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A Place to Call Home: A Synthesis of Delta Smelt Habitat in the Upper San Francisco Estuary

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ABSTRACT

We used a combination of published literature and field survey data to synthesize the available information about habitat use by delta smelt *Hypomesus transpacificus*, a declining native species in the San Francisco Estuary. Delta smelt habitat ranges from San Pablo and Suisun bays to their freshwater tributaries, including the Sacramento and San Joaquin rivers. In recent years, substantial numbers of delta smelt have colonized habitat in Liberty Island, a north Delta area that flooded in 1997. The species has a more upstream distribution during spawning as opposed to juvenile rearing periods. Post-larvae and juveniles tend to have a more downstream distribution during wetter years. Delta smelt are most common in low-salinity habitat (<6 psu) with high turbidities (>12 NTU) and moderate temperatures (7 °C to 25 °C). They do not appear to have strong substrate preferences, but sandy shoals are important for spawning in other osmerids. The evidence to date suggests that they generally require at least some tidal flow in their habitats. Delta smelt also occur in a wide range of channel sizes, although they seem to be rarer in small channels (<15 m wide). Nonetheless, there is some evidence that open water adjacent to habitats with long water-residence times (e.g. tidal marsh, shoal, low-order channels) may be favorable. Other desirable features of delta smelt habitat include high calanoid copepod densities and low levels of submerged aquatic vegetation (SAV) and the toxic algae *Microcystis*. Although enough is known to plan for large-scale pilot habitat projects, these efforts are vulnerable to several factors, most notably climate change, which will change salinity regimes and increase the occurrence of lethal temperatures. We recommend restoration of multiple geographical regions and habitats coupled with extensive monitoring and adaptive management. An overall emphasis on ecosystem processes rather than specific habitat features is also likely to be most effective for recovery of the species.

INTRODUCTION

The San Francisco Estuary (Figure 1) is one of the prominent features of the California coastline. The estuary is both unconventional and complex, supporting diverse habitats that range from marine bays to brackish marshes and tidal freshwater wetlands. Given the extreme level of urbanization and hydrologic alteration of the estuary (Nichols et al. 1986; Brown and Bauer 2010), it is not surprising that many species of endemic plants and animals have severely declined in abundance. Increasingly, habitat has become a target of management and restoration. Of the various declines, the highest-profile has been the collapse of the pelagic fish community of

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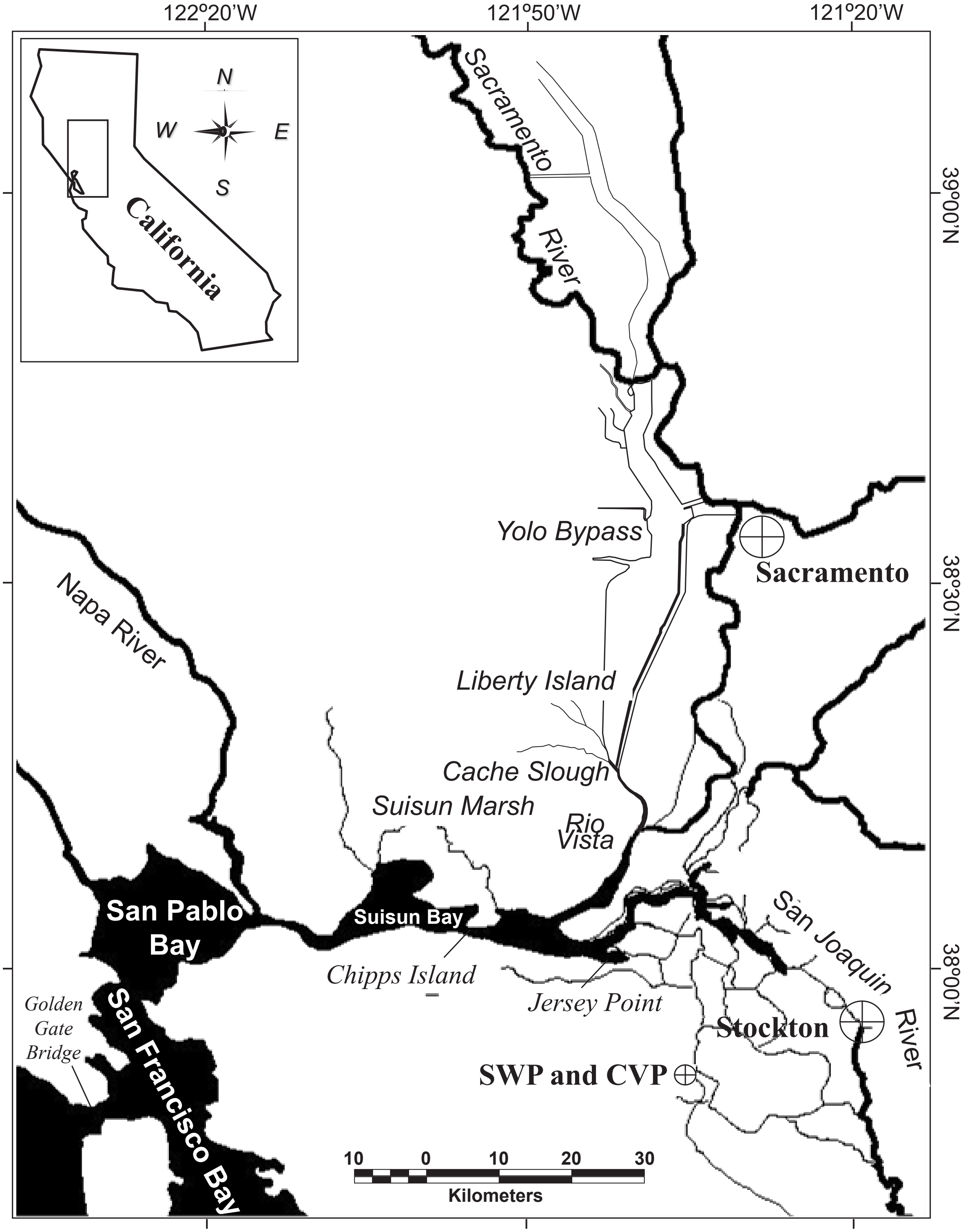

Figure 1 The San Francisco Estuary including key landmarks noted in the text. The Sacramento–San Joaquin Delta is the area between Chipps Island, Sacramento, and just south of Stockton.

the upper Estuary (Sommer et al. 2007). In particular, delta smelt *Hypomesus transpacificus*, has declined precipitously over the past decade, leading to major legal and regulatory actions to try and improve its status (Service 2007; Sommer et al. 2007). The species is currently listed as Threatened under the Federal Endangered Species Act and Endangered under the California Endangered Species Act (USFWS 2008).

This annual species is confined to a single estuary, so maintenance of the population depends in part on habitat conditions in the Sacramento-San Joaquin Delta (herein referred to as the Delta), the upstream region of the San Francisco Estuary from which the species gets its name (Figure 1). The hydrodynamics of the Delta's interconnected channels are especially complex and highly altered, with major changes to key parts of the distribution of delta smelt. One of the biggest hydrologic changes over the past century has been the construction of the large Central Valley Project (CVP) and State Water Project (SWP) water diversions, which supply water to about 25 million California residents and a multi-billion dollar agricultural industry (Grimaldo et al. 2009a). Delta smelt also occur outside the Delta in Suisun Bay, Suisun Marsh, and Napa River (Bennett 2005).

Given its legal status, there has been substantial progress in understanding the life history of this annual species (Moyle et al. 1992; Bennett 2005; Nobriga and Herbold 2009). The typical pattern is for delta smelt to inhabit the oligohaline to freshwater portion of the estuary for much of the year until late winter and early spring, when many migrate upstream to spawn (Sommer et al. 2011a). There is evidence that some may not migrate to spawn. After hatching, their larvae and post-larvae subsequently migrate downstream in spring towards the brackish portion of the estuary (Dege and Brown 2004).

The primary objective of this paper is to synthesize the available information about the habitat of delta smelt and to provide insight into how potential future ecosystem changes will affect the species. Although there are multiple definitions of habitat, we have chosen to consider delta smelt habitat as the physical, chemical, and biological factors in the aquatic environment of this species (Hayes et al. 1996). We assume that the maintenance of appropriate habitat quality is essential to the long-term resilience of the delta smelt population (Rose 2000; Peterson 2003). *We emphasize that this does not mean that our study assumes that habitat is the primary driver of the delta smelt population.* To the contrary, there is substantial evidence that delta smelt are controlled by a complex set of multiple interacting factors such as habitat, food, predation, entrainment, and stock (Sommer et al. 2007; Baxter et al. 2010; Mac Nally et al. 2010). Therefore, it should not be assumed that providing good habitat conditions now or in the future will guarantee delta smelt success. Nonetheless, habitat not only directly affects the species of interest (delta smelt), but also affects other population drivers including "top-down" and "bottom-up" effects. As such, it provides a starting point for evaluating the ecological status of the species and potential restoration options.

A key point in evaluating delta smelt habitat is that it needs to be considered in two different ways. First, it can be considered in a geographical context based on fixed regions that seem to be important, such as the west Delta, Suisun Bay, and Cache Slough Complex (Merz et al. 2011). Because delta smelt are strongly associated with distinct salinity ranges (Dege and Brown 2004; Feyrer et al. 2007; Kimmerer et al. 2009), its habitat must also be considered as constantly shifting in position along the tidal axis of the Estuary. We focused on the following major questions:

1. What are the basic physical, chemical and biological habitat requirements for delta smelt?
2. What geographic areas currently provide these conditions?
3. Given factors such as climate change, which geographic areas and habitat features will improve the survival chances of delta smelt in the future?

Hence, our analysis identified key considerations for large-scale restoration efforts being evaluated under programs such as the Bay Delta Conservation Plan (BDCP) and recent Biological Opinions (USFWS 2008).

Our focus is on the habitat of delta smelt, not a general update and synthesis of life history and biology as has been provided by others (Moyle 2002; Bennett 2005). Although some agency reports have examined delta smelt habitat (Nobriga and Herbold 2009; Baxter et al. 2010), there are no detailed syntheses of this topic in the peer-reviewed literature. We focus on the direct habitat needs of delta smelt, but do not specifically address the role of subsidies from habitats that this fish does not occupy (e.g. tule marsh contributions to the smelt food web). Our goal was to provide a basis for generating testable hypotheses to inform future restoration and research projects. Given the rarity of delta smelt and associated constraints on their field collection, we also hoped that our analyses of existing data would help to set priorities for future studies.

METHODS AND MATERIALS

Assessing the habitat needs of delta smelt is especially challenging because the fish is very small (usually <100 mm FL), fragile, increasingly rare, and has a protected legal status (Moyle 2002; Bennett 2005). A related issue is that the estuary is vast and spatially complex, with multiple tributaries, embayments, and braided channels (Figure 1). High turbidity levels in the estuary present major challenges to direct observations of habitat use. We relied on a combination of published literature, data analyses from long- and short-term fisheries surveys, and the expert opinion of colleagues to synthesize the available information on habitat. We acknowledge that each of the fish surveys that we examined was designed primarily to measure fish abundance and distribution, and often for species other than delta smelt, so conclusions about smelt habitat use may be affected by the inherent bias in each method. Therefore, our approach to delta smelt has a higher uncertainty than direct observational methods; however, the information represents the best available given the many constraints.

Data Sources

Literature

We focused on peer-reviewed literature, the majority of which was from the San Francisco Estuary and about delta smelt. For topics with no journal publications, we also included some agency reports and unpublished manuscripts.

Long-term Surveys

Several long-term Interagency Ecological Program (IEP) monitoring surveys were used to generate data on delta smelt. Details about these surveys are found in Feyrer et al. (2007), Sommer et al. (2011a), and Merz et al. (2011).

Initiated in 1995, the California Department of Fish and Wildlife (CDFW) 20-mm Survey typically sampled post-larvae and juvenile fish during every neap tide between March and July (Dege and Brown 2004). In addition to the fish surveys, zooplankton tows were collected simultaneously using a Clarke–Bumpus net (0.160-mm mesh nylon cloth, outer mouth diameter of 12.5 cm, 76-cm length with a cod-end screened with 0.140-mm mesh). Volume was recorded with a General Oceanics model 2030 flow meter. Zooplankton samples were preserved in 10% formalin with Rose Bengal dye. Preserved samples were concentrated in the laboratory by pouring them through a sieve screened with 0.154-mm mesh wire, rinsed, and then reconstituted to organism densities of 200 to 400 ml^{-1}. A 1-ml subsample was then extracted and counted and identified in a Sedgewick-Rafter cell. For the purposes of this study we focused on counts of calanoid copepods, a key food source for delta smelt (Nobriga 2002; Bennett 2005).

The Summer Townet Survey (TNS) has been conducted annually by CDFW since 1959. The survey was designed to index the abundance of age-0 striped bass, but also collected data on juvenile delta smelt (Kimmerer 2002; Bennett 2005; Nobriga et al. 2008).

The CDFW Fall Midwater Trawl Survey (FMWT) sampled fishes in open-water habitats monthly, from September to December, at 116 stations throughout the northern region of the estuary (Feyrer et al. 2007; Merz et al. 2011). The survey represents one of the best long-term fishery data sets for the San Francisco Estuary and covers the majority of the range of delta smelt.

The CDFW Spring Kodiak Trawl Survey (SKT) has been conducted since 2002 to assess the distribution of adult delta smelt, while they ripen and spawn (Sommer et al. 2011a; Merz et al. 2011; *http://www.delta.dfg.ca.gov/data/skt/*). The SKT samples 39 locations from Napa River upstream through Suisun Bay and the Delta (Figure 1).

The USFWS Beach Seine Survey used a 12-m long by 1.2-m high seine to collect inshore fishes from areas generally less than 1-m deep (Brandes and McLain 2001; Merz et al. 2011). Seine hauls were conducted year-round at 57 current sampling stations from San Francisco Bay upstream to the lower Sacramento and San Joaquin rivers. Unlike most other surveys, basic substrate data was collected for this program. In addition to the core USFWS survey, we examined data from special surveys in Liberty Island, a flooded tidal wetland in the Cache Slough Complex (McLain and Castillo 2010). The surveys during August 2002-October 2004 used similar methods as the regular USFWS Beach Seine program at ten core sites located around the periphery of the lower portion of the island (Figure 2).

Short-term and Geographically-limited Studies

One of the key studies that we used to identify physical habitat used by delta smelt was the CDFW Delta Resident Fishes Survey (Brown and Michniuk 2007). This survey used an electrofishing boat to sample 200-m reaches of shoreline spread across several Delta regions. The timing of this survey has been sporadic, with sampling that collected delta smelt in 1981 to 1982, 1995 to 1997, and 2001 to 2003.

Many of the fish surveys within the range of delta smelt use trawls that require relatively large and deep channels, so there is less information about delta smelt use of smaller channels (e.g., <50 m wide). A source of data that we used to examine the smallest channels that delta smelt use was the California Department of Water Resources (CDWR) Yolo Bypass study, which included larval sampling and rotary screw trapping (Sommer et al. 2004a; Feyrer et al. 2006). This sampling occurred near the base of Yolo Bypass in a 40-m wide perennial channel.

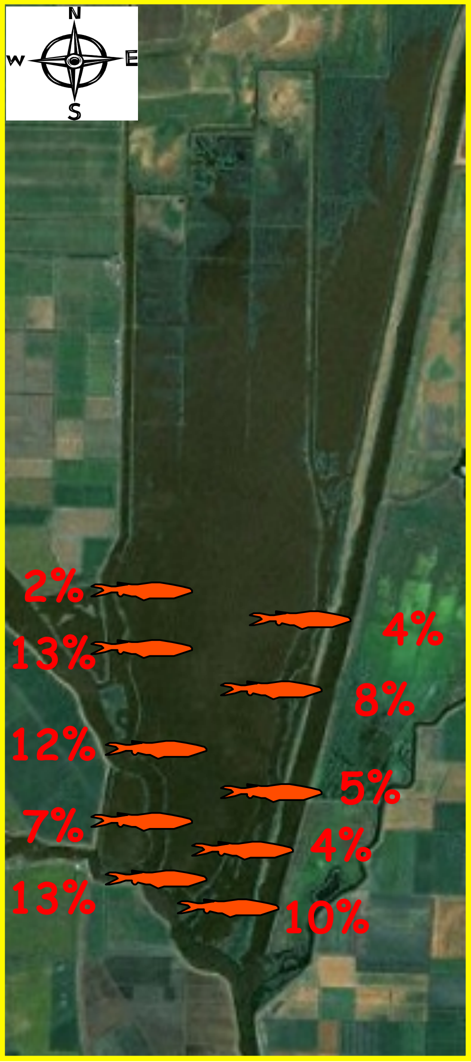

Figure 2 Locations of USFWS beach seine sampling in Liberty Island. The stations starting counter clockwise from the southeast corner of the site are: Liberty Island East #1-5 and Liberty Island #1-5. The data show the percentage of samples with delta smelt in different parts of Liberty Island based on data from August 2002 through October 2004 (n = 607 hauls).

Data Analyses

Delta smelt are a relatively rare and patchy fish, so we summarized most survey data based on presence-absence. To summarize the general locations of delta smelt habitat by life stage, we calculated the upstream and downstream distribution limits for each of the major surveys: FMWT, SKT, 20-mm, and TNS. The center of distribution was calculated for each survey (Sommer et al. 2011b). We summarized data separately for wet and dry years using all years since 1995, when all four surveys were conducted. The 'wet' and 'dry' water year classification system for the Sacramento and San Joaquin river basins was developed by the California State Water Resources Control Board (SWRCB) to provide a way to assess the amount of water originating in each basin (*http://cdec.water.ca.gov/cgi-progs/iodir_ss/wsihist*).

We calculated the percentage of samples with delta smelt present under different conditions (e.g., substrate, geographic locations) and statistically quantified differences where possible. We used a Kruskal–Wallis test to compare delta smelt habitat use in Liberty Island to data concurrently collected (2002 to 2004) from the west and north Delta, where the population is often centered (Sommer et al. 2011a; Figure 3). We used data from six west and north Delta stations (Sandy Beach SR012W; Stump Beach SR012E; Rio Vista SR014W; Brannan Island TM001N; Eddo's SJ005N; Sherman Island MS001N; Antioch Dunes SJ001S) sampled by the USFWS beach seine survey. These data were also analyzed with a Chi-square test to evaluate substrate use. Only data after 1993 were used because they included

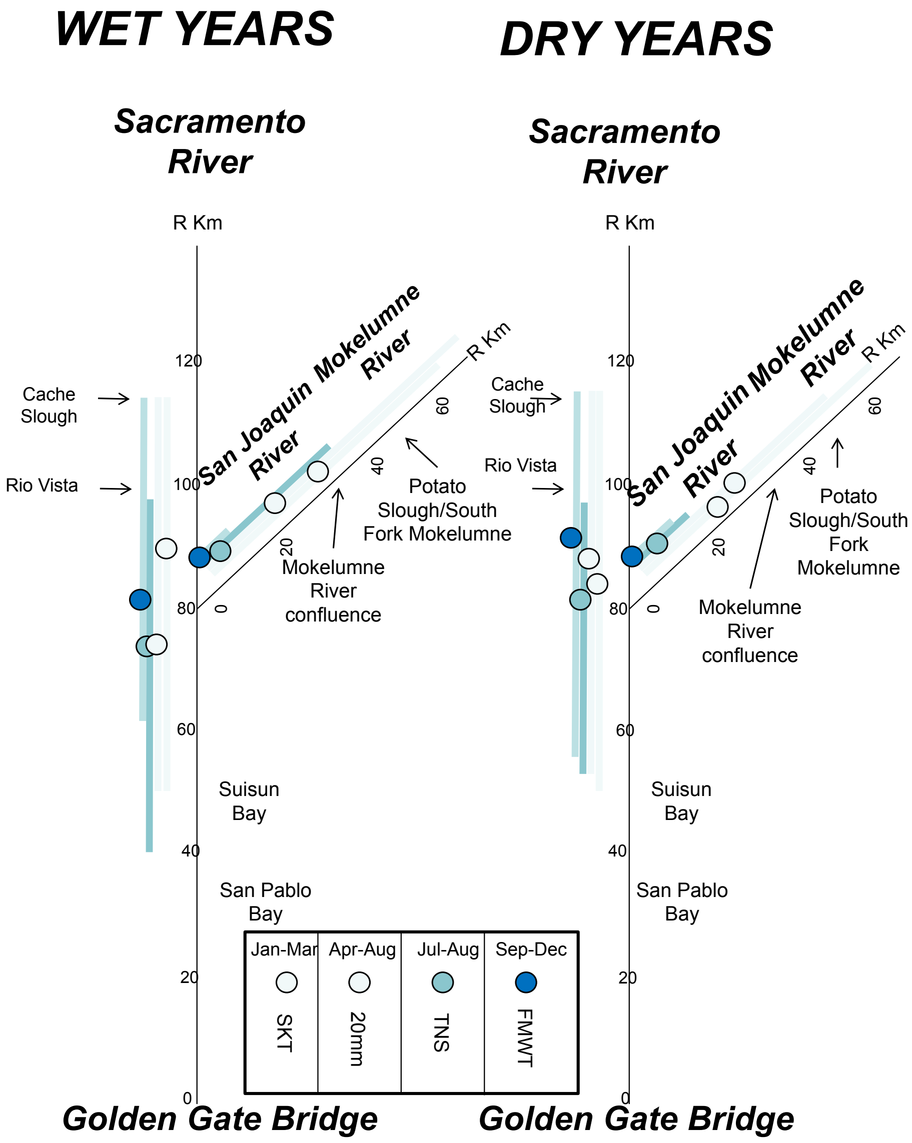

Figure 3 Summary of the extent of delta smelt habitat for four surveys: FMWT, SKT, 20 mm, and TNS. The data are for 2002 to 2010, when all surveys were conducted. The lines show the upstream and downstream limits of catch for wet (left panel) and dry (right panel) years based on the distance from the Golden Gate Bridge. The circles represent the center of distribution for each survey (see text). Note that the surveys do not include inshore habitat or locations around the periphery of the estuary (e.g., Liberty Island, upper Sacramento Deep Water Ship Channel).

substrate information (mud, pavement, vegetated, sand, and gravel).

Potential food organisms for delta smelt (20 to 60 mm) were analyzed for the 20-mm survey in the spring. We used a generalized additive model (GAMs) to examine the associations between fish occurrence, habitat variables (salinity, temperature, and turbidity) and food availability in the form of calanoid copepod density (e.g., Stoner et al. 2001; Feyrer et al. 2007; Kimmerer et al. 2009). All habitat variables and copepod density were obtained from the 20-mm survey. We used calanoid copepod density as the food availability variable in the GAM analysis because larval, post larval and juvenile delta smelt consume mostly copepods (Lott 1998; Nobriga 2002). The GAM analysis uses smoothers to describe the empirical relationships between predictors and response variables and therefore does not assume particular relationships between the two. We used the GAM function in the MGCV package of the statistical program R (R Development Core Team 2011; Wood 2011) with a logit-link function to determine whether there were significant relationships between four predictor variables (mean temperature; mean specific conductance; mean Secchi depth; and mean calanoid copepod density) and the response variable, presence of delta smelt in 20-mm samples for 1995 to 2009. The variables were tested both individually and in combination with each other. We analyzed the GAM results in two ways. First, we examined whether the smoothed results were congruent with expected responses based on laboratory tests and ecological literature. Specifically, we expected that delta smelt would show a unimodal response to temperature and salinity, a declining occurrence relatively to Secchi depth (Feyrer et al. 2007), and an increasing or saturating response to food availability (e.g., Holling 1959). Second, we assessed the statistical significance of the GAM outputs using an approximation of the ability of each variable to reduce null deviance in the models (Venables and Ripley 1997; Feyrer et al. 2007).

DELTA SMELT HABITAT: A SYNTHESIS

Basic Habitat Requirements

Overall, delta smelt occur in a relatively wide range of habitats (Table 1). They occur in regions that

Table 1 Habitat types in which delta smelt have been collected. As noted in the text, historical observations do not ensure that newly created habitats will support delta smelt.

Region	Habitat	Present	Comments	Sources
Marine *Examples:* Lower Napa River, San Pablo Bay	Bay	a	Generally only during high flow events	Bennett (2005); Hobbs et al. (2007); Merz et al. (2011); CDFW Bay Study and Townet Survey
	Channel	a		
	Marsh	b	Collections adjacent to Napa marshes	
Brackish *Examples:* Suisun Bay, West Delta	Bay	c	Core habitat	Moyle et al. (1992); Aasen (1999); Bennett (2005); Feyrer et al. (2007); Dege and Brown (2004); Sommer et al. (2011a); Merz et al. (2011); UCD Suisun Marsh Survey (unpublished).
	Channel	c	Core habitat	
	Marsh	b	Collections adjacent to Suisun Marsh	
Freshwater *Examples:* Sacramento River, Cache Slough, Sacramento Deep Water Ship Channel	Non-tidal	a	Rare, highly seasonal	Aasen (1999); Grimaldo et al. (2004); Nobriga et al. (2005); Sommer et al. (2011a); Merz et al. (2011); CDFW fall midwater and Kodiak trawls; USFWS juvenile salmon and Liberty surveys (unpublished); this paper.
	Tidal channel	c	Primarily North Delta	
	Littoral	c	Primarily North Delta	
	Emergent marsh	?	Little sampling	
	SAV	a	Collections adjacent to SAV	

a = rare; b =periodic, c = common

range from freshwater to brackish areas, and in habitats that include bay, channel, and adjacent marsh habitat. The following provides details about the basic habitat requirements of delta smelt. All conclusions based on literature sources are indicated by citations. New analyses that we conducted are provided with data summaries including tables and figures.

Salinity

Salinity is generally considered a key defining variable for estuaries, so understanding salinity requirements is essential in describing the habitat of estuarine organisms. More so than any other delta smelt habitat variable, salinity has been the subject of intense research and debate. Higher flow levels shift the salt field downstream, as commonly represented by the spatial metric X2, the distance of the 2 psu salinity isohaline from the Golden Gate Bridge (Jassby et al. 1995; Kimmerer 2002). There are no consistent long-term trends in the salinity of the upper Estuary for most months (Jassby et al. 1995; Enright and Culberson 2010); however, there have been salinity increases during fall (Feyrer et al. 2007), when the issue has become most controversial.

Most delta smelt reside the majority of their lives in or near the low-salinity zone, typically <6 psu or <10,000 µS/cm (Feyrer et al. 2007; 2010; Kimmerer et al. 2009). Our GAM results for the 20-mm survey showed a similar pattern (Figure 4; Table 2). The distribution of delta smelt is affected by salinity at all life stages. For example, Dege and Brown (2004) found that the center of distribution of larval and post-larval delta smelt during spring was determined by the location of the salt field as indexed by X2, with a more downstream distribution during wetter years. Similarly, Sommer et al. (2011a) found that the center of distribution of older delta smelt was consistently associated with the location of the salt field (X2) during all months. This does not mean that all smelt are confined to a narrow salinity range because fish occur from fresh water to relatively high salinities (see below).

The effects of salinity on habitat area vary seasonally and therefore by life stage. Kimmerer et al. (2009) found that X2 had a negative association with delta smelt habitat area (i.e. higher flow = more downstream position of X2 and more area appropriate for delta smelt) for all surveys analyzed, but the effect was strongest in spring and summer. They suggest that earlier life stages were more responsive to salinity changes because they tend to occupy fresher water than older delta smelt. Despite a clear effect of estuarine salinity on habitat area, Kimmerer et al. (2009) did not observe strong effects on abundance. Feyrer et al. (2011) also found a negative effect of X2 on habitat area during the fall. Feyrer et al. (2007) report a long-term decrease in habitat area based on the combined effects of salinity and turbidity (as indexed by Secchi depth), and a weak effect of fall conditions on juvenile production the following summer. The significance of these results has been the source of intense debate as part of legal challenges to the USFWS (2008) Biological Opinion for delta smelt, which included new requirements to change X2 to a more downstream position during the fall of wet years.

Tides and Flow

Despite some rare exceptions, the habitat of delta smelt is focused entirely in the tidal zone. There have been occasional collections of delta smelt upstream of the tidal zone north of Sacramento during the winter and spring spawning season (USFWS Juvenile Salmon Survey, unpublished data). It is not known if delta smelt can survive in areas without consistent tidal flows as may be the case for some areas in the future with sea level rise (see below).

Our analyses showed that delta smelt currently are found from small channels such as the Yolo Bypass Toe Drain, where tidal flows are periodically less than ±4 m^3 sec^{-1} during months when smelt are present (Lisbon Gauge, Department of Water Resources, unpublished data), to large channels with stronger tides, such as Chipps Island, where representative summer tidal flows are ±9,400 m^3 sec^{-1} (DWR 1993). It is highly likely that delta smelt use some form of tidal surfing to change their location in the estuary (Swanson et al. 1998; Sommer et al. 2011a). Bennett et al. (2002) provide evidence that young longfin smelt (*Spirinchus thaleichthys*) use tidal surfing to maintain their position in the estuary, so it may be reasonable to assume that a close relative like delta smelt does the same. Sommer et al. (2011a) used a particle tracking model to show that apparent upstream migration rates of adult smelt were consistent with simulations based on a simple tidal surfing behavior.

Velocity

The relative importance of water velocity for pelagic fishes such as delta smelt is challenging to interpret because of the complex and shifting tidal environment in the upper estuary. Even without a clear understanding of the relevance of positive (ebb tide) and negative velocities (flood tide) to delta smelt, it is reasonable to assume that delta smelt respond to covariates of velocity such as turbulence.

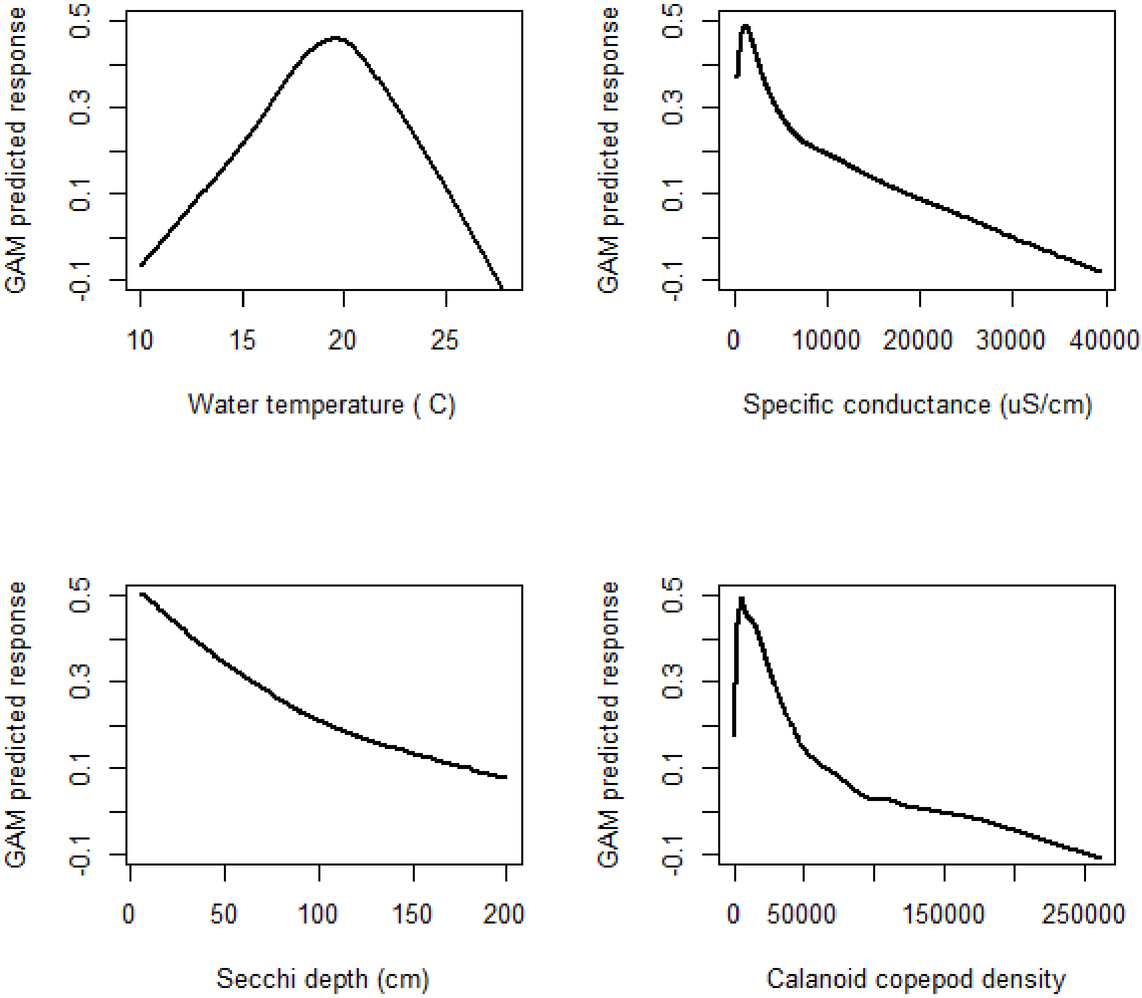

Figure 4 Generalized additive (GAM) model predictions of delta smelt occurrence in the 20-mm Survey (based on all four habitat variables) versus the habitat variables for: **(A)** water temperature; **(B)** specific conductivity; **(C)** Secchi depth; and **(D)** calanoid copepod density. We used a logit-link function to establish the relationship between the mean of the GAM predicted response (probability of delta smelt occurrence) and the smoothed function of the four explanatory variables. Predicted probability of delta smelt occurrence is highest near 20 °C, and low specific conductance, but declines with Secchi depth. Predicted response for calanoid copepod density is contradictory to expectations.

Table 2 Generalized additive modeling (GAM) delta smelt results for the 20-mm Survey including temperature (T), specific conductance (C), Secchi depth (S), and calanoid copepod density (F) based on 4,297 observations. The variances in each model were all statistically significant ($P < 0.00001$) based on approximate Chi square tests.

Model	Residual deviance (percentage of total)
T	5,158 (7.1)
T + C	4,876 (12.2)
T + C + S	4,640 (16.4)
T + C + S + F	4,514 (18.7)

The effects of water velocity on delta smelt are understood primarily from laboratory studies. Swanson et al. (1998) showed that maturing delta smelt probably can swim for long periods at rates of 1 to 2 body lengths sec^{-1}, representing about 6 to 12 cm sec^{-1}. Critical swimming velocities were around 28 cm sec^{-1}. These rates were comparable or somewhat lower than similar-sized fishes for the same temperature range.

Turbidity

Key progress in our understanding of delta smelt is that they are strongly associated with turbid water (Feyrer et al. 2007). Their results showed that, during fall, delta smelt are only present at locations where Secchi depth is less than 1 meter. This finding is consistent with Grimaldo et al. (2009a), who found that delta smelt were not present in upstream areas when turbidities were less than about 12 NTU. Our GAM analyses of the 20-mm data set also showed that delta smelt post-larvae are strongly associated with lower Secchi depths (Figure 4; Table 2).

One potential function of turbidity is predator avoidance (Gregory and Levings 1998): turbidity may help delta smelt avoid visual predators (Baskerville-Bridges et al. 2004; Feyrer et al. 2007; Nobriga and Herbold 2009). Light apparently plays a role in feeding ecology as laboratory studies show that delta smelt consumption of prey is low in clear water (Mager 1996; Baskerville-Bridges et al. 2004). It is possible that turbidity helps create a contrasting background for planktivorous fish to locate their prey (Utne-Palm 2002; Horppila et al. 2004).

One of the most disturbing long-term changes in habitat for delta smelt has been the increase in water clarity in the upper Estuary (Jassby et al. 2002; Wright and Schoellhamer 2004; Feyrer et al. 2007). Modeling by Schoellhamer (2011) suggests that there has been a sudden recent (1999) increase in water clarity as the sediment balance shifted to a much lower supply. In contrast to other habitat variables such as salinity, the trend in turbidity is not driven by hydrology (Jassby et al. 2002). As noted in Baxter et al. (2010), the primary mechanisms suggested to explain the increasing water clarity are (1) reduced sediment supply due to dams in the watershed (Wright and Schoellhamer 2004); (2) major flood events (e.g., 1982 to 1983) that washed out large amounts of sediment (Baxter et al. 2010); and, (3) biological filtering by submerged aquatic vegetation (Brown and Michniuk 2007; Hestir et al., in review). Whatever the mechanisms, this change appears to have had a serious effect on habitat quality for delta smelt during both summer (Nobriga et al. 2008) and fall (Feyrer et al. 2007).

Temperature

Upper temperature limits for delta smelt habitat have been relatively well-studied in both the laboratory and using field data. Interpretation of the laboratory results is somewhat complicated because temperature limits can be affected by various factors including acclimation temperature, salinity and feeding status. The general pattern is that delta smelt cannot tolerate temperatures higher than 25 °C (Swanson et al. 2000), a level that is highly consistent with field collections of young smelt (Nobriga et al. 2008) and our GAM results for the 20-mm data set (Figure 4; Table 2). Hence, the 25 °C is used as a general guideline to assess the upper limits for delta smelt habitat (Wagner et al. 2011; Cloern et al. 2011).

The lower limit to water temperature has not yet been evaluated in detail. However, Bennett and Burau (2010) analyzed the occurrence of adult delta smelt in the SKT based on three water quality variables. Their preliminary results suggest that delta smelt are rare below about 7 °C. Note, however, that temperatures below 10 °C are uncommon in the estuary (Kimmerer 2004; Nobriga and Herbold 2009).

Depth

Like velocity, the relevance of depth to a pelagic fish in a tidal estuary is open to debate. Landscape variables such as depth are, nonetheless, clearly important features that define tidal dynamics such as velocities, excursion, and frequency of inundation. Unfortunately, depth is not recorded for many of the pelagic trawls in the upper estuary, making it difficult to evaluate this variable. Some data are available for littoral surveys, but delta smelt catch is generally too low for a rigorous statistical analysis. Though generally regarded as a pelagic fish (Moyle 2002), delta smelt are clearly caught in shoal and shallow areas such as Suisun Bay and Liberty Island (Moyle et al. 1992; Nobriga et al. 2005; Sommer et al. 2011a). Aasen (1999) found that juvenile smelt densities can be higher in shoal areas than adjacent channels. However, delta smelt use of shallow areas apparently varies with tide (Aasen 1999) and they probably do not substantially use intertidal areas (Matt Nobriga, USFWS, unpublished data). There does not appear to be an obvious maximum depth for delta smelt because the fish are commonly captured along the Sacramento Deep Water Ship Channel (Grimaldo et al., in prep; CDFW SKT), which has most of the deepest habitat in the upper estuary.

Channel Size

Most data have been collected in large channels, making it difficult to evaluate what types of channels delta smelt prefer. Channel width itself is probably not a constraint; instead, related habitat features such as tidal excursion, velocity, temperature, food, and turbidity are likely to influence channel use. The FMWT and TNS surveys found that delta smelt were common in some of the largest channels available in the Estuary, including Cache Slough, (200- to 280-m wide) and the Sacramento Deep Water Ship Channel (170- to 200-m wide).

The lower limit to channel size for delta smelt has not been addressed, but our review suggests that the fish can occur in relatively small channels. Examples in the Delta include a 45-m wide perennial channel of the Yolo Bypass, where adult and larval stages seasonally were collected there in many years (Sommer et al. 2004a), and Miner Slough a 45- to 50-m wide (20-mm station 726) with regular catches of delta smelt larvae. Downstream of the Delta, the smallest channel where adults and juveniles have been reported is Spring Branch Slough in Suisun Marsh, which averages about 15-m wide (Meng et al. 1994; Matern et al. 2002).

Food

Even if physical and chemical requirements are met, delta smelt will not survive if habitat does not contain enough food to support basic metabolic needs. The food source of larval and post-larval delta smelt is fairly specialized, relying primarily on calanoid copepods such as *Eurytemora affinis* and *Pseudodiaptomus forbesi* (Nobriga 2002; Moyle 2002). These copepods also comprise a major part of the diets of sub-adults and adults, although older life stages have a more general diet that includes mysids, cladocerans, and gammarid amphipods (Moyle et al. 1992; Moyle 2002; Slater 2012). There has been a long-term decline in copepods and mysids in the upper estuary (Winder and Jassby 2011), which may account partially for the reduction in the mean size of delta smelt in fall (Sweetnam 1999; Bennett 2005). Overall, food limitation remains a major stressor on delta smelt (Baxter et al. 2010). The importance of food limitation is supported by Kimmerer (2008), who showed that delta smelt survival from summer to fall is correlated with biomass of copepods in the core range of delta smelt. These relationships have led to the recognition that food availability should be included in life cycle models of delta smelt (Maunder and Deriso 2011).

There is evidence of substantial spatial and temporal variation in copepods in the estuary. The most extensive database for zooplankton of the upper estuary is the IEP's Environmental Monitoring Program (EMP) (*http://www.water.ca.gov/iep/activities/emp.cfm*), which includes stations in Suisun Bay, Suisun Marsh, and the west and south Delta. *P. forbesi* and *E. affinis* both frequently show their highest densities in the south Delta and Suisun Marsh (Hennessy 2009; Anke Mueller-Solger, unpublished data). *P. forbesi* is most abundant during summer to fall, while *E. affinis* largely disappears from the EMP sites in summer and fall.

From a restoration perspective, one of the more important recent findings has been that food resources are often more abundant around the periphery of the upper Estuary. In the brackish zone, the smaller channels of Suisun Marsh frequently show relatively high levels of chlorophyll *a* and copepods (Schroeter 2008; Anke Mueller–Solger, Delta Science Program, unpublished data). Similarly, studies by Benigno et al. (in review) show that the channels of the Cache Slough Complex consistently have higher chlorophyll *a* levels than Delta EMP stations. The data suggest that calanoid copepod levels in Cache Slough Complex channels– compared to other parts of the Delta—may be enhanced during key months for delta smelt. Longer residence times are likely a major contributing factor to increased food web production in these regions (Lucas et al. 2009).

Food thresholds for delta smelt have not yet been established, although our GAM analyses provide some insights for spring. Our GAM results of the 20-mm data set suggested that temperature, salinity, Secchi depth, and calanoid copepod density were all significantly associated with occurrence of young delta smelt (Table 2; Figure 4). However, the smoothed GAM results for calanoid copepods (Figure 4) did not follow the expected increasing or saturating responses. Instead, the smoothed response suggested a counter-intuitive decline in delta smelt probability of occurrence at high calanoid copepod densities. Adding calanoid copepods to the model explained only a small additional amount of deviance (2%) compared to models with just the three physical variables (Table 2). Our results, therefore, suggest that calanoid copepod density was not a meaningful predictor of young delta smelt in the 20-mm survey. This does not mean that food is unimportant to young delta smelt; rather, the data may not be at a sufficient scale to detect associations or that other limiting factors may be more deterministic.

Substrate

Most fish surveys in the upper estuary do not record substrate, making it difficult to evaluate the importance of this variable to delta smelt. The relevance of substrate in the deep channel habitat is questionable, since young smelt are typically in the middle or upper portion of the water column, particularly during day time (Rockriver 2004; Grimaldo et al., in review). Nonetheless, substrate may be relevant when delta smelt venture into littoral areas. Delta smelt catches are typically quite low in areas inshore from the current surveys, making it hard to analyze the data in any rigorous way.

The best available data about substrate use are from the USFWS beach seine survey (Table 3). The results of our analyses suggest at least modest differences between observed and expected habitat use (Chi square = 29.15; df = 3; $p < 0.001$). We found that delta smelt were never collected in vegetation, despite 183 samples in such habitats. Habitat use was also much lower than expected at paved locations (boat ramps), but somewhat higher than expected over gravel, mud, and sand. The CDFW Resident Fishes Survey included substrate information with catch results in shallow waters (Brown and Michniuk 2007). Although this survey did not catch enough delta smelt to warrant statistical analysis, they were observed over all substrates sampled, included riprap, mud, and sand. Our summary of the 1981 to 1982 data found that delta smelt were collected in 5% of 360 samples over the following substrates: riprap 41% of fish; mud bank 59% of fish. Sampling effort was much greater in later years (5,645 samples); however, we found that delta smelt were collected in only 0.4% of samples. These fish were collected over rip-rap (38%), mud bank (47.6%), and sand beach (14.3%).

In general, our analyses suggest that delta smelt do not have particularly strong substrate preferences, which is not surprising given their niche as a pelagic fish. Nonetheless, substrate may be an important issue during spawning. The substrate preferences of delta smelt are not known; however, many other smelts are known to favor sandy substrate for spawning (Bennett 2005). This substrate is relatively common in inshore areas of the west Delta (e.g. Sherman

Table 3 Substrate use by delta smelt as sampled by six core USFWS beach seine stations in the west Delta since 1993 (see text for details). The Chi-square analysis[a] excluded vegetated substrate because it included no catch, which violates the assumption of that test.

Substrate	Samples with delta smelt	Total samples (effort)
Gravel	6	338
Mud	39	2,483
Pavement	6	2,508
Sand	116	6,945
Vegetation	0	183

a Chi square = 29.15, df = 3, $p<0.001$ (excluding vegetation)

Island) and north Delta (e.g., Liberty Island and the Sacramento Deep Water Ship Channel).

Other Water Quality Factors

Brooks et al. (2011) recently summarized the current state of knowledge about the effects of water quality problems, including contaminants, on delta smelt and other pelagic fishes. The evidence to date indicates that although acute contaminant toxicity is not a likely cause for the population declines, sublethal stress from multiple factors—including metals, nutrient-rich effluents, toxic algal blooms, and pesticides—all degrade the habitat of delta smelt. For example, sublethal contaminant exposure can impair immune function and swimming ability (Connon et al. 2011). Delta smelt distribution is known to overlap with several key contaminants (e.g., Kuivila and Moon 2004; Brooks et al. 2011) and the effects can be substantial, depending on the level of exposure (Connon et al. 2009).

The highest-profile water quality issue has been inputs of ammonium to the Delta, primarily from municipal discharges (Wilkerson et al. 2006; Dugdale et al. 2007; Glibert 2010; Glibert et al. 2011). The largest source of ammonium to the system is the Sacramento Regional Wastewater Treatment Plant (Jassby 2008). There is no evidence yet of direct effects on delta smelt, but there are concerns about food web effects based on the finding that phytoplankton growth may at times be inhibited by high ammonium concentrations (Wilkerson et al. 2006, Dugdale et al. 2007; Glibert 2010; Glibert et al. 2011). High ammonium concentrations could directly reduce primary productivity and alter phytoplankton species composition, which may in turn affect the zooplankton assemblages that delta smelt rely upon (Glibert et al. 2011).

Another emerging and related concern for delta smelt is that there are periodic blooms of the toxic blue-green alga *Microcystis aeruginosa* during late summer, most commonly August and September (Lehman et al. 2005). These blooms typically occur in the San Joaquin River away from the core summer distribution of delta smelt (Figure 3), but some overlap is apparent. Results by Lehman et al. (2010a) indicate a strong likelihood that delta smelt are exposed to microcystins, which may in turn affect their habitat use (Baxter et al. 2010). Laboratory studies demonstrate that the blue-green alga is toxic to another native fish of the region, Sacramento splittail *Pogonichthys macrolepidotus* (Acuna et al. 2012). Indirect effects are also a major concern because *Microcystis* blooms are toxic to the primary food resources of delta smelt (Ger et al. 2009, 2010a, 2010b).

Pesticide effects are less well understood, although effects may be substantial given that agricultural, commercial, and urban purchases of pesticides within the Delta and the upstream watershed averaged 21 million kg annually from 1990 to 2007 (Brooks et al. 2011). Intermittent toxicity has been reported for *Ceriodaphnia dubia*, an invertebrate surrogate for Delta prey species (Werner et al. 2000) and *Hyalella azteca*, a common invertebrate bioassay species (Weston and Lydy 2010; Werner et al. 2010).

GEOGRAPHICAL RANGE OF HABITAT

A common misconception is that delta smelt habitat only occurs in the Delta. The monitoring data indicate that the center of distribution for the population commonly occurs in the Delta during spring (Dege and Brown 2004) and fall (Sommer et al. 2011a). However, the overall distribution of delta smelt habitat is much broader. To illustrate this point, we summarized survey data for different seasons and water year types by life stage (Figure 3). The surveys do not necessarily capture the extremes of distribution, but provide a general idea of distribution and habitat shifts among years. Our analysis showed that delta smelt habitat is often located well downstream of the Delta, commonly in Suisun Bay. Their habitat also varies substantially by life stage and water year. The habitat tends to be most landward (upstream) for adults (SKT survey) and most seaward for the other life stages (20 mm, TNS, and FMWT). Our results are generally consistent with the smelt distribution summaries reported by Merz et al. (2011). Based on the strong association of younger life stages with salinity (Dege and Brown 2004; Sommer et al. 2011a), our analysis suggested, as expected, that their habitat shifted landward in drier years (Figure 3).

After delta smelt were listed in the early 1990s, one of the most surprising initial discoveries was their presence in the Napa River, a tributary to San Pablo Bay (Figure 1; Merz et al. 2011). Delta smelt are generally caught in wet years (Figure 3): that they can periodically use this down-estuary habitat is significant. Hobbs et al. (2007) found that use of habitat in this region results in a unique chemical signature in the otoliths of delta smelt and revealed that the portion of fish that use the Napa River can be substantial (e.g., 16% to 18% of population in 1999).

Another key finding was that delta smelt heavily use the Cache Slough Complex (Sommer et al. 2011a; Merz et al. 2011). To illustrate the importance of this region delta smelt occurred year-round in Liberty Island (Sommer et al. 2011a, Figure 5) and were present in all stations sampled during 2002 to 2004 beach seine surveys (Figure 2). Similarly, expanded efforts of the 20-mm, TNS and FMWT surveys into the Sacramento Deep Water Ship Channel found delta smelt from June through October (Baxter et al. 2010). The frequency of occurrence in Liberty Island habitats was comparable to USFWS beach seine stations located in core delta smelt Delta habitat during 2002 to 2004 (Figure 6). These findings were relatively unexpected because the general assumption at the time was that delta smelt leave the north Delta after the larval stage (Sommer et al. 2011a). Moreover, flooded islands were generally considered poor-quality habitat for delta smelt in other parts of the Delta because of high predator abundance and the prevalence of aquatic weeds (e.g., Grimaldo et al. 2004; Nobriga et al. 2005). Liberty Island and the Cache Slough Complex may be attractive to delta smelt because of its high diversity of habitats including multiple channel sizes, broad shoals, tidal marsh, and dead-end sloughs (Lehman et al. 2010b; McLain and Castillo 2010; Morgan–King and Schoellhamer 2013). By comparison, most of the Delta is comprised of relatively large rip-rapped channels and weedy flooded islands. Key physical processes in Liberty Island and the Cache Slough Complex include wind-resuspension of sediments that generate higher turbidities than other parts of the Delta (Morgan–King and Schoellhamer 2013), and channels and shoals with long residence times that help generate relatively high levels of phytoplankton and zooplankton (Lehman et al. 2010b; Nelson et al. 2011; Benigno et al., in review).

Although the Napa River and Cache Slough Complex studies provide some cause for optimism regarding the status and extent of delta smelt habitat, it is important to note one of the most troubling changes over the past four decades, the loss of parts of the Delta as year-round habitat for delta smelt. Two studies (Nobriga et al. 2008; Sommer et al. 2011a) note that historical data show many delta smelt remained in the southern portion of the Delta throughout the summer. Though delta smelt still seasonally occur in the southern Delta during winter and spring (Figure 3; Sommer et al. 2011a), they are now absent in summer. Nobriga et al. (2008) suggest that this results from major habitat changes, including the proliferation of aquatic weeds and associated declines in turbidity.

THE FUTURE OF DELTA SMELT HABITAT

There is widespread consensus among scientists that the upper San Francisco Estuary will change drastically in the future because of sea level rise, altered hydrology, and rising temperatures (Knowles 2010; Cloern et al. 2011). Studies by Mount and Twiss (2005) predict a high probability of massive levee failure in the foreseeable future, which will radically

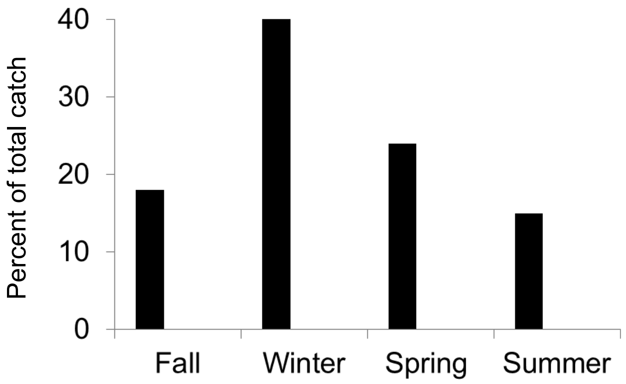

Figure 5 Distribution of catch of delta smelt across seasons in Liberty Island based on USFWS beach seine data from August 2002 through October 2004 (n = 93 fish)

change the salinity distribution along with the types and locations of different habitats (Lund et al. 2007; Moyle 2008). As a consequence, it is especially challenging to use observations on current delta smelt habitat to predict future changes. Model predictions based on future flow conditions through the present landscape are discouraging, suggesting reduced area of low-salinity habitat as soon as 50 years in the future (Feyrer et al. 2011) and increases in the number of lethal temperature days along with decreases in turbidities within 100 years (Wagner et al. 2011; Cloern et al. 2011). At the same time, major biological community changes are inevitable, as are very different physical and chemical regimes (Lund et al. 2007; Cloern et al. 2011). These issues raise the question of whether delta smelt will be able to persist as climate change combines with the effects of current and future changes in land use and water management. At the very least, the analyses show that current habitat conditions are not sustainable (Lund et al. 2007), making it critical to begin planning for ways to react to long-term changes.

MANAGEMENT IMPLICATIONS

Available information suggests a high degree of uncertainty about many aspects of delta smelt habitat (e.g., Brown 2003). This is expected given their low numbers, patchy distribution, the difficulty in directly measuring their habitat use in a highly variable and turbid environment, and the paucity of studies designed specifically to evaluate their habitat needs. Moreover, the data only address delta smelt presence, not how different habitats may affect key processes, such as individual or population growth rates. This does not mean, however, that there is insufficient information

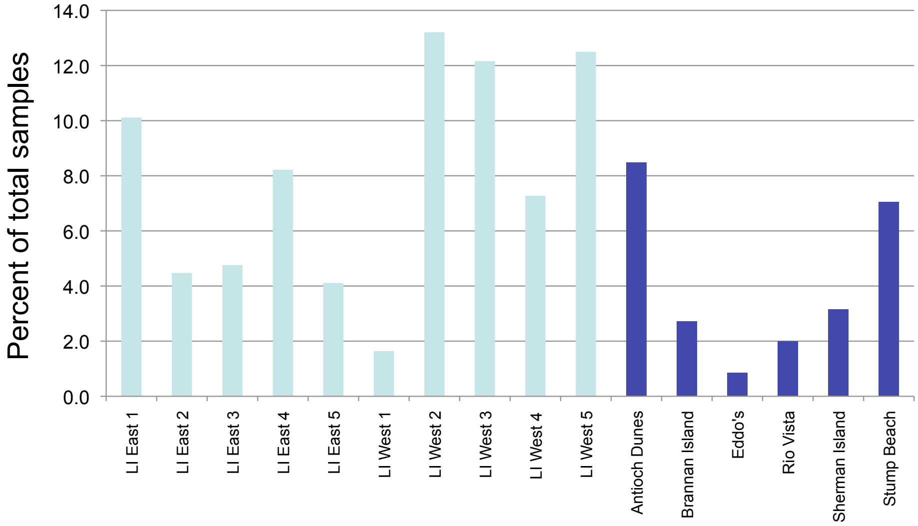

Figure 6 Percentage of beach seine samples with delta smelt in different parts of Liberty Island (ten "LI" stations) as compared to five core west and north Delta sites. Analyses are based on USFWS beach seine sampling in these locations during August 2002 through October 2004. Figure 2 shows the locations of the Liberty Island stations. The differences between the Liberty Island and core Delta stations were not significantly different based on a Kruskal–Wallis test (*p* = 0.065).

to examine some delta smelt habitat management issues. Some basic ideas are provided below. A major part of the problem is that habitat often is not the only factor that controls fish abundance, which is likely the case for delta smelt (Sommer et al. 2007; Mac Nally et al. 2008; Baxter et al. 2010). Note that we do not specifically address how much habitat would be required to generate a measurable increase in the population of delta smelt. Such analyses are notoriously difficult and uncertain, even for better-studied fishes such as salmonids (Roni et al. 2010).

We Know Enough to Attempt Some Large-scale Habitat Projects

The status of delta smelt is so dire that we cannot simply hope that the species will be able to recover without several different types of active management. The salinity, turbidity, temperature, and food requirements outlined here provide a basic description of some of the most important habitat features, and the large unintentional flooding of Liberty Island and subsequent colonization by delta smelt suggests that there is some potential to expand and improve the habitat of this imperiled species.

It therefore seems prudent to proceed with one or more large scale projects provided that there is an intensive field monitoring and adaptive management process.

Since much of the delta smelt habitat restoration activities described in programs such as BDCP and recent Biological Opinions (USFWS 2008) will likely occur in Suisun Marsh and the north Delta, we propose that new habitat projects try to emulate key aspects of these regions. Based on our analyses, some general suggestions are provided in Table 4. Note that habitat features are not intended as the only design criteria for this species. A given project will fail if the constructed habitat is subject to periodic water quality issues such as low dissolved oxygen, pesticide inputs, and toxic algal blooms, or high levels of predators and invasive species. In general, maintaining high levels of hydrologic and structural variability and complexity has been suggested as a key approach to promote native fishes (Moyle et al. 2010).

Habitat Restoration is Highly Vulnerable to Several Factors

In addition to the climate change effects noted above, there are many other factors than can undermine the value of habitat for delta smelt. Of primary concern is the effect of alien species, given the high level of invasions in the estuary (Cohen and Carlton 1998; Winder and Jassby 2011). SAV such as *Egeria* can quickly colonize shallow areas of the Delta (Brown and Michniuk 2007), covering shallow open-water areas that provide part of the habitat for delta smelt. A notable example is Decker Island, where a restoration project was constructed next to a known “hot spot” for delta smelt, yet *Egeria* rapidly choked the small dendritic channels. SAV is especially attractive to invasive predators (Grimaldo et al. 2004; Brown and Michniuk 2007) that likely create mortality risks for delta smelt. However, SAV is not necessary for predator colonization; recently-created open water areas such as Liberty Island now support large numbers of striped bass and inland silverside, both of which are potential predators of delta smelt (Bennett 1995; Moyle 2002; Loboschefsky et al. 2012). In addition, it is possible that new habitat projects may be subject to harmful algal blooms or localized runoff problems. Careful restoration site selection and design coupled with intensive monitoring will be needed to minimize these risks.

Bet-hedging is Critical

Our review of the habitat needs of delta smelt reveals greater diversity in habitat use than previously thought, evident in multiple migration pathways (Sommer et al. 2011a) and occurrence in both higher and lower salinities than expected. Indeed, otolith research by Hobbs (2010) suggests that the range of life histories includes freshwater spawning/freshwater rearing, freshwater spawning/brackish rearing, and brackish spawning/brackish rearing with multiple variations in the specific timing. A sensible approach in habitat restoration efforts for the entire population is to adopt a “bet hedging” strategy including multiple habitat types in multiple geographic areas. This is critical given the projection for future climate change (Wagner et al. 2011; Cloern et al. 2011), the vulnerability of the Delta to floods and earthquakes (Mount and Twiss 2005; Moyle 2008), and likely future changes in development and water use.

Processes May be More Important Than Specific Habitat Features

Habitat restoration projects typically try to maximize the specific features that the target species prefers (Darby and Sear 2008). Obviously, this is a key first step because a fish such as delta smelt cannot colonize a habitat unless its basic environmental needs are met. Unfortunately, excessive emphasis on the few well-understood habitat features can result in over-engineering of habitats, something that may not be justified given the high level of uncertainty about the future of the Delta. We propose that an increased emphasis on processes may be more successful than the construction of well-engineered "gardens." Key processes include sustainability and food web subsidies across habitats.

To be sustainable, habitats need to be designed to accommodate anticipated changes and natural variability that will occur over the next century and beyond. Key changes include a declining sediment load (Wright and Schoellhamer 2004), which will strongly affect accretion and degradation rates of delta habitats, and sea level rise, which is expected to eventually submerge many lower-elevation sites. Careful selection of restoration sites to progressively accommodate sea level rise is therefore a high prior-

Table 4 Suggested habitat features for pilot delta smelt restoration projects. See text for details.

Habitat Feature	Comments	Citations
Low salinities • Typically <6 psu	The best-studied variable that defines the habitat of delta smelt.	Bennett (2005) Feyrer et al. (2007) Kimmerer et al. (2009)
Moderate temperatures • 7 °C to 25 °C	The upper temperature limits appear consistent for laboratory and field studies, but tolerance is strongly affected by food availability and acclimation conditions. Lower limits have not been studied in detail, but stress from very low temperatures is likely.	Swanson et al. (2000) Bennett (2005) Nobriga et al. (2008) Bennett and Burau (2010)
High turbidity • >12 NTU	Regions with shoal habitat and high wind re-suspension may help maintain high turbidities.	Feyrer et al. (2007) Grimaldo et al. (2009a)
Sand-dominated substrate	Evidence from other osmerids indicates sand may be useful as spawning substrate.	Bennett (2005)
At least moderately tidal	Delta smelt are only rarely observed outside tidal areas.	This paper.
High copepod densities	Delta smelt survival appears to be linked to higher levels of calanoid copepods in the low salinity zone.	Nobriga (2002) Moyle (2002) Kimmerer (2008b)
Low SAV	The absence of delta smelt in most SAV sampling indicates that submerged vegetation degrades habitat value.	This paper. Grimaldo et al. (2004) Nobriga et al. (2005)
Low *Microcystis*	The absence of delta smelt in areas with periodic Microcystis levels indicates that these blooms degrade habitat values.	Baxter et al. (2010) Lehman et al. (2010) This paper.
Open water habitat adjacent to long residence time habitat *(e.g., low-order channels; tidal marsh)*	This concept has not been tested statistically, but the frequent occurrence of delta smelt in these habitats suggests that it may be important.	Aasen (1999) This paper.

ity. The declining sediment load is more problematic, but locating restoration sites in areas with relatively higher sedimentation or re-suspension rates may help to maintain turbidity levels (Morgan–King and Schoellhamer 2013).

Although most of the carbon inputs to the delta smelt food web appear to be from riverine sources (Jassby and Cloern 2000; Kimmerer 2004), there is a growing ecological recognition that there may be substantial localized inputs from adjacent habitats such as Yolo Bypass (Schemel et al. 2004; Sommer et al. 2004b), Liberty Island (Lehman et al. 2010b), and tidal marshes (Howe and Simenstad 2011). SAV habitat, in contrast, shows evidence of being trophically decoupled from pelagic food webs (Grimaldo et al. 2009b). In general, phytoplankton and zooplankton levels are higher in small channels that are surrounded by dense emergent vegetation in Suisun Marsh (Rob Schroeter, U.C. Davis, unpublished data). This may be more a function of longer water residence time in these low-order channels, but marsh subsidies are also likely. In any case, it seems wise to consider habitat projects in locations where trophic subsidies are most likely (Jassby and Cloern 2000).

Several Key Studies are Needed

Delta smelt habitat restoration will not succeed without high levels of monitoring and research. Moreover, these types of studies are needed immediately to learn how delta smelt use existing habitat, and to evaluate project success and improve restoration strategies and designs. We have learned quite a bit about the basic needs of delta smelt from long-term monitoring and laboratory studies, but we expect that much more information would be gained from efforts designed specifically to assess habitat use. For example, stratified randomized sampling methods are a more statistically defensible way to assess habitat use than fixed stations and can be customized to evaluate habitat types and features not covered by the existing monitoring network. Such surveys would be a useful supplement to the existing long term monitoring conducted in the estuary. Initial efforts should focus on locations such as Suisun Marsh and the Cache Slough Complex: two major target areas for restoration and the current "hot spots" for delta smelt at several life stages.

An ongoing issue in the study of delta smelt habitat has been that this listed species is rare and fragile, so "take" is a concern. This means that we are unlikely to be able to greatly increase traditional collecting efforts in areas where delta smelt are common. A major priority is, therefore, the development of non-lethal sampling methods such as improved telemetry and marking and imaging techniques. One promising method is the use of underwater cameras. Currently studies are investigating the use of a towed net fitted with a camera at its (open) cod end (Baxter et al. 2010; Feyrer et al., in press). The camera and associated image-processing software were successfully used in fall 2011 and 2012 to identify and record delta smelt in several locations of the low salinity zone. Such methods may allow much more intensive sampling of different habitats without incurring high mortality. Better use of samples from the existing and future monitoring programs using novel approaches such as otolith microchemistry may provide additional insight into delta smelt habitat use and migration patterns (Hobbs et al. 2007; Hobbs 2010).

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