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CENTRAL VALLEY SALMON

A Perspective on
Chinook and Steelhead in the Central Valley of California



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(Photograph: spring Chinook in Butte Creek, by Thomas B. Dunklin)

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Abbreviations and Acronyms

ACE	Army Corps of Engineers
AFRP	Anadromous Fish Restoration Program
CALFED	CALFED Bay-Delta Program
CAMP	Comprehensive Monitoring and Assessment Program
CBDA	California Bay-Delta Authority
CDFG	California Department of Fish and Game
CDWR	California Department of Water Resources
CPOP	Sacramento fall and winter Chinook population model
CVP	Central Valley Project
CVPIA	Central Valley Project Improvement Act
CWWR	Center for Water and Wildlands Resources, University of California
EACH	EA Engineering Chinook Model
FEER	Federal Energy Regulatory Commission
HSRG	Hatchery Scientific Review Group
IEP	Interagency Ecological Program
ISAB	Independent Scientific Advisory Board
ISG	Independent Science Group
JHRC	Joint Hatchery Review Committee
NMFS	National Marine Fisheries Service, also called NOAA Fisheries
NOAA	National Oceanic and Atmospheric Administration
NRC	National Research Council
ORCM	Oak Ridge Chinook Salmon Model
PFMC	Pacific Fishery Management Council
PHABSIM	Physical habitat simulation system
PIT	Passive integrated transponder
PSTRT	Puget Sound Technical Recovery Team
RBDD	Red Bluff Diversion Dam
RSRP	Recovery Science Review Panel
SALMOD	Salmonid Population Model
SRCAF	Sacramento River Conservation Area Forum
SRCSIBM	Sacramento River Chinook Salmon Individual Based Model
SRFCRT	Sacramento River Fall Chinook Review Team
SSJEFRO	Sacramento San Joaquin Estuary Fishery Resource Office
SRFG	Stanislaus River Fish Group
SWP	State Water Project
TBI	The Bay Institute
USBR	United States Bureau of Reclamation
USFWS	United States Fish and Wildlife Service
VAMP	Vernalis Adaptive Management Program
WDFW	Washington Department of Fish and Wildlife
W/LCTRT	Willamette/Lower Columbia Technical Recovery Team
WCSBRT	Winter Chinook Salmon Biological Review Team
WRIMF	Winter-Run Integrated Modeling Framework

River locations

Sacramento River:

Location	River Kilometer (rkm)
Keswick Dam	485
ACID Dam	
Clear Creek confluence	464
Ball's Ferry	442
Cottonwood Creek	438
Battle Creek confluence	435
Jelly's Ferry	426
Bend Bridge	414
Red Bluff	393
RBDD	390
Mill Creek confluence	369
Deer Creek confluence	353
GCID diversion	329
Hamilton City	319
Ord Ferry	295
Mouton Weir	255
Hamilton Weir	234
Colusa	231
Moons Bend (Butte Creek)	221
Tisdale Weir	189
Knights Landing	145
Fremont Weir	131-135
Sutter By-pass	128-136
Feather River confluence	128
Elkhorn	114
American River confluence	97
Freeport	75
Garcia Bend	82
Hood	62
Steamboat Slough	52
Delta Cross Channel	43
Georgiana Slough	42
Ryde	39
Cashe Slough	24
Sacramento-San Joaquin confluence	0

Location	River Kilometer (rkm)

San Joaquin River:

Friant Dam	430
Gravelly Ford	368
Merced River confluence	190
Tuolumne River confluence	133
Durham Ferry	109
Mossdale	90
Old River	86
Port of Stockton	64
Calaveras River confluence	61
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Jersey Point	20
Antioch boat ramp	9

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INTRODUCTION

This is my attempt to review information regarding salmon and steelhead that is relevant to the restoration or rehabilitation of Central Valley habitats and management of Central Valley rivers and the fish that they support. The review was funded by the California Bay-Delta Authority (CBDA, also called CALFED), which has as its mission "...to develop and implement a long-term comprehensive plan that will restore ecological health and improve water management for beneficial uses of the Bay-Delta system." This is easier said than done, and it was thought that a review of relevant information on Chinook salmon and steelhead, species of prominent concern in the Central Valley, could be helpful to the process.

The literature on salmon and steelhead is enormous and growing rapidly. Besides their economic and aesthetic values, various aspects of the life cycle of salmonids make them interesting to scientists working on topics such as animal migration, evolution, genetics, animal behavior, physiology, and life history theory. It is not hyperbole to claim that so many new papers and reports at least marginally relevant to Central Valley Chinook and steelhead are being published that someone reading with a modicum of care could not keep up with them, let alone summarize the literature in a paper of reasonable length. So I have of necessity been selective. As a consequence, although the review tries to take a broad view, the selection of topics and papers—and so the report—is biased by my own interests and predilections, and my screening of what is relevant for restoration and management is tied to my own views of what the problems are, and what actions are feasible or desirable. This kind of bias is unavoidable and I do not apologize for it, but it is fair to describe my point of view at the outset, so that the reader is forewarned.

In the introduction to "Evolution illuminated: salmon and their relatives," Stearns and Hendry (2004:15) remarked that "A major shift in evolutionary biology in the last quarter century is due to the insight that evolution can be very rapid when large populations containing ample genetic variation encounter strong selection (citations omitted)." The first important premise underlying this review is that management can effect strong selection, and so should adopt an evolutionary perspective (Ashley et al. 2003). A second premise is that diversity in life history patterns and related traits contributes to the abundance of populations and to their resilience in the face of environmental variation or change (Thorpe 1989; Hilborn et al. 2003; Greene and Beechie 2004), so that natural variation in life history patterns should be protected. A third premise is that salmon populations can develop adaptations to their environments within the time horizon of management plans (Quinn et al. 2001). In consequence, populations together with their environments are the proper subject of concern and management (Healey and Prince 1995).

The concern with diverse, naturally producing populations reflects one of two major themes in salmon management in the Central Valley. The CALFED Ecosystem Restoration Program, together with the Anadromous Fish Restoration Program (AFRP) mandated by the Central

Valley Project Improvement Act (CVPIA), and the NOAA Fisheries recovery planning for listed runs, are all pursuing or planning ambitious programs for protecting and restoring diversity within and among the various naturally-producing populations of Chinook and steelhead in the Central Valley, and for restoring or rehabilitating the Central Valley habitats upon which the populations depend. On the other hand, the California Department of Fish and Game (CDFG) and the United States Fish and Wildlife Service (USFWS) maintain industrial-scale hatchery programs to support commercial and recreational fisheries. Whether these two programs are compatible seems doubtful. There is evidence that interbreeding between hatchery and naturally produced salmon has largely homogenized Central Valley fall-run in terms of neutral genetic markers (Banks et al. 2000; Williamson and May 2003), and there are good reasons to suspect that this is associated with loss of local adaptation fitness for natural reproduction (Ch. 12). Moreover, there is evidence from the literature (e.g., Unwin and Glova 1997) and from monitoring in the Central Valley (Ch. 2) that hatchery salmon may replace naturally produced salmon, rather than supplement them.

The tension between hatchery programs and restoration programs is not just a Central Valley issue. For example, federal legislation created a Hatchery Scientific Review Group (HSRG) to promote scientifically-sound management of hatcheries in Puget Sound and coastal Washington, with two objectives: “1) helping to recover and conserve naturally spawning populations, and 2) supporting sustainable fisheries” (HSRG 2003:2). Whether the HSRG will be successful with both objectives remains to be seen. In any event, this problem motivates my treatment of some topics such as aspects of reproductive biology that might otherwise seem esoteric, as these topics provide background for understanding the potential effects of hatchery culture on populations that include hatchery fish.

Because my concern is with naturally reproducing fish rather than hatchery fish, I have given less attention to possible modifications of hatchery practice than would have been the case if I were more interested in hatcheries; for example, I have not treated the literature from the Columbia River on barging juveniles downstream, although some may see this as an option for hatchery fish in the Central Valley, and I have treated experimental hatchery programs such as the NATURES program (Maynard et al. 1998) only briefly. As with hatcheries, the treatment of harvest is concerned with its effects on naturally reproducing salmon, rather than economic benefits or angler satisfaction.

Similarly, the screening of what is relevant for restoration and management is tied to my views of what the problems are, what actions are feasible or desirable, and what is inherently interesting. To give some examples, it appears that salmon in the Central Valley do not face the same challenges in their upstream migrations as salmon in, say, the Fraser River, and so I have slighted the considerable literature on the energetics of the upstream migration (e.g., Brett 1995). It also seems to me that we cannot properly understand how we think about salmon unless we understand something of the history of the science, so I have reviewed salient early California salmon studies. I have also tried to understand and in some cases to describe the way points of view have developed and changed within fisheries biology.

Although there are many differences among anadromous salmonids, there are also similarities, and I follow the common practice of citing papers dealing with other salmonids as evidence for or against some point regarding Chinook and steelhead. For example, some of the best evidence for rapid evolution of adaptations to local environments comes from studies of grayling (Haugen and Vøllestad 2001). Such evidence needs to be evaluated in light of the possibility of interspecific differences, but there are also important differences among strains or stocks within species, so this caution is usually appropriate. The extent of the literature also makes it impractical to cite most of the papers bearing on many points. I have tended to cite either the oldest or the most recent papers in preference to others, although sometimes I cite papers that seem particularly strong or that I think deserve more attention. I also favor papers dealing with the Central Valley over others.

Diversity in points of view is important for effective science and management, just as genetic diversity is important for successful species, so I hope that anyone who is interested enough in salmon to read this report will read others as well. To suggest a few sources, two other reports, National Resources Council (1996) and Independent Scientific Group (2000), cover much of the same ground as this one, although they deal primarily with the Columbia River, and deserve the attention of anyone with a serious interest in Central Valley salmon. I have not tried to duplicate some material that is available from these sources. NRC (1996), for example, gives a good history of hatchery culture, and ISG (2000) gives a more extended discussion of some of the genetic processes underlying concerns about the interbreeding between hatchery and naturally-produced fish. Three other books with broad and relevant coverage are Nielsen (1995), Strouder et al. (1997), and the new review of Pacific salmon by Quinn (2005). Lichatowich (1999) provides a good historical account with a broad geographic scope. Evolutionary and life history issues are discussed by Hendry and Stearns (2004) and by Wilson (1997). The literature on the effects of water temperature on steelhead has been reviewed recently by Myrick and Cech (2001) with emphasis on the Central Valley, so I have given that topic less attention than would otherwise have been the case. Similarly, Yoshiyama et al. (2001) deal exhaustively with information on the natural distribution of Chinook in the Central Valley. The chapter on Chinook by Mike Healey in Groot and Margolis (1991) remains a valuable review of the literature to that time. For a less oncorhynchocentric perspective, The Bay Institute (1998) reviews the natural landscape of the Central Valley and the San Francisco Estuary and its subsequent development, as do the opening chapters of Moyle (2002). Naiman and Bilby (1998) cover river ecology with emphasis on the Pacific Northwest. Greco (1999) provides a thorough description of the alluvial section of the Sacramento Valley (downstream from Red Bluff) and associated riparian habitats, both current and historical. Kimmerer (2004) gives an up-to-date review of physical processes in the San Francisco Estuary, and also describes the history of studies of the estuary. Finally, I should note that another John G. Williams publishes on salmon, and citations that do not deal with the Central Valley or instream flow models refer to his work.

On nomenclature

Traditionally, steelhead have been called trout, and in the past they were assigned to the genus *Salmo* along with Atlantic salmon, which steelhead closely resemble in terms of morphology and life history patterns. In 1989, however, steelhead were re-assigned to the genus *Oncorhynchus*, the Pacific salmon (Smith and Stearly 1989). This re-classification was not arbitrary, but rather reflects improved understanding of evolutionary relationships. On that account, it seems justifiable to use the phrase "Central Valley salmon" to include all species of *Oncorhynchus* in the Central Valley. This lets me avoid writing "Chinook and steelhead" over and over again, without resorting to "salmonids," which I reserve for statements that apply to multiple genera, not just multiple species of *Oncorhynchus*. As another complication, it seems that populations of *O. mykiss* in the Central Valley include both anadromous and non-anadromous individuals. Generally, I use steelhead to refer to the anadromous form, and *O. mykiss* to refer to both forms. When describing runs of Chinook, I omit the "-run" when I include Chinook.

There are conflicting uses of the word "wild" in the literature. This review distinguishes naturally produced fish, which include the progeny of naturally spawning hatchery fish, and wild fish, such as the spring-run in Mill, Deer and Butte creeks. Similarly, the term "fry" is used with different meanings. Some studies use the term "fry" for any juvenile that is not a "smolt," usually distinguishing the two by a size criterion. Others distinguish fry and fingerlings, or fry, parr and smolts, often with a 50-mm upper limit for fry. Generally, I call them all juveniles and give lengths, although I sometimes use "fry" to describe juveniles that begin migrating shortly after emergence, and "fingerlings" or "90 day Chinook" to describe those that rear near the spawning areas for one to several months before migrating. I sometimes also use "young of the year" and "yearlings," especially for steelhead, which do not go to sea in their first year. Some Department of Fish and Game reports now distinguish yolk-sac fry, fry, parr, silvery parr, and smolts, based on appearance, which seems a useful approach. I use the terms "ocean-type" and "stream-type" as used first by Gilbert (1913) to distinguish whether the fish migrated to the ocean in their first or second year, but without the connotation of differential use of ocean habitat and run-timing described by Healey (1991), since it appears that most Central Valley spring-run exhibit ocean-type juvenile life history patterns and use the same coastal areas of the ocean as fall-run. Juvenile winter-run and late fall-run migrate into the Delta in the fall and winter, and neither term seems quite apt for them. Finally, I take the San Francisco Estuary to extend as far upstream as the influence of the tides, e.g., as far as Sacramento. Other authors (e.g., MacFarlane and Norton 2002) use a salinity criterion to define the estuary, and so exclude the Sacramento-San Joaquin Delta.

One consequence of the diversity of salmon life history patterns is difficulty in designating ages consistently. For example, the European system used in Groot and Margolis (1991) gives the number of winters spent in freshwater and the number of winters spent in salt water, separated by a period, so typical Central Valley fall-run spawners would be designated as 0.2 or 0.3, and a steelhead that spends two winters in the stream and two in the ocean would be 2.2. This system works well for fish that hatch in the spring, but the life history diversity of Central

Valley Chinook, and the relatively warm water of Central Valley streams that leads to rapid development of eggs and alevins, creates problems. For example, spring-run that emerge in late fall and emigrate the following spring spend a winter in freshwater, but this is quite a different life history than spring-run that incubates in colder water, emerge in the spring, and do not emigrate until the following spring. As another complication, fish in their n th year from emergence are often referred to as n -year olds, so that a 0.2 fall-run spawner is called a three year-old. Ricker (1981:1638) noted that “All systems of designating age have disadvantages,” so it seems unavoidable that different systems will be used to describe particular circumstances. NOAA Fisheries uses somewhat different definitions for winter-run and spring-run: the age in years of a winter-run is increased by one on March 1, if it is in the ocean; for spring-run, the date is May 1. Finally, although age is usually reckoned from emergence, hatcheries often describe fish in terms of “brood years,” referring to the year in which eggs were fertilized.

Organization of the review

Organizing the discussion of a large and complex topic is always a problem. I have not found a satisfactory solution, and suspect that there is none. As it is, the review passes through much of the material on the fish and on their habitats first at a broad level of generalization and again in more detail, with the chapters divided into four sections. This allows for separating background material that is already familiar to many readers from the more detailed discussions. Following the overviews, the more detailed discussions are variously organized by processes (juvenile growth and migration), life stage and habitats (adults in freshwater, gravel, gravel-bed streams, overbank habitat, the estuary, and the ocean), and topics (management approaches and early salmon studies, modeling, and monitoring). Some material has been relegated to appendices. Rather than some rational scheme, this reflects the overall topic being too big for me to hold in my head at one time; I had to work on it piecemeal, and these are the pieces. As one consequence, for readers with some background in the topic, the chapters generally can be read independently, or in an order that matches the reader’s interests. A discussion of salmon diseases is conspicuously absent, and contaminants are mentioned only briefly, in terms of their effect on imprinting by juveniles. I know little about these topics, and the project is already seriously behind schedule, so they were sacrificed.

Because of the wide interest in salmon and steelhead, I have tried to make this paper interesting and accessible to a lay audience, although without sacrificing rigor and scientific standards for citations, units, etc. In consequence, I sometimes include material that is already familiar to fish biologists, and I have favored plain rather than technical language. I have also used more quotations and footnotes than is normal in scientific writing.

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This report is dedicated to the spring Chinook of Butte Creek, and to the memory of Randy Brown.

CHAPTER ONE

THINKING ABOUT SALMON

Nothing in biology makes sense except in light of evolution.

Theodosius Dobzhansky (1973)

The collection and analysis of data does not proceed in a vacuum. Which data to collect and how to analyze them depend on attitudes about what is important and on the conceptual tools that are available for interpreting the data. This chapter briefly describes conceptual foundations for salmon studies and management, and some concepts that have been important for the same purpose. In particular, I try to describe the attitude and concepts that underlie the treatment of topics in this review. The chapter assumes that the reader has some familiarity with salmon and the Central Valley, but if not, reading Chapters 2 and 3 will provide the much of necessary background. On the basis that you cannot really understand where you are unless you know how you got there, the chapter closes with a short historical review of Central Valley salmon studies.

Conceptual foundations

As described by Lichatowich (1998:3), “A conceptual foundation is a set of scientific theories, principles and assumptions, which in aggregate describe how a salmonid-producing ecosystem functions. The conceptual foundation determines how information is interpreted, what problems are identified, and as a consequence also determines the range of appropriate solutions (ISG 1996).”¹ This is similar to what in CALFED parlance is called a conceptual model, but avoids using the word ‘model,’ which has such a range of meanings that its use seems to confuse things more than clarify them.

For most of the twentieth century, management of fish and wildlife had a utilitarian foundation, so that, for example, before passage of the California Environmental Quality Act and other environmental legislation, the basic job of the Department of Fish and Game was to see to it that there were animals for people to harvest for recreation, food, or profit. The conceptual foundation of fisheries management was basically agricultural (Bottom 1997), to the extent that natural production of fish was sometimes referred to as “aquiculture” (e.g., Hatton 1940:334), and the number of salmon that return to spawn is generally called the “escapement,” as if harvest were the right and proper fate of a salmon. Nevertheless, the attitude early in the century seemed to be that one had to understand the biology of an animal in order to manage it. For example, Snyder (1928:25) wrote that: “Believing that measures intended to conserve a fishery can not be intelligently devised and applied until the life history of the species is well known, an investigation of California salmon was begun some years ago, and is still in progress.” Thus, questions of basic biology received attention along with matters of more immediate management concern. This attitude is expressed perhaps most strongly in the many studies of sardines by

¹ This was an earlier version of ISG (2000), Return to the River.

biologists for the California Department of Fish and Game (CDFG) that are published in various early CDFG Fish Bulletins or issues of California Fish and Game, but it is also apparent in early salmon studies by Rutter (1904), Scofield (1913), Rich (1920), Clark (1928), and Snyder 1921; 1923; 1924a,b,c; 1928), and in the work on steelhead by Shapovalov and Taft (1954, but actually conducted in the 1930s).

Starting in the late 1930s, the main thrust of salmon investigations in the Central Valley seems oriented less toward answering basic biological questions and more toward coping with the consequences of civil works projects such as the Central Valley Project (CVP, e.g., Hatton 1940; Hatton and Clark 1942; Clark 1943), debris dams constructed to allow resumption of hydraulic mining (Sumner and Smith 1940), local irrigation diversions (Hallock and Van Woert 1959), and later the State Water Project (SWP, e.g., Sasaki 1966). Ecologically-oriented studies of the Estuary that were highly advanced for their time began in the 1960s, but were directed primarily toward striped bass, and gave surprisingly little attention to salmon. As described in Ch. 5, it was concluded from monitoring studies at the time that juvenile salmon migrated rapidly through the Delta, so studies of habitat use in the Delta by juvenile salmon apparently were regarded as unnecessary, and subsequent studies focused on the survival of smolts migrating through the Delta. Dam construction raised the question of how much water should be released to provide habitat for fish, and “instream flow studies” became a focus of effort, particularly after the development of the Instream Flow Incremental Methodology in the late 1970s and after the legal status of instream resources improved with the 1983 *Audubon v. Superior Court* decision of the California Supreme Court (Appendix C).

Coping with the consequences of civil works projects, and questions relating to hatchery and fisheries management, are still the principal concerns of salmon studies in the Central Valley, although the current emphasis on environmental restoration has increased the level of interest in more basic questions about biological diversity and habitats. The funding for this review is one manifestation of the renewed interest in basing management on better understanding of species of concern and of the ecosystems that support them. As noted earlier, this review takes as a premise that populations together with their environments are the proper subject of concern and of management (Healey and Prince 1995), which requires that attention be given to habitats and to historical changes in habitats, as well as to the populations and historical changes in their abundances and their genomes. The application of this point of view to estuaries, and the reasons for taking it, have been elaborated recently in a major report on the Columbia River Estuary (Bottom et al. 2005).²

Bottom et al. (2005, Ch. 2) argued that the utilitarian foundation of early salmon management resulted in “production thinking,” a point of view that “... measured success by the output on natural resources (e.g., pounds or numbers of salmon, angler-days of use, etc.)” and “emphasized short-term changes in the abundance of salmon, which were defined arbitrarily as

² Bottom et al. (2005) has been available for several years as a draft, and may be cited elsewhere as Bottom et al. (2001).

any geographic unit of management interest (e.g., river basin, state, nation)." As an alternative, Bottom et al. (2005) argued for what they call "population thinking," which they contrast with production thinking in a table, reproduced below. The emphasis is on local populations, diversity in life history patterns, and the varied habitats that support different life history patterns. Although it is applied in this instance to a single genus, it is apparent from the table that population thinking as advocated by Bottom et al. (2005) is consistent with CALFED's emphasis on ecosystem restoration. Bottom et al. (2005) were concerned with the Columbia River Estuary, and the bottom two rows of Table 1.1 are specific to estuaries, but it is easy to generalize them to include upstream habitats as well. The third row in the comparison, time-frame, deserves emphasis. Recent work has demonstrated that salmon, like other organisms, can evolve significantly within a few generations in response to translocation, hatchery culture, and harvest (Kinnison and Hendry 2004 and citations therein). Accordingly, habitat restoration and management should take an evolutionary perspective (Ashley et al. 2003).

Table 1-1. Comparison of production thinking and population thinking, reproduced from Table 2.1 in Bottom et al. (2005), *Salmon at River's End*.

	Production Thinking	Population Thinking
Goals	Efficiency, production	Resilience, reproduction
Population Units	Arbitrarily defined	Biologically defined
Time Frame	Short	Evolutionary
Objectives	Control survival and abundance	Conserve local populations and life-history diversity
Estuary Function	Corridor for a single, homogenous group of salmon	Nursery area for many self-sustaining populations
Estuary Management	Control predators, promote rapid salmon out-migration	Protect habitats of diverse life-history types

A recent report on salmon monitoring (Botkin et al. 2000) demonstrates the importance of making conceptual foundations explicit. Botkin et al. (2000) is the report of a distinguished panel that addressed the following question: "If actions are taken in an attempt to improve the status of salmon (or a specific stock of salmon), what measurements are necessary, feasible, and practical to determine whether the actions are successful?" It appears that the report is in large part a reaction to an argument that because of the difficulties in estimating salmon abundance, assessments of management actions such as timber harvest could be made entirely on the basis of data on habitat conditions. In emphasizing the importance of estimates of abundance in reaction to that argument, however, the panel implicitly, and perhaps inadvertently, adopted a strong production perspective, and says almost nothing about the importance of diversity in life histories.

Population thinking as defined by Bottom et al. (2005) is approximately the conceptual foundation for the CALFED Ecosystem Restoration Program. In the Central Valley, however,

much of local salmon management still embodies production thinking, although concern for meeting numerical goals for harvest and escapement has been largely superseded by concern for not exceeding numerical limits for take of listed species at the CVP and SWP pumps. For example, the passages cited above squarely apply to the 1993 Biological Opinions for the Operation of the CVP and SWP (NMFS 1993) and to the report of the Sacramento River Fall Chinook Review Team (SRFCRT 1994). The Review Team was formed "to determine why the escapement goals for Sacramento River fall chinook (SRFC) were not met in 1990-1992, and to recommend actions to assure future productivity of the stock;" the review team concluded in part (p. 1) that:

Because it is unlikely that we can affect ocean survival,³ the most effective means of increasing adult abundance is to increase the number of juvenile salmon entering the ocean. ... The most efficient and effective way to increase juvenile abundance would be to increase survival during outmigration to the ocean, particularly during passage through the Sacramento-San Joaquin Delta. ... Any improvements in delta survival would benefit natural production at a life stage when natural mortality is not density dependent and would result in a commensurate increase in adults if ocean survival is independent of freshwater survival.

Perhaps the most striking consequence of production thinking regarding salmon in the Central Valley is the lack of good data on the proportion of spawning adults that were naturally or hatchery produced. Unless Central Valley salmon were regarded as interchangeable, distinguishing hatchery and naturally produced fish would seem of prime importance. The limited attention given to the Delta as rearing habitat for juvenile chinook is probably another consequence. The point is not that production thinking is wrong, but that it is limited in ways that tend to undercut objectives for restoration, even when the objectives are embodied in legislation such as the Central Valley Project Improvement Act or the Endangered Species Act.

A conceptual foundation that is somewhat different from but complementary to that of Bottom et al. (2005) has been described for the Columbia Basin in "Return to the River" (ISG 2000), a report by the Independent Scientific Group for the Northwest Power and Conservation Council.⁴ The critical elements of the conceptual foundation that they suggest are, slightly modified (their Box 3.1):

1. Restoration of the [Central Valley] salmonids must address the entire natural and cultural ecosystem, which encompasses the continuum of freshwater, estuarine, and ocean habitats where salmonid fishes complete their life histories. This consideration includes human developments, as well as natural habitats.
2. Sustained salmonid productivity requires a network of complex and interconnected habitats, which are created, altered, and maintained by natural physical processes in freshwater, the estuary, and the ocean. These diverse and high-quality habitats, which

³ This seems a curious statement in a report published by an agency involved in the control of ocean harvest.

⁴ This is available at <http://www.nwccouncil.org/library/return/2000-12.htm>, as of 3/06; select ch. 3.

have been extensively degraded by human activities, are crucial for salmonid spawning, rearing, migration, maintenance of food webs, and predator avoidance. Ocean conditions, which are variable, are important in determining the overall patterns of productivity of salmon populations.

3. Life history diversity, genetic diversity, and metapopulation organization are ways that salmonids adapt to their complex and connected habitats. These factors are the basis of salmonid productivity and contribute to the ability of salmonids to cope with environmental variation that is typical of freshwater and marine environments.

Frissell et al. (1997) provide another good discussion of the conceptual foundations of salmon management, contrasting what they call the “Production/exploitation” and “Ecosystem/restoration” views. Again, the language is somewhat different, but the essential message is the same.

The implicit expectation in articulating a conceptual foundation (or a conceptual model) is that it will lead to ways of thinking and acting that are more likely to result in successful restoration actions, or in studies that will be useful for guiding or evaluating such restoration. However, there is good reason to maintain a critical attitude toward this proposition. Thirty-five years ago, Don Kelley (1968) ended the summary chapter of a major report to the Bay-Delta Water Quality Control Program with a discussion of the need to develop better understanding of the factors influencing fish and wildlife populations in the Estuary:

... The systems analysis approach described by K. E. F. Watt (1966, 1968) may provide the most useful means of developing that understanding to date. This method involves developing conceptual models like those drawn by the authors of subsequent chapters in this report, using them to sort out the variables that most influence the resource and finally the development of simulation models describing what affects each major resource. This method offers an excellent means of making certain that data collecting on animal populations is relevant and can be fitted together so that the end result is real understanding of the influence of future environmental change.

Two lessons can be drawn from Kelley’s observation. First, it is not enough to have a firm conceptual foundation or coherent conceptual models; to the extent that conceptual models or foundations guide inquiries, they can mislead as well as lead. For example, it is not clear that the conceptual foundations reviewed above adequately frame the challenges posed by anthropogenic climate change. Second, there seems to be a human tendency to imagine that the most recently developed approach will soon yield a major breakthrough in understanding. Based on historical experience, the odds are against this. We need to act, in studies as well as in management, based on the information and concepts that we have available to us, but we should keep in mind the favorite motto of a certain 19th Century German philosopher, disastrously ignored by his followers: *De omnibus dubitandum*.⁵

⁵ Doubt everything. (G. Seldes, 1960, *The Great Quotations*. Lyle Stuart, New York.)

Concepts used in salmon studies and management

The stock concept

Salmon management is generally based on “stocks,” such as the “Sacramento fall Chinook,” which includes populations from the large and small tributaries as well as the Sacramento River itself. The concept of stocks in fisheries biology developed from the recognition that many exploited fishes occur as populations that are “sufficiently discrete to warrant consideration as self-perpetuating ... system[s] which can be managed” (Larkin 1972:11). By this definition, the stock concept is based on management as well as biological considerations, as Larkin emphasized. In particular, the term was recommended by a 1938 Conference on Salmon Problems as not implying significant genetic differences among stocks (Ricker 1972).

The stock concept is important for management of fishes that are subject to mixed stock fisheries, where managing to maximize the yield of more productive stocks results in overfishing of less productive stocks, potentially driving them to extinction (Larkin 1977), and restricting harvest sufficiently to protect less productive stocks (for example, from the Klamath River) may reduce the total harvest potentially available to the fishery. This raises the question of what would be lost with the loss of less productive stocks? If observed differences among stocks were simply the result of rearing in different environments, then the answer might be “not much.” Similarly, moving fish from hatcheries on rivers occupied by one stock to hatcheries on rivers occupied by another would not be a problem. Apparently, the view that observed differences among salmon stocks were primarily environmental was prevalent in the early twentieth century, for reasons based on trends in biological thinking of the time as well as on economic interests (Ricker 1972). The view that differences among stocks were based primarily on environmental differences remained common enough to motivate Ricker to compile evidence in the 1950s on the extent to which such differences were genetically as well as environmentally based (Ricker 1960), and to extend the compilation for a 1970 conference on stock identification (Ricker 1972).

Methods for identifying and distinguishing stocks have continued to evolve as new technologies and analytical methods have developed, and genetic markers are now routinely used in stock assessments (NRC 1996; Begg et al. 1999). Along with the recognition of significant genetic differences among stocks, however, came recognition that in practice, even isolated, spatially uniform populations cannot be managed for harvest without effecting some genetic change in the populations, and most populations are neither completely isolated nor lacking internal structure. Therefore, even if all populations were managed as separate stocks, biologically ideal management would not be feasible, so the practical question is the extent to which stocks should be defined to promote management convenience or economic efficiency (Larkin 1972). In practice, at least in California, the tendency has been to define stocks broadly, as with Sacramento fall Chinook.

Metapopulations

Salmon return to their natal streams with high but not complete fidelity. Straying rates for natural populations are poorly known but probably vary, mainly between ~1 and 15%. Higher

rates have been documented in a population of chum salmon (Tallman and Healey 1994), although apparently the straying fish in this case have little reproductive success. Nevertheless, it is clear from the recolonization of formerly glaciated habitat from Washington to Alaska that salmon stray into unoccupied streams and establish new populations there, and from other evidence it appears that salmon sometimes stray into occupied streams and breed successfully with the local population. This raises the question of the extent to which, or the conditions under which, migrants affect the abundance or the genetic structure of nearby populations.

The concept of a metapopulation (Levins 1969) has been useful in considering such questions. A metapopulation is a group of populations occupying discrete habitats among which migration is frequent enough to have a significant effect on the abundance or genetic structure of each of the populations, but not too frequent for the populations to have separate identities. The term was coined by Levins (1969) in a modeling study in which he explored the conditions under which a highly idealized metapopulation would persist. More realistic metapopulation models account for spatial structure and variability in patch size and in the probabilities of extinction and recolonization (Hanski 1997; Hanski and Gilpin 1997). The metapopulation concept seems applicable to salmon, for which the populations in different tributaries or in adjacent rivers may constitute the metapopulation, and the concept has been used in a number of modeling studies as discussed in Ch. 14. However, it seems important to keep in mind the time scale of the metapopulation processes involved (that a suitable vacant patch has a 1% per year chance of being re-colonized might not seem too relevant to many people), and whether the concept applies to a given population should be taken as an hypothesis, not a given.

Evolutionarily significant unit (ESU)

The federal Endangered Species Act (Sec. 3(15)) provides for the listing of “any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” When the National Marine Fisheries Service (NMFS, also known as NOAA Fisheries) considered petitions to list salmon in the Columbia River system under the ESA, it had to consider and clarify the meaning of “distinct population segment” as applied to salmon. It adopted and elaborated the concept of the ESU for that purpose (Waples 1995). As defined by (Waples 1991:12): “An ESU is a population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of the species.”

Evidently this is a flexible definition, since what is an “important component” or “substantial” reproductive isolation is inherently subjective, but the definition reflects an attempt to respond to the contradictory guidance in the legislative history of the ESA that the classification should be applied so as to preserve genetic variability, but also should be applied sparingly (Waples 1995). Like many legal concepts, the meaning of the ESU concept is best defined by examples of its application, and Waples (1995) discussed examples to which it was and was not applied. By resort to such examples, a better answer can be given to the question of what an ESU is under the ESA than to the question what it ought to be; see other contributions in

Nielsen (1995) for discussions of the difficult issues that this question raises; see Hard (2004) for a recent review.

With regard to the Central Valley, NOAA Fisheries currently recognizes Central Valley steelhead and Central Valley winter-run, spring-run, and fall/late fall-run Chinook as separate ESUs. However, as discussed in Ch. 2, spring-run in Mill and Deer creeks and in Butte Creek can be distinguished genetically, and so appear to be “substantially reproductively isolated” from each other, although they have similar life-histories. Fall-run and late fall-run can be distinguished genetically and have different life histories. Nevertheless, all spring-run are in one ESU, and fall-run and late fall-run are another. Moreover, naturally-producing Feather River “spring-run,” which are genetically similar to Feather River fall-run, are also in the spring-run ESU, but spring-run in the Feather River Hatchery, which are not reproductively isolated from naturally producing Feather River spring-run, were excluded from the ESU until a recent court decision, *Alsea Valley Alliance v. Evans*,⁶ made that distinction legally untenable. Finally, naturally produced steelhead in the American River are included in the Central Valley steelhead ESU, even though most steelhead spawning in the river are hatchery fish, and genetically all steelhead in the American River appear to be derived from a coastal stock introduced at the hatchery (Nielsen et al. 2003). It is not clear how an introduced, hatchery-based population “represents an important component in the evolutionary legacy” of Central Valley steelhead.

The *Alsea* decision has renewed controversy over the definition of ESUs and whether hatchery fish that are closely related to listed wild fish should be given the same protection (Myers et al. 2004; Recovery Science Review Panel 2004; Hey et al. 2005). Hey et al. (2005:6), stated in the report of a panel convened at the request of NOAA Fisheries:

By holding to a phylogenetic criterion and overlooking a population perspective of exchangeability, salmon ESUs are sometimes treated largely as taxonomic units rather than as evolutionary and ecological role players. This can lead to lumping of hatchery fish with related wild populations when in fact the two groups are different in many ways. In addition, it can lead to reduced reproductive success and viability of wild populations in cases where hatchery-reared fish are admixed at high rates with wild populations.

It seems likely that this issue will continue to be controversial.

Viable salmonid population (VSP)

As suggested by the metapopulation concept, Pacific salmon do not occur in crisply separated populations, but rather in populations with various degrees of interaction. As is usually the case with legal concepts, however, implementation of the ESA requires that lines be drawn to divide this gradient of interactions into distinct segments. For listings, this is done with ESUs. For recovery planning, however, it is necessary to make distinctions within ESUs, and NOAA Fisheries has developed the VSP concept for this purpose (McElhany et al. 2000). There are

⁶ *Alsea Valley Alliance v. Evans*, 161 F. Supp.2d 1154 (D. Oregon 2001).

several reasons that distinctions need to be made within ESUs, but an obvious one is the need to distinguish self-sustaining populations from populations that are maintained by migration from other populations (source and sink populations).

Whether a population is viable under the VSP concept depends on two tests. First, the population must be independent, in the sense that its population dynamics or its risk of extinction “over a 100-year time period are not substantially altered by exchanges of individuals with other populations (McElhany et al. 2000: xiii).” Independent populations of listed Chinook in the Central Valley are identified in Lindley et al. (2004). The second test is whether the population has a “negligible risk of extinction due to threats from demographic variation, local environmental variation, and genetic diversity changes” over a period of 100 years. Whether a population is viable should be considered in terms of its abundance, growth rate, spatial structure, and diversity. In recognition of the diversity of situations in which the VSP concept will be applied, however, McElhany et al. (2000) provide guidelines rather than explicit rules by which the judgment of viability should be made. More specific criteria for Central Valley populations are under development by the NMFS Central Valley Technical Recovery Team.

Abundance, growth rate, spatial structure, and diversity should also be considered in the assessment of ESUs. The importance of spatial structure and diversity for the long-term stability and persistence of groups of populations has been demonstrated by a study of sockeye populations at Bristol Bay, Alaska (Hilborn et al. 2003). The importance to the Bristol Bay fishery of different populations, and populations using different kinds of freshwater habitats, has varied considerably over the twentieth century, so that populations that were minor contributors to the fishery at some times were important contributors at other times. Thus, population diversity has contributed to the stability of the fishery, and presumably the same would be true for the persistence of ESUs.

Density-dependent mortality

For any biological population, causes of mortality can be divided into those that depend upon the density of the population and those that do not. Generally, the mortality rate increases as the population increases (negative density-dependent mortality), so that populations tend to increase when they are small and to decrease when they are very large. The mortality rate may also increase when populations decrease below some threshold, for either genetic or ecological reasons, but negative density-dependence is much more common, and the qualifier ‘negative’ is often omitted. The relative importance of density-dependent and density-independent mortality has long been the subject of argument in ecology and fisheries management, but there is little question that density-dependent mortality helps regulate many populations of salmonids, especially in more stable habitats (Elliott 1994).

Among salmon, the mortality rate of eggs from disturbance by the spawning of other salmon clearly depends upon population density (e.g., McNeil 1971; Fukushima et al. 1998). On the other hand, the percentage of juveniles entrained by diversions probably does not. The relationship between the number of individuals in successive generations depends upon these

two types of mortality and the reproductive potential of the population. Various models have been proposed to describe this relationship. Several such models are described in Ch. 14.

Density-dependent mortality can be important even for stocks with sharply reduced abundances (Achord et al. 2003), especially if reduced abundance results from habitat loss. Spring Chinook in the Central Valley provide a good example; they have been so abundant in Butte Creek in recent years that density-dependent mortality there seems certain, but independent populations are restricted to Butte Creek and two other Sacramento River tributaries, Mill Creek and Deer Creek (Lindley et al. 2004). Similarly, to the extent that salmon mortality in estuarine or early ocean life is negatively density-dependent, hatchery production could adversely affect depleted stocks that share the same estuarine and ocean habitats (Levin et al. 2001).

The extent and nature of density-dependent mortality at different life-stages and in different habitats has important implications for management and for restoration. For example, if density-dependent mortality were confined to spawning, then increasing spawning habitat would result in commensurate increases in the population (Greene and Beechie 2004). However, if there is strong density-dependent mortality at some later life-stage, then increasing the production of fry may do little to increase populations. The situation is further complicated by the variable life-history patterns among juvenile Chinook. If selection of life history patterns is affected by population density, leading to density-dependent migration, then management that changes the capacity of upstream habitats will change the distribution of juveniles over downstream habitats with corresponding changes in their local survival rates (Greene and Beechie 2004). Unfortunately, little is known about the nature and strength of causes of density-dependent mortality among Central Valley salmon. Similarly, little is known about the nature and importance of density-dependent migration or reductions in growth. This is a major impediment to effective management.

Life-history variation

Chinook salmon and steelhead have highly variable life-history patterns, with age at spawning in Chinook varying from one year to seven years, and age at emigration to estuaries or the ocean ranging from a few days to two years. Steelhead have even more variable life histories and may omit ocean rearing altogether, as may commonly be the case in Sacramento River since construction of Shasta Dam. High variability occurs within other salmonid species such as Atlantic salmon (*Salmo salar*), which in many respects is similar to steelhead, and among some other salmonids (Wilson 1997; Quinn 2005). Given that variability in life-history patterns is an important attribute that should be protected, an understanding of the development of life history patterns should be useful for management.

A conceptual model for life-history variation in Atlantic salmon described in Thorpe et al. (1998) posits a set of condition-dependent "switches" that affect or control such aspects of behavior as feeding, migration, and maturation. Individual variation in the thresholds for the switches and variation in environmental conditions can then produce the observed variation in life-history patterns. While the model cannot be directly transferred to Pacific salmon, it does

present a plausible conceptual framework that clarifies the relationships between environments and life-history patterns for salmonids generally. The model embodies two important generalizations about salmonid life histories: that there are photoperiodically-based "windows" of time in which life-history choices are made, and that these choices are based on the condition of the fish at some prior time, as well as on the condition of the fish shortly before the decision becomes manifest by, say, smolting or by sexual maturation (Shapovalov and Taft 1954; Thorpe 1989).

The basic facts of Atlantic salmon life history that the model seeks to explain are these. Atlantic salmon spawn in the fall, with fry emerging in the spring. The distribution of fry sizes is approximately normal at emergence, but then becomes bimodal, at least in some conditions (Thorpe 1977; Thorpe et al.1998). In such conditions, all surviving fry feed actively early in their first summer, but the slower-growing ones restrict feeding in late summer and spend most of the winter hiding in the gravel in the streambed, while others continue actively feeding through the winter. Fish that continue feeding typically emigrate in the spring, after one year in freshwater. Most of the slower-growing group then feeds actively through their second year, and then emigrates, but a fraction again restricts feeding, and spends a third year in freshwater. After emigrating, the fish spend a variable number of years in the ocean before returning to spawn.

The conceptual model described by Thorpe and colleagues was turned into a simulation model by Mangel (1994) that includes the developmental switches listed in Table 1-2. The model assumes that emigration occurs in May and reproduction occurs in November, and includes several restrictions. For example, a fish that continues gonad growth in freshwater cannot smolt, and a fish can move to an advanced state of preparation for emigration or gonad growth only by continuing preliminary preparation (i.e., E2 can equal 1 only if E1 = 1). If preparation for emigration is aborted (E2=0), then E1 is also re-set to zero, and similarly for gonad growth. Also, the state of each switch can affect the others through their effects on growth, since the thresholds for the switches are given in terms of the fish's weight. For example, if a fish does not eat during its first winter, it will not grow to the threshold size for preparing to emigrate.

Table 1-2. Developmental switches in the Mangel (1994) condition-dependent life history model for Atlantic salmon.

Developmental Switch	Date	Description
F	1 August	Whether to feed (F = 1) or to become anorexic during the winter (F = 0)
G1	1 November	Whether to continue gonad growth (G1= 1) or not (G1 = 0)
E1	1 December	Whether to prepare for emigration the next spring (E1 = 1) or not (E1 = 0)
E2	1 March	Whether to continue to prepare for emigration (E2 = 1) or abort (E2= 0)
G2	1 April	Whether to continue gonad growth (G2 = 1) or not (G2 = 0)

Different life history patterns can then be described in terms of the switches. For example, a parr that smolts at age one would have $F=1$, $G1=0$, $E1=1$, $E2=1$, while a parr that smolts at age two might have $F=1$, $G1=0$, $E1=0$ in the first year, and $F=1$, $G1=0$, $E1=1$, $E2=1$ in the second (there are several switch settings that give the same result). A male parr that matures precociously and breeds without going to sea would have $F=1$, $G1=1$, $E1=0$, $G2=1$. The influence of environmental conditions on life-history patterns can also be taken into account. For example, conditions that allow for rapid growth allow more fish to exceed the threshold for feeding through the winter (i.e., set $F=1$ in August), so that more fish smolt after one winter (this could explain why steelhead in the American River emigrate at age 1). Ocean conditions that allow for rapid growth encourage earlier maturation and spawning (i.e., setting $G2=1$). Conditions allowing very rapid growth would cause more fish to mature precociously, which has been a problem for fish farms (Thorpe 2004).

Many Chinook salmon emigrate shortly after emergence, so it is clear that this model would have to be modified before it could be applied to them, but the fundamental insight remains that a fairly simple developmental program, together with environmental variation and genetic variation in thresholds for the switches and in the timing of the developmental windows, can account for the observed variation in life-history patterns within and among species of Pacific salmon. Very low thresholds could explain the early emigration and fixed two-year life cycle of pink salmon, for example. At least within the Asian lineage (see Ch. 2) spring-run Chinook, a photoperiod-sensitive switch something like "F" in the Atlantic salmon model determines whether fish follow an ocean-type or stream-type juvenile life-history pattern (Clarke et al. 1992). Typically, these fish spawn at high enough altitude that winters are cold and embryos and alevins develop slowly (the incubation period is strongly temperature-dependent). Accordingly, fry emerge well after the winter solstice, and do not experience very short-day photoperiods until the following winter. This causes them to grow slowly, and as suggested by the model they do not emigrate. If the fry are exposed experimentally to a short-day photoperiod, however, they will grow rapidly and emigrate in their first year. In California, it appears that the situation is somewhat different, as many spring-run spawn at relatively low elevations, and the fry emerge early enough to experience short winter days. Most juveniles behave like fall-run fish and emigrate in their first year (Ch. 5).

Ideas about variation in life-history patterns have had real consequences. The usual formulation based upon run timing, or the distinction between stream-type and ocean-type Chinook, did not challenge the tendency, formerly almost dogma in the Central Valley, to think of fry migrants as surplus or somehow deviant fish. In consequence, fry migrants and the habitats that they use were ignored for many years, until monitoring with screw traps demonstrated their abundance (Williams 2001a). In contrast, Higgs et al. (1995) distinguished three basic life history types: ocean type (which move to estuaries as newly emerged fry), 90-day type, and stream type. This emphasizes the normality of fry migrants, and directs attention to the importance of the riverine and estuarine habitats that they use.

The Thorpe et al. (1998) model also helps clarify how environmental and genetic influences on age at maturity and other life history traits may interact to produce observed patterns. For example, first-generation hatchery steelhead in the Hood River in Oregon are canalized into one life-history pattern (Kostow 2004), presumably because conditions of hatchery culture make all of them pass their thresholds for smolting after one year, whereas naturally produced fish display variable life-history patterns. In consequence, fish that otherwise would have smolted at age 2 experience a different selective regime after they are released from the hatchery than they would have experienced had they been naturally produced. This may contribute to the lower survival rate of hatchery smolts.

Contemporary evolution

The term “contemporary evolution” has been proposed to describe observable evolution that occurs over periods shorter than a few hundred years (Stockwell et al. 2003). This seems useful, as it distinguishes evolution likely to be important to management from evolution that may seem rapid to paleontologists but slow to others. Perhaps the best documented example of contemporary evolution comes from a thirty-year study of two species of finch on one of the Galápagos Islands (Grant and Grant 2002), in which indices of body size, peak size, and peak shape were derived from measurements of birds that were captured and individually marked. All changed significantly over time, mainly in response to climatically driven changes in the food supply.

Contemporary evolution has also been shown for Chinook and sockeye salmon and for grayling (*Thymallus thymallus*), another salmonid. All three examples involved populations that were introduced into new habitats at known times, and so were selected for substantial research efforts, recently summarized by Quinn et al. (2001) for Chinook, Hendry (2001) for sockeye, and by Haugen and Vøllestad (2001) for grayling. Kinnison and Hendry (2004) give a broader review of contemporary evolution among salmonids.

Fall-run Chinook from the Sacramento River system, probably Battle Creek, were introduced into the Hakaturamea River in New Zealand in the early twentieth century and soon spread to several other rivers on the South Island. Genetic differences developed among these populations within about 30 generations, as demonstrated by rearing experimental families in common conditions (Quinn et al. 2001). These differences are adaptive, as demonstrated by differential survival in a transplantation experiment: fish from the Hakaturamea River and Glenariffe Stream survived equally well when released from a hatchery on a third stream where experimental broods were reared, but fish from the Glenariffe stock survived better when fish were released in Glenariffe stream. Among the traits that have developed is a stream-type life history pattern, although the founding stock was ocean-type.

Sockeye were introduced into Lake Washington early in the twentieth century, and established a population in the Cedar River, which had been re-routed to flow into the lake. In mid-century, spawning sockeye were observed at a beach in the lake. Genetic analyses indicate

that this beach-spawning population is derived from the much larger Cedar River population, and to some degree has diverged from it, although there is continued immigration from the river population. Adult females in the beach population are smaller, and males have deeper bodies than in the river population. In laboratory tests, the populations have diverged in embryonic survival to hatching in relation to temperature, in development rate, and in size at emergence. The differences appear to be adaptive (Hendry 2001).

Grayling were inadvertently introduced into a Norwegian lake around 1880, and fish from this population were carried in buckets to two smaller lakes at higher elevation by a fisherman around 1920. Fish from these populations moved downstream over waterfalls into two other lakes. The lakes also support brown trout, and grayling are captured in a gill net-fishery aimed primarily at brown trout. Biological information such as length at age of maturity were collected on grayling in the first lake as early as 1903. The longitudinal data show a response in length at maturity and age at maturity to the gill-net fishery; both decreased sharply, and then partially recovered after a change in the minimum mesh size in the nets. Comparison among populations showed divergence in various traits, at least some of which are adaptive. For example, grayling reared experimentally survived best in thermal regimes similar to that of their native lakes, which vary because of differences in elevation (Haugen and Vøllestad 2000).

Local adaptation

As emphasized in other chapters, Chinook and steelhead have evolved complex sets of behaviors and other traits that help them to reproduce successfully. Because streams differ and salmon populations in them differ in ways that suggest local adaptation, and because fish transplanted from one area to another usually do poorly, it is commonly assumed that local adaptations exist among salmon populations (see reviews by Ricker 1972; Withler 1982; Taylor 1991; Quinn 2005; but see Adkison 1995).

Local adaptation was demonstrated experimentally with plants over sixty years ago (Clausen et al. 1958), but this has been more difficult with salmonids. Even before the recent studies of Chinook in New Zealand, sockeye in Washington, and grayling in Norway, however, there were at least a few convincing examples of local adaptation (Taylor 1997). For example, most juvenile sockeye rear in lakes, and those from populations that spawn in outlet streams swim upstream to reach the lake, whereas those from populations in inlet streams move downstream (Burgner 1991). Much of the difficulty in proving that local variation is both genetic and adaptive results from the phenotypic plasticity of salmon and the importance of so-called maternal effects, in which the environment and phenotype of the female affects the fitness of the progeny. For example, egg size affects survival, and good ocean conditions produce larger females that produce larger eggs, but females that grow rapidly in early life produce smaller eggs (Jonsson et al. 1996, cited in Fleming et al. 2003). Despite the complications arising from non-genetic explanations for observed variation, however, Taylor (1997) concluded that (p. 8): “Although indirect and circumstantial, the evidence that local adaptation is pervasive and important in natural populations of salmon is compelling.”

The adaptive landscape

A conceptual model called the adaptive landscape (Wright 1932; 1988; Gavrillets 2004) is useful for thinking about contemporary evolution and local adaptation. For an organism in a given environment, there is a particular reproductive potential or fitness associated with every combination of genes (ignoring maternal effects). If attention is restricted to two genetic dimensions, this can be visualized as a contour map, much like a topographic map but with lines of equal fitness rather than equal elevation (Wright 1932; Figure 1-1), or it can be visualized as a three-dimensional plot in which the x and y axes are genetic dimensions and z axis scales fitness. A similar surface can be defined in hyperspace with as many dimensions as are needed to describe the genome; this cannot be visualized, but is qualitatively similar to the two-dimensional case. A similar landscape can be imagined for populations, where each genetic axis shows the frequency of a particular allele in a population, or, alternatively, the axes can be taken as phenotypic traits (e.g., Lande 1976). The adaptive landscape can be defined fairly rigorously (e.g., Gavrillets 2004), or it can be treated more like a metaphor that allows visualization of a complex process.

If all genes acted independently and all traits were determined by single genes, then for a fixed environment there would be a single best combination of genes, or single best combination of allele frequencies, and a single peak in the adaptive landscape for that environment. Because of interactions among genes and because many traits are affected by many genes, however, in general there are multiple peaks in the adaptive landscape, although they may have different shapes and elevations, and may be connected by ridges.

Figure 1-1. The adaptive landscape as depicted by Wright (1932) by analogy with a topographic map.

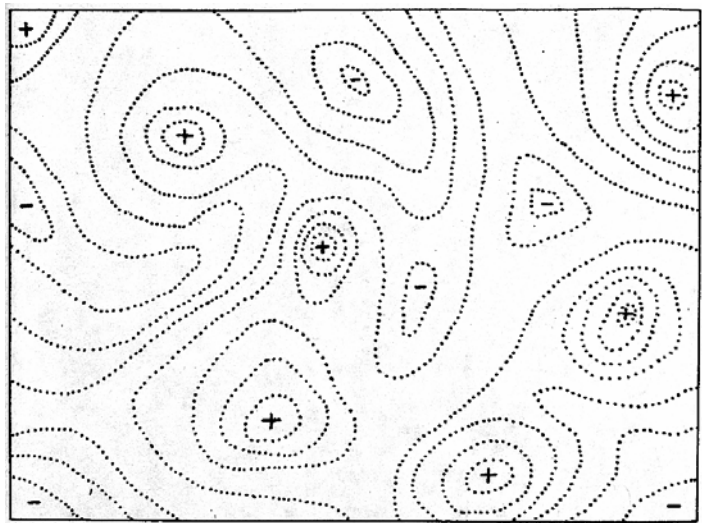


FIGURE 2.—Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect to adaptiveness.

Natural environments vary spatially and temporally, but the adaptive landscape can be considered as reflecting some kind of average condition, or as undulating around some average, so the basic idea still applies, and natural selection results in uphill movement along some path in the adaptive landscape at a rate that depends on the local slope of the surface and the amount of

heritable variation in the population in question. Natural selection is not the only reason for genetic change, however; for small populations random effects can also be important, and these can move a population downhill to and perhaps across a divide to the domain of attraction of a different peak. Natural selection in response to short-term deviations from average environmental conditions might be considered part of such random effects, depending on the time-scale appropriate for the question being addressed.

Because environmental changes can cause changes in the life-history trajectories of salmon without genetic changes, as clarified by the Thorpe et al. (1998) life-history model, not all observed phenotypic changes will be the result of selection. However, major and long-lasting environmental changes, say from building dams, leveeing channels, or harvesting sub-adults, will make major changes in the adaptive landscapes for salmon associated with these environments, and we should expect that salmon will evolve in response to these changes. The same holds for salmon in hatcheries. As a practical matter, the evolutionary response of populations to their environments means that habitats cannot be modified without changing the populations. Management and conservation should deal with populations together with their environments.

Early California salmon studies

Serious study of Central Valley Chinook salmon began at the end of the nineteenth century, with work on Sacramento River Chinook covering all stages of their life in freshwater. This was published by Rutter (1904), although much of the work was actually accomplished or directed by N. B. Scofield. This study established many of the basic facts of Chinook life history, such as the timing of juvenile migration, the variation in size and age of migrants, and the existence of sexually mature male parr—but with some curious lapses. For example, Rutter did not believe that Chinook bury their eggs, even though he watched many of them spawn, and like many biologists of the time he did not believe that salmon homed to their natal streams. Rutter (1904: distinguished only two runs, spring and fall, although he noted that “Adult salmon may be found in the Sacramento River at almost any time of the year.”

Gilbert (1913) studied scales to determine the age at maturity of six species of Pacific Salmon, and concluded that Chinook spawned normally in their fourth or later years, but that grilse spawned in their second or third year. This work was continued for Central Valley Chinook by Rich (1921; 1925) and Clark (1928). Gilbert (1913) distinguished stream-type and ocean-type juvenile life history patterns, and Rich (1920) explored juvenile life history patterns in more detail. Snyder (1924c; 1928) used fin clips on Klamath River Chinook to establish their minimum range at sea and their propensity to home to their natal tributary, although homing remained controversial for some time thereafter (see Rich 1939). Clark (1928) described the streams in the Central Valley that then supported salmon and the areas used for spawning, as well as dams and other habitat problems, and published data on size at age for male and female Chinook captured in the Delta gill net fishery, distinguishing stream-type and ocean-type fish. Snyder (1931) summarized information on the salmon of the Klamath River.

Gross physiological changes in maturing adult salmon were described in the late 19th Century for Atlantic salmon and in the early twentieth century for Pacific salmon. Rutter (1904) described the atrophy and degeneration of the stomach and intestines, and other overt changes. Charles Greene, in a series of papers summarized by Greene (1926) provided much more detail; for example, Greene reported that the lipid content of Sacramento River Chinook dropped from 18% at sea to 1.6% at spawning, but blood pressure and heart rate were relatively unchanged. Rich (1925) described the development of ovaries in the final months at sea. Generally, the basic facts of Chinook life history were known by the 1920s.

Shapovalov and Taft (1954) described a major study of the life histories of steelhead and coho salmon that was conducted during the 1930s on Waddell and Scott creeks, two coastal streams in San Mateo County, between Monterey and San Francisco bays. A weir on Waddell Creek with a two-way fish trap where fish could be counted, measured and marked and where scales could be collected was the centerpiece of the study, but additional investigations such as observations of spawning were conducted as well. A weir on the adjacent Scott Creek that was operated in conjunction with a small hatchery allowed for lethal sampling of fish for egg counts without affecting the population dynamics in Waddell Creek, and also for obtaining information on straying rates. This classic study remains a basic source of information on both species. Shapavalov also contributed to later work on Central Valley steelhead, including operation of a trap for adults near Knights Landing, that was reported in Hallock et al. (1961).

Early Central Valley Project-related studies include Hanson et al. (1940), which reviewed available information on Sacramento River chinook and conducted additional investigations in a mostly failed attempt to develop mitigation measures for Shasta Dam, an effort that was started only after bids for construction of the dam had been received. They described, but did not name, winter Chinook, and also give useful descriptions of Sacramento tributaries below Shasta that were explored for mitigation possibilities. Juvenile migration in the lower rivers and Delta was studied again by Hatton (1940) and Hatton and Clark (1942), as background information for the possible development of mitigation measures for elements of the CVP including a proposed “Cross Delta Canal.” Moffett (1949) assessed the effects of Shasta on Sacramento River Chinook and steelhead, concluding that improved conditions below Shasta more than balanced the loss of upstream habitat, but that future demand for water threatened the downstream improvements. Erkkila et al. (1950) again studied the movement of juveniles into the Delta, and also their distributions within the Delta, to try to clarify the effects of the Delta Cross-Channel and the Tracy Pumping Plant on juvenile salmon. They found that juvenile Chinook from the Sacramento River dispersed widely through the Delta, before pumping affected the movement of water there.

During the 1950s, CDFG participated in a three-state program of marking hatchery fish (Hallock et al. 1952; Fry and Hughes 1952), and put considerable effort into developing estimates of the age composition of the commercial and sport harvest of Chinook, based on analyses of scales. To make the effort more efficient, the samples of fish were stratified by length, and ages

were determined from subsamples within each length category, so that length-at-age data were generated as a by-product, as shown by examples given in appendices of Kutkuhn (1963). Unfortunately, this practice was discontinued. Kutkuhn (1963:8) also noted that information on juvenile life histories could be derived from the scales and might be useful "... in separating oceanic salmon stocks into their component subpopulations, [although] the spatial and temporal relationships involved are not clearly understood let alone defined."

In 1965, the Bay Conservation and Development Commission (BCDC) was established by state law with a mandate to prepare a "comprehensive and enforceable plan for the conservation of the water of San Francisco Bay and the Development of its shoreline" (Delisle 1966).⁷ The CDFG produced a report for the BCDC (Delisle 1966:60) that included a section on use of the Bay by salmon, probably written by CDFG biologist Don Fry. Migration routes of adults were well known from the gill-net fishery, but much less was known about juveniles: "The entire Bay north of the Golden Gate is probably used as a feeding area by young salmonids. The importance of these areas is not known—it could be very great."

When the State Water Project was approved in 1960, many of its features were not well defined, and the CDFG and the Department of Water Resources (CDWR) began a cooperative Delta Fish and Wildlife Protection Study to assess the consequences of various projects that were under consideration. These included a dam and locks at the western edge of the Delta at Chipps Island, and a Peripheral Canal that would carry water from the Sacramento River around the Delta, as well as the dam on the Feather River and the Delta pumping plant that were eventually built. It was probably important for the future direction of studies in the Delta that biologists at the time emphasized the importance of flow reversals in the Delta as part of the argument against the Chipps Island barrier. The Peripheral Canal, their preferred alternative, offered a means to prevent flow reversals, but the barrier did not (e.g., see Ganssle and Kelley 1963).

The Delta Study took a broad ecological perspective, but gave surprisingly little attention to salmon. A review by Ganssle (1962) summarized earlier work on the migration of juveniles into the Delta "...with peak numbers occurring during February or March" (p. 44). However, in 1963, Sasaki (1966) caught juvenile salmon in a mid-water trawl in the lower Sacramento River mainly in May and June, and concluded that the timing of the main downstream migration had changed. Curiously, this rather strong conclusion seems to have been generally accepted without additional field studies (e.g., Heubach 1968; Jensen 1972), although Don Fry apparently cautioned Heubach that the mesh in the trawl was too large to catch fry effectively, and Stevens (1966) noted that the trawl was not effective on fry-sized juvenile shad. In any event, the view that most juvenile salmon migrated rapidly through the Delta apparently reduced the motivation to study the use of Delta habitat by juvenile salmon, and focused attention on survival during smolt migration.

⁷ The BCDC retained an expert advisory committee comprised of an engineer, an ecologist, an economist, and a fish biologist to advise regarding development of the plan.

Independently of the Bay and Delta studies, Richard Hallock and his CDFG colleagues conducted a range of studies on chinook and steelhead from the late 1950s through the 1970s dealing with migration of adult Chinook and steelhead into the Sacramento River (Hallock et al. 1957); losses to irrigation diversions (Hallock and Van Woert 1959); steelhead and steelhead hatcheries (Hallock et al. 1961); Chinook spawning stocks (Fry 1961); the commercial value of salmon (Fry 1963); the occurrence of other species of *Oncorhynchus* (Hallock and Fry 1967); migration of adult Chinook through the Delta (Hallock et al. 1970); and hatchery release strategies (Sholes and Hallock 1979). Estimates of adult returns to various rivers were also developed, mainly by CDFG (Fry 1961; Mills and Fisher 1994), and miscellaneous studies were described in administrative reports. For example, Menchen (1961) described a test of a spawning channel adjacent to the Mokelumne River that was considered as an alternative to a hatchery in planning for Camanche Dam.

Also in the 1950s and 1960s, Harold Gangmark and colleagues in the USFWS conducted a series of studies of eggs and alevins in the gravel in Mill Creek, and in an artificial spawning channel that they constructed in a tributary of the creek (Gangmark and Broad 1955; 1956; Broad and Gangmark 1956; Gangmark and Bakkala 1960). As described in Ch. 8, these studies probably overestimated the danger to eggs from scour. This contributed to subsequent optimism regarding the benefits of flow regulation by dams for downstream spawning habitat (e.g., Dettman et al. 1987).

Monitoring in the Delta continued through the 1970s, and results regarding salmon were published in Kjelson et al. (1982) and Stevens and Miller (1983). Stevens and Miller's report concerned the relationship between flow and the abundance in the Delta of juvenile chinook salmon and other species. Unfortunately, the main conclusion of the report regarding Chinook was based on a flawed analysis that, through careless use of an index, related inflow to [catch / (exports/inflow)]; this would produce a positive relationship even if catch and exports were random variables. Kjelson et al. (1982) described the spatial distribution of juvenile salmon in the Delta based on seine data from 1977 to 1981, and also estimated the growth and survival of tagged fry released into the Delta, as well as of smolts released into the Sacramento River. Coded-wire tag studies relating the survival of smolts migrating through the lower rivers and the Delta, and studies relating to instream flow assessments constituted most of the salmon studies of the 1980s.

The amount and timing of flows that should be released from dams to provide habitat for salmon and other public trust resources has long been a source of controversy in the Central Valley, as elsewhere (Gillilan and Brown 1997). Early instream flow assessments in the Central Valley were based on assumptions about the area of spawning habitat required to produce a given number of fish, and simple statistical analyses between spring flows and adult returns. For example, according to Menchen (1978:4,5):

Spawning gravel area requirements for runs of 32,000 to 52,000 spawners are fairly straightforward. An area of 1,000,000 square feet will accommodate 32,000 spawners on the Tuolumne. Fifty thousand spawners require 1,562,000 square feet. outflows during March through June of around 4,000 cfs are required to produce 32,000 adults and of around 7,500 cfs are required for runs of 50,000 adults (Fry 1965).

Although Fish and Game Code Sec. 5937 has required since 1937 that the owner of any dam release enough water to keep fish below the dam in “good condition,” the interpretation and enforcement of the section historically fell rather short of what the language seemed to require⁸ (e.g., Baiocchi 1980), and until after the development of environmentalism as a political force in the late 1960s Fish and Game biologists believed, probably accurately, that they had little power to require releases to accommodate fish.

In the late 1970s, a federal interagency group developed the Instream Flow Incremental Methodology (IFIM) for estimating the habitat value of a stream as a function of flow, and for using these estimates in negotiations for setting “instream flows,” especially requirements for releases from dams (Bovee et al. 1998). The heart of the IFIM is a set of computer models, the Physical Habitat Simulation System (PHABSIM), critiqued Ch. 14, that has been applied to many Central Valley streams. PHABSIM calculates a statistic called weighted usable area (WUA) at different rates of flow.

It may be useful to distinguish several kinds of studies from among those described above. Most are mainly descriptive (e.g., Rutter 1904; Hatton and Clark 1942; Erkkila et al. 1950), but some are experimental (e.g., Snyder 1924c; Sholes and Hallock 1979). Descriptive studies can be necessary when not enough is known about a topic to devise useful experiments, but making assessments or decision regarding management based on descriptive studies generally involves making stronger assumptions. For example, Erkkila et al. (1950) assumed that juvenile salmon in the Delta “go with the flow” and would be transported toward the Delta pumping facilities in proportion to the pumping rate. It can be reasonable and conservative to make such assumptions when the time or the means to test them are not available, but experimental tests of important assumptions should not be neglected.

⁸ To make a long and complicated story very short, the legal context for instream flow protection was substantially changed by the 1983 decision of the California Supreme Court in *Audubon v. Superior Court*, which outlined the application of the public trust doctrine regarding appropriative water rights. This is discussed further in Appendix C.

CHAPTER TWO

CENTRAL VALLEY SALMON

I will say from my personal experience that not only is every contrivance employed that human ingenuity can devise to destroy the salmon of our west coast rivers, but more surely destructive, more fatal than all is the slow but inexorable march of these destroying agencies of human progress, before which the salmon must surely disappear as did the buffalo of the plains and the Indian of California. The helpless salmon's life is gripped between these two forces – the murderous greed of the fisherman and the white man's advancing civilization – and what hope is there for the salmon in the end?

Livingston Stone (1892)⁹

Before the gold rush, streams draining into the San Francisco Estuary supported five anadromous species of Pacific salmon, genus *Oncorhynchus*: Chinook, steelhead, pink, chum, and coho. The two surviving species, Chinook and steelhead, probably were most widely distributed, and Chinook most abundant, but even after debris from hydraulic mining had degraded lowland river habitats there were occasional reports of significant numbers of chum and pink salmon (Moyle 2002). Coho used streams draining into San Francisco Bay and probably the Sacramento River as well (Moyle 2002). Sockeye occasionally appear in the Sacramento River, as do chum and pinks (Hallock and Fry 1967), but there is no historical evidence of persistent populations of sockeye (Moyle 2002). This chapter provides an introduction to the Pacific salmon and to Chinook and steelhead in the Central Valley.

The Pacific salmon

The Pacific salmon apparently arose around 20 million years ago, during the early Miocene (McPhail 1997). Although specialists disagree on the details of subsequent speciation or the number of species (e.g., Stearley and Smith 1993; Shedlock et al. 1992; Stearns and Hendry 2004), McPhail (1997) notes that there is agreement that the pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) lineages represent the most recent divergences. Since these are represented by fossils that are ~six million year-old (Smith 1992), this implies that the Chinook (*O. tshawytscha*) lineage is even older, considerably older than was thought until recently (e.g., Healey 1991).

The *Oncorhynchus* all spawn in fresh or brackish water, burying their eggs in gravel nests called redds where the eggs incubate. The redds protect the eggs, and *Oncorhynchus* have relatively few (usually <10,000), large eggs. The young hatch as alevins, larvae with a large egg yolk attached to their bellies. The alevins grow and develop in the gravel, living on egg yolk rather than feeding, and emerge as small fish about the time the egg yolk is fully absorbed. Most species are at least partly anadromous, although some populations or subspecies of steelhead/rainbow (*O. mykiss*), cutthroat (*O. clarkii*) and masu salmon (*O. masou*) live only in

⁹ Address to the American Fisheries Society. Copied from Joel Hedgpeth, *The Passing of the Salmon*, in Lufkin (1991).

streams (e.g., golden trout), and other salmon can mature in lakes. Masu occur only in Asia, and some Pacific “trout” (e.g., gila trout, *O. gilae*) occur only in North American, but other Pacific salmon occur on both sides of the North Pacific (Groot and Margolis 1991; Moyle 2002). Chinook and coho salmon have been successfully introduced to the Great Lakes (Carl 1982), and Chinook populations are established in New Zealand as well; *O. mykiss* is now widely distributed around the world (Moyle 2002).

The anadromous Pacific salmon are major pelagic predators in the North Pacific, feeding on crustaceans, mollusks, tunicates, and other fish (Groot and Margolis 1991; Moyle 2002). Central Valley Chinook, however, forage primarily in coastal waters off California and Oregon, and Central Valley steelhead may do so as well (Ch. 11). All adult Chinook, coho (*O. kisutch*), sockeye, chum, pink and anadromous masu salmon die shortly after spawning, as do most steelhead and cutthroat. Since these fish grow mainly in the ocean, they carry nutrients from the ocean to streams that benefit juvenile salmon and other aquatic organisms. Spawning salmon are also important food for many terrestrial animals, and by various routes marine-derived nutrients from salmon carcasses also move into riparian and adjacent terrestrial ecosystems (Stockner 2003).

Salmon are also important to people. In the Central Valley, as elsewhere, Chinook were an important food for Native Americans (Yoshiyama 1999, but see Gobalet et al. 2004), and a commercial fishery developed as soon as the gold rush created a market. Salmon canning began at Sacramento in 1864, and there was a gill net fishery in the Delta until 1957, although in California most salmon have been taken by trolling in the ocean since 1917 (Clark 1928; Fry and Hughes 1951). Both Chinook and steelhead also support popular recreational fisheries, in both fresh and salt water for Chinook, and in fresh water for steelhead. However, salmon are important to people not only as something to catch and eat; there is something mythical about their spawning migrations that touches a deep chord in the human psyche.

Most anadromous Pacific salmon have variable life history patterns, but pink salmon has such a rigid two-year life cycle that populations spawning in the same stream in even and odd years are genetically isolated, and some streams have runs only every other year (Heard 1991). Juvenile pinks, like juvenile chum, migrate to sea directly after emerging from the redds, but chum may spend two to five years at sea, most commonly four (Salo 1991). Coho salmon life cycles are also rather rigid, with almost all females spawning at age three, although males commonly mature at two or three, and at higher latitudes many coho spend two years in streams and spawn at three or four (Sandercock 1991). Chinook salmon may rear in streams for a few days to two years, and spend a few months to seven years at sea, and some males mature precociously as parr (Rutter 1904; Healey 1991; Zimmerman 2003). The life histories of anadromous steelhead are even more variable; they may spend a few months to three years in streams, and a few months to five years at sea (Shapovalov and Taft 1954; Withler 1966). Some do not go past the estuary of their home stream, but others make far-ranging sea migrations (Pearcy et al. 1990). Not all die after spawning, and survivors may spawn again after another trip to sea. As one consequence, while simple statements can be made about pink salmon or even

coho life histories, the same cannot be done for Chinook and steelhead; rather, the great variability of their life histories, both among and within populations, must always be kept in mind.

The life history stages of Pacific salmon are generally described by the same terms used for other salmonids (Moyle 2002). Newly hatched fish with external yolk are “alevins”, or “sac-fry.” When the yolk is nearly depleted and fully enclosed in the body or “buttoned-up,” usually about the time the fish emerge from the gravel, they become simply “fry.” They become “parr” when they develop dark vertical bars or parr-marks on their sides. Larger juveniles migrating toward the sea become silvery and are called “smolts.” Fish that return to spawn after a single year at sea are called “grilse,” or “jacks” if they are male (as almost all are), and “jills” if female; jills appear to be more common in the Central Valley than elsewhere (Ch. 6).

Salmon famously “home” to their natal streams, with enough fidelity that populations in different streams or with different run-timing often seem to be sufficiently isolated genetically to develop local adaptations, and there is good evidence that such adaptations exist (Taylor 1991, 1997; Quinn 2005; but see Adkison 1995). Thus, historical variation within and among the Central Valley runs presumably reflects adaptation to differing environments. However, Chinook salmon and steelhead, like many other salmonids, are highly flexible in their phenotypic responses to environments, so observed phenotypic variation does not necessarily imply genetic variation. For example, age at maturity is affected by both genes and environment (Hankin et al. 1993). This phenotypic plasticity allows salmon to survive in more variable environments than would otherwise be the case (Thorpe 1989), but it also makes it hard to demonstrate conclusively that observed variation is genetically determined. In particular, it is hard to demonstrate that differences between hatchery and naturally-produced fish are genetically based, although, as discussed in Ch. 12, there are good reasons to believe that hatchery culture involves selection for different traits than does natural production.

Salmon populations are generally described by the season in which the adults return to fresh water. In the Central Valley, there are now fall, late fall, winter, and spring Chinook, and winter steelhead, and there may once have been summer Chinook and steelhead (Commissioners of Fisheries 1875; McEwan 2001; Moyle 2002). Chinook are also often described as “ocean-type” or “stream-type.” Biologists have long realized that some Chinook salmon smolt and go to sea in their first year, while others spend a year or more in fresh water before doing so (Figure 1-1); Gilbert (1913) described these as ocean-type and stream-type Chinook. These juvenile life-history patterns are often but not always associated with adult run-timing and the physiological state of the returning fish. Generally, stream-type Chinook re-enter fresh water in the spring as sexually immature fish, and ripen in fresh water before spawning in early fall; ocean-type Chinook typically re-enter fresh water shortly before spawning. Healey (1983; 1991) pointed out other differences: stream-type chinook predominate north of about 55°N on the North American coast, and on the Asian coast, while ocean-type Chinook predominate south of 55°N. Ocean-type Chinook typically forage in coastal waters, while stream-type Chinook forage mainly in the open ocean.

Figure 2-1. Scales of stream-type (A) and ocean-type (B) Chinook, captured as juveniles in the ocean. Closely spaced growth-rings in A reflect slow growth in fresh water after an initial period of more rapid growth. Scale A is from a 128 mm fish captured with sardines in Monterey Bay in June 1923. Scale B came from a fish captured either off Half Moon Bay in 1921 or near Bolinas in 1922, captured by bait fishers. Copied from Snyder (1924).

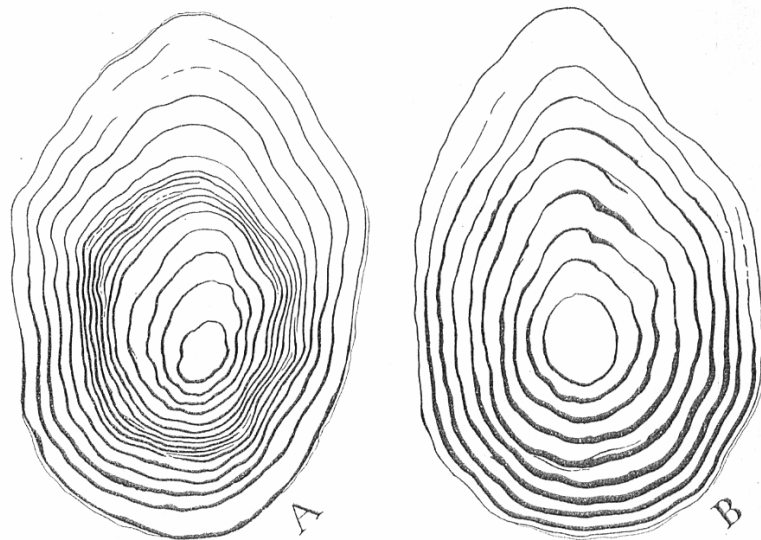


FIG. 16. Types of scales of young sea-caught salmon. Scale A indicates that the fish remained in the stream during its first year or somewhat longer. Scale B indicates that the fish did not stay long in fresh water but migrated to sea at an early age.

More southerly populations of spring Chinook do not share the set of characteristics identified by Healey (1991), however. It now appears likely that an incomplete divergence occurred within Chinook salmon during the Pleistocene, when much of the current North American range of the species was under glacial ice, so that Asian or Beringean and Cascadian/Sierran populations were geographically isolated (Healey 1991; Teel et al. 2000). The resulting lineages correspond largely but not completely with life-history patterns. Genetic evidence suggests that in broad terms the Beringean lineage constitute spring-run as described by Healey (1991), which now ranges from Asia to as far south in North America as the Columbia River; but in detail the situation is more complex and still unresolved (Rasmussen et al. 2003; Waples et al. 2004). In any event, most spring-run in the Central Valley exhibit an ocean-type life history pattern (Ch. 5), although some are stream-type, but both the stream-type and ocean-type forage mainly in coastal waters (Myers et al. 1998).¹⁰

Steelhead also exhibit life histories in which fish spawn within a few months after entering freshwater, or after holding in pools for more extended periods. Historically, Central Valley steelhead probably exhibited both patterns, but the pattern with longer freshwater residency did not persist. Unfortunately, the nomenclature for these runs is not standardized. McEwan (2001) calls the extant and extinct runs “winter-run” and “summer-run,” but the former are sometimes called “fall-run” as well (Moyle 2002), which seems reasonable as they enter the Sacramento River mainly in that season (Hallock et al. 1961).

As described in more detail below, diversity in life history patterns of Central Valley Chinook has also declined. For example, the range of age of maturity in Chinook has declined by

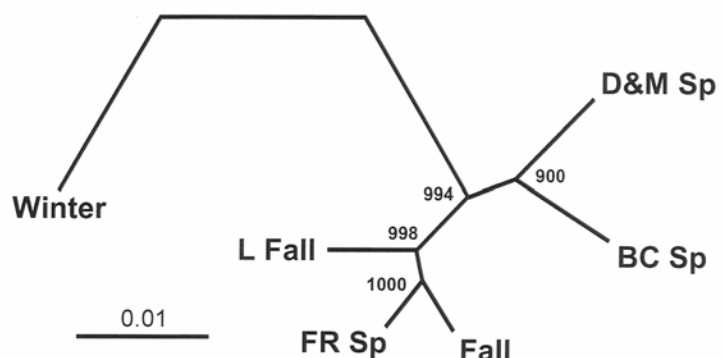
¹⁰ Unfortunately, the terms ocean-type and stream-type are sometimes used in the literature to describe what are probably the Beringian and Cascadian/Sierran lineages (e.g. Myers et al. 1998), which compounds an already confused situation.

about a year, probably in response to ocean harvest (Ch. 13). It is not clear how rapidly such changes can be reversed. Some traits can evolve rapidly, for example, a stream-type phenotype developed in New Zealand from a population founded from ocean-type fall Chinook from the Sacramento River (Quinn and Unwin 1993), and a “reservoir-type” life history pattern apparently has developed in fall Chinook from the Snake River (Connor et al. 2005). On a geological time scale salmon adapt rapidly to new environments, perhaps because they are tetraploid (Wilson 1997; Moyle 2002). Thus, salmon have reoccupied large areas of Washington, British Columbia, and Alaska that were under ice less than 15,000 years ago. Nevertheless, there are constraints to the evolution of life history patterns or complex local adaptations, for which coordinated sets of traits may be needed. On a human time scale, however, the evolution of such co-adapted complexes of genes is likely to be slow (Law 2000), and few of the many attempts to transplant anadromous salmonids have been successful (Quinn 2005).

Central Valley salmon

Rutter (1904) distinguished only spring and fall Chinook, although he noted that some adults could be found in the river year round. Winter and late fall Chinook were recognized later (Hanson et al. 1940; Fry 1961).¹¹ Studies using neutral genetic markers show that the runs are distinct, but there are also three distinct groups of spring-run (e.g., Figure 2-2). Neutral markers, such as slightly different base-pair sequences that code for the same protein, are not associated with traits conferring fitness, so differences in neutral markers reflect genetic drift, rather than natural selection. To date, the genes controlling traits such as run-timing that affect fitness have not been identified, although efforts to do so are underway (M. Banks, pers. comm. 2004). The development of a salmon “gene chip” (Rise et al. 2004) should facilitate identification of fitness genes.

Figure 2-2. Genetic relationships among runs of Central Valley Chinook, based on distances (Cavalli-Sforza and Edwards) calculated from 12 microsatellite loci. The clustering analysis (UPGMA) distinguishes spring-run from Deer and Mill creeks (D&M Sp) and Butte Creek (BC Sp). Numbers next to nodes show the number of bootstrap trees, out of 1,000, showing this node. Nominal spring-run from the Feather River (FR Sp) group close to fall-run. Other genetic studies, reviewed by Hedgecock et al. (2001) have produced similar results. Copied from Hedgecock 2002.



¹¹The Commissioners of Fisheries (1875:10) also described a summer-run that migrated up the San Joaquin River in July and August that appeared to be “...of the same variety as those in the Sacramento, but smaller in size.” The Commission was particularly interested in them because their tolerance of high water temperature “... would indicate that they will thrive in all the rivers of the southern states, whose waters take their rise in mountainous or hilly regions”

Phylogenetic tree of 100 *Drosophila* species based on 18S rDNA. The tree is rooted at the bottom left and branches outwards. Species are represented by symbols: open circles for species with no data, filled circles for species with data, and half-filled circles for species with partial data. Bootstrap values are indicated at the nodes. The tree is divided into several major clades: L (top left), K (top right), C1 (middle right), J1 (middle left), J2 (bottom left), and A (bottom right). A scale bar of 0.01 is shown at the bottom left.

Fall Chinook

26

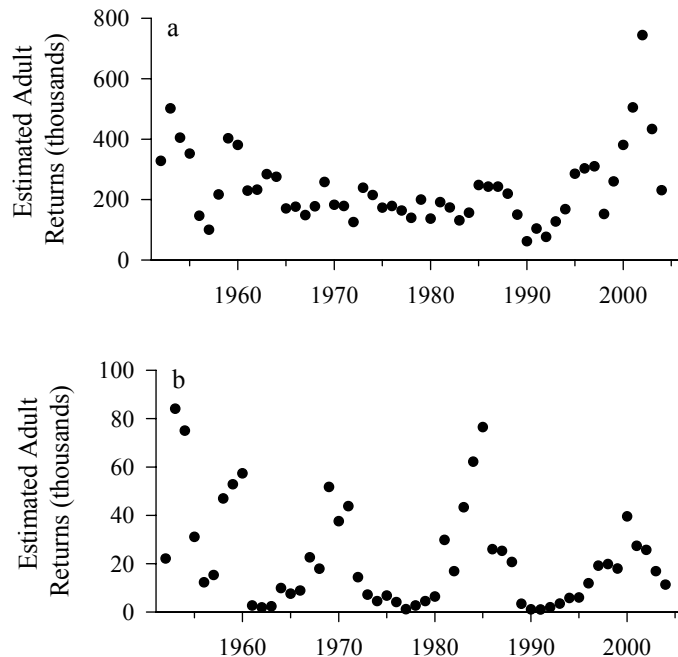
of kilometers upstream. However, a good deal of the historical spawning habitat of the fall-run remains available below existing dams. Spawning typically begins when water cools to about 14 or 15°C, and extends into December (Ch. 6).

Fall-run fry emerge from December into April, depending on the date of spawning and water temperature during incubation, and exhibit two main life-history patterns. Most begin migrating as fry, shortly after emergence (Rutter 1904, Hatton 1940), and most of these apparently rear for one to three months in the Delta before moving into the bays (Ch. 5). However, some continue directly through Carquinez Strait into San Pablo Bay (Hatton 1940). Analogous groups in Puget Sound have recently been described as “delta users” and “fry migrants” (Greene and Beechie 2004). Of the Chinook that do not leave the gravel-bed reaches as fry, most do so as parr or silvery parr by May or early June, before the lower rivers become intolerably warm, and pass fairly quickly through the Delta. These larger migrants are sometimes called “fingerlings” or “90-day Chinook” or “smolts,” although few of them develop the full suite of developmental characteristics of smolts while they are still in the rivers (Ch. 5). The relative contributions of fry and pre-smolt migrants to returns are not known, although there is good evidence that the survival of the larger migrants is much higher (Ch. 10).

Where hypolimnetic releases from reservoirs such as Shasta on the Sacramento River keep water temperature low, some juvenile fall-run remain near the spawning grounds through the summer (Anderson et al. In press), and a few hold over through the winter and migrate as yearlings (SRFG 2004). Except for these last two groups, and some early-arriving adults, the fall-run do not occupy freshwater during the summer, and so can use river habitat that is suitable for them for only part of the year. Reservoirs also keep rivers warmer in the winter than was the case historically, so that embryos and alevins develop more rapidly, and current monitoring (e.g., Snider and Titus 2000a,b,c; SSJEFRO 2003) indicates that fry migrants in the Sacramento River now begin their migration about a month earlier than indicated by pre-dam monitoring reported by Rutter (1904) and Hatton and Clark (1942).

Fall-run abundance has varied considerably through the period of record, with extreme lows in the early 1990s and more recent highs (Figure 2-4). Based on records of commercial harvest, abundance was also highly variable in earlier years (Skinner 1962; Dettman et al. 1987). Abundance is increased by extensive hatchery production (Ch. 12) and decreased by harvest (Ch. 13). The pronounced cyclicity of the San Joaquin tributary escapements remains to be satisfactorily explained, but appears to be influenced both by flow and by internal population dynamics (Speed 1993), and presumably also by ocean conditions.

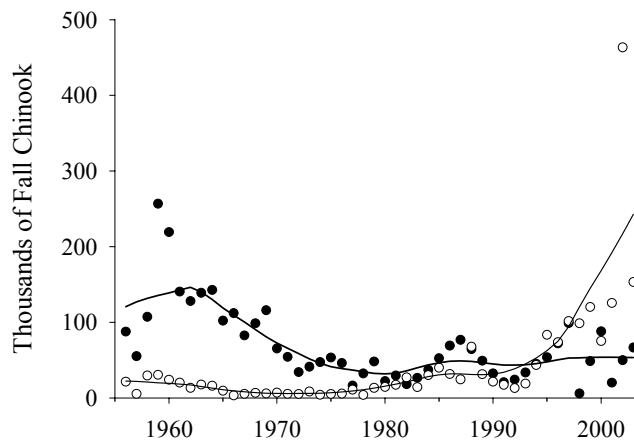
Figure 2-4. Abundance of naturally spawning fall Chinook salmon in (a) the Sacramento River and tributaries, and (b) San Joaquin River tributaries plus the Mokelumne River. Note the eightfold difference in the vertical axes. A poorly quantified but large proportion of these are hatchery fish; fish collected in hatcheries not included. Data from the CDFG GrandTab database, 2002-2004 data are provisional. The accuracy of the GrandTab data is uncertain and variable, especially for earlier years.



Fall-run are raised in five hatcheries in the Central Valley: Coleman (Battle Creek), Feather River, Nimbus (American River), Mokelumne River, and Merced River; about 24 million juveniles are released annually. Hatcheries have come under increasing criticism in recent years (Ch. 12). The National Resource Council (NRC 1996) identified demographic risks, genetic and evolutionary risks, behavior, fish health, physiology, and ecological problems as issues concerning the interaction of hatchery and naturally produced salmon. Genetic risks seem most serious, since genetic effects will persist even if hatchery production is ended. A group of distinguished scientists recently asserted that “Inevitably, hatchery brood stock show domestication effects, genetic adaptations to hatchery environments that are generally maladaptive in the wild” (Myers et al. 2004:1980). Few fall-run hatchery fish are marked, but based on recoveries of tagged fish during spawner counts it appears that fall-run populations in some streams without hatcheries are heavily affected by straying hatchery fish. The NOAA Fisheries status review concluded regarding fall Chinook that “...high hatchery production combined with infrequent monitoring of natural production make assessing the sustainability of natural production problematic, resulting in substantial uncertainty regarding this ESU” (Myers et al. 1998).

In the upper Sacramento River, the relative proportions of fall-run spawning in the mainstem and in Battle Creek have approximately reversed over the last half-century, with more fish now spawning in Battle Creek than in the Sacramento River above Red Bluff (Figure 2-5). Assuming that hatchery strays spawning in the mainstem roughly balance naturally produced fish spawning in Battle Creek, and given that the total number of fish in the years around 2000 is about the same as in the years around 1960, it appears that hatchery fish are replacing naturally produced ones, as has happened elsewhere (Unwin and Glova 1997).

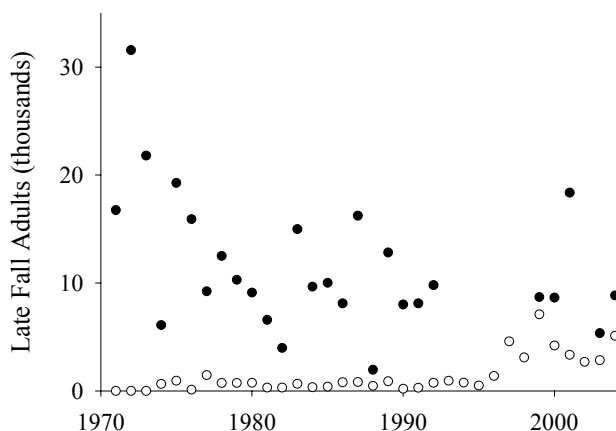
Figure 2-5. Returns of adult fall Chinook to the mainstem Sacramento River above Red Bluff and to Battle Creek. Returns to Battle Creek, including Coleman Hatchery (open circles) have increased dramatically in recent years; returns to the mainstem (filled circles) have not (Fig. 2-4a includes large runs in major tributaries in recent years). Trend lines fit by lowess, with smoothing parameter = 0.3. Data from CDFG GrandTab database; data for 1996 and 1997 overlap.



Late fall Chinook

Maturing late fall Chinook follow the fall-run into fresh water, with peak migration past the RBDD in December or January; spawning occurs from January to early April. The fry emerge from April to June, and the juveniles typically rear in the stream through the summer before beginning their emigration in the fall or winter (Fisher 1994). Historically, late fall-run probably spawned farther upstream than fall-run, where water temperatures remained tolerable for the juveniles through the summer. However, rivers are generally higher and more turbid in winter, so late fall-run adults are hard to observe, and less is known about them and their historical range than about other runs. There are conflicting statements in the literature. For example, Fry (1961:59) wrote that “In addition to the winter run fish there are some very late fall run fish which enter most of the Central Valley salmon streams in winter and spawn almost immediately,” but Fisher (1994) stated that late-fall run spawned “at the northern and southern extremes of the valley floor where summertime water temperatures afforded suitable juvenile rearing conditions.” Late fall-run persist mainly in the Sacramento River, where total numbers have been more or less stable over the last 30 years, but hatchery returns have been increasing (Figure 2-6). Although late fall-run apparently spawn in various streams where recently emerged fry are captured as late as May (e.g., Ward et al. 2004a,b for Butte Creek), genetic analyses to confirm their presence have not yet been done, and some of these fry may be progeny of hatchery strays. Genetically, late fall-run are closely related to fall-run (Figure 2-2), and the NOAA Fisheries (aka NMFS) has treated them as part of the fall-run “evolutionarily significant unit,” or ESU, under the federal Endangered Species Act (Myers et al. 1998).

Figure 2-6. Estimated returns of late fall Chinook to the Sacramento River above the RBDD (filled circles) and to Coleman Hatchery (open circles). River estimates before 1987 were based on counts at the RBDD, and are more accurate than more recent data; the gap in the mid-1990s reflects lack of sampling, not a population crash. Data from CDFG GrandTab database; 2002-2004 data are provisional.



Late fall Chinook have been raised at Coleman National Fish Hatchery since the early 1950s, but were not formally distinguished from fall-run until 1973 (USFWS 2001). Current production is about one million smolts, all marked with adipose fin clips and coded-wire tags (CWTs). Most are released at the hatchery, but a substantial proportion is released in or near the Delta for survival studies, and presumably have a greater propensity to stray. Initially, late fall Chinook broodstock was collected at a trap at Keswick Dam, but Keswick collections were slowly phased out between 1982 and 1996, and for several years fish were taken only at the hatchery. Since 2002 ~10% of the broodstock has been collected at Keswick (K. Niemela, USFWS, pers.comm. 2005). All fish that enter the hatchery are retained, to reduce natural spawning by hatchery fish. Returns to the Colman National Fish Hatchery have increased in recent years relative to returns of naturally produced fish (Figure 2-6), and there is a suggestion of an increasing trend in the percentage of marked fish among spawners examined during carcass surveys, but the percentage is still low (Table 2-1).

Table 2-1. Recoveries of late fall Chinook with clipped adipose fins during carcass surveys on the upper Sacramento River. All hatchery late fall are marked. Data from Snider et al. (1998; 1999; 2000; 2001; D. Killam, CDFG, pers. comm. 2005)

Year	1997-98	1998-99	1999-00	2000-01	2001-02	2002-03	2003-04	2004-05
# fresh carcasses	182	435	365	605	828	205	560	630
# ad-clipped	2	5	29	9	1	5	25	71
% ad-clipped	1	1	8	2	0	2	4	11

Winter Chinook

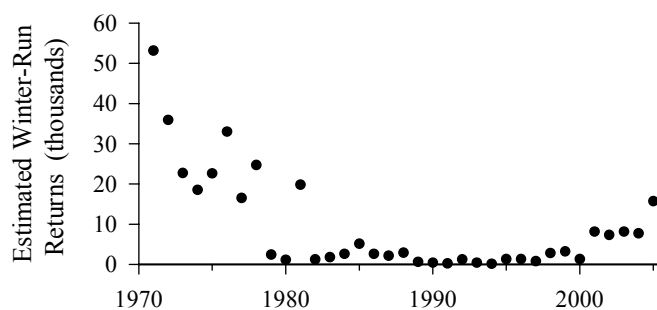
Winter Chinook occurred naturally in upper tributaries of the Sacramento River that drain large areas of fractured basalt or lava: the McCloud River, Little Sacramento, Fall, and Pit rivers,

and in the North Fork of Battle Creek (Yoshiyama et al. 2001; Lindley et al. 2004).¹² Inflow of cool water from springs makes these streams suitable spawning habitat in summer. Winter-run were blocked from their holding and spawning habitat in Battle Creek by early hydroelectric dams, and from the rest of their natural habitat by early dams on the Pit River and finally by Shasta Dam. It seems likely that the run nearly went extinct during the construction of Shasta, since there were several years when migration past the dam was blocked, but releases of cool hypolimnetic water had not begun. Subsequently, the run increased dramatically and supported a substantial recreational fishery (Slater 1963), but then declined to very low number in the early 1990s. More recently the run has increased, but it is still well below mid-century levels (Moyle 2002; Figure 2-7).

Adult winter Chinook pass the RBDD mainly between January and May, with runs peaking in mid-March, based on the assignments to runs made at the RBDD fish ladder.¹³ They spawn from late April through early-August, after holding near the spawning areas for several months, and fry emerge from July through mid-October (Fisher 1994). Most juveniles migrate past the RBDD as fry in summer or early fall, but apparently rear for some time in the river below Red Bluff before reaching the Delta in early winter.

Winter-run have been listed as endangered under the California Endangered Species Act (ESA) since 1993 and under the federal ESA since 1994. Winter-run have recovered to some degree in the last few years, probably in response to changed operations in the RBDD, restrictions on harvest, and improved ocean conditions. About 200,000 winter-run smolts are produced annually at Livingston Stone Hatchery on the Sacramento River (Ch. 12). All are marked and tagged. The percentage of hatchery fish among those spawning in the river has increased in recent years, and probably exceeded 18% in 2005 (K. Niemela, USFWS, pers.comm. 2005). This is high enough to be worrying.

Figure 2-7. Abundance of winter Chinook salmon spawning in the Sacramento River. Returns to hatcheries are minor, and are not included. Data from the CDFG GrandTab database, 2002-2004 data are provisional; 2005 datum from NMFS.



¹² A population of late-running fish that appeared in the Calaveras River in the 1970s and 1980s was reported to be winter-run (e.g., NMFS 1997), but were more likely late fall-run (Yoshiyama et al. 2001). Whatever it was, habitat for this run was created by releases from New Hogan Dam; in natural conditions the river would have been unsuitable for it.

¹³ The winter-run run-timing overlaps with late fall-run and spring-run, and assignments of adults to runs made at the RBDD were based on external appearances and were subject to error. For example, some of the fish selected in the early 1990s for a hatchery supplementation program for winter-run turned out to be spring-run (Banks et al. 2000).

Spring Chinook

Spring Chinook enter freshwater in the winter and spring and hold over through the summer in pools while they mature sexually, and then spawn in the late summer. This life history requires that they migrate far enough upstream to find habitat that remains cool enough ($<21^{\circ}\text{C}$) for the adults to survive (Ch. 6). Embryos are less tolerant of warm water than adults, and as with fall-run, spawning begins when water cools to ~ 14 or 15°C , usually by September. The spring-run life history is well adapted to streams with snowmelt runoff, which provides relatively dependable sustained high flows that allow fish to ascend to high enough elevations that the water will remain tolerably cool through the summer. Snowmelt runoff is relatively more important in the San Joaquin River and its major tributaries, and historically spring-run probably were numerically dominant there.

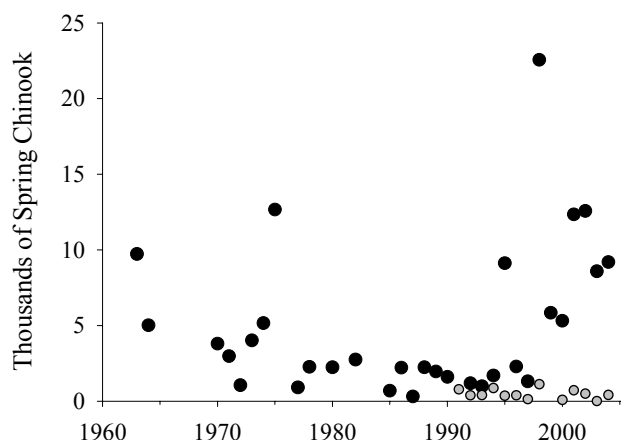
Adults pass upstream into their holding areas from February into early July, with migration peaking in mid-April in Butte Creek, mid or late May in Mill and Deer creeks, and May and June on the Feather River. Most Central Valley spring-run now follow an ocean-type life history, beginning their downstream migration in the winter as fry, although some rear in the stream for several months or more before migrating in later spring or in the following fall, winter, or spring. Before dams blocked most of their high altitude habitat, a larger proportion may have been stream-type. Yearling migrants are more common in Mill and Deer creeks than in Butte Creek (Ch. 5). A substantial tagging program on Butte Creek has demonstrated that adults returning to that stream in recent years are almost all from juveniles that emigrated into the valley as fry (Paul Ward, CDFG, pers.comm. 2005).

Spring-run were extirpated in most rivers by mining or early dams, and populations thought to be self-sustaining now survive only in three tributaries of the Sacramento River: Mill, Deer, and Butte creeks, although small populations also occur in several other tributaries (Lindley et al. 2004; CDFG 2004b). Spring-run were listed as threatened under the federal ESA in 1999. As with fall-run, spring-run abundance has increased in recent years (Figure 2-8), especially in Butte Creek. However, spring-run in the mainstem Sacramento River have been reduced to very low numbers. Spring-run apparently occurred in reasonable numbers in the Sacramento River through the 1980s, but counts at the Red Bluff Diversion Dam through 1990 probably included enough fall-run that the data are not reliable (C. Harvey-Arrison, CDFG, pers.comm. 2005).

Typically, spring-run spawned farther upstream and at higher elevations than did fall-run, where water cools to suitable temperatures earlier than in the fall-run spawning areas. Historically, spatial segregation helped to maintain reproductive isolation, but early reports noted that spring-run spawning was also temporally isolated from fall-run spawning on the McCloud River (CDFG 1998), and Moffett (1949) reported the same for the Sacramento River below Shasta. However, Slater (1963) reported that the spawning periods of the two runs overlapped, with resulting hybridization, and that in recent years the spring-run "... have not been noted to have been abundant" Hybridization between spring and fall Chinook apparently also occurred in the Feather River (Lindley et al. 2004). Although several thousand fish continue to return to the Feather River each year at the appropriate time for spring-run, they are very similar

genetically to Feather River fall-run (Figure2-1). Alternatively, the original Feather River spring-run may have been extirpated by hydraulic mining, and the small population present in the 1960s when Oroville Dam was built may have developed recently from surviving or recolonizing fall-run.¹⁴ Whatever it is, this population is heavily supported by production at the Feather River hatchery, all now marked. Because it is very hard to hold fish over the summer in the hatchery, fish in the past were left in the river until spawning, which presumably led to mixing with fall-run in the hatchery. Early arriving fish are now being marked so that they can be spawned separately. Spring-run in the Yuba River probably are similar to those in the Feather.

Figure 2-8. Estimated abundance of spring Chinook in the Sacramento River mainstem (gray circles) for 1991-2003 and in Mill, Deer and Butte creeks (black circles) for 1970-2004. Note that data for one or more of the creeks are missing for some years. Data from the CDFG GrandTab database, 2002-2004 data are provisional.



Steelhead

As with Chinook, some steelhead enter streams many months before spawning and hold over in pools while maturing sexually, while others begin sexual maturation in the ocean and spawn within a few months after entering streams. Probably both forms once existed in the Central Valley, but remaining anadromous steelhead are now primarily ocean-maturing fall or winter-run fish (McEwan 2001).

Steelhead were once widely distributed in the Central Valley (McEwan 2001), and even in the mid-twentieth century Hallock et al. (1961:16) reported that they “spawn in practically every tributary of the upper Sacramento River and appear to do so in numbers more or less proportional to the amount of runoff.” For five years in the 1950s, they estimated from mark-recapture studies that number of wild adults returning to the Sacramento River above Knights Landing averaged about 18,000. Anadromous steelhead enter freshwater mainly from August through November, but RBDD ladder records show that a few enter at all times of year. Spawning occurs mainly from December through April (Hallock et al. 1961), so adults typically

¹⁴ Waples et al. (2004) note that the genetic differences between spring and fall-run populations in the lower Columbia River basin are small enough that they could have developed in 80-100 years.

spend a few months in freshwater before spawning, but since spawning occurs in the winter and early spring it is much harder to observe than spawning by spring, winter, and fall Chinook.

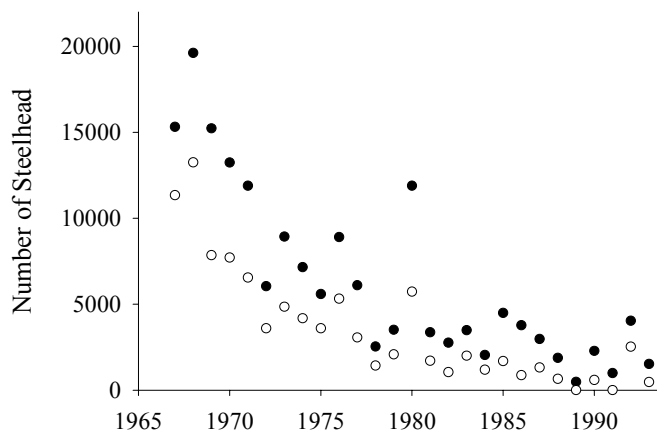
Juvenile steelhead emerge from late winter to summer. Naturally produced steelhead from the upper Sacramento River and tributaries spend one to three, but usually two, years in fresh water before emigrating, usually in the spring; fish from lower tributaries such as the American River mainly emigrate after one year (Titus et al. 2004). Historically, steelhead spawned high enough in stream systems that the water remained tolerably cool for juveniles in the summer. Steelhead can ascend steeper streams and spawn in smaller tributaries than Chinook. Like spring Chinook, steelhead lost most of their natural spawning habitat in the Central Valley to dams.

Many populations of *O. mykiss*, including existing Central Valley populations, consist of both anadromous and non-anadromous individuals (McEwan 2001; Moyle 2002). It seems likely that dams that release cool water through the summer, such as Shasta on the Sacramento River, New Melones on the Stanislaus River, and New Bullard Bar on the Yuba River, have encouraged a shift toward the non-anadromous life history pattern. This is not a unique situation; dramatic changes in the proportions of anadromous and non-anadromous individuals have been reported in other populations of salmonids (Thorpe 1987; Morita et al. 2000; Hendry et al. 2004). Whether this entails genetic change or is simply a phenotypic response to the changed environment is not certain, although in the long term a genetic response to the changed environment seems inevitable. In any event, examples of anadromous progeny of non-anadromous females and vice versa have been documented (Titus et al. 2004).¹⁵

Abundance data on anadromous *O. mykiss* are discouraging. Counts at the Red Bluff Diversion Dam until 1993 showed a rapidly declining population in the upper Sacramento River (Figure 2-9). More recent data are scant. The NOAA Fisheries updated status report (Good et al. 2005) estimated the average number of naturally spawning female steelhead for 1998-2000 at 3,628, based on ratio of unclipped to clipped smolts captured in the USFWS at Chipps Island, an assumed average fecundity (5,000), and a 1% estimate of egg to smolt survival. This estimate may be low, because 3,000 seems a more reasonable estimate for the average fecundity of Central Valley steelhead (Ch. 5), but 1% egg to smolt survival may also be low (e.g., Kostow 2004). Central Valley steelhead were listed as threatened under the Federal ESA in 1998.

¹⁵ The strontium: calcium ratio of the core of the otoliths that forms before emergence reflects that of the egg, and is higher in the eggs of anadromous females (Zimmerman and Reeves 2002). The ratio is also higher in the outer regions of the otoliths of anadromous adults. This allows the life history patterns of an adult and its mother to be determined.

Figure 2-9. Steelhead in the upper Sacramento River. Counts of steelhead at the Red Bluff Diversion Dam (filled circles) and estimated naturally spawning steelhead (open circles). Counts ended after 1993, when the dam gates were held open in the fall to protect winter-run Chinook. Data from Dennis McEwan, CDFG.



Whether steelhead naturally occurred in the San Joaquin basin has been questioned (e.g., Cramer et al. 1994), but descriptions of “salmon trout” reported by Yoshiyama et al. (1996) support the view that steelhead occurred wherever spring Chinook did. The historical abundance of steelhead is much less clear. McEwan (2001) suggests that they were as abundant as Chinook, by analogy to North Coast streams. However, given that Central Valley steelhead spend at least a year in fresh water, whereas few Chinook do so, limited juvenile habitat would be expected to keep steelhead populations smaller than Chinook populations (Quinn 2005). In any event, at the beginning of the twentieth century steelhead were invisible to Rutter (1909), whose entire discussion of steelhead took five lines:

Salmo gairdeneri (Richardson). *Steelhead*.

Reported from the Sacramento River by Jordan & Gilbert, 1881. If it is found in the basin we have been unable to distinguish it from rainbow trout. A specimen weighing 7½ pounds, taken at Battle Creek hatchery in November, 1897, was identified by us as a *Salmo irideus*. Scales in lateral line (not cross rows) 129.

Steelhead are raised in Coleman, Feather River, Nimbus, and Mokelumne River hatcheries. Hatchery culture and planting of *O. mykiss* has a long history in California that probably accounts for the lack of coherent genetic structure among current Central Valley populations described by Nielsen et al. (2005). However, the genetics of American River steelhead clearly reflect the use of coastal steelhead to found hatchery populations, and the same fish were used in the Mokelumne River hatchery. Most steelhead observed spawning in the American River are hatchery fish (Hannon et al. 2003), and it seems likely that the same is true of the Mokelumne.

CHAPTER THREE

CENTRAL VALLEY SALMON HABITATS

Multitudes of streams and bayous wind and ramify through hundreds of square miles -- yes, I should say thousands of square miles -- about the mouths of the San Joaquin and Sacramento rivers, and then away up both of these rivers in opposite directions, until nothing can be seen but the straight line of the horizon. G. H. Brewer (1966:264), written 1861.

If salmon populations together with their habitats are the appropriate units for conservation and management, as argued in Chapter 1, then some understanding of salmon habitats is necessary for dealing effectively with salmon. This understanding should extend beyond the habitats that are now used most extensively, as long-term restoration of diverse, naturally producing populations will require that populations be given the opportunity to use diverse habitats that support diverse life history patterns (Hilborn et al. 2003). This chapter reviews the habitats that were and are available to Central Valley salmon populations, and speculates briefly about future habitats.

Historical habitats

The natural habitats of anadromous Central Valley salmon extended from the upper tributaries of the Sacramento River in the north to the Kings River in the south, through the rivers to the Delta and the bays, and into the ocean (Plate 1). The Central Valley is bounded by the coast ranges to the west and the Sierra Nevada and Cascade Mountains¹⁶ to the east (Plate 2). Salmon habitat in the Central Valley spans about 5 degrees of latitude and a corresponding gradient in precipitation, which generally decreases southward, especially on the west side of the valley (Plate 3), and the wet season normally begins and peaks earlier in the north than farther south. However, the Sierra Nevada is higher in the south than in the north (Plate 2), so in the south more of the precipitation falls as snow, and runs off as snowmelt in late spring (Figures 3-1, 3-2). The mountains around the northern Sacramento Valley get precipitation mostly as rain, so flows respond strongly to individual storms, although some areas are high enough to develop a significant snowpack and generate spring runoff. Glacial meltwater is not significant in the hydrology of any Central Valley streams. In the south, the west side of the valley generates little runoff, and the San Joaquin River has no tributaries of consequence from the west.

These regional patterns combine with local differences in basin shape, geology (Plate 4), relief, and altitude to determine the unregulated flow regimes in the streams historically used by salmon. For example, streams draining areas of fractured basalt or lava, such as the McCloud River or Battle Creek, receive more water as inflow from springs and less as surface runoff than streams draining less permeable terrain with similar precipitation, and so have unusually stable

¹⁶ The Sierra Nevada and Cascade Mountains merge between the Feather River basin and Mount Lassen; trying to define a sharp boundary between them seems pointless.

flow and temperature regimes. Runoff patterns also depend on the particular shapes of the watersheds; for example, the Cosumnes and Calaveras river watersheds do not extend high into the Sierra Nevada, so these rivers get little snowmelt runoff, unlike the intervening Mokelumne River. Similarly, although the geology of a watershed can have strong effects on the streams draining it, these effects depend on attributes that may vary greatly within general types of rock. Sandstones or volcanic rocks, for example, can be highly permeable or nearly impermeable. The regional patterns invite generalizations, but local variation confounds them, and consideration of particular cases is necessary before the generalizations are depended upon.

Figure 3-1. Comparison of the estimated unimpaired monthly and annual average natural runoff for the Sacramento, American, and San Joaquin rivers, 1921-1994. The vertical axes are on the same scale. For each month, the shaded box spans the 25th to 75th percentile flows, the line crossing the box shows the median, the “whiskers” show the 10th and 90th percentiles, and the circles the 5th and 95th

percentiles. Note that months with consistently high flows occur later southward. Data from USACE.

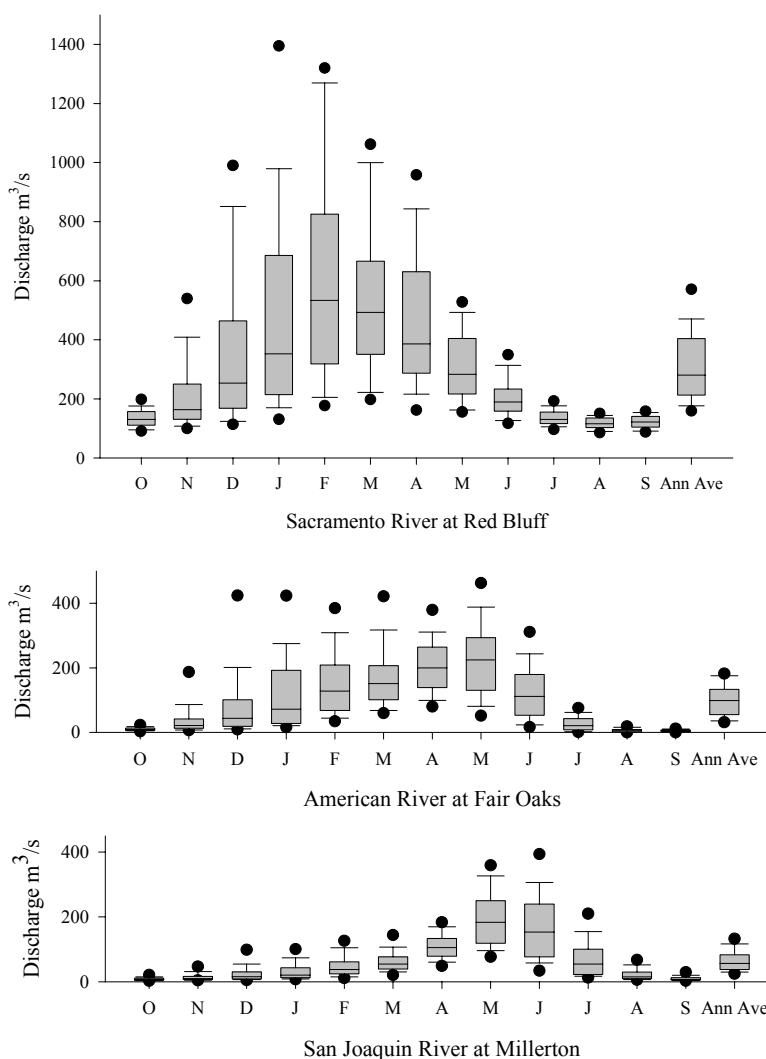
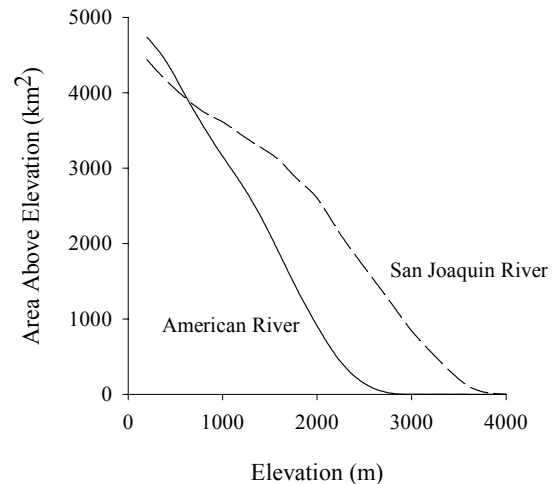


Figure 3-2. Area – elevation curves for the American and San Joaquin rivers for areas above 200 m; the San Joaquin has more area at high elevations, which results in more runoff as snowmelt. Although the areas of the basins are approximately equal, the total runoff is considerably greater in the American River (Figure 3-1), reflecting its more northerly location.



The lowland habitats that supported salmon were documented in early maps showing the progress of the public surveys in the 1850s (Plate 1). The San Francisco Estuary, here taken as including all inland waters affected by the tides, extends from the Golden Gate approximately to Sacramento and Stockton, and formerly included extensive tidal wetlands in the Sacramento-San Joaquin Delta (hereafter the Delta) and around the margins of the bays (Figure 3-3).

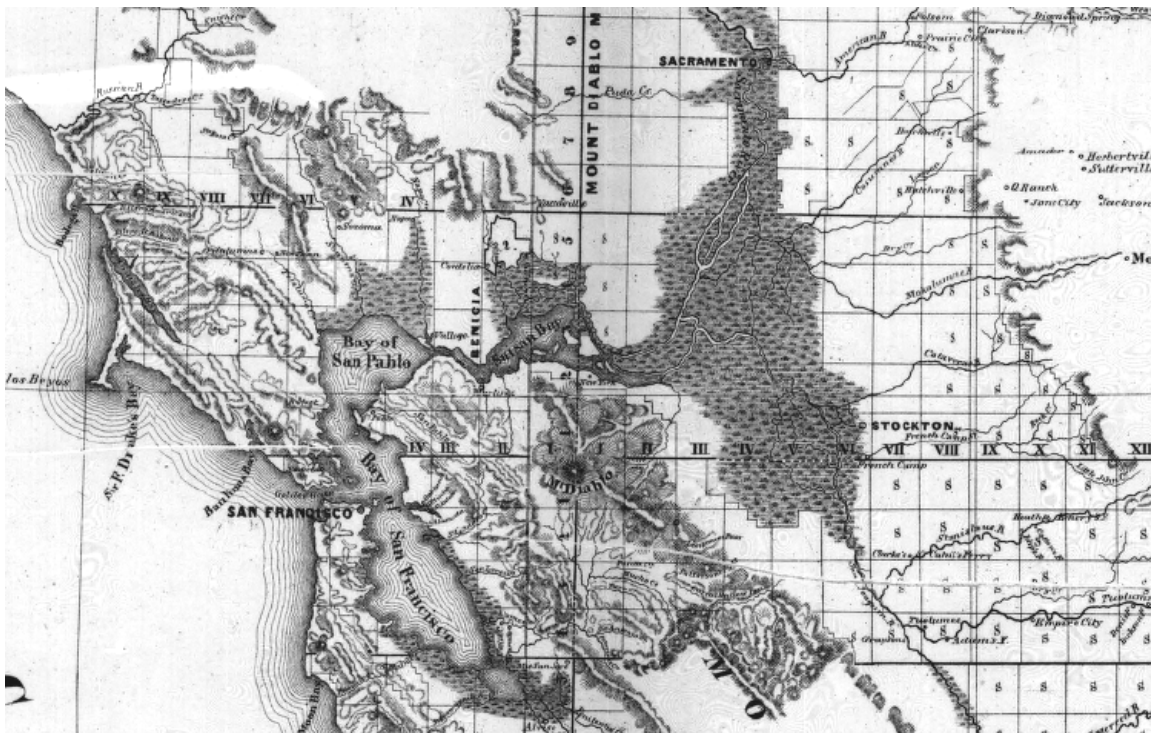


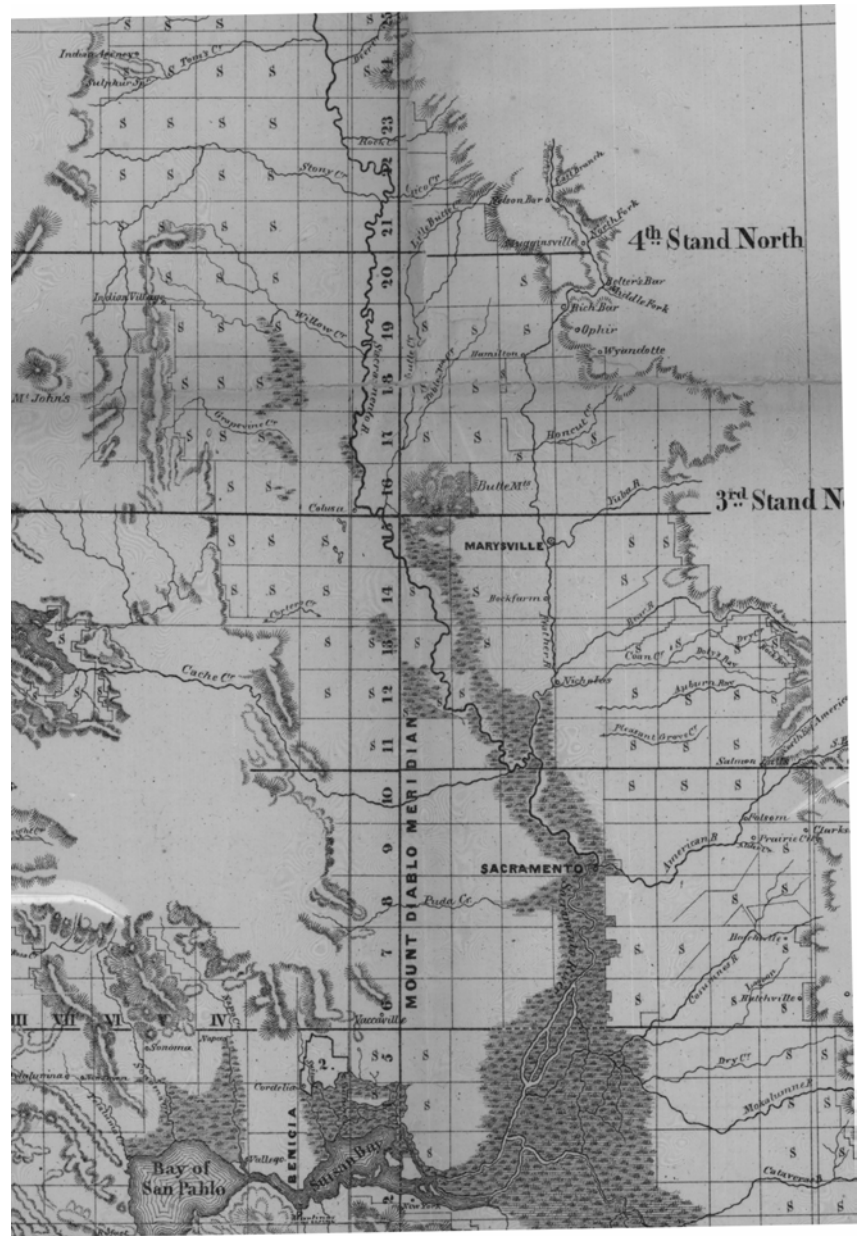
Figure 3-3. A section of the map of public surveys in California in 1856, showing the San Francisco Estuary, extending from the Delta, Suisun, San Pablo, and San Francisco bays, and the shallow Gulf of the Farallones (unlabeled) offshore from San Francisco. Note the extensive wetlands north of San Pablo and Suisun bays. The grid on the maps shows townships, 9.64 km (6 mi) square.

Seasonal variation in the salinity gradient in the estuary presumably was somewhat more pronounced than it is now, as was seasonal variation in Delta inflow, and brackish water intruded into the western Delta in late summer, although the natural extent and year to year variation in the intrusion was not well documented (TBI 1998). Tidal wetlands covered about 800 km² around the bays (Goals Project 1999; Figure 3-3) and probably were generally similar to similarly situated tidal wetlands elsewhere, but the geographic situation of the Delta is unusual and its historical condition more uncertain. Although only a few Delta channels are shown in Figure 3-3, a reconstruction by TBI (1998) based largely on Atwater (1980; 1982) and historical descriptions, indicates a branching and reconnecting network of channels with numerous shallow patches of open water (Figure 3-4). Tidal wetlands in the Delta covered about 1,300 km². Nearer Carquinez Strait, which separates San Pablo and Suisun bays, tules and bulrushes (*Scirpis* spp.) dominated the vegetation, although many other plants were also common. Further upstream, natural levees along the distributary channels of the Sacramento River divided the wetlands and supported impressive riparian forests. Natural levees were less developed in the southern Delta but there were extensive areas of slightly higher elevation dominated by willows.

In the 1856 map of public surveys, wetland was shown extending continuously from Suisun Bay to the Sutter Buttes, and discontinuously along the San Joaquin River and Fresno Slough to Tulare Lake and beyond (Figure 3-5 – 3-7). The valley wetlands apparently covered ~ 5,500 km², including 1,200 km² along the Sacramento River north of the Delta (TBI 1998). The mapping in Figure 3-6 seems conservative, as it does not include the Butte Sinks northwest from the Sutter Buttes that still remain seasonal wetlands, and some other areas of the Sacramento River flood basins. These basins, although seasonally dry and isolated from the Sacramento, Feather, and American rivers by natural levees during periods of low flow, probably carried more water during floods than the main channel of the Sacramento (TBI 1998), and created an “inland sea” (Kelley 1989) that provided ~2,500 km² of shallow habitat for juvenile Chinook and other native fishes in normal winters and springs.

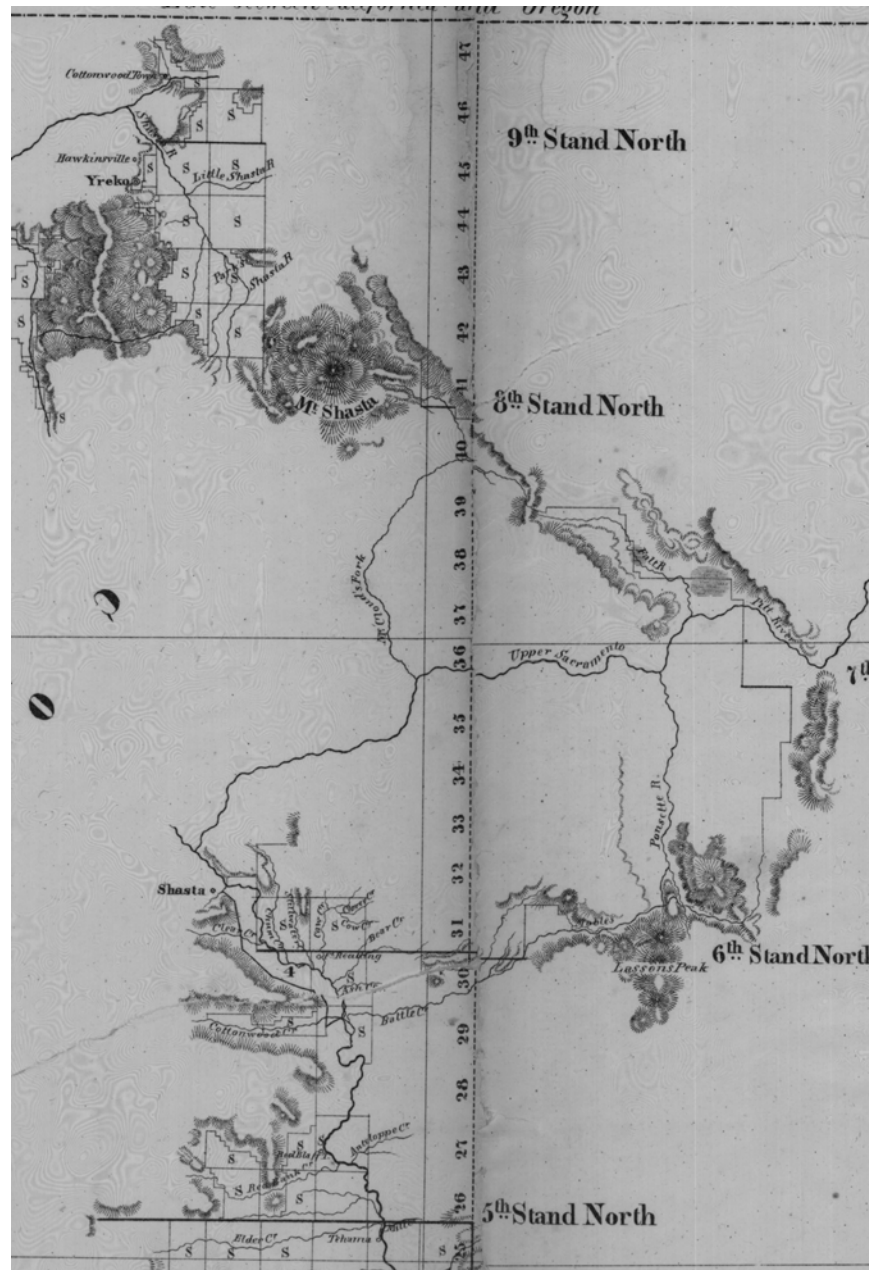
Together, the flood basins, the Delta, and bay marshes offered a vast corridor of habitat for juvenile salmon that began migrating seaward shortly after emerging from the gravel. Just how the habitat was used and how important it was for Central Valley salmon can be only a matter of speculation, although this can be informed by the use of lowland habitats by salmon elsewhere. But it is worth noting that the most successful wild population remaining in the valley, Butte Creek spring Chinook, have access to a remnant of flood basin habitat in the Sutter Bypass.

Figure 3-5. The Sacramento Valley, as shown in the 1856 map of public surveys. Note the extensive wetlands shown east of the Sacramento River to the Sutter Buttes, with higher ground along the river. Some of the wetland edges are suspiciously straight, for example south of Sacramento, so the general depiction of the landscape is probably more reliable than the details. The grid shows townships, 9.64 km (6 mi) square.



The upper Sacramento River system (Figure 3-6), especially the McCloud River, was the center of salmonid diversity in the Central Valley. The McCloud and upper Sacramento rivers, and Hat, Fall, and Battle creeks supported all four runs of Chinook and steelhead, and the McCloud also supported red band *O. mykiss*, bull trout (*Salvelinus confluentus*), and perhaps coho (Yoshiyama et al. 2001; Moyle 2002; P. Moyle, UC Davis, pers.comm. 2005). In 1890, the California Fish Commission described the McCloud as “the best salmon breeding river in the world” (CFC 1890:33, cited in Yoshiyama et al. 2001). Large areas of permeable basalt and lava associated with Mt. Lassen and Mount Shasta supported large springs that gave these streams unusually stable flow that remained cool year-round.

Figure 3-6. A section of the map of public surveys in California in 1856. The Little or Upper Sacramento River, which drains the area southwest from Mt. Shasta, is shown only as a stub upstream from the town of Shasta, and the Pit River is labeled as the Upper Sacramento River. Note Battle Creek, draining the western side of Mt. Lassen. The Shasta River, a tributary of the Klamath River, drains the area to the northwest of Mt. Shasta. The grid on the map shows townships, 9.64 km (6 mi) square.



The San Joaquin River and its tributaries flow west-southwest out of the southern Sierra Nevada and turn to flow northwest along the main axis of the Central Valley (Figure 3-7). Where the streams leave the mountains they have incised into gently sloping Pleistocene alluvial fans that skirt the edge of the foothills, forming shallow valleys that historically were active floodplains with braided channels in the gravel-bedded reaches nearer the foothills, becoming meandering channels as the gradient lessened and the bed material became finer near the axis of the valley.

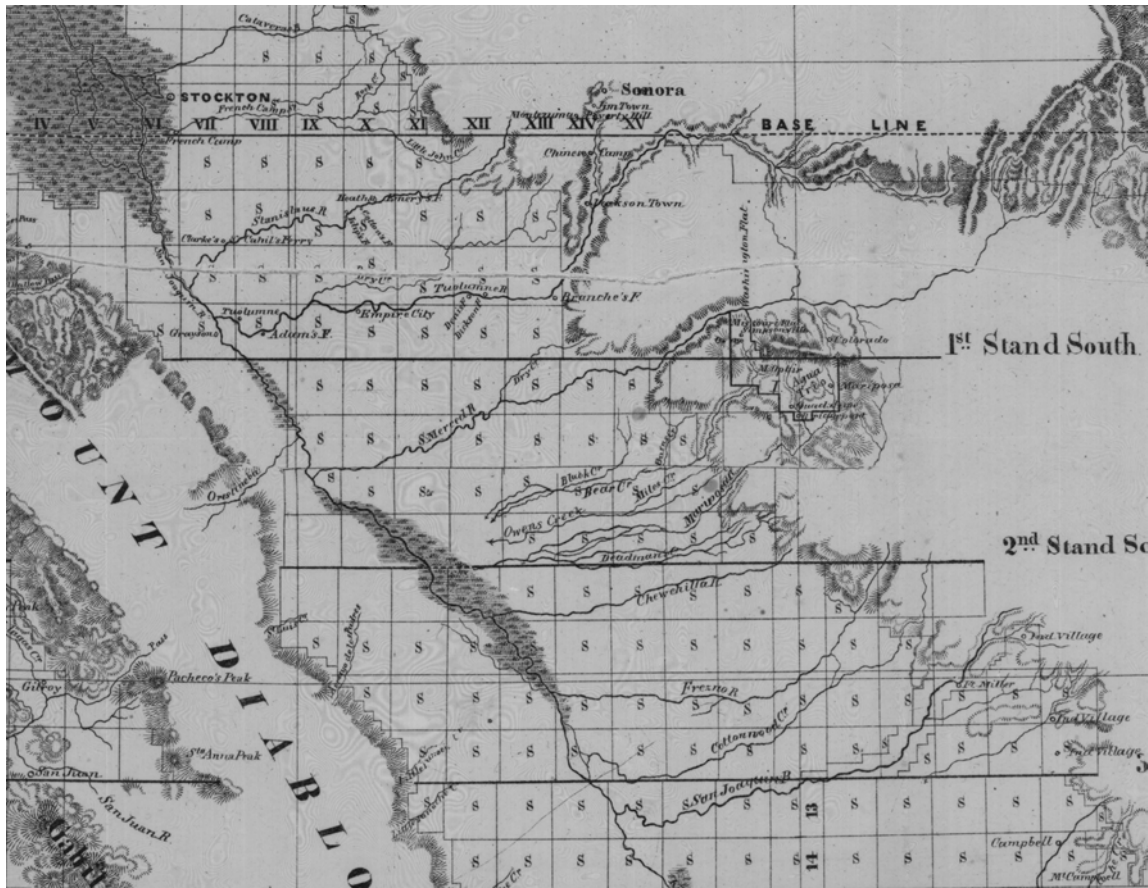


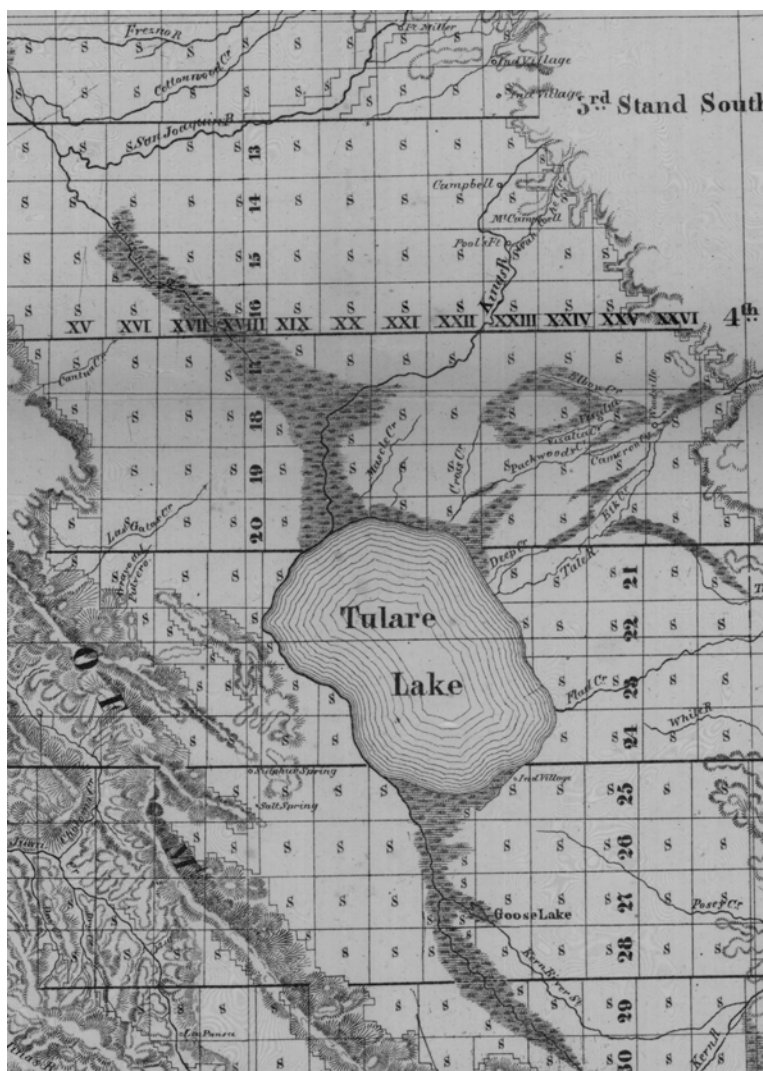
Figure 3-7 The northern San Joaquin Valley, as shown in the 1856 map of public surveys. The streams between the San Joaquin River and the Merced River did not extend high into the Sierra Nevada Mountains, and apparently did not support significant populations of Chinook. The grid shows townships, 9.64 km (6 mi) square.

Snowmelt runoff (Figure 3-1) provided flows that allowed spring Chinook to ascend the San Joaquin and its tributaries to roughly 1,000 m elevation (Yoshiyama et al. 2001; Lindley et al. 2004), but their distribution along the elevational gradient and their main spawning areas are unknown. Fish from redds at higher elevations likely emerged late enough in the year to adopt a stream-type life history, while those incubating at lower elevations probably were ocean-type.

Braided channels can provide good habitat for salmon spawning and rearing, for example on the Fraser River in British Columbia (Rempel and Church 2002), provided that sediment transport is not too active during the incubation period. Even when they are unsuitable for spawning, braided channels may be used extensively for rearing, as with Chinook in the Rakaia River in New Zealand (Unwin 1986). Whether salmon spawned in the braided reaches of the San Joaquin and its major tributaries is unknown, but even if not, it seems likely that the ocean-type fish reared there.

Flood basins did not occur in the San Joaquin Valley, where natural levees were less developed and overbank habitat less separated from the channel than along the Sacramento. Historically, at least during wet years, overflow from Tulare Lake passed down Fresno Slough to the San Joaquin River, allowing anadromous fishes access to the Kings River (Figure 3-8; Yoshiyama et al. 2001), and there may well have been a better developed channel between the Kings and San Joaquin rivers than indicated by the map of public surveys.

Figure 3-8. The southern San Joaquin valley, as shown in the 1856 map of public surveys. Fresno Slough, connecting Tulare Lake and the San Joaquin River, is labeled Kings River on this map, although it is not drawn as a distributary of the main Kings River that is shown flowing into Tulare Lake. Whether there was an open channel between Kings River and the San Joaquin is of interest, because spring chinook were reported in the Kings River. The grid on the map shows townships, 9.64 km (6 mi) square.



Conditions in the upland streams of the Central Valley were less well documented than lowland habitats before they were profoundly altered by hydraulic mining, logging, and other human activities, but conditions there can be reasonably inferred from conditions in the less altered streams and from streams in other areas with similar terrain. Rivers carry sediment as well as water, and with some over-simplification, rivers draining mountainous terrain can be

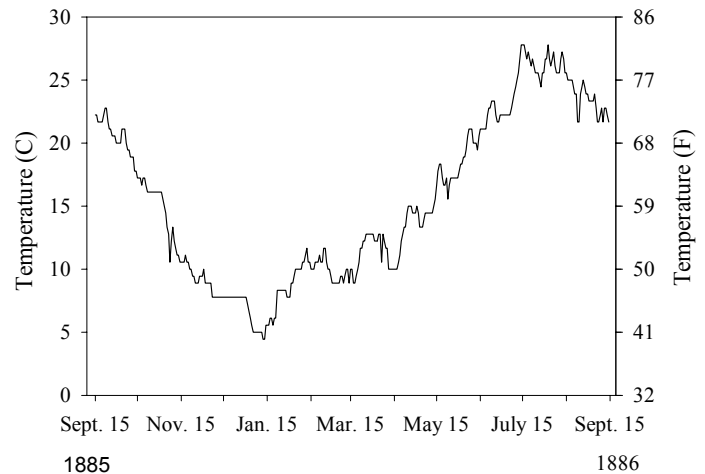
divided into an upland zone of erosion, a zone of transport, and a lowland zone of deposition (Schumm 1977). Salmon spawned mostly in the zone of transport and the lower portions of the zone of erosion, where gravel is in temporary storage in bars in the channel. Rivers also carry wood (Collins et al. 2002), and tree trunks from large conifers higher in the watershed (Figure 3-9), or from riparian trees, interacted with the flows of water and sediment to increase the geometrical complexity of stream channels and the movement of water through sediments in the channels (Maser and Sedell 1994; TBI 1998; Bilby and Bisson 1998; Gregory et al. 2003).

Figure 3-9. The McCloud River. Large springs increase the average flow in the McCloud River by about an order of magnitude a few kilometers below these falls, and keep the temperature suitable for salmonid spawning year-round. Note the size of the trees in the background in this photograph, and the log in the falls itself; a man in a white shirt at left provides scale. Copied from Rutter (1904).



In summer, the entire Central Valley (Plate 5) is hot, although it is hotter both north and south than near the Delta, where there is usually a sea breeze in the afternoon. Unregulated flows were also lowest in late summer and fall, so water in the lowland region, including the Delta, was seasonally very warm (Figure 3-10).

Figure 3-10. Temperature of the Sacramento River at Sacramento, as measured at 4 PM each day by the watchman for the Central Pacific Railroad. Data from Commissioners of Fisheries (1886).



Thus, the different streams offered different opportunities and constraints for salmon. Some of the ways that salmon adapted to these differences are clear enough: for example, juvenile Chinook do not migrate to the Estuary in the summer, as they do in the Columbia River; winter-run exploited the stable thermal regimes of the McCloud and a few other spring-fed rivers to spawn in summer; and spring-run migrated upstream during high spring flows far enough that they could hold over in pools through the summer before spawning early in the fall. Other differences are more subtle, such as the gradient in the timing of fall-run migration, earlier in the north and later in the south. Presumably there were also other differences, in migratory behavior, age at maturity, etc., but many of these can only be guessed at from studies of salmon elsewhere, since they were not documented before salmon habitats were drastically modified by hydraulic mining, irrigation dams and diversions, logging, draining of wetlands, and clearing and snagging channels, and many local populations probably were driven extinct.

Anthropogenic changes in Central Valley rivers

The second half of the nineteenth century was not kind to Central Valley rivers. Hydraulic mining for gold in the late nineteenth century introduced about 6.5 million cubic meters per year of sediment into Central Valley rivers (Kondolf, in Anderson et al. In press), causing meters of aggradation of river channels and devastating salmon habitat and populations. Early dams and diversions blocked salmon from their spawning habitat or intercepted juveniles migrating to the sea. Dams and siltation from hydraulic mining probably extirpated salmon populations in many rivers, in which case existing populations probably are the result of natural re-colonization. The 1886 Biennial Report of the Commissioners of Fisheries summarized the effects of mining and diversion dams on Central Valley rivers and salmon as follows:

The Sacramento, the largest river in the State, runs from north to south through the counties of Modoc, Lassen, Tehama, Butte, Colusa, Sutter, Yolo, Sacramento and Solano, a distance of nearly five hundred miles. It has its origins from the springs and melting snows of the mountains, and, as it drains an immense area during protracted and heavy rains, it overflows its banks and floods a large area of lowlands along the lower

part of its course. The river is a pure, clean mountain stream above the mouth of the Feather, but below that point it is heavily charged with detritus from the mining districts, the streams flowing from which are tributary to the Feather. The water in the mountains is cold, while in the lower reaches during the summer months it gets quite warm, reaching at times a temperature of eighty degrees.

The American is a shallow, muddy stream and empties into the Sacramento at Sacramento City. But few fish are found in the lower part of the stream. Trout are found in some of its branches above the mining districts -- notably Silver Creek and the Rubicon. This river, prior to placer mining, was one of the best salmon streams in the State. Of late years no salmon have ascended it.

The Yuba is a branch of the Feather River. It is a shallow stream, except during the rainy season. Considerable mining is carried on in its bed and along its banks, and its water is muddy. Trout are found in its headwaters above the mining districts.

Bear has lost all claim to the name of river. Above the town of Wheatland it has lost its channel and volume as a summer stream. It never was noted as a fish stream, although a few salmon and perch were taken from its waters in early days.

The San Joaquin, once a noted salmon stream; of late years few salmon have been taken in its waters. The principal cause of abandonment is the great number of dams upon its various branches, which are so constructed as not to allow the fish to reach their spawning grounds. Salmon and other varieties of fish are taken in considerable quantities near the mouth of the river. Most of the fishing in this stream is done below the city of Stockton.

The Tuolumne, a branch of the San Joaquin, at one time was one of the best salmon streams in the State. Salmon have not ascended the stream for some years.

What has been said of the Tuolumne is true of the Stanislaus. Occasionally a salmon may be seen trying to get over one of its numerous dams.

Large but poorly quantified amounts of wood have been removed from Central Valley rivers, especially in the late nineteenth and early twentieth centuries (Sedell et al 1990), but continuing still (Williams et al. 2002). In the 1883 trial of *People v. Gold Run*, John Bidwell testified:

... I can speak generally that our streams there are less likely to overflow than formerly from the fact that we cut out the drifts from them. Nearly all our streams are bordered by timber, sometimes by very large timber and sometimes oaks and other large trees that will fall into the streams, and now the farmer everywhere within the valley will have cut away those drifts. They have for navigation purposes been removed to a very large extent in the Sacramento River.

From a partial compilation of Army Corps of Engineers (ACE) reports, Sedell et al. (1990) estimated that the Corps removed 91 snags per km from the Sacramento River. The effects of such clearing have been better documented for other rivers (e.g., the Willamette River in Oregon, Moser and Sedell 1994), but presumably resulted in sharp decreases in the complexity of habitat in Central Valley rivers as well. While streams in lowland reaches were cleared for human

navigation, fish passage in mountain streams was sometimes blocked by debris from railroad construction (Skinner 1958).

More recently, mining for sand and gravel for construction aggregate has removed about 40 million cubic meters from stream channels or floodplains annually (Kondolf, in Anderson et al. In press). Between this putting and taking, the floodplains along the gravel-bedded reaches of many Sacramento and San Joaquin River tributaries were dredged for gold in such a way that fine sediments settled to the bottom of migrating dredge ponds and were subsequently covered by piles of coarse sediment, leaving uneven terrain with an inverted soil profile. Particularly along the San Joaquin River and its tributaries, mining for aggregate in the floodplains left large, deep pits that provide good habitat for bass and other introduced centrachids, which become predators on juvenile salmon when streams “capture” these pits through channel migration (Stillwater Sciences 2001).

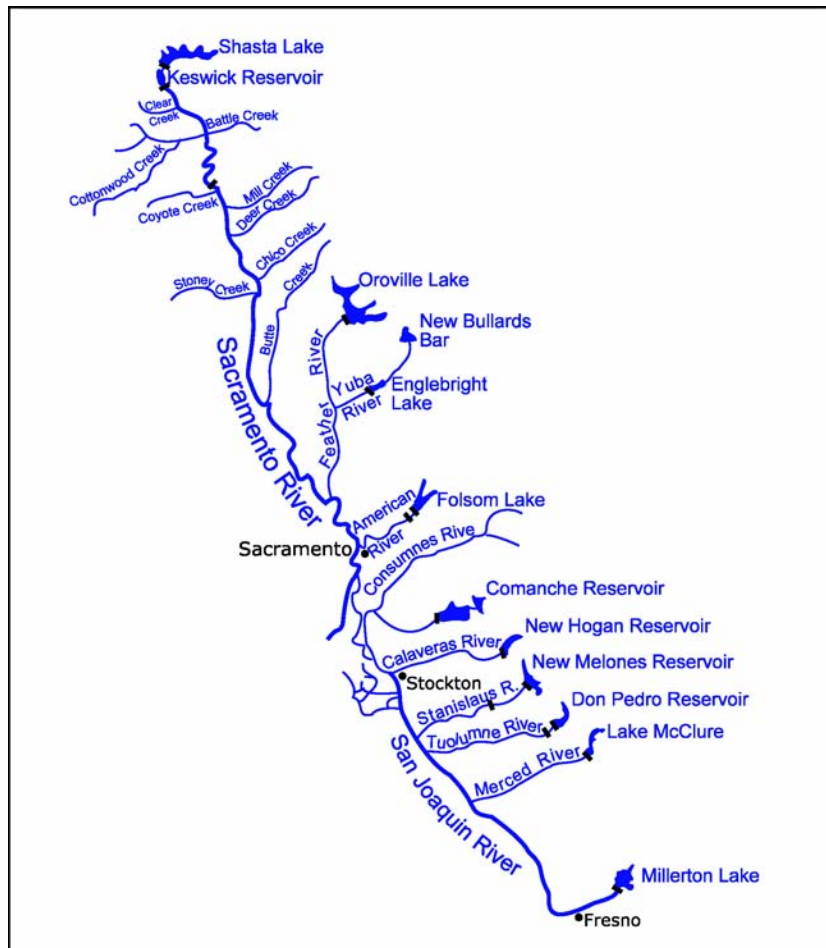
The gold mining industry used large quantities of mercury, most of which escaped into the environment, as did mercury from mercury mines on the west side of the Central Valley. Older resident fish in the Bay and Delta now contain enough mercury to be hazardous to eat, and residual mercury in sediments presents problems for restoration activities such as removing sediment-filled or otherwise unnecessary dams, or using dredger tailings as a source for spawning gravel (Wiener et al. 2003).

Existing habitats

The present landscape is much different from the historical landscape. Impassable dams restrict salmon habitat to the lower reaches of all but a few streams. Schematically, the Sacramento and San Joaquin rivers run along the long axis of the Central Valley, and tributaries (and the upper San Joaquin River) flow in parallel out of the mountains, generally more or less normal to the main rivers in the axis of the valley (Figure 3-11). Of the great spring-fed streams of the upper Sacramento, only Battle Creek is downstream from the impassable Shasta Dam, and salmon are blocked from most of the creek by hydroelectric facilities. Spring Chinook survive mainly in Butte, Mill and Deer creeks, which drain into the Sacramento from the northern Sierra Nevada and southern Cascades, lack impassable dams below natural migration barriers, and lack fish hatcheries. Salmon migration up the Sacramento River is now blocked near Redding by Keswick Dam (rkm 585), a re-regulating dam for hydropower production at Shasta Dam. Rivers have been separated from their floodplains by levees. The dams have changed the flow and thermal regimes in the rivers downstream, making them cooler in the summer and warmer in the winter. Embryos and alevins of fall and winter-spawning runs develop more rapidly in the warmer water, and juvenile fall-run in the Sacramento River migrate to the Delta a month or more earlier than before (Ch. 9). However, releases of cool water from Shasta Reservoir now keep summer temperatures in the Sacramento River suitable for salmon spawning approximately to Bend Bridge (rkm 414). This provides habitat for winter Chinook that is also used by fall-run and late fall-run, but very few spring-run. Some steelhead also use this habitat, but the changed environmental conditions appear to have caused a shift in life-history away from anadromy (Ch.

3); in any event, there are now many large *O. mykiss* in the river near Redding. Habitat below most other Central Valley dams supports fall-run, perhaps some late-fall run, and small numbers of steelhead. A sizable population of nominal spring-run persists in the Feather River below Oroville Dam, but mixes with fall-run to a degree that the populations are hard to distinguish genetically (Lindley et al. 2004), and it is strongly influence by hatchery production.

Figure 3-11. Dams on Central Valley rivers. All major Central Valley rivers are blocked by large, impassable dams. Comanche Reservoir is on the Mokelumne River. Note that the rivers without dams are drawn ending at arbitrary points, not the upstream limit for anadromous fish. Copied from Brown and Greene (1992).

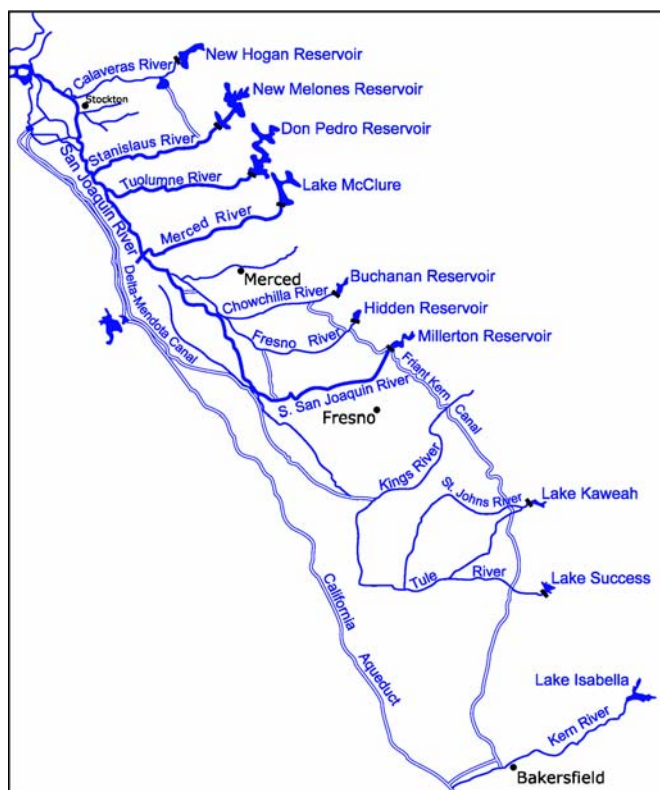


In the Central Valley there are opposing geographic and seasonal gradients of water supply and demand, and the main objective of the federal Central Valley Project (CVP) and the State Water Project (SWP) is to move water from north to south. In the Sacramento Valley, water is stored in Shasta, Oroville, and Folsom dams in the winter and spring for release into the rivers, mostly during the summer irrigation season, to supply downstream diversions and other uses of water. Low diversion dams on the Sacramento River at Redding and Red Bluff have created major problems for migrating salmon in the past, although improved ladders and operations have

reduced them. An instream flow standard, originally for navigation, keeps flow in the lower Sacramento River above $\sim 100 \text{ m}^3 \text{ s}^{-1}$.

Although much water is diverted into canals along the Sacramento River, particularly at Red Bluff and at Hamilton City, more passes down to the Delta, where massive pumps at the CVP and SWP diversion facilities in the Delta supply canals that carry water south along the western edge of the San Joaquin Valley (Figure 3-12, Plate 6), mainly for immediate distribution for agricultural use, but also for storage in the San Luis Reservoir on the west side of the San Joaquin Valley, or for transport to Southern California, and to parts of the San Francisco Bay Area. Many small diversions supply irrigation water in the Delta itself. A gated canal, the Delta Cross Channel, operates as an artificial distributary of the Sacramento to facilitate movement of water across the Delta to the pumps. The effect of these Delta diversions on juvenile Chinook has been a major point of controversy.

Figure 3-12. Major canals in the San Joaquin Valley. Water is diverted from distributary channels of the San Joaquin River in the southern Delta into the Delta Mendota Canal by CVP diversion facilities at Tracy, and into the California Aqueduct by SWP diversions facilities at Banks. Water is distributed along the east side of the valley by the Friant-Kern Canal (south from Millerton Reservoir) and between the San Joaquin and Chowchilla rivers by the Madera Canal (unlabeled).

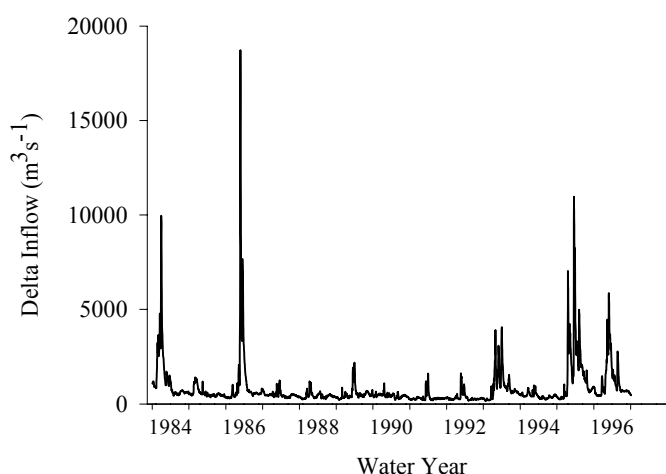


Water is also moved from east to west. O'Shaughnessy Dam on the Tuolumne River drowned a valley much like Yosemite to supply water to San Francisco. The Mokelumne River supplies the East Bay, and some water from the American River will go there, as well, although litigation reduced the amount and shifted the proposed point of diversion from the American River to the Sacramento. Other reservoirs on the San Joaquin River tributaries serve mainly local

demand, with water distributed along the eastern edge of the San Joaquin Valley in the Friant-Kern Canal and in other smaller canals.

The major reservoirs in the Central Valley serve both for water storage and flood control, and although there is variation among dams in the details, the basic management is the same. Floods come mainly from winter storms, so the reservoirs are drawn down below specified elevations at the beginning of winter and operated to maintain that level, with temporary increases following storms, until early spring, when the reservoir levels are allowed to increase. The reservoirs then capture and store snowmelt runoff for release later in the season. Although this operation dampens variability in flow, the large year to year variability in precipitation still results in large year to year variation in flow below the dams (e.g., Figure 3-13). The extent of day to day fluctuations varies among rivers and from dry years to wet years, with more variation in rivers such as the American with relatively small reservoirs, and more variation in wet years. There are re-regulating reservoirs downstream from most major dams, so within-day flow fluctuations from hydropower operations are smoothed out, and flow variation from hydropower operations is generally not as significant a factor for Central Valley salmon as it is for salmon in other river systems, such as the Columbia.

Figure 3-13. Year to year variation in Delta inflow, water years 1984-1997. This sequence of years includes a very high flow in 1986 and an unusually long drought. Data from CDWR's Dayflow program.

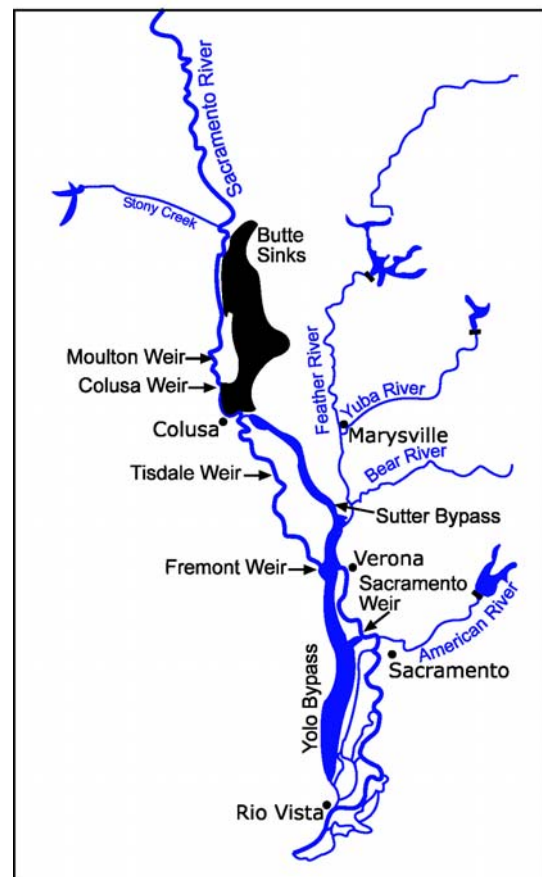


In the Sacramento River and its major tributaries, flows for migration to habitat below dams are seldom a problem. In the San Joaquin Valley, water typically is diverted into canals at the dams, as well as farther downstream, so that the total amounts as well as the seasonal distributions of flows in the lower rivers have been altered, in some cases drastically; the San Joaquin River is usually dry where the channel approaches the main axis of the valley. Friant Dam extirpated spring-run in the San Joaquin River not so much because it blocked access to spawning habitat, of which a good deal remained below the dam (Hatton 1940), but because too little water was released into the river to allow migration (Warner 1991). High temperatures and low dissolved oxygen levels in the lower San Joaquin River near Stockton in the fall often block or delay migration for fall-run (Hallock et al. 1970; Mesick 2001a). Essentially the entire flow of

the lower San Joaquin River may be diverted to the Delta pumps in the fall, raising concerns that olfactory cues for migration may be missing (Mesick 2001a).

Along the Sacramento River, flood bypasses have been constructed by leveeing off swaths of the former flood basins into which water from the river passes over weirs during high flows (Figure 3-14). Thus, the river has been separated from its floodplain. However, earth to make the bypass levees was excavated from the bypass side of the levees, leaving “toe drains” next to the levee that are always inundated, and recent work has shown that the bypasses can provide valuable habitat (Ch. 10).

Figure 3-14. The flood bypass system along the Sacramento River. Water passes from the river through several weirs into the Butte Sinks, from which it flows into the Sutter Bypass, and then across the Sacramento River to the Yolo Bypass, which flows into the Delta.



To mitigate for salmon habitat blocked by the dams, hatcheries have been constructed on the Sacramento, Feather, American, Mokelumne, and Merced rivers. These annually produce ~30 million mostly fall Chinook and over a million steelhead that support commercial and recreational fisheries for Chinook and recreational fisheries for steelhead. Returns of adult fall-run have been very high since the late 1990s (e.g., Figure 2-5), and a poorly quantified but probably a large percentage of the naturally spawning salmon is hatchery fish. Since the hatchery environment selects for different traits than the natural environment, the likelihood of genetic

harm to naturally reproducing salmon from interbreeding with hatchery salmon seems high (Ch. 12). The hatchery-supported fishery normally takes a heavy toll on Chinook populations from hatchery-free streams, on the coast as well as in the Central Valley, although harvest has been sharply reduced in recent years to protect listed runs, especially in the Klamath River (Ch. 13).

Only about 20% of tidal wetlands remain around the bays, and about 5% remain in the Delta, where channels have been leveed and the tidal wetlands converted to agricultural land. Most of the Delta has subsided so much under agricultural use that breaching levees creates shallow lakes rather than tidal marsh, and at current rates of sedimentation the lakes will remain for hundreds of years (Orr et al. 2003). Enough water is released from the Sacramento Valley dams to keep water in the Delta fresh enough for local diversion and use through the summer, expanding the habitat for salt-intolerant plants and animals. Introduced species now dominate the Delta ecosystem, and some of these eat juvenile salmon. The Delta pumps are located on a distributary of the San Joaquin River (Plate 6), and often pump so much water that the net (tidally averaged) flow in much of the Delta is toward the pumps, rather than toward the San Francisco Bay. These “reverse flows” were formerly regarded as a major problem for emigrating salmon (e.g., Ganssle and Kelley 1963), but they are very small compared to the tidal flows that dominate the hydrodynamics of the Delta, and now receive much less attention (Kimmerer 2004).

Future habitats

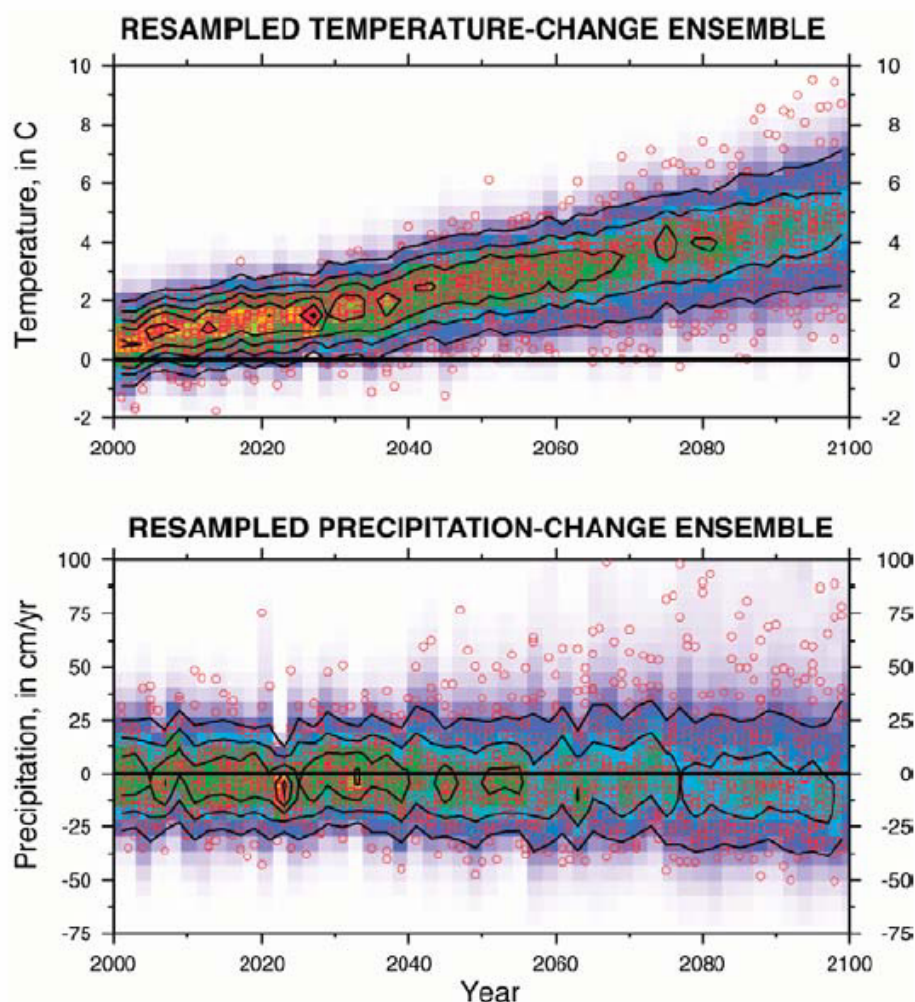
Major efforts at habitat restoration (or rehabilitation) are now underway in many parts of the Central Valley, involving everything from addition of gravel below dams to removal of small dams to re-structuring large areas of floodplain or restoring large areas of tidal wetland. Although the efforts aim at ecosystem restoration, it is fair to say that salmon are “more equal” than most other animals, so improvements in salmon habitat have and should continue to occur. On the other hand, given that the human population will continue to increase, and with it demand for land and water for direct human use, maintaining habitat for salmon will be a continuing challenge.

To make matters much worse for salmon, the global climate is now warmer than it was a century ago and getting even warmer,¹⁷ and more precipitation is falling as rain, shifting the timing of runoff to earlier in the year (Roos 1991; Dettinger et al. 2004). The predicted warming varies depending on the particular global climate model used and on estimates of future emissions of CO₂ and other greenhouse gases, but by a statistical analysis of predictions from six

¹⁷ That the global climate is warming is the consensus of qualified scientists (Oreskes 2004). According to the December, 2003, position statement of the American Geophysical Union (Eos 84:574) “Human activities are increasingly altering the Earth’s climate.” The statement continues that “It is virtually certain that increasing carbon dioxide and other greenhouse gases will cause global surface climate to be warmer,” and “The hydrological cycle will change and intensify, leading to changes in water supply as well as flood and drought patterns,” despite uncertainty about “...exactly how fast [climate change] will occur, exactly how much [climate] will change, and exactly where these changes will take place,” Additional evidence that global warming is already under way is accumulating rapidly (e.g., Oerlemans 2005; Hansen et al. 2005).

climate models using three emissions scenarios, Dettinger (2005) determined that the most likely projection of annual average warming over Northern California is about 5°C by 2100 (Figure 3-15), together with a decrease in precipitation of about 12 cm yr⁻¹. Using a downscaling method to make predictions more spatially and temporally specific, and smaller sets of models and emissions scenarios, Hayhoe et al. (2004) found that the predicted warming is greater for summer than for winters.

Figure 3-15. Projected climate change in the twenty-first century for a model grid cell over Northern California, based on the results of six global climate models and three emissions scenarios. Red circles show raw projections; contours and shading show resampled joint temperature-precipitation probabilities, with a contour interval of 0.025. Copied from Dettinger (2005).



Warming is already affecting Central Valley Chinook. Spring-run in Butte Creek, which increased dramatically in recent years, suffered heavy summer mortalities during hot weather in 2002 and 2003 (~25 and 65%; Ch. 6). Because the run is restricted to low elevations, it seems unlikely that they could persist if summers warm even by one or two degrees. If climate warms by 5°C, it is questionable whether any Central Valley salmon can persist.

The predicted increase in temperature begs the question whether Central Valley salmon are a lost cause, so that efforts to protect salmon are a waste of resources that should be applied elsewhere. The answer seems to be, probably not yet, because the modeling also shows that the

extent of future warming depends largely on future emissions (Hayhoe et al. 2004). Although it may be too late for spring-run in Butte Creek, or perhaps for any Central Valley salmon, if the more extreme predictions considered most likely by Dettinger (2005) turn out to be correct, there is still time for effective actions to reduce future greenhouse gas emissions. Effective actions to reduce the extent of warming are desperately needed for many reasons besides salmon conservation, and may yet be taken.

CHAPTER FOUR

JUVENILE GROWTH

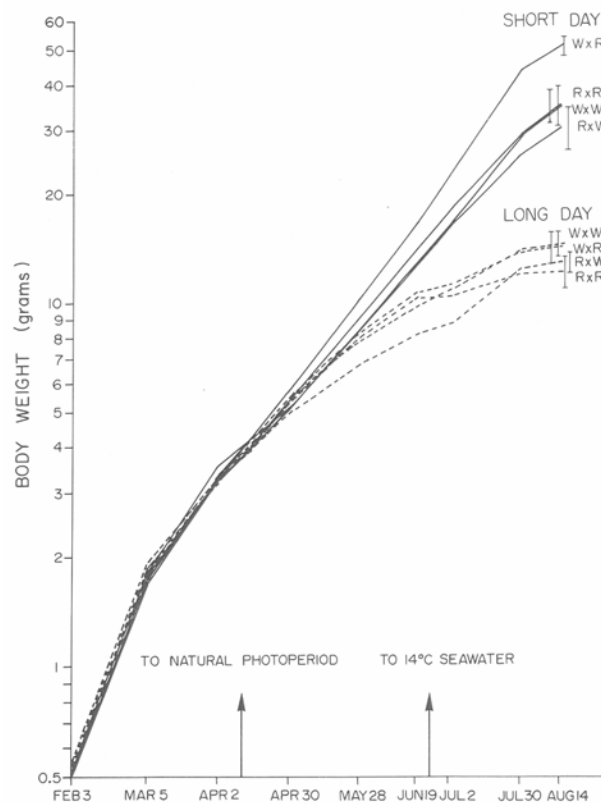
Although from the same brood, hatchery practice and rearing pond, there was great variation in the size of the [Chinook] yearlings at the time of marking, the extremes in length being 1 3/16 to 5 inches, measured from the tip of the snout to the tip of the central ray of the caudal fin.
Scofield (1920)

... it will soon be apparent that, although there are voluminous data on the growth of these [Pacific salmon juvenile life] stages under field conditions, conclusions regarding field measurement of growth may be difficult to evaluate. The reason is simply that somatic growth of salmon, and most other fish, is plastic in response to the major environmental factors of temperature, photoperiod, food supply, and the presence of other fish.
Weatherby and Gill (1995:108)

As these quotations suggest, the growth rate of juvenile salmonids is a vexing topic. Not only do environmental factors and fish size strongly influence growth, but not all juveniles respond to the environment in the same way. Elliott (1994) provides a useful review, although focused on brown trout. In this chapter I describe three examples to illustrate some of the complications regarding growth, one each for Chinook, sockeye, and Atlantic salmon, and then review laboratory and field data for Chinook and steelhead, with an emphasis on Central Valley data. Two empirical models that predict growth in juvenile brown trout as a function of water temperature and fish size are briefly described.

Where winters are cold, stream-type Chinook normally emerge in spring, because low water temperatures make their embryonic and larval development very slow. They rear in the streams until the following spring, when their rate of growth increases and they smolt. However, experiments with juvenile Chinook in British Columbia showed that if the newly hatched fish are experimentally exposed to a short-day photoperiod, they grow much more rapidly and smolt in their first spring, as do ocean-type Chinook (Clarke et al. 1992; Figure 4-1). Further experimental work showed that this effect is controlled by a single gene with two alleles (Clarke et al. 1994). It is likely but not certain that spring-run in the Central Valley share the same trait, so that the progeny of fish that spawn at higher elevations, where water is colder, are less likely to be exposed to days short enough to trigger rapid growth and early emigration. This rather dramatic example illustrates that the trajectory of development and behavior of juvenile salmon results from an interaction with the environment. In a sense, the fish decide how rapidly to grow, based on cues from the environment.

Figure 4-1. Growth of juvenile stream-type Chinook exposed to short and long-day photoperiods. Note the log scale on the vertical axis. R and W refer to red and white-fleshed Chinook; flesh color is under genetic control, but white fleshed Chinook apparently do not occur in California. Copied from Clarke et al. (1992), courtesy of the *Canadian Journal of Fisheries and Aquatic Sciences*.



Juvenile Atlantic salmon from a single brood reared together may grow and smolt at different rates (Thorpe 1977; Figure 4-2), which motivated development of the life history model described in Ch. 1. Diversity in growth rates and smolting in many other salmonids is similar to that in Atlantic salmon (Thorpe 1989), and although the Atlantic salmon model is not directly applicable to Pacific salmon, it seems that something similar most likely applies. In any event, patterns of growth of Pacific salmon with diverse life histories, such as Chinook and steelhead, are far from simple.

The interactive effects of temperature and food supply (ration) on the growth of juvenile Pacific salmon are illustrated by experimental work by Brett et al. (1969) on juvenile sockeye (Figure 4-3). Both the growth rate and the temperature at which growth is maximal depend strongly on the amount of energy ingested, the ration. Similar data exist for brown trout (Elliott 1976; 1994), but similar comprehensive experiments have not been done with Chinook, although the effects of water temperature on growth have been central to water management controversies such as the *EDF v. EBMUD* litigation regarding the American River (Williams 1995). Brett et al. (1982) determined the relation between growth of juvenile Chinook and temperature at full ration, but estimated the relation at reduced ration from the sockeye data (Figure 4-3).

Figure 4-2. Diversity in juvenile growth patterns. Growth and size distributions of juvenile Atlantic salmon from a single brood, raised in identical conditions in a laboratory. Presumably, in nature, the upper modal group would smolt in their second year, and almost all of the lower modal group would smolt in their third year. Copied from Thorpe (1977), courtesy of the *Journal of Fish Biology* and Blackwell Publishing.

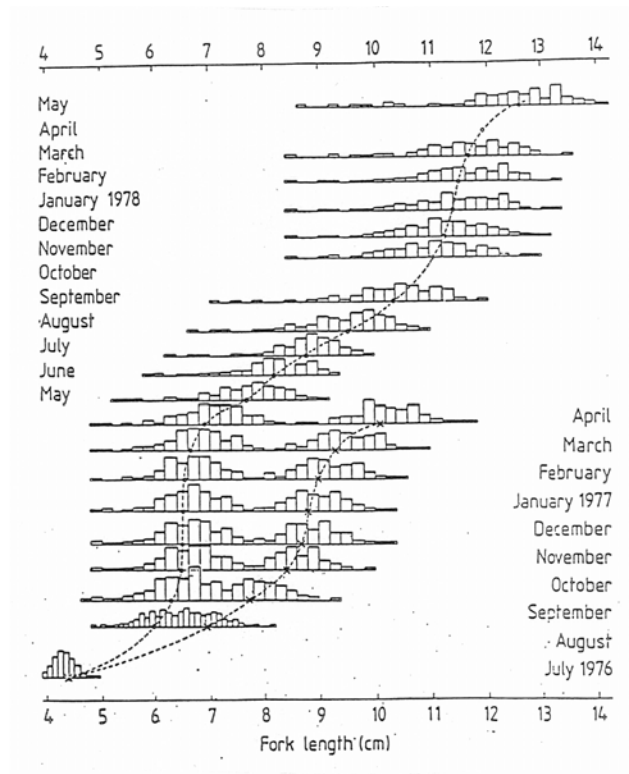
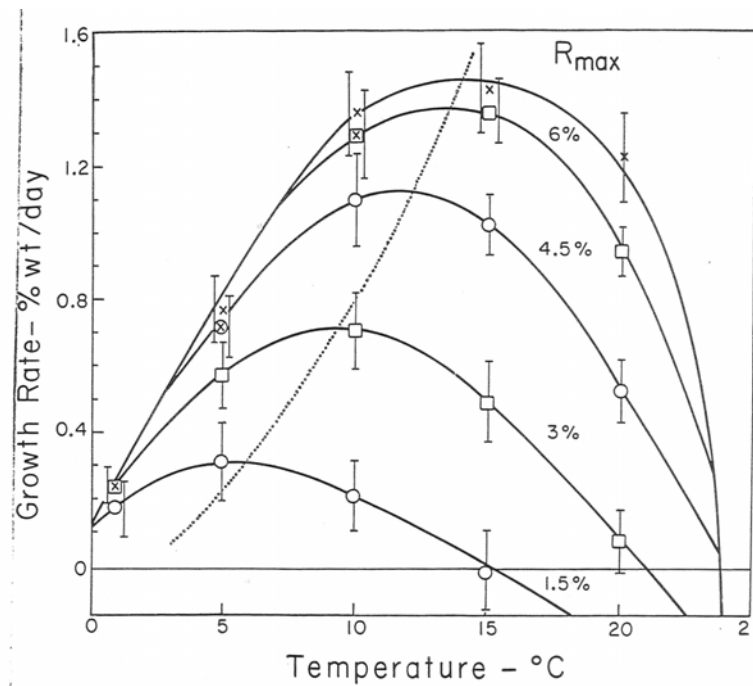


Figure 4-3. The relation between growth rate and temperature for different levels of ration for juvenile sockeye salmon. Dotted line connects temperature of maximum growth at each level of ration. Bars are two standard errors. Copied from Brett et al. 1969



Laboratory data on growth of Chinook and steelhead

Growth experiments intended to simulate existing and modified conditions in the Nechako River in interior British Columbia, where summer water temperatures are rather similar to Central Valley streams, showed limited growth benefit from reducing water temperatures from about 18.5 to 15°C (Shelbourn et al. 1995). Groups of ~ 30 juvenile stream-type Chinook were reared in 200 L tanks. Replicated treatments consisted of full, 80% and 60% ration, with water temperatures matching recorded (ambient) temperatures in the river and with 30 day (d) reductions in temperature to ~ 10, 12.5, and 15°C, as might result from increased releases for hydropower into the river. The ration level strongly affected growth. The 15°C treatment did not affect growth rates at full and 80% ration; fish grew more slowly in one replicate but not in the other at 60% ration, and the overall difference was not significant by the standard criterion of a >5% probability that it could have occurred by chance (Figure 4-4).

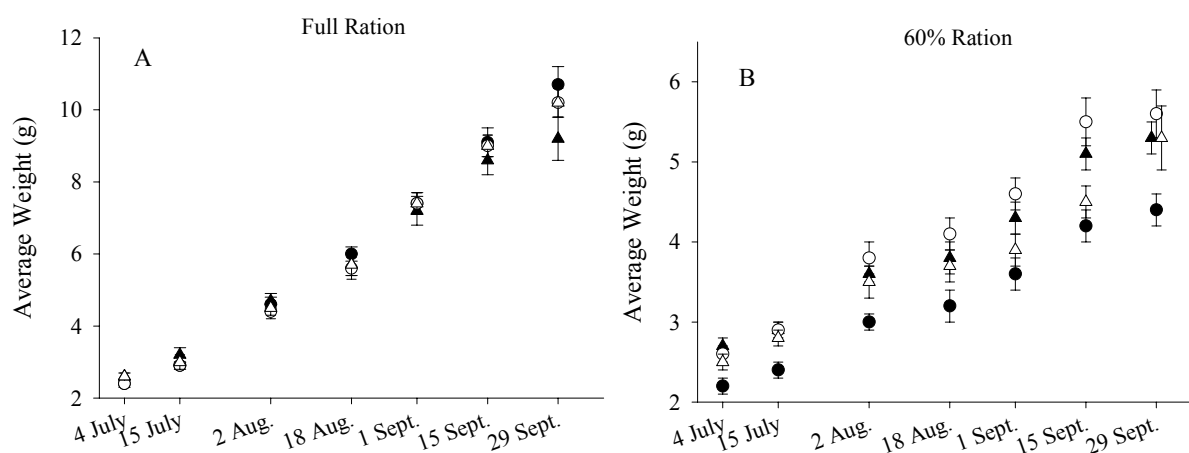
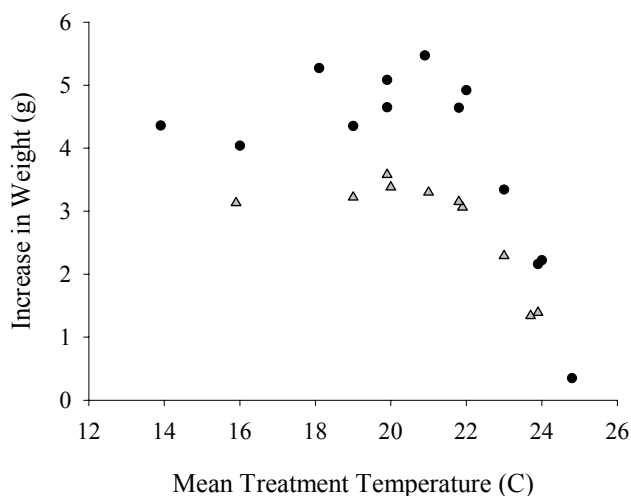


Figure 4-4. The seasonal change in weight of juvenile stream-type Chinook from the Nechako River in British Columbia, for two temperature and ration treatments, with replicates (circles and triangles) for each treatment; note different scales on the vertical axes. A, full ration; B, 60% ration. One temperature treatment simulated measured temperatures in the river (filled symbols) while the other simulated a 30 d decrease as might result from increased releases into the river from a hydropower project. Data from Shelbourn et al. 1995; error bars show standard errors, $n \sim 30$.

Brett et al. (1982) reared juvenile Big Qualicum River and Nechako River Chinook at temperatures ranging from 14 to 25°C for 28 days at full ration (Figure 4-5); only 36% survived the 25°C treatment, but 97% survived the 24°C treatment. Growth dropped off sharply above 22°C, but a clear optimum temperature for growth is not apparent. The ocean-type Big Qualicum Chinook grew somewhat faster than the stream-type Nechako Chinook.

Figure 4-5. The effect of temperature on growth of Big Qualicum (filled circles) and Nechako (gray triangles) Chinook raised at various temperatures for 28 d. Big Qualicum averaged about 0.8 g heavier at the beginning of the experiment. Data from Brett et al. (1982) Table 2.



Three studies have evaluated the relation between growth and temperature of Central Valley Chinook (Rich 1987; Marine 1997 (also Marine and Cech 2004); Cech and Myrick 1999), and their contrasting results illustrate some of the complexities associated with growth studies that can result from using different procedures and different strains of fish. Marine (1997; also reported in Marine and Cech 2004) and Cech and Myrick (1999, also reported in Myrick and Cech 2002) both worked at UC Davis, but Marine used juveniles from Coleman Hatchery, while Cech and Myrick used juveniles from Nimbus Hatchery. Marine used temperature treatments of 13-16, 17-20, and 21-24°C, and a feeding regime of 60-80% ration, while Cech and Myrick used treatments of 11, 15, and 19°C at full ration and 25% ration. Marine (1997) found no difference in growth rates between his low and intermediate temperature treatments (Figure 4-6). Cech and Myrick (1999) found that growth rate at full ration increased up to 19°C (Figure 4-7b). The average weights declined at all temperatures at 25% ration.

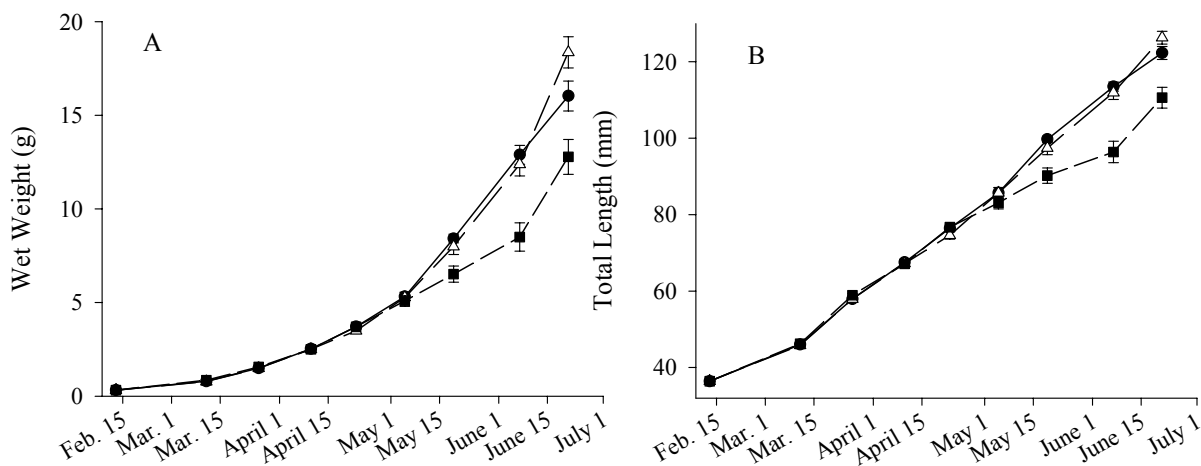


Figure 4-6. Growth of juvenile Chinook at three temperatures. Weight (A) and length (B) over time for juvenile Chinook salmon from Coleman Hatchery fed 60-80% ration at three different temperature treatments: 13-16°C (filled circles), 17-20°C (open triangles), and 21-24°C (filled squares). Temperature treatments began in mid-April. Bars show standard errors. Data from Table 4 in Marine (1997).

Rich (1987) reported maximum growth at 15.3°C (Figure 4-7a), and no survivors at 24°C, in contrast to Marine (1997), Cech and Myrick (1999), and Brett et al. (1982). Possible reasons for the difference are tank effects and disease. Marine (1997) used 400 L circular tanks with filtered surface water from Putah Creek and initial density of 550 fish per tank (0.73 L per fish). Cech and Myrick (1999) used 110 L circular tanks and pathogen-free well water and 30 fish per tank (3.67 L per fish). Both used directed sprays to maintain a current in the tanks. Brett et al. (1982) did not describe their experimental tanks, each of which held 25 fish. Rich (1987) used 57 L rectangular tanks with unfiltered surface water from the American River, and a high density of fish (initially 160 per tank, or 0.36 L per fish). The densities in both the Myrick and Rich experiments decreased over time as fish were sacrificed for various assays.

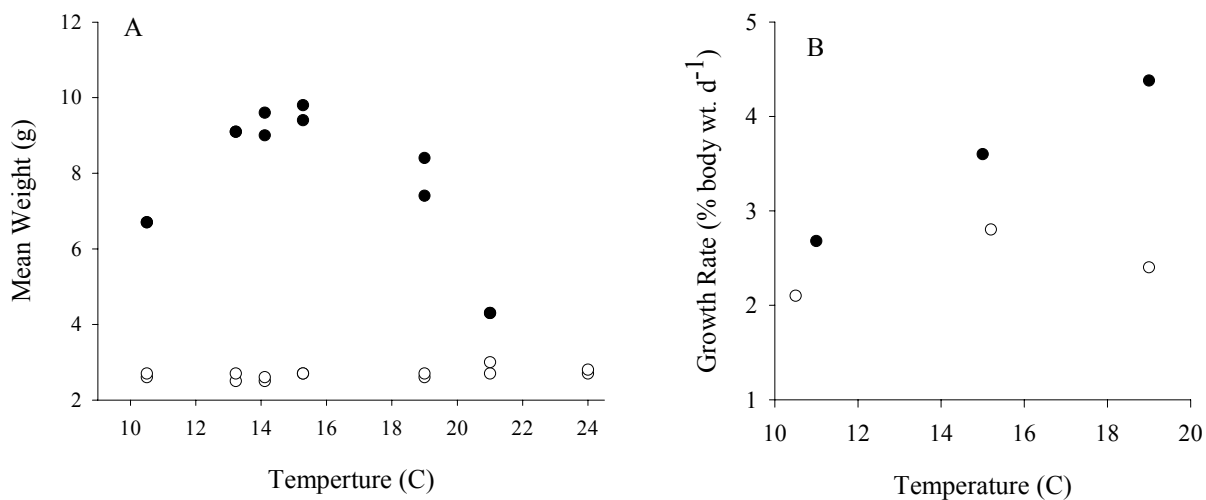
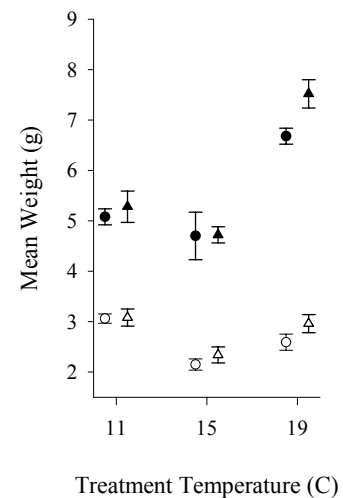


Figure 4-7. Growth of juvenile Chinook in two studies. A: Initial (open circles) and final (filled circles) weights of juvenile Chinook salmon from Nimbus Hatchery reported by Rich (1987); the duration of the study was not stated clearly but apparently was ~45 d. Initial Data from Table 1 in Rich (1987). B: Comparison of average growth rates reported by Rich (1987) open circles), and by Cech and Myrick (1999; filled circles), for three temperature treatments. Rich used two replicates per treatment; Cech and Myrick used four. Data from Table 9 in Cech and Myrick (1999).

Rich noted disease as an indicator of stress for the 19°C and higher treatments, and this, together with confinement in tanks with little current, may explain the difference between her results and those from other studies (there is evidence that confinement in aquaria without current causes stress (Milligan et al. 2000), and the unfiltered surface water probably introduced pathogens). Rich's results underscore the need to consider the extent to which higher temperatures increase the virulence of pathogens (Myrick and Cech 2001), but whether her experimental conditions reasonably reflect natural conditions is questionable. The differences between the results of Marine (1997) and Cech and Myrick (1999) are not easy to explain. Myrick and Cech (2002) suggest either differences between the two hatchery populations, or differences in water quality.

Steelhead from Nimbus Hatchery grew faster at 19°C than at 11°C or 15°C at both full ration and ~90% ration over 30 d (Cech and Myrick 1999; Figure 4-8). However, steelhead at Nimbus are derived from Eel River stock and are not part of the Central Valley steelhead ESU, and data on growth of Central Valley steelhead at different temperatures are not available. Myrick and Cech (2000) measured the growth at full ration of two strains of rainbow trout from the Eagle Lake and Mount Shasta hatcheries at 10, 14, 19, 22 and 25°C. Growth rates were slightly higher at 19 than at 14°C, and decreased at the higher and lower temperatures. Growth for the hatchery trout was somewhat higher than for the Nimbus Hatchery steelhead, as was their food consumption (Cech and Myrick 1999).

Figure 4-8. Initial and final weights of juvenile steelhead from Nimbus Hatchery grown at three temperatures over 30 d at full ration (triangles) and at ~90 ration (circles); open symbols show initial weights. Data from Cech and Myrick (1999); bars show standard errors, $n > 60$.

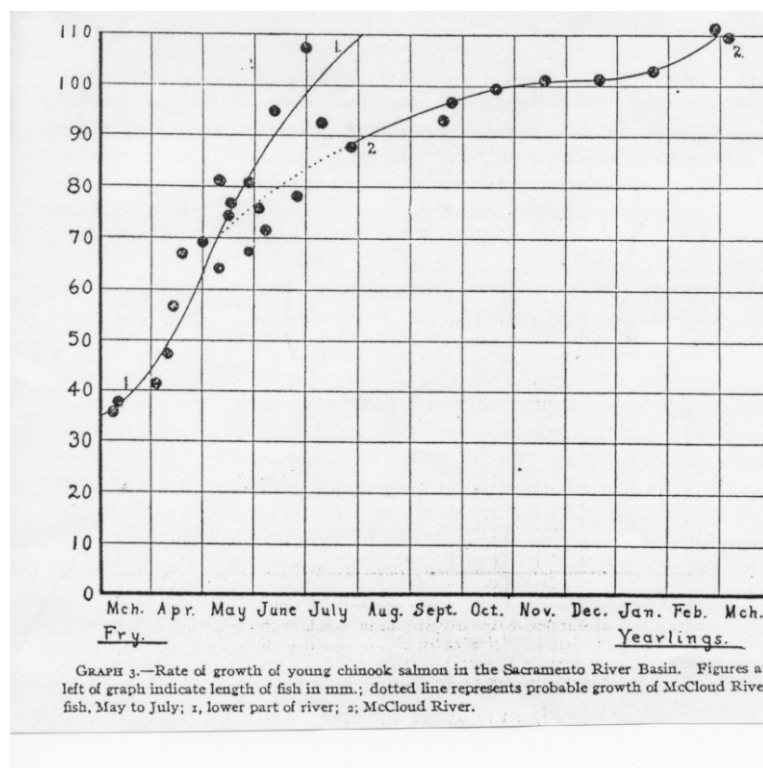


Field data on growth of juvenile Chinook and steelhead

Most early estimates of the growth of juvenile Chinook salmon were developed from the size distributions of sequential field observations. For example, Rutter (1904) used such observations to estimate the growth of migrating Chinook fry at 0.25 mm d^{-1} and the summer and fall growth of juveniles in the upper Sacramento and tributaries at 0.25 to 0.33 mm d^{-1} . Rich (1920) fit lines to sequential measurements of Sacramento River Chinook that give a spring growth rate of $\sim 0.66 \text{ mm d}^{-1}$, and indicate different growth trajectories for stream and ocean-type fish (Figure 4-9). Healey (1991) estimated average growth rates in several rivers in British Columbia and Oregon at 0.21 to 0.62 mm d^{-1} based on the size of juveniles in June and assuming an age of 60 d. However, marked fry had growth rates as high 1.32 mm d^{-1} . Weatherley and Gill (1995) estimated growth at 0.07 to 0.33 mm d^{-1} from estimates of smolt size in various rivers. Tagged hatchery juveniles 40 to 50 mm long, released into the Sacramento River at Red Bluff and recaptured in the Delta, grew at an average rate of 0.33 mm d^{-1} . Similar fish released into the estuary grew at an average rate of 0.86 mm d^{-1} in 1980, and 0.53 mm d^{-1} in 1981 (Kjelson et al. 1982). Juvenile Chinook in small, warm, tributaries of the Sacramento River apparently grew faster than juveniles in the Sacramento River (Maslin et al. 1997; 1998; 1999; Moore 1997). The estimated median growth rates of Butte Creek spring-run fry tagged near Chico and recovered in the Sutter Bypass in 1996, 2001, and 2002 were 0.76 , 0.60 , and 0.35 mm d^{-1} (Ch. 6). In the Yolo

Bypass, estimated mean growth rates for juvenile fall-run in 1998 and 1999 were 0.80 and 0.55 mm d⁻¹ (Sommer et al. 2001). Estimates from sequential measurements of groups of fish are questionable, however, as size-selectivity in migration, mortality, or sampling methods can introduce bias. Moreover, although growth rates in length can be linear for periods of months (Figure 4-6-b), in general growth is non-linear, especially for weight, so that growth rates averaged over times or over fish of different sizes can be misleading (Elliott 1994).

Figure 4-9. The growth trajectories of ocean-type (1-1) and stream-type (2-2) Chinook in the Sacramento River, as inferred by Rich (1920) from the average size of fish collected at various times and places along the river. The ocean-type growth trajectory shows growth of 40 mm in April and May, or ~0.66 mm d⁻¹.



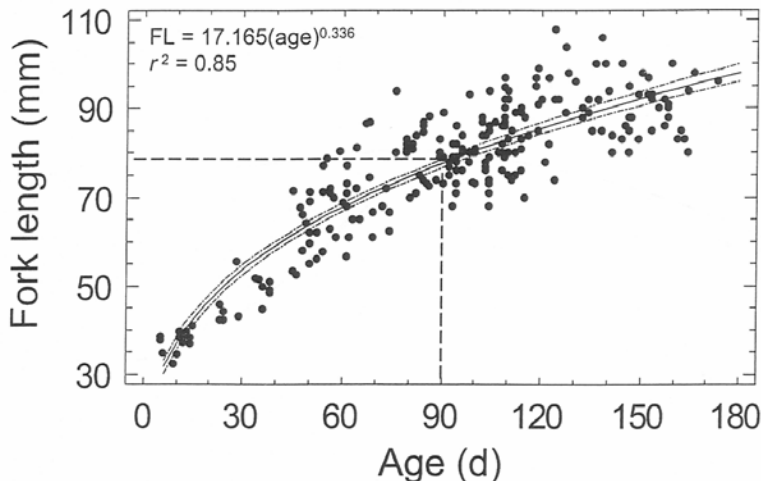
Estimates of growth rates for individual juvenile Chinook and steelhead in the American River have been developed from measurements of length and otolith increments (Castleberry et al. 1991; 1993; Titus et al. 2004). Fish otoliths are composed of alternating layers of protein and calcium carbonate that in cross-section look rather like tree rings, and juvenile salmonids ordinarily add a new increment each day (Bradford and Geen 1987; Campana 1983; Neilsen et al. 1985; Castleberry et al. 1994). Typically, salmonid otoliths show groups of tightly spaced increments or “checks” at hatching and at the transition to active feeding (Zhang et al. 1995).

The number of increments at a given length provides an index of long-term growth rate, and if a length is assumed at formation of the first increment or at the hatching or emergence check, the subsequent absolute growth rate can be estimated. Simulations indicate that such estimates probably become usefully accurate for fish >~50 mm (Williams 1995). Estimating the size of each fish at formation of the first feeding check from the size of its otolith allows more accurate

estimates of the growth rates (Titus et al. 2004). For a sample of 32 juvenile Chinook from the American River, Titus et al. (2004) estimated an average (s.d.) growth rate of 0.48 (0.20) mm d⁻¹, using an estimate of size at first feeding based a relationship they developed between otolith-width and fork length.

Based simply on the relation between number of otolith increments and length reported by Castleberry et al (1993), juvenile Chinook in the American River in 1992 grew ~0.39 mm d⁻¹ on average at 50 mm length (Williams 1995; estimates given in Castleberry et al. 1991; 1993 are incorrect). Titus et al. (2004) also fit a power equation to length at age in days since first feeding check: fork length = 17.917 (age)^{0.334}, r² = 0.81. This gives an average growth rate at 50 mm of 0.77 mm d⁻¹, slightly higher than a comparable group from Nimbus Hatchery. However, their equation over-predicts size for fish from both habitats from about 10 to 45 days in age (~40 to 65 mm), and by inspection a growth rate of about 0.5 mm d⁻¹ at 50 mm fork length seems more appropriate. To cover a larger range in age, Titus et al. (2004) also fit another power curve to their data combined with data on larger fish captured in the bays and the Gulf of the Farallones, reported by MacFarlane and Norton (2002), (Figure 4-10). Again, the equation tends to overpredict length for younger fish, and a sigmoidal curve probably would give a better fit to the data, but the figure shows that growth in the bays is slow, as shown also by Figure 4-11a, b, copied from MacFarlane and Norton (2002)..

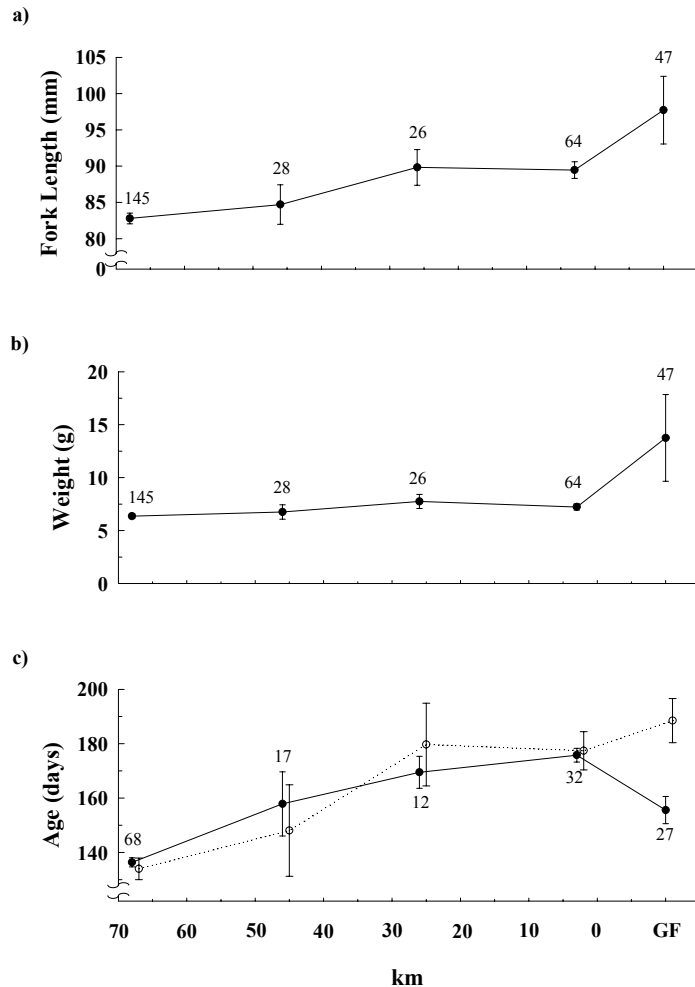
Figure 4-10. Size at age of juvenile Chinook salmon from the American River and from the San Francisco Estuary. Copied from Titus et al. (2004), courtesy of the American Fisheries Society.



A complication with the MacFarlane and Norton (2002) data is that fish captured in the Gulf of the Farallones were on average about 20 days younger, as well as 8 mm longer and 6.5 g heavier, than fish captured just inside the Golden Gate, based on otolith analyses of 27 of the 47 fish captured in the gulf (Figure 4-11). This may be a sampling problem; the Gulf of the Farallones sample was unusual, in that 8 of the 47 fish (17%) had coded-wire tags, and these had unusually high migration rates (Table 1 in MacFarlane and Norton 2002). Based on a length-age relationship, MacFarlane and Norton estimated an age for the entire Gulf of the Farallones sample shown by the open symbols in Figure 4-11c. In any event, the estimated average growth

rate between Chipps Island and the Golden Gate was 0.18 mm d^{-1} in length and 0.02 g d^{-1} in weight, based on the sizes and ages of the fish collected at Chipps Island and near the Golden Gate. As noted by MacFarlane and Norton (2002), these are much slower rates than those reported for other estuaries (Ch. 11). Data are being processed for additional years and should provide more definitive information on growth rates in the bay. However, the sampling has not covered the early part of the run (it began on April 30 in 1997), and so has missed any fry migrants that move directly into the bays.

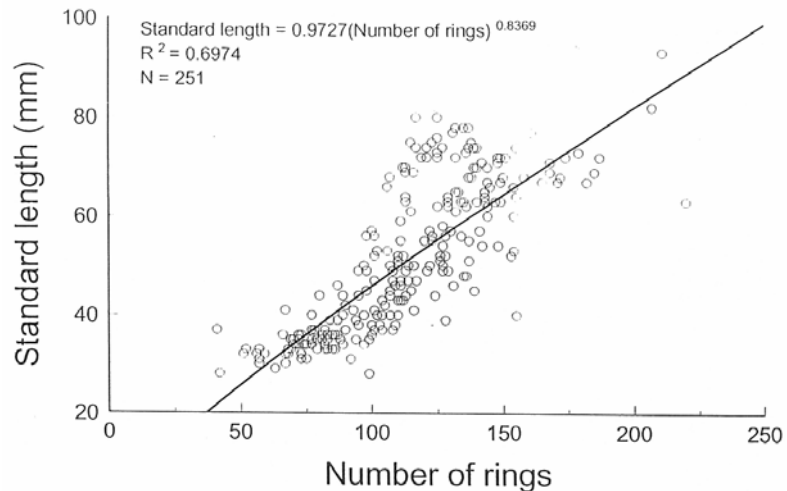
Figure 4-11. Mean fork lengths (a), weights (b), and ages since hatching (c) of juvenile Chinook captured at four stations in the San Francisco Estuary and in the Gulf of the Farallones from April 30 to June 27, 1997; distances are upstream from the Golden Gate. Km 68 is Chipps Island, just downstream from the Delta. Error bars show standard errors, and numbers near means show sample sizes. The dashed line in c shows ages estimated from a length-age relationship. Copied from MacFarlane and Norton (2002).



Variability in growth rates

Growth rates of juvenile Chinook and steelhead are highly variable. Juvenile Chinook in the American River in 1992 with 125 otolith increments ranged from about 40 to 80 mm standard length (Figure 4-12), and from <1 to about 7 g in weight. Steelhead with 110 increments varied from about 45 to almost 100 mm standard length, and from <2 to about 13 g in weight (Castleberry et al 1993). The range in the Titus et al. (2003-4) data is not so large, but their sample size was smaller (Titus et al. 2004 is primarily a methods paper; more extensive results should be published soon).

Figure 4-12. Variability in growth of juvenile Chinook. Length v. number of otolith increments in 251 juvenile Chinook sampled in the American River in 1992. Note the large variation in length of Chinook with ~100-150 increments. Copied from Castleberry et al. (1993).



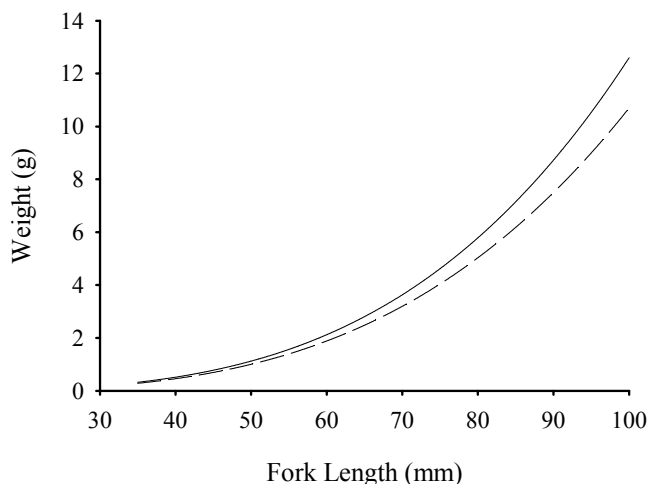
Comparison of the growth rates reported by Castleberry et al (1993) and by Titus et al. (2004) is not straightforward, however, because of the possibility that the more rapidly growing juveniles leave the American River, and because different methods were used to estimate growth. Most of the fish analyzed by Castleberry et al. were captured with seines, while those analyzed by Titus et al. (2004) were captured in rotary screw traps, and were more likely to be actively emigrating. MacFarlane and Norton (2002) reported that juvenile Chinook captured at Chipps Island at the seaward edge of the Delta averaged 83 mm fork length at ~135 days post-hatch. Assuming around 15 pre-hatch otolith increments, this size corresponds to the more rapidly growing juveniles in the Castleberry et al. (1993) sample. In the Castleberry et al. (1991; 1993) studies, growth was estimated simply by fitting a line to a plot of length over the number of otolith increments. If the interest is in growth since emergence, as is usually the case, the accuracy of these estimates is reduced by uncertainty in the size at emergence. Titus et al. (2004) estimated the size of the fish at emergence, and so reduced this error.

High mean growth rates were reported for larger (>60 mm) fall run Chinook parr and smolts in the Snake River, based on sequential measurements of > 40 tagged fish in each of six years (Conover and Burge 2003). Growth rates of parr averaged 1.2 ± 0.04 and 1.0 ± 0.04 mm d⁻¹ in the upper and lower reaches of the river. Growth rates of juveniles tagged in the upper and lower reaches but recaptured in Lower Granite Reservoir averaged 1.3 ± 0.03 and 1.4 ± 0.04 mm d⁻¹. Water temperatures in the lower and upper reaches and in the reservoir averaged 12.0, 11.1, and 15.1°C, respectively. These temperatures are generally cooler than the American River in late spring, but are similar to Marine's 13-16°C treatment, for which the mean growth rate for fish > 60 mm was 0.76 mm d⁻¹ (Figure 4-6). The reason for the more rapid growth by the Snake River Chinook is unclear; Myrick and Cech (2002) present a comparison of growth rates of juvenile Chinook in laboratory studies that shows Central Valley fish growing as rapidly as others.

Length-weight relationships

Length - weight equations have been reported by Petrusso and Hayes (2001b) for the Sacramento River between Chico and Redding in 1995 and 1996, and by Castleberry et al. (1993) for juvenile Chinook and steelhead in the American River in 1992. The equations use different units and measurements, and are most easily compared graphically (Figure 4-13); the juvenile Chinook sampled from the Sacramento River were somewhat heavier at length than fish from the American River.¹⁸

Figure 4-13. Length-weight relationships for juvenile Chinook reported by Petrusso and Hayes (2001) for the Sacramento River in 1995 and 1996 (solid line) and by Castleberry et al. (1993) for the American River in 1992.



Modeling growth

Growth for juvenile salmon in streams is of interest in part as an index of habitat quality. Since temperature and fish size strongly affect growth rates, a growth model that accounts for temperature and size could provide a useful standard for assessing growth rates for individual fish, whether from individually tagged fish or estimated from otoliths. Elliott (1975; 1994) described such a model for brown trout fed full ration:

$$dW/dt = (a + b_2T)W^{-b_1}$$

$$W_t = [(a + b_2T)b_1 + W_0^{b_1}]^{1/b_1}$$

where W_0 is the initial weight, W_t is the weight after t days at temperature $T^\circ\text{C}$, and a , b_1 and b_2 are estimated from laboratory data at different temperatures.

More recently, Elliott et al. (1995) described a new model,

¹⁸ The equations are: Castleberry et al. (1993), American River Chinook: $\text{weight (g)} = 0.000004(\text{standard length})^{**3.2578}$ ($r^2 = 0.9858$, $n = 745$); $\text{fork length} = 1.031(\text{standard length, mm}) + 3.054$ ($r^2 = 0.9989$, $n = 1383$). Steelhead: $\text{weight (g)} = 0.000009(\text{standard length, mm})^{**3.0868}$ ($r^2 = 0.9954$, $n = 385$); $\text{fork length} = 1.062(\text{standard length, mm}) + 1.891$ ($r^2 = 0.9993$, $n = 644$). Petrusso and Hayes (2001), Sacramento River Chinook: $\ln \text{weight (mg)} = -6.6088 + 3.4852 \ln(\text{fork length})$

$$W_t = [W_0^b + bc(T - T_{lim}) t / \{100(T_m - T_{lim})\}]^{1/b}$$

where T_m is the optimum temperature for growth, T_{lim} is the high or low temperature at which growth goes to zero, depending upon whether T is greater or less than T_m , and b and c are parameters; b is the power transformation of weight that makes growth linear with time, and c is the growth rate of a 1 g fish at optimum temperature T_m .

Both models have been applied to populations of brown trout in various streams (Elliott 1994; Nicola and Almódvar 2004), and similar models for Chinook and steelhead could be useful. Data from Brett et al. 1982 and Cech and Myrick (1999) might be used for an initial exploration of this approach for Chinook, but more comprehensive data probably would be needed. Moreover, the shapes of the growth over temperature curve for brown trout at lower rations (Figure 4.13 in Elliott 1994) seem different than Brett's curves for sockeye, so it is not obvious that Elliott's model is directly transferable to Pacific salmon.

Seasonal growth

Although the growth rate of juvenile salmonids is not wholly dependent on the immediate environment (Figures 4-1 and 4-2), a consequence of the dependence of growth on water temperature is that growth typically slows in winter, as shown in Figure 4-9. Similar reductions in winter growth for Chinook are described by others, for example Levings and Lauzier (1991), Ewing et al. (1998), and Beckman et al. (2000). Curiously, salmon management in the Central Valley has used growth curves (Fisher 1992; Johnson et al. 1992; Greene 1992) that do not show any slowing of growth in winter, even though the data analyzed by Fisher (1992) actually do show the expected decline in growth in winter. These curves are used to allocate fish to runs, depending upon their size at date. As described in Chapter 11, genetic analyses have shown that the curves give a high rate of false positives when used to identify winter-run in the Delta. There is enough variation in growth rates within runs (e.g., Figure 4-12) and enough overlap in size among runs (Ch. 6) that in most parts of the watershed such curves would be of limited utility, even if their shapes were biologically plausible. This is not a new idea; Rutter (1904:90): observed that:

Adult salmon can be found in some part of the river throughout the year, and the spawning season is therefore very long. It is probable that there are salmon spawning at some place in the river or its tributaries in every month of the year. They are spawning in considerable numbers from July till January, inclusive. With such an extensive spawning period, it is obviously difficult to separate the young according to size, and say that those of a certain size belong to the spring or fall run of a certain year. A variation in rate of growth, noted elsewhere, adds to the difficulty.

Generally, the size criteria seem to be usefully accurate for distinguishing winter-run in the Sacramento River upstream from tributaries with significant populations of spring-run, for example at the RBDD, but not farther downstream.

CHAPTER FIVE

JUVENILE MIGRATION

As reported by Hasler and Scholz (1983) 15 years ago, “the mechanism of the seaward migration of salmon smolts has been the subject of much study, speculation, and argument,” and any definite solution still does not exist. H. R. Høgåsen (1998:42)

Like other aspects of their life histories, the downstream migration of juvenile salmonids is characterized by complexity and variation: a variety of environmental and biological factors influence the timing, mode, and rate of migration, and a hierarchy of environmental cues is used in navigation. Complex physiological changes that prepare the fish for the transition to seawater occur during the migration, but, particularly for Chinook, not in a set pattern. This chapter reviews salient features of the downstream migration, using examples from the Central Valley when possible, and then presents data on the juvenile migratory behavior of the different Central Valley runs.

Sometime between hours and two years after emerging from the gravel, juvenile Chinook begin migrating downstream toward the ocean (Healey 1991); most steelhead go to sea in their second or third year, but some migrate or disperse downstream in their first spring (e.g., Cavallo et al. 2003), and at least in coastal streams some reach and rear in estuaries (e.g., Dettman and Kelley 1986). There is good evidence for genetic variation in the propensity of ocean-type Chinook to migrate as fry (Carl and Healey 1984), although year to year variation in the proportion of fry and fingerling migrants in some Central Valley rivers, described below, shows that environmental factors also matter. It seems likely that there is some genetically influenced but variable threshold for fish to migrate as fry, analogous to the threshold for smolting in the Thorpe et al. (1998) life history model for Atlantic salmon, discussed in Ch. 1. The Thorpe et al. model may be more directly applicable to steelhead, which are similar to Atlantic salmon in many respects, but this remains to be established.

Physiological changes associated with migration

Juvenile salmonids that rear for a year or more in freshwater before migrating to sea typically undergo a set of behavioral, physiological, and morphological changes that is associated with their downstream migration and the transition from freshwater to marine habitats, and the transition from being parr to being smolts (Clarke and Hirano 1995). Typically, the smolting process occurs in spring, and if the fish are prevented from migrating most of these changes reverse and they “residualize” to being parr, but will smolt again the following spring. The physiological changes associated with migration are reviewed in detail by Høgåsen (1998), so the discussion here is brief and focused on matters relevant to monitoring. As summarized by Jobling (1995:241), the changes associated with smolting are:

“Silvering” due to increased deposition of guanine and hypoxanthine in skin and scales;

More streamlined body form and reduced condition factor due to rapid growth of the caudal peduncle region;

Development of chloride cells, with increased Na^+/K^+ ATPase and succinic dehydrogenase enzyme activity;

Increased salinity tolerance and improved hypo-osmoregulatory ability;

Metabolic changes leading to increased body water content, reduced lipid content, and changes in fatty acid composition;

Reduced territorial behavior and increased formation of schools;

Increased activity, negative rheotaxis and downstream migration;

Preference for water of increased salinity;

Decreased ability to hold station against water current.

With *Oncorhynchus* that go to sea in their first year, however, the process is less well defined (Clarke and Hirano 1995). At one extreme, pink salmon in short coastal streams may migrate to the ocean the same night that they emerge from the gravel (Heard 1991). Ocean-type Chinook exhibit a range of migratory behaviors, and some migrate directly to brackish estuaries as fry (Healey 1991). Accordingly, statements in the literature regarding older smolts should not be applied uncritically to ocean-type Chinook.

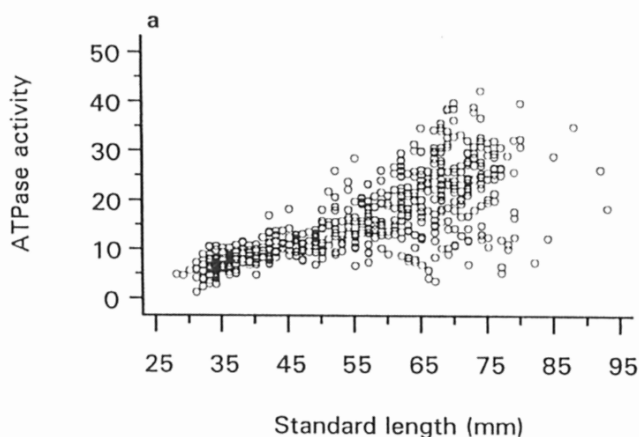
Although it is common for biologists in the Central Valley to refer to juvenile Chinook that rear in the river for two or three months and migrate toward the Delta in April to June as smolt migrants, most are only part way along in the smolting process, at least when they begin migrating. CDFG biologists recently began describing fish sampled in screw traps as sac fry, fry, parr, silvery parr, and smolts; in a trap below the main spawning area in the American River, the percentage of smolts for 1994-2000 varied from 0.0 to 0.4%, and that of silvery parr from 0.1 to 3.9% (Snider and Titus 2001). The lipid content of juvenile Chinook sampled in the American River in 1991 and 1992 increased with length, and moisture content decreased (Castleberry et al. 1991; 1993), contrary to the expectation for smolting fish. However, critical swimming velocity¹⁹ did not increase with length after Chinook reached about 50 mm, and Na^+/K^+ ATPase activity levels increased with length for most but not all sampled fish (Castleberry et al. 1991; 1993; Figure 5-1). Thus, larger (~60+ mm) fall Chinook in the American River share some but not all of the characteristics of smolts listed above.

Like other bony fishes, salmonids maintain their body fluids at about one-third the salt concentration of sea water. In freshwater, they take up water through their gills by osmosis and

¹⁹ Critical swimming velocity is measured by making fish swim in a tube in which water velocity is slowly increased until the fish are pinned against a screen in the tube.

excrete water in dilute urine to maintain ionic balance. In the ocean the osmotic gradient is reversed, so the fish lose water through their gills that they replace by drinking sea water, and excrete the salts by active transport through specialized cells in their gills. The enzyme Na^+-K^+ ATPase (hereafter simply ATPase) helps power the function of these chloride cells, and has been used as an assay for the readiness for release of juvenile salmon in hatcheries or as an index of progress in smolting (Clarke and Hirano 1991). As part of developing tolerance for sea water, at whatever age, juvenile salmonids develop higher ATPase activity.

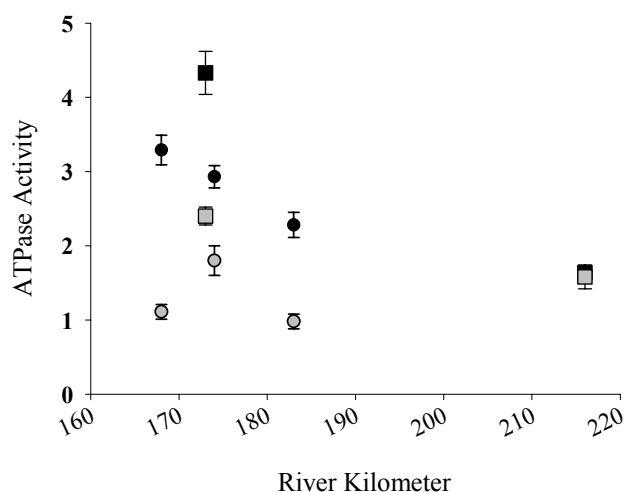
Figure 5-1. ATPase activity²⁰ of juvenile Chinook salmon in the lower American River in 1992, in $\mu\text{mol P}_i \text{ mg protein}^{-1} \text{ h}^{-1}$. Some samples for fish under 60 mm were pooled. Note the large variation in ATPase activity for the larger fish. Copied from Castleberry et al. 1993.



ATPase activity levels are also correlated with the rate of migration, and both can vary within a population at a given time and place along a river (Ewing et al. 2001). In the Rogue River, Oregon, juvenile spring-run Chinook follow an ocean-type life-history pattern, with ~99% migrating to sea in the summer and early fall of their first year. In the late 1970s juveniles were sampled with various gear at various places along the river, and were marked with week-specific brands at two locations so that approximate migration rates could be calculated when branded fish were recaptured. Generally, the data show that fish began migrating before their ATPase activity levels increased, but subsequently those migrating down the center of the channel and captured there in traps had on average higher ATPase activity levels and higher migration rates than fish captured along the margin of the river with seines (Figure 5-2). That is, the population could be divided approximately into two groups, with different migratory behavior and ATPase activity levels, that were most effectively sampled with different gear. Unfortunately for the use of ATPase activity in monitoring, there can also be strong temporal variation, reflected in the higher July values in the samples collected between river kilometers 168 and 183.

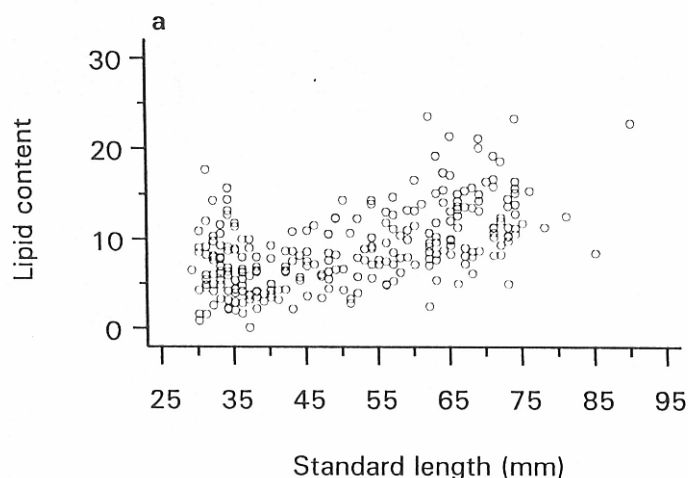
²⁰ Castleberry et al. (1993) did not specify the units for ATPase activity, but presumably they are the same as in Zaugg (1982), since Zaugg performed the assays. The activity levels differ by a factor of about 10 from those described by Ewing et al. (2001). Why this should be is not clear.

Figure 5-2. ATPase activity from fish collected with seines (circles) and traps (squares) in July (black symbols) and August (grey symbols) in the Rogue River. Data for RK 168 to 183 are from single days; upstream data are averages. Bars show standard errors. The units of specific ATPase activity are $\mu\text{moles P h}^{-1} \text{mg protein}^{-1}$. Data from Tables 1 and 3 in Ewing et al. (2001).



It seems intuitive that energy reserves in lipids are important for migrating fish, but surprisingly little information has been published on the lipid content of wild juvenile *Oncorhynchus* (Beckman et al. 2000), and different reports use different methods or units, which complicates comparisons of published values. For example, Castleberry et al. (1991;1993) reported the non-polar lipid content of juvenile Chinook and steelhead in the American River as percent dry weight, and Beckman et al. (2000) and Congleton et al. (2004) reported the same as percent wet weight for juvenile Chinook in the Yakima River. MacFarlane and Norton (2002) removed the head, fins and stomachs from juvenile fall Chinook collected between Chipps Island and the Gulf of the Farallones before extracting all lipids from the remainder, and reporting several classes of lipids. One of these, triacylglycerols, is approximately equivalent to non-polar lipids (B MacFarlane, NOAA Fisheries, pers.comm. 2004). In terms of trends, however, non-polar lipid content increased with length for Chinook and steelhead in the American River in 1991 and 1992 (Figure 5-3), and the triacylglycerol content of juvenile Chinook migrating through the bays was roughly constant while the fish grew slowly, but then dropped sharply when the fish reached the Gulf of the Farallones and began growing rapidly (MacFarlane and Norton 2002). In the Columbia River system, the average lipid reserves for yearling hatchery smolts declined from 6.9% of wet weight before release to 2.0% at Lower Granite Dam and 0.74% at Bonneville Dam, which is 461 km farther downstream. The mean lipid percentage for naturally produced yearling smolts was lower than for hatchery smolts at Lower Granite Dam (1.03%), but only slightly lower at Bonneville Dam (0.67%). Adjusted for length (to 110 mm), naturally produced smolts lost 39% of their lipid reserves between the two dams, compared to 68% for the hatchery smolts (Congleton et al. 2004).

Figure 5-3. Percentage of dry weight of non-polar lipids of juvenile fall Chinook in the American River in 1992. Copied from Castleberry et al. 1993.



Proximate factors influencing migration

In a recent review, Høgåsen (1998) listed the following as influencing the onset of migration: photoperiod, temperature, rainfall, increased flow or turbidity, lunar cycle, size, condition, growth rate, age, sex and sexual maturation, social facilitation, and perhaps endogenous rhythms. For orientation and navigation, she listed stream direction and velocity, odors, visual cues, magnetic fields, and temperature gradients. She summarized the relative importance of the factors that influence the beginning of migration as follows (Høgåsen 1998:10-11):

The number of factors suggested to influence migratory behavior and the number of apparently conflicting results concerning their influence clearly demonstrates the complexity of the regulation of migration in anadromous salmonids. Each stock seems to respond to a specific selection of stimuli, possibly ranged in a specific hierarchy. When the dominant stimulus is absent at a certain time or physiological stage, backup systems may be used. Once the fish have reached a given physiological state, they could use the first-occurring stimulus among a number of environmental changes to ensure mass migration. It seems that photoperiod, temperature, and growth most often regulate the development of migratory readiness, whereas moon cycles, light intensity, water discharge, or temperature changes are responsible for triggering downstream migration. The relative importance of all these factors seems to vary greatly among species, places, times of year, and successive years.

It appears that juvenile salmonids can recognize siblings by scent, probably by proteins of the major histocompatibility complex or their breakdown products, and that this recognition affects their social and migratory behavior (Olsén 1999; Olsén et al. 2004). This can have practical consequences for monitoring; to the extent that siblings tend to migrate together, small samples may not be representative of the population. In a genetic study, Hedgcock et al. (2001) were able to identify likely sibs, and so could make adjustments to allele frequencies in samples of juvenile spring-run in order to estimate the allele frequencies of the parents, but with other kinds of monitoring such adjustments are not possible.

Navigation and orientation seem to involve a similarly variable complex of hierarchically-organized factors, as described in an earlier review by Smith (1985; 207), who concluded in part that:

One of the salient points to emerge from this survey of controlling mechanisms is the variety of different stimuli which can be involved in fish migration. These stimuli also interact in complex ways. Compass mechanisms, for example, are arranged in hierarchical order, one mechanism being used preferentially when its stimuli are present, then the other mechanism taking over in the absence of the preferred stimulus.

...

The variety and subtlety of the controlling mechanisms means that it is difficult to foresee the consequences of interference with natural ecosystems.

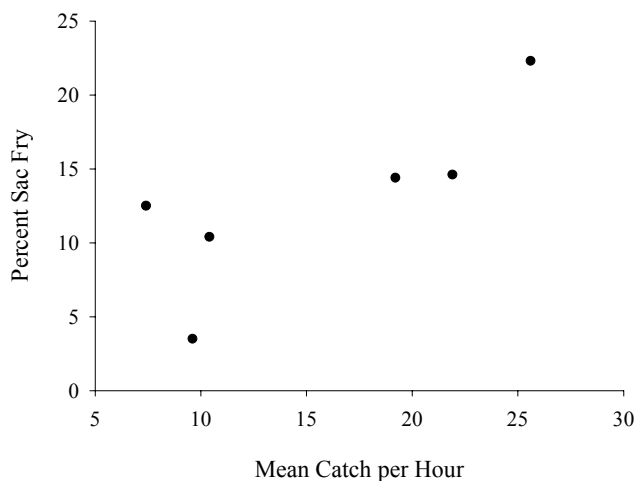
There is also good evidence for genetic differences in responses to migratory cues. Variation in migratory behavior among local populations has been studied particularly in juvenile sockeye, which typically spawn in streams but rear in lakes. Fry hatched in streams flowing into the lake move downstream, while fry hatched in streams that drain the lake must swim upstream, to reach their rearing habitat (Raleigh 1971). Breeding experiments show that this trait is genetically controlled (Quinn 1980). This is not the only example; Smith (1985; 204) observed that "The general conclusion that arises from this handful of experimental tests is that genetic differences in migratory behavior between local populations have been found wherever they have been sought." One implication of possible genetic differences and the variety of migratory cues used by various stocks of salmonids is that while studies from other areas may suggest hypotheses to be tested, studies of Central Valley stocks will be needed to clarify the particular combinations of cues that the various runs and life-history types use to migrate to and through the Estuary.

Smith also noted that (1985:207): "The evidence for genetic adaptation of fish stocks to their specific migration routes means that contamination of these genotypes with fish from other locations may seriously interfere with migratory ability." This raises the issue that hatchery practices in the Central Valley, which have notoriously increased straying rates (JHRC 2001), may have compromised the migratory ability of naturally-produced stocks. It also helps explain a report that fish from eggs collected at the Feather River Hatchery, but raised at the Mokelumne River Hatchery, strayed in greater numbers than fish raised from eggs collected at the Mokelumne River Hatchery (Joe Miyamoto, EBMUD, pers.comm. 2005). Similar results have been reported for Chinook in British Columbia (Candy and Beacham 2000), although the straying rates they reported are an order of magnitude lower.

It is unclear whether ocean-type Chinook that will migrate as fry begin migration immediately, whether they spend a few days in shallow water in the spawning reach before doing so, or whether both behaviors are common. Myers et al. (1998:28) note that such fry migrate "... soon after yolk sac resorption at 30-45 mm in length," but considerable numbers of sac-fry are captured in screw traps downstream from the main spawning areas on the American River in some years, even during periods of low flow such as January 1996 (Snider et al. 1998; Snider

and Titus 2002). Moreover, the seasonal percentage of sac fry appears to increase with mean catch rate (Figure 5-4), suggesting that some density-dependent process, perhaps occurring in the hyporheic zone, may be involved. In any event, the appearance of sac fry in the screw trap samples suggests premature emergence. and the reasons for it should be investigated.

Figure 5-4. Percentage sac fry v. mean catch per hour in screw traps on the lower American River, 1995 – 2000, both on a seasonal basis. Data from Snider and Titus (2002).



Juvenile Chinook may move upstream as well as downstream (Murray and Rosenau 1989), as demonstrated by their presence in Sacramento River tributaries that are too small to support spawning (Maslin et al. 1997; 1998; 1999). This movement is not trivial: Maslin et al. (1999) estimated that a million juveniles may use these streams in some years. There is also evidence of movement up larger tributaries. For example, juvenile Chinook infected with *Ceratomyxa shasta* were captured in the American River in 1992 about 3 km above its mouth; since *C. shasta* occurs in the Sacramento River but not in the American, these probably were Sacramento River fish that traveled upstream in the American (Okimoto et al. 1992). The extent of such movements is unknown. Coded-wire tagged fish are not released into the American River, and only a few tagged fish are captured in the screw traps there (R. Titus, CDFG, pers.comm. 2004), but the traps are 14 km up the American River, and hatchery fish may migrate downstream more directly than naturally produced fish (e.g., Kostow 2004).

Some speculation about navigation by juvenile Central Valley Chinook and steelhead follows, based largely on the material in the reviews by Smith (1985) and Høgåsen (1998). Probably the dominant cues available to migrating juveniles are the flow of water and the position of the sun. Smith (1985:140) observed that "The use of water current as a directional cue in river or stream migration has seemed so obvious that it has received little analysis." Even the Delta, where the current regularly changes direction with the tide, the current should provide useful information. Perception of the current depends largely on the apparent motion of objects in the visual field, however, and although salmon have excellent night vision, current may not be

reliably detected visually in highly turbid water.²¹ It appears that juvenile salmon can track the changing position of the sun over the day, and so use it or other celestial cues to maintain a compass orientation. Salmon are also sensitive to and can orient themselves to the polarization of light, but again highly turbid water seems an obstacle. Salmon can also detect and orient themselves in relation to the Earth's magnetic field, although not as accurately as with visual cues, and this may provide the "fallback" method of navigation.²² The receptors for odors are well developed even in very young salmon, as evidenced by the sequential imprinting on odors that seems to guide their return migration (Chapter 8), but the role of odor in navigating during the downstream migration is unclear. The salinity gradient seems an obvious cue for orientation, but Smith (1985:77) notes that "... there is little evidence that salinity is a guiding mechanism," although the preference and tolerance of juveniles to salinity is appropriate for their migratory behavior. If salinity is really not a factor, then navigation through the bays is probably guided mainly by celestial and magnetic cues.

There are conflicting reports regarding the effect of flow on the number of migrants in Central Valley rivers. For example, Rutter (1904:92) reported that it was "... ascertained that a large migration is not coincident with remarkably high water" on the Sacramento River, and Workman (1999, 2002) found no significant relation between flow and juvenile passage on the Mokelumne River. However, more fry are caught at sites in the Sacramento River near the Delta and in North Delta in January through March in wet years, as indexed by the mean February flow, and catches of the Chipps Island trawling and the seine sampling in the bays also increase with flow (Kjelson et al. 1982; Brandes and McLain 2001). Similar relationships between flow and the movement of fry into the estuary have been reported elsewhere (e.g., Healey 1980), but surges in migration rate can occur even on declining flows (Erkkila et al. 1950). The literature provides other examples of conflicting findings (Healey 1991; Høgåsen 1998).

It seems clear that during very high flows, fry simply get swept downstream; for example, Hatton and Clark (1942) reported catching sac fry at Martinez in 1940, a few days after the daily average discharge on the American River reached 1,600 m³s⁻¹, high enough to scour redds. Based on screw trap data, however, fry move downstream in very large numbers even in dry years, when flow along the edge of the channel is quite slow. It seems plausible that up to some threshold range of discharge, the fish can adjust their rate of migration by adjusting their lateral position in the channel, but above the threshold range the fish lose control of their position because the turbulence is too strong for them to resist, even near the banks in leveed channels (fish that have access to floodplains could find slowly moving water there). Fish may try to avoid the higher turbulence in higher velocity sections of the channel during high flows, which could account for negative relationship between flow and catch of >70 mm fish in trawls at Sacramento

²¹ Salmonids can detect and exploit the vortices shed by objects in the water to decrease the energetic cost of swimming (Liao et al. 2003), so it seems highly plausible that juvenile salmon can sense current speed from the associated turbulence, but if this is described in the literature Høgåsen (1998) did not find it, nor did I.

²² It has recently been reported that green sea turtles use the magnetic field to return to their natal beaches after years at sea (Lohmann et al. 2004), so perhaps this factor is even more important for salmonids than has been supposed.

described by Brandes and McLain (2001). Such behavior could also make the seine catches increase with flow.

Relating migration to flow can be difficult because other factors such as turbidity and temperature commonly change along with flow, and the vulnerability of fish to various sampling gear, and to predators, may also change with flow or turbidity, or turbidity itself may encourage migration. Overall, the evidence suggests that increases in migration are often associated with increases in flow, but migration will occur in any event, although it may be delayed. Whether temporary increases in flow intended to “flush” larger juveniles out of streams before water temperature gets too high are worthwhile remains to be demonstrated (e.g., Demko and Cramer 1996).

Recently, DeVries et al. (2004) reported that lunar gravitation affects the timing with which juvenile Chinook, coho and chum moved from Lake Washington into Puget Sound, although they did not suggest a mechanism by which the fish might sense it. Nevertheless, their data are persuasive enough that it seems worthwhile to test whether this effect is evident in screw trap data or in the Chipps Island trawling data.

Diurnal variation in migration

There is good evidence for diurnal patterns in migratory behavior, but these also vary. A fyke trap operated at Balls Ferry in 1899 was checked in the morning, at noon, and in the evening, and much higher numbers of fish were found in the morning (Figure 5-5), in contrast to catches in turbid water at Georgiana Slough, where day and night catches were roughly equal (Rutter 1904). Rutter interpreted these data as showing that the fish migrated mainly at night where the water was clear, but greater gear avoidance during the day would tend to give the same result. However, data from Battle Creek, where “the trap was so set that they could not have avoided it had they traveled during the day” (p. 90) also indicated primarily nocturnal migration, as did observations of hatchery fry released into small streams. More recent data from screw traps at the RBDD also show greater migration at night or during crepuscular periods (Gaines and Martin 2002), as do data from the Mokelumne River (Workman 2002).

Diurnal variation in migratory behavior has implications for monitoring programs and for management. For example, the recent Delta Cross-Channel studies have shown that the juvenile Chinook migrating past the Cross-Channel in the late fall tend to hold along the edges or the bottom of the channel during the day, and to move out into the main current near the surface at night (B. Herbold, EPA, pers.comm. 2003). Since the main current moves into the Delta Cross-Channel only on the flood tide, keeping the gates closed during flood tides at night should reduce the number of salmon that pass through the Cross-Channel into the Central Delta, where they suffer higher mortality. In the spring, however, migrating juvenile chinook were captured in trawls near the Cross-Channel mainly during the day (C. Hanson, pers.comm. 2003), so the strategy for operating the gates would need to be modified. Similarly, if fish are holding along the channel margins during the day, trying to monitor their passage by trawling in the middle of

the channel during the day is unlikely to be effective. This may be the case for the trawling at Sacramento, which catches very few fish, as discussed below.

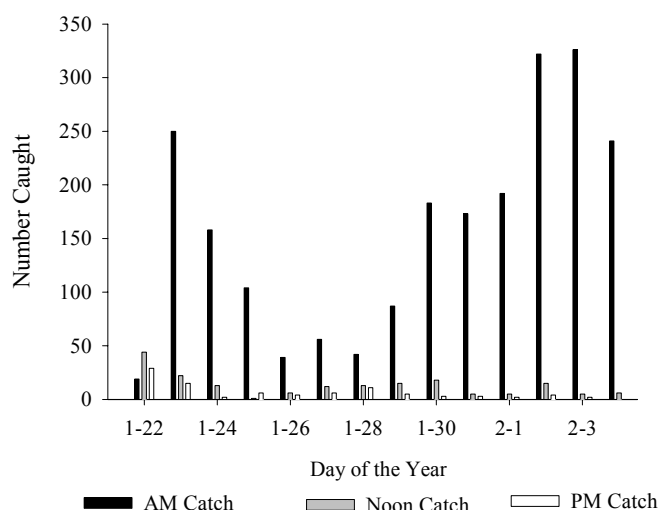
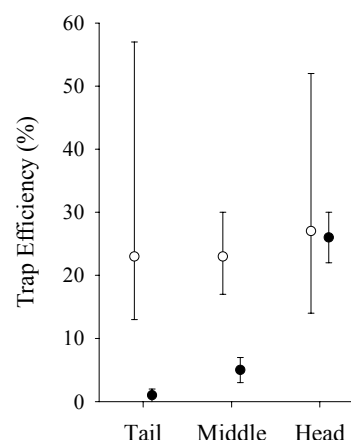


Figure 5-5. The temporal distribution of catches of juvenile Chinook in the Sacramento River in a fyke trap at Balls Ferry in 1899. The trap was checked three times a day, so fish collected in the morning had been captured the night before. Note that the sampling periods are not equal, especially given the long nights in January and February. Data from Rutter (1904).

Diurnal variation in behavior may also affect estimates of trap efficiency. In a study on the South Umpqua River in Oregon, Roper and Scarnecchia (1996) compared the efficiency of a screw trap, measured as the percentage of marked fish that were recaptured, for wild and hatchery young of the year Chinook. The trap was fished in three locations: at the head of a pool below a riffle, in the middle of the pool, and at the tail of the pool. The efficiency of the trap varied strongly among the positions for hatchery Chinook, which moved mainly during the day, but not for wild Chinook, which moved mainly at night. Diver observations indicated that the hatchery Chinook backed down the riffle, and were unable to detect and avoid the trap when it was positioned near the head of the pool. Once in the pool the hatchery fish turned and faced downstream, so that most avoided the trap when it was in the middle of the pool, and almost all did do when it was near the tail. Wild fish, in contrast, traveled mainly at night, and trap efficiencies for them were similar for all three positions (Figure 5-6).

Figure 5-6. Estimated efficiencies for juvenile Chinook salmon of a screw trap in three positions in a pool in the South Umpqua River, Oregon, for fish of hatchery (filled symbols) and wild (open symbols) origin. Bars show 95% confidence intervals. Data from Roper and Scarnecchia (1996).



Traps on the Mokelumne River positioned below the Woodbridge Dam recapture a high proportion of juveniles released into the spillway. However, the recaptures indicate significant differences in trap efficiency between day and night (Figure 5-7) that affect estimates of the percentage of fish passing during those periods (Figure 5-8). Day and night efficiency tests in 2002 exhibited similar differences, but the variation lacked the temporal pattern of 2001. Cramer et al (1992, cited in Roper and Scarnecchia 1996) reported that re-capture rates of hatchery Chinook in the Sacramento River varied from 1.6% when fish were released during the day to 26% when they were released at night.

Figure 5-7. Diel variation in the efficiency of screw traps operated on the Mokelumne River near the Woodbridge Dam in 2001. Turbidity was generally higher but variable through February, and averaged about 3 NTU in April and May. Average fork length increased from about 40 mm through Feb. 23 to nearly 80 mm by April 1. Data from Workman (2002)

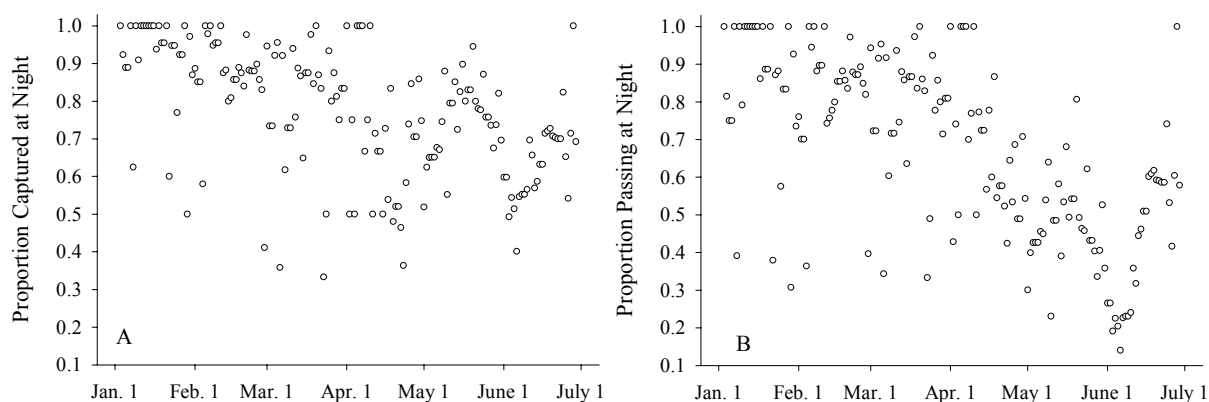
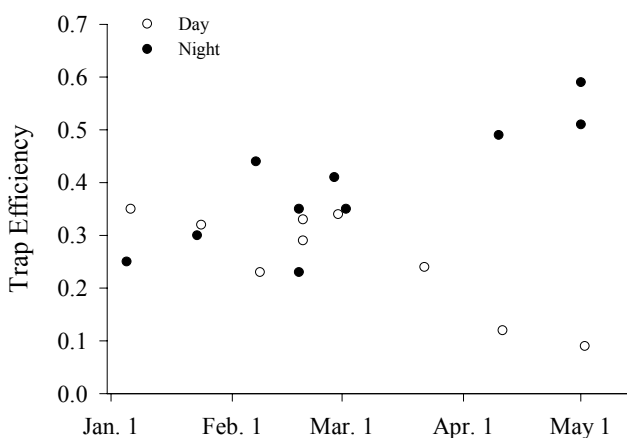


Figure 5-8. The proportion of emigrating young of the year Chinook captured at night in screw traps below Woodbridge Dam on the Mokelumne River in 2002 (a), and the proportions adjusted by estimated trap efficiency (b). Data from M. Workman of EBMUD.

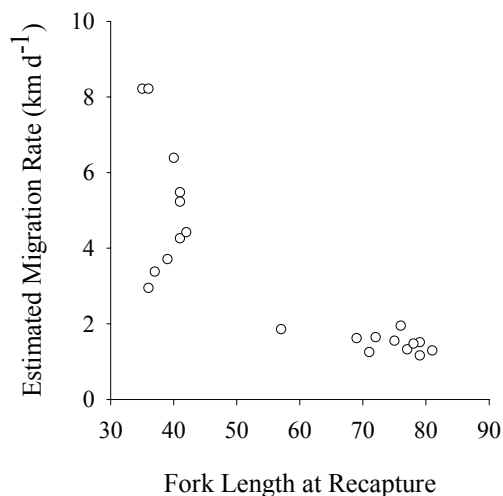
In a summary of his findings, Rutter (1904:100) noted “Much of the time the fry float downstream tail first, and in larger streams they travel more or less in schools.” Others have also reported that juveniles migrate in schools. For example, in a report on trawling conducted from

late April into June, 1988 near the mouth of the American River, Beak Consultants (1988) reported that “During the trawl surveys, tightly schooled groups of fish occasionally were observed traveling downstream and feeding on the surface of the water. Catch data reflect these observations; usually no fish or small groups of 15-30 fish were collected during a standard 10 minute haul.” Monitoring data frequently exhibit this “overdispersion,” with more zero catches and more large catches than would be expected if fish did not travel in schools.

Rate of migration

Probably the first estimate of the rate of migration by juvenile Chinook was by Rutter (1904), who saw that two peaks in the catch of juvenile Chinook at Georgiana Slough in 1899 lagged peaks in the catch at Balls Ferry by 34 days, from which he surmised that on average the fish migrated 16 km d^{-1} , more slowly than the mean current, even if they traveled only at night. However, since fry tend to keep toward the margins of large rivers (Hatton 1940; Healey 1991), they would move downstream more slowly than the water, even if they did not swim against the current. Moffett (1949) described a lag of six weeks between peak catches in fyke nets at Balls Ferry and at Squaw Hill Bridge, about 95 km downstream, suggesting a migration rate of only 2.3 km d^{-1} . Naturally produced fry ($\sim 41 \text{ mm}$) marked by Hallock et al. (1952) near Red Bluff traveled 24 km in as little as 18 hours. In any event, the rate of migration is highly variable. Tagged spring-run fry in Butte Creek that were recaptured in the Sutter Bypass in 2002 fell roughly into two groups: fish that migrated at 3 to 8 km d^{-1} and grew little, and fish that lingered in the lower reaches of the creek or bypass and grew to 70-80 mm (Figure 5-9).

Figure 5-9. Estimated migration rate and length at recapture for 21 wild juvenile spring-run tagged as fry in Butte Creek near Chico in 2002 and recaptured 115 km downstream in the Sutter Bypass. Fish were batch marked with coded-wire tags, but tag codes were used for only 3 d, so the estimates of migration rate are fairly good. Data from Ward et al. (2003).



In the Rogue River, fingerling ($>70 \text{ mm}$) wild spring-run Chinook generally averaged $< 5 \text{ km d}^{-1}$ early in their migration, but later picked up the pace to average $10\text{-}15 \text{ km d}^{-1}$ (Ewing et al. 2001). Migration rates for individuals in the Rogue River ranged from 6 to 24 km d^{-1} (Cramer and Lichatowich 1978 cited in Healey 1991).

Many more data are available on the migration rate of hatchery fish than of naturally produced fish. Most tagged fall-run hatchery juveniles (mean length 57 mm at release) moved slowly ($\sim 1 \text{ km d}^{-1}$) through the Yolo Bypass (Sommer et al. 2005), but some moved as rapidly as

11 km d⁻¹. Some tagged hatchery fry released near the RBDD were recaptured in the Delta in as little as 11 d (Kjelson et al 1982), implying a migration rate over 30 km d⁻¹. The migration rate of larger juvenile fall-run released from Coleman Hatchery and recaptured at Chipps Island averaged about 32 km d⁻¹ over four years. Releases were distributed over almost two months in 1998, and in that year migration rate increased both with release date and with fish size at release (Figure 5-10). The median migration rate to Chipps Island of late fall Chinook released from Coleman Hatchery was about 25 km d⁻¹ over four years, but there was considerable variation among years and even more among batches (Figure 5-11).

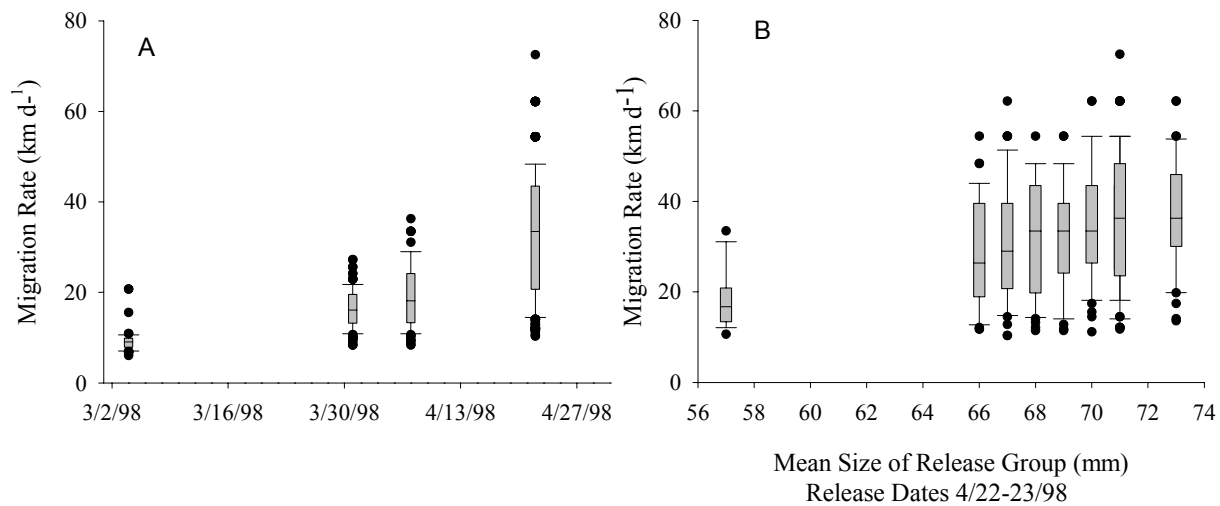


Figure 5-10. Migration rate of juvenile fall Chinook released from Coleman Hatchery and recaptured at Chipps Island. A. Migration rate by release date; juveniles released later in the year migrated more rapidly. B. Migration rate by estimated mean size of release group for fish released on April 22 or 23, 1998. Fish released on 4/22/98 with a mean length of 57 mm were about the same size as fish released on 3/2/98, but migrated more rapidly.

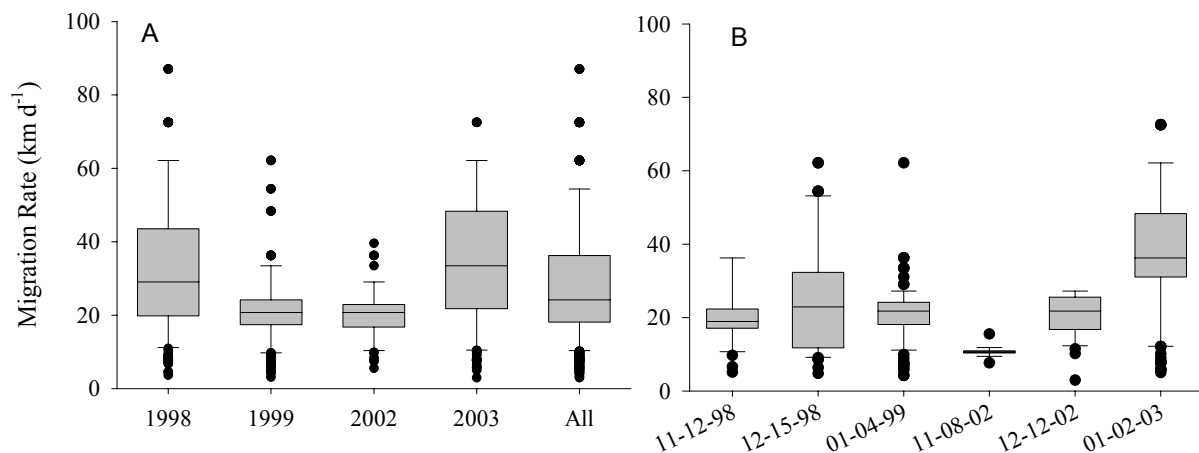
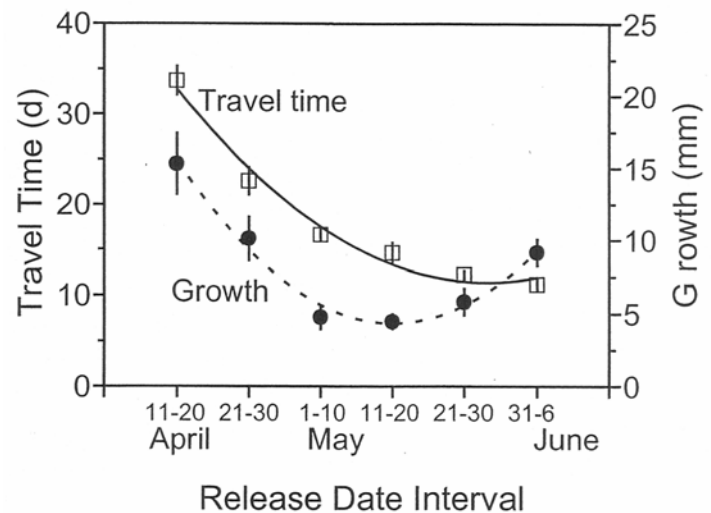


Figure 5-11. A. Migration rate of juvenile late fall Chinook released at Coleman Hatchery and recaptured at Chipps Island in four years. B. Migration rate of six batches of late fall Chinook released at Coleman Hatchery and recaptured at Chipps Island. Data from USFWS.

The most detailed information on migration rates comes from fish in the Columbia River that are individually marked with passive integrated transponder (PIT) tags that are detected when fish move through passage facilities on the dams. Rates for individual Chinook, sockeye, and steelhead between Rock Island and McNary dams were all highly variable (Giorgi et al. 1997). For age 0 Chinook, the average migration rate over four years was 15.5 km d^{-1} , but increased with size from about 5 km d^{-1} on average at 60 mm to about 30 km d^{-1} on average at 140 mm. Migration rates varied directly with flow and inversely with temperature and day of the year, but not as strongly as with length. For yearling Chinook, the average migration rate was about 20 km d^{-1} , and was independent of length but increased somewhat with temperature, mean flow, and day of the year. Time of year had a strong effect on the migration rate of naturally produced yearling Chinook from the Snake River (Congleton et al. 2004).

Figure 5-12. Migration and growth rates for naturally produced yearling Chinook salmon between Lower Granite Dam on the Snake River and Bonneville Dam on the Columbia in 2002; bars show standard errors. The dams are 461 km apart, so 20 d travel time = 23 km d^{-1} . Copied from Congleton et al. 2004.



The association between migration rate and environmental factors differed somewhat for wild and hatchery steelhead in the Columbia River (Giorgi et al. 1997). For naturally produced steelhead in the Columbia River, the average migration rate decreased with fish length, increased with mean temperature and flow, and was independent of the day of the year. The migration rate of hatchery steelhead in the Columbia River decreased more strongly with length than for wild steelhead, and also increased with day of the year, as well as with mean flow and temperature. Overall, steelhead had a mean migration rate of 30.4 km d^{-1} ($\text{SD} = 10.9 \text{ km d}^{-1}$).

There seems to be little published information on the migration rates of steelhead in the Central Valley. Hallock et al. (1961:16) noted that "... hatchery reared steelhead of a size larger than 10 to the pound [$>45 \text{ g}$] usually move downstream rapidly," and that "... fish averaging seven to the pound [65 g] released in Mill Creek, about one mile [1.6 km] above its confluence with the Sacramento, ... within an hour were spilling over a shallow bar into the Sacramento River."

Timing of juvenile Chinook migrations in the Central Valley

The timing of the juvenile migration by the various runs of Chinook in the Sacramento River is less discrete than is suggested by the size-at-date criteria currently used to assign fish to runs (Johnson et al. 1992; Greene 1992). The authority usually cited on the timing of the migration by the various runs in the Sacramento River is Vogel and Marine (1991), which is based largely on unpublished data from CDFG, on Vogel et al. (1989), and on the size distributions of juvenile Chinook samples with seines by USFWS (Figure 5-13). The source of the size criteria for the different runs shown in Figure 5-13 is not cited, but probably was then unpublished work by Fisher (1992). As with the more recent sampling at Red Bluff Diversion Dam (RBDD; Figure 5-14), the sampled fish do not fall neatly within the criteria. As a further complication, the seine sampling was probably biased toward smaller fish (Vogel and Marine 1991).

The current timing of migration and size of the migrants in the upper Sacramento River is best illustrated by data from screw traps operated in fast water just downstream of the RBDD, which presumably are more representative of the fish passing the dam than were the USFWS seine data. The traps capture juvenile Chinook, including newly emerged fry, at all times of the year (Figure 5-14). The lengths of commonly captured juveniles vary from about 30 to 120 mm, but juveniles as large as 250-300 mm are occasionally taken.

The criteria currently used to assign juvenile Chinook to runs based on their size at date, given by Johnson et al. (1992), are shown in Figure 5-14. Although the size data clearly do not fit neatly into the categories, they do seem usefully accurate for winter-run at the RBDD. Of 62 fish using non-natal habitat in Mud Creek, a small tributary near Chico, genetic testing showed that the size criteria gave 3 false positives and 43 correct assignments for fish within the winter-run size category, and 2 false positives and 14 correct assignments for fish just outside the size category (Maslin et al. 1998). However, as shown below, there is considerable overlap between winter-run and spring-run, so the rate of false positives for winter-run will increase if significant populations of spring-run become established in Clear Creek and Battle Creek upstream from the RBDD. In general, then, even in the upper Sacramento River there is some uncertainty about the timing of the migration for the different runs and about the size of the migrants within the runs, and the uncertainty increases downstream. Genetic analyses of tissue samples taken from fish collected in the screw traps at the RBDD and at other downstream locations should clarify the temporal distribution of migration for the different runs of Chinook, but as discussed below there is enough overlap between runs and year to year variation within runs that size-at-date criteria have limited utility for assigning individual fish to runs in the lower river.

Although some juveniles pass the RBDD in all months, most pass from December through March, with a smaller pulse passing in August and September (Figure 5-15). This is a somewhat broader temporal distribution than that indicated by fyke trapping at Balls Ferry, about 50 km upstream from Red Bluff, in 1889 (Figure 5-16), when the migration of newly emerged fry did not begin until mid-January, and catches in the fyke trap dropped off sharply in late March. However, the average size of the fish captured in 1899 increased very little through March, and few fish >50 mm were captured (Rutter 1904), which suggests that the fyke trap was not

effective for capturing larger fish. This has been confirmed in other studies. Hallock et al. (1952:311) observed that a fyke trap set in “only moderately fast water to insure a live catch” was ineffective in catching larger fish: “Numerous salmon up to five or six inches in length could be observed feeding around the nets in the every morning and evening, yet these fish never appeared in the catches.”

Figure 5-14. Size at day of capture of (A) unmarked juvenile Chinook < 180 mm, and (B) marked hatchery Chinook < 200 mm fork length, sampled from screw traps at the Red Bluff Diversion Dam from July 1994 through June 2000. Note that a few fish are too large to display on this graph, and that multiple fish of the same size captured on the same day of the year are represented by a single point. Some of the unmarked fish are hatchery fall-run, presumably of the same size as the smaller fish in March-June in (B); but because naturally produced fall-run are abundant these unmarked hatchery fish probably do not affect the appearance of the figure. The curves show the criteria commonly used to assign fish to runs. Some hatchery fall-run and winter run fall into the spring-run size category. Note that the scales on the vertical axes are offset by 20 mm to accommodate the larger size of hatchery fish. Data from Phillip Gaines, CDFG, Red Bluff.

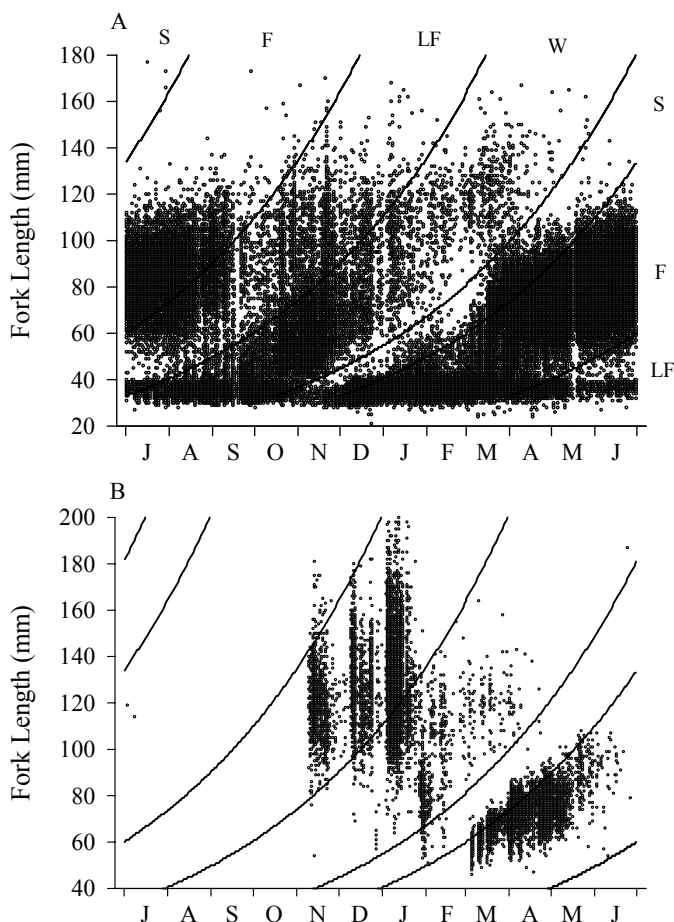
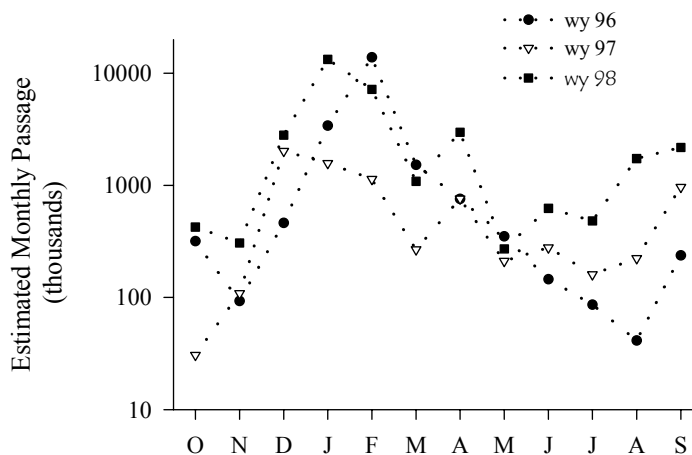


Figure 5-15. Estimated number of juvenile chinook of all runs passing the Red Bluff Diversion Dam in water years 1996, 1997, and 1998. Year-to-year and seasonal variation is high (note log scale). Data from Gaines and Martin (2002).



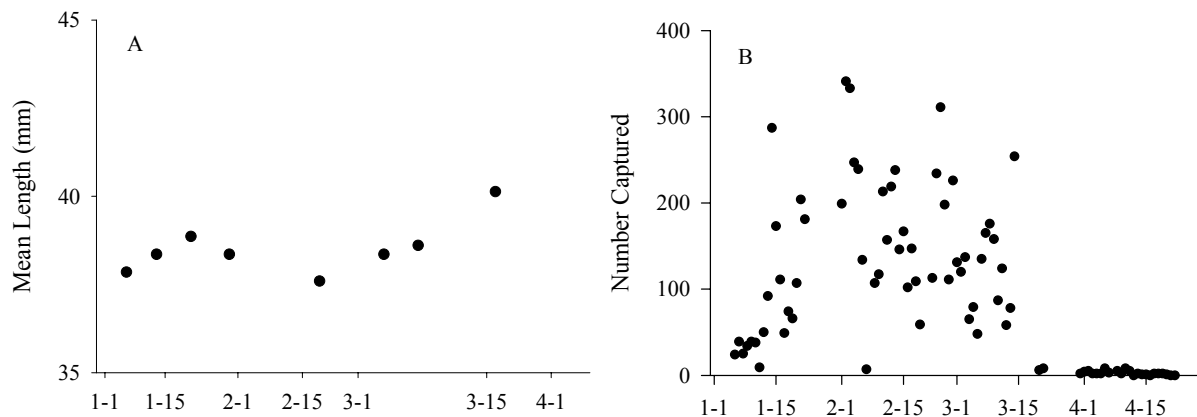


Figure 5-16. The average length (a) and number (b) of juvenile Chinook captured in a fyke net in the Sacramento River at Balls Ferry in 1899, reported by Rutter (1904). Lengths (whether fork or total not specified) were measured only occasionally.

Additional fyke trapping at Balls Ferry was conducted by USFWS shortly after the closure of Shasta Dam; according to Hallock and Van Woert (1959:235):

... Salmon migration studies by the United States Fish and Wildlife Service in the Sacramento River at Balls Ferry, including 10 seasons of fyke netting between 1944 and 1953, show a measurable downstream movement between early October and the latter part of May in most years. The majority of the young salmon, however, migrate between early December and late April. The peak of the downstream movement varies from year to year; it may occur in late December, as in 1946, or even in late February, as in 1952. More often than not, however, two or even three peaks are evident between January and early March. Results of the 1944-1953 salmon migration studies at Balls Ferry are in agreement with the findings of studies made near the same location in 1899 (Rutter, 1903²³).

The fyke traps were operated only from October through May, however, so fish passing in other months were not detected, and again the average size of the fish collected in the fyke traps seems rather small in the spring months (Figure 5-17).

²³ This is the same as Rutter (1904), which is cited differently by different authors; arguably it could be 1902, 1903, or 1904. Most authors use 1904, however, and I have followed their example.

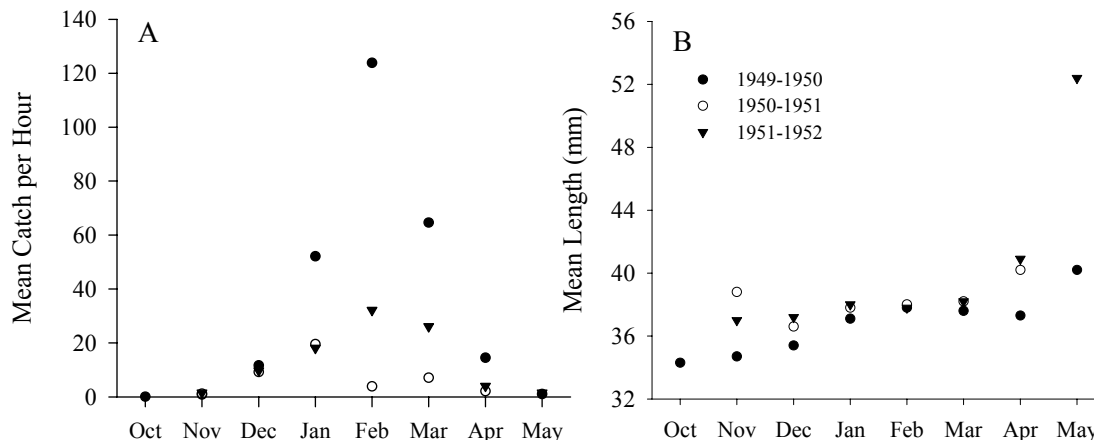


Figure 5-17 The catch per hour (A) and mean length (B) of juvenile Chinook captured in a fyke net operated on the Sacramento River at Balls Ferry, upstream from Red Bluff, for three years. The small average size of juveniles in April and May suggests that the net was not effective at capturing larger fish. Data from Azevedo and Parkhurst (undated).

Fall chinook migration

In the Sacramento River and its tributaries, most fall-run juveniles migrate toward the Delta from December through March as fry. For example, there was very little change in the size of the migrants leaving the American River from December through mid-March of 2000, when most migrants passed the trap (Figures 5-18); the size increased from mid-March to early-May, and then stabilized at ~0.1 fish per hour until June when the catch dropped to almost zero. The pattern at the RBDD is similar (Gaines and Martin 2002), except that larger (60-110 mm) migrants pass the dam from March into September. The American River is warmer in the summer than the upper Sacramento River, which probably accounts for this difference.

Juvenile Chinook migrating out of the spawning reaches of the American and Mokelumne rivers move directly into low gradient, tidally affected reaches of the rivers; that is, into the outer edge of the Delta. Fish migrating from farther north or south in the valley have a longer migration through the valley lowlands, but reach the Delta in patterns similar to but somewhat less distinct than migration from the nearby spawning areas. As discussed below, these data also include juvenile spring-run, most of which follow an ocean-type life history pattern like that of the fall-run. The pattern of migration into the Delta was established at the end of the nineteenth century by monitoring at Georgiana Slough, a distributary that conveys water from the Sacramento River toward the central Delta (Figure 5-19): the catch rate peaked in March when fish were mainly < 50 mm, and the size of the fish captured increased rapidly during April. The water was turbid with sediment from mining debris coming down the Feather and American rivers, and it seems likely that these data were less affected by trap avoidance than the early monitoring at Balls Ferry (Figures 5-16), where the water was clear.

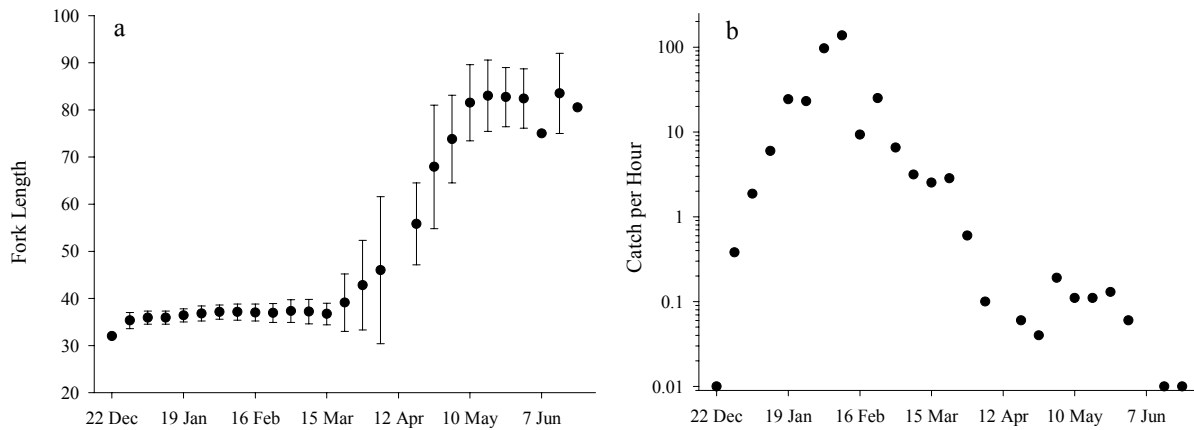


Figure 5-18. Mean length (a) and catch per hour (b) of juvenile Chinook salmon sampled in screw traps in 1999-2000 on the lower American River near the downstream limit of spawning habitat. Error bars show standard deviations. Note log scale in (b); the catch dropped sharply as size increased in March. Dates are approximately the middle of the sampling period. Data from Snider and Titus 2002.

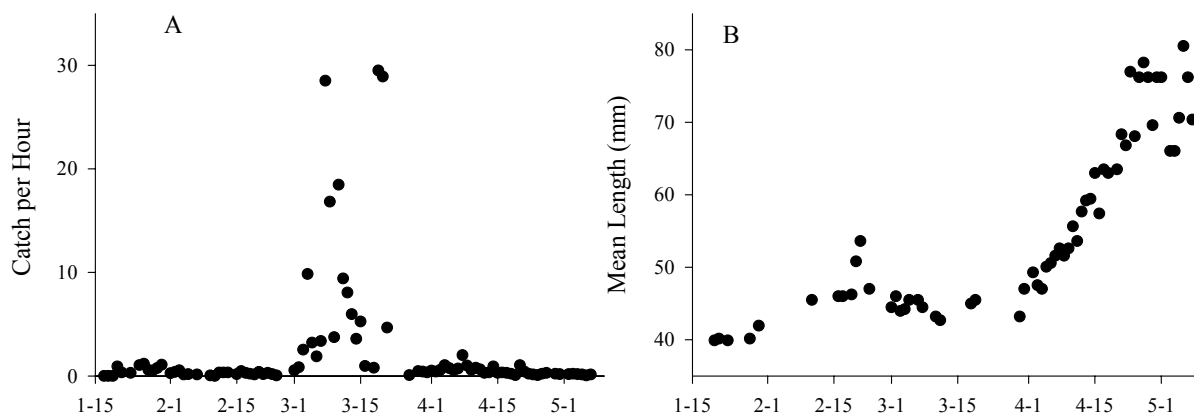


Figure 5-19. Juvenile Chinook sampled in 1899 in Georgiana Slough near Walnut Grove on the Sacramento River, with a 1.0 m (4 ft) diameter hoop net with 6.2 (20 ft) m wings. A: catch per hour. B: mean length. Data from Rutter (1904); length measurement not specified.

The same timing of migration in the Sacramento River was reported by Hatton and Clark (1942), from monitoring conducted with fyke traps at Hood (rkm 62) in 1939-1941, just before closure of Shasta Dam (Figure 5-20). In 1940 and 1941 the size of the migrants increased rapidly

through April, as it did in 1889 data. Curiously, however, migrants in April 1939 were unusually small, and no fish were captured after mid-May.

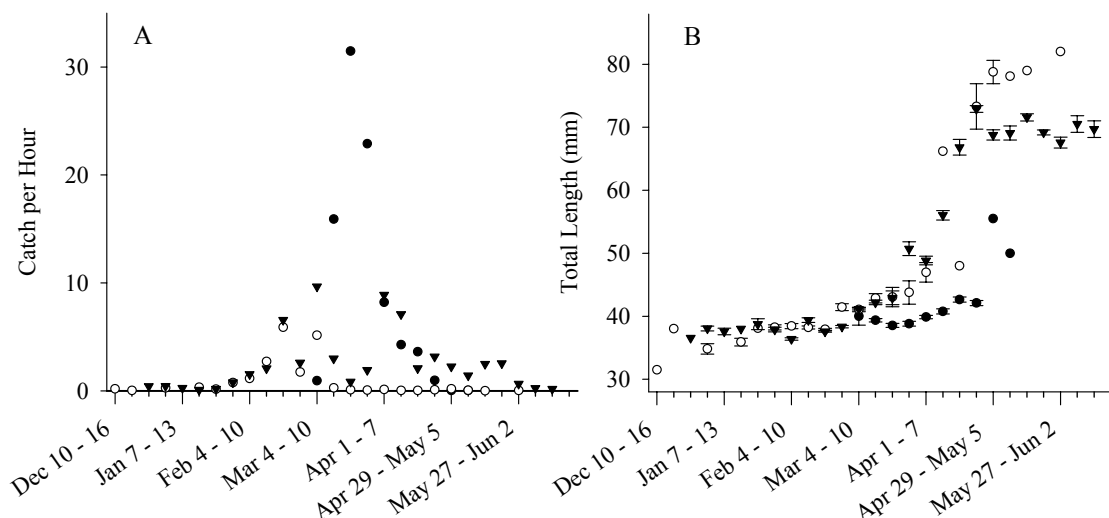


Figure 5-20. Catch per hour (A) and total length (B) of juvenile Chinook entering the Delta from the Sacramento River at Hood in 1939 (filled circles), 1940 (open circles), and 1941 (filled triangles). Bars show standard errors; symbols without bars represent <10 fish. The gear used was a fyke net with a 152 cm (5 ft) circular opening. Data from Hatton and Clark (1942).

Erkkila et al. (1950) operated fyke traps in the lower Sacramento River in 1947 and 1948, and reported that catches peaked in March in both years. There were significant catches in February 1947, but not in 1948, which Erkkila et al. (1950) attributed to low flow until late March in 1948. Based on tow-net data, migration into the Delta from the Sacramento River peaked at the beginning of March in 1949, as in Hatton and Clark’s 1939 data, when most of the fish were 35-45 mm fork length.

In more recent monitoring with screw traps at Knights Landing (RK 145), the catch rate of naturally produced Chinook peaked earlier in the year, in January or February (Figure 5-21); later peaks in the catch rate follow releases from Coleman National Fish Hatchery (Snider and Titus 2000a, b, c). This difference in timing seems too great to attribute to the time needed to travel the 80 km between the sampling sites. The shift in timing probably is due to the changed temperature regimes in the Sacramento and Feather rivers, where the thermal inertia of Shasta and Oroville reservoirs keeps temperatures higher in the winter than was formerly the case. In the Sacramento River, this “...unquestionably accelerated the development of eggs and advanced the time of migration seaward” (Moffett 1949:98). Earlier migration is not apparent in the Erkkila et al. (1950) data, but the late migration in 1947-49 may reflect the drought of the time. Early hatchery practice, which disproportionally spawned early-arriving fish, may also be partly responsible. The significance of this change in migration timing is unknown.

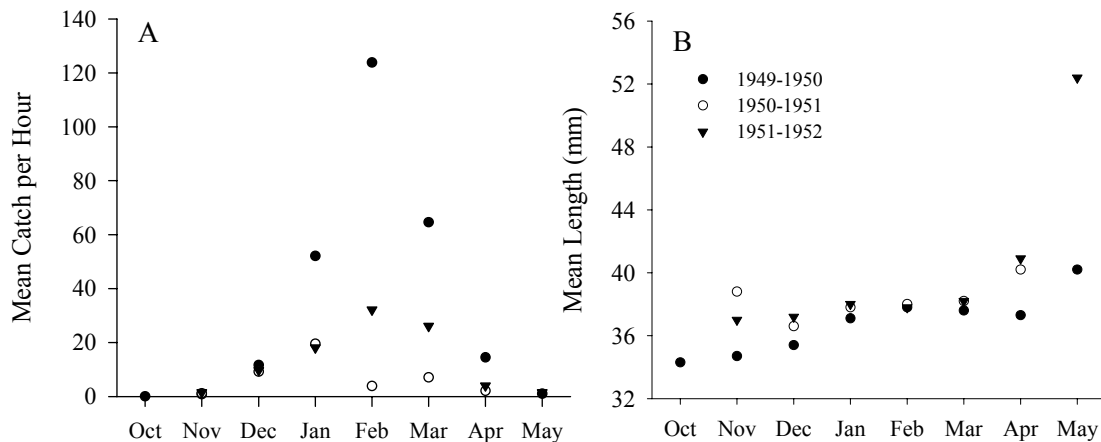
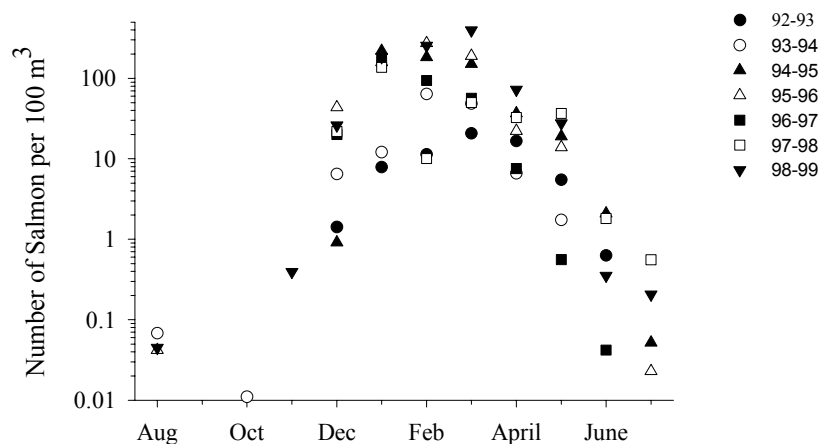


Figure 5-21. Catch per hour (A) and mean fork length (B) of juvenile Chinook captured with a rotary screw trap at Knights Landing, about 80 km upstream from Hood, in water years 1997 (block symbols), 1998 (grey symbols), and 1999 (open symbols). Data from Snider and Titus (2000a, b, c).

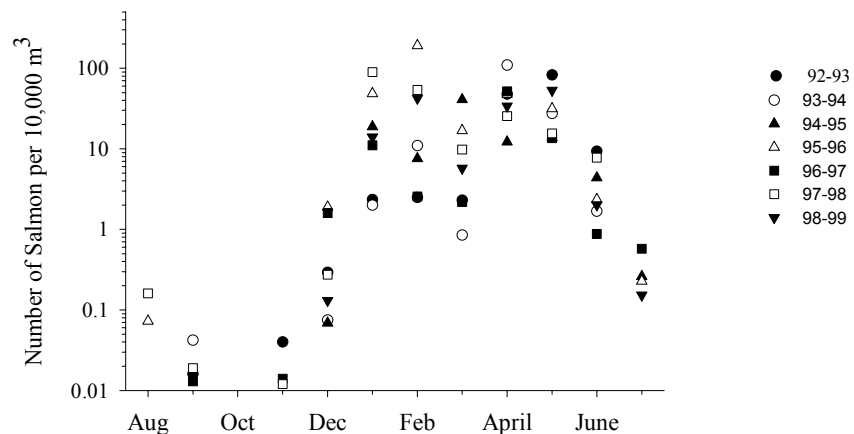
A shift toward earlier arrival at the Delta is also suggested by monitoring in the lower Sacramento River with beach seines, reported in SSJEFRO (2003). Monthly mean catches in beach seines at seven sites on the lower Sacramento from Colusa (RK 231) downstream to Elkhorn (rkm 114) peak from January to March, and vary from year to year by over an order of magnitude (Figure 5-22). As discussed below, the migration timing of spring-run overlaps that of the fall-run in the Central Valley to an extent that SSJEFRO (2003) does not try to separate them, but the overwhelming majority of the migrants are fall-run. Only one seine haul is made at each site every week, so a good deal of the variation probably reflects sampling uncertainty as well as actual variation in the density of fish. However, the general seasonal pattern in the catches of spring/fall-run juveniles seems clear.

Figure 5-22. Juvenile spring/fall Chinook in the lower Sacramento River: monthly average catch in beach seine monitoring: Data from Table 3 in SSJEFRO (2003)



Juvenile salmon are also sampled at Sacramento with trawls fished in the middle of the channel. Both Kodiak and mid-water trawls are now used, depending on the time of year. The timing of the peak trawl catch is highly variable, ranging from January to May (Figure 5-23), and catches are particularly variable for January-March. Note that the units on the vertical axes of graphs showing trawl data are catch per 10,000 m³, rather than per 100 m³ as in the graphs showing seine data. The indication from the Delta Cross-Channel studies, mentioned above, that during the winter larger juvenile Chinook in the lower Sacramento River migrate mainly at night, raises questions about the utility of this sampling for larger juveniles in the winter. For four of the seven years shown, catches peaked in April or May, which strongly suggests that the trawls are not effective for capturing fry migrants.

Figure 5-23. Juvenile spring/fall Chinook at Sacramento: monthly average catch in mid-water or Kodiak trawls. Data from Table 11 in SSJEFRO (2003); averages are shown for months for which catch for both types of trawl was reported.



In the San Joaquin River in 1940 and 1941, the migration of juvenile Chinook into the Delta also peaked in February or March, when the fish were still < 50 mm (Figure 5-24). However, Erkkila et al. (1950) reported that juvenile Chinook from the San Joaquin River first appeared in the Delta in early April, and at > 60 mm fork length. More recent seine catches on the lower San Joaquin River were more similar to Hatton and Clark's (1942) data (Figure 5-25), but the data are extremely variable and catches of zero are reported for each month in at least one of the six years shown. SSJEFRO (2003) also reports data from trawling at Mossdale for 1995-1999 (not shown); catches are low (<10 per 10,000 m³), with no obvious trend between January and May.

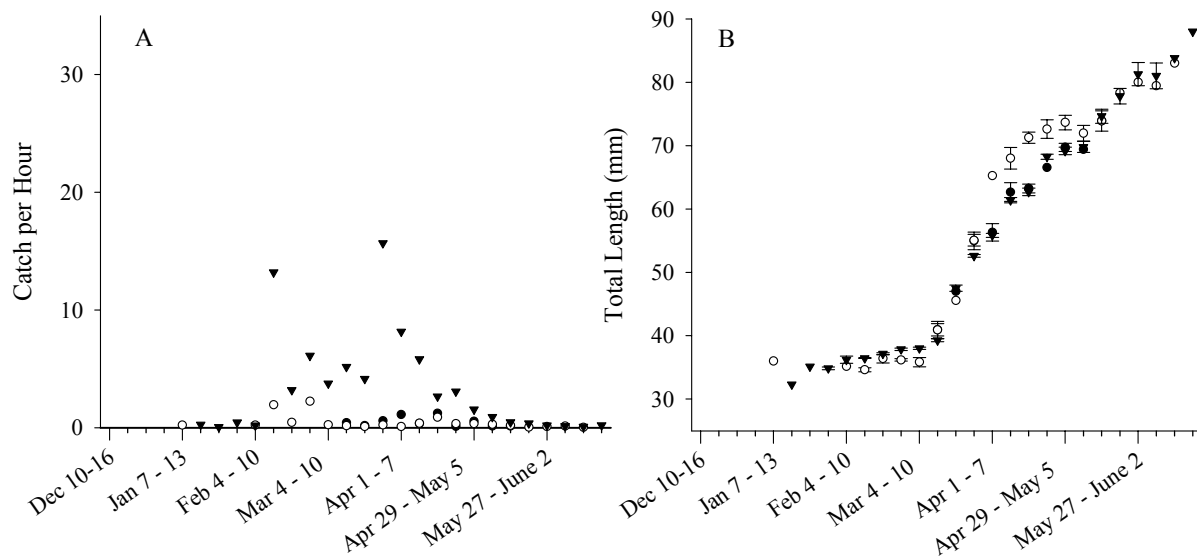
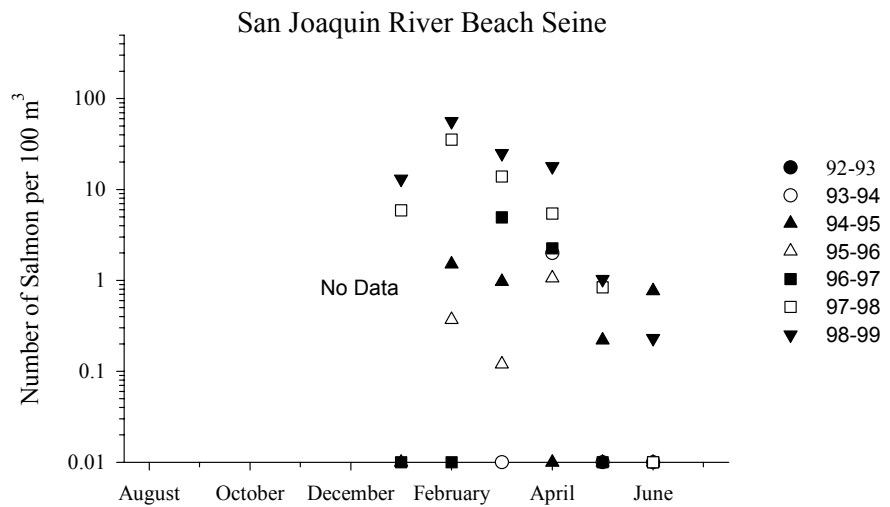


Figure 5-24. Juvenile Chinook in the San Joaquin River at Mossdale: catch per hour (A) and total length (B) of juvenile Chinook entering the Delta, 1940 (open circles), and 1941 (filled triangles). Bars show standard errors, symbols without bars represent <10 fish. Data from Hatton and Clark (1942). Symbols as in Figure 5-22.

Figure 5-25. Juvenile Chinook in the San Joaquin River: mean monthly catch in beach seines at 10 sites on the lower river. Catches of zero are shown as 0.01. Data from Table 8 in SSJEFRO (2003).



In the Mokelumne River and in San Joaquin River tributaries a higher proportion of juvenile fall Chinook, even a majority in some cases, rears in the river for some time before migrating, unlike the fish in the Sacramento system (Figures 5-26:5-27). The reason for the difference in the proportion of fry migrants among fall Chinook in the two systems is unknown, but apparently is not new; a discussion of San Joaquin River Chinook in Hallock and Von Woert (1959) suggests that few San Joaquin River fall-run migrated as fry at that time. This may vary from year to year,

however (Figure 5-26B). On the Mokelumne River, Chinook migrate mainly as fry in wetter years, and mainly as larger juveniles in drier years such as 2002 (M. Workman, EBMUD, pers.comm. 2004; Figure 5-27).

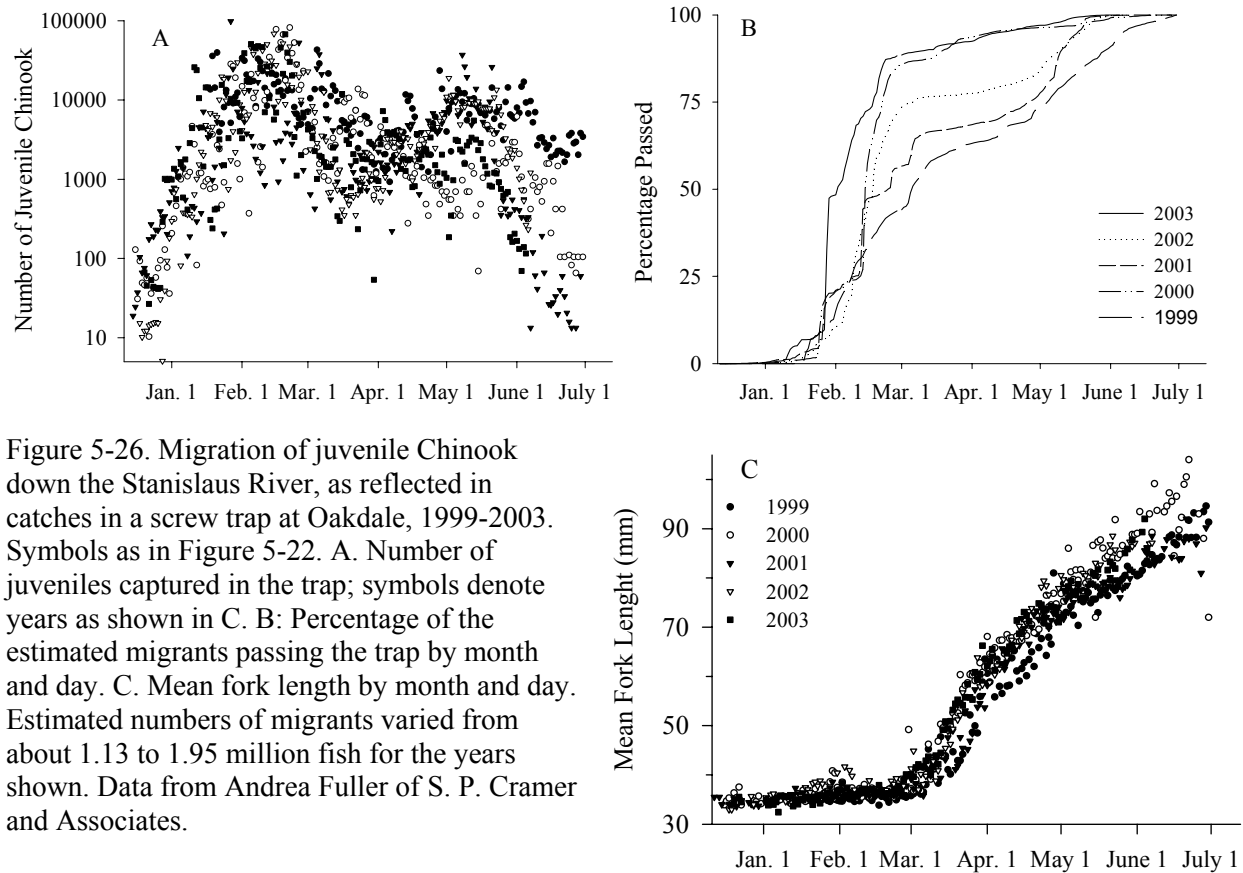
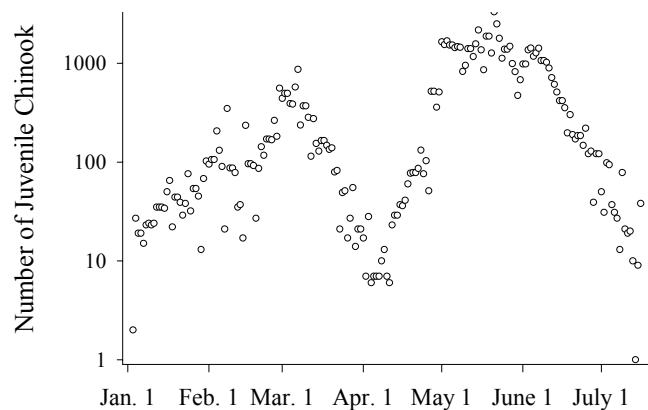


Figure 5-26. Migration of juvenile Chinook down the Stanislaus River, as reflected in catches in a screw trap at Oakdale, 1999-2003. Symbols as in Figure 5-22. A. Number of juveniles captured in the trap; symbols denote years as shown in C. B. Percentage of the estimated migrants passing the trap by month and day. C. Mean fork length by month and day. Estimated numbers of migrants varied from about 1.13 to 1.95 million fish for the years shown. Data from Andrea Fuller of S. P. Cramer and Associates.

Figure 5-27. Juvenile Chinook in the Mokelumne River: estimated numbers passing Woodbridge Dam on the lower Mokelumne River in 2002, based on captures in two screw traps fished side by side. Data from M. Workman of EBMUD.



Juvenile Chinook leaving the Delta are monitored by trawling at Chipps Island, the seaward margin of the Delta; Brandes and McLain (2001) give details on the sampling. The mean monthly catch of nominal fall/spring-run peaks in April or May, but smaller juveniles are captured in February and March, especially in wet years (Figures 5-28, 5-29).

Figure 5-28. Juvenile Chinook leaving the Delta: mean monthly catches of fall/spring-run size juvenile chinook in the midwater trawl at Chipps Island. Data from SSJEFRO (2003).

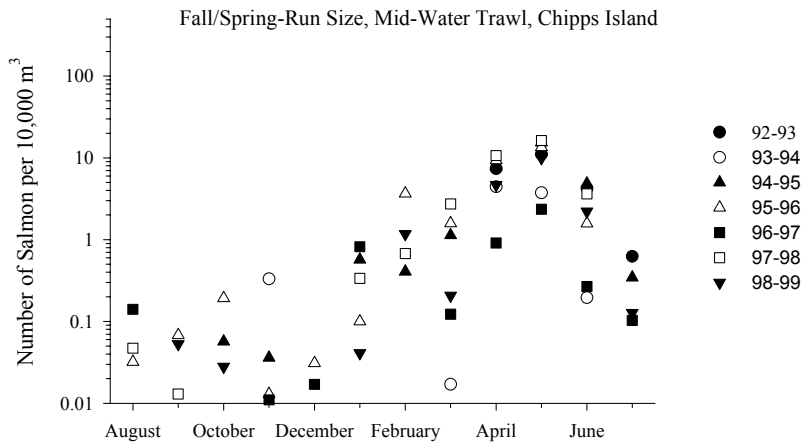
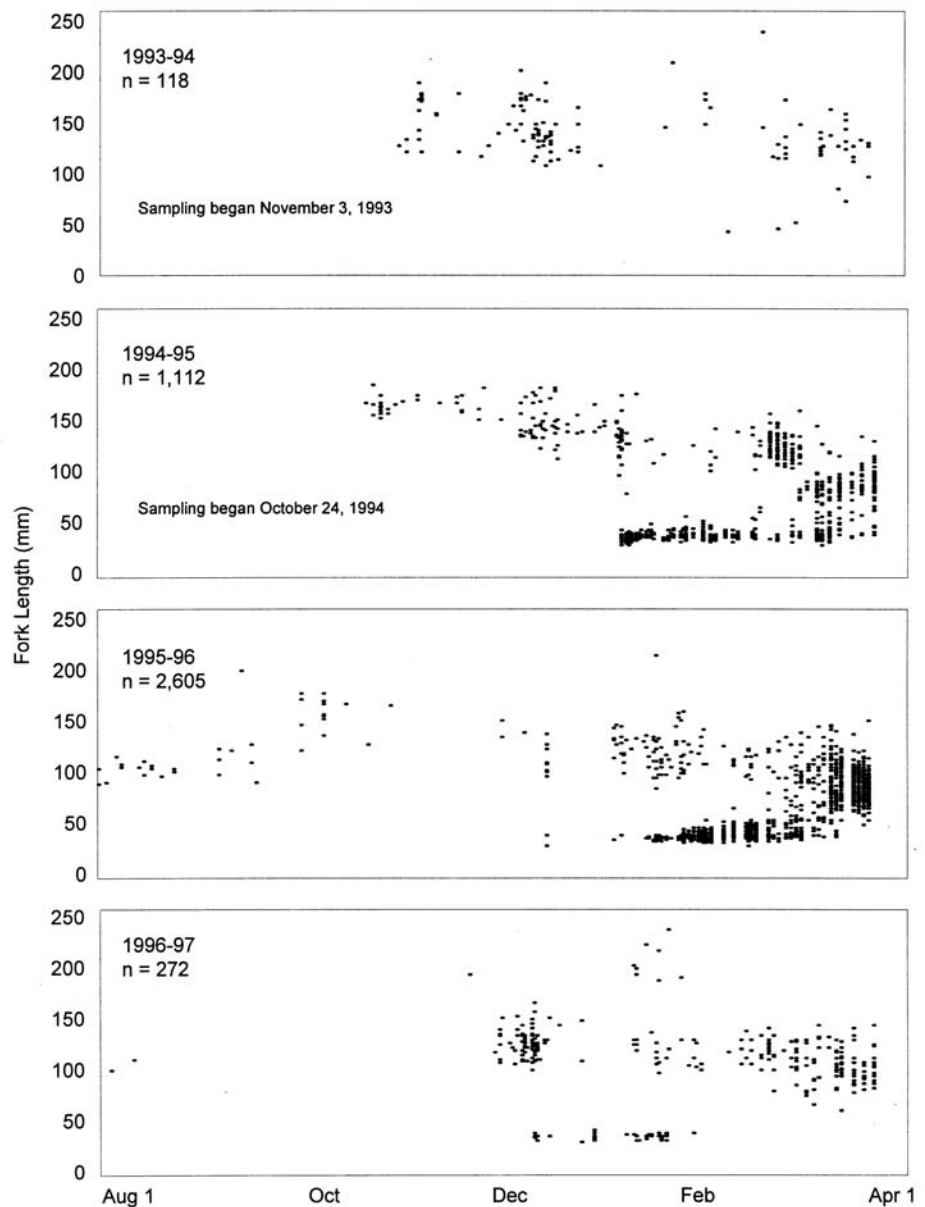


Figure 5-29. Size at date of juvenile Chinook salmon captured in the midwater trawl at Chipps Island between August 1 and March 31. As with Figure 5-14, multiple fish of the same length may be represented by a single dot. Small (<50 mm) Chinook are captured in January through March, especially in wet years such as 1995 and 1996. Copied from Brandes and McLain (2001).



Catches in the Chipps Island trawl peak two to four months later than in the lower Sacramento River beach seine data (Figure 5-22), and two to three months later than in the Delta seine data. There are three possible explanations for this, all of which may be partially correct: (1) most of the early arrivals to the Delta perish there, and most of the fish sampled at Chipps Island reared longer in the upper rivers and passed rapidly through the Delta, (2) juvenile spring and fall-run rear for some time in the lower river and in the Delta before moving into the bays, or (3) the Chipps Island trawl does not capture smaller fish effectively, so that more fish are leaving the Delta from February to early April than the data indicate. Wherever they rear, the age of chinook sampled at Chipps Island in late spring over five years has consistently averaged about 135 days from hatching, based on otoliths (B. MacFarlane, NMFS, pers.comm. 2003).

Early sampling at Martinez, between Suisun and San Pablo bays, supports the hypotheses that more small juveniles leave the Delta than the trawling suggests. Sampling with fyke nets in 1939 and 1940 at Martinez captured mainly small (~40 mm) Chinook in March and early April (Hatton and Clark 1942; Figure 5-30). The peak weekly catch rate in 1939, a dry year, was $\sim 10 \text{ h}^{-1}$, compared to over 30 h^{-1} at Hood (Figure 5-20). However, few fish were captured in 1940, a wet year.

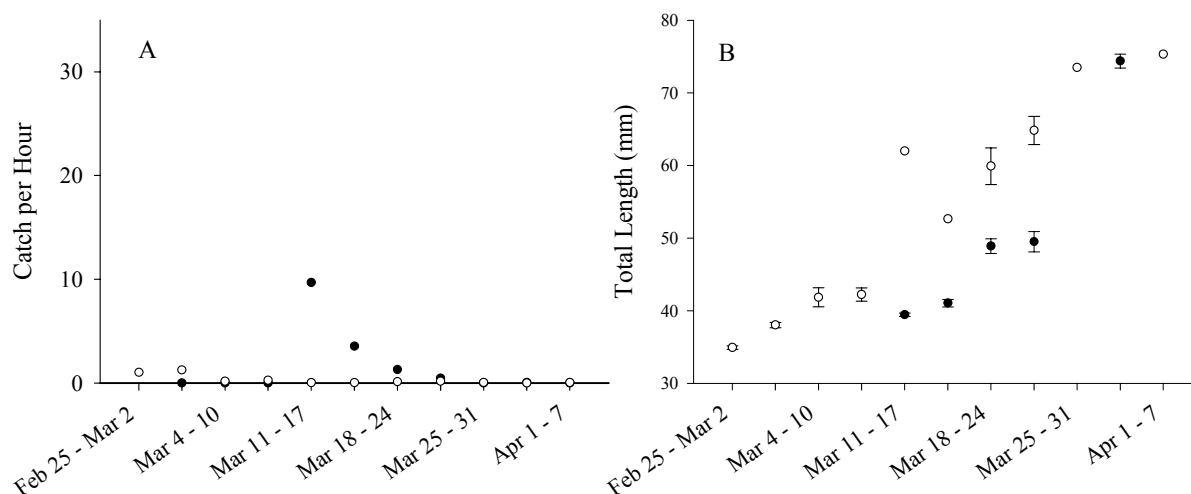


Figure 5-30. Juvenile Chinook sampled in fyke nets at Martinez in 1939 (filled circles) and 1940 (open circles). A: Catch per hour, same scale as Fig. 5-19; B: total length; error bars show standard errors, symbols without bars represent <10 fish. Data from Hatton and Clark (1942).

Few juvenile Chinook are captured in the bays. From 1981 to 1986, and since 1997, juvenile chinook have been sampled with seines at 10 stations around San Pablo and San Francisco bays from January through March. The density of fry at these sites averages about 1.3 per 100 m^3 , well over an order of magnitude lower than in the Delta (SSJEFRO 2003). The area of potential habitat around the margins of the bays is large, however. Few chinook are collected by the IEP at

mid-water trawl stations in the western Delta and throughout the bay; the average catch for 1980-1995 was only 124 fish per year (Orsi 1999).

Based on the mean age of samples collected between Chipps Island and the Gulf of the Farallones from April into June, 1995, juvenile Chinook migrated through Suisun, San Pablo, and San Francisco bays at an average rate of 1.6 km d⁻¹ (MacFarlane and Norton 2002). However, migration rates calculated for tagged fish, based on the time and distance between release and recapture, were all higher than the estimated mean for all fish collected. Data from other years are now being processed, and may clarify the migration rate. Hatchery and wild fish can be distinguished from the microstructure of their otoliths (Zhang et al 1994; R. Barnett-Johnson, NOAA Fisheries, pers.comm. 2005), and it would be useful to compare the average migration rates for the two groups. Temporal variation in migration rate, shown for Chinook in the Columbia River (Figure 5-12), should also be investigated.

Spring Chinook migration

High variability characterizes the timing of migration and size of migrants in the Sacramento River tributaries that still support independent populations²⁴ of spring-run: Mill, Deer, and Butte creeks (Figures 5-31; 5-32). Most juveniles migrate downstream as newly emerged fry, especially in Butte Creek, but some migrate as larger parr from March through June, and others hold over through the summer and migrate in fall or winter; only a few hold over until the following spring. As noted above, there is great overlap in size between the spring-run and fall-run, and there is also considerable overlap between spring-run and winter-run. These data demonstrate the problem with using size at date criteria to assign fish to runs.

The finding that most spring-run from Mill, Deer, and Butte creeks emigrate in their first year contradicts many statements in the literature (e.g., Moyle 2002), which seem to assume that Central Valley spring-run follow a typical stream-type life history pattern. However, several lines of evidence suggest that an ocean-type life history pattern was typical for Central Valley spring-run through the twentieth century, although the stream-type life history pattern may have been more common before higher altitude habitat in the San Joaquin system was blocked by early dams. First, Clark (1928) classified only 13% and 9% of his 1919 and 1921 samples from the Delta gill-net fishery as stream-type, based on the growth patterns on scales. Unless spring-run made up only 20% or less of the catch, this indicates that stream-type fish were a minority among returning spring-run. An even smaller minority of emigrating fish would have been stream-type, since older juveniles presumably survived better than younger ones. Clark did not say when his sample was collected, but did report that the season was closed for most (1919) or all (1921) of June and from Sept. 25 to Nov 14, so presumably fishing occurred around the closed periods and the catch includes both spring and fall Chinook. Second, biologists familiar with Central Valley spring-run apparently thought that spring-run migrated mainly in

²⁴ The populations of spring-run in Mill, Deer and Butte creeks are independent in the sense used in ESA recovery planning for Pacific salmon (Lindley et al. 2004).

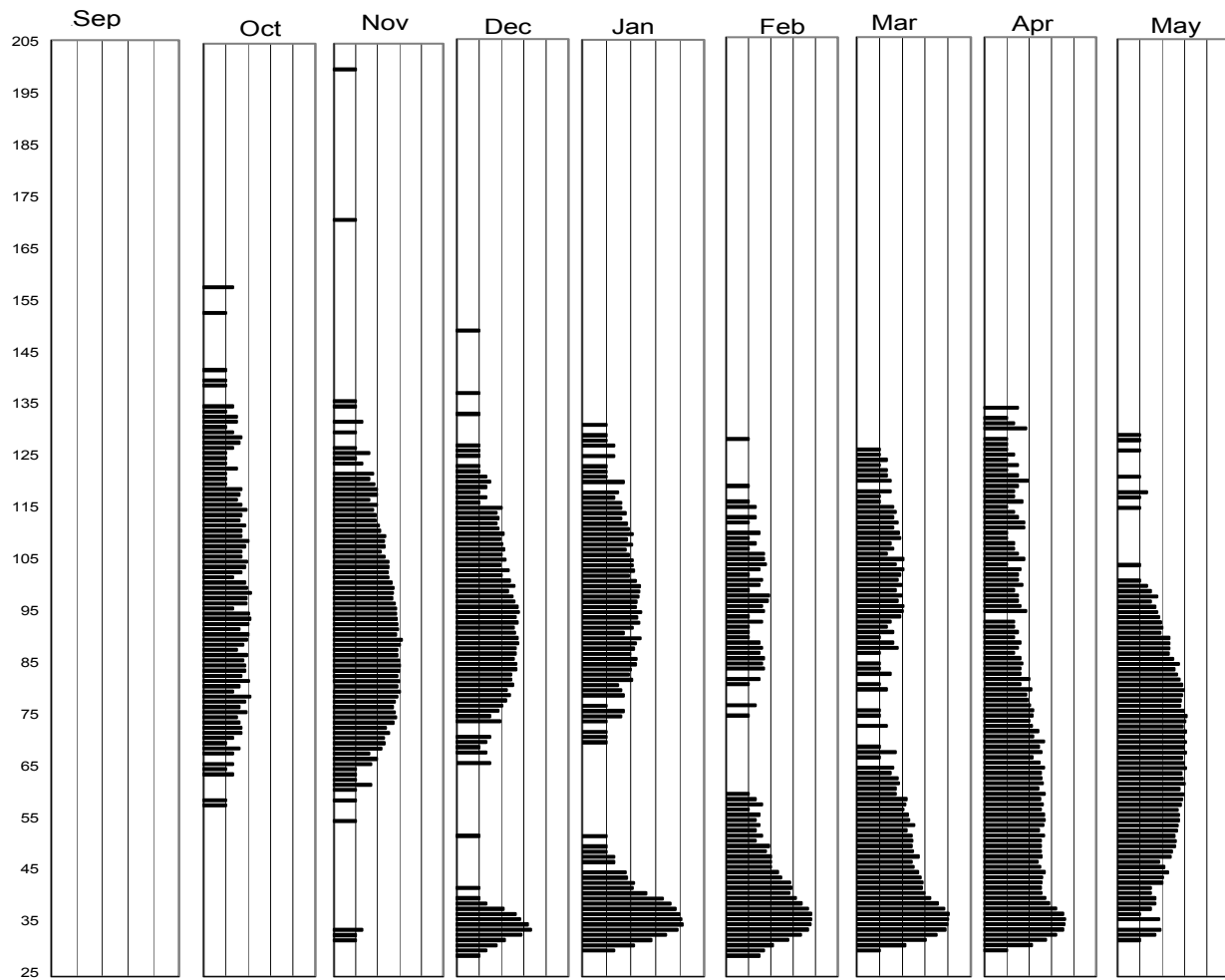


Figure 5-31. Number and size of juvenile spring-run Chinook captured in a screw trap in Mill Creek, 1995 to 2003. The trap is positioned upstream from almost all fall-run spawning, but a few of the fish may be fall-run. The vertical axis is fork length in mm; the horizontal axis is the number captured at size on a log scale, so for each month the vertical lines represent 1, 10, 100, 1,000, and 10,000 fish. Most fish leave as fry, although some leave as fingerlings in spring or as yearlings. Figure from Colleen Harvey of CDFG. [One reviewer objected that bar graphs are unsuitable for logged data. In this case, however, the figure provide such an effective visual summary of the data that this normally valid objection should be set aside.]

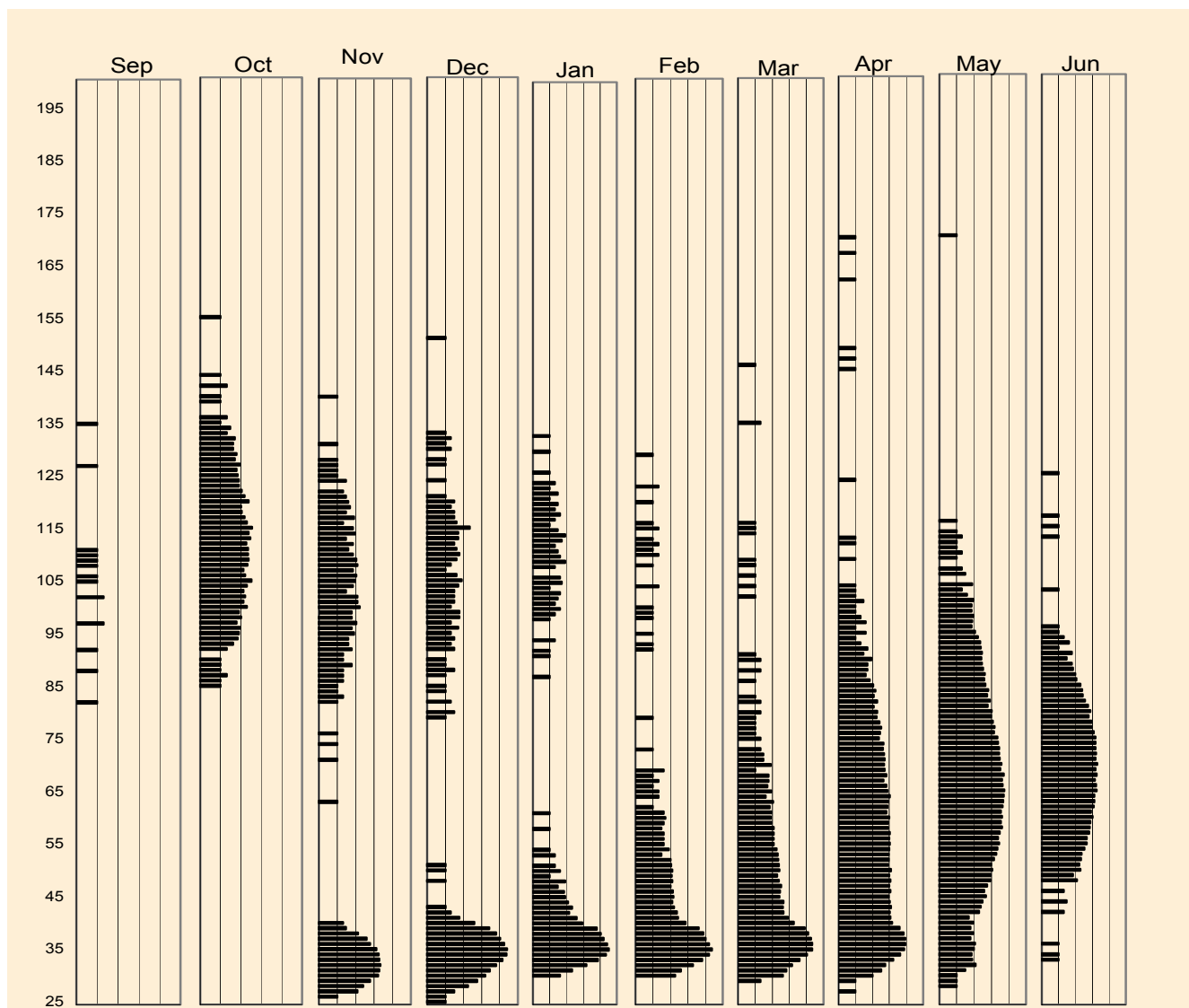


Figure 5-32. Number and size of juvenile spring-run Chinook captured in a screw trap in Butte Creek, 1995 to 2002. The trap is positioned upstream from almost all fall-run spawning, but a few of the fish may be fall-run. The vertical axis is fork length in mm, the horizontal axis is the number captured at size on a log scale, so for each month the vertical lines represent 1, 10, 100, 1,000, and 10,000 fish. Most fish leave as fry, although some leave fingerlings in spring, or as yearlings. Figure from Colleen Harvey Arrison of CDFG.

their first year. Hallock and Van Woert (1959) attributed a shift in the timing of peak migration in the San Joaquin River from January-March to March-mid May in the late 1940s to the loss of the San Joaquin River spring-run following the closure of Friant Dam.²⁵ Hallock et al. (1952:

²⁵ According to Hallock and Von Woert (1959), CDFG operated fyke nets at Mendota from 1944 to 1949. The data from that trapping would clarify the age distribution of emigrating San Joaquin River spring-run, if they could be found. However, in 1939 and 1940, Hatton and Clark (1942) captured mainly sub-yearling sized juveniles at Mossdale in fyke nets, with numbers peaking in February and March, and Hallock and Von Woert also cited these data as reflecting the influence of the San Joaquin River spring-run.

323), in discussing the Sacramento River, observed that "... there are usually two peaks in the seaward migration of the young. The first and earlier peak is presumed to consist of spring-run fish." In context, it is clear that they were talking about fry migrants. Similarly, Azevedo and Parkhurst (undated) thought that < 40 mm juveniles captured in fyke traps at Balls Ferry in December and January of 1950-52 were spring-run. Third, the remaining spring-run spawning habitat, in the San Joaquin River at least, was mostly at relatively low elevation—two-thirds of it was downstream from the site of Friant Dam (Hatton 1940)—which implies relatively warm water during incubation, and emergence of juveniles early enough to be exposed to short-day photoperiods. Based on experiments with stream-type Chinook in British Columbia (Clarke et al. 1992), this would trigger rapid development and early migration, as discussed Ch. 4. Fourth, spring-run Chinook in the Rogue River also emigrate almost entirely as sub-yearlings (Ewing et al. 2001); like Central Valley Chinook, these are from the Cascadian lineage (Ch. 1).

Winter Chinook migration

Winter-run sized Chinook pass the RBDD (rkm 390) mainly as fry in late summer and early fall, and in small numbers but at larger size in late fall and winter (Figures 5-33 and 5-34). The size-at-date criteria appear to work reasonably well in this part of the river, as noted above, so the general pattern shown in Figure 5-33 seems reliable. However, there is overlap among the runs, so some proportion of winter-run fall outside the size range traced on Figure 33a, and some of the fish shown are not winter-run. Note that a higher proportion of fish passed the RBDD in August of some of the years shown in Figure 5-34 than in those shown in Figure 5-33. The gates at the RBDD are not raised until mid-September, so a substantial proportion of the run still passes through highly turbulent water just downstream of the dam, where they presumably are subjected to an unnaturally high rate of predation.

Farther downstream, the size criteria fail, at least for hatchery fish, as shown by captures of tagged hatchery winter Chinook and late fall Chinook in screw traps fished at rkm 144, near Knights Landing (Table 5-1); for 1995-97 to 1998-99, only a quarter of the winter-run sized fish with coded-wire tags were winter-run.

Table 5-1. Numbers of winter-run, late fall-run, and fish without tags among winter-run sized juvenile Chinook that were captured in screw traps near Knights Landing and sacrificed for tag reading because they lacked adipose fins, which are clipped to mark tagged fish. Most winter-run sized fish were actually late fall-run, and 13% had shed tags. Data from Snider and Titus (2000a, b, c.)

Season	No. Checked	No. Winter	No. Late Fall	No. Tagless
1995-97	69	0	60	9
1997-98	67	9	48	10
1998-99	113	45	55	13
Total	249	54	163	32

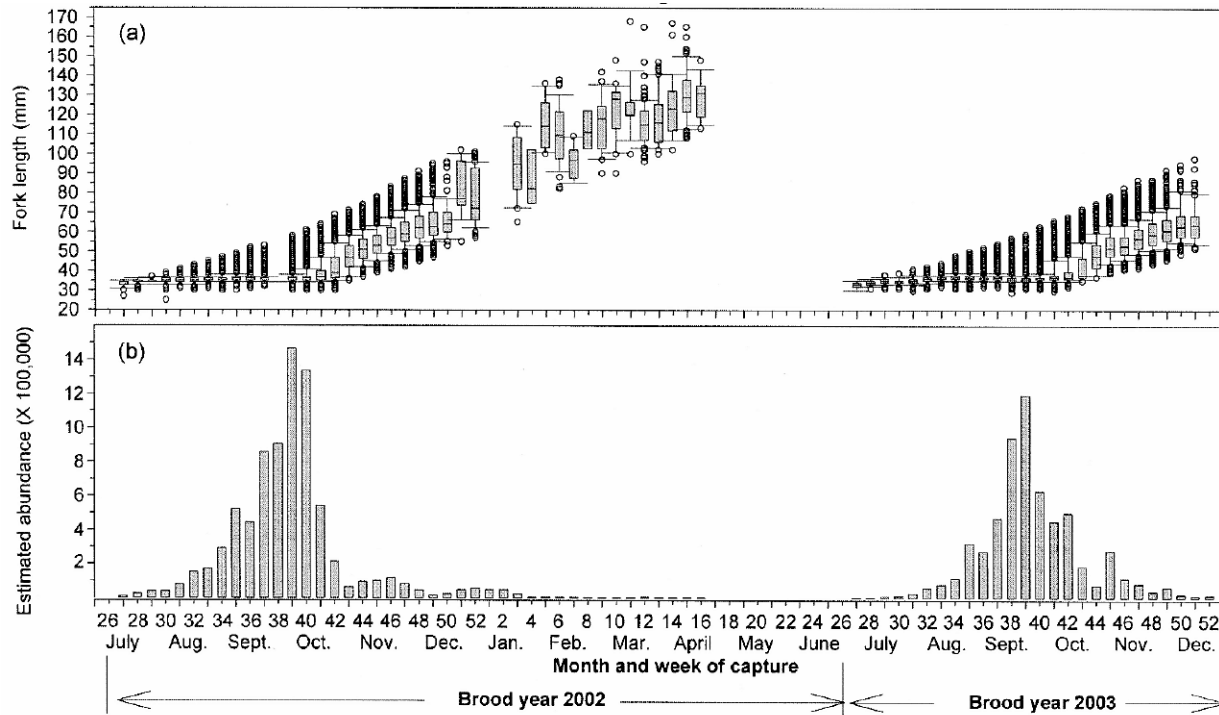
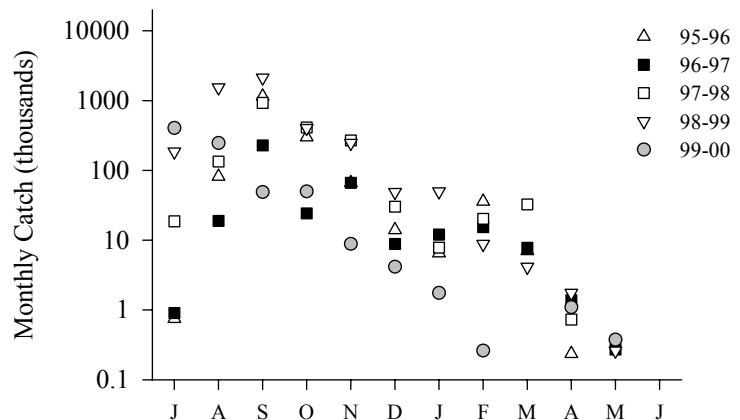


Figure 5-33. Size distributions (a) and numbers (b) of winter-run size juvenile Chinook salmon captured in screw traps at the RBDD in July 2002 through December 2003. Box plots in (a) show the 10th, 25th, 50th, 75, and 90th percentiles, plus outliers. Note that the outliers simply trace the size criteria when abundance is high. Copied from Gaines and Poytress (2004).

Figure 5-34. Numbers of winter-run sized Chinook captured in the screw traps at the RBDD from 1995-96 to 1999-2000, by month. Data from Gaines and Martin (2002).

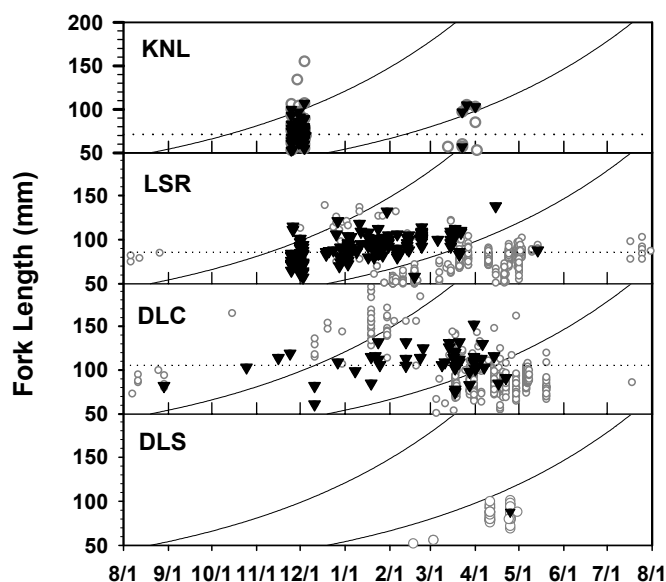


The situation seems somewhat better for naturally-produced winter-run, based on genetically-identified winter-run sampled at Knights Landing, other locations on the lower Sacramento River, and the Delta (Figure 5-35). Nevertheless, the size-at-date criteria still produce many false positives and some false negatives; for a larger sample of fish collected at the CVP and SWP Delta pumps, only about half the fish identified as winter-run by the size

criteria were so identified by genetic analysis, and among years the percentage of false positives varied from 16 to 95% (Hedgecock 2002). However, if winter-run increase more rapidly than the runs producing the false positives, the percentage of false positives should decrease.

Focusing on the genetically identified winter-run in Figure 5-35, the data suggest a slow movement down the Sacramento River and into the Delta. However, the fish were captured over six seasons, and there is considerable year to year variation in the collections. For example, over 80% of the Knights Landing sample was collected in 1997/98, but only 15% of the Central Delta sample was collected in that season, so the apparent slow movement may be an artifact of the sampling.

Figure 5-35. Size at date of capture for 2,280 juvenile Chinook salmon captured in screw traps or trawls in 1995-96 to 2000-01 at Knights Landing (KNL), the lower Sacramento River (LSR), the central Delta (DLC), and the southern Delta (DLS), and assigned to winter-run (filled triangles) or other runs (open circles) by genetic analysis of small clips of tissue from the caudal fin (what appear as filled circles are triangles overlying open circles). Dotted lines show mean size of winter-run for the site; curved lines show size at date criteria. 317 fish were assigned to winter-run; many false positives are obscured on the graph. Copied from Hedgecock et al. (2002).



Given the problems with the size-at-date criteria, it does not seem useful to apply them in the lower river and Delta, and monitoring programs should begin taking tissue samples so that fish can be assigned to runs by genetic analyses. In the meantime, sampling data should be reported in term of the size distributions of fish collected at given times. The box plot and bar graph format used in Figure 5-33 is one good way to do this, although the horizontal bar format used in Figures 5-31 and 5-32 may be better if the data are strongly bimodal. In the meantime, to provide some information on the passage of larger juveniles from late summer through the winter, data summarized by SSJEFRO (2003) for winter-run size and late fall-run size are combined and presented below, although some of these fish probably are spring or fall run.

Larger juvenile Chinook appear in the Lower Sacramento Beach Seine data mainly in November through February, and do so most consistently in December (Figure 5-36). The catches generally are small, however, as might be expected for gear that is better suited for

smaller fish. Catches are even smaller, and without much pattern, in the data from the Kodiak trawl fished at Sacramento (Figure 5-37). Catches in the Chipps Island trawl are also without much pattern and somewhat lower than in the Kodiak trawl (Figure 5-38), but the difference between catches in the two trawls is much less than for spring/fall-run (Figures 5-23 and 5-28). Probably this reflects the tendency of larger Chinook migrants in the fall to migrate down the river at night, as shown by recent work at the Delta Cross Channel, described above. There are also data from a midwater trawl at Sacramento, but this has not been fished in January and February since 1994, and it is not obvious how to combine the per-volume sampled data. Given the tenor of the comments here about the utility of these data, however, it seems fair to point out that the relationship between annual total catches in the trawling at Sacramento and at Chipps Island for winter-run size is rather good (Figure 5-39). However, the relations deteriorates when the winter and late fall-run data are combined, and in any event the origin of the relationship in Figure 5-39 is hard to understand.

Figure 5-36. Larger juvenile Chinook in the lower Sacramento River, fall through winter. Combined catch of winter-run and late fall-run sized fish in the lower Sacramento River beach seine sampling. There are many catches of zero, which do not show on the log scale. Data from Tables 1 and 2 in SSJEFRO (2003).

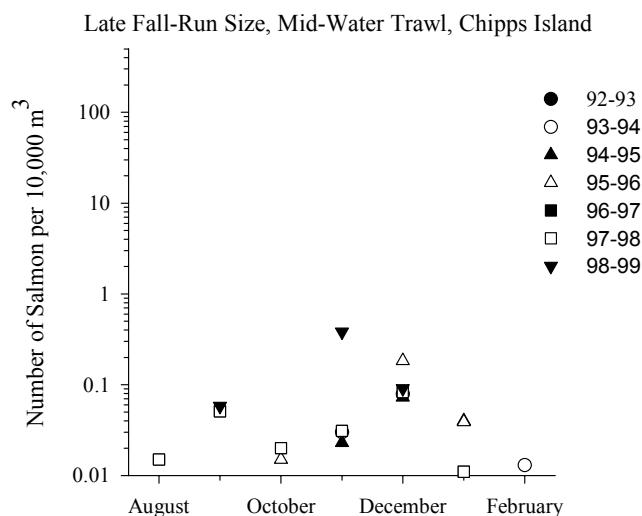


Figure 5-37. Larger juvenile Chinook entering the Delta, fall through winter. Combined catch of winter-run and late fall-run sized fish in the Kodiak trawl at Sacramento, 5 years of sampling except 4 for October. See cautions regarding the data in the text. Symbols as in Figure 5-36. Data from Tables 10 and 11 in SSJEFRO (2003).

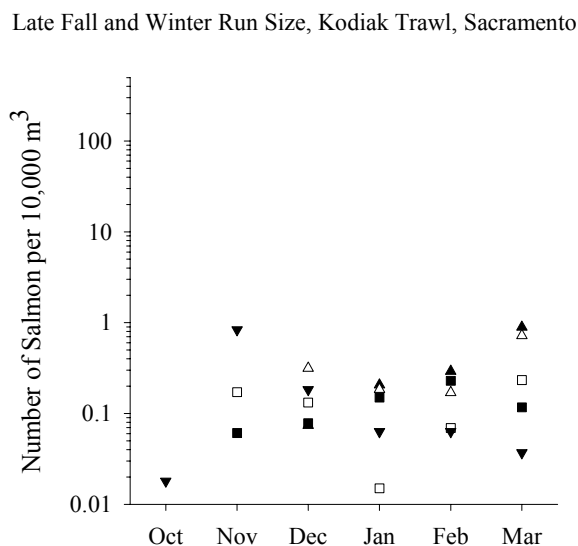


Figure 5-38. Larger juvenile Chinook leaving the Delta, late summer through winter. Combined catch of winter-run and late fall-run sized fish at Chipps Island. Years of sampling vary from 3 for August to 7 for April and May. Symbols as in Figure 5-35. Data from Tables 13 and 14 in SSJEFRO (2003).

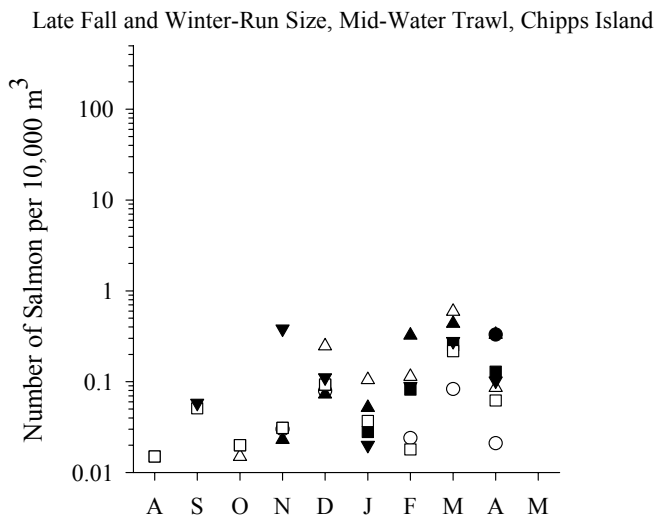
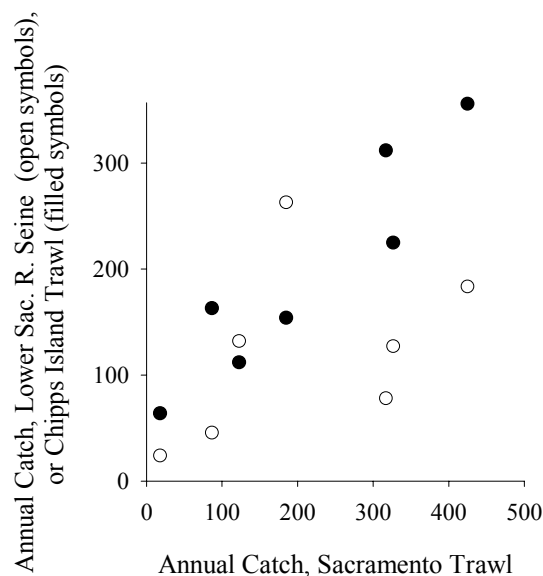


Figure 5-39. Comparison of the number of Winter-run sized Chinook captured by three monitoring programs, 1992-93 to 1998-99. Total annual catches of winter run sized juvenile chinook in the lower Sacramento beach seines (open symbols), and in the Chipps Island trawling (filled symbols), plotted against the total annual catches in the trawling at Sacramento. Axes are on the same scale. Data from SSJEFRO (2003).



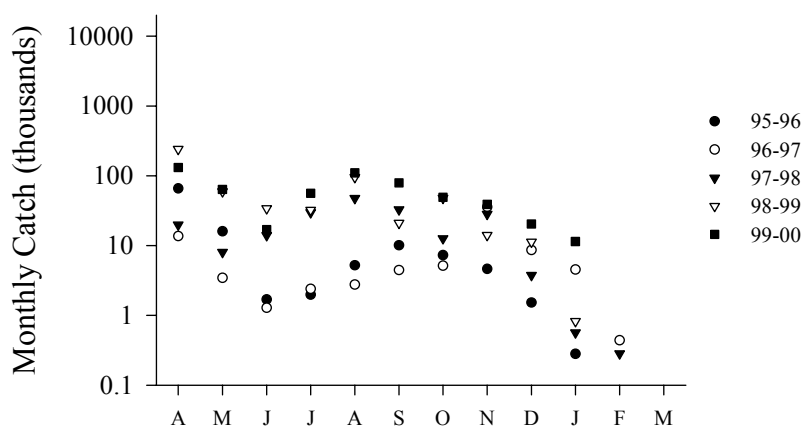
Late fall Chinook migration

Late fall-run and winter-run, and some fall-run, begin migrating downstream in late summer and fall. Late fall-run are usually older and larger than winter-run, so that, for example, Hallock and Riesenbichler (1980) used a length criterion of 45 mm to separate them in seine samples collected just upstream from the RBDD in September and October of 1969, 1970, and 1971. However, they assumed that some fraction of the <45 mm fish would be late fall-run.

Late fall Chinook, as defined by size at date, appear in screw traps at the RBDD as fry in spring, especially in April, and as larger juveniles in the summer and fall (Figure 5-40), but made up only 1.4% of the catch in the screw traps from 1995-1999 (Gaines and Martin 2002). Even some of these may have been fall-run, especially in July and August. Farther downstream, below

the confluences of Mill and Deer creeks, some juvenile spring-run also fall into the late fall-run size range (Figures 5-31, 5-32). The few nominal late fall-run collected by monitoring in the lower Sacramento River fall into two groups; small migrants in the spring (<50 mm), and larger migrants in the fall and winter. The spring migrants are captured in low numbers in the lower Sacramento River seine sampling (<1 per 100 m³); the larger migrants are discussed above.

Figure 5-40. Catch by month of juvenile late fall Chinook, as defined by size at age, at the RBDD. Data from Phillip Gaines, CDFG.



Timing of juvenile steelhead migration

Less is known about the migration of juvenile steelhead in the Central Valley than about juvenile Chinook, but better information is now becoming available from screw traps that are located in fast enough water to catch yearlings in significant numbers. However, interpretation of the data is complicated by the large proportion of the population that has adopted a resident life history pattern; it is not clear whether juveniles captured in the traps are migrating to the ocean.

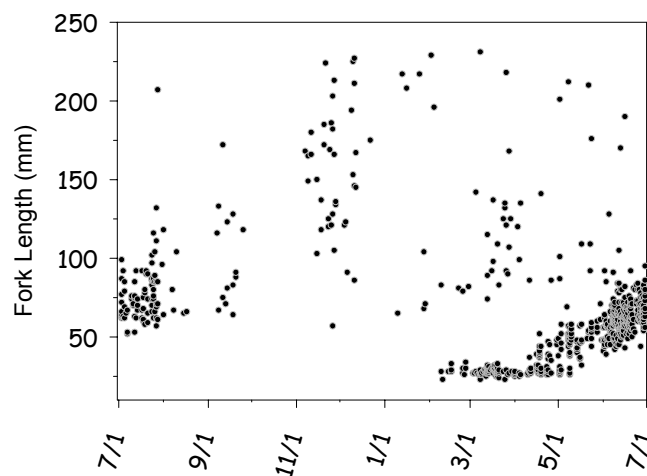
What determines the selection of anadromous v. non-anadromous life history patterns is unknown, although there are several plausible hypotheses, recently reviewed by Hendry et al. (2004). Migration may be viewed as a response to the lack of opportunity for growth (Thorpe 1987; Jonsson and Jonsson 1993), and the behavior of Central Valley *O. mykiss* is consistent with that view. However, this explanation does not address the particular mechanisms or cues that determine the behavior. Generally, anadromous salmonids that grow rapidly as juveniles emigrate at a younger age than conspecifics that grow more slowly, although rapidly growing males may mature as parr (Hendry et al. 2004). Dramatic changes in the proportions of anadromous and non-anadromous individuals have been reported in other populations in response to fishing mortality of anadromous adults (Thorpe 1987) or changes in stream conditions following dam construction (Morita et al. 2000), but decreased survival of migrating juveniles or of sub-adults in the ocean would have the same selective effect. In any event, the change in life history patterns raises the question whether genotypic as well as phenotypic change is involved: that is, have Sacramento River *O. mykiss* evolved to adapt to changed circumstances, or are they simply responding to changed circumstances? Either or both seems

plausible, and it might be possible to address this question by experimental comparisons of the behavior of progeny from fish from the Sacramento River and, say, Butte Creek.

Older information on migration timing was summarized by Hallock et al (1961:14), who reported that “An attempt to determine the time pattern of the juvenile steelhead migration past the mouth of the Feather River was made by trapping. This method proved unsuccessful, because insufficient numbers of fish were captured. However, in the upper river all evidence indicates a heavy seaward migration of yearlings in the spring and a much smaller one in the fall.” Data on migration from the tributaries into the river was available from a trap operated on a dam on Mill Creek, however. These showed that “... young fish migrated downstream during most months of the year, but the peak periods for yearling and two-year-old fish were reached during the first heavy runoff of fall and again in early spring” (Hallock et al. 1961).

As an example of more recent data, in 2001-2002 juvenile steelhead, or at least juvenile *O. mykiss*, moved out of Clear Creek into the upper Sacramento River mainly as young of the year, based on captures in a screw trap about 2.7 km upstream from the confluence with the Sacramento River (Greenwald et al. 2003); fry were captured from February into May, and older fish from the same cohort were captured mainly through July (Figure 5-41). Larger fish were captured mainly in November and December, but captures were scattered broadly through the year. Data for other years are similar, but with some differences in timing. For example, in 2002-2003, fry did not appear in the trap until the end of February.

Figure 5-41. Length at date of juvenile *O. mykiss* captured in a screw trap in Clear Creek from 1 July 2001 to 1 July 2002. Redrawn from Greenwald et al. (2003).



At the RBDD, juvenile steelhead ranging in size from ~30 to over 250 mm are captured in the screw traps (Gaines and Martin 2002), along with a few larger fish. Most larger juveniles pass in the first half of the calendar year, with the hatchery fish passing mainly in January, and the naturally-produced fish passing through the winter and spring (Figure 5-42). Naturally-produced young of the year pass mainly in summer, although passage of fry occurs from March

through August, and older young of the year are captured through the fall. The data suggest the existence of distinct groups that pass in the spring and in the summer (Gaines and Martin 2002); if this is confirmed by more recent data it deserves more study.

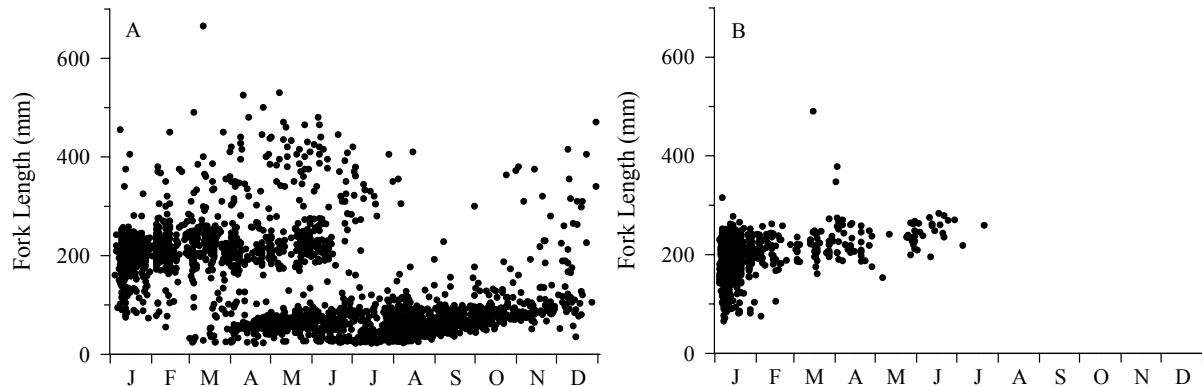


Figure 5-42. Size at day of capture of (A) unmarked *O. mykiss*, and (B) marked hatchery steelhead at the RBDD for July 1994 through June 2000. Note that not all hatchery fish were marked before 1999, so some of the fish shown in (A) are hatchery fish, and that multiple fish of the same size captured on the same day of the year are represented by a single point. Data from Phillip Gaines, CDFG, Red Bluff.

Relatively few migrating juvenile steelhead are captured farther downstream in the Sacramento River. For example, the CDFG screw trap at Knights Landing, close to the site of the failed trapping described by Hallock et al. (1961), captured only 45 naturally-produced juveniles in 1999, mostly in April and May (Snider et al. 2000). Two screw traps are operated in the Feather River, one near the downstream end of the “low flow channel” where most steelhead spawn, and one farther downstream. Many small juveniles are captured in the upstream trap, but few juveniles of any size are captured in the downstream trap (Kindopp 2003). A few dozen to a few hundred juvenile steelhead, most of them young-of-the-year, are captured each year in screw traps on the American River (e.g., Snider and Titus 2002). Nevertheless, CDFG biologists have developed useful information on the age, sex, and background of emigrating steelhead from analyses of relatively small numbers of individuals (Titus et al. 2004), including information on differences between hatchery and naturally produced steelhead. All hatchery steelhead are now marked, which facilitates such analyses.

Based on the small numbers of emigrating steelhead that are captured in the lower Sacramento River, it appears that most hatchery steelhead smolts pass Knights Landing soon after they are released from Coleman National Fish Hatchery in January, and pass rapidly through the Delta to Chipps Island, although some linger for several months. Naturally produced fish mainly pass Knights Landing in April and May, and pass rapidly through the Delta (Figure 5-43). The hatchery smolts are all one year old (one winter in freshwater), whereas the naturally produced smolts from the Sacramento River are mostly aged two, with ~ 15% each age one and

age three (Titus et al. 2004). Naturally produced steelhead in the American River mainly smolt at age one, however, so that on average, smolts at Knights Landing are older than smolts at Chipps Island. However, smolts at Chipps Island are larger on average (Figure 5-44).

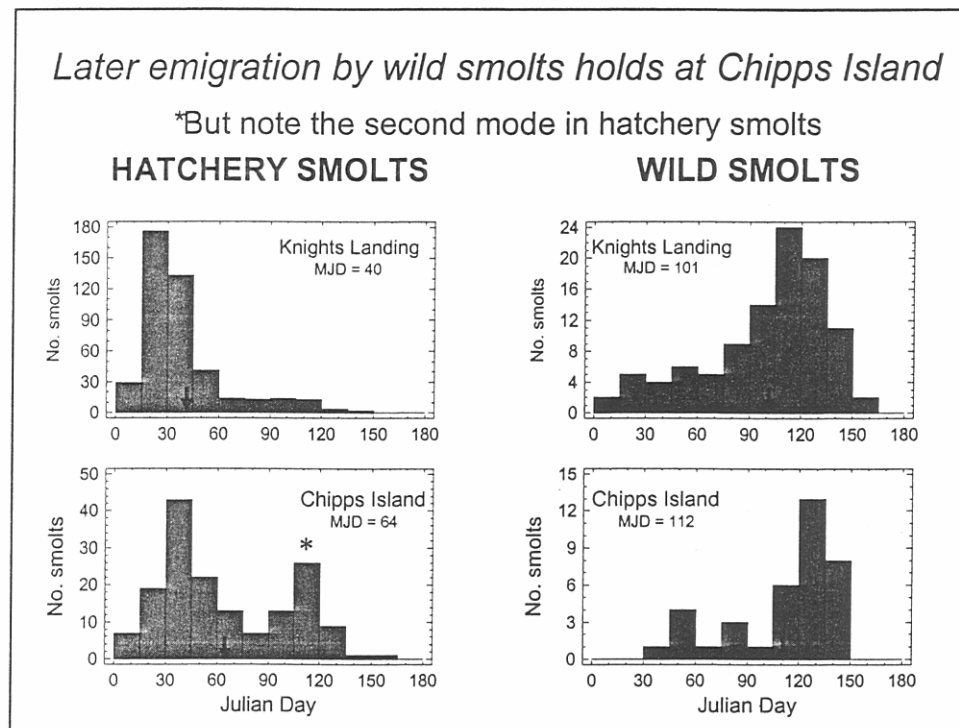


Figure 5-43. Temporal distribution of captures of juvenile steelhead at Knights Landing on the Sacramento River and at Chipps Island at the seaward limit of the Delta, 1999-2002. Sampling is with a screw trap at Knights Landing, and a trawl at Chipps Island. Copied from Titus et al. (2004).

Most naturally produced steelhead smolts are females (Titus et al. 2004). In samples collected from 1999–2002, 70% of 71 fish at Knights Landing and 66% of 29 fish collected at Chipps Island were females. Among hatchery fish, males and females were about evenly represented at Knights Landing, but 59% of 118 fish captured at Chipps Island were females. In salvage at the Delta pumps, however, the sex ratio of hatchery fish was even. This suggests that some hatchery males may not migrate farther than the Delta. The skewed sex ratio for migrating naturally produced steelhead is consistent with theoretical predictions for partially anadromous populations (Hendry et al. 2004), since the advantages of large size for females (e.g., more eggs) are largely independent of the fraction of the population that is anadromous, whereas the advantages of large size for males (e.g., access to females) are not.

Juvenile steelhead are captured in small numbers in the screw traps below Woodbridge Dam on the Mokelumne River; for 2001-2002; Workman (2002) estimated that 540 naturally produced young-of-the-year passed the dam, mainly from mid-April to late July. One hundred one naturally produced steelhead smolts were also captured between January and June, along with 495 hatchery smolts that had been released downstream from the dam.

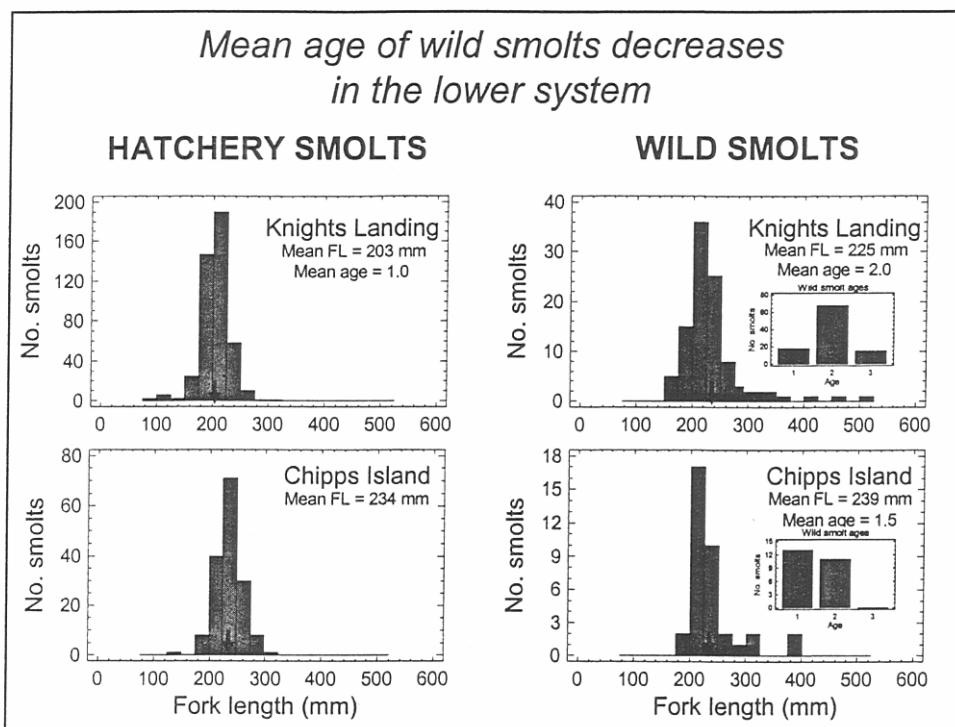


Figure 5-44. Length and age distributions of hatchery and naturally produced steelhead smolts captured at Knights Landing on the Sacramento River and Chipps Island at the seaward edge of the Delta, 1999-2002. Copied from Titus et al. (2004).

Only a little information is available on the migration of juvenile *O. mykiss* in the San Joaquin River system. Screw traps are operated on the Stanislaus River from December through July, and small numbers of juvenile *O. mykiss* are captured in them (Figure 5-45). As in Clear Creek, fry are captured in spring, and smolt-sized (or larger) fish are captured throughout the sampling season, but mainly in January through April. Assuming that the captures are proportional to the number of migrants and the percentage of the flow going through the trap, the estimated number of emigrating fish has averaged around 250 for 1955-2003 (SRFG 2004). However, the trap efficiency presumably is low for smolt-sized steelhead, so probably this is an underestimate. Like the *O. mykiss* in the Sacramento River, the population in the Stanislaus River may be largely resident.

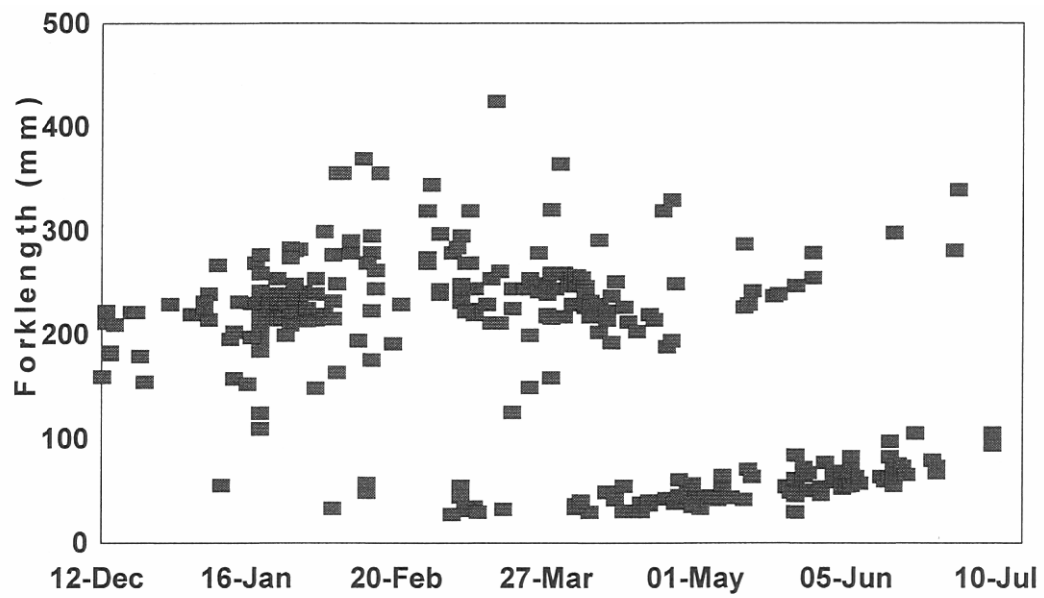


Figure 5-45. Lengths of steelhead captured in screw traps at Caswell and Oakdale on the Stanislaus River, 1995-2003. Copied from SRFG (2004).

CHAPTER SIX

ADULTS IN FRESH WATER

Tens of thousands, not to say hundreds of thousands, which would perhaps be nearer the truth, passed the line of our barricade before it was completed.

Livingston Stone (1876:44)

The salmon of the summer run where they were intercepted by the racks all died before becoming ripe enough to spawn, death being due to the extremely warm weather. ... As it has been found impossible to secure eggs from the summer run of fish at Mill Creek Station, during the early spring temporary racks were constructed across the mouth of the creek in order to turn the salmon back into the Sacramento River with the hopes that a large proportion of them would continue up the river and on to Baird Station (on McCloud River), where the water is colder and more eggs can be taken. A large run of fish passed up the river in May and June, and the fish were continually fighting the racks, but all were compelled to return to the river.

Commissioner of Fish and Fisheries (1904:74-75)²⁶

Concentrations of adult salmon in freshwater are impressive visually as well as biologically, and have made salmon a totemic animal of the Pacific Northwest. This chapter describes the migration, holding, spawning, and fecundity of adult salmon, and provides some related recommendations.

The maturation process in salmon is gradual, but some unknown cue motivates maturing salmon to leave their feeding grounds and return to their natal streams. The relative timing of migration and sexual maturation varies among the runs of Chinook: fall-run and late-fall run may be ready to spawn shortly after arriving at their spawning grounds, but spring-run and winter-run complete maturation as they hold for several months in the spawning areas or nearby. This difference was of practical importance for early gill net fisheries, because spring-run have higher lipid concentrations and better color as they pass through the estuaries and lower rivers than do fall-run (Rich 1920). It remains important for managing freshwater habitats, because winter-run and particularly spring-run need holding habitat as well as spawning habitat.

Adult migration

Navigation

How salmon find their way in the ocean is still uncertain, because adult salmon at sea are difficult to study experimentally, but probably involves direct beam and polarized solar radiation and the Earth's magnetic field, cues also used by juveniles. Green sea turtles apparently use a geomagnetic map to find their way back to their natal beaches after living in the open ocean (Lohmann et al. 2004), so this may be a sufficient mechanism. As the fish approach their natal streams and can detect its odor, olfactory cues become the primary means of navigation (Dittman and Quinn 1996). The use of chemical cues for homing by adults was described in the nineteenth century, although many biologists in the early the twentieth century thought the idea was

²⁶ Quoted in Hanson et al. 1940, p. 71.

romantic nonsense,²⁷ and even the fact of homing was debated through the 1930s. The alternative explanation for evidence of homing was the assumption that salmon do not travel far at sea, so that when salmon seek freshwater they usually find their natal stream simply by chance. Early marking experiments on the Klamath River (Snyder 1924 b, c) showed that Chinook return to their natal tributaries after migrating long distances at sea, but did not determine the mechanism. Opposition to conservation measures apparently motivated some of the reluctance to accept homing as a fact (Rich 1939).

The importance of odor for homing was established by Arthur Hasler and colleagues in the 1950s and 1960s (Hasler 1966). The home-stream odor hypotheses was stated as follows by Hasler et al. (1978, quoted in Smith 1985:89-90):

(1) because of local differences in soil and vegetation of the drainage basin, each stream has a unique chemical composition and, thus, a distinctive odor; (2) before juvenile salmon go to the sea they become imprinted to the distinctive odor of their home stream; and (3) adult salmon use this information as a cue for homing when they migrate through the home-stream network to the home tributary.

The propensity of people to move fish from place to place has provided a number of inadvertent experiments in which fish return to the site of their release rather than to their natal hatchery (e.g., Jensen and Duncan 1971); these and deliberate experiments have shown that imprinting can occur rapidly at certain times in the development of young fish. The diversity of life history patterns among wild salmonids precludes any fixed time for imprinting, however, even within populations (Quinn 1990), and especially for Chinook and steelhead. The sequential odor hypothesis (Harden Jones 1978) proposed that emigrating salmon learn a sequence of odors as they pass downstream, and follow the sequence in reverse order in the return migration. Most subsequent work is consistent with this hypothesis (Quinn 1997). However, there also appears to be a genetic component to homing, demonstrated by transplantation experiments with Chinook from stocks native to upper and lower reaches of the Columbia River (McIsaac and Quinn 1988); 9% of fish from the upstream stock returned to their native habitat despite being bred and reared at a downstream hatchery.

Estuaries may be a transition zone in which fish switch from primarily visual and magnetic guidance to olfactory cues for navigation (Dittman and Quinn 1996), and acclimate to reduced salinity (Greene 1926). Marking and tracking experiments show that adult Chinook may spend considerable time in estuaries moving with the tides without appreciable movement upstream,

²⁷ Rutter (1903:121) wrote that "There is a widespread belief that when a salmon returns to freshwater to breed it seeks the stream in which it was hatched, though there is very little evidence that such is true," and David Starr Jordan had a similar opinion. On the other hand, Smith (1985) quotes Buckland (1880: 320) as follows: "When the salmon is coming in from the sea he smells about till he scents the water of his own river. This guides him in the right direction, and he has only to follow up the scent, in other words to 'follow his nose,' to get to up into freshwater, i.e., if he is in a traveling humour. Thus a salmon coming up from the sea into the Bristol Channel would get a smell of water meeting him. 'I am a Wye salmon,' he would say to himself. 'This is not the Wye water; it's the wrong tap, it's the Usk. I must go a few miles further on,' and he gets up stream again."

although some move through estuaries fairly quickly (Greene 1926; Hallock et al. 1970; Olson and Quinn 1993). Some returning Chinook even move actively downstream for considerable distances after starting upriver, as demonstrated by tagging studies in the 1950s. Over five percent of recoveries of Chinook that were trapped and tagged at the Fremont Weir, upstream of the Sacramento-Feather River confluence, were made in the gill net fishery in the Delta. For fish tagged during the August 10 to September 26 gill net season, 15 percent of recoveries were in the Delta (McCully 1956). One fish actually returned to sea and was caught by an angler the following spring. These were mostly smaller fish, and may have been reacting to their capture. Nevertheless, the considerable number that returned to the Delta illustrates the variability of the migratory behavior of adult Chinook. As a practical consequence, this variability makes it difficult to determine whether some factor or situation is delaying migration into the rivers.

Rate of migration

Rutter (1904) branded and released 150 Chinook at Rio Vista in September 1901, and three were recovered at hatcheries; these traveled ~ 6 to 8 km d^{-1} on average. From this and evidence from the fishery he inferred that fall-run took about 2 months to reach the McCloud River from Collinsville, and spring-run took about 6 weeks. However, it is clear that Chinook can migrate more rapidly. Gilbert (1921-22, cited in Greene 1926) recovered 18 marked Chinook in the Yukon River that migrated 69 km d^{-1} on average (range $34\text{--}84 \text{ km d}^{-1}$). The median migration rate of PIT-tagged spring Chinook passing dams 460 km apart on the Columbia River was about 28.9 km d^{-1} , ranging from 9.5 to 51.5 km d^{-1} (Matter and Sandford 2003); the tagged fish tended to migrate more rapidly as the season progressed, and the data suggest that medium-sized fish ($70\text{--}80 \text{ cm}$) may migrate more rapidly than smaller or larger fish.

Straying

Salmon return to their natal streams with high but not complete fidelity. The various advantages and disadvantages of homing and straying are reviewed by Hendry et al. (2004), who concluded that adaptations to local environments provide the main advantage for homing, while buffering temporal variation in local habitats is the strongest short-term reason for straying; on longer time-scales, straying also facilitates colonization of vacant habitats. For example, Shapovalov (1947) reported that considerable numbers of fall Chinook reached Capay Dam on Cache Creek in 1938; this could have founded a new population, had Cache Creek been suitable habitat. Straying rates for natural populations of salmon are poorly known but probably vary between ~ 1 to 15% , although some populations of chum show much higher rates (Tallman and Healey 1994). Appendix 1 in Hendry and Stearns (2004) gives a summary of published studies.

In local studies, Shapovalov and Taft (1954) reported straying rates of 2 or 3 percent for steelhead between Waddell and Scott creeks during a period when weirs were operated on both streams, which enter the Pacific Ocean about 7 km apart, between Monterey and San Francisco bays.²⁸ Straying of naturally produced fall Chinook in the Mokelumne River has been estimated

²⁸ Straying rates for coho reported by Shapovalov and Taft (1954) were much higher than for steelhead: 15% of naturally spawned coho marked in Waddell Creek were recovered in Scott Creek, and 27% of coho marked in Scott

at 7.3% (J. Miyamoto, EBMUD, pers.comm., 2004), but this population has been heavily affected by hatchery production, including the introduction of eggs and fry from the Feather River. Naturally-produced spring-run are also tagged in Butte Creek, but too few have been recovered yet to allow a reasonable estimate of straying. Straying rates are difficult to determine accurately, because the probability that a marked fish will be recovered in a stream, given that it is there, varies over streams and over time. For example, among the Mokelumne River fish recorded as straying, 439 were recovered in the Feather River, but only 14 were recovered in the Yuba River. It seems likely that this difference reflects a higher probability of detection in the Feather River. Generally, straying rates can be high enough for exchanges to affect the population dynamics and genetics of neighboring populations, and make the metapopulation concept (Ch.1) applicable to analyses of groups of adjacent populations, provided that migrants are reproductively successful.

Straying rates for hatchery fish are generally higher than for naturally-produced fish. Rates for fall Chinook from five lower Columbia Basin hatcheries varied from 9.9 to 27.5% (Quinn et al. 1991; Quinn 1997). The straying rate for Chinook from hatcheries in British Columbia varied considerably, from ~1 to 18%; on average, hatchery fish derived from local stocks and released on site had the lowest rates (1.2% average), and fish trucked directly to estuaries had higher rates (5.3% average; Candy and Beacham 2000). Straying rates for stream-type Chinook from an experimental hatchery in Alaska were also low, averaging 1.4% over years (Hard and Heard 1999); off-site recoveries decreased with distance from the release site, and young males were most likely to stray.

Trucking Chinook smolts away from hatcheries for release increases the rate of straying (Quinn 1993; Pascual et al. 1995; Candy and Beacham 2000). Approximately 12 million Chinook smolts are trucked annually from Central Valley hatcheries and released downstream from the Delta (Ch. 12); most of these are unmarked. Additional hundreds of thousands are released at various locations for mark-recapture studies such as the Vernalis Adaptive Management Plan (VAMP).

Central Valley studies of straying rates for hatchery fish transported away from the hatchery for release have given widely varying results, but some indicate very high rates. For Chinook reared at the Feather River and released at Rio Vista as yearlings, 73% of recoveries were in the American River (Sholes and Hallock 1979). Straying rates of fish released into the Delta were estimated at 70 percent by JHRC (2001; see its App. 1 for a discussion), based mainly on comparisons of the percentages of groups of tagged fish released on and off-site that were captured in the ocean fishery and that returned to the hatchery (USFWS 2001, App. 10.C). The

Creek (which were all hatchery fish) were recovered in Waddell Creek. However, the Waddell and Scott Creek weirs were low enough in the streams that it is possible that some fish recorded as strays would have moved back downstream (like the tagged Chinook recovered in the Delta gill net fishery) and eventually to their natal streams; One marked steelhead did so (Taft and Shapovalov 1938). In any event, recent genetic analyses of California coho populations show differences among populations that suggest lower effective straying rates (C. Garza, NMFS, pers.comm., 2004).

straying rate estimated for fall Chinook smolts from Coleman Hatchery approximately doubled for fish released at Knights Landing or farther downstream, compared with smolts released at the RBDD (Cramer 1991; USFWS 2001, App. 10.C). However, over 90% of recoveries of fall Chinook reared at the Feather River Hatchery and released into the Estuary when smolts normally would be migrating through it were in the Feather River (Brown et al. 2004). Marking all hatchery fish with hatchery-specific marks would allow for better estimates of straying. The percentage of strays in streams should be the focus, rather than straying rates per se, since the loss of fish to straying is unlikely to harm hatchery populations.

Increased straying by trucked hatchery fish is consistent with the sequential odor hypothesis, since trucking would interrupt the normal sequence of odors encountered by emigrating fish. Increased straying exacerbates the negative ecological and genetic effects of hatchery production on naturally reproducing fish (Ch. 12), especially in streams without hatcheries. For example, enough marked hatchery strays have been found among fall-run returning to the Tuolumne River, Mill Creek and Deer Creek (Brown and Ford 2001; Table 12-4) to indicate that hatchery strays constitute significant proportions of returns. This issue requires more study, if off-site releases are to continue.

Other factors besides trucking may affect straying rates. Diversions at the state and federal facilities in the fall reduce the amount of San Joaquin River water reaching the lower channel of the river, and Mesick (2001a) argued that they may do so to the point that San Joaquin River salmon lose their olfactory cues and stray. Data on the timing of returns at a new weir on the Stanislaus River and from water quality monitoring in the lower San Joaquin River should allow this suggestion to be tested.

Heavy metals or pesticides may present another anthropogenic problem for migrating adults by affecting the olfactory neurons of juveniles; transient exposures during emigration may interfere with the normal sequential imprinting on odors, leading to increased straying. Fish detect odors when dissolved odorant molecules bind with olfactory receptor molecules that are carried on the olfactory rosettes. Contaminants can affect olfaction in several ways: by competing with natural odorants for binding sites, by affecting activation of the olfactory receptor neurons, or by affecting intracellular signaling in the neuron (Scholz et al. 2000). Brief exposure to copper at ecologically relevant concentrations can impair the function of olfactory receptor neurons in coho salmon, and longer exposures (4 hours) can kill the neurons (Baldwin et al. 2003). The current EPA freshwater quality criterion for dissolved copper of 13 µg/L for a 1-hour average maximum concentration (at 100 mg/L hardness) is approximately equivalent to one of the experimental exposures reported by Baldwin et al. (2003), and based on their results a pulse of stormwater just meeting the criterion "...could be expected to cause a >50% loss of sensory capacity among resident coho ...", at least temporarily. Longer exposures that kill the neurons would have an effect lasting perhaps weeks. A two hour exposure to 1.0 µg/L diazinon interferes with anti-predator behaviors in Chinook, and a 24-hour exposure to 10.0 µg/L interferes with homing (Scholz et al. 2000). Diazinon and a carbamate pesticide, carbofuran, also interfere with reproductive behavior in Atlantic salmon by inhibiting perception by males of a

pheromone released by females that are ready to spawn (Moore and Waring 1996; Waring and Moore 1997). Like organophosphates, carbamates inhibit the activity of acetyl cholinesterase, an enzyme important for the transmission of signals in nerves. A number of organophosphate and carbamate pesticides are used in the Central Valley and likely have additive effects, but this has not yet been studied (Scholz et al. 2000)

Energetics

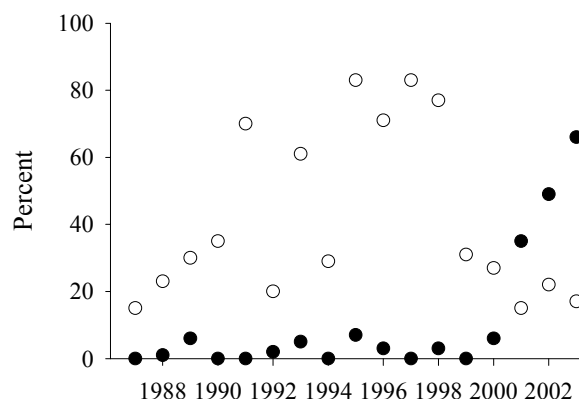
Chinook salmon famously stop eating during their spawning migrations and depend on energy reserves to swim to their spawning grounds and to complete elaboration of reproductive tissues. In many rivers the migrations are difficult, and apparently involve a trade-off in energy allocation between migration and reproductive tissue (Lister 1990; Kinnison et al. 2001). Chinook marked by Gilbert (1921-22, cited in Greene 1926) traveled as far as 2,400 km up the Yukon River in as few as 52 days. In streams such as the Fraser River, major spawning areas are upstream from steep, high velocity reaches that are difficult for salmon to pass (e.g., Cooke et al. 2004). In the Central Valley, however, the access to most major spawning areas in natural conditions was relatively easy, except for the steep Little Sacramento River, or unless flows were low, as may have been common for San Joaquin tributaries in the fall. The easier access to spawning areas may help explain why the fecundity of Central Valley Chinook was higher than Chinook in the Klamath River, as reported by McGregor (1922; 1923). Salmon habitat on most Central Valley rivers is now limited by impassible dams in the foothills, so that salmon migrating to the remaining spawning habitat do not encounter steep reaches except in the spring-run streams such as Mill, Deer, and Butte creeks.

Barriers to migration

Barriers to adult migration are usually evident from the salmon holding below them. Migration barriers in the Central Valley are detailed in various reports (e.g., USFWS 1995; 1998), and many of the smaller ones have been mitigated or removed by CALFED or CVPIA restoration activities, so only selected examples are described here.

Dams: The Anderson-Cottonwood Irrigation District (ACID) maintains a seasonal flashboard dam on the Sacramento River at Redding, which is normally in operation from April to October. McGregor (1922) described observations of the almost entirely unsuccessful attempts of salmon to pass the dam. The dam was a nearly complete barrier to migration from 1917 to 1927, when a fishway was constructed (Moffett 1949). However, the fishway was not highly effective (NMFS 1997), and new ladders were installed on each end of the dam in 2001; spawning by winter-run in the three miles of habitat above the dam has since increased dramatically (Figure 6-1).

Figure 6-1. Percentage of winter-run redds observed above the ACID Dam (filled circles) between the dam and the Highway 44 bridge (open circles) in CDFG aerial surveys. Data from Doug Killam, CDFG, Red Bluff).



The Red Bluff Diversion Dam, constructed in 1966, was a major barrier to adult migration, as well as a cause of mortality for juveniles migrating downstream, even though it was built with fishways (USFWS 1988; NMFS 1997). The ladders do not attract fish effectively; tagging studies indicated that almost half of migrating winter-run failed to pass the dam, and those that did were delayed for days to weeks (Hallock et al. 1982; Vogel and Smith 1986; USFWS 1987; Vogel et al. 1998, all cited in NMFS 1997). Passage problems at the dam have been sharply reduced by restricting the period when the gates on the dam are closed to May 15 to September 14. Further changes, including installation of screened pumps to replace the gravity diversions allowed by the dam, are now being considered, along with plans to develop additional off-stream storage in the area (Tucker et al. 2003). Extending the gates' open period in the spring may be important for re-establishing spring Chinook upstream from the dam, and having the gates open in August and early September presumably would reduce predation on early-migrating juvenile winter-run.

Small diversion dams can be serious obstacles to migration, even if they have fishways that allow some fish to pass. Moffett (1949) noted that many spring Chinook died or were injured trying to get over the Stanford-Vina Dam on Deer Creek, before a new ladder was installed there. Biologists with long experience on Butte Creek report that adults holding in pools have fewer head injuries than was the case before several dams were recently removed or rebuilt (John Icanberry, USFWS, pers.comm. 2001). Diversions from Mill Creek probably continue to block late arriving spring Chinook by reducing the flow in the lower reach of the stream.

In the Delta, the Montezuma Slough tide gates and the Delta Cross Channel gates have the potential to delay migrating adults. Studies cited in NMFS (1997) indicate that tide gates at Montezuma Slough can increase passage time by about a day. Whether this delay is significant is unknown, but seems unlikely given the extent to which fish apparently linger in the Delta. The Yolo Bypass presents a more serious problem. When discharge in the Sacramento River at Knight's Landing exceeds about $2,000 \text{ m}^3 \text{ s}^{-1}$, water from the river passes over the Fremont Weir and flows down the bypass. Migrating adults are attracted into the bypass, but are unable to pass over the weir (T. Sommer, CDWR, in Anderson et al. 2006). A fishway should be provided.

Dissolved oxygen: On the San Joaquin River, dissolved oxygen concentrations near Stockton can be low enough to block migration of adult salmon (Hallock et al. 1970; Alabaster 1989). This is a continuing problem, resulting from complex interactions among factors such as diversion of San Joaquin River water toward the Delta pumps, modifications of channel morphology to allow shipping, and wastewater discharge, that is the subject of much current work (Lee and Jones-Lee 2003; Jassby and Van Nieuwenhuyse 2005). Usually this problem eases in late October.

Water temperature: Hallock et al. (1970) reported that water warmer than 21°C blocks migration of Chinook into the San Joaquin River and water warmer than 19°C inhibits it. However, data from the new weir on the Stanislaus River indicate that in 2003 over 500 Chinook passed through water 21°C daily average, or warmer, in the lower San Joaquin River (SRFG 2004). The role of temperature in blocking migration should be clarified as data from this weir or others that may be installed on other tributaries accumulate. Whether migration through such warm water harms gametes should also be considered.

Diversions: In dry years such as 2001, diversions from Mill Creek can reduce flow in the lower few miles of Mill Creek enough to create a migration barrier (Figure 6-2). This seems like a problem that should have a solution, since water from the Sacramento River is available nearby. Diversions from the San Joaquin River block salmon migration near Gravelly Ford (rkm 368) except in wet years, but this may change as a result of litigation (App. C).

Run timing

Rutter (1904:121) remarked that “Adult salmon may be found in the Sacramento River at almost any time of year” and this is still true, as demonstrated by counts at the ladder at the RBDD (Figure 6-3). The temporal distribution of adult migration of Chinook in the Sacramento River is now heavily concentrated between August and November, reflecting the numerical dominance of the fall-run, but presumably was more evenly distributed when other runs, especially the spring-run, were more abundant.

It seems likely that historically, adult Chinook also migrated up the San Joaquin River in every month. The Commissioners of Fisheries (1875) described what may have been a now extinct summer-run of Chinook in the San Joaquin River that migrated in July and August, despite average water temperatures over 25°C. Unequivocal evidence of late-fall Chinook in the San Joaquin system is lacking, but suitable conditions existed, and there are accounts of adults in good condition in the system in January and February (Yoshiyama et al. 1996). Fall-run and spring-run would have migrated into the system in the remaining months. There is no equivalent to the RBDD on the San Joaquin River, however, so data from counts exist only for 2003 on the Stanislaus River where a new weir has been installed.

Figure 6-2. Discharge in lower Mill Creek during the period of spring-run migration. During wet years such as 2004 there is enough water for spring-run migration except perhaps at the very end of the migration period. In drier years such as 2001, passage may be curtailed by inadequate flows during the peak of the run. This results from diversions. The dashed line in the lower panel shows discharge in 2001 at the USGS gage, which is upstream from the diversions. The solid line shows discharge at the CDWR gage downstream from the diversions. Circles show the timing of migration based on ten years of weir counts (Van Woert 1964). About 25% of years are as dry or drier than 2001, based on 76 years of USGS gage data.

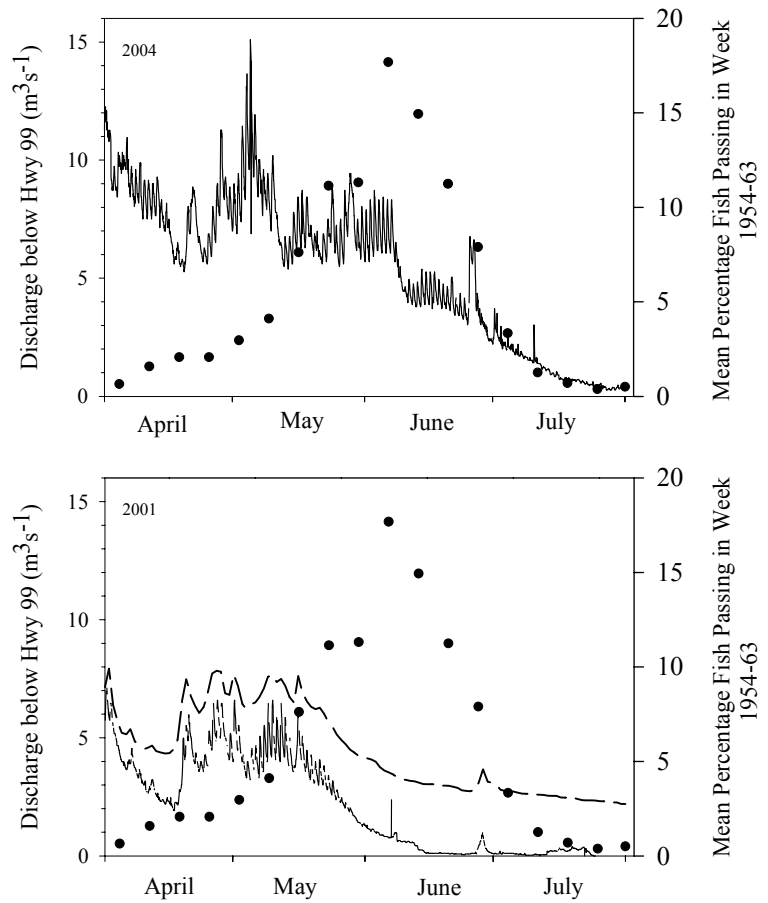
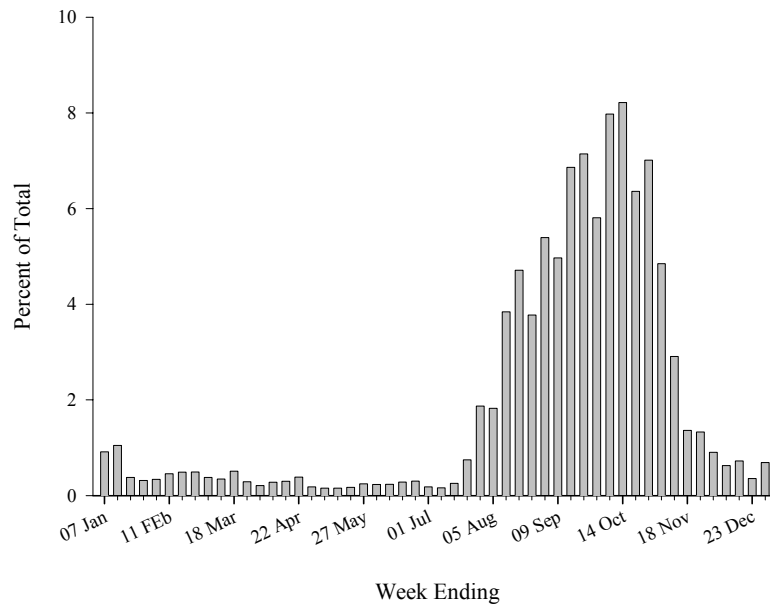


Figure 6-3. The temporal distribution of adult Chinook salmon passing the ladder at the Red Bluff Diversion Dam, 1983-1985. The gates at the dam have been opened for part of the year since 1986, so more recent data are not available. Data from CDFG, as given in Table 5 of Cramer and Demko 1986.



The RBDD ladder counts formerly provided the best information on the timing of migration of Chinook and steelhead in the Sacramento River, as well as on their abundance. Since 1987 the gates have been open for large parts of the year, so more recent information for those periods is based on estimates from carcass surveys or on extrapolation from periods when the dam gates are closed. Chinook passing through the ladder at the RBDD are assigned to runs based on inspection of a sample of about 50 fish and the time of year. These assignments involve some error, particularly around the beginning and end of the fall-run migration. Even a small error in assignment for the more numerous fall-run would have a large effect on the estimated timing of the other, much smaller, runs (Cramer and Demko 1986), and estimates of the number of spring-run for ~1970 – 1990 probably are inflated by misidentified fall-run (C. Harvey-Harrison, CDFG, pers.comm. 2005).

Fall Chinook

The timing of the fall-run migration past the RBDD is represented by the pronounced hump from August into November in Figure 6-2. The timing of the fall-run migration is less well documented in other rivers, but the period of spawning is generally well defined from carcass surveys conducted to estimate abundance (Table 6-1).

Table 6-1. Temporal distribution of fall-run Chinook spawning in selected Central Valley salmon streams.

Fall-Run Spawning			
River or Creek	5% By	Peak	95% By
American ²⁹	late Oct. to mid Nov. ³⁰	early Nov. to late Nov.	late Nov. to early Dec.
Mokelumne ³¹	Late Oct. to early Nov.	mid Nov. to Late Nov.	Late Nov. to Mid Dec.
Yuba ³²	early Oct	late Oct	late Nov
Tuolumne ³³	mid Sep to late Oct.	Early Nov to late Nov	Early Dec to late Dec
Sacramento	Mid-Sept. to mid-Oct.	Mid-Oct.-early Nov.	Early Nov.-early Dec.

Late-fall Chinook

Late fall Chinook follow the fall-run into fresh water, but because they arrive when flows are often high and turbid they are more difficult to observe than fall-run. Again, the best data on the timing of their migration are from the RBDD on the Sacramento River, where their run peaked in December and January (Vogel and Marine 1991). Their presence in other streams such as Butte Creek is inferred from the appearance of newly emerged fry in late spring.

²⁹ Based on redd counts from aerial surveys for 1991-95 reported by CDFG; note that when escapements are large it becomes impossible to distinguish individual redds.

³⁰ Significant spawning begins about the time the water temperature cools to 15° C, which depends upon management of the cool-water pool in Folsom Reservoir as well as on the weather.

³¹ Based on weekly redd counts: data from Jose Setka, East Bay Municipal Utility District

³² Data from Stephanie Thies, Jones & Stokes, pers. comm., 2004

³³ Data from Steve Kiriara, consultant for Tuolumne Irrigation District, pers. comm. 2004

Table 6-2. Temporal distribution of late fall Chinook spawning in major Central Valley salmon streams.

Late fall-Run Spawning			
River or Creek	5% By	Peak	95% By
Sacramento ³⁴	early Dec. – late Dec.	Late Dec. – late Jan.	late Mar. – late April

Winter Chinook

Winter-run begin to appear in the Sacramento River in late December, based on RBDD records and on recoveries of coded wire tagged fish from Livingston Stone hatchery (NOAA BRT 2003). Fish at the RBDD are assigned to winter-run as late as July, but some of these have been demonstrated to be spring-run (Cramer and Demko 1996). Spawning by winter Chinook begins in late April, peaks in May and June, and continues into mid-August (NMFS 1997). The spatial distribution of spawning has shifted farther upstream over time as partial blockages to migration at the RBDD and the ACID dam have been corrected (Figure 6-1). Eggs deposited farther upstream are less likely to be exposed to unfavorably warm water, and upstream from tributaries such as Cottonwood Creek, the permeability of gravels is likely to be higher, because transport of fine sediments in the Sacramento River is blocked by Shasta Reservoir.

Table 6-3. Temporal distribution of winter Chinook spawning in major Central Valley salmon streams.

Winter-Run Spawning			
River or Creek	5% By	Peak	95% By
Sacramento ³⁵	early May - mid-May	early June - early July	early Aug – mid-Aug.

Spring Chinook

Spring Chinook enter Mill, Deer and Butte creeks from March through June, based on observations by CDFG biologists (CDFG 2004a,b). In counts at a weir on Mill Creek between 1954 and 1963, the migration peaked in late May and early June, but the tail of the migration extended through July (Figure 6-4). Passage at the RBDD was somewhat later, from early April to mid-October. Although the timing of spring-run passage varied from year to year, before 1980 half the Spring-run were usually past the RBDD by early July; by 1983-85, the last years for which complete data are available, the run peaked in August (Cramer and Demko 1996). This could reflect hybridization with fall run, or errors in assignment for the more numerous fall-run. Chinook also enter the Feather and Yuba rivers in the spring, but the nature of these run is uncertain; genetically, the Feather River fish are closely related to fall-run (Ch 2).

³⁴ Doug Killam, CDFG Red Bluff, personal communication, 2004

³⁵ Doug Killam, CDFG Red Bluff, personal communication, 2004

Figure 6-4. Average weekly counts of spring Chinook passing a weir on Mill Creek at Clough Dam, 1954-1963. Data from Van Woert (1964).

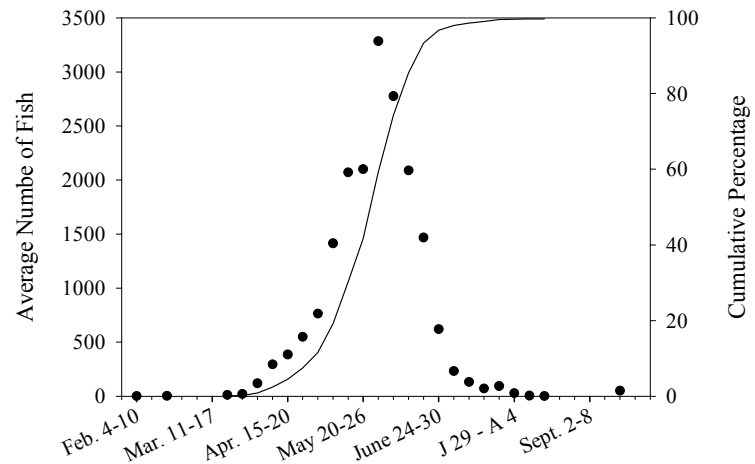


Table 6-4. Temporal distribution of spring Chinook spawning in major Central Valley salmon streams.

Spring-Run Spawning			
River or Creek	5% By	Peak	95% By
Butte Creek		Late Sept. – early Oct.	
Deer Creek	late Aug.	Sept.	Oct.
Mill Creek	late Aug.	Sept.	Oct.
Sacramento River ³⁶	late Aug – early Sept.	mid-Sept. – early Oct.	late Oct.

Steelhead

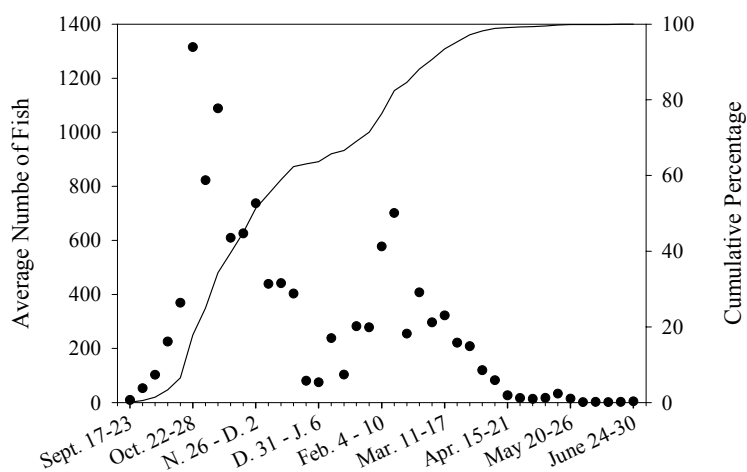
Like some Chinook, some steelhead exhibit a life-history pattern in which adults hold over through the summer in pools before spawning. There is evidence that these spring or summer-run steelhead occurred in the Central Valley (McEwan 2001); for example, steelhead passed the old Folsom Dam on the American River mainly in May, June, and July of 1943-47 (McEwan and Nelson 1991). Although a few steelhead passed the fish ladders at the RBDD in every month (McEwan 2001), the spring or summer-run seems effectively extinct.

Steelhead now move up the Sacramento River mainly from August through November, but some migrate upstream in all months (Hallock et al. 1961; McEwan 2001). Data on run timing comes mainly from trapping conducted just upstream from the mouth of the Feather River (Hallock et al. 1961) and from the ladders at the RBDD. The timing of movement into spawning tributaries is less well documented. Hallock et al. (1961:14) reported that most steelhead remain in the mainstem Sacramento, “where they concentrate on riffles occupied by spawning king salmon ...and near the mouths of the larger tributary streams,” until mid November or until

³⁶ Doug Killam, personal communication, 2004.

flows increase in the tributaries. However, counts at a dam on Mill Creek from 1953-62 peaked in late October – early November, although there was a second, smaller peak in February. Counts on the Feather River during construction of Oroville Dam peaked in September or October (Brown et al. 2004).

Figure 6-5. Average weekly counts of steelhead passing a weir on Mill Creek at Clough Dam, 1953-1963. Data from Van Woert 1964. It seems likely that some fish bypassed the counting weir during high winter flows, but the general temporal pattern is probably correct.



Although some steelhead survive spawning, it is commonly observed that they eat little if anything during the spawning migration (e.g., Shapovalov and Taft 1954). The timing of the steelhead migration and the pause near spawning Chinook is suggestive, however, and there is evidence that adult Central Valley steelhead consume Chinook eggs. Burns (1974) reported that 79 of 83 stomachs of adult steelhead collected in Mill and Deer creeks in 1969-71 contained small amounts of food, mainly Trichoptera, although salmon eggs were also common in stomachs collected in November and December. Only 11% of the stomachs of steelhead from the Cowlitz River in Washington examined by Vander Haegen et al. (1998) contained food.

Native winter-run Central Valley steelhead spawn mainly from late December through April (Hallock et al. 1961), so most spend several months in the river before spawning. Steelhead are normally tributary spawners (McEwan 2001), and according to Hallock et al. (1961:16) “spawn in practically every tributary of the upper Sacramento River and appear to do so in numbers more or less proportionate to the amount of runoff.” Steelhead tend to migrate farther upstream than Chinook, and may spawn in small tributaries that go dry in late summer. Because steelhead spawn mainly in the winter months they are difficult to observe, and fewer data are available on spawning than is the case for Chinook. The best data are from steelhead in the American River (Hannon et al. 2003), but this population appears to be derived from coastal steelhead that were brought to Nimbus Hatchery (McEwan and Nelson 1991; Nielsen et al. 2005).

Native Central Valley steelhead tend to be small. Fish trapped by Hallock et al. (1961) between 1953-54 and 1958-59 averaged 46 cm fork length, or 47.5 cm if small fish that may have been moving downstream are ignored. The length distribution is broad and bimodal, however, with a standard deviation of 8.6 cm, and modes at 39.5 and 52 cm. Average weight was

about 1.4 kg. The age distribution of 100 fish, based on scales, was: 17 two-year-olds, 41 three-year-olds, 33 four-year-olds, 6 five-year-olds, 2 six-year-olds, and 1 seven-year-old. Eighty-three were on their first spawning migration. (Information on the size and age of adult Chinook is given in Ch. 14, on ocean harvest.)

Table 6-5. Fork length in centimeters of Central Valley steelhead at various life stages, estimated from scale measurements of steelhead on their first spawning migration, for four life history patterns (age at return = years in freshwater/years in salt water). Data from Table 1 in Hallock et al. (1961).

Age at return	No. of fish	Length at salt water entry	Length at end of year 1	Length at end of year 2	Length at end of year 3	Length at capture
1/1	17	20.3	12.2			33.0
1/2	10	18.3	12.2	33.5		52.1
2/1	30	22.9	10.7	19.8		40.6
2/2	26	21.3	9.4	18.0	41.9	59.2

Steelhead now appear in small numbers in several tributaries of the San Joaquin River (McEwan 2001). Few data are available on them, but more should be forthcoming from the weir on the Stanislaus River. There is a lively recreational fishery for large *O. mykiss* in the Stanislaus (SRFG 2004), but many of these may be resident rather than anadromous fish.

Holding habitat

Both spring and winter Chinook hold in freshwater for months before spawning. Holding habitat is not a problem for winter-run in their existing habitat in the Sacramento River below Keswick Dam: flow is reliable, water temperatures are suitable, and the river is big enough to provide cover. There appear to be few if any spring-run remaining in the Sacramento River mainstem, however (Lindley et al. 2004), and holding habitat for the remaining populations in tributaries is critical: water temperatures are marginal or worse in the remaining spring-run streams, and fish are vulnerable to predators and poachers.

Water temperature has been extensively monitored in Butte Creek (Figure 6-6), where high temperatures in the summers of 2002 and 2003 caused high mortality among adult spring-run: 20-30% in 2002 and about 65% in 2003 (Ward et al. 2003; Paul Ward, CDFG, pers.comm. 2004). Summer mortality did not appear to be a serious problem in other recent years, but may have been underestimated since intensive surveys did not begin until 2002. However, holding habitat extends into the settled portions of the Butte Creek canyon (Williams et al. 2002), and local residents would likely have noticed large numbers of dead fish, had they been there. Assuming that high mortality did not occur in previous years, the data suggest that it results from more than a few days with mean temperature greater than 21°C at a monitoring site (Pool 4) in the central portion of the holding habitat (temperatures are about 1° C cooler at the upstream end of the holding habitat, and about 2°C warmer at the downstream end). There was also high

mortality from high water temperature in 1960 (Salo 1960), but releases into the stream from a hydropower dam above the holding habitat were then much lower ($\sim 0.15 \text{ m}^3/\text{s}$ rather than $1.15 \text{ m}^3/\text{s}$). Mortality in 2002 and 2003 was primarily from columnaris, a bacterial disease that affects the gills or skin (Ward et al. 2003; CDFG 2004b). Very few juveniles were captured in downstream migrant traps in the winter and spring of 2002-2003, raising concern that the viability of the gametes had been compromised by temperature stress, as might be expected from the literature (Marine 1992). However, high winter flows interrupted trapping, making that result inconclusive. Good numbers of young of the year were captured in 2003-2004, but no yearlings (Paul Ward, CDFG, pers.comm., 2004).

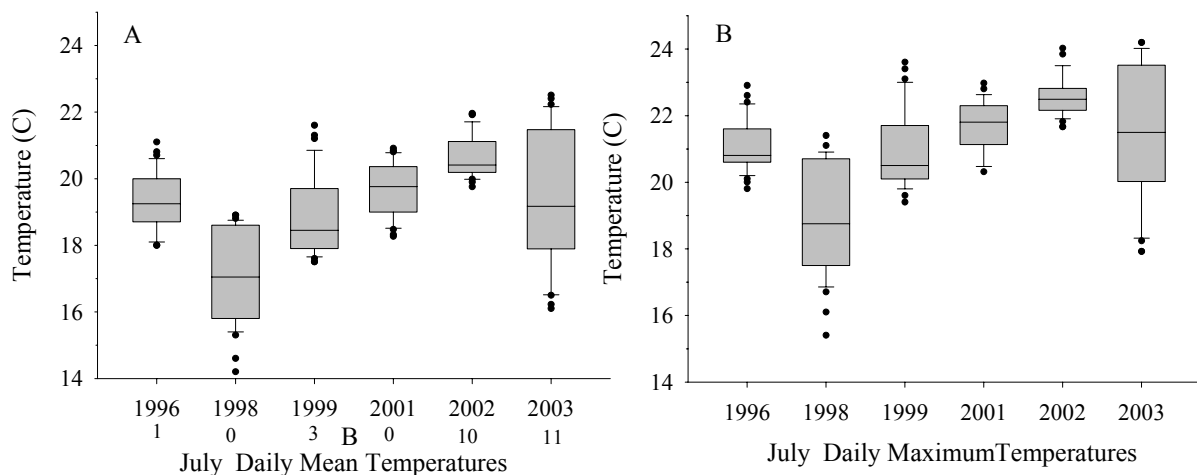


Figure 6-6. Daily mean (A) and daily maximum (B) water temperatures at the Pool 4 monitoring site in the reach of holding habitat on Butte Creek: The number of days with mean $> 21^{\circ}\text{C}$ in each year is shown below the date in A. Data from CDWR and CDFG. July 2002 was consistently warm; July 2003 was cool early but warm later.

Uncertainty regarding temperature-induced mortality before 2002 notwithstanding, the population of spring-run in Butte Creek increased rapidly in the late 1990s (Ch. 2), despite temperatures that exceed conventional assessments of the temperature tolerance of adult Chinook (e.g., Boles et al. 1988; McCullough 1999). Spring-run in Butte Creek are genetically distinct from spring run in Mill and Deer creeks (Hedgecock 2002), but Mill and Deer creek spring-run also seem tolerant of high temperatures; an early study of spring-run in Mill Creek gave the lethal temperature as 81° to 82°F ($27.2 - 27.7^{\circ}\text{C}$; Cramer and Hammack 1952). There is evidence that spring-run in the San Joaquin River were also tolerant of quite warm water (Clark 1943),³⁷ and spring-run also experience warm water in Beegum Creek (CDFG 2004b). Accordingly, evaluations of potential habitat for spring-run such as the Yuba River or the San

³⁷ Clark (1943) stated that water in a pool where spring-run were holding in 1942 “reached a maximum of 72°F (22.2°C) in July,” but did not give more details regarding the measurement; he did say that in September the fish were “in good condition.”

Joaquin River should use temperature criteria based on data from Central Valley streams rather than criteria from the general literature. In the long term, however, expected climate change makes prospects for spring-run dim. The estimates for mid-century summer warming in California using version 3 of the “medium-sensitivity” Hadley Centre Climate Model range from 2.2 to 3.1°C, depending on the scenario selected for future emissions of greenhouse gases (Mote et al. 2003; Hayhoe et al. 2004); such an increase in water temperature would make Butte Creek intolerably warm for Chinook in most years.

Reproductive behavior

Females select and defend territories and build redds, and males compete for access to the females. Successful spawning requires closely coordinated release of gametes by the spawning fish, which follows courtship behavior that may last for several hours. The spawning behavior of wild Chinook has not been described in detail, but for hatchery fish in an experimental stream the time between spawnings in successive egg pockets was 9.6 hours for females paired with large males, and 16.2 hours for females paired with small males (Berejikian et al. 2000a). Presumably the delay in spawning with smaller males reflects preference for larger ones, since it allows more time for a larger male to displace the smaller one (see Fleming and Reynolds 2004, for a review of salmonid breeding systems). Spawning by steelhead can last from one or two days to a week (Briggs 1953). Average residence time for steelhead on redds in the American River is about three days, (Hannon et al. 2003), which is consistent with the observations by Briggs (1953) and Shapovalov and Taft (1954).

Breeding male Chinook vary strongly in their morphology (Figure 6-7), although not so strikingly as with coho salmon. Larger male Chinook develop a hooked snout, “breeding teeth,” and dark colors, and try to drive others away from a nesting female. Grilse, generally two-year old males but also some three year-olds³⁸ (Rich 1920), undergo less morphological change than larger males, and try to participate in breeding by lurking near a redd and darting in to contribute gametes as the dominant male and female are doing so. Grilse are less attractive to anglers and in the past were regarded as somehow abnormal, but the current view is that early maturation and “sneaker” mating tactics can be the preferred alternative from an evolutionary perspective (Fleming and Reynolds 2004). The conditions under which this should be so and the factors controlling the development of one form or the other have been the subject of recent scientific interest. The issue is complex and does not yet seem well enough understood to inform management, except that rapid growth in juveniles tends to lead to early maturation (Thorpe 2004).

³⁸ Quinn (2005) argues that the term grilse properly applies to Atlantic salmon that have spent one year at sea, but early salmon biologists such as Rutter and Rich also used the term for Pacific salmon.

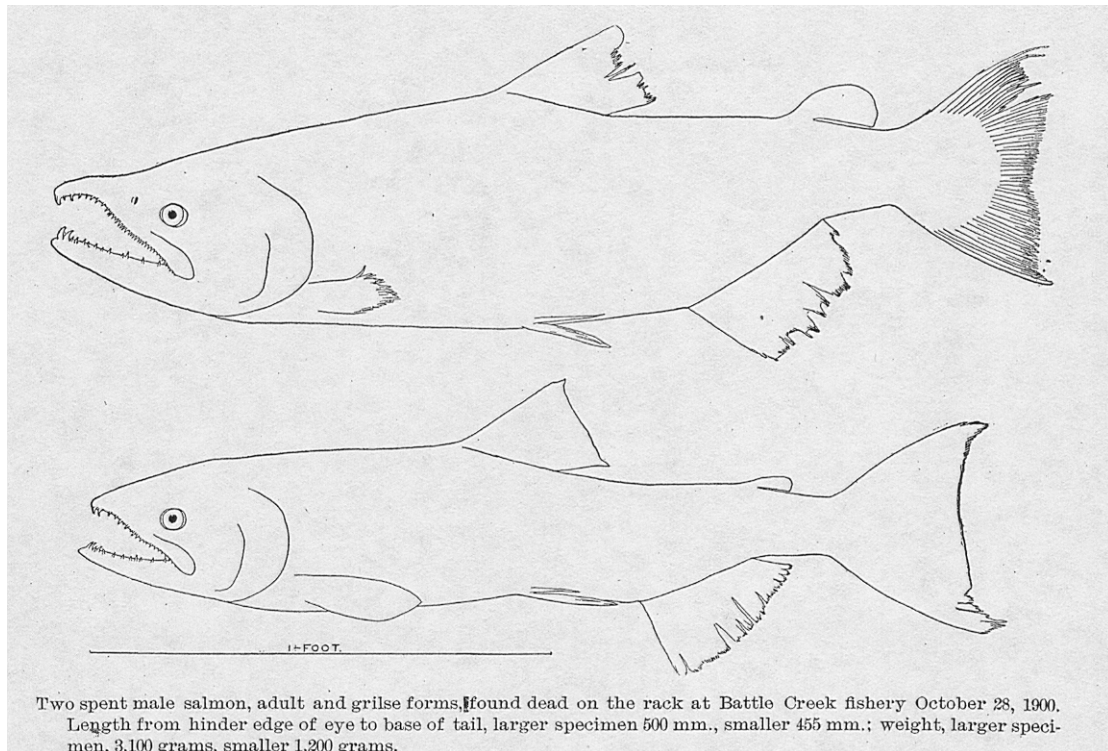


Figure 6-7. “Hooknose” and grilse or “jack” morphs of adult male Chinook salmon. Copied from Rutter (1904).

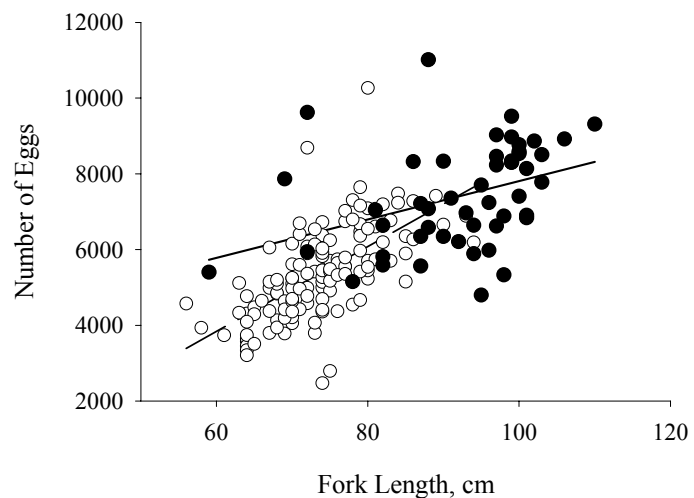
After spawning, female Chinook defend their redds for as long as they are able to do so, sometimes for several weeks, but steelhead do not (Briggs 1953; Healey 1991). Males of both species leave the redd in search of other females. Although some steelhead survive to spawn again, most do not; the median of repeat spawners reported for 23 populations was only 10% (Fleming 1998).

Fecundity

The number and size of eggs laid by Chinook and steelhead are highly variable, among both individuals and populations (Lister 1990; Healey and Heard 1984; Healey 2001; Beacham and Murray 1993; Moyle 2002), but surprisingly few good data are available from the Central Valley, except for winter Chinook at Livingston Stone Hatchery. Available data are presented below. Moyle (2002) offers as a rule of thumb that steelhead carry about 2,000 eggs per kilogram of body weight. Based on Hallock et al.’s (1961) length and weight data and Moyle’s rule of thumb, Central Valley steelhead of average weight would carry about 3,000 eggs. The fecundity of 23 steelhead from Scott Creek, a coastal stream south of San Francisco, varied from under 2,000 to over 11,000, and the relation between fecundity and length was reasonably well described by $F = 0.9471 \text{ Length}^{2.1169}$ (Shapovalov and Taft 1954). Individual variation was considerable, however, and Shapovalov and Taft remarked that a 60 cm female could have from 3,800 to 7,800 eggs.

The fecundity of 50 wild fall Chinook taken in the gill net fishery in Suisun Bay around 1920 averaged 7,422, varied from 4,795 to 11,012, and was only weakly related to length (McGregor 1922; Figure 6-8). Unfortunately McGregor did not describe how the fish were selected, and he did not specify the length measurement, but fork length was conventional at the time (Snyder 1922). The fecundity of 56 fall-run collected in Battle Creek or in the Sacramento River near Redding in 1939 averaged 6,404 and varied from 3,861 to 11,223, and was only weakly related to length (Hanson et al. 1940, App. A). The fecundity of 135 randomly sampled fall Chinook at Nimbus Hatchery in 1996 averaged 5,386, varied from 2468 to 10,264 and was moderately related to length (K. Vyverberg, CDFG, unpublished data; Figure 6-8). The change in the age distribution of Central Valley Chinook toward younger fish (Chapter 14) may help explain the change in the strength of the relationship between length and fecundity as well as the difference in size, since older fish at a given size tend to have higher fecundity (Healey 2001).

Figure 6-8. Fecundity v. length with regression lines for 50 Chinook sampled by McGregor (1922) from the gillnet fishery in Suisun Bay around 1920 (filled circles), and 135 Chinook sampled at Nimbus Hatchery in 1996 by Kris Vyverberg of DFG (unpublished data; open circles). For the 1923 data, $r^2 = 0.14$, slope = 50.74, intercept = 2734.2; for the 1996 data, $r^2 = 0.41$, slope = 112.09, intercept = -2886.7.



Fecundity in Chinook varies considerably among populations as well as within them (Healey and Heard 1984; Healey 2001). McGregor (1923b) reported that the average fecundity of 68 fall Chinook from the Klamath River was only 3,891, although the fish were intermediate in size between McGregor's and Vyverberg's Central Valley samples (mean fork lengths 81.4, 92.4, and 73.8 cm; Figure 6-9). Winter-run appear to be smaller but more fecund than the Nimbus Hatchery fall-run in Vyverberg's sample. The average fecundity of winter Chinook at Livingston Stone Hatchery between 1998 and 2003 varied from 3,416 to 4,891, depending mainly on the size of the fish (Figure 6-10). The recent average fecundity for winter-run at Livingston Stone Hatchery is considerably greater than the estimate of 3,800 given in NMFS (1997), probably because of an increase in length starting in 2000.

Figure 6-9. Distributions of size (open boxes) and fecundity (shaded boxes) for fall Chinook salmon collected in Suisun Bay ~ 1920, Klamath River ~ 1920, and Nimbus Hatchery on the American River, 1997, and for winter Chinook from Livingston Stone Hatchery. Data from McGregor 1923b, Kris Vyverberg, DFG, and John Rueth, USFWS.

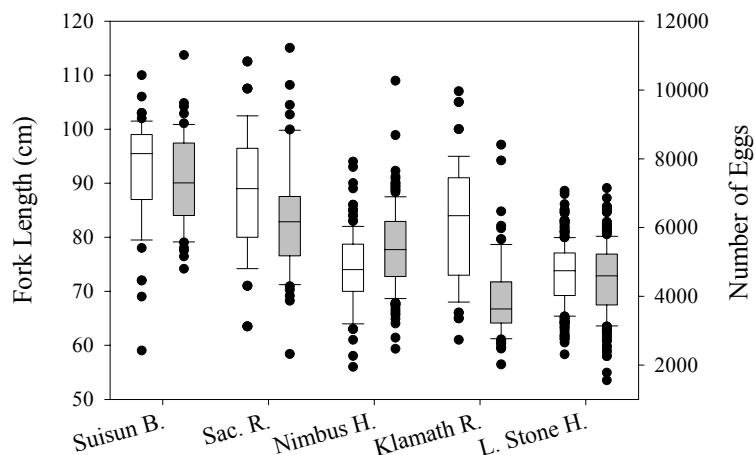
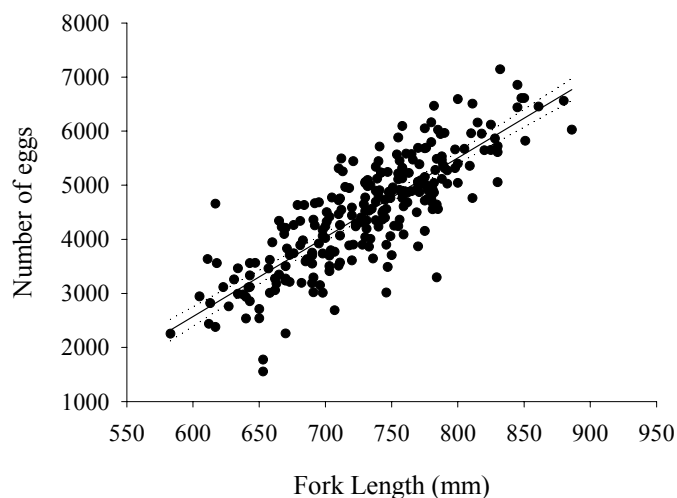


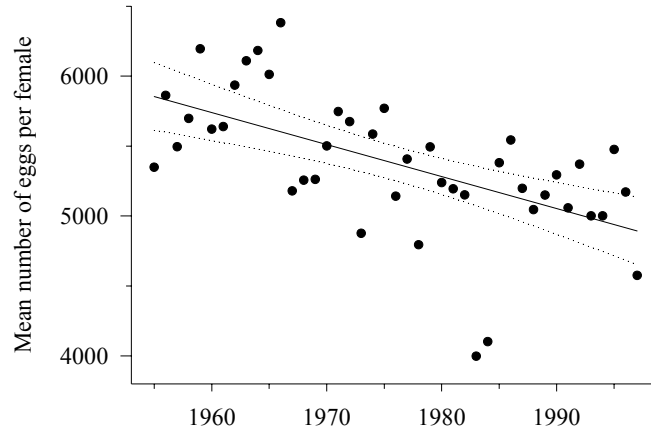
Figure 6-10. Fecundity of winter-run salmon at Livingston Stone Hatchery, 1998–20003, with regression line and 95% confidence intervals; length accounts for 68% of the variation in egg number. (intercept = -6237.85, slope = 14.769). Weight accounts for almost as much of the variance in egg number (65%) as does length. Data from John Rueth, USFWS.



Production hatcheries estimate only average fecundity, and based on these estimates average fecundity at Nimbus Hatchery has declined significantly (Figure 6-11). Possible reasons include a decrease in adult size (Williams 2001) and changes in hatchery practices; with current hatchery practices more eggs are expressed before fish are stripped, and more two-year old females are selected for stripping (Terry West, CDFG, pers.comm. 2003). The estimates are also of variable accuracy, since they depend on sometimes problematical estimates of the egg size.³⁹ Winter-run eggs at the Livingston Stone Hatchery are counted more carefully, but the counts are of expressed eggs and some eggs that adhere to the ovaries are missed.

³⁹ For Nimbus hatchery, for example, the recorded number of eggs per ounce for each batch of fish processed is constant in some years and highly variable in others, indicating that the number was sometimes assumed rather than measured. Moreover, egg size is highly variable among females (Rombough 1985) so there is ample opportunity for sampling error, and there is no record of how samples were taken in the past, even when the eggs in the samples were counted.

Figure 6-11. Average fecundity at Nimbus Hatchery over time; dotted lines show 95% confidence intervals. Data from Frey Meyer and Terry West. Note the caveats about the data in the text.



Fecundity is important for management and should be better documented. For example, goals for adult returns are set in terms of numbers of adults, but for most purposes the number of viable eggs is of more interest. Setting goals in terms of adults assumes some average number and quality of eggs, but these vary from year to year. For example, fecundity at Nimbus Hatchery in 1983 and 1984 was unusually low (Figure 6-11), presumably because of the strong El Niño, so an assessment of this run based on numbers of spawners alone would be unduly optimistic. Fecundity or related measures such as the gonosomatic index ($100 \times \text{gonad mass} / \text{body mass}$) might also be used for an index of ocean conditions.

Egg size should be considered together with egg number, since larger eggs are more likely to produce surviving offspring (Heath et al. 1999; Klemetsen et al. 2003), particularly if habitat quality is poor (Einum and Fleming 1999). Since the total energy that can be dedicated to reproduction is limited, there is a trade-off between egg size and egg number. For a constant environment, there should be an optimum egg size, but real environments are variable and females vary in their ability to detect and occupy higher quality spawning habitat, and individual factors also influence egg size: larger fish tend to have larger eggs (Hankin and McKelvey 1985), older fish of a given size may have larger eggs (Kinnison et al. 2001), and other factors probably are involved as well. For example, Atlantic salmon that grow rapidly before migrating to the ocean have smaller eggs (Jonsson and Flemming 1996). Presumably in consequence, egg size varies a great deal within populations, although it varies little within individual females; for example, in experimental work on the relationships between initial egg weight and time to maximum wet weight of the alevins, Rombough (1985) found females from the Qualicum Hatchery, British Columbia, with mean egg weights ($\pm$ sd) ranging from $0.163 (\pm 0.007)$ g to $0.437 (\pm 0.008)$ g. Egg size also varies among life-history types and populations. Stream-type Chinook have smaller eggs than ocean type (Healey 2001), and within life-history types populations with long freshwater migrations tend to have smaller eggs (Kinnison et al. 2001). For reviews dealing with the evolution of egg size and number in Chinook specifically and salmonids generally, see Healey (2001) and Einum et al. (2004).

Just what limits the advantages of larger eggs in salmon is unclear. It has been commonly assumed that oxygen supply was such a factor. Before hatching, dissolved oxygen reaches the embryo by diffusion through the wall of the egg, and metabolic wastes disperse by the same passive process, at rates that vary directly with the concentration gradients. As egg size increases, the area of egg surface per unit volume of egg decreases, and if the oxygen demand of the embryo varies directly with the volume of the egg, the demand for oxygen per unit area of egg wall would increase. However, recent experimental work indicates that the oxygen demand of embryonic brown trout scales with the 0.44 power of the volume, well below the 0.66 power that would result in a constant oxygen demand per unit area of cell wall⁴⁰ (Einum et al. 2002). Einum et al. (2002), citing Beacham et al. (1985), suggested as an explanation that the variation in egg size at the critical period just before hatching reflects variation in the amount of yolk, rather than the size of the embryo. This should be confirmed with Chinook.

Rapid selection for smaller egg size has been reported in a captive population of Chinook (Heath et al. 2003). The finding has been challenged (Fleming et al. 2003; Beacham 2003) and defended (Fox and Heath 2003; Heath et al. 2003), and additional work on this topic can be expected.

⁴⁰ The oxygen demand of an egg can be described as a power function of the volume/surface ratio: $VO_2 = a(4/3\pi r^3)^b/4\pi r^2$. If $b > 2/3$, oxygen demand per unit surface area would increase with egg diameter.

CHAPTER SEVEN

HYPORHEIC HABITAT

"The alevins have many enemies in the streams; fry but few." Rutter (1904:69)

"Most of the eggs deposited are eaten by other fishes, or are killed by being covered with sand and gravel. Those not destroyed hatch in from seven to ten weeks, according to the temperature of the water. ... It requires about six weeks and more for the yolk-sac to be absorbed, when the fry are able to swim and are ready for their seaward migration. Most of the alevins, however, are devoured by other fishes before they are able to swim. It is to prevent this great mortality among eggs and alevins that artificial propagation has been employed." Rutter (1904:72)

"Operation of hatcheries was originally based on the assumption that natural spawning was inefficient and that the eggs of a few females sheltered in a hatchery would produce as many fry as the eggs of many females spawning naturally. Today we know that the percentage of hatch under normal stream conditions is about as high as in the hatchery." Murphy and Shapovalov (1951:506)

"... there is no doubt that, during the period of study, substantially more young fish were introduced into Prairie Creek via natural propagation than could be supplied through standard hatchery methods utilizing the entire run in the creek." Briggs (1953:58)

"... mortality of king salmon to fry stage ranges from 85.2 to 100 percent and averages 95.8 percent. It is quite obvious that the incubation stage is the most critical period in the life history of king salmon. From these studies it was determined that unstable streamflow was the principal cause of these losses." Gangmark and Bakkala (1960:152)

"It is obviously time for a serious study of the behavior and ecology of the salmonid alevin." Dill (1969:97)

"... the distribution of bed material sizes, depths of scour and fill, and rates and grain sizes of sediment transported over a streambed are characterized better by their variability than by their average condition." Lisle (1989:1317)

"Published estimates of the mortality rate between egg laying and fry emergence are so few and so variable that it is difficult to draw any firm generalizations." Healey (1991:329)

Salmon start life underground as well as under water. This chapter deals with the underground phase of the salmon life cycle and with some related aspects of salmon biology. The topic is treated in some detail, because most naturally spawned salmon die in this phase of

life, and most of this mortality is avoided in hatcheries. This is the rationale for hatcheries. For the same reason, however, hatchery culture relaxes selection for traits that increase survival in natural reproduction, and may select against some such traits. Accordingly, an understanding of the hyporheic phase of the salmon life cycle is necessary for understanding the potential effects of interbreeding between hatchery and naturally produced fish, as well as for managing the rivers.

Female salmon dig nests called redds in gravel deposits on the beds of streams, where they lay their eggs and bury the eggs directly after they are fertilized. The embryos and alevins develop there, and juveniles often burrow back into the gravel for cover. Thus, salmon habitat extends below the bed of the stream into the “hyporheic” zone, the saturated sands and gravels in the beds of streams that exchange significant amounts of water with the surface stream. The quality of hyporheic habitat for embryonic and larval salmon is highly variable, so reproductive success depends heavily on the sites selected for redds and on the construction of the redds, as well as on the quality of the eggs. In a discussion of larval adaptations to hyporheic conditions in sockeye, Bams (1969:72) noted that: “These adaptations are consequences of the inter-gravel requirement and show by their very existence and their being maintained in the face of a tremendous scope for selection (some 90% of the brood dies in each cycle before reaching the migrant stage) that development in the gravel is a very important requirement and that it is maintained by a continuing strong selective pressure.” Presumably, Chinook exhibit similar adaptations.

Hyporheic habitat

For organisms the size of humans, the surface of a streambed seems like a definitive boundary, but in alluvial streams it can be highly permeable to water and to organisms whose size is scaled in millimeters or even in centimeters, and there is often considerable exchange of water, nutrients, and organisms between the stream and the water in the permeable sediments. Although some scientists have long been aware of the hyporheic zone, interest in and understanding of it has increased rapidly in the last two decades (Stanford and Ward 1988; Gilbert et al. 1994; Boulton et al. 1998; Jones and Mulholland 2000). There is no official definition of hyporheic flow or of the hyporheic zone in which it occurs, but generally it involves water that has been part of the surface flow somewhere upstream, or the area occupied by organisms that are particularly adapted to live in the spaces between grains of sand or gravel, but spend part of their lives in the surface stream or are in some way dependent on it.

The extent of the hyporheic zone varies with the geological setting of a stream. In bedrock streams it is limited to small patches of sand and gravel that occur in the lee of logs or boulders or in eddy zones downstream from bedrock constrictions. In fully confined alluvial reaches such as the lower canyon reach of Butte Creek or lower Clear Creek, or the Sacramento River between Redding and Jellys Ferry (rkm 475-426), the hyporheic zone extends to the bedrock below and on either side, with clear boundaries. In larger alluvial basins there is often no clear boundary, but rather a gradient across which hyporheic water fades into groundwater that is not

significantly affected, chemically or biologically, by interactions with the surface stream, except over long periods of time.

Hyporheic flow occurs over a large range of spatial scales. It is often apparent at short spatial scales at gravel bars, when water can often be seen seeping out of the gravel into areas that are lower in elevation than the adjacent surface stream. Similarly, hyporheic flow typically enters gravels at the downstream end of pools and resurfaces in the riffle downstream. In valleys with meandering streams, the gradient of the valley is steeper than the gradient of the stream, inducing subsurface flow that cuts across the meanders. Where alluvial basins are separated by bedrock constrictions, water downwells into the alluvium where the basin expands, and upwells where it contracts. Hyporheic flow at all of these scales may be important for salmonids; for example, bull trout tend to select spawning sites where water is upwelling at the basin scale but downwelling locally (Baxter and Hauer 2000).

The hyporheic zone is also important for basic ecological processes such as nutrient spiraling (Brunke and Gonser 1997). Because the flow of a stream tends to carry nutrients downstream, ecologists speak of nutrients in streams as spiraling rather than cycling (Elwood et al. 1983). The average distance downstream that nutrients move in the course of a cycle is called the spiraling length (Duff and Triska 2000), and in general, streams with shorter spiraling lengths have higher biological productivity. Particles of gravel and sand or pieces of wood in the hyporheic zone are covered with a thin “biofilm” of organic material containing bacteria that take up dissolved organic matter from the water and process it in various ways, depending upon the amount of dissolved oxygen in the water. Since the total surface area of hyporheic particles is very large, this bacterial processing can substantially shorten spiraling lengths. For example, nitrogen in dissolved or particulate organic material may be converted to nitrate or ammonium in the hyporheic zone, making it available to algae and other organisms when the hyporheic water returns to the surface stream (Duff and Triska 2000). When hyporheic flow passes under vegetated surfaces such as riparian habitat inside a stream meander, the nutrients may become available to vegetation (O’Keefe and Edwards 2003). Hyporheic processing of nutrients should be particularly important in salmon streams, which receive pulses of marine-derived nutrients from the carcasses of returning adults (Bilby et al. 1998; Wipfli et al. 1998, 1999, 2003; Stockner 2003).

Juvenile salmonids often take cover in the interstitial spaces between gravel and cobbles on the bed of the stream (Chapman 1966). Chinook as large as 70 mm were captured in emergence traps set on redds in the Tuolumne River (EA 1991b), and presumably had burrowed under the 30 cm skirts of the traps. In other words, salmonid habitat extends down into the hyporheic zone for juveniles (and for adults of smaller species) as well as for eggs and alevins. However, the ability to use this habitat depends on the size distribution of the substrate. Concentrations of fine sediment are high in many Central Valley streams, and this likely results in loss of shelter for juvenile salmon, as well as lower egg and alevin survival and lower production of invertebrates. The use of substrate for shelter has received little attention in studies or restoration projects in the Central Valley, which may be a significant oversight. For example, it could be useful to consider

the role of the substrate as shelter in designing gravel restoration projects, since particles too large for spawning may be important for this purpose. Similarly, larger juveniles holding position in riffles frequently utilize cobbles for velocity cover (Jackson 1992). This suggests that gravel enhancement projects should include some percentage of larger clasts, so that the projects do not result in riffles that lack velocity shelters. The desirable percentage of cobbles in added gravels seems another good subject for field experiments.

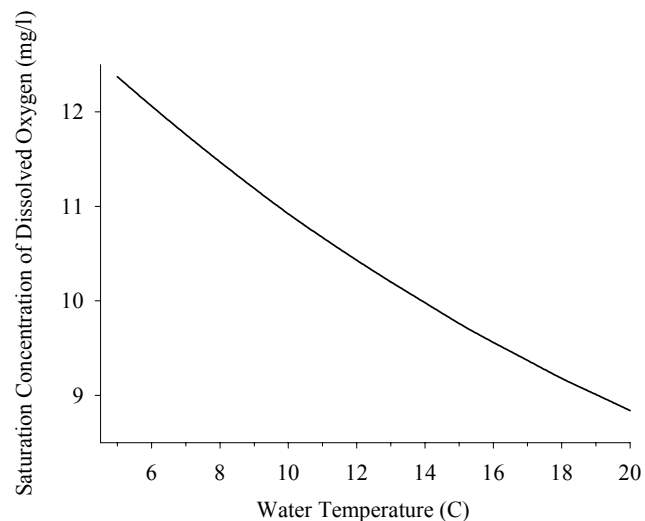
Spawning gravels consist mainly of clasts or particles of rock that form an open framework that supports the weight of the deposit and encloses considerable pore space. Some of this space usually is occupied by smaller particles, but the rest is filled with hyporheic water that is more or less free to flow through the deposit, depending mainly on the number and size of the connections among the spaces. This permeability or conductivity of the deposit, and the local hydraulic pressure gradient, determine the rate of hyporheic flow. Permeability can be highly variable spatially, especially vertically (e.g., Peterson and Quinn 1996).

The permeability of gravel deposits can be estimated from information about the size, shape and packing of the particles using the Kozeny-Carman equation (Johnson 1980, Vogel 1994). Obtaining the necessary information about size, packing, and shape for spawning gravels in the field would not be practicable, but the Kozeny-Carman equation could nevertheless be useful for simulations exploring, for example, the effects of fine sediment on permeability (Johnson 1980), and laboratory experiments in which parameters are measured for samples of spawning gravels could provide guidance on the plausible ranges of the parameters. For most practical work at the scale of redds, it seems simpler to measure permeability. Unfortunately, the standpipe method normally used to measure permeability (Terhune 1958) may not be reliable in the field, since work in progress at California State University Sacramento (CSUS) indicates that more water may leak from the surface stream down along the standpipe than Terhune realized (T. Horner, CSUS, pers.comm. 2005). Approaches to modeling flow through the hyporheic zone at larger spatial scales are developing rapidly (e.g., Packman and Bencala 2000; Wörman et al. 2002).

Much effort, probably too much, has gone into measuring the distributions of particle sizes in spawning gravels and relating these to the survival of eggs and alevins, in order to develop methods for assessing the quality of spawning habitat (see Kondolf 2000 for a review). Gravel size is only indirectly related to egg survival, and matters mainly as it affects rates of hyporheic flow, the quality of hyporheic water, and the stability of the bed. Since permeability is affected by the shape and packing of the gravel as well as the size distribution (Pollard 1955), relations between permeability and the size distribution, or between survival and the size distribution, are likely to be specific to the conditions in which they were developed. Nevertheless, equations predicting survival as a function of gravel size (e.g., Tappel and Bjorn 1983) seem useful if they are taken as approximations. Some rules of thumb regarding sediment size can also be useful. Permeability varies inversely with the amount of fine sediment, so the percentage less than 1 mm should be less than 10 or 12% (Kondolf 2000). Particles between 1 and 10 mm may hinder movement of alevins through the gravel, but studies supporting this idea (e.g., Bjorn 1969) may be confounded by the effects of low oxygen levels on the strength of the alevins.

The concentration of dissolved oxygen in redds is a critical factor for developing eggs and alevins, as discussed below. The dissolved oxygen concentration of downwelling water from the surface stream is limited by the water temperature (Figure 7-1), and at temperatures at which some Chinook incubate in Central Valley streams, the saturation concentration of oxygen is below optimal for developing embryonic and larval salmon. Biological activity in the hyporheic zone can be sufficiently intense to reduce the concentration of dissolved oxygen along hyporheic flowpaths over distances of meters, such as between downwelling areas such as at the tail of a pool and the upwelling regions in the riffle downstream (Hendricks and White 2000), so the dissolved oxygen concentration in water reaching the eggs may be well below that of the surface stream. Finally, metabolic activity and so the need of embryos for oxygen also increases with temperature. Accordingly, the quality of hyporheic habitat may be particularly important in the Central Valley, at the southern limit of the Chinook's range.

Figure 7-1: The saturation concentration of dissolved oxygen as a function of water temperature, over the environmentally relevant range for Central Valley salmon.



The importance of hyporheic flow for spawning habitat was recognized early in the twentieth century, and considerable experimental work regarding hyporheic conditions for salmonid eggs and larvae was conducted in mid-century (e.g., Wickett 1954; McNeil 1962, Vaux 1962; Sheridan 1962; McNeil and Ahnell 1964; Gangmark and Bakkala 1960). With the development of the popular Physical Habitat Simulations System or PHABSIM (Bovee et al. 1998) in the late 1970s, however, much more attention was given to describing spawning habitat in terms of the PHABSIM “microhabitat” variables: depth, velocity, and substrate size (e.g., Smith 1973; Bovee 1978). Hyporheic conditions, which are not addressed by PHABSIM, were largely ignored in instream flow assessments, except for estimates of sediment size. More recently, attention shifted back to subsurface or hyporheic flow and the geomorphic context of spawning habitat (e.g., Vyverberg et al. 1997; Geist and Dauble 1998, Geist 2000; Mesick 2001b; Geist et al 2002; Merz et al. 2004), although some recent reports still emphasize depth, velocity and substrate (e.g., Gallagher and Gard 1999; Geist et al. 2000). However, gravel permeability and hyporheic water quality distinguish selected from non-selected areas better than

the PHABSIM microhabitat variables (Vyverberg et al. 1997; Geist and Dauble 1998; Geist et al. 2002).

Unfortunately, ideas about “proper” gravel sizes have compromised restoration projects and even experimental studies. Some restoration projects in the Central Valley have replaced large but usable gravels with smaller gravel that has been scoured away in normal winter flows, resulting in a net loss of spawning habitat (Kondolf et al. 1996). Gangmark and Broad (1955) added five cubic yards of $\frac{3}{4}$ inch (19 mm) gravel to the site of their study of Chinook egg survival in Mill Creek, because they thought the existing gravel was too coarse, even though salmon spawned there. The added gravel was inherently unstable at the site, and to an unknown degree compromised the study results.⁴¹ Assessments of the suitability of gravel need to take account of the geomorphic context of the deposit.

Spawning

Unlike most other teleost fishes, most salmonids bury their eggs in gravel, typically 15 to 50 cm below the surface of the streambed for Chinook and steelhead (DeVries 1997).⁴² Provided that hyporheic conditions are favorable, and that the nest is not disturbed by other spawning salmon or by scour of the streambed during high flows, most of the eggs develop and hatch in the redd. The larval fish, called alevins (Hubbs 1943), normally rear there living off egg yolk until the remaining yolk is enclosed by the body of the fish, when the fry is described as “buttoned up.” The young salmonids then move up into the surface stream as juveniles called fry.

Redd site selection

Redd sites are selected by females, which defend territory within which they construct their redds (Briggs 1953; Shapovalov and Taft 1954). Most often, salmon and steelhead select redd sites where the topography of the streambed induces flow through the gravel, as in the transitional area between a pool and a riffle (Hobbs 1937; Chapman 1943; Shapovalov and Taft 1954),⁴³ or where larger channel features induce upwelling or downwelling (Geist and Dauble 1998; Geist 2000; Geist et al. 2002). Redds are also often located near logs or debris dams that induce localized downwelling or upwelling (Vronskiy 1972; Merz 2001). The quality of water is also important. Although Chinook spawn in areas where hyporheic water is either downwelling or upwelling, they tend to avoid areas with upwelling groundwater (Geist 2000; Mesick 2001b).

⁴¹ This was a multi-year experiment, and it is not clear whether gravel was added in only one year or more frequently.

⁴² The depths of egg burial given by DeVries (1997) are below the surface of the original streambed, not the surface of the redd tailspill, which may be 5-15 cm higher unless it is leveled by high flows.

⁴³ “According to Chapman (1943:169-170), (I)t is generally considered that one reason salmon choose the vicinity of a riffle is that the difference in waterhead forces a flow of water subterraneously through the gravel, in which the eggs are buried, in such a manner as to ventilate and aerate the water around the growing embryos.” Regarding steelhead, Shapovalov and Taft (1954:143) reported that “...the site is typically near the head of a riffle (which is also the lower end of the a pool) composed of medium and small gravel. ... The nature of the redd site insures a good supply of oxygen for the eggs, since in streams a considerable portion of the water flowing through a swift riffle passes through the gravel.”

The reported mean values for depth and velocity of water at Chinook redds are fairly consistent at ~ 0.3 to 0.55 m and ~ 0.4 to 0.6 m s⁻¹ (e.g., Healey 1991, Table 2). The reported ranges are broad, however, and there are occasional strong exceptions for reported means; for example, in one reach of the Snake River, the mean depths and vertically-averaged water velocity at redds were 2.8 m and 1.1 m s⁻¹ (Groves and Chandler 1999), and Chapman (1943) described Chinook spawning in water 4 or 5 m deep in the Columbia River. Hanrahan et al. (2004) recently described the “suitable” ranges of depth and depth-averaged velocity for Chinook spawning as 0.30 to 9.5 m and 0.25 to 2.25 m s⁻¹. The size of the gravels used for spawning by Chinook and steelhead is also highly variable. Median grain sizes from examples reviewed by Kondolf and Wolman (1993) ranged from about 10 to nearly 80 mm for Chinook and from 10 to 45 mm for steelhead. As a rule of thumb, salmon and steelhead can use gravels with a median grain size of about one-tenth the length of the fish (Kondolf and Wolman 1993), so larger fish can spawn in larger gravels. Healey (1991:323) summarized a short review of the topic by noting that “Provided that the condition of good subgravel flow is met, Chinook apparently will spawn in water that is shallow or deep, slow or fast, and where the gravel is coarse or fine.”

Other factors also influence selection of spawning sites. Spawning Chinook often concentrate near dams that block further migration (e.g., Gallagher and Gard 1999; Vyverberg et al. 1997), even if there is not a hatchery near the base of the dam (K. Vyverberg, CDFG, pers. comm. 2003). Logs, rootwads, or large stones may provide visual separation between spawners that allows closer spacing of redds (Merz 2001), and also induces local deposition of suitable gravel and upwelling or downwelling of water through it. Spring-run salmon in Beegum Creek seem to select deep spawning sites, perhaps in response to predation by the locally abundant bears (D. Killam, CDFG, pers. comm. 2003).

The details of the process of selecting redd sites and the relevant environmental cues remain unclear, however. It seems likely that, as with the remarkable navigational abilities of anadromous salmonids, a hierarchy of cues is involved, and that fish will select unfavorable areas when better areas are not available. In any event, spawning behavior has been shaped and presumably is maintained by natural selection, which raises the question whether hatchery fish that spawn in rivers may be less effective than wild fish in selecting and constructing habitat for their progeny. This seems plausible, as hatchery fish are less effective in other aspects of their breeding behavior (Fleming and Gross 1993; Fleming and Petersson 2001), but evidence bearing directly on the question is lacking.

Redd construction

Redd construction was described by Briggs (1953:19):

... all of the redd construction was accomplished by the female.⁴⁴ At fairly regular intervals, once every two to three minutes, she turned on her side and dug vigorously. This “digging” was accomplished by placing the tail flat against the substrate and suddenly lifting it upward with a powerful muscular contraction. The resultant hydraulic suction was generally strong enough to loosen stones and finer materials and to move them several inches upward. This material, once having been detached from the redd surface, was then carried by the current for a short distance before coming to rest again. This motion of the tail was usually repeated very rapidly five or six times, after which the individual rested before continuing the process.

Although this description was written about coho, Briggs stated that it applied as well to Chinook and steelhead, except that “the digging labors were conducted at a more leisurely pace than was noted with the silver [coho] salmon, with bouts of digging about five minutes apart. Steelhead, on the other hand, dug more rapidly than coho.” Jones (1959, quoted in Needham 1961), provided a more detailed description, based on slow-motion photography, of redd construction by Atlantic salmon, and suggested that the downward movement of the tail before the vigorous upstroke may also help to loosen the gravel; DeVries (1997) similarly noted that “... the female uses her tail to redirect and accelerate higher momentum fluid from the main flow field down into the redd, ...”

Redds normally consist of a series of pockets, usually three to six for Chinook (Burner 1951; Hawke 1978), each containing the eggs from one act of spawning. Hawke (1978) excavated seven stranded Chinook redds in New Zealand, and found that the first (farthest downstream) egg pockets tended to be deeper and to contain more eggs. Chapman (1988:2) provided a good narrative description applicable to large salmonids generally:

The salmonid redd in a stream begins as a pocket from which the female has removed fines and small gravels. ...

The female cannot or does not lift the largest particles in the substrate within the initial pocket; these form the clean egg pocket centrum, commonly a grouping of two to four large gravel or cobble particles that lie on the undisturbed substrate that forms the floor of the redds (Hobbs 1937; Burner 1951; Jones and Ball 1954; Vronskiy 1972). The female deposits the first group of eggs into this centrum and the male simultaneously fertilizes them. The eddying currents within the pocket help retain sperm in contact with the eggs. Currents at the bottom of the pocket deposit most eggs around the upstream bottom edges of large centrum components (Hobbs 1937).

The female quickly begins digging again directly and obliquely upstream from the first pocket. Current again carries the finer materials downstream from the redd, and gravels and some sands lifted from this newly excavated area drop into the first egg pocket or onto the tailspill, depending on the size of the excavated material. The female then

⁴⁴ Briggs notes that Jordan (1885) incorrectly reported that redds were dug by males using their noses as well as their tails, and this description was repeated by Jordan or by others as late as 1937. However, male sockeye do exhibit digging behavior (McCart 1968), which may account for Jordan’s error.

prepares a new egg pocket centrum of several large gravel or cobble particles cleaned of fine materials, and the egg deposition and fertilization process continues.

During excavation of the egg pockets, the female periodically drifts over the pocket, apparently testing the depth and shape with her caudal fin. When the redd is completed, there is a depression called the pot or the pit at the upstream end, and a mound called the tail or the tailspill at the downstream end; egg pockets are normally near the long axis of the redd and under the upstream portion of the mound. (Chapman 1988; Crisp and Carling 1989; Figure 7-2).

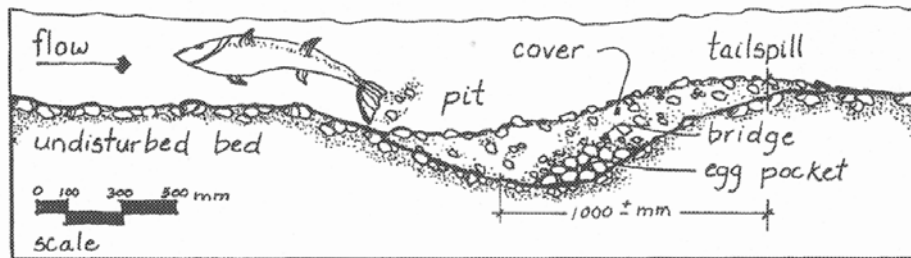


Figure 7-2. Sketch of a redd, showing features often mentioned in the relevant literature. This is actually of a chum salmon redd, so the spatial scale is small for larger Chinook, which are larger. Copied from Rennie and Miller (2000), courtesy of *the Canadian Journal of Fisheries and Aquatic Sciences*.

Whatever the importance of the downstroke or the downward deflection of higher-velocity water, it is clear that the current normally plays a role in redd construction. However, much current is not an absolute requirement for redd construction; successful spawning by introduced Chinook has been reported on a gravel shoal in a bay off Lake Huron (Powell and Miller 1990),⁴⁵ and there are lake-spawning populations of sockeye.

The process of creating the redd flushes some fine sediments from the gravel, but on average about 60% of the fine sediments (< 1 mm) remains, and the particle size distribution in the redd after construction is best predicted from the pre-existing distribution (Kondolf et al. 1992). It seems intuitive that the efficiency with which fine sediments are winnowed from the redd should increase with water velocity, but Kondolf et al. (1992) found that the effect was small.

Fine-scale patterns of flow around the redd are important in two respects. Local velocities within the egg pocket are low, so that eggs and sperm tend to remain there, and the percentage of viable eggs fertilized is very high, generally over 90% (Briggs 1953). After the redd is completed, the geometry of the tailspill induces downwelling into the redd (Stuart 1954), although the tailspill is often obliterated by high flows during incubation (Lisle 1989).

⁴⁵ Powell and Miller (1990) do not say anything about currents at the shoal where Chinook were observed spawning.

The reported size of Chinook redds varies substantially (Healey 1991). This might be expected, since the weight of spawning females can vary by a factor of ten, but it can also vary with the method for measurement. Redds on the American River averaged 5.8 m² when measured on the ground and 18.2 m² when measured from aerial photographs (Snider and Vyverberg 1996). When the density of spawning Chinook is high the boundaries of the disturbed areas frequently overlap, so that it is impossible to distinguish individual redds (e.g., Snider and Vyverberg 1996).

Existing redds may be excavated and destroyed by later-spawning females. This “superimposition” can be a source of significant mortality for embryonic Chinook; in four of six redd pairs excavated in a study on the Tuolumne River, the estimated mortality in the superimposed redd was > 80% (EA 1991e). The area of disturbed gravel is considerably larger than that of the egg pockets, so estimates of superimposition based on overlapping areas of disturbed gravel may be overestimates, but there is little reason to doubt that superimposition is an important cause of density-dependent mortality among Chinook, especially fall-run, in the Central Valley. Better quantification of the problem seems important for proper evaluation of the impacts of hatchery fish on naturally produced fish.

A possible complication for quantifying superimposition is that Chinook may construct more redds than they use (Hobbs 1937; Briggs 1953); 17 of 25 redds excavated by Briggs in Prairie Creek contained no eggs.⁴⁶ Briggs (1953) distinguished “trial redds,” which were constructed and abandoned before spawning, and “postspawning redds.” The population that Briggs studied was fairly sparse, however, and it is not clear that false redds are common where fish are more crowded and competition for spawning territory is more intense.

Steelhead redds on the American River average about 2 m² but some redds are over 6 m² (Hannon et al. 2003). However, the steelhead population in the American River is derived at least in part from coastal fish introduced to Nimbus Hatchery (Myers et al. 1998), and may be larger than other Central Valley steelhead. Steelhead also may construct more than one redd, but all 14 excavated by Briggs (1953) contained eggs. Hannon et al. (2003) reviewed reports on the average number of redds per female steelhead from other rivers and could conclude only that the average probably lies between one and two.

Single redds are minor features from a geomorphic perspective, but they can be numerous enough to modify the packing and sorting of bed materials in spawning areas, perhaps sufficiently to affect survival and risk of scour (Montgomery et al. 1996). Especially on regulated rivers with infrequent high flows, spawning by Chinook can create transverse ridges of gravel or “spawning dunes.” Shirvell (1989) described spawning dunes on the Nachako River in British Columbia as 0.5-0.75 m high, and averaging 20 m long and 13 m apart; Chinook spawned

⁴⁶ Rutter (1904) also excavated several redds and found no eggs, which contributed to his belief that Chinook broadcast eggs over the gravel, and that the digging motions of the females were really attempts to loosen the eggs in their ovaries. These may have been false redds, or he may not have dug deeply enough.

mainly on the upstream sides of these dunes. Spawning dunes are common in the San Joaquin River tributaries (Tim Heyne, CDFG, pers.comm., 2003), and also occur in Sacramento River tributaries (Huntington 1985), although they are washed by high flows. Where dunes do not develop, perhaps because flows are high enough for some sediment transport, but not enough for deep scour, the large clasts in the egg pocket centrum may accumulate as a lag deposit that appears to inhibit spawning, as apparently has happened on the American River (Vyverberg et al. 1997).

Temporal change in redds

The structure and sediment size distribution of redds in natural streams change over time. This may involve a gradual change, generally back toward the conditions at the site before redd construction, or it may involve an abrupt change during a high flow event that may sharply modify the redd or even destroy it. Unfortunately, the processes involved are complex, highly variable in time and space even within a single flow event (Hassan 1990), and inherently difficult to study. Some generalizations are nevertheless possible; as summarized by Lisle (1989:1317):

1. Fish excavate a pit, deposit eggs, and cover them with a mound of bed material that has reduced amounts of fine sediment.
2. During the rising stages of a subsequent storm flow, increasing amounts of suspended sediment and fine bed load are transported over the bed. Some enters the bed, and because of its small size, deposits at all depths down to the level that eggs were laid.
3. As the entrainment threshold of the bed surface is exceeded, the topography of the redd is obliterated, and a surface seal of sand forms [within the upper layer of gravel]. The seal inhibits further infiltration of fine sediment, despite the increase of suspended sediment concentration in the surface flow.
4. As bed load transport fluctuates during peak flow, the bed scours, eroding and forming seals at progressively lower levels. Scour may be deep enough to excavate and wash away the eggs.
5. Alternatively, bed load is deposited over the bed and forms a thick seal in combination with sand deposited below the original bed surface. Bed load deposited at riffle crests may be coarser than in transport because of local sorting. Other scenarios are possible with different sequences of scour and fill.
6. Little change in bed material occurs after scour and fill cease during waning stages of the hydrograph.

Incubation

After fertilization, the embryos of Chinook and steelhead develop and hatch in the redd, and remain there as alevins, nourished by the yolk from the large eggs, through the larval stage. Developing alevins in laboratory experiments move downwards and seek contact with solid

objects (Godin 1981), and presumably settle toward the bottom of the egg pockets in natural redds. They are also repelled by light. Near the end of their development, however, the aversion to light decreases, and for steelhead may reverse. Eventually, the alevins move upwards through the gravel, but if Chinook are like sockeye (Bams 1969) they retain enough aversion to light that they emerge mainly at night. The young fish, now called fry, are generally 30 to 40 mm long for Chinook and 20 to 30 cm for steelhead.

Emergence normally occurs after the remaining yolk is fully enclosed by the body (Bams 1969), but sac-fry (older alevins) are frequently captured in seines or screw traps even in the absence of high flows that might have exposed them involuntarily (e.g., Snider and Titus 2002). Although the alevins are capable of feeding (Bams 1969; Merz 2001), the external yolk must make them even more susceptible to predation. The emergence of alevins before they are buttoned up apparently represents a response to poor hyporheic conditions (Bams 1969). If so, then the frequency of sac-fry in monitoring samples could be useful as an index of the condition of hyporheic habitat in the stream. Presumably, poor conditions would also result in smaller fry, so the index could be used with more confidence if there is also a negative correlation between the percentage of sac-fry and their size.

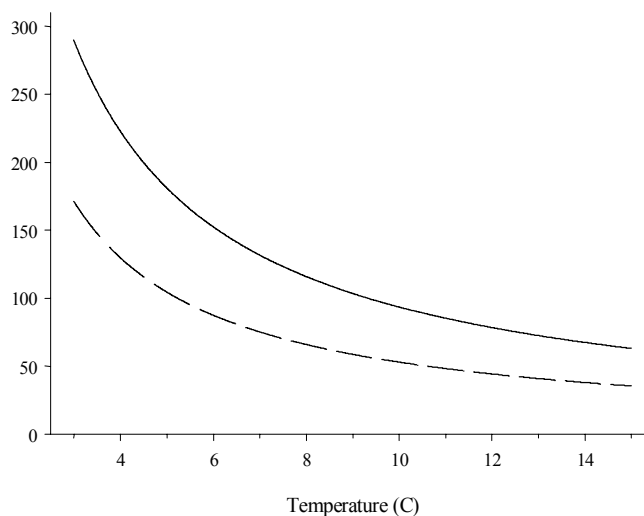
Alevins follow a developmental pathway directed toward achieving fry morphology by the time the yolk is exhausted, and growth is subordinated to that objective, as is nicely demonstrated by occasional twin larvae on a single yolk, each of which develops into a fully formed fry but about half normal size (Bams 1969). In consequence, alevin size and presumably subsequent survival is affected by egg size and environmental conditions. An Excel program for calculating incubation timing, based on empirical relationships, is available on the internet,⁴⁷ and more mechanistic models are also available (Beer and Anderson 1997; Beer 1999).

Temperature

Temperature strongly affects the rate of development of embryos and alevins (Beacham and Murray 1990; Figure 7-3) and their need for oxygen (Rombough 1988). Incubation temperatures in the Central Valley span approximately the range shown in Figure 7-3, being lowest for spring-run and steelhead in the higher reaches of Mill and Deer creeks, and highest for summer-spawning winter-run in the Sacramento River. Water temperature in the streams varies over time, however, so incubation periods cannot be calculated directly from Figure 7-3. In the American River, for example, early-spawned eggs may begin incubation at around 15°C and emerge at around 10°C. Size at hatching and emergence also depend upon temperature (Figure 7-4). Water temperature in redds usually tracks that of the surface stream but with less diurnal variation and some delay, but in some situations it is affected by upwelling water with different thermal characteristics (e.g., Mesick 2001b).

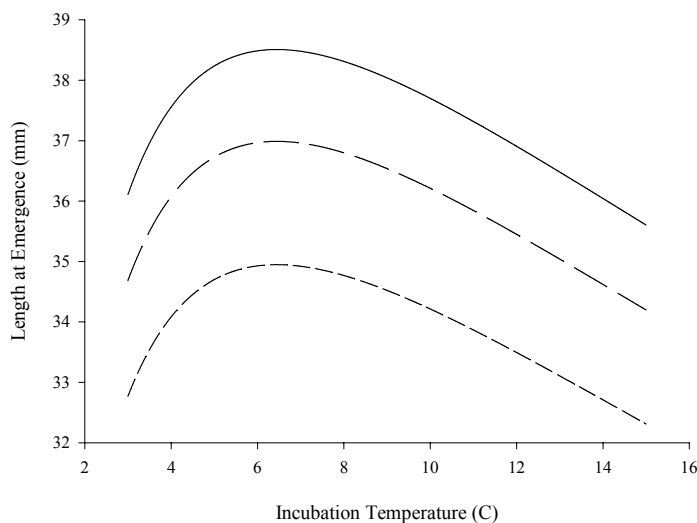
⁴⁷ The program, called WINSIRP, is available from John Jensen of the Pacific Biological Station at Nanaimo: jensen@dfo-mpo.gc.ca. Besides temperature, the model takes account of dissolved oxygen, pH, NH₃, flow rate, and initial egg weight. Although it is designed for hatchery conditions, it may be applicable to natural redds, given some data or assumptions. Selecting the correct flow rate probably would be the greatest challenge.

Figure 7-3. Days to hatching (dashed line) and emergence (solid line) for Chinook embryos and larvae raised at constant temperatures, from Model 2 in Beacham and Murray (1990). Model 2 gives good fits to the data, with values of r^2 of 0.991 for hatching and 0.955 for emergence, but does not apply directly to natural streams with varying temperatures.



The thermal inertia of water in reservoirs dampens the annual cycle in the thermal regime in the rivers downstream, so that water in most remaining spawning habitat in the Central Valley is now warmer in the winter than it was historically. This affects the duration of incubation, such that fry emerge earlier (Moffett 1949), and the migration of fall-run fry down the Sacramento River now begins about a month earlier than indicated by data collected before the construction of Shasta Dam (Ch. 5). The consequences of the change in timing are unknown, but could be significant.

Figure 7-4. Length at emergence for Chinook salmon incubated at constant temperatures, for three initial egg weights: 0.2, 0.3, and 0.4 g, from Model 11 in Beacham and Murray (1990).



Embryos and alevins are less tolerant of warm or very cold water than are juveniles or adults. Chinook and steelhead eggs and alevins in the Central Valley seldom experience water cold enough to be harmful, but high temperatures are a problem that has received considerable attention; Myrick and Cech (2001) give a recent review with emphasis on the Central Valley. Various studies of effects of water at constant temperature on Chinook embryos give generally consistent results, although there is considerable scatter in the data (Combs and Barrows 1957; Healey 1979; Velsen 1987; USFWS 1999). Some mortality occurs above about 12 or 13 °C and

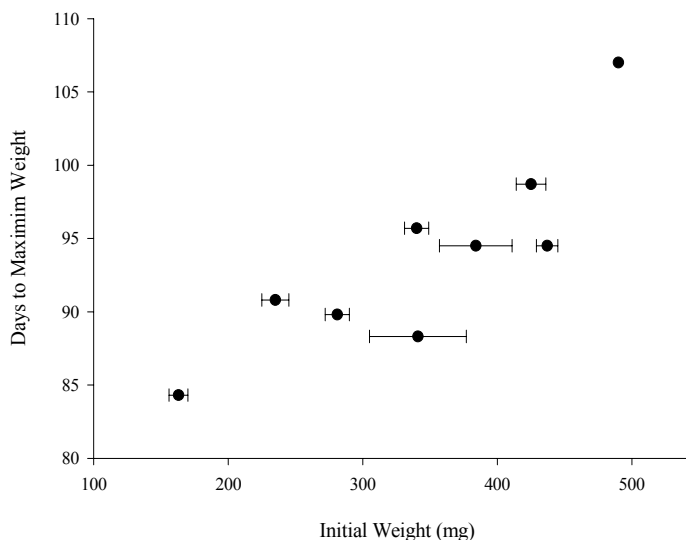
it becomes serious above about 14 or 15°C. Based on their study of winter-run eggs, the USFWS (1999) recommended a temperature criterion of 13.3 °C above Bend Bridge (rkm 414) for management of releases of cool water from Shasta Dam.

Fall and spring Chinook spawn when water temperatures are decreasing, however, and there is evidence that their eggs are more tolerant of warm water shortly after fertilization than they are later. Eggs exposed to water temperatures that tracked the temperature of the Columbia River, plus a 2.5 °C increment, showed no effect of an initial exposure to 16.1 °C (Olson and Foster 1957). This suggests, for example, that Chinook in the American River that begin to spawn when temperatures reach about 15 °C (Williams 2001a) may experience no ill effects, provided that normal seasonal cooling occurs. Chinook eggs exposed to warmer water at fertilization apparently survive better than eggs reared at a uniformly low temperature (Combs 1965, cited in McNeil 1969).

Egg size

Egg size also effects the rate of development, as does activity level. At a given temperature, it takes longer for alevins from larger eggs to reach maximum unfed weight (Rombough 1985; Figure 7-5).⁴⁸ However, it appears that larger eggs tend to have more yolk rather than larger embryos, so that embryos in larger eggs are not more sensitive to low levels of dissolved oxygen than embryos in smaller eggs (Einum et al. 2002).

Figure 7-5. Relationship between initial egg weight and day post-fertilization to maximum alevin wet weight, at an incubation temperature of 10°C, for Qualicum Hatchery, B.C., Chinook. Error bars show standard deviations for egg size; the two points with wider error bars include eggs from more than one female. Note the large variation in egg size. Data from Rombough (1985).



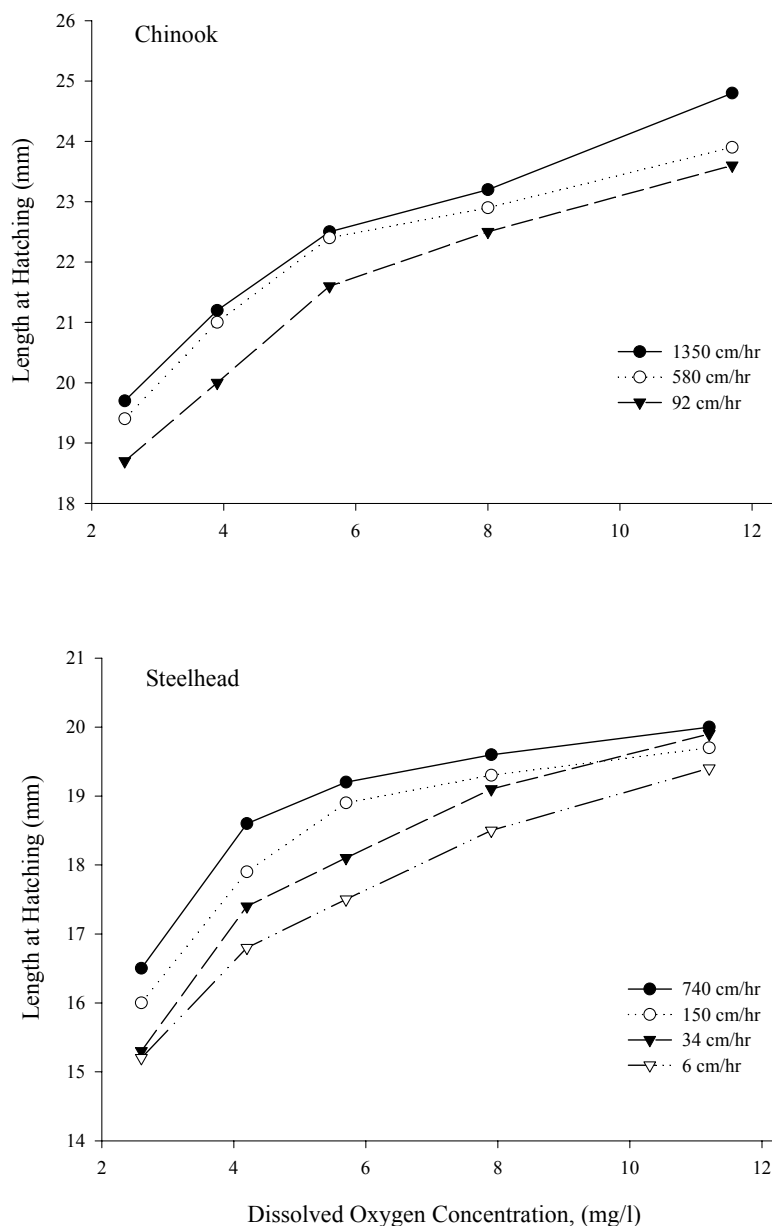
Dissolved oxygen and irrigation rate

At temperatures of 9-13°C, the mean length of Chinook larvae increased with the dissolved oxygen concentration of the water up to ~11 mg O₂ L⁻¹, the highest concentration studied, and

⁴⁸ Maximum unfed weight includes yolk, and normally precedes emergence (Beer and Anderson 1997), but unlike emergence can be observed unambiguously in the laboratory.

also with the velocity of flow around the eggs (Silver et al. 1963; Figure 7-6). Eggs at the 2.5 mg O₂ L⁻¹ took five to eight days longer to hatch than the eggs at 11 mg O₂ L⁻¹. Similar results were obtained for steelhead at temperatures of 7-10°C, and with coho (Shumway et al. 1964), although the rates of change were not quite as steep (Figure 7-6). Although over 95% of Chinook eggs hatched at 2.5 mg O₂ L⁻¹ oxygen, over 20% of the fry from the lower water velocity treatments died within a week, as did 8.5% of those at the highest velocity, and many of these were malformed.

Figure 7-6. Relation between length at hatching and dissolved oxygen concentration at various water velocities for Chinook and steelhead. Data from tables 3 and 6 in Silver et al. 1963). Note that the water velocities are through the experimental apparatus, rather than adjacent to the eggs; the latter are the matter of real concern, but could not be measured.



Although fry incubated at intermediate oxygen levels survived well in the laboratory, despite their smaller size, Silver et al. (1963) thought that likely they would not do so in the wild, and recommended that this be evaluated in future studies. Nevertheless, most studies of the effects of

hyporheic conditions on embryos and alevins use survival to emergence as an end point (e.g., Tappel and Bjorn 1983; Snowden and Power 1985; Lisle and Lewis 1992; Peterson and Quinn 1996; Wu 2000). Such studies may not detect biologically significant effects of poor hyporheic conditions. The temperatures in the Silver et al. (1963) experiments are relevant for many Central Valley streams. Levels of dissolved oxygen in or near redds in the Central Valley are typically less than 11 mg O₂ L⁻¹ (e.g., Mesick 2001b), indicating that Chinook embryos and alevins in the Central Valley may be typically more or less stunted. A review of the literature on the relation between hyporheic water quality and the survival and condition of Chinook embryos and larvae concluded that (Chapman 1988:9):

The key inference from the body of work described above is that deprivation of dissolved oxygen leads to subtle problems often not detectable in tests of survival in various oxygen concentrations. It appears incorrect to set critical oxygen levels at any arbitrary point, or to assume that survival to time of emergence is sufficient evidence of ecological success. *Any* decremented reduction in dissolved oxygen from saturation probably reduces survival to emergence or post-emergent survival.

Dissolved oxygen levels may be particularly a problem for eggs of winter Chinook in redds constructed far enough below Shasta that temperatures approach their tolerance limits (~13 or 14°C), and the saturation concentration of dissolved oxygen is below optimal levels (Figure 7-1). Where water is colder and development correspondingly slower, moderately reduced levels of dissolved oxygen may be less detrimental.

Dissolved oxygen in hyporheic water is most critical just before hatching, as the large embryos must obtain oxygen and dispose of metabolic wastes by diffusion through the egg wall. After hatching, the barrier of the egg wall is removed, resulting in a sudden drop in critical dissolved oxygen levels (Rombough 1988). As they develop, the alevins are increasingly capable of moving through the gravel, and presumably can take advantage of small-scale variation in hyporheic conditions.

Although aspects of development must be constrained by the nature of the physiological processes involved, the duration of incubation can vary among populations, perhaps in response to natural selection. Beacham and Murray (1990) noted that the embryos of Pacific salmon that spawn in fall when water temperatures are declining require more thermal units (e.g., degree-days⁴⁹) for hatching at higher temperatures, whereas steelhead and grayling (*Thymallus thymallus*) that spawn in the spring require fewer thermal units at higher temperatures. They interpreted this as adaptive variation intended to avoid premature emergence in winter for the salmon following unusually warm weather, and to promote early emergence in the spring for steelhead and grayling if conditions are favorable. Similarly, three populations of chum salmon in two adjacent streams in British Columbia emerge at approximately the same and presumably

⁴⁹ Degree days are calculated as the number of degrees above some threshold temperature for each day, summed over days.

favorable time despite considerable differences in the times of spawning and the accumulation of temperature units (Tallman and Healey 1994; Healey and Prince 1995).

Behavior of alevins

Most information on the behavior of *Oncorhynchus* alevins is based on observations of sockeye (Bams 1969) or pinks (Dill 1969). Differences in behavior have been reported for alevins of various salmonids (Dill 1981), but in the absence of contrary evidence it seems reasonable to assume that the sockeye and pink salmon observations apply to Chinook and steelhead as well. Unfortunately, Dill's 1969 call for "serious study of the behavior and ecology of the salmonid alevin" has not yet been answered.

Energy spent on activity reduces alevin size. Alevins exhibit a "righting response" to return to an upright position, which is normally maintained by the physical support of the gravel. Hatchery methods that do not provide such support induce enough activity in sockeye alevins to reduce fry size by up to 20% (Bams 1969), and alevins that incubate in very coarse gravel are smaller than those incubating in finer gravel (Dill 1969; Marr 1963, 1965, cited in Dill 1969).

Infusion of fine sediments or formation of a sand seal in the surface layers of gravel will reduce hyporheic circulation through the egg pockets, although this problem is still poorly quantified. However, embryonic and larval salmonids display various behavioral adaptations to poor hyporheic conditions (Bams 1969 and citations therein). Low levels of dissolved oxygen induce release of a hatching hormone by embryos resulting in early hatching, removing the egg membrane as a barrier to oxygen transport. Elevated CO₂ induces movement thorough the gravel by alevins; younger alevins moved randomly, older ones moved toward the surface as in normal emergence. Alevins clear larger suspended particles from their mouths by a "coughing" reflex, and clear finer particles such as silt from their gills by secreting mucus which "passes from underneath the gill covers in strings loaded with silt" (Bams 1969:79). Very high sediment concentrations induce movement, presumably as an escape mechanism. Emerging sockeye alevins also have well-developed behaviors for moving through the substrate, including a method for moving through a layer of sand (Bams 1969:81):

When the fish confronted a sand barrier near the surface of an experimental gravel bed, they exhibited "butting" behavior, which may be of great value in a natural habitat where a sandy layer over the redds is a common occurrence. The fish butted into the sand with repeated short upward thrusts. This action loosened the grains, which fell down and past the butting fish, thus forming an open passage as the fish worked along.

Mortality in the hyporheic zone

Estimates of the mortality rates of eggs and alevins are generally high but also highly variable. According to Healey (1991:329) "Published estimates of the mortality rate between egg laying and fry emergence [for Chinook] are so few and so variable that it is difficult to draw any firm generalizations," and this seems still to be true. Based on the studies he reviewed and his own experience, Healey suggested that under natural conditions, survival to emergence is usually

less than 30%. In another review, Bradford (1995) could not find enough studies on which to base an estimate of egg to fry survival for Chinook, but suggested that average survival to smolting is over 8% for ocean-type Chinook. Given reasonable estimates of fry mortality, this implies that average egg to fry survival must be in the tens of percent. Some early reports of egg to fry survival were quite high. Hobbs (1937) reported over 90% survival, and Briggs (1953) reported that the average egg to fry survival in 18 redds was 86%. More recently, Unwin (1997) estimated egg to fry survival at 48% for Chinook in a spring-fed stream in New Zealand.

The survival of eggs and embryos reported in studies in the Central Valley is also highly variable, but generally low. In a study of gravel enhancement projects on the Mokelumne River, the average survival to late alevin stage of eggs incubated in tubes buried in gravel was 29% in enhanced sites and 22% in unenhanced sites, but the average survival of controls grown in the Mokelumne River Hatchery was only 63%, suggesting a problem with egg quality (Merz et al. 2004). In another component of the study, the average survival was 58% for Chinook and 61% for steelhead, compared to 88% and 84% for controls in the hatchery. The estimated survival of eggs and alevins in 19 redds under emergence caps on the Tuolumne River ranged from 0 to 60%, and averaged 32% EA 1991b). Survival of eggs in plastic baskets buried in gravel in Mill Creek averaged 4.2% and ranged from 0 to 14.8% (Gangmark and Bakkala 1960), but this may have resulted from setting the eggs in gravel that was too small for the site, as noted above. In experiments in a control section,⁵⁰ where flow was controlled and silt had been flushed from the gravel, egg survival was bimodal: all eggs died in 22% of the baskets and a few had low survival, but survival averaged 75% for 72% of the baskets; survival was strongly related to the velocity of the hyporheic flow. In summary, survival can be very high when hyporheic conditions are good and redds are not disturbed, (Hobbs 1937; Briggs 1953; Unwin 1997), but it can also be zero; the practical problem is knowing the shape of the distribution of survival, and how the distribution is affected by human activity that can be changed.

Bradford (1994) reported that average egg to fry survival for pink, chum, and sockeye salmon is about 7%. This estimate seems low for steelhead; extensive monitoring in Waddell Creek indicated that egg to smolt survival for steelhead in Waddell Creek averaged about 3% (Shapovalov and Taft 1954), which implies an egg to fry survival higher than 7%. Shapovalov, who had extensive experience with steelhead in California, thought that survival typically “is about as high as in the hatchery” (Murphy and Shapovalov 1951:506), and Briggs (1953) reported that the average survival in 13 redds was 65%. These estimates seem high, however. Information on egg to fry survival for steelhead in the Central Valley is lacking.

Scour and infiltration of fines

Many egg and larval salmonids perish when the beds of streams are mobilized during high flows and the eggs or alevins are either crushed or expelled from the hyporheic zone. Others suffocate when infiltration of fine sediments reduces rates of hyporheic flow and dissolved

⁵⁰ The control section in the Gangmark and Bakkala studies was the upstream end of the North Fork of Mill Creek, a tributary that is now dry except in very high flows. It is described in Broad and Gangmark (1956).

oxygen levels, or when fines on the surface of eggs blocks oxygen transport into the eggs (Cordone and Kelley 1961). However, sediment transport also creates and renews both spawning and rearing habitat, by separating coarse and fine sediments and by modifying channel geometry, so high flow events that devastate one year-class may create improved conditions for those that follow. Moderate scour also affects stream food webs to the benefit of juvenile salmonids (Wootton et al. 1996), and the view that the “natural flow regime” is normally beneficial overall is a cornerstone of much current thinking on the restoration of stream ecosystems (e.g., Power et al. 1996; Poff et al. 1997). It is certainly the case that many Central Valley streams historically supported large populations of salmon despite variable hydrographs and frequent sediment transport, although scour and sedimentation presumably affected year to year variation in the populations.

Very high rates of loss of Chinook eggs to scour (95-99%) were reported for Mill Creek by Gangmark and Bakkala (1960), but these seem hard to reconcile with the apparently high productivity of the stream (Clark 1928),⁵¹ and there were problems with the study, described above. On the other hand, the very high rate of survival (86%) reported by Briggs (1953) probably reflects the scarcity of flows high enough to mobilize sediment during the year in which he collected most of his data.⁵² Greene et al. (2005) found that a measure of high flows during incubation was a useful predictor of adult Chinook returns in the Sakgit River, Washington.

Bed mobility may explain why salmon do not show a stronger preference than they do for spawning in the tails of pools, where water is downwelling and hyporheic dissolved oxygen levels are higher than in the riffle downstream. Redds in these areas may be more susceptible to infiltration of sand that can be mobilized in the upstream pool at flows below the threshold for gravel transport (Lisle 1989), and scour to the depth of egg pockets apparently occurs at lower discharge in the tails of pools than on the riffles (Schuett-Hames et al. 2000). However, mobilization of the bed per se does not mean that eggs are scoured; generally, the thickness of the mobilized layer is less than 1.7 times the diameter of the larger particles in the bed (Wilcock et al. 1996), which is often less than the depth of normal egg pockets, so eggs are unlikely to be scoured unless the surface of the bed lowers enough that the mobile layer reaches the egg pockets (Lapointe et al. 2000). A recent study of chum redds found deeper scour below downstream parts of tailspills than over egg pockets, indicating that some earlier studies in which scour was measured in tailspills overestimated mortality from scour (Rennie and Miller 2000). Moreover, depth of scour and fill within a reach is highly variable (Lisle 1989; Montgomery et al. 1996; Lapointe et al. 2000; Rennie and Miller 2000; Schuett-Hames et al. 2000), so some redds survive even extreme events.

⁵¹ Clark (1928) documents the number of fall-run eggs collected there in the early twentieth century, which peaked at 30 million in 1905.

⁵² Briggs investigated Chinook redds mainly in the winter of 1949-1950, for which he reported a peak discharge of just under 3.9 m³/s, which is about the critical discharge for gravel mobility in Prairie Creek estimated by Lisle (1989, his Fig. 8); Lisle reported little movement of sand in Prairie Creek until flow reached critical discharge.

The probability of damage to redds occurring while eggs or alevins are still present depends on the timing of spawning and the temperature of the hyporheic water, which affects the time between spawning and emergence. The risk seems greatest for later spawning fall and for late-fall Chinook. It is virtually nil for winter Chinook, and is perhaps intermediate for spring-run and for steelhead that spawn in late winter or spring.

Sediment transport clearly is a hazard for Central Valley salmon, but it does not seem to exert a strong control on the timing of spawning, except perhaps for steelhead and spring-run. Many fall-run and all late fall-run spawn late enough that their eggs incubate during a period of maximal risk of both scour and infiltration by fine sediment. Perhaps other advantages of spawning in this season outweigh the hazards from sediment transport. Winter-run historically occupied streams with unusually stable hydrographs and low frequency of sediment transport, and avoiding competition with spring-run by spawning in summer probably conferred a greater benefit than avoiding infrequent episodes of sediment transport during incubation. Snowmelt runoff allows more reliable access to areas used for spawning by spring-run, probably providing a stronger advantage to that life history pattern than avoiding scour. However, scour to the depth of egg pockets appears to be less frequent in smaller streams (Lisle 1989), which may explain the tendency of fish such as steelhead and coho to spawn in small tributaries.

Although indices of scouring flows can help explain variation in the numbers of juveniles emigrating from streams (Wales and Coots 1954; Holtby and Healey 1985) and the numbers of adults returning to them (Greene et al. 2005), the population consequences of even extreme events are not always apparent. For example, high flows on January 1, 1997, caused major channel change on Butte Creek, including an avulsion⁵³ away from the diversion structure where DFG maintains an out-migrant trap, scour and widening of the channel at the USGS gaging station, and partial filling of many of the pools that provide summer holding habitat for adult spring-run (Williams et al. 2002). Although DFG re-established a trap farther downstream after only 16 days, they captured only 32 juveniles for the remainder of the season (Hill and Webber 1999). The holding pools scoured out again the following winter, indicating that there was again significant movement of gravel. Nevertheless, spring-run returns to Butte Creek seem not to have suffered: estimated returns in 1996 were 1,412, compared with 3,690 in 1999, 4,118 in 2000, and 9,605 in 2001. Clearly, there is more to learn.

Stranding and dewatering

Redds are described as stranded when flows drop so much that the surface of the redd is above the surface of the stream, and as dewatered when the surface of the saturated hyporheic zone drops below the egg pockets. Eggs tolerate temporary dewatering provided that the temperature remains suitable (Becker et al. 1983; McMichael et al. 2005), since oxygen exchange continues as long as the eggs remain moist, but alevins perish quickly. Alevins cannot emerge from stranded redds, but the consequences of temporary stranding depend upon its

⁵³ In hydrology, an avulsion occurs when a stream shifts suddenly from one course to another, without occupying the area in-between.

effects on dissolved oxygen levels in the hyporheic flow. However, a link between flow and dissolved oxygen levels in hyporheic water has long been recognized (e.g., Wickett 1954), so reduced oxygen concentrations should be expected during stranding events.

In managed rivers, stranding can be a consequence of deliberate choices regarding reservoir releases. Central Valley dams commonly serve for both flood control and water storage, and are required to maintain the reservoirs below specific elevations during the flood season, except for temporary increases during storms. Inflow rises when storms occur, so if the reservoir level is at the limit, releases must also be increased. This raises the question whether it is better, in terms of stranding redds, to limit the extent or the duration of the increase of flow below the dam. The best course of action probably depends on the particulars of the situation, so the issue is best dealt with by consultation between the dam operators, biologists and other interested parties. This has become increasingly institutionalized in the Central Valley, for example with the Lower American River Operations Group. Redds may also be stranded if reservoir releases are reduced to save water. Probably the most serious serious example is the frequent stranding of fall-run redds below Keswick Dam (Killam, in Anderson et al. 2006).

Predation

Although salmon eggs and alevins in redds are relatively safe from predation, they are not completely so. Up to 400 oligochaete worms were found in redds in Prairie Creek and were associated with egg mortality (Briggs 1953). Small sculpins can burrow down into redds, especially in coarse gravel (Phillips and Claire 1966) and there is indirect evidence that they consume eggs of pink salmon (McNeil 1969), although these are smaller than eggs of Chinook. Atlantic salmon parr up to 122 mm total length have been found in redds, but their stomachs contained invertebrates rather than eggs (Erkinaro et al. 1994). Some Chinook eggs are eaten during spawning (Briggs 1953; Vronskiy 1972) and predation on eggs that are dislodged by superimposition is probably high. Newly emerged fry that have not yet filled their air bladders are also highly susceptible to predation (Bams 1969).

Density-dependent mortality

Density-dependent mortality among Chinook in the Central Valley in the spawning and incubation stages presumably occurs, but is not well quantified. Several different processes are involved. When the density of potential spawners is very high, as among fall-run in some streams during the last few years, many fish may die without spawning. On Battle Creek in 2002, with over 400,000 spawners, the estimated pre-spawning mortality was greater than 85% (Table 12-3). Superimposition of redds also results in density-dependent mortality. Again, however, the extent of the mortality is not well quantified; although it is easy to observe whether the margins of redds overlap, it is difficult to determine whether egg pockets have been disturbed. Presumably, the hazards of scour and superimposition have opposing effects on the timing of spawning for fall-run, as later spawning fish enjoy lower risk of superimposition but suffer higher risk of scour. Territorial behavior that forces some females to build redds in suboptimal or unsuitable areas also results in density-dependent mortality, although this would not be readily apparent. Healey (1991) noted that density-dependent mortality resulting from territorial

behavior may an important process, and that the amount of good spawning habitat may be less than is indicated by the occurrence of redds. A logical consequence of density-dependent mortality in spawning and incubation is that the appearance of hatchery fish on the spawning grounds reduces the productivity of naturally-produced fish, whether or not hatchery fish are less fit, unless the number of spawners is low.

Local adaptations to hyporheic habitat

Concern for maintaining diversity within and among salmon populations is based on the assumption of local adaptations to habitats. It seems clear that local adaptations to hyporheic conditions exist among Central Valley salmon: for example, the summer spawning of winter Chinook is an adaptation to the low temperature of hyporheic water in their native habitat, but the extent of such adaptations is unclear. The importance of the tradeoff between egg size and egg number for fitness and the potential influence of hyporheic conditions on this trade-off make other local adaptation seem likely. However, the recent showing that larger eggs are not less tolerant of low oxygen concentrations (Einum et al. 2002), contrary to what was assumed from consideration of the surface to volume ratio of eggs, shows how poorly we understand these matters, and the effects of migration distance and difficulty on egg size and number (Kinnison et al. 2001) shows that adaptations to hyporheic conditions are complicated by other aspects of the life cycle.

CHAPTER EIGHT

GRAVEL-BED STREAMS

We might conclude from the foregoing that fish go where the food is, but we have not been able to assess the relative importance of food supply versus the cover provided by depth and turbulence in causing fish to move toward faster, deeper water as they grow.
Chapman and Bjorn (1969:157)

One of the main limitations in estimating the impact of habitat losses on salmon populations is the lack of knowledge of juvenile salmon habitat use in larger rivers ...
Beechie et al. (2005:727)

Most naturally spawned salmon in the Central Valley begin life in gravel-bedded reaches of large rivers below dams, and some rear there for months to a year before migrating downstream toward low gradient, sand-bedded reaches, the Estuary, and the ocean. Studying small fish in large rivers is difficult, and the understanding of ways that juvenile salmon use habitats in large rivers is limited (Beechie et al. 2005). In this section I review selected studies from the Central Valley and elsewhere, and discuss some concepts that have been used in studying habitat use. I also describe the available information on the diet of juvenile Chinook and steelhead in gravel-bedded reaches of Central Valley streams, and touch on two topics related to these reaches: stranding, and large wood as a component of salmon habitat.

Emergence and initial stream life

Newly emerged fry are more dense than water, so to attain neutral buoyancy and adjust to life in the stream, they must swim to the surface and swallow air to inflate their swim bladders. Then they return to the bottom to find shelter (Tait 1960; Bams 1969; Smith 1985). Some fish make several attempts to reach the surface before they succeed. Except for fry emerging from redds in relatively slow and shallow water, this process must involve more or less dispersal, as the newly-emerged fry are not strong swimmers. For Chinook fry emerging from redds four meters below the surface of the Columbia River (Chapman 1943), the dispersal must be considerable. There may also be deliberate downstream movement and dispersal directly after emergence (Healey 1991). Fry are highly susceptible to predation at this time, but may reduce the risk by a tendency to emerge at night (Reimers 1971, cited in Healey 1991). The diel timing of emergence among salmonids is variable, however, and is affected by factors such as water temperature (Godin 1981).

Although there is variation among streams and years, most fall-run and spring-run fry in Central Valley streams begin migrating downstream soon or directly after emerging from the redds, although others rear in the streams for weeks to months, or even for a full year, before migrating. Why some fry migrate soon after emerging but some do not remains unclear (Ch. 5). Fry that will take up longer residency in the stream, and probably some of those that will soon migrate downstream, move to shallow water along the margins of the stream after emerging, to

find sheltered habitat in which to complete absorption of the egg yolk and make the transition to active feeding. As they grow, juvenile steelhead and the non-migratory Chinook move away from the shallow margins of the stream into deeper and sometimes more rapidly moving water (Chapman and Bjorn 1969; Everest and Chapman 1972; Figure 8-1). Presumably they disperse longitudinally as well.

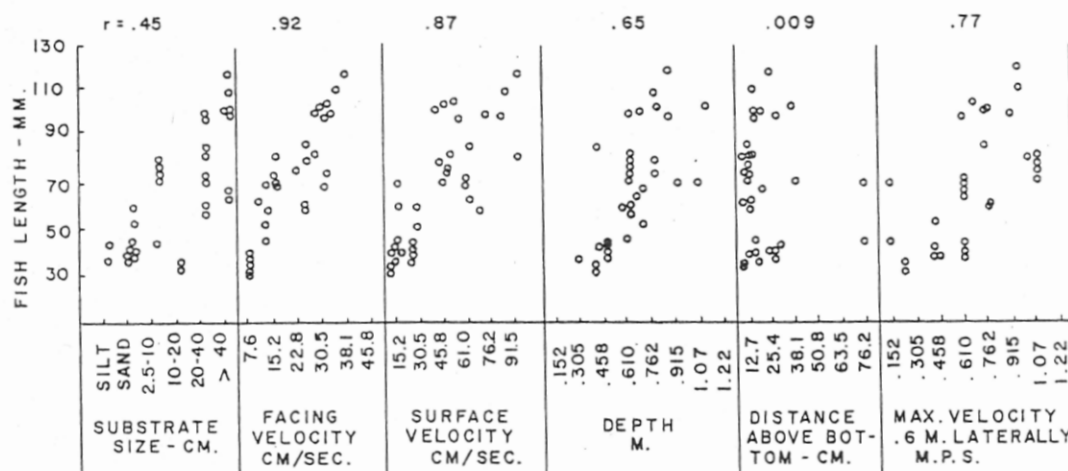


FIGURE 2
THE RELATIONSHIP BETWEEN CHINOOK SALMON OF VARIOUS LENGTHS AND
SELECTED PHYSICAL VARIABLES OF THE LOCHSA RIVER AND JOHNSON
CREEK (EVEREST, UNPUBLISHED).

Figure 8-1. The classic figure demonstrating that juvenile Chinook move into faster and deeper water as they grow, copied from Chapman and Bjorn (1969); see also Everest and Chapman (1972), courtesy of *Canadian Journal of Fisheries and Aquatic Sciences*.

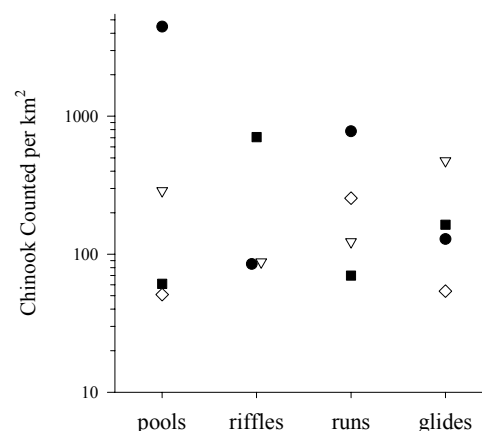
Habitat use during juvenile rearing

The use of stream habitat by juvenile salmonids is of theoretical as well as practical interest, and is the subject of a very large and sometimes contradictory literature. Overall, the literature indicates that the way juvenile salmonids use habitat depends on the nature of the available habitats and on the life history pattern followed by the fish. Accordingly, although studies elsewhere may establish important facts or illustrate important principles, several factors limit their relevance for Central Valley salmon. First, for practical reasons, most of this work has been done in smaller streams, but most remaining habitat in the Central Valley is in larger streams below dams. Second, the literature mainly concerns fish that defend individual territories, while juvenile Chinook in Central Valley rivers often occur in schools (Rutter 1904; Jackson 1992; Cavallo et al. 2003), as they do elsewhere (Everest and Chapman 1972). Third, many studies have been conducted at fine spatial scales, and much of the grey literature on stream habitat use is further restricted to observations at fine spatial scales of the PHABSIM microhabitat variables: depth, velocity, substrate, and sometimes cover. However, the importance of taking multiple spatial scales into account is now recognized (e.g., Fausch et al. 2002), and has been demonstrated locally by Cavallo et al. (2003), as described below. Finally, many of the studies of

habitat use in streams by Chinook concern stream-type Chinook, while most Central Valley Chinook are ocean-type. Thus, the literature is likely to be most relevant for steelhead or the fraction of spring Chinook that rears in smaller streams through the summer and emigrate the following winter or spring, and local studies are generally most informative regarding fish that rear in the rivers. Selected examples are discussed below, together with studies from other areas that illustrate particular points.

In the lower American River in late April, 1989, Jackson (1992) found juvenile Chinook in all habitat types that he sampled, but mainly in small to large schools in upstream pools (Figure 8-2). He also observed smaller numbers of larger fish defending feeding territories in riffles. Within the pools on the American River, the fish were associated with instream cover such as rootwads, logs, or submerged vegetation, or with overhead cover, and were also associated with eddies or other areas with steep velocity gradients (Jackson 1992); such positions allow fish to hold in slower water but make forays into faster water to capture drifting insects, their main food. For example, juvenile Chinook may hold in slower water in the head of a pool under the current flowing off the upstream riffle, especially when the current creates a “bubble screen” that provides overhead cover. Similar observations have been reported by others (e.g., Reimers manuscript, cited in Chapman and Bjorn 1969; Everest and Chapman 1972; Hampton 1988; Roper et al. 1994). Juvenile steelhead are generally more territorial than Chinook (e.g., Keeley 2000), but Jackson (1992) reported that some were seen schooling together with juvenile Chinook.

Figure 8-2. Counts of juvenile Chinook observed per km² on April 25-29, 1989, in different habitats in the lower American River (circles: upper reach, bar complex; triangles: upper reach, flat water; squares: middle reach, bar complex; diamonds, middle reach, flat water). Data from Jackson (1992), Table 4a. Note the log scale on the vertical axis.



Jackson (1992) was concerned mainly with developing suitability information for a PHABSIM study. In that regard, he found that the water depth and vertically-averaged velocity at positions occupied by 4,315 juvenile Chinook usually varied significantly among different habitats and between pairs of sites within habitat types, based on t-tests ($\alpha = 0.05$) ; Figure 8-3 shows median values and ranges for the 15 sites sampled in 1989 at relatively high flow, 105 m³s⁻¹. This variation in microhabitat selection raises questions about the biological meaning of the suitability criteria used in PHABSIM.

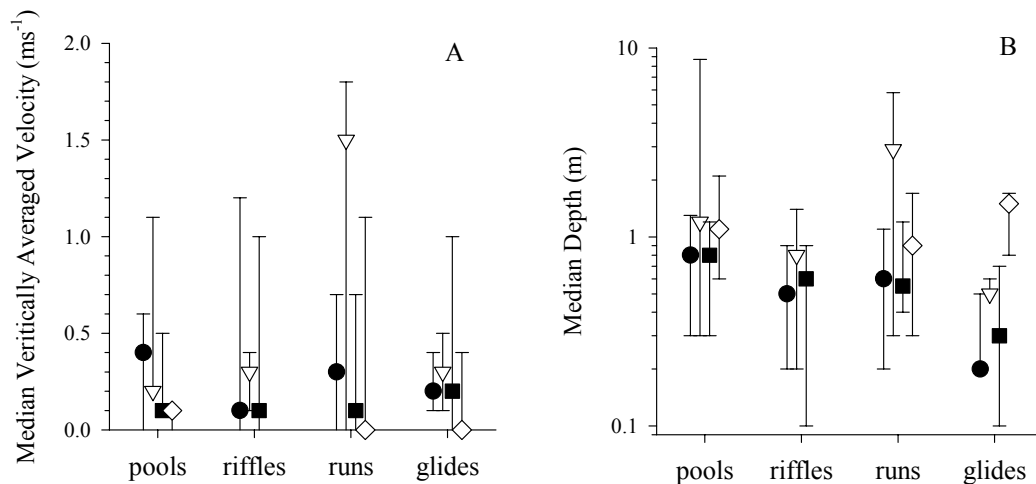


Figure 8-3. Median velocities (A) and depths (B) at which fish were observed at 15 sites on the American River, April 25-29, 1989, at a discharge of $105 \text{ m}^3 \text{ s}^{-1}$ (circles: upper reach, bar complex; triangles: upper reach, flat water; squares: middle reach, bar complex; diamonds, middle reach, flat water, bars show ranges.). Data from Table 6a in Jackson (1992).

In the Sacramento River, very high densities of juvenile Chinook, probably fall-run, were documented in video photography by Doug Killam of CDFG in the late spring and summer of 2002 (Killam, in Anderson et al. In press). In the pool above the ACID Dam in Redding, fish were distributed broadly through the water column. Although quantitative data on the availability of food were not obtained, Killam reported that caddis larvae were abundant and that the fish shown probably were satiated by feeding earlier in the day (pers.comm. 2004). Downstream from the dam, small schools of fish were holding behind velocity shelters near the bottom, with individuals moving up into the current to capture drifting prey. Killam reported that many of these fish stay in the area until August or September and emigrate at $>100 \text{ mm}$ fork length (Killam, in Anderson et al. In press), in the temporal pattern typically described for late-fall Chinook. This change in migratory timing, like the resident life history pattern exhibited by *O. mykiss* in this area, seems to be a response to the hydrologic conditions created by Shasta Dam. The proportion of Chinook migrating in the fall that is fall-run could be determined if genetic analyses were made part of monitoring in the Delta. Relatively large ($\sim 175 \text{ mm}$) fall-run have been collected in the Delta in early November (Ch. 10).

In a study on the Feather River using snorkel surveys and seining, Cavallo et al. (2003) found small ($<100 \text{ mm}$) steelhead mainly in the upper 1.5 km of the available habitat where most steelhead spawning occurs. Larger steelhead ($>100 \text{ mm}$) and juvenile Chinook were spread more widely over the upper 13 km of the river, the “low flow channel” around which all but $17 \text{ m}^3 \text{ s}^{-1}$ of flow is normally diverted through an afterbay (Figure 8-4). Most smaller steelhead were in glides, although they shifted to riffles as they grew, so that more steelhead $>80 \text{ mm}$ were in riffles than in glides. Juvenile Chinook were seen mainly in glides, with a less pronounced shift

to riffles as they grew. Chinook often occurred in small schools, apparently with dominance hierarchies (B. Cavallo, CDWR, pers.comm. 2004). Pools were used relatively little, in contrast to Jackson's (1992) observations on the American River.

The Cavallo et al. (2003) study is notable for a multi-scale sampling design, which included annual coarse-scale surveys in May or June that covered the entire 26 km study area in 1999, 2000, and 2001, monthly (March to August) intermediate-scale surveys of nine 200-665 m sections of streams that included at least one riffle-pool sequence, and monthly fine-scale surveys of twenty-four 4 x 25 m habitat patches in riffle-glide habitats in 2001. At the spatial scale of the river, the longitudinal position was the most important factor affecting the presence of smaller (<100 mm) steelhead (Figure 8-4). Within that reach, most fish were observed in glide or riffle habitat, but distance from shore probably was most important, since almost all steelhead < 80 mm were observed within ~2 m of shore. Within that 2 m strip, other microhabitat variables, especially depth and cover, were important, based on binary logistic regression analysis.

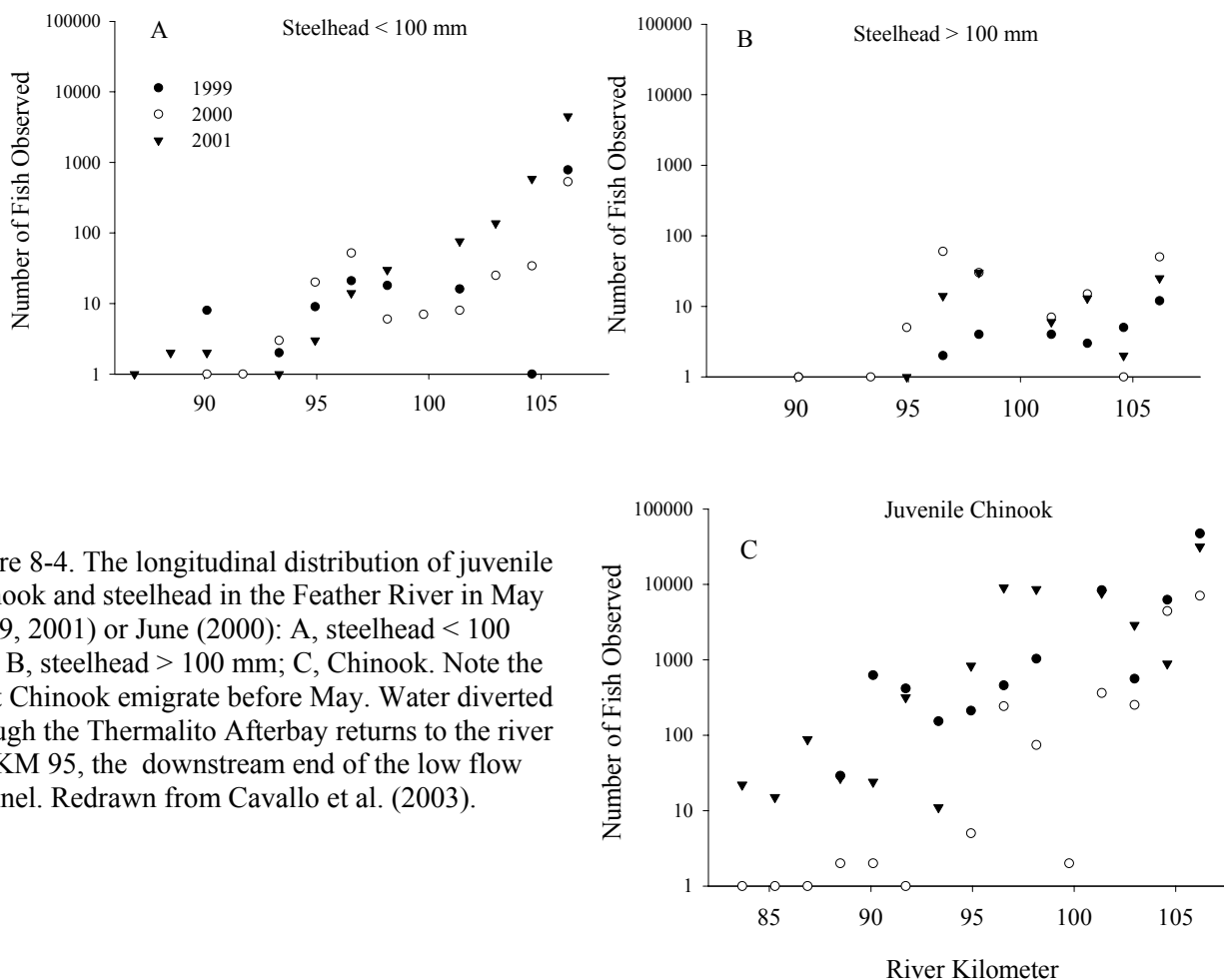


Figure 8-4. The longitudinal distribution of juvenile Chinook and steelhead in the Feather River in May (1999, 2001) or June (2000): A, steelhead < 100 mm; B, steelhead > 100 mm; C, Chinook. Note the most Chinook emigrate before May. Water diverted through the Thermalito Afterbay returns to the river at RKM 95, the downstream end of the low flow channel. Redrawn from Cavallo et al. (2003).

As Cavallo et al. (2003) pointed out, habitat analyses that focus on one spatial scale may give misleading results. Analyses based on microhabitat variables may miss coarser-scale factors affecting fish distributions; for example, areas with apparently favorable fine-scale conditions at the downstream end of the low flow channel may get much less use by small steelhead than similar areas farther upstream. On the other hand, analyses based on categories such as habitat types may miss important differences in the detailed morphologies of the habitats, or differences arising from the size of the stream. At a fine spatial scale, a pool in a small stream may be similar to a patch in a riffle in a larger one (Roper et al. 1994). Issues of spatial scale should be given more attention in studies of Central Valley salmon.

A recent study of habitat use by juvenile Chinook and steelhead in two reaches of the Bridge River in British Columbia (Bradford and Higgins 2001) demonstrates that water temperature can strongly affect habitat use, and that temporal as well as spatial factors may need to be taken into account in studies of habitat use. Except for occasional spills, the entire flow of the Bridge River has been diverted for hydropower,⁵⁴ so flow in the lower river is limited to contributions from springs and tributaries, one of which is considerably larger and colder than the remnant river upstream from their confluence, (4.3 v. 0.7 m³s⁻¹ annual mean); this tributary and the river below their confluence also support piscivorous bull trout. Eight diel snorkel surveys conducted between August 1995 and August 1996 in the Bridge River above and below the tributary confluence recorded mainly juvenile Chinook and 0, 1, and 2 year-old steelhead. In the lower reach, where the water temperature was never above about 12°C, all fish were strongly crepuscular in all seasons, emerging from cover in the substrate to forage at dusk. In the upper reach, which was several degrees warmer in summer, there was variation among seasons and fish. In winter, activity was strongly crepuscular, as in the lower reach. In summer, age-0 steelhead were most active during the afternoon, age-1 steelhead were almost as active during the afternoon as at night, and age-2 steelhead were most active at night; juvenile Chinook were most active at dusk but many were observed at other times as well. Observations in spring and fall were intermediate, except that age 2 steelhead were then most active at dusk. Age-0 steelhead and Chinook were significantly larger in the upper reach, in samples collected by net.

Juvenile salmonids often become nocturnal when water temperatures decline into the range of 8-12°C, presumably to reduce the risk of predation (Campbell and Neuner 1985; Fraser et al. 1995). However, fish were active in the water column in the afternoon in the upper reach of the Bridge River at temperatures and in seasons in which fish a few kilometers downstream remained concealed, and apparently did not grow as rapidly.

In a study of juvenile fall-run Chinook in the Hanford Reach of the Columbia River, Venditti and Garland (1994) sampled juveniles with fyke traps and underwater video on three occasions in 1994: April 27-30, May 3-6, and June 6-11. The fyke traps were fished in pairs, one

⁵⁴ Releases of 1 to 3 m³s⁻¹ into the Bridge River are now in effect, as part of an application of adaptive management to instream flow assessment (Paul Higgins, pers. comm. 2006.)

nearer and one farther from shore, and the traps were checked every few hours. In June, traps were set facing downstream as well as upstream, and although many fewer fish were present in June, the downstream facing traps captured more fish than the upstream facing traps. Venditti and Garland (1994) attributed this to local movements associated with feeding. The fyke trap catches showed that juvenile Chinook were more active during the day, and the video photography showed that they were distributed throughout the water column and not associated with any particular structural features in the channel; at least in late April and early May, most juveniles were settled near the bottom at night. In June, however, most fish were captured in the fyke traps at night. Lister and Genoe (1970) reported that juvenile Chinook in the Big Qualicum River in British Columbia were active at night and associated with shoreline cover.

Concepts regarding habitat use

As the studies reviewed above show, there is still a good deal to be learned about habitat use by juvenile salmon, and a need for understanding underlying principles that can help explain observed differences in behavior. Metcalfe et al. (1999) proposed that juvenile salmonids should use stream habitats in ways that minimize the risk of mortality per increment of growth or feeding. Bradford and Higgins (2001) interpreted their Bridge River results as showing that, on average, fish were not acting to maximize growth, but rather were weighing growth or feeding opportunities against predation risk, as predicted by Gilliam and Fraser (1987) for other fishes and by Metcalfe et al. (1999) for salmon.

This posits a sort of rational behavior on the part of the fish, but such behavior need not arise from foresightful calculation. It seems more likely that the behavior results from the application of behavioral “rules of thumb” mediated by urges or impulses that result from responses to physiological conditions that can be selected for or against (Kramer et al. 1997). That is, a fish may forage despite some risk of predation because it is hungry (Gotceitas and Godin 1991; Damsgård and Dill 1998), and the tendency to do this should be subject to selection. On average, unless the habitat has changed, the evolved behavior should be adaptive, but it may not always be so, as illustrated by the territorial behavior of young-of-the-year brown trout in a small stream in England (Elliott 1994). When the population density is high, smaller fish that are unable to establish territories perish, but largest individuals that defend larger territories do so even at the expense of foraging, and also perish, so that the size distribution of surviving fish is narrower in years with high initial density. Most likely, the impulse of the larger juveniles to defend larger territories is adaptive in years with low to moderate population densities. If so, the optimal size and aggressiveness depend upon the population density, which varies from year to year. Environmental conditions in the stream Elliott studied are unusually stable, but presumably adaptive traits or sets of traits in more variable streams will depend upon variable environmental conditions, as well as on population density. Adaptive behavioral rules may also vary from stream to stream or among life-history types (Taylor 1991), and so provide additional scope for local adaptation by salmonids, and for confusion among fish biologists. Despite these complications, and the effect of individual experience in modifying behavior, the idea that fish should behave so as to minimize the risk of mortality per unit of growth or feeding opportunity

seems useful for studies of habitat use as a kind of null hypothesis; if there is good evidence that a particular behavior violates the rule, then it is probably worth exploring why.

Where juvenile salmonids are territorial, the productivity of streams may be limited by their behavior (Elliott 1994). At a conceptual level, differences between the distributions of animals over habitats when they are territorial and when they are not has been modeled in terms of the “ideal free distribution” and “ideal despotic distribution” (Fretwell and Lucas 1970; Fretwell 1972), assuming that the animals can accurately assess the value of habitats. These models were intended not so much to predict actual distributions as to provide idealized examples against which to compare actual distributions, and have been applied to salmon (e.g., Giannico and Healey 1999) as well as other animals. Similarly, the models could be used to clarify the biological meaning of habitat indices developed from observations of habitat use or measures of habitat quality derived from them, such as the “weighted usable area” (WUA) an index of physical habitat, used in PHABSIM.

Grant and Kramer (1990) and Grant et al. (1998) proposed that percent habitat saturation (PHS) is a useful statistic for assessing whether populations are limited by the area of rearing habitat: $PHS = 100 \sum D_i T_i$, where D_i is the density (no. m^{-2}) of the size class i , and T_i (m^2) is the territory size for size class i . In a survey of published studies of salmonids in shallow streams, density-dependent population effects in growth, emigration, or mortality were common when PHS was greater than about 27% (Grant and Kramer 1990). However, juvenile salmonids are not always territorial, especially in deeper habitats such as pools.

Percent habitat saturation may be useful for assessing instream flow needs in streams such as Battle Creek. Dedual (2004) argued from estimates of PHS that the population of adfluvial⁵⁵ *O. mykiss* in the Tongariro River, New Zealand, which is somewhat similar to Battle Creek, is limited by food rather than by space. This was part of an argument that releases from a hydropower project into the river should be increased, in order to increase the area of food-producing riffle habitat, despite an argument by consultants for the power company that increasing flow would lead to a decrease in WUA for the fish. Percent habitat saturation can also be used as a framework for estimating the effects of factors that change territory size. For example, territory size decreases as the availability of food increases. Based on data from the literature, Grant et al. (1998) estimated that territories decrease to 0.76 of their initial size if food supply doubles. Provided that space were otherwise the limiting factor, this would result in the population increasing by a factor of 1.3.

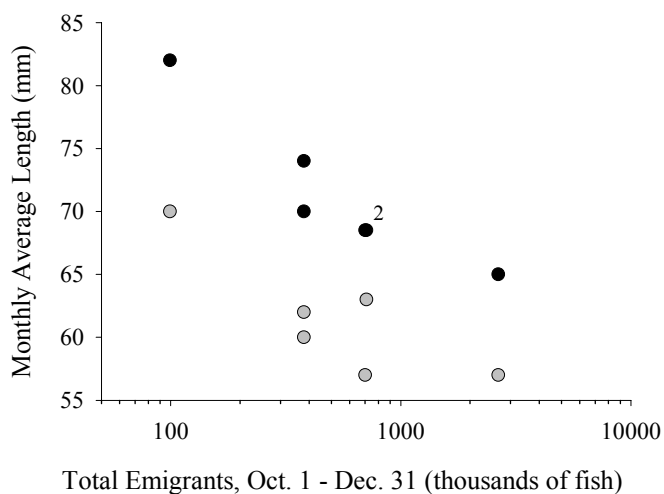
Although the concept of PHS seems useful, particularly for smaller streams that support steelhead or stream-type Chinook, like other generalizations about salmonids it should be approached with due caution. As applied by Grant and Kramer (1990), PHS is really a length-weighted density estimate, since they estimated territory size for each size class from $\log T = 2.61 \log \text{fork length (cm)} - 2.83$, based on data in the literature that exhibit considerable scatter

⁵⁵ Fish that grow in lakes but move into streams to spawn are adfluvial.

(their Figure 1). Moreover, as noted above, territory size in a given stream will depend on the food supply there, which may vary from year to year and change over the course of a season. Local information on territory size would make the concept more reliable.

Unfortunately, there do not seem to be concepts analogous to PHS that might assist in evaluating habitat use by schools of juvenile Chinook. However, there are abundant data from existing monitoring programs that could be analyzed for evidence of density-dependent growth or migration that might shed light on the productivity of large river habitats. For example, there is evidence of density-dependent growth in juvenile winter-run that rear upstream from the RBDD for several months before emigrating (Figure 8-5). Simple models describing this density-dependence could be compared using statistical measures such as the AIC (Burnham and Anderson 1998; Ch. 14). Questions regarding the influence of environmental factors on size and migration timing could also be explored and modeled. These matters could be explored in more detail if the growth and condition of subsamples of fish were determined, as discussed in Ch. 15.

Figure 8-5. Apparent density-dependent growth in juvenile winter Chinook passing the RBDD. Monthly average length in November (grey circles) and December (black circles), plotted against the estimated number of juveniles passing the dam from October through December, for 1995-99 and 2002. Data points for two Decembers overlap. Note that most juveniles pass at smaller sizes in August and September. Data courtesy of Steve Cramer, S. P. Cramer & Associates.



Modeling can also be useful for testing whether and under what circumstances various behavioral rules are consistent with observations of habitat use. As noted in Chapter 14, such use of models as experimental systems allows for relaxation of the concerns regarding complexity that apply when models are used for prediction. However, simplicity is still a virtue, and simple rules for behavior may produce the same results as more complex considerations. For example, bioenergetic considerations are often invoked to predict the water velocity at feeding stations occupied by stream salmonids (e.g., Fausch 1984). However, Hill and Grossman (1993) found that predictions based only on the efficiency with which rainbow trout could capture prey (a function of velocity) were usually more accurate than predictions based on their full bioenergetic model. It seems likely that it is easier for a fish to tell whether prey are being swept past too quickly to capture than whether their caloric content is worth the effort.

Stranding

When flow in a stream drops, juvenile salmonids and other fishes that live along the margins of the stream may be stranded. Fish that burrow down into the substrate on gravel bars for cover may not sense the decline in water levels in time to move into deeper water, and fish may move into local depressions that become isolated ponds; even if the ponds do not go dry the fish may be easy prey for birds, or the ponds may get lethally warm. In rivers below dams, the rate of decline in the flow is often controlled, and especially below dams operated for hydropower, substantial fluctuations in flow may be chronic. Stranded fish may be highly visible, and sometimes occur in impressive numbers, so considerable effort has gone into developing controls on the rate of change of flow, or “ramping rates,” that are intended to reduce stranding. However, in streams that produce millions of juvenile salmonids, the loss of several thousands may be a minor source of mortality, even if visually impressive, so the actual importance of losses to stranding can be questioned.

Probably the most intensive study of stranding of juvenile Chinook has been on the free-flowing Hanford Reach of the Columbia River, which supports substantial populations of naturally producing salmon, including fall-run Chinook, but is subject to substantial daily fluctuations in flow from hydropower operations at Priest Rapids Dam (e.g., Nugent et al. 2002a,b; Tiffan et al. 2002). Conservatively estimated mortalities (se) for 1998-2002 were 93,943 (30,015), 45,486 (16,643), 2,013,638 (1,408,149), and 67,409 (39,594). Since the Hanford Reach produces over 20 million juveniles annually, it appears that stranding mortality was biologically significant in 2001, a low-flow year, but not in other years. Curiously, flow fluctuations were smaller in 2001 than in other years. However, at the low flows in 2001, substantially more area, especially in island complex habitats, was exposed by the fluctuations (Nugent et al. 2002b). Thus, the threat of stranding depends on local circumstances, so broad generalizations about the importance of stranding seem out of order, although the Hanford Reach studies do indicate that fish longer than ~ 60 mm are much less likely than smaller fish to be stranded.

Studies of stranding in Central Valley streams are roughly consistent with the Hanford Reach studies. Kurth (2003) estimated that less than 0.5% of fall-run Chinook were at risk of stranding in the Feather River in 2002-2003, and CDFG (2001) estimated that 1.5 to 19% of juvenile fall-run were at risk of stranding in the lower American River in 1997-2000. However, actual mortalities were not estimated.

Predation

The natural mortality rate of juvenile salmonids is high, and presumably most of the mortality results from predation. Nevertheless, information about predation on salmon in the Central Valley is limited, for several reasons. Predation is natural, and salmon are sufficiently fecund that populations can increase rapidly even when substantial predation occurs, so simply showing that predation occurs does not show that it is a cause for reasonable concern. Predation is hard to study, especially in large rivers. Quantitative information on survival of juvenile salmon in the Central Valley comes mainly from studies of tagged hatchery fish, which probably

are more vulnerable to predation than naturally produced fish of the same size,⁵⁶ especially when they are first released. Finally, an appropriate reaction against the negative attitudes toward natural predators that characterized the early twentieth century, displayed for example in early issues of California Fish and Game, may have created a reluctance to develop information that might be used to lobby for control of predators, especially birds. More is known about predation in the Columbia River, where dams are arranged in series and allow for extensive use of PIT tags, with which individual fish can be tracked as they move down the river, and there has been considerable study of various salmon predators (e.g., NMFS 2000; Ryan et al. 2003). In any case, the currently prevalent view of predation in the Central Valley is that serious predation problems for salmon result from unnatural conditions, as expressed for example by the proposed recovery plan for Winter Chinook (NMFS 1997:III-89):

Predation by native species is a natural phenomenon and should not have a serious effect in the free flowing river. Winter-run chinook have co-evolved with its native predators and have developed strategies to avoid predation. However, predation by introduced species and increased predation due to artificial in-water structures may have resulted in gross imbalances in the predator-prey relationships and community structure in which winter-run Chinook evolved.

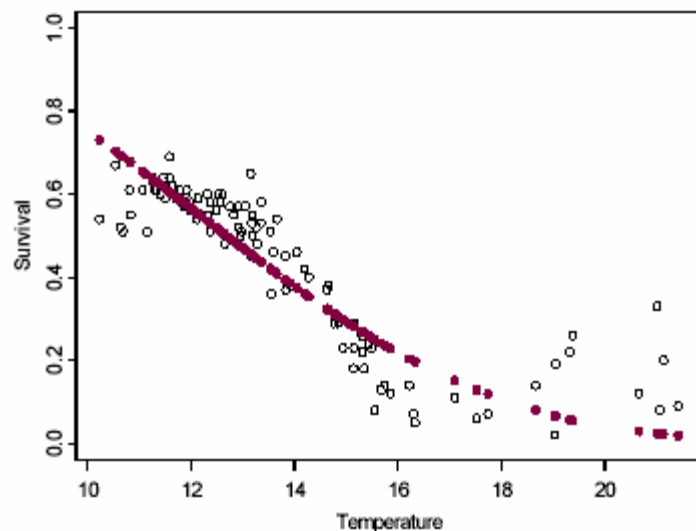
The view that predators did not seriously depress salmon populations in the Central Valley under natural conditions is supported by the literature (e.g., Brown and Moyle 1981), and is necessarily implied by historical accounts of the abundance of Chinook. It is clear that structures such as the Red Bluff Diversion Dam create opportunities for striped bass and pikeminnow to prey on juvenile salmon (Tucker et al 1998; 2003). It is also clear that gravel mining has created ponds and deep runs in San Joaquin River tributaries that provide habitat for striped bass, black bass, and pikeminnow, but the actual rates of predation on naturally produced fish and the relative importance of the different predatory fishes are less so (Tri-Dam Project 2001). Moreover, it is not clear that artificial structures such as piers create more favorable conditions for predators than existed in natural conditions, when snags were abundant in the rivers.

It seems likely that the risk of predation is mediated by water temperature, primarily through its effect on the metabolism (and appetite) of the predatory fish. For example, Anderson (2003) found a good relation between water temperature and survival based on PIT tag data, even at low temperatures (Figure 8-6). It seems hardly plausible that direct physiological effects result in increasing mortality as temperature increases between 11 and 15°C. Similarly, a recent assessment of data on coded-wire tagged late fall Chinook released into the lower Sacramento River or Georgiana Slough found that temperature accounted for variation in survival better than exports from the Delta pumps, over a temperature range of 7 to 11°C (B. Manly, Western Ecosystems Technology, pers.comm. 2005). This also suggests that predation is the actual

⁵⁶ Goodman (2004:218) notes that data on the smolt to adult survival of wild fish are scarce and variable, but “Some available data suggest that often, but not always, the smolt to adult return rates of wild fish are higher than those of the corresponding hatchery-reared fish, often by a factor of about two.” It seems likely that differential losses to predation account for a good part of this difference.

mechanism involved, although Manly cautioned that a single data point with low temperature, low exports, and high survival strongly influenced both relationships. The survival of coded-wire tagged hatchery fall-run smolts released into the lower Sacramento River begins to decline at about 18 or 19°C (Baker et al. 1995), which also suggests that predation rather than direct physiological factors are involved, although the two are related since sublethal physiological stress makes fish more susceptible to predation (Marine and Cech 2004). Similarly, disease makes fish more susceptible to predation (Quinn 2005). Various birds also eat juvenile salmonids (Quinn 2005), but I have not found any studies of this in the Central Valley. Much of the mortality associated with stranding probably results from birds eating fish stranded in isolated ponds.

Figure 8-6. The effect of temperature on survival of juvenile spring Chinook in the Columbia River between Lower Granite Dam and McNary Dam in 2001, estimated from pit tags (open circles) and from a model (filled circles). Copied from Anderson (2003).



Sculpins and larger salmonids are generally significant predators on Pacific salmon eggs and fry (Quinn 2005), and probably this holds true for the Central Valley. Merz (1993) reported that about 9% of the biomass in the stomachs of 115 sculpins from the American River was fry of Chinook or steelhead. Predation on Chinook fry by hatchery Chinook released as yearlings has been documented (Sholes and Hallock 1979), and hatchery steelhead from Coleman Hatchery are now released at Bend Bridge to reduce predation on juvenile Chinook in Battle Creek (USFWS 2001). There seems not to be published information on predation by resident *O. mykiss* below dams with cool summer releases, but presumably it occurs, as does predation on fry by yearling Chinook. Whether such predation significantly limits populations is less clear, however (e.g., Moyle 1977).

Predation on juvenile Chinook by striped bass (*Morone saxatilis*) has been a concern in the Central Valley for some time. Striped bass occur in the rivers as well as in the Delta. For example, adult striped bass hold just downstream from the Red Bluff Diversion Dam (RBDD) when the gates are lowered, and prey on juvenile salmon and other small fishes that are

disoriented by the violent turbulence where the water passing under the gates decelerates. Pikeminnow (*Ptychocheilus grandis*) are less important as predators now that the dam gates are raised during their upstream spawning migration, so that they do not congregate below the dam (Tucker et al 1998; 2003). On the San Joaquin River tributaries, more attention has been given to largemouth and smallmouth bass (*Micropterus salmonides* and *M. dolomieu*) that live in mining pits that are connected to the rivers (e.g., McBain and Trush and Stillwater Sciences 1999; 2000).

Use of habitat in small tributaries

Central Valley salmon streams have many tributaries that are too small to support spawning by Chinook, but nevertheless provide rearing habitat for juveniles, as demonstrated by recent studies of small tributaries of the Sacramento River (Moore 1997; Maslin et al. 1997; 1998). The upshot is that juveniles migrate up even seasonally dry streams to rear before returning to the river to emigrate. These streams are generally warmer than the river, and the abundant food allows juveniles to grow rapidly (Moore 1997; Maslin et al. 1997; 1998). Maslin et al. (1998) estimated that more than a million juveniles use these Sacramento tributaries in some years.

Large wood in streams

Streams carry not only water and sediment to the ocean but also wood, and fallen trees can have major effects on channel form and on both physical and biological processes in streams (Harmon et al. 1986; Bisson et al. 1987; Maser and Sedel 1994; Montgomery et al. 1996; NRC 1996; Bilby and Bisson 1998; Gregory et al. 2003). Large woody debris can create or modify pools, cause bank erosion or deposition of sediments including gravels suitable for spawning, provide cover for fish or substrate for invertebrates, and trap smaller organic debris, including salmon carcasses, allowing the local use of the nutrients they contain. According to NRC (1996:194), "Perhaps no other structural component of the environment is as important to salmon habitat as large woody debris, particularly in coastal watersheds."

The ability of a stream to transport wood increases with the size of the stream and decreases with the size of the wood, so that as stream size increases, the frequency of large wood decreases but the average size increases. In the Central Valley, as elsewhere, large wood historically was more likely important in the smaller streams and tributaries than in the larger rivers, but the history of clearing and snagging on these rivers suggests that large logs were common even in the mainstem Sacramento. Early settlers actively cleared "drift" from streams to increase channel conveyance capacity for winter flows, as described in the 1882 testimony of John Bidwell in the trial of *People v. Gold Run Ditch and Mining Co.* (Ch. 2). Although not as important as hydraulic mining, the early logging of forests around the margins of the Central Valley was another major modification of the landscape that contributed to the degradation of habitat for salmonids, and the forests of very large conifers that so impressed early observers such as the geologist William Brewer (Brewer 1966) are mostly gone even from memory.

Fallen trees enter streams by three main processes (Bilby and Bisson 1998): by bank erosion undercutting riparian trees, by windthrow, or by debris flows. In the Central Valley these processes probably recruit mainly hardwoods, hardwoods and conifers, and conifers,

respectively. Riparian restoration will tend to increase the rate at which hardwoods fall into streams, but the source area for longer-lasting conifer logs in most Central Valley rivers is blocked by dams. Dam operators routinely remove logs from reservoirs, and there could be significant benefit to downstream habitats if the logs were returned to the stream below the dam.

Unfortunately, many bridges are built with spans too narrow to pass large wood effectively, and bank erosion induced by large wood can be a threat to housing or other infrastructure that has intruded into riparian areas. In consequence, what large wood still remains or is recruited to streams is often cut into pieces that are too small to be geomorphically effective. For example, logs in the canyon reach of Butte Creek were cut up with public funding a few years ago (Williams et al. 2002), at the same time that millions of dollars were being spent to improve access by salmon to the habitat.

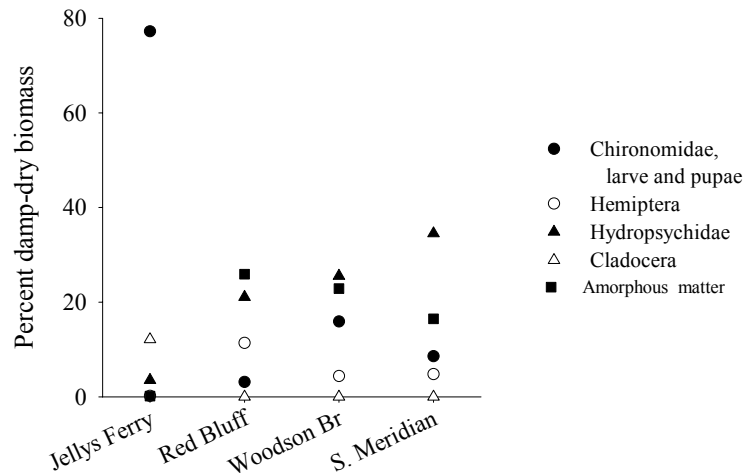
The lack of logs probably is most critical in streams such as Clear Creek, where removal of a small dam has allowed spring Chinook and steelhead access to the bedrock reach below Whiskeytown Dam. From examination of aerial photographs, it appears that gravels have been flushed out of this reach since the supply from upstream was cut off by the dam (Williams and Kondolf 1999), so that gravel replenishment probably is needed for salmonids to make effective use of the habitat. Gravel deposits suitable for spawning typically are scarce in such channels, and many that do occur result from the hydraulic effects of logs jammed across the flow (Montgomery et al. 1996). Accordingly, a shortage of logs will make any gravel replenishment program less effective, and reduce the utility of the large investment that went into removing the dam.

Diet

There is a good deal of local information on the diet of juvenile Chinook salmon in gravel-bedded streams, which generally seems consistent with reports from other areas reviewed by Higgs et al. (1995), who noted that prey size, abundance, and visibility seem to be the most important determinants of diet. In the Central Valley, aquatic insects, especially chironomids and mayflies and sometimes caddisflies, are generally important, but crustaceans, aphids, terrestrial insects, and larval fish such as Sacramento suckers can be so as well.

In the Sacramento River in March to May of 1998, Martin and Saiki (2001) found that midge (chironomid) larvae and pupae dominated the diet of juvenile Chinook at Jelly's Ferry (rkm 426), but caddisfly larvae, other aquatic insects, and bugs (Hemiptera) were more important farther downstream. Cladocera made up 12% of the biomass at Jelly's Ferry (rkm 416), but were absent elsewhere (Figure 8-7). Difference in sampling dates probably accounts for the sharp difference recorded for Jelly's Ferry (May) and Red Bluff (March), given the short distance (36 km) between the two sites.

Figure 8-7. Distribution by biomass of important components of the gut contents of 114 juvenile Chinook from the Sacramento River, reported by Martin and Saiki (2001). Amorphous matter is “mostly unidentifiable insect remains.” Data from Table 1 in Martin and Saiki (2001); items making up more than 10% of the sample at any site are shown.



Martin and Saiki (2001:41-42) summarized the results of earlier studies on the Sacramento River as follows:

According to an early report by Rutter (1904), juvenile Chinook salmon in the Sacramento River and its tributaries consumed mostly adult or terrestrial insects and immature stages of aquatic insects. ... More recently, Schafer et al. (1983) found that juvenile Chinook salmon captured from the river between Red Bluff and Chico fed primarily on midges, baetid mayflies, and Aphididae. In August, 1990, identifiable gut contents of 29 juvenile Chinook salmon from Lake Redding on the upper Sacramento River consisted mostly of Cladocera and midge larvae (M.K. Saiki, unpublished data). ... Finally, Moore (1997) reported that juvenile salmon in the Sacramento River at Red Bluff fed mostly on midges, baetid and ephemereid mayflies, hydropsychid caddisflies, and perlodid stoneflies, whereas juvenile salmon in Dibble and Blue Tent creeks feed mostly on midges, baetid mayflies, capniid stoneflies, and larval fish.

Petrusso and Hayes (2001b) investigated the diet of juvenile Chinook sampled in the Sacramento River between rkm 331 (near Chico) to rkm 444 (between Red Bluff and Redding) from April into June, 1996; they also sampled drifting organisms that were potential prey. Chironomids (63%) and mayflies (14%) were the main prey organisms. Chironomid larvae appeared much less frequently in stomachs than in the drift, but the adults and pupa were strongly selected; there was some selection against oligochaetes and cladocera, but other organisms were taken in rough proportion to their abundance. There was a weak increase in prey size with fish size, but the increase in prey size was much less than the increase in gape width. On average, the wet weight of stomach contents equaled 2.4% of the wet weight of the fish. Petrusso and Hayes estimated that on average, 24 hour consumption was about 12.5% of wet body weight.

Merz (2001) studied the contents of 688 stomachs from juvenile Chinook from the Mokelumne River, sampled from January to June of 1997 and 1998. Zooplankton (daphnids and cyclopids), chironomid larvae and pupae, and larval Sacramento suckers were the dominant food items. Since these varied considerably in size, Merz calculated an index of relative importance, defined as the percentage by number plus percentage by weight, multiplied by the percentage frequency of occurrence, for each major food item and for a lumped category of “others.” The relative importance of these varied by month and year, but generally zooplankton was particularly important in February and March of both years, and in May and June of 1998. Chironomids were particularly important in April, May and June of 1997 and in January and April of 1998. Larval suckers were important in April and June of 1997 and in May and June of 1998; by weight, larval suckers dominated the diet in both years. Mean prey length increased with fish length in both years, from ~1 mm for newly emerged fry to about 4 mm for fish > ~70 mm.

Juvenile and adult *O. mykiss* in the Mokelumne River ate mostly aquatic insects, along with lesser amounts of zooplankton; fish eggs, larvae or juveniles; terrestrial arthropods, and miscellaneous other items including mice. The 179 fish were sampled in each quarter of the year, but mainly in fall and winter, and ranged from 92 to 435 mm. Ranked by the index of relative importance used by Merz (2001), the most important items were caddisfly larvae, chironomid pupae, baetid mayflies, and daphniids.

In the lower American River, the diet of juvenile Chinook and steelhead sampled at three sites varied considerably between 1992, a dry year with stable flow, and 1993, a wet year with several periods of high flow (Merz and Vanicek 1996; Figure 8-8). The diet was more varied in 1992, and fish had more food in their stomachs; averaged over months, an index of fullness (s.e.) for 1992 and 1993 were 2.5 (0.49) and 0.9 (0.13) for Chinook and 3.6 (1.3) and 0.8 (0.12) for steelhead. The fish were smaller in 1993 (Figure 8-9), which was also found in more extensive sampling conducted for other purposes (Williams 1995). However, water temperatures were ~ 3°C cooler in 1993, which would also affect the growth rates of the fish. A growth model like that described in Ch. 4 would be useful for interpreting these results. In any event, assessments of the relation between temperature and the growth of juvenile salmon in the Central Valley need to take food supply into account, since in regulated streams warmer temperatures are generally associated with the lower and more stable flows of dry years. Juvenile Chinook and steelhead grew well in the American River in 1991 and 1992 (Castleberry et al. 1991; 1993), this growth presumably depended on an ample supply of food.

Figure 8-8. The diet of juvenile Chinook (circles) and juvenile steelhead (triangles) in the lower American River in 1992, a year with low and stable flow, and 1993, a year with high and variable flow. The index of relative importance is calculated as $IRI = (FN + FW)FO$, where FN are the food item's percentages of total number and of total weight of ingested items, and FO is the percentage frequency of occurrence in all stomachs examined that contained food. Data from Table 2 in Merz and Vanicek (1996).

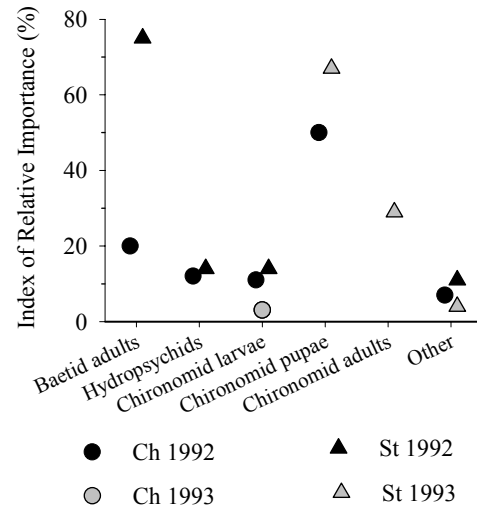
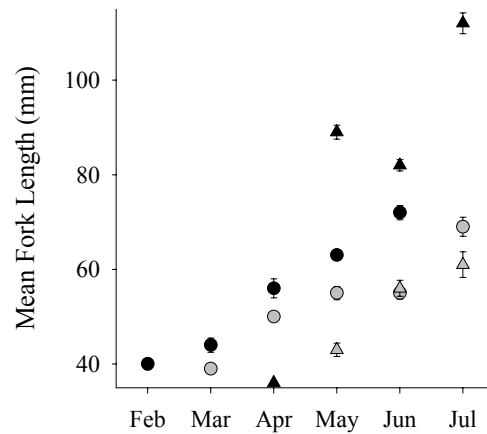


Figure 8-9. Comparison of fork lengths of juvenile Chinook and steelhead sampled from the American River in 1992 and 1993 by Merz and Vanicek (1996); symbols are as in Figure 8-8. Bars show standard errors; samples sizes ranged from 21 to 64. No Chinook were sampled in July 1992.



CHAPTER NINE

OVERBANK HABITAT

Our plans were materially changed in April, when we discovered that great numbers of salmon fry are lost during high water, by being caught in overflow ponds, where they are stranded as the water recedes. Scofield (1913:37)

In this study, we provide evidence that the Yolo Bypass, the primary floodplain of the lower Sacramento River ..., provides better rearing and migration habitat for juvenile Chinook salmon ... than adjacent river channels. Sommer et al. (2001:325)

Juvenile Chinook and steelhead migrating downstream sooner or later pass from the higher-gradient, gravel-bed reaches that support spawning into low-elevation, low gradient habitat along the main axis of the Central Valley. Formerly, except perhaps in very dry years, fish migrating in winter or spring found a vast expanse of non-tidal, shallow habitat in the flood basins of the Sacramento Valley, and in the overbank habitat and sloughs along the San Joaquin River (Kelley 1989; TBI 1998; Greco 1999) . These merged gradually into the tidal Delta. Along the Sacramento River, part of this habitat remains within the Butte Sinks and the Sutter and Yolo bypasses (Figure 3-14), which are at least partly inundated in about 60% of years (Sommer et al. 2001). Sommer et al. (2004) and Feyrer et al. (2006) describe the bypasses and their fish communities. Low elevation overbank habitat in the San Joaquin Valley has been lost except for vestiges remaining within the levees, but some is being restored, particularly along the Cosumnes River.

There is little information about the historical use of flood basin and overbank habitat by juvenile Chinook in the Central Valley, and apparently there is little published information on the use of such habitat elsewhere (Sommer et al. 2001). Losses to stranding and high water temperatures in the Sutter and Yolo bypasses in 1911 were documented and viewed with alarm by Scofield (1913), but were not quantified. Scofield was concerned in part because a net set in the outlet to the Sutter Bypass did not catch juvenile Chinook, although a net set in an inlet did. However, his study of this issue was unplanned, as indicated by the quotation above, and did not begin until April, when the peak of the fall-run emigration was past.

Scofield (1913) remarked on the need for additional study of the flood basins, but if he conducted any he did not publish the results. He did note that the proposed construction of bypasses within the basins would reduce the stranding hazard by improving drainage, which may explain the lack of further work. Nevertheless, even after construction of Shasta and Oroville dams reduced winter and early spring flows in the Sacramento, large volumes of water still flow through the bypasses in wet years, so it does seem remarkable that the bypasses received so little attention from salmon biologists until recently. For example, Hatton (1940), in a discussion of the anticipated effects of the Central Valley Project on fish, did not mention the bypasses.

Similarly, the map of the Estuary and lower rivers given in Kjelson et al. (1982) did not include the Yolo Bypass, nor did they mention it.

Recent work shows that the bypasses do indeed provide habitat for juvenile Chinook, that they grow well there, and that most avoid stranding (Hill and Webber 1999; Sommer et al. 2001; 2004; Ward et al. 2004a,b). Juvenile spring-run Chinook in Butte Creek are captured in a screw trap and a fish screen a short distance below the downstream limit of their spawning area, and for some years were also captured in the Sutter Bypass, at sites that range from 98 to 125 km below the upstream trap. Some of the fish captured at the upstream site are coded-wire tagged, and recaptures at the downstream trap in 1996, 2001, and 2002 allow estimates of migration and growth rates (Figure 9-1). These estimates should be viewed with caution, since they are based on the median date on which fish with the same tag code were released, and on the average size of tagged fish, rather than on paired measurements of individual fish. In at least two years, however, there have been reasonable numbers of recaptures of fish from tag codes that have been used only for 4 or fewer days (2001, 97 recaptures) or 7 or fewer days (2002, 28 recaptures) (Ward et al. 2004a, b). Since the mean intervals between release and recapture in the two years were 71 and 52 days, estimates of individual migration rates in these years are fairly good. There were 56 recaptures in 1996, but only two tag codes were used, so estimates of growth rates of individuals in 1996 are highly uncertain, and because the bypass was flooded it was not possible to install the trap until the bypass began to drain in mid March. Nevertheless, the median estimates are probably reasonable, and show considerable year to year variation, with the median estimated growth rate varying from 0.35 to 0.75 mm d⁻¹ (Figure 9-1).

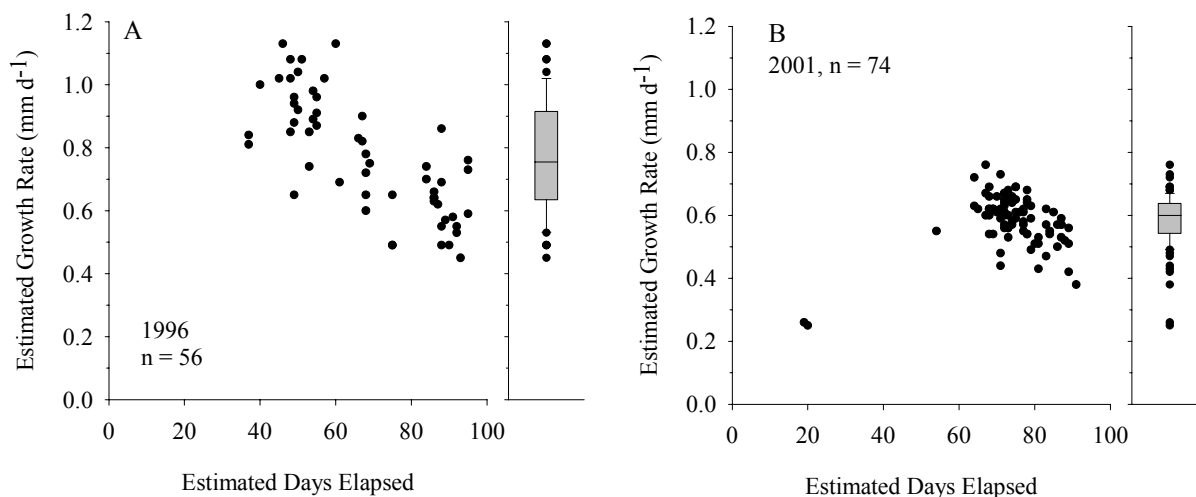
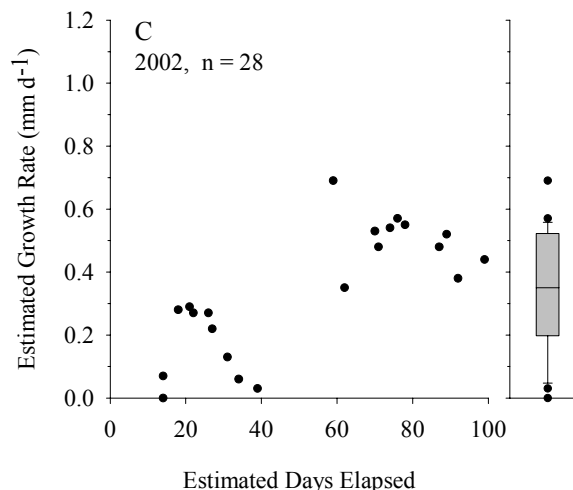


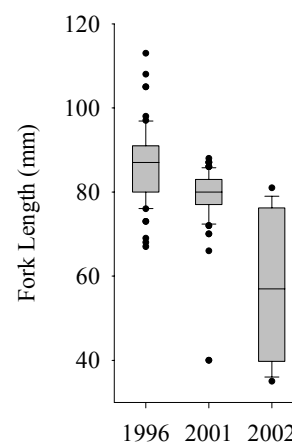
Figure 9-1: See following page for legend.

Figure 9-1. Estimated growth rates v. estimated days elapsed between release and recapture for juvenile spring-run Chinook in Butte Creek in 1996 (A) 2001 (B), 2002 (C); estimates for 1996 are highly uncertain. Box plots show the distribution of estimated growth rates. Data from Hill and Webber (1999) and Ward et al. (2004a,b).



There are intriguing patterns in the data, such as the inverse relation between migration rate and growth rate for fish that spend over 60 days in the lower creek and bypass, but not too much should be made of them unless they are confirmed by future work. Analysis of the otolith microstructure of such fish would also allow more robust interpretation of the data. However, there is no doubt that juvenile Chinook can grow well in the bypass: in 1996, 75% of the recaptured tagged fish were more than 80 mm fork length (Figure 9-2).

Figure 9-2: Distribution of the fork lengths of tagged young-of-the-year spring-run Chinook salmon from Butte Creek, when recaptured in the Sutter Bypass. Data from Hill and Webber (1999) and Ward et al. (2004a,b).



Studies in the Yolo Bypass (Sommer et al. 2001; 2005) have also produced intriguing data. Because juvenile Chinook can migrate to the Delta either through the Yolo Bypass or down the lower Sacramento River, Sommer and his colleagues were able to evaluate the relative survival of juveniles in the bypass and in the river using paired releases of small (~55 mm) tagged juvenile fall Chinook from the Feather River Hatchery in 1998, 1999, and 2000. The tagged fish were released into the bypass near the Fremont Weir, just upstream from the confluence of the Sacramento and Feather rivers, and into the river just downstream from the weir. Based on recaptures of juveniles at Chipps Island and of tagged adults in the ocean fisheries, those released

in the Yolo Bypass survived better than those released in the river in 1998, about the same in 1999, and less well in 2000 (Sommer et al. 2001, 2005). The reasons for the year-to-year differences in relative survival are unknown, but may be related to the greater duration of flooding in the bypass in 1998.

Tagged fish were also recovered in a screw trap operated near the downstream end of the bypass. The average time that tagged fish spent in the bypass in the three years ranged from 30 to 56 days, although one fish traversed the 44 km between the release and recovery sites in 4 days (Sommer et al. 2005). Seining showed that fish distributed themselves widely over the bypass. Although some fish were lost to stranding, especially around engineered structures, stranding losses appeared to be minor (Sommer et al. 2001; 2005); in each year, there were large spikes in the number of fish captured in the screw trap when the bypass was draining, and there was no indication that fish were concentrated in residual pools. Unpublished studies of overbank habitat use along the Cosumnes River also indicate that juvenile Chinook grow well on inundated floodplain, and that most successfully return to the river when the floodplain drains (P. B. Moyle, UC Davis, pers.comm., 2004).

In the Yolo Bypass, juvenile Chinook consumed mainly chironomid pupae and adults in 1998 and 1999; in the river there were fewer chironomids, and the fish consumed mainly zooplankton. Water in the bypass was warmer than in the river, and evidently juvenile Chinook found enough food there to exploit the growth opportunity that the warmer water provided. In any event, juveniles in the bypass apparently grew more rapidly than juveniles in the river in both 1998 and 1999 (Sommer et al. 2001; Figure 9-3).

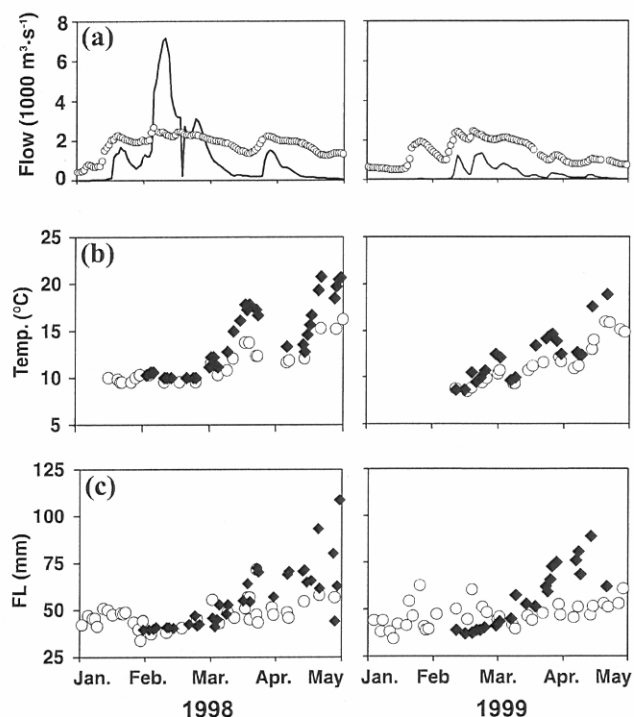


Figure 9-3. Physical conditions (a, b) and size (c) of juvenile Chinook salmon in the Yolo Bypass (line and solid figures) and Sacramento River (open symbols). Temperatures and fork lengths are daily means, fish lengths are from seine samples. Copied from Sommer et al. (2001), courtesy of the CJFAS.

Overall, the data indicate that historically the overflow basins along the Sacramento River and overbank habitat along the San Joaquin River probably were important habitat that afforded a major growth opportunity for juvenile fall-run and spring-run Chinook, although at the cost of some losses to stranding. They also suggest that routing more water down the bypasses in drier years could provide significant benefits for juvenile Chinook.

Juvenile steelhead are also captured in the bypasses, but in much lower numbers than Chinook, and the potential benefit to them of migrating through the bypasses has not been assessed.

CHAPTER 10

THE ESTUARY

We must remember that in the past 120 years, the Delta has changed from a vast tidal marsh to a series of 40 large flat-farmed islands. The old tidal creek channels have been dredged into some 900 miles of navigable waterways. ... Surprisingly enough, a significant wildlife resource remains. It is a far different resource, made up to a very great extent of introduced species dependent on an unnatural environment that man has been changing drastically for a hundred years.

Resources Agency of California (1964:1)

The most efficient and effective way to increase juvenile abundance would be to increase survival during outmigration to the ocean, particularly during passage through the Sacramento-San Joaquin Delta. ... Any improvements in delta survival would benefit natural production at a life stage when natural mortality is not density dependent and would result in a commensurate increase in adults if ocean survival is independent of freshwater survival.

SRFCRT 1994:1

The notion of independent limiting factors to salmon production stems from a traditional agricultural approach to resource management. From this perspective, the estuary was viewed as a hazardous environment where numerous predators or competitors must be controlled to ensure efficient salmon production. This perspective provided little information about the estuarine habitats that salmon need or the processes that link freshwater, estuarine, and marine habitats. A fundamental impediment to salmon and estuary recovery, therefore, is the lack of an explicit conceptual framework to explain the evolutionary and ecological requirements of diverse salmon populations.

Bottom et al. 2005:iv

Many if not most salmon studies in the Central Valley in recent decades concern the passage of larger juveniles through the Delta, or the effects on salmon of the Delta pumps. Most of these studies reflect the view, expressed in the quotation above by the Sacramento River Fall Chinook Review Team, that for salmon the Delta is something to be got through. This view is widespread (Bottom et al. 2005), and in the Central Valley probably has been reinforced by the extensive modification of the Delta and the loss of tidal wetlands there. In contrast to the Delta, there has been little study of juvenile salmon in the bays until a recent effort by NOAA Fisheries that is still in progress, although results from the first year are described in MacFarlane and Norton (2002). This chapter reviews studies of the use of estuaries elsewhere by Chinook and steelhead, and then studies their occurrence of the Delta and of their survival passing through it. There is also information on the growth of juvenile Chinook in the estuary and the timing of their migrations through it in chapters 5 and 6.

The use of estuaries by Chinook and steelhead

The importance of estuaries for Chinook salmon has long been recognized. In the first major publication on salmon in the Central Valley, Rutter (1904; 71) observed that "The quinnat

[Chinook] salmon is found throughout the Pacific coast from Monterey Bay northward, but is less abundant north of Puget Sound. At spawning time it frequents the larger streams, especially those with estuaries." Rutter's associate, N. B. Scofield, monitored the movement of juvenile Chinook into the Delta at Georgiana Slough from January through May, 1899, as discussed in Ch. 6. Rutter knew that very young fry were sometimes found in brackish estuaries, and learned by experiments at the "Hopkins Seaside Laboratory" that even alevins tolerate brackish water: at six days post-hatch alevins can live in 25% seawater, and at 40 days in 50% seawater (Rutter 1904). Rich (1920:51) found from studies of scales of juvenile Chinook in the Columbia River that "The effect of migration into the brackish water of estuary is to decidedly stimulate the growth."

Estuaries are highly variable, as are Chinook life history patterns, so it is not surprising that the use of estuaries by Chinook is also highly variable, as found by Rich (1920) and subsequent workers. Generally, it appears that the importance of estuaries to Chinook varies inversely with the size of the fish reaching the estuary; stream-type Chinook that rear for a year in freshwater spend little time there, but ocean-type Chinook that migrate to the estuary directly after emergence depend on the estuary for rearing habitat, and may spend considerable time there (Healey 1991). For example, Healey (1980) estimated that fry migrants stay as long as 60 days in the Nanaimo River estuary, and tagged hatchery fry remained in the Delta for up to 64 days (Kjelson et al. 1982). Fry migrants initially tend to occupy shallow habitats, often moving far up into tidal wetlands with high tides, but move into deeper water as they grow; Chinook that rear in the river for several months before emigrating rapidly also occupy deeper water (Healey 1991). MacFarlane and Norton (2002) reported that juveniles sampled from April to mid-June took on average around 40 days to migrate through the bays, suggesting a total residence time in the estuary of up to 100 days.

As described in more detail in Ch. 5, most fall-run juveniles in the Central Valley begin migrating toward the lower rivers or the Estuary in January, February or March, shortly after they emerge from the gravel, when they are still less than 50 mm long; however, a considerable number rear near the spawning areas for one to three months before migrating, typically in April and May and at more than 60 mm. A few emigrate in the fall or winter, or in spring as yearlings. Most spring-run in the Central Valley follow a juvenile life-history pattern similar to that of fall-run, although some follow the typical stream-type life history pattern. The timing of migration among winter-run, late fall-run, and yearling spring-run is less clear, because the size-at-date method for distinguishing the runs is unreliable in the Delta (Hedgecock 2002), and they are otherwise distinguishable only by genetic analyses. Generally, however, there are larger (>~100 mm) juveniles moving into the Delta from fall through February or March. There is very little information on the extent to which these fish rear in the Delta, or on the extent to which doing so affects their survival.

Bottom et al. (2002) recently summarized the importance of estuaries for juvenile Chinook. There are enough differences between the Columbia estuary and the San Francisco Estuary that

various details do not apply, but there are enough similarities to make the summary and literature review quite relevant:

More than just a simple corridor for salmon migration, the Columbia River estuary functions as an important transition environment, where individuals should have the opportunity to gradually adapt to salt water, and as a nursery ground, where many young salmon feed and grow to sizes that may increase their chances of surviving in the ocean (Reimers 1973; Simenstad et al. 1982; Thorpe 1994). Juvenile salmon are found in the estuary all months of the year, as different species, size classes, and life-history types continually move downstream and enter tidal waters from multiple upstream sources. The timing and duration of estuarine residence varies widely among salmon species and life-history types with species (Groot and Margolis 1991). Chinook salmon, (*O. tshawytscha*), which has the greatest diversity of juvenile life histories among all Pacific salmon (Healey 1991; Wissmar and Simenstad 1998), has the most varied patterns of estuarine use. Healey (1982) proposed that Chinook are the most estuarine dependent salmonid species since virtually all life-history types spend some time feeding and growing in estuaries, and (ocean-type) fry migrants may depend entirely on the estuary for nursery habitats. ...

The movements of juvenile salmon and their patterns of habitat use within estuaries are size related. Chinook salmon and chum salmon subyearlings (fry) usually occupy shallow, nearshore habitats, including salt marshes, tidal creeks, and intertidal flats (Levy and Northcote 1982; Myers and Horton 1982; Simenstad et al. 1982; Levings et al. 1986). As subyearlings grow to fingerling and smolt stages, their distribution typically shifts toward deeper habitats farther from the shoreline (Healey 1982; 1991; Myers and Horton 1982). In the Columbia River estuary, McCabe et al. (1986) reported that subyearling Chinook salmon in shallow intertidal habitats were smaller than subyearlings captured in deeper pelagic areas. Large yearling migrants, on the other hand, may spend relatively little time in shallow-water habitat. A 1980-81 survey of the Columbia River estuary, for example, found most yearling Chinook salmon at deeper channel sites rather than at intertidal sites sampled near shore (Bottom et al. 1984). Thus, the occurrence of small subyearling salmon, including those life-history types that stay in the estuary for the longest periods, may be closely linked to the availability of certain shallow-water habitats.

Emergent marshes, forested wetlands, and dendritic tidal channel networks may be particularly important to small salmon because they are (1) areas of high secondary production of insect and other invertebrate prey; (2) sources and sinks for detritus; and (3) places where complex structure provides refuge from predators (e.g., Levy and Northcote 1982; McIvor and Odum 1988; Gray et al. In press). ...

Although there has been extensive monitoring of the occurrence of juvenile salmon and steelhead in the Delta, and good evidence that Chinook fry rear there, there has been relatively little study of the actual use of the habitat by those fishes (Brown 2003). One exception is the BREACH studies (<http://depts.washington.edu/calfed/breachii.htm>). Generally, the results for Chinook are consistent with the studies of more northern estuaries reviewed above (L. Grimaldo, CDWR, pers.comm. 2003): small juveniles (< 60 mm) were collected from January to April,

with a peak in March. Most Chinook were collected in open water rather than among submerged aquatic vegetation, and their stomachs contained mainly larval and pupal chironomids (midges) and amphipods.

It appears that juvenile Chinook make less use of the marshes around the edges of Suisun and San Pablo bays than might be expected from the literature. In a review of the use of estuaries in Washington by Pacific salmon, Simenstad et al. (1982:352) noted that “Subyearlings and fry occur mainly in salt marshes where these habitats are available. However, mudflat, foreshore areas can be utilized for some time by larger subyearlings before they move into neritic habitats (Stober et al. 1973; Simenstad and Eggers 1981; Congleton et al. 1981).” Some of the Kjelson et al. (1982) West Delta sites were in brackish areas, and some juvenile Chinook were captured there, particularly in the wet year 1980, when juveniles were captured in San Pablo Bay and central San Francisco Bay as well. The IEP regularly captures juveniles at seine sampling stations around the edge of the bays, particularly in wet years, but the numbers are small (SSJEFRO 2003). Efforts to collect juvenile Chinook with beach seines for the work described in MacFarlane and Norton (2002) were largely unsuccessful (Bruce MacFarlane, NOAA Fisheries, pers.comm., 2003). However, Chinook fry (< 50 mm) are captured by the IEP trawl sampling at Chipps Island in wet years, and fry were found in near-shore habitats near Pittsburg in wet years during studies of the effects of the plume of warm cooling water from a large power plant (C. Hanson, Hanson Environmental, pers.comm.). As summarized by Kjelson et al. (1982:407): “In the Sacramento-San Joaquin system most estuarine rearing occurs in the freshwater Delta supplemented by fry rearing in the brackish bays during high runoff years.”

The scant evidence of use of tidal wetlands and flats around the margins of the bays in drier years is something of an enigma, and may reflect a recent change in Chinook behavior. Considerable numbers of small (< 50 mm) Chinook were captured in a fyke trap at Martinez, in the strait between Suisun and San Pablo bays, in March and early April 1939, a dry year (Hatton 1940; Figure 6-29), and a 1966 report referred to “the proven heavy use of the mud flats of Suisun and Honker Bays by salmon and steelhead” (Delisle 1966:59).⁵⁷ Alternatively, the apparent low densities of juvenile Chinook around the bays may reflect the large area potentially available to them. The extent and circumstances under which juvenile Chinook make significant use of these brackish tidal areas has implications for the value for Chinook of wetland restoration around the bays, and deserves more attention. Repeating Hatton and Clark’s trapping at Martinez would be an initial step.

Studies of the Delta

Erkkila et al. (1950) investigated the spatial distribution of juvenile Chinook within the Delta at 25 stations in April to July 1948 and in late February to July 1949, using a tow net with a 1.5 m (5 ft) circular opening, fished just below the surface (e.g., Figure 10-1). Although their

⁵⁷ Unfortunately, Delise (1966) did not provide a citation for his statement regarding heavy use of mud flats by Chinook and steelhead. However, he also stated that use of mud flats around the rest of the bay was unknown, so presumably he had some study in mind. Don Fry, a CDFG salmon biologist, helped with this report, and the statement about Suisun and Honker bays may reflect his knowledge.

Figure 10-1. A panel from Figure 4 in Erkkila et al. (1950), depicting the estimated spatial distribution of juvenile Chinook in the Delta during the March 22-24, 1949 towing cycle. Areas of the circles are proportional to estimated abundance at the stations; the inset bar graphs show Delta inflow from the Sacramento, San Joaquin, and Mokelumne rivers, minimum and maximum water temperatures, mean salinity, and turbidity at Mossdale and Isleton.

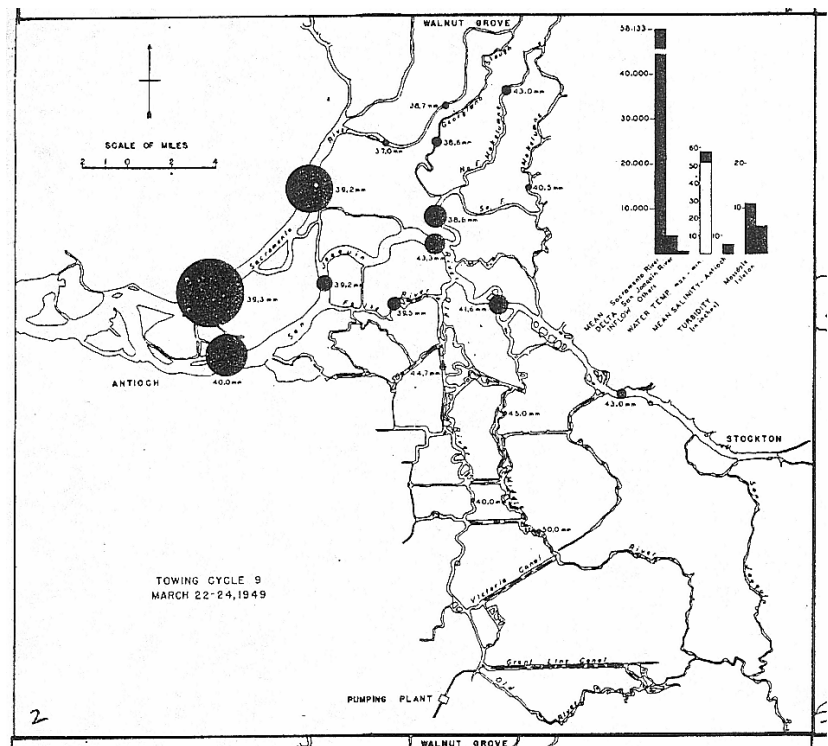
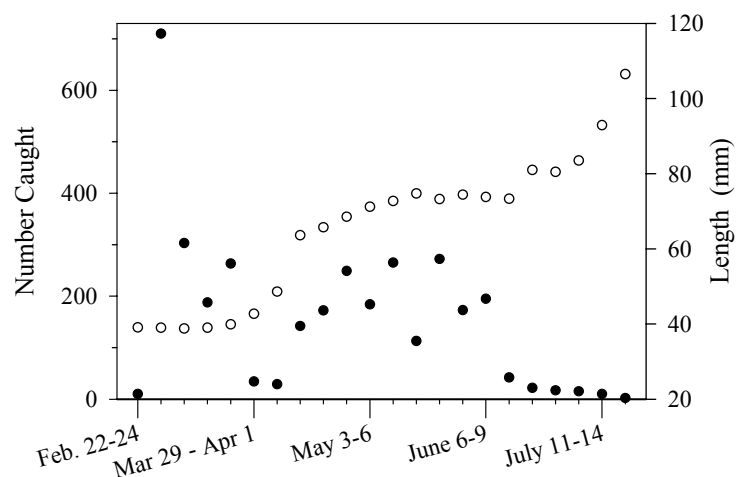


Figure 10-2. Size and abundance of juvenile Chinook in the Delta. Number (filled symbols) and mean fork length (open symbols) of juvenile Chinook captured in the Delta by Erkkila et al. (1950), in 1949, summed over 25 towing stations. Note that the mean length did not increase until late March.



Beach seines (15 x 1.2 m) were used in a subsequent study of the abundance and distribution of juvenile Chinook in the Delta (Kjelson et al. 1982; Figure 10-3); average catches peaked in February or March, and dropped off sharply in April. Monthly average lengths increased most rapidly from April to May, but the number of fish captured decreased sharply over the same period (Figure 10-4). Again, increased catches were associated with pulses of inflow. In diurnal sampling catches were higher during the day than at night, suggesting that the fish moved offshore then.

Figure 10-3. Mean monthly catch per haul of juvenile Chinook collected by beach seine in the Northern Delta in five years. Within months, catches were highly variable (average coefficient of variation 208%). Data from Kjelson et al. 1982.

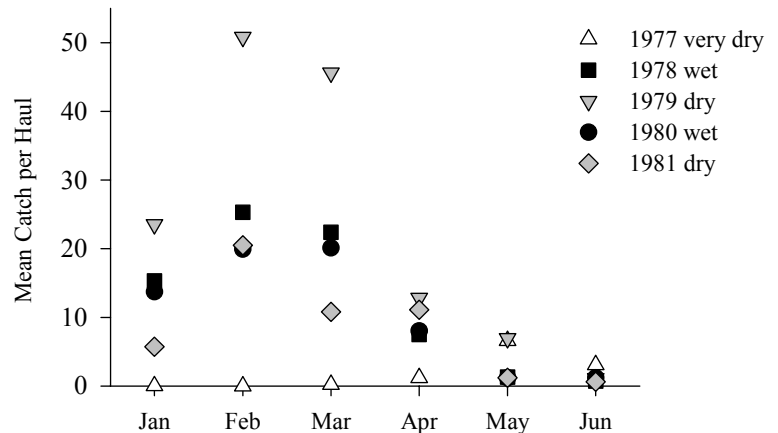
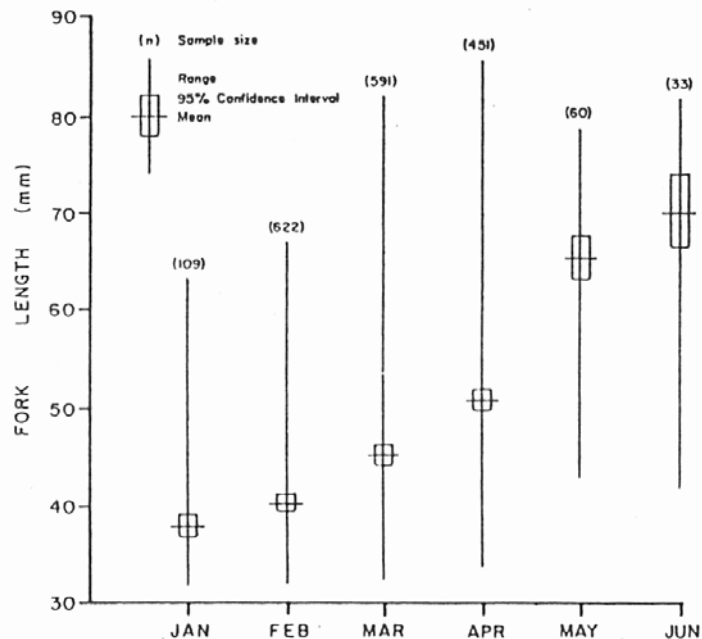


Figure 10-4. Mean size with 95% confidence intervals and range in sizes of 1,866 juvenile Chinook captured with beach seines in the northern Delta between 1978 and 1981. Copied from Kjelson et al. (1982).



Sampling with beach seines in the estuary has been continued by the IEP at ~ 40 stations from Sacramento and Stockton to San Francisco Bay. Summary data from this sampling from 1992-93 to 1998-99 have been reported in SSJEFRO (2003), with fish allocated to runs according to size at date criteria, except that spring and fall-run are reported together because they overlap in size.

Spring/fall-run are most abundant in the Delta in late winter and early spring, as fry, but are captured in significant numbers as larger juveniles in late spring as well, and in small numbers as larger juveniles in late summer and fall (Figure 10-5). The beach seines presumably are less effective for the larger juveniles that tend to occupy deeper water and are better able to escape the net, so the seasonal differences probably are somewhat less extreme than figures 10-3 and 10-5 suggest. Similarly, the nominal late fall-run captured in fall and winter are much larger than those captured in the spring, and probably are relatively more abundant than the seine data suggest.

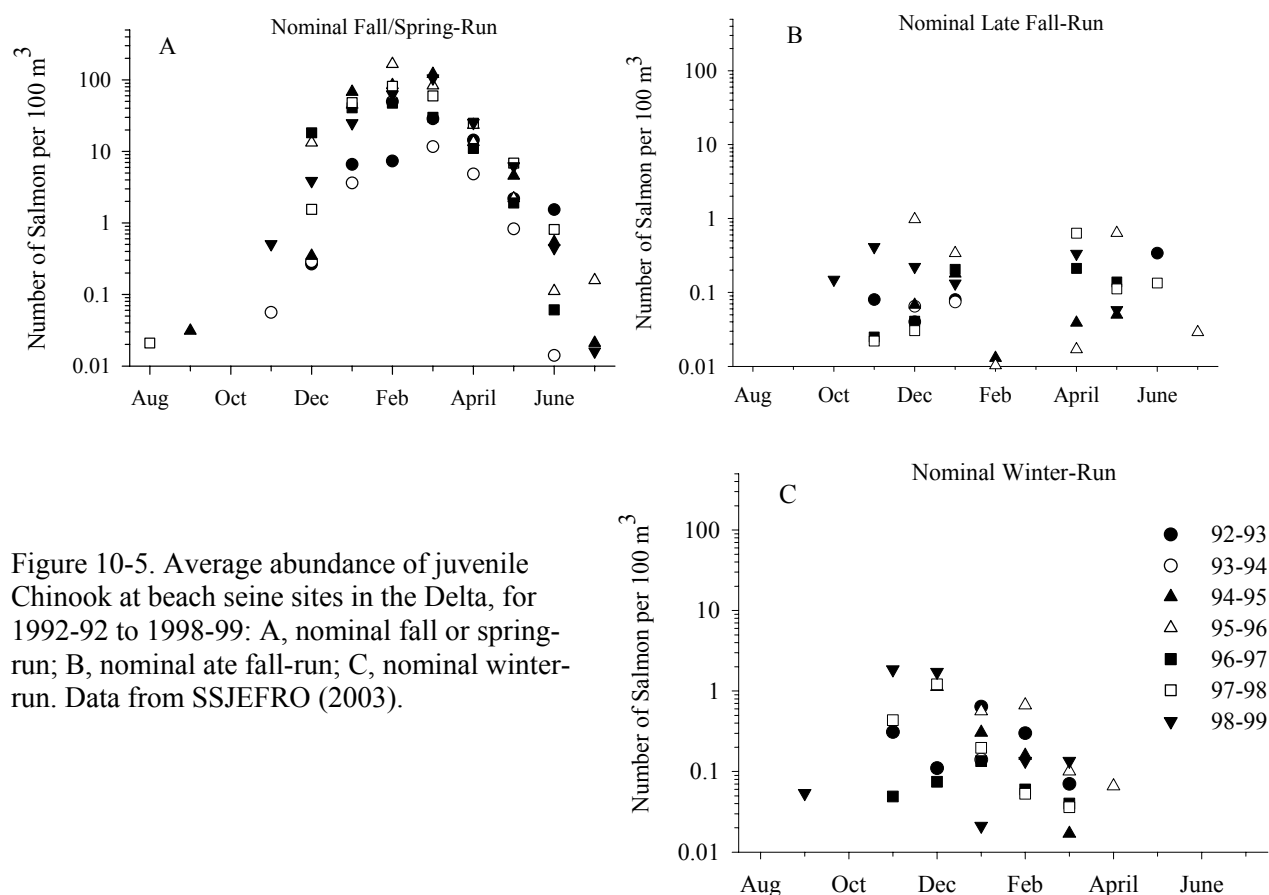


Figure 10-5. Average abundance of juvenile Chinook at beach seine sites in the Delta, for 1992-92 to 1998-99: A, nominal fall or spring-run; B, nominal late fall-run; C, nominal winter-run. Data from SSJEFRO (2003).

Only one haul is taken at each station per sampling cycle, and the catches at individual sites are extremely variable (e.g., Figure 10-6), presumably because the fish occur largely in schools, so the data show only general patterns of temporal distribution. Similarly, it is not clear how well

the stations represent the areas in which they occur. For example, should we believe that there are few juvenile Chinook around the mouth of Steamboat Slough (Figure 10-7), or do the low catches reflect the particular site that is sampled? Nevertheless, the data do show, for example, that on an annual basis the January to March seine catch in the North Delta increases with the mean February flow in the Sacramento River ($r^2 = 0.69$; Brandes and McLain 2001).

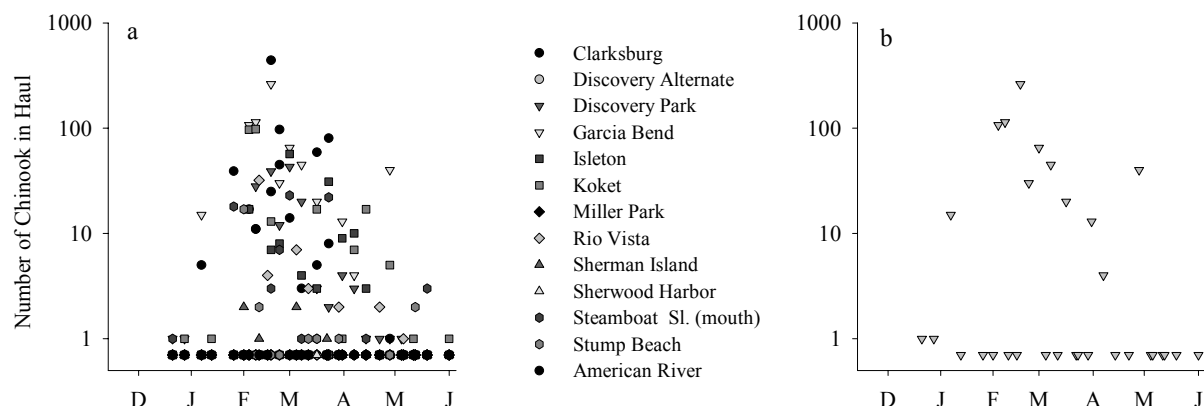
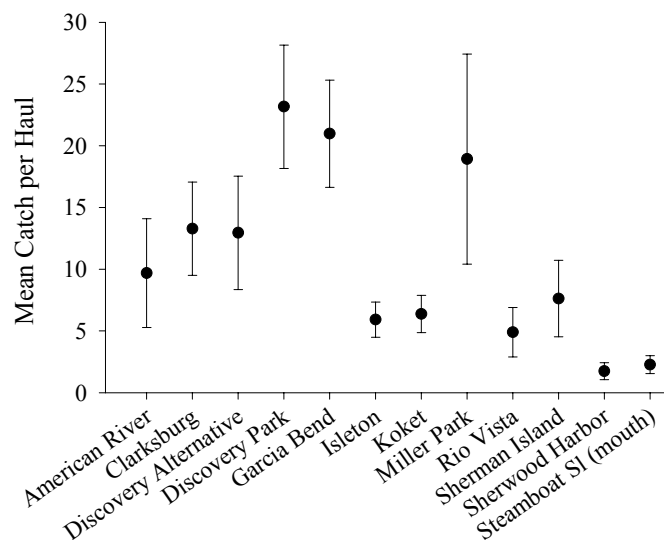


Figure 10-6. Catch per haul of juvenile Chinook in 1993-1994 at (a) 13 seine stations in the North Delta and at (b) one of the stations, Garcia Bend. Catches are extremely variable; note log scale (except that symbols at bottom show catches of zero).

Figure 10-7. Mean catch per haul for 12 sampling stations in the North Delta, 1993-2002. Bars show 95% confidence intervals. Data from IEP.

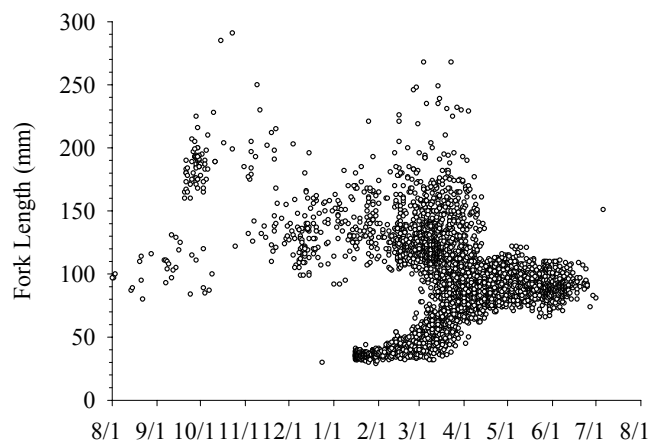


Sampling also occurs at the CVP and SWP diversion facilities at the southern edge of the Delta, where fish are diverted by screens into holding tanks and trucked to the western Delta, and samples are counted and measured (Brown and Greene 1992). The fish sampled are neither a random nor a uniform sample of the fish that make their way to the diversions, since a smaller proportion is sampled when density is high, and the efficiency of the screens varies with factors such as the rate of diversion (Brown and Greene 1992; Hedgecock 2002). Moreover, many fish

may be consumed by predators as they approach the facilities. Nevertheless, it seems likely that the salvage data reasonably reflect major patterns regarding the time of year and conditions under which fish arrive or do not arrive at the diversions. Unfortunately, this source of information has not yet been fully exploited.

The general pattern of arrivals at the diversion facilities is fairly clear (Figure 10-8). Larger (>~ 80 mm) juvenile Chinook arrive from late summer to spring. Small juveniles begin to arrive in winter, and do so with little increase in size until sometime in March. Their average size then increases rapidly for about a month, from < 50 mm to > ~80 mm, and then levels off until July, when salvage of Chinook essentially ends.

Figure 10-8. Juvenile Chinook at the Delta diversions; size at date of 6,752 juvenile Chinook sampled at the CVP and SWP diversion facilities in the Delta from August 1995 through July 2001. Data from Hedgecock (2002).



Flow apparently affects the timing with which juvenile fall and spring-run appear at the pumps. In a wet year (2000), young-of-the-year Chinook appeared at the pumps in mid-February, following a sharp increase in Delta inflow; however, in 2001, a dry year, few fish were sampled until late March (Figure 10-9).

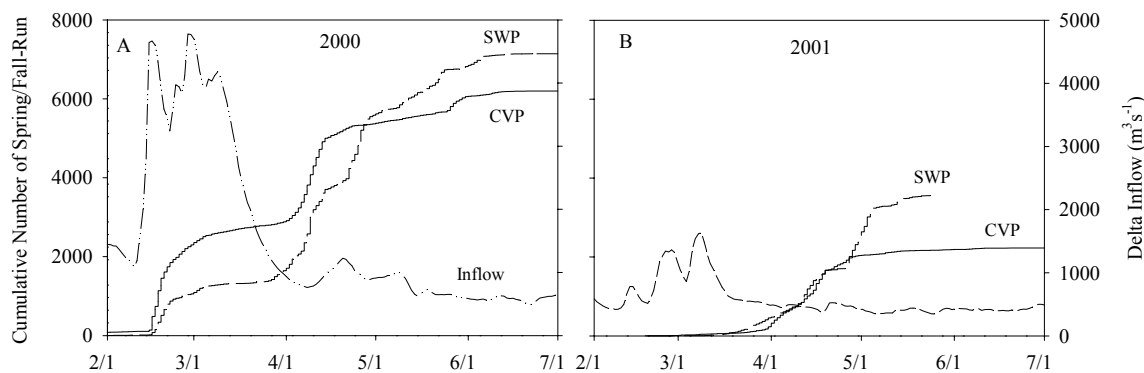


Figure 10-9. Unmarked juvenile spring or fall Chinook sampled at the CVP and SWP diversions in 2000 (A) and 2001 (B). Dashed lines show total inflow to the Delta. Fish appeared at the diversion facilities shortly after a rise in Delta inflow in February 2000. The numbers sampled are not expanded and do not represent the total numbers collected at the pumps (see text), but should reflect major patterns in the arrival of fish at the diversions. Data from the IEP database.

The rate at which juvenile Chinook appear in the samples is affected by the rate of pumping, but the relationship does not appear to be simple; for example, CVP pumping was steady though February and most of March, 2000, then dropped briefly in late March and resumed in early April (Figure 10-10). The peaks in sampling occurred in late February and early April.

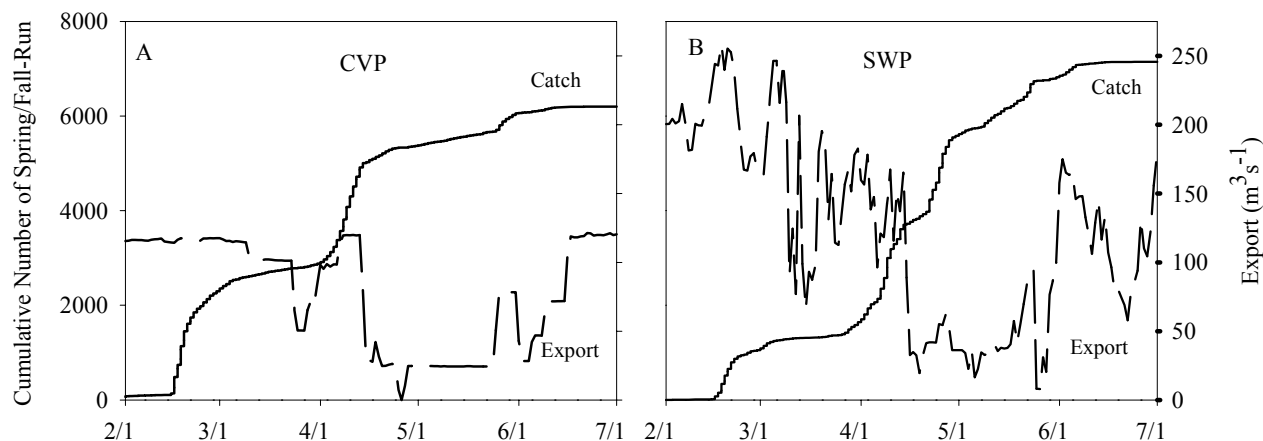


Figure 10-10. Cumulative number of unmarked juvenile spring and fall-run Chinook sampled at the CVP and SWP pumps in January through June of 2000 (solid lines), and exports for the same period (dashed lines). Data from the IEP database.

Besides arriving at the diversion facilities later in 2001 than in 2000, age 0 Chinook were also smaller by ~5 mm in late spring, and they were about ~2 mm larger at the SWP diversion than at the CVP diversion in both years (Figure 10-11). Such year to year variation in size at date may provide a useful index of growth opportunity in fresh water. This should be explored. It would also be useful to look for relations between increases and decreases in the number of fish sampled at the diversions and environmental variables, such as increases in Delta inflow, and in the number of fish collected in other sampling efforts such as the Chipps Island trawl. The objective should be better understanding of the behavior of the fish, as well as better predictions of their arrival at the diversions.

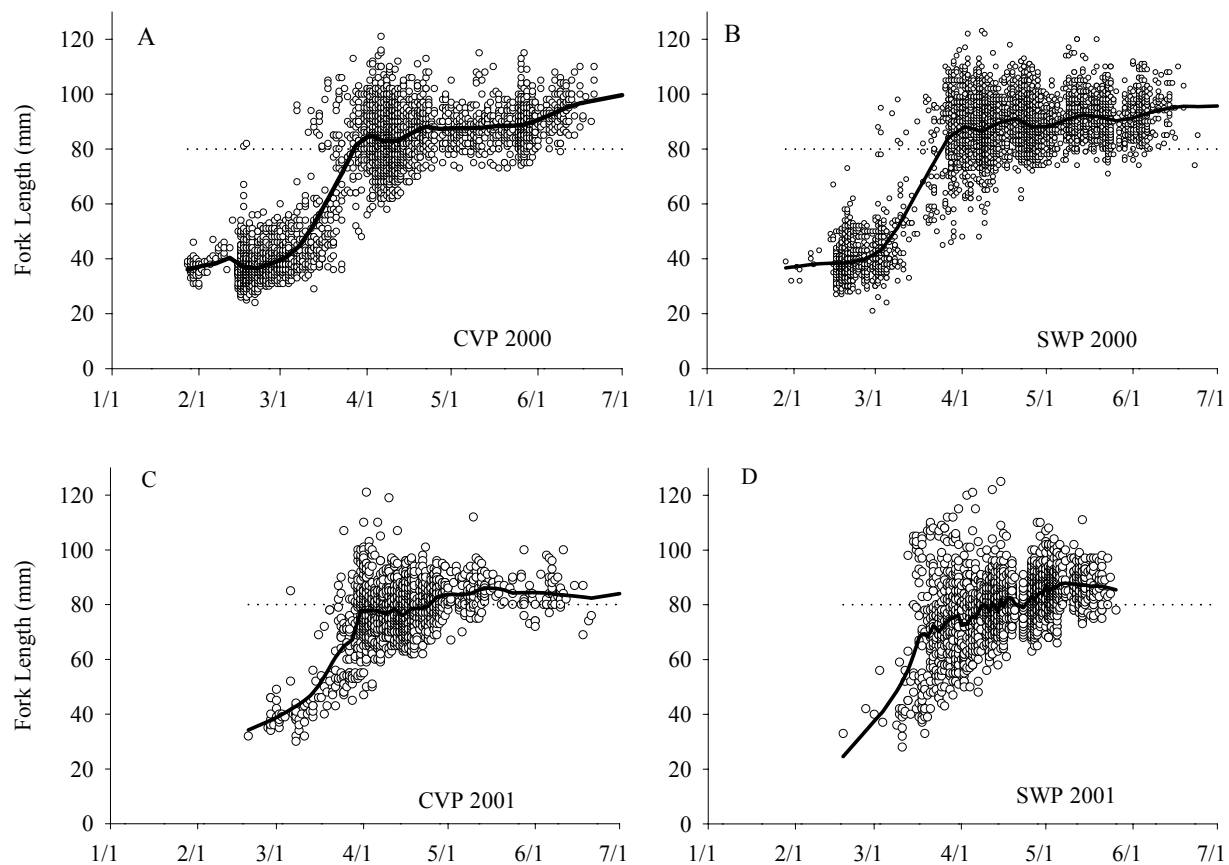
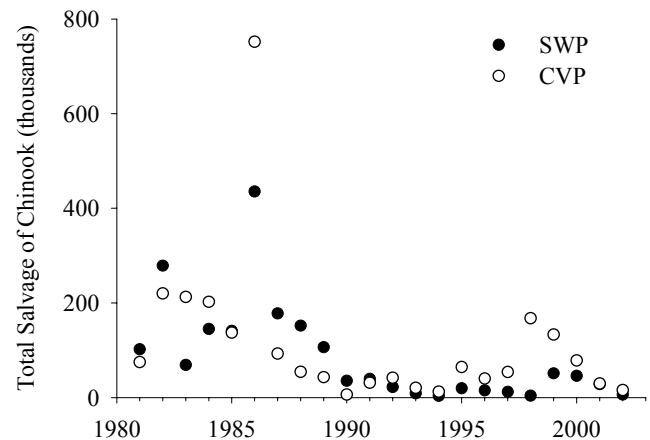


Figure 10-11. Lengths of unmarked fall and spring Chinook sampled at CVP and SWP diversion facilities in 2000, a wet year (A and B), and 2001, a dry year (C and D). Trend lines fit by LOWESS; almost all the change in length occurred March. Data from the IEP data bank.

Even when the numbers of fish sampled are expanded to account for the time intervals between samples (Figure 10-12), the total estimated numbers of juvenile Chinook collected at the diversion facilities do not seem large compared to the total number of juveniles that may arrive at the Delta. For example, if 50,000 Chinook females spawn an average of 5,000 eggs of which 7% survive to reach the Delta (which does not seem unreasonable given Bradford's (1995) estimate of 7% egg to smolt survival), then the few hundred thousand fish that are normally collected at the diversions would be a few percent of the 17.5 million arriving at the Delta. However, there is also indirect mortality associated with the diversions that is not well understood. Most efforts to study it have involved releases of hatchery fish marked with coded-wire tags, as discussed below.

Figure 10-12. Estimated total number of juvenile marked and unmarked Chinook collected at diversion facilities operated by the SWP (solid circles) and CVP (open circles). The high values for 1986 may reflect the very high flows in February of that year. Data from USBR (2003).



False positive identification of winter-run:

Concern about direct and indirect losses of fish to Delta diversions varies inversely with the strengths of the populations involved, and is greatest for ESA-listed runs. All hatchery steelhead are now marked, so that identifying naturally spawned steelhead is straightforward. Chinook are assigned to runs by size at date criteria, as described in Ch. 6, and recent genetic analyses have demonstrated the problems with the size approach as applied to winter-run at the state and federal diversion facilities in the Delta (Hedgecock 2002). The initial objective of the genetic work was to use mixed stock analysis to determine the proportion of the salmon taken at the pumps that were winter run, from which the “take” of the listed winter-run might be estimated. This was abandoned, however, when it was realized that the sampling at the pumps did not allow for accurate estimates of allele frequencies in the impacted group of juvenile Chinook, since mixed-stock analysis depends on such estimates. As an alternative, individuals were assigned to runs. Although this did not allow a calculation of take, it did allow a test of the size criteria, with mixed results. Although 95% of the fish that were assigned to the winter-run by genetic analysis were within the winter-run size criteria, only half of the fish with assignable genotypes that met the size criteria were winter-run. In other words, as applied to winter-run at the pumps, the size criteria have a high rate of false positives (Figure 10-13). To complicate matters further, the rate of false positives has varied from 16.3% to 94.6% over the six years in which fish were sampled (1995/6 - 2000/1). This, together with the likely bias in samples selected from salvage, makes it hard to develop a useful estimate of take using the size criteria, and challenges the validity of analyses such as those summarized in Brown and Kimmerer (2001; 2002) that also depend on the size criteria.

When the Hedgecock (2002) work was performed it was possible to identify individuals as winter-run or non-winter-run with high accuracy by genetic analysis, but it was not yet possible to do this for runs that are more closely related, such as fall-run and late-fall run. Nevertheless, a mixed stock analysis by Vanessa Rashbrook of Hedgecock’s laboratory showed that the large juveniles in September and October in the fall-run band in Figure 10-13 are indeed fall-run (D.

Hedgecock, pers.comm. April 2003). This result is clear enough that the sampling uncertainties described above do not matter. Additional genetic markers have since been developed, and it is now possible to distinguish individuals of all runs except Feather River spring-run (M. Banks, Oregon State U., pers.comm 2004).

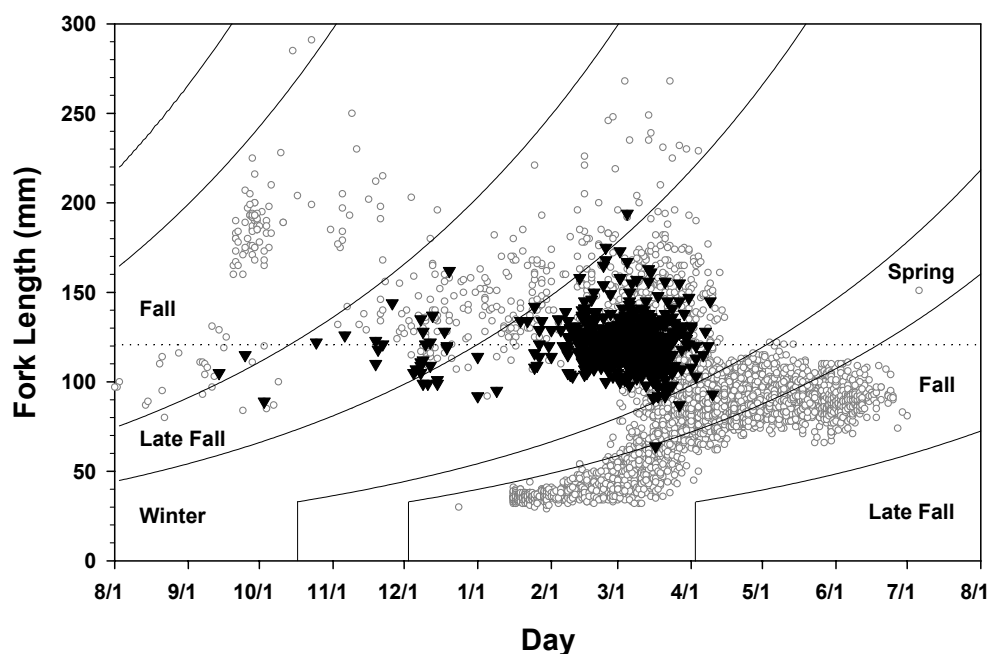


Figure 10-13. Distribution, by fork length and day of capture, of 6,752 juvenile chinook salmon with assignable genotypes over a six-year period, from August 1995 through July 2001. The 711 juveniles assigned to winter-run are shown by dark inverted triangles; fish assigned to other runs are shown by open circles. Note that each symbol may represent more than one fish, and that many non-winter-run are obscured by the tight cluster of winter-run. Mean fork length of winter run juveniles (121 mm) is shown by the dotted line. The figure and most of the caption are copied from Figure 1 in Hedgecock (2002).

Survival studies

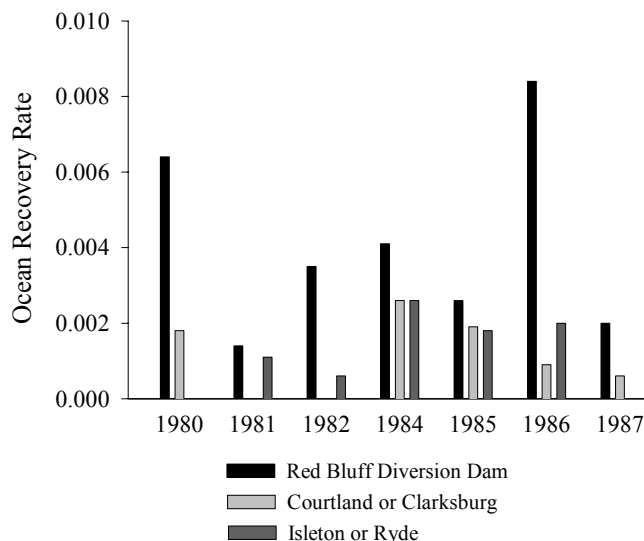
Fry survival

Fry survival was studied using coded-wire tags (CWTs) from 1980 through 1987 (Brandes and McLain 2001). Tagged hatchery fry were released in February or March at various locations in the Delta; mean sizes for the groups ranged from 40 to 53 mm fork length, but most were 45-50 mm.⁵⁸ Fry released below Red Bluff Diversion Dam were recovered in the ocean fishery at a higher rate than fry released in the Sacramento River near the edge of the Delta, particularly in wet years, despite the greater distance that they had to travel. Based on the data in Brandes and McLain (2001), ocean recoveries of fry released in the Delta are roughly an order of magnitude lower than for smolts released there (Figure 10-14). Whether hatchery fry are reasonable

⁵⁸ 0.5 mm "half-tags" were used for these fish, because of their size.

surrogates for naturally produced fry can be questioned, as discussed below. Whatever else happened to the tagged fry, few of them ended up at the pumps; only 46 of about two million were recovered there (Brandes and McLain 2001, App. A).

Figure 10-14. Recovery rates in the ocean harvest for ~50 mm chinook fry marked with CWTs and released near Red Bluff Diversion Dam and at locations on the lower Sacramento River. Data from Brandes and McLain (2001).



Smolt Survival

Most coded-wire tag studies have involved smolts. Analyses of the data have related survival as estimated by trawl and ocean fishery tag recoveries to covariates such as flow, water temperature, or exports, or whether the Delta cross-channel gates were open, for the relevant period. Early analyses of the CWT data (e.g., Kjelson et al. 1989) used multiple regression to estimate survival as a function of several covariates. This approach was criticized by various parties on a number of technical grounds, for example that linear regression is unsuitable for estimating survival rates that are constrained between 0 and 1, or on the selection of the covariates (Newman and Rice 2002). To move the situation beyond arguments, the California Urban Water Agencies and the U.S. Fish and Wildlife Service funded two independent statisticians, John Rice of the University of California Berkeley and Ken Newman of the University of Idaho, to apply more advanced methods to the data. A group of biologists and engineers representing various parties provided assistance in selecting and compiling covariates for 101 releases groups from 1979 to 1995 that were used in the analysis.⁵⁹

The Newman-Rice study was essentially completed by 1998, although it was not published in the professional literature until 2002,⁶⁰ and to a considerable extent the preliminary reports defused the controversy. On the one hand, they generally supported the findings of the earlier

⁵⁹ Some of these covariates are complex and opaque; for example, the tide covariate is described as "a measure of the magnitude of the change in low-low and high-low tides and whether the delta was filling or draining." As far as I know no detailed description of the development of these covariates is available, which is unfortunate.

⁶⁰ The article was submitted in October 1998; apparently a very long lag time for publication is not unusual in statistics.

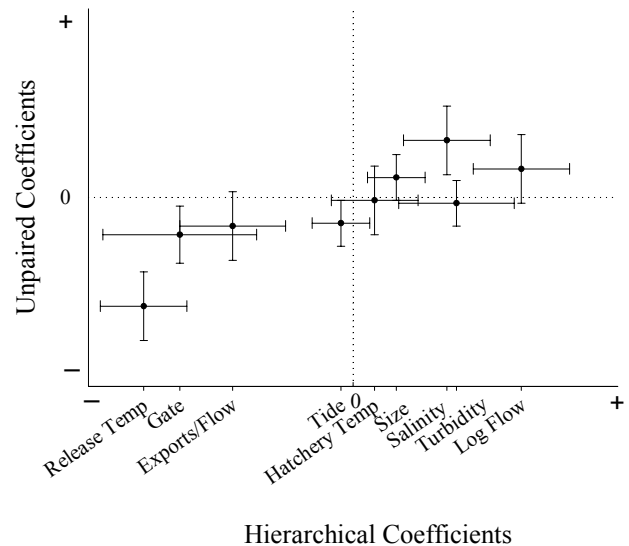
studies, but they also highlighted the limitations of the data and the need to apply the results cautiously. The technical level of the modeling is also beyond the ken of all but a few of the scientists involved with Central Valley salmon, which may have discouraged controversy. Newman continued with additional analyses, but this IEP-funded work has been largely free of the political tension that marked the early phases of the work with Rice. More recently, CUWA has sponsored another statistician, Bryan Manly, to participate in analyses of the cwt data.

One important difference between the Newman and Newman-Rice studies is that Newman and Rice (2002) estimated the effect of various environmental factors on recaptures of a larger number of groups of CWT fish that were released upstream and recovered at Chipps Island and in the ocean fishery. Newman (2003) focused on a subset of these groups for which groups released farther upstream could be paired with groups released just downstream from Chipps Island. Thus, Newman and Rice (2002) estimated the probability of survival times the probability that surviving fish are captured. By assuming equal probability of marine survival and capture for the paired releases, Newman (2003) estimated only probability of survival. Newman and Rice (2002) also used export/inflow ratio as a covariate, while Newman (2003) used exports.

The Newman and Rice analyses are described in more detail in Appendix B, but the main results can be summarized by a comparison of the original Newman and Rice (2002) study and the hierarchical model by Newman (2003). To facilitate comparison with the unpaired model of Newman and Rice (2002), Newman (2003) also reported results from the paired models using the export/inflow ratio rather than exports as a covariate (Figure 10-15); there are strong similarities but some important differences between the paired and unpaired analyses.

By the criterion that strong effects have coefficients more than two standard errors from zero, the temperature of the water into which fish were released (release temperature), whether the Delta Cross Channel gate was closed (gate position), and the export/inflow ratio had strong negative associations with survival for the hierarchical model, and fish size, salinity, turbidity, and the log of flow in the Sacramento River had strong positive associations. Of these, the export/inflow (E/I) ratio, fish size, turbidity, and log flow were not "strong" in the unpaired analysis (although fish size was very close), and only tide was a "strong" effect in the unpaired analysis but not in the hierarchical analysis. The greatest contrast concerns turbidity, which had little effect on predictions of the unpaired model. Newman (2003) speculated that this may result from turbidity increasing survival but also increasing the probability of capture in the trawl, and so having little effect in the unpaired model which estimates probability of survival times probability of capture, rather than probability of survival. Another important difference concerns Sacramento River flow, which has a much stronger association with survival than the hierarchical model.

Figure 10-15. Comparison of estimated coefficients plus/minus two standard errors for the unpaired analysis of Newman and Rice (2002) and the hierarchical analysis of Newman (2003) with release-specific capture probabilities.



Release temperature has been strongly associated with survival in all analyses. An early application of modern statistics to the Central Valley coded-wire tag data, by Baker et al. (1995), focused on the effect of temperature, and estimated a 95% confidence interval for the temperature at which mortality of tagged fish reaches 50% as $23.01 \pm 1.08^{\circ}\text{C}$ ($73.4 \pm 1.94^{\circ}\text{F}$).

Newman and Rice (2002) provided an example of the use of the unpaired model to compare the relative survival that might be expected from two options of management of the river that affects the covariates in the model, in this case the export/inflow ratio and the position of the cross-channel gate. They note, however, in a comment that also seems relevant to the paired-release models, that (p. 990):

Comparisons such as this must be tempered with caution, however. Our model summarizes historical relationships and is relevant to prediction in such a passively observed system. But because a number of unmeasured variables may well be important, it is much less well suited to predicting what would happen if the system were directly manipulated (Box 1966). Thus it would be a mistake to take literally the numerical predictions of the model in the latter case; a more modest and realistic hope is that they point to beneficial management strategies.

Moreover, the models embody assumptions, such as the assumption of equal catchability in the unpaired model and of equal (or constant ratio) survival downstream from Chipps Island for the paired models, that are at best approximately valid. More fundamentally, the data are for hatchery fish, which may not be a reasonable surrogate for naturally produced fish, as discussed below.

It seems likely that Newman and Rice have wrung as much information regarding smolt survival in the Sacramento River and Delta from the historical CWT data as can be got by purely statistical analyses, and that focused studies such as the Delta Cross-Channel studies that can clarify the actual processes underlying the statistical associations are the next logical step. For example, flow and salinity are inversely related, so it seems curious that both should be positively related to survival. The data used for the statistical studies show that salinity was uniformly low when flow in the Sacramento River was above about 20,000 cfs, high when flow was less than about 7,500 cfs, and highly variable in-between (Figure 10-16). There is a group of about 11 data points with low flow (<10,000 cfs) and low salinity, which presumably had poor survival, and it seems worthwhile to investigate the particular circumstances at those times. Eight of these are from April or early May 1994. Investigating the circumstances in which salinity and discharge were both low might suggest testable hypotheses for the association identified by the statistical studies.

The CWT data also include information about ocean conditions, however, in the coefficients for the indicator variables for release year. The effects of ocean conditions on survival will be confounded by year-to-year variation in fishing effort and the variable ages of fish recovered in the ocean (2, 3 or 4 years), but these might be sorted out by state-space modeling (K. Newman, U. of St. Andrews, pers.comm, March 2003). Such an analysis might be most useful as a means to test hypotheses developed from other information about which ocean conditions are favorable or unfavorable for Central Valley Chinook.

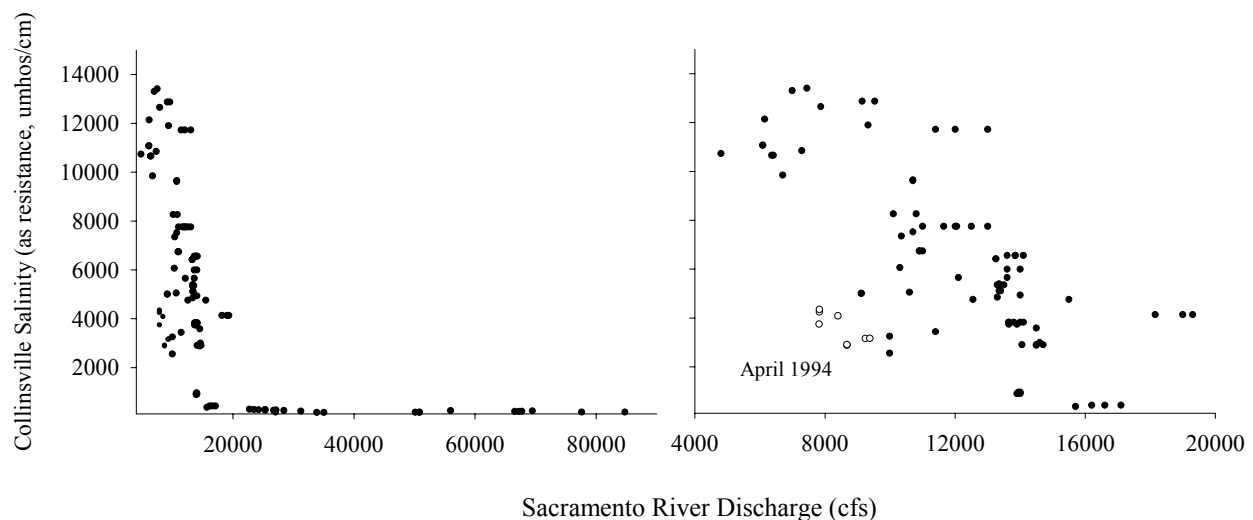


Figure 10-16. Values of salinity and Sacramento River Discharge used to characterize these conditions in the Newman and Rice (2002) analysis. A. all data; B. data for $Q < 20,000$ cfs, with eight data points (one is obscured) from April 1994 shown as open circles. Data from Alison Britton.

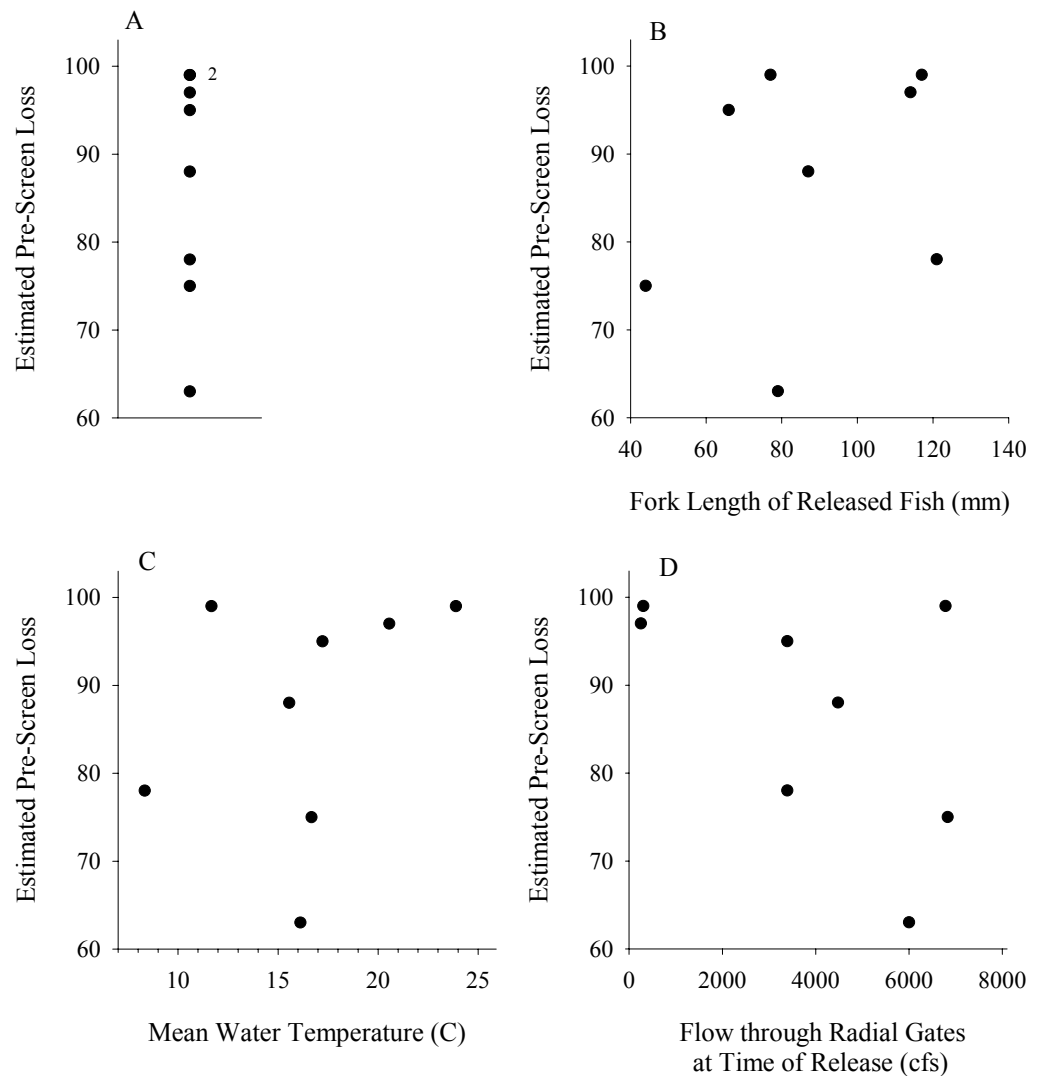
The paired analyses described above assume that the survival of fish released just downstream from Chipps Island is the same as the survival of the fish released at Sacramento or Courtland that pass Chipps Island. Newman (2003) describes several reasons to doubt this, and

the most biologically plausible reasons suggest that fish released downstream from Chipps Island should not survive as well. It seems likely that the hatchery fish used for the studies are not all equally likely to survive, but that there is a distribution of "survivability," so that fish with low survivability would already have been culled from the group released upstream by the time it reached Chipps Island. There is also good evidence that downstream migration is a self-reinforcing process (Høgåsen 1998; Ewing et al. 2001), so fish released upstream will be farther advanced in the smolting process and will be migrating more rapidly when they pass Chipps Island than will the group of fish released downstream from Chipps Island. There may also be an initial period of higher mortality following release, as fish adapt to life in the wild. Whatever the cause, the "shock effect" can be modeled by assuming that the mortality rate of the downstream group is some fixed multiple of the mortality rate of the upstream group. Newman (2003) found that doing this had relatively little effect on the estimated coefficients, although it decreased the estimates of survival and increased the estimates of the probability of capture. Estimates of the multiple or the shock effect were substantial, however, particularly for the hierarchical model.

There is independent evidence for a shock effect. For three experimental releases, hatchery Chinook trucked to the bays but allowed to acclimate in off-shore net pens before release survived ~2.5 times better than control fish released directly into the bays (Brown et al. 2004). Hatchery fish show a growth check in their scales or otoliths at the time of release (Rich 1920; Zhang et al. 1995). Newman (2003) noted that if shock also occurs with the upstream releases, which seems likely, then survival indices estimated from these releases would underestimate the survival of naturally-produced fish or of hatchery fish that are already acclimated to the river.

Coded-wire tags have also been used to estimate mortality in the Clifton Court Forebay to the SWP diversion facilities in the Delta, as described by Gringas (1997). Tagged salmon and striped bass have been released at the radial gates that separate the forebay from Old River and at the trash rack just upstream from the salvage facility, and recovered in the facility. Fish not recovered were assumed to have died. Estimated mortality for salmon in the forebay has ranged from 63 to 99%, with no obvious patterns in the data (Figure 10-17). The estimated forebay mortality is large and plays an important role in the calculation of the take of winter-run Chinook, so it seems that more effort should be made to characterize it well, as urged by the 2002 EWA Review Panel (2002). The estimates should also be reconciled with the observation by Kimmerer (2004) that similar numbers of fish are salvaged at the state and federal facilities, although the federal facilities do not have a forebay. A strong shock effect, from high initial rates of predation on naïve hatchery fish, might help to explain this observation. This could be tested by checking whether water temperature affects the ratio between fish salvaged per volume of water exported at the two facilities, since the rate of predation should increase with water temperature. Such a shock effect could also explain the seemingly low survival rates (~15-20%) for juvenile Chinook in the lower San Joaquin River estimated by the VAMP experiments.

Figure 10-17.
Estimated mortality
of coded-wire tagged
juvenile salmon in
Clifton Court
Forebay: A, overall
distribution; B, as a
function of, fork
length; C, of water
temperature, and D of
flow through the
radial gates; one point
in A represents two
estimates. Data from
Table 1 in Gringas
(1997).



In summary, the main result of the CWT studies seems to be that several factors influence the survival through the Delta of tagged hatchery fish, and of these, only water temperature stands out.

Are hatchery fish reasonable surrogates for naturally produced fish?

The utility of the CWT studies depends on the assumption that hatchery fish are reasonable surrogates for naturally produced fish. Although some studies have addressed questions specific to hatchery fish, such as the relative survival of fish released upstream or downstream of the Delta, most of the interest lies with naturally produced fish. There is good evidence for differences between hatchery and naturally produced fish, but it can be argued that the differences in the survival of hatchery fish with water temperature and other environmental variables also apply to naturally-produced fish, even though the absolute survival rates may

differ. This matter was recently argued in an expert review of proposed methods for measuring smolt survival in the Tuolumne River (CWWR 1999), one of which involved CWTs. On the one hand, Anne Kapuscinski (University of Minnesota) asserted in her comments that:

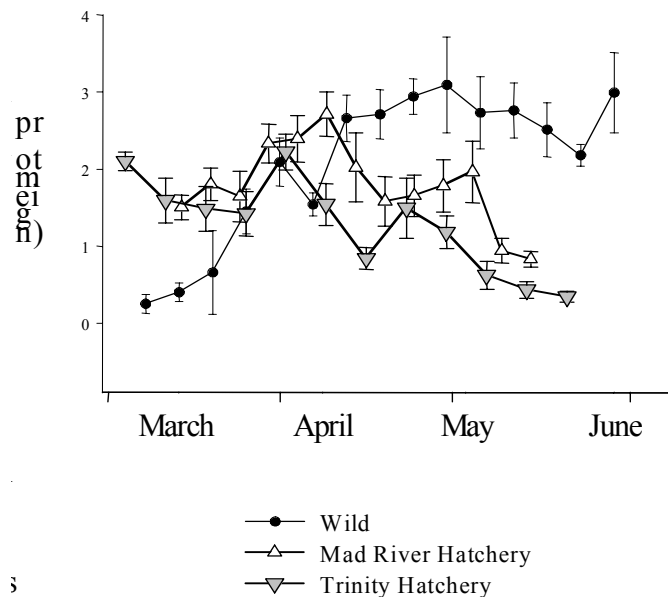
There are numerous behavioral and physiological differences between hatchery-propagated and wild-born fish, differences likely to affect downstream survival. These differences arise, in part, because hatchery fish develop physiologically and learn their behaviors under fundamentally different and often more homogenous environmental conditions than wild fish. If smolt survival assessments rely on hatchery fish, the effects of hatchery rearing on outmigration survival will be confounded with the effects of flow rates or habitat restoration. ... Because we don't understand the complex interactions among environmental and biological factors affecting seaward migration survival, monitoring of hatchery fish could even be misleading about the suite of in-river conditions needed to achieve an increase in naturally reproducing chinook salmon ..."

David Hankin (Humboldt State University) stated the alternative view, that useful inferences can be drawn from studies of hatchery fish.

I find myself less concerned about use of hatchery-reared fish for survival studies than were some of the other peer reviewers. To me, the hatchery fish provide a nice "standardized" and available source of fish. If experiments using hatchery fish show that survival rates of these fish are very poor in the mining reach (as compared to the upper Tuolumne reach), then I am willing to conclude that survival rates of wild fish are probably also lower in the mining reach than in the upper Tuolumne. I would not be willing, however, to conclude that the absolute survival rates of wild and hatchery fish would be the same in the two areas. But I don't think knowledge of the actual survival rates is necessary to provide guidance for restoration or even evidence of improvements in survival rates after restoration activities.

As an example of the kind of difference that concerns Kapuscinski (although she did not cite it), Kerstetter and Keeler (1976) showed that the surge of activity of gill Na⁺K⁺ ATPase, an enzyme associated with smolting, occurred a month or more earlier in two strains of hatchery steelhead in the Trinity River than it did in wild fish, and there were also differences between the two hatchery strains (Figure 10-18). Since increased gill ATPase activity is associated with migratory behavior (Zaug and Wagner 1973, Ewing et al. 2001), and gill Na⁺K⁺ ATPase activity tends to cycle in hatchery chinook but not in wild Chinook (Ewing et al. 2001), it is easy to imagine that the relative survival of hatchery and wild fish could change over the season. However, definitive evidence on this point is lacking.

Figure 10-18. Difference in ATPase activity among wild and hatchery steelhead. Gill Na^+K^+ ATPase activity in wild Trinity River steelhead and two hatchery strains. Bars show standard errors; data from Kerstetter and Keeler (1976).



A related difficulty concerns populations of juvenile chinook in which some appear to be migrating actively (and have higher levels of gill Na^+K^+ ATPase activity) while others seem to be migrating more passively and slowly. This is the situation with spring Chinook in the Rogue River which migrate in their first summer, reaching the estuary in September or October (Ewing et al. 2001). Fish captured in traps in the center of the channel were mainly from the more rapidly migrating part of the population, while those captured in beach seines were mainly not (fish were marked and recaptured at various places along the river so differences in migration rates could be determined). It would seem difficult for a homogenous group of hatchery fish to represent even the relative survival of both segments of the wild population.

Use of the bays by juvenile Chinook

Too little is known about the use of the bays by juvenile Chinook. MacFarlane and Norton (2002) reported one year of a ten-year field study of juvenile fall and perhaps spring-run in the bays (reviewed in Ch. 6), and analyses of the data from subsequent years is now underway (B. MacFarlane, NMFS, pers.comm. 2005), so much new information should be available soon. However, the sampling for these studies began in April, and collected fish with a trawl in relatively deep water. All that is known about fry migrants in the bays is that they are taken in small numbers in the IEP seine sampling, mainly in wet years.

Diet

Information is available on the diet of juvenile Chinook in other estuaries (Healey 1991; Bottom et al. 2005) as well as in the San Francisco Estuary (Rutter 1904; Scofield 1913; Ganssle 1966; Sasaki 1966; Heubach 1968; Fields 1976; Kjelson et al. 1982; MacFarlane and Norton 2002). Healey (1991:346) noted that “Diets vary considerably from estuary to estuary and from

place to place within an estuary,” and also that seasonal changes in diet are typical. The available information for the San Francisco Estuary seems consistent with these observations. From an analysis the stomach contents of 540 juvenile Chinook (< 70 mm) from the Delta and 189 from the bays, Kjelson et al. (1982:402) reported that:

Crustaceans and insects dominated Chinook [< 70 mm] stomach contents, with an increase in crustacean ingestion downstream ... Cladocera and diptera were consumed frequently in the Delta, while in brackish San Pablo and San Francisco Bays, consumption of copepods, amphipods, and fish larvae increased. Similar food habits were reported for older fry and smolts in [earlier] Delta studies ...

MacFarlane and Norton (2002) examined the stomachs of 93 juvenile Chinook collected between Chipps Island and the Gulf of the Farallones from April 30 to July 15, 1997, and reported that fish leaving the Delta contained mainly amphipods, other crustaceans, and insects. In Suisun Bay insects, especially waterboatmen, and crustaceans were the main food items, along with some fish larvae. Crustaceans were the dominant food in San Pablo Bay, and fish larvae were dominant in Central San Francisco Bay.

Given that juvenile Chinook are opportunistic feeders in estuaries (Healey 1991), the more relevant question may not be what juvenile Chinook in the San Francisco Estuary eat, but what quality it is and whether they get enough of it. This seems questionable. MacFarlane and Norton (2002) found that juvenile Chinook moving through the bays grew slowly (0.18 mm d⁻¹ on average) until they reached the Gulf of the Farallones. Kjelson et al. (1982) noted that the scales of fish from the Sacramento-San Joaquin system did not show the pattern of intermediate circuli spacing indicative of enhanced growth in brackish water, as reported by Rich (1920), Snyder (1931) and Reimers (1971; 1973) for the Columbia, Klamath, or Sixes rivers. MacFarlane and Norton (2002:225) concluded that “... juvenile Chinook salmon derive little benefit from their time in the [brackish water part of the] San Francisco Estuary.” In contrast, Magnusson and Hilborn (2003) reported from a comparative study of rivers from northern California through Washington, the survival of tagged hatchery fall Chinook increased with the proportion of the estuary that was in natural condition.

Poor growth in the bays of the San Francisco Estuary may reflect changed conditions in the estuary, as noted by MacFarlane and Norton (2002). Scofield (1913:17), in a report of towing a live car filled with Chinook and steelhead fry from Sacramento to the Golden Gate, reported that there was “a plentiful supply of land insects” on the surface of Suisun and San Pablo bays in May, 1912, so that Chinook fry could continue “their habit of surface feeding until well out in salt water.” Scofield also reported abundant “small crustaceans, especially young shrimp” at the surface of Suisun and San Pablo bays. He caught “quantities” of these with a gauze tow net, and the fry “devoured them greedily.” Unfortunately, old collections of scales apparently have been lost, so the speculation that the estuary formerly offered better conditions for growth cannot be tested.

Although published data from the NMFS study on fish passing through the bays are available only for 1997, data on juveniles passing into the ocean are now available for 1998 and 1999. There is year to year variation in the size and condition of juvenile Chinook leaving the bay (Table 10-1), as might be expected from similar variation elsewhere in the rivers and the Delta. Fish at the Golden Gate were smaller and older in 1997 than in the other two years. The strongest variation is in energy stored as triacylglycerol, normalized to cholesterol (TAG/CHOL). Although growth of juvenile Chinook in the bay has been consistently low and condition (Fulton's K) has consistently declined in fish passing through the bay, TAG/CHOL has been variable from year to year (B. MacFarlane, NMFS, pers.comm. 2006). Why this should be so is not clear.

Table 10-1. Measures of condition of juvenile fall or Chinook captured near the Golden Gate. Data from MacFarlane and Norton (2002) and MacFarlane, et al. (2005).

Year	Length (mm)	Weight g	Age d	TAG/CHOL	Fulton's K
1997	85.5±1.1 (64)	7.23±.3 (64)	176±3 (32)	9.5^l	na
1998	87.6±0.5 (255)	7.1±0.1 (255)	160±1 (106)	4.1±0.4	1.04±??
1999	92.0±1.0 (124)	8.6±0.3 (124)	168±3 (60)	15.37±1.56	1.05±??

CHAPTER ELEVEN

THE OCEAN

Unlike in the freshwater environment, the physical and biological mechanisms and factors in the marine environment that cause mortality of salmon are largely unknown. Predation, inter- and intraspecific competition, food availability, smolt quality and health, and physical ocean conditions likely influence survival of salmon in the marine environment. Brodeur et al. (2004:25)

While numerous retrospective analyses show a strong correlation between past changes in the ocean environment and salmon production within the North Pacific, these correlations rarely make good predictions. Scheuerell and Williams (2005:488)

Salmon that survive to spawn spend most of their lives in the ocean and gain most of their weight there. Central Valley Chinook begin their ocean life in the Gulf of the Farallones, and then spread north and south along the continental shelf, mainly between Point Conception to the south and the coast of Washington to the north, although a few go farther north. The same may be true of Central Valley steelhead (Pearcy et al. 1990), although evidence regarding their ocean distribution is scant. It is now generally recognized that ocean conditions have a substantial effect on survival during the ocean phase of the salmon life cycle. 1983 El Niño had an obvious effect on Chinook size and fecundity (Wells et al. 2006; Figure 7-10). Decadal scale “regime shifts” in ocean conditions have received much recent attention. This chapter briefly describes the use of coastal ocean habitat by Central Valley salmon, the oceanography of the shelf, and the influence of regime shifts on coastal ocean habitat. Use of the North Pacific by Chinook and salmon generally is described by Healey (1991) and Quinn (2005).

Early ocean life

There are a few early descriptions of Chinook in the ocean off California. Snyder (1924b:63) described the diet of 25 ocean-type Chinook, 74 to 100 mm fork length,⁶¹ captured with bait fish in shallow water near Half Moon Bay, south of San Francisco, on June 21, 1921: “The Half Moon Bay fish had fairly gorged themselves with small fish and insects. These small fish, some of which measured 45 mm long, had been swallowed head first in all cases, the heads extending into the alimentary track some distance beyond the stomach.” However, stomachs of 100 others captured on June 29, 1922, with anchovies near shore close to Bolinas were “not well filled,” and 28 were empty. Their lengths ranged from 71-110 mm. The fishermen who captured these fish said they caught them regularly, especially in August.

⁶¹ The length measurement was not specified but fork length was standard at the time.

Published information on juvenile Chinook off the California coast is still limited, but NMFS has been sampling them in the Gulf of the Farallones and the adjacent coast since 1997, and these studies are starting to yield published results (MacFarlane and Norton 2002; MacFarlane et al. 2005), discussed below. More work has been done off the coasts of Oregon and Washington, particularly cruises sampling with seines conducted by Oregon State University between 1979 and 1985 and summarized by Percy (1992), studies by NMFS in the Columbia River plume using seines and trawls, and more recent GLOBEC surveys using trawls off the coast of Oregon in 2000 and 2002 (Brodeur et al. 2003). For the GLOBEC cruises, only results from 2000 have been published (Brodeur et al. 2004).

MacFarlane and Norton (2002) and MacFarlane et al. (2005) describe juvenile Chinook that were sampled with trawls in the Gulf of the Farallones in 1997 to 1999 in late spring to fall, which were respectively “normal,”⁶² El Niño, and La Niña years. Growth and condition varied among years. Juvenile Chinook entered the Gulf of the Farallones at mean ages of 160 to 176 days (estimated from otoliths), mean fork lengths of 85.5 to 92 mm, and mean weights of 7.1 to 8.6 g. There was also considerable variation in energy reserves, measured as triacylglycerol normalized to cholesterol (Table 10-1). Based on the width of otolith increments, fish grew 13% faster between June 1 and August 1 in 1998 than in 1999. Growth in the gulf was 0.85 ± 0.13 and 0.55 ± 0.06 mm d⁻¹ in 1998 and 1999, based on linear fits to the data (Figure 11-1), and was about ~ 0.6 mm d⁻¹ in 1997.⁶³ These rates are much higher than the 0.18 mm d⁻¹ reported for juveniles traversing the bays in 1997 (MacFarlane and Norton 2002). More strikingly, normalized triacylglycerol decreased sharply in the gulf in 1997 and 1999, but increased in 1998. Apparently, fish reacted to the greater availability of food in the gulf compared to the bays by growing at the expense of energy reserves in 1997 and 1999, but were able to store energy as well as grow faster in 1998.

Juvenile Chinook are not randomly distributed in the Gulf of the Farallones. In the summer, most are found in slow eddies at either side of the Golden Gate, south of Duxbury Point and west of Point San Pedro, but their distribution shifts north beyond Point Reyes later in the fall. NMFS collected so few south of the Gulf of the Farallones that trawling for them was abandoned (MacFarlane et al. 2005, MacFarlane, pers.comm. 2006).

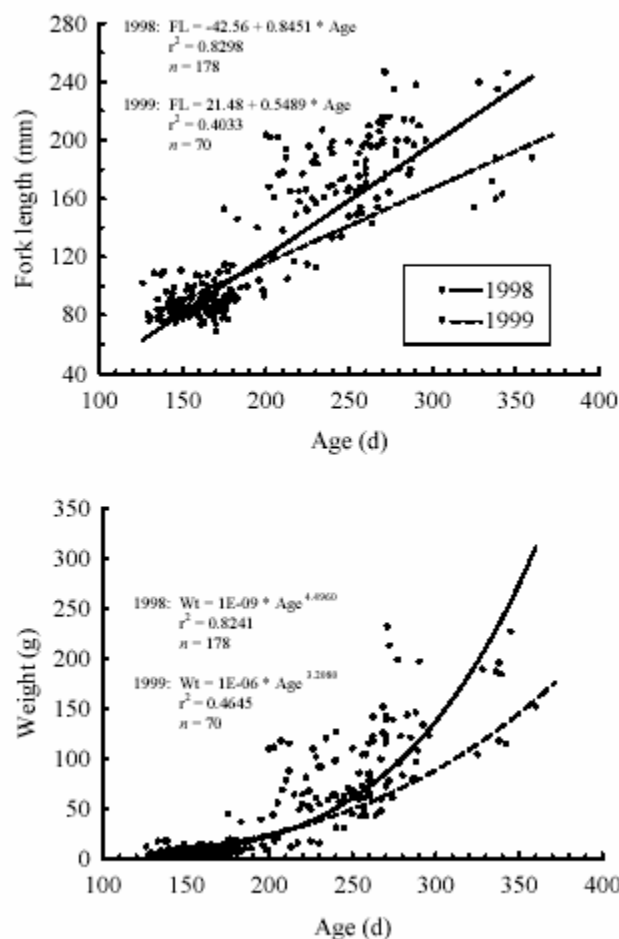
Farther afield, yearling juvenile Chinook from the Central Valley were collected with trawls off Oregon in GLOBEC sampling in 2000. An August sample of 54 collected north of Cape Blanco was estimated to be 90% Central Valley fish by genetic (allozyme) analysis; the sample averaged 229 ± 26 mm fork length, and 164 ± 72 g in weight (Brodeur et al. 2004). Thirty five yearlings that were estimated to be 20% from the Central Valley were collected south of Cape Blanco. Only one of the Central Valley fish was tagged. Generally, the Chinook were captured at nearshore stations in the coastal upwelling zone. Among the 58 steelhead sampled, 14% (~ 8) were from the Central Valley; none were tagged. The steelhead were also taken in nearshore

⁶² The El Niño started in late summer 1997, and so had little effect on MacFarlane et al.’s data. See Chavez et al. (2002) for a description of ocean conditions off central California in 1997-99.

⁶³ The estimate of growth in the Gulf in 1997 is uncertain, as discussed in MacFarlane and Norton (2002).

stations in the upwelling zone, and those collected south of Cape Blanco were from streams in California or southern Oregon.

Figure 11-1. Length and weight at otolith age of juvenile Chinook captured in the Gulf of the Farallones in 1998 and 1999. Copied from MacFarlane et al. (2005).



Juvenile Chinook at sea eat mainly larval and juvenile fishes, but they also eat plankton, especially euphausiids, and even terrestrial insects that have blown offshore (Snyder 1924b; Healey 1991; MacFarlane and Norton 2002). Juvenile Chinook can be voracious eaters, as indicated by Snyder's (1924) description of fish taken off Half Moon Bay. Less is known about the diet of small steelhead in the ocean, but based on a sample 134 collected north of Cape Blanco reported by Percy et al. (1990), it is similar to that reported for small Chinook, except that euphausiids may be more important in the diet of steelhead.

Later ocean life

Information on the spatial distribution of the landings of sub-adult Central Valley Chinook from commercial and sport harvest is available from the PFMC, although recent data are affected by restrictions on harvest. Most are between the Columbia River to the north and

Monterey Bay to the south. Point Conception probably marks the southern extent of their range, and only a few go north beyond Washington (Myers et al. 1998, Table 11-1).

Table 11-1. Coded wire tag recoveries in the ocean recreational and commercial fisheries from releases of Central Valley hatchery Chinook salmon. Data from Regional Mark Information System database, Pacific States Marine Fisheries Commission, compiled by Randy Brown.

Fisheries Mgt Area	FRH* 98 brood year No. (%)	LSNFH* – WR 98-02 brood years No. (%)	CNFH* – late fall 00-02 brood years No. (%)
British Columbia	-	7..(1)	74 (1)
Washington	-	-	125 (1)
Northern Oregon	2,572 (20)	3 (0)	848 (7)
Coos Bay	1,253 (10)	9 (1)	549 (5)
Klamath Zone - OR	135 (1)	3 (0)	45 (0)
Klamath Zone - CA	182 (1)	7 (1)	181 (2)
Fort Bragg	1,001 (8)	16 (1)	1,759 (15)
San Francisco	5,105 (40)	596 (50)	6,850 (57)
Monterey	2,439 (19)	551 (46)	1,533 (13)

*FRH = Feather River Hatchery, LSNFH = Livingston Stone National Fish Hatchery, CNFH = Coleman National Fish Hatchery.

It seems likely that ocean conditions influence the distribution of Chinook in the ocean, and that before harvest restrictions this was reflected in the distribution harvest, or rather, in the delivery of fish to ports. However, I have not found studies that deal with this issue. More specific information on the location of harvest probably could be obtained by fishers, following the example of Healey and Groot (1987), but again I have not found such studies for California Chinook. At a crude level, however, the data in Table 11-1 indicate that winter-run Chinook tend to have a more southerly distribution, while late fall Chinook may be more likely to venture as far as British Columbia.

Temperature and depth preference

Data from 25 archival tags recovered from large subadult Chinook show that they usually occupy habitat where the water temperature is between 8 and 12°C, and they occupy deeper water in the winter, often deeper than 200 m, and shallower habitat in late spring and early summer (Hinke et al. 2005a,b). The temperature selection appears to be a preference rather than

a physiological need, since Chinook in Lake Ontario routinely forage in water that is ~19-20°C (Wurster et al. 2005). Chinook can and do make rapid vertical migrations (Candy and Quinn 1999; Hinke et al. 2005a). Hinke et al. (2005b) suggest that the use of deeper water in winter is a response to lower biological productivity in that season, but Chinook feed largely on fishes that are farther up the food web and live more than a year, and some of the fishes on which Chinook feed, for example sardines, are available at the surface in the winter, so the nature of the link is unclear. However, although based on a relatively small sample, the pattern of depth and temperature selection is striking.

Growth in the ocean

Chinook and steelhead grow rapidly in the ocean, but strong variation in the size at age of spawning fish, discussed in the next chapter, implies that there must also be strong variation in growth rates at sea, both within and among years. Growth is seasonal for Chinook, with little growth in winter (Healey 1991), at least at higher latitudes, and the apparent growth rate declines with age, at least in part because more rapidly growing fish tend to mature early. There is little information on the ocean growth rate of Central Valley steelhead, except what can be inferred from their size and age at Chipps Island (Figure 5-43) and at return (Table 6-5).

Sub-adult diet

The diet of larger sub-adult Chinook off the California coast of California and elsewhere has been described in various papers reviewed by Healey (1991) and Hunt et al. (1999). Generally, subadult Chinook are opportunistic foragers that eat mostly small fish and squid, but they eat plankton as well, especially euphausiids and larval crabs. What fishes are eaten apparently depends on what is available (Healey 1991). Thus, the quantity and quality of the food available probably matters more than the particular species.

Foraging opportunities in the ocean are not static, and are not beyond management influence. For example, early studies reported that sardines were important prey for Chinook (Healey 1991). Sardines were abundant early in the twentieth century, as illustrated by the distribution of sardine catches in Monterey Bay in 1921-22 (Figure 11-2), about the time that Clark (1928) was collecting salmon scales for his analysis of life history patterns and length at age. By mid-century the sardine population crashed, but in recent decades their abundance has increased again. To the extent that humans prey on the same fishes as Chinook, we are competing with them as well as preying on them.

Figure 11-2. The distribution catches of sardines by the Monterey fleet from July 23, 1921, to Feb. 8, 1922, which "... illustrates the concentration of catches in the cove of the bay near the town of Monterey where the canneries re located." Scofield (1929) describes the method of fishing in detail. The fleet used lampara nets from small boats with small engines and no radios that towed lighters (barges) to carry the catch. It is safe to infer from the pattern of catches that sardines were abundant.

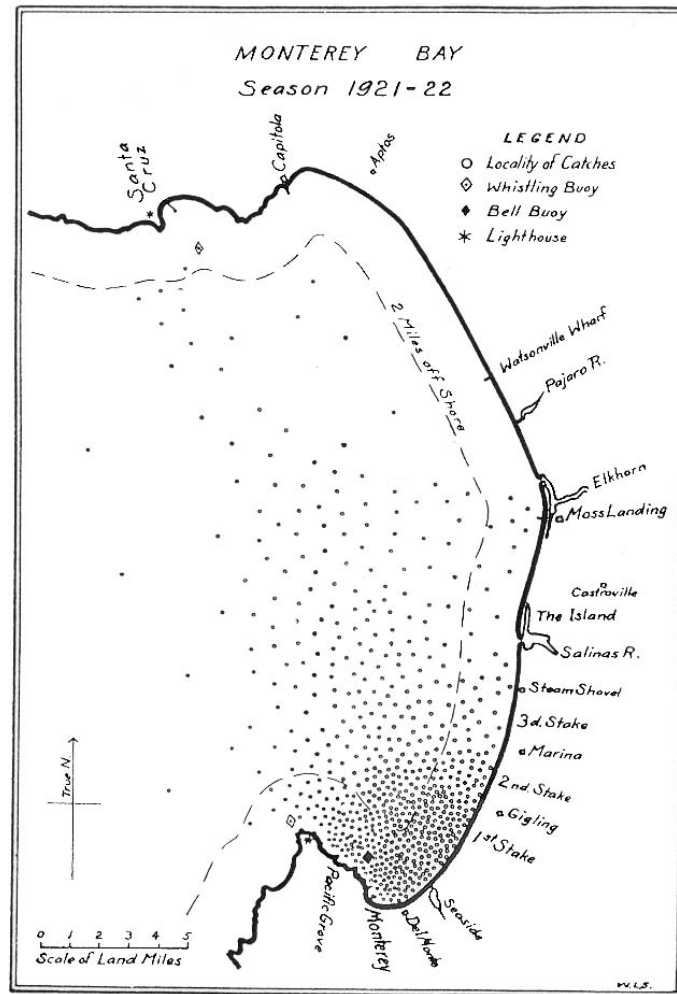
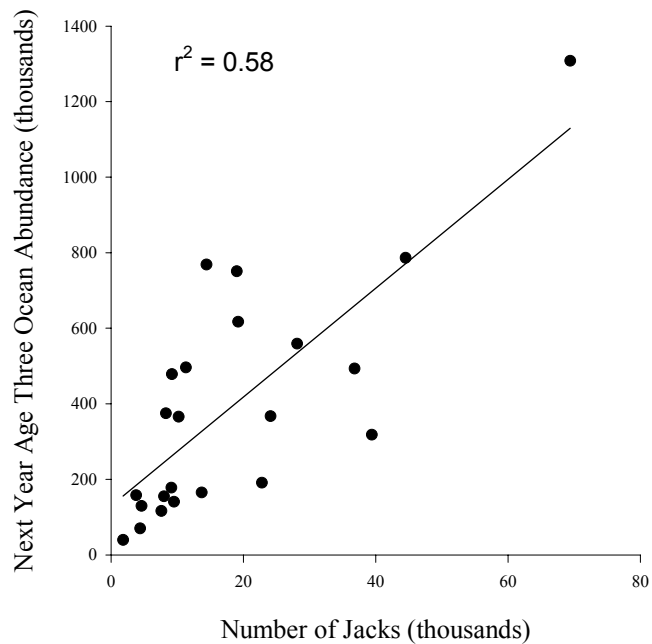


FIG. 3. Locality of the catches made by the boats from which samples were taken. The fishing season 1921-1922 is represented and illustrates the concentration of catches in the cove of the bay near the town of Monterey where the canneries are located. Locality names on this map are those used by fishermen.

Ocean Survival

The first year of ocean life is commonly regarded as a critical period of high mortality that largely determines survival to harvest or spawning (Beamish and Mahnken 2001; Quinn 2005). Thus, the number of jacks is a useful indicator of estimated abundance of three-year olds the following year (Quinn 2005; Figure 11-3). However, conditions at the end of ocean residency can also be important, as indicated by the effect of the 1983 El Niño on the survival, size, and condition of coho and Chinook in Oregon (Johnson 1988), and on size and fecundity of Central Valley fall-run (Wells et al. 2006; Figure 11-3).

Figure 11-3. Estimated abundance of three-year old Klamath River fall Chinook plotted over Klamath River jack returns the previous year, 1981-2003. Age 3 estimates are for Sept. 1. Data from CDFG (2004). The PFMC predicts an index of harvest for Central Valley Chinook from the number of jacks, but the relationship is not as strong, probably because the index covers more than one year class.⁶⁴



In a review of information on survival rates, Bradford (1995) reckoned that for salmon generally, variations in ocean and freshwater conditions account about equally for variations in abundance. Bradford (1995) found fewer data on smolt to adult survival for Chinook than for other salmon, but estimated that smolt to adult survival of wild stock Chinook is relatively low and averages only around 1 or 2%. In a more recent review, Quinn (2005) estimated 3.1% average smolt to adult survival for Chinook, and 13% survival for steelhead. The Chinook estimate was averaged over stream and ocean types, but presumably survival is lower for the smaller ocean-type smolts. For one population of stream-type Chinook in the Snake River, smolt to adult survival has varied from <0.5 to almost 5% over the years 1964 to 2002 (Scheuerell and Williams 2005), so getting a good estimate of average ocean survival for Chinook is apt to be difficult.

Using data on Chinook, coho and chum in the Strait of Georgia, Beamish and Mahnken (2001) tested the hypothesis that there are two primary causes of mortality in the first ocean year: predation in the initial weeks at sea, and size-dependent starvation (or predation on fish that fail to thrive) in the first ocean winter. That is, fish that do not reach some critical size (or perhaps energy storage) before the first winter fail to survive it. Although the results were stronger for coho, the hypothesis seemed to be supported for Chinook as well, but were inconclusive for chum.

⁶⁴ Historically, harvest has been such a large influence on the number of spawners that the relationship between jacks and “adults” the following year at the RBDD is actually negative.

There is considerable variation in the size of juvenile Chinook in the Gulf of the Farallones, both within and between years (Figure 11-1), so the critical size hypothesis may help explain year to year variation in the abundance of Central Valley Chinook. This could be tested by comparing the distributions of otolith size at age for juveniles collected in the Gulf of the Farallones and for fall-run adults, or harvested sub-adults. If the hypothesis holds, the otolith size at age of older fish will average larger than for fish collected in the first ocean summer. Similarly, the hypothesis would predict higher survival through the first ocean winter for 1998 than for 1999. However, the fish captured as yearlings off Oregon in 2000 (Brodeur et al. 2004) do not seem large compared to those of the same cohort captured in the Gulf of the Farallones in 1999 (Figure 11- 1). It may be that the effect of size in the first winter is absent or weaker for Central Valley Chinook, if the contrast between summer and winter conditions is not as strong as at higher latitudes.

Ocean habitat

The Continental Shelf and the Gulf of the Farallones

The continental shelf along the coast of California, Oregon and Washington underlies the main ocean habitat of Central Valley salmon, although a few migrate farther north (Myers et al. 1998). The shelf extends at a gentle slope to a depth 100 to 200 m, ending at the “shelf break,” beyond which the continental slope dips more steeply to the ocean floor below 3,000 m. The width of the shelf varies along the coast, from a maximum of about 50 km off San Francisco to almost nothing south of Point Sur, and is broken by features such as the subsurface Monterey Canyon (Figure 11-4). The Gulf of the Farallones, where Central Valley salmon first enter the ocean, is bounded on the east by the coast, which swings westward at Point Reyes, and on the west by the Farallon Islands and the edge of the coastal shelf (Figure 11-4). The southern boundary is indistinct, and defined more by convention than by topography. USGS Circular 1198 provides a good description of the gulf in non-technical language.

Like the weather on shore, ocean conditions in the Gulf and on the coastal shelf are affected by processes occurring at a various temporal and spatial scales. In consequence, although the major currents are well defined in long-term averages, conditions at any given time or place are highly variable, and meanders and eddies in the currents are prominent (Figure 11-5). The ocean “weather” varies vertically as well as horizontally, so that observations must be similarly distributed to generate a reasonably complete description of the dynamics. Although the technology for collecting such data is improving rapidly, collecting the data is still difficult and expensive, and understanding of oceanographic details is still developing, despite a long history of study, described by Bograd et al. (2003). For example, Collins et al. (2003) reported that advection from the north is not a major source of nutrients for waters over the shelf, as had been thought. A major study of the area just north from San Francisco, the CoOp West project, is now in the synthesis phase, and more information should be available soon.

Figure 11-4. The topography of the Gulf of the Farallones and adjacent continental shelf. Note that contour intervals change from 10 to 100 m at 100 m, so the shelf steepens seaward from the dark 100 m contour. Copied from Chin and Graymer, 1998.

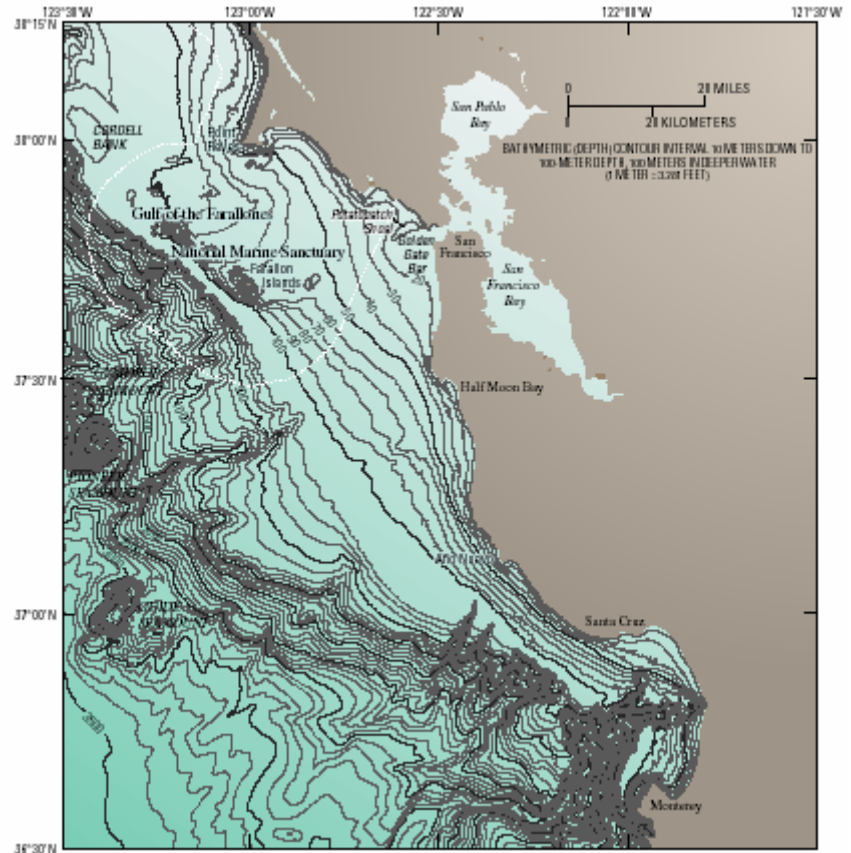
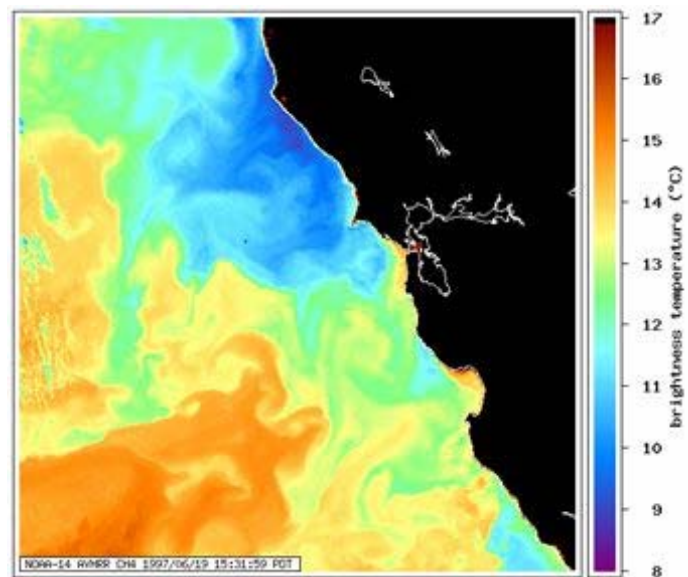


Figure 11-5. Sea surface temperature of California, June 19, 1997, showing eddies and meanders in coastal currents. Copied from WEST overview, <http://www-ccs.ucsd.edu/coop/west/overview.html>. The bar on right is labeled “brightness temperature.”



At a coarse scale, the California Current, a part of the North Pacific gyre, is a dominating influence on the coastal ocean. This cool southward flowing current generally flows above or offshore from the shelf break. The California Undercurrent, a northward flowing, warm counter

current, flows at depth over the continental slope, inshore from the California Current. Closer to shore, the northward flowing Inshore or Davidson⁶⁵ Current predominates in the winter, but southward flow driven by coastal winds predominates in the spring and summer. The region from the California Current inshore is known as the California Current System (CCS).

Although these currents are well defined in long-term average data, they are also variable, with decadal regime shifts and ~ year-long El Niño and La Niña events. At shorter temporal and spatial scales the dynamics of the CCS are dominated by eddies and meanders in the main currents (Figure 11-5) and by seasonal but episodic upwelling events, and on the shelf diurnal currents tidal are also important, especially in the Gulf of the Farallones.

Currents flowing southward along the coast force offshore movement of water through Ekman transport, inducing upwelling. The California Current tends to induce upwelling of water from the continental slope, and wind-driven currents closer to the coast induce upwelling of water from the shelf. Besides affecting temperature, the upwelling also brings nutrients to the “photic” zone, where enough light penetrates to support photosynthesis. The strength of the upwelling, as measured by the Bakun index, has a clear seasonal pattern but considerable year to year variation, much like flow in the rivers. However, from a biological perspective, the intermittency of upwelling may be important. That is, persistent northwest winds and Ekman transport can move the upwelled water off the shelf before the nutrients pass up the food web, so periods of calm between periods of wind may improve productivity close to the coast (Chavez et al. 2002).

The upwelling is stronger in some areas than in others, and topographic forcing of currents also occurs, as can be seen in the plumes of cold water at Point Reyes and Point Arena in Figure 11-5. This results in places where the water temperature along the coast can vary by several degrees over tens of kilometers.

Topographic forcing of the California Undercurrent occurs where the continental slope bends westward at the Farallon Islands. This also contributes to mixing of shelf and slope water (Noble 2001). Accordingly, water in the gulf is a mixture of upwelled shelf water, offshore oceanic water, and outflow from San Francisco Bay, including outflow from Central Valley rivers (Wilkerson et al. 2002). The upwelled water and bay outflow both provide nutrients, and water in the gulf tends to be retained near the coast and warmed. These features make the gulf a distinct environment, in which conditions for juvenile Chinook and steelhead may differ from the more open shelf habitat offshore from smaller coastal rivers.

Strong topographic forcing at places such as Point Conception or Cape Blanco creates persistent gradients in environmental conditions that are reflected in patterns of animal

⁶⁵ The names of currents seem not to be well standardized. Although the California Current is known only by that name, the Inshore Current and the Davidson Current are the same, and the current at the top of the Pacific Gyre is called the West Wind Drift by some, but the North Pacific Current by others. The North Pacific Current seems preferable, since there is a West Wind Drift in the Southern Hemisphere.

abundance and distributions, including those of salmon. For example, Chinook from Oregon streams south of Cape Blanco are genetically disposed to migrate south, while fish from north of Cape Blanco have the opposite tendency (Nicholas and Hankin 1988). Few juvenile steelhead from California have been collected north of Cape Blanco (Pearcy et al. 1990; Brodeur et al. 2004), supporting the suggestion that steelhead from California and southern Oregon remain in the CCS.

In most years there is an abrupt change from downwelling or neutral conditions to strong upwelling along the coast called the spring transition (Figure 11-6), and a more gradual change to mainly downwelling in late summer and fall. Winds blowing down the coast drive southerly flow and upwelling, creating a band of cooler and nutrient-rich water along the coast. The spring transition initiates a plankton bloom that drives a period of high productivity to which many animal populations are attuned. Variation in the timing of the transition can have severe consequences for some animals; for example, the transition occurred late in the spring of 2005, so that seabirds around the Gulf of the Farallones suffered reproductive failure, but conditions were good for juvenile Chinook by June (B. MacFarlane, NMFS, pers.comm. 2006).

Figure 11-6. Changes in dynamic height, surface temperature, and surface salinity between March and April 1995. Contours of dynamic height can be interpreted in the same way as isobars on a weather map. Note the change in temperature contours from roughly perpendicular to roughly parallel to the coast. Copied from Lynn et al. 2003.

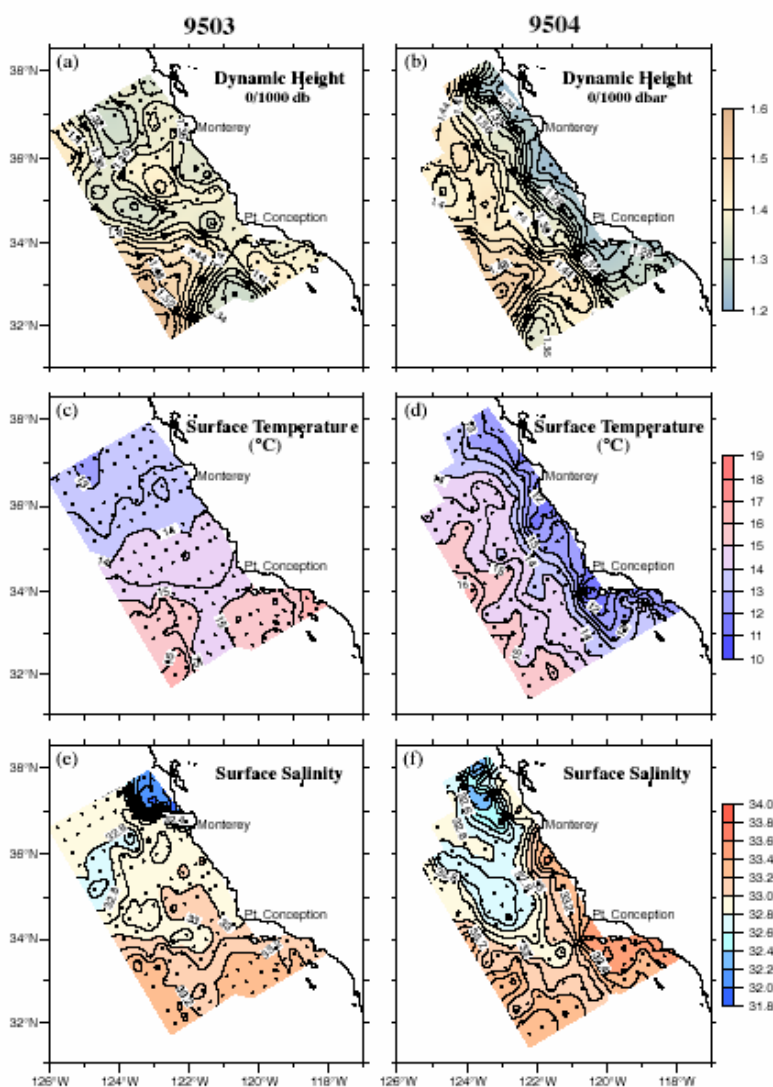
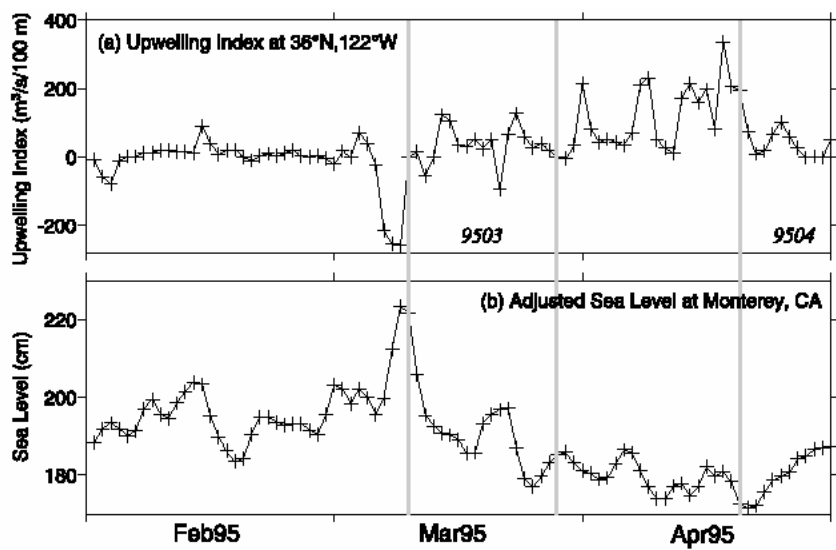


Figure 11-7. Change in the upwelling index and in adjusted sea level at Monterey for February – April 1995. Note that upwelling was episodic, rather than continuous. 9503 and 9504 are the numbers of oceanographic surveys conducted during the intervals marked by the vertical lines. Copied from Lynn et al. 2003.



Regime shifts

The recognition of regionally coherent fluctuations in populations of salmon and other fishes over decadal time scales (e.g., Francis and Silby 1991) has generated a sizable literature on regime shifts, which I have not tried to summarize. In an oversimplified form, for salmon, this involves the notion of alternating patterns of abundance in the Gulf of Alaska and the California Current System (CCS), including the west coast from Vancouver Island through California, as a function of the split in the eastward flowing North Pacific Current into the Alaska Current and the southward flowing California Current. As usual, the details are more complicated (e.g., Mueter et al. 2002; Botsford and Lawrence 2002), and as noted by Hare et al. (1999) and elaborated by Botsford and Lawrence (2002), Chinook fit the pattern less well than other salmon. Changes over longer temporal scales also affect salmon. Finney et al. (2000; 2002) described multi-centennial changes in sockeye abundance that seem climatically driven, although reinforced biologically by changes in the delivery of marine-derived nutrients to the nursery lakes.

Regime shifts in the CCS were described as follows in a recent PICES⁶⁶ report (King 2005:38):

Conditions in the California Current System are subject to decade-scale regime behavior with an overlay of episodic warm El Niño and cold La Niña events that last a year or two. In the CCS, there have been strong ecosystem responses to the 1977 and 1989 regime shifts. The 1977 regime shift led to a protracted period of warm surface waters, with a deepening of the thermocline and the implication of lower productivity. However, available zooplankton time series suggest that scallop biomass declined after 1977, while euphausiid biomass remained unchanged and copepod biomass actually

⁶⁶ North Pacific Marine Science Organization.

increased. Following the 1977 regime shift, overall recruitment improved for species such as Pacific sardine, and other species experienced intermittent very strong year classes (Pacific hake and Pacific cod). After the 1989 regime shift, the warm surface waters intensified and became unproductive for many coastal species. In coastal waters, zooplankton shelf species were replaced by more southerly and oceanic species. Many fish species (Pacific salmon,⁶⁷ Pacific hake, Pacific cod, and rockfish species) experienced almost a decade of poor recruitment. Southern migratory pelagics (Pacific sardines and Pacific hake) extended their northern limit of their distribution to northern British Columbia, and in some years, to the Gulf of Alaska.

After an intense El Niño in 1998, the CCS experienced a very cold La Niña in 1999. Since 1999, sea surface temperatures have tended to return gradually to warm conditions similar to those of the 1980s and early 1990s, but the thermocline depths are now much shallower and nutrient levels are higher, generating higher primary and secondary production. Beginning in 1999, coastal waters saw a return of shelf zooplankton, and many coastal fish stocks experienced substantial improvements in year class success. Some stocks produced good year classes in 1999 (*e.g.*, Pacific hake), and recent returns of several salmon stocks have improved; Columbia River salmon runs have been extraordinary. In addition, the distribution of migratory pelagic fishes (Pacific sardine and Pacific hake) contracted to a more southerly distribution. There is growing evidence, based on a strong and diverse biological response, that a regime shift favoring coastal organisms occurred in 1998.

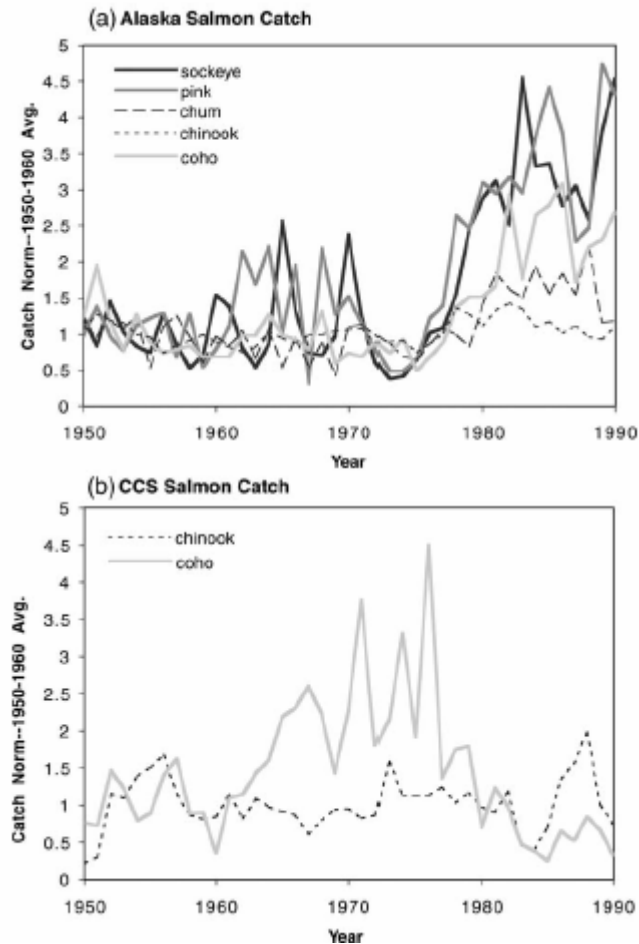
Correlating indices of recruitment or abundance with environmental variables seems the obvious way to clarify the effects of ocean condition on salmon, but technical problems make this difficult (Walters and Collie 1998; Kope and Botsford 1988). For example, it is desirable to do such analyses by year-class, but estimating Chinook abundance by year-class is difficult and involves more or less error. Unless the errors are small, it may be better to use simpler indices such as overall abundance or harvest (Kope and Botsford 1990), as was done by Botsford and Lawrence (2002). Moreover, simply finding correlations is not enough, as noted in the introductory quotation from Scheuerell and Williams (2005); effective predictions are needed if ocean conditions are to influence management. Scheuerell and Williams (2005) report a method for predicting the survival of Snake River spring/summer Chinook from the Coastal Upwelling Index (also called the Bakun Index) for April, September and October. Whether the same approach will be successful for other populations remains to be seen.

Botsford and Lawrence (2002) assessed the relationship between the abundance as indexed by harvest of Chinook and coho salmon and Dungeness crab in the CCS with sea surface temperature, sea surface height, and an index of upwelling, as well as with a mathematically derived variable that expresses the main patterns in the three physical variables. They also investigated the relationship between these variables and various basin-scale indices such as the Pacific Decadal Oscillation. While they found a simple pattern in the catch of coho that varied

⁶⁷ The statement that Pacific salmon experienced almost a decade of poor recruitment refers to salmon in the CCS generally; it is not true for Central Valley Chinook.

inversely with the catch of Alaskan stocks, they did not find such a pattern with Chinook (Figure 11-8). The reason for this difference is unknown. Although catch is an imperfect index of abundance, problems with the index seem unlikely to account for it.

Figure 11-8. Comparison of normalized catch records for salmon in Alaska (A) with catch records for coho and Chinook in the California Current System (ports in California, Oregon and Washington). Copied from Botsford and Lawrence (2002).



Botsford and Lawrence (2002) did find relationships between the state of the ocean environment and the catch of Chinook, for conditions in both the year of ocean entry and the final year. The importance of conditions in the year of ocean entry is intuitive and consistent with critical period concept. Migration and sexual maturation are energetically expensive, and it seems likely that mortality for maturing fish may increase significantly in years when feed is very scarce, as in 1983, but it also seems plausible that the vulnerability of Chinook to harvest may vary with ocean conditions, say from factors affecting the spatial distribution or aggregation of the fish, so that Botsford and Lawrence (2002) may have detected patterns in catchability rather than abundance. If ocean conditions in the normal range of variation do affect the condition of maturing Chinook enough to affect survival, they should also affect size at age and perhaps fecundity. Conditions in the ocean do affect size at return, as might be expected. Based on analysis of the size of coded-wire tagged fish that returned at age three (after two ocean winters) from Washington, Oregon, and California (WOC), Wells et al. (2006) found

correlations between size at return and both regional and basin scale indices of ocean conditions, but the correlations were for the late winter of, and the spring and summer after, the first ocean winter, rather than the year of return. That is, Wells et al. (2006) argue that size at return for WOC Chinook is determined before the year of return, although for ocean-type Chinook in the Puget Sound – British Columbia region they found that size was related to conditions in the final year. From a physiological point of view, it seems curious that size at age of return should be affected by conditions after one sea winter in one region and after two sea winters in another.

The Gulf of the Farallones data for 1997-1999 may help explain why Botsford and Lawrence did not find coast-wide patterns for Chinook. In 1998, when juvenile Chinook grew best, the gulf was unusually warm. However, upwelling was also locally strong, and high runoff from the Central Valley rivers also contributed nutrients to water in the gulf. In consequence, the biological productivity of the gulf was high, and enough food was available for juvenile Chinook to realize the growth opportunity afforded by the high temperatures. The same favorable suite of conditions may not have occurred elsewhere along the coast where other populations of Chinook enter the ocean. Generally, the highly productive region of the CCS along the coast was unusually narrow in 1998 (Chavez et al. 2002).

In summary, it seems clear that growth and survival in the ocean is affected by ocean conditions, that ocean conditions vary at a range of spatial and temporal scales, and that ocean conditions affect different species differently and salmon of the same species in different areas differently, but there is still much to learn about the causal relations involved. To complicate matters more, ocean conditions will be also affected by climate change. For Central Valley salmon, conditions in the Gulf of the Farallones are likely to be most important, although conditions farther north along the coast should also be important if first-year survival depends strongly on mortality in the first winter, as argued by Beamish and Mahnken (2001).

CHAPTER TWELVE

HATCHERIES

Although one can hypothesize that exposure to the hatchery environment for even a small portion of the fish's life cycle allows some genetic divergence from the wild genome, the nature, degree, and consequences of the change will remain largely unknown until we can better understand the determinants of [wild stock productivity]. Cuenco 1994:28

*Although several studies have shown genetic differences between hatchery and wild anadromous Pacific salmon (*Oncorhynchus* spp.), none has provided compelling evidence that artificial propagation poses a genetic threat to conservation of naturally spawning populations. When the published studies and three studies in progress are considered collectively, however, they provide strong evidence that the fitness for natural spawning and rearing can be rapidly and substantially reduced by artificial propagation.*

Reisenbichler and Rubin (1999:1054)

The role of hatcheries is affected by society's choice between continual high human inputs to salmon ecosystems and rehabilitation of their natural regenerative capacity. ... Under the option of rehabilitation, the role of hatcheries would be much more limited and refined than their historical role because rehabilitation of the natural regenerative capacity of an ecosystem requires congruence of each human intervention with natural structures and processes of genetics, evolution, and ecology.

NRC (1996:315-316)

We believe that these experimental results, considered in light of widely recognized evolutionary and population genetics theory, provide convincing evidence that:

- *Domestication selection can genetically alter hatchery populations in a relatively few generations.*

- *Hatchery-reared adults returning from the ocean and spawning in the wild generally produce progeny that do not survive as well as progeny from adults of wild origin.*

And persuasive evidence that:

- *Interbreeding between hatchery reared adults and wild fish can reduce the fitness of wild populations.*

ISAB (2002:24)

A fundamental goal of an integrated [hatchery] program is to minimize genetic divergence between the hatchery broodstock and a naturally spawning population ... A hatchery supporting an integrated program can be viewed conceptually as an artificial extension of the natural environment, where the population as a whole (hatchery plus wild) is sustained at a much higher level of abundance than would occur without the hatchery. A properly-managed integrated broodstock program can serve as a genetic repository, in the event of a major decline in abundance of natural-origin fish.

HSRG (2003:12)

Inevitably, hatchery brood stock show domestication effects, genetic adaptations to hatchery environments that are generally maladaptive in the wild.

Myers et al. (2004:1980)

Chinook and steelhead reproduce in hatcheries in the Central Valley as well as in streams, and Chinook have done so since the late nineteenth century (Black 1994; 2001). Although hatchery practices and attitudes toward hatcheries have changed in response to new information

about the life history and biology of salmon, the basic idea has remained the same: mortality in the early life stages is high, and by reducing that mortality more progeny can be produced from a given number of adult fish than would result from natural spawning.

Given the very large numbers of returning fall-run Chinook in recent years, the hatcheries in the Central Valley now seem successful. The situation was different a decade ago, however, when returns of fall-run were low (SRFCRT 1994), and the general success of hatcheries continues to be questioned (e.g., Hilborn 1998, NRC 2003). Although the increase in returns is due in part to changes in hatchery practices, such as trucking juveniles from some hatcheries to San Pablo Bay and letting them acclimate in net pens there before release (Brown et al. 2004), presumably the increase also resulted from favorable ocean conditions and restrictions on the ocean fishery, and it is not clear what returns will be when these conditions change. Moreover, hatchery fish do not exist in isolation from naturally-produced fish, and there have long been concerns that wild fish may be harmed by interactions with hatchery fish (see NRC 1996; Flagg et al. 2000; ISG 2000, and ISAB 2002 for reviews). This chapter briefly describes historical and current hatchery practices in the Central Valley, and describes at greater length the more fundamental issues involved with hatcheries and recommendations regarding them that have been made by various expert panels. Recommendations specific to the Central Valley are also presented.

Early hatchery practices

Culture of Chinook began in California to obtain fertilized eggs that could be planted elsewhere; only later were cultured fish released back into the stream from which the adults were taken (Clark 1929). The early practice in the Central Valley was to plant out alevins a few days after they hatched; over forty million were released from a hatchery on Battle Creek in 1897 (Rutter 1904). Apparently this practice was based on the view that in natural spawning many eggs remained unfertilized or that “Most of the eggs deposited are eaten by other fishes, or are killed by being covered with sand and gravel” (Rutter 1904:72). On the basis that “alevins have many enemies in the stream; fry but few,” Rutter recommended that fish be planted after the yolk was fully absorbed. Rich (1920) repeated this recommendation. Despite Rutter’s concerns about releasing alevins, however, he began his report with the observation that “Within the last few years, ... artificial propagation has reached such efficiency that the species is again increasing, especially in the Sacramento River, California.”

The species did not continue to increase, however, and enthusiasm for hatcheries waned, as it did in other parts of the Northwest (Lichatowich and McIntyre 1987; ISG 2000). Even the basic rationale for hatcheries was challenged. According to Briggs (1953:7):

It was frequently supposed, until very recently, that by far the greatest losses took place during the egg and larval stages, and that once the young fish were free swimming they were relatively safe from predation. This belief of most early authorities gave impetus to the practice of artificial hatching. The advantage of artificial rearing during the early stages of the life cycles was fully accepted by most biologists, in spite of some evidence

to the contrary, until Hobbs (1937; 1940) published the results of his extensive New Zealand redd sampling projects on introduced salmonid species.

Although Briggs (1953) cautioned against uncritical acceptance of Hobbs's high estimates of the survival of early life-stages of salmonids, he concluded from his own work (p. 58): "... there is no doubt that, during the period of study, substantially more young fish were introduced as fry into Prairie Creek via natural propagation than could be supplied through standard hatchery methods utilizing the entire run in the creek." It now appears that the survival rates observed by Hobbs and by Biggs were unusually high. In any event, hatchery practices and the thinking supporting them changed. Murphy and Shapovalov (1951) noted that:

The thought has been advanced that better results than from natural propagation could be obtained by taking eggs from natural runs, hatching the fry, and, instead of planting them soon after, rearing the offspring until their normal downstream migration period. Theoretically, at least, this procedure should circumvent a considerable amount of stream mortality and result in an increase in the number of returning adults over the number that would have been produced if all fish had been allowed to spawn naturally.

With the development of better disease control and fish food, this approach worked well, and rearing salmon to smolt stage or even beyond has become standard in the Pacific Northwest as well as in California (Lichatowich and McIntyre 1987; Mahnken et al. 1998; ISG 2000). Overall hatchery production of Chinook and steelhead increased rapidly after about 1950 and peaked at about 400 million and 35 million annually in the late 1980s, with a subsequent slight decline (Mahnken et al. 1998).

Current hatchery programs in the Central Valley

There are six hatcheries for anadromous salmon in the Central Valley, two operated by the USFWS, and four operated by the CDFG (Table 1). The operation of the USFWS hatcheries is described in detail in a recent biological assessment (USFWS 2001), and the operation of the Feather River Hatchery and Nimbus Hatchery are described in Brown et al. (2004) and Brown (2006), but no comparable documents exist for the Mokelumne and Merced River hatcheries.

Table12-1. Summary List of Central Valley Hatcheries

Hatchery	River	Run by	Purpose	Stocks
Livingston Stone	Sacramento	USFWS	Conservation	Winter
Coleman	Sacramento	USFWS	Mitigation	Fall, Late Fall, Steelhead
Feather River	Feather	CDFG	Mitigation	Spring, Fall, Steelhead
Nimbus	American	CDFG	Mitigation	Fall, Steelhead
Mokelumne River	Mokelumne	CDFG	Mitigation	Fall, Steelhead
Merced River	Merced	CDFG	Mitigation	Fall

The relationship between salmon populations in streams and hatcheries can take different forms, depending upon the source of hatchery broodstock and the disposition of returning adults (Figure 12-1). Except for Livingston Stone Hatchery, existing hatcheries for salmon or steelhead in the Central Valley fall into the category of Production Hatchery A in Figure 12-1, with some naturally produced fish introduced into the broodstock each year or periodically, and some hatchery fish spawning naturally. For example, Coleman Hatchery currently has targets of 25% and 10% unmarked fish for late-fall Chinook and steelhead broodstock respectively. The objective is that there be enough genetic mixing that the hatchery and naturally producing fish on a given river constitute a single population.

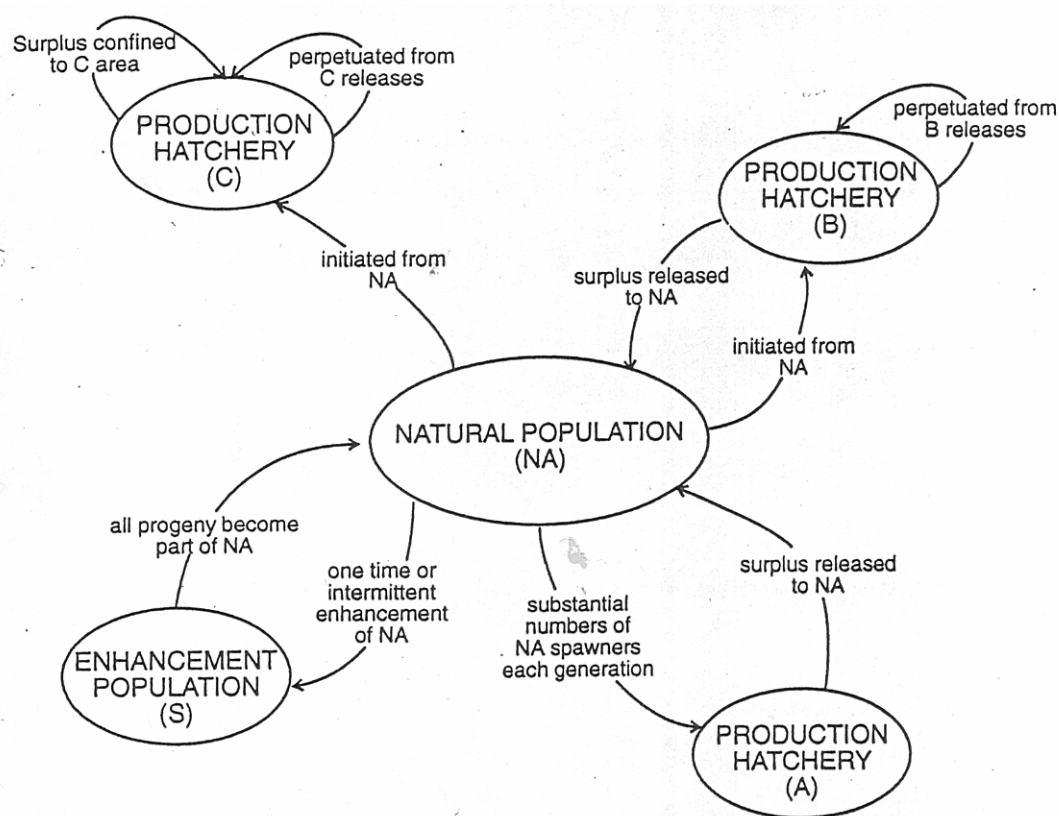


Figure 12-1. Possible patterns of migration between a natural population and derived hatchery populations. These patterns and the number of fish produced determine the extent of hatchery influence on the natural population. Copied from Utter (1998), courtesy of *Bulletin of Marine Science*.

The Central Valley hatcheries are intended to mitigate for the loss of habitat to large dams built in the mid-twentieth century: Shasta, Folsom, Oroville, Camanche, and New Exchequer, although some also produce additional fish for enhancement and for coded-wire tag experiments.

As such, these mitigation hatcheries are intended to produce large numbers of fish on a continuing basis, regardless of the status of naturally-producing populations that utilize habitat below the dams or in other streams. They routinely produce and release over 30 million juvenile Chinook and over a million juvenile steelhead each year (Table 12-2), so hatcheries are an important habitat for both species. In contrast, the recently opened Livingston Stone Hatchery is intended to assist the recovery of winter Chinook, follows the model of the enhancement hatchery in Figure 12-1, has much smaller production, and presumably will be phased out as the population recovers.

Chinook hatcheries in Southeast Alaska exemplify the approach of Production Hatchery C in Figure 12-1. These hatcheries are located near tidewater on streams that do not have wild runs of Chinook (Heard et al. 1995), so except for strays, interactions with naturally produced fish occur only in the ocean, and straying rates from these hatcheries seem to be low (Hard and Heard 1999).

Hatcheries take advantage of the tendency of salmon returning to their natal streams to migrate upstream until they reach some obstacle, and have collection works so constructed that the fish enter the hatcheries of their own accord. Under current procedures, all Chinook that enter the production hatcheries during the spawning seasons are retained; steelhead are returned to the river after being stripped. Older practices are reviewed in Brown et al. (2004).

All Central Valley hatcheries now try to obtain broodstock over the length of the spawning season, although in the past there was a tendency to concentrate egg collection in the earlier part of the season to ensure that goals for eggs collection would be met even if the run dropped off. The different hatcheries use different mating protocols, but generally aim for an equal opportunity for “adult” fish to contribute to the next generation; grilse are limited to a 5% contribution (USFWS 2001; Armando Quinones, CDFG, personal communication 2003; Brown et al. 2004). In the past, grilse generally were not used for broodstock, and there may have been informal selection for larger fish.

Although Chinook fry were released into rivers in the past, particularly when more were on hand than needed to reach production goals for smolts, hatcheries now release only smolts and a much smaller number of yearlings (Table 2). About half the smolts are released in net pens in San Pablo Bay; smolts from Coleman National Hatchery and most smolts from the Mokelumne River Hatchery are released into the river. About 85% of smolts from the Merced River hatchery are used in experimental releases, and the rest are released into the Merced River. Steelhead are released into the rivers at sites downstream from the hatcheries, to reduce their predation on Chinook fry.

Table12-2. Production and release data for salmon and steelhead in the Central Valley, data from JHRC (2001, Appendix V) and Brown et al. (2004). M = mitigation, E = enhancement.

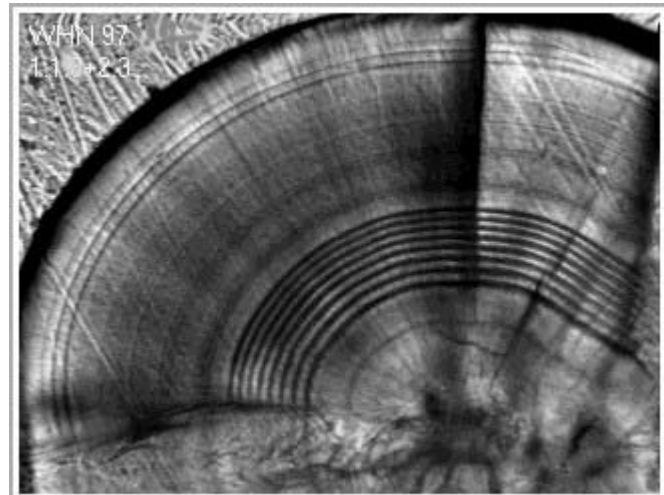
Hatchery	Species or Run	Production Goal (millions)	Maximum Egg Take (millions)	Tag or Marks	Size and Time of Release	Release Location
Coleman	Fall	12, smolts		~ 8% cwt BY 95-02	90/lb. Apr.	Battle Creek
Coleman	Late-Fall	1, smolts		100% cwt	13-14/lb. Nov.-Jan	Battle Creek
Coleman	Steelhead	0.6, smolts		100% ad-clip, some cwt	~4/lb Jan.	75% Balls Ferry; 25% Battle Creek
Livingston Stone	Winter	0.2, smolts		100% cwt	~85 mm Jan.	Sac. R. at Redding
Feather River	Spring	5, smolts	7	100% cwt	May-June	50% F. R., 50% S. P. Bay
Feather River	Fall	M 6, smolts E 2, post-smolts	12	~10% cwt	April-June	San Pablo Bay
Feather River	Steelhead	0.45, yearlings		Ad-clip		
Nimbus	Fall	4, smolts				San Pablo Bay
Nimbus	Steelhead	0.43, yearlings		100% ad-clip		
Mokelumne River	Fall	M 1, smolts M 0.5 post smolts E 2, post-smolts		few cwt	May-July Sept.-Nov. May-June	various Lower M. R. San Pablo B.
Mokelumne River	Steelhead	0.1	0.25	100% ad-clip	Jan.	Lower M. R.
Merced River	Fall	0.96, smolts or yearling		100% cwt	Apr. – June Oct. – Dec	Merced R. + exper. releases elsewhere

Marking and tagging methods

All hatchery winter, late-fall, and spring Chinook are now marked with coded wire tags as well as adipose fin clips, and all hatchery steelhead are marked with adipose fin clips; however, only a small percentage of hatchery fall-run are marked (Table 12-2). Although coded-wire tags have been a mainstay of salmon studies in the Central Valley, other methods are now standard elsewhere. Coded-wire tags have a limited number of codes, and so can only be used to mark batches of fish. Passive integrated transponder (PIT) tags, however, can be used to mark individuals, although the individuals must pass close to a receiver in order to be detected. PIT tags are extensively used on the Columbia River, where migrating juveniles can be detected in the fish passage facilities in the dams. Tag detectors can also be mounted on open-ended trawls, although this approach seems still to be experimental (Ledgerwood et al. 2004). The 2002 EWA Review Panel has recommended that use of PIT tags for Central Valley salmon be considered.

Otolith thermal marking (OTM) allows all hatchery fish to be marked at less expense than other methods. The growth of embryos or alevins in hatchery incubators can be varied by manipulating the temperature of the water, producing patterns of light and dark bands on the otoliths to create bar codes that can mark batches of fish (Volk et al. 1994; Figure12-2). Otolith thermal marking is now the dominant method for marking fish in Alaska, with billions of salmon, mostly pinks, being marked each year (E. Volk, WDFW, pers.comm., 2003). Otoliths must be removed and processed in order to read the marks, but otoliths can be processed for OTM reading quickly enough that OTM is used for real-time management of mixed stock fisheries (Heard 1998; Hagen et al. 2001). Adipose fins of OTM fish can be clipped if an external mark is needed. Coleman Hatchery has experimented with otolith marking, and the Feather River hatchery is moving toward using them (Brown et al. 2004). This is a welcome development.

Figure12-2. Section of an otolith from a juvenile Chinook salmon, showing a pattern of dark bands produced by manipulating the water temperature in the hatchery tray. Image from Eric Volk.



The otoliths of hatchery and naturally produced fish can be distinguished by examination of the otolith bands or of otolith microchemistry, even if the fish are not deliberately marked. The spacing of otolith bands is more regular in hatchery fish (Zhang et al. 1995; R. Barnett-Johnson, NOAA Fisheries, pers.comm. 2005), and marine-derived hatchery feed affects the isotopic ratio of sulfur in the otolith (Weber et al. 2002). However, these methods require more careful preparation and analysis of the otoliths than is required to read thermally marked otoliths.

The hatchery environment

Hatchery culture is a blend of art and science, and procedures vary among hatcheries and over time. Pennell and Barton (1996) provide a review as well as much information on salmon biology. Rather than in redds, eggs and alevins in salmon hatcheries grow and develop in shallow trays arranged in stacks so that water trickles from one to the next, or in “jars” made from short sections of large diameter plastic pipe through which water upwells. About the time that alevins reach maximum wet weight (MAWW), approximately the completion of yolk absorption, they are transferred to rearing troughs or ponds and presented with food. Usually

they are transferred again to larger raceways where they rear until release. The eggs, alevins and fry are raised at high densities, but with modern facilities and procedures, problems with disease generally are not severe if cool water is available.

In the hatcheries, ~90% of the eggs collected are fertilized and survive initial development, and for populations with a longer history of hatchery culture ~99% survive through the alevin stage to ponding; survival for winter-run, which have been cultured for only a few generations, averaged 86% in 1998 and 1999. Survival during ponding seems inversely proportional to its duration, ranging from 97% for fall-run to 85% for steelhead (S. Hamelberg, USFWS, pers.comm. 2003). For Coleman Hatchery, estimated survival from smolt to harvest or maturity for fall-run during 1973 to 1995 varied from 0.2% to 2.9% and averaged 0.78% (USFWS 2001). Survival for smolts to harvest or maturity for late fall-run was slightly lower (0.75%), but data are available for fewer years.

Straying

One particularly controversial aspect of salmon culture in the Central Valley involves trucking fish from hatcheries to San Pablo Bay, to avoid the mortality associated with migration through the river and Delta. Although this practice results in substantial increases in harvest and returns (Brown et al. 2004), it also results in high rates of straying (Pascual et al. 1995; Quinn 1997), estimated at over 70% by the JHRC (2001).⁶⁸ Mating between strays and other fish probably is a major reason for the lack of detectable genetic variation among Central Valley populations of fall-run Chinook (Banks et al. 2000; Williamson and May 2003); other reasons are the deliberate movement of eggs or fry among hatcheries, which used to be common (Williamson and May 2003), and recolonization of streams after hydraulic mining. This lack of genetic structure is in strong contrast to the genetic variation in other large river basins such as the Klamath-Trinity basin (Banks and Barton 1999; Waples et al. 2004). In view of the evidence for adaptive variation among populations of salmonids (Ricker 1972; Withler 1982; Wilson 1997; Taylor 1997; Unwin et al. 2003), the apparent lack of genetic structure of Central Valley fall-run is cause for serious concern. However, Banks et al (2000) and Williamson and May (2003) studied neutral genetic markers that are not associated with traits conferring fitness. Despite the lack of detectable genetic structure in the sets of neutral markers used in these studies, there may still be differences among populations in genes that are subject to natural selection (Utter et al. 1992; Williamson and May 2003).

Differences between hatchery and wild or naturally produced salmonids

Differences between wild and hatchery fish were studied first in trout that were reared to catchable size before release (e.g., Moyle 1969), and the existence of the differences was not controversial (Reisenbichler and Rubin 1999). Hatchery salmon, however, spend most of their lives in the wild, and mortality in the hatchery is low. These considerations gave rise to doubts that hatchery culture of anadromous fish would have significant genetic effects (e.g., Cuenco

⁶⁸ In the past, some biologists apparently thought that straying was a good thing because, as noted by Meyer (1982), "... the strays will be going from rivers with adequate escapement to areas with poor escapements."

1994). According to Busack and Currens (1995:76): “The biggest obstacle to serious consideration of the hazard of domestication is a tenacious belief that hatcheries can not impose selection simply because they allow so many fish to survive.” Waples (1999) described this belief as a myth, and Goodman (2004) elaborates the reasons that it is. For example, although survival in the hatchery is high, selection after release operates on traits such as rapid early growth that are expressed in the hatchery (Busack and Currens 1995; Reisenbichler and Rubin 1999; Waples 1999; Kostow 2004).

Differences between hatchery and wild salmonids have been reported in survival, foraging and social behavior, habitat preference, morphological and physiological attributes, life history variation, response to predators, and reproductive biology (Flagg et al. 2000; Einarsson and Fleming 2001; Reinhardt 2001; Weber and Fausch 2003). Even “first-generation” hatchery steelhead can exhibit significant differences in life history variation and in smolt to adult survival, as demonstrated by a study of steelhead in the Hood River, Oregon (Kostow 2004).

The Hood River supports a natural population of winter-run steelhead, and a hatchery there has long maintained a population of summer-run steelhead, some of which spawn in the river. Recently, a hatchery program was established for the winter-run population, with broodstock selected from naturally spawned fish to the extent feasible. A dam downstream from the hatchery and spawning habitat allows for monitoring the survival of these groups of fish (Kostow 2004). For both populations, hatchery fish had much higher egg to adult survival (Figure 12-3a), which supports the rationale for hatcheries. For both populations, however, the smolt to adult survival of the naturally-produced fish was considerably higher (Figure 12-3b); that is, the advantage of the hatchery fish was entirely in the egg to smolt survival. Moreover, on average, egg to adult survival was highest for the summer-run population, with a long history of hatchery culture, but that population also had the lowest egg to adult survival for naturally-produced fish. This is an out-of-basin stock, but nevertheless the extremely low egg to adult survival of the progeny of those that do spawn in the river suggests that adaptation to hatchery culture has decreased their fitness to survive in the wild.

Juvenile steelhead in the Hood River were also sampled with traps at several locations, one of which was downstream of known rearing areas, and fish collected there were assumed to be leaving the river. There was considerable variation in the size and age of naturally-produced fish from the native winter-run population collected in the various traps, as might be expected from the normal diversity in life history patterns among steelhead; however, the hatchery-produced fish, which were larger, all migrated rapidly out of the Hood River, and based on scale analyses almost all of them proceeded directly to the ocean. That is, hatchery culture canalized the fish into a single life history pattern (Kostow 2004), probably through enhanced growth. Thus, after their release, many of them experienced the natural environment differently than they would have, had they been naturally produced, and so were exposed to different selective regimes. Despite their larger size at age, their smolt-to-adult survival was considerably less than that of the naturally produced fish.

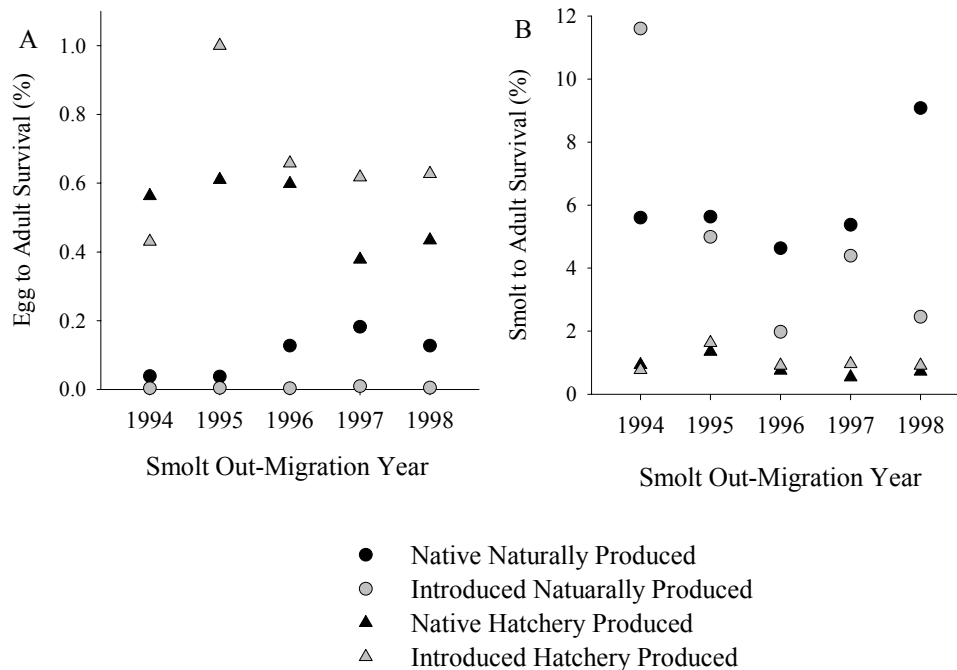


Figure 12-3. Comparison of the survival of hatchery and naturally produced steelhead from a native and introduced stock. A: Egg to adult and B: smolt to adult survival of native winter-run steelhead (black symbols) and an introduced stock of summer-run steelhead (grey symbols) that are naturally (circles) or hatchery (triangles) produced, in the Hood River, Oregon. Data from Kostow (2004).

Alternative rearing systems

Experiments with more natural hatchery environments have been one response to concerns about the quality of hatchery fish (e.g., Maynard et al. 1995; 1998), and considerable work is now underway in the Columbia River basin, mostly with Chinook but now also with steelhead (Berejikian et al. 1999; 2000; 2001; Maynard et al. 2003). Fish reared in the Natural Rearing Enhancement System (NATURES) generally had better survival than conventionally-reared controls, probably because of more cryptic coloration. In other tests, predator conditioning also improved survival. NATURES fish were generally somewhat smaller, but had higher scores on a health index and more natural behavior than control fish reared conventionally (Maynard et al. 2003). Overall, the results suggest that changes in hatchery practice can lead to moderate increases in survival (but see Kostow 2004); whether they can significantly reduce unfavorable genetic effects remains unknown. Nevertheless, increased survival would allow smaller releases to produce the same number of adults, and smaller releases should have fewer negative indirect or ecological effects on naturally produced fish.

Effects of hatchery fish on naturally produced fish

Concern about the effects of hatcheries on naturally-producing stocks is not new, but its expression has been increasingly common and sometimes vociferous in the last decade (e.g., Hindar et al. 1991; Meffle 1992; Hilborn 1992; 1998; NRC 1996; Reisenbichler and Rubin 1999;

Waples 1999; ISG 2000; Levin et al. 2001; Einum and Fleming 2001; Fleming and Petersson 2001; Lynch and O'Hely 2001; Ford 2002; ISAB 2003; NRC 2003; McGinnity et al. 2003; Myers et al. 2004; Hey et al. 2005; see Incerpi 1996; Armand et al. 2000; Brannon et al. 2004 for contrary views). Effects can be either indirect, ecological, or genetic (Utter 1998; Levin et al. 2001; JHRC 2001).

Indirect effects of hatchery fish on wild or naturally producing fish

There has long been concern that fisheries targeted at strong stocks may result in unsustainable rates of harvest on weaker stocks (e.g., Ricker 1973), as is recognized in the management of mixed-stock fisheries. The same issue arises regarding hatchery populations, which can sustain a higher harvest rate than can non-hatchery populations (Lichatowich and McIntyre 1987; NRC 1996; Myers et al. 2004). Although Central Valley winter-run that return in their third year are vulnerable to the ocean fishery for a relatively short time, over 20% of hatchery winter-run are caught there (CDFG 2004a). The estimated harvest rate for spring-run was 0.36 and 0.42 for 1998 and 1999 (CDFG 2004b), although probably it has decreased in the last few years when harvest has been severely restricted to protect Klamath River Chinook (Ch. 14).

In a related problem, the presence of unmarked hatchery fish may block recognition that populations of naturally-produced are low. This is particularly a problem for Central Valley fall-run, where the proportion of hatchery fish in spawning runs is large but poorly known.

Ecological effects of hatchery fish on wild or naturally producing fish

Ecological effects arise mainly from interactions among hatchery and non-hatchery fish. However, ecological effects can also be indirect. For example, hatchery fish that die in streams contribute marine-derived nutrients to stream ecosystems, which may benefit non-hatchery fish rearing there. Other interactions have been described in spawning, rearing in streams, downstream migration, and ocean life; unfortunately, these effects are generally negative. Weber and Fausch (2003) provide an up-to-date review.

Spawning

Whenever the progeny of wild fish and hatchery fish use the same habitat, there is a potential for density-dependent effects (Einum and Fleming 2001). Although naturally-produced salmon and steelhead appear to survive better in the wild (Unwin and Glova 1997; Kostkow 2004) and to have greater reproductive success than hatchery fish (McLean et al. 2003), large numbers of hatchery fish on the spawning grounds probably limit the success of naturally-produced fish, even if successful interbreeding that could lead to genetic effects does not occur. This could result from later-spawning hatchery fish disturbing the redds of naturally-produced fish, from larger hatchery fish displacing smaller naturally-produced fish from good spawning habitat, or from hatchery females diverting the reproductive effort of naturally-produced males (Flagg et al. 2000). If the population density is high enough, substantial percentages of fish may die without spawning at all, as happened in recent years with fall-run in several Central Valley streams with high escapements; Battle Creek is an extreme example, with almost 90% pre-

spawning mortality in 2002 (Table 12-3). At least some of the unspawned fish must have been naturally produced.

Table12-3. Estimated adult returns and the observed percentage of unspawned female fall-run Chinook in Battle Creek and Clear Creek, tributaries joining the Sacramento River near Redding, for years 2000 – 2003. Coleman National Fish Hatchery is on Battle Creek. Pre-spawning mortality data from Colleen Harvey, CDFG, Red Bluff; adult return estimates from CDFG GrandTab data base.⁶⁹

		2000	2001	2002	2003
Battle Creek	Est. adult returns	53,447	100,604	397,149	67,764
	% P-S Mortality, ♀	26.3	28.5	87.5	60.1
Clear Creek	Est. adult returns	6,687	10,865	16,071	9,475
	% P-S Mortality, ♀	0.8	0.3	0.8	0.7

Rearing in streams

Current hatchery practice in the Central Valley avoids direct interactions between hatchery and naturally produced fish during the pre-smolt life stages. However, interactions can still occur between “first generation” naturally produced fish and others that are farther removed from hatchery rearing. In the Clackamas River, for example, progeny of naturally-spawning hatchery steelhead from a non-native stock compete with wild fish for juvenile habitat, although few return as adults (Kostow et al. 2003). The importance of such interactions among Central Valley salmon is unknown, but presumably depends both on the population density and on the extent of remaining genetic differences between hatchery fish and more naturalized fish.

When hatcheries release large juveniles there is also a potential for predation on younger naturally produced fish. For example, 532,000 yearling Chinook were released into the Feather River in 1972. The fish did not immediately migrate downstream, and stomachs of those sampled in January and February contained 1.3 Chinook fry on average; DFG estimated total predation at about 7.5 million fry (Sholes and Hallock 1979). Yearling Chinook are no longer released into the rivers (Table12-2), and Coleman Hatchery now releases steelhead into the mainstem Sacramento to reduce their predation on juvenile Chinook in Battle Creek (USFWS 2001).

Downstream migration

Releasing smolts at the hatcheries where they rear reduces straying, but increases the potential for density-dependent mortality or adverse ecological interactions with naturally produced fish as both groups move out of the river and through the Delta and the bays. For example, releases of hatchery coho in Oregon rivers apparently attract predators that incidentally consume more wild smolts than would have been the case without the releases (Nickelson 2003).

⁶⁹ The GrandTab data for adult returns in Table 23-3 are as given, down to the last salmon, but without confidence intervals or standard errors. This is an unfortunately typical example of spurious precision in Central Valley salmon data.

Hatchery managers at Coleman try to reduce this kind of risk by releasing fish toward the end of the smolt migration period (USFWS 2001), but there is still overlap. Weber and Fausch (2003b) found some evidence for competitive interactions among hatchery and naturally produced Chinook in the Sacramento River in enclosure experiments, and recommended more study of the issue. Twenty years ago, Kjelson et al. (1982:409) noted that “The problem of exceeding estuarine rearing capacity [through hatchery releases] is of some concern in the Sacramento-San Joaquin (hatchery releases total about 26 million smolts annually), but as yet has not been studied.” This is still true.

Ocean life

It is now generally accepted that ocean conditions strongly affect salmon populations, but the extent to which abundance affects this relationship is unclear (Heard 1998; Ch. 12). Whether significant density-dependent mortality occurs in the ocean may depend on conditions there; Levin et al. (2001) found a negative association between the survival of wild Snake River Chinook and the number of hatchery smolts released in years with poor ocean conditions, but not in years with good conditions. Returns of Chinook in British Columbia provide “a relatively strong suggestion of density-dependent mortality” (Perry 1995:152). Similarly, the proportion of naturally produced coho in the Strait of Georgia decreased when ocean conditions for salmon deteriorated, although hatchery production remained relatively constant (Sweeting et al. 2003). Reduced fish size may also indicate density-dependent effects. Although salmon populations in most of the North Pacific increased sharply from 1975 to 1993, the size of returning adults generally decreased; however, Chinook in California were an exception to this trend in decreasing size (Bigler et al. 1996).

Salmon spawning in hatcheries typically produce more adult progeny than naturally spawning salmon, but the post-release survival rate of hatchery fish is typically lower than that of non-hatchery fish of the same size and life stage (Waples 1991; Unwin 1997; Kostow 2004). For example, estimated average survival rates for hatchery and non-hatchery Chinook smolts from the Deschutes River over six years were 0.04 and 3% (Lindsay et al. 1989, cited in Waples 1991). Because of the typically low survival rates of hatchery smolts, they are produced in large numbers; it has been estimated that there are now more smolts leaving the Columbia River than before European settlement (HSRG 2003). Survival of hatchery Chinook from Coleman National Fish Hatchery averages about 0.78% (USFWS 2001), almost twice that cited for Deschutes River Chinook. In any event, hatcheries in the Central Valley now produce about 34.5 million smolts or post-smolts per year, suggesting considerable potential for competition with non-hatchery fish in early ocean life.

Genetic effects

Studies clearly demonstrating biologically significant genetic effects from hatchery culture of anadromous salmonids are not common, because differences between hatchery and wild fish can also have non-genetic causes. Differences in ecologically relevant traits between wild salmonids and crosses between hatchery and wild salmonids have been demonstrated, however (e.g., Reisenbichler and McIntyre 1977; Petersson and Järvi 2003). Because there are strong

theoretical reasons for expecting that deleterious effects should occur (Lynch and O’Hely 2001; Ford 2002) and considerable if not completely conclusive evidence that they do occur, it is clear from the literature that the mainstream of professional thought accepts that such effects do occur (e.g., Busack and Currens 1995; NRC 1996; Grant 1997; Utter 1998; Reisenbichler and Rubin 1999, Waples 1999, ISG 2000; RSRP 2001; ISAB 2002; HSRG 2003; Goodman 2004; 2005; Hey et al. 2005; see Brannon et al. 2004 for a contrary view). This is not some effect that is unique to hatcheries and salmon; in comments on research regarding evolution in bacteria, Elena and Sanjún (2005) remarked that “Evolutionary biologists have long recognized that an organism’s performance (or fitness) in one specific environment is accompanied by the organism’s decreased performance (or fitness) in other environments.” Myers et al. (2004) asserted that “Inevitably, hatchery broodstock show domestication effects, genetic adaptations to hatchery environments that are generally maladaptive in the wild.”

Production hatcheries in the Central Valley generally produce enough salmon that more return as adults than the hatchery needs for producing the next generation of fish, and many hatchery fish remain in the river where they may spawn naturally and presumably interbreed with naturally-produced fish. The percentage of naturally-spawning salmon of hatchery origin in Central Valley streams is uncertain and probably varies from year to year, but it is certainly large (Cramer 1991; Williams 2001). Even if there is no hatchery on the stream, hatchery fish may stray into the stream and spawn there, as on Mill Creek. If the progeny of such fish also reproduce successfully, the genetic composition of the naturally produced populations may be affected.⁷⁰ Even if some allele⁷¹ that is selected for in the hatchery is selected against in the wild, the allele will increase in the naturally producing population if gene flow for the allele from the hatchery exceeds the strength of selection against the allele in the wild (Felsenstein 1997).

One clear difference in selection in hatcheries and in the streams concerns mating. Salmon in streams do not select mates randomly; rather, there is often intense competition for redd sites and for mates (reviewed by Fleming and Petersson 2001; Fleming and Reynolds 2004). Random mating in hatcheries by-passes this competition and the associated selection; in effect, the hatchery adaptive landscape is simply flat with respect to traits associated with breeding and the genes that affect them. According to NRC(1996:308), “Although not all of the effects of this inadvertent interference with natural selection are precisely known, it is almost certain that one result is loss of general vigor, adaptation to local environments, and evolutionary fitness.”

Possible genetic effects on naturally producing salmon in the Sacramento River from interbreeding were considered recently in a biological assessment of the activities of Coleman National Fish Hatchery and Livingston Stone National Fish Hatchery (USFWS 2001, App. 6D.) The views expressed in the biological assessment are very similar to those of the Hatchery Scientific Review Group, described below. The assessment recognizes that some genetic harm

⁷⁰ For an introductory review of this issue see Waples (1999); for more technical detail see Grant (1997).

⁷¹ An allele is one form of a gene for a variable trait, such as the smooth and wrinkled skins in the peas in the classic studies by Mendel.

from mixing between hatchery and naturally produced fish is for practical purposes inevitable, but is justified by the need to mitigate the effects of Shasta Dam (USFWS 2001, App. 6D:3-4):

The only strategy to ensure artificial propagation programs at Coleman NFH do not impart any deleterious genetic impacts on co-occurring natural populations of Pacific salmonids is to terminate the hatchery programs. However, cessation of the hatchery propagation programs at Coleman NFH would result in failure of the Service to fulfill its responsibility to mitigate for negative effects resulting [from] habitat losses caused by Shasta Dam, and would have unknown and potentially harmful effects to Chinook salmon and steelhead trout populations in the upper Sacramento River system.

Non-genetic explanations for variation generated controversy regarding a recent report of rapid selection for smaller egg size in a captive population of Chinook (Heath et al. 2003a). Fleming et al. (2003) argued that environmental or maternal effects could account for the observed change in egg size. Although Fox and Heath (2003) accepted some of the points made by Fleming et al. (2003), they asserted that reciprocal hybridization experiments showed that at least some of the change was genetic, and that (p. 59c) "... none of these issues detract from our main point: minimizing juvenile mortality in the captive rearing program relaxes selection on the traits required for juvenile survival, allowing the evolution of traits that maximize adult reproduction (i.e., fecundity) at the expense of traits that affect juvenile survival in nature (e.g., egg size)."

If there is significant interbreeding between two populations adapted to different environments, say after a dam blocks one population from reaching its natural spawning habitat, then the gene frequencies in the mixed population may be less favorable than in either of the original populations; that is, they may fall in a valley in the relevant adaptive landscape. This is outbreeding depression (Emlen 1991; Lynch 1997).⁷² Perhaps surprisingly, outbreeding depression can occur with isolated populations adapted to the same environment, as demonstrated by experimental crosses between odd and even-year runs of pink salmon from a single stream; progeny from the matings had low fitness (Gharrett and Smoker 1991). Pink salmon have a strict two-year life cycle, so odd and even year runs are reproductively isolated, and the crosses were produced with cryogenically preserved sperm. In this case, the populations apparently occupied different peaks in the adaptive landscape associated with the stream.

Since a hatchery has a different adaptive landscape from the adjacent stream, it can be expected that selection in the hatchery should shift gene frequencies in the hatchery population toward a peak in the hatchery adaptive landscape. In general, this would move the population away from peaks in the adaptive landscape associated with the stream. If there is significant interbreeding between the hatchery and the naturally producing population, the result may be a

⁷² Hybrid vigor, or increased fitness in progeny of crosses, results from an escape from the effects of disadvantageous recessive alleles for which one of the populations was homozygous; the beneficial effects decline as alleles recombine in subsequent generations. The effects of outbreeding depression are longer lasting, since they involve the breakdown of coadapted complexes of traits.

population that is maximally fit for neither environment. Because hatchery fish have higher egg to adult survival, under plausible conditions the population may shift strongly toward the adaptive peak associated with hatchery, with a corresponding loss of fitness in natural conditions (Goodman 2005; Hey et al. 2005).

Do hatchery fish supplement or replace naturally-produced fish?

Several articles have argued that hatchery salmon tend to replace naturally-produced fish, rather than supplement them (Richards and Olsen 1993, cited in NRC 1996; Unwin and Glova 1997; Cooney and Brodeur 1998; Hilborn and Eggers 2000; but see Wertheimer et al. 2001 and response by Hilborn and Eggers 2001; Noakes et al. 2000; Levin et al. 2001; Sweeting et al. 2003; Kostow et al. 2003). Unwin and Glova (1997) described such a substitution in Glenariffe Stream, New Zealand, a tributary of the Rakaia River, which supports fall Chinook introduced from the Sacramento River in the early 20th Century. Population estimates on the stream are good because it arises from springs fed by the hyporheic flow of the Rakaia, and so has usually stable flow that has allowed successful operation of a counting fence. After a hatchery was put into operation the number of fish returning to Glenariffe Stream increased by a small, statistically insignificant amount, but the proportion of hatchery fish increased to over 60%.

As a matter of logic, hatchery fish can both replace non-hatchery fish and increase the total run, so the question is one of degree rather than of kind. Replacement could result either from density-dependent mortality in early ocean life (e.g., Unwin and Glova 1997; Noakes et al. 2000; Levin et al. 2001) or in streams (e.g., Kostow et al. 2003); from gene flow from hatchery fish reducing the fitness of naturally-spawning fish; from fisheries supported by hatchery fish (Noakes et al. 2000); or by combinations of these effects (Sweeting et al. 2003).

Whether hatchery fish have replaced naturally-spawning fish in the Central Valley is unknown, because too few fall Chinook are marked to allow accurate estimates of the proportion of hatchery fish among returning adults. However, it appears that replacement may have occurred in the Sacramento River; returns to Battle Creek are now greater than returns to the upper mainstem, in contrast to the situation in the 1960s and 70s (Figure 2-5). If the mainstem and Battle Creek returns approximate the naturally spawning and hatchery fractions, then, compared to the 1960s, replacement has occurred.

For another example, the percentages of marked fall-run among fish examined in Mill and Deer creeks are not strikingly lower than the percentage of marked fish in Battle Creek (Table 12-4), where most returning fall-run presumably are products of Coleman Hatchery. Although the percentage of fall-run from various hatcheries that are marked is too small and variable to allow an accurate estimate of the percentage of hatchery fish in Mill and Deer creeks from the percentage of tagged fish, it must be large. The strong indication from these data that the Mill Creek population is largely stray hatchery fish is particularly distressing because habitat in the creek is relatively intact, and Mill Creek historically supported a large population of fall-run; an egg-taking station was established on Mill Creek in 1901 for that reason, and 30 million eggs were taken there in 1905 (Clark 1928; 1929).

Table 12-4. Marked hatchery fish (adipose fin clip) found during fall-run carcass surveys in Battle, Mill, and Deer Creeks in 2003 and 2004. Some marked fish in Mill and Deer Creeks were from hatcheries other than Coleman National Fish Hatchery on Battle Creek. Data from Colleen Harvey-Addison, CDFG, Red Bluff.

	Battle Creek: Ad-clipped fish of fish inspected %	Mill Creek: Ad-clipped fish of fish inspected %	Deer Creek: Ad-clipped fish of fish inspected %
2003	105 of 945 11.6%	69 of 1,295 5.3%	2 of 21 9.5%
2004	161 of 2,151 7.5%	23 of 405 5.7%	4 of 130 3.1%

To the extent that hatchery fish replace naturally produced fish, hatchery production is self-defeating, so these studies raise a basic challenge to the idea of hatcheries, and the hatchery on the stream studied by Unwin and Glova (1997) was closed in response to their findings. Moreover, when most hatchery fish are unmarked, as they are in the Central Valley, even partial substitution can mask the decline of the naturally-spawning populations (JHRC 2001). Sweeting et al. (2003:500) proposed that "... hatchery-reared coho salmon should no longer be considered as additive to the wild production. Rather, hatchery fish should be considered as ones that interact with wild coho through the natural competitive processes that select the individuals that will successfully occupy the available marine habitat." It seems prudent to adopt a similar attitude toward hatchery salmon in the Central Valley.

Recent management recommendations regarding hatcheries

The concerns described above have given rise to a number of agency or independent panels that have made management recommendations. The reports of these panels express a range of points of view, and support the hypothesis that agency scientists are less likely than independent scientists to recommend significant changes to the status quo.

National Research Council, Committee on Protection and Management of Pacific Northwest Anadromous Salmon (NRC). In a book-length report, "Upstream, Science and Society in the Pacific Northwest," a committee of the NRC73 devoted a chapter to hatcheries, grouping problems under the following categories: demographic risks, genetic and evolutionary risks, behavior, fish health, physiology, and ecological problems. The report made several recommendations that seem consistent with CALFED goals and applicable to the Central Valley (NRC 1996:321-323):

The approach to hatchery operations should be changed in accordance with the goal of rehabilitation and the ecological and genetic ideas that inform that goal.

⁷³ The members of the committee were John J. Magnuson, Fred W. Allendorf, Robert L. Beschta, Peter A. Bisson, Hampton L. Carson; Donald W. Chapman, Susan S. Hanna, Anne R. Kapuscinski, Kai N. Lee, Dennis P. Lettenmaier, Bonnie J. McCay, Gordon M. MacNabb, Thomas P. Quinn, Brian E. Riddell, and Earl E. Werner.

All hatchery programs should adopt a genetic-conservation goal of maintaining genetic diversity that exists between and within hatchery and naturally spawning populations.

All hatchery fish should receive identifiable marks.

Decision-making about uses of hatcheries should occur within the context of fully implemented adaptive-management programs that focus on watershed management, not just on the fish themselves.

Joint Hatchery Review Committee (JHRC). Issues regarding hatchery practices in California in relation to the ESA were jointly reviewed by a Joint Hatchery Review Committee of NMFS and CDFG (JHRC 2001). There seemed to be agreement within the committee that interbreeding between naturally-produced fish and straying hatchery fish has largely eliminated genetic diversity among fall-run populations in Central Valley rivers. Disagreement centered instead on the significance and implications of this interbreeding: whether any pre-existing differentiation reflected adaptations to local environments rather than simply reproductive isolation; whether gene flow from hatchery to naturally-producing populations carried deleterious effects of domestication; and whether reducing the rate of straying would allow adaptive variation to develop. As summarized by JHRC (2001:15):

There was disagreement among members of the committee over the relative benefits and risks of trucking hatchery fish to the Delta. The debate reflected skepticism regarding the importance of conserving (or attempting to restore) genetic diversity among the remaining Central Valley natural fall-run populations as well as a reluctance to make changes to hatchery operations that would likely reduce their effectiveness in preserving the salmon fishing industry. Those in favor of continued off-site release point out that locally adapted fall-run populations may no longer exist in the Central Valley. The lack of clear genetic differentiation among Central Valley fall Chinook populations sampled to date supports this view, ...

Similarly, although the committee discussed the general question of ecological and genetic interactions between hatchery and naturally-produced fish, apparently it did not reach consensus beyond recognition that problems exist.

Because of concerns regarding straying, the JHRC (2001) recommended that trucking of Feather River Hatchery spring-run be halted, and that fall-run from the Feather River, Nimbus, and Mokelumne hatcheries “be considered for release ‘in river,’ rather than being trucked to San Pablo Bay” (JHRC 2001:17). In response, the Feather River Hatchery now releases half of its production of spring-run on-site and trucks the other half (Brown et al. 2004). Comparing the proportion of these groups that are captured in the ocean fishery and that return to the Feather River should provide additional information on the relationship between trucking and straying.

Independent Scientific Advisory Board (ISAB). Whether surplus hatchery fish should be allowed to spawn naturally⁷⁴ became a point of controversy a few years ago regarding a listed stock of Chinook in the Columbia River basin, and NMFS requested that the Independent Scientific Advisory Board (ISAB) for the basin review the relevant biological evidence. A version of the review was published in *Fisheries*, the bulletin of the American Fisheries Society (ISAB 2002). According to the abstract:

... Substantial experimental evidence demonstrates that domestication selection can genetically alter hatchery populations in a few generations and that hatchery-origin adults returning from the ocean and spawning in the wild produce fewer progeny than adults of wild origin spawning in the wild. More limited evidence suggests that interbreeding between hatchery-origin adults and wild fish can reduce the fitness of wild populations. We conclude that decisions about whether or not to permit hatchery-origin adults should be based on the needs of wild⁷⁵ populations and the ability of the habitat to support additional reproduction, not based simply on the availability of hatchery-origin adults returning from the ocean. ...

Recovery Science Review Panel (RSRP). Interactions between hatchery and wild stocks were also considered by the Recovery Science Review Panel, convened by NMFS to advise on recovery planning for salmon and steelhead throughout the Northwest. The RSRP (2001a:7-8) concluded that “Theory, experimental evidence from other species, measurements, and short-term small-scale experiments comparing wild and hatchery salmon in rivers all suggest that the release of hatchery fish into wild populations may be having detrimental effects on the fitness of wild salmon stocks.” However, the RSRP also emphasized that the extent of the effects remains unclear (p. 8):

At least three questions remain unanswered:

- (1) what are the actual fitness effects of hatchery releases on wild stocks, and to what extent are these direct demographic or ecological effects rather than genetic or evolutionary effects?
- (2) What is the contribution of hatchery releases relative to other potential negative effects (harvesting, habitat degradation, and hydropower) on wild stock performance?
- (3) What is the potential for, and the time scale of, demographic and evolutionary recovery of wild stocks, once hatchery releases cease?

⁷⁴ For the Livingston Stone Hatchery or other conservation hatcheries that are designed to increase depleted runs, natural reproduction by fish raised in the hatchery is the desired result. These hatcheries generally have protocols intended to reduce genetic effects, although such effects cannot be avoided altogether (Waples 1999). For example, Livingston Stone Hatchery marks all the winter-run Chinook that it produces, but prefers spawn only unmarked fish, so that selection for hatchery conditions is limited to a single generation at a time. Such a procedure is not an option for hatchery culture of fall-run Chinook, however, because few fall-run are currently marked.

⁷⁵ The ISAB used the term “wild” to describe any progeny from natural spawning, so their discussion is directly applicable to the Central Valley.

The RSRP (2001) suggested experimental (aka adaptive) management of hatcheries to address the uncertainties that it identified, but recognized that implementing such experiments would be politically difficult. The RSRP (2002:6,7) restated its concerns and reiterated its recommendation:

The RSRP continues to be concerned with and intrigued by hatcheries given their mixed contribution to salmonid ESU recovery. For instance, hatcheries increase rates of straying; inappropriate hatchery management can lead to genetic mixing of discrete stocks; massive fish production can increase mortality of outmigrating smolts as can harvest of mixed stocks on their spawning run. On the other hand, conservation hatcheries may represent the last and best chance to retain seriously threatened ESUs; others can be used to rebuild natural runs; still others are required under treaty obligations.

...

The panel emphasizes the necessity of an experimental approach to determine the positive and negative ecological and genetic influences of hatchery fish on the natural spawning population. This approach is also lauded by the ISAB. The goal of such experiments is not to determine whether hatcheries are unconditionally good or bad, but to clarify conditions under which hatcheries will aid recovery of the wild population versus impeding recovery or contributing to decline.

The relation between hatchery and naturally produced fish was revisited in RSRP (2004:2), which concluded that “We believe that the loss of fitness in the wild is an inevitable consequence of adaptation to hatcheries and evidence suggests that this loss can occur even in the initial generations of breeding stock.” Hey et al. (2005:9), the report of a workshop convened at the request of NOAA Fisheries, probably in response to a recommendation in RSRP (2004), came to a similar conclusion: “Taken together, the evidence that hatchery fish have reduced fitness when released to the wild, relative to wild fish, is quite strong.”

Hatchery Scientific Review Group (HSRG). The Hatchery Scientific Review Group is a congressionally established panel charged with promoting scientifically-sound management of hatcheries in Washington to achieve two potentially conflicting objectives: “1) helping to recover and conserve naturally spawning populations, and 2) supporting sustainable fisheries” (HSRG 2003:2). The group comprises four scientists from agencies dealing with salmon and steelhead around Puget Sound, and five independent scientists, and has recently published a summary of its findings in Fisheries (Morbrand et al. 2005). The HSRG (2003) proposes that hatchery programs be either integrated or segregated, depending on the genetic objectives of the hatchery. The Chinook hatcheries in Southeast Alaska described by Heard et al. (1995) are examples of a segregated program. For integrated hatchery programs, such as those in the Central Valley (HSRG 2003:12):

A fundamental goal ... is to minimize genetic divergence between the hatchery broodstock and a naturally spawning population, in areas where fish are released and/or collected for broodstock. The long-term goal is to maintain genetic characteristics of a

local, natural population among hatchery-origin fish, by minimizing genetic changes resulting from artificial propagation and potential domestication. In an idealized integrated hatchery program, natural-origin and hatchery-origin fish are genetically equal components of a common gene pool. A hatchery supporting an integrated program can be viewed conceptually as an artificial extension of the natural environment, where the population as a whole (hatchery plus wild) is sustained at a much higher level of abundance than would occur without the hatchery.

Unfortunately, HSRG (2003a) does not provide any analysis showing the conditions necessary to realize the long-term goal of maintaining “the genetic characteristics of a local, natural population,” or that realizing the goal is feasible. Rather, it offers guidelines that 10-20% of the hatchery broodstock be naturally produced fish and that not more than a third of the naturally spawning fish be of hatchery origin, and analysis showing that as a result “the mean fitness ... of the population as whole [will] be closer to the optimum for the natural environment than to the optimum for the hatchery environment” (HSRG 2003b:5); this falls considerably short of maintaining the genetic characteristics of a locally adapted natural population.

Hatcheries and CALFED objectives

The contrasting positions of the ISAB (2002) and the HSRG (2003a) effectively frame a major question facing salmon management in the Central Valley: should hatchery operations be substantially modified to reduce the number of hatchery fish that spawn naturally? Meeting HSRG recommendations would not mean major disruption of existing hatchery programs, except perhaps for trucking fish around the Delta.⁷⁶ The ISAB puts higher priority on the conservation requirements of naturally producing populations, while the HSRG implicitly puts higher priority on maintaining hatchery production of fish for harvest. The ISAB cites risks to naturally producing populations that it cannot quantify, while the HSRG cites an objective that it has not shown to be feasible. The uncertainties involved raise policy questions regarding priorities and the burden of proof, a point discussed explicitly by the ISAB (2002:25):

For situations in which there is scientific uncertainty, a precautionary approach has been recommended as a desirable fishery management option (Dayton 1998; Musick 1999). This precautionary approach requires those proposing potentially harmful activities to demonstrate that they will not produce adverse impacts or to establish precautionary measures to detect problems and intervene if those problems are realized (Hilborn 1997). A precautionary approach also suggests that management actions be reversible if found to yield unintended results. Because it is virtually impossible to “undo” the genetic changes caused by allowing hatchery and wild salmon to interbreed, the ISAB advocates great care in permitting hatchery-origin salmon to spawn in the wild.

This guidance may seem compelling where naturally producing populations have not already been heavily affected by interbreeding with hatchery fish, but less compelling in the Central Valley, particularly for fall Chinook, where there is question regarding any remaining

⁷⁶ The HSRG (2003) recommendations for outplanting and net pen releases are somewhat vague, but at least discourage outplanting.

local adaptations. However, given the CALFED emphasis on restoring or rehabilitating environments and promoting diversity within and among salmon populations, and the evidence that local adaptation can develop in relatively few generations (Hendry et al. 2000; Unwin et al. 2000; 2003), a precautionary approach may well be appropriate. This would seem to be the view of the ISAB (2002:21): “We believe the real issue is not whether a given population is now “optimally fit” for some specific environment, but rather how some management action (e.g., allowing hatchery fish to interbreed in the wild) would affect the relative fitness of that population in the future.”

Taken as a whole, the available evidence strongly indicates an inherent conflict between existing hatchery programs and the objective of protecting or rehabilitating diverse, naturally adapted populations of salmon in the Central Valley. It does not appear that there is an easy resolution to this dilemma. The HSRG has struggled to discover one for the similar dilemma in Puget Sound and coastal Washington, and although it has made useful recommendations, the result seems to fall short. A basic policy decision establishing priorities for the competing objectives seems a precondition for a rational approach. Such a decision is inherently political, not scientific, although science can inform the political decision that must be made.

Options for changes in hatchery programs

Implicitly, the HSRG (2003a) has given commercial harvest at least equal priority to rehabilitating naturally adapted populations, at least in part because of treaty obligations. This perspective led to a set of recommendations, some of which are currently implemented in Central Valley hatcheries:

- Take a regional approach to managing hatchery programs;
- Operate hatcheries with the context of their ecosystems;
- Measure success in terms of contribution to harvest and conservation goals;
- Emphasize quality, not quantity, in fish releases;
- Incorporate flexibility into hatchery design and operation;
- Evaluate hatchery programs regularly to ensure accountability and success;
- Develop a system of wild steelhead management zones;
- Use in-basin rearing and locally-adapted broodstocks;
- Take eggs over the natural period of adult returns;
- Develop spawning protocols to maximize effective population size;
- Take into account both freshwater and marine carrying capacity in sizing hatchery programs.

The position of the ISAB, which puts priority on the naturally producing population, leads logically to different and more radical recommendations. These might include (as points on a continuum):

Abandon production hatcheries altogether:

A strong argument can be made that even with changes such as recommended by the HSRG (2003a), hatchery operations will remain fundamentally incompatible with the objective of protecting or rehabilitating diverse, naturally adapted populations of salmon in the Central

Valley. If that objective is taken seriously, then closing hatcheries on Central Valley rivers should be considered. Commercial and sport harvest would then be limited to what could be supported by natural production. It is unclear what this level of harvest would be, because it is unclear to what degree hatchery fish have replaced naturally produced fish, rather than augmented them. There will always be uncertainty on this point. If, as seems likely, naturally produced fish have suffered significant loss of fitness from interbreeding with hatchery fish, it would take decades before the productivity of natural stocks stabilizes, and by that time climate change will have altered the environment, presumably to the detriment of salmon. There are very large numbers of naturally produced juveniles in some Central Valley rivers, however, and absent interactions with hatchery fish, the productivity of naturally producing populations may be considerable.

Move fall-run hatcheries to the coast

This would follow the example of Chinook hatcheries in Southeast Alaska (Heard et al. 1995) and could satisfy the objective of supporting the ocean fishery without sacrificing the fitness of fall-run reproducing naturally in the Central Valley. Ecological interactions in the ocean would still occur, as would harvest effects. However, ecological interactions in early ocean life probably would be reduced if hatcheries were located say on Monterey Bay,⁷⁷ away from the Gulf of the Farallones or other areas used by naturally produced fish when they first enter the ocean.

Concentrate fall-run hatchery production in one river

Rather than moving fall-run production to the coast, it could be concentrated on one Central Valley river, with releases to that river to minimize straying. This would concentrate harm to the naturally-spawning population in that river. The lower American River might be a logical choice, since it is close to the Delta.

Substantially reduce hatchery production

This might be accomplished by reducing production in all hatcheries, or by experimentally closing selected hatcheries as suggested for the Klamath River by NRC (2003).

Recommendations

1. Thoroughly reconsider hatchery operations:

The actions listed above are major steps that should be undertaken only after careful review and consideration, so the main recommendation of this paper is that such a review be undertaken. Since the basic problems with hatcheries are generic, advantage can be taken of the considerable attention being given to these problems elsewhere. However, the available information does support several less drastic steps that could be taken quickly.

⁷⁷ A hatchery near Moss Landing could use slightly brackish groundwater, and release fish into a slough that drains into the harbor from the south.

2. Mark all hatchery fish:

All hatchery fish should be marked, which can be done economically with otolith thermal marking (Volk 1994). This will allow determination of the proportion of naturally-spawning fish that are of hatchery origin. The true extent of the problems resulting from past and current hatchery programs will be unknown without such data. It is remarkable that, more than twelve years after the CVPIA mandated doubling the number of naturally produced anadromous fish, the proportion of hatchery fish among returns remains unknown, despite the availability of a proven method for economically marking all hatchery fish.

3. Release fish only at hatcheries, or nearby:

High straying rates are incompatible with the objective of protecting or rehabilitating diverse, naturally adapted populations of salmon in the Central Valley. Either that objective or the practice of trucking fish around the Delta should be abandoned. Production should be decreased if that is necessary to reduce negative interactions with naturally produced fish in the rivers and the Delta.

4. Avoid overproduction:

There has been clear overproduction of fall-run Chinook in recent years, and all indications are that this will be true for 2005 as well. Overproduction results in harm to naturally spawning populations through ecological effects such as density-dependent mortality during spawning (Table 12-3), and probably in high rates of interbreeding, as well. Presumably, the overproduction has resulted in part from good ocean conditions and from low harvest rates, and hatchery production should be adjusted according to projections for these two factors.

5. Review and document practices in the Mokelumne River, and Merced River hatcheries, in documents comparable to USFWS (2001), Brown et al. (2004), or Brown (2006).

6. Look for evidence of domestication:

The hypothesis that fall-run have lost fitness in the natural environment from hatchery influences should be tested, which could be done experimentally for the egg and alevin life stages. The simplest such experiment would compare the size at maximum wet weight of hatchery fry reared in conventional hatchery conditions with that of fry reared in trays with groves in the bottom of an appropriate size to accommodate alevins. If the sizes are similar, this would indicate that selection has occurred against the normal “righting response” of alevins, described by Bams (1969). Other experiments along the same lines could compare the growth, behavior and survival of fall-run embryos and alevins with embryos and alevins from a wild stock such as Butte Creek spring-run, in simulated hyporheic conditions. Such experiments could not demonstrate that no loss of fitness has occurred, since such loss could occur in attributes not tested in the experiments, but findings of no apparent loss of fitness in hyporheic conditions could substantially alleviate concerns on this issue.

CHAPTER THIRTEEN

HARVEST

Among the king salmon taken ... by trolling in the salt water of Monterey Bay, Cal., are found 4-year-old male and female individuals which are mature, and others of the same size and age which show no activity of the gonads and would not mature until a later year. The same is true of five-year old fish, but the undeveloped individuals of this age are more largely males.
Gilbert (1913:14)

In the river the fish that escape the nets will go up the river to spawn. On the other hand a great many of the salmon taken in the ocean are immature. The immature fish taken early in their lives, of course, will never get an opportunity to go up the streams and spawn...
Clark (1928:11)

There can be no question that fishing causes evolution of phenotypic traits of fish; the existence of additive genetic variation has been demonstrated beyond reasonable doubt, and directional selection pressures on this variation caused by fishing are substantial. What is much less clear is how fast evolution is taking place. It is uncertain whether such evolution contributes significantly to the phenotypic change happening in many fish stocks, or whether it is operating on an altogether longer time scale.
Law (2000:666)

Despite mounting evidence of rapid life history evolution in wild fish population (citations), the unexpectedly slow recovery of populations from overexploitation (citations) and warnings from theorists (citations), current models and management plans for sustainable yield ignore the Darwinian consequences of selective harvest.
Conover and Munch (2002:94)

Our study provides new evidence that intense fishing may indeed lead to rapid evolution of key life-history traits in harvested populations. Olsen et al. (2004:935)

Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery..
Magnuson-Stevens Act, National Standard I.

The problem is not that we do not know enough, but that we do not allow what we know to constrain our behavior.
Young (2004:376)

Humans are the main predators on large sub-adult Chinook in the ocean, and there is good evidence that harvest has reduced the mean age at maturity of Central Valley Chinook, but apparently not size at age. At least part of this change probably results from contemporary evolution, as has occurred with other fishes such as cod (Olsen et al. 2004). This chapter briefly reviews harvest, harvest management, and the effects of harvest on the age distribution of adult

Chinook. Steelhead are taken in the ocean only as bycatch, and since high seas gillnetting ended in 1993 (Myers 1997) ocean harvest has been of little importance for Central Valley steelhead.

Early commercial harvest of salmon in the Central Valley used gill nets and sometimes seines to capture fish as they passed through the bays and up into the rivers on their spawning migrations. Such “terminal” fisheries have the advantage that immature fish are spared, runs can be fished selectively, and the catch provides a good estimate of adult returns that allows effective real-time management of harvest. However, an ocean troll fishery began in Monterey Bay in the 1890s and became the dominant method of harvest by 1917 (Clark 1928; 1929). Trolling is inherently a “mixed stock fishery,” since fish from different rivers and runs occur together in the ocean. When runs declined in the 1920s, CDFG took the position that one fishery or the other should be closed, and “As the river fishing has more to commend it than the sea trolling, we proposed that the trolling be stopped” Scofield (1929:13).⁷⁸ This recommendation was ignored, however; the troll fishery continues, and the gill-net fishery ended in 1957.

Harvest management

Ocean harvest of is managed by the Pacific Fishery Management Council, according to the Pacific Coast Salmon Plan (PFMC 1984, amended in PFMC 2003). Normally, management is intended to ensure that the adult returns of “Sacramento River fall Chinook” meet goals set by the PFMC in 1984, but in recent years fishing has been sharply restricted in order to protect listed Chinook in the Central Valley and in north coastal streams, and to satisfy tribal fishing rights on the Klamath River. Ocean harvest has declined substantially since a high in the late 1980s because there were few fish in the early 1990s, and fishing has since been restricted (Figure 13-1); fishing in recent years has been good when it was allowed (Figure 13-1B.)

Management of ocean fisheries is constrained by the Magnuson-Stevens Act as well as the ESA, as indicated by the quotation above, but the Magnuson-Stevens Act seems to allow considerable leeway. For example, the “optimum yield” that management should achieve is the maximum sustainable yield, “as reduced by any relevant economic, social, or ecological factor.” Nevertheless, harvest management raises a dilemma. On the one hand, harvest is a major reason that salmon are valued; on the other, as discussed below, there is good reason to think that the early CDFG concerns about the troll fishery were justified; in particular, Central Valley Chinook are now younger and therefore smaller than they used to be. Especially in the recreational fishery, Chinook are valued for their size.

⁷⁸ The legislature declined to close either fishery, and instead opened a season for salmon spearing, much to Scofield’s disgust. The language of Scofield (1929) suggests that early CDFG biologists felt more license to criticize the state government than now seems to be the case.

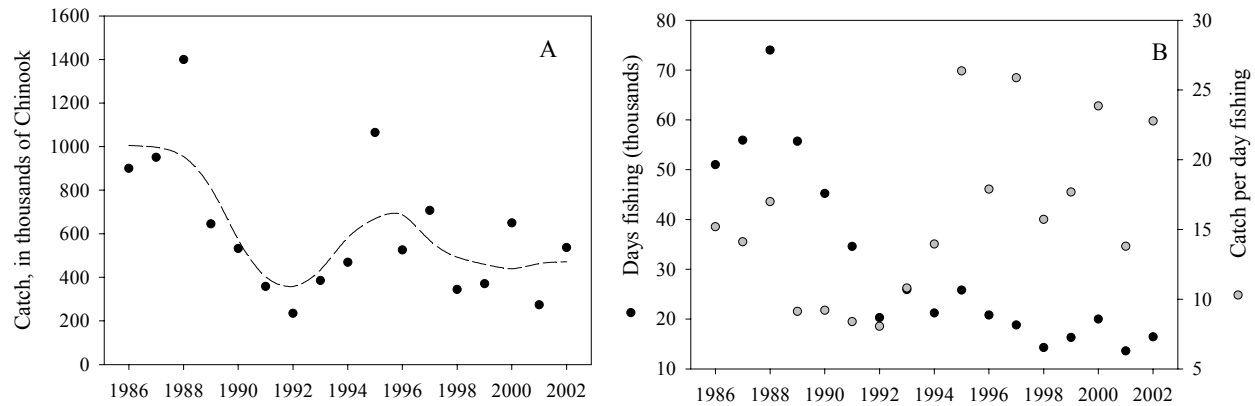
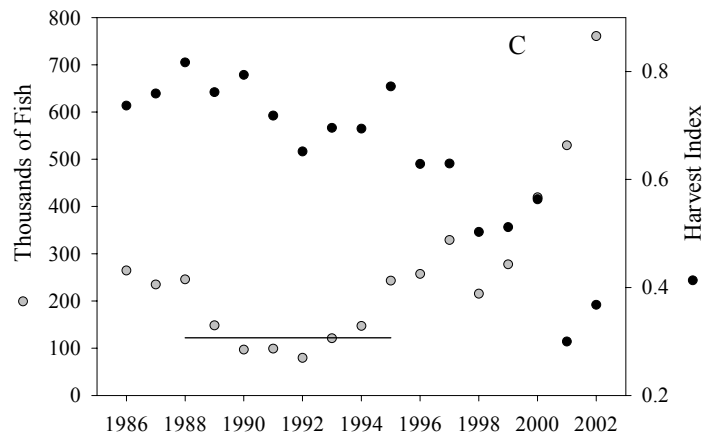


Figure 13-1. Ocean harvest of Chinook. A: Combined commercial and recreational landings of Chinook from Horse Mountain south, with trend line fit by locally weighted regression (lowess). (Horse Mt. is just north of Shelter Cove in Humboldt County.) Data from PFMC (2003). The data include some Klamath River and north coastal Chinook, but exclude Central Valley Chinook taken farther north. B: Number of commercial fishing days (black symbols) and catch per day (gray symbols) of from Horse Mountain (Humboldt County) south. Note the sharp drop in catch per day in 1989. Data from PFMC (2003). C: Index of ocean harvest (black symbols) and Central Valley adult returns (gray symbols); the index is calculated as the total ocean harvest (sport and commercial) divided by the sum of the total ocean harvest and adult returns for all runs (including jacks). Data from PFMC (2003); data for 2000 overlap. Solid horizontal line shows the lower escapement goal for “Sacramento River fall Chinook.”



Escapement goals

Goals for adult returns of fall-run Chinook for the Sacramento and San Joaquin rivers were established in 1978, based on estimates of average adult returns to the Sacramento River and major tributaries for prior decades, developed by CDFG biologists (Hallock 1977; Menchen 1978). However, the goals were amended in 1980 and 1984 to be a range from 122,000 to 180,000 in the Sacramento system only (PFMC 1984). The upper limit of the range is the sum of the DFG goals for the Sacramento and its major tributaries (Table 13-1). The lower limit was developed from the assumption that fish losses at the Red Bluff Diversion Dam (RBDD) would make it impossible to reach the upper Sacramento goal of 108,000 fish without so restricting harvest that “gross over-escapement” would result in the lower Sacramento tributaries (PFMC

1984:3-19). Therefore, the goal for the upper Sacramento was reduced from 108,000 to 50,000 until problems associated with the diversion dam were resolved.

Although it did not say so explicitly, PFMC (1984) implied that meeting escapement goals in the San Joaquin tributaries would also require undue restrictions on harvest of the healthy lower Sacramento tributary stocks, because of deteriorating environmental conditions on the tributaries. In any event, PFMC simply stated (p. 3-19) that “Ocean management for Sacramento River within the escapement range adopted will provide adequate escapement of San Joaquin stocks to achieve spawning requirements.” This assumption should be reconsidered, especially in light of efforts to restore San Joaquin River tributaries.

Although CDFG set separate goals for naturally produced and hatchery fish, with rather modest goals for hatchery fish, PFMC (1984:3-19) declined to follow that example on the grounds that “The separation of hatchery and natural fish ... is artificial.” This attitude probably is responsible for the continuing uncertainty about the percentage of hatchery fish among returning adults. Methods exist to mark all hatchery fish economically (Volk et al. 1994), and doing so should have high priority.

Table 13-1. CDFG distribution goals for Sacramento River fall-run, modified from PFMC (1984). Note that the total goal of 20,000 for hatchery fish is only 11% of the goal of 160,000 for naturally produced fish.

River	Environment	Escapement Goal
Upper Sacramento	Natural	99,000
	Hatchery	9,000
Feather River	Natural	27,000
	Hatchery	5,000
Yuba	Natural	10,000
American	Natural	24,000
	Hatchery	6,000

In recent years, concern about gross overescapement has been overshadowed by concerns about ESA-listed stocks, and restrictions on fishing have sharply reduced the ocean harvest. Arguably, this resulted in very large returns of fall-run in 2001 and 2002 in the Sacramento River and tributaries, resulting in high prespawning mortality (Ch. 12). However, hatchery production has not been modified to take account of the restrictions or the large escapements.

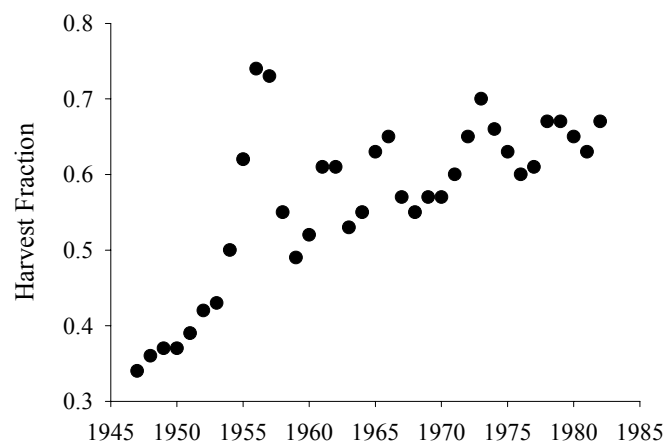
Estimates of harvest

Quantifying the harvest of Chinook is not straightforward, because Chinook mature at different ages. For example, for a given year, one could estimate the percentage of potential spawners that was harvested, or the percentage of fish available to be harvested that was harvested, or the percentage of fish of each age that was harvested. CDFG develops an index of ocean harvest by dividing the estimated ocean harvest by the sum of estimated harvest and

estimated adult returns. This would be an estimate of the actual harvest rate for the year only if all fish matured after being vulnerable to the fishery for one year (Hankin and Healey 1986), which is approximately the case for winter-run, of which few spawn as four year-olds, and if inland harvest were negligible. The harvest index underestimates the effect of harvest on late-maturing fish (Hankin and Healey 1986), and as applied in the Central Valley does not account for harvest in the inland recreational fishery, which is estimated only sporadically, but is substantial for fall-run. Based on sampling from 1990 to 1994 and 1998 to 2000, inland harvest for fall-run was estimated at about 25% of the spawning migration on average (PFMC 2003). Neglecting inland harvest (which would go in the denominator) inflates the ocean harvest index. In any event, the harvest index has dropped sharply from $\sim 0.7 - 0.8$ before 1996 to < 0.4 since 2001 (Figure 13-1c).

Reisenbichler (1986) estimated a combined harvest fraction for California coastal and Central Valley Chinook from data on unpublished CDFG data on landings and estimates of adult returns through 1985 (Figure 13-2). As he defined it, the harvest fraction is the ratio of the number of fish caught that would have spawned in a given year, and the number that would have spawned if there had been no fishing.⁷⁹ Early estimates of returns are questionable (Fry 1961), but the general trend is for increased harvest over this period.

Figure 13-2. Combined harvest fraction for California coastal and Central Valley Chinook, 1947-1982, estimated by Reisenbichler (1986).



Not all runs are equally susceptible to the ocean fishery, or to all parts of it. Winter-run, for example, are taken mainly in the recreational ocean fishery, and south from San Francisco, with estimated spawner reduction rates (the fraction of potential spawners taken by the fishery) of 0.26, 0.23, and 0.24 for 1998-2000 (CDFG 2004a). The rate is low because most winter-run do not reach legal size for harvest until their third year, and most of them leave the ocean in the spring of that year, before the commercial fishing season begins. Spring-run also avoid most of the fishing season in the year in which they mature, with spawner reduction rates estimated at

⁷⁹ To add to the confusion, the 23 February 1996 NMFS Biological Opinion for Ocean Harvest defined harvest fraction as catch/(catch + escapement), i.e., as the harvest index. The 1997 Addendum described catch/(catch + escapement) as an approximation of the harvest rate, the “fraction of available adults landed by a fishery.”

0.36 and 0.42 in 1998 and 1999 (CDFG 2004b). The rates for Central Valley fall-run presumably is higher but is not well known, although CDFG is currently developing estimates for several hatchery populations from coded-wire tag data (Allen Grover, CDFG, pers.comm. 2003). The analysis is not straightforward because mortality estimates are needed for fish that are hooked but not landed, and these depend upon size at age which varies from year to year. Generally, better data and models are available for harvest management of the Klamath River Chinook than of Central Valley Chinook (e.g., Goldwasser et al. 2001; Prager and Mohr 2001), and CDFG recognizes the need to develop comparable information and models for management of harvest of Central Valley stocks (Allen Grover, CDFG, pers.comm. 2003).

Natural mortality in the ocean is poorly known (Healey 1991). The Klamath Harvest Rate Model assumes annual survival rates of 0.5, 0.8 and 0.8 for fish in their second, third, and fourth year (Prager and Mohr 2001), which probably are equally applicable to Central Valley fish.

Effects of harvest

Demographic effects of harvest

Harvest affects salmon populations in both obvious and subtle ways. Most obviously, it reduces the number of fish that return to spawn and the potential number of their progeny, and mixed-stock fisheries supported by strong stocks may overharvest weaker ones (Ricker 1980; Hilborn 1985). Whether harvest tuned to hatchery-supported populations of Central Valley fall-run has over-harvested naturally producing populations in other streams is unknown, but seems likely. Such over-harvest could be masked by hatchery strays, and loss of fitness from mixing with hatchery-adapted fish (Ch. 13) could exacerbate the problem.

Ecological effects of harvest

Returning adult salmon carry marine-derived nutrients (MDNs) to riverine and riparian ecosystems (Stockner 2003). The presence of MDNs in vegetation along the Mokelumne River has been documented (Merz and Moyle 2006), and it seems intuitive that in streams with large runs MDNs could contribute substantially to riverine, riparian, and nearby terrestrial ecosystems.⁸⁰ Salmon also modify spawning gravels when the females dig redds, and where fish are abundant this also may have significant ecological effects (Montgomery et al. 1996). To the extent that harvest reduces the number of adults returning to spawn in the rivers, it must also reduce their ecological role (Wilson et al. 1998).

Genetic effects of harvest

The potential evolutionary effects of harvest on size and age at maturity has been a matter of concern for some time (e.g., Ricker 1980; 1981; Healey 1986; Hankin and Healey 1986; Thorpe 1993; Reisenbichler 1997; Law 2000; Ernande et al. 2004). The ocean troll fishery selects against fish that mature at greater age and so are vulnerable to harvest for more years (Ricker

⁸⁰ I snorkeled down Butte Creek with a CDFG crew during a thermally-induced die-off of spring-run in 2002, and viewing the more or less decayed fish through somewhat murky water it was impossible to avoid the thought that we were swimming through a dilute salmon broth.

1981; Hankin and Healey 1986), and age at maturity has moderate heritability⁸¹ (Hankin et al. 1993). A change in life-history traits in a few generations' response to harvest has been demonstrated experimentally with Atlantic silverside (*Menidia menidia*; Conover and Munch 2002), and has been observed with grayling (Haugen and Vøllestad 2001). Smaller escapements may also relax selection for traits such as large size that are advantageous at high population densities (Young 2004). As shown below, the age distribution of returning to Central Valley rivers has shifted toward younger fish, although it is uncertain how much of this change is genetic.

Several factors complicate estimating the genetic contribution to an observed change in age at maturity. The presumed mechanism for evolutionary change involves the biochemical thresholds for maturation at specific times of the year (Thorpe 1993), so that whether a fish's physiological condition in a given year exceeds the thresholds depends on environmental conditions. Uncertainty also arises because harvest continues to remove older fish, and because the age distribution may be affected by ecological feedbacks (e.g., the reduction of population density by harvest may allow salmon to grow faster and therefore mature younger than would otherwise have been the case). Finally, even if harvest does select for earlier maturity, there may be counter-selection for greater size, and so age, during spawning (Reisenbichler 1997).

The best early data on the size and age of Central Valley Chinook give the length and age of Chinook sampled from the Delta gill net fishery in 1919 and 1921, distinguishing ocean-type and stream-type fish (Clark 1928; Figure 13-3). This was not a random sample of returning adults, as 2-year old and small 3-year old fish are seriously underrepresented;⁸² it is nevertheless striking that five- year olds made up 35% of the catch of ocean-type fish (Table 13-2), especially because Chinook were already subject to an ocean troll fishery. Thirteen percent of Clark's sample were stream-type fish, which had an even older age distribution. In another sample from the gill net fishery taken about 30 years later, in 1947-51, half the fish were still 4 year-olds, but 3 year-olds had become the second most common group, and the 5 year-olds were reduced to 10% (Table 13-2). In the 1955 harvest, 3 year-olds were most common, followed closely by 4 year- olds, and 5 year-olds were reduced to 3% (Table 13-2). Contemporary data on the age distributions are available only for coded-wire tagged Central Valley fish, and unfortunately these are not often analyzed for length and age distributions, although as noted above that work is in progress. For fish returning to the Feather River in 2002, the modal age increased to 4, probably because of reduced harvest (Figure 13-1), but 5 year-olds were rare (Table 13-2).

⁸¹ Heritability (h^2) measures the degree to which genes affecting a trait make relatives more alike, compared to unrelated individuals. From returns from breeding experiments on Elk River, Oregon, Hankin et al. (1993) estimated the heritability h^2 of age of maturity at between 0.49 and 0.57 for males, and between 0.39 and 0.41 for females, depending on adjustments made to the data. Estimates of heritability depend on the particular context (Law 2000), and so may be smaller for wild fish subject to greater environmentally induced variation.

⁸² Rutter (1904:130) reported that "(A)t Battle Creek fishery in 1900 the males were nearly all grilse, though there were almost as many of the adult males as there were females. The great preponderance of the grilse over the adult males and females is due to their being too small to be taken by the nets of lawful mesh." Thus, populations had been subjected to a size-selective fishery for some time.

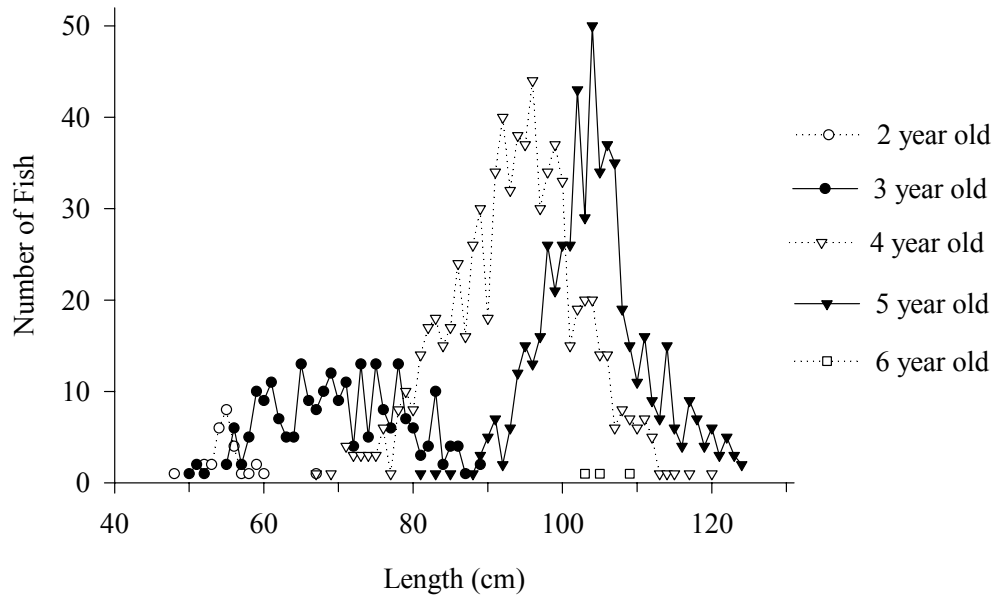


Figure 13-3. Length distributions at age of ocean-type salmon captured in the Delta gill net fishery in 1919 and 1921. Data from Clark (1928); the length measurement was unspecified, but presumably was fork length, which was customary at the time (see Snyder 1922).

Table 13-2. Age distributions of Central Valley Chinook from harvest or adult returns. 1919 and 1921 data for ocean-type Chinook captured by the Delta gill-net fishery, reported by Clark (1928); 1947-51 data for fall-run Chinook from the Delta gill-net fishery, data from Cope and Slater (1957) as given in Reisenbichler (1986); 1955 ocean harvest data from Kutkuhn (1963); 1973-77 data for fall-run returning to the Tehama Colusa Fish Facility, data from Vogel and Clemens (1982) as given in Reisenbichler (1986); 1976-81 data from coded-wire tag returns in the American and Feather rivers (Dettman et al. 1987); 2002 data for fall-run returning to the Feather River or Feather River Hatchery, provided by B. Cavello. Fisher (1994) gave the age distribution of maturing female fall-run as 3% 2 year-old, 77% 3 year-old, and 11% 4+ year-old, but did not give the source for these estimates.

Years	N	% 2 yr-old	% 3 yr-old	% 4 yr old	% 5 yr-old	% 6 yr-old
Samples from harvest						
1919-21	1,574	1.8	15.4	47.7	34.9	0.2
1947-51	1,200	4	35	50	10	1
1955 Ocean Harvest		0.8	52.7	43.5	3.1	0
Samples from adult returns						
1973-77	4,500	24	57	19	<1	
1976-81	3,125	15.1	66.3	18.5	0.1	
2002	1,722	22	36	41	0.002	

Other early data are consistent with a decrease in age at maturity. N. B. Scofield released fry into Paper Mill Creek, a tributary of Olema Creek in Marin County, in 1897. None of these fish returned until 1900, and most returned in 1901, as five year olds (i.e., age 0.4; Rutter 1904). Gilbert (1913:14) reported that “The commercially valuable portion of the king salmon run consists mainly of 4 and 5 year fish, with less frequent 6-year individuals,” although this did not refer specifically to the Central Valley. He noted that “A single large male, weighing 67 pounds, observed by Mr. N. B. Scofield in the Sacramento River, was in its seventh year.” Gilbert also stated emphatically that he had not found a mature female Chinook less than four years old, and seemed doubtful of a marking experiment at an Oregon hatchery in which mature three year-olds were reported. Rich (1920) summarized and endorsed Gilbert’s findings on age at maturity, although he added in a footnote that “More recently [ocean type] females have been seen maturing in their third year.” Rich (1921) noted that 15 of 51 (29%) three year-old females taken in the troll fishery in Monterey Bay in 1918 contained maturing eggs, and Clark (1928) reported that 47% and 26% of 3 year-old ocean-type Chinook in his 1919 and 1921 samples were females.

Depletion of older fish in the harvest at Monterey Bay was evident in the 1920s. Of 1,326 ocean-type Chinook taken by the troll fishery in Monterey in 1919 (Figure 13-4), 48% were four year-olds, with 38% three year-olds and 8% five year-olds. A change in the size distribution was noted in the 1920s, so another large sample of was collected in 1929 (Snyder 1931). Of 2,477 ocean-type Chinook, only 13% were four year-olds, 64% were three year-olds, and 1% were five year-olds.

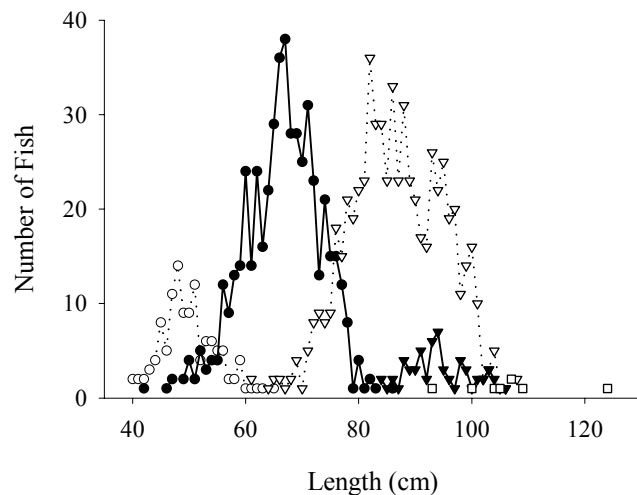
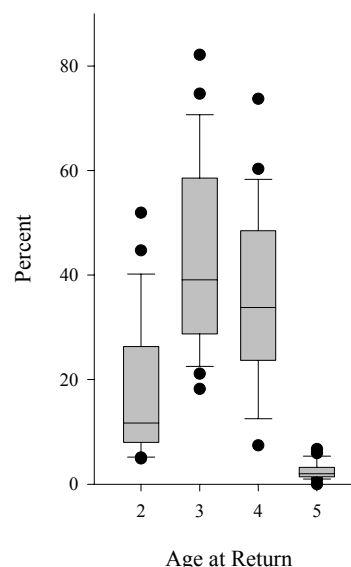


Figure 13-4. Age distribution of 1,326 ocean-type fish taken in the troll fishery at Monterey Bay in 1919. Data from Table 63 in Snyder (1931), symbols as in Figure 13-3.

Much better recent data are available for the Klamath River Chinook than for Central Valley Chinook, and these show that age distributions are highly variable from year to year (Figure 13-5). Accordingly, the data for isolated years in Table 13-2 should be taken cautiously. Nevertheless, the decline in the fraction of 5 year-olds in the Central Valley samples seems too great to attribute to year to year variation, and the documented change in the age distribution of

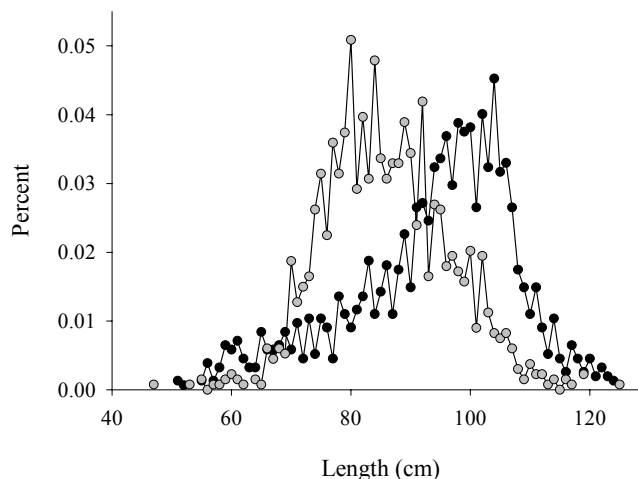
the Monterey Bay harvest was consistent with smaller samples and casual observations in other years.

Figure 13-5. Estimated percentages of Klamath River fall-run of different ages in adult returns to the river, 1979-1999. For each age, the box plot shows the distribution of the contribution of that age to adult returns. The shaded box extends from the 25th to the 75th percentiles, the line crossing the box shows the median, the lines extending from the box show the 10th and 90th percentiles, and filled circles show outliers. Data from Goldwasser et al. (2001), Table 3.



Data on size are much more common than data on age, and much of the discussion of the effects of harvest in the literature concerns size (e.g., Ricker 1981; Healey 1986; Bigler et al. 1996; see Hard 2004 for a modeling study). Age at maturity is not independent of size, as the faster growing fish in any age group are more likely to mature (Healey 1986; Goldwasser et al. 2001; Scheurell 2005); however, size may be more responsive than age at maturity to variation in environmental conditions. In any event, comparison of the overall length distributions from Clark's gill net sample and the 2002 Feather River sample for 3 year-old or older fish suggests that fish are now smaller than they were (Figure 13-6).⁸³

Figure 13-6. Comparison of the overall size distributions for fish from gill net samples in 1919 and 1921 (black symbols), and for coded-wire tagged fish 3 years-old or older recovered in the Feather River in 1922 (gray symbols; data from Clark 1928 and Brad Cavallo of DWR).



⁸³ Williams (2001) presented a similar comparison of Clark's data with recent length data from the American River, making the conservative assumption that Clark reported total length. However, measuring fork-length was the convention at the time (Snyder 1922), so it seems much more likely that Clark reported fork lengths.

Comparison of size at age gives a different picture, however (Figure 13-7): 3 year-olds in the Feather River in 2002 were larger than in the 1919 and 1921 gillnet sample. Assuming again that Clark reported fork lengths, the size distributions of 4 year-olds for the two samples are very similar (Figure 13-6), and the downward shift in the overall size distribution results from the shift in the age distribution, not size at age. Although data from one year are far from conclusive, they do support the report by Bigler et al. (1996) that California Chinook are an exception to the general trend toward smaller size at age among Pacific salmon.

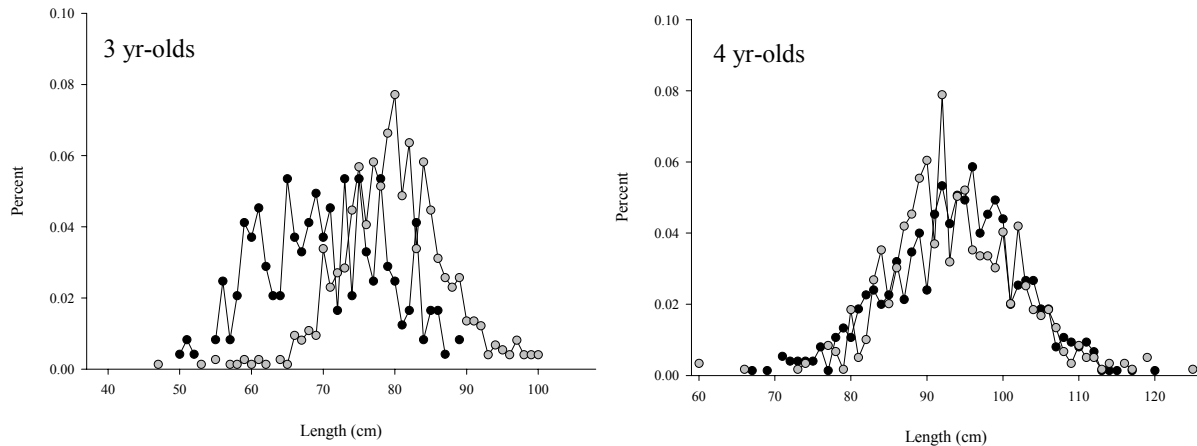


Figure 13-7. The size distribution of 3 and 4 year-old salmon from the Delta gill-net fishery in 1919-21 (black symbols) and from the Feather River (gray symbols). The Feather River data are fork length; the 1919-21 length measurement is uncertain, but probably is fork length. The graphs do not show two outliers from the Feather River, a 26.5 cm 3 year-old and a 134 cm 4 year-old.

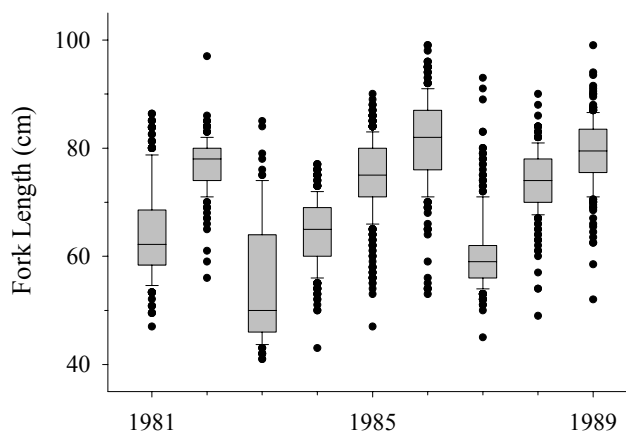
Although the apparent lack of change in size at age four is encouraging, the apparent decrease in age at maturity, demonstrated most clearly by the loss of the 5 year-old component of the population, may be hard to reverse, even if the ocean harvest rate remains low (Law 2000). Removal of larger fish may change the selection that occurs among the surviving fish. The selective advantages of size, say in competition for good spawning sites or for mates, presumably are relative to the size of the other fish in the population. Other potential advantages, such as the ability to move larger stones or to place eggs deeper in the gravel where they are less likely to be scoured, depend on absolute rather than relative size, but unless the benefit for greater age from these advantages to absolute size outweighs the expected harvest and natural mortality during another year in the ocean, selection for greater age will not occur.

Whether the percentage of grilse has increased significantly in recent years is unclear from the available data, since small fish are strongly underrepresented in the early harvest data. Rutter (1904:130) noted that “At the Battle Creek fishery in 1900 the males were nearly all grilse,” but attributed this to the size selective gill-net fishery. Nevertheless, it seems clear that grilse were common; Gilbert (1913) noted that “Conspicuous in every spawning run of king salmon are the numerous undersized males, known locally as grilse, jack salmon, or sachems.” Gilbert

described 2 year-old ocean-type Chinook from the Columbia River as short as 34 cm. He also described grilse as being either 2 or 3 years old, with the three year-olds grilse mostly 48-66 cm (19-26 inches) in length, and over a third of the 3 year-olds in Clark's sample of ocean-type fish were 66 cm or less. In the 2002 Feather River sample, small 3 year-olds are much less frequent.

The percentage of 2 year-old females among Central Valley Chinook does seem unusual, however, since Healey (1991:377) remarked that "two-year old females are virtually unknown...." Fisher (1994) reported that 3% of female fall-run mature at age 2, and 4% of females in the 2002 Feather River sample were 2 year-old. They appear to be even more common in the Tuolumne River, where a majority of females is less than 60 mm fork length in some years (Figure 13-8).

Figure 13-8. Length distributions of female salmon in the Tuolumne River, 1981-1989. Although ages were not determined, many of the smaller fish must be two year-olds. Data from EA 1991f.



Inland harvest

Inland harvest of Chinook is a significant and variable cause of mortality that is not well monitored. For 1991-1994, the estimated inland harvest in the Sacramento River system varied between about 10,000 to 30,000 (Wixom et al. 1995), but in 1998 it was estimated to be about 45,500 (CDFG 2000). The creel censuses required to estimate the inland harvest are expensive, and consistent funding has not been available. Returns of coded-wire tags from fish reared at Livingston Stone Hatchery recently showed unexpected but significant harvest of winter-run in the first two weeks of January, 2003, the end of the inland season for Chinook (NOAA Fisheries WCSBRT 2003); the season has been shortened in consequence. Poaching is hard to quantify, but there are some indications that it can be significant (Williams 1995; SRFG 2004). Spring-run are particularly vulnerable while the adults hold in pools through the summer.

Recommendations

1. Harvest management should be harmonized with the CALFED restoration objectives.

Apart from ESA considerations, PFMC manages the ocean fishery with an objective of 122,000 – 180,000 adult returns of “Sacramento River fall Chinook.” The “escapement” objective is based on old information of uncertain validity, lumps hatchery and naturally produced fish, lumps populations in major rivers that should be managed separately, and ignores Chinook in the San Joaquin River tributaries. The objective should be revised and put on a scientifically supportable basis. In particular, separate goals for adult returns should be established for major populations of naturally-produced fall-run, including populations in San Joaquin River tributaries, and spawner goals should be set in terms of expected numbers of progeny, rather than numbers of returning adults. This would give more weight to older and larger fish, since fecundity and expected survival of offspring increase with the size and age of the female parent.

The NRC (1996:321) recommendation regarding hatchery operations seems to apply as well to harvest management, which also “... should be changed in accordance with the goal of rehabilitation and the ecological and genetic ideas that inform that goal.” The idea that diversity within and among populations is necessary to preserve the long-term productivity of a basin is not new (Rich 1939) but is now receiving renewed attention (e.g., Riddell 1993; NRC 1996; Bottom et al. 2001), and underlies much of the rationale for CALFED restoration efforts regarding salmon. Harvest management should take this into account.

As a first step, efforts to modernize management of the harvest of Central Valley stocks along the lines of Klamath River management should be encouraged. This would include estimating the percentage of fish of each age that are harvested each year. Inland harvest should also be accounted for.

2. Harvest management should take account of the evolutionary and ecological effects of harvest, as well as demographic effects.

Terminal fisheries that target only returning adults may be size selective, depending upon the gear used, but fish that mature at whatever age are exposed to them only once. A shift to a terminal fishery, for example using gill nets in the bays, may be necessary to avoid continued selection against late-maturing fish, and continued narrowing of age at maturity. In the past, CDFG favored a terminal fishery over the troll fishery for such reasons (Clark 1929), as did Stanford professor Willis Rich (1925). Commercial harvesting in a terminal fishery would also allow a much tighter focus on unlisted runs, although the early-season recreational fishery has the greatest impact on winter-run (CDFG 2004a). At the least, a shift to a terminal fishery deserves serious study.

CHAPTER FOURTEEN

MODELING

Models should be as simple as possible, but not more so.

Albert Einstein, quoted in May (2004)

I would not give a fig for the simplicity on this side of complexity, but I would give my life for the simplicity on the other side of complexity.

Attributed to Oliver Wendell Homes

Because they offer insights into the population dynamics of salmon, it is inevitable that models such as ours will be used to assist in management or in the determination of policy questions. This will happen despite the protestations of statisticians who at times are forced to explain that the available data and scientific understanding of the issues under discussion might not be an adequate basis for answering such questions. A far more satisfactory situation is when the model is used in conjunction with a programme of research into the mechanisms underlying the empirical relations in the field.

Terry Speed (1993:291)

In this section I review selected aspects of modeling that seem particularly relevant for modeling salmon in the Central Valley, and offer some recommendations. I then briefly discuss instream flow models. It is far from a comprehensive review of biological modeling,⁸⁴ which is a huge topic, and many important topics are not treated at all. Other models are discussed in other chapters. Generally, I take the view that the most important uses of modeling in salmon management are to provide clear summaries of the empirical relations among variables, as exemplified by the various models in Elliott (1994), and to promote clear thinking. As stated by Walters (1986:45): “The value of modeling in fields like biology has not been to make precise predictions, but rather to provide clear caricatures of nature against which to test and expand experiences.”

Proponents of adaptive management sometimes observe that all management is experimental, whether it is intended to be or not, and that much can be gained by accepting this and treating management explicitly as experimental (Hennessey 1994). Similarly, all salmon management is based on some kind of model, even if only a qualitative conceptual model, and clarity in thinking can be gained by making this modeling explicit. For whatever reason, however, modeling and data analysis have not become parts of the culture of salmon management in the Central Valley in that same way that they have in fisheries management and science elsewhere. This is unfortunate, but it offers those concerned with managing Central Valley salmon the opportunity to learn from the experience of others.

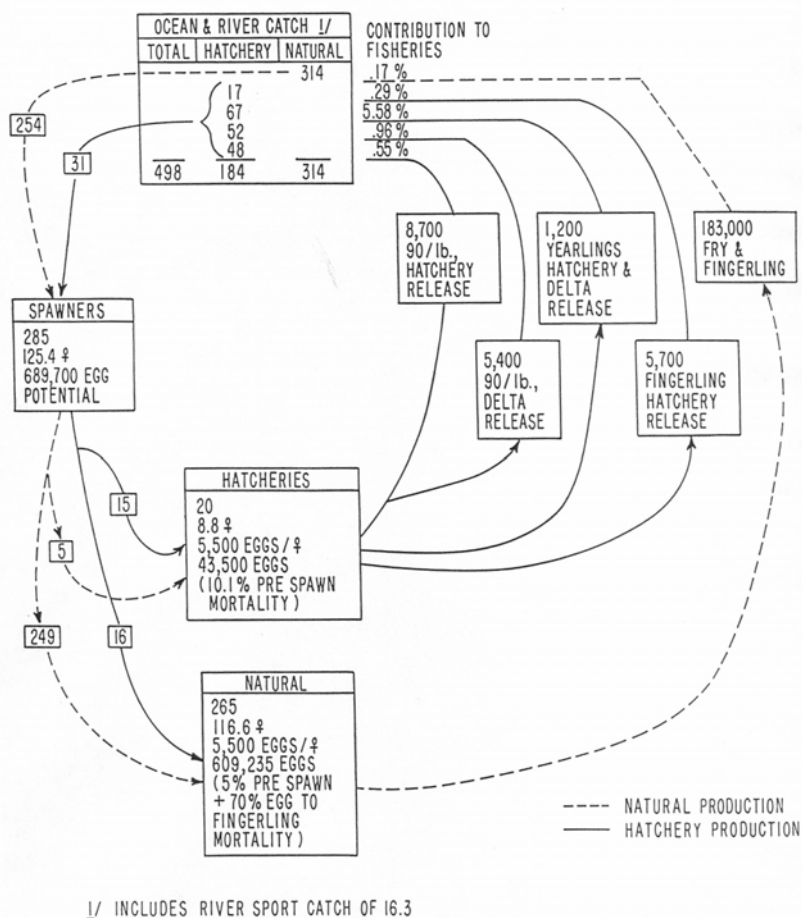
⁸⁴ For a good brief discussion of biological modeling generally, see Ch. 2 in Hilborn and Mangel (1997).

The term “modeling” describes a range of activities that can be categorized in various ways. For example, Hilborn and Mangel (1997), with an emphasis on ecological modeling, distinguish deterministic and stochastic models; statistical and scientific models; static and dynamic models; quantitative and qualitative models; and models used for understanding, prediction, and decision. Other sources use similar but not identical categories. The main dichotomy used in this chapter distinguishes simulation models, for which parameter values are taken from the literature or other sources or simply made up, and estimation models, for which parameter values are estimated directly by fitting the model to the data available on the subject at hand. On close inspection his distinction turns out to be somewhat blurred (Schnute 2003), but it emphasizes an important point regarding the use of models for prediction, as explained below.

Simulation models

A simple but often effective use of models is to explore the consistency of existing information or current assumptions. For example, Hallock (undated) developed a simple conceptual model for Sacramento River Chinook using averaged data or estimates for 1971-1975 (Figure 14-1). The model implied that hatchery Chinook were much more vulnerable to the ocean fishery than naturally produced Chinook. Hallock thought this unlikely, and instead inferred that CDFG was seriously underestimating the proportion of naturally spawning fish that came from hatcheries. Similarly, a quantified conceptual model of a proposed restoration project might be used to assess the plausible size of the effect of the project on the target population.

Figure 14-1. Quantified conceptual model of the hatchery and naturally reproducing components of Sacramento River Chinook. Numbers are thousands of fish. Copied from Hallock (undated).



Adding rules for stepping through time and coding the conceptual model in some computer language turns the conceptual model into a simulation model. The model could also be elaborated, so that, for example, the runs in different Sacramento River tributaries might be treated separately, the juvenile life stage might be divided into phases that are treated separately, juvenile survival might be made to vary as a function of flow, pumping in the Delta, etc. The result is a complex population model. If the population is further divided into individuals or classes of individuals with different attributes that are tracked through time, the result is an individual-based model (IBM).

Several complex population or individual-based models have been or are being developed for Central Valley Chinook: CPOP (Kimmerer et al. 1989); EACH (EA 1991f); SALMOD (Bartholow et al. 1993); ORCM (Jager et al. 1997) SRCSIBM (Kimmerer and Jones & Stokes 1999; and WRIMF (Cramer et al. 2003). The schematic for juvenile Chinook in freshwater from SRCSIBM illustrates the detail in which some of these models describe fish behavior (Figure 14-2). It should be clear from other chapters in the review that many of these details are not well understood, as is recognized by the developers of the models. For example, Kimmerer and Jones & Stokes (1999:17) note that “Rules for the occupancy of rearing habitat are not well known.”

Not all simulation models focus on the salmon life cycle. For example, the simple metapopulation model developed by Levins (1969) has been very influential in ecology (Hanski and Gilpin 1997) and has also been applied to salmon. The basic conceptual model assumes a number of equally suitable patches of habitat, some of which are occupied by populations that have the same probability of extinction, with the unoccupied patches all having the same probability of colonization. The model is characterized by the rate m at which vacant patches are colonized and the rate e at which populations in patches go extinct. If the rate of colonization is proportional to both the number of occupied patches and the number of empty patches, and the rate of extinction is proportional to the number of occupied patches, then the rate of change in the proportion p of occupied patches of habitat is $dp/dt = mp(1-p) - ep$.

Even though this seems obvious once it is stated, Hanski and Gilpin (1991) argue that the model was an important advance in ecological thinking because it focused attention on the dynamics of a group of populations rather than individual populations, and because it clarified the importance for those dynamics of the proportion of suitable habitats that are occupied. It also emphasized that suitable patches may be temporarily unoccupied, so that unoccupied habitats are not necessarily unsuitable. Again, the conceptual model can be turned into a simulation model by developing rules for stepping through time. The Levins model is clearly general and unrealistic, but extensions of the model that include spatial structure and variation in habitat size and colonization and extinction rates have been developed (Hanski 1997). These need not be complex. Cooper and Mangel (1999) used a simple metapopulation model with source and sink populations to show that abundance data could mislead managers if the relations between source and sink populations were not recognized and taken into account. Young (1999) used another simple metapopulation model to consider the circumstances in which it makes sense to increase the colonization rate of threatened salmon by rearing eggs taken from fish occupying one stream

and planting them in nearby and similar unoccupied streams. It is worth noting that while Levins's model may seem abstract and academic, it was developed in an article on insect pest control.

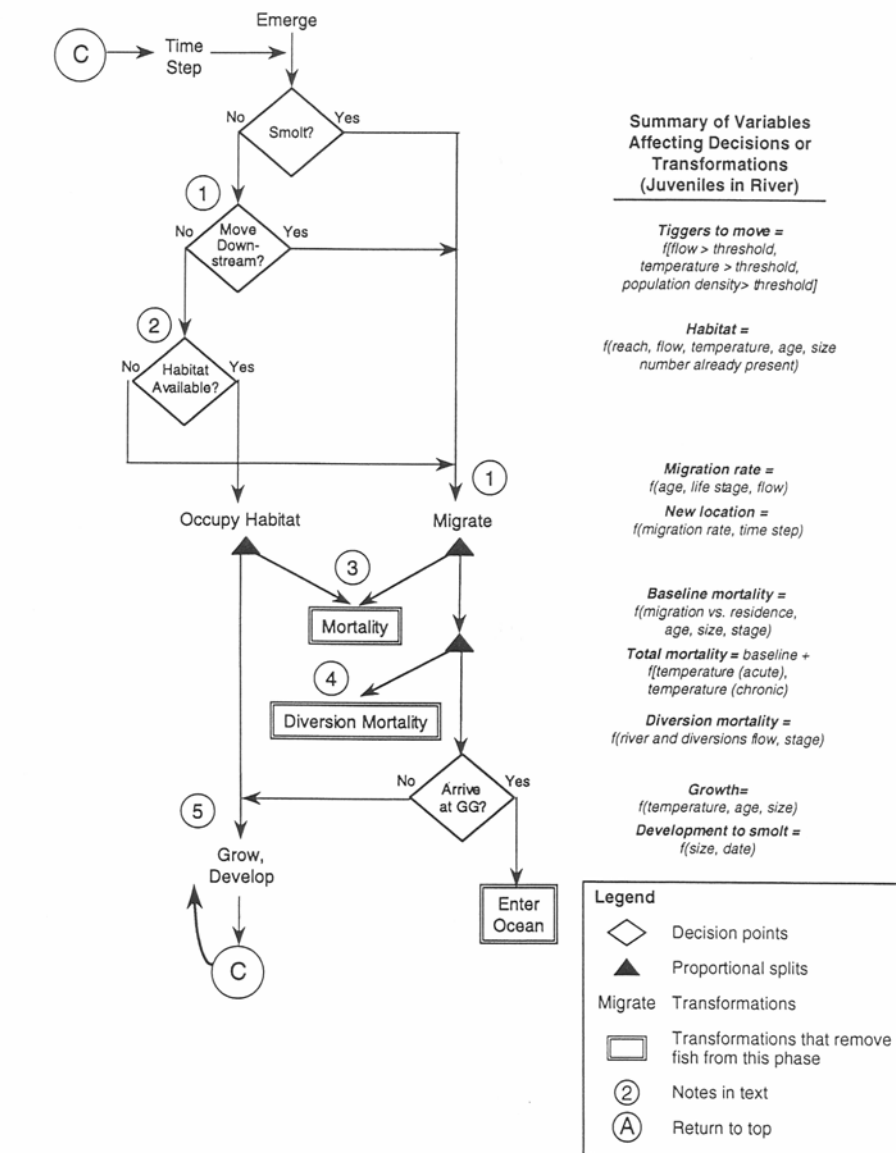


Figure 6
Flow Diagram for Juveniles in River

Figure 14-2. Schematic for the simulation of the juvenile life stage in SRCSIBM, copied from Kimmerer and Jones & Stokes (1999).

Essentially, simulations are thought experiments (Starfield 1997; Schnute 2003), in which parameter estimates may be more or less well founded in data. For example, Hard (2004) used data from a breeding experiment with ocean-type hatchery Chinook to estimate parameters for simulations of the effects of size-selective harvest over five generations on size at age (and found generally a modest response). For other purposes, such as simulating monitoring programs, it may be enough that the parameter values be plausible. In either case, the basic objective is to clarify thinking, or to make qualitative predictions, rather than quantitative predictions.

Estimation models

With estimation models, as the term is used here, parameter values are obtained by fitting the model to data. Estimation models are essentially statistical, although the terms of the models may be intended to have biological meaning. Stock-recruitment models are usually used as estimation models, and provide a useful example of this kind of model. They have also been important in salmon management, although not in the Central Valley, and deserve attention on that account as well.

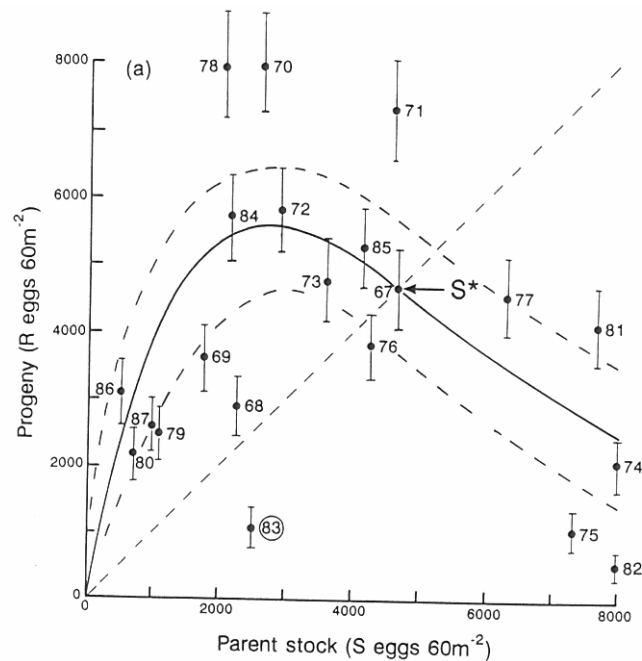
Stock-recruitment modeling relates the abundance of progeny to the abundance of parents, and involves the concepts of density-dependent and density-independent mortality, discussed in Ch. 1. A number of models, briefly reviewed by Elliott (1994), has been proposed to describe this relationship. Applied to fisheries, these are called stock-recruitment relationships, where the parental generation is the stock (S) and the filial generation is the recruits (R). These can be written in a general form as $R = aSf(S)$, where the parameter a describes the rate of increase in the absence of density-dependent mortality (say when the population is small), and the function $f(S)$, which varies from model to model, relates survival to population density (Elliott 1994).

The stock-recruitment model applied most commonly to salmon probably is the Ricker model, which can be written as $R = aSe^{-bS}$. This specifies a dome-shaped relationship in which R peaks when $S = 1/b$, and is equal to S when $S = \ln(a)/b$ (Figure 14-3). Thus, when the model is fit to data, the value of b depends on the size of the population, and values of b for different populations must be adjusted to a common equilibrium size to allow comparisons. Hankin and Healey (1986:1751) suggested that “pessimistic, reasonable(?) and optimistic” values of a are 5, 10, and 15. Corresponding values for b for early maturing populations such as those in the Central Valley are 0.00183, 0.00292, and 0.00357, given a few other assumptions and adjusted to give equilibrium populations of 1,000. For Central Valley rivers, Reisenbichler (1986) found values of a generally in the neighborhood of 10, and Rein (1993) estimated a for San Joaquin River Chinook at 5.01 or 6.91, depending upon the assumptions made about errors in escapement estimates.

Stock-recruitment models traditionally are applied to salmon as part of harvest management, to estimate the number of fish that should be allowed to escape the fishery and reproduce, but they can be applied to non-exploited populations as well. Elliott (1985; 1994) found that the Ricker model gave the best fit of six models to his data on the population of anadromous brown trout in a section of a small stream in England (Figure 14-3). In this case, Elliott’s interest was in

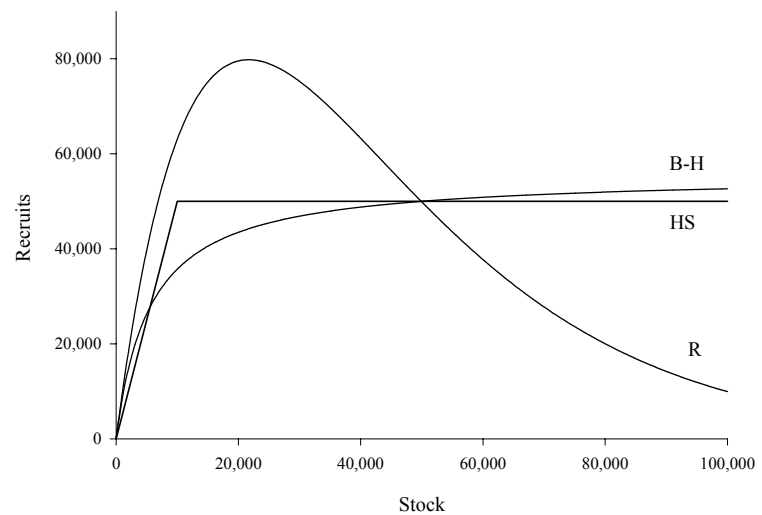
understanding the nature of the density-dependent processes in the study population. Although there are now better methods for comparing models than the ones used by Elliott (1985), his basic approach was sound. Hilborn and Mangel (1997) emphasize the importance of evaluating models against other models, rather than against some abstract criterion of “validation” or “verification.” There are strong arguments that these terms cannot usefully be applied to models (Oreskes et al. 1994; Oreskes and Belitz 2001), as suggested by the aphorism “All models are wrong, but some are useful” (Box 1979).

Figure 14-3. The Ricker model fit to data on brown trout in a section of a small stream in England. Dashed lines around the fit show 95% confidence intervals. Error bars around points show two standard errors; numbers give brood years. Numbers of fish in both generations are given in eggs per area, based on measured lengths of spawners and a length fecundity relationship. The outlier year 1983 was a drought year, and was not used in fitting the model. S* is the equilibrium population. Reproduced from Elliott (1994), courtesy of Oxford University Press.



The Beverton-Holt model, $R = aS/(1 + bS)$, which gives an asymptotic spawner-recruit relationship (Figure 14-4), is also frequently applied to salmon. The Ricker and Beverton-Holt models predict very different consequences of large numbers of spawners, but both assume that, below an equilibrium level, survival increases as population decreases, even when populations are very low. This does not matter much for management of healthy stocks, but can lead to dubiously optimistic expectations when the models are applied to very small populations (Myers et al. 1999). This prompted development of another model, the “hockey stick model,” in which survival is constant up to some level of escapement, above which recruitment is constant (Barrowman and Myers 2000). Since a piecewise linear model seems implausible and introduces numerical problems in fitting the model to data, Barrowman and Myers (2000) also describe generalizations of the hockey-stick, in which the sharp bend is rounded off. In another approach, Munch et al. (2005) apply a Bayesian nonparametric approach to estimating the stock-recruitment relationship. For purposes of this discussion, however, the main point is that the parameter values for these models usually are estimated by fitting the model to data directly from the population of interest.

Figure 14-4. Comparison of Ricker and Beverton-Holt models, with $a = 10$ and b set to give an equilibrium population of 50,000, and a hockey stick model.

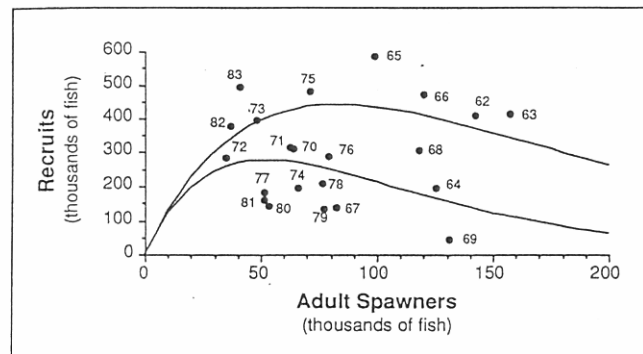


Although the parameters of the Ricker model are reasonably well defined with Elliott's data, there is a great deal of scatter among the data for individual years. Thus, the model does not generate good predictions of the population in a particular future year, based on previous escapement. This has implications for proper use of the model. It would be one thing to set a target escapement based on the model fit to these data (assuming that this were a harvested population), but it would be quite another thing to set a target harvest for a particular year by subtracting the desired future escapement from the predicted recruitment, even though predicting recruitment from escapement is what the model seems to do. Put differently, the model estimates the average escapement for a given stock, and it is necessary to know something about the variability in recruitment to understand how the model should or should not be used. Proper use of models requires an understanding of what is being modeled, as well as of the strengths and weaknesses of the model itself.

In Elliott's data, there is a great deal of scatter in the number of recruits over the range of stock values that is predicted to produce many recruits ($> \sim 4,500$). Hence, data on recruits in this range are not very informative, and Elliott was able to get a good fit because he had data on recruits from both small and large values of stock. The need for such data for estimating parameters well creates a dilemma for fishery managers. If the fishery is successfully managed to allow approximately the desired escapement, as determined from an initial estimate of the parameters of the model, then subsequent recruitment will be of little use in refining the parameter estimates. The idea of adaptive management was developed in the context of estimating the value for fisheries management of data on recruits from high or low values of stock (Walters and Hilborn 1976); that is, whether the fishery should forego some harvest in current years in order that future management could be based on better parameter estimates. This point generalizes to other kinds of adaptive (experimental) management: unless the experiment covers a broad range of conditions, the response will be obscured by normal variation.

Stock-recruitment models have uses beyond managing harvest. For example, Reisenbichler (1986) compared the parameters of the Ricker model fit to escapement data from California streams for different periods of time and found statistically significant changes, suggesting that management of the streams was making them less productive. Kope and Botsford (1990) found a similar change (Figure 14-5), probably resulting from the installation of the Red Bluff Diversion Dam. Speed (1993) developed a state-space model incorporating stock-recruitment models to analyze abundance data for Chinook in the San Joaquin River, and found (p. 290) “that there is a discernable effect of spring flow (or related variables) on the number of recruits over and above that resulting from the size of the parent stock.” Stock-recruitment models can also be used to generate plausible synthetic population data in simulations to evaluate monitoring programs (e.g., Korman and Higgins 1997; Williams 1999). In such cases the particular values used for the parameters of the stock-recruitment model may have little importance, although they should be plausible.

Figure 14-5. The Ricker Model fit to data for Sacramento River fall-run Chinook before and after construction of the Red Bluff Diversion Dam. Data points are labeled by year; upper curve was fit to 1962-66, lower curve to 1967-83. Copied from Kope and Botsford (1990)

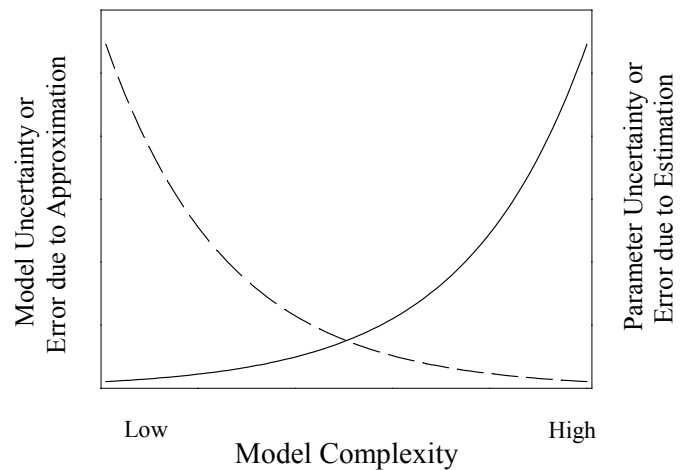


Stock-recruitment models are simple population models, although their implementation can be very sophisticated (e.g., Punt and Hilborn 1997; Schnute and Kronlund 2002), and more complex population models are in a sense stock-recruitment models that take environmental or other factors that influence mortality explicitly into account. Individual-based models (e.g., Jager et al. 1997; Kimmerer and Jones & Stokes 1999) take this elaboration a step farther by tracking variation among individuals, or groups of individuals, within the population. Such models are attractive because they seem more realistic, but many mathematically sophisticated modelers think that this advantage is illusory (e.g., May 2004), at least for models used for making predictions. One fundamental problem is the need to estimate parameters.

The Deriso model, $R = aS(1-bcS)I/c$ (Deriso 1980), illustrates the point that more complex models may not perform as well as simpler models. Although the extra parameter allows the Deriso model to mimic the Ricker and Beverton-Holt models and to fit intermediate cases, it performs poorly in practice (Schnute 1985). When parameters must be estimated from data that are measured with error, as is almost always the case with fishery data, a simpler model may give better predictions. Ludwig and Walters (1985) demonstrated this by generating synthetic population data with an age-structured population model based on the Deriso model.

Measurement errors were simulated by adding modest random terms to the data. Different models were then fit to the simulated data to estimate optimal yield. A model based on the Ricker Model that did not account for age did as well or better than the model used to generate the data. There is a fundamental trade-off between model uncertainty, or error due to approximation, and parameter uncertainty, or error due to estimation (Figure 14-6); accordingly, “Effective management models cannot be realistic” (Ludwig 1994:516).

Figure 14-6. Conceptual model of the trade-off between model uncertainty (dashed line) and parameter or estimation uncertainty (solid line). In a good predictive model these two types of uncertainty are balanced. Redrawn from Ludwig (1994).



A common and seemingly persuasive response to arguments such as those just made is to show that the model in question can accurately reproduce historical data such as escapement, given historical data on flows, etc., as input. It seems, intuitively, that in such a case the model cannot be far wrong, but this is a case where intuition fails. Often, a model with many adjustable parameters can give good fits to data with more than one set of parameter values, a problem known as equifinality. Since all the sets of parameter values cannot be “right,” getting a good fit does not “validate” the parameter values.

An alternative defense of the use of more complex models is the plea that although the actual predictions are not reliable, the relative performance of simulated management actions can still be compared (e.g., Kimmerer et al. 2001). This argument depends on the assumptions that the aspects of the actions that matter to salmon are accurately reflected in the model, and that the rest of the system is more or less linear. These are both brave assumptions.

In evaluating models used for prediction, then, the number of parameters must be taken into account. Several statistical criteria can be used to do this. One criterion is the adjusted residual squared error, which is the residual sum of squares divided by $n-2p$, where n is the sample size and p is the number of parameters (Efron and Tibshirani 1993). Another is the Akaike information criterion (AIC), advocated by Burnham and Anderson (1998); it is the negative log likelihood of the data given the model (a measure of how well the model fits the data, where more negative is better) plus twice the number of parameters in the model. Burnham and Anderson (1998) give a good discussion of model selection, and use of the AIC has become common in the ecological literature. However, some good statisticians think that the AIC tends

to select models with too many parameters (T. Speed, personal communication 2002), so it may be prudent to apply several criteria and proceed with caution if different methods rank models differently. Similarly, Burnham and Anderson (1998) suggest that if the ranking of two models with the AIC is close then the best course may be to use both, and this also seems good advice for cases where different criteria give different rankings. Moreover, any of these statistical criteria may select models that are biologically implausible, so models should be evaluated on that basis as well (Burnham and Anderson 1998), and even if a model is plausible and fits the existing data well, the biological idea expressed by the model may still prove wrong. For example, if flow and temperature are highly correlated, a model based on flow may give good predictions of an effect that is really a consequence of temperature.

Using models to evaluate restoration strategies

Managers often want to use models to evaluate restoration strategies, in the sense of predicting whether a given set of restoration actions will allow a population to meet some abundance criterion. For such purposes, more statistical approaches are needed. The analyses of smolt survival by Newman and Rice (2002) and Newman (2003) described in Ch. 10 and Appendix B are examples. In another example, Lindley and Mohr (2003) used an elaboration of the Ricker model in a Bayesian framework to model the effects of striped bass predation on winter Chinook. This allowed them to assess whether resumption of stocking striped bass would significantly increase the risk that winter-run will go extinct. This approach uses the simplest models that describe the biology relevant to the problem at hand. In this case, the interest was on the effects of striped bass, so the model included a term for the effects of striped bass predation on the growth rate of the winter-run population, a term for the effect of density-dependent mortality on the population growth rate, a term for the mean population growth rate in the absence of bass predation and density-dependent mortality, a term for the possible change in the population growth rate resulting from conservation actions after 1989, and a “process error” with a mean of zero and a variance estimated, along with the parameters in the other terms, from the data. The data in this case are estimates of winter-run escapements and of the abundance of adult striped bass. Thus, the model includes five parameters to be estimated from data, and a few such as the proportion of winter-run that mature at age three and age four that were taken from the literature. Five is not a small number of parameters to estimate from data, but the model is much simpler than models such as SCSIFM and the others described above.

Models such as Lindley and Mohr’s have several important advantages over other types of models. They meet management needs for a basis upon which to make decisions, in this case whether to allow stocking of striped bass to resume, and they also provide assessments of the range that the parameters might plausibly take. With Bayesian models, these assessments come in the form of the posterior distributions (e.g., Figure 14-7). In this case, for example, the posterior distribution for α , the per-bass predation rate, has a median that translates into about a 9% chance that a juvenile winter-run will be eaten by a bass (Lindley and Mohr 2003). The distribution shows that small values of α are most likely, but large values are plausible. Generally, the posterior distributions summarize the information in the data, given the model, in a form that is useful for management.

Besides the estimate of bass predation, this model also provides an assessment of the post-1989 conservation measures. The median estimate and 0.9 confidence interval for the relevant parameter indicate that, based on this model and the data, more likely than not the post-1989 conservation measures did some good. Although this study was not published until 2002, the actual work was done years before when data were available only through 1996, before the recent increase in winter-run escapements (Figure 2-7). Even using the pre-1997 data, however, allowing for a change in the mean population growth rate resulted in an assessment that winter-run are less likely to go extinct, compared to the results of Botsford and Brittnacher (1998), who assumed a constant mean population growth rate.

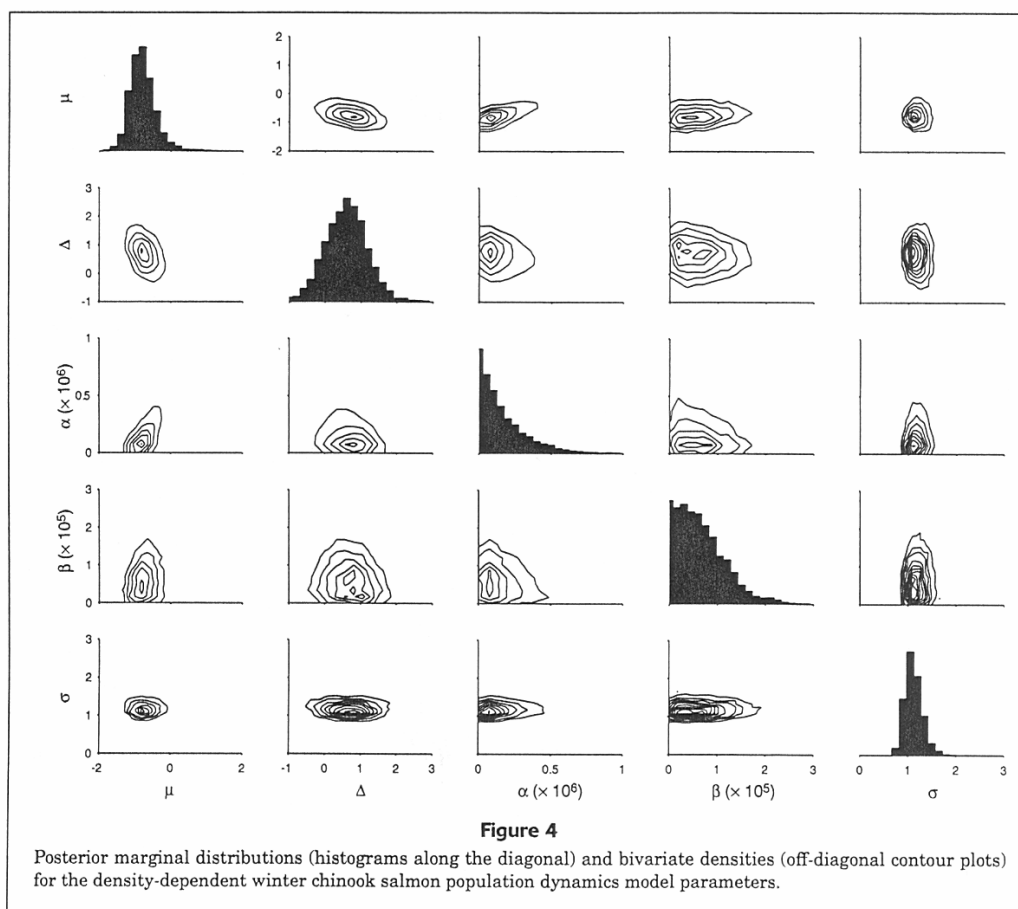


Figure 14-7. Posterior distributions (main diagonal) and bivariate densities for the parameters of the models used to assess the effects of stocking striped bass on the population of winter-run Chinook: μ (growth rate), Δ (growth rate change), α (predation rate), β (density dependence), and σ (process error). These show, for example, that the bass predation rate is probably small but large values are not inconsistent with the data. Note that values of α and β are very small and are multiplied here to make the axes legible. Copied from Lindley and Mohr (2002).

One potential problem with this model is that it does not account explicitly for changes in ocean conditions, which could inflate the apparent success of post-1989 conservation measures and lead to an overly optimistic assessment of the condition of winter-run, since conservation

measures can be made permanent but changes in ocean conditions cannot. This could be dealt with by comparing the results of this model with the result of a model that included a parameter for ocean conditions. However, if the interest is in the post-1989 conservation measures rather than the effects of stocking striped bass, then probably the model should be revised by leaving out the striped bass parameter.

The main disadvantage of models such as Lindley and Mohr's (2003) is that most biologists and managers, including the author of this review, have a limited grasp of the statistics and mathematics involved. This is even more true of "hidden process models," described by Newman et al. with an application to winter-run (In press). Although models such as SRCSIBM are complex (e.g., Figure 14-2), the individual steps are easy enough for people with limited quantitative background to understand, and this allows for a level of comfort that does not extend to modeling that in a sense has to be accepted on faith. However, the basic ideas of this kind of analysis arguably are more intuitive than those of conventional frequentist statistics, so the problem is largely one of language and familiarity. This problem should ease over time, as people become more accustomed to hearing about prior and posterior distributions, conditional probability densities, etc. It will also help if managers provide appropriate training opportunities for their staffs, and if more people with strong training in these methods become involved in Central Valley salmon studies. Recruiting such people should be a priority for agencies concerned with salmon management in the Central Valley.

When too few data are available to fit an estimation model, simulation models are the only available option for exploring the plausible outcomes of some management action. The question again arises, how complex should the model be? Two basically different approaches are advocated in the literature. Some modelers, for example Starfield (1997), advocate the use of simple simulation models tailored to the particular problem at hand. Others, for example Jager et al. (1997) and Kimmerer and Jones & Stokes (1999), propose the use of highly complex simulation IBMs that seem too expensive to develop except as general purpose models, intended to address a whole range of questions. The CALFED Environmental Water Account (EWA) Review Panel has recently recommended development of such a model for Central Valley Chinook (2002 EWA Review Panel 2002).

This recommendation can be questioned, for several reasons. One is that many aspects of Chinook life history remain poorly understood. It is possible to define rules that generate what seems like reasonable approximations to observed behavior, but this does not show that the model has "got it right." On the one hand, important aspects of the behavior may not be well observed, and on the other hand, other sets of rules may produce equally reasonable behavior. Even where the rules or relationships are relatively well known, there can still be the need to select values for parameters, as discussed above and elaborated below.

Another objection to complex simulation models is based on experience with human nature. Schnute (2003:409) remarked that "Everyone recognizes that simulation provides a thought experiment, not an accurate representation of nature." Unfortunately, experience shows that

many people do not recognize this, and even people who do recognize it intellectually may forget it in the often difficult process of making decisions. There is less danger that a simple model will be confused with “an accurate representation of nature.”

A third and related objection is that the level of detail in the models varies among life stages, depending upon the amount of information available. Less is known about the ocean phase of the salmon life cycle, for example, so of necessity this is modeled in less detail. To the extent that the model is intended to serve as a summary of available understanding, this is unobjectionable. However, if the model is intended to assess restoration or mitigation measures, then the model is only as strong as its weakest link, and the scientific purpose of detailed simulation in some aspects of the model while other aspects are generalized is unclear. May (2004:793) noted that “It makes no sense to convey a beguiling sense of ‘reality’ with irrelevant detail, when other equally important factors can only be guessed at.” The Recovery Science Review Panel, convened by NOAA Fisheries to provide guidance for salmon recovery efforts coast-wide, was sharply critical of the Ecosystem Diagnosis and Treatment (EDT) model, which is now widely used in Washington and Oregon, largely on that basis: “The inclusion of so much detail may create an unjustified sense of accuracy, but actually introduces sources of inaccuracy, uncertainty, and error propagation” RSRP (2000:6).

A final objection is based on the view that models should be used as aids to thought. When models become complex they become “black boxes” that are not well suited for this purpose, and tend to become substitutes for thought instead. This is particularly true when models appear to provide answers to important management questions. Instream flow models, discussed below, are a good example of this problem.

A simulation model that explores the consequences of density-dependent mortality and density-dependent migration on the potential utility of classes of restoration actions for ocean-type Chinook salmon in Puget Sound (Greene and Beechie 2004) seems to occupy a reasonable middle ground of complexity. This is a modified Leslie Matrix model that uses survival estimates at various life-stages to step the simulated population through multiple life cycles. The stages are: redds, streams, tidal deltas, nearshore habitats, and the ocean. It uses Beverton-Holt density-dependence, and allows for three different juvenile life history patterns: parr migrants, that rear in the stream, delta users, that rear largely in the tidally influenced area near the river mouth, and fry migrants, that migrate directly to nearshore areas in Puget Sound. Altogether, the model has 40 parameters for which values were taken from other sources. The model seems sufficiently generalized that to minimize the risk that it will be mistaken for an “accurate representation of nature,” but sufficiently detailed to characterize the main elements of the Chinook life cycle and their use of habitats.

In using their model, Greene and Beechie simulated a base case, in which density-dependent mortality occurs only at spawning, and ran the model until the simulated population stabilized, for four model watersheds with different areas of spawning, stream, delta, and nearshore habitat, and two real watersheds with contrasting distributions of habitat area. They also simulated cases

with density-dependent mortality and density dependent migration, again running the model until the population stabilized. Finally, they adjusted various parameters by 5% for each case to explore how the equilibrium population responded to the adjustment in the various cases.

The Greene and Beechie (2004) model seems most useful not for indicating what kinds of restoration actions would have the most effect on a particular population of Chinook, but rather for showing what one needs to believe about the density-dependent processes affecting the population in order to believe that a certain kind of action would have the most effect. That is (p. 598), “understanding how restoration actions may effect salmon populations depends upon knowledge of density-dependent mechanisms.” Unfortunately, little is known about density-dependent mechanisms or processes affecting Central Valley Chinook. The model also suggests, at least as parameterized for Puget Sound Chinook, that nearshore habitats in the sound are particularly important. We know relatively little about comparable habitats for Central Valley Chinook.

Other uses of models

Models have other uses than making predictions, and complex models may serve such purposes well. Models may also help structure discussions or negotiations among different parties involved in natural resources management (Volkman and McConnaha 1993), and relatively simple simulation models play a central role in adaptive management process described by Walters (1986). Complex models may also be useful in this context. Despite the RSRP’s harsh assessment of the EDT, it is nevertheless being used for recovery planning in Washington and Oregon (PSTRT 2002; W/LCTRT 2003), apparently because it proved useful in the political processes that are involved in recovery planning and in other restoration activities (J. Anderson, UW, personal communication 2004). The spatially-explicit description of the system in the model allowed people from different areas to contribute their knowledge to the modeling process, and various parties could set up model runs that reflected their views of the main problems and favored remedies. When these produced implausible results, the parties were persuaded to become more open-minded to alternative views of the problems. These are real virtues, but effective management needs to be sound scientifically as well as politically.

The process of developing complex simulation models can be useful as a way of organizing existing knowledge and identifying gaps in understanding, even if the model predictions are unreliable. In this use, however, the main benefit may go to the people who develop the model, and there is a danger of confusing the ability to specify rules that give plausible results with real understanding.

A more fruitful use of complex simulation models is to treat them as experimental systems, distinct from the “real world,” in which the consequences of various sets of assumptions can be examined (Peck 2004). For example, complex simulation models can be used to assess other modeling approaches. Railsback et al. (2003) used a complex individual-based model (IBM) of trout to show that, given reasonable assumptions about trout behavior, the depth and velocity at foraging sites selected by simulated fish in a simulated stream should change with discharge.

This finding challenges a basic assumption of the Physical Habitat Simulation System (PHABSIM), which is discussed below.

Complex simulations that are focused on specific questions may also be useful. For example, Haefner and Bowen (2002) have developed an IBM for the behavior of fish near fish screens, which is intended to be used in designing a new facility. Physical models may also be useful for this purpose (e.g., Swanson et al. 2004), and the two types of modeling could be used in conjunction.

More on parameters

With estimation models, as defined above, parameters are estimated by fitting the models to data, as described for example by Hilborn and Mangel (1997). With simulation models, parameter values are obtained independently. This can raise problems. The RSRP was particularly critical of using professional judgment for setting many parameter values in the EDT model. Alternatively, parameter values may be taken from the literature, although the values may be adjusted later to give a better fit to data (e.g., Jager et al. 1997). Obtaining parameter values from the literature has its own set of dangers, as detailed by Trudel et al (2004) in terms of parameters for bioenergetic models. They compared the predictions of four published models with observations and found that (p. 337):

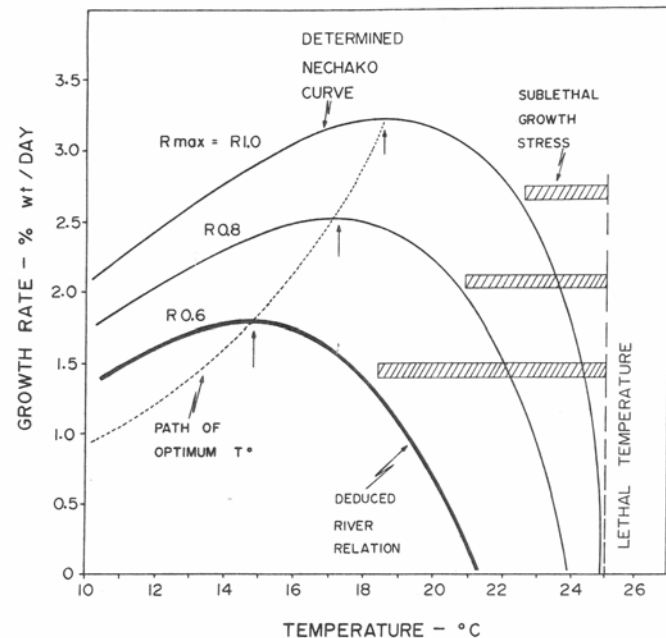
(1) oxygen consumption rates for sockeye salmon and steelhead were not always accurately predicted by models that were derived specifically for these species, (2) metabolic rates of Pacific salmon and steelhead were not accurately predicted by models developed from closely related species, and (3) allometric equations of metabolic rates were not stable when measured over small ranges of sizes, and were inaccurate when extrapolated to smaller or larger fish.

The situation can be even worse for parameters that cannot be determined in laboratory experiments, as illustrated here by the example of the ration parameter, which appears in various salmon models. The ration parameter is the ratio of the food consumed by juvenile salmon in the circumstances modeled to the food that would be consumed were food readily available. The ration parameter matters because it strongly affects estimates of the relation between water temperature and growth (Figure 14-8), as demonstrated by extensive experiments with juvenile sockeye (Brett et al. 1969).

The Oak Ridge Chinook model (Jager et al. 1997; Jager and Rose 2003) has a parameter for the maximum ration at feeding stations, set at 0.6. Jager et al. (1997) do not cite an authority for the estimate, but the value 0.6 probably comes from Brett et al. (1982), a litigation-driven study of Chinook in the Nechako River, British Columbia, an interior tributary to the Fraser River where diversions for hydropower decreased flow and increased water temperature. Brett et al. (1982) was published as a Canadian Technical Report of Fisheries and Aquatic Sciences, that is, as grey literature, not subject to formal peer review. Moreover, Brett et al.'s objective was to estimate the effect of the increase in temperature on the growth of Nechako River Chinook, for

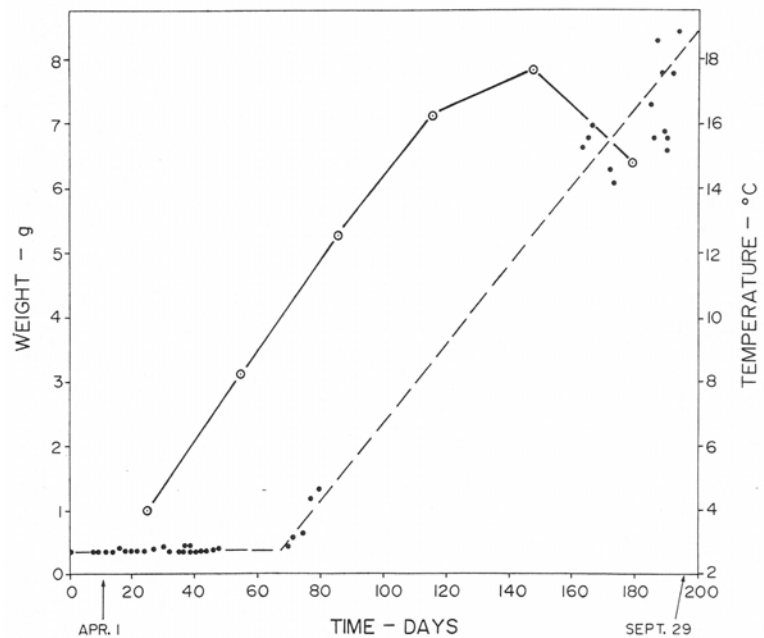
which they needed the estimate of ration level (Figure 14-8). In other words, estimating ration level was not the primary purpose of the study, but rather a step in the main process at hand, and the estimate of ration level actually came from application of a growth-ration model that is described only in theses (Stauffer 1973; McLean 1979) to an estimate of growth developed from 5 and 14 samples of 10 to 50 fish collected in early June and September in the Nechako River, and mean monthly temperature data (Figure 14-9).

Figure 14-8. Growth rate v. temperature curves for Nechako River Chinook. The top curve is derived from laboratory experiments. The lower curves are estimated based on data for juvenile sockeye and data on the size of juvenile Chinook in the Nechako River (see Fig. 5). Copied from Brett et al. 1982.



These data are sparse at best, and estimating growth rate from sequential samples entails strong assumptions, for example that neither mortality nor the capture efficiency of the gear used is size-selective. Brett was a prestigious salmon biologist, which probably accounts for the ready acceptance and wide application of the 0.6 value, but it is a weak reed to lean upon. Even if the estimate of ration level were accurate for the Nechako River in 1981, it is a bold step to apply it elsewhere, particularly since not that many data would be required to develop a comparable estimate for the stream in question, and the fit of the model to the data could be assessed. In that case, however, the citation would be to unpublished theses, rather than to an established expert in the field.

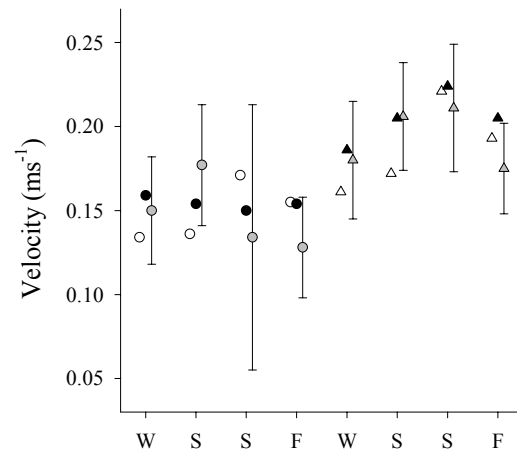
Figure 14-9. Data used by Brett et al. (1982) to develop the estimate that juvenile Chinook in the Nechako River in 1981 experienced a ration level of 0.6. The dashed line is the estimated growth rate. Fish were collected by seining and by trapping, but no specifics were given. Copied from Brett et al. (1982).



Although it is easy to imagine improving on the estimates developed by Brett et al. (1982), there are practical limits to what can be done with wild living resources. It may be useful to contrast the use of complex models in fisheries management with, say, detailed models of the growth and development of crop plants that are used in conjunction with field and laboratory studies. Unlike wild Chinook and steelhead, crop plants have been selected for uniformity in life-history patterns, at least within varieties, and their environments are more or less controlled. More importantly, the growth and development of crop plants can be observed in detail, so intermediate predictions of the model can be tested, and parameter values can be obtained from replicated field or growth chamber experiments. Wild fish are more variable and enormously more difficult to observe, let alone experiment upon, and effective management models for them therefore must take statistical considerations regarding the estimation of parameters into account. These considerations limit the optimal complexity of the model.

A final example may illustrate the benefits of simplicity in modeling for making predictions. Hill and Grossman (1993) used a bioenergetics model to develop good predictions of the water velocity at positions selected by rainbow trout and rosyside dace of different sizes in different seasons. However, they got better predictions from a simpler model based only on prey capture success rate (Figure 14-10), which is a decreasing function of water velocity (as velocity increases beyond some threshold, the fish miss drifting prey more often). In this case, the results of the bioenergetic model clarify why the simpler model works better. The energetic cost of holding position at realistic water velocities increases only slowly with velocity, and is small compared to the energy gained from successful foraging. Thus, the energy balance is determined mainly by the rate at which prey are captured. The more complex and mechanistic bioenergetics simulation may be satisfying intellectually, but serves less well for predictions.

Figure 14-10. Predicted and observed water velocity of positions selected by 52-7 mm rainbow trout (circles) and by 71-125 mm rainbow trout (triangles), for winter, spring, summer and fall. Observed mean values have error bars showing 95% confidence intervals; open symbols show predictions of the bioenergetic model, filled symbols of the capture-rate based model. Data from Hill and Grossman 1993.



Instream flow models

In the complex population models discussed above, a salient weak link is the need to relate the habitat value of streams to the rate of flow. How to do this is an unsolved problem (Castleberry et al. 1996). The model most commonly used is the Physical Habitat Simulation System (PHABSIM). This model, developed by an interagency group in the late 1970s, combines hydraulic and simple biological models to estimate a parameter called “weighted usable area” (WUA) as a function of flow (Bovee et al. 1998). Other “numerical habitat models” that combine hydraulic and simple biological models have also been proposed (Guay et al. 2000), as have others with more complex biological models (Van Winkle et al. 1996; EPRI 2000), but PHABSIM is still the standard method. At least two of the salmon population models used in the Central Valley (SALMOD and ORCM) are built on PHABSIM, and SRCSIBM uses WUA as an input, at least as an option.

WUA is intended to be a metric of the habitat value of a reach of stream. In most applications of PHABSIM, patches of habitat are characterized in terms of three “microhabitat” variables: depth, water velocity, and substrate size, at different rates of flow, for the species and life stage in question. Within each patch or “cell,” substrate size is estimated from field data, and either one or two-dimensional hydraulic models are used to estimate mean depth and water velocity. At each discharge, the habitat value of each patch is evaluated according to “suitability curves” ranging from zero to one for each variable, and the product of these values and the area of the patch produces an estimate of WUA. These are summed over the patches, producing a curve of WUA over discharge for the reach. PHABSIM is normally used as a spatially-explicit model, because the estimates of WUA are made patch by patch.

Since the 1980s, PHABSIM has been applied to many Central Valley streams to estimate the relation between flow and habitat for Chinook or steelhead. In some cases, however, flow recommendations were based on considerations such as water temperature rather than WUA (e.g., Aceituno 1993). Recent or ongoing applications include the studies of spawning habitat in

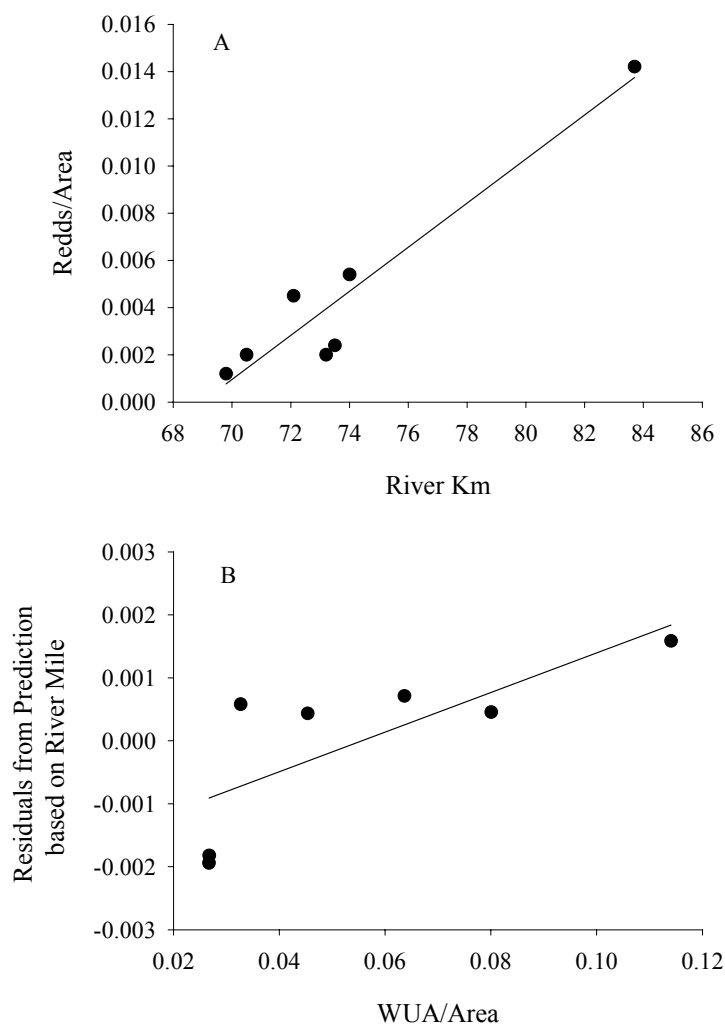
the Merced and American rivers (Gallagher and Gard 1998), the Feather River (Thomas R. Payne & Assoc. 2002), and on Butte Creek and the Sacramento River by USFWS..

Although PHABSIM is widely used, it has long been sharply criticized on biological, hydraulic, and statistical grounds (Marthur et al. 1985; Shirvell 1986; 1994; Scott and Shirvell 1987). These criticisms have recently been extended (e.g., Castleberry et al. 1996; Williams 1996; Bult et al. 1999; Kondolf et al. 2000; Bradford and Higgins 2001; Williams 2001b; Holm et al. 2001, Heggenes 2002; Railsback et al. 2003; Kemp et al. 2003), and the method has much more support among agency scientists and consultants than among academic scientists.

In the Central Valley, some biologists who are critical of PHABSIM nevertheless think that it “works” for Chinook spawning. Support for this view is provided by Gallagher and Gard (1999), who applied PHABSIM to sites “known to be heavily used for spawning” on the Merced and American rivers, and found a moderate but highly significant correlation between WUA and the density of Chinook redds in PHABSIM cells in the Merced River (cell by cell results for the American River were not reported). However, it is not clear what they would have found if they had applied PHABSIM to riffle areas generally, rather than only to areas that were heavily used and presumably had good hyporheic conditions. More seriously, based in the data in tables 1 and 5 of Gallagher and Gard (1999), position along the river (River km) explains most of the variation in the density of the redds considered in the Merced River (Figure 11-15a; similar data were not given for the American River). Spawning habitat quality, as estimated by PHABSIM, is related to the residuals from estimates based on river kilometer, but the residuals are not large compared to the reported range in spawning density, and the relationship is not strong (Figure 11-15b).

Gallagher and Gard (1999) found stronger relationships between WUA and redds in both rivers when the data were aggregated by site. Since PHABSIM is calculated cell by cell, however, the meaning of this finding is unclear. The belief that the aggregated findings strengthen the cell by cell findings seems to be an example of the “ecological fallacy” (Freedman 1999), that is, the belief that relationships observed for groups necessarily hold for individuals. One problem in this case is that the density of redds increases with distance upstream. Hence, the site-level analyses are confounded by a location variable, even if stream and hyporheic conditions are otherwise equal in all sites. This holds even if the most upstream site is excluded, as it was in some of the reported analyses.

Figure 14-11. A. Density of spawning in the Merced River is determined primarily by position along the river, or distance from Crocker-Huffman Dam ($r^2 = 0.91$). B. Spawning habitat quality as estimated by PHABSIM helps to explain the residuals in A ($r^2 = 0.58$), but the residuals are not large and the relationship is not quite significant by the standard criterion ($p = 0.054$). Data from tables 1 and 5 in Gallagher and Gard (1999).



Castleberry et al. (1996), who called PHABSIM “not defensible scientifically,” recommended that an adaptive approach be applied instead, pointing to the example of the Hodge Decision (Hodge 1990) in the case of EDF et al. v. EBMUD. Judge Hodge set flows that conditioned EBMUD’s ability to divert from the American River at Nimbus Dam, based on the evidence presented. However, he also recognized the great uncertainty in the evidence, so he retained jurisdiction and ordered the parties to cooperate in studies intended to determine whether changes should be made in the standards. Probably the best work of this sort is being conducted by BC Hydro (e.g., Higgins 2001; McDaniels and Gregory 2004; Gregory et al. 2006) as part of the British Columbian equivalent of a FERC relicensing process.

PHABSIM seems to provide information that managers and decision-makers want on the relation between the flow in a stream and its value as habitat. Probably on that account, it continues to be used, despite the unanswered scientific objections to it cited above. At the least,

however, managers and decision-makers should be aware of these objections, and should require the following from parties presenting PHABSIM results for their consideration:

1. Scatter plots comparing the predictions of the hydraulic model used with measured data at randomly located sites in the study area, as described in Williams (2001b);
2. Scatter plots of WUA predicted by PHABSIM with WUA calculated from the measured data at the same locations.
3. Scatter plots of the data used to develop the habitat suitability criteria used, overlain with line plots of the criteria, together with bootstrap confidence intervals for the criteria (see Williams et al. 1999, for an example of such confidence intervals).
4. Plots comparing WUA calculated with the selected suitability criteria with WUA calculated using selected 5th and 95th percent confidence intervals for the suitability criteria.⁸⁵
5. For PHABSIM studies using 1-dimensional hydraulic models, a plot showing bootstrap confidence intervals around the curve of WUA over discharge, as described in Williams (1996).
6. Comparisons of the PHABSIM results with results of alternative models, e.g., that redd density depends on position along the stream.

Recommendations

1. For most purposes, models should be tailored to the problem at hand, and simpler models should be favored over more complex models. Unnecessary complexity should be avoided.
2. Where adequate data exist, the potential effects of important restoration measures should be evaluated with estimation models; simulations should be used otherwise.
3. Monitoring programs should be assessed with simulations.
4. More people with good training in modeling and statistics should be employed or retained by agencies concerned with Central Valley salmon issues, and training opportunities should be provided for existing staff.

⁸⁵ With confidence intervals with three habitat suitability criteria, there are 720 possible comparisons to be made, so clearly some judgment must be exercised in selecting examples to plot for this recommendation to be practical.

CHAPTER FIFTEEN

MONITORING

How odd it is that anyone should not see that all observation must be for or against some view if it to be of any service.

Charles Darwin

Science is the art of not fooling yourself.

Richard Feynmann

Programs for monitoring Chinook and steelhead in the Central Valley are extensive (Table 15-1; 15-2) and increasingly coordinated, but they are funded or operated by various agencies for various purposes, and do not yet constitute a well integrated system. Some are required by FERC licenses or other binding agreements; others have less secure funding. Programs that collect data on winter-run, spring-run and steelhead are thoroughly described in Pipal (2005); these and other programs are also described in Low (2005). This chapter briefly reviews existing monitoring programs, and offers both general and specific recommendations and suggestions for improving existing programs.

Existing programs

Monitoring ocean harvest and adult returns has the longest history, and for many streams estimates of returns extend back to the early 1950s. In the Delta, routine monitoring of juveniles began in the late 1970s and continues with the institutional support of the IEP and the CVPIA. Monitoring juveniles in the rivers was more sporadic until the early 1990s. Various multi-year programs did occur earlier, but consistent funding was not available until winter-run Chinook were listed under the ESA and the CVPIA became law in 1992.

Adult returns

Central Valley rivers are too diverse for a single approach to be appropriate for estimating adult returns in all of them, and various methods are used (Table 15-1). Most Central Valley salmon can reach their spawning grounds without passing a dam, so estimates of adult returns cannot be based on ladder counts. Instead, estimates are usually based on mark-recapture approaches applied to carcasses: spawning reaches are surveyed repeatedly, unmarked carcasses are tagged and tallied, and “recaptures” of previously marked carcasses are also tallied. Estimates of adult returns are then developed, usually using an estimator described by Schaefer (1951) or (and increasingly) by Seber (1982), but sometimes also using a modified Petersen formula. These estimators entail assumptions—for example that all carcasses are equally likely to be found, that are more or less seriously violated in different streams or at different times—and they can give significantly different estimates. For the American River in 1995, for example, the Schaefer and Jolly-Seber estimates were 70,096 and 42,973, respectively (Williams 2001a). Compared to weir counts on the Stanislaus River, Jolly-Seber estimates were 18% higher and 24% lower in 2003 and 2004 respectively, while Schaefer estimates were 37% higher and 9% lower. Unfortunately, it has not been standard practice to report confidence intervals for the

estimates, although programs are available that can generate them, at least for the Jolly-Seber method.

The carcass surveys typically distinguish fish by length as “grilse,” presumably two years old, or as “adults.” The rationale for this seems more traditional than biological; usually the length criterion for the distinction is around 65 cm, close to the minimum legal length for commercial ocean harvest. More complete information on length distributions is increasingly being collected, although often the information is not reported. Heads are collected from fish that lack adipose fins, and so presumably carry coded-wire tags, but the attention given to this task varies among programs, and often there are not enough workers to carry it out properly when there are many carcasses to handle. Few hatchery fall Chinook are marked in any event, so hatchery and naturally produced fall Chinook are not distinguished.

For smaller rivers with relatively stable flow, resistance board weirs (Tobin 1994) seem to be a practical means of estimating returns accurately. Such a weir equipped with an automatic Vaki infrared scanner, is now in use on the Stanislaus River (SRFG 2004). A Vaki scanner is also being tested at Daguerre Point Dam on the Yuba River. The images from these scanners are often good enough for determining size, sex, and whether fish have adipose fins, and provide precise information on the time at which fish pass the weir; use of these systems probably will increase. Fish are also counted at Woodbridge Dam on the Mokelumne River, at the Coleman Hatchery weir on Battle Creek, and at the Red Bluff Diversion Dam, when its gates are lowered. Morphometric features to use for distinguishing males and females in video images are discussed by Merz and Merz (2004).

Aerial redds counts are used for estimating spring-run adult returns on Mill Creek, where other methods are too difficult, and on the Sacramento River. Snorkel surveys are used on several streams for spring Chinook or for steelhead, but a comparison of estimates from snorkel surveys and from carcass counts on Butte Creek indicated that the snorkel surveys seriously underestimate returns, at least when fish are numerous (P. Ward, CDFG, pers.comm. 2004). Steelhead sometimes survive spawning, and even if they do not they are less likely to die on the spawning grounds than are Chinook, so carcass counts are ineffective for estimating the number of steelhead spawners. Steelhead redds are too small to show effectively on aerial photographs, but surveys by canoe have been used successfully on the American River (Hannon et al. 2003). Resistance board weirs should also be effective for steelhead.

Redds

Besides the redd surveys just mentioned, CDFG monitors the spatial and temporal distribution of fall-run spawning in the American River and of winter-run and spring-run spawning in the Sacramento, using aerial photography in which redds are visible because undisturbed gravel is darkened by algae. This method is effective only when turbidity is low.

Eggs and alevins

There are no regular programs for monitoring conditions in redds or the survival of eggs and alevins there, but this has been done in various Central Valley studies (e.g., Vyverberg et al. 1997; Merz et al. 2004). Variables most often measured are permeability, upwelling or downwelling, dissolved oxygen, and temperature. Alternatively, eggs may be planted in baskets or tubes so that eggs and alevins can be recovered at intervals to assess their survival and condition, for example their ability to orient themselves in a slight current in a bucket (Merz et al. 2004). Redd caps have been used successfully to monitor the survival of eggs and alevins in highly regulated Central Valley streams (e.g., EA 1991c), but they have failed in applications where winter flows are more variable (K. Vyverberg, CDFG, pers.comm. 2003).

Juveniles

Rotary screw traps have become the preferred method for monitoring emigrating juvenile Chinook and steelhead where there is enough current to operate the traps (Table 15-2), although fyke nets are also used on the Merced River. The screw traps consist of conical drums set between pontoons; angled vanes inside the drum catch the current to make the drum rotate, and move fish into a holding tank at the back of the trap. Typically, groups of captured fish are marked with dye and released above each trap or set of traps, and the efficiency of the trap(s) is estimated as the percentage that are recaptured; on large rivers, the recapture rate is often under one percent. Snorkel surveys and seines are also used for assessments of habitat use in a few streams. Generally, fish lengths and sometimes weights are recorded for samples of juveniles, although when catches are large only a haphazard subsample is measured.

The IEP has a long-standing program of seine sampling at several dozen specific sites in the lower rivers and around the Delta and the bays (Brandes and McLain 2001; SSJEFRO 2003). Although these data provide a general picture of habitat use through time by juvenile Chinook, only one seine haul is made at each site during each sampling interval, and the sampling variance is too great to provide useful information at finer spatial and temporal scales. Whether the particular sites sampled are representative of areas around them is also questionable (Ch. 10).

The IEP also samples juveniles moving into the Delta by trawling at Sacramento and at Mossdale (rkm 87) on the San Joaquin River. The effectiveness of this sampling varies with the season; recent and still unpublished studies at the Delta Cross Channel have demonstrated that older juveniles passing Sacramento in the late fall and early winter migrate mostly at night (Ch. 10), but the trawling is done during the day.

Juveniles moving out of the Delta are sampled by trawling at Chipps Island. The trawl used is intended for smolts, however, and probably is less effective for sampling smaller (<50 mm) Chinook that migrate into the bays, at least in wet years. Besides monitoring the movement of juvenile Chinook and steelhead from the Delta to the bays, the trawl serves as a recovery site for studies using fish marked with coded-wire tags. These are described briefly below, and in more detail in Brandes and McLain (2001). Juveniles are also sampled at the CVP and SWP export facilities in the Delta, as discussed in Ch. 10

Studies of the survival of juvenile chinook marked with coded wire tags have been a mainstay of work on Central Valley salmon. Coded-wire tags (CWT) are 0.5 or 1 mm lengths of stainless steel wire, marked with a binary code, that can be inserted into the snouts of juvenile salmonids or other fish. The tags are not externally visible, so tagged salmon are marked by removing the adipose fin. Coded wire tags are practical only for marking batches of fish, however, since the number of distinguishable codes is limited. In the Central Valley the batches usually include 50,000 or more fish, so that enough tags can be recovered to provide useful data. Use of CWTs in the Central Valley began in 1969, and continues in studies such as the Vernalis Adaptive Management Plan (VAMP), the Delta Cross-Channel studies, and survival studies in tributaries to the San Joaquin River. A prominent use has been a set of survival studies conducted by the USFWS. The most common procedure has been to release batches of tagged fish at different locations in the river or in the Delta, and to recover marked fish in a trawl fished near Chipps Island and in the ocean fishery. On average roughly ten times as many fish are captured in the ocean fishery as at Chipps Island, but ocean recoveries are estimated from sampling and so include additional sampling error. Brandes and McLain (2001) provide a summary of CWT releases and recoveries, and more detail is available in earlier summaries such as Kjelson et al. (1981) and USFWS reports cited in Brandes and McLain (2001). Brandes and McLain (2001) and Baker and Morhardt (2001) provide discussions of the data from somewhat differing points of view, and recent statistical studies of the data are described in Chapter 10 and Appendix B. Coded wire tags have also been used for growth studies (e.g., Kjelson et al 1982), and to mark steelhead, spring, late-fall and some fall Chinook reared in hatcheries.

Recommendations for monitoring

Given that all natural resources management is experimental, whether deliberately so or not (Hennessey 1994), monitoring should be considered as obtaining the experimental results. Even in the absence of deliberate management experiments intended to test alternative hypotheses about the system being managed, hypotheses can still be tested, provided that there is sufficient variation in the main variables of interest. Year to year variation in precipitation and runoff in California makes this generally the case for many factors affecting salmon. From this point of view, monitoring should be approached in terms of what can be learned about the system and its management, and not just in terms of tracking whether targets for variables such as adult returns have been met; in other words, we should think of monitoring as part of science as well as part of management. In any event, monitoring deserves careful attention, in part because it is hard to do well. One aspect is the difficulty of sampling consistently through highly variable field conditions, which requires skill and diligence from boat operators and field crews. A good monitoring program is impossible without good execution; however, a good program also requires a good sampling design, and good data analysis.

Table 15-1. Monitoring for adult Chinook and steelhead. Fall-run (FR), late fall-run (LFR), winter-run (WR), spring-run (SR), steelhead (ST). Data from Alice Low, CDFG.

Monitoring Activity	Variable	Stream	Agency
Carcass Counts	Adult Returns, FR	Sacramento River	CDFG/USFWS
		Clear Creek	CDFG/USFWS
		Battle Creek	CDFG
		Butte Creek	CDFG
		Yuba River	YCWA/JSA⁸⁶
		Feather River	DWR/CDFG
		American River	DFG
		Cosumnes River	CDFG, DWR, TNC
		Stanislaus River	CDFG
Snorkel Surveys	Adult Returns, SR, St	Tuolumne River	CDFG
		Merced River	CDFG
		Clear Creek	USFWS
		SR, WR, St	Battle Creek
		SR	USFWS
		SR	Antelope Creek
		SR	CDFG
Dam or Weir Counts	FR, WR	Big Chico Creek	CDFG
		SR	Beegum Creek
		SR	CDFG
		SR	Deer Creek
		SR	CDFG
		FR, WR	Sacramento River
		FR, WR, St	USFWS
Redd Surveys	FR, LFR, SR, St	Battle Creek	USFWS
		FR, ??	Yuba River
		FR, St	CDFG?
		FR	Mokelumne River
		FR	EBMUD
		FR	Stanislaus River
		FR	S. P. Cramer & Assoc.
Spawning Distributions, all runs	FR, LFR, SR, St	Clear Creek	USFWS
		SR, WR, St	Battle Creek
		SR	USFWS
		SR	Mill Creek
		SR	CDFG
		SR	Sacramento River
		FR, St	CDFG
		FR	Yuba River
		FR	CDFG
		FR	American River
Angler Survey	Sport Harvest	FR	CDFG
		FR, St	Cosumnes Rivers
		FR	CDFG, DWR, TNC
		FR	Mokelumne River
		FR	EBMUD
		FR	Merced River
		FR	CDFG
Angler Survey	Sport Harvest	Sacramento River	CDFG
		Yuba River	CDFG
		Feather River	CDFG
		American River	CDFG
		Mokelumne River	CDFG
		Stanislaus River	CDFG

⁸⁶ Funded by Yuba County Water Agency, performed by Jones & Stokes

Table 15-2. Monitoring for juvenile Chinook and steelhead. Data from Alice Low, CDFG.

Monitoring Activity	Variable; Run	Stream	Agency
Snorkel Surveys	Habitat use; FR, LFR, SR, St Habitat use, survival; St Habitat use; FR Abundance, habitat use; FR Presence; FR	Clear Creek Feather River Yuba River Calaveras River Stanislaus River	USFWS DWR YCWA/JSA ⁸⁷ USFWS, Fishery Fnd. USFWS/ Fishery Fnd.
Screw traps	Emigration; all All FR, LFR, SR, St FR, LFR, SR, St SR SR SR SR All All FR, SR?, St FR, ST FR, ST FR, ST FR, ST FR FR, ST FR, St FR	S.R., RBDD S. R., GCID Clear Creek Battle Creek Big Chico Creek Mill Creek, Deer Creek Butte Creek, Chico Sutter By-Pass S. R., Knights Lndg Feather River Yuba River American River Cosumnes River Mokelumne River Calaveras River Stanislaus River Tuolumne River Merced River	USFWS CDDFG USFWS USFWS CDFG CDFG CDFG CDFG CDFG CDFG CDFG DWR CDFG CDFG USFWS, Fishery Fnd. EBMUD S. P Cramer Assoc. S. P. Cramer Assoc. CDFG CDFG
Beach seines	Distribution, emigration; all Distribution, abundance; FR ; FR, St Abundance; FR Distribution; FR	S. R., S.J. R., Delta, bays Cosumnes River Mokelumne River San Joaquin River Tuolumne River	USFWS TNC EBMUD USFWS TID
Trawls	Emigration; All Emigration; FR, St Emigration, Survival; All	S. R. at Sacramento S. J. R. at Mossdale Chippis Island	USFWS CDFG USFWS
Fyke nets	Emigration; FR, St	Merced River	CDFG

Although some basic level of monitoring will be needed for all streams, the nature and intensity of monitoring should vary according to need and the suitability of conditions in the stream for addressing particular questions. Given the inevitable constraints of time and money and the magnitude and variability of the system to be monitored, developing a well designed program is a major challenge. This section presents some generalities about monitoring and suggestions for elements of a monitoring program for Central Valley salmon, and offers some suggestions for evaluating and improving existing programs.

⁸⁷ Funded by Yuba County Water Agency, performed by Jones & Stokes.

General Recommendations on monitoring

1. Monitoring should evaluate the condition of organisms as well as of populations and habitats.

Traditional approaches to monitoring try to measure attributes of populations, especially abundance, and attributes of habitats such as water temperature, discharge, etc. These are necessary, but attention should also be given to measuring attributes of individuals, such as growth rates and aspects of physiological condition such as lipid content. In a study monitoring the environmental effects of off-shore oil production in the Santa Barbara Channel, Osenberg et al. (1994) found that individual-based parameters were more effective at detecting impacts than population-based or physical parameters, because they have better statistical properties and because they provide better evidence of the mechanisms that control populations. Castleberry et al. (1996) urged that individual-based measures of condition and performance be monitored, in addition to population measures, for effective adaptive management of instream habitats. Potential individual-based parameters of salmon include growth rates from otolith microstructure, measures of lipid content, RNA/DNA ratios, and levels of stress proteins, as well as simpler “condition factors” such as relative weight. These are described in more detail below.

2. Monitoring programs should emphasize collecting data on naturally produced fish. Great effort and expense is now devoted to restoring runs of naturally produced Chinook and steelhead, but hatchery and naturally produced fish are not distinguished in many monitoring programs. Hatchery fish may have different life history patterns and behave differently than naturally produced fish (Ch. 12), and to the extent that they do, management based on information about hatchery fish may be counterproductive for naturally produced fish.

3. Monitoring should address specific questions. In most cases, monitoring should be linked to specific hypotheses or management activities. Basic biological monitoring is sometimes justified, however, especially where lack of data inhibits the development of useful hypotheses (Power et al. 2001), but there is a danger that monitoring for “status and trends” can become rote, producing data that are never thoughtfully analyzed or critically evaluated for utility. This danger can best be avoided by making data analyses that address specific questions, as well as exploratory analyses, basic parts of the monitoring program. This will clarify which aspects of the monitoring program are producing useful data, and which are not.

4. Data collection and analysis should be closely linked. Monitoring produces better and more useful data if the person responsible for analyzing the data is closely associated with the data collection. This gives the analyst a better understanding of the strengths and weaknesses of the data, and promotes more careful work by the field crews. If no one is interpreting the data, the need for the monitoring should be reconsidered.

5. Monitoring programs should try to answer multiple questions. Just as a good move in chess attacks and defends at the same time, so a good monitoring program should develop new knowledge at the same time that it checks the performance of management actions in light of existing knowledge. By addressing multiple scientific questions, a monitoring program can

develop data that allow management questions to be addressed from several points of view. This can be important, because field observations of single variables will seldom provide unambiguous answers; almost always, different conceptual models or “stories” can be invoked to explain observations of a single variable, and the monitoring program should include enough elements to test multiple stories and rank their plausibility. For example, using PIT tags to monitor the survival of individual smolts passing down the Columbia River has not settled a long-standing dispute about the relation between flow and survival, because decreased flow increases travel-time, and there is evidence that increased travel-time reduces the smolts’ energy reserves and so reduces their viability, even if they survive past the last tag detector (Congleton et al. 2004; NRC 2004).

6. Monitoring should use up-to-date statistical and graphical methods. The statistical methods now most commonly used were developed for use on mechanical hand-calculators. Computers have allowed the development of computationally intensive statistical methods that allow more useful information to be developed from monitoring programs (Efron and Tibshirani 1991; Hilborn and Mangel 1997). Bayesian statistics arguably provide a more useful guide to management of natural resources than do the more traditional and familiar frequentist methods (e.g., Hilborn and Ludwig 1993). Very few of the scientists now working on Central Valley salmon are familiar with these newer methods, however, so a deliberate effort should be made to introduce the methods and train people in their application. With frequentist methods, more attention should be given to developing estimates of effect size and confidence intervals, rather than tests of whether an observed change is statistically significant (Stewart-Oaten 1996; Steidl et al. 1997; Johnson 1999). As a first step, however, better use should be made of available software for graphical presentation of data; for example, box plots can be a useful way to summarize information about distributions of fish size, etc. Graphical presentation of data is discussed at greater length below.

7. Monitoring programs should be evaluated by simulations. Analyses of simulated data that include realistic amounts of uncertainty can help determine whether a proposed monitoring program will provide useful answers to the questions it is designed to address. For example, Williams (1999) used simulations incorporating reasonable amounts of measurement or sampling error to argue that the Comprehensive Monitoring and Assessment Program (CAMP), set up under the CVPIA, is unlikely to meet its objectives. Similarly, Meekan et al. (1998) used simulations to show the effect of measurement errors on the ability of regression analysis to detect the relationship between the size of Atlantic salmon at emergence and two measures of otolith size. Monitoring programs are expensive, and experimental programs such as the Vernalis Adaptive Management Program (VAMP) are very expensive; simulations can be an inexpensive way to avoid costly mistakes in the design of these programs (Hilborn and Mangel 1997), or to assess the results. For example, the estimates of smolt survival through the Delta developed by the VAMP using hatchery fish marked with coded-wire tags are low (~15-20%), and simple simulations of the salmon life cycle could be used to assess whether it is reasonable to think that these survival estimates are also applicable to naturally-produced smolts; that is, given current

estimates of mortality in other life stages, is 15-20% survival passing through the Delta compatible with existing population data.

8. Monitoring should be complemented by modeling. To be useful, monitoring data must be converted into information, and one way to do this is to model the biological processes that are thought to underlie the variables being monitored. In an important sense, modeling is simply a formal way of thinking about the data, and many different kinds of models can be used (Ch. 14). As with statistics, modeling is a rapidly developing field that has been stimulated by the rapid development of computers and computer-based methods. More people with good training in modeling and statistics should be employed or retained by agencies concerned with Central Valley salmon, and training opportunities should be provided for existing staff.

9. The monitoring program should provide for extra sampling of unusual events. Extra sampling during unusual events or situations, such as the aftermath of floods, can sometimes produce particularly valuable information. By their nature, unusual events are hard to plan for, but funding for contingency sampling can be made part of the monitoring program. The utility of contingency sampling probably depends upon close supervision of the field program.

10. Take sampling bias and uncertainty into account. To an extent that is probably greater than most of us realize, our knowledge of salmon is shaped by the gear that are used to sample them. As discussed earlier, sampling with a mid-water trawl in the 1960s (Sasaki 1966) led to the mistaken conclusion that the timing of the main migration of juvenile chinook had changed, a view that was corrected only when sampling with floating screw traps started in the early 1990s. Similarly, the existence of a gill net fishery in Suisun Bay allowed for recovering a significant number of adult salmon that had been tagged well up the Sacramento River (McCully 1956), demonstrating an aspect of behavior that seems to have faded from the common awareness of Central Valley salmon biologists. The current view regarding the number of fry that migrate into the bays is based on data from the Chipps Island trawl, which was designed for capturing smolt migrants and presumably is not as efficient for capturing smaller fish (see Stevens 1966). Similarly, current data on the timing of winter-run migration into the Delta is based largely on trawling at Sacramento, but if the findings of the recent Delta Cross Channel experiments using hatchery late fall-run smolts (Ch. 10) also apply to winter-run, the trawling occurs when most fish are holding near the bed and banks of the stream, so the trawl data may be misleading. As another example, it is common to sample juvenile salmonids with traps facing upstream, in order to catch fish moving downstream, but this practice may give a distorted picture of fish behavior if it is assumed that movement is downstream. A study using traps facing downstream as well as upstream, described in Ch. 8, sometimes caught more fish in the downstream-facing trap (Venditti and Garland 1994), presumably because the fish were not actively migrating. Special sampling to assess the relative efficiency and bias of various sampling methods should be conducted, although some uncertainty will always remain. Sampling bias seems inevitable, but at least we can be conscious of it.

11. Make full use of existing data. A great many data have been collected by monitoring programs but have not been thoroughly analyzed. For example, the data on salvage of juvenile Chinook and steelhead have not been analyzed for differences among years in size at date (e.g., Figure 10-11), which could provide a useful index of growth opportunity or habitat conditions in fresh water. Similarly, length at age data from the coded-wire tag database might be used to generate an index of ocean conditions, and both indices could be related to environmental conditions. Generally, these should be exploratory analyses, intended to generate hypotheses that can be tested with future data. Care should be taken to avoid “data dredging,” which occurs when many variables are screened, some are selected for a model, and then the same data are used to evaluate how well the model fits the data (Freedman 1983; Burnham and Anderson 1998).

One reason that data have gone unexplored is that they have been hard to get. The situation has improved recently, with development of the Calfish data base (www.calfish.org) and a new interface for the data managed by the IEP. Good data management is expensive, however, and more money will need to be allocated to this purpose before the data are fully available.

12. Assess monitoring programs periodically. It is natural and appropriate that as interests change, perhaps because older questions have been satisfactorily resolved, efforts will be made to address new questions using data from programs that were not designed to address the new questions. Thus, even if monitoring programs are suitably designed for their original purpose, they may become inadequate as needs change. Moreover, standards of practice evolve, so what may have been an acceptable practice before may no longer be so, and new approaches and technologies may make older methods obsolete or require data not previously collected. Periodic review and assessment of monitoring programs is therefore appropriate, and such a review, with substantial participation by outside reviewers, seems in order for salmon monitoring programs in the Central Valley.

The various recommendations and suggestions offered here should be considered in such a review. It should also take account of the findings of a highly qualified panel (Botkin et al. 2000) that considered the question: “If actions are taken in an attempt to improve the status of salmon (or a specific stock of salmon), what measurements are necessary, feasible, and practical to determine whether the actions are successful?” Many of their comments, or questions, are applicable to assessing other monitoring programs as well. Their list of important considerations is paraphrased and abbreviated below:

Sampling:

Do the sampling sites and methods reasonably represent the area in question and the range of conditions that occur there?

Is the sampling of adequate duration and frequency?

Does the sampling take advantage of replicated actions?

Are the sampling methods sufficiently accurate and precise to meet the monitoring objectives?

Are proposed monitoring activities really feasible?

Is the use of new technology proposed, and if so, are backup methods also proposed?

Data Management:

Are data properly checked for errors?

Are data archived securely?

Are archived data readily available?

Analysis and Interpretation:

Are the analytical techniques used appropriate for the data and questions being addressed?

Are alternative hypotheses properly considered?

Is uncertainty properly described and taken into account in analyses of the monitoring data?

Do the analyses identify and assess risks as well as benefits from management alternatives?

Do the analyses identify opportunities for additional learning?

The review should include special studies to assess the relative efficiency and sampling biases of various sampling methods. It should also consider whether the program is appropriately funded.

Possible Improvements to Existing Programs

The recommendations given above imply changes in existing monitoring programs, most of which would require time, planning, and additional funding to implement. However, there are some changes that can be made more easily.

Improve statistical practice. Monitoring normally involves observations of samples, and observations almost always include some error, so estimates of variables of interest developed from monitoring data are more or less uncertain. Accordingly, the estimate should include both a point estimate and a measure or estimate of the uncertainty around the point estimate; typically, this is done by reporting standard errors or confidence intervals. Unfortunately, this is not done in many Central Valley monitoring programs. Off-the-shelf statistical programs now calculate standard statistics almost instantaneously, and bootstrap methods (Efron and Tibshirani 1991; 1993; Manly 1997) can often be used for unusual statistics as well. Agencies should make training opportunities available for staff who prefer it, and time for independent study available to others.

More attention should also be given to the problem of spurious precision in reporting monitoring results. That is, if an estimate of adult returns is thought to be accurate to within a thousand, then it is spurious precision to give the estimate as, say, 14,351, unless standard errors or confidence intervals are also given. Reporting highly uncertain estimates down to single digits seems to be an unfortunate tradition in the Central Valley.

Present data more effectively. Existing programs could yield additional information with modest additional expense, if more effort were put into displaying the data more effectively. For example, it is common practice to measure the lengths of up to 50 individuals from a seine haul or from the daily or weekly catch of a screw trap, and then to report only means and standard errors or deviations, or means and ranges, or even just means. With modern graphical programs, however, it is simple to create several kinds of figures that emphasize different aspects of the data, and this should be standard practice. Good graphics convey information clearly, just as good writing does. As with writing, there is no single best style for graphics, but Cleveland (1985) provides useful guidance. Agencies should provide their staffs with training opportunities, and with better graphics programs than Excel.

One positive development for Central Valley monitoring programs has been the development of “project work teams,” in which biologists working on various aspects of monitoring Chinook and steelhead meet periodically to discuss problems and developments. These meetings provide a good venue in which to implement the suggestions just made. To some extent this has already happened. For example, a training workshop on the use of software for calculating confidence intervals around escapement estimates was organized for members of the Escapement Project Work Team. This kind of activity should be encouraged.

Elements of monitoring programs for salmon

Potential elements of monitoring programs for Chinook and steelhead are described below. Which should be included in actual monitoring programs depends on the questions at play in each case; that is, this list is intended as a menu, not a recipe.

Adult returns: The number of returning adults is a basic measure of the quality of habitats and of management, so estimates of adult returns are a fundamental objective of a monitoring program. Numbers by themselves are not enough, however, and accuracy is subject to diminishing returns, so decisions regarding the allocation of resources among elements of a monitoring program will always be in order. For example, if the interest is in stock-recruit relationships, or the number of progeny that can be expected from a spawning run, then the real quantity of interest is the number of viable eggs, and uncertainty about the size and fecundity of the enumerated fish limits the useful accuracy of the estimate of numbers of fish, unless information is also collected on sex and on fecundity and perhaps on egg size, both of which vary with the size and age of the female (Ch. 6). If adult returns are of interest as a measure of habitat quality, then the useful accuracy of estimates is limited by uncertainty about ocean and inland harvest, including illegal harvest. Developing a good allocation of resources in a monitoring program will require careful consideration of the marginal utility of accuracy for the various parameters that are estimated, and the importance of other aspects of the monitoring program such as data management.

Where fish need to pass over existing dams, or where weirs can be operated, as on the Mokelumne and Stanislaus rivers, accurate estimates can be obtained. Elsewhere, the accuracy of the estimates will vary depending upon the resources available for surveys and conditions in the stream. Where fish spawn in remote areas of streams where access is difficult, as on Deer Creek,

obtaining accurate estimates may be prohibitively expensive. Estimates of returns on most Central Valley streams are obtained by mark-recapture methods applied to carcasses. As delicately put by JHRC (2001:12) “The accuracy and variance of most Central Valley escapement estimates are currently unknown and may not be sufficient to meet management needs, ...” The accuracy will depend on percentage of carcasses that can be recovered and the extent to which various assumptions of the methods, for example that all carcasses are equally likely to be recovered, are violated in the particular circumstances in which the method is applied. A careful and critical review of the use of mark-recapture methods in the various Central Valley streams is in order, and could make use of the results of particularly intensive surveys that have been done recently on the Feather River (B. Cavallo, CDWR, pers.comm. 2005). This would be a serious project, on the order of a Ph.D. project in statistics. Currently two different methods are commonly used to estimate the total run for carcass survey data, and until it is clearly established which is more appropriate in which circumstances, the best course probably is to use and report both. In any event, estimates of adult returns, like other estimates from monitoring, should include confidence intervals or standard errors. Methods for estimating confidence intervals are available, at least for the Jolly-Seber estimator, and confidence intervals should be reported routinely, along with appropriate caveats if important assumptions of the method may be invalid.

Natural Production: The proportions of adult returns that are naturally and hatchery produced should be estimated for most if not all streams. For this and other purposes, all hatchery fish should be marked, as recommended by NRC (1996). Economical marking that can identify the hatchery of origin and brood year can be accomplished by varying the temperature of water in hatchery trays, creating alternating light and dark bands in the otoliths that serve as a bar-code (Volk et al. 1994, Fraley and Munk 1997). Otolith thermal marking is a mature technology that is widely used around the North Pacific; the otoliths of more than a billion salmon are now marked annually (E. Volk, WDFW, pers.comm. 2004). Preparing otoliths well enough to read thermal marks is easy enough that they are used for in-season management of mixed-stock fisheries (Hagen et al. 2001). Collecting otoliths from a modest number of carcasses in each stream should allow reasonable estimates of the proportions of hatchery and naturally-produced fish, but enough should be collected to meet some specified objective. For example, on a stream without a hatchery, the objective might be to determine with 80% accuracy whether fewer than 5% of the spawners are hatchery fish. This approach would also produce a collection of otoliths that could be analyzed for other purposes, such as estimating the distributions of length at age for naturally produced fish and determining the juvenile life histories of naturally produced fish that survive to spawn.

Hatchery fish can also be marked by clipping their adipose fins, as is done when fish are marked with coded-wire tags. Clipping fins is relatively inexpensive, so all hatchery fish could be given an external mark by clipping the fins, in addition to the otolith thermal marks. Because the fin clip is used to identify coded-wire tagged fish, however, there is reluctance to clip the fins of fish without tags. On the other hand, marking all hatchery fish with coded-wire tags would be expensive. A compromise approach currently in planning for the Central Valley is to tag a

constant fraction of hatchery fish (25%), so that the proportion of hatchery fish among adult returns can be estimated from the proportion with tags. However, it is hard to see any advantage of constant fractional marking over otolith thermal marking, except that coded-wire tags are a familiar technology to Central Valley salmon biologists. On the other hand, constant fractional marking has the disadvantage of focusing attention and learning on hatchery fish, rather than on naturally produced fish. In monitoring programs for juveniles, for example, the origin of unmarked fish would be difficult and expensive to determine. Hatchery and naturally produced fish can be distinguished by the isotopic composition of their otoliths, since the otoliths of the hatchery fish carry the isotopic composition of the hatchery feed (Weber et al. 2002), and they can be distinguished with about 80% accuracy by the greater regularity in the widths of early increments in hatchery fish (Zhang et al. 1995), but sorting fish by origin using these methods may be too difficult and expensive for routine use in monitoring, or even in many focused studies. If fish need to be marked for special studies using coded-wire tags, such as the VAMP, clips on fins other than the adipose fin could be used.

Size at age, age distribution, life history information: The age distribution of returning adults and size at age should be determined, using otoliths collected for tracking the proportion of hatchery and naturally-produced fish. The sample sizes needed should be determined by experience, but should be large enough to meet defined objectives. Better estimates will be justifiable on streams selected for active adaptive management, and might be omitted altogether for some others, although any otoliths collected could be archived in case a need arises for the data. Although preparing adult otoliths for microstructural analysis is more difficult and time consuming than preparing them for reading thermal marks and age in years, analyses of otolith microstructure from early life can also provide information on the prevalence of different life-history patterns among fish that survive to maturity. Such work is currently in progress for Chinook in the Skagit River in Washington (R. Reisenbichler, USGS, pers.comm. 2005).

Timing and location of spawning, approximate number of redds, and estimates of superimposition: The spatial and temporal distributions of spawning can be determined by repeated aerial surveys in some streams but not in others, depending upon depth and clarity of the water. Ground or boat surveys may be effective for tracking redds where aerial photography fails. Where it is effective, aerial photography also provides a lasting record of conditions in the channel that may prove useful for other purposes. Data on the location and timing of spawning seem useful for developing empirical estimates of the relation between discharge and spawning habitat (Williams 2001a), and significant changes in either distribution should provoke inquiries into causes. Estimates of the extent of superimposition can be developed from aerial photography, but this should be done cautiously since redd size estimated by aerial photography on the American River was about three times larger than redd size measured on the ground (Snider and Vyverberg 1996). If adult returns are estimated by carcass surveys, some information on the timing and spatial distribution of spawning is obtained as a by-product.

Fecundity: Fecundity is a basic biological parameter that deserves more attention (Ch. 6), and can easily be measured at hatcheries. Average fecundity is routinely estimated at hatcheries by

dividing an estimate of the total number of eggs taken by the number of females stripped, but the data are of uncertain quality and data on variation in fecundity among individuals are scarce. Collecting data on the fecundity of individual fish is not difficult and should be routine, although proper protocols for selecting females to sample need to be developed and used. Besides providing a check on possible effects of hatchery culture, fecundity data contains information on ocean conditions (Figure 6-11). Fecundity data for naturally-produced fish generally should be obtained on an opportunistic basis to check for consistency with hatchery data, but if there is a specific question to be addressed then deliberate collection of a sample of appropriate size may be in order. Data on egg size should be collected along with egg numbers.

Hyporheic conditions: Salmon begin their lives buried in gravel and probably most die there as well (Ch. 7), but very little information is available on the quality of the hyporheic habitat of Chinook and steelhead in the Central Valley. This is a difficult but important area of inquiry. Components of hyporheic water quality, particularly dissolved oxygen content and temperature, are important variables that can be monitored. Permeability is commonly measured with standpipes, but work in progress indicates that in gravel the standpipes are subject to considerable leakage along the pipe, casting doubt on the validity of the data (Tim Horner, CSUS, pers.comm. 2005), so such data should be treated with caution until this question is clarified. Unfortunately, such data as are available suggest that hyporheic habitat is highly variable in time and space, so direct monitoring of hyporheic conditions may be difficult, and should be supplemented by information inferred from the condition of fish that do emerge. For example, the size of recently emerged juveniles that are captured in screw traps and the percentage of them that have not fully absorbed the yolk sac are easily measured and probably vary with hyporheic conditions. Data on otolith microstructure or aspects of physiological condition or histology of newly emerged fry probably would be more informative but would be more difficult and expensive to obtain. As with length-weight indices of condition, standards for comparison would need to be developed to allow better interpretation of the data.

Emergence, early emigration: The timing of emergence and early emigration is most often monitored in the Central Valley using screw traps, but fyke traps or seines can also be used. Data from seines also provide some measure of populations, but in most larger streams there will be so much uncertainty in seine data that they are better regarded as qualitative (none or few, some, many, lots) rather than quantitative. Screw or fyke traps provide more accurate estimates of the numbers of migrants, but on large streams where only a small percentage of migrants is sampled the estimates may still be subject to considerable error, and the traps may be more effective for smaller than for larger fish. Software for calculating confidence intervals around screw trap estimates exists (e.g., Bjorkstedt 2005) and should be used, but these depend on assumptions such as constant capture efficiency over sampling periods (e.g., weeks) that may not be valid. Simulations could clarify the potential errors involved. Sampling with seines or screw traps also allows for collecting subsamples of fish for measures of condition, etc., and sampling with seines or fyke traps near the margins of larger stream may collect fish that avoid screw traps fished farther from shore (Ewing et al. 2001; S. Williamson, USGS, pers.comm., 2005)

Population density: A promising approach for estimating the density of juveniles in rivers has been described by Weber and Fausch (2004). Essentially, the method involves outlining a section of channel with posts set in the stream bed (in their case 6.1 x 30.5 m), and attaching a modified seine that can be raised and dropped on the posts. The seine is raised long enough to allow fish to move into the area, and then dropped, and the number within the enclosure is estimated by depletion sampling with a standard seine. This method should allow better estimates of population density and size distributions than conventional seining.

Habitat use by juveniles: Methods for observing fish and estimating their abundance in smaller streams are well established (Dolloff et al. 1996). The problem is more difficult in larger streams, and when water is turbid, but presence and qualitative estimates of abundance can be determined using seines or other traditional gear. Migration rates and habitat use can also be monitored by marking naturally-produced fish with coded-wire tags and appropriate fin clips and recapturing them farther downstream. If many fish of approximately the same size can be marked with a particular tag code, as has been done in a project on Butte Creek (Ch. 5), then growth rates can be estimated as well.

Methods from landscape ecology (e.g., Jongman et al. 1987; Ford and Brown 2001) seem appropriate for summarizing the relationships between observations of fish and environmental variables. Often, however, there is a desire to relate observations of fish to habitat features in terms of habitat selection or habitat preference, but doing this well is difficult. Kramer et al. (1997) noted that "Studies of habitat selection frequently fail to acknowledge the statistical complexity underlying even simple questions of distribution." Manly et al. (2002) have provided a more secure theoretical basis for studies of resource selection in terms of a "resource selection function," which is "a function such that its value for a resource unit is proportional to the probability of that unit being used, " which seems similar to what a PHABSIM suitability curve is often taken to be. The assumptions of their approach are (Manly et al. 2002:43):

- a. the distributions of the measured X variables for the available resource units and the resource selection probability function do not change during the study period;
- b. the population of resource units available to the organisms has been correctly identified;
- c. the subpopulations of used and unused resource units have been correctly identified;
- d. the X variables which actually influence the probability of selection have been correctly identified and measured;
- e. organisms have free and equal access to all available resource units; and
- f. when studies involve the sampling of resource units, these units are sampled randomly and independently.

People familiar with field studies will realize that some of the assumptions are difficult to meet, but Jones and Tonn (2004) have reported resource selection functions for Arctic grayling.

Other difficulties with studies of habitat selection involve questions of scale. A study of substrate use by various species darters (Welsh and Perry 1998) provides a particularly clear example. One of the darters typically holds on top of submerged boulders, while two others typically hold in the gaps between them. Since gravel often occurs in the gaps, these species are associated with smaller substrate when data are taken using small quadrats, whereas the other species is associated with larger substrate. If larger quadrats are used, this difference disappears, and the selected substrate size of two species seems to increase while it seems to decrease for the other. Cavallo et al. (2003) showed that large scale features strongly affect habitat selection by juvenile steelhead in the Feather River. In short, monitoring that tries to relate distributions of fish to habitat features should be approached with due caution, and with good statistical guidance. Generally such work should be regarded more as research than as monitoring, and should be concentrated in the streams selected for active adaptive management, or that offer good study conditions. Monitoring of habitat use is also appropriate for restoration projects justified by specific hypotheses regarding habitat use, and there is a particular need for information on habitat use by small Chinook in the Delta and in the bays.

Condition: One difficulty with monitoring habitat use is that the presence or abundance of organisms in a habitat is not necessarily a good index of the quality of the habitat (Van Horne 1983; Manly et al. 2002), which may be more reliably inferred from measures of the organisms' condition. Which measures will prove most useful needs to be determined by experience, since this depends in large part on the strength of the response to the environmental variable of interest and on the background variability, and in many cases the data needed to estimate these factors do not yet exist. For example, there are few data on the lipid content of wild juvenile chinook in rivers (Beckman et al. 2000; Congleton et al. 2003). Similarly, there may be various ways to estimate a particular factor such as lipid content with varying costs and information returns, and some experience will be necessary to determine which way makes sense in particular situations (e.g. Weber et al. 2003). Sutton et al. (2000) calculated and compared seven different indices based on length, wet weight, dry weight, or lipid content, for a sample of 284 Atlantic salmon parr. Similar comparisons, using a wider array of variables, would be useful for Central Valley salmon, particularly fall-run Chinook.

Length and wet weight can be determined non-lethally from lightly anesthetized fish, and several measures of condition can be calculated from these measurements. Fulton's Condition Factor K ($\text{wet weight}/\text{length}^3$) is perhaps the best known index of condition and has been reported for juvenile Central Valley salmon in some studies (e.g., Snider and Titus 2001; Petrusso and Hayes 2001b). However, K can be misleading for comparing fish of different length (Cone 1989), and better indices compare individual fish to standardized length-weight relationships for the study population (relative condition K_n ; Le Cren 1951) or the species (relative weight W_r ; Wege and Anderson 1978). Residuals from standard length-weight relationships can also be used (residualized wet weight; Sutton et al. 2000). Whichever index is

used, lengths and weights should also be reported, so that other workers can calculate the other indices. Proper interpretation of these indices as indicators of environmental quality depends on the realization that both environmental and genetic factors affect the weight at length of a particular fish. Ideally, the index should reflect the deviation of the individuals' weights at length from a genetically-determined standard, although in practice probably the best that can be done is to compare the weights to a standard for a species, a population or a sample (Sutton et al. 2000). Given the diversity of life history patterns expressed by salmonids, any such group will be genetically heterogeneous.

More informative indices can be developed if fish are sacrificed and the contributions of water and polar lipids to wet weight are determined. Again, comparisons with relationships standardized to length may be useful, and the same caveats apply as for condition factors based on length and wet weight. Difficulties in comparing the results of different studies that use different indices can be mitigated if authors also publish their basic data. Dry weight and percent water is easier and less expensive to determine than percent lipid, but percent lipid is more biologically meaningful and is simple enough to determine that it seems hard to justify sacrificing fish simply to determine dry weight.

A number of measures of growth and condition that can help address such questions have been applied to chinook salmon and steelhead in the Central Valley, especially in the American River (Castleberry et al. 1991; 1993), in the bays (MacFarlane and Norton 2002), and in the Gulf of the Farallones (MacFarlane et al. 2005), and others have been applied elsewhere. For example:

Otolith microstructure: Because juvenile salmonids generally form one otolith growth increment each day, with distinctive tightly spaced increments at hatching and first feeding (Bradford and Geen 1987; Campana 1983; Neilsen et al. 1985; Castleberry et al. 1994), the number of otolith increments divided by length provides an index of long-term growth rate (e.g., Figure 4-12), and if a length is assumed at formation of the hatching or first feeding mark, the subsequent absolute growth rate can be estimated; simulations indicate that such estimates become usefully accurate by the time juveniles reach 45 to 50 mm (Williams 1995). More accurate estimates can be developed if the length at first feeding is also estimated for each individual from the size of the otolith at the first feeding check (Titus et al. 2004). Increment widths are also closely related to growth rate over extended periods (e.g. 50 days), although not for shorter periods (Bradford and Geen 1987).

RNA/DNA ratios: RNA/DNA ratios provide a measure of short-term growth rates, because the amount of RNA in cells increases during active growth but the amount of DNA is relatively constant (Buckley et al. 1999). A measure of short-term growth rate would be useful for evaluating the utility of specific habitats for juvenile salmon; rapid growth rates would be more powerful evidence of benefit to juvenile salmon than the mere presence of the fish in the habitat. In starved rainbow trout, however, the amount of DNA decreases over time, so that an initial decline in the RNA/DNA ratio leveled off, although it stayed below the ratio for fed fish (Weber

et al. 2003). In the American River, mean RNA/DNA ratios for juvenile Chinook in the American River rose rapidly with size to about 45 mm, but only slowly thereafter, and some of the variation may have been from the analytical technique used (Castleberry et al. 1993).

Lipids: Lipids are an important source of potential energy that reflects the physiological capacity of fish for growth or activity (Busacker et al. 1990), and lipid levels of juvenile salmonids from hatcheries affect their survival (Peterson 1973, Rondorf et al. 1985). Castleberry et al. (1991; 1993) analyzed lipid levels for juvenile chinook salmon and steelhead from the American River for two similar years (1991 and 1992), and found the levels to correspond with the lower range of levels for fed fish in hatcheries or laboratory experiments. However, few other data are available on lipid levels in naturally produced juvenile salmonids in rivers, so interpretation of such data will be hampered until more are accumulated. Also, lipids occur in various forms. Castleberry et al. reported data for non-polar lipids, which can be determined by a simple ether extraction technique. Chromatographic analysis allows a more detailed and informative but also more expensive breakdown of lipids into sterol/wax esters, triacylglycerol, nonesterified fatty acids, cholesterol, and polar lipids, and was used in a study of salmon smolts from Chipps Island to the Gulf of the Farallones by MacFarlane and Norton (2002), who reported data as triacylglycerol normalized to cholesterol. Weber et al. (2003) describe methods for measuring whole body total lipids, whole body triglycerides, muscle RNA:DNA ratio and muscle protein from the same juvenile *O. mykiss*.

Gill Na^+K^+ ATPase activity: Gill sodium, potassium-activated adenosine triphosphatase activity levels have been used as a quantitative measurement of the progress of smolting of migrating salmon in routine monitoring on the Columbia River (Beeman et al. 1991), and have been used elsewhere to clarify patterns in life history trajectories (Ewing et al. 2001). The enzyme is involved with maintenance of proper ionic balance of fishes in seawater. There is concern that temperature stress may lead to reduced ATPase activity (Zaugg 1981), which could further compromise salmon smolts migrating through the Delta. Assays of the ATPase activity of fish exposed in the laboratory to thermal stress simulating migration through the lower Sacramento River in unfavorable conditions could provide a reference from known conditions. ATPase activities may also be helpful for interpreting monitoring data for larger juveniles migrating down the Sacramento River in late fall and winter, especially if combined with genetic analyses to assign fish to runs. ATPase activity can be sampled non-lethally by taking a small clip from one gill filament (McCormick 1993).

Stress proteins: Exposure to thermal or other stresses induces synthesis of small "heat shock " proteins, particularly members of the hsp70 family (Morimoto et al. 1990 and 1994; Feige et al. 1996). Although the functions of heat shock proteins continues to be elucidated it is known that some, including the hsp70 family, function as molecular chaperones that reduce damage to other proteins, and account for acclimation to warmer water (Feige et al. 1996). The potential of hsp assays for monitoring temperature stress was confirmed by Werner et al. (2005; see also Viant et al. 2003); elevated levels of hsp-72 were detected in juvenile steelhead in the Navarro River that had been exposed to water with daily mean temperatures of 18-19°C and daily maximum

temperatures of 20-22.5°C. Smolting fall-run chinook salmon are frequently subjected to high water temperatures in the lower Sacramento and San Joaquin rivers. Previous attempts to relate smolt survival to water temperature have used paired releases of coded-wire tagged fish. Although the data have been given competent statistical analysis (Baker et al. 1995, Newman and Rice 2002, Newman 2003) and it is clear that high temperatures reduce survival, considerable uncertainty remains regarding the level at which temperature begins to be a significant problem. Assays for hsp72 would provide an independent measure of the temperature stress that fish experience. Hsp70 synthesis is also induced by other stressors such as various toxins that, like high temperatures, act by altering the biologically effective three-dimensional geometry of proteins. Accordingly, the presence of hsp70 proteins that cannot be accounted for by temperature stress probably indicates exposure to such stressors.

Field dissection: Sublethal stresses such as low levels of contaminants commonly induce changes in the color or gross appearance of organs and tissues that can be detected by field necropsy, and protocols have been developed for recording these systematically to obtain a profile of the health of a fish population based on percentages of observed anomalies (Goede and Barton 1990; Foott 1990, Adams et al. 1993).

Stomach Contents: Recently ingested prey provide a measure either of habitat quality, or of the ability of the fish to feed successfully. For example, terrestrial insects in stomachs provide evidence of the importance of riparian vegetation as a source of food. The amount of food in stomachs of recently emerged fry captured in screw (outmigrant) traps could provide evidence about the viability of early-emigrating fry.

Otolith microchemistry: The chemical composition of otoliths, particularly isotopic ratios, provides information about the habitats occupied by fish (e.g., Kennedy et al. 2002). Because of geological gradients along the Central Valley, otolith composition can even be used to identify the river from which the fish probably came (Barnett-Johnson et al. in prep), and if hatcheries use feed derived from marine organisms, hatchery fish can be similarly identified (Weber et al. 2002). The age at which fish enter brackish water can be determined by analyzing both the microchemistry and microstructure of otoliths (Secor 1992). The cost of analyzing otolith microchemistry is decreasing rapidly, so that it may soon be feasible for routine use in monitoring programs. If fish can be identified to stream by microchemistry and to run by genetic analysis, then the use of lower elevation habitats by different populations can be tracked, and it may be possible to manage the habitats for particular populations of concern.

Genetic markers: Enough genetic markers have been identified to allow Central Valley Chinook to be assigned to runs with good confidence (M. Banks, pers.comm. 2004). Given the importance attached to take of winter-run at the pumps, and the inadequacy of size-at-date criteria for assigning fish at the pumps to runs (Hedgecock 2002), genetically based assignments seem appropriate. They should also be used in monitoring of juveniles elsewhere, at least until better understanding is developed of the migratory behavior of the various runs. As genetic typing develops from a research endeavor to a standard practice, however, laboratories will be needed

that can do the analyses on a contract basis, and appropriately trained staff will be needed to develop sampling protocols, oversee the laboratory work, and interpret the laboratory results.

Smolt and pre-smolt emigration: Generally the same methods can be used to monitor emigration by larger juveniles as for smaller ones, but with gear such as screw traps the efficiency is higher for smaller fish than for larger ones. Counting fences may be an option for pre-smolt and smolt migrants because the fish are larger and spring flows are less variable than winter flows. Dempson and Stansbury (1991) and Warren and Dempson (1995) describe the use of a counting fence with juvenile Atlantic salmon. Studies or adaptive management that require good estimates of numbers of juveniles should be conducted where good estimates can be obtained.

Survival in lower rivers and Delta: Much effort has gone into estimating survival in the lower rivers and the Delta by marking fish with coded-wire tags, and relating recoveries to environmental conditions, with significant but somewhat limited results (Ch. 10). A basic problem is that several weak effects, rather than a few strong ones, seem to control survival, at least in the lower Sacramento River (Newman and Rice 2002; Figure 10-15). Unfortunately, as noted above, even where good estimates of survival rates can be obtained, there still may be controversy regarding their meaning. Generally, future coded-wire tag studies should be designed to address specific questions, such as the relative survival of fish in bypasses versus fish in the rivers, or take place in the context of an experimental design such as the VAMP or the Delta Cross Channel studies. The increased straying rate of fish used in such studies should be taken in to account in assessing the costs and benefits of the studies, however. Although the actual effects of such increased straying are uncertain, modeling studies such as Lynch and O'Hely (2001) or Goodman (2005) provide a logical framework for analyzing the issue.

CHAPTER SIXTEEN

HYDROSYSTEM MANAGEMENT

At the present time, no salmon enter these streams [Feather, Yuba, American, Mokelumne, Tuolumne rivers]. It would be safe to estimate that one-half the streams in this State to which salmon formerly resorted for spawning have, for this purpose, been destroyed by mining. As mining is the more important industry, of course, for this evil there is no remedy, other than by artificial means to increase the supply in those tributaries that are still the resort of these fish.

Report of the Commissioners of Fisheries for 1876 and 1877

Although the plans to build a huge dam on the Sacramento River had been in print for at least seven years (citation), it was not until complete specifications for the Shasta Dam were published and the bids received for consideration that a study of the probable effects of this dam on the fishery resources of the river system was begun.

Hanson et al. (1940:1)

Development of the California Water Plan [i.e., the SWP] will create considerable environmental changes in the Sacramento-San Joaquin Delta. Major changes will occur in the amount and pattern of water flow, water quality and salinity incursion. A knowledge of the major factors affecting fish distribution and abundance is essential if we are to protect and enhance, if possible, the fishery resources of the Delta ...

J. L. Turner (1966:9)

There is a growing public recognition that one of the most important public uses of tidelands – a use encompassed within the tidelands trust – is the preservation of those lands in their natural state, so that they may serve as units for scientific study, as open space, and as environments which produce food and habitat for birds and marine life, and which favorably affect the scenery and climate of the area.

Marks v. Whitney (1971) 6 Cal.3d 251

The prosperity and habitability of much of this state requires the diversion of great quantities of water from its streams for purposes unconnected to any navigation, commerce, fishing, recreation, or ecological use relating to the source stream. The state must have the power to grant unvested usufructuary rights to appropriate water even if diversions harm public trust uses. Approval of such diversion without considering public trust values, however, may result in needless destruction of those values. Accordingly, we believe that before the courts and agencies approve water diversions they should consider the effect of such diversions upon interests protected by the public trust, and attempt, so far as feasible, to avoid or minimize any harm to those interests.

National Audubon v. Superior Court (1983) 33 Cal.3d 419

This chapter gives a brief review of water management in the Central Valley as it affects salmon, and is intended mainly as background for readers who are unfamiliar with the area. More detailed descriptions can be found in various documents, such as NOAA Fisheries (2004),

and the 2005 California Water Plan (<http://www.waterplan.water.ca.gov>). Management of harvest is discussed briefly in Chapter 14; legal issues related to instream flows, particularly regarding the Public Trust Doctrine as applied to water in California, are described in Appendix C.

All major Central Valley rivers are blocked by large dams with substantial reservoirs, as well as by various smaller dams (Ch. 3). Water stored in major reservoirs in the Sacramento Valley is mostly released into the rivers for diversion farther downstream, particularly in the Delta, so on annual average, flows in the rivers below the dams are not much reduced from natural levels. Shasta Dam on the Sacramento River and Folsom Dam on the American are part of the Central Valley Project (CVP), while Oroville Dam is part of the State Water Project (SWP). New Bullards Bar Dam on the North Fork Yuba River is owned by a local agency, and unlike the others, supplies mainly local demand. In the San Joaquin Valley, stored water is applied mainly to local uses, and major canals divert directly from the reservoirs, so that average flows in the downstream reaches available to salmon are much reduced from their natural level. In the extreme case of Friant Dam on the San Joaquin River, not enough water is released to satisfy downstream water rights, water from the Sacramento system is pumped south in the Delta-Mendota Canal to satisfy those water rights, and not enough water remains in parts of the river to allow fish migration. Friant Dam and Goodwin Dam on the Stanislaus River are part of the CVP, while New Don Pedro Dam on the Tuolumne River and New Exchequer Dam on the Merced River are owned by local agencies, as is Pardee Dam on the Mokelumne River, which drains directly to the Delta. This patchwork of ownership does not facilitate coordinated management.

For historical reasons including the importance of the mining industry, California recognizes both riparian and appropriative water rights (Littleworth and Garner 1995). The Mediterranean climate of the state, with an annual summer drought, makes extensive irrigation necessary, and large areas of the Central Valley were subject to frequent winter and spring flooding before the development of levees, flood bypasses, and multi-purpose dams. These and other developments had disastrous effects on Central Valley salmon (Ch. 3). Over time, however, more attention has been given to protection of fish and the environment. Fish protection was essentially an afterthought in the design of the CVP (Hanson et al. 1940), but major studies of the Delta were conducted during the design of the SWP (e.g., Fish Bulletins 133 and 136). This trend continued as the environmental movement developed as a political force, laws such as the Endangered Species Act and National Environmental Policy Act and their California counterparts were enacted, and the public trust doctrine was extended by the California Supreme Court to provide environmental protection to tidelands and to navigable waters or their tributaries in *Marks v. Whitney* (6 Cal.3d 251) in 1971 and *National Audubon Society v. Superior Court* (33 Cal.3d 419) in 1983. Thus, water management in the Central Valley is based on a complex web of rights and regulations that has evolved over time to accommodate new projects and changing legal and political environments.

The 1987-1992 drought created great tension between instream and consumptive needs for water, particularly because of the recent listing of winter Chinook under the Endangered Species Act. Political gridlock ensued, but was eased by the 1994 Delta Accord, which provided for interim protection for listed species, along with certain principles for managing the Delta and water diversions in the short term. The Delta Accord was implemented largely through Decision 1641 by the State Water Resources Control Board (SWRCB), in 1995.

The SWRCB deals with water quality as well as water rights, and because water quality in the Delta depends on inflows, water quality standards are in effect flow standards. In the abstract, the SWRCB has great authority in California water issues, but in practice has played a cautious and limited role in the Central Valley in recent decades. Instead, the lead role was taken by CALFED, a consortium of state and federal agencies which was transformed by the Delta Accord into a multi-agency effort to develop a comprehensive resolution to Central Valley water issues. This effort now has independent institutional existence as the California Bay-Delta Authority. CALFED has programs dealing with such matters as new water storage facilities, levee stability, and water transfers, but also with ecosystem restoration and science. Notably, the ecosystem restoration program emphasizes the importance of geomorphic processes in the creation and maintenance of habitats. Generally, money for restoration programs has been distributed through a process of competitive proposals. However, the organizational structure of CALFED has been sharply criticized (CLHC 2005), and CALFED is now going through a period of “re-focusing” and “re-invigoration” (CALFED 2005).

The Environmental Water Account (EWA) is a major CALFED program that is designed to reduce conflicts between exports from the Delta pumps and protection of ESA-listed fish. Water is acquired and moved south of the Delta when the diversions are thought to be less harmful, or is acquired south of the Delta, and banked. The banked water is used to replace water that is not pumped at times that are thought to be more harmful (CALFED 2005). Water is acquired in several ways, but mainly by purchasing water from willing sellers, by temporarily relaxing normal restrictions on Delta pumping, or by using water allocated to environmental uses under other programs. In another aspect of the program, hydropower producers can be compensated for foregone power generation, for example when cool water is released from outlets below the hydropower intakes, in order to reduce temperatures in the river downstream. Although the EWA has been successful in reducing conflicts, it is less clear that it has benefited listed Chinook or steelhead (NOAA Fisheries 2004).

The Central Valley Project Improvement Act (CVPIA), enacted in 1992, made fundamental changes in the CVP authorization, giving protection and restoration of fish and wildlife and associated habitats equal priority to municipal and irrigation uses of water, and enhancement equal priority with hydropower production. In particular, section 3406(b) called for implementation of a program “which makes all reasonable efforts to ensure that, by the year 2002, natural production of anadromous fish in Central Valley rivers and streams will be sustainable, on a long-term basis, at levels not less than twice the average levels attained during the period of 1967-1991.” It also specified a number of measures intended to effect the new fish

and wildlife purposes, including dedication of 986.7 million m³ [800,000 acre feet] of “CVP yield” to fish and wildlife purposes, and setting up a restoration fund to provide up to \$50 million annually for fish and wildlife restoration. Section 3406(g) calls for development of “readily usable and broadly available models and supporting data to evaluate the ecologic and hydrologic effects of existing and alternative operations of public and private water facilities and systems in the Sacramento, San Joaquin, and Trinity River watershed.” These should provide improved scientific understanding of, among other things, “measures needed to restore anadromous fisheries”, and “development and use of base flows and channel maintenance flows to protect and restore natural channel and riparian habitat values.” The Secretary of the Interior was also charged with determining instream flow needs for all CVP controlled streams (3406(b)(1)(B)), based on recommendations of the USFWS after consultation with the CDFG.

Although some progress has been made, the CVPIA has made less difference than its proponents expected (McCarthy 1997). For one thing, litigation resulted in most of the 800,000 acre feet of CVP yield effectively being assigned to maintaining the status quo in the American River.⁸⁸ More fundamentally, implementation of the CVPIA revealed the limitations of current scientific knowledge and understanding, and the resulting difficulty in developing effective restoration programs. As a simple example, the estimate of natural production of Chinook salmon during the 1967-1991 base period is little more than an educated guess; estimates of harvest and estimates of varying quality of adult returns existed for most streams, but these were simply divided by two to estimate natural production (Mills and Fisher 1994).

All major Central Valley dams except Friant release water to provide habitat for fish below the dams, and as a result of current litigation, water presumably will soon be released from Friant, as well (Appendix C). Instream flow requirements are determined by the Federal Energy Regulatory Commission (FERC) for non-CVP projects with hydropower licenses,⁸⁹ and for other dams by the SWRCB, or alternatively, by a court, since the California courts also have jurisdiction over instream flow questions. From time to time instream flow requirements are reconsidered, for example when FERC licenses expire, and in most cases, instream flow requirements have been increased when permits were reviewed. For example, the license for Oroville Dam is currently under active review. For Shasta, a standard originally intended to protect navigation, 99 to 142 m³s⁻¹ (3,000 – 5,000cfs) depending on storage in Shasta, now effectively operates as a fish protection standard. Important legal developments affecting

⁸⁸ *San Luis and Delta Mendota Water Authority v. US* (U.S. District Court, E.D. Cal, CV-F-97-06140-OWW). As of 1992, the legally binding instream flow standards in the American River were set in the permit for Folsom Dam. These called for flows of 250 or 500 cfs (7.1 or 14.2 m³s⁻¹), depending on the time of year. Subsequently, the SWRCB set higher standards, in a 1972 decision permitting the proposed Auburn Dam. These called for 1,500 cfs (42.5 m³s⁻¹) unless CVP contractors were rationed, in which case somewhat lower flows applied. Since Auburn Dam was not built, the higher standards did not go into legal effect, although the Bureau of Reclamation operated Folsom as if they were. The CVPIA provided that the 800,000 acre-feet would go, among other things, to meet new legal obligations placed on the CVP following its enactment; thus, most of it has gone into the difference between the two sets of standards on the American River. Presumably, this was not the result intended by proponents of the CVPIA.

⁸⁹ Federal authority regulating hydropower production normally preempts state authority regarding instream flows (*California v. FERC*, 1990), but the Reclamation Act that provided authority for building the CVP explicitly required that state law be observed.

instream flows in the last few decades have mostly come from court decisions. In essence, these require that instream and consumptive uses of water be balanced, with considerable weight given to instream uses, and allow the balancing to be reconsidered in light of new information (Appendix C). To do such balancing in a straightforward way would require better information about the effects of water management on stream ecosystems than is generally available, which makes an adaptive (i.e., experimental) approach appropriate (Castleberry et al. 1996).

The major Central Valley reservoirs serve for both flood control and water storage. The reservoirs are drawn down in late fall to provide temporary storage for regulating runoff from winter storms, and then allowed to refill, mainly from snowmelt runoff, as the risk of major storms declines in the spring. During the winter, releases from the dams are increased during and after the storms, and then “ramped down” as the reservoir level drops back toward to the appropriate level. Maximum controlled releases are set at levels intended to prevent or at least minimize flood damage. Controls on the rate of change of the releases (ramping rates) to avoid stranding fish, or on decreases in flow after fish have spawned to avoid stranding redds, are other aspects of instream flow management. Generally these controls are specified in agreements, or are negotiated on a case by case basis by project operators and biologists for regulatory agencies, since the best course of action can depend strongly on the particular circumstances. Although there is no doubt that stranding does kill juvenile salmon, the importance of stranding mortality as a control of populations remains unclear (Ch. 8). Probably the stranding of fall-run redds below Keswick Dam is the most serious example.

During the summer a temperature gradient develops in reservoirs of much depth, with cooler and denser water lying below warmer water, so the temperature of releases from dams can be managed by adjusting the depth at which water is withdrawn and the amount of water discharged. Temperature management is simpler with reservoirs such as New Melones that are large relative to the annual flow in the river. Dams such as Shasta and Folsom were built without facilities for regulating the depth of withdrawals effectively, but these have been added recently, at considerable expense.

When cool water is released into a river during warm weather, its temperature rises toward an equilibrium temperature for the immediate environment at a rate that increases with the difference between the actual and equilibrium temperatures, and decreases with the mass of water involved (Deas and Lowney 2000). Thus, the temperature in the river at a given point downstream from the dam depends on the discharge, which affects both the amount of water to be warmed and the duration of the warming, since the velocity of the flow increases with discharge. Conversely, during cool weather in the fall-run spawning season, the rate of cooling may also decrease with discharge. Management of water temperature and management of instream flows are therefore linked, and temperature standards may act as flow standards.

Releasing cool water from dams can maintain habitat for salmonids for considerable distances. Even in the hot summer in the northern Central Valley, releases of cool water from Shasta Dam normally keep the Sacramento River cool enough for eggs of winter-run

Chinook to survive ($<14^{\circ}\text{C}$) for over 50 km (Deas et al. 1997). For the Sacramento River in the summer, the river usually approaches equilibrium temperature near the city of Sacramento. Managing water temperature is particularly challenging on the American River, where authorities try to maintain summer habitat for steelhead using a limited pool of cool water in Folsom Reservoir, and also to retain some cool water in reserve to accelerate cooling in the fall for spawning by fall-run Chinook. Management of water temperature on the Feather River is directed toward rice cultivation rather than fish; most of the water released from Oroville Dam passes through the shallow Thermalito Afterbay, where it warms enough that water diverted to irrigate rice will promote good growth, and cool water habitat in the river is restricted to the 13 km of channel upstream from the Thermalito Afterbay Outlet.

Since 1995, flows in the Delta have been managed largely in terms of an outflow-related salinity index called “ X_2 ,” as specified in Decision 1641 of the State Water Resources Control Board (SWRCB). X_2 is an ecologically-based index that is roughly the distance in kilometers up the axis of the Estuary from the Golden Gate to where the tidally-averaged, near-bottom salinity is 2 practical salinity units (psu) (Kimmerer 2004), and is determined by recent and current outflow from Delta.⁹⁰ The management requirements for “ X_2 days” vary according to the flow in specified Central Valley rivers, with X_2 held farther down-Estuary in wetter years and vice versa. Besides X_2 , SWRCB Decision 1641 imposes constraints or standards for diversions at the CVP and SWP pumps, specified in terms of an Export/Inflow (E/I) ratio and total export rates, minimum Delta outflow requirements, flow requirements in the lower San Joaquin and Sacramento rivers, and municipal and industrial (M&I) water quality standards at specific points in the Delta. Restrictions on the take of listed salmon and steelhead may also constrain pumping.

Three basic “knobs” are available for managing Delta water quality. First is regulating the rate of pumping itself; shifting diversions from one pump to the other allows for minor adjustments. Second is managing the routes of flow into the Delta, either by opening or closing the Delta Cross Channel, an artificial distributary that connects the Sacramento River with the interior Delta, or by closing the head of Old River, a distributary of the San Joaquin through which water flows to the pumps. Closing these channels causes water and associated fish to flow farther downstream in the mainstem rivers before moving toward the pumps, but closing the Delta Cross Channel causes more saline water to be entrained into the flow to the pumps, and blocking the head of Old River may cause more Delta smelt, another ESA listed species, to be so entrained. The third approach is to adjust Delta inflows, mainly by releases from CVP and SWP reservoirs. Thus, management of the Delta directly affects conditions in the rivers, and vice versa.

SWRCB Decision 1641 also established a major program to test the rationale for a controversial proposed standard for Delta inflow in the San Joaquin River to protect Chinook smolts. Although the data were clear that smolt survival was higher in wet years when spring discharge is high, a relation between flow and survival was not apparent at the lower range of

⁹⁰ See Kimmerer (2002) for a thorough discussion the history of and basis for X_2 .

flows that usually occur. Following negotiations by parties involved, a 12 year Vernalis Adaptive Management Program (VAMP) was designed to investigate the influence of flow and exports on the survival of fall-run smolts moving into the Delta from the San Joaquin River. The VAMP uses hatchery fish marked with coded-wire tags, released above and below the reach most affected by the pumps: upstream releases at Durham Ferry (rkm 109) and Mossdale (rkm 90), and downstream releases at Jersey Point. Recoveries are at Antioch (rkm 9) and Chipps Island. The experimental design of the VAMP calls for targeting flow and export combinations for a 31 day period between April 15 and May 31 (Table 16-1), although as a practical matter flows in the San Joaquin vary around the selected target by around $10 \text{ m}^3 \text{ s}^{-1}$. Results to date are inconclusive (Figure 16-1). The estimated survivals through the lower river seem low, given that runs persist in San Joaquin tributaries.

Table 16-1. Combinations of exports and flow into the Delta from the San Joaquin River that are targeted by the Vernalis Adaptive Management Program (VAMP).

Flow ($\text{m}^3 \text{ s}^{-1}$)	Exports ($\text{m}^3 \text{ s}^{-1}$)		
	42.5	63.7	84.9
90.6	X		
127.4	X		
161.4		X	
198.2	X		X

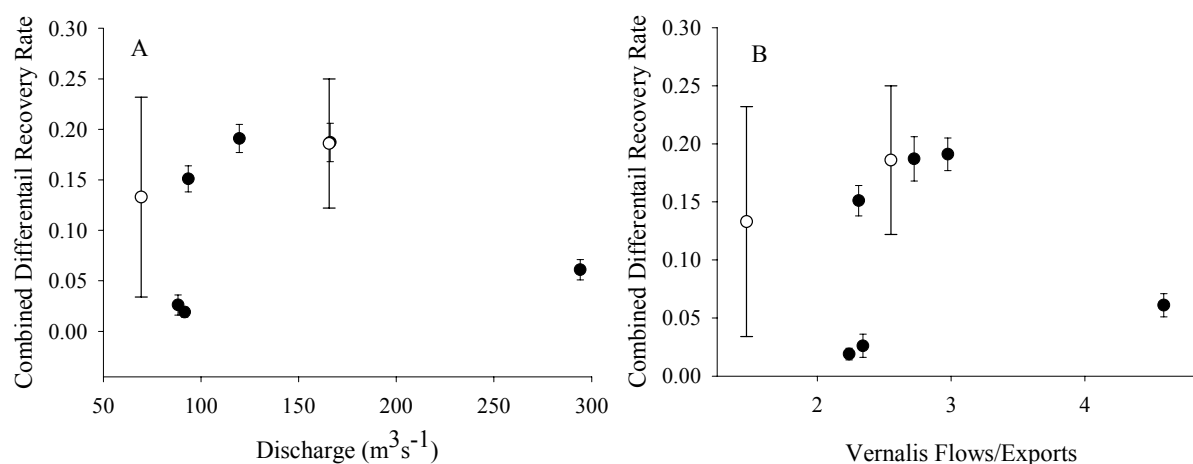


Figure 16-1. Combined differential recovery rate (a measure of survival) plotted (a) over discharge at Vernalis, and (b) the flow/export ratio, for the years of the VAMP experiment, 2000-2005 (filled circles) and two prior years, 1994 and 1997 (open circles). The two low survival years are 2003 and 2004. The combined differential recovery rate is the ratio of the recovery rates for the upstream and downstream release groups, which in turn are the ratios of the recoveries at both recovery sites to the number of fish released upstream. Bars show one standard error. Data from SJRGA (2004) and Lowell Ploss.

In general, the trend in management of the hydrosystem has been toward increased accommodation of environmental concerns, and the legal and institutional means for this trend to continue are in place. Whether the trend will continue is uncertain. The basic problem is that the increasing human population and climate change will place increasing stress on both the system and the web of legal and institutional arrangements by which it is managed. Warmer winters will mean that more precipitation will fall as rain, during individual storms as well as over the season, so to maintain the same level of flood control, dams may need to be drawn down farther in the winter, and there will be less snowmelt runoff to fill them in the spring. Like the Red Queen in Alice and Wonderland, hydrosystem management will need to run faster and faster just to stay in the same place.

CHAPTER 17

SUMMARY AND RECOMMENDATIONS

The impression that it is sought to convey throughout this paper is that in order to conserve our fisheries, there are many problems to be solved, all of them important. Among them that of the adoption of statistical methods having for their object the ascertainment of the abundance, rather than the amount taken, easily comes first. But such a substitution cannot be made without a knowledge of biology to supplement and guide it. And the biological phases of fishery science are in themselves many and important, dealing as they do with the rate of growth and movements of the fish. Then, finally, there is almost no adequate knowledge concerning the methods of conservation, or the prevention of depletion. We are at the threshold of a period of exploitation of our fisheries and we must be sure to begin an era of scientific investigation of our fisheries in time to adequately guide and control the exploitation.

W. F. Thompson (1919:59)

This chapter provides a brief summary of the main points presented in earlier chapters, followed by a summary review of the current status and future prospects of the various runs of Chinook and of steelhead. Some recommendations relevant to each of the runs are given, followed by general recommendations regarding management of salmon and their habitats.

Summary

For thousands of years, since the post-Pleistocene rate of increase in sea level slowed and allowed the formation of vast tidal wetlands in the Delta, five species of Pacific salmon in the Central Valley adapted to conditions more or less like those existing when the gold rush began (Ch. 3). Occasionally, salmon in the Central Valley were subject to severe stresses, such as major episodes of drought around 1,000 and 700 years ago (Stine 1994), but evidently they survived. By the time of the first serious study of salmon at the end of the nineteenth century, however, Central Valley rivers had already been heavily modified by hydraulic mining, dams and diversions, levees, clearing and snagging, and logging. Pink, chum, and coho salmon were effectively extinct in the Central Valley, as were many of the pre-existing populations of Chinook and steelhead, and perhaps also summer-run Chinook in the San Joaquin River (Ch. 2). Statements about the life histories and habitat use of natural salmon populations in the Central Valley are therefore more or less speculative, as are statements about their abundance, although from the historical accounts there is no doubt that Chinook were abundant, and from the documentation of the natural landscape such as the Map of Public Surveys and inferences about the habitats that it offered, it is not hard to imagine why; the Central Valley was a good place to be a salmon (Ch. 3).

Modifications of Central Valley rivers continued through most of the twentieth century. Impassable dams were built on all major Central Valley rivers where the rivers emerge from the foothills, fundamentally changing the hydrologic conditions in the moderate to low gradient

reaches downstream from the dams where Chinook and steelhead are now mainly confined. The loss of upstream habitat and other changes such as loss of wetlands, increased diversions, bank stabilization and gravel extraction are detrimental to salmon, but not all modifications of the rivers were adverse. Particularly in the Sacramento system, water is released from dams into the channels rather than into canals for conveyance to users, and this creates habitat that to some degree substitutes for habitat above the dams that has been lost to salmon. For example, winter Chinook now reproduce in parts of the Sacramento River that formerly were far too warm during their summer spawning season, and for a time, until the Red Bluff Diversion Dam (RBDD) went into operation, this substitute habitat was highly productive. Problems associated with the RBDD have been reduced by keeping the dam gates open for much of the year, but the productivity of the habitat with current salmon populations remains uncertain, as explained below.

Based on analysis of functionally neutral genetic markers, five distinct groups of Chinook populations persist in the Central Valley: fall-run, late fall-run, winter-run, and two groups of spring-run. These are grouped into three Evolutionarily Significant Units (ESUs) for purposes of the federal Endangered Species Act (ESA): fall-run (including late fall-run), winter-run, and spring-run. Of these, winter-run are listed as endangered under the ESA, and spring-run are listed as threatened. The spring-run ESU includes a population in the Feather River that groups very close to fall-run in genetic analyses. The remaining steelhead are winter-run (sometimes called fall-run), although formerly there were also summer-run. However, existing Central Valley steelhead populations in the American and Mokelumne rivers are derived from a coastal population that was introduced into hatcheries on those rivers (Ch. 2). Central Valley steelhead are also listed as threatened under the ESA.

Naturally reproducing Central Valley salmon pass through a series of environments during their lives, beginning in the gravel-beds of streams, and continuing through the lower gradient reaches of the streams, the San Francisco Estuary, the Gulf of the Farallones, the ocean, and back again (Chapters 6-11). All of these habitats have been highly modified (Ch. 3).⁹¹ Salmon have responded to these changes in various ways. Demographically, their numbers vary from year to year, depending both on natural variation in climate, ocean conditions, etc., and on variation in human activities such as harvest, hatchery production, and water management. Chinook populations have always varied substantially (Dettman et al. 1987), but, at least for fall Chinook in the Sacramento River and its tributaries, have done so particularly in the last two decades, from extreme lows around 1990 to much higher numbers around 2000 (Ch. 2).

Genetically, salmon have responded to the changed conditions in the Central Valley over tens of generations, enough time for considerable evolution to occur. As one example, age at maturity is genetically influenced, and the range of age at maturity in Chinook has decreased by about a year, presumably in response to selection by ocean harvest; 85 years ago there were many five year-olds and a few six year-olds, and now there are many four year-olds and a few

⁹¹ From a salmon's point of view, ocean habitats have been highly modified in the last century by the appearance of a major new predator that also harvests small fish on which salmon feed.

five year-olds. Size increases with age, so on average Central Valley Chinook are now smaller as well as younger (Ch. 13). Other changes have not been documented, but probably for lack of baseline data rather than absence of changes.

Developmentally, salmon may follow one or another life-history pattern, depending on both natural and anthropogenic conditions as well as on their genotypes. Currently, the great majority of naturally produced juvenile Chinook in the Sacramento River and its tributaries begins migrating downstream shortly after they emerge from the gravel, mainly in late winter or early spring, although some rear in the streams for a few months to a year before emigrating in late spring or in the following fall, winter, or spring (Ch. 2). The propensity to migrate at different times varies among runs and among populations, and among years. For example, in the San Joaquin tributaries, juvenile fall-run migrate mainly in winter in some years and in spring in others. Spring-run in several Sacramento River tributaries, the last wild salmon in the Central Valley, exhibit great diversity in life history patterns. Various cues, including the Earth's magnetic field, the angle and duration of sunlight, and the specific odors of different streams, are used to accomplish the required navigation and scheduling for these migrations, although just how it is accomplished remains unclear (Ch. 5). Similarly, although a good deal is known about the control of salmonid life history patterns (Ch. 1), just what determines the repertoire of behaviors used by Central Valley salmon to survive, grow and reproduce in these various habitats remains uncertain.

Whether or not "mitigation, protection, and restoration of fish and wildlife" have become co-equal with water supply as purposes of the Central Valley Project, as called for by the Central Valley Project Improvement Act (CVPIA), there is no doubt that in recent years salmon have been given much more consideration in the management of Central Valley rivers than was formerly the case (Ch. 16). Moreover, the conceptual foundation underlying salmon management is changing. The CALFED environmental restoration program, with an emphasis on restoring populations by restoring the natural processes that create habitat for the populations is one aspect of this change, which provides a basis for optimism regarding the future of salmon and steelhead in the Central Valley. Other aspects of salmon management, especially hatcheries and harvest, reflect an older, production-oriented approach based on an agricultural model (Ch. 1). Management actions based on these different points of view will be in conflict until a clear set of priorities is developed.

As one example, hatcheries now provide habitat for a large percentage of Central Valley Chinook and steelhead. In one sense the hatcheries have been successful, especially for fall Chinook, as evidenced by the very high returns in recent years. However, hatcheries have come under increasing criticism (Ch. 12). The National Resource Council (NRC 1996) identified demographic risks, genetic and evolutionary risks, behavior, fish health, physiology, and ecological problems as issues concerning the interaction of hatchery and naturally produced salmon. Genetic risks seem most serious, since genetic effects will persist even if hatchery production is ended. A group of distinguished scientists recently asserted that "Inevitably, hatchery brood stock show domestication effects, genetic adaptations to hatchery environments

that are generally maladaptive in the wild” Myers et al. (2004:1980), and there is evidence, discussed below and in Ch. 2, that hatchery fall Chinook have tended to replace naturally reproducing fish in the Central Valley, rather than supplement them. Thus, hatchery production tends to undercut the CALFED objective of promoting locally adapted, naturally reproducing populations of Chinook and steelhead.

As another example, there is little doubt that harvest is slowing the recovery of winter and spring Chinook. Almost a quarter of subadult winter-run were killed by the ocean fishery in 1998-2000, as were over a third of subadult spring-run in 1998 and 1999 (Feb. 2004 Interagency Workgroup Report to the PPMC, cited in CDFG 2004a and 2004b). Not all of these would have survived to spawn. Nevertheless, given the high mortality rate of small fish in the ocean, the ~1% of juvenile winter-run that are killed at the Delta pumps pales into insignificance by comparison.

Salmon monitoring in the Central Valley is conducted by a number of agencies or their consultants (Ch. 15). Coordination among the monitoring programs has improved in recent years, but the programs do not constitute a well integrated system, and primarily address questions based in the older production-based approach to salmon management.

The greatest threat facing Central Valley salmon is the projected warming of the regional climate (Ch. 3). The high mortality of adult spring-run in Butte Creek in two recent summers (Ch. 6) underscores this problem. Although the details remain uncertain, the world is getting warmer (Hansen et al. 2005; Barnett et al. 2005), and California increasingly will get less precipitation as snow (Mote et al. 2003; Hayhoe et al. 2004). Based on an analysis of an ensemble of climate models and emission scenarios and a reference temperature from 1951-1980, the most plausible projection for warming over Northern California is 2.5°C by 2050 and 5°C (9°F) by 2100, with a modest decrease in precipitation (Dettinger 2005). Climate change will complicate all the CALFED programs, but Chinook in the Central Valley are at the southern limit of their range, and it seems unlikely that any could survive a 5°C warming. These projections depend heavily on assumptions about future emissions of greenhouse gases, however, and because there are many other compelling reasons to reduce emissions, there may still be time to moderate warming enough to allow salmon to persist in the Central Valley.

The current status and future prospects of Chinook and steelhead in the Central Valley

Fall Chinook

The typical life history patterns of fall Chinook avoid freshwater during the summer, with juveniles migrating toward the Delta within a few days to a few months of emerging from the gravel. Much of the natural spawning habitat for fall-run is downstream from dams, habitat conditions on many streams seem good in many years, and large numbers of naturally spawned juveniles are produced in many years.

Fall-run returns have increased dramatically over the last decade, but much of the increase probably results from improved ocean conditions, together with stable hatchery production and

sharply reduced harvest. Few hatchery fall-run are marked, so the proportion of hatchery fish among returning adults is unknown, but presumably it is large (Ch. 12). The NOAA Fisheries status review concluded regarding fall Chinook that "...high hatchery production combined with infrequent monitoring of natural production make assessing the sustainability of natural production problematic, resulting in substantial uncertainty regarding this ESU" (Myers et al. 1998). This uncertainty remains.

There is good reason to believe that salmon populations that breed both in hatcheries and in streams can lose fitness for breeding in streams (Ch. 12; Hey et al. 2005), and that hatchery salmon may tend to replace rather than supplement naturally producing fish in consequence of this and of density-dependent mortality (Cooney and Brodeur 1998; Hilborn and Eggers 2000; Sweeting et al. 2003). Such replacement has been demonstrated for a Chinook population in New Zealand (Unwin and Glova 1997), and there is evidence from the Sacramento River system that it is happening in the Central Valley. Enough marked fall-run have been found recently in Mill and Deer creeks to indicate that these populations are largely hatchery strays (Ch. 2). A century ago, Mill Creek was known for its large run of fall Chinook, and its watershed is still largely undeveloped, so the heavy presence of hatchery fish there is an ominous sign. Recent trends in returns to Battle Creek and to the mainstem river also suggest replacement (Figure 2-5). Assuming that the number of Coleman Hatchery fish that stray to the mainstem Sacramento River roughly balances the number of naturally produced fish returning to Battle Creek, so that the mainstem and Battle Creek returns approximate the naturally produced and hatchery fractions of the population, it appears that the hatchery fraction is now dominant. If the early estimates of returns reasonably reflect the actual returns, the total numbers of fall Chinook upstream from Red Bluff were about the same in the years around 1960 as they have been in recent years, but most fall-run now return to Battle Creek.

Some problems with hatcheries have been recognized and are in various stages of correction in the Central Valley; for example moving fish from one stream to another has largely been stopped, although CDFG policy still permits it. Some problems, such trucking fish around the Delta, which increases straying, could be stopped but have not been. Other problems, such as the lack of natural mate selection and the different selective regimes in hatchery and natural environments, probably cannot be avoided.

For fall-run, probably the greatest near-term need is to revise hatchery and harvest policies and practices to be more consistent with restoration objectives. Recommendations in this regard are given in Chapters 12 and 13, and below. Climate change is the greatest long term hazard, as it is with other runs. At the least, warming will shorten the period in which the low elevation habitats used by naturally producing fall-run are thermally acceptable. This should particularly affect fish that emigrate as fingerlings, mainly in May and June, and especially those in the San Joaquin River and its tributaries.

Late fall Chinook

Late fall Chinook spawn in winter, and the juveniles pass a summer in freshwater before emigrating in the fall. Less is known about late fall-run than about other runs of Chinook, for several reasons. First, they spawn when field work in the rivers is much more difficult than in other seasons, and since the RBDD gates have been raised seasonally the estimates of adult returns of late fall-run have been less reliable than for other runs. Second, until recently, it was not possible to distinguish individual late fall-run fish from fall-run fish using genetic markers, so confirming ideas about late fall-run has been very difficult. Third, because late-fall are included in the unlisted Central Valley fall-run ESU (Myers et al. 1998), there is less motivation to study them. There were good returns of late fall Chinook in 1998 and 2002, but they have not increased as strongly in recent years as other runs. Returns to the Colman National Fish Hatchery have increased in recent years relative to returns of naturally produced fish, and although the percentage of hatchery fish among natural spawners is still low, it seems to be increasing (Ch. 2).

More needs to be learned about late fall-run. A good first step would be regular genetic typing of subsamples of juvenile Chinook captured in monitoring programs. Initial questions that could be addressed include an assessment of which streams support late fall-run on a regular basis, whether populations in smaller streams are strongly influenced by hatchery strays, and whether there are differences in the life history patterns of naturally produced and hatchery fish. It is also important to learn whether juvenile late fall-run from the hatchery are reasonable surrogates for naturally produced Chinook from other runs, as assumed in some survival studies.

Winter Chinook

Winter Chinook have increased sufficiently over the last decade to ease concerns about their near-term prospects (Ch. 2). If the population continues to increase, the biological significance of reversible sources of mortality such as losses of juveniles at diversions will become increasingly questionable. The population is already large enough to raise questions about the desirability of hatchery supplementation, and to justify loosening restrictions on mortality in monitoring programs, especially those producing information that will be useful for managing winter-run or other listed runs or species. Besides ocean conditions and reduced harvest, changes in the management of freshwater habitat, especially raising the RBDD gates, probably account for most of the recent increase in numbers of winter-run, although probably hatchery supplementation has also helped. The long-term prospects for winter-run are still poor, however. For winter-run, the embryonic and larval life stages that are most vulnerable to high temperatures occur during the summer, so winter-run are particularly at risk from climate warming. Currently there is only a single population. Removal of dams on Battle Creek should allow for re-establishment of a second population there, but whether the Battle Creek habitat will remain cool enough to be suitable as the climate warms seems doubtful.

Now that the temperature of releases from Shasta can be better managed, the RBDD is operated seasonally, and passage over the ACID Dam has been improved, the actions that seem most likely to help winter-run in the short term are extending the “gates out” period at RBDD to include the beginning of juvenile migration period, further reductions in harvest, and

improvements to the habitat used by juveniles during their slow migration down the Sacramento River. Implementation of the “meanderbelt” concept between Red Bluff and Colusa (SRCAF 2003) through continued acquisition of riparian land or easements to allow more natural processes of channel behavior and habitat creation may be particularly important; most of the bank protection works in this reach were constructed from the 1960s to the 1980s (Greco 1999), when the winter-run population was declining. More needs to be learned about the way that juvenile winter-run use this habitat, but studying small fish in large rivers is difficult, and new approaches probably are needed. Collecting samples with seines by itself will be of limited value, absent well-defined questions that the sampling can reasonably be expected to answer.

Installing an operable gate with a fish ladder at the Fremont Weir, so that some water could be diverted into the Yolo Bypass in all years, should also be helpful. This would allow adults that are attracted into the bypass to continue their upstream migration, and make the toe drain a regular distributary of the Sacramento River, with better prospects for a more natural connection to a floodplain than are available for the main channel. Passage down the bypass also keeps migrating juveniles away from the central Delta and the pumps.

As far downstream as the RBDD, juvenile winter Chinook can be reasonably well identified using length at date criteria, but this will change if spring Chinook populations increase in upper Sacramento mainstem or tributaries. Below the confluences of Mill and Deer creeks the utility of these criteria deteriorates, because of overlap with spring-run, and fish or subsamples of fish should be assigned to runs by genetic analyses. Making genetic analyses a routine part of monitoring for juvenile Chinook will allow better understanding of the actual spatial and temporal distribution of juveniles of all runs. The existing data from the RBDD screw traps seem like a rich vein for exploratory data analyses. For example, the length and number of emigrating winter-run appear to be inversely related, suggesting a density-dependent effect (Figure 8-5). As patterns are identified they should be fit with models that can be tested with future data.

It is probably time to begin modeling the effects of different scenarios for climate change on water temperature in the Sacramento River, to allow assessment of their consequences for all runs.

Spring Chinook

Spring Chinook have made a spectacular recovery in Butte Creek in recent years and have increased in other streams as well, although the population in the mainstem Sacramento River apparently has dwindled to very low numbers (Ch. 2). Favorable ocean conditions, including reduced harvest, doubtless has contributed to the increases in the tributaries. Why spring-run declined in the mainstem Sacramento River is less clear, but interbreeding with fall-run seems the most plausible explanation. Why spring-run have increased more in Butte Creek than in Mill and Deer creeks is also unclear. Substantial efforts have been made to improve adult passage in Butte Creek, and this may have released the potential of inherently more productive habitat in Butte Creek, but the question remains why the habitat is more productive, if it is. The low elevation habitat in lower Butte Creek and the Sutter Bypass may be responsible, and the use of

this habitat by juvenile spring-run deserves continued study. In any event, the population in Butte Creek has been high enough in some recent years that strong density-dependent mortality seems inevitable, and further large increases should not be expected.

Despite recent increases in several populations, the prospects for spring-run are dampened by global warming. Spring-run in Butte Creek are limited to low elevation habitat that is thermally marginal now, as demonstrated by high summer mortality of adults in 2002 and 2003, and will become intolerable within decades if the climate warms as expected. The same is true for other streams such as Beegum Creek, a tributary of Cottonwood Creek, where modest numbers of spring-run have been observed in recent years. However, suitable conditions should persist longer in Mill and Deer creeks, where fish can reach higher altitudes. Some existing or potential habitat should also remain for some time below various dams that currently release cool water through the summer. More habitat could be opened up in Battle Creek if the proposed restoration plan for that stream is implemented; although it seems doubtful that the habitat will remain cool enough in the summer for the eggs of winter-run to survive if the predicted warming occurs, it may remain cool enough to provide holding habitat for adult spring-run, which are considerably more tolerant of warm water. Opening the Yuba River to spring-run is also under study. Temperature criteria developed from Butte Creek data should be used to evaluate the thermal suitability of habitats there, since temperature criteria developed from the literature are likely to be too conservative. On the other hand, the investigations should consider future as well as current temperatures.

Spring-run are restricted to low elevations in Butte Creek by natural barriers as well as PG&E dams. The Butte Creek canyon is so steep that opening access to higher elevation habitat would be difficult, but the possibility of doing so should be reassessed in light of global warming. In the meantime, consideration should be given to trucking a few adults around the PG&E dams to avoid losses of complete year classes, as may have happened in 2002, although the trucking would work only if the PG&E diversions were screened.

Chinook return to the Feather River in spring, but genetic analyses show that these are very closely related to fall-run (Figure 2-2). These fish hold over through the summer in the river, and until recently attempts at the hatchery to isolate them reproductively from fall-run have not been fully effective. Fish also appear in the Yuba River in spring, and it seems likely that these are similar. Whether or not these fish belong in the spring-run ESU, they do contribute to the phenotypic diversity of Central Valley Chinook, and so deserve attention, especially given the possibility that appropriate habitat for spring-run will become available in the Yuba River. In the meantime, a portion of the low-flow channel in the Feather River might be fenced off in early summer to keep these early fish spatially isolated from fall-run. The hatchery production target for Feather River spring-run has recently been reduced, from five to two million smolts. The appropriate level of hatchery production should be considered carefully, using analytical approaches such as those reported in Lynch and O'Hely (2001) or Goodman (2005).

Opening new habitat for reproduction raises the question whether fish from other streams should be introduced to seed the new habitat, or whether fish should be allowed to colonize it on their own. There is not an obvious answer to this question. Past transfers of fish from one stream to another are now commonly regarded as mistakes, and this history cautions against deliberate transfers. That is, we may think that we now understand enough to avoid past mistakes, but probably biologists in the past also thought that they understood enough to make wise choices. However, opening habitat that may not be colonized for decades does not seem feasible politically, even if it were desirable biologically. Where some fish are using the habitat, as in Clear Creek, it seems appropriate to give them a chance to colonize it. On the other hand, it seems far less likely that fish would spontaneously recolonize the San Joaquin River in any reasonable time, assuming that adequate instream flows are restored, so deliberate transfers seem appropriate.

Steelhead

The current status of naturally-produced anadromous steelhead in the Central Valley is poor; abundance data are scant, but based on the ratio of marked and unmarked smolts captured in the Chipps Island trawl, it appears that the anadromous populations total only a few thousand adults, and an unknown percentage of these are progeny of hatchery fish, some from an out-of-basin stock. On the other hand, if the non-anadromous component of the population is taken into account, the status of *O. mykiss* in the Central Valley is much less dire. Like spring Chinook, steelhead have been cut off from most of their natural spawning habitat on most Central Valley rivers by dams. Some of these dams, for example Shasta and New Melones, release enough cool water through the summer to provide good habitat for non-anadromous *O. mykiss*, and it appears that many fish are taking advantage of it. It is also possible that *O. mykiss* in Sacramento River tributaries such as Clear Creek have become potadromous rather than anadromous; that is, they may migrate downstream to the river, but not continue to the ocean.

Steelhead are heavily influenced by hatchery production in several rivers, with unknown consequences for the fitness of naturally spawning fish. This is particularly a problem on the American River, where the naturally spawning population is included in the Central Valley steelhead ESU although the hatchery population is not, but naturally spawning fish are mainly hatchery fish from a coastal stock (Hannon et al. 2002; 2003; Nielsen et al. 2005). If fish that really belong in the Central Valley ESU actually occur in the American River, then hatchery production is a major threat for them, and should at least be sharply curtailed. It seems more sensible to recognize that the steelhead in the American River are the legacy of a past mistake,⁹² and to manage the river for fall Chinook instead. A similar situation exists in the Mokelumne River.

⁹² When Nimbus Hatchery began operations it was unsuccessful at propagating the existing population of steelhead in the American River, and eggs from the northern California coast were introduced to found the existing population.

General recommendations for management

1. Take climate change into account.

Regional climate models are improving (Hayhoe et al. 2004), and before long may provide more specific forecasts that are usefully reliable for guiding management, but the reality of warming is certain enough that it should be factored into planning for restoration activities. As a practical matter, this means that restoration activities that will benefit multiple species or ecosystems should be preferred over those that are specific to salmon, especially along streams where water temperatures are less likely to remain tolerable for salmon. Restoration activities in lowland areas such as tidal marsh restoration should also take account of projected increases in sea level. Change in the amount and distribution of precipitation should also be expected, so designing restoration projects to match historical hydrology is problematic. This seems particularly so for restoration plans that aim to reconstruct floodplains to match miniaturized but more naturally variable hydrology downstream from dams; whether such plans are robust to plausible changes in climate should be considered before large amounts of money are committed to them.

Managers should resist the temptation to allow uncertainty regarding precisely how climate will change to be used to justify not taking future climate change into account in restoration planning. One reason for this is that uncertainty about the extent of global warming results mainly from uncertainty about future emissions of greenhouse gases (Hayhoe et al. 2004); ignoring climate change will likely make it worse.

2. Recognize the limitations of concepts, and use multiple approaches to evaluate problems and policies.

It is well known that the concepts of waves and particles can both be usefully applied to light, but that neither concept allows a complete description of its behavior. In a similar way, various conceptual models or analytical approaches can be usefully applied to salmon or habitats or ecosystems, but none allows complete or even generally sufficient descriptions of them. For example, concepts from population, behavioral, and physiological ecology might all be usefully applied to different aspects of some problem regarding salmon management. The saying that “all models are wrong, but some are useful” applies to conceptual models as well as other kinds, and different concepts or approaches will be more or less useful depending on the particular aspect of an issue that is under consideration. Which concepts or points of view are useful often depends on the spatial and temporal time scales involved, so problems and policies should be considered in terms of various spatial and temporal scales.

3. Take evolutionary considerations into account.

Evolution can occur rapidly in salmon populations. For example, a stream-type life-history pattern has developed in Chinook populations in New Zealand that were founded from ocean-type, fall-run fish about 100 years ago, as have other differences in life history patterns among Chinook in different New Zealand Rivers (Quinn et al. 2000; Quinn et al. 2001). In a statement supported by citations to studies of salmon as well as other organisms, Stearns and Hendry (2004:15) observed that “A major shift in evolutionary biology in the last quarter century is due

to the insight that evolution can be very rapid when large populations containing ample genetic variation encounter strong selection (citations omitted).” Management can impose strong selection, and managers should consider the consequences.

4. Take populations and their habitats as the unit for management.

The different runs of salmonids in the Central Valley, and the different life history patterns expressed by the runs, historically were associated with and presumably represented adaptations to particular habitats. If the runs and diversity in life history patterns are to be maintained, access to these habitats or their equivalents must be preserved or restored (Healey and Prince 1995). As a consequence, highest priority should be given to restoration actions that match fish with appropriate environments; for example, restoring access for steelhead to the South and Middle Yuba should have higher priority than managing temperature in the lower American River for steelhead, where the habitat is more appropriate for fall Chinook (and the existing steelhead population is derived from an out-of-basin stock). Maximizing access for winter-run and spring Chinook and steelhead to appropriate habitat in Battle Creek, and providing seasonal access for juvenile salmon to flooded overbank habitat, e.g., in the Yolo Bypass, should also have high priority.

Lichatowich (1998) noted that stocks have been the traditional unit of management, but, building on Healey and Prince (1995), argued that the management units need to be stocks and their habitats. Booke (1999) similarly argued that acceptable stock concepts must be based on inherited markers that define a specific group of fish plus its habitat. In practice, however, management convenience has sometimes resulted in the development of multi-population stocks such as Sacramento River Fall Chinook. Restoration, on the other hand, typically deals with habitats that are occupied by particular populations, and these habitats and populations should be the basic units of management.

5. Take account of the evolutionary and ecological effects of hatcheries and harvest, as well as the demographic effects.

In a recommendation that seems well directed to CALFED, NRC (1996:321) advised that “The approach to hatchery operations should be changed in accordance with the goal of rehabilitation and the ecological and genetic ideas that inform that goal.” This is a major undertaking. To this end, CALFED should sponsor a major review of Central Valley hatcheries in which all options are up for consideration; these include sharply reducing hatchery production, consolidating hatchery production to one or two streams, moving Chinook hatcheries to coastal streams without natural populations, and abandoning hatchery production altogether (Ch. 12). In the meantime, all hatchery fish should be marked, as recommended by NRC (1996) and as legally required for salmon intended for harvest that are produced by federally funded hatcheries.⁹³

⁹³ Public Law 108-7, enacted in Feb. 2003, contains the following language in sec. 138: “The U.S. Fish and Wildlife Service shall, in carrying out its responsibilities to protect threatened and endangered species of salmon, implement a system of mass marking of salmonid stocks, intended for harvest, that are released from Federally

The ocean troll fishery inherently selects against more slowly maturing fish, because it targets subadult as well as maturing fish (Clark 1929; Ricker 1980). The available evidence indicates that ocean harvest of sub-adults has narrowed the range of age at maturity for Central Valley Chinook by about a year. A shift to a terminal fishery, for example using gill nets in the bays, may be necessary to avoid continued selection against late-maturing fish, and continued decrease in average age at maturity. In the past, the California Fish and Game Commission favored a terminal fishery over the troll fishery for such reasons (Scofield 1929). Commercial harvesting in a terminal fishery would also allow a much tighter focus on unlisted runs, although the early season recreational fishery has the greatest impact on winter-run (CDFG 2004a). At the least, a shift to a terminal fishery deserves serious study.

PFMC objectives for adult returns should be harmonized with CALFED objectives. Goals for adult returns should be revised and put on a scientifically supportable basis. In particular, separate goals for adult returns should be set for naturally produced fall Chinook in major streams, including the San Joaquin River tributaries. Goals should be set in terms of the expected number of progeny, which would give more weight to larger females.

6. Treat management as experimental, and try to learn from it.

The California Department of Fish and Game recently suspended stocking trout in a sample of alpine lakes in the Sierra Nevada, and studied whether the existing populations were able to maintain themselves by natural reproduction (Armstrong and Knapp 2004); by and large they were, and comparisons of otoliths from fish in stocked and unstocked lakes indicated that density-dependent reductions in growth rates occurred in the stocked lakes. CALFED has properly emphasized the importance of such active adaptive management, in which actions are taken deliberately to perturb the system being managed, in order to learn from its response. For example, hatchery production of Chinook might be sharply reduced for some number of years to test whether there are density-dependent interactions between hatchery and naturally produced fish, such that increased productivity of the naturally produced fish would compensate for part or all of the foregone hatchery production. Unfortunately, the scarcity of good examples of active adaptive management demonstrates how difficult such management experiments are to arrange, and particularly in the short term, the political feasibility of active adaptive management does not seem likely to increase.

Deliberate management experiments are necessary where there is otherwise little variation in some variable that is central to the problem at hand, such as the hatchery production of juvenile salmon and steelhead. For many problems, however, there is substantial variation in the important variables because of natural variability in climate, and this makes a more passive approach to adaptive management viable. The critical element for success in such passive adaptive management is a state of mind: looking always for opportunities to learn. This leads to

operated or Federally financed hatcheries including but not limited to fish releases of coho, chinook, and steelhead species.”

thinking of management actions as experiments, formulating hypotheses, and trying to conduct monitoring that is adequate to get the experimental results and test the hypotheses. Monitoring should be approached from this point of view.

7. Simulate major restoration actions and monitoring programs.

Restoration actions are expensive experiments. CALFED has properly stressed the importance of articulating the conceptual model or hypotheses upon which proposed actions are based. For actions of any magnitude, it should be worthwhile to develop a numerical formulation of the conceptual model so that likely outcomes of the action can be evaluated quantitatively, and the sensitivity of the outcomes to various parameters in the model can be assessed. This process can help identify key uncertainties and avoid expensive mistakes. The Clear Creek Decision Analysis and Adaptive Management Model (Alexander et al. 2003) that has been developed with CALFED funding is an example of this approach; unfortunately, as that example demonstrates, such modeling can be very difficult. The Water Use Planning (WUP) process in British Columbia, more or less a Canadian equivalent of the FERC relicensing process, provides more successful examples (e.g., McDaniels and Gregory 2004).

In many cases, the monitoring that is proposed to accompany the action should also be simulated, with appropriate random noise added to simulate measurement uncertainty, to determine how strong a signal the restoration action must generate to be detected with reasonable probability. Monitoring programs not associated with specific restoration actions should also be simulated. Ludwig and Walters (1985) urged that "all estimation schemes should be tested with simulated data where the parameter values are known in advance, since accuracy and consistency cannot in principle be determined from 'real data' where parameter values are unknown." Williams (1999) used such simulations to show the limitations of the salmon monitoring proposed by the Comprehensive Monitoring and Assessment Program (CAMP). This should be standard practice, especially for major efforts such as the VAMP.

Developing a larger group of modelers and statisticians to work on Central Valley salmon issues would be a major step forward. Ideally, this group should be large enough to raise the general standard of numeracy among Central Valley salmon biologists, but small enough that it remains focused on issues of importance to other biologists and managers, rather than on modeling itself. It is also important that training opportunities be offered to biologists who are less well versed in statistics and data analysis, so that good communication is possible.

8. Take account of developments in other areas of biology that may help address questions regarding salmon biology and management.

The development of genetic markers for the various runs of Chinook has substantially improved understanding of questions concerning take of listed Chinook at the Delta pumps, and should allow better understanding of the migratory behavior of the various runs as genetic typing is incorporated into existing monitoring programs. With a few exceptions, however, the markers are not associated with traits conferring fitness. The development of a "gene chip" for salmon (Rise et al. 2004) may provide a means to address other genetic questions that do involve fitness.

For example, it may be possible to determine whether domestication has occurred in hatchery fish by examining whether patterns of gene expression in the face of low oxygen levels or other stresses are the same in wild fish and in fish with long histories of hatchery culture. Appropriate advantage should be taken of this and other technological advances.

9. Put the effects of the pumps on Chinook and steelhead into proper perspective.

It seems clear that the Delta pumps are a problem for Central Valley Chinook, especially for San Joaquin River Chinook, and presumably the problem will increase as pumping increases. Nevertheless, it does not appear that the pumps *per se* are **the** problem. Probably because of the assumption that juvenile salmon would passively follow the water (e.g., Erkkila et al. 1950), the pumps have received more attention as a factor in the decline of salmon and other fishes than seems justified by the available evidence. That said, it seems artificial to consider the pumps separately from truncated habitat, reduced spring flows, freshening of the Delta, and other changes in Central Valley salmon habitats that result from the entire system for water management, of which the pumps are an important part. The critical point is that Central Valley salmon would benefit from a more rational allocation of management attention over problems.

10. Put human intervention into proper perspective.

Restorationists have properly emphasized the desirability of maintaining or re-creating conditions such that natural processes maintain habitat in which wildlife can go about its business without human intervention. Thus, for example, CALFED has emphasized the importance of allowing high flows to power natural fluvial processes that sort bed sediments in streams and create spawning habitat. This is the best approach for protecting Chinook and steelhead in the Central Valley, as with the meanderbelt concept, mentioned above. However, the prevalence of dams on Central Valley rivers and human intervention in global climate limit the practicable scope for this approach, and alternatives should be entertained where it is not feasible. For example, on heavily regulated rivers where it is not feasible to provide “flushing flows,” mechanical cleaning of spawning gravels should be considered, if gravel quality is a problem. Similarly, where dams prevent natural spatial segregation between runs, artificial separation is necessary if the distinct runs are to be maintained. For example, fall-run are now restricted to the valley reach of Clear Creek, to protect spring-run that spawn farther upstream in the canyon reach. Potentially, this approach could be followed on the Sacramento and Feather rivers, as well, if the fish ladder on the ACID Dam were closed say from the end of July to when the dam is removed in October, or if fall-run were blocked from part of the low-flow channel of the Feather River. In other words, the desirability of restoring ecological functions does not justify an ideological opposition to direct human intervention in the affairs of Chinook and steelhead when there is no good alternative. However, it should be a last resort.

11. Allocate streams to different treatment groups.

Central Valley streams vary in the extent to which they have been modified or degraded, and have different prospects for restoration, so it makes sense to treat them differently. Although this variation probably is more continuous than discrete, it seems useful to consider three basic treatment groups to which different restoration approaches or objectives should be applied.

Restore selected streams to a semblance of natural conditions. For several streams, restoration to an approximation of natural conditions seems feasible, and should be pursued. An approximation of natural conditions does not mean pristine, and this objective does not require curtailing all diversions or ending human occupancy and use of the land along the streams, but it does mean trying to maintain or restore the main features and functions of natural stream ecosystems. Mill Creek and Deer Creek are the obvious candidates; the significant problems with these streams are concentrated at their lower ends and seem tractable, and a major restoration program is planned for Battle Creek. This objective also seems feasible for Butte Creek and for the Cosumnes River. In a sense, the conceptual foundation for this treatment is "If it's natural, it's right," although biological, practical and legal considerations will require that this be relaxed more or less frequently. Management should still be adaptive, with explicit hypotheses and monitoring for restoration work, but rehabilitation of natural conditions and processes would be the default objective.

Restoration actions appropriate for this set of streams include acquiring land or easements along the streams from willing sellers; providing substitute sources of water for diversions, especially during critical periods; removing or modifying dams that block or impede migration; removing inappropriate bank stabilization works, setting back or removing levees, and rebuilding bridges with longer spans to allow passage of tree trunks.⁹⁴

Select other streams for intensive restoration or active adaptive management of instream flows. Focusing active adaptive management efforts in some streams should make it easier to do things on a large enough scale to get clear responses. Streams should be selected primarily in terms of opportunity for large-scale restoration, or suitability for experimental management. The Yuba River, for example, apparently offers the best opportunity for restoration of holding and spawning habitat for spring-run salmon and access to tributary habitat for steelhead, although a recent court decision may result in the reintroduction of spring-run to the San Joaquin River below Friant Dam (Appendix C). The "low flow" channel of the Feather River, between Oroville Dam and the return from the Thermalito Afterbay, seems well suited for instream flow experiments. The river is large enough to be a reasonable model for other Central Valley streams, but it is small enough to allow populations to be monitored with reasonable accuracy, and flows are normally well controlled. Some streams may be suitable for an active adaptive approach to certain questions, but not to others, so this grouping should be flexible. For example, the installation of a temperature control device has made the water temperature in the lower American River controllable to a useful degree, so that stream is well suited for temperature-related experiments in the summer and fall, but it is less suited for flow-related experiments.

Apply passive adaptive management or more "status quo" management to the remaining streams, at least for the time being. Passive adaptive management can be effective when there is

⁹⁴ It is also important to stop cutting fallen trees into smaller pieces, as was done recently along Butte Creek (Williams et al. 2002).

substantial variation in the factor of interest. For example, flow in most Central Valley rivers varies more from year to year variation in the weather than it would from any plausible experimental variation, so passive adaptive management seems appropriate for flow-related questions, and is much easier and less expensive to implement than active adaptive management. Passive adaptive management nevertheless requires clear hypotheses and good monitoring to be effective, so in subtle but important ways it is quite different from traditional or status quo management. Good monitoring is difficult and expensive, however, and within this group of streams it should be concentrated where it is most likely to be effective. This means that some streams may be left with status quo management and minimal monitoring. Restoration will be difficult enough in the best of circumstances. Adding a requirement of geographical "fairness" to the program will make it that much more difficult.

12. Develop a unified and consistent conceptual foundation for salmon management.

Salmon management in the Central Valley, as in most other areas, suffers from a kind of schizophrenia. Much of it, especially hatchery and fisheries management, is still based on a production perspective, but much of it is now often based on a population perspective.⁹⁵ This schizophrenia is well reflected in the CVPIA, which mandated efforts to increase the populations of naturally-produced anadromous fishes by a program that gives "first priority to measures which protect and restore natural channel and riparian habitat values," but at the same time provided for rehabilitation and expansion of the Coleman National Fish Hatchery. Similarly, CALFED is undertaking an ecosystem-based restoration program, in part to restore depleted and listed stocks of Central Valley Chinook, while state and federal agencies maintain industrial-scale hatcheries that support mixed-stock fisheries.

The very high returns of fall Chinook in recent years that resulted in high rates of prespawning mortality in streams with hatcheries (e.g., Table 12-3) provides a clear example of objectives in conflict. The ocean fishing season has been sharply cut back in order to reduce harvest of winter-run and spring-run, and of Chinook from the Klamath River. However, hatchery production has been maintained at the same level, either to support high catch rates during periods when fishing was allowed, or from management inertia. The result has been so many hatchery fish spawning in the rivers that the spawning success of naturally produced fish has been compromised. Given the evidence that hatchery fish are genetically less well adapted to natural conditions (Ch. 12), there is a conflict between the objectives of trying to support the coastal fishing industry, and trying to allow recovery of the genetic integrity of Central Valley fall-run. This conflict may have a partial physical solution, in moving hatcheries to coastal streams that do not support wild Chinook, but ocean harvest of sub-adults will continue to select against more slowly maturing fish. Hatchery release practices provide another example of conflicting objectives. On the one hand, trucking smolts around the Delta results in more sub-adults in the ocean and more adult returns than releasing smolts at the hatcheries. However, the resulting increased straying rate will tend to obliterate any local differentiation and adaptation that may still exist, or to prevent them from redeveloping.

⁹⁵ Population and production perspectives are described in Ch. 1.

Because management actions based on these differing perspectives can be at cross-purposes, it is important that managers be given clear guidance on priorities. This can best be done by developing a unified and consistent conceptual foundation for the management of Central Valley rivers and the salmon that inhabit them. This review has advocated a population perspective, and clearly I hope that such a point of view will be adopted, but in fairness to the people who are expected to implement our policies, the temptation to finesse conflicts among management objectives should be resisted.

Reference List

- 2002 EWA Review Panel. 2002. http://science.calwater.ca.gov/pdf/EWAReviewFinal_1-27-03.pdf
- Aceituno, ME. 1990. Habitat preference criteria for fall-run Chinook holding, spawning, and rearing in the Stanislaus River, California. Sacramento, California: U. S. Fish and Wildlife Service.
- Aceituno, ME. 1993. The relationship between instream flow and physical habitat availability for Chinook salmon in the Stanislaus River, California. Sacramento, California: United States Fish and Wildlife Service.
- Achord, S, Levin, PS, Zabel, RW. 2003. Density-dependent mortality in Pacific salmon: the ghosts of impacts past? *Ecology Letters* 6:335-342.
- Adams, SM, Brown, AM, Goede, RW. 1993. A quantitative health assessment index for rapid evaluation of fish condition in the field. *Transactions of the American Fisheries Society* 122:63-73.
- Adkison, MD. 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? *Canadian Journal of Fisheries and Aquatic Sciences* 52:2762-2777.
- Alabaster, JS. 1989. The dissolved oxygen and temperature requirements of king salmon, *Oncorhynchus tshawytscha*, in the San Joaquin Delta, California. *Journal of Fish Biology* 34:331-332.
- Alderdice, DF, Wickett, WP, Brett, JR. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. *Journal of the Fisheries Research Board of Canada* 15:220-250.
- Alexander, CAD, Marmorek, DR, Peter, CN, Porter, M. 2003. Clear Creek decision analysis and adaptive management model: design document, draft 1.5. Vancouver, B. C.: ESSA Technologies.
- Allen, MA. 2000. Seasonal microhabitat use by juvenile spring Chinook salmon in the Yakima River basin, Washington. *Rivers* 7:341-332.
- Anderson, J, May, B, Williams, J, Lindley, S, Greene, S, Hanson, C, Low, A, McEwan, D, MacFarlane, R, Swanson, C, Yoshiyama, R, Teel, D, Banks, M, Williamson, K, Arden, W, Werner, I, Ainley, D, Viele, DCS, Kondolf, M, Grimaldo, L, Sommer, T, Killam, D, Brown, M, Ward, P, Hamilton, A. In press. Report from the Central Valley Technical Recovery Team Salmon Workshop. To be published as a NOAA Technical Memorandum.
- Anderson, JJ. 2003. Toward a resolution of the flow/survival debate and the impacts of flow augmentation and water withdrawal in the Columbia/Snake River system. Seattle: Columbia Basin Research, School of Aquatic and Fishery Science, University of Washington.
- Arkoosh, MR, Johnson L., Rossignol, PA, Collier, TK. 2004. Predicting the impact of perturbations on salmon (*Oncorhynchus* spp.) communities: implications for monitoring. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1166-1175.
- Armand, DF, Lannan, J, McNeil, WJ, Smith, C, Wedemeyer, GA. 2000. <http://www.steelheadclub.com/pdfdocs/Perspectiveonhatcheries.pdf>
- Armstrong, TW, Knapp, RA. 2004. Response by trout populations in alpine lakes to an experimental halt to stocking. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2025-2037.
- Ashley, MV, Wilson, MF, Pergams, ORW, O'Dowd, DJ, Gemde, SM, Brown, JS. 2003. Evolutionarily enlightened management. *Biological Conservation* 111:115-123.
- Atwater, BF. 1980. Attempts to correlate the late Quaternary climatic records between San Francisco Bay, the Sacramento-San Joaquin Delta, and the Mokelumne River, California [dissertation]. Newark: University of Delaware.
- Atwater, BF. 1982. Geologic maps of the Sacramento-San Joaquin Delta, California. San Mateo, California: U. S. Geological Survey. MF-1401.
- Azevedo, RL, Parkhurst, ZE. undated. The upper Sacramento River salmon and steelhead maintenance program, 1949-1956. United States Fish and Wildlife Service.
- Bacon, CR, Weber, PK, Larsen, KA, Reisenbichler, R, Fitzpatrick, JA, Wooden, JL. 2004. Migration and rearing histories of Chinook salmon (*Oncorhynchus tshawytscha*) in ion microprobe Sr isotope and Sr/Ca transects of otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2425-2439.
- Baiocchi, JC. 1980. Use it or lose it: California Fish and Game Code Section 5937 and instream fishery resources. *U. C. Davis Law Review* 14:431-460.

- Baker, PF, Morhardt, JE. 2001. Survival of chinook salmon smolts in the Sacramento-San Joaquin Delta and Pacific Ocean. In: Brown, RL, editor. Fish Bulletin.2. p. 163-182.
- Baker, PF, Speed, TP, Ligon, FK. 1995. Estimating the influence of temperature on the survival of chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento - San Joaquin River Delta of California. Canadian Journal of Fisheries and Aquatic Sciences 52:855-863.
- Baldwin, DH, Sandahl, JF, Labenia, JS, Scholz, NL. 2003. Sublethal effects of copper on coho salmon: impacts on nonoverlapping receptor pathways in the peripheral olfactory nervous system. Environmental Toxicology and Chemistry 22:123-131.
- Ballard, WW. 1973. Normal embryonic stages for salmonid fishes, based on *Salmo gairdneri* Richardson and *Salvelinus fontinalis* (Mitchell). Journal of Experimental Zoology 184:7-26.
- Baltz, DM, Vondracek, B, Brown, LR, Moyle, PB. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Trends in Ecology and Evolution 116:12-20.
- Baltz, DM, Vondracek, B, Brown, LR, Moyle, PB. 1991. Seasonal changes in microhabitat use by rainbow trout in a small stream. Transactions of the American Fisheries Society 120:166-176.
- Bams, RA. 1969. Adaptations in sockeye salmon associated with incubation in stream gravels. In: Northcote, TG, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Vancouver: Institute of Fisheries, University of British Columbia. p. 71-88.
- Banks, M, Barton, M. 1999. Microsatellite DNA variation among Klamath River chinook salmon sampled from fall and spring runs. Bodega Marine Laboratory, Bodega Bay, California.
- Banks, MA, Rashbrook, VK, Calvaetta, MJ, Dean, CA, Hedgecock, D. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Canadian Journal of Fisheries and Aquatic Sciences 57:915-927.
- Barnett-Johnson, RC, Ramos, FC, Grimes, CB, MacFarlane, RB. In prep. Identifying the natal origin and migration history of adult salmon using Sr isotopes obtained by ablation MC-ICPMS. NMFS, Southwest Fisheries Science Center, Santa Cruz, California:
- Barnett-Johnson, RRFC, Grimes, CB, MacFarlane, RB. 2005. Sr isotopes in otoliths reveal river of origin of wild adult salmon [abstract]. Program, American Fisheries Society, California-Nevada Chapter, Annual Meeting; Sacramento. p. 39.
- Barnett-Johnson, R, Ramos, FC, Grimes, CB, MacFarlane, RB. 2005. Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. Canadian Journal of Fisheries and Aquatic Sciences 62:2425-2430:
- Barnett-Johnson, R. 2004. Determining the importance of stock structure, and production sources, to population dynamics of California Chinook salmon using otoliths and geochemical signatures. eScholarship Repository, University of California Paper 010: <http://repositories.edlib.org/ucmarine/ceqi/010>
- Barnett, TP, Pierce, DW, AchutaRao, KM, Gleckler, PJ, Santer, BD, Gregory, JM, Washington, WM. 2005. Penetration of human-induced warming into the World's oceans. Science Express www.scienceexpress.org/2 June 2005 / Page 1/ 10.1126Science.1112418
- Barrowman, NJ, Myers, RA. 2000. Still more spawner-recruit curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences 57:665-676.
- Bartholow, JM, Laake, JL, Stalnaker, CB, Williamson, SC. 1993. A salmonid population model with emphasis on habitat limitations. Rivers 4:265-279.
- Baxter, CV, Hauer, FR. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1470-1481.
- The Bay Institute (TBI). 1998. From the Sierra to the sea: the ecological history of the San Francisco Bay-Delta watershed. Novato, California: The Bay Institute. http://www.bay.org/sierra_to_the_sea.htm (2005)
- Beacham, TD, Murray, CB. 1993. Fecundity and egg size variation in North Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42:485-508.
- Beacham, TD, Withler, FC, Morley, RB. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 63:847-850.
- Beacham, TD. 2003. Comment on "Rapid evolution of egg size in captive salmon". Science 302:59d.

- Beacham, TD, Murray, CB. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Transactions of the American Fisheries Society* 119:927-949.
- Beak Consultants, Inc. 1988. Smolt emigration assessment. Sacramento, CA: Beak Consultants, Inc.
- Beamish, RJ, Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423-437.
- Beamish, RJ, Noakes, DJ, McFarlane, GA, Klyashtorin, L, Ivanov, VV, Kursashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 56:516-526.
- Beamish, RJ, Riddell, BE, Neville, C-EM, Thompson, BL, Zhang, Z. 1995. Declines in Chinook salmon catches in the Strait of Georgia in relation to shifts in the marine environment. *Fisheries Oceanography* 4:543-554.
- Becker, CD, Neitzel, DA, Abernethy, CS. 1983. Effects of dewatering on chinook salmon redds: tolerance of four developmental stages to one-time dewatering. *North American Journal of Fisheries Management* 3:372-382.
- Beckman, BR, Larsen, DA, Lee-Pawlak, B, Moriyama, S, Dickhoff, WW. 1998. Insulin-like growth factor-I and environmental modulation of growth during smoltification of spring chinook salmon, (*Oncorhynchus tshawytscha*). *General and Comparative Endocrinology* 109:325-335.
- Beckman, BR, Larsen, DA. 2005. Upstream migration of minijack (age-2) Chinook salmon in the Columbia River: behavior, abundance, distribution, and origin. *Transactions of the American Fisheries Society* 134:1520-1541.
- Beckman, BR, Larsen, DA, Sharpe, C, Lee-Pawlak, B, Schreck, CB, Dickhoff, WW. 2000. Physiological status of naturally-reared juvenile spring chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. *Transactions of the American Fisheries Society* 129:727-753.
- Beechie, TJ, Liermann, M, Beamer, EM, Henderson, R. 2005. A classification of habitat types in a large river and their use by juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 134:717-729.
- Beeman, JW, Rondorf, DW, Fler, JC, Free, ME, Haner, PV, Sauter, ST, Venditti, DA. 1991. Assessment of smolt condition for travel time analysis. Portland, Oregon: Bonneville Power Administration. Annual Report 1990 (Contract DE-A179-8-87BP-35245).
- Beer, WN. 1999. Comparison of mechanistic and empirical methods for modeling embryo and alevin development in chinook salmon. *North American Journal of Aquaculture* 61:126-134.
- Beer, WN, Anderson, JJ. 1997. Modeling the growth of salmonid embryos. *Journal of Theoretical Biology* 189:297-306.
- Begg, GA, Friedland, KD, Pearce, JB. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research* 43:1-8.
- Ben-David, M, Hanley, TA, Schell, DM. 1998. Fertilization of riparian vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83:47-55.
- Berejikian, BA, Fairgrieve, WT, Swanson, P, Tezak, EP. 2003. Current velocity and injection of GnRHa affect reproductive behavior and body composition of captive reared offspring of wild chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:690-699.
- Berejikian, BA, Smith, RJF, Tezak, EP, Schroder, SL, Knudsen, CM. 1999. Chemical alarm signals and complex hatchery rearing habitats affect antipredatory behavior and survival of chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:830-838.
- Berejikian, BA, Tezak, EP, LaRue, AL. 2000a. Female mate choice and spawning behavior of chinook salmon under experimental conditions. *Journal of Fish Biology* 57:647-661.
- Berejikian, BA, Tezak, EP, Flagg, TA, LaRae, AL, Kummerow, E, Mahnken, CVW. 2000b. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Sciences* 57:628-636.
- Bigler, BS, Welch, DW, Helle, JH. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 53:455-465.
- Bilby, RE, Fransen, BR, Bisson, PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164-173.

- Bilby, RE, Fransen, BR, Bisson, PA, Walter, JK. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1909-1918.
- Bilby, RE, Bisson, PA. 1998. Function and distribution of large woody debris. In: Naiman, RJ, Bilby, RE, editors. *River ecology and management*. New York: Springer. p. 324-346.
- Bisson, PA, Bilby, RE, Bryant, MD. 1987. In: Cundy, T, Salo, EO, editors. *Proceedings of a symposium: streamside management-forestry and fisheries interactions*; University of Washington. p. 143-190.
- Bjorkstedt, Eric P. 2005. DARR 2.0: updated software for estimating abundance from stratified mark-recapture data. NOAA Technical Memorandum, NMFS-SWFSC-368.
- Bjorn, TC. 1969. Embryo survival and emergence studies. Idaho Department of Fish and Game. Salmon and steelhead investigations, Project F-49-R-7.
- Black, M. 1994. Recounting a century of failed fishery policy toward California's Sacramento River salmon and steelhead. *Conservation Biology* 8:892-894.
- Black, M. 2001. Shasta salmon salvage efforts: Coleman National Fish Hatchery on Battle Creek, 1895-1992. In: Brown, Randall L., editor. *Contributions to the biology of Central Valley salmonids*. Fish Bulletin. California Department of Fish and Game.
- Blackwell, BG, Brown, ML, Willis, DW. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. *Reviews in Fisheries Science* 8:1-44.
- Bograd, SJ, Checkley, DA Jr, Wooster, WS. 2003. CalCOFI: a half century of physical, chemical, and biological research in the California Current System. *Deep-Sea Research II* 50:2349-2353.
- Boles, GL, Turek, SM, C. D. Maxwell, D. M. McGill. 1988. Water temperature effects on Chinook salmon (*Oncorhynchus tshawytscha*) with emphasis on the Sacramento River. Red Bluff, California: California Department of Water Resources, Northern District.
- Booke, HE. 1999. The stock concept revisited: perspectives on its history in fisheries. *Fishery Bulletin* 43:9-11.
- Botkin, DB, D. L. Peterson, Calhoun, JM. 2000. The scientific basis for validation monitoring of salmon for conservation and restoration plans. Forks, Washington: University of Washington, Olympic Natural Resources Center. Olympic Natural Resources Technical Report.
- Botsford, LW, Lawrence, CA. 2002. Patterns of co-variability among California Current Chinook salmon, coho salmon, Dungeness crab, and physical oceanographic conditions. *Progress in Oceanography* 53:283-305.
- Botsford, LW, Lawrence, CA, Hill, MF. 2005. Differences in dynamic response of California Current salmon species to changes in ocean habitat. *Deep-Sea Research II* 52:331-345.
- Botsford, LW, Brittnacher, JG. 98. Viability of Sacramento River winter-run chinook salmon.
- Bottom, DL. 2002. Historic habitat opportunities and food-web linkages of juvenile salmon in the Columbia River estuary and their implications for managing river flows and restoring estuarine habitat. Proposal to Bonneville Power Administration. NMFS.
- Bottom, DL. 1997. To till the water: a history of ideas in fish conservation. In: Stouder, DJ, Bisson, PA, Naiman, RJ, Editors. New York: Chapman & Hall.
- Bottom, DL, Simenstad, CA, Baptista, AM, Jay, DA, Burke, J, Jones, KK, Casillas, E, Schiewe, MH. 2005. *Salmon at River's End: the role of the estuary in the decline and recovery of Columbia River salmon*. Seattle: National Marine Fisheries Service.
- Boulton, AJ. 2000. The subsurface macrofauna. In: Jones, JB, Mulholland, PJ, editors. *Streams and ground waters*. San Diego, CA: Academic Press. p. 337-362.
- Boulton, AJ, Findlay, S, Marmonier, P, Stanley, EH, Valett, HM. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* 29:59-81.
- Bovee, KD. 1978. Probability of use criteria for the family Salmonidae. United States Fish and Wildlife Service. Instream Flow Information Paper 4. FWS/OBS-78/07.
- Bovee, KD, Lamb, BL, Bartholow, JM, Stalnaker, CB, Taylor, J, Henriksen, J. 1998. Instream habitat analysis using the instream flow incremental methodology. U. S. Geological Survey. Biological Resources Division Information and Technology Report.
- Box, GEP. 1979. Robustness in the strategy of scientific model building. In: Launer, RL, Wilkinson, GN,

Robustness in Statistics
. New York: Academic Press.

- Brabrand, A, Koestler, AG, Borgstrom, R. 2002. Lake spawning brown trout related to groundwater influx. *Journal of Fish Biology* 60:751-763.
- Bradford, JJ, Geen, GH. 1987. Size and growth of juvenile Chinook salmon back-calculated from otolith growth increments. In: Summerfelt, RC, Hall, GE, editors. *The age and growth of fish*. Ames, Iowa: Iowa State University Press . p. 453-461.
- Bradford, MJ. 1995. Comparative review of Pacific salmon survival rates. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1327-1338.
- Bradford, MJ, Higgins, PS. 2001. Habitat-, season-, and size specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:365-374.
- Bradford, MJ, Korman, J, Higgins, PS. 2005. Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus spp.*) to experimental habitat alterations. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2716-2726.
- Brandes, PL, McLain, JS. 2001. Juvenile chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin estuary. In: Brown, RL, editor. *Contributions to the biology of Central Valley salmonids*, Vol 2. Fish Bulletin No. 179. Sacramento: California Department of Fish and Game. p. 39-138.
- Brannon, EO, Amend, DF, Cronin, MA, Lannan, JE, LaPatra, S, McNeil, WJ, Noble, RE, Smith, CE, Talbot, AJ, Wedenmyer, GA, Westers, H. 2004. The controversy about hatcheries. *Fisheries* 29:12-31.
- Brenden, TO, Murphy, BR, Birch, JB. 2003. Statistical properties of the relative weight (W_t) index and an alternative procedure for testing W_t differences between groups. *North American Journal of Fisheries Management* 23:1136-1151.
- Brett, JR. 1995. Energetics. In: Groot, C, Margolis, L, Clarke, WC, editors. *Physiological ecology of Pacific salmon*. Vancouver: UBC Press. p. 1-68.
- Brett, JR, Clarke, WC, Shelbourn, JE. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon. Nanaimo, British Columbia: Department of Fisheries and Oceans. Canadian Technical Report of Fisheries and Aquatic Sciences .
- Brett, JR, Shelbourn, JE, Shoop, CT. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363-2394.
- Brewer, WH. 1966. Up and down California in 1860-1864. Farquhar, Francis P., Editor. University of California Press.
- Briggs, JC. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. Fish Bulletin No. 94. Sacramento, California: California Department of Fish and Game.
- Broad, RD, Gangmark, HA. 1956. Establishment of a controlled-flow area and construction of king salmon spawning pens at Mill Creek, California. *Progressive Fish Culturist* 18:131-134.
- Brodeur, RD, Boehlert, GW, Casillas, E, Eldridge, MB, Helle, JH, Peterson, WT, Heard, WR, Lindley, ST, Schiewe, MH. 2000. A coordinated research plan for estuarine and ocean research on Pacific salmon. *Fisheries* 25:716.
- Brodeur, RD, Myers, KW, Helle, JH. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* 3:89-131.
- Brodeur, RD, Fisher, JP, Teel, DJ, Emmett, RE, Casillas, E, Miller, TW. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. *Fishery Bulletin* 10:25-46.
- Brown, LR. 2003. Will tidal wetland restoration enhance populations of native fishes. *San Francisco Estuary and Watershed Science* (online serial) 1:Article 2. <http://repositories.cdlib.org/jmie/sfews.vol1/iss1/aart2>
- Brown, LR, Ford, T. 2001. Distribution and abundance of Chinook salmon and resident fishes of the lower Tuolumne River, California. In: Brown, RL, editor. *Contributions to the biology of Central Valley salmonids*, Fish Bulletin No. 179. 2. p. 253-304.
- Brown, LR, Ford, T. 2002. Effects of flow on the fish communities of a regulated California River: implications for managing native fishes. *Regulated Rivers: Research and Management* 18:331-342.

- Brown, LR, Moyle, PB. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptycholcheilus grandis*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:849-856.
- Brown, LR, Moyle, PB. 1981. The impact of squawfish on salmonid populations: a review. *North American Journal of Fisheries Management* 1:104-111.
- Brown, R, Cavallo, B, Jones, K. 2004. The effects of the Feather River Hatchery on naturally spawning salmonids. California Department of Water Resources.
- Brown, R, Greene, S. 1992. Biological assessment: effects of Central Valley Project and State Water Project Delta operations on winter-run Chinook salmon. Sacramento, California: California Department of Water Resources.
- Brown, R, Kimmerer, W. 2002. Chinook salmon and the Environmental Water Account: a summary of the 2002 salmonid workshop. Sacramento, California: CALFED Science Program.
- Brown, R, Kimmerer, W. 2001. Summary report of the June 21, 2001 salmonid workshop for the CALFED Environmental Water Account. Sacramento, California:
- Brunke, M, Gonser, T. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37:1-33.
- Buckley, LJ, Caldaroni, E, Ong, TL. 1999. RNA-DNA ratio and other nucleic acid-based indicators for growth and condition in marine fishes. *Hydrobiologia* 401:265-277.
- Buer, K. 1985. Sacramento River spawning gravel studies. Red Bluff, California: California Department of Water Resources, Northern District.
- Buffington, JM, Montgomery, DR, Greenberg, HM. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2085-2096.
- Bult, TP, Haedrich, RL, Schneider, DC. 1998. New technique describing spatial scaling and habitat selection in riverine habitats. *Regulated Rivers: Research and Management* 14:107-118.
- Bult, TP, Riley, SC, Haedrich, RL, Gibson, RJ, Heggenes, J. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1298-1306.
- Burgner, RL. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). In: Groot, C, Margolis, L, editors. *Pacific salmon life histories*. Vancouver: UBC Press. p. 1-118.
- Burner, CJ. 1951. Characteristics of spawning nests of Columbia River salmon. *Fishery Bulletin* 52:97-110.
- Burnham, KP, Anderson, DR. 1998. Model selection and inference: a practical information-theoretic approach. New York: Springer.
- Burns, DC. 1974. Feeding by mature steelhead (*Salmo gairdnerii gairdnerii*) in the spawning stream. *California Fish and Game* 60:
- Busack, C, Hankin, D, Hedrick, RP, Lichatowich, JA, Reisenbichler, R. 2004. Compatibility of Coleman National Fish Hatchery operations and restoration of anadromous salmonids in Battle Creek. Report of Technical Review Panel. Sacramento, California: CALFED Bay-Delta Program.
- Busack, CA, Currens, KP. 1995. Genetic risks and hazards in hatchery operations. In: Schramm, HLJ, Piper, RG, editors. *Uses and effects of cultured fishes in aquatic ecosystems*. American Fisheries Society Symposium 15. American Fisheries Society. p. 71-80.
- Busacker, GP, Adelman, IR, Goolish, EM. 1990. Growth. In: Schreck, CB, Moyle, PB, Editors. *Methods for fish biology*. Bethesda, Maryland: American Fisheries Society. p. 363-388.
- CALFED Bay-Delta Program. 2005. 10-year action plan framework, final draft. Sacramento, California: CALFED Bay-Delta Program. http://calwater.ca.gov/Revitalizing_CALFED/Revitalizing_Calfed.shtml
- CALFED Bay Delta Program. 2005. Environmental Water Account Final EIS/EIR. Sacramento, California: <http://calwater.ca.gov/Programs/EnvironmentalWaterAccount/EnvironmentalWaterAccount.shtml>
- California Department of Fish and Game (CDFG). 2004b. Sacramento River spring-run Chinook salmon: 2003-2004 biennial report. Sacramento, California: California Department of Fish and Game, Native Anadromous Fish and Watershed Branch.
- California Department of Fish and Game (CDFG). 2001. Evaluation of effects of flow fluctuations on the

- anadromous fish populations in the Lower American River. Sacramento: California Department of Fish and Game. Stream Evaluation Program Technical Report.
- California Department of Fish and Game (CDFG). 2004a. Sacramento River winter-run Chinook salmon: biennial report 2003-2003. Sacramento, California: California Department of Fish and Game, Native Anadromous Fish and Watershed Branch.
- California Department of Fish and Game (CDFG). 1998. A status review of the spring-run Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River drainage. Sacramento, California: Candidate Species Status Report 98-01.
- California Little Hoover Commission. 2005. Still imperiled, still important: the Little Hoover Commission review of the CALFED Bay Delta Program. Sacramento, California: Little Hoover Commission of California. <http://www.lhc.gov/hcdir/report183.html>
- Campana, SE. 1983. Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Canadian Journal of Zoology 61:15912-1597.
- Campbell, EA. 1998. Influence of streamflow and predators on habitat choice by trout [dissertation]. University of California, Davis.
- Campbell, RF, Neuner, JH. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain streams. In: Olsen, FW, White, RG, Hamre, RH, Editors. Symposium on small hydropower and fisheries; Bethesda, Maryland: American Fisheries Society.
- Campton, DE. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: what do we really know. In: Schramm, HL Jr, Piper, RG, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15. p. 337-353.
- Candy, JR, Beacham, TD. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. Fisheries Research 47:41-56.
- Candy, JR, Quinn, TP. 1999. Behavior of adult Chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry. Canadian Journal of Zoology 77:1161-1169.
- Carl, LM. 1982. Natural reproduction of coho salmon and Chinook salmon in some Michigan streams. North American Journal of Fisheries Management 2:375-380.
- Carl, LM, Healey, MC. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 41:1070-1077.
- Castleberry, DT, Cech, JJJ, Erman, DC, Hankin, D, Healey, MC, Kondolf, GM, Mangel, M, Mohr, M, Moyle, PB, Nielsen, J, Speed, TP, Williams, JG. 1996. Uncertainty and instream flow standards. Fisheries 21:20-21.
- Castleberry, DT, Cech, JJ Jr, Saiki, MK, Martin, BA. 1991. Growth, condition and physiological performance of juvenile salmonids from the American River, February through June, 1991. Dixon, California: U. S. Fish and Wildlife Service.
- Castleberry, DT, Cech, JJ Jr, Saiki, MK, Martin, BA. 1993. Growth, condition and physiological performance of juvenile salmonids from the American River, February through July, 1992. Dixon, California: U. S. Fish and Wildlife Service.
- Castleberry, DT, Saiki, MK, Martin, BA. 1994. Field validation of daily increment formation on the sagittal otoliths of juvenile Chinook salmon. Dixon, California: U. S. Fish and Wildlife Service.
- Cavallo, B, Kurth, R, Kindoff, J, Seesholtz, A, Perrone, M. 2003. Distribution and habitat use of steelhead and other fishes in the lower Feather River, 1999-2001. Sacramento, California: California Department of Water Resources.
- Cech, JJ Jr, Myrick, CA. 1999. Steelhead and Chinook salmon bioenergetics: temperature, ration and genetic effects. University of California Water Resources Center, University of California, Davis.
- Cederholm, CJ, Kunze, MD, Murota, T, Sibitani, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24:6-15.
- Centers for Water and Wildland Resources (CWWR). 1999. Tuolumne River technical advisory committee peer review forum for methodologies of measuring salmon smolt survival, University of California, Davis, December 18, 1998. Davis, California: Centers for Water and Wildland Resources, University of California,

Davis .

- Chapman, DW. 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist* 100:345-357.
- Chapman, DW, Bjornn, TC. 1969. Distribution of salmonids in streams, with special reference to food and feeding. In: Northcote, TG, editor. Symposium on salmon and trout in streams; Vancouver: UBC Press. p. 153-176. H. R. MacMillan Lectures in Fisheries.
- Chapman, DW. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117:1-21.
- Chapman, WM. 1943. The spawning of Chinook salmon in the main Columbia River. *Copeia* 3:168-170.
- Chavez, FP, Pennington, JT, Castro, CG, Ryan, JP, Michisaki, RP, Schlining, B., Walz, P., Buck, KR, McFadyen, A, Collings, CA. 2002. Biological and chemical consequences of the 1997-1998 El Niño in central California waters. *Progress in Oceanography* 44:205-232.
- Chilcote, MW. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:1057-1067.
- Chin, JL, Graymer, RW. 2001. Regional setting of the Gulf of the Farallones. In: Karl, HA, Chin, JL, Ueber, E, Stuaffner, PH, Hendley, JW, editors. Beyond the Golden Gate -- Oceanography, geology, biology, and environmental issues in the Gulf of the Farallones. USGS Circular 1198.
- Clark, GH. 1929. Sacramento River salmon fishery. *California Fish and Game* 15:1-11.
- Clark, GH. 1928. Sacramento- San Joaquin salmon (*Oncorhynchus tshawytscha*) fishery of California. *Fish Bulletin* 17:1-73.
- Clark, GH. 1943. Salmon at Friant Dam -- 1942. *California Fish and Game* 29:89-91.
- Clarke, WC, Whithler, RE, Shelbourn, JE. 1992. Genetic control of juvenile life history pattern in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 49:2300-2306.
- Clarke, WC, Hirano, T. 1995. Osmoregulation. In: Groot, C, Margolis, L, Clarke, WC, editors. Physiological ecology of Pacific salmon. Vancouver, British Columbia: UBC Press. p. 317-438.
- Clarke, WC, Withler, RE, Shelborn, JE. 1994. Inheritance of smolting phenotypes in backcrosses of hybrid stream-type X ocean-type chinook salmon (*Oncorhynchus tshawytscha*). *Estuaries* 17:13-25.
- Clausen, J, Keck, DD, Hiesey, WM. 1958. Experimental studies on the nature of species. I. Effect of varied environments on Western North American plants. Washington, D. C.: Carnegie Institution of Washington.
- Cleveland, WS. 1985. The elements of graphing style. Monterey, CA: Wadsworth Books.
- Collins, BD, Montgomery, DR. 2002. Forest development, wood jams, and restoration of floodplain rivers in the Puget Lowland, Washington. *Restoration Ecology* 10:237-247.
- Collins, BD, Montgomery, DR, Haas, AD. 2002. Historical changes in the distribution and function of large wood in Puget Lowland rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 59:66-76.
- Collins, CA, Pennington, JT, Castro, CG, Rago, TA, Chavez, FP. 2003. The California Current system of Monterey, California: physical and biological coupling. *Deep-Sea Research II* 50:2389-2404.
- Combs, BD. 1965. Effect of temperature on the development of salmon eggs. *Progressive Fish-Culturist* 27:134-137.
- Combs, BD, Barrows, RE. 1957. threshold temperatures for the normal development of Chinook salmon eggs. *Progressive Fish-Culturist* 19:3-6.
- Commissioners of Fisheries of the State of California. 1886. Biennial Report for 1885-1886. Sacramento, California:
- Commissioners of Fisheries of the State of California. 1875. Report for the years 1874 and 1875. Sacramento, California:
- Commissioners of Fisheries of the State of California. 1877. Report for the years 1876 and 1877. Sacramento, California:
- Cone, RS. 1989. The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* 118:510-514.

- Congleton, JL, Davis, SK, Foley, SR. 1981. Distribution, abundance and outmigration timing of chum and chinook salmon fry in the Skagit salt marsh. In: Brannon, EL, Salo, EO, editors. Salmon and trout migratory behavior symposium; Seattle, Washington: University of Washington, School of Fisheries.
- Congleton, JL, Wagner, T, Evavold, J, Hafner, J, Fryer, D, Sun, B. 2004. Evaluation of physiological differences in transported, in-river migrating, and multiple-bypassed juvenile salmon (DACW68-00-C-0031), Annual Report, 2002. Walla Walla, Washington: Dept. of Fish and Wildlife Resources, University of Idaho.
- Connor, WP, Sneva, JG, Tiffan, KF, Steinhorst, RK, Ross, D. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 134:291-304.
- Conomos, TJ. 1979. San Francisco Bay, the urbanized estuary. San Francisco, California: American Association for the Advancement of Science.
- Conover, DO, Munch, SB. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94-96.
- Conover, WP, Burge, HL. 2003. Growth of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management 23:594-599.
- Cooke, SJ, Hinch, SG, Farrell, AP, Lapointe, MF, Jones, SRM, Macdonald, JS, Patterson, DA, Healey, MC, Van Der Kraak, G. 2004. Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. Fisheries 29:22-33.
- Cooney, RT, Brodeur, RD. 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implications. Bulletin of Marine Science 6:443-464.
- Cooper, AB, Mangel, M. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fishery Bulletin 97:213-226.
- Cope, PB, Staler, DW. 1957. Role of Coleman Hatchery in maintaining a king salmon run. United State Fish and Wildlife Service. Research Report 47.
- Cordone, AJ, Kelly, DW. 1961. The influence of inorganic sediment on the aquatic life of streams. California Fish and Game 47:189-228.
- Cramer, FK, Hammack, DF. 1952. Salmon Research at Deer Creek, California. Washington, D. C.: U.S. Fish and Wildlife Service. Special Scientific Report.
- Cramer, SP. 1991. Contribution of Sacramento Basin hatcheries to ocean catch and river escapement of fall Chinook salmon. Corvallis, Oregon: S. P. Cramer & Associates.
- Cramer, SP, Daigeault, M, Teply, M. 2003. Conceptual framework for an integrated life cycle model of winter-run Chinook salmon in the Sacramento River. Gresham, Oregon: S. P. Cramer & Associates.
<http://www.spcramer.com/imf.htm>
- Cramer, SP, Lichatowich, JA. 1978. Factors influencing the rate of downstream migration of juvenile Chinook salmon in the Rogue River. In: Shepard, BC, Ginetz, RMJ, Compilers. Proceedings of the 1977 Northwest Pacific Chinook and Coho Salmon Workshop; Fish. Mar. Serv. (Can). p. 43-48. Technical Report 759.
- Cramer, SP, Alley, D, Baldridge, J, Bernard, K, Demko, D, Dettman, D, Farrell, B, Hagar, J, Laird, A, Mitchell, B, Orton, R, Taylor, T, Van Dyke, E. 1994. The status of steelhead populations in California in regards to the Endangered Species Act. Gresham, Oregon: S.P. Cramer & Associates.
- Cramer, SP, Demko, DB. 1986. The status of late-fall and spring Chinook salmon in the Sacramento River Basin regarding the Endangered Species Act. Gresham, Oregon: S. P. Cramer & Associates.
- Crisp, DT. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11:361-368.
- Crisp, DT. 1988. Prediction, from temperature, of eyeing, hatching, and 'swim-up' times for salmonid embryos. Freshwater Biology 19:41-48.
- Crisp, DT, Carling, PA. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34:119-134.
- Cuenco, ML. 1994. A model of an internally supplemented population. Transactions of the American Fisheries Society 123:277-288.
- Curry, RA, Gehrels, J, Noakes, DLG, Swainson, R. 1994. Effects of river flow fluctuations on groundwater discharge through brook trout, *Salvelinus fontinalis*, spawning and incubation habitats. Hydrobiologia 227:121-134.

- Daley, WJ. 1993. The use of fish hatcheries: polarizing the issue. *Fisheries* 18 (3):4-5.
- Damsgard, B, Dill, LM. 1998. Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behavioral Ecology* 9:26-32.
- Dauble, DD, Watson, DG. 1997. Status of fall chinook salmon populations in the mid-Columbia River 1948-1992. *North American Journal of Fisheries Management* 17:283-300.
- Dayton, PK. 1998. Reversal of the burden of proof in fisheries. *Science* 279:821-822.
- Deas, ML, Lowney, CL. 2000. Water temperature modeling review.
<http://www.cwemf.org/Pubs/TempReview.pdf>: Bay-Delta Modeling Forum.
www.cwemf.org/Pubs/BDMFTemp.Review.pfd
- Deas, ML, Meyer, GK, Lowney, CL, Orlob, GT, King, IP. 1997. Sacramento River Temperature Modeling Project. Department of Civil and Environmental Engineering, University of California, Davis.
- Dedual, M. 2004. Case study: the Tongariro River. Workshop on IFIM in New Zealand; Nelson, New Zealand.
<http://www.doc.govt.nz/Explore/hunting-and-fishing/Taupo-Fishery/PDF/IFIM%20PDFs/Tongariro-River-Case-Study.pdf>
- Dedual, M. 2003. Sonoma Creek: where it all began for New Zealand rainbow trout. *Target Taupo* 44:54-55.
- del Rosario, RB, Ruch, VH. 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? *Journal of the North American Benthological Society* 19:680-696.
- Delisle, G. 1966. Preliminary fish and wildlife plan for San Francisco Bay-Estuary. Prepared for the San Francisco Bay Conservation and Development Commission. California Department of Fish and Game.
- Demko, DB, Cramer, SP. 1996. Effects of pulse flows on juvenile Chinook migration in the Stanislaus River. Gresham, Oregon: S. P. Cramer & Associates.
- Dempson, JB, Stansbury, DE. 1991. Using partial counting fences and a two-sample stratified design for mark-recapture estimation of an Atlantic salmon smolt population. *North American Journal of Fisheries Management* 11:27-37.
- Deriso, RB. 1980. Harvesting strategies and parameter estimate for an age structured model. *Canadian Journal of Fisheries and Aquatic Sciences* 37:268-282.
- Dettinger, MD. 2005. From climate-change spaghetti to climate-change distributions for 21st Century California. *San Francisco Estuary and Watershed Science* 3:Issue 1, Article 4.
<http://repositories.edlib.org/jmie/sfews/vol3/iss1/art4>
- Dettinger, MD, Cayan, DR, Meyer, MK, Jeton, AE. 2004. Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American river basins. *Sierra Nevada, California, 1900-2099. Climate Change* 62:283-317.
- Dettman, DH, Kelley, DW. 1986. Assessment of the Carmel River steelhead resource. Volume I. Biological Investigations. Newcastle, California: D. W. Kelley & Associates.
- Dettman, DH, Kelley, DW. 1987. The roles of Feather and Nimbus salmon and steelhead hatcheries and natural reproduction in supporting fall run chinook salmon populations in the Sacramento River basin. Newcastle, California: D. W. Kelley & Associates.
- Dettman, DH, Kelley, DW, Mitchell, WT. 1987. The influence of flow on Central Valley salmon. Newcastle, California: D. W. Kelley & Associates.
- DeVries, P. 1997. Riverine salmonid egg burial depths: a review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1685-1698.
- DeVries, P, Goetz, F, Fresh, K, Sheiler, D. 2004. Evidence of a lunar gravitation cue on timing of estuarine entry by Pacific salmon smolts. *Transactions of the American Fisheries Society* 133:1379-1395.
- Dill, LM. 1969. The sub-gravel behaviour of Pacific salmon larvae. In: Northcote, TG, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. University of British Columbia. p. 89-99.
- Dill, PA. 1981. Behavior of alevin influencing distribution in gravel. In: Brannon, EL, Salo, EO, editors. Salmon and trout migratory behavior symposium; Seattle, Washington: University of Washington, School of Fisheries. p. 61-70.
- Dittman, AH, Quinn, TP. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* 199:83-91.

- Dobzhansky, T. 1973. Nothing in biology makes sense except in light of evolution. *The American Biology Teacher* 35:125-129.
- Dolloff, A, Kershner, J, Thurow, R. 1996. Underwater observation. In: Murphy, BR, Willis, DW, editors. *Fisheries Techniques*. Bethesda, Maryland: American Fisheries Society. p. 533-554.
- Duff, JH, Triska, FJ. 2000. Nitrogen biogeochemistry and surface-subsurface exchange in streams. In: Jones, JB, Mulholland, PJ, editors. *Streams and ground waters*. San Diego, CA: Academic Press. p. 197-220.
- Dunning, HC. in press. California instream flow protection law: then and now. *McGeorge Law Review*
- EA Engineering, Science, and Technology. 1991a. Lower Tuolumne River 1990 Predation Study, Interim Report . Lafayette, California: EA Engineering, Science, and Technology. Unpublished report to the Turlock Irrigation District and Modesto Irrigation District.
- EA Engineering, Science and Technology. 1991e. Lower Tuolumne River Chinook salmon redd excavation report. Unpublished report to the Turlock Irrigation District and Modesto Irrigation District.
- EA Engineering, Science and Technology. 1991b. Lower Tuolumne River Chinook salmon redd excavations interim report. Unpublished report to the Turlock Irrigation District and Modesto Irrigation District.
- EA Engineering, Science and Technology. 1991c. Lower Tuolumne River spawning gravel availability and superimposition report. Unpublished report to the Turlock Irrigation District and Modesto Irrigation District.
- EA Engineering, Science and Technology. 1991d. Lower Tuolumne River spawning gravel studies interim report. Unpublished report to the Turlock Irrigation District and Modesto Irrigation District.
- EA Engineering, Science and Technology. 1991f. San Joaquin River system Chinook salmon population model documentation.
- Ebersole, JL, Liss, WJ, Frissell, C. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States.
- Efron, B, Tibshirani, R. 1993. An introduction to the bootstrap. New York: Chapman & Hall.
- Efron, B, Tibshirani, R. 1991. Statistical data analysis in the computer age. *Science* 252:390-395.
- Einum, S, Fleming, IA. 2002. Does within-population variation in fish egg size reflect maternal influences on optimal values. *The American Naturalist* 160:756-765.
- Einum, S, Fleming, IA. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405:565-567.
- Einum, S, Fleming, IA. 2001. Implications of stocking: ecological interactions between wild and released salmon. *Nordic Journal of Freshwater Resources* 75:56-70.
- Einum, S, Fleming, IA. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proceedings of the Royal Society of London, Series B* 266:2095-2100.
- Einum, S, Flemming, IA. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* 54:628-639.
- Einum, S, Hendry, AP, Fleming, IA. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size? *Proceedings of the Royal Society of London, Series B* 269:2325-2330.
- Einum, S, Kinnison, MT, Hendry, AP. 2004. Evolution of egg size and number. In: Hendry, AP, Stearns, SC, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press. p. 126-153.
- Elena, SF, Sanjuán, R. 2003. Climb every mountain? *Science* 302:2074-2075.
- Elliott, JM. 1985. The choice of a stock-recruitment model for migratory trout, *Salmo trutta*, in a Lake District stream, 1966-83. *Archiv für Hydrobiologie* 104:145-168.
- Elliott, JM. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature, and ration size. *Journal of Animal Ecology* 45:923-948.
- Elliott, JM. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *Journal of Animal Ecology* 44:805-821.
- Elliott, JM. 1994. Quantitative ecology and the brown trout. *Oxford Series in Ecology and Evolution*. Oxford University Press .
- Elliott, JM. 2002. Shadow competition in wild juvenile sea-trout. *Journal of Fish Biology* 61:1268-1281.
- Elliott, JM, Hurley, MA, Fryer, RJ. 1995. A new, improved growth model for brown trout, *Salmo trutta*.

Functional Ecology 9:290-298.

- Elwood, JW, Newbold, RV, O'Neil, RV, Van Winkle, W. 1983. Resource spiraling: an operational paradigm for analyzing lotic systems. In: Fontainne, TD, Bartell, SM, editors. Dynamics of Lotic Ecosystems. Ann Arbor, MI: Ann Arbor Science (Butterworth). p. 3-27.
- Emlen, JM. 1991. Heterosis and outbreeding depression: a multi-locus model and an application to a salmon population. Fisheries Research 12:187-212.
- EPRI. 2000. Instream flow assessment methods: guidance for evaluating instream flow needs in hydropower licensing. Palo Alto, CA: Electric Power Research Institute.
- Erande, B, Dieckmann, U, Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturity. Proceedings of the Royal Society of London, Series B 271:425-423.
- Erkinaro, J, Shchurov, IL, Saari, T, Niemela, E. 1994. Occurrence of Atlantic salmon parr in redds at spawning time. Journal of Fish Biology 45:899-900.
- Erkkila, LF, Moffett, JW, Cope, OB, Smith, BR, Nielson, RS. 1950. Sacramento - San Joaquin Delta Fishery Resources: Effects of Tracy Pumping Plant and Delta Cross Channel. Sacramento, California: U.S. Fish and Wildlife Service. Special Scientific Report: Fisheries No. 56.
- Everest, FH, Chapman, DW. 1972. Habitat selection and spatial interaction by juvenile Chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.
- Ewing, RD, Ewing, GS, Satterthwaite, TD. 2001. Changes in gill Na^+ , K^+ -ATPase specific activity during seaward migration of wild juvenile chinook salmon. Journal of Fish Biology 58:1414-1426.
- Ewing, RD, Fustish, CA, Johnson, SL, Pribble, HJ. 1980. Seaward migration of juvenile chinook salmon without elevated gill (Na^+K^+)-ATPase activities. Transactions of the American Fisheries Society 109:349-356.
- Ewing, RD, Sheaham, JE, Lewis, MA, Palmisano, AN. 1998. Effects of rearing density and raceway conformation on growth, food conversion, and survival of juvenile spring Chinook salmon. Progressive Fish-Culturist 60:167-178.
- Fausch, KD. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 50:1198-1207.
- Fausch, KD. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.
- Fausch, KD, Torgersen, CE, Baxter, CV, Li, HW. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483-496s.
- Feige, U, Morimoto, RI, Yahara, I, Polla, BS. 1996. Stress-inducible cellular responses. Basel, Switzerland: Birkhauser Verlag.
- Felsenstein, J. 1997. Population differentiation and evolutionary processes. In: Grant, WS, Editor. Genetic effects of straying of non-native hatchery fish into natural populations, NOAA Technical Memorandum NMFS NWFSC 30. <http://www.nwfsc.noaa.gov/publications/techmemos/tm30/felsenstein.htm>
- Feyrer, F, Sommer, T, Harrell, W. 2006. Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities: evidence from two adjacent engineered floodplains on the Sacramento River, California. North American Journal of Fisheries Management 26:408-417. DOI: 10.1577/M05-113.1
- Fields, W. 1976. Food habits of juvenile king salmon in the Sacramento-San Joaquin Delta, 1975-1976. Newcastle, California: Hydrozoology.
- Finney, BP, Gregory-Evans, I, Douglas, MSV, Smol, JP. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature 416:729-723.
- Finney, BP, Gregory-Evans, I, Sweetman, J, Douglas, MSV, Smol, JP. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290:795-799.
- Fisher, FW. 1992. Chinook salmon, *Oncorhynchus tshawytscha*, growth and occurrence in the Sacramento-San Joaquin River system. California Department of Fish and Game, Inland Fisheries Division.
- Fisher, FW. 1994. Past and present status of Central Valley chinook salmon. Conservation Biology 8:870-873.
- Fisher, JP, Percy, WG. 1990. Distribution and residence times of juvenile fall and spring chinook salmon in Coos Bay, Oregon. Fishery Bulletin 88:51-58.

- Five Agency Delta Salmon Team, Fish Facilities Subcommittee. 1991. Evaluation of the Feasibility of protecting downstream migrant chinook salmon smolts in the Sacramento River and San Joaquin River with physical facilities.
- Flagg, TA, Berejikian, BA, Colt, JE, Dickhoff, WW, Harrell, LW, Maynard, DJ, Nash, CE, Strom, MS, Iwamoto, RN, Mahnken, CVW. 2000. Ecological and behavioral impacts of artificial production strategies on the abundance of wild salmon populations. National Marine Fisheries Service. NOAA Technical Memorandum NMFS-NWFSC-41.
- Flagg, TA, Nash, CE. 1999. A conceptual framework for conservation strategies for Pacific salmonids. NOAA Technical Memorandum NMFS-NWFSC-38.
- Fleming, IA. 1998. Pattern and variability in the breeding systems of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1):59-76.
- Fleming, IA, Agustsson, T, Finstad, B, Johnsson, JI, Björnsson, BT. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 59:1323-1330.
- Fleming, IA, Einum, S, Jonnson, B, Jonnson, N. 2003. Comment on "Rapid evolution of egg size in captive salmon". Science 302:59b. www.sciencemag.org/cgi/content/full/302/5642/59b
- Fleming, IA, Gross, MR. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications 3:230-245.
- Fleming, IA, Gross, MR. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 71:1-11.
- Fleming, IA, Gross, MR. 1992. Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): does it differ? Aquaculture 103:101-121.
- Fleming, IA, Jonnson, B, Gross, MR. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences 51:2808-2824.
- Fleming, IA, Petersson, E. 2001. The ability of released, hatchery salmonids to breed and contribute to the natural productivity of wild populations. Nordic Journal of Freshwater Resources 75:71-98.
- Fleming, IA, Reynolds, JD. 2004. Salmonid breeding systems. In: Hendry, AP, Stearns, SC, Editors. Evolution illuminated, salmon and their relatives. Oxford University Press.
- Foott, JS. 1990. The organosomatic analysis system: a tool for the evaluation of smolt quality. In: Hauser, TJ, editor. Proceedings of the 1990 Northwest Pacific Chinook and coho salmon workshop; Arcata, California: California Cooperative Fishery Research Unit, Humboldt State University.
- Foott, JS, Walker, RL, Williamson, JD, True, KC. 1994. Anderson, California: U.S. Fish and Wildlife Service, California-Nevada Fish Health Center.
- Ford, MJ. 2004. Conservation units and preserving diversity. In: Hendry, AP, Stearns, SC, editors. Evolution illuminated: salmon and their relatives. Oxford University Press. p. 338-357.
- Ford, MJ. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16:815-825.
- Ford, T, Brown, LR. 2001. Distribution and abundance of Chinook salmon and resident fishes in the lower Tuolumne River, California. In: Brown, RL, Editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin 179. Sacramento, CA: California Department of Fish and Game.
- Fowler, RT, Scarsbrook, MR. 2002. Influence of hydrologic exchange patterns on water chemistry and hyporheic invertebrate communities in three gravel-bed rivers. New Zealand Journal of Marine and Freshwater Research 36:471-482.
- Fox, CW, Heath, DD. 2003. Response to comment on "Rapid evolution of egg size in captive salmon". Science 302:59c. www.sciencemag.org/cgi/content/full/302/5642/59c
- Fraley, EV, Munk, K. 1997. Incidence of thermally marked pink, chum and sockeye salmon in the coastal waters of the Gulf of Alaska. Juneau, Alaska: National Marine Fisheries Service, NOAA, Alaska Science Center.
- Francis, RC, Sibley, TH. 1991. Climate change and fisheries: what are the real issues? Northwest Environmental Journal 7:295-307.
- Fraser, NHC, Heggenes, J, Metcalfe, NB, Thorpe, JE. 1995. Low summer temperatures cause juvenile fish to

- become nocturnal. *Canadian Journal of Zoology* 73:446-451.
- Freedman, DA. 1999. Ecological inference and the ecological fallacy. Department of Statistics, University of California, Berkeley. Technical Report No. 549.
- Freedman, DA. 1983. A note on screening regression equations. *The American Statistician* 37:152-155.
- Fretwell, SD. 1972. *Populations in a seasonal environment*. Princeton, New Jersey: Princeton University Press.
- Fretwell, SD, Lucas, HL. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16-36.
- Frissell, CA, Liss, WJ, Gresswell, RE, Nawa, RK, Ebersole, JL. 1997. A resource in crisis: changing the measure of salmon management. In: Stouder, DJ, Bisson, PA, Naiman, RJ, editors. *Pacific salmon and their ecosystems*. New York: Chapman & Hall. p. 411-446.
- Fry, DH Jr. 1961. King salmon spawning stocks of the California Central Valley, 1940-1959. *California Fish and Game* 47:55-71.
- Fry, DH Jr. 1963. Potential profits in the California salmon fishery. *California Fish and Game* 49:256-267.
- Fry, DH Jr, Hughes, EP. 1952. A sampling program for recovery of marked king and silver salmon. *California Fish and Game* 38:535-540.
- Fry, DH Jr, Hughes, EP. 1951. The California salmon troll fishery. *Pacific Marine Fisheries Commission Bulletin* 2:7-42.
- Fry, DH Jr, Hughes, EP. 1952. A sampling program for recovery of marked king and silver salmon. *California Fish and Game* 38:535-540.
- Fukushima, M, Quinn, TP, Smoker, WW. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Canadian Journal of Fisheries and Aquatic Sciences* 55:618-625.
- Fulton, TW. 1904. The rate of growth of fishes. *Fisheries Board of Scotland, Annual Report* 22 (Part 3) 141-241.
- Gaines, PC, Martin, CD. 2004. Feasibility of dual-marking age-0 Chinook salmon for mark-recapture studies. *North American Journal of Fisheries Management* 24:1456-1459.
- Gaines, PD, Martin, CD. 2002. Abundance and seasonal, spatial, and diel distribution patterns of juvenile salmonids passing the Red Bluff Diversion Dam, Sacramento River. Red Bluff, California: United States Fish and Wildlife Service.
- Gallager, SP, Gard, MF. 1999. Relationship between Chinook salmon (*Oncorhynchus tshawytscha*) redd densities and PHABSIM-predicted habitat in the Merced and Lower American rivers, California. *Canadian Journal of Fisheries and Aquatic Sciences* 56:570-577.
- Gangmark, HA, Bakkala, RG. 1960. A comparative study of unstable and stable (artificial channel) spawning streams for incubating king salmon at Mill Creek. *California Fish and Game* 46:151-163.
- Gangmark, HA, Broad, RD. 1955. Experimental hatching of king salmon in Mill Creek, a tributary of the Sacramento River. *California Fish and Game* 41:233-242.
- Gangmark, HA, Broad, RD. 1956. Further observations on stream survival of king salmon spawn. *California Fish and Game* 42:37-49.
- Gangmark, HA, Sanford, FB. 1963. Theory on development of mounds near Red Bluff, Calif. *Fishery Bulletin* 63:213-200.
- Ganssle, D. 1966. Fishes and decapods of San Pablo and Suisun bays. In: Turner, JL, Kelley, DW, editors. *Ecological studies of the Sacramento-San Joaquin estuary*. *Fish Bulletin* 133. p. 64-94.
- Ganssle, D. 1962. *Annual Report (1961-1962)*. Sacramento, California: Delta Fish and Wildlife Protection Study, Resources Agency of California.
- Ganssle, D, Kelley, DW. 1963. *Sacramento, California: Resources Agency of California. Delta Fish and Wildlife Protection Study, Appendix A*.
- Garcia, A. 1989. The impacts of squawfish predation on juvenile Chinook salmon at Red Bluff Diversion Dam and other locations in the Sacramento River. U.S. Fish and Wildlife Service. USFWS Report No. AFF/FAO- 89-05.
- Gavrilets, S. 2004. *Fitness landscapes and the origin of species*. Monographs in Population Biology. Princeton University Press.

- Geist, DR. 2000. Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia river. Canadian Journal of Fisheries and Aquatic Sciences 57:1647-1656.
- Geist, DR, Dauble, DD. 1998. Redd site selection and spawning habitat use by fall chinook salmon: the importance of geomorphic features in large rivers. Environmental Management 22:655-669.
- Geist, DR, Hanrahan, TP, Arntzen, EV, McMichael, GA, Murrya, CJ, Chien, Y-J. 2002. Physiochemical characteristics of the hyporheic zone affect redd site selection by chum salmon and fall chinook salmon in the Columbia River. North American Journal of Fisheries Management 22:1077-1085.
- Geist, DR, Jones, J, Murray, CJ, Dauble, DD. 2000. Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat use in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1636-1646.
- Gharrett, AJ, Smoker, WW. 1991. Two generations of hybrids between even- and odd-year pink salmon (*Oncorhynchus gorbuscha*); a test for outbreeding depression. Canadian Journal of Fisheries and Aquatic Sciences 48:1744-1749.
- Giannico, GR. 2000. Habitat selection by juvenile coho salmon (*Oncorhynchus kisutch*) in response to food and woody debris manipulations in suburban and rural stream sections. Canadian Journal of Fisheries and Aquatic Sciences 57:1804-1813.
- Giannico, GR, Healey, MC. 1999. Ideal free distribution theory as a tool to examine juvenile coho salmon (*Oncorhynchus kisutch*) habitat choice under different conditions of food abundance and cover. Canadian Journal of Fisheries and Aquatic Sciences 56:2362-2373.
- Gilbert, CH. 1913. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. Bulletin of the Bureau of Fisheries.
- Gilbert, J, Danielopol, DL, Stanford, JA. 1994. Groundwater ecology. San Diego, California: Academic Press.
- Gilliam, JF, Fraser, DF. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:
- Gillilan, DM and Brown, TC. 1997. Instream flow protection: seeking a balance in western water use. Washington, D.C.: Island Press.
- Gingras, M. 1997. Mark/recapture experiments at Clifton Court Forebay to estimate pre-screening loss to juvenile fishes: 1976-1993. Interagency Ecological Program for the San Francisco Bay/Delta Estuary.
- Ginzburg, LR, Jensen, CXJ. 2004. Rules of thumb for judging ecological theories. Trends in Ecology and Evolution 19:121-126.
- Giorgi, AE, Hillman, TW, Stevenson, JR, Hays, SG, Peven, CM. 1997. Factors that influence the downstream migration rates of juvenile salmon and steelhead through the hydroelectric system in the mid-Columbia River basin. North American Journal of Fisheries Management 17:268-282.
- Girard, P, Bosclair, D, Leclerc, M. 2004. The effect of cloud cover on the development of habitat quality indices for juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1386-1397.
- Goals Project. 1999. Baylands ecosystem habitat goals. A report of habitat recommendations prepared by the San Francisco Bay Area wetlands ecosystem goals project. U. S. Environmental Protection Agency, San Francisco, California San Francisco Regional Water Quality Control Board, Oakland, California.
- Gobalet, KW, Schulz, PD, Wake, TA, Siefkin, N. 2004. Archaeological perspectives on Native American fisheries of California, with emphasis on steelhead and salmon. Transactions of the American Fisheries Society 133:801-833.
- Godin, J-GJ. 1981. Migrations of salmonid fishes during early life history phases: daily and annual timing. In: Brannon, EL, Salo, EO, editors. Proceeding of the salmon and trout migratory behavior symposium. Seattle, Washington: School of Fisheries, University of Washington. p. 22-50.
- Goede, RW, Barton, BA. 1990. Oganosomatic indices and an autopsy-based assessment as indicators of health and condition of fish. American Fisheries Society Symposium 8:93-108.
- Goldwasser, L, Mohr, MS, Grover, AM, Plamen-Zwahlen, ML. 2001. The supporting databases and biological analyses for the revision of the Klamath ocean harvest model. National Marine Fisheries Service and California Department of Fish and Game.

- Good, TP, Waples, RS, Adams, P. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U. S. Dept. of Commerce, NOAA Tech. Memo. NMFS-WSFSC-66.
- Goodman, D. 2004. Salmon supplementation: demography, evolution, and risk assessment. In: Nickum, MJ, Mazik, PM, Nickum, JG, MacKinley, DD, editors. Propagated fish in resource management. American Fisheries Society, Symposium 44. Bethesda, Maryland: American Fisheries Society. p. 217-232.
- Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences 62:374-389.
- Gotceitas, V, Godin, J-G. 1991. Foraging under risk of predation in juvenile Atlantic salmon (*Salmo salar*): effects of social status and hunger. Behavioral Ecology and Sociobiology 29:255-261.
- Gowan, C, Fausch, KD. 2002. Why do foraging salmonids move during summer? Environmental Biology of Fishes 64:139-153.
- Grant, JWA, Kramer, DL. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737.
- Grant, JWA, Steinrimsson, SO, Keeley, ER, Cunjak, RA. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1):181-190.
- Grant, PR, Grant, BR. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707-711.
- Grant, WS. 1997. Genetic effects of straying of non-native hatchery fish into wild populations: proceedings of the workshop . NOAA NMFS-NWFSC Technical Memorandum 30 .
- Greco, SE. 1999. Monitoring riparian landscape change and modeling habitat dynamics of the yellow-billed cuckoo on the Sacramento River, California [dissertation]. University of California, Davis.
- Greene, CW. 1926. The physiology of the spawning migration. Physiological Review 6:201-241.
- Greene, CM, Beechie, TJ. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:590-602.
- Greene, CM, Jensen, DW, Pess, GR, Steel, EA, Beamer, E. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. Transactions of the American Fisheries Society 134:1562-1581.
- Greene, S. 1992. Daily fork-length table from data by Frank Fisher, California Department of Fish and Game. Sacramento, California: California Department of Water Resources, Environmental Services Division.
- Greenland, S, Robins, J. 1994. Invited commentary: ecologic studies --biases, misconceptions, and counter-examples. American Journal of Epidemiology 139:747-760.
- Greenwald, GM, Earley, JT, Brown, MR. 2003. Juvenile salmonid monitoring in Clear Creek, California, from July 2001 to July 2002. Red Bluff, California: United States Fish and Wildlife Service.
- Gregory, RS, Levings, CD. 1998. Turbidity reduces predation on migrating Pacific salmon. Transactions of the American Fisheries Society 127:275-285.
- Gregory, R, Failing, L, Higgins, P. 2006. Adaptive management and environmental decision making: a case study application to water use planning. Ecological Economics 58:434-447.
- Gregory, SV, Boyer, KL, Gurnell, AM. 2003. The ecology and management of wood in world rivers. American Fisheries Society Symposium. Bethesda, Maryland: American Fisheries Society.
- Gringas, M. 1997. Mark/recapture experiments at Clifton Court Forebay to estimate pre-screening loss to juvenile fishes: 1976-1993. Interagency Ecological Program for the San Francisco Bay/Delta Estuary. Technical Report.
- Groot, C, Margolis, L. 1991. Pacific salmon life histories. Vancouver: UBC Press.
- Groot, C, Margolis, L, Clarke, WC. 1995. Physiological Ecology of Pacific salmon. Vancouver: UBC Press.
- Gross, MR. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1):131-144.
- Groves, PA, Chandler, JA. 1999. Spawning habitat used by fall Chinook salmon in the Snake River. North American Journal of Fisheries Management 19:912-922.
- Guay, JC, Boisclair, D, Rioux, D, Leclerc, M, Lapointe, MLP. 2000. Development and validation of numerical

- habitat models for juveniles of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:2065-2075.
- Guay, JC, Bosclair, D, Leclerc, M, Lapointe, M. 2004. Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1398-1408.
- Haefner, JW, Bowen, MD. 2002. Physical-based model of fish movement in fish extraction facilities. Ecological Modeling 152:227-245.
- Hagen, P, Meerburg, D, Myers, K, Rogatnykh, A, Urawa, S, Volk, E. 2001. Workshop on salmonid otolith marking, 21 March 2001, Seattle, Washington. Technical Report 3. North Pacific Anadromous Fish Commission.
- Hallock, RJ, Elwell, RF, Fry, DHJr. 1970. Migrations of adult king salmon (*Oncorhynchus tshawytscha*) in the San Joaquin Delta as demonstrated by the use of sonic tags. Fish Bulletin 151. California Department of Fish and Game.
- Hallock, RJ, Warner, GH, Fry, DHJr. 1952. California's part in a three-state salmon fingerling marking program. California Fish and Game 38:301-332.
- Hallock, RJ. undated. The status of inland habitat and factors adversely impacting salmon resources. California Department of Fish and Game, Anadromous Fisheries Branch .
- Hallock, RJ. 1977. Status of Sacramento River system salmon resource and escapement goals. California Department of Fish and Game.
- Hallock, RJ, Fry, DH. 1967. Five species of salmon, *Oncorhynchus*, in the Sacramento River. California. California Fish and Game 53:5-2.
- Hallock, RJ, Fry, DH, LaFaunce, DA. 1957. The use of wire fyke traps to estimate the runs of adult salmon and steelhead in the Sacramento River. California Fish and Game 43:271-298.
- Hallock, RJ, Reisenbichler, RR. 1979. Evaluations of returns from Chinook salmon, *Oncorhynchus tshawytscha*, released at Coleman and Nimbus hatcheries and in the Sacramento River estuary. California Department of Fish and Game, Anadromous Fisheries Branch. Office report.
- Hallock, RJ, Reisenbichler, RR. 1980. Freshwater and ocean returns of marked winter-run and late fall-run Chinook salmon, *Oncorhynchus tshawytscha*, from the Sacramento River . California Department of Fish and Game, Anadromous Fisheries Branch. Office report.
- Hallock, RJ, Van Woert, WF. 1959. A survey of anadromous fish losses in irrigation diversions from the Sacramento and San Joaquin rivers. California Fish and Game 45:227-296.
- Hallock, RJ, Van Woert, WF, Shapovalov, L. 1961. An evaluation of stocking hatchery-reared steelhead rainbow trout (*Salmon gairdnerii gairdnerii*) in the Sacramento River System. Fish Bulletin No. 114. California Department of Fish and Game.
- Ham, KD, Pearsons, TN. 2000. Can reduced salmonid population abundance be detected in time to limit management impacts. Canadian Journal of Fisheries and Aquatic Sciences 57:17-24.
- Hampton, M. 1988. Development of habitat preference criteria for anadromous salmonids in the Trinity River. Sacramento, California: U. S. Fish and Wildlife Service.
- Hankin, DG, Healey, MC. 1986. Dependence of exploitation rates for maximum yield and stock collapse on age and sex structure of chinook salmon (*Oncorhynchus tshawytscha*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 43:1746-1759.
- Hankin, DG, McKelvey, R. 1985. Comment on fecundity of chinook salmon and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 42:393-394.
- Hankin, DG, Nicholas, JW, Downey, TW. 1993. Evidence for inheritance of age at maturity in chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:347-358.
- Hannon, J, Healey, M. 2002. American River steelhead redd surveys, 2001-2002. Sacramento, California: U. S. Bureau of Reclamation and California Department of Fish and Game.
- Hannon, J, Healey, M, Deason, B. 2003. American River steelhead (*Oncorhynchus mykiss*) spawning, 2001-2003. Sacramento, California: U. S. Bureau of Reclamation and California Department of Fish and Game.
- Hanrahan, TP, Dauble, DD, Geist, DR. 2004. An estimate of Chinook salmon (*Oncorhynchus tshawytscha*)

- spawning habitat and redd capacity upstream of a migration barrier in the upper Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 61:23-33.
- Hansen, J, Nazakrenko, L, Ruedy, R, Sato, M, Willis, J, Del Genio, A, Kock, D, Lacis, A, Lo, K, Menon, S, Novakov, T, Periwitz, J, Russell, G, Schmidt, GA, Tausnev, N. 2005. Earth's energy imbalance: confirmations and implications. *Science* 308:1431-1435.
- Hanski, IL. 1997. Metapopulation dynamics: from concepts and observations to predictive models. In: Hanski, IL, Gilpin, ME, editors. *Metapopulation biology: ecology, genetics, evolution*. New York: Academic Press. p. 69-92.
- Hanski, IL, Gilpin, ME. 1997. *Metapopulation biology: ecology, genetics, evolution*. New York: Academic Press.
- Hanski, I, Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Hanson, HA, Smith, OR, Needham, PR. 1940. An investigation of fish salvage problems in relation to Shasta Dam. United States Fish and Wildlife Service. Special Scientific Report # 10.
- Hanson, HA, Smith, OR, Needham, PR. 1940. An investigation of fish salvage problems in relation to Shasta Dam. Special Scientific Report # 10. Washington, D. C.: U. S. Bureau of Fisheries.
- Hard, JJ. 2004. Evolution of Chinook salmon life history under size-selective harvest. In: Hendry, AP, Stearns, SC, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press. p. 315-337.
- Hard, JJ, Heard, WR. 1999. Analysis of straying variation in Alaskan hatchery Chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. *Canadian Journal of Fisheries and Aquatic Sciences* 56:578-589.
- Harden Jones, FR. 1978. *Fish Migration*. London: Arnold.
- Hare, SR, Mantua, NJ, Francis, RC. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries* 24:6-14.
- Harmon, ME, Franklin, JF, Swanson, FJ, Sollings, P, Gregory, SV, Lattin, JD, Anderson, NH, Cline, SP, Sumen, NG, Sedell, JR, Lienkaemper, GW, Cromack, KJr, Cummins, KW. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Hasler, AD, Scholz, AT, Hornall, RM. 1978. Olfactory imprinting and homing in salmon. *American Scientist* 66:347-355.
- Hasler, AD. 1966. *Underwater Guideposts*. Madison, Wisconsin: University of Wisconsin Press.
- Hassan, M. 1990. Scour, fill, and burial depth of coarse material in gravel bed streams. *Earth Surface Processes and Landforms* 15:341-356.
- Hatchery Scientific Review Group (HSRG) - Lars Mobrand (chair), John Barr, Lee Blankenship, Don Campton, Trevor Eyelyn, Conrad Mahnken, Bob Piper, Lisa Seeb and Bill Smoker. 2003b. *Emerging issues in hatchery reform: marine carrying capacity*. Seattle, Washington: Long Live the Kings.
- Hatchery Scientific Review Group (HSRG) - Lars Mobrand (chair), John Barr, Lee Blankenship, Don Campton, Trevor Eyelyn, Conrad Mahnken, Bob Piper, Lisa Seeb and Bill Smoker. 2003a. *Hatchery reform recommendations for the Puget Sound and coastal Washington Hatchery Reform Project*. Seattle, Washington: Long Live the Kings.
- Hatton, SR. 1940. Progress report on the Central Valley fisheries investigations, 1939. *California Fish and Game* 26:334-369.
- Hatton, SR, Clark, GH. 1942. A second progress report on the Central Valley fisheries investigation. *California Fish and Game* 28:116-123.
- Haugen, TO, Vøllestad, LA. 2001. A century of life-history evolution in grayling. *Genetica* 112-113:475-491.
- Haugen, TO, Vøllestad, LA. 2000. Population differences in early life-history traits in greyling. *Journal of Evolutionary Biology* 13:897-905.
- Hawke, SP. 1978. Stranded redds of quinnat salmon in the Mathias River, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 12:161-78.
- Hayhoe, K, eighteen others. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences* 101:12422-12427.
- Healey, MC. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook

- salmon, *Oncorhynchus tshawytscha*. Canadian Field Naturalist 97:427-433.
- Healey, MC. 1982. Juvenile Pacific salmon in estuaries: the life support system. In: Kennedy, VS, Editor. Estuarine comparisons. New York: Academic Press. p. 315-341.
- Healey, MC. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). In: Groot, C, Margolis, L, editors. Pacific salmon life histories. p. 311-394.
- Healey, MC. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. In: Meerburg, DJ, editor. Salmonid age at maturity; p. 39-52. Canadian Special Publication in Fisheries and Aquatic Sciences.
- Healey, MC. 2001. Patterns of gametic investment by female stream- and ocean-type chinook salmon.
- Healey, MC. 1980. Utilization of the Nanaimo River estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. Fishery Bulletin 77:653-668.
- Healey, MC. 1994. Variation in the life history characteristics of chinook salmon and its relevance to conservation of the Sacramento winter-run of chinook salmon. Conservation Biology 8:876-877.
- Healey, MC, Groot, C. 1987. Marine migration and orientation of ocean-type chinook and sockeye salmon. American Fisheries Society Symposium 1. p. 298-312.
- Healey, MC, Heard, WR. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41:476-483.
- Healey, MC, Prince, A. 1995. Scales of variation in life history tactics of Pacific salmon and conservation of phenotype and genotype. In: Nielsen, JL, Powers, DA, editors. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17. Bethesda, Maryland: American Fisheries Society. p. 176-184.
- Healey, TP. 1979. The effect of high temperature on the survival of Sacramento River Chinook (king) salmon, *Oncorhynchus tshawytscha*, eggs and fry. California Department of Fish and Game. Anadromous Fisheries Administrative Report 79-10.
- Heard, WR. 1998. Do hatchery salmon affect the North Pacific Ocean ecosystem. North Pacific Anadromous Fish Commission Bulletin 1:405-411.
- Heard, WR. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). In: Groot, C, Margolis, L, editors. Pacific salmon life histories. Vancouver: UBC Press. p. 119-230.
- Heard, WR, Burkett, R, Thrower, F, McGee, S. 1995. A review of chinook salmon resources in Southeast Alaska and development of an enhancement program designed for minimal hatchery-wild stock interaction. In: Schramm, HLJ, Piper, RG, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium.
- Heath, DD, Blouw, DM. 1998. Maternal effects in fish: are they adaptive or merely physiological side effects? In: Mousseau, TA, Fox, CW, editors. Adaptive maternal effects. Oxford University Press. p. 178-201.
- Heath, DD, Fox, CW, Heath, JW. 1999. Maternal effects on offspring size: variation through early development of chinook salmon. Evolution 53:1605-1611.
- Heath, DD, Heath, JW, Bryden, CA, Johnson, RM, Fox, CW. 2003. Rapid evolution of egg size in captive salmon. Science 299:1738-1740.
- Heath, DD, Moya-Laraño, J, Fox, CW. 2003. Response to comment on "Rapid evolution of egg size in captive salmon". Science 302:59e. www.sciencemag.org/cgi/content/full/302/5642/59e
- Hedgecock, D, Banks, MA, Rasbrook, VK, Dean, CA, Blankenship, SM. 2001. Applications of population genetics to conservation of Chinook salmon diversity in the Central Valley. In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids. Fish Bulletin .1. p. 45-70.
- Hedgecock, D. 2002. Microsatellite DNA for the management and protection of California's Central Valley chinook salmon (*Oncorhynchus tshawytscha*). University of California, Davis, Bodega Marine Laboratory.
- Heggnes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society 131:287-298.
- Heintz, RA, Nilson, BD, Hudson, J, Larsen, M, Holland, L. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Transactions of the American

- Fisheries Society 133:559-567.
- Helsel, DR, Hirsch, RM. 1992. Statistical methods in water resources. Studies in Environmental Sciences . New York: Elsevier.
- Hendricks, SP, White, DS. 2000. Stream and groundwater influences on phosphorus biogeochemistry. In: Jones, JB, Mulholland, PJ, editors. Streams and ground waters. San Diego: Academic Press. p. 221-235.
- Hendry, AP. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. *Genetica* 112/113:515-534.
- Hendry, AP, Bohlin, T, Jonsson, B, Berg, OK. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. In: Hendry, AP, Stearns, SC, Evolution illuminated: salmon and their relatives. Oxford University Press. p. 92-125.
- Hendry, AP, Stearns, SC. 2004. Evolution illuminated: salmon and their relatives. Oxford University Press.
- Hendry, AP, Weinberg, John K., Bemtzen, P, Volk, EC, Quinn, TP. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516-518.
- Hennessey, TM. 1994. Governance and adaptive management of estuarine ecosystems: the case of Chesapeake Bay. *Coastal Management* 22:119-145.
- Heubach, W. 1968. Fish and wildlife resources of the San Francisco Bay and Delta: description, environmental requirements, problems, opportunities and the future. California Department of Fish and Game.
- Hey, J, Brannon, EL, Campton, DE, Dowle, RW, Fleming, IA, Kinnison, MT, Lande, R, Olsen, J, Philipp, DP, Travis, J, Wood, CC, Doremus, H. 2005. Considering life history, behavioral, and ecological complexity in defining conservation units for Pacific salmon. An independent panel report, requested by NOAA Fisheries.
- Higgins, PS, Bradford, MJ. 1996. Evaluation of a large-scale fish salvage to reduce the impacts of controlled flow reduction in a regulated river. *North American Journal of Fisheries Management* 16:666-673.
- Higgins, P. 2001. Using adaptive management for instream flow assessment for water use planning in British Columbia. Burnaby, British Columbia: BC Hydro, Water Use Planning, Fisheries Advisory Team.
- Higgs, DA, Macdonald, JS, Levings, CD, Dosanjh, BS. 1995. Nutrition and feeding habits in relation to life history stage. In: Groot, C, Margolis, L, Clarke, WC, editors. Physiological ecology of Pacific salmon. Vancouver: University of British Columbia Press. p. 159-316.
- Hilborn, R. 1985. Apparent stock-recruitment relationship in mixed stock fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 42:718-723.
- Hilborn, R. 1998. The economic performance of marine stock enhancement projects. *Bulletin of Marine Science* 62:661-674.
- Hilborn, R. 1992. Hatcheries and the future of salmon in the Northwest. *Fisheries* 17:5-8.
- Hilborn, R. 1997. Statistical hypothesis testing and decision theory in fisheries science. *Fisheries* 22:19-20.
- Hilborn, R, Coronado, C. 1997. Changes in ocean survival of coho and Chinook salmon in the Pacific Northwest. In: Emmett, RI, Schiewe, MH, editors. Estuarine and ocean survival of northeastern Pacific salmon: proceedings of the workshop. NOAA Technical Memorandum. U. S. Dept. of Commerce.
- Hilborn, R, Eggers, D. 2000. A review of hatchery programs in Prince Williams Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society* 129:333-350.
- Hilborn, R, Eggers, D. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society* 129:333-350.
- Hilborn, R, Eggers, D. 2001. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska: response to comment. *Transactions of the American Fisheries Society* 130:720-724.
- Hilborn, R, Ludwig, D. 1993. The limits of applied ecological research. *Ecological Applications* 3:550-552.
- Hilborn, R, Mangel, M. 1997. The ecological detective: confronting models with data. Monographs in Population Biology. Princeton, New Jersey: Princeton University Press.
- Hilborn, R, Quinn, TP, Schindler, DE, Rogers, DE. 2003. Biocomplexity and fisheries sustainability . *Proceedings of the National Academy of Sciences* 100:6564-6568.
- Hilborn, R and Walters, CJ. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. New York: Chapman & Hall.

- Hill, J, Grossman, GD. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74:685-698.
- Hill, KA, Webber, JD. 1999. Butte Creek Spring-Run Chinook Salmon, *Oncorhynchus tshawytscha*, Juvenile Outmigration and Life History, 1995-1998. California Dept. of Fish and Game . Inland Fisheries Administrative Report No. 99-5.
- Hindar, KRN, Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48:945-957.
- Hinke, JT, Foley, DG, Wilson, C, Watters, GM. 2005. Persistent habitat use by Chinook salmon *Oncorhynchus tshawytscha* in the coastal ocean. *Marine Ecology Progress Series* 304:207-220.
- Hinke, JT, Watters, GM, Boehlert, GW, Zedonis, P. 2005. Ocean habitat use in autumn by Chinook salmon in coastal waters of Oregon and California. *Marine Ecology Progress Series* 285:181-192.
- Hobbs, DF. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. *New Zealand Marine Department Fishery Bulletin* 6:
- Hobbs, DF. 1940. Natural reproduction of trout in New Zealand and its relation to density of populations. *New Zealand Marine Department Fishery Bulletin* 8:
- Hobbs, NT, Hanley, TA. 1990. Habitat evaluation: do use/availability data reflect carrying capacity. *Journal of Wildlife Management* 54:515-522.
- Hodge, RJ. 1990. Statement of Decision, Environmental Defense Fund, Inc. et al., v. East Bay Municipal Utility District, et al. Hayward, California: Superior Court, Alameda County, California. Case No. 425955.
- Høgåsen, HR. 1998. Physiological changes associated with the diadromous migration of salmonids. *Canadian Special Publication of Fisheries and Aquatic Sciences* 127.
- Holm, CF, Armstran, JD, Gilvear, DJ. 2001. Investigating a major assumption of predictive instream habitat models: is water velocity preference of juvenile Atlantic salmon independent of discharge. *Journal of Fish Biology* 59:1653-1666.
- Holtby, LB, Healey, MC. 1985. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1946-1959.
- Horner, T, Titus, R, Brown, M. 2003. Phase 3 gravel assessment on the lower American River, draft. California State University Sacramento:
- Hubbs. C. L. 1943. Terminology of the early stages of fish. *Copeia* 4:260.
- Hughes, NF, Dill, LM. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2939-2048.
- Hughes, NF. 2000. Testing the ability of habitat selection theory to predict interannual movement patterns of a drift-feeding salmonid.
- Hughes, NF, Grand, TC. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. *Environmental Biology of Fishes* 59:285-298.
- Hughes, NF, Hayes, JW, Shearer, KA, Young, RA. 2003. Testing a model of drift-feeding using three-dimensional videography of wild brown trout, *Salmo trutta*, in a New Zealand River. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1462-1476.
- Hunt, SL, Mulligan, TJ, Komori, K. 1999. Oceanic feeding habitats of chinook salmon, *Oncorhynchus tshawytscha*, off Northern California. *Fishery Bulletin* 97:717-721.
- Huntingford, FA. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology* 65(SA):122-142.
- Huntingford, FA, Metcalf, NB, Thorpe, JE. 1988. Choice of feeding station in Atlantic salmon, *Salmo salar*, parr: effects of predation risk, season and life history strategy. *Journal of Fish Biology* 33:917-924.
- Huntington, CW. 1985. Deschutes River spawning gravel study, Volume 1. Beaverton, Oregon:
- Incerpi, A. 1996. Hatchery-bashing: a useless pastime. *Fisheries* 21:28.
- Independent Scientific Advisory Board (ISAB). 2002. Hatchery surpluses in the Pacific Northwest. *Fisheries* 27:16-27.
- Independent Scientific Advisory Board (ISAB). 2003. Review of salmon and steelhead supplementation. Portland,

Oregon:

- Independent Scientific Group (ISG). 2000. Return to the River - 2000. Portland, Oregon: Northwest Power and Conservation Council. Council Document 2000-12.
- Independent Scientific Group (ISG). 1999. Scientific issues in the restoration of salmonid fishes in the Columbia River. *Fisheries* 24 (3):10-19.
- Iron Mountain Mine Trustee Council (IMMTC). 2002. Final restoration plan for natural resource injuries from Iron Mountain Mine.
- Isaac, DJ, Thurow, RF. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 63:285-296.
- Wilma, GK, Thomas, PT, Forsyth, RB, Vijay an, MM. 1998. Heat shock protein expression in fish. *Reviews in Fish Biology and Fisheries* 8:35-56.
- Jackson, TA. 1992. Microhabitat utilization by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in relation to discharges in the lower American River [ms thesis]. Corvallis: Oregon State University.
- Jager, HI, Cardwell, HE, Sale, MJ, Bevelheimer, MS, Coutant, CC, Van Winkle, W. 1997. Modeling the linkages between flow management and salmon recruitment in rivers. *Ecological Modeling* 103:171-191.
- Jager, HI, Rose, KA. 2003. Designing optimal flow patterns for fall chinook salmon in a Central Valley, California, river. *North American Journal of Fisheries Management* 23:1-21.
- Jassby, A, Van Nieuwenhuysse, EE. 2005. Low dissolved oxygen in an estuarine channel (San Joaquin River, California): mechanisms and models based on long-term time series. *San Francisco Estuary and Watershed Science* (online serial) 3:Article 2. <http://repositories.cdlib.org/jmie/sfews/vol2/iss2/art2>.
- Jensen, AL, Duncan, RN. 1971. Homing of transplanted coho salmon. *Progressive Fish-Culturist* 33:216-218.
- Jensen, P. 1972. King salmon. In: Skinner, JE, editor. *Ecological studies of the Sacramento-San Joaquin estuary*. Report No. 8. Sacramento, California: Delta fish and wildlife protection study, Resources Department of California.
- Jobling, M. 1995. *Environmental Biology of Fishes*. Fish and Fisheries Series 16. London: Chapman & Hall.
- Johnson, DH. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763-772.
- Johnson, N, Jonsson, B. 2003. Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. *Canadian Journal of Fisheries and Aquatic Sciences* 60:506-516.
- Johnson, RA. 1980. Oxygen transport in salmon spawning gravels. *Canadian Journal of Fisheries and Aquatic Sciences* 37:155-162.
- Johnson, RR, Weigand, DC, Fisher, FW. 1992. Use of growth data to determine the spatial and temporal distribution of four runs of juvenile Chinook salmon in the Sacramento River, CA. United States Fish and Wildlife Service.
- Johnson, SL. 1988. The effect of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon. *Fisheries Research* 6:105-123.
- Jonsson, J, Clarke, WC. 1988. Development of seawater adaptation in juvenile steelhead trout (*Salmo gairdneri*) and domesticated rainbow trout (*Salmo gairdneri*) - effects of size, temperature and photoperiod. *Aquaculture* 71:247-263.
- Jonsson, JI, Blackburn, J, Clarke, WC, Withler, RE. 1997. Does presmolt growth rate in steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) predict growth rate in seawater. *Canadian Journal of Fisheries and Aquatic Sciences* 54:430-433.
- Johnston, NT, MacIsaac, EA, Tschaplinski, PJ, Hall, KJ. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 61:384-403.
- Joint Hatchery Review Committee (JHRC). 2001. Final Report on Anadromous Salmonid Fish Hatcheries in California, Review Draft. California Department of Fish and Game and National Marine Fisheries Service Southwest Region.
- Jones, JW. 1959. *The salmon*. London: Collins.

- Jones, JB, Mulholland, PJ. 2000. Streams and ground waters. San Diego: Academic Press.
- Jones, NE, Tonn, WM. 2004. Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation. Canadian Journal of Fisheries and Aquatic Sciences 61:1736-1746.
- Jongman, RHG, ter Braak, CJF, van Tongeren, FR. 1987. Data analysis in community and landscape ecology. Wageningen, the Netherlands: Center for Agricultural Publishing and Documentation (PUDOC).
- Jonsson, B, Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348-365.
- Jonsson, NJB, Flemming, IA. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon. General and Comparative Endocrinology 10:89-96.
- Jordan, DS. 1885. The lower vertebrates. In: Kingsley, JS, The riverside natural history. 3. Cambridge: The Riverside Press. p. 134-168.
- Kapuscinski, AR. 1997. Rehabilitation of Pacific salmon in their ecosystems: what can artificial propagation contribute? In: Stouder, DJ, Bisson, PA, Naiman, RJ, Editors. Pacific salmon and their ecosystems. Chapman and Hall. p. 493-512.
- Karl, HA, Chin, JL, Ueber, E, Stuaffer, PH, Hendley, JWI. United States Geological Survey. 1991. Beyond the Golden Gate - oceanography, geology, biology and environmental issues in the Gulf of the Farallones. Reston, Virginia: USGS Circular 11-98.
- Keeley, ER. 2003. An experimental analysis of self-thinning in juvenile steelhead trout. Oikos 102:543-550.
- Keeley, ER. 2000. An experimental analysis of territory size in juvenile steelhead trout. Animal Behavior 59:477-490.
- Kelley, DW. 1968. Fish and wildlife resources of the San Francisco Bay and Delta: description, environmental requirements, problems, opportunities and the future. Sacramento: Resources Agency of California.
- Kelley, DW. 1966. Ecological studies of the Sacramento-San Joaquin Estuary. Part 1: zooplankton, zoobenthos, and fishes of San Pablo and Suisun bays, zooplankton and zoobenthos of the Delta. Fish Bulletin 133. California Department of Fish and Game.
- Kelley, R. 1989. Battling the inland sea. Berkeley: University of California Press.
- Kemp, P. S., Gilvear, DJ, Armstrong, JD. 2003. Do juvenile Atlantic salmon parr track local changes in water velocity. Rivers: Research and Applications 19:569-575.
- Kennedy, BP, Klaue, A, Blum, JD, Folt, CL, Nislow, KH. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences 59:925-929.
- Kerstetter, TH, Keeler, M. 1976. Smolting in steelhead trout (*Salmo gairdneri*): a comparative study of populations in two hatcheries and the Trinity River, Northern California, using gill Na, K, ATPase assays. Arcata, California: Humboldt State University Publication SG 9.
- Kimmerer, W, Hagar, JM, Garcia, J, Williams, T. 1989. Chinook population model for the Sacramento River basin, version CPOP-2. Tiburon, California: Biosystems Analysis, Inc.
- Kimmerer, WJ. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological response. San Francisco Estuary and Watershed Science (online serial) 2:Article 1. <http://repositories.edlib.org/jmie/sfews/vol2/iss1/art1>.
- Kimmerer, WJ. 2002. Physical, biological, and management responses to variable freshwater inflow into the San Francisco Estuary. Estuaries 25:1275-1290.
- Kimmerer, W, Jones & Stokes Associates. 1999. Conceptual framework for the Sacramento River Chinook salmon individual-based model. Sacramento, California: Draft report to U. S. Fish and Wildlife Service.
- Kimmerer, W, Mitchell, B, Hamilton, A. 2001. Building models and gathering data: can we do this better? In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin 179. 2. 2001: California Department of Fish and Game.
- Kincaid, HL. 1993. Selective breeding and domestication. In: Cloud, JG, Thorgaard, GH, editors. Genetic conservation of salmonid fishes; New York: Plenum Press.
- Kindopp, J. 2003. Growth investigations of wild juvenile steelhead (*Oncorhynchus mykiss*) in the Feather River using mark and recapture techniques. California Department of Water Resources. Interim Report SP-F10, Task B.

- King, HR, Pankhurst, NW, Watts, M, Pankhurst, PM. 2003. Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. *Journal of Fish Biology* 63:153-167.
- King, J. 2005. Sidney, British Columbia: North Pacific Marine Science Organization (PICES). Pices Scientific Report No. 28.
- Kinnison, MT, Hendry, AP. 2004. From macro- to micro-evolution: tempo and mode in salmonid evolution. In: Hendry, AP, Stearns, SC, editors. *Evolution illuminated, salmon and their relatives*. p. 208-231.
- Kinnison, MT, Unwin, MJ, Hendry, AP, Quinn, TP. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* 55:1656-1667.
- Kjelson, MA, Greene, S, Brandes, PL. 1989. A model for estimating mortality and survival of fall-run Chinook smolts in the Sacramento River Delta between Sacramento and Chipps Island. Stockton, California: United States Fish and Wildlife Service.
- Kjelson, M. A., Raquel P. F., and Fisher, F. W. Influences of freshwater inflow on Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin Estuary. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS 81/04. p. 88-108. . FR 32(4). 81.
- Kjelson, MA, Raquel, PF, Fisher, FW. 1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary, California. In: Kennedy, VS, editor. *Estuarine comparisons*. New York: Academic Press. p. 393-411.
- Klemetsen, A, Amundsen, P-A, Dempson, JB, Jonsson, B, Jonsson, N, O'Connell, MF, Mortensem. E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12:1-59.
- Knowles, N, Cayan, DC. 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. *Geophysical Research Letters* 29:1891, doi:10.1029/2001GLO14339.
- Kondolf, GM, Falzone, A, Schneider, DK. 2001. Reconnaissance-level assessment of channel change and spawning habitat on the Stanislaus River below Goodwin Dam. Berkeley, California: GM Kondolf.
- Kondolf, GM. 2000. Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society* 129:262-281.
- Kondolf, GM, Larsen, EW, Williams, JG. 2000. Measuring and modeling the hydraulic environment for assessing instream flows. *North American Journal of Fisheries Management* 20:1016-1028.
- Kondolf, GM, Sale, MJ, Wolman, MG. 1992. Modification of fluvial gravel size by spawning salmonids. *Water Resources Research* 29:2265-2274.
- Kondolf, GM, Vick, JC, Ramirez, TM. 1996. Salmon spawning habitat rehabilitation in the Merced, Tuolumne, and Stanislaus Rivers, California: an evaluation of project planning and performance. Centers for Water and Wildland Resources, University of California .
- Kondolf, GM, Wolman, MG. 1993. The sizes of spawning gravels. *Water Resources Research* 29:2275-2285.
- Kope, RG, Botsford, LW. 1988. Detection of environmental influence on recruitment using abundance data. *Canadian Journal of Fisheries and Aquatic Sciences* 45:448-458.
- Kope, RG, Louis W. Botsford. 1990. Determination of factors affecting recruitment of chinook salmon *Oncorhynchus tshawytscha* in Central California. *Fishery Bulletin* 88:257-269.
- Korman, J, Higgins, PS. 1997. Utility of escapement time series data for monitoring the response of salmon populations to habitat alteration. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2058-2067.
- Koskinen, MT, Haugen, TO, Primmer, CR. 2002. Contemporary fisherian life-history evolution in small salmonid populations. *Nature* 419:826-830.
- Kostow, KE, Marshall, AR, Phelps, SR. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Transactions of the American Fisheries Society* 132.:780-790.
- Kostow, KE. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61:577-589.
- Kramer, DL, Rangely, RW, Chapman, LJ. 1997. Habitat selection: patterns of spatial distribution from behavioral

- decisions. In: Godin, J-GJ, editor. Behavioral ecology of teleost fishes. Oxford University Press. p. 37-80.
- Krebs, CJ. 1998. Ecological methodology. Longman.
- Kurth, R. 2003. Redd dewatering and juvenile steelhead and Chinook salmon stranding in the lower Feather River, 2002-2003. California Department of Water Resources.
- Kutkuhn, JH. 1963. Estimating absolute age composition of California salmon landings. Sacramento: California Department of Fish and Game. Fish Bulletin 120.
- Kwain, W, Thomas, E. 1984. The first evidence of spring spawning by Chinook salmon in Lake Superior. North American Journal of Fisheries Management 4:227-228.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314-334.
- Lapointe, M, Eaton, B, Driscoll, S, Latuippe, C. 2000. Modeling the probability of salmonid egg pocket scour due to floods. Canadian Journal of Fisheries and Aquatic Sciences 57:1120-11130.
- Larkin, PA. 1977. An epitaph for the concept of maximum sustained yield. Transactions of the American Fisheries Society 106:1-11.
- Larkin, PA. 1972. The problem. In: Simon, RC, Larkin, PA, editors. The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries. Vancouver, British Columbia: University of British Columbia. p. 1-18.
- Larsen, DA, Beckman, BR, Dickhoff, WW. 2001. The effect of low temperature and fasting during the winter on growth and smoltification of coho salmon. North American Journal of Aquaculture 63:1-19.
- Law, PW. 1994. A simulation study of salmon carcass survey by capture-recapture method. California Fish and Game 80:14-28.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57:659-668.
- Lawson, PW, Logerwell, EA, Mantua, NJ, Francis, RC, Agostini, VN. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61:360-373.
- Le Cren, ED. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). Journal of Animal Ecology 20:201-219.
- Ledgerwood, RD, Ryan, BA, Dawley, EM, Nunnallee, EP, Ferguson, JW. 2004. A surface trawl to detect migrating juvenile salmonids tagged with passive integrated transponder tags. North American Journal of Fisheries Management 24:440-451.
- Lee, GF, Jones-Lee, A. 2003. Synthesis and discussion of findings on the causes and factors influencing low DO in the San Joaquin River deep water ship channel near Stockton, CA: including 2002 data. El Macero, CA: G. Fred Lee & Associates.
- Lehamn, PW, Sevier, J, Guilianotti, J, Johnson, M. 2004. Sources of oxygen demand in the lower San Joaquin River, California. Estuaries 27:405-418.
- Levin, PS, Zabel, RW, Williams, JG. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London, Series B 268B:1153-1158.
- Levings, CD, Lauzier, RB. 1991. Extensive use of the Fraser River basin as winter habitat by juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Zoology 69:1759-1767.
- Levings, CD, McAllister, CD, Chang, BD. 1986. Intertidal habitats used by juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 43:1386-1397.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of American 15:237-240.
- Levy, DA, Northcote, TG. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Canadian Journal of Fisheries and Aquatic Sciences 39:270-276.
- Lewis, SL. 1969. Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society 89:14-19.
- Liao, JC, Beal, DN, Lauder, GV, Triantafyllou, MS. 2003. Fish exploiting vortices decrease muscle activity. Science 302:1566-1569.
- Lichatowich, J. 1999. Salmon without rivers. Washington, D. C.: Island Press.

- Lichatowich, JA, McIntyre, JD. 1987. Use of hatcheries in the management of anadromous salmonids. In: Dadswell, MJ, Kluada, RJ, Moffitt, CM, Saunders, RL, Rulifson, RA, Cooper, JE, Editors. Common strategies of anadromous and catadromous fish. American Fisheries Society Symposium 1. p. 131-136.
- Lichatowich, J. 1998. A conceptual foundation for the management of native salmonids in the Deschutes River. Portland, Oregon: Portland General Electric Company.
- Lindley, ST. 2003. Estimation of population growth and extinction parameters from noisy data. *Ecological Applications* 13:806-813.
- Lindley, ST, Mohr, MS. 2003. Modeling the effects of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*). *Fishery Bulletin* 101:321-331.
- Lindley, ST, Schick, R, May, BP, Anderson, JJ, Greene, S, Hanson, C, Low, A, McEwan, D, MacFarlane, RB, Swanson, C, Williams, JG. 2004. Population structure of threatened and endangered Chinook salmon ESUs in California's Central Valley Basin. NOAA-TN-NMFS-SWFSC-370.
- Lindsay, RB, Jonasson, BC, Schroeder, RK, Cates, BC. 1989. Spring Chinook in the Deschutes River, Oregon. Oregon Department of Fish and Wildlife. Information Report 89-4:1.92.
- Lisle, TE. 1989. Sediment transport and resulting deposition in spawning gravels, North Coastal California. *Water Resources Research* 25:1303-1319.
- Lisle, TE, Lewis, J. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2337-2344.
- Lister, DB, Genoe, HS. 1970. Stream habitat utilization by cohabiting underyearlings of Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) in the Big Qualicum River, British Columbia. *Journal of the Fisheries Research Board of Canada* 27:1215-1224.
- Lister, RB. 1990. Egg size and fecundity as indicators of life history patterns in southern British Columbia Chinook stocks. In: Hassler, TJ, Proceedings of the 1990 Northeast Pacific Chinook and coho salmon workshop; Arcata, CA. California Cooperative Fishery Research Unit, Humboldt State University. p. 128-140.
- Littleworth, AL and Garner, EL. 1995. California water. Point Arena, California: Solano Press Books.
- Lohmann, KJ, Lohmann, CMF, Ehrhart, LM, Bagley, DA, Swing, T. 2004. Geomagnetic map used in sea-turtle navigation. *Nature* 428:909-910.
- Low, A. 2005. Existing program summary: Central Valley salmon and steelhead monitoring programs. Sacramento, California: California Department of Fish and Game.
- Ludwig, D, Walters, CJ. 1985. Are age-structured models appropriate for catch and effort data? *Canadian Journal of Fisheries and Aquatic Sciences* 42:1066-1072.
- Ludwig, D. 1994. Uncertainty and fisheries management. In: Levin, SA, editor. *Frontiers in Mathematical Biology*. Springer-Verlag. p. 516-528.
- Lufkin, A. 1991. California's salmon and steelhead. Berkeley: University of California Press.
- Lund, SG, Caissie, D, Cunjak, RA, Vijayan, MM, Tufts, BL. 2002. The effects of environmental heat stress on heat-shock mRNA and protein expression in Miramichi Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1553-1562.
- Lynch, M. 1997. Inbreeding depression and outbreeding depression. Grant, W. S. Genetic effects of straying of non-native hatchery fish into natural populations; NOAA Technical Memorandum NMFS NWFSC-30.
- Lynch, M, O'Hely, M. 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2:363-378.
- Lynn, RJ, Bograd, SJ, Chereskin, TK, Huyer, A. 2003. Seasonal renewal of the California Current: the spring transition off California. *Journal of Geophysical Research* 108:3279. doi:10.1029/2003/JC001787
- MacFarlane, BR, Ralston, S, Royer, C, Norton, EC. 2005. Juvenile chinook salmon (*Oncorhynchus tshawytscha*) growth on the Central California coast during the 1980 El Niño and the 1999 La Niña. *Fisheries Oceanography* 14:
- MacFarlane, RB, Norton, EC. 2002. Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and the Gulf of the Farallones,

- California. Fishery Bulletin 100:244-257.
- Madenjian, CP, O'Conner, DV, Chernyak, SM, Rediske, RR, O'Keefe, JP. 2004. Evaluation of a Chinook salmon (*Oncorhynchus tshawytscha*) bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 61:627-635.
- Magnusson, A, Hilborn, R. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U. S. Pacific Coast. Estuaries 26:1094-1103.
- Mahnken, C, Ruggerone, G, Waknitz, W, Flagg, T. 1998. A historical perspective on salmonid production from Pacific Rim hatcheries. North Pacific Anadromous Fish Commission Bulletin 1:38-53.
- Mangel, M. 1994. Climate change and salmonid life history changes. Deep-Sea Research II 41:75-106.
- Mangel, M. 1996. Computing expected reproductive success of female Atlantic salmon as a function of smolt size. Journal of Fish Biology 49:877-882.
- Mangel, M. 1994. Life history variation and salmonid conservation. Conservation Biology 8:879-880.
- Manly, BFJ. 1997. Randomization, bootstrap and Monte Carlo methods in biology, second edition. London: Chapman & Hall.
- Manly, BFJ. 2001. Statistics for environmental science and management. Boca Raton, Florida: Chapman & Hall/CRC.
- Manly, BFJ, McDonald, LL, Thomas, DL, McDonald, TL, Erickson, WP. 2002. Resource selection by animals. Kluwer Academic Publishers.
- Mantua, NJ, Hare, SR, Zhang, Y, Wallace, JM, Francis, RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.
- Marine, KR. 1992. A background investigation and review of the effects of elevated water temperature on reproductive performance of adult Chinook salmon (*Oncorhynchus tshawytscha*). Department of Wildlife and Fisheries Biology, University of California, Davis.
- Marine, KR. 1997. Effects of elevated water temperature on some aspects of the physiological and ecological performance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*): implications for management of California's Central Valley salmon stocks [ms thesis]. University of California Davis.
- Marine, KR, Cech, JJr. 2004. Effects of high temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. North American Journal of Fisheries Management 24:198-210.
- Marr, DHA. 1965. The influence of light and surface contour on the efficiency of development of the salmon embryo. Report of the Challenger Society 3(XVII):33.
- Marr, DHA. 1963. The influence of surface contour on the behavior of trout alevins, *S. trutta* L. Animal Behavior 11(2-3):412.
- Marthur, D, Bason, WH, Purdy, EJr, Silver, CA. 1985. A critique of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825-831.
- Martin, BA, Saiki, MK. 2001. Gut contents of juvenile Chinook salmon from the upper Sacramento River California, during spring 1998. California Fish and Game 87:38-43.
- Maser, C, Sedell, JR. 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. Delrey Beach, Florida: St. Lucile Press.
- Maslin, P, Kindopp, J, Storm, C. 1999. Intermittent streams as rearing habitat for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*): 1999 update. California State University Chico, Dept. of Biological Sciences.
- Maslin, P, Lenox, M, Kindopp, J, McKinney, W. 1997. Intermittent streams as rearing habitat for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*). California State University Chico, Dept. of Biological Sciences.
- Maslin, PLM, Kindopp, J. 1998. Intermittent streams as rearing habitat for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*): 1998 update. California State University Chico, Dept. of Biological Sciences.
- Mason, JC. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26:63-91.

- Matter, AL, Sandford, BP. 2003. A comparison of migration rates of radio- and PIT-tagged adult Snake River Chinook salmon through the Columbia River hydropower system. 23:967-973.
- Matthews, KR, Berg, NH. 97. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools.
- May, RM. 2004. Uses and abuses of mathematics in biology. Science 303:790-793.
- Maynard, DJ, Flagg, TA, Mahnken, CVW. 1995. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids. In: Schramm, HLJr, Piper, RG, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium. p. 307-316.
- Maynard D. J., Flagg, TA, Mahnken, CVW, Schroder, SL. 1998. Natural rearing enhancement system technology for salmon culture. In: Brannen, EL, Kinsel, WC, editors. Proceedings of the Columbia River Anadromous Salmonid Rehabilitation and Passage Symposium; Moscow, Idaho. Aquaculture Research Institute, University of Idaho.
- Maynard, DJ, Berejikian, BA, Flagg, TA, Riley, S. Resource Enhancement and Utilization Technologies Division, NSC. 2003. Development of a natural rearing system to improve supplemental fish quality: progress report (performance period 1 March 1999 through 28 February 2003). Seattle, Washington: National Marine Fisheries Service.
- McCain and Trish and Stillwater Sciences. 2000. Tuolumne River restoration project monitoring : Special Run Pools 9/10, 7/1 Mining Reach, Ruddy Mining Reach. Arcata, California:
- McBain and Trush and Stillwater Sciences. 1999. Tuolumne River restoration project monitoring : Special Run Pools 9/10 and Gravel Mining Reach 7/1. Arcata, California:
- McCabe, GTJr, Emmett, TC, Muir, WD, Blahm, TH. 1986. Utilization of the Columbia River estuary by subyearling Chinook salmon. Northwest Science 60:133-124.
- McCart, P. 1969. Digging behavior of *Oncorhynchus nerka* spawning in streams at Babine Lake, British Columbia. In: Northcote, TG, Editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Vancouver: University of British Columbia.
- McCarthy, E. 1997. CVP Improvement Act update. Western Water <http://www/water-ed.org/mayjune97.asp#cvp>
- McCormick, SD. 1993. Methods for non-lethal gill biopsy and measurement of Na^+, K^+ - ATPase activity. Canadian Journal of Fisheries and Aquatic Sciences 50:656-658.
- McCormick, SD, Saunders, RL. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth and metabolism. American Fisheries Society Symposium . p. 211-229.
- McCullough, DA. 1999. A review and synthesis of effects of alteration to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. Environmental Protection Agency EPA 910-R-99-010. <http://www/critfc.org/tech/EPAreport.pdf>
- McCully, H. 1956. An undescribed type of migration in king salmon, *Oncorhynchus tshawytscha* (Walbaum). California Fish and Game 42:189-918.
- McDaniels, TL, Gregory, R. 2004. Learning as an objective within a structured risk management decision process. Environmental Science and Technology 38:1921-1926.
- McElhany, P, Ruckelshaus, MH, Ford, MJ, Wainwright, TC, Bjorkstedt, E. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42.
- McEvoy, AF. 1986. The fisherman's problem. Cambridge University Press.
- McEwan, D, Nelson, J. 1991. Steelhead restoration plan for the American River. Sacramento, California: California Department of Fish and Game.
- McEwan, D. 2001. Central Valley Steelhead. In: Brown, RL, Editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin 179. Fish Bulletin 179.1. California Department of Fish and Game. p. 1-44.
- McGinnity, P, Proh hl, P, Ferguson, A, Hynes, R,   Maoil idigh, Niall, Baker, N, Cotter, D, O'Hea, B, Cooke, D, Rogan, G, Taggart, J, Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London, Series B 270:2443-2450.
- McGregor, EA. 1923. Notes on the egg yield of Sacramento River king salmon. California Fish and Game 9:134-138.

- McGregor, EA. 1922. Observations on the egg yield of Klamath River king salmon. California Fish and Game 8:160-164.
- McHugh, P, Budy, P. 2004. Patterns of spawning habitat selection and suitability for two populations of spring Chinook salmon, with an evaluation of generic versus site-specific suitability criteria. Transactions of the American Fisheries Society 133:89-97.
- McIsaac, DO, Quinn, TP. 1988. Evidence for a hereditary component in homing behavior of chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 45:2201-2205.
- McLain, Jeff, Burmester, R. 1999. Juvenile fall-run and winter-run Chinook salmon abundance. IEP Newsletter 12:35-38.
- McLean, JE, Bentzen, P, Quinn, TP. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. Canadian Journal of Fisheries and Aquatic Sciences 60:433-440.
- McLean, WE. 1979. A rearing model for salmonids [ms thesis]. Vancouver: Department of Interdisciplinary Studies, University of British Columbia.
- McMichael, GA, Rakowski, CL, James, BB, Lukas, JA. 2005. Estimated fall Chinook salmon survival to emergence in dewatered redds in a shallow side channel of the Columbia River. North American Journal of Fisheries Management 25:876-884.
- McNabb, CD, Liston, CR, Brothwick, SM. 2003. Passage of juvenile Chinook salmon and other fish species through Archimedes lifts and a hidrostral pump at Red Bluff, California. Transactions of the American Fisheries Society 132:326-334.
- McNeil, WJ. 1969. Survival of pink and chum salmon eggs and alevins. In: Northcote, TG, editor. Symposium on salmon and trout in streams. H. R. MacMillian Lectures in Fisheries. Vancouver: p. 101-117.
- McNeil, WJ. 1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of Southeastern Alaska. United States Fish and Wildlife Service Special Report - Fisheries No. 402.
- McNeil, WJ, Ahnell, WH. 1964. Success of pink salmon spawning relative to size of spawning bed materials. United States Fish and Wildlife Service. Special Scientific Report-Fisheries No. 469.
- McPhail, JD. 1997. The origin and speciation on *Oncorhynchus* revisited. In: Stouder, DJ, Bisson, PA, Naiman, RJ, editors. Pacific salmon and their ecosystems. New York: Chapman & Hall. p. 29-40.
- Meekan, MG, Dodson, JJ, Good, SP, Ryan, DA. 1998. Otolith and fish size relationships, measurement error, and size selective mortality during the early life of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:1663-1673.
- Meekan, MG, Ryan, DAJ, Dodson, JJ, Good, SP. 1998. Does mortality select size or growth potential in young sockeye salmon (*Oncorhynchus nerka*)? A simulation based on otolith - fish size relationships. Canadian Journal of Fisheries and Aquatic Sciences 55:1674-1681.
- Meffle, GK. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific Coast of North American. Conservation Biology 6:350-354.
- Menchen, RS. 1978. A description of California Department of Fish and Game management program for the San Joaquin River system salmon resource. California Department of Fish and Game, Anadromous Fisheries Branch.
- Menchen, RS. 1961. The Mokelumne River artificial spawning channel experiment. California Department of Fish and Game, Marine Resources Branch.
- Merz, JE, Setka, JD. 2004. Evaluation of a spawning habitat site for Chinook salmon in a regulated California River. North American Journal of Fisheries Management 25:48-56.
- Merz, JE. 2001. Association of fall-run chinook salmon redds with woody debris in the lower Mokelumne River, California. California Fish and Game 87:51-60.
- Merz, JE. 2001. Diet of juvenile fall-run Chinook salmon in the lower Mokelumne River, California. California Fish and Game 87:102-114.
- Merz, JE. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne River, California. California Fish and Game 88:95-111.
- Merz, JE. undated. Striped bass predation on juvenile salmonids at the Woodbridge Dam afterbay, Mokelumne

- River, California. Lodi, California: East Bay Municipal Utility District.
www.delta.dfg.ca.gov/sfrg/docs/MokelumneStriperPredation.pdf
- Merz, JE. 1993. A survey of drift and epibenthic communities and their utilization as forage by target fish in the Lower American River, California, February-July, 1992. Sacramento, California: California State University Foundation.
- Merz, JE, Merz, WR. 2004. Morphological features used to identify Chinook salmon sex during fish passage. *Southwest Naturalist* 49:197-202.
- Merz, JE, Moyle, PB. 2006. Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of Central California. *Ecological Applications* 16:999-1009.
- Merz, JE, Setka, JD. 2004. Evaluation of a spawning habitat enhancement site for Chinook salmon in a regulated California river. *North American Journal of Fisheries Management* 24:397-407.
- Merz, JE, Vanicek, CD. 1996. Comparative feeding habits of juvenile Chinook salmon, steelhead, and Sacramento squawfish in the lower American River, California. *California Fish and Game* 82:149-159.
- Merz, JJ, Setka, JD, Pasternack, GB, Wheaton, JM. 2004. Predicting benefits of spawning -habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1433-1446.
- Mesick, C. 2001a. The effects of San Joaquin River flows and Delta export rates during October on the number of adult San Joaquin chinook salmon that stray. In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin 179. Fish Bulletin.2. California Department of Fish and Game. p. 139-162.
- Mesick, C. 2001b. Studies of spawning habitat for fall-run chinook salmon in the Stanislaus River between Goodwin Dam and Riverbank from 1994 to 1997. In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin 179. Fish Bulletin.2. p. 217-252.
- Metcalfe, NB, Fraser, NHC, Burns, MD. 1999. Food availability, and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology* 68:371-381.
- Metcalfe, NB, Huntingford, FA, Thorpe, JE. 1988. Feeding intensity, growth rates, and the establishment of life history patterns in juvenile Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 57:463-474.
- Metcalfe, NB. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 55(Suppl. 1):93-103.
- Meyer, KA, Gregory, JS. 2000. Evidence of concealment behavior by adult rainbow trout and brook trout in winter. *Ecology of Freshwater Fish* 9:138-144.
- Miller, JA, Simenstad, CA. 1997. A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile chinook and coho salmon. *Estuaries* 20:792-806.
- Milligan, CL, Hooke, GB, Johnson, C. 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. *Journal of Experimental Biology* 203:921-926.
- Mills, KL. Undated. Comparison of the Central Valley Chinook salmon stock predictor performance. Stinson Beach, California: Point Reyes Bird Observatory.
- Mills, TJ, Fisher, F. 1994. Central Valley anadromous sport fish annual run-size, harvest, and population estimates. Sacramento, California: California Department of Fish and Game, Inland Fisheries Division.
- Mills, TJ, McEwan, DR, Jennings, MR. 1997. California salmon and steelhead: beyond the crossroads. In: Stouder, DJ, Bisson, PA, Naiman, RJ, editors. Pacific salmon and their ecosystems. New York: Chapman & Hall. p. 91-112.
- Milner, NJ, Elliot, JM, Armstrong, JD, Gardiner, R, Welton, JS, Ladle, M. 2003. The natural control of salmon and trout populations in streams. *Fisheries Research* 62:111-125.
- Ministry of Environment, Lands, and Parks (British Columbia). 1997. Ambient water quality criteria for dissolved oxygen. Vancouver:
- Minshall, GW, Thomas, SA, Newbold, JD, Monaghan, MT, Cushing, CE. 2000. Physical factors influencing fine organic particle transport and deposition in streams. *Journal of the North American Benthological Society* 19:1-16.
- Modde, T, Hardy, TB. 1992. Influence of different microhabitat criteria on salmonid habitat simulation. *Rivers* 3:37-44.

- Moffett, J. 1949. The first four years of king salmon maintenance below Shasta Dam, Sacramento River, California. *California Fish and Game* 35:77-102.
- Montgomery, DR, Beamer, EM, Pess, GR, Quinn, TP. 1999. Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 56:377-387.
- Montgomery, DR, Buffington, JM, Peterson, NP, Schuett-Hames, D, Quinn, TP. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1061-1070.
- Montgomery, DR, Collins, BD, Buffington, JM, Abbe, TB. 2003. Geomorphic effects of wood in rivers. In: Gregory, SV, Boyer, KL, Gurnell, AM, editors. *The ecology and management of wood in world rivers*. Bethesda, Maryland: American Fisheries Society. p. 21-48.
- Moore, AP, Waring, CP. 1996. Sublethal effects of the pesticide diazinon on olfactory function in mature male Atlantic salmon parr. *Journal of Fish Biology* 48:758-775.
- Moore, TL. 1997. Condition and feeding of juvenile chinook salmon in selected intermittent tributaries of the upper Sacramento River [ms thesis]. California State University, Chico.
- Morbrand, LE, Barr, J, Blankenship, L, Campton, DE, Trevor, TPE, Flagg, TA, Mahnken, CVW, Seeb, LW, Seidel, PR, Smoker, WW. 2005. Hatchery reform in Washington state: principles and emerging issues. *Fisheries* 30:11-23.
- Morimoto, RI, Tissieres, A, Georgopoulos, C. 1990. *Stress proteins in biology and medicine*. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.
- Morita, K, Yamamoto, S, Takashima, Y, Matsuiishi, T, Kanno, Y, Nishimura, K. 1999. Effect of growth history on egg number and size in wild white-spotted char (*Salvelinus leucomaenis*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:1585-1589.
- Morita, K, Yanamoto, S, Hoshino, N. 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1300-1306.
- Mote, PW, Parson, EA, Hamlet, AF, Keeton, WS, Lettenmaier, D, Mantua, N, Miles, EL, Peterson, DW, Peterson, DL, Slaughter, R, Snover, AK. 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. *Climate Change* 61:45-88.
- Moyle, PB. 1970. Occurrence of king (Chinook) salmon in the Kings River, Fresno County. *California Fish and Game* 56:314-315.
- Moyle, PB, Marchetti, MP, Baldridge, J, Taylor, TL. 1998. Fish health and diversity: justifying flows for a California stream. *Fisheries* 23:6-15.
- Moyle, PB. 1969. Comparative behavior of young brook trout of wild and hatchery origin. *Progressive Fish-Culturist* 31:51-56.
- Moyle, PB. 1994. The decline of anadromous salmonids in California. *Conservation Biology* 8:869-870.
- Moyle, PB. 1977. In defense of sculpins. *Fisheries* 2:20-23.
- Moyle, PB. 2002. *Inland Fishes of California*. University of California Press.
- Moyle, PB, Israel, JA. 2005. Untested assumptions: effectiveness of screening diversions for conservation of fish populations. *Fisheries* 30:20-28.
- Mueter, FJ, Peterman, RM, Pyper, BJ. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59:456-463.
- Munch, SB, Kottas, A, Mangel, M. 2005. Bayesian nonparametric analysis of stock-recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1808-1821.
- Murphy, GI, Shapovalov, L. 1951. A preliminary analysis of northern California salmon and steelhead runs. *California Fish and Game* 37:497-507.
- Murray, CB, Rosenau, ML. 1989. Rearing of juvenile Chinook in nonnatal tributaries of the lower Fraser River. *North American Journal of Fisheries Management* 118:284-289.
- Muscik, JA. 1999. Criteria to define extinction risk in marine fishes. *Fisheries* 24:6-14.
- Myers, JM, Kope, RG, Bryant, GJ, Teel, D, Lierheimer, LJ, Wainwright, TC, Grant, WS, Waknitz, FW, Neely, K, Lindley, ST, Waples, RS. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and

- California. U. S. Department of Commerce, National Oceanic and Atmospheric Administration NOAA Technical Memorandum NMFS-NWFSC-35.
- Myers, KW, Horton, HF. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. In: Kennedy, VS, editor. Estuarine comparisons. New York: Academic Press. p. 388-392.
- Myers, KW. 1997. Offshore distribution and migration patterns and ocean survival of salmon. In: Emmett, RL, Scjoeve, MH, editors. Estuarine and ocean survival of Northeastern Pacific salmon: proceedings of the workshop. U. S. Dept. of Commerce. NOAA Technical Memorandum NMFS-NWFSC-29.
- Myers, RA, Bowen, KG, Barrowman, NA. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404-2419.
- Myers, RA, Levin, SA, Lande, R, James, FC, Murdock, WW, Paine, RT. 2004. Hatcheries and endangered salmon. Science 303:1980.
- Myrick, CA, Cech, JJr. 2002. Growth of American River fall-run Chinook salmon in California's Central Valley: temperature and ration effects. California Fish and Game 88:35-44.
- Myrick, CA, Cech, JJr. 2001. Temperature effects on Chinook salmon and steelhead: a review focusing on California's Central Valley populations. <http://www.cwemf.org>: Bay-Delta Modeling Forum.
- Myrick, CA, Cech, JJr. 2000. Temperature influences on California rainbow trout physiological performance. Fish Physiology and Biochemistry 22:245-254.
- Naiman, RJ, Bilby, RE. 1998. River ecology and management. New York: Springer.
- National Marine Fisheries Service (NMFS). 1993. Biological opinion for the operation of the federal Central Valley Project and the California State Water Project. Silver Springs, Maryland:
- National Marine Fisheries Service (NMFS). 1997. NMFS proposed recovery plan for the Sacramento Rive winter-run Chinook salmon. Long Beach, California:
- National Marine Fisheries Service (NMFS). 2000. Predation on salmonids relative to the Columbia River Power System. Seattle, Washington: Northwest Fisheries Science Center. White Paper.
- National Research Council (NRC) Committee on Endangered and Threatened Fishes in the Klamath River Basin. 2003. Endangered and threatened fishes in the Klamath River basin: causes of decline and strategies for recovery. Washington, D.C.: National Academies Press.
- National Research Council (NRC) Committee on protection and management of Pacific Northwest anadromous salmonids, board on environmental studies and toxicology, commission on life sciences . 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press.
- National Research Council (NRC), Committee on water resources management, instream flows, and salmon survival in the Columbia River Basin. 2004. Managing the Columbia River: instream flows, water withdrawals, and salmon survival . Washington, D. C. : National Academies Press.
- Naughton, GP, Bennett, DH, Newman, KB. 2004. Predation on juvenile salmonids by smallmouth bass in the Lower Granite Reservoir system, Snake River. North American Journal of Fisheries Management 24:534-544.
- Needham, PR, Hanson, HA, Parker, LP. 1943. Supplementary report on investigations of fish-salvage problems in relation to Shasta Dam. U.S. Fish and Wildlife Service. Special Scientific Report No. 26.
- Needham, PR, Smith, OR. 1940. Salmon salvage problems in relation to Shasta Dam, California, and notes on the biology of the Sacramento River salmon. Transactions of the American Fisheries Society 70:55-69.
- Needham, PR. 1961. Observations on the natural spawning of eastern brook trout. California Fish and Game 47:27-40.
- Neilsen, JD, Geen, GH. 1986. First-year growth of rate of Sixes River chinook salmon as inferred from otoliths: effects of mortality and age at maturity. Transactions of the American Fisheries Society 115:28-33.
- Neilson, JD, Geen, GH, Bottom, DL. 1985. Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 42:899-908.
- Neilson, JD, Banford, CE. 1983. Chinook salmon (*Oncorhynchus tshawytscha*) spawner characteristics in relation to redd physical features. Canadian Journal of Zoology 61:1524-1531.

- Newman, KB, Buckland, ST, Lindley, ST, Thomas, L, Fernández, C. 2006. Hidden process models for animal population dynamics. *Ecological Applications* 16:74-86.
- Newman, KB. 1999. Estimating the chinook salmon production for watersheds within the Sacramento-San Joaquin river system. Moscow, Idaho: University of Idaho, Department of Statistics.
- Newman, KB. 2003. Modeling paired release-recovery data in the presence of survival and capture heterogeneity with application to marked juvenile salmon. *Statistical Modeling* 3:157-177.
- Newman, KB, Rice, J. 2002. Modeling the survival of chinook salmon smolts outmigrating through the lower Sacramento River system. *Journal of the American Statistical Association* 97:983-993.
- Nicholas, JW, Hankin, DG. 1988. Chinook salmon populations in Oregon coastal river basins: descriptions of life history and assessment of recent trends in run strength. Portland, Oregon: Oregon Department of Fish and Wildlife. Information Report, Series Number 88-1.
- Nichols, FH, Cloern, JE, Luoma, S, Peterson, DH. 1986. The modification of an estuary. *Science* 231:567-573.
- Nichols, K, Foott, JS. 2002. Health monitoring of hatchery and natural fall-run Chinook salmon juveniles in the San Joaquin River and tributaries, April - June 2001. Anderson, California: U.S. Fish and Wildlife Service, California-Nevada Fish Health Center. FY2001 Investigational Report.
- Nickleston, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1050-1056.
- Nicola, GG, Almodóvar, A. 2004. Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society* 133:66-78.
- Nielsen, JF, Pavey, SA, Wiacek, T, Williams, I. 2005. Genetics of Central Valley *O. mykiss* populations: drainage and watershed scale analyses. *San Francisco Estuary and Watershed Science* 3:article 1
<http://repositories.cdlib.org/mie/sfews/vol3/iss2/art3>. <http://repositories.cdlib.org/mie/sfews/vol3/iss2/art3>
- Nielsen, JL. 1995. Evolution and the aquatic ecosystem: defining unique units in population conservation. *American Fisheries Society Symposium* 17. Bethesda, Maryland:
- Nielsen, JL, Pavey, S, Wiacek, T, Sage, GK, Williams, I. 2003. Genetic analyses of Central Valley trout populations 1999-2003. Anchorage, Alaska: USGS Alaska Science Center.
- Nielsen, JL, Pavey, SA, Wiacek, T, Williams, I. 2005. Genetics of Central Valley *O. mykiss* populations: drainage and watershed scale analyses. *San Francisco Estuary and Watershed Science* (online serial) 3:
<http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art3>
- Nislow, KH, Einum, S, Foults, CL. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* 65(SA):188-200.
- Nislow, KH, Sepulveda, AJ, Folt, CL. 2004. Mechanistic linkage of hydrological regime to summer growth of age-0 Atlantic salmon. *Transactions of the American Fisheries Society* 133:79-88.
- NOAA Fisheries. 2004. Biological opinion on the long-term Central Valley Project and State Water Project operations criteria and plan. National Marine Fisheries Service, Southwest Region.
- NOAA Fisheries, West Coast Salmon Biological Review Team (NOAA WCSBRT). 2003. Updated status of federally listed ESUs of West Coast salmon and steelhead. <http://santacruz.nmfs.noss.gov/files/pubs/00682.pdf>
- Noakes, DJ, Beamish, RJ, Sweeting, R, King, J. 2000. Changing the balance: interactions between hatchery and wild Pacific coho salmon in the presence of regime shifts. *North Pacific Anadromous Fish Commission Bulletin* 2:155-163.
- Noble, MA. 2001. Current patterns over the continental shelf and slope. In: Karl, HA, Chin, JL, Ueber, E, Stuaffer, PH, Hendley, JW, editors. *Beyond the Golden Gate -- Oceanography, geology, biology, and environmental issues in the Gulf of the Farallones*. USGS Circular 1198.
- Northcote, TG. 1984. Mechanisms of fish migration in rivers. In: McCleave, JD, Arnold, GP, Dodson, JJ, Neil, WH, editors. *Mechanisms of migration in fishes*. New York, N.Y.: Plenum Publishing Company. p. 317-355.
- Novartis Crop Protection, Inc. 1997. An ecological risk assessment of diazinon in the Sacramento and San Joaquin river basins. Novartis Crop Protection. Technical Report.
- Nugent, J, Hoffarth, P, Brock, W. 2002b. 2002 evaluation of juvenile fall Chinook salmon stranding on the

- Hanford Reach of the Columbia River. Washington Department of Fish and Wildlife.
- Nugent, J, Newsome, T, Hoffarth, P, Nugent, MBW, Kuklinski, MJr. 2002a. 2001 evaluation of juvenile fall Chinook salmon stranding on the Hanford Reach of the Columbia River. Washington Department of Fish and Wildlife.
- O'Keefe, TC, Edwards, RT. 2003. Evidence for hyporheic transfer and removal of marine derived nutrients in a sockeye salmon stream in Southwest Alaska. In: Stockner, J, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society Symposium. Bethesda, Maryland: American Fisheries Society. p. 99-110.
- Oerlemans, J. 2005. Extracting a climate signal from 169 glacier records. *Science* 308:675-677.
- Okihiro, MS, Ostrach, D, Hinton, DE. 1992. American River juvenile Chinook and steelhead histological and morphometric evaluation. School of Veterinary Medicine, University of California. Davis.
- Olsén, H. 1999. Present knowledge of kin discrimination in salmonids. *Genetica* 104:295-299.
- Olson, AF, Quinn, TP. 1993. Vertical and horizontal movements of adult chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. *Fishery Bulletin* 91:171-181.
- Olson, PA, Foster, RF. 1957. Temperature tolerances of eggs and young of Columbia River chinook salmon. *Transactions of the American Fisheries Society* 85:203-207.
- Olsén, KH, Petersson, ERB, Lundqvist, H, Järvi, T. 2004. Downstream migration in Atlantic salmon (*Salmo salar*) smolt sibling groups. *Canadian Journal of Fisheries and Aquatic Sciences* 61:328-331.
- Oreskes, N, Belitz, K. 2001. Philosophical issues in model assessment. In: Anderson, MG, Bates, PD, editors. Model validation: perspectives in hydrological science. John Wiley & Sons. p. 23-42.
- Oreskes, N, Shrader-Frechette, K, Belitz, K. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. *Science* 263:641-646.
- Oreskes, N. 2004. The scientific consensus on climate change. *Science* 306:1686.
- Orr, M, Crooks, S, Williams, PB. 2003. Will restored tidal marshes be sustainable. *San Francisco Estuary and Watershed Science* 1:Article 5 <http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art5>
- Orsi, JJ. 1999. Report on the 1980-1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Sacramento, California: The Interagency Ecology Program for the Sacramento-San Joaquin Estuary.
- Osenberg, CW, Schmitt, RJ, Holbrook, SJ, Abu-Aba, KE, Flegal, AR. 1994. Detection of environmental impacts; natural variability, effect size, and power analysis. *Ecological Applications* 4:16-30.
- Pacific Fishery Management Council (PFMC). 1984. Final framework agreement for managing the ocean salmon fisheries off the coasts of Washington, Oregon, and California commencing in 1985. Portland, Oregon:
- Pacific Fishery Management Council (PFMC). 2003. Fishery Management Council plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California as revised through Amendment 14. Portland, Oregon: Pacific Fishery Management Council.
- Packman, AI, Bencala, KE. 2000. Modeling surface - subsurface hydrologic interactions. In: Jones, JB, Mulholland, PJ, editors. Streams and ground waters. San Diego, CA: Academic Press. p. 46-82.
- Parker, LP, Hanson, HA. 1944. Experiments on transfer of adult salmon into Deer Creek. *Journal of Wildlife Management* 8:192-197.
- Parker, RR, Larkin, PA. 1959. A concept of growth in fishes. *Journal of the Fisheries Research Board of Canada* 16:721-745.
- Pascual, MA, Quinn, TP, Fuss, H. 1995. Factors affecting the homing of fall chinook from Columbia River hatcheries. *Transactions of the American Fisheries Society* 124:308-320.
- Payne, BA, Lapointe, MF. 1997. Channel morphology and lateral stability: effects on distribution of spawning and rearing habitat for Atlantic salmon in a wandering cobble-bed river. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2627-2636.
- Pearcy, WC. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press.
- Pearcy, WG, Brodeur, RD, Fisher, JP. 1990. Distribution of juvenile cutthroat trout *Oncorhynchus clarki clarki* and steelhead *O. mykiss* in coastal waters off Oregon and Washington. *Fishery Bulletin* 88:697-711.

- Pearson, TN. 2002. Chronology of ecological interactions associated with the life-span of salmon supplementation programs. *Fisheries* 27:10-15.
- Peck, SL. 2004. Simulation as experiment: a philosophical reassessment for biological modeling. *Trends in Ecology and Evolution* 19:530-534.
- Peery, CA, Bjorn, TC. 2004. Interactions between natural and hatchery chinook salmon parr in a laboratory stream channel. *Fisheries Research* 66:311-324.
- Pennell, W, Barton, BA. 1996. Principles of salmonid culture. Elsevier.
- Perry, EA. 1995. Salmon stock restoration and enhancement: strategies and experience in British Columbia. In: Schramm, HLJ, Piper, RG, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15. p. 152-160.
- Peterman, RM. 1987. Review of the components of recruitment of Pacific salmon. In: Dadswell, MJ, Klauda, RJ, Moffitt, CM, Saunders, RL, Rullifson, RA, Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1.
- Peterson, HH. 1973. Adult returns to date from hatchery-reared one-year old smolts. In: International Atlantic Salmon Foundation, Special Publication 4. p. 219-226.
- Peterson, NP, Quinn, TP. 1996. Spatial and temporal variation in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington. *Journal of Fish Biology* 48:131-143.
- Petersson, E, Järvi, T. 2003. Growth and social interactions of wild and sea-ranched brown trout and their hybrids. *Journal of Fish Biology* 63:673-686.
- Petrusso, PA, Hayes, DB. 2001b. Condition of juvenile Chinook salmon in the upper Sacramento River, California. *California Fish and Game* 87:19-37.
- Petrusso, PA, Hayes, DB. 2001a. Invertebrate drift and feeding habits of juvenile Chinook salmon in the upper Sacramento River, California. *California Fish and Game* 87:1-18.
- Phillips, RW, Claire, EW. 1966. Intragravel movement of the reticulate sculpin, *Cottus perplexus*, and its potential as a predator on salmon embryos. *Transactions of the American Fisheries Society* 95:210-212.
- Pipal, KA. 2005. Summary of monitoring activities for ESA-listed salmonids in California's Central Valley. NOAA-TM-NMFS-SWFSC-373.
- Poff, NL, Allan, JD, Bain, MB, Karr, JR, Prestegard, KL, Richter, BD, Sparks, RE, Stromberg, JC. 1997. The natural flow regime. *BioScience* 47:769-784.
- Pollard, RA. 1955. Measuring seepage through salmon spawning gravel. *Journal of the Fisheries Research Board of Canada* 12:706-741.
- Powell, MJJ, Miller, M. 1990. Shoal spawning by Chinook salmon in Lake Huron. *North American Journal of Fisheries Management* 10:242-244.
- Power, ME, Dietrich, WE, Finlay, JC. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management* 20:887-895.
- Power, ME, Dietrich, WE, Sullivan, KO. 2001. Experimentation, observation, and inference in river and watershed investigations. In: Reserits, WJ, Bernardo, J, editors. Issues and perspectives in experimental ecology. Oxford, U.K.: Oxford University Press. p. 113-132.
- Prager, MH, Morh, MS. 2001. The harvest rate model for Klamath fall chinook salmon, with management applications and comments on model development and documentation. *North American Journal of Fisheries Management* 21:533-547.
- Price, CS, Schreck, CB. 2003. Stress and saltwater-entry behavior of juvenile chinook salmon (*Oncorhynchus tshawytscha*): conflicts in physiological motivation. *Canadian Journal of Fisheries and Aquatic Sciences* 60:910-918.
- Puget Sound Technical Recovery Team (PSTRT). 2002. Planning ranges and preliminary guidelines for the delisting and recovery of the Puget Sound Chinook Salmon Evolutionarily Significant Unit. Seattle, Washington: NOAA Fisheries, National Marine Fisheries Service, Northwest Fisheries Science Center.
- Punt, AE, Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* 7:35-63.
- Quinn, TJI. 2003. Ruminations on the development and future of population dynamics models in fisheries. *Natural*

Resources Modeling 16:341-392.

- Quinn, TJI, Deriso, RB. 1999. Quantitative Fish Dynamics. Biological Resources Management. New York: Oxford University Press.
- Quinn, TP. 2005. The behavior and ecology of Pacific salmon and trout. Bethesda, Maryland: American Fisheries Society.
- Quinn, TP. 1990. Current controversies in the study of salmon homing. *Ethology Ecology & Evolution* 2:49-63.
- Quinn, TP. 1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon. *Journal of Comparative Physiology* 137:243-248.
- Quinn, TP. 1997. Homing, straying, and colonization. In: Grant, WS, editor. Genetic effects of straying of non-native hatchery fish into wild populations: proceedings of the workshop. NOAA Tech Memo . Seattle, Washington: NWFSC, NOAA Tech Memo 30.
- Quinn, TP. 1993. A review of homing and straying of wild and hatchery-produced salmon. *Fishery Bulletin* 18:29-44.
- Quinn, TP, Hendry, AP, Wetzel, LA. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* 74:425-438.
- Quinn, TP, Kinnison, MT, Unwin, MJ. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate and process. *Genetica* 112-113:493-513.
- Quinn, TP, Nemeth, RS, McIsacc, DO. 1991. Patterns of homing and straying by fall Chinook salmon in the lower Columbia River Basin. *Transactions of the American Fisheries Society* 120:150-156.
- Quinn, TP, Nielsen, JL, Gan, C, Unwin, MJ, Wilmot, R, Guthrie, C, Utter, FM. 1996. Origin and genetic structure of chinook salmon, *Oncorhynchus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence. *Fishery Bulletin* 94:506-521.
- Quinn, TP, Unwin, MJ. 1993. Variation in life history patterns among New Zealand Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1414-1421.
- Quinn, TP, Unwin, MJ, Kinnison, MT. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. *Evolution* 54:1372-1385.
- Quinn, TP, Volk, EC, Hendry, AP. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 77:766-775.
- Railsback, SF, Stauffer, HB, Harvey, BC. 2003. What can habitat preference models tell us? Tests using a virtual trout population. *Ecological Applications* 13:1580-1594.
- Raleigh, RF. 1971. Innate control of migrations of salmon and trout from natal gravels to rearing areas. *Ecology* 52:291-297.
- Randall, RG, Healey, MC, Dempson, JB. 1987. Variability in length of freshwater residence of salmon, trout, and char. *American Fisheries Society Symposium* 1.
- Rasmussen, C, Ostberg, C, Clifton, DR, Holloway, James L., Rodriquez, RJ. 2003. Identification of a genetic marker that discriminates ocean-type and stream-type chinook salmon in the Columbia River Basin. *Transactions of the American Fisheries Society* 132:131-142.
- Recovery Science Review Panel (RSRP). 2004. Report for the meeting held August 30, September 2, 2004. <http://www.nwfsc.noaa.gov/trt/rsrp.cfm>: NOAA Fisheries, NWFSC.
- Recovery Science Review Panel (RSRP). 2002. Report for the meeting held December 11-13, 2002. <http://www.nwfsc.noaa.gov/trt/rsrp.cfm>: NOAA Fisheries, NWFSC.
- Recovery Science Review Panel (RSRP). 2001. Report for the meeting held March 13-14, 2001. <http://www.nwfsc.noaa.gov/trt/rsrp.cfm>: NOAA Fisheries, NWFSC.
- Recovery Science Review Panel (RSRP). 2000. Report of December 4-6, 2000, meeting. <http://www.nwfsc.noaa.gov/trt/rsrp.cfm>: NOAA Fisheries, NWFSC. <http://www.nwfsc.noaa.gov/trt/rsrp.cfm>
- Reimers, PE. 1971. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Corvallis, OR: Oregon State University.
- Reimers, PE. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Portland: Fish Commission of Oregon. Research Reports of the Fish Commission of Oregon.

- Reimers, PE. 1968. Social behavior among juvenile fall Chinook salmon. Journal of the Fisheries Research Board of Canada 25:2005-2008.
- Rein, SR. 1993. Model of Chinook salmon population dynamics [dissertation]. University of California Berkeley, Department of Statistics.
- Reinhardt, UG. 2001. Selection for surface feeding in farmed and sea-ranched masu salmon juveniles. Transactions of the American Fisheries Society 130:155-158.
- Reisenbichler, RR, McIntyre, D, Hallock, RJ. 1982. Relation between size of chinook salmon, *Oncorhynchus tshawytscha*, released at hatcheries and returns to hatcheries and ocean fisheries. California Fish and Game 68:57-59.
- Reisenbichler, RR. 1997. Genetic factors contributing to declines of anadromous salmonids in the Pacific Northwest. In: Stouder, DJ, Bisson, PA, Naiman, RJ, Editors. Pacific salmon and their ecosystems. Chapman and Hall. p. 223-244.
- Reisenbichler, RR. 1988. Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. North American Journal of Fisheries Management 8:172-174.
- Reisenbichler, RR. 1986. Use of spawner-recruit relations to evaluate the effect of degraded environment and increased fishing on the abundance of fall-run chinook salmon, *Oncorhynchus tshawytscha*, in several California streams [dissertation]. Seattle: University of Washington.
- Reisenbichler, RR, Brown, G. 2003. Potential risks and benefits of hatchery supplementation to naturally spawning populations of salmon. In: MacDonald, AD, Wainwright, TC, editors. Assessing extinction risks for West Coast salmon; NOAA. NOAA Technical Memorandum NMFS-NWFSC-56.
- Reisenbichler, RR, McIntyre, JD. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:123-128.
- Reisenbichler, RR, McIntyre, JD, Solazzi, MF, Landing, SW. 1992. Genetic variation in steelhead of Oregon and Northern California. Transactions of the American Fisheries Society 121:158-169.
- Reisenbichler, RR, Rubin, SP. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES Journal of Marine Science 56:459-466.
- Reiser, DW, White, RG. 1990. Effects of streamflow reduction on chinook salmon egg incubation and fry quality. Rivers 1:110-118.
- Rempel, L, Church, M. 2002. Morphological and habitat classification of the lower Fraser River gravel-bed reach: confirmation and testing. Vancouver, British Columbia: Department of Geography, University of British Columbia.
- Rennie, CD, Millar, RG. 2000. Spatial variability of stream bed scour and fill: a comparison of scour depth in chum salmon (*Oncorhynchus keta*) redds and adjacent bed. Canadian Journal of Fisheries and Aquatic Sciences 57:928-938.
- Rennie, CD, Miller, RG. 2000. Spatial variability of stream bed scour and fill: a comparison of scour depth in chum salmon (*Oncorhynchus keta*) redds and adjacent bed. Canadian Journal of Fisheries and Aquatic Sciences 57:928-938.
- Resources Agency of California. 1964. The effect of water development on the Delta environment. Sacramento: Resources Agency of California. Delta fish and wildlife protection study, report no. 3.
- Reynolds, FL, Mills, TJ, Benthin, R, Low, A. 1993. Restoring Central Valley streams: a plan for action. Sacramento, California: California Department of Fish and Game.
- Rice, C, Beamer, E, Lomax, D, Henderson, R, Pess, G. 2003. Distribution and abundance of hatchery and wild juvenile chinook salmon in nearshore waters of Skagit Bay, Puget Sound, Washington. Program, 2003 Georgia Basin/Puget Sound Research Conference. www.psat.wa.gov/Publications/2003research/rc03_abstracts/oral_sessions/session_5c
- Rich, AA. 1987. Report on studies conducted by Sacramento County to determine the temperatures which optimize growth and survival in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Sacramento, California: McDonough, Holland & Allen.
- Rich, WH. 1920. Early history and seaward migration of chinook salmon in the Columbia and Sacramento Rivers. Bulletin of the Bureau of Fisheries 37:3-77.
- Rich, WH. 1925. Growth and degree of maturity of chinook salmon in the ocean. Bulletin of the Bureau of

- Fisheries 41:15-90.
- Rich, WH. 1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. In: Moulton, FR, editor. The migration and conservation of salmon. p. 45-50.
- Rich, WH. 21. The relative maturity of the chinook salmon taken in the ocean along the Pacific Coast.
- Rich, WH, Holmes, HB. 1928. Experiments in marking young chinook salmon on the Columbia River, 1916 to 1927. Bulletin of the Bureau of Fisheries 44:
- Richards, J, Olsen, D. 1993. Inter-basins comparison study: Columbia River salmon production compared to other West Coast production areas. Phase 1 analysis for U. S. Army Corps of Engineers.
- Ricker, WE. 1980. Causes of the decrease in age and size of Chinook salmon. Canadian Technical Report of Fisheries and Aquatic Sciences.
- Ricker, WE. 1981. Changes in average size and age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636-1656.
- Ricker, WE. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 191.
- Ricker, WE. 1972. Hereditary and environmental factors affecting certain salmonid populations. In: Simon, RC, Larkin, PA, editors. The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries. Vancouver: University of British Columbia. p. 19-160.
- Ricker, WE. 1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. Journal of the Fisheries Research Board of Canada 30:1275-1286.
- Ricker, WO. 1960. The effect of environmental factors and heredity on the morphology and behavior of the Pacific salmon. VNIRO, Nauchnaya Informatsiya 4:1-12.
- Riddell, BE. 1986. Assessment of selective fishing on the age at maturity in Atlantic salmon (*Salmo salar*): a genetic perspective. In: Meerburg, DJ, editor. Salmonid age at maturity. Canadian Special Publication in Fisheries and Aquatic Sciences 89; p. 102-109.
- Riddell, BE. 1993. Spatial organization of Pacific salmon: what to conserve? In: Cloud, JG, Thorgaard, GH, editors. Genetic conservation of salmonid fishes. New York: Plenum Press. p. 22-41.
- Rieman, BE, Dunham, JB. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64.
- Rieman, BE, Beamesderfer, RC, Vigg, S, Poe, TP. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448-458.
- Riley, SC, Fuss, HJ, LeClair, LL. 2004. Ecological effects of hatchery-reared juvenile Chinook and coho salmon on wild juvenile salmonids in two Washington streams. North American Journal of Fisheries Management 4:506-517.
- Rise, ML, von Schalburg, D, Brown, GD, Mawer, MA, Devlin, RH, Kuipers, N, Busby, M, Beetz-Sargent, M, Alberto, R, Bobbs, A, Ross, Hunt, P, Shukin, R, Zeznik, JA, Nelson, C, Jones, SRM, Smailus, DE, Jones, SJM, Schein, JE, Marra, MA, Butterfield, YSN, Stott, JM, Ng, SHS, Davidson, WS, Koop, BF. 2004. Development and application of a salmonid EST database and cDNA microarray: data mining and interspecific hybridization characteristics. Genome Research 13:478-490.
- Rombough, PJ. 1988. Growth, aerobic metabolism, and dissolved oxygen requirements of embryos and alevins of steelhead, *Salmo gairdneri*. Canadian Journal of Zoology 66:651-660.
- Rombough, PJ. 1985. Initial egg weight, time to maximum alevin wet weight, and optimal ponding times for chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 42:287-291.
- Rombough, PJ. 1986. Mathematical model for predicting the dissolved oxygen requirements of steelhead (*Salmo gairdneri*) embryos and alevins in hatchery incubators. Aquaculture 59:119-137.
- Rondorf, DW, Dutchuk, MS, Kolok, AS, Gross, ML. 1985. Bioenergetics of juvenile salmon during the spring migration. Bonneville Power Administration. Annual Report 1983 (Contract DE-A179-82BP35346).
- Roni, P, Quinn, TP. 1995. Geographic variation in size and age of North American Chinook salmon. North American Journal of Fisheries Management 15:325-345.
- Roos, M. 1991. A trend of decreasing snowmelt runoff in California. Proceedings of the 59th Western Snow

- Conference; Juneau, Alaska. p. 29-36.
- Roper, B, Scarnecchia, DL. 1996. A comparison of trap efficiencies for wild and hatchery age-0 Chinook salmon. *North American Journal of Fisheries Management* 16:214-217.
- Roper, BB, Scarnecchia, DL, La Marr, TJ. 1994. Summer distribution of and habitat use by Chinook salmon and steelhead with a major basin of the South Umpqua River, Oregon. *Transactions of the American Fisheries Society* 123:298-308.
- Rosenfeld, JS, Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles.
- Ruggerone, GT. 2000. Differential survival of juvenile sockeye and coho salmon exposed to low dissolved oxygen during winter. *Journal of Fish Biology* 56:1013-1016.
- Rutter, C. 1909. The fishes of the Sacramento-San Joaquin Basin, with a study of their distribution and variation. *Bulletin of the United States Fish Commission* 27:103-152.
- Rutter, C. 1904. Natural history of the Quinnet Salmon. *Bulletin of the United States Fish Commission* 22:65-142.
- Ryan, BA, Smith, SG, Butzerin, JM, Ferguson, JW. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary. *Transactions of the American Fisheries Society* 132:275-288.
- Sacramento River Conservation Area Forum (SRCAF). 2003. Handbook. <http://www.sacramentoriver.ca.gov/publications/handbook/handbook.html>. (as of 1/05)
- Sacramento River Fall Chinook Review Team (SRFCRT). 1994. Sacramento River Fall Chinook Review Team Report. Portland, Oregon: Pacific Fishery Management Council.
- Sacramento San-Joaquin Estuary Fishery Resource Office (SSJEFRO). 2003. Abundance and survival of juvenile chinook salmon in the Sacramento-San Joaquin Estuary. Stockton, California: U.S. Fish and Wildlife Service.
- Saiki, MK, Castleberry, DT, May, TW, Martin, BA, Bullard, FN. 1995. Copper, cadmium, and zinc concentrations in aquatic food chains from the upper Sacramento River (California) and selected tributaries. *Archives of Environmental Contamination and Toxicology* 29:484-491.
- Salo, EO. 1991. Life history of chum salmon (*Oncorhynchus keta*). In: Groot, C, Margolis, L, editors. *Pacific salmon life histories*. Vancouver, British Columbia: UCB Press. p. 231-310.
- Salo, EO. 1960. Report on Butte Creek investigations, July 27 - August 3, 1960. Arcata, California: Humboldt State College, Division of Natural Resources.
- San Joaquin River Group Authority. 2004. 2003 Annual Technical Report. Modesto, California:
- San Joaquin River Group Authority. 2005. 2004 Annual Technical Report. Modesto, California:
- Sandahl, JF, Baldwin, DH, Jenkins, JJ, Scholz, NL. 2004. Odor-evoked field potentials as indicators of sublethal neurotoxicity in juvenile coho salmon (*Oncorhynchus kisutch*) exposed to copper, chlorpyrifos, or esfenvalerate. *Canadian Journal of Fisheries and Aquatic Sciences* 61:404-413.
- Sandercock, FK. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In: Groot, C, Margolis, L, editors. *Pacific salmon life histories*. Vancouver, British Columbia: UCB Press. p. 395-446.
- Sasaki, S. 1966. Distribution and food habits of king salmon, *Oncorhynchus tshawytscha*, and steelhead rainbow trout, *salmo gairdnerii*, in the Sacramento-San Joaquin delta. In: Turner, JL, Kelley, DW, compilers. *Ecological studies of the Sacramento-San Joaquin delta, part II*. Fish Bulletin 136. California Department of Fish and Game. p. 108-114.
- Savereide, JW, Quinn, TJ. 2004. An age-structured assessment model for Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:974-985.
- Schaefer, MB. 1951. Estimation of the size of animal populations by marking experiments. U. S. Fish and Wildlife Service Bulletin 52:189-203.
- Schaffter, RG. 1980. Fish occurrence, size, and distribution in the Sacramento River near Hood, California during 1973 and 1974. California Department of Fish and Game. Anadromous Fisheries Branch Administrative Report.
- Schaffter, R. G., Jones, PA, Karlton, JG. 1983. Sacramento River and tributaries bank protection and erosion control investigation - evaluation of impacts on fisheries: final report. Stockton, California: California Department of Fish and Game.

- Scheuerell, MD, Williams, JG. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography* 14:448-457.
- Scheuerell, MD. 2005. Influence of juvenile size on the age at maturity of individually marked wild Chinook salmon. *Transactions of the American Fisheries Society* 134:999-1004.
- Schindler, DE, Scheuerell, MD, Moore, JW, Gende, SM, Francis, TB, Palen, WJ. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1:31-37.
- Schlosser, IJ. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- Schmitt, RJ, Osenberg, CW. 1996. Detecting ecological impacts. Editors. _San Diego: Academic Press.
- Schnute, J. 1985. A general theory for analysis of catch and effort data. *Canadian Journal of Fisheries and Aquatic Sciences* 42:414-429.
- Schnute, JT. 2003. Designing fishery models: a personal adventure. *Natural Resources Modeling* 16:393-413.
- Schnute, JT, Haigh, R. 2003. A simulation model for designing groundfish trawl surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 60:640-656.
- Schnute, JT, Kronlund, AR. 2002. Estimating salmon stock-recruitment relationships from catch and escapement data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:433-449.
- Schnute, JT, Richards, LJ. 2001. Use and abuse of fishery models. *Canadian Journal of Fisheries and Aquatic Sciences* 58:10-17.
- Scholz, NL, Truelove, NK, French, BL, Berejikian, BA, Quinn, TP, Casillas, E, Collier, TC. 2000. Diazinon disrupts antipredator and homing behaviors in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:1911-1918.
- Schrank, AJ, Rahel, FJ, Johnstone, HC. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. *Transactions of the American Fisheries Society* 132:100-109.
- Schreck, CB. 1981. Parr-smolt transformation and behavior. In: Brannon, EL, Salo, EO, editors. *Salmon and trout migratory behavior symposium*; Seattle, Washington : University of Washington, School of Fisheries.
- Schrock, RM, Beeman, JW, Rondorf, DW, Haner, PV. 1994. A microassay for gill sodium, potassium-activated ATPase in juvenile Pacific salmonids. *Transactions of the American Fisheries Society* 123:223-229.
- Schuett-Hames, DE, Peterson, NP, Conrad, R, Quinn, TP. 2000. Patterns of gravel scour and fill after spawning by chum salmon in a Western Washington stream. *North American Journal of Fisheries Management* 20:610-617.
- Schumm, SA. 1977. *Drainage Basin Morphology*. Benchmark Papers in Geology 41. New York: Halstead Press.
- Scofield, N. 29. The status of salmon in California. *California Fish and Game* 15:13-18.
- Scofield, NB. 1913. A general report on a quinnat salmon investigation, carried on during the spring and summer of 1911. *Fish Bulletin* 1:35-41.
- Scofield, WL. 1920. King salmon marking experiment at Klamath River, 1919. *California Fish and Game* 6:101-103.
- Scott, D, Shirvell, CS. 1987. A critique of the Instream Flow Incremental Methodology and observations of flow determinations in New Zealand. In: Craig, JF, Kemper, JB, Editors. *Regulated streams: advances in ecology*. New York: Plenum Press.
- Seber, GA. 1982. *The estimation of animal abundance and related parameters*. New York: MacMillian.
- Secor, DH. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. *Fishery Bulletin* 90:798-806.
- Sedell, JR, Reeves, GH, Hauer, RF, Stanford, JA, Hawkins, CP. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14:711-724.
- Shackley, PE, Talbot, C, Cowan, A. 1993. The use of whole-body sodium, potassium and calcium content to identify the nutrient status of first year salmon fry. *Journal of Fish Biology* 43:825-836.
- Shapovalov, L. 1967. Biology and management of steelhead trout in California. California Department of Fish and Game. Inland Fisheries Administrative Report.
- Shapovalov, L. 1937. Experiments in hatching steelhead eggs in gravel. *California Fish and Game* 23:208-214.
- Shapovalov, L. 1947. Report on fisheries resources in connection with the proposed Yolo-Solano Development of the United States Bureau of Reclamation. *California Fish and Game* 33:61-88.

- Shapovalov, L, Taft, AC. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*). Sacramento: California Department of Fish and Game. Fish Bulletin No. 98.
- Shaw, PA, Maga, JA. 1943. The effect of mining silt on the yield of fry from salmon spawning beds. California Fish and Game 29:29-41.
- Shedlock, AM, Parker, JD, Crispin, DA, Pietsch, TW, Burner, GC. 1992. Evolution of the salmonid mitochondrial control region. Molecular Phylogenetics and Evolution 1:179-192.
- Shelbourn, JE, Clarke, WC, Levings, CD. 1995. Effect of lowered temperature on growth of juvenile Nechako River Chinook salmon (*Oncorhynchus tshawytscha*) at three ration levels. Canadian Data Report of Fisheries and Aquatic Sciences.
- Shelton, JM, Pollock, RD. 66. Siltation and egg survival in incubation channels.
- Shepherd, JG. 1982. A versatile new stock-recruitment relationship for fisheries and the construction of sustainable yield curves. Journal du conseil. conseil permanent international pour l'exploration de la mer 21:
- Sheridan, WL. 1962. Waterflow through a salmon spawning riffle in Southeastern Alaska. United States Fish and Wildlife Service Special Report -- Fisheries No. 407.
- Shirvell, CS. 1989. Ability of PHABSIM to predict chinook salmon spawning habitat. Regulated Rivers: Research and Management 3:277-289.
- Shirvell, CS. 1994. Effect of changes in stream flow on the microhabitat use and movements of sympatric juvenile coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) in a natural stream. Canadian Journal of Fisheries and Aquatic Sciences 51:1644-1652.
- Shirvell, CS. 1986. Pitfalls of physical habitat simulation in the Instream Flow Incremental Methodology. Prince Rupert, British Columbia: Department of Fisheries and Oceans, Fisheries Research Branch. Canadian Technical Report of Fisheries and Aquatic Sciences.
- Sholes, WH, Hallock, RJ. 1979. An evaluation of rearing fall-run chinook salmon, *Oncorhynchus tshawytscha*, to yearling at Feather River Hatchery, with a comparison of returns from hatchery and downstream releases. California Fish and Game 65:239-255.
- Shreffler, DK, Simenstad, CA, Thom, RM. 1992. Foraging by juvenile salmon in a restored estuarine wetland. Estuaries 15:204-213.
- Shumway, DL, Warren, CE, Doudoroff, P. 1964. Influence of oxygen concentration and water movement on growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society 93:342-356.
- Silver, SJ, Warren, CE, Doudoroff, P. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos and different water velocities. Transactions of the American Fisheries Society 92:327-343.
- Simenstad, CA, Eggers, DM. 1981. Juvenile salmonid and baitfish distribution, abundance, and prey resources in selected areas of Grays Harbor, Washington. Seattle, Washington: University of Washington, Fisheries Research Institute. FRI-UW-8116.
- Simenstad, CA, Fresh, KL, Salo, EO. 1982. Role of Puget Sound and Washington coastal estuaries in the life histories of Pacific salmon: an unappreciated function. In: Kennedy, VS, editor. Estuarine Comparisons. New York: Academic Press. p. 343-364.
- Simpkins, DG, Hubert, WA, Martinez del Rio, C, Rule, DC. 2003. Effect of swimming activity on relative weight and body composition of juvenile rainbow trout. North American Journal of Fisheries Management 23:283-289.
- Smith, BD, Ward, BR. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for coastal regions of British Columbia support the variable marine survival hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 57:271-284.
- Skinner, JE. 1972. Ecological studies of the Sacramento-San Joaquin estuary. Delta Fish and Wildlife Protection Study. Sacramento : California Department of Fish and Game.
- Skinner, JE. 1962. Fish and wildlife resources of the San Francisco Bay Area. Sacramento, California: California Department of Fish and Game.
- Skinner, JE. 1958. Some observations regarding the king salmon runs of the Central Valley. Sacramento,

- California: California Department of Fish and Game.
- Slater, DW. 1963. Winter-run chinook salmon in the Sacramento River, California with notes on water temperature requirements at spawning. U. S. Fish and Wildlife Service.
- Smith, AK. 1973. Development and application of spawning velocity and depth criteria for Oregon salmonids. Transactions of the American Fisheries Society 102:312-316.
- Smith, BD, Ward, BR. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for coastal regions of British Columbia support the variable marine survival hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 57:271-284.
- Smith, CC, Fretwell, SD. 1974. The optimal balance between size and number of offspring. The American Naturalist 108:499-506.
- Smith, GR. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. Systematic Biology 41:41-57.
- Smith, GR, Stearley, RF. 1989. The classification and scientific names on rainbow and cutthroat trouts. Fisheries 14:4-10.
- Smith, RJF. 1985. The control of fish migration. Berlin: Springer-Verlag.
- Smith, TR, Buckley, LJ. 2003. RNA-DNA ratio in scales from juvenile cod provides a nonlethal measure of feeding condition. Transactions of the American Fisheries Society 132:9-17.
- Snider, B, Reavis, B, Hill, S. 1998. Upper Sacramento River late fall-run Chinook salmon escapement survey, December 1997-May 1998. Sacramento: California Department of Fish and Game, Environmental Services Division.
- Snider, B, Reavis, B, Hill, S. 1999. Upper Sacramento River late fall-run Chinook salmon escapement survey, December 1998-May 1999. Sacramento: California Department of Fish and Game, Environmental Services Division.
- Snider, B, Reavis, B, Hill, S. 2000. Upper Sacramento River late fall-run Chinook salmon escapement survey, December 1999-April 2000. Sacramento: California Department of Fish and Game, Habitat Conservation Division.
- Snider, B, Titus, R. 1998. Evaluation of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, November 1995-July 1996. California Department of Fish and Game, Stream Evaluation Program. Technical Report.
- Snider, B, Titus, RG. 2001. Lower American River emigration survey, October 1997-September 1998. Sacramento, CA: California Department of Fish and Game, Stream Evaluation Unit. Technical Report No. 01-6.
- Snider, B, Titus, RG. 2002. Lower American River emigration survey, October 1999-September 2000. Sacramento, CA: California Department of Fish and Game, Stream Evaluation Unit. Technical Report No. 02-4.
- Snider, B, Titus, RG. 2000a. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1996 - September 1997. Sacramento, California: California Department of Fish and Game, Habitat Conservation Division.
- Snider, B, Titus, RG. 2000b. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1997 - September 1998. Sacramento, California: California Department of Fish and Game, Habitat Conservation Division.
- Snider, B, Titus, RG. 2000c. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1998 - September 1999. Sacramento, California: California Department of Fish and Game, Habitat Conservation Division.
- Snider, B, Vyverberg, K. 1996. Chinook salmon redd survey, lower American River, fall 1995. Sacramento, CA: California Department of Fish and Game, Stream flow and Habitat Evaluation Program.
- Snowden, TK, Power, G. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114:804-812.
- Snyder, JO. 1924c. An experiment relating to the homing instinct of the king salmon. California Fish and Game 10:8-64.

- Snyder, JO. 1922. The return of marked salmon grilse. *California Fish and Game* 8:103-107.
- Snyder, JO. 1928. Salmon Investigation. *California Fish and Game* 14:25-29.
- Snyder, JO. 1931. Tagging and marking. Report from California Department of Fish and Game. Proceedings, 1930 Annual Meeting of the International Pacific Salmon Federation; Stanford University, Palo Alto, California.
- Snyder, JO. 1924a. Third report on return of king salmon marked in 1919 in the Klamath River. *California Fish and Game* 10:110.
- Snyder, JO. 1921. Three California marked salmon recovered. *California Fish and Game* 7:1-5.
- Snyder, JO. 1924b. Young salmon taken at sea. *California Fish and Game* 10:63-64.
- Snyder, JO. 1931. Salmon of the Klamath River, California. Sacramento, California: Division of Fish and Game of California. Fish Bulletin No. 34.
- Sommer, TR, Nobroga, ML, Harrell, WC, Batham, W, Kimmerer, WJ. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:325-333.
- Sommer, TR, Harrell, WC, Mueller Solger, A, Tom, B, Kimmerer, W. 2004. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:247-261.
- Sommer, TR, Harrell, WC, Nobriga, M. 2005. Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. *North American Journal of Fisheries Management* 25:1493-1504.
- Sophocleous, M. 2002. Interactions between groundwater and surface water: the state of the science. *Hydrogeology Journal* 10:52-67.
- Soulsby, C, Malcolm, IA, Youngson, AF. 2001. Hydrogeochemistry of the hyporheic zone in salmon spawning gravels: a preliminary assessment in a degraded agricultural stream. *Regulated Rivers: Research and Management* 17:651-665.
- Sowden, TK, Power, G. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrate. *Transactions of the American Fisheries Society* 114:804-812.
- Speed, T. 1993. Modeling and managing a salmon population. In: Barnett, V, Turkman, KF, editors. *Statistics for the Environment*. John Wiley & Sons. p. 265-290.
- Stanford, JA, Ward, JV. 1998. The hyporheic habitat of river ecosystems. *Nature* 335:64-66.
- Stanislaus River Fish Group. 2004. A summary of fisheries research in the lower Stanislaus River: working draft.
- Starfield, AM. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61:261-270.
- Stauffer, GD. 1973. A growth model for salmonids reared in hatchery environments [dissertation]. Seattle: University of Washington, Department of Zoology.
- Stearley, RF, .Smith, GR. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. *Transactions of the American Fisheries Society* 122:1-33.
- Stearns, SC, Hendry, AP. 2004. The salmonid contribution to key issues in evolution. *Evolution illuminated: salmon and their relatives*. New York: Oxford University Press.
- Steen, RP, Quinn, TP. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* 77:836-841.
- Stefansson, SO, Björnsson, BTH, Sundell, K, Nyhammer, G, McCormick, SD. 2003. Physiological characteristics of wild Atlantic salmon post-smolts during estuarine and coastal migration. *Journal of Fish Biology* 63:942.
- Steidl, RJ, Hayes, JP, Schaubert, E. 1997. Statistical power analysis in wildlife research. *Journal of Wildlife Management* 61:270-279.
- Stevens, DE. 1966. Distribution and food habits of the American shad (*Alosa sapidissima*) in the Sacramento-San Joaquin Delta. In: Turner, JL, Kelley, DW, Editors. *Ecological studies of the Sacramento-San Joaquin Delta, Part II*. Fish Bulletin 136.
- Stevens, DE, Miller, LW. 1983. Effects of river flow on abundance of young Chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin River system. *North American Journal of Fisheries Management* 3:425-437.

- Steward, CR, Bjorn, TC. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: a synthesis of published literature. Portland, Oregon: Bonneville Power Administration.
- Stewart, IJ, Marison, SM, Boatright, CP, Buck, GB, Quinn, TP. 2004. Site fidelity of spawning sockeye salmon (*Oncorhynchus nerka* W.) in the presence and absence of olfactory cues. *Ecology of Freshwater Fish* 13:104-110.
- Stewart-Oaten, A. 1996. Goals in environmental monitoring. In: Schmitt, RJ, Osenberg, CW, editors. *Detecting ecological impacts*. San Diego: Academic Press. p. 17-28.
- Stillwater Sciences. 2004. Lower Calaveras River Chinook salmon and steelhead limiting factor analysis, first year report (revised). Stillwater Sciences, Berkeley, California.
- Stillwater Sciences. 2001. Merced River Restoration Baseline Studies. Berkeley, CA: Stillwater Science.
- Stine, S. 1994. Extreme and persistent drought in California and Patagonia during mediaeval time. *Nature* 369:546-549.
- Stockner, J. 2003. Nutrients in salmonid ecosystems: sustaining production and biodiversity, American Fisheries Society Symposium 34. Bethesda, Maryland: American Fisheries Society.
- Stockwell, CA, Hendry, AP, Kinnison, MT. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18:94-101.
- Stone, L. 18876. Report on operations during 1874 at the United States salmon hatching establishment on the McCloud River, California. Washington, D.C.: U.S. Commission of Fisheries. Report of the Commissioner for 1873-4 and 1874-5. Appendix 22:437-478.
- Storber, QJ, Walden, SJ, Griggs, DT. 1973. Juvenile salmonid migration through Skagit Bay. In: Storber, QJ, Salo, EO, editors. *Ecological studies of the proposed Kilet Island nuclear power site*. Seattle, Washington: University of Washington, Fisheries Research Institute. p. 35-70.
- Stouder, DJ, Bisson, PB, Naiman, RJ. 1997. *Pacific salmon and their ecosystems*. New York: Chapman & Hall.
- Stuart, TA. 1954. Spawning sites of trout. *Nature* 173:354.
- Sullivan, K, Martin, DJ, Cardwell, RD, Toll, JE, Duke, S. 2000. An analysis of the effect of temperature on salmonids of the Pacific northwest with implications for selecting temperature criteria. Portland, Oregon: Sustainable Ecosystems Institute.
- Sumner, FH, Smith, OR. 1940. Hydraulic mining and debris dams in relation to fish life in the American and Yuba rivers of California. *California Fish and Game* 26:2-22.
- Sutton, SG, Built, TP, Jaedrocj. Richard L. 2000. Relationships among fat weight, body weight, water weight, and condition factor in wild Atlantic salmon parr. *Transactions of the American Fisheries Society* 129:527-538.
- Swan, GA. 1989. Chinook salmon spawning surveys in deep waters of a large, regulated river. *Regulated Rivers: Research and Management* 4:355-370.
- Swanson, C, Young, PS, Cech, JJr. 2004. Swimming in two-vector flows: performance and behavior of juvenile Chinook salmon near a simulated scree water diversion. *Transactions of the American Fisheries Society* 133:265-278.
- Sweeting, RM, Beamish, RJ, Noakes, DJ, Neville, CM. 2003. Replacement of wild coho salmon by hatchery-reared coho salmon in the Strait of Georgia of the past three decades. *North American Journal of Fisheries Management* 23:492-502.
- Tabor, RA, Shivley, R. S., Poe, TP. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management* 13:831-838.
- Taft, AC, Shapovalov, L. 1938. Homing instinct and straying among steelhead trout (*Salmo gairdnerii*) and silver salmon (*Oncorhynchus kisutch*). *California Fish and Game* 24:118-125.
- Tait, JS. 1960. The first filling of the swim bladder in salmonids. *Canadian Journal of Zoology* 38:179-187.
- Tallman, RF, Healey, MC. 1994. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta*. *Canadian Journal of Fisheries and Aquatic Sciences* 48:661-671.
- Tappel, PD, Bjornn, TC. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. *North American Journal of Fisheries Management* 3:123-135.
- Taylor, EB. 1998. Adaptive variation in rheotactic and agonistic behavior in newly emerged fry of Chinook

- salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. Canadian Journal of Fisheries and Aquatic Sciences 45:237-243.
- Taylor, EB. 1997. Local adaptation. In: Grant, WS, editor. Genetic effects of straying of non-native hatchery fish into wild populations: proceedings of the workshop. NOAA Technical Memorandum NMFS NWFSC 30.
- Taylor, EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.
- Teel, DJ, Milner, GB, Winans, GA, Grant, WS. 2000. Genetic population structure and origin of life history types in chinook salmon in British Columbia, Canada. Transactions of the American Fisheries Society 129:194-209.
- Terhune, LDB. 1958. The Mark VI groundwater standpipe for measuring seepage through salmon spawning gravel. Journal of the Fisheries Research Board of Canada 15:1027-1063.
- Thomas, AE, Banks, JL, Greenland, DC. 1969. Effect of yolk sac absorption on the swimming ability of fall Chinook salmon. Transactions of the American Fisheries Society 89:406-410.
- Thomas, CD, Cameron, A, Green, RE, Bakkenes, M, Beaumont, LJ, Collingham, Y, Erasmus, BFN, Ferreira de Siqueira, M, Grainger, A, Hannah, L, Hughes, L, Huntley, B, van Jaarsveld, AS, Midgley, GF, Miles, L, Ortega-Huerta, Peterson, AT, Phillips, OL, Williams, SE. 2004. Extinction risk from climate change. Nature 427:145-148.
- Thomas R. Payne & Associates. 2002. Evaluation of project effects on instream flows and fish habitat. Arcata, California: Oroville Facilities Relicensing (Project No. 2100), SP-F16.
- Thompson, WF. 1919. The conservation of our fisheries. California Fish and Game 51:49-59.
- Thorpe, JE. 1977. bimodal distribution of lengths of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. Journal of Fish Biology 11:175-184.
- Thorpe, JE. 1989. Developmental variation within salmon populations. Journal of Fish Biology 35(Supplement A):295-303.
- Thorpe, JE. 1993. Impacts of fishing on the genetic structure of salmonid populations. In: Cloud, JG, Thorgaard, GH, editors. Genetic conservation of salmonid fishes; New York: Plenum Press.
- Thorpe, JE. 2004. Life history responses of fishes to culture. Journal of Fish Biology 65 (Supplement A):263-285.
- Thorpe, JE. 1994. Performance thresholds and life-history flexibility in salmonids. Conservation Biology 8:877-879.
- Thorpe, JE. 1994. Salmonid fishes and the estuarine environment. Estuaries 17:76-93.
- Thorpe, JE. 1998. Salmonid life-history evolution as a constraint on marine stock enhancement. Bulletin of Marine Science 62:465-475.
- Thorpe, JE. 1987. Smolting versus residency: developmental conflicts in salmonids. In: Dadswell, MJ, Klauda, RJ, Moffitt, CM, Saunders, RL, Rulifson, RA, Cooper, JE, editors. Common strategies of anadromous and catadromous fishes, American Fisheries Society Symposium 1. American Fisheries Society Symposium 1. p. 224-252.
- Thorpe, JE, Mangel, M, Metcalfe, NB, Huntingford, FA. 1998. Modeling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12:581-599.
- Tiffan, KF, Garland, RD, Rondorf, DW. 2002. Quantifying flow-dependent changes in subyearling fall Chinook salmon rearing habitat using two-dimensional spatially-explicit modeling. North American Journal of Fisheries Management 22:713-726.
- Tiffan, KF, Rondorf, DW, Wagner, PG. 2000. Physiological development and migratory behavior of subyearling fall Chinook salmon in the Columbia River. North American Journal of Fisheries Management 20:28-40.
- Titus, RG, Volkoff, MC, Snider, WM. 2004. Use of otolith microstructure to estimate growth rates of juvenile Chinook salmon from a Central Valley, California stock. In: Feyrer, FL, Brown, RL, Orsi, JJ, editors. Early life history of fishes in the San Francisco Estuary and watershed. American Fisheries Society Symposium 39. Bethesda, Maryland : American Fisheries Society. p. 181-202.
- Tobin, JHI. 1994. Construction and performance of a portable resistance board weir for counting migrating adult salmon in rivers. Kenai, Alaska: United States Fish and Wildlife Service, Region 7.
- Travis, J, Cokeman, FC, Grimes, CB, Conover, D, Bert, TM, Tringali, M. 1998. Critically assessing stock enhancement: an introduction to the Mote Symposium. Bulletin of Marine Science 62:305-311.

- Tri-Dam Project. 2001. Three year evaluation of predation in the Stanislaus River.
<https://ecosystem.calfed.ca.gov/WRRC/CalFed/people/spcramer/proposal/99982173764/compilation-b>
- Trudel, M, Geist, DR, Welch, DW. 2004. Modeling the oxygen consumption rates in Pacific salmon and steelhead: as assessment of current models and practices. Transactions of the American Fisheries Society 133:326-348.
- Tucker, ME, Martin, CD, Gaines, PD. 2003. Spatial and temporal distribution of Sacramento pikeminnow and striped bass at the Red Bluff Diversion Complex, including the Research Pumping Plant, Sacramento River, California: January, 1997 to August, 1998. Red Bluff, California: U. S. Fish and Wildlife Service. Red Bluff Research Pumping Plant Report Series.
- Tucker, ME, Williams, CM, Johnson, RR. 1998. Abundance, food habits and life history aspects of Sacramento squawfish and striped bass at the Red Bluff Diversion Complex, including the Research Pumping Plant, Sacramento, California, 1994-1996. Red Bluff, California: U. S. Fish and Wildlife Service.
- Turner, JL. 1966. Introduction to fisheries studies in the Sacramento-San Joaquin Delta. In: Turner, JL, Kelley, DW, Editors. Ecological studies of the Sacramento-San Joaquin Delta, Part II. Fish Bulletin 136.
- United States Bureau of Reclamation (USBR). 2000. Draft environmental assessment/initial study for Mill Creek anadromous fish adaptive management enhancement plan. Shasta Lake, California: USBR, Northern California Area Office.
- United States Bureau of Reclamation (USBR). 2004. Long-term Central Valley Project operations criteria and plan, CVP-OCAP. Sacramento, California: Bureau of Reclamation.
- United States Fish and Wildlife Service (USFWS). 2001. Biological assessment of artificial propagation at Coleman National Fish Hatchery and Livingston Stone National Fish Hatchery: program description and incidental take of chinook salmon and steelhead trout. Red Bluff, California:
- United States Fish and Wildlife Service (USFWS). 1998. Central Valley Project Improvement Act tributary production enhancement report. Sacramento, CA:
- United States Fish and Wildlife Service (USFWS). 1999. Effects of temperature on early-life survival of Sacramento River fall- and winter-run chinook salmon. Red Bluff, California: USFWS.
- United States Fish and Wildlife Service (USFWS). 1988. Fish passage action program for the Red Bluff Diversion Dam. Final report on fishery investigations.
- United States Fish and Wildlife Service (USFWS). 2000. Impacts of riprapping to ecosystem functioning, lower Sacramento River, California. Sacramento, California: USFWS.
- United States Fish and Wildlife Service (USFWS). 1984. Results of the food habitats study on juvenile Chinook salmon in the lower American River - March to June 1983. Sacramento, California:
- United States Fish and Wildlife Service (USFWS). 1995. Working paper on restoration needs: habitat actions to double natural production of anadromous fish in the Central Valley of California. Stockton, CA:
- Unwin, M. J. 1986. Stream residence time, size characteristics, and migration patterns of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from a tributary of the Rakaia River, New Zealand. New Zealand Journal of Marine and Freshwater Research 20:231-252.
- Unwin, MJ. 1997. Fry-to-adult survival of natural and hatchery-reared chinook salmon (*Oncorhynchus tshawytscha*) from a common origin. Canadian Journal of Fisheries and Aquatic Sciences 54:1246-1254.
- Unwin, MJ, Glova, GJ. 1997. Changes in life history parameters in a naturally spawning population of chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. Canadian Journal of Fisheries and Aquatic Sciences 54:1235-1245.
- Unwin, MJ, Kinnison, MT, Boustead, NC, Quinn, TP. 2003. Genetic control over survival in Pacific salmon (*Oncorhynchus* spp.): experimental evidence between and within populations of New Zealand chinook salmon (*O. tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 60:1-11.
- Unwin, MJ, Quinn, TP, Kinnison, MT, Boustead, NC. 2000. Divergence in juvenile growth and life history in two recently colonized and partially isolated chinook salmon populations. Journal of Fish Biology 57:943-960.
- Utter, F, Milner, G, Stahl, G, Teel, D. 1989. Genetic population structure of chinook salmon, *Oncorhynchus tshawytscha*, in the Pacific Northwest. Fishery Bulletin 87:239-264.
- Utter, FMWRS, Teel, DJ. 1992. Genetic isolation of previously indistinguishable chinook populations from the Snake and Klamath Rivers: limitations of negative data. Fishery Bulletin 90:770-777.

- Utter, F. 1998. Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. *Bulletin of Marine Science* 62:623-640.
- Utter, F. 2001. Patterns of subspecific anthropogenic introgression in two salmonid genera. *Reviews in Fish Biology and Fisheries* 10:265-279.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Van Hying, JM. 1957. Stock-recruitment relationships for Columbia River chinook salmon. *Conseil International pour l'Exploration de la Mer* 164:89-97.
- Van Winkle, W, Jager, HI, Holcomb, BD. 1996. An individual-based instream flow model for coexisting populations of brown and rainbow trout. Palo Alto, CA: EPRI.
- Van Woert, W. 1964. Mill Creek Counting Station. Memorandum to Elden Hughes. California Dept. of Fish and Game.
- Vander Haegen, GE, Ashbrook, CE, Yi, KW, Dixon, JF. 2004. Survival of spring Chinook salmon captured and released in a selective commercial fishery using gill nets and tangle nets. *Fisheries Research* 68:123-133.
- Vander Hagen, GE, Tipping, JM, Hammer, SA. 1998. Consumption of juvenile salmonids by adult steelhead in the Cowlitz River, Washington. *California Fish and Game* 84:48-50.
- Vaux, WG. 1968. Intergravel flow and interchange of water in a streambed. *United States Fish and Wildlife Service Fishery Bulletin* 66:479-489.
- Vaux, WG. 1962. Interchange of stream and intragravel water in a salmon spawning riffle. *United States Fish and Wildlife Service Special Report - Fisheries*.
- Velsen, FPJ. 1987. Temperature and incubation in Pacific salmon and rainbow trout: compilation of data on median hatching time, mortality, and embryonic staging. *Canadian Data Report in Fisheries and Aquatic Sciences*.
- Venditti, DA, Garland, RD. 1994. Nearshore movement and feeding behavior of juvenile fall Chinook salmon in the Columbia River. In: Rondorf, DW, Tiffan, KF, editors. Identification of the spawning, rearing and migratory requirements of fall Chinook salmon in the Columbia River. 1994 Annual Report to Bonneville Power Administration. Portland, Oregon: p. 80-98.
- Viant, MR, Werner, I, Rosenblum, ES, Gantner, AS, Tjeerdema, RS, Johnson, ML. 2003. Correlation between heat-shock protein induction and reduced metabolic condition in juvenile steelhead trout (*Oncorhynchus mykiss*) chronically exposed to elevated temperature. *Fisheries Board of Scotland, Annual Report* 22 (Part 3) 29:159-171.
- Vick, J, McBain and Trush. 2004. Tuolumne River floodway restoration, project design approach and rationale. Arcata, California: McBain and Trush.
- Vogel, DA. 1982. Preferred Spawning Velocities, Depths, and Substrates for Fall Chinook Salmon in Battle Creek, California. Red Bluff, California: U.S. Fish and Wildlife Service.
- Vogel, DA. 1989. Tehama-Colusa Canal Diversion and Fishery Problems Study. Red Bluff, California: U.S. Fish and Wildlife Service. Final Report. USFWS Report No. AFF1/FAO-89-06.
- Vogel, DA, Marine, KR, Smith, JG. 1988. Fish passage action program for Red Bluff Diversion Dam - final report on fishery investigations. Red Bluff, California: U. S. Fish and Wildlife Service, Northern Central Valley Fishery Resource Office.
- Vogel, DA, Smith, JG, Marine, KR. 1988. Fish passage action program for Red Bluff Diversion Dam: Final report on fishery investigation, including executive summary. Report No. FR1/FAO-88-19. U.S. Fish and Wildlife Service.
- Vogel, DA, Marine, KR. 1991. Guide to upper Sacramento River chinook salmon life history. Redding, California: CH2M Hill.
- Vogel, S. 1994. Life in moving fluids. Princeton, New Jersey: Princeton University Press.
- Volk, EC, Schroder, SL, Grimm, JJ. 1994. Use of a bar code symbology to produce multiple thermally induced otolith marks. *Transactions of the American Fisheries Society* 123:811-816.
- Volkman, JM, McConnaha, WE. 1993. Through a glass darkly: Columbia River salmon, the Endangered Species Act, and adaptive management. *Environmental Law* 23:1249-1272.

- Vøllestad Asbjørn, L, Peterson, J, Quinn, TP. 2004. Effects of freshwater and marine growth rates on early maturity in male coho and Chinook salmon. *Transactions of the American Fisheries Society* 133:495-503.
- von Schalburg, KR, Rise, ML, Brown, GD, Davidson, WS, Koop, BF. 2005. A comprehensive survey of the genes involved in maturation and development of the rainbow trout ovary. *Biology of Reproduction* 72:687-699.
- Vronskiy, BB. 1972. Reproductive biology of the Kamchatka River Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)). *Journal of Ichthyology* 12:259-273.
- Vyverberg, K, Snider, B, Titus, RG. 1997. Lower American River chinook salmon spawning habitat evaluation. California Department of Fish and Game, Environmental Services Division.
- Wagner, T, Congleton, JL. 2004. Blood chemistry correlates of nutritional condition, tissue damage, and stress in migrating juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:1066-1074.
- Wales, JH, Coots, M. 1954. Efficiency of chinook salmon spawning in Fall Creek, California. *Transactions of the American Fisheries Society* 84:137-149.
- Walters, CJ, Collie, JS. 1988. Is research on environmental factors useful to fisheries management? *Canadian Journal of Fisheries and Aquatic Sciences* 45:2848-2854.
- Walters, CJ, Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058-2070.
- Walters, CJ. 1986. Adaptive management of renewable resources. New York: Macmillian.
- Walters, CJ, Hilborn, R. 1976. Adaptive control of fishing systems. *Journal of the Fisheries Research Board of Canada* 33:145-159.
- Wang, S, Hard, JJ, Utter, F. 2002. Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries* 11:301-319.
- Waples, RS. 1999. Dispelling some myths about hatcheries. *Fisheries* 24:12-21.
- Waples, RS. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. In: Nielsen, JL, Editor. *Evolution and the aquatic ecosystem: defining unique units in population conservation*; Bethesda, Maryland: p. 8-27. American Fisheries Society Symposium 17.
- Waples, RS. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 48 (Supplement 1):124-133.
- Waples, RS. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *U.S. National Marine Fisheries Service Marine Fisheries Review* 53:11-22.
- Waples, RS, Teel, DJ, Myers, JM, Marshall, AR. 2004. Life history divergence in Chinook salmon: historic contingency and parallel evolution. *Evolution* 58:386-403.
- Ward, BR. 1996. Population dynamics of steelhead trout in a coastal stream, the Keogh River, British Columbia. In: Cox, IG, editor. *Stock assessment in inland fisheries*. Blackwell Publishing. p. 308-323.
- Ward, PD, McReynolds, TR. 2001. Butte and Big Chico creeks spring-run Chinook salmon, *Oncorhynchus tshawytscha*, life history investigations 1998-2000. Inland Fisheries Administrative Report 2001-2. California Department of Fish and Game.
- Ward, PD, McReynolds, TR, Garman, CE. 2004b. Butte and Big Chico creeks spring-run Chinook salmon, *Oncorhynchus tshawytscha*, life history investigation, 2001-2002. Chico, California: California Department of Fish and Game. Inland Fisheries Administrative Report No. 2004-4.
- Ward, PD, McReynolds, TR, Garman, CE. 2004a. Butte and Big Chico creeks spring-run Chinook salmon, *Oncorhynchus tshawytscha*, life history investigation, 2000-2001. Chico, California: California Department of Fish and Game. Inland Fisheries Administrative Report No. 2004-3.
- Ward, PD, McReynolds, TR, Garman, CE. 2003. Butte Creek spring-run Chinook salmon, *Oncorhynchus tshawytscha* pre-spawn mortality evaluation, 2003. Chico, California: California Department of Fish and Game. Inland Fisheries Administrative Report No. 2004-5.
- Waring, CP, Moore, AP. 1997. Sublethal effects of a carbamate pesticide on pheromonal mediated endocrine function in mature male Atlantic salmon (*Salmo salar*). *Fish Physiology and Biochemistry* 17:203-211.
- Warner, G. 1991. Remember the San Joaquin. In: Lufkin, A, editor. *California's salmon and steelhead*. Berkeley:

- University of California Press. p. 61-72.
- Warner, GH, Fry, DHJr, Culver, AN. 1961. History of yearling king salmon marked and released at Nimbus Hatchery. *California Fish and Game* 47:343-355.
- Warren, WG, Dempson, JB. 1995. Does temporal stratification improve the accuracy of mark-recapture estimates of smolt production? A case study based on the Conne River, Newfoundland. *North American Journal of Fisheries Management* 15:126-136.
- Weatherley, AH, Gill, HS. 1995. Growth. In: Groot, C, Margolis, L, Clarke, WCC, editors. *Physiological ecology of Pacific salmon*. Vancouver, British Columbia: University of British Columbia Press.
- Weber, ED, Fausch, KD. 2004. Abundance and size distribution of ocean-type juvenile Chinook salmon in the upper Sacramento River margin before and after hatchery release. *North American Journal of Fisheries Management* 24:1447-1455.
- Weber, ED, Fausch, KD. 2003a. Competition between hatchery-reared and naturally spawned juvenile chinook salmon in the Sacramento River, California. Fort Collins: Colorado State University, Department of Fishery and Wildlife Biology.
- Weber, ED, Fausch, KD. 2005. Competition between hatchery-reared and wild juvenile Chinook salmon in enclosures in the Sacramento River, California. *Transactions of the American Fisheries Society* 134:44-58.
- Weber, ED, Fausch, KD. 2003b. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1018-1036.
- Weber, LP, Higgins, PS, Carlson, RI, Janz, DM. 2003. Development and validation of methods for measuring multiple biochemical indices of condition in juvenile fishes. *Journal of Fish Biology* 63:637-658.
- Weber, PK, Hutcheon, ID, McKeegan, KD, Ingram, BL. 2002. Otolith sulfur isotope method to reconstruct Chinook salmon (*Oncorhynchus tshawytscha*) life history. *Canadian Journal of Fisheries and Aquatic Sciences* 59:587-591.
- Wege, GJ, Anderson, RO. 1978. Relative weight (R_w): a new index of condition for largemouth bass. In: Novinger, GD, Dillard, JG, editors. *New approaches to the management of impoundments*. Special Publication 5. Bethesda, Maryland: American Fisheries Society, North Central Division. p. 79-91.
- Weissmar, RC, Simenstad, CA. 1998. Variability of estuarine and riverine ecosystem productivity for supporting Pacific salmon. In: McMurray, GR, Bailey, RJ, editors. *Change in Pacific Northwest Coastal Ecosystems*. MOAA Decision Analysis Series. Silver Springs, Maryland: NOAA Costal Ocean Program. p. 253-301.
- Welch, DW, Ishida, Y, Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Canadian Journal of Fisheries and Aquatic Sciences* 55:937-948.
- Welch, DW, Ward, BR, Smith, BD, Everson, JP. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. *Fisheries Oceanography* 9:17-32.
- Wells, BK, Rieman, BE, Clayton, JL, Horan, DL, Jones, CM. 2003. Relationships between water, otolith, and scale chemistries of west slope cutthroat trout from the Coeur d'Alene River, Idaho: the potential application of hard-part chemistry to describe movements in freshwater. *Transactions of the American Fisheries Society* 132:409-424.
- Wells, BK, Grimes, CB, Field, JC, Reiss, CS. 2006. Co variation between the average lengths of mature coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) and the ocean environment. *Fisheries Oceanography* 15:67-79.
- Wells, RA, W. J. McNeil. 1970. Effect of quality of the spawning bed on the growth and development of pink salmon embryos and alevins, Special Scientific Report-fisheries 616. U.S. Fish and Wildlife Service.
- Welsh, SA, Perry, SA. 1998. Influence of spatial scale on estimates of substrate use by benthic darters. *North American Journal of Fisheries Management* 18:954-959.
- Werner, I, Smith, TB, Feliciano, J, Johnson, ML. 2005. Heat shock proteins in juvenile steelhead reflect thermal conditions in the Navarro River Watershed, California. *Transactions of the American Fisheries Society* 134:399-410.
- Wertheimer, AC, Smoker, WW, Joyce, TL, Heard, WR. 2001. Comment: a review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society* 130:712-720.

- White, J, Kjelson, M, Brandes, PL, McLain, JS, Greene, SOB, Sitts, R. 2001. The use of the Environmental Water Account for the protection of anadromous salmonids in the Sacramento-San Joaquin Delta in 2000-2001. Sacramento, California: CALFED Bay-Delta Program.
- Wickett, WP. 1954. The oxygen supply to salmon eggs in spawning beds. *Journal of the Fisheries Research Board of Canada* 11:933-953.
- Wickwire, RH, Stevens, DE. 1971. Migration and distribution of young king salmon, *Oncorhynchus tshawytscha*, in the Sacramento River near Collinsville, Anadromous Fisheries Branch, Administrative Report 71-4. California Department of Fish and Game.
- Wiener, JG, Gilmour, CC, Krabbenhoft, DP. 2003. Mercury strategy for the Bay-Delta ecosystem: a unifying framework for science, adaptive management, and ecological restoration. University of Wisconsin-La Crosse.
- Wilcock, PR, Barta, AF, Shea, CC, Kondolf, GM, Matthews, WVG, Pitlick, J. 1996. Observations of flow and sediment entrainment on a large gravel-bed river. *Water Resources Research* 32:2897-2909.
- Wilkerson, FP, Dugdale, RC, Marchi, A, Collins, CA. 2002. Hydrography, nutrients and chlorophyll during El Niño and Laña 1997-99 in the Gulf of the Farallones, California. *Progress in Oceanography* 54:293-310.
- Willamette/Lower Columbia Technical Recovery Team (W/LCTRT). 2003. Interim report on viability criteria for Willamette and Lower Columbia Basin Pacific salmonids. Seattle, Washington: NOAA Fisheries, National Marine Fisheries Service, Northwest Fisheries Science Center.
- Williams, JG. 2001a. Chinook salmon in the lower American River, California's largest urban stream. In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids, Fish Bulletin No. 179. 2. p. 1-38.
- Williams, JG. 1996. Lost in space: minimum confidence intervals for idealized PHABSIM studies. *Transactions of the American Fisheries Society* 125:458-465.
- Williams, JG. 1995. Report of the Special Master, Environmental Defense Fund et al. v. East Bay Municipal Utility District, Alameda County (California) Superior Court Action No. 425955.
- Williams, JG. 1999. Stock dynamics and adaptive management of habitat: an evaluation based on simulations. *North American Journal of Fisheries Management* 19:329-341.
- Williams, JG. 2001b. Testing models used for instream flow assessment. *Fisheries* 26:19-20.
- Williams, JG, Kondolf, GM. 1999. Rehabilitation concepts for Clear Creek, Shasta County, California. Berkeley, California: G. M. Kondolf.
- Williams, JG, Kondolf, GM, Ginney, E. 2002. Geomorphic assessment of Butte Creek, Butte County, California. Report to the USFWS, Stockton, CA. http://www.delta.dfg.ca.gov/afro/ws_docs.asp?code=BUTTC
- Williams, JG, Speed, TP, Forrest, WF. 1999. Comment: transferability of habitat suitability criteria. *Transactions of the American Fisheries Society* 128:623-625.
- Williamson, KS, May, B. 2003. Homogenization of fall-run chinook salmon gene pools in the Central Valley of California, USA. Completion Report for CALFED Grant #97-C09. University of California Davis.
- Williamson, KS, May, B. 2005. Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* 25:993-1009.
- Williamson, KS, May, Bernie. 2005. Inheritance studies implicate a genetic mechanism for apparent sex reversal in Chinook salmon. *Transactions of the American Fisheries Society* 134:1253-1264.
- Williamson, SC, Bartholow, JM, Stalnaker, CB. 1993. Conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. *Regulated Rivers: Research and Management* 8:15-28.
- Wilson, MF. 1997. Variation in salmonid life histories: patterns and perspectives. Portland, Oregon: USDA, Forests Service, Pacific Northwest Research Station. Research Paper.
- Wilson, MF, Gende, SM, Mars ton, BH. 1998. Fishes and the forest: expanding perspectives on fish-wildlife interactions. *Bioscience* 48:455-462.
- Winans, GA, Viele, D, Grover, A, Plamer-Zwahlen, M, Teel, D, Van Doornik, D. 2001. An update of genetic stock identification of chinook salmon in the Pacific Northwest: test fisheries in California. *Reviews in Fisheries Science* 9:213-237.
- Wipfli, MS, Hudson, JP, Caouette, JP. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and*

- Aquatic Sciences 55:1503-1511.
- Wipfli, MS, Hudson, JP, Caquetter, JP, Chaloner, DT. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* 132:371-381.
- Wipfli, MS, Hudson, JP, Chaloner, DT, Caoutte, JP. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1600-1611.
- Wipfli, MS, Hudson, JP, Caquette, JP. 2004. Restoring productivity of salmon-based food webs: contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. *Transactions of the American Fisheries Society* 133:1440-1454.
- Withler, FC. 1982. Transplanting Pacific salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1079.
- Withler, IL. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific Coast of North America. *Journal of the Fisheries Research Board of Canada* 23:365-393.
- Wixom, LH, Pisciotto, J, Lake, C. 1995. Final performance report - Sacramento river system sport fish catch inventory. Sacramento, California: California Department of Fish and Game, Inland Fisheries Division.
- Woods, PF, Nolan, KM, Kelsey, HM, Marron, DC. 1995. Geomorphic processes and aquatic habitat in Redwood Creek Basin, Northwestern California. U. S. Geological Survey Professional Paper 1454-T.
- Wootton, JT, Parker, MS, Power, ME. 1996. Effects of disturbance on river food webs. *Science* 273:1558-1561.
- Workman, ML. 99. An assessment of the downstream migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the lower Mokelumne River [ms thesis]. California State University, Sacramento.
- Workman, ML. 2002. Downstream migration monitoring at Woodbridge Dam on the Lower Mokelumne River, California, December 2000 through July 2001. Lodi, California: East Bay Municipal Utility District.
- Worman, A, Packman, AI, Johansson, H, Jonsson, K. 2002. Effect of flow-induced exchange in hyporheic zones on longitudinal transport of solutes in streams and rivers. *Water Resources Research* 38:2-1 - 2-15.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the 6th International Congress on Genetics*; p. 356-366.
- Wright, S. 1988. Surfaces of selective value revisited. *American Naturalist* 131:115-123.
- Wu, FC. 2000. Modeling Embryo Survival Affected by Sediment Deposition Into Salmonid Spawning Gravels: Application to Flushing Flow Prescriptions. ISI:000087226800020
- Wurster, CM, Patterson, WP, Stewart, DJ, Bowlby, JN, Stewart, TJ. 2005. Thermal histories, stress, and metabolic rates of Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario: evidence from intra-otolith stable isotope analyses. *Canadian Journal of Fisheries and Aquatic Sciences* 62:700-713.
- Yoshiyama, RM. 1999. A history of salmon and people in the Central Valley region of California. *Reviews in Fisheries Science* 7:197-239.
- Yoshiyama, RM, Fisher, FW. 2001. Long time past: Baird Station and the McCloud Wintu. *Fisheries* 26(1):6-22.
- Yoshiyama, RM, Gerstang, ER, Fisher, FW, Moyle, PB. 2000. Chinook salmon in the California central valley: an assessment. *Fisheries* 25(2):6-20.
- Yoshiyama, R. 1999. A history of salmon and people in the Central Valley region of California. *Reviews in Fisheries Science* 7:197-239.
- Yoshiyama, RM, Gerstung, Eric R., Fisher, FW, Moyle, PB. 2000. Chinook salmon in the Central Valley of California: an assessment. *Fisheries* 25:6-20.
- Yoshiyama, RM, Gerstung, ER, Fisher, FW, Moyle, PB. 2001. Historical and present distribution of Chinook salmon in the Central Valley drainage of California. In: Brown, RL, editor. *Fish Bulletin 179: Contributions to the biology of Central Valley salmonids*. 1. Sacramento: p. 71-176.
- Yoshiyama, RM, Gerstung, ER, Fisher, FW, Moyle, PB. 1996. Historical and present distributions of Chinook salmon in the Central Valley drainage of California. In: *Sierra Nevada Ecosystem Project, Status of the Sierra Nevada, Volume III. Final Report*. p. 309-362.
- Young, KA. 1999. Managing the decline of Pacific salmon: metapopulation theory and artificial recolonization as ecological mitigation. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1700-1706.
- Young, KA. 2004. Toward evolutionary management. In: Hendry, AP, Stearns, SC, editors. *Evolution*

- illuminated: salmon and their relatives . Oxford University Press. p. 358-376.
- Young, MK, Hubert, WA, Wesche, TA. 1990. Comment: fines in redds of large salmonids. Transactions of the American Fisheries Society 119:156-162.
- Zabel, RW. 2002. Using "travel time" data to characterize the behavior of migrating animals. The American Naturalist 159:372-387.
- Zabel, RW, Williams, JG. 2002. Selective mortality in chinook salmon: what is the role of human disturbance? Ecological Applications 12:173-183.
- Zaugg, WS. 1981. Relationships between smolt indices and migration in controlled and natural environments. In: Brannon, EL, Salo, EO, editors. Salmon and trout migratory behavior symposium; Seattle: University of Washington Press. p. 173-183.
- Zaugg, WS, Wagner, HH. 1973. Gill ATPase activity related to parr-smolt transformation in steelhead trout *Salmo gairdneri*: influence of photoperiod and temperature. Comparative Biochemistry and Physiology 45:955-965.
- Zhang, Z, Beamish, RJ, Riddell, BE. 1995. Differences in otolith microstructure between hatchery-reared and wild Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 52:344-352.
- Zimmerman, CE. 2003. Migration of precocious male hatchery Chinook salmon in the Umatilla River, Oregon. North American Journal of Fisheries Management 23:1006-1014.
- Zimmerman, CE, Reeves, GH. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry.
- Zimmerman, CE, Reeves, GH. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152-2162.

PERSONAL COMMUNICATIONS

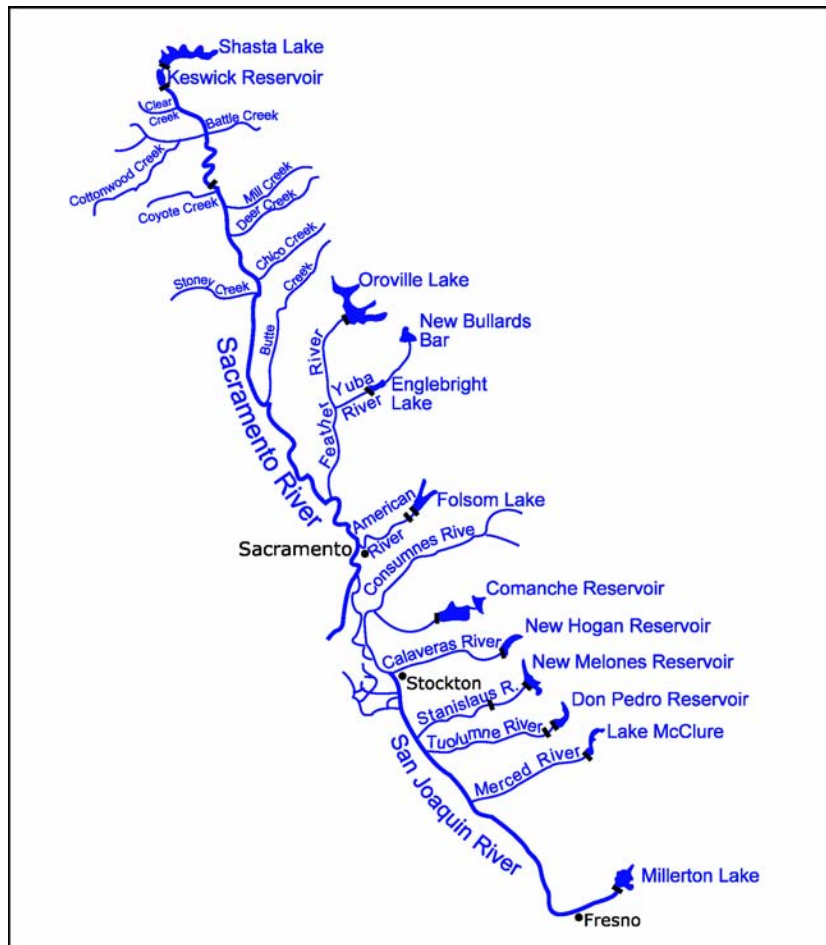
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APPENDIX A

MAJOR SALMON STREAMS

This appendix provides brief descriptions of Central Valley streams that currently support major runs of Chinook or steelhead, or where restoration of a major run seems feasible. For other descriptions, see Yoshiyama et al. (2001) and USFWS (1995). The NOAA Fisheries Southwest Region website includes a “Central Valley Chinook salmon current stream habitat distribution table.”

Figure A-1. Major streams of the Central Valley, plus Coyote, Chico, and Stony creeks. Streams as drawn end at impassable dams, or at arbitrary points along the stream, so that, for example, the length of the Cosumnes River is overemphasized. Comanche Reservoir is on the Mokelumne River. Copied from Brown and Greene (1992).



Mainstem Sacramento River

Keswick Dam (rkm 485) near Redding, a re-regulating dam for hydropower releases from Shasta Dam, is now the upstream limit to salmon migration in the lower Sacramento River. Flow regulation by Shasta Dam dampens variability and shifts flow from winter/spring to summer (Figure A-2). Releases from Shasta keep the discharge higher and the temperature lower in the summer than it was in the past, and have the opposite effect in the winter. A recently installed

device for adjusting the elevation of water intakes for hydroelectric turbines facilitates management of downstream water temperature. Large quantities of gravel were mined from the river for constructing Shasta, which blocks sediment transport from upstream, and gravel is now added to the river just below Keswick.

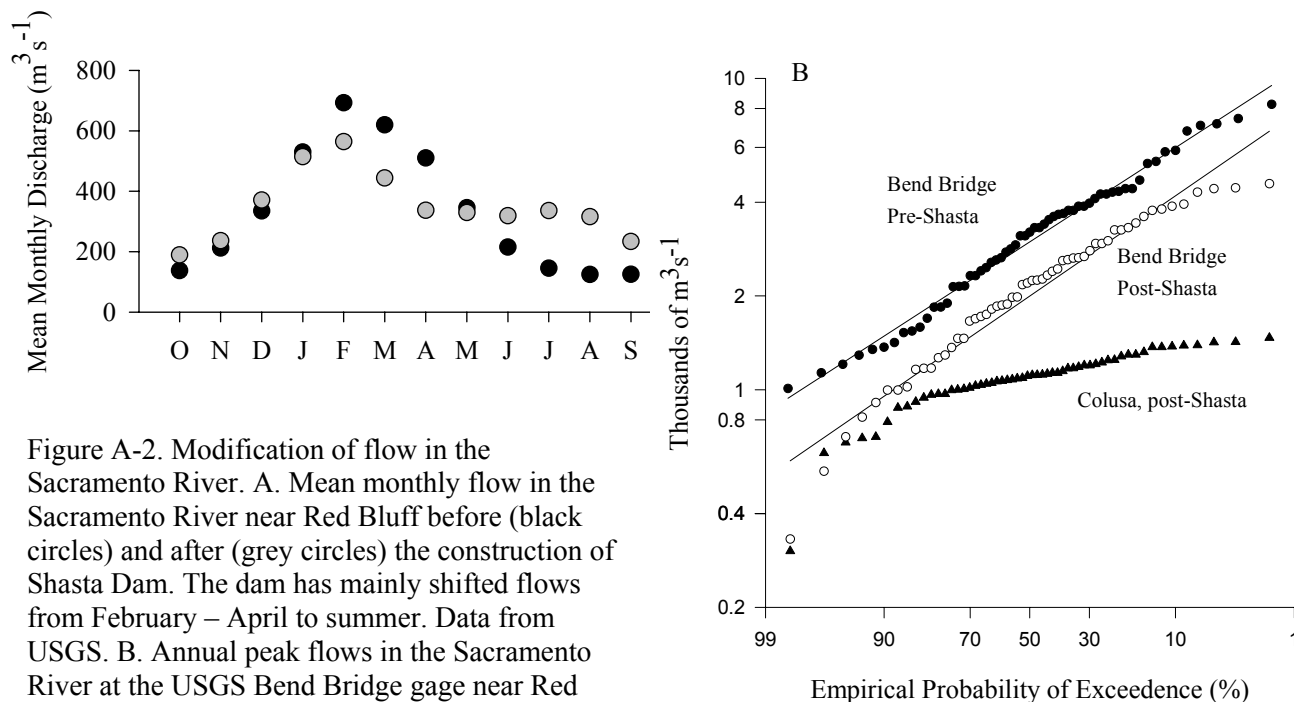


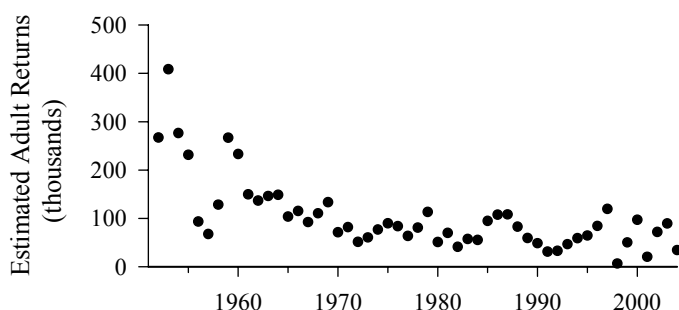
Figure A-2. Modification of flow in the Sacramento River. A. Mean monthly flow in the Sacramento River near Red Bluff before (black circles) and after (grey circles) the construction of Shasta Dam. The dam has mainly shifted flows from February – April to summer. Data from USGS. B. Annual peak flows in the Sacramento River at the USGS Bend Bridge gage near Red Bluff have been reduced by Shasta Dam; diversion of water into the Butte Bypass sharply reduces peak flows at Colusa, 183 km downstream from Bend Bridge. Data from USGS.

The river crosses a small alluvial basin between Redding (~rkm 475) and Jelly’s Ferry (rkm 426), and enters the Sacramento Valley proper at Red Bluff (rkm 393), historically the head of navigation (Brewer 1966). There are major diversions from the river at Redding (rkm 479), Red Bluff (rkm 390), and Hamilton City (rkm 329), and many minor diversions. In years when flow exceeds about $1,000 \text{ m}^3 \text{s}^{-1}$, water passes over one or more weirs into the Butte Sinks, to the east of the river (Figure 2-14), so that during high flows the river is a losing stream between Red Bluff and Colusa (rkm 231; Figure A-2). Water in the Butte Sinks flows to the west of the Sutter Buttes into the Sutter-Bypass, which joins the Sacramento River near its confluence with the Feather River. Just upstream (rkm 113), water passes over the Fremont Weir from the Sacramento River into the Yolo Bypass (Figure A-1). Thus, the river has been for the most part separated from its floodplain, although some floodplain remains in the upper basin, and in the reach between Red Bluff and Colusa. Public and non-profit agencies have been active in acquiring riparian property in this reach, with an eye toward creation of a “meanderbelt” in which more natural fluvial processes could occur. Downstream from Colusa, the river is tightly controlled by levees.⁹⁶

⁹⁶ For a more detailed description of this reach of the river see the Sacramento River Conservation Area Handbook (SRCAF 2003).

The Sacramento River below Keswick includes much of the natural spawning habitat for fall Chinook, and the changed thermal conditions allow successful spawning of late-fall and winter-run, as well. Early assessments regarded this habitat as favorable for spring-run (Moffett 1949), but the run has declined to almost nothing, probably as a result of interbreeding with fall-run (Slater 1963). Steelhead also spawn there, but habitat conditions below the dam apparently are favorable to a resident life history pattern, which a large percentage of the population seems to have adopted (Ch. 3). Small numbers of winter-run are produced at the Livingston Stone Hatchery, just below Keswick Dam. Estimated fall-run returns to the mainstem are well below mid-century levels (Figure A-3), and below recent estimates of Battle Creek, a tributary with a major hatchery (see below).

Figure A-3. Estimated returns of fall Chinook to the mainstem Sacramento River upstream from the RBDD. Mainstem returns are well below mid-century levels, and below recent Battle Creek levels (Figure A-7). Data from CDFG GrandTab; post 1997 data are preliminary.

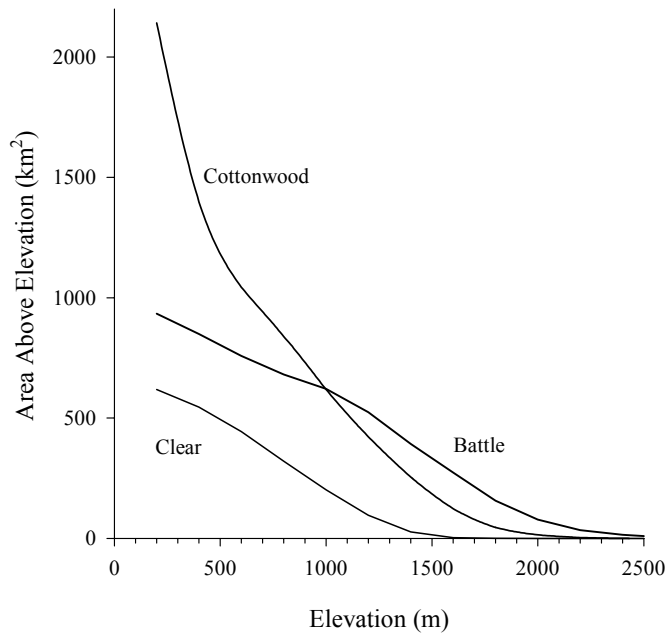


Observations at the fish ladder at the Red Bluff Diversion Dam (RBDD) from 1967 to 1986 provide the best available data on the abundance and migration timing of adult Chinook and steelhead, but the dam gates have been raised for part of the year since 1987, and are now raised from Sept. 15 to May 15. Current estimates of escapements are based mainly on mark-recapture estimators applied to carcasses. When the dam gates are lowered, water and fish pass at high velocity below the gates, which do not completely block the river, and juvenile salmon are particularly subject to predation when they encounter severe turbulence as the water decelerates after passing under the gates. Four screw traps stationed in fast water a short distance below the dam provide good data on juveniles. Salmon monitoring on the upper Sacramento is conducted mainly by the USFWS and the CDFG.

Tributaries above Red Bluff

The three largest tributaries joining the Sacramento River between Keswick Dam and Red Bluff are Clear Creek and Cottonwood Creek, joining from the west, and Battle Creek, joining from the east (Figure A-1). Cottonwood Creek has the largest watershed, but Battle Creek has more watershed area at higher elevations (Figure A-4). The USFWS and the CDFG conduct most of the salmon monitoring on these streams.

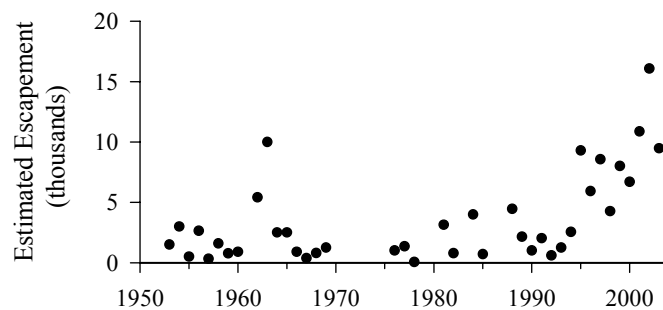
Figure A-4. Area-elevation curves for Clear, Battle, and Cottonwood creeks, for elevations above 200 m. These tributaries join the Sacramento River near Redding. Data from NOAA Fisheries.



Clear Creek

Clear Creek flows southward through the Trinity Mountains and then turns east to join the Sacramento River at rkm 464, just downstream from Redding. Whiskeytown Dam, part of the Central Valley Project (CVP) involved in the transfer of water from the Trinity River to the Sacramento River, blocks fish migration 31 km upstream from the mouth. Downstream from the dam, Clear Creek flows southward for ~17 km through a steep canyon, then eastward for ~14 km at a lower gradient through a valley to the Sacramento. Releases from Whiskeytown make the canyon reach suitable habitat for spring-run, now that a small diversion dam on the creek that blocked migration has been removed, and a small population may be establishing itself. Small numbers of steelhead also use the canyon reach, and fall-run and perhaps late fall-run use the valley reach. Clear Creek was severely degraded by gold and gravel mining, and is the site of a major habitat restoration project. Juveniles are sampled with screw traps above and below the fall-run spawning reach.

Figure A-5. Estimated returns of fall Chinook to Clear Creek. Data are not available for all years. Data from CDFG GrandTab; post 1997 data are preliminary.



Battle Creek

Battle Creek drains about 760 km², mostly on the western slope of Mt. Lassen, the southernmost volcano in the Cascade Mountains, and joins the Sacramento River at rkm 435 near the town of Anderson. Battle Creek is a classic basalt-terrain spring-fed stream with high summer flows (Figure A-5) that probably supported all four runs of Central Valley Chinook as well as steelhead (Table A-1). The reliable supply of cool water also make the stream an attractive site for a fish hatchery, and Coleman National Fish Hatchery was built there to mitigate for habitat blocked by Shasta. The hydrology of Battle Creek has long been highly modified by Pacific Gas and Electric Company hydropower dams and diversions, and passage of salmon and steelhead into the upper watershed has been restricted by a weir at the Coleman National Fish Hatchery, 10.5 km from the Sacramento River. The hydropower facilities are run-of-the-river, however, so discharge near the mouth (Figure A-6) is not highly modified. Plans for a major restoration project that would re-open most of the natural habitat in the watershed to anadromous fish have been developed, but whether the project will be implemented remains uncertain.

Small numbers of Chinook and steelhead pass the hatchery weir, but flows farther upstream are still severely depleted by hydropower operations. Fall-run also spawn in the ~10 km reach downstream from the hatchery, recently in greater numbers than in the mainstem Sacramento River (Figure A-7); presumably, these are mainly hatchery fish. A few late fall-run, probably also hatchery-reared, spawn there as well.

Figure A-6. Flow in Battle Creek. Distributions of mean monthly discharge in Battle Creek, 1961-2004. Data from USGS gage 11376550. Flows farther upstream are highly modified by run-of-the-river hydropower operations.

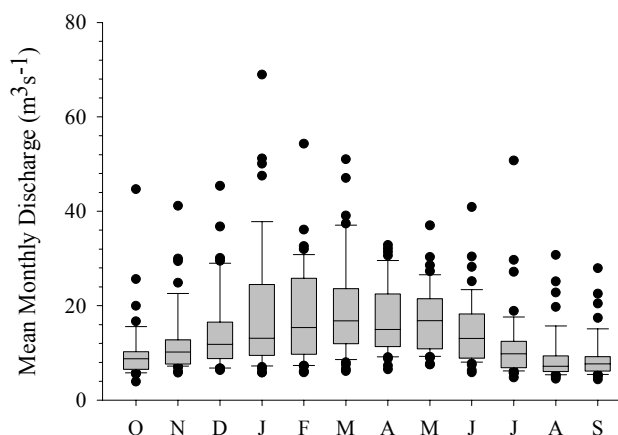
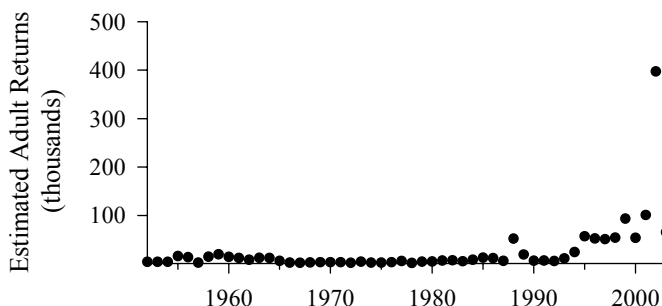


Figure A-7. Estimated returns of fall Chinook to Battle Creek downstream from CNFH. Presumably most of these are hatchery fish. Data from CDFG GrandTab; post 1997 data are preliminary.



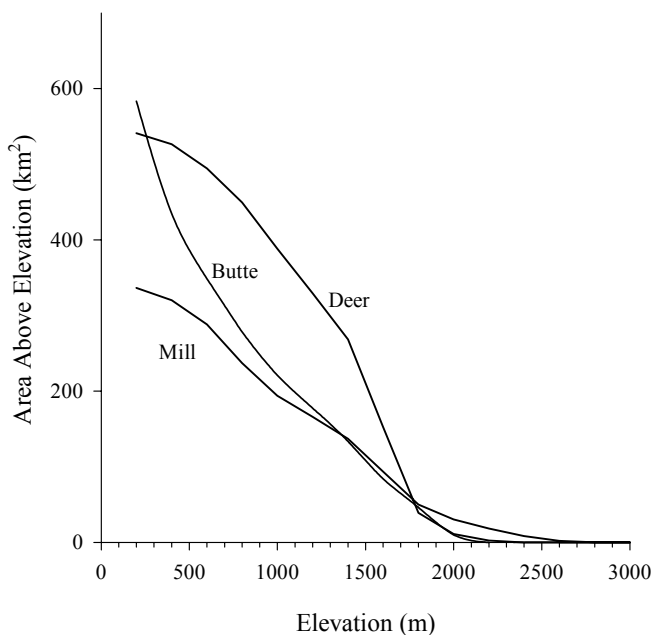
Cottonwood Creek

Cottonwood Creek drains 2,400 km² of the Coastal Range, including some area of high elevation, and joins the Sacramento just downstream from the Battle Creek confluence, at rkm 438. There are irrigation diversions but no storage reservoirs on the creek. Fall-run returns have been monitored irregularly, but range from several hundred to several thousand. Clark (1928) reported that Cottonwood Creek formerly supported spring-run, and a small population now occurs in a tributary, Beegum Creek (Killam, in Anderson et al. In press). The creek is an important source of gravel for the Sacramento, but the potential supply is sharply reduced by gravel mining.

The spring-run tributaries

Three streams that drain the Cascade Mountains from Mt. Lassen south to the transition to the Sierra Nevada support independent populations of spring Chinook (Lindley et al. 2004), and steelhead. This is mainly rugged country with little development. Two of these streams, Mill Creek and Deer Creek, flow directly to the Sacramento (Figure A-1). Early mapping (Figure 2-5) shows Butte Creek flowing south to bifurcate west of the Sutter Buttes, with one branch joining the Sacramento and one flowing into the Sutter Basin. The branch joining the Sacramento River is now controlled by gates, and most of the stream passes down the Sutter Bypass. CDFG monitors adult returns and juvenile outmigration in these streams.

Figure A-8. Area-elevation curves for Butte, Mill and Deer creeks, for elevations above 200 m. These streams support the remaining independent populations of spring Chinook in the Central Valley. Note the steepness of the lower portion of Deer Creek, and the relatively low gradient, high elevation reach. Although it is the smallest of the three watersheds, Mill Creek extends to higher elevations on Mount Lassen.

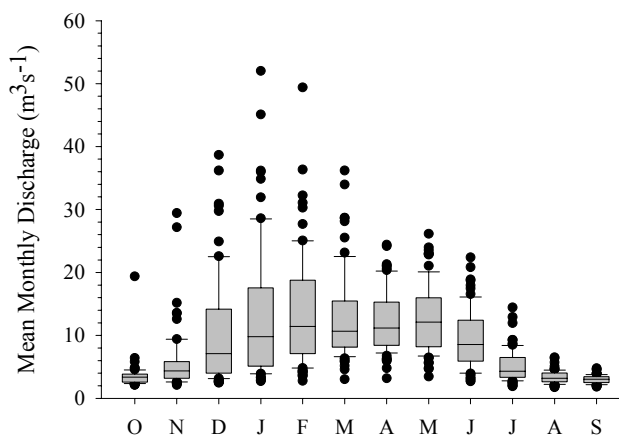


Mill Creek

Mill Creek drains part of the southern slopes of Mt. Lassen, and snowmelt runoff in the creek is cloudy with volcanic silt, but the stream lacks the strong influence of springs that characterizes Battle Creek (Figure A-9). For all but the last two kilometers of the reach between the mountains and the Sacramento River, Mill Creek flows in a channel of varying width incised into cemented Pleistocene gravels, so in the narrower sections of this reach shear stresses on the bed are very high during high flows. Mill Creek joins the Sacramento River at rkm 369;

backwater from the Sacramento causes gravel to deposit near the mouth of the stream, creating difficult access for adult salmon during low flows.

Figure A-9. Distributions of mean monthly discharge in Mill Creek, 1928-2004. Data from USGS gage 11381500. Water is diverted for irrigation downstream from the gage, and diversions probably prevent late-arriving spring-run from reaching their holding habitat.



Although the watershed of Mill Creek is the smallest of the three streams currently supporting independent populations of spring-run, it extends to high elevations (Figure A-8). The stream formerly supported large numbers of fall-run and a U. S. Bureau of Fisheries egg-taking station and hatchery (Clark 1928). A counting weir was operated on the creek by the California Department of Fish and Game from 1953-54 to 1962-63, but only summary data (e.g., Van Woert 1964) remain (1,857 spring-run and 1,116 steelhead on annual average). The US Fish and Wildlife Service conducted studies of incubation there at the same time and found high losses of eggs to scour, (e.g., Gangmark and Bakkala 1960), but these studies were compromised because the investigators did not appreciate the unusual geomorphic conditions of the stream. Water is diverted for irrigation from two small dams, which can deny late-arriving spring-run access the stream (USBR 2000). Recent estimates of spring-run returns are somewhat below the mid-century average (Figure A-10). Many of the fall-run in Mill Creek apparently are now hatchery strays, as noted in the overview description of fall-run.

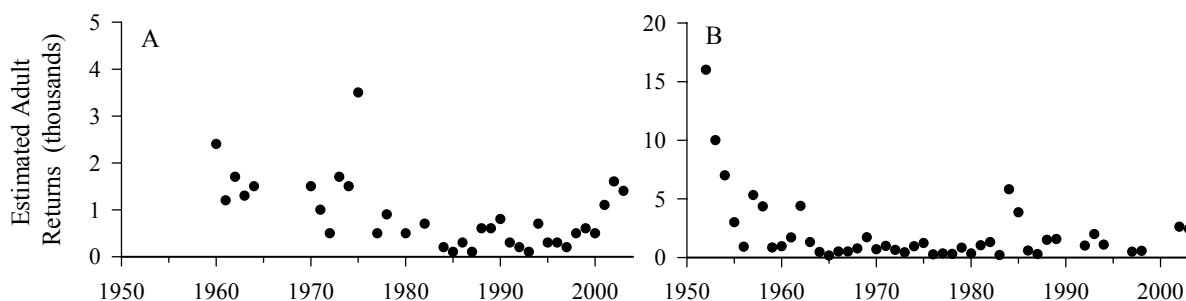


Figure A-10. Estimated returns of Chinook to Mill Creek: A, spring-run; B fall-run. Chinook. Data are of variable accuracy, and are not available for all years, but probably shows trends reliably. Data from CDFG GrandTab; post 1998 data are preliminary.

Deer Creek

Deer Creek also drains part of the southern slopes of Mt. Lassen, with a narrow watershed of 520 km² to the east and south of the Mill Creek watershed, and joins the Sacramento at rkm 353. The creek supports a respectable population of spring Chinook, and a smaller population of fall-run also spawns there (Figure A-11), but as with Mill Creek many of these probably are hatchery strays. According to Clark (1928:39), “The salmon were very numerous in Deer Creek until dams were built which took most of the water from the creek,” and agricultural diversions in the spring along the lower reaches of the creek are still a problem (J. Icanberry, USFWS, pers.comm. 2005).

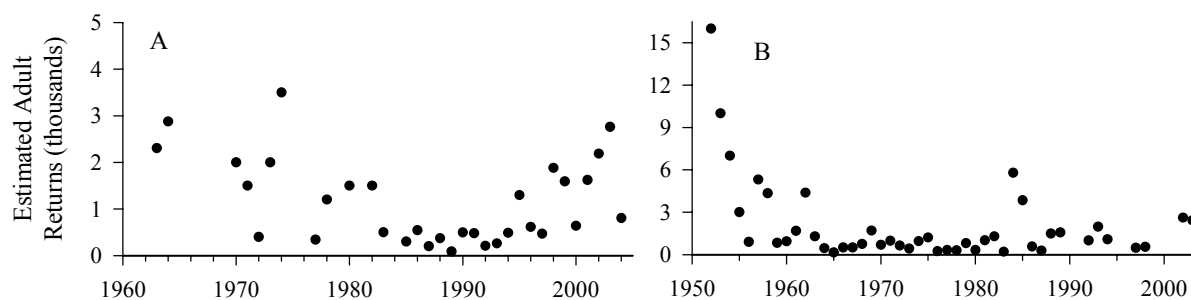


Figure A-11. Estimated returns of Deer Creek Chinook: A, spring-run; B, fall-run. Data are of variable accuracy, and are not available for all years, but probably shows trends reliably. Data from CDFG GrandTab; post 1998 data are preliminary.

Butte Creek

Butte Creek drains an area in which the Sierra Nevada and Cascade ranges come together, and after leaving the mountains near Chico runs almost parallel to the Sacramento River for about 50 km (Figure 2-6). Most of the stream flows down the Sutter bypass and joins the Feather River just upstream from its confluence with the Sacramento, but it is also connected to the Sacramento River by gated culverts at rkm 221. Several small diversion dams on the creek have been removed or reconstructed with new ladders in recent years, and a canal carrying water from the Feather River has been routed under it in a siphon; previously, the canal simply added water to one side of the pool behind a low dam, and took an equal amount out the other side, so that water from the Feather River and Butte Creek were mixed.

Chinook habitat in Butte Creek extends only to about 300 m elevation, where a natural barrier blocks all migration by spring-run in most years, although a few pass in exceptionally wet springs. A hydropower dam now blocks even steelhead about 1.4 km farther upstream, but there are more natural barriers farther upstream, and the natural limit to Chinook and steelhead passage is unknown. Spring-run now hold and spawn in about 21 km of the stream, upstream from the Parrot-Phelan Diversion Dam, and fall-run spawn mostly downstream from the dam. Butte Creek spring-run are genetically distinct from those in Mill and Deer creeks (Figure 2-1),

and have increased sharply in recent years after decades of low numbers (Figure A-12). A screw trap operated at the Pharrot-Phelan Diversion Dam by CDFG monitor the migration of juvenile Chinook, and substantial numbers of migrants have been marked with coded-wire tags in recent years. Until recently, diversions made conditions unfavorable for adult fall Chinook.

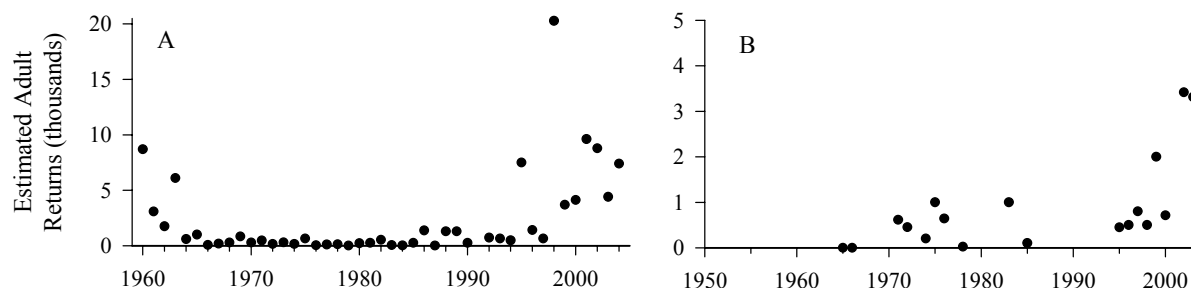


Figure A-12. Estimated adult Chinook returns to Butte Creek: A, spring-run; B, fall-run. Note different scaling on the vertical axes. Data are of variable accuracy, and are not available for all years for spring-run, but probably show trends reliably; fall-run data are fragmentary until the last decade. Data from CDFG GrandTab; post 1997 data are preliminary.

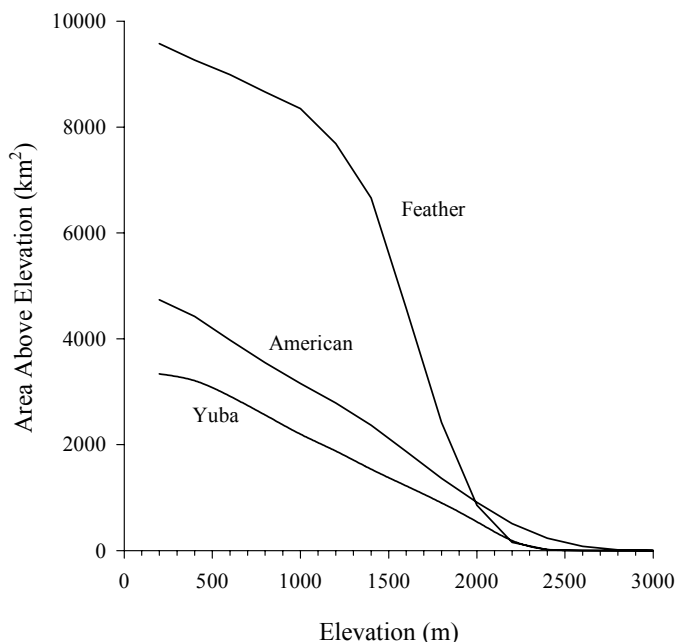
Lower Sacramento River tributaries

Two major tributaries, the Feather and the American rivers, flow out of the northern Sierra Nevada to join the Sacramento River near the upstream limit of tidal influence; the Yuba River is a major tributary of the Feather (Figure A-1). The northern Sierra Nevada are of moderate elevation, and the natural hydrographs of these streams reflect a balance of rainfall and snowmelt runoff (Figure A-13). Historically these streams supported spring-run, fall-run, and steelhead, and probably late fall-run as well. Chinook reportedly were extirpated in these streams by hydraulic mining (Commissioners of Fisheries 1877), but apparently populations were quickly reestablished (Clark 1928). Impassable dams now block these streams where they emerge from the foothills.

Feather River

The Feather River flows southwest out of the mountains and turns almost due south to join the Sacramento River at rkm 128, near Verona (Figure A-1). The State Water Project's Oroville Dam at rkm 108 blocks salmon migration and controls the hydrology of the lower river (Figure A-14). The dam has an unusual feature in the Thermalito Afterbay, a large, shallow re-regulating reservoir that serves to warm the water in the summer so that water supplied to rice farmers in the area is not too cool for optimal plant growth. Water from the afterbay rejoins the river 13 km downstream from the dam, but releases at the dam create a "low flow reach" with nearly constant flow of $17 \text{ m}^3 \text{ s}^{-1}$ upstream from the Thermalito outlet.

Figure A-13. Area-elevation curves for the Feather, Yuba, and American rivers, for elevations above 200 m.



The Feather River supports fall Chinook (Figure A-15), steelhead, and a sizable run of Chinook that return in the spring but are very similar genetically to fall-run (Hedgecock et al 2001).⁹⁷ The Feather River Hatchery contributes substantially to these populations. Fisheries studies are conducted mainly staff biologists of the California Department of Water Resources.

Figure A-14. Modification of flow in the Feather River. Estimated unimpaired mean monthly flow in the Feather River near Gridley (black circles) and after the construction of Oroville Dam. The data includes return flow from the Thermalito afterbay. Unimpaired data from ACE, post-dam data from USGS.

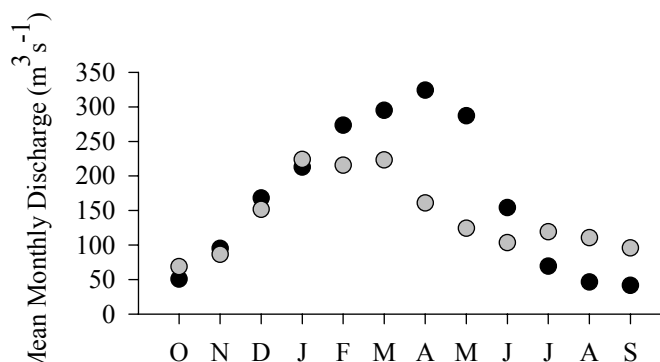
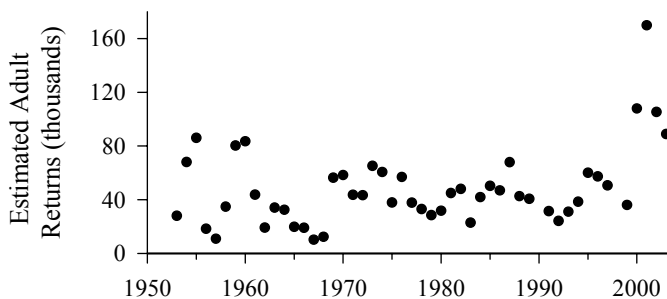


Figure A-15. Estimated adult returns of fall Chinook spawning naturally in the Feather River. Data are of variable accuracy, but probably show trends reliably. Data from CDFG GrandTab; post 1998 data are preliminary.

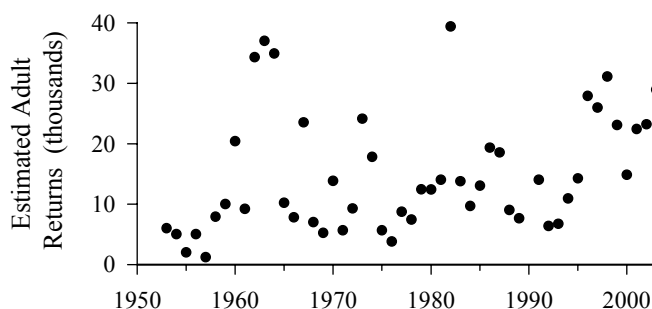


⁹⁷ In 2004, the Feather River hatchery ladder was opened from May 17 to June 17, and 3,650 Chinook were marked and returned to the river. This is the first reliable estimate of the number of spring-run. No doubt other fish remain in the river as well (B. Cavallo, DWR, pers.comm. 2005).

Yuba River

The Yuba River is a major tributary of the Feather that was especially affected by hydraulic mining. Between the hills and the Feather River, the Yuba deposited a corridor of mining debris into which its current channel has incised. Fish passage is currently blocked by Englebright Dam, a small dam at rkm 38 that was built as a sediment trap to allow hydraulic mining to resume, and now provides recreation and minor hydropower generation. A large storage reservoir on the North Fork, New Bollards Bar, releases cool water that passes through Englebright Reservoir and moderates summer temperatures in the lower river, so that the temperature above a laddered diversion dam at ~ rkm 17 normally remains below 15°C. The Yuba River supports mainly fall Chinook (Figure A-16), but a few spring-run and fewer late fall-run also spawn there. There is an active fishery for *O mykiss*, both anadromous and resident. Fisheries studies on the river are conducted mainly by consultants for the Yuba County Water Agency and CDFG. A major study of the feasibility of providing anadromous fish access the Middle Fork and the South Fork of the Yuba is underway.

Figure A-16. Estimated of naturally spawning fall Chinook in the Yuba River. Data are of variable accuracy, and for 1990 are missing, but probably show trends reliably. Data from CDFG GrandTab; post 1998 data are preliminary.



American River

The American River flows eastward to join the Sacramento River at Sacramento (rkm 96). Salmon are now confined to a 37 km reach below Nimbus Dam, part of the CVP, which smoothes hydropower releases from the larger Folsom Dam and diverts water into the aborted Folsom-South Canal.⁹⁸ The Lower American River flows through a parkway that is a major recreational area for the Sacramento region. Fall-run and probably some late fall Chinook spawn in the lower American River, as do steelhead. Fall-run spawning extends about 28 km down the river, almost to the upstream limit of tidal influence. Nimbus Hatchery produces fall-run and steelhead, and many fall-run and most steelhead spawning naturally are hatchery fish. Water temperature is marginal for juvenile steelhead in the summer. Attempts to propagate the native steelhead failed when the hatchery began operations, and the current population was founded with a coastal stock. Litigation over proposed diversions by the East Bay Municipal Utility District from the Folsom-South Canal motivated considerable study of salmon and steelhead in the river in the late 1980s and early 1990s (Williams 1995). Fisheries studies now are conducted mainly by the California Department of Fish and Game.

⁹⁸ Construction of the Folsom-South Canal was halted by litigation, and the canal actually diverts only minor amounts of water.

Figure A-17. Modification of flow in the American River. Estimated unimpaired mean monthly flow at Fair Oaks (black circles) and mean monthly flow after the construction of Folsom Dam (1955-2000). Unimpaired data from ACE, post-dam data from USGS.

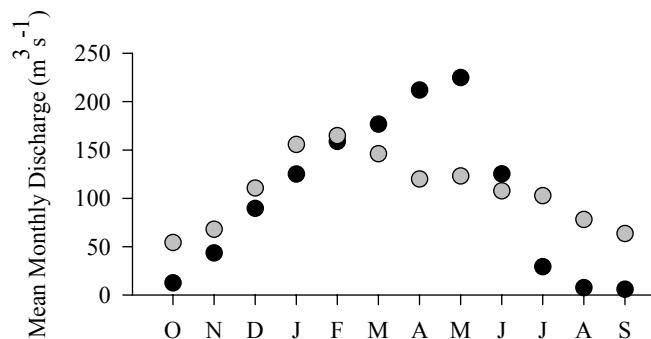
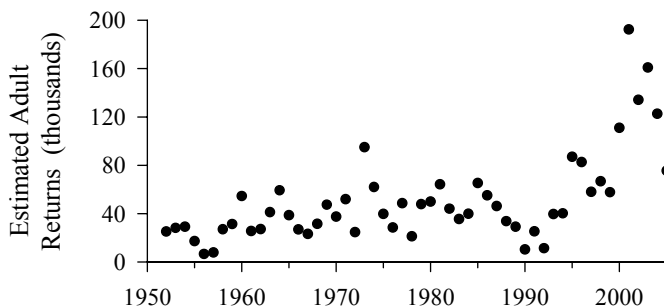


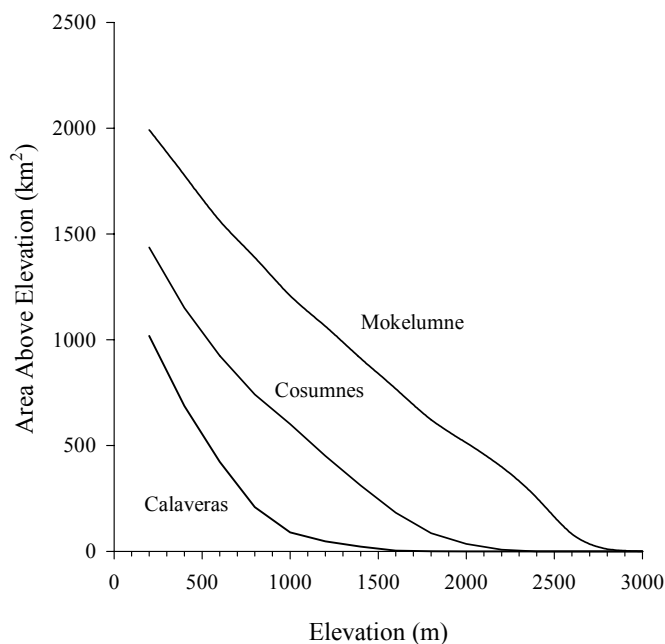
Figure A-18. Estimated escapement of naturally spawning fall Chinook in the American River. Data are of variable accuracy, but probably show trends reliably. Data from CDFG GrandTab; post 1998 data are preliminary.



Delta tributaries

The Cosumnes, Mokelumne, and Calaveras rivers flow directly from the western slope of the Sierra Nevada into the eastern Delta (Figure A-1). These are relatively small streams, and only the Mokelumne drains enough high elevation terrain to have significant snowmelt runoff (Figure A-19).

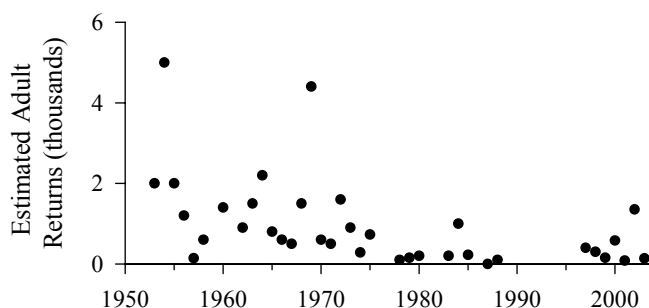
Figure A-19. Area-elevation curves for the Cosumnes, Mokelumne, and Calaveras rivers, for elevations above 200 m.



Cosumnes River

The Cosumnes River joins the Mokelumne within the Delta (Figure A-1), and supports a small population of fall Chinook. The river and its aquifer are heavily exploited for irrigation, so that above tidewater the river goes dry every summer; although the river is perennial in the Sierra foothills, and water for migration is marginal in many years and lacking in some. Salmon migration is blocked by a natural barrier about 54 km from the confluence with the Mokelumne. The Nature Conservancy owns much of the land along the lower Cosumnes and has been removing levees to restore the natural connection between the river and its floodplain; the University of California has a major program of ecological studies underway there.

Figure A-20. Estimated returns of naturally spawning fall Chinook in the Cosumnes River. Data are sparse and of variable accuracy, but probably show trends reliably. Other data from CDFG GrandTab; post 1998 data are preliminary.



Mokelumne River

The Mokelumne River provides water supply for the eastern side of San Francisco Bay as well as for the valley region through which it flows. Most storage is behind Pardee Dam, but Comanche Dam at rkm 47.5 blocks anadromous fish. The elevation of the afterbay below Camanche Dam is only about 30 m, so the potential for spawning habitat is limited, but it is spread out over about 16 km below the dam. A hatchery near the dam raises fall Chinook, and steelhead derived from a coastal stock. A diversion dam low on the river allows for effective monitoring of upstream and downstream migrants. Most fisheries work is conducted by biologists for the East Bay Municipal Utility District (EBMUD).

Figure A-21. Modification of flow in the Mokelumne River. Estimated unimpaired mean monthly flow at Pardee Dam (black circles) and mean monthly flow below Camanche Dam (1963-2000). Unimpaired data from ACE, post-dam data from USGS.

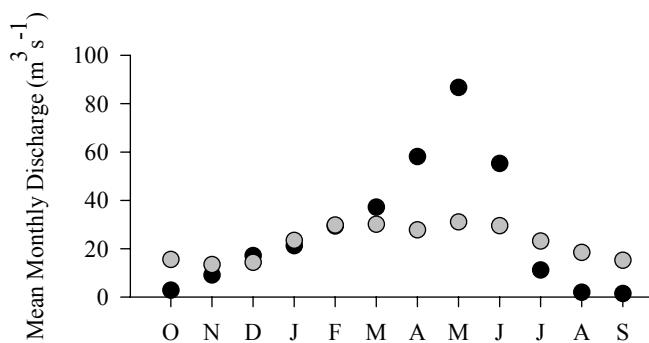
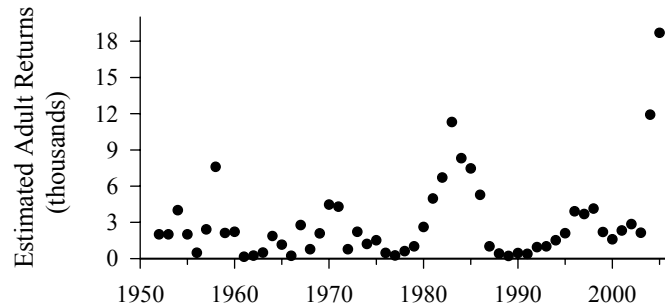


Figure A-22. Estimated returns of naturally spawning fall Chinook in the Mokelumne River. Data are of variable accuracy, but probably show trends reliably. 2001 datum from EBMUD, other data from CDFG GrandTab; post 1998 data are preliminary.



Calaveras River

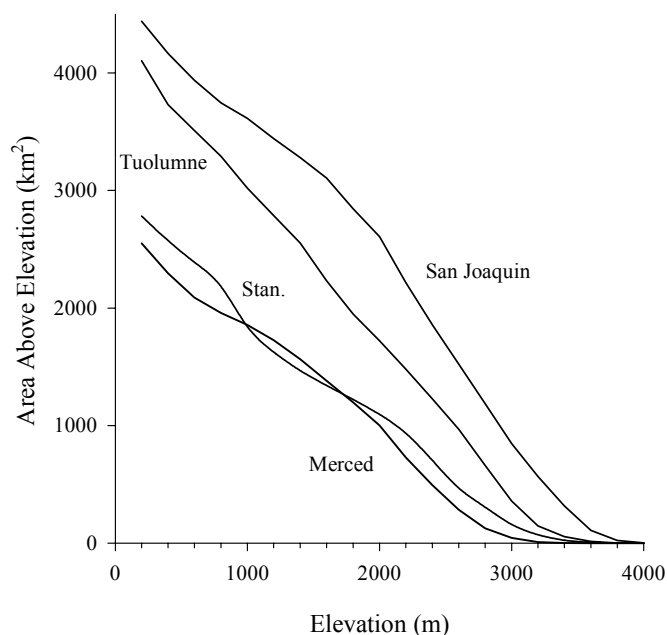
The hydrology of the Calaveras River is driven by rainfall, and in natural conditions the river sometimes went dry in summer or fall but apparently supported fall Chinook in some years (Stillwater Sciences 2004). New Hogan Dam, at ~rkm 60, now dampens variability in the flow downstream and moderates summer temperatures in most years, and the river now supports a popular recreational fishery for resident *O. mykiss*: fall Chinook and anadromous *O. mykiss* occasionally appear there as well (Stillwater Sciences 2004). An unusual run of 100 to 1,000 Chinook that spawned in late winter or spring was documented in the Calaveras River between 1972 and 1984, but has since died out (Reynolds et al. 1993). These fish are sometimes referred to as winter-run (e.g., Myers et al. 1998), but more likely they were late fall-run (Yoshiyama et al. 2001). In either case they were a recent development, since the pre-dam hydrology was not suitable for late-spawning Chinook. Most current fisheries work is conducted by the Fishery Foundation of California and S. P. Cramer & Associates.

The San Joaquin River and tributaries

The San Joaquin River and its tributaries flow west-southwest out of the southern Sierra Nevada Mountains and turn to flow northwest along the main axis of the Central Valley. The three major tributaries, from north to south, are the Stanislaus, the Tuolumne, and the Merced (Figure A-1). These streams drain high elevation terrain (Figure A-23), and their natural annual hydrographs were dominated by snowmelt. Flows in the tributaries are now much reduced and stabilized by diversions to use and to storage, and the hydrology of the area is complicated by a patchwork of canals. Flow in the San Joaquin has been reduced to zero upstream from its confluence with the Merced except in wet years, but it now appears that some flow may be restored (Appendix C).

Spring-run probably were the dominant run of Chinook in the San Joaquin River and its major tributaries, but these streams also supported fall-run and probably late fall Chinook, as well as steelhead. Fall-run and a few late-fall Chinook remain in the tributaries, as well as resident populations of *O. mykiss*, and a few steelhead appear in the Stanislaus River. Dams block all these rivers where they leave the foothills, and the remaining habitat for salmon and steelhead is below the dams.

Figure A-23. Area-elevation curves for the Stanislaus, Tuolumne, Merced, and upper San Joaquin rivers, for elevations above 200 m.



Geomorphically, the streams below the dams are incised into gently sloping Pleistocene alluvial fans that skirt the edge of the foothills, forming shallow valleys that historically were active floodplains with braided channels in the gravel-bedded reaches nearer the foothills, becoming meandering channels as the gradient lessened and the bed material became finer farther downstream. The gravel-bedded reaches have been dredged for gold and mined for aggregate, and gravel pits that provide good habitat for bass are common features. Major stream restoration projects are in planning or underway for the three major tributaries; work is farthest along on the Tuolumne (Kondolf et al. 2001).

Stanislaus River

The Stanislaus River is the northernmost of the major tributaries of the San Joaquin, and supports a modest population of naturally spawning fall Chinook. The hydrograph of the river was dominated by snowmelt, but is now highly modified by storage in the New Melones Reservoir (Figure A-24), and overbank flow is now rare (Kondolf et al. 2001).

Fall Chinook (Figure A-25) and perhaps a few late fall-run spawn in the Stanislaus River for about 40 km below Goodwin Dam, an impassable diversion dam at rkm 94. New Melones, a large CVP storage reservoir farther upstream, releases cool enough water to allow some Chinook to rear there through the summer. Most fisheries studies on the Stanislaus have been conducted by consultants, especially Carl Mesick Consultants and S. P. Cramer & Associates, who now operate a weir on the river, but CDFG also does carcass surveys.

Figure A-24. Mean monthly unimpaired (black symbols) and recent (gray symbols) discharge in the Stanislaus River. Unimpaired data estimated for the Melones Dam by USACE; 1979-2000 data from USGS.

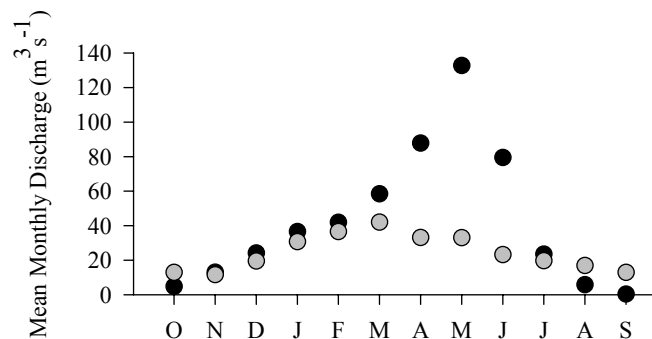
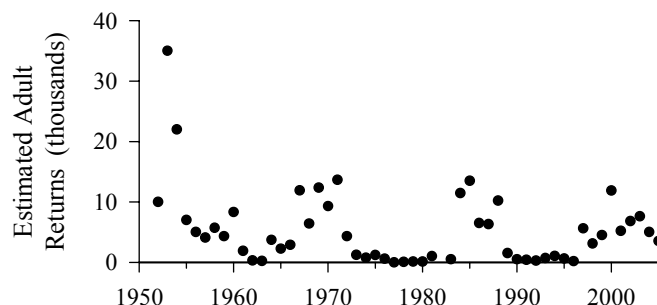


Figure A-25. Estimated escapement of naturally spawning fall Chinook in the Stanislaus River. Data are of variable accuracy, but probably show trends reliably. Data from CDFG GrandTab; post 1997 data are preliminary.



Tuolumne River

The Tuolumne River is the largest tributary of the San Joaquin, and supplies water to San Francisco as well as adjacent areas of the San Joaquin Valley. The watershed area above 2,000 m elevation exceeds 1,700 km² (Figure A-23). Fall Chinook spawn in a 35 km reach below LaGrange Dam (rkm 84), a re-regulating and diversion facility for New Don Pedro Dam. Adult returns have varied strongly, but with a downward trend (Figure A-27). Fry (1961:64) noted that “In some years the Tuolumne River has had fall runs which were larger than those of any Central Valley stream except the Sacramento River;” 130,000 were counted passing a diversion dam in 1944. Major restoration projects are planned for two reaches affected by dredging and gravel mining (Vick and McBain & Trush 2004). Biologists for the Turlock and Modesto irrigation districts and CDFG conduct salmon studies on the river.

Figure A-26. Mean monthly unimpaired (black symbols) and recent (gray symbols) show discharge in the Tuolumne River below LaGrange Dam. Unimpaired flow data from USACE; 1971-2000 data from USGS.

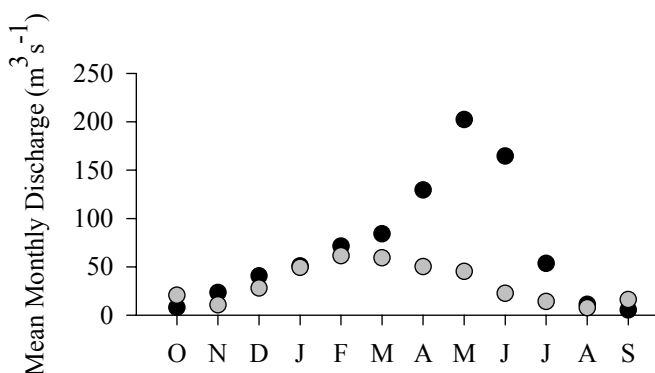
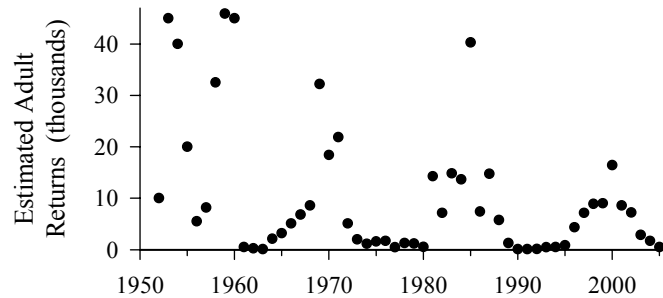


Figure A-27. Estimated escapement of naturally spawning fall Chinook in the Tuolumne River. Data are of variable accuracy, but probably show trends reliably. Data from CDFG GrandTab; post 1997 data are preliminary.



Merced River

The Merced River drains Yosemite Valley and adjacent areas of the southern Sierra-Nevada, but has less watershed area at high elevations than the Tuolumne or San Joaquin rivers (Figure A-23). Fall Chinook now spawn downstream from the Crocker-Huffman Dam, in a ~40 km gravel-bed reach where the river has incised an active floodplain up to 7 km wide into old fan deposits that form bluffs on either side. This is currently the southernmost spawning habitat for Chinook salmon. Farther downstream, the material in the channel bed becomes finer and more cohesive and the floodplain narrows to the dimensions of channel meanders. The gravel-bed reach of the river has been extensively dredged and mined, and the river now flows about 8 km through mining pits (Stillwater Sciences 2001). Flows are highly modified and reduced by storage and diversions (Figure A-28), and normally are effectively confined to the channel by private levees. Planning for restoration in an 11 km reach downstream from the Crocker-Huffman Dam is well advanced (e.g., Stillwater Sciences 2004). A small hatchery operated by CDFG rears fall Chinook, and about 35% of returning fish are of hatchery origin (J. Wickert, USFWS, pers.comm. 2005).

Figure A-28. Mean monthly unimpaired (black symbols) and recent (gray symbols) show discharge in the Merced River. Unimpaired data at Exchequer Dam from ACE; 1968-2000 data from USGS gage 11270900 (below Merced Falls).

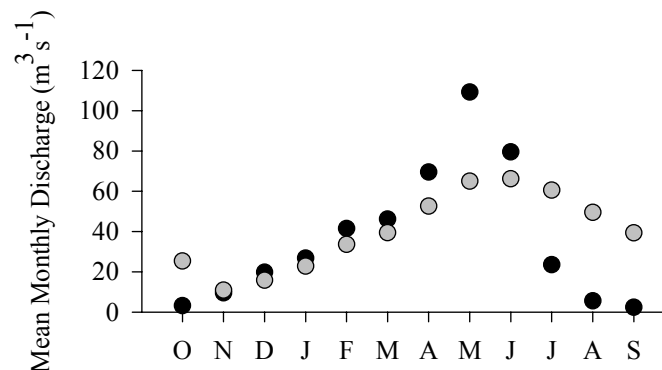
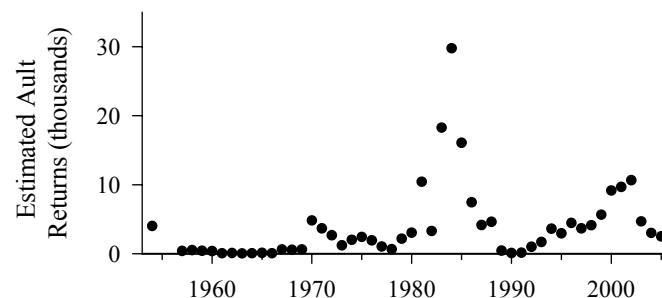


Figure A-29. Estimated escapement of naturally spawning fall Chinook in the Merced River. Data are of variable accuracy, and are not available for all years, but probably shows trends reliably. Data from CDFG GrandTab; post 1997 data are preliminary.



San Joaquin River

The upper San Joaquin River drains a large area of the high country in the southern Sierra Nevada, and formerly supported a large population of spring Chinook as well as fall and late fall Chinook. Salmon were extirpated in the river following construction of Friant Dam, part of the CVP. Water is conveyed to use from Friant primarily by canals, and not enough water is released into the river to allow migration to and from spawning habitat that remains below the dam (Warner 1991). In 2006, tentative agreement was reached for settling long-standing litigation regarding instream flows below Friant Dam, that would provide for enough flow to allow restoration of salmon. The settlement requires federal action, however, and whether this will be forthcoming remains uncertain.

Table A-1. Historical and present runs of Chinook salmon for Central Valley streams that now support significant populations, based on Yoshiyama et al (2001) except for Clear Creek.

River or Creek	Historical Runs	Present Runs	Upstream Limit
Sacramento R.	S, F, LF, W	S, F, LF, W	Keswick Dam
Clear Cr.	S?, F, LF?	S, F, LF?	Whiskeytown Dam
Cottonwood Cr.	S, F, LF?	S, F, LF?	Natural Barrier
Battle Cr.	S, F, W	S ^o , F ^o	
Mill Cr.	S, F, LF??	S, F, LF ^o	Natural barrier
Deer Cr.	S, F	S, F	Natural barrier
Butte Cr.	S, F, LF	S, F, LF	Natural barrier
Feather R.	S, F	F	Oroville Dam
Yuba R.	S, F	S(?), F	Englebright Dam
American R.	S, F, LF??	F	Nimbus Dam
Cosumnes R.		F	Natural barrier
Mokelumne R/	S, F, LF?	F	Comanche Dam
Calaveras R.	F?	F ^o	New Hogan Dam
Stanislaus R.	S, F, LF??	F	Goodwin Dam
Tuolumne R.	S, F, LF??	F	La Grange Dam
Merced R.	S, F	F	Crocker Huffman Dam

o occasional, probably strays; ? substantial but inconclusive evidence; ?? fragmentary evidence; S Spring-Run; F Fall-Run; LF Late Fall-Run; W Winter-Run.

APPENDIX B

MORE ON THE NEWMAN-RICE STUDIES

This appendix supplements the discussion in Chapter 11 of the statistical analyses of the survival of coded-wire tagged fall Chinook smolts released into the Sacramento River and the Delta that were conducted by John Rice and Ken Newman (Newman and Rice 2002; Newman 2003).

The Newman-Rice study was essentially completed by 1998, although it was not published in the professional literature until 2002,⁹⁹ and to a considerable extent the preliminary reports defused the controversy. On the one hand, they generally supported the findings of the earlier studies, but they also highlighted the limitations of the data and the need to apply the results cautiously. The technical level of the modeling is also beyond the ken of all but a few of the scientists involved with Central Valley salmon, which may have discouraged controversy. Newman continued with additional analyses, described below, but this IEP-funded work has been largely free of the political tension that marked the early phases of the work with Rice.

Covariates used in the Newman-Rice study

1. Fish size (average length in mm)
2. Log-transformed median flow (ft³/sec) during the outmigration period
3. Salinity of water as measured by resistance (µmho/cm)
4. River temperature at time of release (°F)
5. Temperature of the hatchery water on the day of release (°F)
6. Temperature shock, the difference between the temperature of the water in the truck carrying the fish from the hatchery to the release location and the river temperature.
7. A tide-related variable that measured the magnitude of the change in low-low and high-low tides and whether the Delta was filling or draining
8. Turbidity of the water (formazine turbidity units)
9. Position of the cross-channel gate located just below Courtland; 1 if open and 0 if closed
10. Ratio of amount of water exported to amount of water flowing in the mainstem.

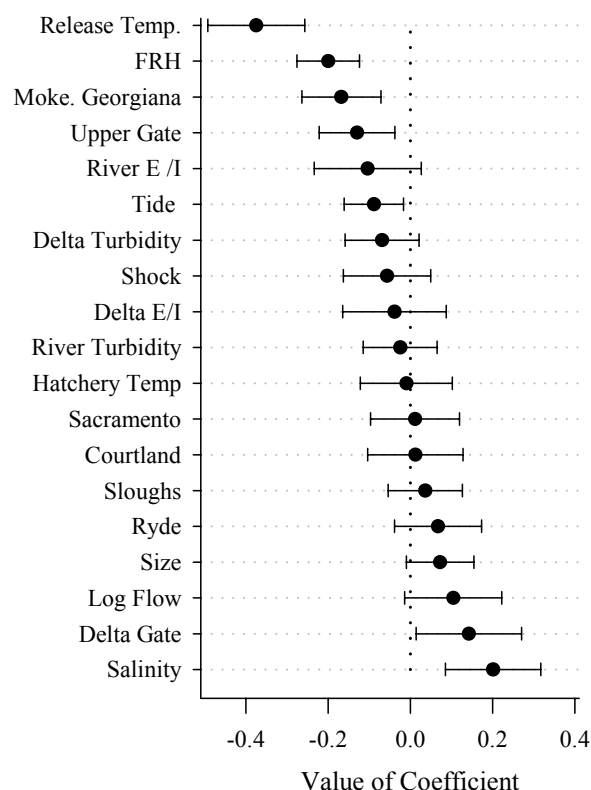
The Newman-Rice model also included indicator variables for each year of the study and for the sites at which fish were released, and so required estimates of 36 coefficients. This is a large number, more than a third the number of release groups, which raised the question whether a model of the same basic structure with a smaller number of parameters might not be better, but tests with appropriate methods for selecting covariates to include in the model resulted in no change.¹⁰⁰

⁹⁹ The article was submitted in October 1998; apparently, a very long lag time for publication is not unusual in statistics.

¹⁰⁰ A ridge parameter was included in the model because of the large parameter to sample size ratio, however; this helps to increase the precision and stability of the parameter estimates, but at the cost of some bias (Ken Newman, personal communication, 3/03).

The main results, estimates of the coefficients of the covariates and twice their standard errors, allow an assessment of the strength of the effects associated with the covariates (Figure B-1); roughly speaking, the effect of the variable can be called strong if twice the standard errors (the bars in the figure) do not include zero, and weak otherwise (Newman and Rice 2002), although as the figure makes clear this is drawing a line across a gradient. By the two-standard-error criterion, release temperature, release at the Feather River Hatchery, release in the Mokelumne River or Georgiana Slough, tide, and (for releases in the Sacramento River) the cross-channel gate being open have a strong negative association with survival, and salinity and (for releases into the Mokelumne River or Georgiana Slough) the cross-channel gate being open have strong positive associations. Flow in the Sacramento and fish size have "almost strong" positive associations.

Figure B-1. Estimated coefficients for covariates and indicator variables in the Newman and Rice (2002) model with ridge parameter, plus or minus two standard errors. The covariates were standardized before the analysis. Positive coefficients indicate a positive association with survival. There are six covariates indicating release site (which take a value of 1 if the fish were released there and zero otherwise): Feather River hatchery (FRH), Sacramento, Courtland, Ryde, Sutter or Steamboat Slough, Georgiana Slough or Mokelumne River (and, implicitly, Jersey Point); three water temperature variables: water temperature where fish were released, water temperature at the hatchery, and the difference between the water temperature in the truck and the receiving water (shock); Export/inflow ratio for releases in the rivers or in the Delta, position of the Delta cross-channel gate for releases in the Sacramento River and the Delta; turbidity for releases in the rivers and the Delta; flow in the Sacramento River (log transformed); average size of the fish; salinity at Collinsville, and a covariate based on tide. The coefficients for the effect of years are not shown. Data from Table 1 in Newman and Rice (2002).



Following the work with Rice, Newman (2003) applied three different approaches to data from situations in which upstream releases could be matched with releases just downstream from Chipps Island (Newman 2003). If survival in the bay and ocean and recoveries of adults are assumed to be the same for both groups, then survival (S) in the river and Delta between the upstream release site and Chipps Island can be estimated separately from the probability of capture at Chipps Island (p). The unpaired analysis in Newman and Rice (2002) estimated the product Sp . Newman (2003) compared a trinomial/binomial product (TBP) model, another pseudo-likelihood (PL) model, and a hierarchical model. All modeled survival as a function of nine covariates: length of fish, Sacramento River flow, salinity at Collinsville, water temperature

at the release site and at the hatchery, tide, exports (rather than the export/inflow ratio), position of the Delta cross-channel gate, and turbidity, and "indicator variables" that account for whether fish were released at Sacramento or Courtland, rather than Ryde. The gate and export covariates were assumed to affect only fish released at Sacramento or Courtland, upstream from the cross-channel gate.

The mathematical details of the models are unimportant for this discussion, but it is important to understand that the models make different assumptions. The TBP model is based on the assumptions that all fish in a release group act independently and are equally likely to be captured, either in the Chipps Island trawl or in the ocean. These are dubious assumptions for a number of reasons described by Newman, who included the TBP model in the study mainly for comparative purposes (Newman, personal communication. 3/03). For example, emigrating salmonids typically form schools, which creates correlations among individuals and "overdispersion" in the data, or greater variance in the recoveries than would be expected if the assumptions held. Errors in the estimates of ocean recoveries have the same effect. In the pseudo-likelihood model, the expected number of recoveries is the same as for the TBP model, but the variances in the recoveries are inflated by dispersion parameters. The inflated variances result in different estimates of the importance of the different covariates, and in their estimated standard errors. The hierarchical model uses a Bayesian approach to add further adjustments to the TBP model, which again affect the estimates of the coefficients of the covariates and their estimated standard errors. All three models were fit to the data with two different assumptions about the probability that a given fish passing Chipps Island would be captured: that it varies by release group, or by year, but the results for the pseudo-likelihood and hierarchical models are of most interest (Figure B-2).

The standard errors of the coefficients for the hierarchical model are generally smaller than for the pseudo-likelihood model, with the result that more of the variables have a strong association with survival, especially when the capture probability is allowed to vary by release. For example, even though the coefficient for the gate indicator is larger for the pseudo-likelihood model, the standard error of the coefficient is so large that the plus or minus two standard error range includes zero, although it does not with the hierarchical model. Thus, by that criterion, release temperature, gate, release at Sacramento, and exports all have strong negative associations with survival with the hierarchical model, but only release temperature does so with the pseudo-likelihood model. For positive associations with survival, flow, turbidity, salinity and size have strong effects with the hierarchical model, and flow, turbidity and salinity do with the pseudo-likelihood model. Results are generally similar when the capture probability varies by year, except that release at Sacramento and at Courtland and size have a strong negative association with survival with the pseudo-likelihood model. Newman (2003) describes two reasons to give more weight to the hierarchical model: the coefficients of the hierarchical model are more stable when the models are applied to subsets of the data (Table 4 in Newman 2003), and the sign of the coefficient for fish size is consistent with independent information on the association between fish size and survival.

The analyses described above assume that the survival of fish released just downstream from Chipps Island is the same as the survival of the fish released at Sacramento or Courtland that pass Chipps Island. Newman (2003) describes several reasons to doubt this, and the most biologically plausible reasons suggest that fish released downstream from Chipps Island should not survive as well.¹⁰¹ This can be modeled by assuming that the mortality rate of the downstream group is some fixed multiple of the mortality rate of the upstream group. Newman (2003) found that doing this had relatively little effect on the estimated coefficients, although it decreases the estimates of survival and increases the estimates of the probability of capture. Estimates of the multiple or the "shock effect" were substantial, however, particularly for the hierarchical model. There is independent evidence for a shock effect, for example in the higher survival of fry released below Red Bluff Diversion Dam than those released in the Delta, and hatchery fish released in British Columbia as smolts showed a growth check in their otoliths at the time of release (Zhang et al. 1995). Newman notes that if shock also occurs with the upstream releases, which seems likely, then survival indices estimated from these releases would underestimate the survival of naturally-produced fish or of hatchery fish that are already acclimated to the river.¹⁰²

To facilitate comparison with the unpaired model of Newman and Rice, Newman (2003) also reported results from the paired models using the export/inflow ratio rather than exports. There are strong similarities but some important differences between the paired and unpaired analyses, especially the paired analysis with the hierarchical mode (Figure B-3).

By the two-standard-error criterion, release temperature, gate position, and the export/inflow ratio had strong negative associations with survival for the hierarchical model, and size, salinity, turbidity, and flow had strong positive associations. Of these, the E/I ratio, size, turbidity, and flow were not "strong" in the unpaired analysis (although size was very close), and only tide was a "strong" effect in the unpaired analysis but not in the hierarchical analysis. The greatest contrast concerns turbidity, which had little effect on predictions of the unpaired model. Newman (2003) speculates that this may result from turbidity increasing survival but also increasing the probability of capture in the trawl, and so having little effect in the unpaired model, which estimates probability survival times probability of capture, given survival, rather

¹⁰¹ It seems probable that the hatchery fish used for the studies are not all equally likely to survive, but that there is a distribution of "survivability," so that fish with low survivability would already have been culled from the group released upstream. Moreover, there is good evidence that downstream migration is a self-reinforcing process (Høgåsen 1998; Ewing et al 2001), so fish released upstream will be farther advanced in the smolting process and will be migrating more rapidly when they pass Chipps Island than will the group of fish released downstream from Chipps Island.

¹⁰² Suppose that hatchery fish suffer a shock effect, resulting in an initially high mortality rate upon release, which drops more or less rapidly to the mortality rate of similar fish that are already acclimated to the release environment. If these fish bear CWTs and are recaptured at some later time farther downstream, the proportion that are recaptured will be proportional to the product of the short-term, lower survival rate and the longer-term, higher survival rate. The shock effect estimated by Newman (2003) would be the ratio of the Delta shock and the upstream shock. Whatever the causes of the shock effect, they are likely to be variable over time, environmental conditions, or batches of fish, more or less independently of the variables of interest in the study.

than probability of survival. Another important difference concerns Sacramento River flow, which has a much stronger association with survival with the hierarchical model.

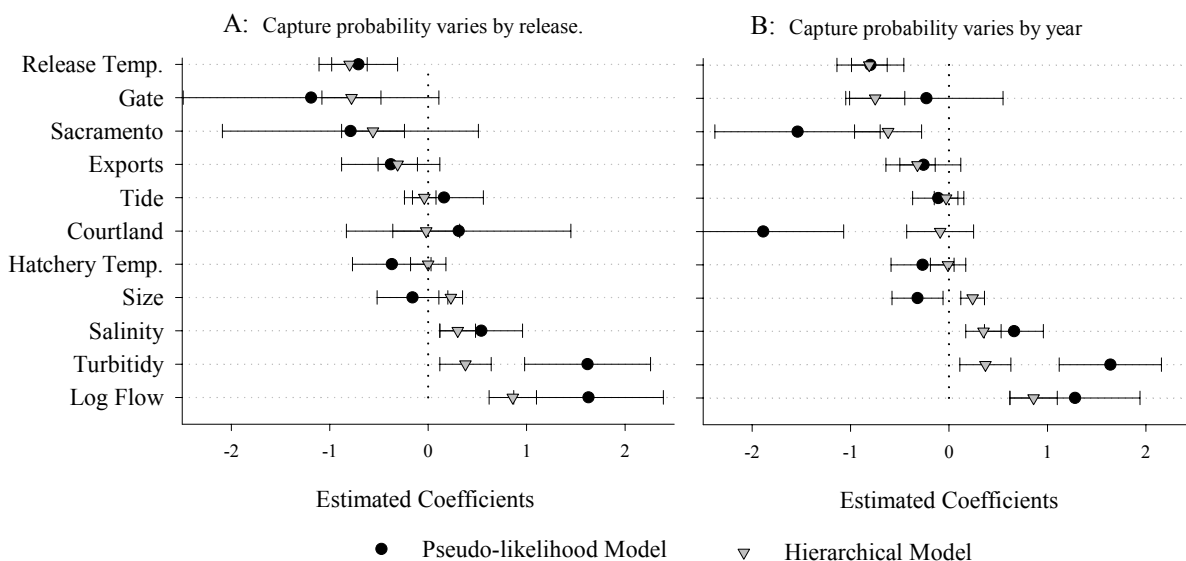
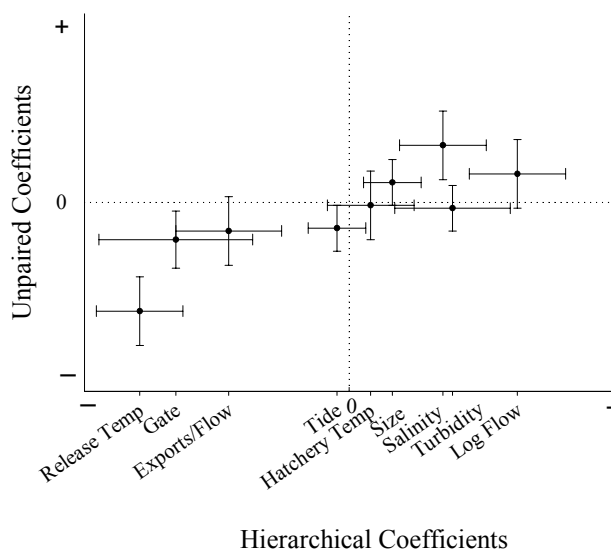


Figure B-2. Estimated coefficients for the covariates and indicator variables listed on the vertical axis, for the pseudo-likelihood and hierarchical models of Newman (2003), with capture probability varying by release group (A) or by year (B); bars show two standard errors. The covariates were standardized before the analysis. Positive coefficients indicate a positive association with survival. Data from Table 3 in Newman (2003).

Figure B-3. Comparison of estimated coefficients plus/minus two standard errors for the unpaired analysis of Newman and Rice (2002) and the hierarchical analysis of Newman (2003) with release-specific capture probabilities.



APPENDIX C

LEGAL ISSUES AFFECTING INSTREAM FLOWS

The Public Trust Doctrine and instream flows

The Public Trust Doctrine has emerged as a major factor in California water law since 1983. The doctrine developed out of ideas about the public nature of waterways that have influenced law for thousands of years.¹⁰³ Essentially, the doctrine is that the state holds navigable waterways and the land under them, up to the elevation of “ordinary high water,” in trust for use by the public. Even if the land is transferred to private ownership, the state ordinarily retains an easement for public trust uses.

In 1971, in *Marks v. Whitney* (6 Cal.3d 251), a decision about tidelands in Tomales Bay, the California Supreme Court broadened the uses that are protected by the trust to include providing environments for birds and marine life, and scientific study. In pertinent part, the decision states that:

Public trust easements are traditionally defined in terms of navigation, commerce and fisheries. They have been held to include the right to fish, hunt, bathe, swim, to use for boating and general recreation purposes the navigable waters of the state, and to use the bottom of the navigable waters for anchoring, standing, or other purposes (citations). The public has the same rights in and to tidelands. ... The public uses to which tidelands are subject are sufficiently flexible to encompass changing public needs. In administering the trust the state is not burdened with an outmoded classification favoring one mode of utilization over another (citations). There is a growing public recognition that one of the most important public uses of tidelands – a use encompassed within the tidelands trust – is the preservation of those lands in their natural state, so that they may serve as units for scientific study, as open space, and as environments which produce food and habitat for birds and marine life, and which favorably affect the scenery and climate of the area. ...

This broadening of trust uses was extended to navigable lakes and streams and their tributaries in 1983 in *National Audubon Society v. Superior Court* (33 Cal.3d 419), when the California Supreme Court reversed a lower court ruling that the public trust doctrine was “subsumed in the water rights system of the state,” and found instead that the Los Angeles Department of Water and Power (DWP) did not have a vested right to divert water from tributaries to Mono Lake. The Court noted that:

¹⁰³ In *National Audubon Society v. Superior Court* (33 Cal.3d 419), the California Supreme Court began its discussion of the Public Trust Doctrine by quoting the Institutes of Justinian: “By the law of nature these things are common to mankind – the air, running water, the sea and consequently the shore of the sea.”

This case brings together for the first time two systems of legal thought: the appropriative water rights system which since the days of the gold rush has dominated California water law, and the public trust doctrine which, after evolving as a shield for the preservation of tidelands, now extends its protective scope to navigable lakes. Ever since we first recognized that the public trust protects environmental and recreational values (*Marks v. Whitney*), the two systems of legal thought have been on a collision course. ...

Attempting to integrate the teachings and values of both the public trust and the appropriative water rights system, we have arrived at certain conclusions which we briefly summarize here. In our opinion, the core of the public trust doctrine is the state's authority as sovereign to exercise a continuous supervision and control over the navigable waters of the state and the lands underlying those waters. This authority applies to the waters tributary to Mono Lake and bars [the Los Angeles Department of Water and Power] or any other party from claiming a vested right to divert waters once it became clear that such diversions harm the interests protected by the public trust. The corollary rule which evolved in tideland and lakeshore cases barring conveyance of rights free of the trust except to serve trust purposes cannot, however, apply without modification to flowing waters. The prosperity and habitability of much of this state requires the diversion of great quantities of water from its streams for purposes unconnected to any navigation, commerce, fishing, recreation, or ecological use relating to the source stream. The state must have the power to grant unvested usufructuary rights to appropriate water even if diversions harm public trust uses. Approval of such diversion without considering public trust values, however, may result in needless destruction of those values. Accordingly, we believe that before the courts and agencies approve water diversions they should consider the effect of such diversions upon interests protected by the public trust, and attempt, so far as feasible, to avoid or minimize any harm to those interests.

In short, *Audubon* held that public trust and other uses of water must be balanced, and this requirement applies retroactively. Moreover, the balancing can be reconsidered in light of new information. *Audubon* did not provide clear guidance regarding the relative weight to be given to instream and consumptive uses of water. This has been considered in two subsequent cases, reviewed below, although both of these are superior court decisions rather than appellate court decisions, and are binding only on the parties to the cases. *Audubon* did confirm that public trust uses must be reasonable, however. The California Constitution, in Article 10 section 2,¹⁰⁴ limits the right to use water to reasonable and beneficial uses, and the Court noted that this restriction also applies to public trust uses. The Court also reiterated that public trust uses are beneficial

¹⁰⁴ "It is hereby declared that because of the conditions prevailing in this State the general welfare requires that the water resources of the State be put to beneficial use to the fullest extent of which they are capable, and that the waste and unreasonable use or unreasonable method of use of water be prevented, and that the conservation of such waters is to be exercised with a view to the reasonable and beneficial use thereof in the interest of the people and for the public welfare. The right to water or to the use or flow of water in or from any natural stream or water course in this State is and shall be limited to such use as shall be reasonably required for the beneficial uses to be served, and such right does not and shall not extend to the waste or unreasonable use of water or unreasonable method of use or unreasonable method of diversion of water ..."

uses (although the framers of Article 10 section 2 may not have had them in mind); there is case law on this point, and Water Code section 1243 provides that “The use of water for recreation and preservation and enhancement of fish and wildlife resources is a beneficial use of water.” However, the Court rejected the argument, apparently made by the then Attorney General of California, that all public uses of water, including consumptive uses, were trust uses; the Court noted that if this were the case, the public trust doctrine “would impose no restrictions on the state’s authority to allocate trust property.”

Although Audubon laid down basic principles, their actual meaning will be determined in subsequent cases. There have been three major cases in the Central Valley, which are described below. However, two of these are superior court decisions, and so are not binding as precedent for other cases, and one of these, concerning Putah Creek, was replaced by a negotiated settlement following appeal.

Environmental Defense Fund v. East Bay Municipal Utility District

The basic issue of EDF v. EBMUD was whether EBMUD could divert water from the American River at Nimbus Dam, through the Folsom-South Canal, or whether it must divert the water from some point farther downstream. After a long trial in 1989, Judge Hodge ruled that EBMUD could divert water through the canal, provided enough water remained in the river to protect public trust resources, and he set flow standards in the river that were intended to provide that protection, based on the evidence presented at the trial. However, he also found that the evidence presented was inadequate to support a final determination of the flows necessary to protect public trust resources, so he retained jurisdiction, ordered the parties to cooperate in doing scientific studies to reduce the uncertainty regarding the necessary flows, and appointed me as special master to supervise the studies (Hodge 1990:95):

The task for this court is to recognize the fundamental inadequacy of existing studies as they relate to the American River, to extract from the “consensus¹⁰⁵” and from the testimony those factors which can provide a guide for protecting fishery values, and significantly, to retain jurisdiction until the scientific community can provide definitive answers.

Five years later, I reported back that “In my opinion the court, while grasping the great uncertainty in the evidence, did not appreciate the full depth of the problem: not only are we without good evidence, but methods to develop much of the needed evidence are not at hand” (Williams 1995:17).

By 1995, a change in the EBMUD Board of Directors had shifted that agency’s attention to alternatives to diversion at Nimbus Dam, and the study program was terminated. Moreover, as a superior court decision, the Hodge Decision applies only to the parties. However, by confronting

¹⁰⁵ The “consensus” referred to by Judge Hodge was a statement developed by biologists who testified for the parties, who at the judge’s suggestion met without lawyers present to determine areas of agreement regarding fisheries issues.

the uncertainty in the scientific basis for managing public trust resources and by taking positive steps to reduce that uncertainty, the Hodge decision remains as an example of the application of adaptive management to setting instream flow standards (Castleberry et al. 1996).

The need for balancing public trust and consumptive uses is another major theme in the Hodge decision. Hodge explicitly rejected the argument that because Audubon requires that public trust resources be protected “whenever feasible” and EBMUD had feasible alternative diversion sites farther downstream, that EBMUD must use those alternatives (p. 28):

The logic is defective. The crux of *Audubon* is that public trust values require consideration and protection. It is simply not a fact that diversion below the confluence of the American/Sacramento rivers is the only way to achieve that protection. And if protection of public trust resources can be accomplished consistently with diversion at Folsom-South Canal, then plaintiffs and intervenors can have no sustainable complaint. ... In the absence of harm, plaintiff is not entitled simply to achieve a different diversion site as a question of policy or preference. ... There is simply no escape from the administrative and judicial necessity of providing a comprehensive allocation of water rights, considering all factors currently manifest or reasonably to be anticipated, and considering the cumulative impact of all known and anticipated diversions and appropriations. ... In assessing appropriation values versus public trust values, it is impossible to avoid a balancing analysis.¹⁰⁶

However, as important qualification, Hodge also noted that (p. 30) “If harm to public trust resources becomes significant, then the fullest beneficial use of water may be precluded as a violation of the public trust, i.e., protection of public trust resources may prevail over the constitutional requirement to put the state’s waters to their fullest beneficial use, when the two are irreconcilable.”

The Putah Creek cases and Fish and Game Code section 5937:

Section 5937 of the California Fish and Game Code, enacted in 1937, provides that “The owner of any dam shall allow sufficient water at all times to pass through a fishway, or in the absence of a fishway, allow sufficient water to pass over, around, or through the dam, to keep in good condition any fish that may be planted or exist below the dam.” In the past this language has been interpreted to mean not very much, as detailed by Baiocchi (1980), but an important effect of Audubon was to breathe new life into it. This is exemplified by the 1996 decision in the Putah Creek cases, in which Judge Park accepted an argument advanced by Peter Moyle that the meaning of “good condition” had to consider the condition of the fish at three scales: community, population, and individual (Moyle et al. 1998). However, Judge Park also emphasized that enforcement of section 5937 entails balancing (Statement of Decision, Sacramento Superior Court Case No. JC 2565:7):

¹⁰⁶ Note that whole sentences have been omitted from this quotation at the points marked by the ellipses; however, the meaning is intact.

Finding that the public trust resources have been harmed and that the fish are not in good condition, I do not believe is the end of the case, because it is clear under the case law that I am to then engage in a balancing process. National Audubon makes it clear that public trust values in theory can be sacrificed altogether if it is more appropriate under all the facts and circumstances to allow a complete diversion of the water to Solano County.

In my opinion critical to the analysis is the amount of additional water needed to satisfy these public trust values and to keep the fishery in good condition, weighed against the impact that taking this water from the Solano parties will have on them.

Natural Resources Defense Council v. Patterson

A question of long standing is whether section 5937 applies to the dams of the Central Valley Project, but a recent (August 2004) order by Judge Karlton in NRDC v. Patterson concerning Friant Dam on the San Joaquin River confirms that it does, and settlement discussions to determine what the flows should be have begun. Presumably, some balancing will be involved. After noting that to comply fully with section 5937, enough water be released to restore the historic fishery, Judge Karlton found that the past operation of Friant by the Bureau of Reclamation has violated the section as it applies to the Bureau by virtue of section 8 of the Reclamation Act of 1902. However, he added in a footnote

That this court has reached the conclusion that the Bureau has violated its duty hardly begins to address the problem of remedies. In that regard, the court notes not only the issues of whether the reasonableness component of the CVPIA constitutes an overlay on the Bureau's duties, but as the non-federal defendants have noted in oral argument, farmers throughout the valley have dedicated their lives and fortunes to making the desert bloom. They did so in reliance on the availability of CVP water. That reality most likely should be taken into account when the court comes to address a remedy.

The need to balance public trust and consumptive uses of water implies the need for good scientific understanding of public trust resources, so that the consequences of a given allocation of water between consumptive and instream uses of water can be weighed. Unfortunately, scientific understanding is not yet good enough to allow this to be done in a straightforward way, and an adaptive approach is called for (Castleberry et al. 1996).

Instream uses are still denied legal parity with other uses in some contexts, however. *California v. FERC* (495 U.S. 490; 1990) considered the meaning of language in the Federal Power Act to the effect the Act did not supercede "laws ... relating to the control, appropriation, use or distribution of water used in irrigation or for municipal or other uses, or any vested rights acquired therein," and upheld a 1946 decision that the language is limited to irrigation or municipal or other uses "of the same nature," and did not apply to state laws concerning instream uses. Therefore, FERC has exclusive jurisdiction to set minimum flows for non-federal

hydroelectric projects,¹⁰⁷ and instream flows below Oroville Dam on the Feather River and on the Mokelumne River, for example, are set by FERC.

¹⁰⁷ Section 8 of the Reclamation Act makes state law regarding instream flows applicable to the CVP. That federal law controls instream flows for non-federal hydroelectric projects but California law controls instream flows for the CVP is yet another example showing that water law is incomprehensible outside of its historical context.