



Tidal Wetlands Associated with Foraging Success of Delta Smelt

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Received: 22 February 2018 / Revised: 8 January 2019 / Accepted: 9 January 2019
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Abstract

Delta smelt (*Hypomesus transpacificus*), an annual fish endemic to the San Francisco Estuary (SFE), is imperiled. One recovery strategy is to restore tidal wetlands, thereby increasing productivity and prey abundance. However, the link between tidal wetlands and foraging of delta smelt is not yet established. Using GIS, we quantified the area of tidal wetlands (km²) within a 2-km radius around sampling stations from which 1380 delta smelt were collected over 4 years (2011–2015). We quantified stomach fullness, a metric of foraging success, for each fish and regressed it against tidal wetland area, turbidity, water temperature, and other factors known to influence foraging success of delta smelt. Stomach fullness increased with both increasing tidal wetland area and increasing water temperature and was reduced at turbidities > 80 NTU. Model estimates show that stomach fullness increased twofold from the minimum (0 km²) to the maximum (4.89 km²) tidal wetland area. Of this increase, 60% was due to increased predation on larval fish, while 40% was due to increased predation on zooplankton. Delta smelt collected from areas with the highest tidal wetland area were six times more likely to have a larval fish in their guts than those collected from areas with the lowest. Thus, tidal wetland appears to confer substantial benefits to the foraging success of delta smelt, mainly via increased predation on larval fish.

Keywords GIS · Stomach fullness · Zooplankton · Turbidity · Temperature · Tidal marsh

Introduction

An apparent pattern in aquatic ecosystems is that the combination of stable substrate and sunlight elevates productivity, and this pattern holds across gradients of both salinity and current. In freshwater lakes for example, the shallow areas close to shore tend to be more productive than the surface waters offshore (i.e., littoral versus limnetic zones; Kalff 2002; Vadeboncoeur et al. 2011; Vander Zanden et al. 2011).

Similarly, the sunlit bottoms of streams provide habitat for benthic algae and plants, while the primary producer community in the water column is relatively depauperate (Allan and Castillo 2007). Shallow, tidally influenced areas within estuaries, called tidal wetlands or tidal marshes, are extremely productive (Shaffer and Sullivan 1988; Beck et al. 2001). Tidal wetlands are therefore potentially important sources of productivity for nearby pelagic ecosystems, where they may provide both foraging habitat and subsidies of primary and secondary production to the surrounding channels (i.e., the outwelling hypothesis; Odum and de la Cruz 1967; Dame et al. 1986).

California's San Francisco Estuary (hereafter SFE) is formed by the confluence of the Sacramento and San Joaquin rivers and the San Francisco Bay, and is a relatively unproductive estuary (i.e., < 100 g C m⁻² year⁻¹; Cloern et al. 2014; Wilkerson and Dugdale 2016). Although approximately 97% of the tidal wetland in the estuary was drained during the nineteenth and early twentieth centuries (Whipple et al. 2012), loss of tidal wetland habitat is not a proximate cause of its oligotrophy. The estuary was productive as recently as the early 1980s, well after the bulk of the tidal wetland was drained (Jassby and Powel 1994). Instead, several other factors are hypothesized to suppress productivity, including grazing by invasive clams (Alpine and Cloern 1992; Jassby et al.

Communicated by Paul A. Montagna

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12237-019-00521-5>) contains supplementary material, which is available to authorized users.

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2002), low residence times and loss of phytoplankton due to fresh water export from the south Sacramento–San Joaquin Delta (i.e., upstream and south of the SFE; Jassby and Powell 1994), and possibly changes in nitrogen concentration or form (e.g., Glibert et al. 2011; Parker et al. 2012; Wilkerson and Dugdale 2016), although nutrients are generally considered replete (Jassby et al. 2002; Cloern and Jassby 2012).

There is increasing evidence that the low productivity of the SFE is contributing to the declining abundance of several fish species, including the delta smelt (*Hypomesus transpacificus*; Feyrer et al. 2003; Sommer et al. 2007; Miller et al. 2012; Hammock et al. 2015). Delta smelt is listed on the state and federal endangered species acts and is endemic to the SFE (Bennett 2005). It is pelagic, migratory, and annual, spawning mainly in freshwater in the spring (Bennett 2005; Sommer et al. 2011). One current recovery strategy is to restore tidal wetland habitat, in part to increase the food supply for delta smelt (USFWS 2008; California Natural Resource Agency 2017). Tidal wetlands support both detrital and autochthonous food web pathways via high rates of primary production (e.g., macrophytes, phytoplankton; Conway-Cranos et al. 2015). In consequence, tidal wetlands are rich in zooplankton, larval fish, and benthic invertebrates (Shaffer and Sullivan 1988; Beck et al. 2001; Visintainer et al. 2006; Howe et al. 2014), prey of delta smelt (Slater and Baxter 2014; Hammock et al. 2017). Many tidal wetland restoration projects are planned in the SFE, and several are underway or completed (USFWS 2008). A second recovery strategy is to release additional water from reservoirs, pushing the salinity field seaward and increasing the area of the low salinity zone (salinity ranging from 0.5–6)—a relatively productive salinity range occupied by delta smelt (Kimmerer et al. 1998; Feyrer et al. 2011; California Natural Resource Agency 2017). This strategy may also increase habitat quality because seaward areas are less channelized and have more remnants of tidal wetland (e.g., Grizzly Bay, Suisun Marsh; Matern et al. 2002; Feyrer et al. 2011; Hammock et al. 2015). Given the general importance of shallow water habitat to the productivity of aquatic ecosystems, these strategies appear sound. However, there is currently no direct evidence linking tidal wetland to increased foraging success of delta smelt (Hobbs et al. 2017).

Here, we examine whether the amount of surrounding tidal wetland correlates with foraging success of delta smelt, while accounting for covariables and examining underlying mechanisms. Delta smelt are associated with higher turbidities in the wild (Feyrer et al. 2007; Grimaldo et al. 2009), potentially because it improves their foraging success while limiting predation (Feyrer et al. 2007; Bennett and Burau 2015; Hasenbein et al. 2016; Kimmerer and Slaughter 2016). In laboratory experiments, foraging success decreased linearly with increasing turbidity for juvenile delta smelt (Hasenbein et al. 2013), and at both high and low turbidities for larval delta smelt (optimal foraging success occurred between ~ 12

or 25 and 80 NTU, Hasenbein et al. 2016). Temperature is a well-known driver of foraging in other ectotherms (Brown et al. 2004), but is less well studied for delta smelt. We suggest that there are two mechanisms by which tidal wetland could directly improve the foraging success of delta smelt. Wetlands may export zooplankton into open water habitat (Odum and de la Cruz 1967; Dame et al. 1986), or delta smelt may forage within or along the edge of tidal wetland before returning to the open water where they were collected (Herbold et al. 2014). We consider the likelihood of these mechanisms for delta smelt, and whether area of adjacent tidal wetland—nursery habitat for many fishes (Baltz et al. 1993; Beck et al. 2001; Grimaldo et al. 2004, 2017)—increases the probability of observing larval fish in the guts of delta smelt.

Materials and Methods

Fish Collection, Dissection, and Diet

Juvenile, sub-adult, and adult delta smelt were sampled with trawls conducted by California Department of Fish and Wildlife (CDFW) Interagency Ecological Program surveys in bays and channels in the SFE (Bennett 2005; Merz et al. 2011; Hammock et al. 2015; Damon et al. 2016). Delta smelt were flash-frozen in dewars of liquid nitrogen on CDFW boats and then measured for a variety of growth, health, reproduction, and condition endpoints at UC Davis (e.g., Hammock et al. 2015 and 2017; Teh et al. 2016; Kurobe et al. 2016). Juveniles were collected in summer during the Summer Towntnet survey (40 stations sampled twice per month, June–Aug), sub-adults in fall during the Fall Midwater Trawl survey (122 stations sampled monthly, Sept–Dec), and adults in winter and spring during the Spring Kodiak Trawl survey (40 stations sampled monthly, Jan–May). At each station, temperature (°C), turbidity (Nephelometric Turbidity Units; NTU), and specific conductance ($\mu\text{S cm}^{-1}$) were measured. This study focuses on delta smelt that were collected over a 4-year period, from Aug 23, 2011, through Aug 12, 2015, from 55 stations (Fig. 1, Table S1, $n = 1380$). During summer and fall surveys, a zooplankton tow (160- μm mesh size) accompanied the fish trawl at all 40 Summer Towntnet stations and 32 of the 122 Fall Midwater Trawl stations.

The flash-frozen delta smelt were kept immersed in liquid nitrogen until individuals were weighed, measured for fork length, and dissected as each fish thawed (5–10 min per fish; Teh et al. 2016). Following excision, the digestive tract was preserved in 70% ethanol, and sent to the CDFW Diet Study Lab for stomach fullness and content analysis. At CDFW, stomach contents were weighed, identified, and enumerated, with lengths measured for larger prey items (i.e., amphipods, mysids, and fish). The wet weight of prey was determined by either multiplying the count of each prey type by a wet weight

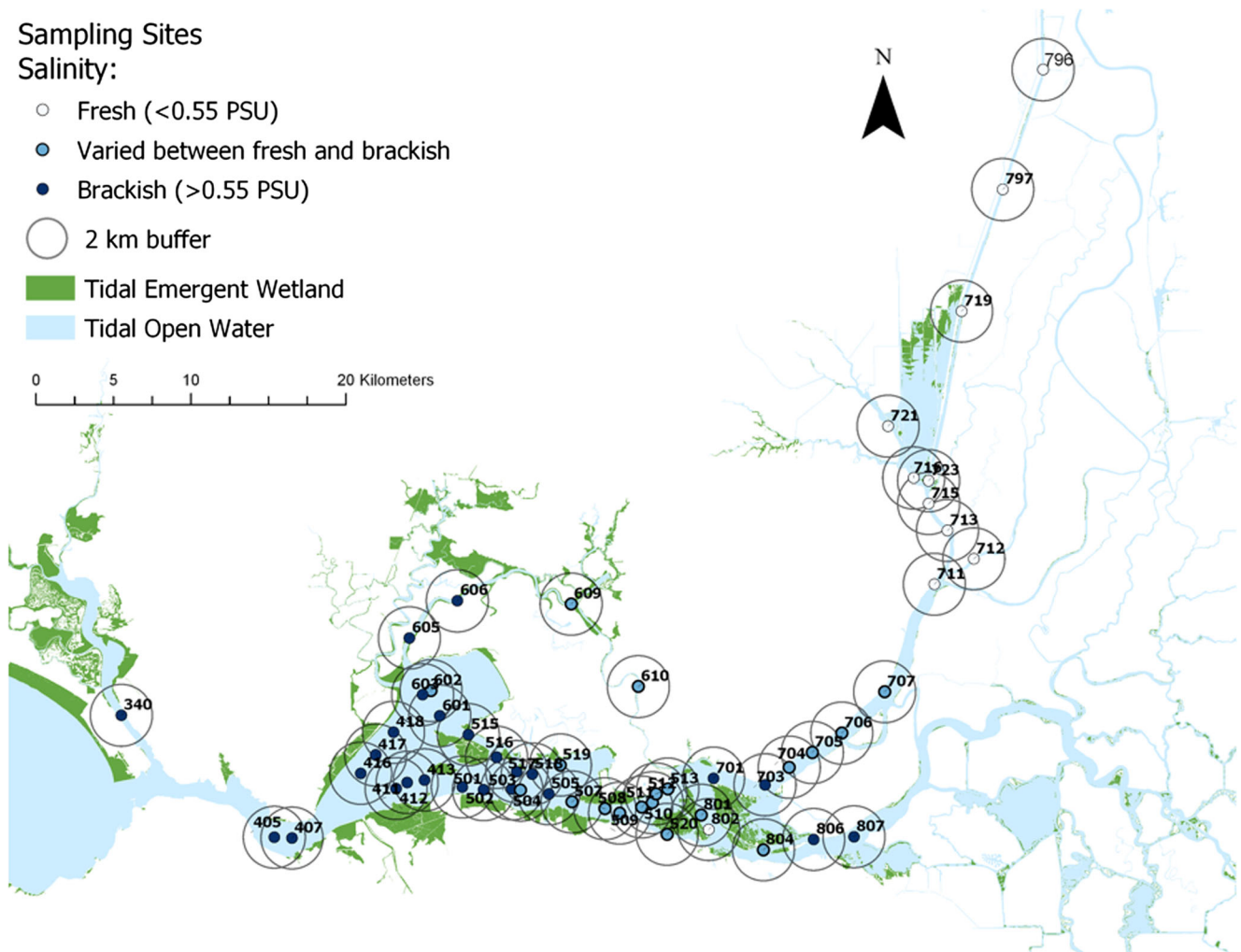


Fig. 1 Tidal wetland areas and CDFW sampling stations in the San Francisco Estuary positive for delta smelt catch (Aug 2011–Aug 2015). The circles show the 2-km ArcGIS buffers used to quantify tidal wetland area (km^2) around the 55 stations in our analysis. Salinity bins are based on salinities during which the 1380 delta smelt were collected. Sites that

were < 0.55 when every delta smelt was collected are designated ‘fresh’, brackish is analogous but > 0.55, and ‘varied’ means that the site varied between fresh and brackish depending on time of year and amount of freshwater flow

estimate, or from calculations based on length-weight equations for larger zooplankton (Slater and Baxter 2014). Stomach fullness was calculated as the weight of the gut contents divided by the weight of the delta smelt, multiplied by 100. Detailed diet analysis methods are available in Slater and Baxter (2014), and dissection methods and flash-freezing justification are available in Teh et al. (2016).

Determining Tidal Wetland Area

To obtain a metric that reflects the foraging access of delta smelt to tidal wetland, we quantified the combined areas of tidal emergent wetlands, tidal flats, tidal pannes, and muted tidal emergent wetlands within circles around each of the 55 sampling stations with positive delta smelt catch using ArcGIS (ESRI, Redlands, CA; Fig. 1, Table S1). We based the radius of these circles (i.e., ArcGIS buffers) on our

estimate of the area within which delta smelt, which feed during daylight, potentially foraged before collection (Hammock et al. 2015, 2017). Potential foraging area was based on the mean time delta smelt had to forage during the day up until collection (4 h; $n = 1380$), movement speed of delta smelt (0.72 km h^{-1} in slack water, Swanson et al. 1998), and trawl length, which is strongly influenced by tidal strength (median distance traveled over land by Fall Midwater Trawl and Summer Towntnet was 0.32 km). Therefore, an average delta smelt collected during a typical trawl could have foraged up to 3.3 km from the sampling station coordinates, although this requires that the boat trawled in the opposite direction that the fish swam at 0.72 km h^{-1} from sunrise until collection, and that the fish was collected at the end of the trawl.

Given the multiple uncertainties in precise collection point and foraging range, and the circuitous routes taken by pelagic fish (e.g., Marsac and Cayré 1998; Dagorn et al. 2000), we

quantified tidal wetland area within both a 1- and a 2-km radius around each station (i.e., buffers). While our estimate above of 3.3 km suggests that delta smelt collected from a station could conceivably have been foraging beyond this range, larger buffers would have overlapped one another considerably (Fig. 1). Preliminary results were quite similar between the two radii, so we chose to use 2-km buffers. We note that obstructions and channel networks may prevent access to all areas within this buffer in some cases, but a standard circular buffer allowed us to apply the same metric across all stations, and nearby wetland area is a first approximation of wetland availability.

We quantified areas of tidal wetlands using data compiled from three sources: the Bay Area Aquatic Resources Inventory (BAARI, <http://www.sfei.org/baari#sthash.palEXR8x.dpbs>); a data set compiled by Wetlands and Water Resources, Inc. from three sources: the Delta Plan, the Cache Slough Conservation Assessment, and the Bay Delta Conservation Plan (<http://baydeltaconservationplan.com/Home.aspx>; Jeff Schlueter *personal communication*); and the CDFW VegCAMP survey of Suisun Marsh plants from 2009 (<https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=48108&inline>).

The data were updated where necessary to reflect known changes to wetland areas caused by levee breaches. We used the “Intersect” tool in ArcGIS to calculate the overlap between the tidal wetlands in the data sets listed above and the buffers around the sampling stations. We then calculated the area of the intersection features in km². Wetland areas around each station ranged from 0.0 to 4.89 km².

To provide a variable with which to test whether simply open-water area, rather than wetland area, might be driving foraging success, we quantified the area of open-water habitat around the stations using the same method and data sets described above for wetland area (i.e., all wetted area except tidal wetlands). The calculated tidal wetland area and open water area values were visually checked against the map to ensure the areas were reasonable (2-km buffers shown in Fig. 1).

Data Analysis

We used model comparison to identify predictors of stomach fullness for delta smelt ($n = 1380$). An arcsin square-root transformation was applied to the proportional stomach fullness data to improve normality (examined using quantile-quantile plots), and used as the response variable in 13 Gaussian models (Table 1). The main goal was to determine whether tidal wetland area predicted stomach fullness, while accounting for potential confounding and masking variables (McElreath 2016). We built models of increasing complexity, beginning with an intercept model (model 1, Table 1) and adding potential cofactors known or hypothesized to be important to delta smelt foraging success. Pairs of models were built that were identical except that they either included

(models 3, 5, 6, 7, 8, 10, and 13) or omitted (models 1, 2, 4, 9, 11, and 12) tidal wetland area.

Following Hammock et al. (2017), time of collection (binned into 6:00–8:00, 8:00–10:00, 10:00–12:00, 12:00–14:00, and 14:00–16:00), season (summer, fall, and winter/spring), and salinity (<0.55 and >0.55) were included in models 2–13 (Table 1). Salinity was included because there is twice the tidal wetland area in brackish habitat in the SFE (see “Results”), and stomach fullness of delta smelt is higher in brackish habitat most of the year (Hammock et al. 2017). Models 3–13 included an interaction of known importance between salinity (<0.55 and >0.55) and season (summer, fall, winter/spring; Hammock et al. 2017). Turbidity was included because it is known to affect delta smelt foraging success (Feyrer et al. 2007; Bennett and Burau 2015; Hasenbein et al. 2016; Kimmerer and Slaughter 2016, and Hasenbein et al. 2013) and could conceivably increase with tidal wetland area if export of particulate matter from the wetland affects turbidity in adjacent channels or bays (Shaffer and Sullivan 1988). To distinguish between reduced foraging at both high and low turbidity, reduced foraging at only high turbidity, or a continuous response to turbidity, turbidity was left as a continuous variable (model 6), divided into three bins (< 12, 12–80, and > 80 NTU; model 7), and divided into two bins (< and > 80 NTU; model 8). The model with two turbidity bins (model 8) outperformed models 6 and 7, as well as an identical model without a turbidity variable (model 5), so turbidity (< and > 80 NTU) was included in models 9–13 (Table 1). Relatively shallow tidal wetland habitat may be more strongly influenced by air temperature than channels, potentially influencing water temperature and the metabolic demand of delta smelt at nearby sampling stations (Brown et al. 2004), so temperature was included in models 10–13 (Table 1). To test whether delta smelt foraging success was driven by simply the availability of aquatic habitat, we replaced tidal wetland area with open-water area in the top-ranked of models 1–11 (model 12). Finally, water year type varied from wet (2011) to critically dry (2014, 2015) during the study period (<http://cdec.water.ca.gov/reportapp/javareports?name=wsihist>). Therefore, a variable for year-class of delta smelt was included in the top-ranked of models 1–12 to account and test for potential differences in foraging success due to water year type.

All models were fit in R using the ‘lm’ command (R Core Team). The models were compared using Akaike information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002; McElreath 2016), and ANCOVAs were used to determine significance of variables. The ‘visreg’ R package was used to plot the partial residuals to show the influence of each variable on stomach fullness (Breheny and Burchett 2013). The top-ranked model was used to make predictions across the ranges of tidal wetland area, turbidity, and temperature to calculate the effect sizes of each variable on stomach fullness (additional details in Supplemental material, *Effect sizes*).

Table 1 Comparison of stomach fullness models fit to the full dataset ($n = 1380$). ‘Tw’ is tidal wetland area (km^2), ‘Hr’ is time of day divided into 2-h blocks (treated as a continuous variable), ‘Seas’ is season (summer, fall, winter/spring), ‘Sal’ is salinity (fresh (< 0.55) or brackish (> 0.55)), ‘Yc’ is delta smelt year-class, ‘Turb2’ is turbidity divided into two bins (< 80 and > 80 NTU), ‘Turb3’ is turbidity divided among three bins (< 12 , > 12 and < 80 , and > 80 NTU), ‘Turb’ is turbidity as a continuous variable, ‘Temp’ is water temperature in $^{\circ}\text{C}$, and ‘Ow’ is open-water area (km^2)

Model #	Model	ΔAIC_c	df	AIC_c wt
10	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp}$	0	11	0.74
13	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp} + \text{Yc}$	2.1	15	0.26
12	$\sim \text{Ow} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp}$	21.4	11	< 0.001
11	$\sim \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp}$	23.9	10	< 0.001
8	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2}$	27.5	10	< 0.001
7	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb3}$	29.5	11	< 0.001
6	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb}$	43.6	10	< 0.001
9	$\sim \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2}$	64.1	9	< 0.001
5	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas}$	70.4	9	< 0.001
4	$\sim \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas}$	115.8	8	< 0.001
3	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal}$	125.7	7	< 0.001
2	$\sim \text{Hr} + \text{Seas} + \text{Sal}$	165.2	6	< 0.001
1	$\sim \text{Intercept only}$	260.5	2	< 0.001

ΔAIC_c difference between model of interest and top-ranked model in Akaike information criterion units corrected for small sample size, df degrees of freedom, AIC_c wt Akaike weight

Some of the delta smelt had extremely high stomach fullness due to the presence of larval fish in their guts (Figs. 2 and 3). To determine to what extent our results were driven by these outliers, we excluded all 69 delta smelt with fish in their guts and reanalyzed the dataset with models 1–11 described above ($n = 1311$). This also allowed us to determine the extent to which the benefit of tidal wetland area was due to predation on larval fish versus zooplankton.

If delta smelt feed directly on zooplankton in the pelagic zone and do not forage within or along tidal wetland, replacing tidal wetland area with zooplankton density should improve the foraging models. Zooplankton density is a direct measure of food availability where the fish was collected, whereas tidal wetland area is a proxy for food availability (either via export or direct foraging). Thus, if tidal wetland area is a better predictor of stomach fullness than zooplankton density, tidal wetland likely confers foraging benefits beyond simple zooplankton export, perhaps because delta smelt utilize tidal wetland—or the edges of tidal wetland—for foraging (Herbold et al. 2014). We note that wetlands can also export nutrients, detritus, and phytoplankton to stimulate the open-water food web (e.g., Lehman et al. 2010), but we do not address this less direct mechanism here.

To differentiate between the two mechanisms (tidal wetland export versus foraging within/along tidal wetland), we excluded all delta smelt without an associated zooplankton sample (all Spring Kodiak Trawl fish and Fall Midwater Trawl fish from stations where zooplankton were not sampled), and five Fall Midwater Trawl delta smelt that had larval fish in their guts, leaving 434 delta smelt. To obtain an estimate of local food availability using the associated zooplankton samples we summed across all species of Cladocera and Copepoda, two major prey items of delta smelt (Nobriga 2002; Slater and Baxter 2014; Hammock et al. 2017, Table S2). While this is

a very rough metric of food availability (not all zooplankton are of equivalent food quality for delta smelt; Nobriga 2002), the variable nevertheless correlated positively with stomach fullness (Hammock et al. 2017). As with the previous models, the response variable was ‘proportion stomach fullness’ that was arcsin square-root transformed. The models for this comparison included an intercept model (model 1), the top-ranked model from the previous analysis (\sim tidal wetland area + time of day + season + salinity + salinity \times season + turbidity + temperature; model 2), the same model except that tidal wetland area was replaced with zooplankton density (model 3), a

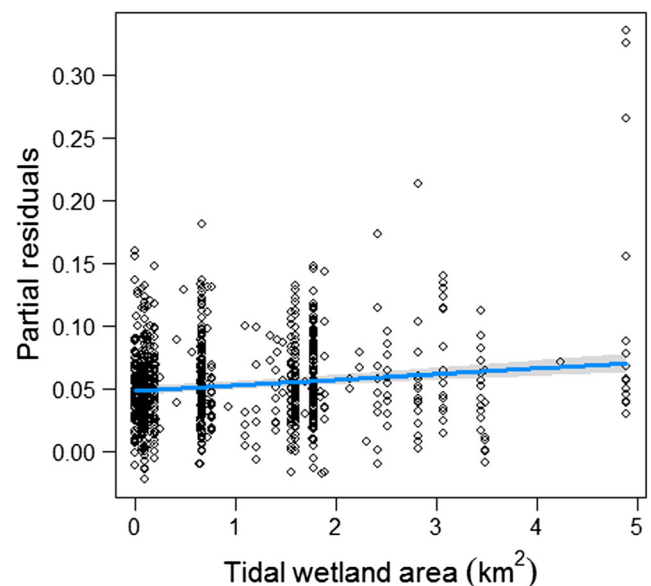
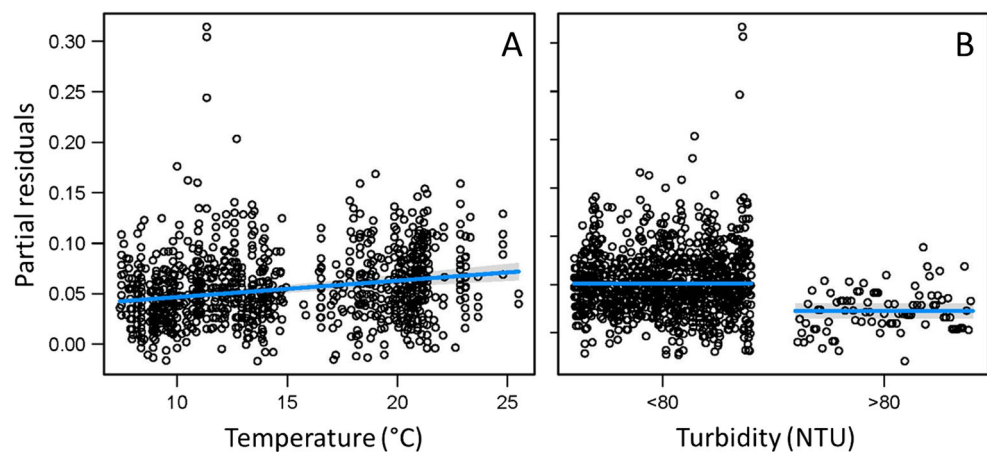


Fig. 2 Partial residuals of the top-ranked model in Table 1, plotted against tidal wetland area (km^2). Note that the y -axis is on the ‘arcsin(square-root)’ of ‘proportion stomach fullness’ scale. The gray shading represents the 95% confidence interval

Fig. 3 Partial residuals of the top-ranked model in Table 1, plotted against water temperature ($^{\circ}\text{C}$; panel **a**) and turbidity (NTU; panel **b**). The y-axis is on the ‘arcsin(square-root)’ of ‘proportion stomach fullness’ scale, and is identical in panels **a** and **b**. The gray shading represents the 95% confidence interval



model that included both zooplankton density and tidal wetland area (model 4), and a model that included a zooplankton density by temperature interaction (model 5; Table 2). This final model was included because metabolic theory predicts that temperature should increase feeding rate and therefore stomach fullness, if food is available and the critical thermal optima is not exceeded (Brown et al. 2004), but decrease stomach fullness at low food availability due to increased metabolic demand (Vinagre et al. 2007).

Next, we used model comparison to determine whether the incidence of larval fish in the guts of delta smelt increases with tidal wetland area, since tidal wetland acts as nursery habitat for fishes (Baltz et al. 1993; Beck et al. 2001; Grimaldo et al. 2004, 2017). Because the response variable was a proportion (i.e., the proportion of delta smelt at each station with fish in their guts) with an uneven distribution of fish among stations (Table S1), we fit beta-binomial models to the data (McElreath 2016). Two models were built: an intercept model and a model with tidal wetland area as a linear predictor. The models were fit using `mle2` from the `bbmle` package in R (Bolker 2010). More complex models were not included because the dataset was far smaller than above ($n = 69$) and mostly included delta smelt collected during winter/spring (92.8%).

Finally, stations were divided between ‘fresh’ and ‘brackish’ based on weighted average salinity (as above, 0.55 was the boundary). Mean proportion of tidal wetland area within the 2-km buffer was calculated for both categories and compared with a generalized linear model with a beta distribution, since the data were non-normal (Cribari-Neto and Zeileis 2009).

Results

The 1380 delta smelt ranged in fork length from 23 to 90 mm (mean 58.7 mm) and in body weight from 0.09 to 6.69 g (mean 1.70 g). Tidal wetland area, higher temperatures, and turbidities below 80 NTU were strongly associated with

increased stomach fullness of delta smelt (Table 1, Figs 2 and 3). The top-ranked model included a parameter for tidal wetland area (ANCOVA, $F_{1, 1370} = 57.75$, $P < 0.0001$, Fig. 2), temperature (ANCOVA, $F_{1, 1370} = 33.68$, $P < 0.0001$; Fig. 3a), and turbidity (<80 and >80 NTU; ANCOVA, $F_{1, 1370} = 43.55$, $P < 0.0001$; Fig. 3b). It also included other variables that previous work has shown to be important (Hammock et al. 2017). Time of day was significant (ANCOVA, $F_{1, 1370} = 92.90$, $P < 0.0001$), with stomach fullness increasing during the day (Hammock et al. 2017). Salinity (fresh vs brackish; ANCOVA, $F_{1, 1370} = 13.42$, $P = 0.0002$), season (summer, fall, winter/spring; ANCOVA, $F_{2, 1370} = 1.52$, $P = 0.220$), and a salinity by season (summer, fall, winter/spring) interaction (ANCOVA, $F_{1, 1370} = 31.11$, $P < 0.0001$) were included in the top-ranked model (Hammock et al. 2017). During summer, stomach fullness was higher in freshwater, but stomach fullness was higher in brackish habitat during fall and spring/winter (further explanation of this interaction in Hammock et al. 2017). Parameter estimates and their 95% confidence intervals are in Table S3. In all cases, including tidal wetland area as a predictor substantially improved the AIC_c score of the model (Table 1). That is, model 3 outperformed model 2, model 5 outperformed model 4, model 8 outperformed model 9, and model 10 outperformed model 11, all by substantial margins (Table 1). In addition, model 10 outperformed model 12, indicating that stomach fullness increases with tidal wetland area, not simply availability of open-water habitat. Model 13, which included a variable for year-class, received some AIC_c weight (0.26, Table 1). However, year-class was not a significant predictor of stomach fullness (ANCOVA, $F_{4, 1366} = 0.7313$, $P = 0.570$).

Based on predictions from the top-ranked model (Table 1), increasing tidal wetland area from the minimum of 0.0 km² to the maximum of 4.89 km² increased stomach fullness by 2.0-fold, from 0.28 to 0.55%. For turbidity, predicted stomach fullness was 0.32% at <80 NTU and 0.09% at >80 NTU, a 3.7-fold difference. Increasing temperature from 7.4 to

Table 2 Comparison of stomach fullness models fit to dataset with associated zooplankton abundance data ($n = 434$). 'Tw' is tidal wetland area (km^2), 'Hr' is time of day divided into 2-h blocks (a continuous variable), 'Seas' is season (summer, fall, winter/spring), 'Sal' is salinity(fresh (< 0.55) or brackish (> 0.55)), 'Turb2' is turbidity divided into two bins (< 80 and > 80 NTU), 'Temp' is water temperature in $^{\circ}\text{C}$, and 'Z' is zooplankton abundance

Model #	Model	ΔAIC_c	df	AIC_c wt
2	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp}$	0.0	9	0.6111
4	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp} + \text{Z}$	2.0	10	0.2296
5	$\sim \text{Tw} + \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp} + \text{Z} + \text{Temp} \times \text{Z}$	2.7	11	0.1572
3	$\sim \text{Hr} + \text{Seas} + \text{Sal} + \text{Sal} \times \text{Seas} + \text{Turb2} + \text{Temp} + \text{Z}$	11.4	9	0.0021
1	$\sim \text{Intercept only}$	83.4	2	< 0.001

ΔAIC_c difference between model of interest and top-ranked model in Akaike information criterion units corrected for small sample size, df degrees of freedom, AIC_c wt Akaike weight

25.5 $^{\circ}\text{C}$ increased predicted stomach fullness 2.7-fold, from 0.21 to 0.56%.

When the 69 delta smelt with fish in their guts were excluded from the analysis ($n = 1311$), the top-ranked model remained the same, with a ΔAIC_c value 4.3 units better than the next best model and an AIC_c weight proportion of 0.90 (Table S4). However, while tidal wetland area was still included in the best model, and it was still significant (ANCOVA, $F_{1, 1301} = 16.65$, $P < 0.0001$), its influence on stomach fullness was diminished. Predicted stomach fullness was 0.28% at zero tidal wetland area and 0.40% at 4.89- km^2 tidal wetland area, a 1.4-fold difference. Thus, of the approximate doubling of stomach fullness as tidal wetland area increased from the minimum to the maximum for the top-ranked model fit to the full dataset, 60% can be attributed to increased predation rates on larval fish, and 40% to increased predation rates on zooplankton. Parameter estimates and 95% confidence intervals are in Table S5.

Mean stomach fullness for the 1311 delta smelt without fish in their stomachs was 0.39%, while, for the 69 delta smelt with fish in their stomachs, it was 1.41%, a 3.7-fold difference. Of the organisms found in delta smelt guts, 78.8% were invertebrates, 19.2% were larval fish, and 1.9% were unidentified by weight (Table S2). Of the 464 larval fish found in delta smelt stomachs, 52% were Pacific herring, 8% were prickly sculpin, 1% were longfin smelt, 1% were *Tridentiger* spp., and 38% were unidentified.

Comparing models fitted to the delta smelt dataset that included zooplankton tows ($n = 434$), tidal wetland area was a better predictor of foraging success than zooplankton abundance (model 2 vs 3; Table 2). Overall, the models that included tidal wetland area received an AIC_c weight proportion of 0.998 (Table 2). The ANCOVA results for the top-ranked model were tidal wetland area ($F_{1, 426} = 7.14$, $P = 0.008$), time of day ($F_{1, 426} = 22.81$, $P < 0.0001$), season ($F_{1, 426} = 0.51$, $P = 0.477$), salinity ($F_{1, 426} = 2.41$, $P = 0.122$), turbidity ($F_{1, 426} = 16.03$, $P < 0.0001$), and the season by salinity interaction ($F_{1, 426} = 36.07$, $P < 0.0001$). Parameter estimates and 95% confidence intervals are in Table S6.

The proportion of delta smelt with fish in their guts increased substantially with increasing tidal wetland area. The top-ranked beta-binomial model included tidal wetland area and received an AIC_c weight proportion of 0.925 (Table 3). The tidal wetland area parameter was positive and significant (parameter = 0.42; 95% CI 0.17, 0.67; $P = 0.0012$). Based on model estimates, increasing tidal wetland area from the minimum to the maximum increased the probability of observing fish in the gut of a delta smelt by 6.4-fold, from 3.3 to 21.2%.

Tidal wetland area was lower in fresh water than in brackish water (beta regression of proportion of wetland area with the 2-km buffer, $z = -6.61$, $P < 0.001$). Mean tidal wetland area in fresh water was 0.69 km^2 , and in brackish water it was 1.44 km^2 , a 2.1-fold difference.

Discussion

Over a 4-year period, wild delta smelt collected from stations with proximity to greater tidal wetland area exhibited increased stomach fullness. As with any observational study, this result could be misleading if a covariable is in fact responsible for the relationship. However, we somewhat mitigated this possibility by including potential confounders in the models (e.g., salinity, turbidity, and temperature; McElreath 2016) and tidal wetland area remained an important predictor of stomach fullness. Moreover, tidal wetlands are productive

Table 3 Comparison of beta-binomial models in which the proportion of delta smelt at each station with fish in their guts was the response variable ($n = 1380$). 'Tw' is tidal wetland area (km^2)

Model #	Model	ΔAIC_c	df	AIC_c wt
2	$\sim \text{Tw}$	0.0	3	0.925
1	$\sim \text{Intercept only}$	5.0	2	0.075

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

habitat (Shaffer and Sullivan 1988; Beck et al. 2001) and are well known to act as nurseries for larval fish (e.g., Baltz et al. 1993; Grimaldo et al. 2004), to which 60% of the influence of tidal wetland area on stomach fullness was attributed. Therefore, we suggest that tidal wetlands, or more specifically the productivity of tidal wetlands, improved the foraging success of delta smelt collected nearby through increased access to prey.

The influence of tidal wetland area on delta smelt foraging success is consistent with previous work on other fishes. Allen et al. (1994) found that mummichogs exiting tidal marsh had fuller stomachs than when they entered. Gulf killifish had greater foraging success on the surface of brackish marsh than in subtidal areas (Rozas and LaSalle 1990). In southern California, California killifish collected on tidal marsh had six times more food in their guts than individuals restricted to tidal creeks within the marsh (West and Zedler 2000). Our study is a less direct test of the influence of tidal wetland on fish foraging because it did not compare delta smelt collected from inside and outside of tidal wetland. Instead, we used GIS to quantify tidal wetland area in the vicinity of delta smelt sampling stations and regressed that area against stomach fullness. This methodology assumes that delta smelt have equal access to all tidal wetland within the buffers and no access to tidal wetland outside the buffers, and these assumptions are unlikely to be fully met. Routes to areas of tidal wetland may be circuitous or impossible in some cases, and riverine or tidal currents could make certain areas of tidal wetland relatively inaccessible. Despite these assumptions, tidal wetland area was an important predictor of delta smelt foraging success.

We compared two possible mechanisms for how tidal wetland area improved the foraging success of delta smelt. One possibility is that tidal wetlands export phytoplankton, detritus, and zooplankton to bays and channels, increasing prey availability directly and indirectly. This potential mechanism was first proposed by Odum and de la Cruz (1967) and is known as the outwelling hypothesis (Dame et al. 1986). Two local studies indicate that tidal wetlands are net exporters of organic material, though it is highly variable temporally (Lehman et al. 2010; Lucas et al. 2006). However, a third SFE study found a tidal marsh to be a sink for the mysid *Neomysis kadiakensis* (Dean et al. 2005) so support in the SFE for the outwelling hypothesis is mixed. In any case, Herbold et al. (2014) suggest that, given the relatively small volume of water in tidal wetlands compared to channels, the flux of phytoplankton and zooplankton to the pelagic food web is likely inconsequential. Herbold et al. (2014) argue instead that tidal wetland improves prey availability for fish by providing rich foraging habitat within or along the edges of wetlands. Indeed, the edges of tidal wetland habitat, either around the outside of wetlands or along tidal creeks within wetlands, are considered to be particularly important to fish foraging success (Gewant and Bollens 2012).

Rich foraging is perhaps why Baltz et al. (1993) found that larvae and juvenile fishes in estuarine wetlands in Louisiana were concentrated within 0–1.25 m of the edge of wetlands. In the SFE, Grimaldo et al. (2004) observed densities of larval fish that were over three times higher in marsh edge habitat than in adjacent river channels. Given that the ‘tidal wetland area’ model outperformed the ‘zooplankton density’ model, our results suggest that there is a foraging benefit provided by tidal wetland that is unrelated to purely zooplankton export (model 2 versus 3, Table 2). The most abundant larval fish taxon in delta smelt guts was Pacific herring, which occurred in high densities in brackish tidal marsh during recent SFE surveys (L. Grimaldo *personal communication*). Thus, our results are more consistent with the hypothesis that tidal wetlands provide foraging habitat than substantial export of prey, although both mechanisms may occur. However, this result should be considered preliminary, given that the zooplankton variable is likely a crude measure of delta smelt food availability.

This potential mechanism—that delta smelt forage within or along tidal wetlands—could explain why delta smelt appear to be far more efficient predators in brackish than in freshwater habitat (Fig. 3D, Hammock et al. 2017). If delta smelt forage along the periphery of tidal wetlands, zooplankton tows in channels near tidal wetlands may underestimate prey availability. Because tidal wetland is more prevalent in brackish habitat in the SFE (see “Results”), relative prey availability may be underestimated by zooplankton tows compared to those in fresh water. Delta smelt may also be able to take advantage of other resources in wetlands that are not available in channels, such as increased access to epibenthic and epiphytic chironomids and amphipods (Whitley and Bollens 2014; Howe et al. 2014), although demersal prey are of relatively limited use compared to pelagic prey like copepods (Table S2). While our study provides only indirect evidence that delta smelt use tidal wetlands as foraging habitat, other studies provide stronger evidence that delta smelt use relatively shallow habitat. Sommer et al. (2004), Sommer and Mejia (2013), and Mahardja et al. (2015) show that delta smelt inhabit tidal sloughs in the Yolo Bypass floodplain, and Aasen (1999) found that densities of delta smelt were higher in shallow water habitat in Sherman Lake and Honker Bay than in channels. But whatever the mechanism, our study indicates that tidal wetlands improve the foraging success of delta smelt.

The relationship between stomach fullness and temperature is consistent with metabolic theory and physiological work on cultured delta smelt. Depending on the temperature of acclimation, the critical thermal maximum (CT_{max}) of delta smelt is 27–29 °C (Komoroske et al. 2014). In our study, stomach fullness increased linearly with increasing temperature, up to a maximum of 25.5 °C (Fig. 3a). Thus, delta smelt behaved as expected, continuing to increase food consumption as temperature

approached their CT_{max} (e.g., Fonds et al. 1992). Because stomach fullness increased with temperature, the increase in feeding rate must have outpaced the increase in gastric evacuation rate, which also increases with temperature in fishes (e.g., Persson 1981; Booth 1990; Handeland et al. 2008). However, as temperature increases toward the CT_{max} of ectotherms, metabolic demand increases (Brown et al. 2004). With energy shifting from growth to metabolism, it is possible for fish to eat more at higher temperature but grow more slowly (e.g., Handeland et al. 2008). Delta smelt in the 2013/2014 year-class, collected during an extreme drought in CA, had significantly higher stomach fullness than those in the previous two year-classes, both of which were substantially cooler (Hammock et al. 2017). However, the elevated stomach fullness in 2013/2014 did not lead to improved fitness, as sexually mature females from 2013/2014 were smaller and less fecund than those of the previous two year-classes (B. Hammock, *unpublished results*). Thus, the positive influence of temperature on stomach fullness does not indicate that high temperature improves conditions for delta smelt (Fig. 3a).

The influence of turbidity on stomach fullness was also consistent with previous research. Turbidity has been depressed in the SFE for decades (Feyrer et al. 2007), which may be problematic for delta smelt because its occurrence is associated with turbid water (Feyrer et al. 2007; Grimaldo et al. 2009). For delta smelt, clear water is thought to increase predation pressure, decrease prey availability as zooplankton exhibit predator avoidance behaviors, and decrease foraging success by, counterintuitively, reducing visual acuity (Feyrer et al. 2007; Bennett and Burau 2015; Hasenbein et al. 2016; Kimmerer and Slaughter 2016). For example, to promote feeding of larval delta smelt in aquaculture, an alga is added to rearing systems to bring turbidity up to 9 NTU (Lindberg et al. 2013). In concurrence, Hasenbein et al. (2016) found a parabolic response of prey consumption of larval delta smelt to turbidity, with optimal foraging success between ~25 and 80 NTU and relatively low cortisol levels (cortisol is a stress hormone; Hasenbein et al. 2016). While we also observed reduced foraging success above 80 NTU, we found no reduction in stomach fullness below 12 NTU ($n = 152$). In fact, mean stomach fullness was higher below 12 NTU than it was from 12 to 80 NTU (0.51 and 0.44%, respectively), although not significantly so (Table 1). However, the fish in our study were more mature than those used by Hasenbein et al. (2016), and it is larval delta smelt that require turbid water to feed successfully (Lindberg et al. 2013). Juvenile delta smelt show a more linear decrease in foraging efficiency with turbidity (Hasenbein et al. 2013), similar to our results.

In summary, stomach fullness of delta smelt increased with increasing tidal wetland area and increasing temperature and at turbidities below 80 NTU. We detected no difference in foraging success between moderate and low turbidity in juvenile through adult delta smelt. Our results appear inconsistent

with the outwelling hypothesis, because tidal wetland area was a better predictor of foraging success than zooplankton density (Table 2). Our results are more consistent with the hypothesis that delta smelt forage within or along tidal wetlands, although detections of delta smelt in tidal wetlands and their peripheries are needed to support this conclusion. Overall, our results support two recommendations from the Delta Smelt Resiliency Strategy meant to benefit delta smelt: (1) restoration of tidal wetlands and (2) outflow actions that maximize the amount of tidal wetland area within the low salinity zone (California Natural Resource Agency 2017; USFWS 2008).

Acknowledgements We are grateful to the many people who contributed to this study, including CDFW boat crews, UCD AHP dissection teams, and the Interagency Ecological Program. We thank Randy Baxter for facilitating the Diet and Condition Study, Tricia Bippus for leading the CDFW Fish Diet Lab, and Sally Skelton for processing zooplankton samples. We also thank Ted Sommer, Andrew Shultz, and an anonymous reviewer for comments that greatly improved the paper.

Funding Information Partial funding for this study was provided by US Bureau of Reclamation R17AC00129, US Geological Survey G15AS00018, and CDFW Ecosystem Restoration Program E1183004.

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