SAN FRANCISCO ESTUARY & WATERSHED SCIENCE
Sponsored by the Delta Stewardship Council and UC Davis Institute of the Environment

RESEARCH

Thermal Stress and Suitability for Aquatic Species in the San Francisco Estuary

Catarina Pien[1,2], Rosemary Hartman[2], Eva Bush[3], Peggy W. Lehman[2], Brittany E. Davis[2]

ABSTRACT

Increases in water temperature caused by climate change will challenge the management of water and species in the San Francisco Estuary. Our goals were to describe spatial and seasonal patterns in water temperature across the upper estuary, and evaluate how temperature stress and suitability vary across the aquatic ecosystem. We synthesized 10 years of continuous water-temperature data at 75 stations across six regions of the estuary between 2010 and 2019. We identified stressful temperature thresholds for species of interest using published physiological limits and observed distributions, including Endangered Species Act-listed native fishes (e.g., osmerids, salmonids), native fishes (e.g., cyprinids), non-native species (e.g., centrarchids, bivalves), and nuisance species such as invasive aquatic vegetation, and harmful cyanobacteria. We then quantified thermal stress across varying spatial and temporal scales and metrics. Analyses indicated there were detectable regional temperature differences, and that Suisun Bay was the only region to provide regular thermal refuge during the warmer parts of the year, though portions of the confluence and Suisun Marsh also provided potential thermal refuge during summer/fall and during cooler parts of the day. Meanwhile, the Central and South Delta experienced the warmest temperatures, exceeding thresholds for listed species throughout summer and early fall. We found that listed species such as juvenile salmonids and osmerids experience more thermal stress across a number of metrics. Fishes with higher heat tolerance (including non-natives and select natives), aquatic vegetation, and *Microcystis* (a harmful cyanobacteria) had the lowest average number of thermal stress days. This study demonstrates that the estuary is already exhibiting stressful conditions for species of concern, and thermal stress will only increase with climate change. We identify at what times of year and where the estuary may provide refuge from thermal stress conditions across a variety of species, which has important implications for restoration prioritization, design, and species management.

SFEWS Volume 23 | Issue 2 | Article 3
https://doi.org/10.15447/sfews.2025v23iss2art3

Corresponding author: *cpien@usbr.gov*

1 US Bureau of Reclamation
Bay–Delta Office, Region 10
Sacramento, CA 95814 USA

2 California Department of Water Resources
Division of Integrated Science and Engineering
West Sacramento, CA 95691 USA

3 Delta Stewardship Council
Delta Science Program
Sacramento, CA 95814 USA

KEY WORDS

water temperature, estuary, thermal stress, habitat suitability, climate change, refugia, Sacramento–San Joaquin Delta, long-term monitoring, fish

INTRODUCTION

The San Francisco Estuary (estuary), including the Sacramento–San Joaquin Delta (Delta), Suisun Bay, and Suisun Marsh, has been experiencing the effects of global climate change for at least the past 40 years. Each of the past 4 decades has been successively warmer than all previous decades, and the 2010s have been the warmest decade on record (Cloern et al. 2010; Goss et al. 2020; IPCC 2021). Climate change models predict a continuation of these trends, with mean temperature increases of 2 to 4 °C over the next century (Dettinger et al. 2016; Knowles et al. 2018; Pierce et al. 2018), more precipitation falling as rain instead of snow (Dettinger et al. 2016), increased precipitation variability (Swain et al. 2018), increased extreme precipitation (Polade et al. 2017; He 2022), and increased saltwater intrusion from a combination of reduced freshwater outflow and sea level rise (Dettinger et al. 2016; Polade et al. 2017; Knowles et al. 2018; Pierce et al. 2018; Swain et al. 2018; Ghalambor et al. 2021).

The effect of climate change on estuaries is of worldwide concern because estuaries provide key ecosystem services, including nursery habitat for fisheries, buffering development from storms, carbon sequestration, transportation, and recreation (Barbier et al. 2011). However, estuaries are also frequently highly developed, and thus already threatened by human actions in addition to climate change. A 12-year monitoring study of 166 estuaries in Australia showed an increase in temperature and acidification rate over that time-span, with the rates of both parameters an order of magnitude higher than those predicted by the Intergovernmental Panel on Climate Change (IPCC) (Scanes et al. 2020). The changes observed are significantly more extreme than the predictions from global models, which indicates a need for regional-scale estuarine models (Collins et al. 2012; Knowles et al. 2018; Scanes et al. 2020). Analysis of expected and potential effects on estuaries in Australia, the United Kingdom, and Chesapeake Bay found wide-ranging effects on species from the locally predicted changes in precipitation, water temperature and chemistry, salinity, flow, primary productivity, turbidity, and geomorphology (Gillanders et al. 2011; Robins et al. 2016).

Within the estuary, measured water temperature varies considerably by region (Bashevkin, Mahardja, et al. 2022). While water temperature is controlled primarily by air temperature (Vroom et al. 2017), precipitation and resulting inflow interact with air temperature to influence seasonal and spatial water-temperature patterns in the system (Bashevkin and Mahardja 2022; Bashevkin, Mahardja, et al. 2022). As with estuaries worldwide, climate change will increase temperatures in the estuary, and local models have projected up to a 4 °C increase in annual mean water temperature between 2020 and 2099, with greater increases in temperature predicted during the summer than the winter (He 2022).

The estuary is home to many native fish species, including several that are listed as threatened or endangered under the state or federal Endangered Species Acts (ESAs; (hearafter “listed species”; CDFW 2025). How water temperature affects these species on a regional scale is important for identifying climate-change refugia and potential conservation actions for such listed species. This idea has been applied to many cold-water stream systems across the US, where restoration of riparian vegetation, bank structure, and flows has been targeted to preserve habitat for sensitive fish species (Kurylyk et al. 2015; Ebersole et al. 2020), but has rarely been evaluated in estuaries. To enhance our understanding of ecological interactions and implications for water temperature, we examined spatial and seasonal water-temperature trends in relation to a number of listed and unlisted species that focused on (1) resource management (e.g., state or federally listed endangered or threatened species), (2) species that may negatively affect management-relevant species (e.g., non-native predators and competitors, benthic invertebrates that affect the lower trophic food web, aquatic vegetation, which may negatively affect habitat, and toxic cyanobacteria), and (3) less-studied native fishes.

Listed fishes in the estuary including Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), spring-run and winter-run Chinook Salmon (*Oncorhynchus tshawytscha*), and Green Sturgeon (*Acipenser medirostris*) are particularly sensitive to warm water temperature (Mayfield and Cech 2004; Komoroske et al. 2014; Jeffries et al. 2016; Zillig et al. 2021). Each species has a limited temperature optimum (the temperature range for optimal performance) such that increasing water temperature may increase chronic temperature stress and decrease health, growth, and/or reproductive fitness (Fangue et al. 2020). Negative changes in physiological and behavioral performance can affect growth, survival, and recruitment; and limit or exclude native species from the estuary (Jeffries et al. 2016; Lewis et al. 2021; Herbold et al. 2022). For example, an analysis of the spawning window of the endangered Delta Smelt predicted that under most climate-change scenarios, they may no longer be able to reproduce in the estuary (Brown et al. 2016; Hobbs et al. 2019), though an alternative model found their spawning window may expand, but shift earlier in the year (Huntsman et al. 2024). Warming water temperature increases stressful days for juveniles and initiates earlier spawning, which would decrease the maturation window and also likely negatively affect fitness (Brown et al. 2016). Therefore, to focus conservation and habitat-restoration efforts, it is important to identify when and where thermally suitable habitats occur for native species of concern.

To better understand how warming temperatures may affect aquatic species, here we use continuous (real-time) water-temperature data and literature on fish physiology and field detections to address the three study objectives:

1. Describe the inter-annual and seasonal variation in water temperature in the estuary between 2010 and 2019 and determine whether spatial differences were detectable
2.
    a. Determine species' thermal sensitivities based on cited literature and field data
    b. Evaluate how thermal stress varies by species and ESA-listed vs. non-listed status
3. Assess what parts of the estuary may provide thermal refuge at different temporal scales

We combined records from continuous temperature probes from the past 10 years with data on the thermal sensitivity of aquatic organisms to assess how future warming will affect the Delta ecosystem. First, we examined how temperature has varied temporally over the previous decade and how temperature varies regionally across the Delta. Next, we conducted a literature review to describe thermal sensitivities of native and non-native fishes, invertebrates, and primary producers. We then combined thermal sensitivity data to establish thresholds for each taxon and examine how habitat suitability and thermal stress is likely to vary spatially and through time as the climate continues to warm.

Resource managers rely on the use of temperature thresholds and habitat-suitability models to assess risk to listed species, make decisions for real-time water operations, and inform potential locations for habitat improvements via restoration or flow augmentations. This information will help guide the management and conservation measures needed to lessen how stressful thermal conditions affect species as a result of continued drought periods and climate change.

MATERIALS AND METHODS

Study Area

The study was conducted in the upper estuary, including the Sacramento–San Joaquin Delta (Delta), Suisun Bay, and Suisun Marsh. The Delta is a tidal inland delta with fresh to brackish water in the Central Valley of California. The Sacramento River provides freshwater from the north, while the San Joaquin River provides freshwater from the south. From the Delta, water flows into Suisun Bay and Suisun Marsh before it enters the San Francisco Bay on its way into the Pacific Ocean. The system plays an important role in water delivery to the state of California, and, as a result, has an extensive network of environmental monitoring stations (Figure 1; Table A1).

Data Compilation, Cleaning, and Filtering

We compiled data from the California Data Exchange Center (CDEC; *https://cdec.water.ca.gov/*), which hosts non-quality-controlled, real-time water-quality data from several different monitoring programs. We downloaded all available event (15-minute) and hourly water temperature data in the estuary using the '`CDECRetrieve`' package (Rodriguez 2022). We then standardized all data to hourly data by taking the first value of each hour. The full integrated dataset and associated meta-data, including details on the sensors and data contacts, are available on the Environmental Data Initiative (EDI) (IEP et al. 2020).

We removed data that were of questionable quality based on the following criteria: (1) values outside a range of 1–40°C based on our knowledge of the system, (2) any day with fewer than 20 values (e.g., 83% of day's values), (3) any day with 18 or more repeating values (e.g., 75% of day's values), (4) outliers—defined as values outside 3 times above or below the interquartile range—on the remainder component of the seasonally decomposed dataset, and (5) values where there was greater than a 5- degree change in temperature within an hour. We selected filters based on recommendations from subject matter experts, and by visually examining data across stations to balance accuracy and the quantity of data retained. Approximately 2.8% of values were removed as a result of these steps. Additional details and code for downloading data and QA/QC are available on EDI (IEP et al. 2020). We then removed 15 stations that did not represent our study (non-contiguous stations, stations not in the estuary, some duplicate stations), and filtered to 2010–2019 because most of the stations initiated monitoring by 2010, removing 36.2% of remaining values. We then removed station-years with 275 days or fewer days per year (75% of the year) and 10 or fewer months of data per year to avoid biasing calculated summary statistics. Based on these filters, we then removed stations with fewer than 8 years of data. Approximately 26.9% of remaining data were removed as a result of these filters, with a final dataset composed of 6,149,782 values across 75 stations (Table A1; see *https://deltascience.shinyapps.io/ContinuousWaterTempQC/* for spatial representation of all stations originally considered).

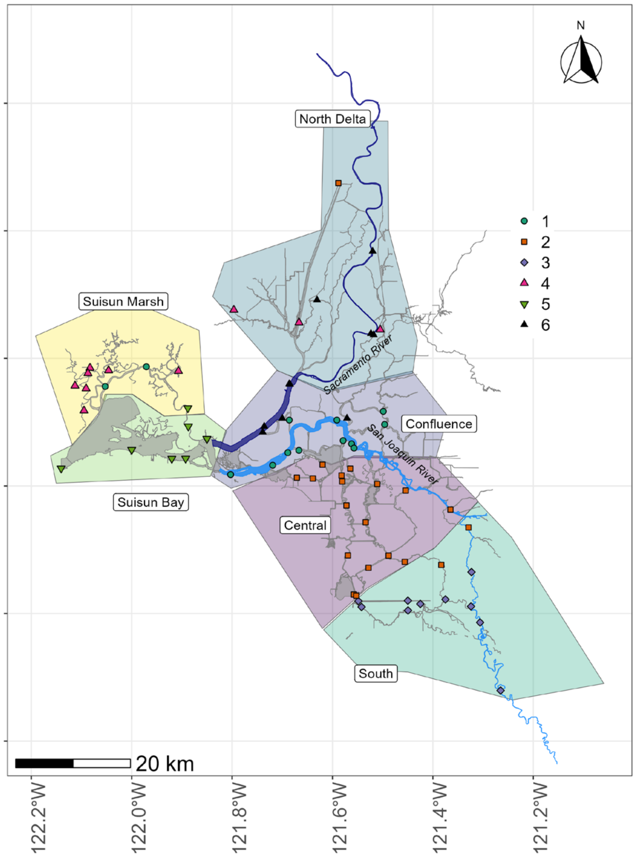

Figure 1 Map of stations and cluster assignments based on cluster analysis of daily mean temperatures. Shapes and colors of points indicate cluster assignments; polygons indicate final regions used for analyses. Regions were drawn to maximize the number of stations in a cluster within each region, but also to incorporate hydrologic landmarks, so some regions contain some stations in different clusters.

Region Assignments

To identify regions within the study area with similar thermal regimes, we calculated the daily mean temperature (T_{avg}) for each station for each day of the year over the entire time-frame of the dataset (2010 to 2019). We then used hierarchical cluster analysis on the Euclidian distance between the T_{avg} for each day of the year (function "*hclust*" in R version 4.1.1; R Core Team 2021) with Ward's minimum variance method. We based geographic regions on cluster assignments, but did adjust assignments slightly based on spatial proximity. In particular, the North Delta region included stations from three different clusters but were grouped together because the three clusters were intermixed and hydrologically connected. Similarly, the confluence region included two clusters that were mixed throughout the area (Figure 1).

Water Temperature Patterns

To address Objective 1, we used our compiled water-temperature dataset and tested for trends in average maximum (T_{max}) and minimum (T_{min}) water temperature. Recent studies have detected trends over time (Bashevkin, Mahardja, et al. 2022), and because of the limited temporal scale of our dataset and the known variability between years, we focused on looking at differences between individual years and region–season combinations. Specifically, we evaluated whether some years were warmer than others, whether some regions were warmer than others, and whether those regional patterns differed by season. To reduce temporal auto-correlation, we condensed hourly data to monthly average T_{max} and T_{min} and ran separate mixed-effects models for each, with maximum likelihood as an estimation method. We conducted analyses in R version 4.2.1 (R Development Core Team 2021). We used the '`lme4`' package to run mixed-effects models (Hothorn et al. 2008; Bates et al. 2015; Wood 2017). We included the fixed effects of water year (October 1 of calendar year-1 to September 30 of next calendar year), season, and region, with an interaction term between season and region. We also included station and month as random effects. We conducted post-hoc tests using the '`emmeans`' package, which assesses significance based on the statistical properties of the differences of the estimated marginal means (Lenth et al. 2024; see Explanations Supplement). Because of the greater number of comparisons, we included a Bonferroni correction, and we used a more conservative alpha = 0.01 to distinguish differences between pairs due to some remaining temporal auto-correlation.

$$Temp \sim WY + Season * Region + (1|Station) + (1|Month) \quad \textbf{Eq 1}$$

where

Temp = average monthly maximum or average monthly minimum water temperature (°C),

WY = water year as a factor, where WY_i = October 1_{i-1} to September 30_i

Season = season as a factor,
where wet season = October–April and dry season = May–September

Region = region as a factor, as defined by Figure 1,

Station = station as a factor, included as a random effect on the intercept (denoted by '(1|...)') to account for spatial auto-correlation

Month = month as a factor, included as a random effect on the intercept (denoted by '(1|...)').

Species Temperature Thresholds

To evaluate the biological implications of water-temperature patterns and address Objective 2a, we selected key native and non-native fishes, invertebrates, and primary producers relevant to the estuary. We then conducted a literature review of available temperature thresholds, and summarized long-term field survey data to develop a single integrated table of temperature thresholds. We define different temperature threshold terms in Table 1.

Details of species' upper-temperature thresholds developed for the current study (e.g., species,

Table 1 Description of abbreviated terms used to describe habitat temperatures, and species temperature thresholds for sub-optimum and tolerance exceedance

Term	Description
T_{max}	Maximum daily water temperature
T_{avg}	Average daily water temperature
T_{tol}	Tolerance temperature threshold for species
T_{sopt}	Sub-optimal temperature threshold for species
E_{tol}	Annual daily tolerance exceedance; number of days/yr that $T_{max} > T_{tol}$
E_{sopt}	Annual daily sub-optimum exceedance; number of days/yr that $T_{max} > T_{sopt}$
T_{mar}	Temperature margin; difference of T_{tol} and average T_{max} in a region and season

thresholds, and supporting literature) were published to a data repository (Davis et al. 2022). For each species and life stage (where possible), we included two documented or estimated temperature thresholds: sub-optimum temperature (T_{sopt}) and maximum temperature tolerance (T_{tol}). We defined T_{sopt} as the temperature value outside documented thermal optima at which physiology "turns for the worse" and performance decreases (Fangue et al. 2020). Sub-optimal temperatures are considered moderately stressful and can reduce energy diverted to growth, reproduction, and activity as a result of the increased energy demand for basic maintenance mechanisms (Sokolova et al. 2012). Temperatures both warmer and cooler than the optimum can influence mechanisms responsible for growth, survival, and recruitment (Volkoff and Rønnestad 2020; He et al. 2025); however, in this study, we focus only on T_{sopt} when temperatures are warmer than optimal, given rising temperatures in the estuary (Bashevkin, Mahardja, et al. 2022) associated with climate change and concerns of effects to native species (Herbold et al. 2022). The second species threshold, T_{tol}, we described as the upper temperature limit for survival. We used combined literature on critical thermal maxima, similar end-point measures, and mortality to assign T_{tol} thresholds; thus, we list a range of threshold values found in Table 2.

As a quality check of the T_{sopt} and T_{tol} assignments—many of which came from laboratory studies—we compared threshold values to temperatures associated with fish field detections (i.e., the field detection temperatures should not be greater than the tolerances obtained from literature). We calculated the mean, 75% quantile, and maximum water temperature at which species were detected in field surveys using data from the '`deltafish`' R package (Clark and Bashevkin 2022), which accesses an integrated dataset of nine long-term fish-monitoring surveys in the estuary from 1959 to 2021 (Bashevkin, Nguyen, et al. 2022). While some species have distinct life-stage nomenclature (e.g. salmonid alevins, fry, etc.), given variation in life-stage designations within the literature and among monitoring surveys, we standardized all species into three life stages (larvae, juveniles, adults) for consistency and generalization of analyses. We subsequently use species thresholds to inform the following analysis of heat stress in the estuary and species' sensitivity to estuary temperature (Table 2). Additional details about threshold and life-stage determinations have been published in Davis et al. (2022).

Thermal Stress and Suitability

We compared water-temperature data to species' thresholds to determine how thermal stress varied among different species and life stages (Objective 2b), and to determine which times and areas of the estuary might provide thermally suitable habitat or refuge (Objective 3). These analyses all use measured, continuous temperature data to examine data at different scales.

Regional and Seasonal Vulnerability

We calculated an average 'temperature margin' (T_{mar}) for species-life stages by season and region to indicate how close species were to experiencing temperatures above their thresholds. We first filtered seasonal and regional presence for each species–life stage of interest using fish monitoring data. We used the '`deltafish`' R package (Clark and Bashevkin 2022) to access the integrated fish dataset (Bashevkin, Nguyen, et al. 2022), plus additional fish datasets from fish salvage counts

Table 2 Species temperature thresholds summarized from the literature (as documented in Davis et al. 2022). Sub-optimum (T_{sopt}) and tolerance (T_{tol}) thresholds are reported by life stage (adult, juvenile, larvae) based on lengths estimated from the literature. For consistency with other species' life stages, early life stages of salmonids were not differentiated; juveniles start at the fry life stage. Maximum field detection temperature indicates the maximum temperature species–life stage combinations were detected by monitoring data from the estuary. NA indicates thresholds were not found in the literature. Asterisks in the Status column indicate listed species. Additional details and supporting literature for thresholds are described in "Metadata for Species Thresholds" document in Davis et al. (2022).

Taxon	Species	Assigned life stage	Status	Maximum field detection temperature (°C)	75% quantile field detection temperature (°C)	T_{sopt} range (°C)	T_{tol} range (°C)
Acipenser medirostris	Green Sturgeon	Adult	Native*	NA	NA	19	NA
Acipenser medirostris	Green Sturgeon	Juvenile	Native*	28.5	20.6	20–21	30–34
Acipenser medirostris	Green Sturgeon	Larvae	Native*	NA	NA	20–24	26–28
Acipenser transmontanus	White Sturgeon	Adult	Native*	23.6	15.8	NA	NA
Acipenser transmontanus	White Sturgeon	Juvenile	Native*	26.7	19.4	21–24	31
Acipenser transmontanus	White Sturgeon	Larvae	Native*	24.8	20	20	27–32
Arundo donax	Giant Reed EAV	Undifferentiated	Non-native	NA	NA	<24 & >30	32
Catostomus occidentalis	Sacramento Sucker	Adult	Native	32.1	20.6	20	30
Catostomus occidentalis	Sacramento Sucker	Juvenile	Native	31.8	20.3	NA	NA
Catostomus occidentalis	Sacramento Sucker	Larvae	Native	19	17.4	NA	NA
Corbicula spp. *(manilensis; fluminea)*	Asian Clams	Undifferentiated	Non-native	NA	NA	<22 & >30	37
Cottus asper	Prickly Sculpin	Adult	Native	32.1	21.7	22–24	32
Cottus asper	Prickly Sculpin	Juvenile/Larvae	Native	32.1	20.3	NA	NA
Egeria densa	Brazilian waterweed	Undifferentiated	Non-native	NA	NA	3–16 & 26–30	20–30
Eichhornia crassipes	Water Hyacinth FAV	Undifferentiated	Non-native	NA	NA	<10 & >30	34
Gasterosteus aculeatus	Three-spined Stickleback	Adult	Native	26.7	18.6	NA	26–29
Gasterosteus aculeatus	Three-spined Stickleback	Juvenile/Larvae	Native	32.1	19.5	NA	25–29
Hypomesus nipponensis	Wakasagi	Adult	Non-native	27.6	20.9	NA	NA
Hypomesus nipponensis	Wakasagi	Juvenile	Non-native	28.8	21.1	NA	29.1
Hypomesus nipponensis	Wakasagi	Larvae	Non-native	23.3	16.1	NA	NA
Hypomesus transpacificus	Delta Smelt	Adult	Native*	27.8	17.8	19–22	26.5–28.5
Hypomesus transpacificus	Delta Smelt	Juvenile	Native*	27.8	21.2	20–22	27–29
Hypomesus transpacificus	Delta Smelt	Larvae	Native*	25.5	19.9	20–23	27.6–29
Hysterocarpus traskii	Tule Perch	Adult	Native	32.1	20.8	21	34
Hysterocarpus traskii	Tule Perch	Juvenile/Larvae	Native	32.1	21.8	NA	NA
Lavinia exilicauda	Hitch	Adult	Native	29.6	21.1	29	38
Lavinia exilicauda	Hitch	Juvenile/Larvae	Native	29.6	21.8	NA	NA
Menidia spp. *(audens/beryllina)*	Mississippi Silverside	Adult	Non-native	31.8	17.8	NA	31
Menidia spp. *(audens/beryllina)*	Mississippi Silverside	Juvenile	Non-native	31.8	23.3	26	35
Menidia spp. *(audens/beryllina)*	Mississippi Silverside	Larvae	Non-native	24	22.5	25	34
Microcystis spp.	Microcystis	Undifferentiated	Non-native	NA	NA	< 19 & >25	36
Micropterus salmoides	Largemouth Bass	Adult	Non-native	29.1	20.6	NA	33–35

Table 2 continued

Taxon	Species	Assigned life stage	Status	Maximum field detection temperature (°C)	75% quantile field detection temperature (°C)	T_{sopt} range (°C)	T_{tol} range (°C)
Micropterus salmoides	Largemouth Bass	Juvenile	Non-native	31.8	24	27–29	33–40
Micropterus salmoides	Largemouth Bass	Larvae	Non-native	29.4	23.6	NA	NA
Morone saxatilis	Striped Bass	Adult	Non-native	28.3	20	24	28
Morone saxatilis	Striped Bass	Juvenile	Non-native	32.1	22.2	25	32
Morone saxatilis	Striped Bass	Larvae	Non-native	32.1	22.3	25	NA
Oncorhynchus mykiss	Steelhead/Rainbow Trout	Adult	Native*	25.6	16.7	20	25.5
Oncorhynchus mykiss	Steelhead/Rainbow Trout	Juvenile	Native*	28.3	14.4	17–21	24-29
Oncorhynchus mykiss	Steelhead/Rainbow Trout	Larvae	Native*	21.7	13.3	10–12	15–19
Oncorhynchus tshawytscha	Chinook Salmon	Adult	Native*	25.9	20.6	21	23–26
Oncorhynchus tshawytscha	Chinook Salmon	Juvenile	Native*	28.5	18.3	16–20	24–28
Oncorhynchus tshawytscha	Chinook Salmon	Larvae	Native*	21.7	11.7	13–16	16.7–29
Orthodon microlepidotus	Sacramento Blackfish	Adult	Native	27.7	20	NA	32
Orthodon microlepidotus	Sacramento Blackfish	Juvenile/Larvae	Native	31.1	22.8	24	32
Pogonichthys macrolepidotus	Sacramento Splittail	Adult	Native	32.1	19	24	29
Pogonichthys macrolepidotus	Sacramento Splittail	Juvenile	Native	32.1	21.5	21–25	28–33
Pogonichthys macrolepidotus	Sacramento Splittail	Larvae	Native	26.7	20	22–27	32
Potamocorbula amurensis	Overbite Clam	Undifferentiated	Non-native	NA	NA	<12 & > 28	NA
Potamogeton crispus	Curly-leaf Pondweed	Undifferentiated	Non-native	NA	NA	<5 & > 25	25
Ptychocheilus grandis	Sacramento Pikeminnow	Adult	Native	26.5	20	22–25	35–38
Ptychocheilus grandis	Sacramento Pikeminnow	Juvenile/Larvae	Native	31.1	20	NA	NA
Spirinchus thaleichthys	Longfin Smelt	Adult	Native*	25.6	12	15	25.6
Spirinchus thaleichthys	Longfin Smelt	Juvenile	Native*	28.3	19.3	15	26.4
Spirinchus thaleichthys	Longfin Smelt	Larvae	Native*	24	13.5	15–20	24.8

collected at the State Water Project pumping facility (*https://filelib.wildlife.ca.gov/Public/salvage/*), from the Yolo Bypass Fish Monitoring Program (IEP et al. 2022), and from CDFW Trammel Net Survey (Stompe and Hobbs 2023) to determine regional and seasonal presence of fishes. Presence of species and life stages were determined by there being >1 detection of that species–life stage combination in the given region and season during the entire duration of the dataset, based on life stage–length designations specified in Davis et al. (2022). Thus, a species–life stage classified as "present" in a region and season may not currently or commonly be present in a region where it is labeled as "present," but there is some historical precedence for its presence there. It is also important to note that cases in which species were classified as "not present," do not mean species are absent in the region, but that they were not detected in the particular surveys we used.

We calculated T_{mar} as the difference between a species' T_{tol} (lower value if there was a range of values) and the average T_{max} (average maximum daily water temperature for a given station, month, and water year averaged across season and region; Figure A2), which is an approach to add ecological relevance to fish presence. This was in contrast to previous temperature–margin models that calculated the difference between a species' tolerance and maximum field temperature measured in a single point (Deutsch et al. 2008; Davis et al. 2019). We then binned the T_{mar} values to visually assess level of vulnerability across species and life stages where possible. T_{mar} bins from most vulnerable to least vulnerable included <0 °C, 0 to 3 °C, 3 to 6 °C, and >6°C. Season was designated as follows: Winter = January–March, Spring = April–June, Summer = July–September, Fall = October–December.

Thermal Stress by Species Life Stages

We calculated the number of stressful days experienced per year based on T_{sopt} and T_{tol} thresholds for a range of species and life stages (Table 2). Species and life stages that lacked T_{sopt} and T_{tol} were not included in analyses. To reduce inflation of stressful days, for each species–life stage, water-temperature data were filtered to season–region combinations where the species–life stage was present, based on fish monitoring data. T_{sopt} and T_{tol} were compared to daily T_{max} at each station to determine whether the observed temperature was above the species threshold. To be moderately conservative with our estimates of suitability, within each region, if >30% of stations in a region were above the water temperature threshold (T_{sopt} or T_{max}) for a particular day, that entire region was considered to be above the threshold for that day. For each species–life stage, we summed days that exceeded the water temperature thresholds for the sub-optimum (E_{sopt}) or tolerance (E_{tol}) by water year and created boxplots to show the range of days exceedance across the 10 years of the dataset. We were not able to acquire both kinds of thresholds for all species of interest and life stages; hence, not all species were included in exceedance analysis, but available threshold information is provided in Table 2. If a range of thresholds were reported in the literature, we used the lower threshold value for our visualizations, and reported results for lower and upper thresholds.

Thermal Stress by Listing Status

To assess differences in E_{tol} by species ESA listing status (i.e., listed or non-listed), we filtered the datasets to the adult life stages of fishes, and repeated the model for both the upper and lower range values of T_{tol}. We did not conduct analyses for T_{sopt} because of a lack of available threshold values in the literature. We ran a mixed-effect**s** models with a binomial distribution to represent proportional data using the '`lme4`' package (Bates et al. 2015), with the fixed effect of listed status and the random effect of species:

$$p_{\mathrm{TOL}} \sim status + (1 \mid species), \qquad \textbf{Eq 2}$$

where

p_{TOL} = proportion of days per year exceeding tolerance threshold,

$status$ = ESA-listed or unlisted, and

$(1 \mid species)$ = random effect of species

We assessed residuals for assumptions of homogeneity of variance and normality. We used the '`lmerTest`' R package to assess measures of statistical significance (Kuznetsova et al. 2017).

Daily Thermal Stress by Station

We calculated, then visualized the proportion of each day that temperatures were >22 °C. While other analyses have focused on mean and maximum daily temperatures, these visualizations allow us to better understand, on multiple scales, when and where certain species may be able to recover. We were also able to note differences within a region to identify particularly warm or cool stations.

We used the continuous water-temperature dataset to calculate, for each station and day of the year between April and September, the proportion of each day that was >22 °C. We selected 22 °C to represent the T_{sopt} of Delta Smelt, which is a species for which management actions occur in the summer, when temperatures are warmest. This 22 °C also represents temperatures that are sub-optimal for Green Sturgeon, White Sturgeon, Sacramento Sucker, Prickly Sculpin, Tule Perch, *O. mykiss*, Chinook Salmon, Sacramento Splittail, Sacramento Pikeminnow, and Longfin Smelt (see T_{sopt} in Table 2). Temperatures at each station were averaged across the dataset for each calendar day. To further put the analysis in the context of warming temperatures, we also examined how potential recovery temperatures might differ between the whole dataset and warm years by comparing the same metric for the whole dataset (2010–2019) and the three warmest (2014, 2015, 2016) years in our dataset.

RESULTS

Region Assignments

After clustering stations into six thermal regimes based on T_{avg} across the year (Figure A1), we saw the thermal regimes frequently fit into geographic regions (Figure 1). Most stations in the far south of the Delta had a similar thermal regime (Cluster 3), the Central Delta also had a similar thermal regime (Cluster 2), Suisun Marsh were mostly in the same thermal regime (Cluster 4), as was Suisun Bay (Cluster 5). The lower San Joaquin River and the lower Sacramento River had two clusters interspersed (Custers 1 and 6), but were combined into a single "Confluence" region because of geographic proximity. The Cache Slough and Sacramento River in the northern Delta also had stations that represented several thermal regimes, but were combined for ease of analysis.

Water-Temperature Patterns

We ran a mixed-effects model on maximum and minimum water temperature to statistically test for variation among years, regions, and seasons. The wet years had negative anomalies of maximum daily temperatures, whereas most of the dry years had positive anomalies, with 2015 experiencing the highest anomaly (Figure 2A). We found significant differences of T_{max} and T_{min} between year, region, season, and the interaction between region and season ($P < 0.05$, Tables A2 and A3 [T_{max}], A4, and A5 [T_{min}]). Monthly average T_{max} and T_{min} in 2015 were particularly high (95% CI: 17.7 to 21.0 °C for maximum temperature; 16.4 to 20.0 °C for minimum temperature), with 2014 and 2016 following as the next hottest years (Figure 2B). For our comparison of region by wet and dry season, we found that during the dry season (May–September), the Central and South Delta experienced the highest average maximum temperatures, and Suisun Bay experienced the lowest average maximum temperatures (Figure 2C). During the wet season (October–April), we found less difference in temperature between regions (0.9 °C difference in mean in wet seasons compared with 2.3 °C difference in dry seasons). Suisun Marsh, and the South and Central Delta experienced the warmest average maximum temperatures, and the North Delta and Confluence experienced the coolest average maximum water temperatures. Trends in model results were generally similar for mean minimum water temperatures, except mean minimum temperatures in Suisun Marsh were cooler than those in Suisun Bay, reflecting the larger range that the region can experience (Figure 3A and Figure 3B; see Appendix A for additional results and model validation).

Thermal Stress and Suitability

Regional and Seasonal Vulnerability

Estimated T_{mar} varied broadly across species and life stages. Several species—particularly ESA-listed fishes—were within 3 °C of their T_{tol} or were detected in regions that exceeded their T_{tol} (Figure 4). Most species had wider T_{mar} in fall (October–December; >3 °C), and all species had wide margins in the winter (January–March; 3 to 6 °C or >6 °C). We found negative T_{mar} (i.e., habitat temperatures were warmer than species thresholds in the <0 °C category) for all life stages of Rainbow Trout/Steelhead and Chinook Salmon during spring and summer in at least some of the regions in which they were detected. Species in the 0 to 3 °C T_{mar} bin included listed salmonids and osmerids, and additional species such as Striped Bass (adult), Sacramento Splittail (juvenile), and Three-spined Stickleback. Sturgeon, Tule Perch, Sacramento Blackfish, Sacramento Sucker, Sacramento

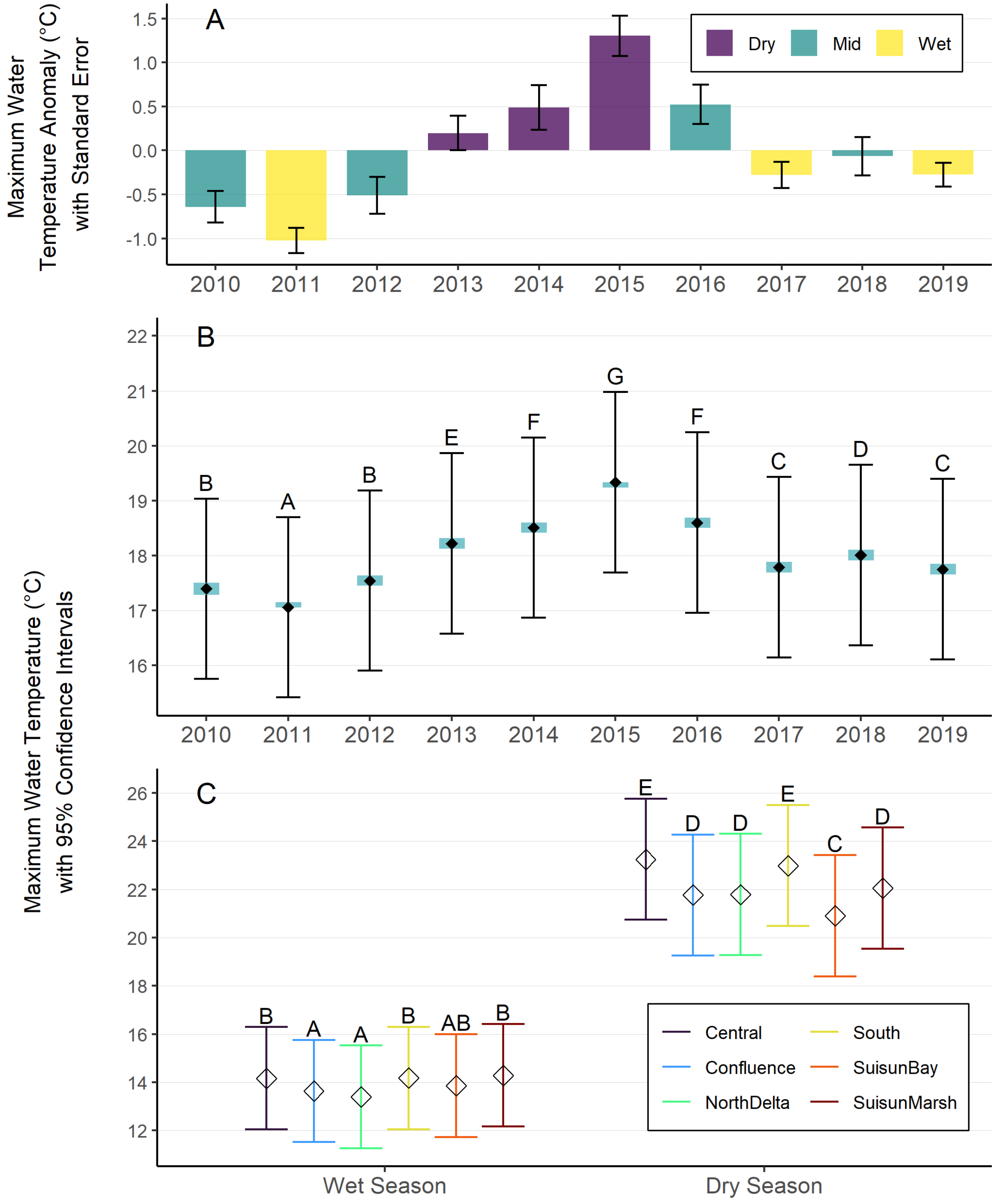

Figure 2 Trends in maximum daily water temperature (T_{max}, °C) by water year, region, and season. (**A**) Temperature anomalies calculated (from raw data) as the difference between the mean of the T_{max} across the dataset and T_{max} for a given station and date. Mean anomalies are plotted with standard errors that account for different results by region. Results are plotted by water year type. Designations of water year type are from CDEC (*https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST*), which are based on unimpaired runoff. Dry = CDEC "Critical" and "Dry" designations, Mid = CDEC "Above Normal" and "Below Normal" designations, and Wet = CDEC "Wet" designation. (**B**) Mean maximum monthly water temperature with 95% confidence intervals by water year. Results are from Equation 1. *Blue boxes* are calculations based on standard error generated by the 'emmeans,' R package, *non-overlapping boxes* indicate significantly different years, and *letters* indicate whether groups are significantly different from each other. (**C**) Mean maximum monthly water temperature with 95% confidence intervals by season and region. *Letters* indicate whether groups are significantly different from each other. Dry Season encompasses May–September; Wet Season encompasses October–April.

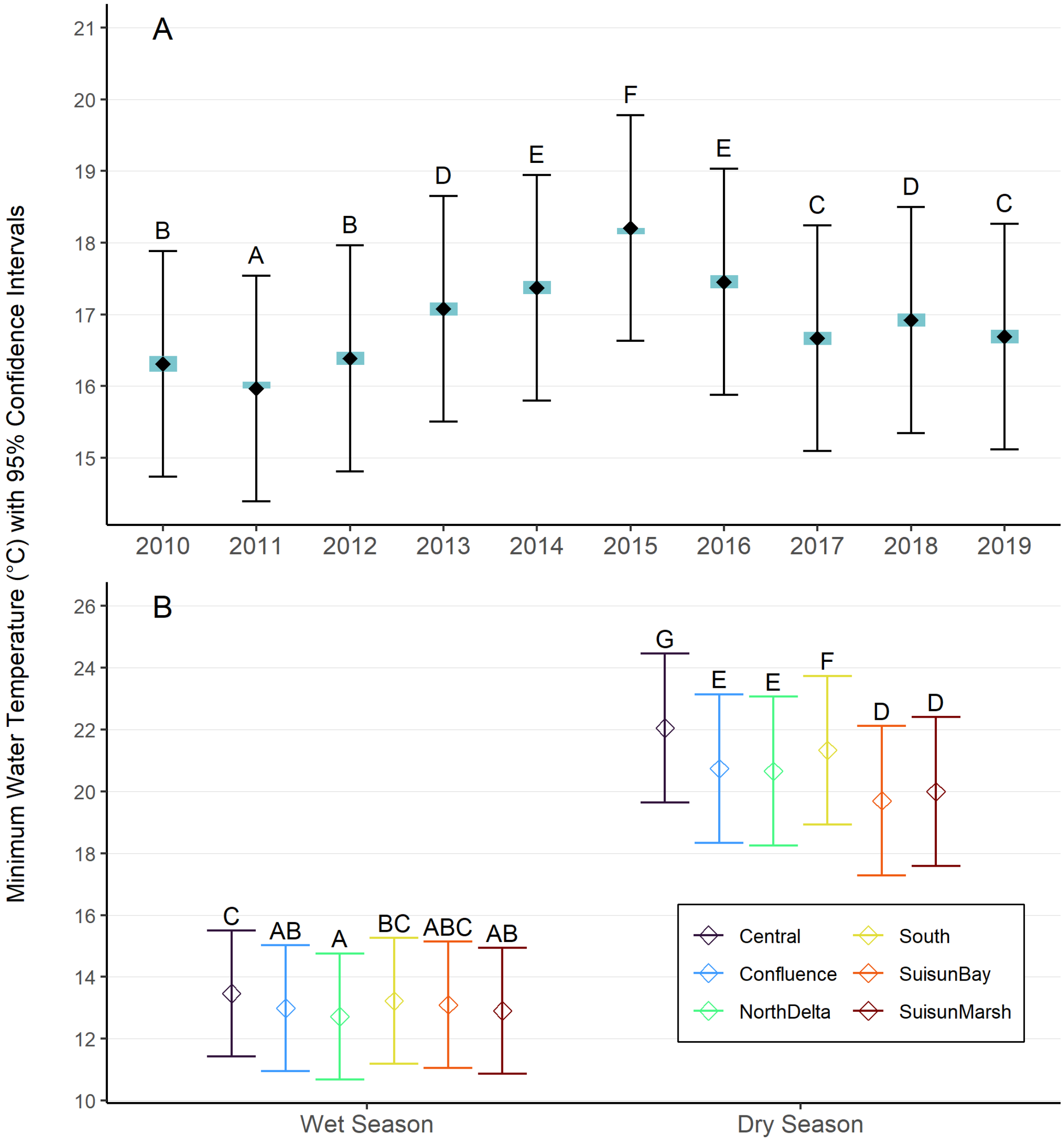

Figure 3 Trends in minimum daily water temperature (T_{min}, °C) by water year, region, and season. (**A**) Mean minimum monthly water temperature with 95% confidence intervals by water year. *Blue boxes* are calculations based on standard error generated by 'emmeans' R package, *non-overlapping boxes* indicate significantly different years, and *letters* indicate whether groups are significantly different from each other. (**B**) Mean minimum monthly water temperature with 95% confidence intervals by season and region. Dry Season encompasses May–September; Wet Season encompasses October–April.

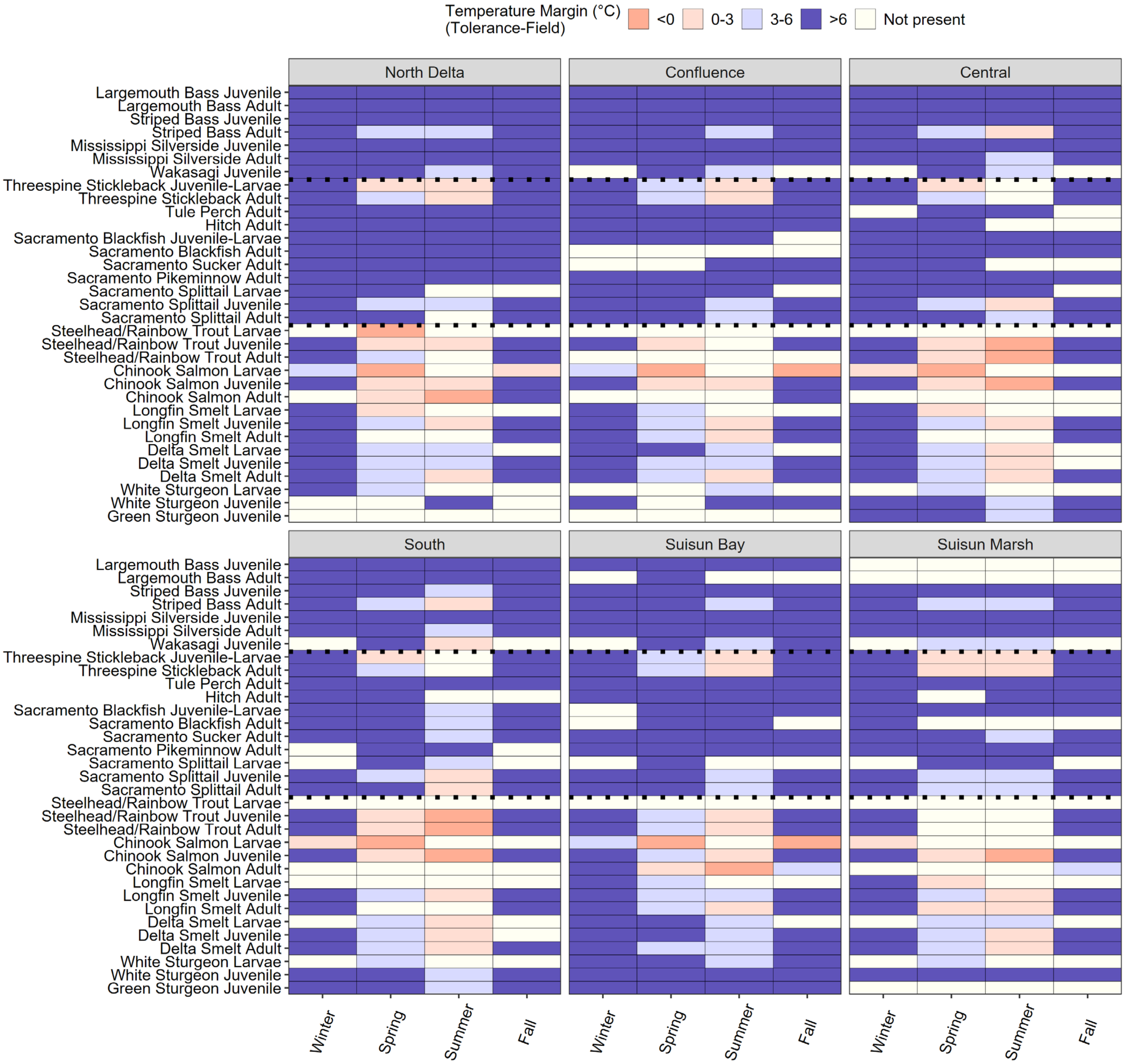

Figure 4 Heat map of temperature margins (Tmar, °C) between water years 2010 and 2019 using continuous water-temperature data. *White* indicates the species–life stage combination is not present or not detected in the monitoring dataset at a particular region–season combination, based on monitoring data and life stage–length designations from Davis et al. (2022). Species are organized from non-native fishes, to native unlisted fishes, to native listed fishes and their relatives. *Dotted lines* indicate these separations.

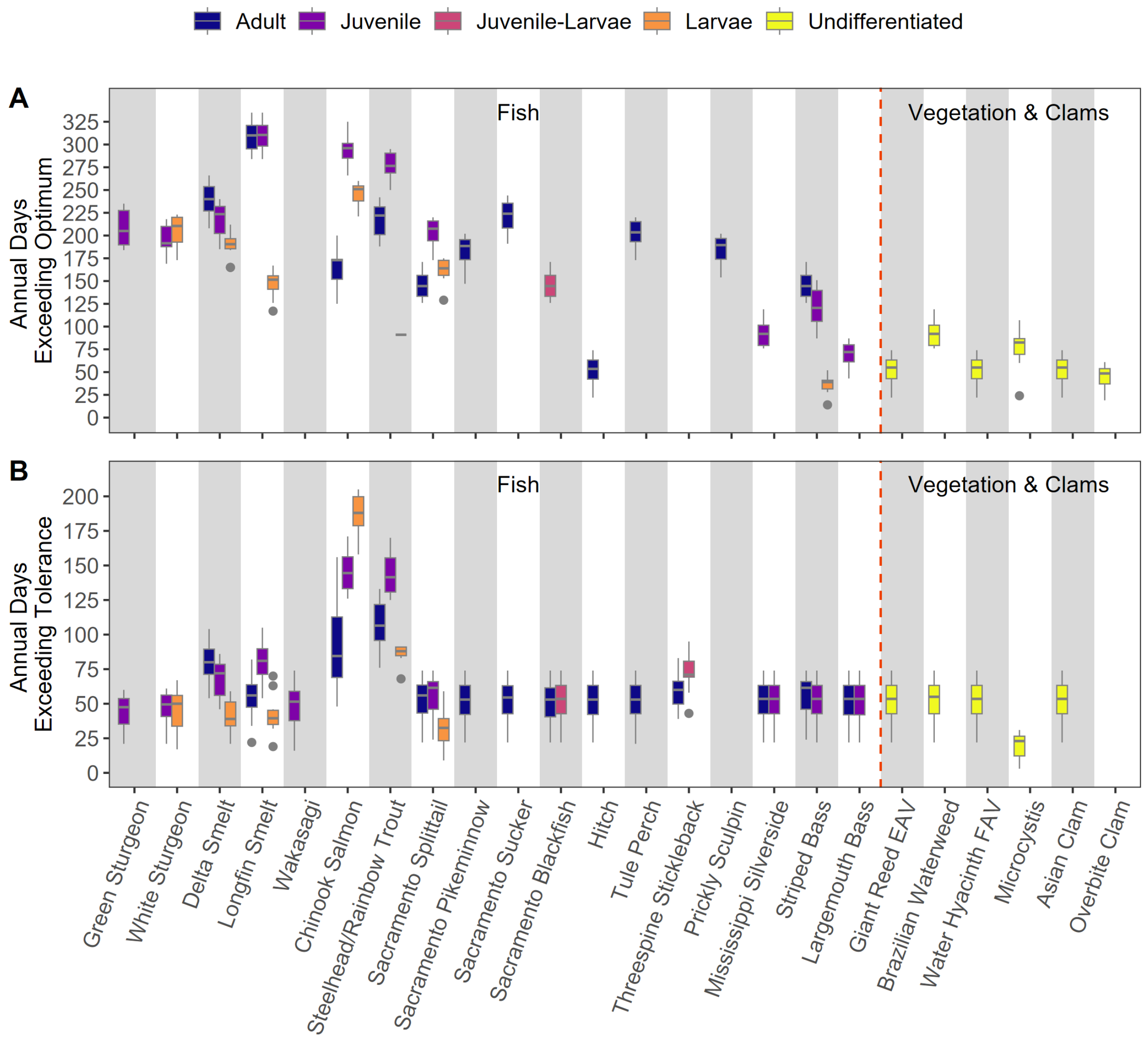

Figure 5 Boxplot of the annual number of days that water temperature exceeded heat thresholds of species and life stage between 2010 and 2019 across the entire upper estuary. *Boxplots* represent (**A**) E_{sopt} and (**B**) E_{tol}, as the sum of days per year where water temperature exceeded species T_{sopt} and T_{tol}, respectively. The number of days for some species–life stage combinations were not computed because of a lack of available threshold data. Thresholds used are listed in Table 2.

Pikeminnow, and most of the non-native fishes also had relatively wide temperature margins. The North Delta, Central Delta, and South Delta had the greatest number of species–life stage combinations in which T_{mar} was negative or in the 0 to 3 °C bin, and the Confluence and Suisun Bay had the fewest species–life stage combinations that might experience negative or small T_{mar}.

Thermal Stress by Species Life Stages

The mean number of exceedance days across all fish species and life stages between 2010 and 2019 was 138 days for E_{sopt} and 52 days for E_{tol}, based on the temperature thresholds selected from the literature (Figure 5). Many of the listed species, such as osmerids and salmonids, have lower T_{sopt} and T_{tol} relative to other species (Table 3) and thus exhibited greater vulnerability to thermal

Table 3 Mean days exceeding species sub-optimum (E_{sopt}) and tolerance (E_{tol}) thresholds by life stage. Days exceedance was calculated for the "lower" and "upper" end of the threshold, where ranges were reported. Values in parentheses represent the minimum to maximum exceedance across the 10-year dataset (water years 2010–2019) and entire upper estuary.

Species	Life stage	E_{sopt} (lower)	E_{sopt} (upper)	E_{tol} (lower)	E_{tol} (upper)
Green Sturgeon	Juvenile	208 (184–235)	188 (164–213)	45 (21–60)	44 (21–60)
White Sturgeon	Juvenile	196 (169–218)	141 (122–170)	46 (21–61)	46 (21–61)
White Sturgeon	Larvae	206 (173–223)	206 (173–223)	45 (17–67)	43 (17–66)
Giant Reed EAV	Undifferentiated	52 (22–74)	52 (22–74)	52 (22–74)	52 (22–74)
Sacramento Sucker	Adult	221 (191–244)	221 (191–244)	52 (22–74)	52 (22–74)
Asian Clam	Undifferentiated	52 (22–74)	52 (22–74)	52 (22–74)	52 (22–74)
Prickly Sculpin	Adult	185 (154–202)	147 (126–171)	NA	NA
Brazilian Waterweed	Undifferentiated	93 (76–119)	52 (22–74)	52 (22–74)	52 (22–74)
Water Hyacinth FAV	Undifferentiated	52 (22–74)	52 (22–74)	52 (22–74)	52 (22–74)
Three-spined Stickleback	Adult	NA	NA	60 (39–83)	52 (22–74)
Three-spined Stickleback	Juvenile–Larvae	NA	NA	72 (43–95)	52 (22–74)
Wakasagi	Juvenile	NA	NA	48 (16–74)	48 (16–74)
Delta Smelt	Adult	239 (208–266)	185 (154–202)	80 (54–104)	54 (22–74)
Delta Smelt	Juvenile	218 (185–240)	180 (147–201)	68 (46–86)	52 (22–74)
Delta Smelt	Larvae	190 (165–212)	146 (109–160)	41 (21–59)	34 (9–59)
Tule Perch	Adult	201 (173–220)	201 (173–220)	52 (21–74)	52 (21–74)
Hitch	Adult	51 (22–74)	51 (22–74)	51 (22–74)	51 (22–74)
Mississippi Silverside	Adult	NA	NA	52 (22–74)	52 (22–74)
Mississippi Silverside	Juvenile	93 (76–119)	93 (76–119)	52 (22–74)	52 (22–74)
Microcystis	Undifferentiated	76 (24–107)	76 (24–107)	19 (3–31)	19 (3–31)
Largemouth Bass	Adult	NA	NA	52 (22–74)	52 (22–74)
Largemouth Bass	Juvenile	69 (43–87)	53 (22–74)	52 (22–74)	52 (22–74)
Striped Bass	Adult	147 (126–171)	147 (126–171)	56 (24–74)	56 (24–74)
Striped Bass	Juvenile	121 (87–151)	121 (87–151)	52 (22–74)	52 (22–74)
Striped Bass	Larvae	36 (14–52)	36 (14–52)	NA	NA
Steelhead/Rainbow Trout	Adult	218 (188–242)	218 (188–242)	107 (76–133)	107 (76–133)
Steelhead/Rainbow Trout	Juvenile	276 (250–295)	198 (169–218)	144 (125–170)	53 (22–74)
Steelhead/Rainbow Trout	Larvae	91 (91–91)	91 (91–91)	86 (68–91)	59 (21–83)
Chinook Salmon	Adult	166 (125–200)	166 (125–200)	90 (48–156)	44 (21–64)
Chinook Salmon	Juvenile	293 (266–325)	223 (192–246)	147 (126–171)	56 (24–74)
Chinook Salmon	Larvae	246 (221–260)	198 (167–220)	186 (158–205)	51 (22–74)
Sacramento Blackfish	Adult	NA	NA	51 (22–74)	51 (22–74)
Sacramento Blackfish	Juvenile-Larvae	147 (126–171)	147 (126–171)	52 (22–74)	52 (22–74)
Sacramento Splittail	Adult	147 (126–171)	147 (126–171)	53 (22–74)	53 (22–74)
Sacramento Splittail	Juvenile	203 (173–220)	121 (87–151)	56 (24–74)	52 (22–74)
Sacramento Splittail	Larvae	162 (129–175)	50 (34–69)	33 (9–59)	33 (9–59)
Overbite Clam	Undifferentiated	44 (19–61)	44 (19–61)	NA	NA
Sacramento Pikeminnow	Adult	183 (147–202)	120 (86–150)	51 (22–74)	51 (22–74)
Longfin Smelt	Adult	309 (284–335)	309 (284–335)	55 (22–82)	55 (22–82)
Longfin Smelt	Juvenile	310 (284–335)	310 (284–335)	81 (54–105)	81 (54–105)
Longfin Smelt	Larvae	146 (117–167)	96 (73–116)	42 (19–70)	42 (19–70)

stress compared with non-native fishes and heat-tolerant native fishes. The fishes with the lowest T_{tol}—adult Steelhead/Rainbow Trout and juvenile Longfin Smelt—had the greatest E_{tol} (mean 81–107 days), and all other species had fairly similar T_{tol}, and thus similar E_{tol} (33–59 days). When assessing vulnerability by T_{sopt}, adult and juvenile Longfin Smelt had the greatest E_{sopt} (309 to 310 days), followed by juvenile Chinook Salmon, adult Sacramento Sucker, adult Steelhead/Rainbow Trout, adult Tule Perch, and larval White Sturgeon (>200 days) (Figure 5; Table 3). While E_{tol} were relatively similar among fishes, certain life stages of Sacramento Splittail, Hitch, Striped Bass, Largemouth Bass, and Mississippi Silverside had lower E_{sopt}, suggesting they may better withstand warmer water temperature compared with other species and life stages of fishes. Adult fishes tended to have higher E_{sopt} and E_{tol} than juvenile and larval fishes (Figure 5, Table 3). Among nuisance species, *Microcystis* only exceeded its T_{tol} a few days each year (mean 19 E_{tol}). Aquatic vegetation and non-native clams also had high T_{tol}, with only a mean of 52 E_{tol} (Figure 5, Table 3).

Thermal Stress by Listing Status

ESA-listed species experienced a significantly greater proportion of days that exceeded the lower range of adult T_{tol} ($P < 0.001$, Table A6), with listed species experiencing stressful days for 18.1% of the year (95% CI: 16.3 to 20.2%) and unlisted species experiencing stressful days for 12.7% of the year (95% CI: 11.7 to 13.6%), though there was no difference detected between listed and unlisted species based on the upper range of adult T_{tol} values ($P > 0.05$, Table A7).

Daily Thermal Stress by Station

The days exceeding 22 °C (the threshold derived from multiple species' T_{sopt} based on Table 2) have ranged from April to October and primarily occur between June and September (Figure 6). Across years and stations, the Central Delta clearly exceeds 22 °C for the majority of the day between mid-June and mid-September across stations, allowing for few opportunities to mitigate exposure to stressful water temperature. Although Suisun Bay reaches 22 °C during most of July and August, on average, this is for less than 50% of the day, potentially allowing for periods of recovery.

Comparing a particularly warm period—which was also a drought period—with the entire dataset, the period of daily stress increases to incorporate more stations, notably in the Central and South Delta, as well as many of the more eastward stations of the Confluence, and more days extending through the rest of June and September (Figure 6). Much of the Confluence, Central, and South Delta provide sub-optimal temperatures for all of July and most of August, with no periods for recovery during the day.

DISCUSSION

With growing evidence of climate change effects on the San Francisco Estuary, we show how spatial and seasonal patterns in water temperature may affect select special- status species, as well as other native, non-native, and nuisance species. We found that across all 10 years and all regions of our study, late spring, summer, and early fall water temperatures may cause sub-lethal and lethal effects on listed and unlisted native species, severely limiting the habitat they can occupy. Many native fishes in the estuary are already living near the edge of their thermal limits, and increasing temperatures favor non-native fishes, invertebrates, and aquatic weeds which further threaten native fishes through altered predator–prey interactions, competition, and food availability.

Water-Temperature Patterns

Over the past decade, we found there was ~1.3 °C (modeled mean annual maximum) and ~2.2 °C (modeled mean annual minimum) difference between the warmest and coolest years in the dataset. The warmest period we observed (2014 to 2016) overlapped with the extended and extreme drought that occurred between 2012 and 2016, which in addition to elevated water temperature, was associated with low streamflow (Swain et al. 2018). Regional variation was more pronounced in the dry season, with ~2.3 °C difference between the warmest (Central and South Delta) and coolest (Suisun) regions for both

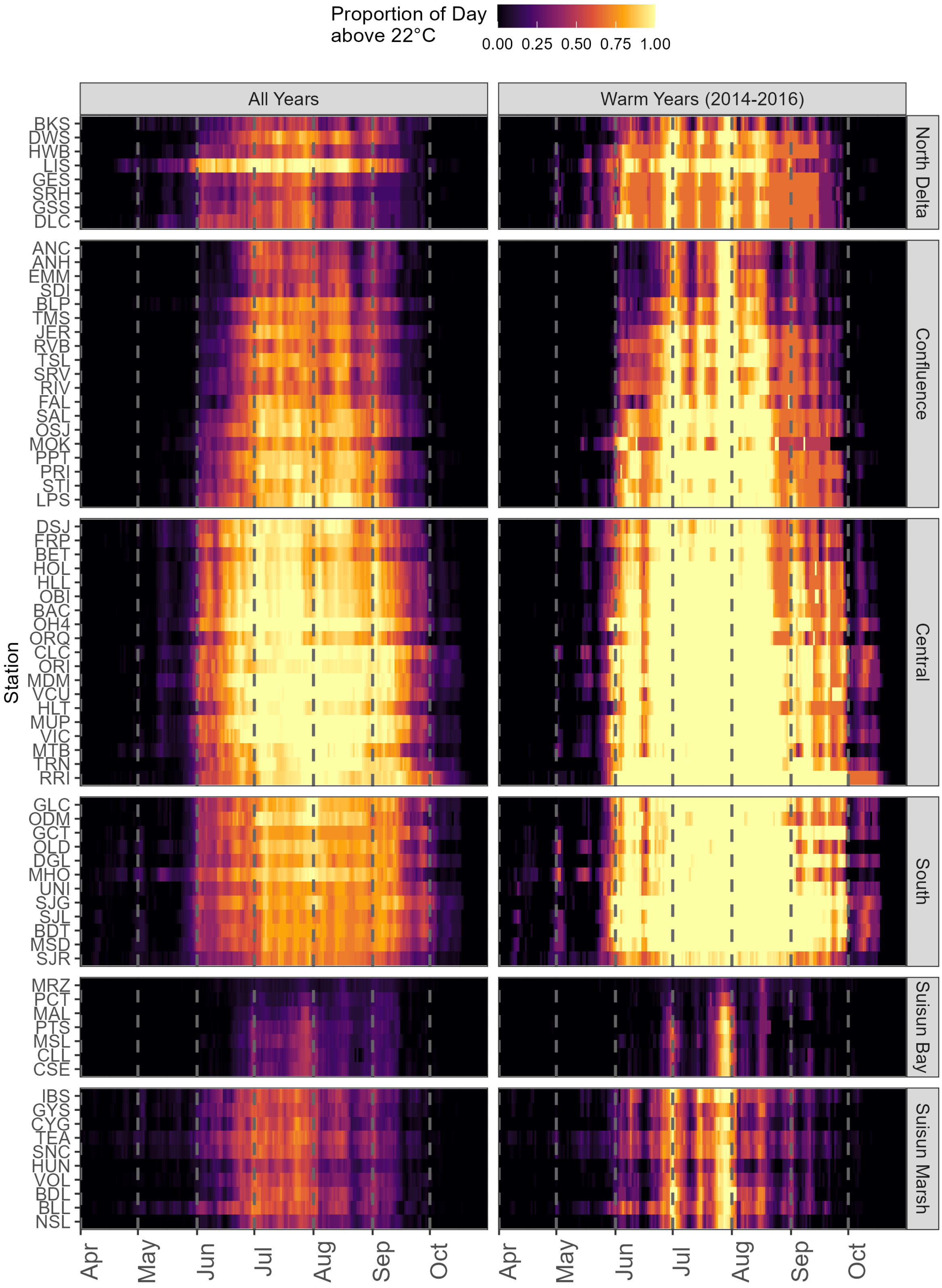

Figure 6 Daily thermal stress by station and day of year. Colors represent the average proportion of each day that exceeded 22 °C for each station from 2010 to 2019, based on continuous water-temperature data. Stations (listed as CDEC station code; see Table A1 for descriptions) are ordered by longitude from west to east.

maximum and minimum water temperatures (Figure 2), and these differences are greater when looking at individual stations and days. Maximum temperatures have reached 24 °C at all stations in our dataset over the decade, and up to 30 °C at several stations in the South Delta region (Table A1). Climate-change modeling has indicated that these extreme water temperatures will become more common in the next few decades during the summer (Huntsman et al. 2024), as evidenced in July 2024, which was the hottest July on record globally and in California (NCEI 2024; NOAA c2024).

Comparison of Stress by Species

While several studies have used different analyses to demonstrate that increases in water temperature will affect ESA-listed fishes in the estuary such as Delta Smelt and Chinook Salmon (Cloern et al. 2011; Brown et al. 2016; Halverson et al. 2022; Mahardja et al. 2022), we wanted to apply observed temperature patterns to a range of species, and examine both sub-lethal and lethal effects.

The degree of vulnerability and stress for each species depended on the type of threshold used (lethal vs. sub-optimal, as well as the particular T_{tol} or T_{sopt} metric considered). Across analyses, we found that listed species such as native osmerids and salmonids are more vulnerable to increased temperatures associated with climate change, and experience significantly more days of thermal stress compared to unlisted species (particularly if behavioral movement to cooler habitat is limited). Many of the listed species are cold-water species, which use the warmer Delta during their life history, though they no longer thrive in today's warmer waters. Meanwhile, many of the unlisted native species—such as Sacramento Blackfish, adult Hitch, adult Prickly Sculpin, adult Sacramento Pikeminnow, adult Sacramento Sucker, adult Tule Perch, and larval Sacramento Splittail—are more thermally tolerant, with $T_{tol} > 30$ °C, and are thus likely more resilient to current and future temperatures.

In contrast to many of the listed and some unlisted native fishes, non-native fishes such as Mississippi Silversides and Largemouth Bass may be less vulnerable to warming estuary temperatures, and continue to thrive, as demonstrated by lower E_{sopt}, E_{tol}, and larger temperature margins. Higher thermal tolerance may explain Silverside population increases in recent years. The increase of non-native fishes expected to coincide with increasing water temperature may intensify predation and competition with native fishes (Baerwald et al. 2012; McInturf et al. 2022).

In addition to non-native fishes, warming temperatures are likely to promote harmful cyanobacteria and aquatic weed growth, and support growing invasive clam populations because of the higher temperature thresholds and lower E_{sopt} and E_{tol} of these species. *Microcystis* blooms and their toxins have been linked to decreased health and survival for native fish and zooplankton (Ger et al. 2009; Ger et al. 2010; Acuña, Baxa, et al. 2012; Acuña, Deng, et al. 2012; Kurobe et al. 2018; Acuña et al. 2020), and the invasion of aquatic weeds, particularly *E. densa*, into sub-tidal habitat can also permanently affect native fish communities by promoting alien sunfishes and Largemouth Bass over native fishes (Brown 2003; Brown and Michniuk 2007; Conrad et al. 2016). Low abundances of *Microcystis* and *E. densa* in Suisun Marsh and Suisun Bay have partly been attributed to high salinity and turbidity in these regions (Moisander et al. 2009; Borgnis and Boyer 2015; Durand et al. 2016). Our analysis suggests that lower temperatures may also limit their growth in these regions compared with the Central and South Delta regions.

Non-native clams—such as the Overbite Clam (*Potamocorbula amurensis*), and particularly the Asian Clam (*Corbicula fluminea*)— can tolerate high temperatures (Table 2), although it should be noted that temperature tolerance for *Potamocorbula amurensis* is based on a congener, because lab studies have not been conducted on this species. These clams have been implicated in decreasing primary productivity in the estuary and thus food availability for estuarine fishes (Cloern and Jassby 2012; Kimmerer and Thompson 2014). Both spatially and temporally, much of the estuary is suitable for both species of non-native clams.

Stress by Region and Season

For all listed species besides sturgeon, the Central and South Delta are already above or within 0 to 3 °C of their lethal T_{tol} during the summer, and salmonids are also vulnerable in most regions during the spring (Figure 4), similar to findings in Mahardja et al. (2022) and Munsch et al. (2019). In some seasons, fish species may be able to find cooler temperatures, though fish behavior and the ability to adapt can vary by and within species (Myrick and Cech 2000; Cocherell et al. 2012). For example, juvenile Chinook Salmon and *O. mykiss* T_{mar} in most regions in spring are 0 to 3 °C, respectively, such that additional increases in warming may exacerbate mortalities directly or indirectly from predation, disease, respiratory stress, or other factors. However, we found Chinook juvenile T_{mar} are more robust in the Suisun Bay in the spring (3 to 6 °C), potentially allowing them to find suitable thermal habitat before they migrate to cooler temperatures in the San Francisco Bay. While little is known about juvenile Chinook use of Suisun Bay, they are known to leave areas of high temperatures for cooler temperatures during migration (Sykes et al. 2009), so they may move into the bay as the Delta warms. Similar refugia may occur for Delta and Longfin Smelt in the summer if salinities are low enough for them to access these regions.

Species comparisons with T_{sopt} indicate the entire study area exceeds thresholds for optimal physiological performance throughout the entirety of the summer for many listed species. The modeled average T_{max} during the dry season (May–September) ranged from 20.9 to 23.3 °C (95% CI: 18.1–20.4 °C to 23.8–26.1 °C) across regions during the dry season, exceeding Delta Smelt, Green Sturgeon T_{sopt}, and Steelhead/Rainbow Trout, Longfin Smelt, and Chinook Salmon T_{sopt} and T_{tol}, and leading to potentially >146 days and >33 days of sub-lethal and lethal stress, respectively, across native species (Table 3). While T_{tol} describes what the estuary species may survive in the short-term (particularly from laboratory studies), T_{sopt} may also approximate what could eventually be lethal over a longer time-frame (i.e., chronic T_{sopt} may not be tolerable because of combined sub-lethal effects). We found that summer temperatures in certain regions exceeded T_{sopt} for the entire day during July and August, limiting a species' ability to recover over the course of a day. These cumulative stress days occurred across the estuary, with the greatest frequency in the Central Delta, and with spatial extent extending to the lower San Joaquin River portion of the confluence and the South Delta during warmer years (Figure 6). Chronic stress from prolonged exposure to higher temperatures may result in long-term changes to stress responses, diminished ability to cope with other stressors, and increased energy demands when compared with acute temperature stress (Alfonso et al. 2021).

Study Limitations

This study relied on the usage of available data published on data repositories and in the literature. Thus, metrics and types of studies used for species thresholds were not consistent across all species and life stages (Davis et al. 2022). Additionally, surveys were not equally sampled across all regions, habitats, seasons, species, and life stages. Thus, we may have over- or under-estimated the number of stressful days for certain species and life stages, depending on the metrics and biological data available.

During our calculations of T_{mar}, we observed that some fish were detected in field surveys at temperatures higher than the physiological T_{tol} thresholds recorded in literature (Figure A3; Table 2). This was contrary to other studies that have found lower field tolerances than laboratory tolerances (Eaton et al. 1995). We attribute these to either life stage cut-offs being slightly different between studies and our literature, fish being dead or in very poor condition when caught, field identification errors, or some level of field or local acclimation/adaptation that is either different from what is experienced in the laboratory or has changed over time and with warming temperatures (McCullough et al. 2009). In particular, acclimating fishes to variable temperatures can result in higher thermal tolerances (Schaefer and Ryan 2006); therefore, the highly variable field temperatures may produce greater thermal plasticity than that seen in a laboratory settings. More research is warranted to describe species' ability to acquire temperature tolerance in variable and complex field conditions vs. laboratory conditions.

Potential for Refugia

While habitat suitability depends on species and life stage, we found that the only region to provide consistently suitable temperatures for cool-water native species life stages is Suisun Bay. Cooler thermal habitat also exists in the western and Sacramento River portions of the Confluence, Suisun Bay, and Suisun Marsh, as well as in some locations in the North Delta, which is consistent with Brown et al. (2016). The cool-water temperature corridor has been identified as an area to target for tidal wetland restoration (Durand 2013; Hobbs et al. 2017), and has been the key location for recent releases of cultured Delta Smelt into the estuary to support the population (USFWS et al. 2021). The higher diversity and abundance of native fish in this region has been attributed to relatively high turbidity, hydrodynamic complexity, and increased tidal wetland area, which benefits numerous native species (Sommer and Mejia 2013; Bever et al. 2016; Young et al. 2018; Feyrer et al. 2021). Our research demonstrates that cool water temperature in this region may also be a reason why this area benefits native fishes, many of which have lower temperature tolerances compared with non-native fishes (Davis et al. 2022).

Understanding how temperature regimes vary across regions and seasons will help inform restoration and/or reinforcement efforts for native species. For example, certain parts of the North Delta may be too warm in the summer, such that benefits of restored or enhanced habitat and food enhancement actions may not outweigh the negative effects associated with warming water temperature (e.g., increased energy demands, increased non-native predators, etc.). However, restoration in these areas can still be valuable, as much of the estuary experiences suitable temperatures during the rest of the year such that restoration can target life stages present in those seasons, and can also produce food and benefit other species (e.g., mammals, waterfowl).

Climate-Change Effects

Recent modeling studies based on historical data have found average increases in temperature on the order of 0.017 °C per year, with specific regions and months exhibiting greater than 0.15 °C increases per year, and more recent periods exhibiting significant increases in March–June across much of the upper estuary (Bashevkin, Mahardja et al. et al. 2022). Heatwave incidents have been prevalent in many recent years (Mahardja et al. 2025) and climate-change modeling indicates significant temperature increases in the next few decades across the estuary (Huntsman et al. 2024). Comparisons of the 10-year temperature dataset with the warmest 3 years of the dataset indicate a large increase of stations and days in the confluence, and in the Central and South Delta regions that become stressful for native species for entire months, with no nighttime recovery to temperatures below thresholds (Figure 6, Figure A4). Warmer spring temperatures may provide benefits in certain cases, potentially providing longer spawning periods for certain species (Huntsman et al. 2024). However, given existing conditions and predicted increases, the next few decades will likely lead to further narrowing of temperature margins across the estuary, and a shift toward higher numbers of E_{tol} and E_{sopt}, especially of the cold-water native species of interest.

Because most life stages of fish are mobile, it is possible that fish species may find additional refuge in unsampled parts areas of the estuary, such as deeper areas of the estuary (Mahardja et al. 2022). Some species may also be able to acquire additional thermal tolerance, shift the distribution and timing of their migration/residence, or compensate by finding additional food resources (Lusardi et al. 2020; Alfonso et al. 2021). However zooplankton—which comprise the major food source for pelagic fishes—shift to smaller body size or smaller species when temperatures warm, limiting available food resources (Richardson 2008), and rapid shifts in the composition and timing of food resources may make adaptation difficult as climate change and non-native species drive phenological mismatches between predators and prey (Merz et al. 2016; Renner and Zohner 2018).

CONCLUSIONS

While this study covered a large portion of the upper estuary and leveraged the long-term efforts of monitoring programs and existing research across agencies, we identified areas for additional research. We found that most of the water-temperature data were collected within 1 meter of the surface, which may not reflect additional suitable habitat at depth that could be > 3 °C cooler (Mahardja et al. 2022) and more suitable for species. Understanding temperature regimes in off-channel habitats such as sloughs and marshes will be important for understanding climate-change effects, given that many restoration projects are happening in these habitats (Herbold et al. 2014; Sherman et al. 2017). We found less long-term water-temperature data available in the northern parts of the North Delta, the northern part of Suisun Bay and Grizzly Bay, and the western Delta to San Francisco Bay. Since many of these areas provide potential temperature refuge and areas of restoration, having more long-term monitoring stations across various habitats in these areas would be informative. We also found temperature threshold data (particularly for optimal physiological performance) lacking for many species and life stages. Additional laboratory and field studies could better define and validate thresholds or identify differences with lab and field-determined thresholds.

Through managed actions, environmental parameters such as salinity and streamflow can be modified to increase suitable habitat, and potentially increase food resources for species (Sommer 2020; Sommer et al. 2020; Beakes et al. 2021). However, the community is uncertain whether inflow can be used to adjust water temperature in the estuary. In upstream tributaries, reservoir releases can provide cooler water for early life stages of Chinook Salmon (Yates et al. 2008). While some studies have found relationships between inflow/ discharge and water temperature (Vroom et al. 2017; Bashevkin and Mahardja 2022), reservoir releases have not been found to affect downstream temperatures in the estuary (Daniels and Danner 2020). Restoration of tidal wetlands, deeper pools, and riparian vegetation—including the addition of shade—may provide thermal refugia (Enright et al. 2013; Kurylyk et al. 2015) or an acute escape from high water temperatures. Areas with cooler suitable temperatures can also be identified as release locations for cultured Delta Smelt, should juvenile life stages be released in the future. In the estuary, water temperature is mainly driven by air temperature (a function of solar radiation) and day length (Vroom et al. 2017; Sommer 2020). One consideration for restoration projects is to incorporate shade into restored habitat, which could reduce insolation and mitigate warming temperatures (Greenberg et al. 2012; Fuller et al. 2022).

Regional habitat- and food-restoration efforts should (1) focus on restoring areas of cooler habitat within at-risk fish habitat ranges, (2) consider inter-annual as well as daily variability at a given location—because minimum temperatures may also play an important role in species stress—and lastly, (3) consider effects on other species. While efforts to restore habitat (in acreage and suitable conditions) continue, many of the estuary's listed species are already (Chinook Salmon, *O. mykiss*, Delta Smelt) or soon to be (Longfin Smelt) cultured and genetically managed in hatchery facilities. Direct supplementation of species during cooler periods may be required annually to support species resiliency and conservation, and if species continue to decline, additional human interventions and contingency actions may warrant consideration (Sommer et al. 2024).

DATA ACCESSIBILITY

You may access datasets associated with this manuscript at:

- *https://doi.org/10.6073/pasta/f06807bddf8b32613ffc5d73605a6175* (species thresholds)
- *https://doi.org/10.6073/pasta/7385985f68b02c0deb2a9e425a9f3ad8* (continuous water temperature data)

You may access code used for modeling and creating figures at GitHub: *https://github.com/InteragencyEcologicalProgram/TempSynthesis/tree/master*

See "Readme" at the repository for a list of relevant files.

You may access the majority of relevant code located in a subfolder at GitHub: *https://github.com/InteragencyEcologicalProgram/TempSynthesis/tree/master/manuscript_code*

You may access model validation plots at: *https://github.com/InteragencyEcologicalProgram/TempSynthesis/tree/master/manuscript_code/Figures/model_validation_plots*

ACKNOWLEDGMENTS

The views expressed are those of the authors and do not represent the views of the respective agencies.

We would like to thank staff from various monitoring programs who collected the continuous water-temperature data we used in our analyses, including staff from the California Department of Water Resources, United States Geological Survey, California Department of Fish and Wildlife, and Bureau of Reclamation. We would like to thank Sam Bashevkin, Brian Schreier, and Brian Mahardja for providing expertise on analysis techniques and/or fish distribution. We would also like to thank Sam Bashevkin, Elissa Buttermore, Lauren Damon, Karen Gehrts, Daphne Gille, Josh Israel, Nicole Kwan, Laurel Larsen, Dean Messer, Shaun Philippart, and John Franco Saraceno for reviewing and providing valuable comments on the manuscript.

REFERENCES

Acuña S, Baxa D, Lehman P, Teh F–C, Deng D–F, Teh S. 2020. Determining the exposure pathway and impacts of *Microcystis* on Threadfin Shad, *Dorosoma petenense*, in San Francisco Estuary. Environ Toxicol Chem. [accessed 2023 Jan 12];39(4):787–798. *https://doi.org/10.1002/etc.4659*

Acuña S, Baxa D, Teh S. 2012a. Sublethal dietary effects of microcystin producing *Microcystis* on Threadfin Shad, *Dorosoma petenense*. Toxicon. [accessed 2023 Jun 22];60:1191–1202. *https://doi.org/10.1016/j.toxicon.2012.08.004*

Acuña S, Deng DF, Lehman P, Teh S. 2012b. Sublethal dietary effects of *Microcystis* on Sacramento splittail, *Pogonichthys macrolepidotus*. Aquat Toxicol. [accessed 2023 Feb 6];110–111:1–8. *https://doi.org/10.1016/j.aquatox.2011.12.004*

Alfonso S, Gesto M, Sadoul B. 2021. Temperature increase and its effects on fish stress physiology in the context of global warming. J Fish Biol. [accessed 2025 Jan 14];98(6):1496–1508. *https://doi.org/10.1111/jfb.14599*

Baerwald MR, Schreier BM, Schumer G, May B. 2012. Detection of threatened Delta Smelt in the gut contents of the invasive Mississippi Silverside in the San Francisco Estuary using TaqMan assays. Trans Am Fish Soc. [accessed 2023 Jun 22];141:1600–1607. *https://doi.org/10.1080/00028487.2012.717521*

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecol Monogr. [accessed 2014 Aug 15];81(2):169–193. *https://doi.org/10.1890/10-1510.1*

Bashevkin SM, Mahardja B. 2022. Seasonally variable relationships between surface water temperature and inflow in the upper San Francisco Estuary. Limnol Oceanogr. [accessed 2023 Jan 4];67:684–702. *https://doi.org/10.1002/lno.12027*

Bashevkin SM, Mahardja B, Brown LR. 2022b. Warming in the upper San Francisco Estuary: patterns of water temperature change from five decades of data. Limnol Oceanogr. [accessed 2023 Jan 3];67(5):1065–1080. *https://doi.org/10.1002/lno.12057*

Bashevkin SM, Nguyen TX, Tham EJ, Gaeta JW, Mitchell L, Khanna S. 2022a. Fish abundance in the San Francisco Estuary (1959–2024), an integration of 10 monitoring surveys. Ver. 2. Enviornmental Data Initiative. [accessed 2025 Feb 5]. *https://doi.org/10.6073/pasta/a29a6e674b0f8797e13fbc4b08b92e5b*

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using '`lme4`'. J Stat Softw. [accessed 2023 Mar 15];67(1):1-48. *https:/doi.org/10.18637/jss.v067.i01*

Beakes MP, Graham C, Conrad JL, White JR, Koohafkan M, Durand J, Sommer T. 2021. Large-scale flow management action drives estuarine ecological response. N Am J Fish Manage. [accessed 2023 Jun 22];41(1):64–77. *https://doi.org/10.1002/nafm.10529*

Bever AJ, MacWilliams ML, Herbold B, Brown LR, Feyrer FV. 2016. Linking hydrodynamic complexity to Delta Smelt (*Hypomesus transpacificus*) distribution in the San Francisco Estuary, USA. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];14(1). *https://doi.org/10.15447/sfews.2016v14iss1art3*

Borgnis E, Boyer KE. 2015. Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the upper San Francisco Estuary. Estuaries Coasts. [accessed 2023 Jun 22];39(3):707–717. *https://doi.org/10.1007/s12237-015-0033-5*

Brown LR. 2003. Will tidal wetland restoration enhance populations of native fishes? San Franc Estuary Watershed Sci. [accessed 2024 Apr 18];1(1). *https://doi.org/10.15447/sfews.2003v1iss1art2*

Brown LR, Komoroske LM, Wagner RW, Morgan–King T, May JT, Connon RE, Fangue NA. 2016. Coupled downscaled climate models and ecophysiological metrics forecast habitat compression for an endangered estuarine fish. PLOS ONE. [accessed 2023 Jun 20];11(1):e0146724. *https://doi.org/10.1371/journal.pone.0146724*

Brown LR, Michniuk D. 2007. Littoral fish assemblages of the alien-dominated Sacramento–San Joaquin Delta , California, 1980–1983 and 2001–2003. Estuaries Coasts. [accessed 2025 Feb 5];30(1):186–200. *https://doi.org/10.1007/BF02782979*

[CDFW] California Department of Fish and Wildlife. 2025. California Natural Diversity Database: endangered and threatened animals list. [accessed 2025 May 20]. Sacramento (CA): CDFW. 28 p. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=109405&inline*

Clark J, Bashevkin SM. 2022. '`deltafish`': an R package to access an integrated dataset of fish count and length from the San Francisco Delta. version 1.0.0. [accessed 2024 Jan 4]. Available from: *https://github.com/Delta-Stewardship-Council/deltafish/releases/tag/v1.0.0*

Cloern JE, Hieb KA, Jacobson T, Sansó B, Di Lorenzo E, Stacey MT, Largier JL, Meiring W, Peterson WT, Powell TM, et al. 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. Geophys Res Lett. [accessed 2025 Feb 5];37(21):L21602. *https://doi.org/10.1029/2010gl044774*

Cloern JE, Jassby AD. 2012. Drivers of change in estuarine–coastal ecosystems: discoveries from four decades of study in San Francisco Bay. Rev Geophys. [accessed 2023 Jan 14]:50(4):RG4001. *https://doi.org/10.1029/2012rg000397*

Cloern JE, Knowles N, Brown LR, Cayan D, Dettinger MD, Morgan TL, Schoellhamer DH, Stacey MT, van der Wegen M, Wagner RW, et al. 2011. Projected evolution of California's San Francisco Bay–Delta-River system in a century of climate change. PLOS ONE. [accessed 2023 Jan 5]:6(9):e24465. *https://doi.org/10.1371/journal.pone.0024465*

Cocherell SA, Chun SN, Cocherell DE, Thompson LC, Klimley AP, Cech JJ. 2012. A lateral-displacement flume for fish behavior and stranding studies during simulated pulsed flows. Environ Biol Fishes. [accessed 2025 Feb 5];93(1):143–150. *https://doi.org/10.1007/s10641-011-9894-z*

Collins M, Chandler RE, Cox PM, Huthnance JM, Rougier J, Stephenson DB. 2012. Quantifying future climate change. Nat Clim Change. [accessed 2025 Feb 5];2(6):403–409. *https://doi.org/10.1038/nclimate1414*

Conrad JL, Bibian AJ, Weinersmith KL, De Carion D, Young MJ, Crain P, Hestir EL, Santos MJ, Sih A. 2016. Novel species ineractions in a highly modified estuary: association of Largemouth Bass with Brazilian waterweed *Egeria densa*. Trans Am Fish Soc. [accessed 2023 Jan 3];145:249–263. *https://doi.org/10.1080/00028487.2015.1114521*

Daniels ME, Danner EM. 2020. The drivers of river temperatures below a large dam. Water Resour Res. [accessed 2023 Jan 5];56(5):e2019WR026751. *https://doi.org/10.1029/2019WR026751*

Davis B, Bush E, Lehman P, Pien C. 2022. Temperature thresholds for aquatic species in the Sacramento San–Joaquin Delta. version 2. Environmental Data Initiative. [accessed 2023 Feb 13]. *https://doi.org/10.6073/pasta/0ffa27c1302fd8f6197ea5ffd9feff9e*

Davis BE, Cocherell DE, Sommer T, Baxter RD, Fangue NA, Hung T–C, Todgham AE, Fangue NA. 2019. Sensitivities of an endemic, endangered California smelt and two non-native fishes to serial increases in temperature and salinity: implications for shifting community structure with climate change. Conserv Physiol. [accessed 2019 Apr 4];7(1):coy076. *https://doi.org/10.1093/conphys/coy076*

Dettinger M, Anderson J, Anderson M, Brown L, Cayan D, Maurer E. 2016. Climate change and the Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jan 12];14(3). *http://doi.org/10.15447/sfews.2016v14iss3art5*

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci. [accessed 2023 Jun 22];105(18):6668–6672. *https://doi.org/10.1073/pnas.0709472105*

Durand J. 2013. October 26, 2013. 'North Delta Arc' lifts hope for recovery of native fish. California Water Blog. [accessed 2013 Oct 26]. Available from: *https://californiawaterblog.com/2013/10/26/north-delta-arc-lifts-hope-for-recovery-of-native-fish/*

Durand J, Fleenor W, McElreath R, Santos MJ, Moyle P. 2016. Physical controls on the distribution of the submersed aquatic weed *Egeria densa* in the Sacramento–San Joaquin Delta and implications for habitat restoration. San Franc Estuary Watershed Sci. [accessed 2023 Jun 22];14(1). Available from: *http://www.escholarship.org/uc/item/85c9h479*

Eaton JG, McCormick JH, Goodno BE, O'Brien DG, Stefany HG, Hondzo M, Scheller RM. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries. [accessed 2023 Jun 22];20(4):10–18. *https://doi.org/10.1577/1548-8446(1995)020<0010:AFISFE>2.0.CO;2*

Ebersole JL, Quiñones RM, Clements S, Letcher BH. 2020. Managing climate refugia for freshwater fishes under an expanding human footprint. Front Ecol Environ. [accessed 2024 Jan 8];18(5):271–280. *https://doi.org/10.1002/fee.2206*

Enright C, Culberson S, Burau J. 2013. Broad timescale forcing and geomorphic mediation of tidal marsh flow and temperature dynamics. Estuaries Coasts. [accessed 2024 Apr 18];36(6):1319–1339. *https://doi.org/10.1007/s12237-013-9639-7*

Fangue NA, Todgham AE, Schulte PM. 2020. Thermal biology. In: Currie S, Evans DH, editors. The physiology of fishes. 5th ed. [accessed 2023 Jan 10]. Boca Raton (FL): CRC Press. p. 91–104. Available from: *https://www.taylorfrancis.com/chapters/edit/10.1201/9781003036401-7/thermal-biology-nann-fangue-anne-todgham-patricia-schulte*

Feyrer F, Young MJ, Huntsman BM, Brown LR. 2021. Disentangling stationary and dynamic estuarine fish habitat to inform conservation: species-specific responses to physical habitat and water quality in San Francisco Estuary. Mar Coast Fish. [accessed 2024 Apr 18];13(5):548–563. *https://doi.org/10.1002/mcf2.10183*

Fuller MR, Leinenbach P, Detenbeck NE, Labiosa R, Isaak DJ. 2022. Riparian vegetation shade restoration and loss effects on recent and future stream temperatures. Rest Ecol. [accessed 2023 Feb 13];30(7):e13626. *https://doi.org/10.1111/rec.13626*

Ger KA, Teh SJ, Baxa DV, Lesmeister S, Goldman CR. 2010. The effects of dietary *Microcystis aeruginosa* and microcystin on the copepods of the upper San Francisco Estuary. Freshw Biol. [accessed 2023 Jun 22]; 55(7):1548–1559. *https://doi.org/10.1111/j.1365-2427.2009.02367.x*

Ger KA, Teh SJ, Goldman CR. 2009. Microcystin-LR toxicity on dominant copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* of the upper San Francisco Estuary. Sci Tot Environ. [accessed 2023 Jun 22];407:4852–4857. *https://doi.org/10.1016/j.scitotenv.2009.05.043*

Ghalambor CK, Gross ES, Grosholtz ED, Jeffries KM, Largier JK, McCormick SD, Sommer T, Velotta J, Whitehead A. 2021. Ecological effects of climate-driven salinity variation in the San Francisco Estuary: can we anticipate and manage the coming changes? San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];19(2). *http://dx.doi.org/10.15447/sfews.2021v19iss2art3*

Gillanders BM, Eldson TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ. 2011. Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar Freshw Res. [accessed 2023 Feb 13];62:1115–1131. *https://doi.org/10.1071/MF11047*

Goss M, Swain DL, Abatzoglou JT, Sarhadi A, Kolden CA, Williams AP, Diffenbaugh NS. 2020. Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. Environ Res Lett. [accessed 2023 Jun 22];15(9):094016. *https://doi.org/10.1088/1748-9326/ab83a7*

Greenberg JA, Hestir EL, Riano D, Scheer GJ, Ustin SL. 2012. Using LiDAR data analysis to estimate changes in insolation under large-scale riparian deforestation. J Am Wat Res Assoc. [accessed 2023 Jun 20];48(5):939–948. *https://doi.org/10.1111/j.1752-1688.2012.00664.x*

Halverson GH, Lee CM, Hestir EL, Hulley GC, Cawse–Nicholson K, Hook SJ, Bergamaschi BA, Acuña S, Tufillaro NB, Radocinski RG, et al. 2022. Decline in thermal habitat conditions for the endangered Delta Smelt as seen from Landsat satellites (1985–2019). Environ Sci Tech. [accessed 2023 Jan 5];56(1):185–193. *https://doi.org/10.1021/acs.est.1c02837*

He K, Li Z, Yan H, Shi L, Yang H, Liu Q, Song K, Hu Y, Wang B, Yang S, et al. 2025. Cold temperature delays ovarian development of Largemouth Bass by inhibiting sex hormone release, angiogenesis, apoptosis and autophagy during out-of-season reproduction. Comp Biochem Physiol A. [accessed 2024 Jun 20];301:111795. *https://doi.org/10.1016/j.cbpa.2024.111795*

He M. 2022. Assessing changes in 21st century mean and extreme climate of the Sacramento–San Joaquin Delta in California. Climate. [accessed 2025 Feb 5];10(2). *https://doi.org/10.3390/cli10020016*

Herbold B, Baltz DM, Brown L, Grossinger R, Kimmerer W, Lehman P, Moyle PB, Nobriga M, Simenstad CA, Wilcox C, et al. 2014. The role of tidal marsh restoration in fish management in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2024 Dec 10];12(1). *https://doi.org/10.15447/sfews.2014v12iss1art1*

Herbold B, Bush E, Castillo G, Colombano D, Hartman R, Lehman P, Mahardja B, Sommer T. 2022. Climate change impacts on San Francisco Estuary aquatic ecosystems: a review. San Franc Estuary Watershed Sci. [accessed 2024 Jan 23];20(2). *http://doi.org/10.15447/sfews.2022v20iss2art1*

Hobbs J, Moyle PB, Fangue N, Connon RE. 2017. Is extinction inevitable for Delta Smelt and Longfin Smelt? An opinion and recommendations for recovery. San Franc Estuary Watershed Sci. [accessed 2023 Jan 3]; 15(2). *https://doi.org/10.15447/sfews.2017v15iss2art2*

Hobbs JA, Denney C, Lewis L, Willmes M, Xieu W, Schultz A, Burgess OT. 2019. Exploring life history diversity in a critically-endangered species during a period of extreme environmental variability. In: Schultz AA, editor. Directed Outflow Project: Technical Report 1. Sacramento (CA): US Bureau of Reclamation, Bay–Delta Office, Mid-Pacific Region. [accessed 2023 Jan 10]. p. 124–146. Available from: *https://www.baydeltalive.com/docs/24818*

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometr J. [accessed 2023 Jan 8];50(3):346–363. *https://doi.org/10.1002/bimj.200810425*

Huntsman B, Brown LR, Wulff M, Knowles N, Wagner RW, Feyrer F. 2024. Climate change scenarios for air and water temperatures in the upper San Francisco estuary: implications for thermal regimes and Delta Smelt. San Franc Estuary Watershed Sci. [accessed 2023 Feb 13];22(2). *http://doi.org/10.15447/sfews.2024v22iss2art1*

[IEP] Interagency Ecological Program, Pien C, Hamilton J, Hartman R, Nelson M, Saraceno JF, Schreier BM, Davis B. 2020. Hourly water temperature from the San Francisco Estuary, 1986–2019. version 2. Environmental Data Initiative. [accessed 2025 Feb 5]. *https://doi.org/10.6073/pasta/7385985f68b02c0deb2a9e425a9f3ad8*

[IEP] Interagency Ecological Program, Pien C, Kwan N. 2022. Interagency Ecological Program: fish catch and water quality data from the Sacramento River floodplain and tidal slough, collected by the Yolo Bypass Fish Monitoring Program, 1998–2021. version 3. Environmental Data Initiative. [accessed 2023 Jun 21]. *https://doi.org/10.6073/pasta/f5c4362f4a1f370723e2b9113432909f*

IPCC] Intergovernmental Panel on Climate Change. 2021. Summary for policymakers. In: Climate change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the IPCC. [accessed 2025 Feb 5.] Available from: *https://www.ipcc.ch/report/ar6/wg1/*

Jeffries KM, Connon RE, Davis BE, Komoroske LM, Britton MT, Sommer T, Todgham AE, Fangue NA. 2016. Effects of high temperatures on threatened estuarine fishes during periods of extreme drought. J Exp Biol. [accessed 2023 Jan 3];219(11):1705–1716. *https://doi.org/10.1242/jeb.134528*

Kimmerer WJ, Thompson JK. 2014. Phytoplankton growth balanced by clam and zooplankton grazing and net transport into the low-salinity zone of the San Francisco Estuary. Estuaries Coasts. [accessed 2023 Jan 4];37:1202–1218. *https://doi.org/10.1007/s12237-013-9753-6*

Knowles N, Cronkite–Ratcliff C, Pierce DW, Cayan DR. 2018. Responses of unimpaired flows, storage, and managed flows to scenarios of climate change in the San Francisco Bay–Delta Watershed. Water Resour Res. [accessed 2023 Jun 22]; 54(10):7631–7650. *https://doi.org/10.1029/2018wr022852*

Komoroske LM, Connon RE, Lindberg J, Cheng BS, Castillo G, Hasenbein M, Fangue NA. 2014. Ontogeny influences sensitivity to climate change stressors in an endangered fish. Conserv Physiol. [accessed 2023 Jun 22];2:cou008. *https://doi.org/10.1093/conphys/cou008*

Kurobe T, Lehman PW, Haque ME, Sedda T, Lesmeister S, Teh S. 2018. Evaluation of water quality during successive severe drought years within *Microcystis* blooms using fish embryo toxicity tests for the San Francisco Estuary, California. Sci Tot Environ. [accessed 2023 Jan 6];610–611:1029–1037. *https://doi.org/10.1016/j.scitotenv.2017.07.267*

Kurylyk BL, MacQuarrie KTB, Linnansaari T, Cunjak RA, Curry RA. 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology. [accessed 2023 Jun 22];8(6):1095–1108. *https://doi.org/10.1002/eco.1566*

Kuznetsova A, Brockhoff PB, Christensen RH. 2017. ‘`lmerTest`’ package: tests in linear mixed-effects models. J Stat Softw. [accessed 2024 Jun 14];82(13):1–26. *https://doi.org/10.18637/jss.v082.i13*

Lenth RV, Buerkner P, Herve M, Love J, Riebl H, Singmann H. 2024. ‘`emmeans`’ package: estimated marginal means, AKA least-squares means. version 1.10.4. CRAN: Comprehensive R Archive Network. [accessed 2023 Jun 22] Available from: *https://CRAN.R-project.org/package=emmeans*

Lewis LS, Denney C, Willmes M, Xieu W, Fichman RA, Zhao F, Hammock BG, Schultz A, Fangue N, Hobbs JA. 2021. Otolith-based approaches indicate strong effects of environmental variation on growth of a critically endangered estuarine fish. Mar Ecol Prog Ser. [accessed 2023 Feb 13];676:37–56. *https://doi.org/10.3354/meps13848*

Lusardi RA, Hammock BG, Jeffres CA, Dahlgren RA, Kiernan JD. 2020. Oversummer growth and survival of juvenile coho salmon (*Oncorhynchus kisutch*) across a natural gradient of stream water temperature and prey availability: an in situ enclosure experiment. Can J Fish Aqua Sci. [accessed 2023 Feb 13];77(2):413–424. *https://doi.org/10.1139/cjfas-2018-0484*

Mahardja B, Bashevkin S, Pien C, Khanna S, Pearson D, Davis B, Basu R. 2025. Heatwaves and rising temperatures in the upper San Francisco Estuary: trends and impacts on ecosystems and humans. San Franc Estuary Watershed Sci. [accessed 2025 May 15];23(1). *https://doi.org/10.15447/sfews.2025v23iss1art4*

Mahardja B, Bashevkin SM, Pien C, Nelson M, Davis BE, Hartman R. 2022. Escape from the heat: thermal stratification in a well-mixed estuary and implications for fish species facing a changing climate. Hydrobiologia. [accessed 2023 Jan 4];49:2895–2918. *https://doi.org/10.1007/s10750-022-04886-w*

Mayfield RB, Cech JJ. 2004. Temperature effects on Green Sturgeon bioenergetics. Trans Am Fish Soc. [accessed 2023 Jun 22];133:961–970. *https://doi.org/10.1577/T02-144.1*

McCullough DA, Bartholow JM, Jager HI, Beschta RL, Cheslak EF, Deas ML, Ebersole JL, Foott JS, Johnson SL, Marine KR, et al. 2009. Research in thermal biology: burning questions for coldwater stream fishes. Rev Fish Sci. [accessed 2023 Jun 22];17(1):90–115. *https://doi.org/10.1080/10641260802590152*

McInturf AG, Zillig KW, Cook K, Fukumoto J, Jones A, Patterson E, Cocherell DE, Michel CJ, Caillaud D, Fangue NA. 2022. In hot water? Assessing the link between fundamental thermal physiology and predation of juvenile Chinook Salmon. Ecosphere. [accessed 2023 Jun 22];13(11):e4264. *https://doi.org/10.1002/ecs2.4264*

Merz JE, Bergman PS, Simonis JL, Delaney D, Pierson J, Anders P. 2016. Long-term seasonal trends in the prey community of Delta Smelt (*Hypomesus transpacificus*) within the Sacramento–San Joaquin Delta, California. Estuaries Coasts. [accessed 2021 Sep 07];39(5):1526–1536. *https://doi.org/10.1007/s12237-016-0097-x*

Moisander P, Lehman P, Ochiai M, Corum S. 2009. Diversity of *Microcystis aeruginosa* in the Klamath River and San Francisco Bay delta, California, USA. Aquat Microb Ecol. [accessed 2023 Jun 22]; 57:19-31. *https://doi.org/10.3354/ame01320*

Munsch SH, Greene CM, Johnson RC, Satterthwaite WH, Imaki H, Brandes PL. 2019. Warm, dry winters truncate timing and size distribution of seaward-migrating salmon across a large, regulated watershed. Ecol Appl. [accessed 2021 Sep 7];29(4):e01880. *https://doi.org/10.1002/eap.1880*

Myrick CA, Cech JJ. 2000. Swimming performances of four California stream fishes: temperature effects. Environ Biol Fishes. [accessed 2023 Jun 15];58(3):289–295. *https://doi.org/10.1023/A:1007649931414*

[NCEI] National Centers for Environmental Information. c2024a. National climate report for July 2024. [webpage]. National Oceographic and Atmospheric Administration. [accessed 2025 Feb 5]. Available from: *https://www.ncei.noaa.gov/access/monitoring/monthly-report/national/202407*

[NOAA] National Oceanic and Atmospheric Administration. c2024b. Earth just had its warmest July on record. [webpage]. August 12, 2024. NOAA: news and features. [accessed 2025 Jan 15]. Available from: *https://www.noaa.gov/news/earth-just-had-its-warmest-july-on-record*

Pierce DW, Kalansky JF, Cayan DR. 2018. Climate, drought, and sea level rise scenarios for the fourth California climate change assessment. In: [year?]. California's Fourth Climate Change Assessment, California Energy Commission. Publication Number: CNRA-CEC-2018-006. [accessed 2023 Jun 22.] 78 p. Available from: *https://www.energy.ca.gov/sites/default/files/2019-11/Projections_CCCA4-CEC-2018-006_ADA.pdf*

Polade SD, Gershunov A, Cayan DR, Dettinger MD, Pierce DW. 2017. Precipitation in a warming world: assessing projected hydro-climate changes in California and other Mediterranean climate regions. Sci Rep. [accessed 2023 Jun 22];7(1):10783. *https://doi.org/10.1038/s41598-017-11285-y*

R Development Core Team. 2021. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. [accessed 2023 Jun 22]. Available from: *https://www.R-project.org/*

Renner SS, Zohner CM. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu Rev Ecol Evol Syst. [accessed 2024 Jun 14]:49:165–182. *https://doi.org/10.1146/annurev-ecolsys-110617-062535*

Richardson AJ. 2008. In hot water: zooplankton and climate change. ICES J Mar Sci. [accessed 2020 Jul 14];65(3):279–295. *https://doi.org/10.1093/icesjms/fsn028*

Robins PE, Skov MW, Lewis MJ, Giménez L, Davies AG, Malham SK, Neill SP, McDonald JE, Whitton TA, Jackson SE, et al. 2016. Impact of climate change on UK estuaries: a review of past trends and potential projections. Estuar Coast Shelf Sci. [accessed 2023 Jun 22];169:119–135. *https://doi.org/10.1016/j.ecss.2015.12.016*

Rodriguez E. 2022. 'CDECRetrieve': an R package to retrieve California Data Exchange Center data. version 0.1.5. GitHub. [accessed 2023 Jun 29]. Available from: *https://github.com/FlowWest/CDECRetrieve*

Scanes E, Scanes PR, Ross PM. 2020. Climate change rapidly warms and acidifies Australian estuaries. Nat Comm. [accessed 2023 Jun 22];11(1):1803. *https://doi.org/10.1038/s41467-020-15550-z*

Schaefer J, Ryan A. 2006. Developmental plasticity in the thermal tolerance of zebrafish *Danio rerio*. J Fish Biol. [accessed 2023 Jun 22];69(3):722–734. *https://doi.org/10.1111/j.1095-8649.2006.01145.x*

Sherman S, Hartman R, Contreras D. 2017. Effects of tidal wetland restoration on fish: a suite of conceptual models. Interagency Ecological Program Technical Report 91. Sacramento (CA): Department of Water Resources. [accessed 2024 Apr 18], Available from: *https://cadwr.app.box.com/v/InteragencyEcologicalProgram/file/571038692179*

Sokolova IM, Frederich M, Bagwe R, Lannig G, Sukhotin AA. 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Mar Environ Res. [accessed 2023 Jun 15];79:1–15. *https://doi.org/10.1016/j.marenvres.2012.04.003*

Sommer T. 2020. How to respond? An introduction to current Bay–Delta natural resources management options. San Franc Estuary Watershed Sci. [accessed 2023 Feb 28];18(3). *https://doi.org/10.15447/sfews.2020v18iss3art1*

Sommer T, Hartman R, Koller M, Koohafkan M, Conrad JL, MacWilliams M, Bever A, Burdi C, Hennessy A, Beakes MP. 2020. Evaluation of a large-scale flow manipulation to the upper San Francisco Estuary: response of habitat conditions for an endangered native fish. PLOS ONE. [accessed 2023 Jan 4];15(10). *https://doi.org/10.1371/journal.pone.0234673*

Sommer T, Mejia F. 2013. A place to call home: a synthesis of Delta Smelt habitat in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Jan 3];11(2). *https://doi.org/10.15447/sfews.2013v11iss2art4*

Sommer T, Mount J, Gray B, Grenier L, Harder J, Sencan G. 2024. Climate-smart tools to protect California's freshwater biodiversity. [accessed 2025 Jan 15]. San Francisco (CA): Public Policy Institute of California. 48 p. Available from: *https://www.ppic.org/?show-pdf=true&docraptor=true&url=https%3A%2F%2Fwww.ppic.org%2Fpublication%2Fclimate-smart-tools-to-protect-californias-freshwater-biodiversity%2F*

Stompe DK, Hobbs JA. 2023. California Department of Fish and Wildlife Adult Sturgeon Study, Sacramento–San Joaquin Watershed 1954–2022. version 1. Environmental Data Initiative. [accessed 2025 Jan 15]. Available from: *https://doi.org/10.6073/pasta/521d2adb9362113812a04f2bc4623a31*

Swain DL, Langenbrunner B, Neelin JD, Hall A. 2018. Increasing precipitation volatility in twenty-first-century California. Nat Clim Change. [accessed 2023 Jan 4];8(5):427–433. *https://doi.org/10.1038/s41558-018-0140-y*

Sykes GE, Johnson CJ, Shrimpton JM. 2009. Temperature and flow effects on migration timing of Chinook Salmon smolts. Trans Am Fish Soc. [accessed 2023 Jan 4];138(6):1252–1265. *https://doi.org/10.1577/T08-180.1*

[USFWS et al.] US Fish and Wildlife Service, California Department of Fish and Wildlife, California Department of Water Resources, US Bureau of Reclamation, US States Geologic Survey, University of California Davis. 2021. Delta Smelt experimental release study plan. Draft 5. Sept 2021. [accessed 2024 Jan 4]. Available from: *https://water.ca.gov/-/media/DWR-Website/Web-Pages/Programs/State-Water-Project/Endangered-Species-Protection/2024-FEIR-Long-Term-Ops/Appendices/App-2E/SWP_LTO_FEIR_App2E_Delta-Smelt-Supplementation-Strategy_508.pdf*

Volkoff H, Rønnestad I. 2020. Effects of temperature on feeding and digestive processes in fish. Temperature. [accessed 2023 Jan 3];7(4):307–320. *https://doi.org/10.1080/23328940.2020.1765950*

Vroom J, van der Wegen M, Martyr–Koller R, Lucas L. 2017. What determines water temperature dynamics in the San Francisco Bay–Delta system? Water Resour Res. [accessed 2023 Jan 4];53(11):9901–9921. *https://doi.org/10.1002/2016WR020062*

Wood S. 2017. Generalized Additive Models: an introduction with R. 2nd ed. New York (NY): Chapman and Hall/CRC. 496 p. Available from: *https://www.taylorfrancis.com/books/mono/10.1201/9781315370279/generalized-additive-models-simon-wood*

Yates D, Galbraith H, Purkey D, Huber–Lee A, Sieber J, West J, Herrod–Julius S, Joyce B. 2008. Climate warming, water storage, and Chinook Salmon in California's Sacramento Valley. Clim Change. [accessed 2023 Jun 22];91(3):335–350. *https://doi.org/10.1007/s10584-008-9427-8*

Young MJ, Feyrer FV, Colombano DD, Conrad JL, Sih A. 2018. Fish-habitat relationships along the estuarine gradient of the Sacramento–San Joaquin Delta, California: implications for habitat restoration. Estuaries Coasts. [accessed 2024 Apr 18];41:2389–2409. *https://doi.org/10.1007/s12237-018-0417-4*

Zillig KW, Lusardi RA, Moyle PB, Fangue NA. 2021. One size does not fit all: variation in thermal eco-physiology among Pacific salmonids. Rev Fish Biol Fish. [accessed 2023 Jun 22];31:95–114. *https://doi.org/10.1007/s11160-020-09632-w*