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Patterns and predictors of condition indices in a critically endangered fish

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Abstract Condition indices are key predictors of health and fitness in wild fish populations. Variation in body condition, therefore, can be used to identify stressful conditions that may impact endangered species, such as California's endemic Delta Smelt (*Hypomesus transpacificus* McAllister, 1963). Here, we examined spatiotemporal variation in the condition indices of > 1600 Delta Smelt collected over nine years (2011–2019), a period characterized by tremendous variability in hydrodynamic and water quality conditions. The population exhibited low hepatosomatic index (HSI) and condition factor (CF) during September/October/November (fall), and both condition indices declined over the nine-year study during fall. HSI was positively correlated with indicators of pelagic productivity (e.g., Chlorophyll *a*, zooplankton biomass, and proximity to tidal wetlands), whereas CF was negatively correlated with temperature, peaking at a relatively cool 10–13 °C. In sum, seasonal and interannual variation in body condition corresponded most strongly with pelagic productivity and water temperature, with little correlation to freshwater outflow. Management actions that increase pelagic productivity, restore and freshen productive wetlands during late summer-fall, and reduce water

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temperatures overall are likely to benefit condition indices and, therefore, fitness of the Delta Smelt population.

Keywords Hepatosomatic index · Condition factor · Estuary · Outflow · Chlorophyll *a* · Temperature · Delta Smelt

Introduction

Estuaries occur where freshwater from rivers and streams tidally mixes with salt water from the ocean. These ecosystems are typically hotspots for productivity (Hopkinson & Smith, 2005), but also anthropogenic influence, leading to declines in many estuarine fishes. These declines are often attributed to some combination of anthropogenic stressors, including overfishing, freshwater abstraction, climate change, contaminants, invasive species, eutrophication, and habitat loss [e.g., Africa (Guastella, 1994; Baird et al., 1996; James et al., 2018), North America (Hughes et al., 2002; Kemp et al., 2005; Buchheister et al., 2013), South America (Belarmino et al., 2021), Australia (Cottingham et al., 2018)]. Thus, understanding the causes of the declines in estuarine fishes, and how those declines can be reversed, are major goals of scientists and managers.

The San Francisco Estuary and Sacramento-San Joaquin Delta of North America (SFE) has many of these same stressors, including freshwater abstraction by pumping plants in the South Delta, contaminants, loss of tidal wetland, and invasive species (Nichols et al., 1986; Kuivila & Moon, 2004), although notably not eutrophication despite high nutrient concentrations (Jassby, 2008). Together, these perturbations are thought to suppress abundance of pelagic fishes (Feyrer et al., 2007; Sommer et al., 2007). One such species is the Delta Smelt (*Hypomesus transpacificus*, McAllister 1963), a small, mostly annual osmerid that is endemic to the SFE (Bennett, 2005). The species spawns in the spring, and has freshwater, brackish water, and migratory phenotypes (Hobbs et al., 2019). Previously one of the most abundant pelagic fishes in the SFE (Moyle et al., 2016), it is currently listed under the California Endangered Species Act and the US Endangered Species Act (USFWS, 1993; California Fish and Game Commission, 2009). Given its historical abundance and small size it was likely an important prey species for SFE fishes, but is too uncommon to meaningfully contribute to the SFE foodweb today (Moyle et al., 2016; Fig. 1A). The species' habitat overlaps with the largest source of fresh water in California, so water resource management within the SFE aims to prevent further declines in abundance (Moyle et al., 2018). Like many imperiled species, much of the information on the habitat requirements of Delta Smelt is based on its distribution (Jarnevich et al., 2015). However, determining habitat quality based on distribution can be misleading because detrimental habitat is frequently occupied (Weldon & Haddad, 2005; Faldyn et al., 2018; Hale et al., 2018), and otherwise high-quality habitat may be unoccupied due to biotic interactions or limited dispersal (Guisan & Thuiller, 2005).

Current information on suitable habitat for Delta Smelt focuses on salinity, temperature, and turbidity, with much of this information coming from abundance and distribution surveys. Delta Smelt occur almost entirely at salinities below 15 (Feyrer et al., 2007), and 90% of the population occurs below a salinity of 7 (Bennett, 2005). The species rarely occurs above 25 °C (Sommer & Mejia, 2013), and the critical thermal maxima of hatchery fish ranges from 24 to 29 °C, depending on acclimation temperature and life stage (Komoroske et al., 2014). Delta Smelt abundance peaks at turbidities above 12 NTU (Sommer & Mejia, 2013), perhaps because foraging success is improved (Hasenbein et al., 2016), predation risk is lowered (Ferrari et al., 2014), or behavioral changes associated with higher turbidity increase the efficiency of sampling gear. Indeed, stimulating feeding of larval Delta Smelt in culture requires inputs of phytoplankton, which is used to increase turbidity up to 9 NTU (Baskerville-Bridges & Lindberg, 2004; Tigan et al., 2020). However, stomach fullness in juveniles through adults is not influenced by a wide range of turbidities (0-80 NTU) and only shows a small decrease at turbidities above 80 NTU. Moreover, Delta Smelt do not require increased turbidity in culture to feed after the larval stage (Baskerville-Bridges & Lindberg, 2004; Hasenbein et al., 2016; Hammock et al., 2019a; Tigan et al., 2020). Thus, the decrease in catch at low turbidity may be unrelated to foraging.

Freshwater outflow is not well correlated with abundance of Delta Smelt (Stevens & Miller, 1983; Dege & Brown, 2003), but there are hints that it is

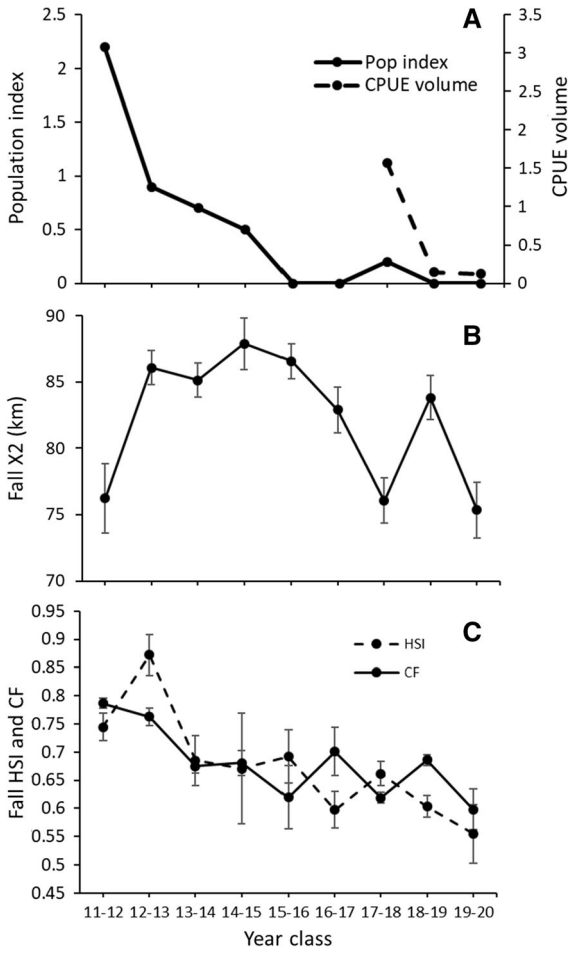

Fig. 1 Delta Smelt abundance estimates (**A**), mean fall *X*2 (distance from the Pacific Ocean to the bottom isohaline of 2; **B**), and HSI and CF (**C**) during fall, by year-class (fall includes September, October, November). Nomenclature 11–12 is the 2011–12 year-class, 12–13 is the 2012–13 year-class, etc. (e.g., 11–12 refers to the year-class of Delta Smelt that hatched in 2011 and reached sexual maturity in 2012). The solid line in (**A**) is the Delta Smelt population index, calculated from CDFW's Fall Midwater Trawl (details in Miller et al., 2012; https://www.dfg.ca.gov/delta/data/townet/indices.asp?species=3). The dashed line in (**A**) is Delta Smelt catch per unit effort (water volume sampled, in units of $m^3 \times 10{,}000$) calculated from USFWS Kodiak trawls (Enhanced Delta Smelt Monitoring Program [EDSM]). Note: EDSM's CPUE values and CDFW's population index in (**A**) are not directly comparable. EDSM's sampling effort is more intensive, so the survey detects Delta Smelt even when CDFW's population index is zero. The three lowest *X*2 values in (**B**) correspond to 3 years classified as 'wet' by CA Department of Water Resources. The two highest values of *X*2 correspond to 'critically dry' years (2014–2015 and 2015–2016; https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST). For (**C**), n = 131, 34, 11, 8, 5, 7, 81, 98, and 13 for each year-class (fall). Error bars are ± SD in (**B**) and ± SE in (**C**)

important to the species. A recent study showed that spring recruitment and survival of subsequent life-stages of Delta Smelt were positively correlated with greater outflow (Polansky et al., 2021). However, out of five previous droughts, Delta Smelt abundance rebounded following only two, with warm water temperatures possibly preventing population rebounds following the other three (Mahardja et al., 2021). For example, abundance estimates reached historical lows during a recent, severe drought in California (2012–2016), and abundance remained low during the subsequent wet period (Teh et al., 2020; Fig. 1A and B). Periods of low outflow are thought to stress the population because the volume of physically suitable habitat becomes restricted by encroaching salinity (Moyle et al., 1992; Bennett, 2005; Feyrer et al., 2011). As the salinity field shifts upstream of the confluence of the Sacramento and San Joaquin rivers, Delta Smelt rapidly loses access to the more seaward portions of its range, including the relatively intact habitat of Suisun Marsh (Moyle et al., 1992; Feyrer et al., 2011; Fig. 2). Consequently, late summer into fall may represent a seasonal bottleneck for the species as freshwater flows reach their annual nadir and access to seaward habitat is lost, particularly during droughts.

While multiple stressors are thought to have contributed to the decline of Delta Smelt (Sommer et al., 2007), food limitation may be a primary factor (Maunder & Deriso, 2011; Hamilton & Murphy, 2018). The species' decline, like other pelagic fishes, has roughly coincided with negative exponential declines in primary and secondary pelagic productivity in the SFE (Winder & Jassby 2011; Moyle et al., 2016; Hammock et al., 2019b). Calanoid copepods are a major prey item for Delta Smelt (Nobriga, 2002; Slater & Baxter, 2014), and summer to fall survival is correlated with calanoid copepod biomass (Kimmerer, 2008). Declines in productivity and introductions of invasive zooplankton have caused Delta Smelt to rely on smaller, potentially less nutritious prey items in the fall (Winder & Jassby, 2011; Slater & Baxter, 2014). Several observational studies show that stomach fullness of Delta Smelt varies regionally, increases with mesozooplankton abundance, and increases with tidal wetland proximity, indicating that individuals would consume more prey if conditions were more suitable or prey more available (Hammock et al., 2015, 2017, 2019a).

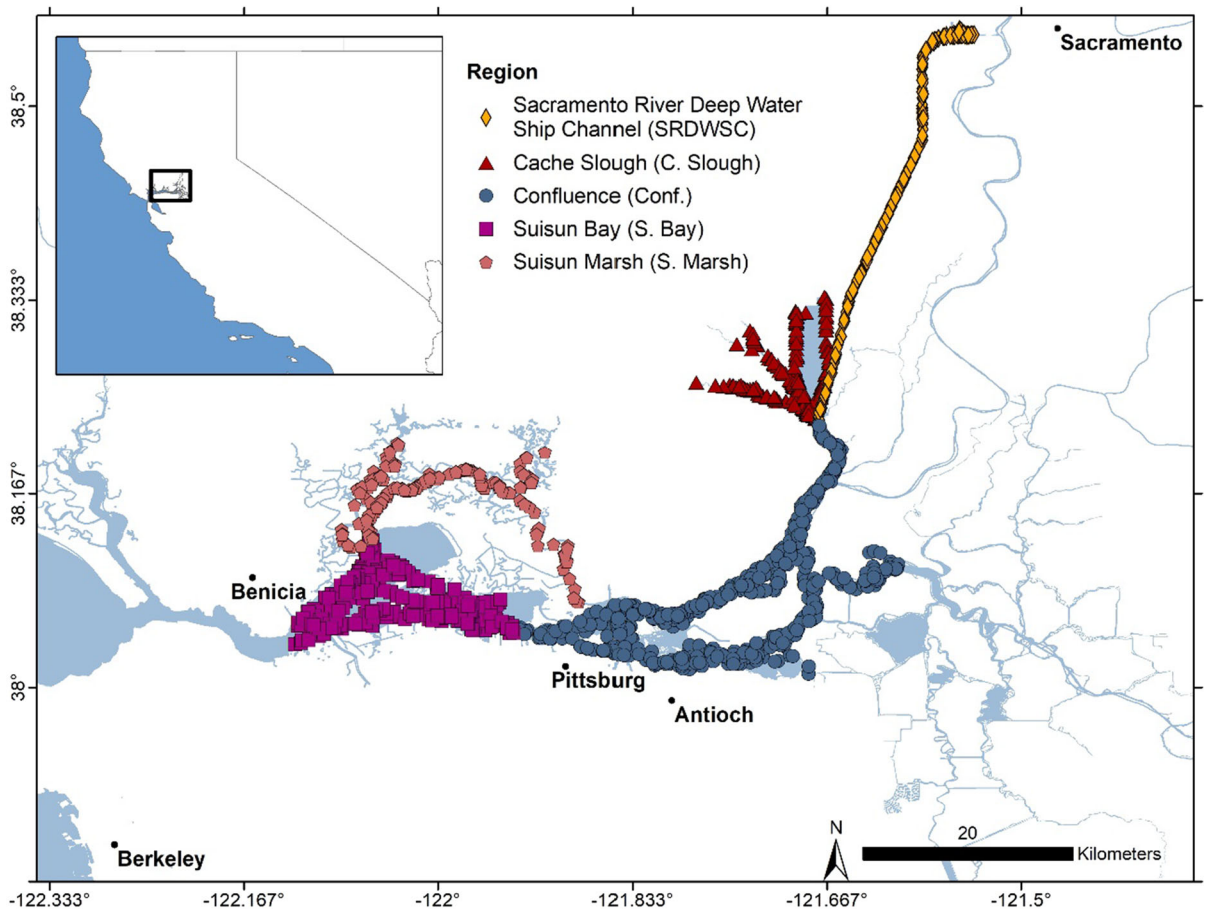

Fig. 2 Study area within the Sacramento-San Joaquin Delta and San Francisco Estuary (SFE; CA, USA). The map depicts the five regions from which Delta Smelt were collected and compared in terms of HSI and CF. Each point represents an EDSM trawl site. CDFW fish were collected from the same five regions

While much is known regarding the environmental conditions associated with Delta Smelt abundance, far less is known regarding the influence of environmental conditions on Delta Smelt condition. Here, we used a nine-year collection of Delta Smelt to examine spatio-temporal patterns and predictors of the species' condition throughout the upper SFE. The study period encompassed a wide range in hydrologic conditions in California, from wet years (2011, 2017, 2019) to critically dry (2014–2015), based on classifications by California Department of Water Resources (Fig. 1B). The study has two major objectives. In objective one, we describe the influence of region, season, and year-class on condition of Delta Smelt collected from 2011 through 2019 (i.e., spatio-temporal models). Based on previous studies, we hypothesized that Delta Smelt condition would vary regionally, and be lowest during fall and during drought years (Bennett, 2005; Feyrer et al., 2011; Hammock et al., 2015). In objective two, we explore the predictors of Delta Smelt condition to better understand its spatio-temporal drivers (i.e., environmental models). We hypothesized that Delta Smelt would exhibit relatively poor condition at temperatures above $\sim$ 20 °C, at low turbidities ($<$ 12 NTU), and in fresh water, where foraging is depressed much of the year (Bennett, 2005; Sommer & Mejia, 2013; Hasenbein et al., 2016; Hammock et al., 2017, 2019a; Lewis et al., 2021). We further hypothesized that Delta Smelt condition would decline with decreased phytoplankton abundance, decreased zooplankton biomass, greater distance to tidal wetlands, and under low outflow conditions (Bennett, 2005; Feyrer et al., 2011; Hammock et al., 2017, 2019a). By quantifying how Delta Smelt condition varies in space

and time, and in relation to environmental variation, we aim to inform management efforts to conserve the species. Proposed and ongoing efforts include fall reservoir releases to shift the salinity field seaward, tidal wetland restoration to improve habitat quality and prey availability, and operation of salinity control gates to freshen Suisun Marsh, a region relatively rich in tidal wetlands (Brown, 2003; USFWS, 2008, 2019; CNRA, 2016; Sommer et al., 2020).

Materials and methods

We focused on two indicators of Delta Smelt condition: Hepatosomatic index (HSI; the percentage of body weight comprised by the liver) and Condition factor (CF; body weight divided by fork length cubed; Bolger & Connolly, 1989). We examined HSI and CF for four main reasons. First, both variables are widely used indicators of the general condition of fish, with HSI generally indicating the availability of shorter-term energy reserves (i.e., liver glycogen), protein, and lipid, and CF generally associated with muscle, protein and mesenteric fat (Boujard & Leatherland, 1992; Zamal & Ollevier, 1995; De Pedro et al., 2003; Hards et al., 2019). Second, in a recent experiment on cultured Delta Smelt, HSI was the most sensitive to fasting of the many biomarkers examined, becoming significantly depressed after four days without food at 15.9 °C, and CF was also relatively sensitive to food limitation, becoming significantly depressed after 7 days of fasting (Hammock et al., 2020). The relative sensitivities of these indices make them ideal for assessing environmental conditions, because individuals have less time for movement to homogenize their responses to local conditions. Third, other known stressors in the SFE, such as contaminants and adverse water temperatures, are also known to affect HSI and CF, hence HSI and CF are considered good indicators of general habitat suitability (Bolger & Connolly, 1989; Verma & Prakash, 2019; Morrison et al., 2020). Finally, HSI and CF can correlate with survival, reproductive fitness, and growth, such that changes in both metrics are likely to influence abundance (e.g., Ruthsatz et al., 2018).

HSI and CF were calculated from Delta Smelt collected during fish monitoring surveys conducted by California Department of Fish and Wildlife (CDFW) and United States Fish and Wildlife Service (USFWS). CDFW provided our study with fish at juvenile through adult life-stages throughout the study, from August 2011 through December 2019, collected during three surveys: Fall Midwater Trawl, Spring Kodiak Trawl, and Summer Townet Survey (Honey et al., 2004; Feyrer et al., 2007; Sommer & Mejia, 2013; Damon et al., 2016). However, Delta Smelt became nearly undetectable by CDFW surveys beginning in 2014. Consequently, USFWS began their own, more intensive effort in 2017, the Enhanced Delta Smelt Monitoring survey (EDSM; USFWS et al., 2020). EDSM specifically targets Delta Smelt and provided our study with juvenile through sub-adult life stages from August through November 2017, and July through November 2018 and 2019. Thus, sharply declining abundance led to low sample sizes through the middle of the study (2014–2016), before increasing with the addition of the EDSM samples in 2017 (e.g., annual fall sample sizes in Table 1). Together, these surveys covered most of the contemporary range of Delta Smelt.

CDFW and USFWS preserved Delta Smelt using the same method, so although gear types varied among the four surveys it is unlikely that fish condition was affected. Moreover, focusing on a single survey was not an option due to the limited number of fish available from any single survey. Individuals that were caught in trawls were wrapped in labeled aluminum foil packets and immediately frozen in Dewar flasks of liquid nitrogen onboard survey boats. Water temperature, turbidity, specific conductivity, and GPS coordinates were recorded during the trawls and associated with individual fish in a relational database. Dewar flasks were transported to University of California, Davis (UCD) for subsequent measurement and dissection of fish as they thawed (5–10 min per fish; Teh et al., 2016). Each fish was measured for fork length and weighed on an analytical balance. The liver was excised and weighed. HSI was calculated as $HSI = W_l/W_b \times 100$ and CF was calculated as $CF = W_b/L^3 \times 100$, where W_l is liver weight (mg), W_b is the body weight (mg), and L is the fork length (mm).

Statistical analysis

To avoid conflating habitat quality with reproductive maturity, all female fish collected during January, February, and March were excluded from analyses (females collected from June-December were left in

Table 1 Mean Chl *a* (µg/L), water temperature (Temp; °C), zooplankton biomass density (Zoop; mg/m^3), tidal wetland area (TW; km^2), and sample size (after removal of sexually mature females) by region, season, and year-class (YC)

Region/season/year-class	Chl *a*	Temp	Zoop	TW	n
C. Slough	4.4	16.8	109.7	0.5	126
SRDWSC	3.7	16.9	150.2	1.7	533
Conf	2.7	15.1	155.5	1.6	461
Suisun Bay	2.2	16.8	71.4	2.2	292
Suisun Marsh	3.0	13.6	20.3	6.8	215
Summer	3.8	21.5	232.1	1.7	490
Fall	3.3	18.1	83.1	1.9	374
Winter	1.9	9.7	16.7	3.1	603
Spring	4.5	13.9	74.2	2.6	160
11–12	2.4	17.3	43.2	3.1	121
12–13	13.6	17.0	198.2	2.0	34
13–14	1.9	17.6	104.6	2.4	11
14–15	2.9	21.1	219.6	0.5	8
15–16	2.1	22.2	178.0	0.4	5
16–17	1.5	16.9	35.9	0.6	7
17–18	2.1	17.9	139.1	1.9	81
18–19	2.2	19.4	120.6	0.6	98
19–20	2.7	19.4	120.6	1.4	13

The year-class data only include fish collected during fall (September–November), while the regional and seasonal means include all data. Note that the means represent the average conditions that the fish were experiencing at collection, and do not necessarily represent the region, seasons, and years overall. Water temperature was measured during trawls and tidal wetland area was estimated using ArcGIS (Hammock et al., 2019a). Chl *a* and zooplankton biomass were not measured during trawls, but obtained from ancillary studies

the analyses; Fig. S1). These exclusions eliminated a clear relationship between HSI and fork length (Fig. S1C). One fish with a liver enlarged by a tumor was also excluded. In the resulting dataset, HSI and CF were poorly correlated (Fig. S2) and therefore provide unique information and required separate analyses. The analyses of HSI and CF were divided into two parts: spatio-temporal and environmental models. The spatio-temporal models are purely descriptive, whereas the environmental models attempt to characterize the mechanisms underlying the spatio-temporal patterns in HSI and CF. Individuals in the dataset ranged in fork length from 21 to 90 mm and females ranged in sexual maturity from immature to early vitellogenic stage (males were not assessed for sexual maturity; Kurobe et al., 2016).

Spatio-temporal models

Fish were divided into five regions, four seasons, and nine year-classes based on collection location and date. These categories were kept coarse to maintain a sufficient number of samples within each category (e.g., season rather than month; Table S1). The regions analyzed encompass the bulk of the range of Delta Smelt and were described and justified previously (Hammock et al., 2015; Teh et al., 2020). The regions include the Cache Slough Complex, Sacramento River Deep Water Ship Channel (SRDWSC), the confluence of the Sacramento and San Joaquin rivers (the Confluence), Suisun Marsh, and Suisun Bay (Fig. 2). Briefly, the Cache Slough Complex is a freshwater, relatively shallow area in the North Delta. The SRDWSC is also fresh, and was constructed to allow shipping to access the Port of West Sacramento. The Confluence ranges from fresh to brackish and deep to shallow depending on the tide, freshwater outflow and location. Suisun Marsh is a brackish region with relatively intact tidal wetland habitat. Suisun Bay is an open water, brackish region that has both deep and shallow areas. Fish were divided into seasons based on collection date (summer: June–August, fall:

September–November, winter: December-February, and spring: March–May). Year-classes began in June (juveniles) and ended the following May (adults), except in a few cases where adult fish from the previous year-class were collected in June (Damon et al., 2016). Large differences in size made these year-class classifications clear. Larvae were not collected as part of this study.

HSI and CF were compared among regions and seasons with mixed model ANOVAs fit to the entire dataset (HSI ~ region + season and CF ~ region + season). Year-class was included as the random effect in both models to account for possible year effects and sample size imbalance among year-classes. Sample sizes were 1628 and 1749 for the HSI and CF ANOVAs, respectively. Year-class was analyzed separately using ANOVAs for both HSI and CF, using only fish collected during fall (HSI ~ year-class, CF ~ year-class). Only the fall model was fit to a subset of the data, all other models in this study were fit to the entire dataset. We focused on fall because this season is thought to be relatively stressful to Delta Smelt due to low-flow conditions (Moyle et al., 1992; Bennett, 2005; Feyrer et al., 2011), a hypothesis which was confirmed by the seasonal ANOVAs of the full dataset (Fig. 3). We reasoned that if fall was generally stressful due to low flow, condition indices should improve during wet years. Residual plots were checked for conformity with test assumptions. Significant results for the ANOVAs ($P < 0.05$) were followed by Tukey Honestly Significant Difference (HSD) mean separations. ANOVAs were performed using JMP Pro 15.

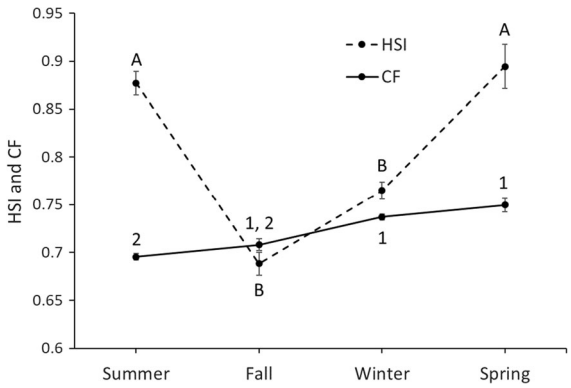

Fig. 3 Hepatosomatic index (HSI: dashed line) and condition factor (CF: solid line) by season, averaged across years. For HSI, n = 491, 374, 603, and 160 for each season, left to right. For CF, n = 607, 378, 603, and 161, left to right. Differing letters represent significantly different HSI means and differing numbers represent significantly different CF means ($P < 0.05$; Tukey HSD)

Environmental models

To identify and quantify drivers of spatio-temporal variation in HSI and CF, a series of multiple regression models were compared. Predictors of HSI (n = 1483) and CF (n = 1604) used in the model comparisons included three variables recorded during trawls: salinity, water temperature, and turbidity. We also examined five additional variables: Chlorophyll *a* concentration (Chl *a*), zooplankton biomass, tidal wetland area, the *X*2 index (distance from the Golden Gate Bridge [Pacific Ocean] to the bottom isohaline of 2; Jassby et al., 1995), and fork length, which are described below. A correlation matrix of the predictor variables was examined to check for independence ($r < 0.53$ for all pairs), including the relationship between zooplankton biomass and Chl *a* (r = 0.29). The 'dredge' function from the R package MuMIn was used to fit all possible main effects models (Barton, 2009). Models were compared using Akaike information criterion corrected for small sample size (AIC_c; Burnham & Anderson, 2002). The five top-ranked HSI and CF models, plus the intercept model, are presented in the results. We also report the effect size for each predictor, the ΔAIC_c of the selected model with and without each predictor, and the P value for each predictor. Effect sizes were calculated as the percent change in model prediction from the min to the max of each predictor, with the other predictors held constant. The error distributions were Gaussian. However, because HSI is a percentage and is therefore not normally distributed, we fit the same set of models to liver weight as the response variable ($\log_{10}$-transformed), with individual body weight as a predictor. The HSI and liver weight model comparisons yielded nearly identical results, so the HSI model comparison is presented here.

Zooplankton biomass was estimated using zooplankton abundance data from five sources: Environmental Monitoring Program Zooplankton Survey, 20-mm Survey, Summer Townet Survey, Fall Midwater Trawl, and a UCD/United States Bureau of Reclamation (USBR) project that monitored

zooplankton in the SRDWSC. The first four datasets were merged following Bashevkin et al. (2020) and then combined with the UCD/USBR-SRDWSC data. See Kayfetz et al. (2020) for full details of the collection and enumeration methods for the first four datasets, but in brief: A 160-µm mesh zooplankton net was mounted on a steel sled and towed obliquely through the water column for ten minutes at sites throughout the SFE. Samples were preserved in formalin and all zooplankton were identified to the lowest feasible taxon at the CDFW Laboratory in Stockton, CA. Samples were identified in 1-ml aliquots on Sedgewick-rafter slides with a concentration of 200–400 organisms per slide. Between 5 and 20 slides were processed per sample. Methods were similar for the UCD/USBR surveys. A vertical tow of the water column was made using a 150-µm mesh zooplankton tow net with a retrieval rate of $\sim$ 0.33 m/s. Samples were preserved in Lugol's solution and zooplankton were identified to the lowest feasible taxon by BSA Environmental Services (Beechwood, OH). Zooplankton identifications were made and abundances measured on three 1-ml aliquots using a Wilovert inverted microscope at 100× with a target tally of 200–400 specimens.

All zooplankton samples collected within a region over the course of a month were used to calculate a monthly regional mean of zooplankton biomass to use as an indicator of Delta Smelt prey availability (Fig. 2). Zooplankton biomass only included taxa common in Delta Smelt diets; all copepods and Cladocera were included, while barnacle nauplii, rotifers, and crab zoea were excluded (Slater & Baxter, 2014). Abundance was converted to biomass (mg carbon) by multiplying by life-stage specific factors from the literature (references and conversion factors in Kayfetz et al., 2020). We note that the estimates of zooplankton biomass leave out important prey for which data were less available, such as amphipods, mysids, and larval fish (Hammock et al., 2019a). Therefore, it is only a proxy for prey availability, and likely is more applicable to younger, more zooplanktivorous fish than for older fish that eat larger prey in addition to zooplankton.

Tidal wetland area was defined as the area of tidal wetlands within a 2-km radius from where each fish was collected and was calculated using ArcGIS as described in Hammock et al. (2019a). The *X*2 index data were downloaded from the California Department of Water Resources Dayflow website: https://data.cnra.ca.gov/dataset/dayflow. Of the eight predictors examined, the *X*2 index is under the greatest human control and is therefore of particular interest to scientists and managers. *X*2 declines with increased flow as the salinity field shifts seaward. Its position is regulated for several reasons, including to avoid contaminating freshwater exports with saltwater from the Pacific Ocean, and to benefit native fishes, including Delta Smelt (Gartrell et al., 2017). Fork length was included as a possible predictor in the CF model comparison to ensure that seasonal changes were not simply due to CF changing with maturation. To ensure that any influence of *X*2 was not obscured by its inclusion in a complex model (e.g., if *X*2 appeared less important because tidal wetland area was included in the same model), we also fit HSI and CF to *X*2 individually (see Supplemental Results).

Chl *a* was measured monthly throughout the range of Delta Smelt by a variety of projects. We merged these data to create a 'Chl *a* index' variable. For 94% of the fish in our analysis, we obtained Chl *a* specific to the five regions in our study (Fig. 2), measured during the same month as the fish were collected. The data sources were the Discrete Water Quality Environmental Monitoring Program (IEP, 2020), the UCD/USBR-SRDWSC project (which has paired Chl *a* and zooplankton data), and the Liberty Island Study of primary productivity in tidal wetlands by P. Lehman (CA Department of Water Resources). In cases with multiple Chl *a* measurements collected from the same region and month, the measurements were averaged. For the remaining 6% of fish, which were collected in the Cache Slough Complex and the SRDWSC where Chl *a* was not routinely measured, an average of the freshwater Chl *a* measurements by EMP was used (salinity < 0.55), specific to the month of collection. We ran the model comparisons both with and without the 6% of fish lacking associated Chl *a* data and obtained nearly identical results; thus, we present the results that include all fish.

In preliminary analyses, water temperature, salinity, turbidity, and *X*2 were modeled both as continuous variables and binned in several different ways to account for potential nonlinearities and thresholds. The most predictive variables (lowest AIC_c), and what we present here, were water temperature divided into six bins (7–10, 10–13, 13–16, 16–19, 19–22, and 22–26 °C), salinity divided into fresh and brackish

bins (< or > 0.55 salinity), turbidity divided into two bins (< or > 80 NTU), and *X*2 divided into two bins (< and > 80 km). The salinity threshold was used in previous Delta Smelt studies, including as a predictor of foraging success by Hammock et al. (2017) and as a cutoff between fresh and brackish water life history strategies by Hobbs et al. (2019). The thresholds for turbidity and *X*2 were initially selected because Delta Smelt foraging success declines at high turbidity (> 80 NTU; Hasenbein et al., 2016; Hammock et al., 2019a), and Delta Smelt habitat availability has an inflection point at 80 km (i.e., physical habitat volume declines rapidly above an *X*2 of 80 km, and vice versa; Feyrer et al., 2011). Chl *a*, fork length, and zooplankton biomass were modeled as continuous, linear predictors.

Zooplankton data were unavailable for 102 fish collected in the SRDWSC and the Cache Slough Complex. Analyses run with and without the zooplankton biomass variable yielded nearly identical results for the other variables. Therefore, the analysis with zooplankton biomass (and without the 102 fish) is presented here. These exclusions left sample sizes of 1483 and 1604 Delta Smelt for the HSI and CF model comparisons, respectively.

Results

Spatio-temporal models

There were significant differences in HSI among the five regions (ANOVA, $F_{4,\ 1611} = 11.73$, $P < 0.0001$; Fig. 4A). The highest HSI means occurred in the Cache Slough Complex and Suisun Marsh, with an intermediate mean in the SRDWSC, and the lowest means in the Confluence and Suisun Bay (Fig. 4A). The difference between the highest and lowest regional means was 24%. There was also a significant effect of season on HSI (ANOVA, $F_{3,\ 1570} = 30.16$, $P < 0.0001$; Fig. 3). Delta Smelt exhibited the lowest mean HSI during fall, an intermediate value in winter, and the highest values in spring and summer. The difference between the highest and lowest mean was 30.0% (i.e., between spring and fall).

There were significant differences among regions in CF (ANOVA, $F_{4,\ 1722} = 6.32$, $P < 0.0001$; Fig. 4B), which exhibited a similar pattern to HSI. The highest CF means were observed in the Cache Slough Complex and Suisun Marsh, the SRDWSC and Suisun Bay means were intermediate, and the Confluence had the lowest mean CF (Fig. 4B). The difference between the highest and the lowest regional mean was 5.6%. There was also a significant effect of season on CF (ANOVA, $F_{3,\ 1671} = 4.72$, $P = 0.0028$; Fig. 3), with fish collected during summer and fall having the lowest and next lowest CFs, respectively. Fish collected from winter and spring had the highest CFs. The difference between the highest (spring) and lowest (summer) mean was 8.0%.

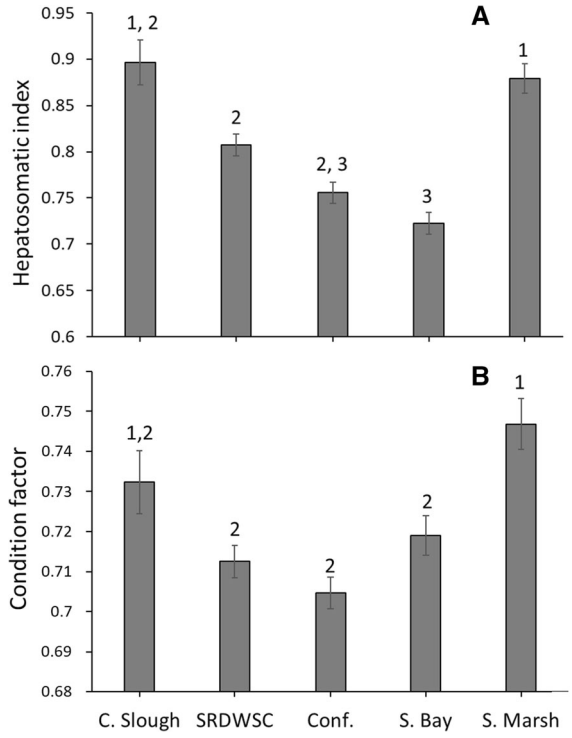

Fig. 4 Mean (± SE) HSI (**A**) and CF (**B**) by region, averaged across all seasons. For HSI, sample sizes for each region were 126, 533, 461, 293, and 215, left to right. For CF, sample sizes for each region were 130, 577, 520, 304, and 218, left to right. Note that only 5 of the 126 fish collected from the Cache Slough Complex were from the fall, the season with the lowest mean HSI (Fig. 3). Differing numbers above the bars denote significant differences based on Tukey HSD tests

Fall HSI showed significant variation among year classes (ANOVA, $F_{8,\ 365} = 6.76$, $P < 0.0001$), as did CF (ANOVA, $F_{8,\ 369} = 22.86$, $P < 0.0001$). However, fish collected during drier years did not display poorer condition than in other years (Table 2). For example, the 2019/20 year-class, classified as 'wet', had the lowest mean HSI and CF of any year. While the

Table 2 Fall HSI and CF mean comparisons following the significant ANOVA

Year-class	Water year type	HSI	HSI group	CF	CF group
2011–12	Wet	0.744	A, B	0.786	A
2012–13	Below normal	0.872	A	0.763	A, B
2013–14	Dry	0.685	A, B, C	0.675	B, C, D
2014–15	Critically dry	0.670	A, B, C	0.680	A, B, C, D
2015–16	Critically dry	0.692	A, B, C	0.619	B, C, D
2016–17	Below normal	0.597	A, B, C	0.701	A, B, C, D
2017–18	Wet	0.662	B, C	0.619	D
2018–19	Below normal	0.603	C	0.686	C
2019–20	Wet	0.555	B, C	0.598	C, D

The water year type refers to CA Department of Water Resources water year classifications for the Sacramento River Valley. Year-classes with the same letter are not significantly different (Tukey HSD)

highest CF did occur in 2011/2012, a wet year, the highest HSI occurred in 2012/2013, a below normal year. Rather than responding to water year type, fall HSI and CF instead declined steadily over the nine-year study (Fig. 1C). The difference between the highest mean fall HSI (2012–13 year-class) and the lowest (2019–2020) was 57%. Fall CF also declined over the nine-year study, and the difference between the highest mean fall CF (2011–12 year-class) and the lowest (2019–2020) was 10.3%.

Environmental models

The top-ranked HSI model included seven predictor variables (Table 3). Chl *a*, the predictor with the largest effect size, was associated with a 54% increase in HSI (Table 4). HSI also increased substantially with zooplankton biomass (39%) and tidal wetland area (22%; Table 4). Temperature was the fourth most important predictor, with the highest HSI occurring between 10 and 13 °C, and the lowest between 16 and 19 °C (Fig. 5; Table 4). HSI also decreased at turbidities over 80 NTU, in brackish habitat (> 0.55 salinity), and at $X2 > 80$ km (i.e., HSI declined under low outflow conditions). These last three variables had relatively small effect sizes ($< 10\%$, Table 4, Fig. S3).

There was parity among the top-ranked CF models, so we selected the most parsimonious of the five highest-ranked models, namely the second ranked model (Table 5). Temperature and Chl *a* were by far

Table 3 Comparison of the top five environmental HSI models, plus the intercept model

Model	df	ΔAIC_c	Weight
~ Chl *a* + Sal + Temp + Turb + TW + *X*2 + Z	13	0.00	0.76
~ Chl *a* + Sal + Temp + TW + *X*2 + Z	12	2.47	0.22
~ Chl *a* + Sal + Temp + Turb + TW + Z	12	9.64	0.01
~ Chl *a* + Sal + Temp + TW + Z	11	10.21	0.00
~ Chl *a* + Temp Turb + TW + Z	12	11.53	0.00
~ Intercept	2	206.5	< 0.0001

The first-ranked model was selected. Chl *a* is chlorophyll *a* as a continuous variable, 'Sal' is a dummy variable for salinity (< or > 0.55), 'Temp' is temperature bin (7–10, 10–13, 13–16, 16–19, 19–22, 22–26 °C), 'Turb' is a dummy variable for turbidity (< or > 80 NTU), 'TW' is tidal wetland area, '*X*2' is a dummy variable for the *X*2 index (< or > 80 km), and '*Z*' is zooplankton biomass

df degrees of freedom, ΔAIC_c difference between model of interest and top-ranked model in Akaike Information Criterion Units corrected for small sample size, *Weight* AIC_c weight.

Table 4 Effect size, ΔAIC_c, and *P* value for each variable in the selected environmental HSI and CF models

	Response	Predictor						
		Chl *a*	Zoop	Wetlands	Temp	Turb	Sal	*X2*
Effect size	HSI	54.3 (+)	38.7 (+)	21.9 (+)	16.9 (NA)	8.6 (−)	7.7 (−)	6.3 (−)
ΔAIC_c	HSI	52.2	27.8	41.0	19.2	2.5	11.5	9.6
P value	HSI	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0102	0.0002	< 0.0001
Effect size	CF	7.8 (+)	–	3.7 (+)	13.0 (NA)	–	–	2.8 (+)
ΔAIC_c	CF	7.1	–	10.5	163.7	–	–	16.0
P value	CF	0.0002	–	0.0025	< 0.0001	–	–	< 0.0001

Effect sizes were calculated as the percent change in model prediction from the min to the max of each predictor, with the other predictors held constant. ΔAIC_c is the difference in AIC_c between the selected model with and without each variable. Chl *a* is chlorophyll *a* as a continuous variable, 'Zoop' is zooplankton biomass density, 'Wetlands' is tidal wetland area, Temp is temperature bin (7–10, 10–13, 13–16, 16–19, 19–22, 22–26 °C), 'Turb' is a turbidity dummy variable (< or > 80 NTU), 'Sal' is a salinity dummy variable for fresh vs brackish (< or > 0.55), and 'X2' is a dummy variable for the X2 index (< or > 80 km). The sign in parentheses indicates the sign of each parameter, if applicable

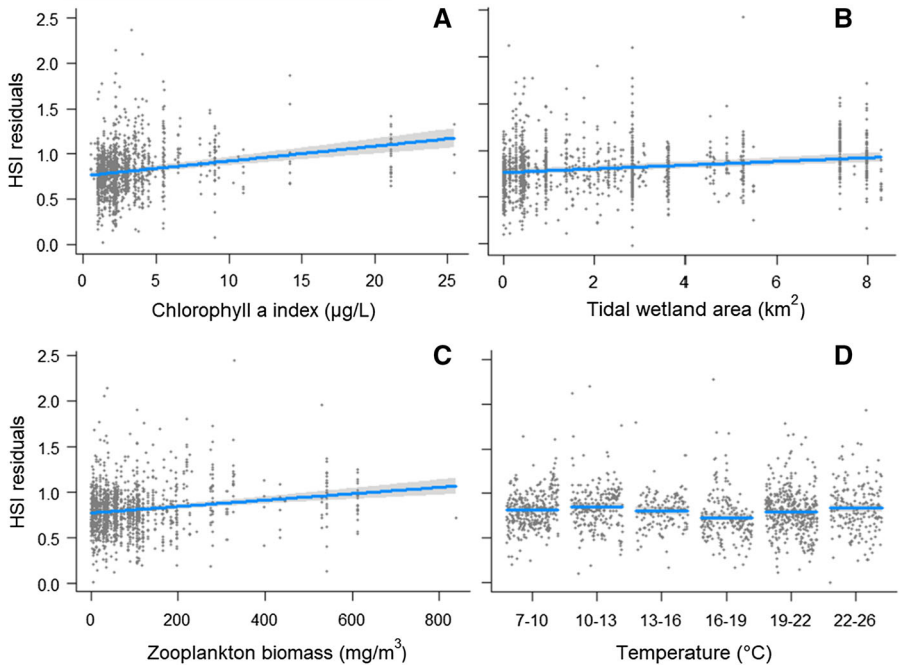

Fig. 5 Partial residuals from the selected (top-ranked) environmental HSI model (Table 3). Fish from all seasons were included in the analysis. The four variables with the largest effect sizes are presented here; the other three variables are displayed in Fig. S3 (effect sizes in Table 4). The shaded regions are 95% confidence intervals of the model. Water temperature was binned to capture possible nonlinearities

the most important predictors, accounting for effect sizes of 13.0 and 7.8%, respectively (Table 4). CF peaked at 10–13 °C and increased with Chl *a*. CF also increased with tidal wetland area, but to a lesser extent (Fig. 6; Table 4). CF was higher under lower outflow conditions (*X2* > 80; Fig. 6D), the opposite of *X2*'s influence on HSI. Fork length was not a significant predictor of CF (Fig. S4).

Table 5 Model comparison of the top five environmental CF models, plus the intercept model

Model	df	ΔAIC_c	Weight
~ Chl *a* + Temp + TW + *X*2 + Z	11	0.00	0.21
~ Chl *a* + Temp + TW + *X*2	10	0.37	0.18
~ Chl *a* + Sal + Temp + TW + *X*2 + Z	12	0.39	0.18
~ Chl *a* + Sal + Temp + TW + *X*2	11	0.82	0.14
~ Chl *a* + Temp + TW + X2 + Z + Turb	12	1.93	0.08
~ Intercept	2	204.7	< 0.0001

The second-ranked model was selected. Chl *a* is chlorophyll *a* as a continuous variable, 'Sal' is a dummy variable for salinity (< or > 0.55), 'Temp' is temperature bin (7–10, 10–13, 13–16, 16–19, 19–22, 22–26 °C), 'Turb' is a dummy variable for turbidity (< or > 80 NTU), 'TW' is tidal wetland area, '*X*2' is a dummy variable for the *X*2 index (< or > 80 km), and '*Z*' is zooplankton biomass

df degrees of freedom, ΔAIC_c difference between model of interest and top-ranked model in Akaike Information Criterion Units corrected for small sample size, *Weight* AIC_c weight

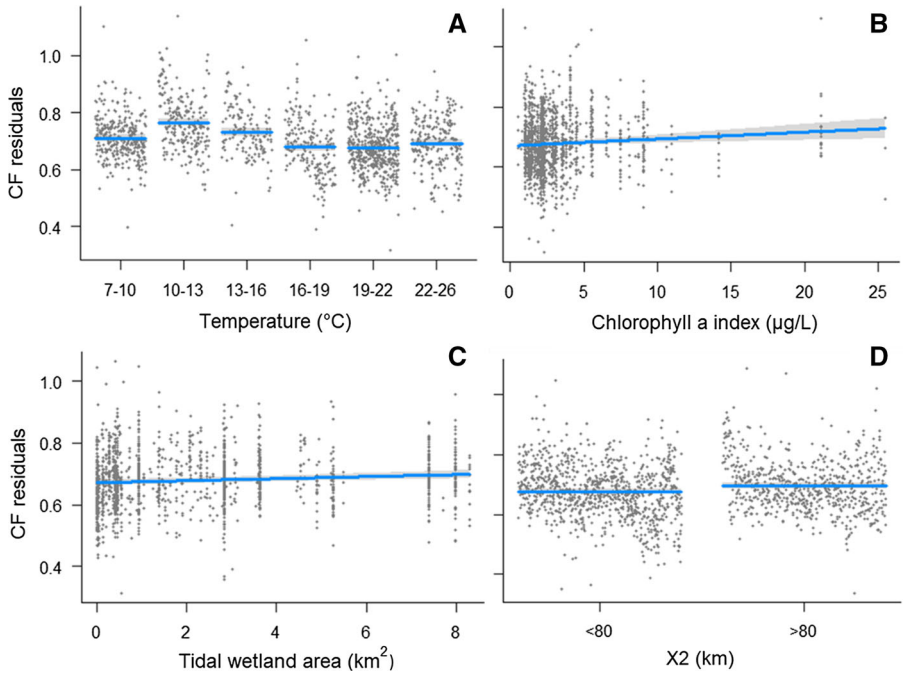

Fig. 6 Partial residuals for each variable in the selected (2nd ranked) environmental CF model (Table 5). Fish from all seasons were included in this analysis. The shaded regions are 95% confidence intervals of the model. Temperature was binned to detect possible nonlinearities, and *X*2 was binned because Delta Smelt habitat volume shrinks rapidly above an *X*2 of 80 km. Effect sizes are in Table 4

Habitat characterization

Means by region, season, and year-class (during fall only) of the four most important HSI and CF predictors are presented in Table 1, including Chl *a*, water temperature, zooplankton biomass, and tidal wetland area. These means reflect what the fish were experiencing at the time of collection, and do not necessarily represent the region, season or year-class overall. Notable results include relatively high Chl *a* and zooplankton biomass and low temperature during fall 2012, a period that coincided with collections of relatively good condition fish (Fig. 1C, Table 1). Summer and fall, the seasons with the worst

condition fish, had considerably higher temperatures and lower Chl *a* concentrations than spring, when fish were in relatively good condition (Fig. 3).

Discussion

Delta Smelt is nearing extinction in the wild, and a large body of work suggests that food limitation is a major contributor to its decline (Kimmerer, 2008; Maunder & Deriso, 2011; Hamilton & Murphy, 2018). In a recent laboratory study, HSI and CF responded relatively rapidly to food limitation in Delta Smelt, and are therefore sensitive metrics for evaluating the quality of habitat from which individuals are collected (Hammock et al., 2020). In objective one of our study, we assessed the spatio-temporal variation in HSI and CF of more than 1600 Delta Smelt collected over nine years (2011–2019). Relatively poor condition indices were observed in Suisun Bay and the Confluence (Fig. 4), and during fall (Fig. 3). Relatively good condition indices were observed in Suisun Marsh and C. Slough (Fig. 4), and during spring (Fig. 3). We also observed a steady decline in both HSI and CF during fall over the nine-year study, a period of tremendous hydrologic variability (Fig. 1B and C). Given that HSI and CF are tightly coupled to fitness and survival (e.g., Robinson et al., 2008; Mion et al., 2018), which dictate the population dynamics of fishes (Maunder & Starr, 2003; Rose et al., 2013), the downward trajectory in both condition indices is alarming.

In objective two, we identified and quantified predictors of HSI and CF using model comparisons. Conditions that were most strongly associated with improved Delta Smelt condition indices were high Chl *a*, low water temperature (10–13 °C), high zooplankton biomass, and proximity to tidal wetlands (Figs. 5 and 6). The range in condition indices of wild Delta Smelt observed in this study are likely to be ecologically meaningful because the range in HSI and CF of wild fish spanned roughly 2/3 of the difference between fully-fed and severely-starved hatchery Delta Smelt (i.e., fasted three weeks at 15.9 °C; Hammock et al., 2020). We note that although HSI varied more than CF with its predictors (i.e., the effect sizes were larger; Table 4), the HSI results should not be considered more important because a far smaller change in CF than HSI indicates an equivalent level of starvation (Hammock et al., 2020). For example, 21 days of fasting resulted in significant declines in both HSI and CF, but the effect sizes were 131% and 32%, respectively (Hammock et al., 2020). Although turbidities less than 80 NTU improved HSI somewhat, we found no change in HSI and CF from 0–80 NTU. The 0–80 NTU turbidity range also did not influence Delta Smelt foraging success (Hammock et al., 2019a), suggesting that the decline in catch at turbidities below 12 NTU is unrelated to stressors that affect condition indices, such as food limitation (Sommer & Mejia, 2013).

The regional patterns we observed in HSI and CF are consistent with previous studies. Hammock et al. (2015) reported depressed stomach fullness, RNA–DNA ratio in muscle, HSI, and CF in Suisun Bay and the Confluence, whereas fish collected from Suisun Marsh had relatively good nutritional and condition indices. Here we observed this same pattern in HSI and CF (Fig. 4), but over more years and seven times the sample size. Hobbs et al. (2006) also reported better Delta Smelt feeding success in the north of Suisun Bay, near Suisun Marsh. The Cache Slough Complex appeared to be beneficial to Delta Smelt condition, which is consistent with several studies indicating that the region is an important area for Delta Smelt and other native fishes due to its relatively high productivity, zooplankton abundance and historical spawning of Delta Smelt (Sommer et al., 2011; Sommer & Mejia, 2013; Kimmerer et al., 2018a). The model comparison suggests that causes for regional differences may include low Chl *a* in Suisun Bay and the Confluence, and low zooplankton biomass in Suisun Bay (Table 1). Although zooplankton biomass was even lower in Suisun Marsh (Table 1), this may have been offset by lower water temperature and the prevalence of tidal wetlands in the region, which improves foraging success of Delta Smelt (Table 1; Bever et al., 2016; Hammock et al., 2019a; Sommer et al., 2020). For example, tidal wetlands provide key nursery habitat for larval fishes, an important prey item for Delta Smelt that was not captured by our zooplankton biomass metric (Beck et al., 2001; Hammock et al., 2019a).

Although our results are consistent with the hypothesis of a survival bottleneck during summer into fall (Fig. 3), they are less consistent with the proposed mechanism of decreased access to more seaward habitat (Moyle et al., 1992; Bennett, 2005; USFWS, 2008; Feyrer et al., 2011). As outflow

declines, salt water encroaches on the seaward portions of Delta Smelt habitat, restricting the species to more channelized habitat upstream (Feyrer et al., 2011). This mechanism is the basis for targeting late summer and fall with several management actions designed to benefit the species, including reservoir releases and freshening Suisun Marsh with tidally timed salinity control gate operations (Sommer et al., 2020). In our study, while an improvement in HSI for fish collected in fresh water was observed, the effect size was modest (Table 4). In addition, *X*2 had only a minor influence on HSI and CF and its effects were in opposing directions, even when *X*2 was used as the only predictor (Figs. 6D and S3D, Supplemental Results). In addition, despite the tremendous range in hydrologic conditions in the SFE during the study, HSI and CF steadily declined (Fig. 1). In fact, fall 2019 exhibited both the lowest *X*2 (wettest conditions) and poorest condition Delta Smelt in our study (Fig. 1). Rather than being driven by low outflow, the modeling results suggest that fall condition indices of Delta Smelt declined over the nine-year study due to some combination of low pelagic productivity and high water temperatures.

The lack of a clear relationship between *X*2 and Delta Smelt condition is consistent with other studies that found an unclear or inconsistent relationship between Delta Smelt population indices and outflow or *X*2 (e.g., Stevens & Miller, 1983; Kimmerer, 2002; Dege & Brown, 2003; Bennett, 2005; Miller et al., 2012). However, our results present an apparent paradox. While *X*2 does not correlate with Delta Smelt condition, two variables with well established relationships to *X*2 did correlate with improved condition: collection from Suisun Marsh and proximity to tidal wetlands. That is, Delta Smelt have greater access to Suisun Marsh and tidal wetlands as outflow increases, but *X*2 had little overall influence on condition, even when modeled on its own. One possibility is that while high outflow provides Delta Smelt access to higher quality habitat, it may also reduce phytoplankton and zooplankton abundance by advection. Another possibility is that low *X*2 increases accessibility to both high and low quality habitat, possibly offsetting the benefits of low *X*2 to Delta Smelt. In any case, our results suggest that low flow is not the primary driver of poor condition indices of Delta Smelt during summer and fall. Instead, the seasonal analysis, in combination with the environmental modeling, suggests that the poor CF during summer was driven largely by high water temperature, whereas poor HSI during fall was driven more by food web related factors (Chl *a*, zooplankton, and tidal wetland access). We note, however, that abundance of Delta Smelt is generally suppressed during dry years (Fig. 1), suggesting that increased flow may benefit Delta Smelt abundance, even if it does not appear to improve condition.

None of the predictors of HSI and CF is necessarily causative, but Chl *a* seems especially likely to be a proxy for another key variable. Condition indices may have increased with Chl *a* because the chronically low secondary productivity of the SFE was stimulated by increased phytoplankton concentrations, leading to improved foraging success and condition. For example, increased productivity is thought to explain the positive relationship between Chl *a* and larval abundance of another osmerid endemic to the SFE, the Longfin Smelt (*Spirinchus thaleichthys* Ayres, 1860; Grimaldo et al., 2017). However, the relationship between Chl *a* and zooplankton is complex. While zooplankton generally increases with Chl *a* in other systems (McCauley & Kalff 1981; Yuan & Pollard, 2018), Chl *a* is a poor predictor of zooplankton biomass in the SFE (Montgomery et al., 2015; Kimmerer et al., 2018B), and a poor predictor of production for some of the major copepods that make up Delta Smelt diets (Kimmerer et al., 2014; Slater & Baxter 2014; Jungbluth et al., 2021). Moreover, Chl *a* was a stronger predictor of HSI and CF than zooplankton biomass (Table 4), suggesting that stimulation of secondary productivity is not the primary cause for the association between Chl *a* and condition indices. Another possibility is that the energetic costs for Delta Smelt decline with longer residence times, and longer residence times also favor phytoplankton. For example, many fish avoid fast water to reduce energy expenditure (Bisson et al. 1988; Korman & Campana, 2009), including migrating Delta Smelt (Bennett & Burau 2015; Bever et al., 2016). Elevated phytoplankton levels may also improve foraging success and condition, as they do for larval Delta Smelt in captivity (Baskerville-Bridges & Lindberg 2004; Bennett & Burau, 2015; Tigan et al., 2020). Thus, elevated phytoplankton, or the conditions associated with it, appear to confer substantial benefit to Delta Smelt, but the reasons remain unclear.

Water temperature was the most important predictor of CF, peaking in the 10–13 °C range, likely because metabolic demand of Delta Smelt was low. Delta Smelt also exhibited the highest HSI at 10–13 °C, although the differences in model predictions across the temperature range were small. Lewis et al. (2021) largely corroborates our temperature results, reporting that Delta Smelt growth peaked in the 12–13 °C range, and declined rapidly over 20 °C. However, Lewis et al. (2021) does not corroborate the small but surprising secondary peak in HSI at 22–26 °C, which is likely due to another, unknown variable associated with summer, rather than a direct benefit of high water temperature on HSI (Fig. 5D). The far more pronounced influence of temperature on CF may be due to differences in the biochemical pathways underlying short versus long-term energy storage. It may indicate an evolutionary strategy that favors lipid accumulation in muscle and mesenteric fat, and muscle growth over liver glycogen accumulation at low temperatures. For example, evidence of increased energy substrate mobilization (i.e., amino acids) was reported in salmonid species after prolonged exposure to high temperatures, which could be an indication of enhanced protein catabolism (Liu et al., 2019) or a reflection of increased lipolysis or decreased lipid accumulation in muscle and mesenteric adipose tissue, as showed for Atlantic Salmon exposed to high water temperature (Kullgren et al., 2013). Given that optimal body condition occurred at 10–13 °C, which is 10–15 °C below the critical thermal maximum of hatchery Delta Smelt (Komoroske et al., 2014), it is likely that greater foraging success would increase the optimal temperature range of wild Delta Smelt, as in other fishes (e.g., Lusardi et al., 2020). Under the current, oligotrophic conditions of the SFE, however, water temperatures above 13 °C depressed Delta Smelt body condition (Fig. 6A).

Assuming that poor fall condition indices lead to depressed abundance, our study is more consistent with bottom-up rather than top-down causes of Delta Smelt declines. Predators, parasites, or disease could have depressed Delta Smelt condition directly or indirectly, but there is no evidence that any of these factors became progressively more pronounced during the study, and parasites and parasitoids are rare in wild Delta Smelt (He & Kitchell, 1990; Foott & Bigelow, 2010; Teh et al., 2020). Entrainment in the South Delta pumps, another top-down effect, could not have caused the steady, nine-year decline in fall HSI and CF (Grimaldo et al., 2021; Korman et al., 2021). However, the pumping plants may contribute to depressed condition indices via bottom-up effects if water exports suppress phytoplankton abundance (Hammock et al., 2019b). Contaminants, another stressor for Delta Smelt (Kuivila & Moon, 2004; Teh et al., 2020), could depress condition indices (e.g., Verma and Prakash, 2019). However, liver condition of Delta Smelt improved substantially from 2011 to 2016 (Teh et al., 2020), even as fall condition indices and overall abundance of Delta Smelt declined (Fig. 1A and C). In addition, the strongest evidence for contaminants in the SFE comes from the Cache Slough Complex (Werner et al., 2000; Kuivila & Moon, 2004; Weston et al., 2014, 2019), which was highly underrepresented during fall in our study. The best fall condition indices occurred in 2012 during a period of relatively high phytoplankton biomass and low water temperature for our Delta Smelt collections (Fig. 1C; Table 1). More recently, fall conditions were generally characterized by low Chl *a* and high water temperature (e.g., 2015–2016, Table 1). Thus, our results suggest that low Chl *a* and high water temperatures have contributed substantially to declines in Delta Smelt condition indices.

Management implications

The downward trajectory in fall condition indices and abundance shows a species at increasing risk of extinction, but there may be ways to improve environmental conditions for Delta Smelt. Our results are consistent with the USFWS Biological Opinion and CDFW Incidental Take Permit that specifically target fall for management actions to benefit the species (USFWS, 2019; CDFW, 2020). Increasing Chl *a* appears to be a promising option to improve conditions for Delta Smelt because it was associated with the largest improvement in HSI, and the second largest improvement in CF (Figs. 5A and 6B). In addition, increasing Chl *a* may increase zooplankton biomass (Williams & Poulet 1986; Mozetič et al., 2012), which was also associated with improved HSI (Fig. 5C). However, the success of management actions to increase Chl *a* likely depend on the composition of the primary producer community, and the method used. For example, stimulating

primary production with nutrient addition may not improve conditions for Delta Smelt if the primary producers are toxic or provide poor quality food for zooplankton (Cloern, 2018; Ger et al., 2010, 2018). The cyanobacterium *Microcystis* has increased within the SFE since 1999, and fish exposed to the microcystin toxins it produces exhibit reductions in condition indices (Lehman et al., 2010; Acuña et al., 2012a, b, 2020). Moreover, the correlation between Delta Smelt and Chl *a* concentration may not represent a food web link. For example, perhaps Delta Smelt and phytoplankton both benefit from longer hydrologic residence times, and phytoplankton does not provide a benefit itself. In this case, nutrient additions would not be expected to benefit Delta Smelt, even if they stimulate phytoplankton growth. Thus, understanding why Chl *a* correlates with improved condition indices, and whether primary producer community structure explains additional variation in condition indices, are key next steps.

Multiple outflow-related actions geared toward benefitting Delta Smelt habitat and ultimately its population are ongoing or planned (USFWS, 2008, 2019; CNRA, 2016). Operation of the salinity control gates to freshen Suisun Marsh should benefit Delta Smelt, because the region is associated with improved condition indices, as is fresh water itself (Figs. 4, S3; Sommer et al., 2020). We found little evidence that fall reservoir releases would benefit Delta Smelt because *X*2 had little net influence on the condition indices, and the poorest condition fish occurred during the fall with the lowest *X*2 (Fig. 1). This stated, high outflow years with low fall *X*2 may produce system-wide beneficial effects beyond the scope of our study (IEP-MAST, 2015). Potential for flow actions to have the desired ecological effects may increase the more their design mirrors the natural seasonal hydrograph that the system's native biota evolved with, and and fall was historically the period of the year when flow was lowest (Propst & Gido, 2004; Kiernan et al., 2012; Schultz et al., 2019). While it is uncertain to what extent managers can influence water temperature (Sommer et al., 2020), especially in a warming world, management actions to decrease water temperature during summer would almost certainly improve Delta Smelt CF (Fig. 3, Table 4). Finally, our results suggest that efforts to restore tidal wetland in the SFE should benefit Delta Smelt condition (Brown, 2003).

Conclusions

This study examined the predictors of HSI and CF of more than 1600 Delta Smelt collected over nine years (2011–2019), a period of tremendous variability in hydrodynamic and water quality conditions. The population exhibited low HSI and CF during September/October/November, supporting the long-standing hypothesis that the species is disproportionately stressed during fall. Chlorophyll *a*, zooplankton biomass, and proximity to tidal wetlands were all positively associated with HSI. Water temperature was the strongest predictor of CF, with condition peaking at 10–13 °C, and exhibiting its worst level during summer. *X*2, a correlate of outflow, was a poor predictor of Delta Smelt condition overall. Our results therefore suggest that the condition of Delta Smelt during fall declined over the nine-year study largely due to a combination of low pelagic productivity and high water temperature. Management actions to increase primary and secondary pelagic productivity, freshen Suisun Marsh during late summer and fall, restore tidal wetlands, and decrease water temperature should benefit condition indices of Delta Smelt, and therefore population fitness.

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Data availability Data and code are available upon request from the corresponding author.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

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