Title:
Diet, Prey Selection, and Body Condition of Age-0 Delta Smelt, *Hypomesus transpacificus*, in the Upper San Francisco Estuary

Journal Issue:
San Francisco Estuary and Watershed Science, 12(3)

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Publication Date:
2014

Publication Info:
San Francisco Estuary and Watershed Science

Permalink:
http://www.escholarship.org/uc/item/52k878sb

Acknowledgements:
This study was supported by the Interagency Ecological Program for the San Francisco Estuary as part of the Pelagic Organism Decline special studies. We thank Julio Adib–Samii and April Hennessy for providing project data. We acknowledge CDWR's Dayflow program provided valuable environmental data. We thank numerous California Department of Fish and Wildlife staff that provided invaluable assistance during field collections and sample processing in the laboratory. We thank Jason Dubois for his considerable and detailed effort in review of this document. Lastly, we thank Gonzalo Castillo and two other reviewers who provided valuable comments that considerably improved this manuscript.

Keywords:
Smelt, zooplankton, diet, selectivity, fullness, length–weight, condition, allometric growth, San Francisco Estuary

Local Identifier:
jmie_sfews_15840

Abstract:
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doi: http://dx.doi.org/10.15447/sfews.2014v12iss3art1

The Delta Smelt, an endangered fish, has suffered a long-term decline in abundance, believed to result from, in part, to changes in the pelagic food web of the upper San Francisco Estuary. To investigate the current role of food as a factor in Delta Smelt well-being, we developed reference criteria for gut fullness and body condition based on allometric growth. We then examined monthly diet, prey selectivity, and gut fullness of larvae and juvenile Delta Smelt collected April through September in 2005 and 2006 for evidence of feeding difficulties leading to reduced body condition. Calanoid copepods Eurytemora affinis and Pseudodiaptomus forbesi remained major food items during spring and from early summer through fall, respectively. Other much larger copepods and macroinvertebrates contributed in lesser numbers to the diet of older juvenile fish from mid-summer through fall. In fall, juvenile Delta Smelt periodically relied heavily on very small prey and prey potentially associated with demersal habitat, suggesting typical pelagic food items were in short supply. We found a strong positive selection for E. affinis and P. forbesi, neutral to negative selection for evasive calanoid Sinocalanus doerrii, and neutral to negative selection for the small cyclopoid copepod Limnoithona tetraspina and copepod nauplii, which were consumed only when extremely numerous in the environment. Feeding incidence was significantly higher in 2006, but among successfully feeding fish we found no between year difference in gut fullness. However, we did detect differences in fullness across months in both years. We found no difference in body condition of Delta Smelt between years yet our sample sizes were low in September when Delta Smelt reverted to feeding on very small organisms and fullness declined, so the longer-term effect remains unknown. Our findings suggest that: Delta Smelt had difficulty obtaining prey in spring 2005 or obtaining proper-sized prey in fall of both years. We detected these difficulties in some regional feeding incidence and fullness indices, but not in body condition indices.

Supporting material:

Appendix A: Tables of Values Used to Calculate Percent Wet Weight of Prey and Gut Fullness
Appendix B: Determination of Allometric Growth Phases in Delta Smelt from Length–Weight Data

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Volume 12, Issue 3, Article 1 | September 2014
doi: *http://dx.doi.org/10.15447/sfews.2014v12iss3art1*

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ABSTRACT

The Delta Smelt, an endangered fish, has suffered a long-term decline in abundance, believed to result from, in part, to changes in the pelagic food web of the upper San Francisco Estuary. To investigate the current role of food as a factor in Delta Smelt well-being, we developed reference criteria for gut fullness and body condition based on allometric growth. We then examined monthly diet, prey selectivity, and gut fullness of larvae and juvenile Delta Smelt collected April through September in 2005 and 2006 for evidence of feeding difficulties leading to reduced body condition. Calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* remained major food items during spring and from early summer through fall, respectively. Other much larger copepods and macroinvertebrates contributed in lesser numbers to the diet of older juvenile fish from mid-summer through fall. In fall, juvenile Delta Smelt periodically relied heavily on very small prey and prey potentially associated with demersal habitat, suggesting typical pelagic food items were in short supply. We found a strong positive selection for *E. affinis* and *P. forbesi*, neutral to negative selection for evasive calanoid *Sinocalanus doerrii*, and neutral to negative selection for the small cyclopoid copepod *Limnoithona tetraspina* and copepod nauplii, which were consumed only when extremely numerous in the environment. Feeding incidence was significantly higher in 2006, but among successfully feeding fish we found no between year difference in gut fullness. However, we did detect differences in fullness across months in both years. We found no difference in body condition of Delta Smelt between years yet our sample sizes were low in September when Delta Smelt reverted to feeding on very small organisms and fullness declined, so the longer-term effect remains unknown. Our findings suggest that: Delta Smelt had difficulty obtaining prey in spring 2005 or obtaining proper-sized prey in fall of both years. We detected these difficulties in some regional feeding incidence and fullness indices, but not in body condition indices.

KEY WORDS

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INTRODUCTION

Fisheries biologists commonly conduct diet studies to examine food web interactions, determine feeding success, and supplement body condition and growth information, all of which contribute to the manage-

ment of fish populations (Bowen 1996). Identifying organisms utilized as prey is the first step in assessing the quantity and quality of the available food. Prey availability and feeding success are especially important for the growth and survival of very young fish (Houde 1987). Declines in important zooplankton prey (Winder and Jassby 2010), species introductions, and changes in environmental conditions (Winder et al. 2011) can lead to slow growth in larval fishes and prolong their susceptibility to high predation (Houde 1987; Paradis et al. 1996), all of which have occurred in the upper San Francisco Estuary (estuary) (Bennett and Moyle 1996).

The Delta Smelt, *Hypomesus transpacificus*, is one of several fishes in the upper estuary believed to be food limited during spring (Bennet 2005), summer and fall (Bennett and Moyle 1996). Summer to fall survival has been positively linked to zooplankton biomass (Kimmerer 2008). Historically, Delta Smelt was one of the more common fishes in Suisun Bay (Ganssle 1966) and the Delta (Radtke 1966). Since the 1980s its abundance has declined, leading to its listing as "threatened" in 1993 under the California and Federal Endangered Species Acts (Federal Register 1993) and more recent up-listing to "endangered" by the State (California Fish and Game Commission 2009). This decline has been attributed in part to changes in the food web (Bennett and Moyle 1996; Moyle 2002; Sommer et al. 2007; Mac Nally et al. 2010). Here we examine Delta Smelt diet and prey selectivity, and then relate these observations to a couple of metrics of feeding success and finally body condition to address whether prey and feeding success might be related to current low abundance.

A small and primarily annual fish, the Delta Smelt is endemic to the upper estuary (Moyle et al. 1992). Delta Smelt move into freshwater habitats in winter and early spring before spawning (Moyle 2002; Sommer et al. 2011). Delta Smelt larvae begin hatching in late February or March and are abundant by April and thereafter (Moyle 2002). During spring and summer most Delta Smelt larvae and small juveniles move from freshwater into the low-salinity areas of the lower Sacramento and San Joaquin rivers and downstream through Suisun Bay (Moyle et al. 1992; Dege and Brown 2004); however, some remain in freshwater throughout the year (Sommer et al. 2011; Hobbs 2012, see "Notes"). Thus, rearing and feeding takes place within a broad range of habitats from the Sacramento–San Joaquin Delta (Delta) throughout Suisun Bay and Montezuma Slough, and, more rarely, Napa River and San Pablo Bay (Figure 1).

Delta Smelt is a life-long zooplanktivore, feeding primarily on pelagic crustaceans and consuming larger prey as it grows (Moyle et al. 1992; Lott 1998; Nobriga 2002; Feyrer et al. 2003; Mager et al. 2004). Delta Smelt larvae hatch at 5- to 6-mm fork length (FL) (Wang 1986) and begin feeding within a week at about 6 mm FL (Mager et al. 2004). Before air bladder inflation (ca. 16 to 17 mm FL), Delta Smelt need to actively swim to feed (Mager et al. 2004). Delta Smelt have a prolonged larval stage of up to 70 days and become superficially recognizable as juveniles around 20 to 24 mm FL (Mager et al. 2004), usually in May and June. Nobriga (2002) found that the smallest feeding larvae (≤9 mm FL) consumed mostly copepod nauplii and copepodites, then switched to mostly adult copepods by 14 mm FL, with the calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* and cyclopoid copepods dominant among prey types. Juveniles included larger prey, particularly the mysid shrimp *Neomysis mercedis*, in their diet (Moyle et al. 1992; Feyrer et al. 2003).

The feeding environment for Delta Smelt changed substantially from the 1970s through the 1990s as a result of numerous species introductions (Cohen and Carlton 1995). In particular, the bivalve *Potamocorbula amurensis*, introduced about 1986 (Carlton et al. 1990) rapidly dominated the benthic fauna of the upper estuary. *P. amurensis* became both a competitor and predator of many zooplankton, suppressing phytoplankton blooms (Jassby 2008) and feeding directly on copepod early life stages (Kimmerer et al. 2005a). Abundance declines of *E. affinis* and subsequently *N. mercedis* during the late 1980s have been linked to *P. amurensis* feeding (Orsi and Mecum 1996; Kimmerer and Orsi 1996; Kimmerer 2006). Several zooplankton introductions also occurred since the 1960s adding to and shifting the prey field: copepods—*Oithona davisae* (1963), *Sinocalanus doerri* (1978), *Limnoithona sinensis* (1979), *P. forbesi* (1987), *Acartiella sinensis* (1993),

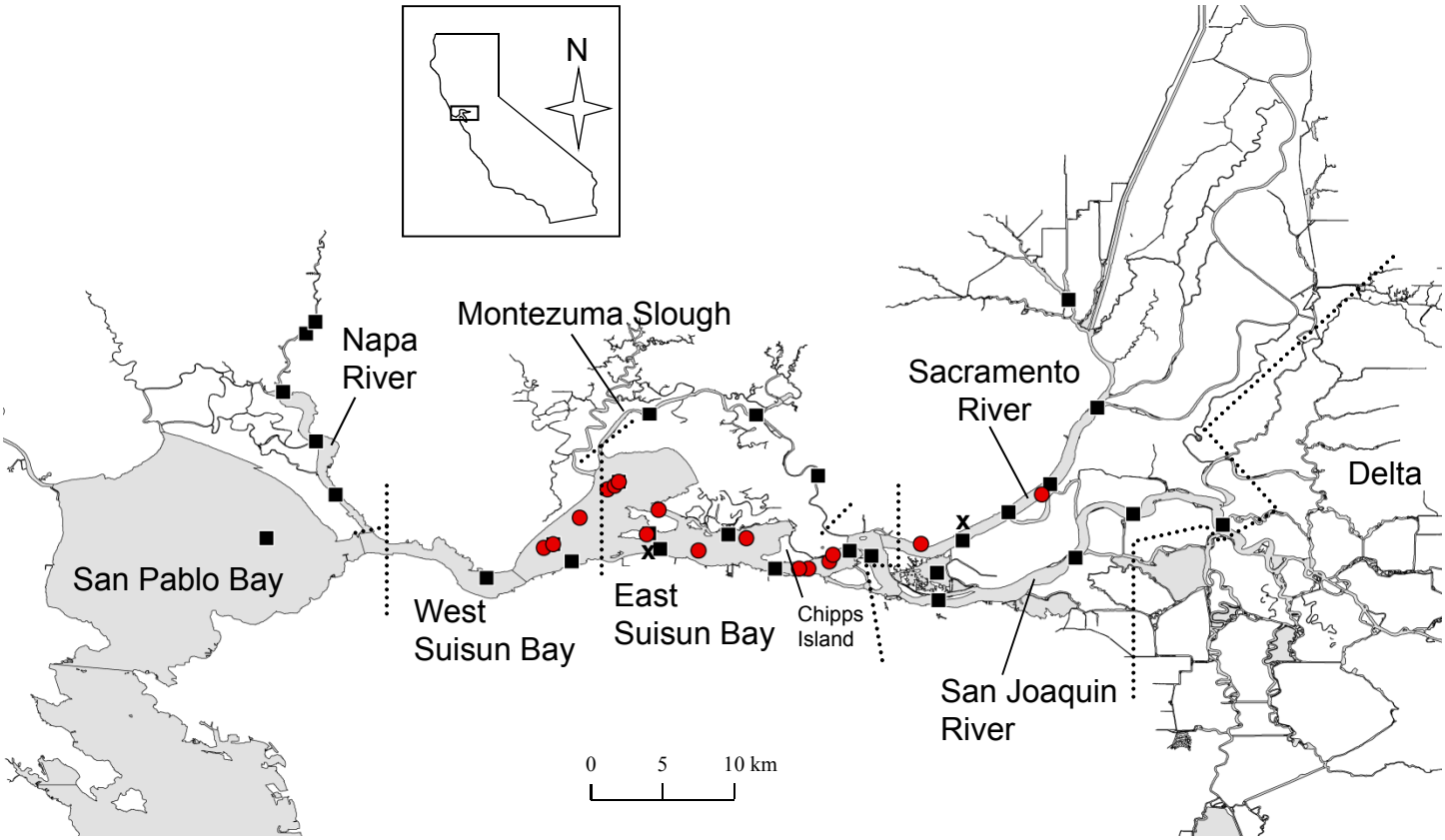

Figure 1 Map of the upper San Francisco Estuary with dashed lines to indicate the separation of regions within the estuary. Points mark station locations of Interagency Ecological Program sampling programs that contributed Delta Smelt to this study: 20-mm Survey (■), Summer Townet, Fall Midwater Trawl, Spring Kodiak Trawl, San Francisco Bay Study (●), and Beach Seine (×).

Tortanus dextrilobatus (1993), and *Limnoithona tetraspina* (1993) (Orsi et al. 1983; Ferrari and Orsi 1984; Orsi and Walter 1991; Orsi and Ohtsuka 1999); and mysid *Hyperacanthomysis longirostris* (formerly *Acanthomysis bowmani*) (1993) (Modlin and Orsi 1997). Of the introduced copepods, the calanoid copepod *P. forbesi* rapidly became very abundant in the upper estuary and an important prey for Delta Smelt (Lott 1998; Nobriga 2002). It remains unclear whether the more-recently-introduced cyclopoid copepod *L. tetraspina* and the calanoid copepods *A. sinensis* and *T. dextrilobatus* (Orsi and Ohtsuka 1999), provide suitable alternative prey. In particular, *L. tetraspina*, currently the dominant copepod by number and biomass in the upper estuary, is believed to be a poor food item because of its small size and predator-avoidance behavior (Bouley and Kimmerer 2006).

Among the older introductions, the calanoid copepod *S. doerrii* exhibits strong predator avoidance behavior (Meng and Orsi 1991), and was rarely eaten by larval Delta Smelt even when abundant (Nobriga 2002).

Researchers often evaluate feeding success in fishes by examining gut fullness and body condition (Bowen 1996). To date, Hobbs et al. (2006) provide the only information on Delta Smelt gut fullness and body condition in relation to food resources, and their analyses were limited to larvae. Gut fullness or body condition comparisons across a broader size or developmental range, such as larvae through juveniles, requires consideration that gut capacity increases with fish size (Knight and Margraf 1982) and body shape may change during growth and development thus complicating condition analyses

(Osse 1990; van Snik et al. 1997; Osse and van den Boogart 2004).

In this study, we examined the diet, prey selectivity, gut fullness, and body condition of age–0 Delta Smelt during spring and summer months in 2005 and 2006. Understanding what prey organisms were used for food in the context of available prey and the associated condition of fish, will help clarify the existence and timing of food limitation for the Delta Smelt population. Questions being investigated here are:

1. What is the diet of Delta Smelt in the estuary?
2. Is there evidence of reduced feeding success at different periods or in certain regions in the estuary?
3. If so, is reduced feeding success associated with changes in body condition?

METHODS

Field Collections

Delta Smelt were collected in the upper estuary from San Pablo Bay to the lower Sacramento and San Joaquin rivers (Figure 1) by California Department of Fish and Wildlife (CDFW) fish sampling programs operated under the auspices of the Interagency Ecological Program (IEP; *http://www.water.ca.gov/iep/*). Sampling programs providing Delta Smelt included: 20-mm Survey, Summer Townet Survey, Fall Midwater Trawl Survey, San Francisco Bay Study, and Pelagic Organism Decline (POD) supplemental Kodiak Trawl and Beach Seine sampling. The 20-mm Survey provided a majority of the fish processed for body condition and diet; it collects larval and juvenile Delta Smelt from late March through early July throughout their historic range using an ichthyoplankton net (1,600 µm knotless mesh) on a fixed-mouth sled (Dege and Brown 2004). A mesozooplankton net (Clarke–Bumpus net, 160-µm mesh) attached to the 20-mm net frame provided zooplankton density data collected concurrently with the fish. The paired fish and zooplankton samples allow calculation of a fish feeding selectivity index. The other fish studies use a variety of sampling gears to collect older juveniles (descriptions are available in Honey et al. 2004). The Delta Smelt examined were collected between April and September in 2005 and 2006, and included larval and juvenile fish. We assigned sampling stations to regions to compare spatial differences in fullness and condition (Figure 1).

Environmental Data

Environmental data including temperature (° C), water clarity (measured as Secchi disk depth [cm]), and salinity (ppt) data were measured at each sampling program station in 2005 and 2006 during the biweekly 20-mm Survey (March to July) and Summer Townet Survey (August), and during the monthly Fall Midwater Trawl Survey (September). Environmental data was collected using the same equipment and methods among sampling programs. Daily freshwater outflow estimates were obtained from the Dayflow website (*http://www.water.ca.gov/dayflow/*) and plotted for 2005 and 2006. Delta Smelt habitat is strongly associated low salinity (1 to 6 ppt) and water clarity which vary in location within the estuary (Dege and Brown 2004; Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009).

Laboratory Methods

Fish collected in the field were placed in labeled containers of 10% buffered formalin and sent to the CDFW laboratory (Stockton, CA) for processing. Fish samples were obtained from 108 individual date-station sampling events during the two study years. The majority of samples (n = 79) contained less than 10 fish (mean = 3.9 fish per sample). For samples containing ≤10 fish, all individuals were processed for diet and condition. For samples containing >10 fish, a random subset of 10 fish was selected for diet and condition processing, with one exception: a single sample collected July 2005 contained 28 individuals and all were processed.

We processed fish following a consistent series of steps. All fish were rinsed then soaked in water for half an hour to reduce formalin fumes. Fish were then blotted dry, measured to the nearest 0.1 mm FL, and then weighed to the nearest 0.0001 grams (g). We performed a two-sample *t*-test ($\alpha < 0.05$) to examine

if there was a significant difference in specimen fork lengths between 2005 and 2006.

Diet analysis began with placing a fish on a glass dish and cutting open its body cavity to reveal its entire digestive tract. Using a dissecting microscope, the entire digestive tract was extracted and gut contents removed from the entire digestive tract of larvae (<20 mm FL), or from the esophagus and fully formed stomach of juveniles (>26 mm FL). For fish in digestive tract developmental transition (ca. 20 to 26 mm FL), gut contents were removed from the entire digestive tract, unless a muscular stomach was detected, in which case we examined only contents from the esophagus and stomach. Gut contents were placed in a drop of water in a Petri dish and all prey types identified to the lowest practical taxon and counted. We categorized amphipods as either *Gammarus* spp. or *Corophium* spp. based on distinct body shapes of the genera. Feeding incidence for each fish was recorded as 'positive' when at least one food item was present in the gut. We examined if there was a difference in feeding incidence between years using a *Chi*-square test ($\alpha < 0.05$).

We determined the total gut-content wet weight (g) for each larvae by multiplying the count of each prey type by its mean wet weight (g) estimate (see Appendix A, Table A-1) or by summing weights derived from length–weight equations for larger zooplankton (see Appendix A, Table A-2), and then summing the various prey-type weights. We measured body lengths (0.1 mm), from the head to the base of the telson, for mysids and amphipods, and if individual organisms were "intact," weighed them to the nearest 0.0001 g. Many mean wet weight (g) estimates of smaller prey and length–weight equations of larger prey were generated during this study using undigested organisms found in gut contents. When such samples were not available, we converted estimates from literature carbon (µg) estimates summarized by Kimmerer (2006) (Table A-1). We converted literature-derived carbon (µg) and dry weight (µg) values to wet weight (µg) using ratios reported by Beers (1966) for copepods: dry weight = carbon weight / 0.42 and wet weight = dry weight / 0.13.

For juvenile fish, we determined gut-content wet weight by directly weighing all prey items combined to the nearest 0.0001 g after they were removed from the esophagus and stomach. Items were then placed in a drop of water and identified to the lowest practical taxon and counted. We determined the proportion by volume of each prey type visually, by spreading the gut contents to an even height over a 1-mm grid, counting the number of squares occupied by each prey type, and dividing by the grand total for all prey types. We then multiplied the prey type proportions by the total gut content weight to determine individual prey type weights for each fish.

We reported monthly diet composition as percent of prey by number (%N), by weight (%W), and by frequency of occurrence (%FO). Unidentified animal and plant material and inorganic debris were not included in determination of %N or %W, because enumeration of these items in larval fish was not possible.

DATA ANALYSES

Prey Size

By dividing the sum total of identifiable prey wet weight (unidentified animal material not included) by the sum total of prey number in each gut, we determined the mean prey size, by wet weight (µg), consumed by fish. We plotted the mean (±SE) monthly prey size values for comparison between years and among months.

Prey Selectivity

We determined Delta Smelt feeding selectivity using Chesson's (1983) index. The index was calculated using paired fish-diet and mesozooplankton samples collected by the 20-mm Survey. The 20-mm Survey sampled 41 stations biweekly from mid-March through early July, 2005 and 2006, during which 75 sampling events collected both Delta Smelt and a zooplankton sample (2005: n = 41 and 2006: n = 34). The index was calculated for each fish as:

$$\alpha_i = \frac{r_i / p_i}{\Sigma_{j=1}^{m} \left(r_j / p_j \right)}, i = 1, \ldots, m$$

where α_i is the selection index for prey type i for an individual or group of Delta Smelt from a given date–station collection, r_i is the proportion of prey type i in the stomachs of the fish from that date-station collection, p_i is the proportion of prey type i in the environment as calculated from the concurrent zooplankton sample, and m is the number of prey types available, also based on the concurrent meso-zooplankton sample. Prey types found in Delta Smelt guts were grouped into nine categories. All copepod nauplii were grouped together and distinguished from older life stages. We combined copepodite and adult life stages for species-specific and general copepod categories. The values of α_i were normalized so that $\sum\alpha_i = 1.0$. The value of α_i can range from 0 to 1. A value of α_i equal to 1/m represents neutral selection for prey type i. In our analyses, neutral selection occurs at values of α_i=0.111, so α_i > or < 0.111 represent positive and negative selection for that prey type, respectively. Monthly mean selectivity index values (±95% CI) were calculated for each prey category, and plotted along with the value of neutral selection. Selectivity measures where 95% confidence intervals do not overlap the neutral selection value where interpreted as significant positive selection when α_i > 0.111 and significant negative selection when α_i < 0.111.

Fullness

To estimate the maximum possible stomach mass for Delta Smelt of any length, we developed a gut fullness relationship (Knight and Margraf 1982) using the maximum observed gut content mass within each 5 mm FL interval (e.g., 7.5 mm to 12.4 mm = group for 10 mm) ranging from 5 mm to 60 mm FL and fit the power function:

$$V = a \times L^b$$

where, V = gut capacity (g), L = fork length (mm), and a and b are parameters. Maximum predicted gut fullness at length allowed us to convert observed gut volumes to a fullness index so to compare fullness among fish of varied length and across time. Our fullness index, modified from Herbold (1986), was calculated for each Delta Smelt with gut contents as: fullness = $\log_{10}$ ([observed gut content mass / maximum predicted gut content mass at length] × 100). On this scale, full guts would have an index of 2. The Delta Smelt is a visual feeder (Baskerville–Bridges et al. 2004) and so to assess whether time of collection influenced gut fullness, we regressed fullness on the number of hours after sunrise fish were collected. If fullness increased substantially after sunrise, then our results could be biased, because fish sampling stations are visited systematically from sunrise through early afternoon. To examine temporal and regional patterns in feeding success, we generated a table of mean (±SE) fullness index values by year, month, and regions within months.

Body Condition

To assess body condition, we calculated Le Cren's (1951) relative condition factor (K_n) for each fish. Relative condition factor was calculated as:

$$K_n = \left(W / a \times L^b\right)$$

Where, W is wet weight (g), L is fork length (mm), a is the intercept, and b is the slope of the logarithmic length–weight relationships (Anderson and Neumann 1996; Craig et al. 2005). Fish preserved for less than 8 weeks at the time of recording body weight (n = 47) were omitted from length–weight and condition analyses because of concerns late in the study of preservation-induced weight changes (Slater 2010, see "Notes"). We also examined the weight at length regression residuals and discovered a pattern that suggests three growth stanzas (Appendix B shows details on how these groups were identified). This indicated the need for three, length–weight relationships to accurately calculate the body condition index through the range of sizes encountered. A change in body shape can result in a positive or negative length-based bias in a condition index that assumes isometric growth (Cone 1989; Rennie and Verdon 2008). We visually examined data plots and used ontogenetic information to establish the lower break point (12 mm) and then used methods similar to Peck et al. (2005) to locate the second break point (28 mm; see Appendix B). Our final body condi-

tion index involved fitting and linking three separate length–weight regression lines to three distinct size groups (<12.0 mm FL, 12.0 to 27.9 mm FL, and >27.9 mm FL) based on growth phases. A plot of K_n values versus FL was evaluated for bias. To examine temporal and regional patterns in body condition, we generated a table of mean (±SE) condition (K_n) index values by year, month, and regions within months.

Prey size, gut fullness, and body condition data were found to violate the normality assumption of parametric testing (Shapiro–Wilk test: $P < 0.001$). Instead we used nonparametric Mann–Whitney U and Kruskal–Wallis tests (Zar 1999), to test for significant ($\alpha < 0.05$) differences between years and among months within years, respectively, for prey size, gut fullness and body condition. All statistical analyses were conducted using SYSTAT (13).

RESULTS

Delta Smelt Examination

We examined 611 Delta Smelt for body condition and diet (Table 1). Most were collected in spring and early summer (Table 1). Fish examined ranged from 4.3 to 60.6 mm FL in 2005 and from 7.0 to 55.7 mm FL in 2006, representing young larval through large juveniles each year (Table 1, Mager et al. 2004). Large fish (>55 mm FL) were considered juveniles because they lacked mature gonads of reproductively active adults. We found no difference in mean length of fish examined between years (Table 1; t-test = −1.397; df = 609; $P = 0.163$).

Of the Delta Smelt examined, we found 488 (80%) contained at least one prey item in the gut and classified positive for feeding incidence (Table 1). The gut contents from four of the 488 fish that were positive for feeding incidence were not quantified because all contents comprised unidentified animal or plant material; these contents did not contribute to determination of diet by %N, %W, or fullness. Unidentified animal material was found at a low frequency in stomachs, 45 of 488 fish containing food. Of these 45 fish, 35 were processed as juveniles for proportion by volume of prey and we found unidentified animal material contributed a small amount, on average 15%, to the total proportion of prey found in stomachs. Feeding incidence was significantly higher in 2006 (87%) compared to 2005 (74%) (Chi-square = 15.886; df = 1; $P < 0.0001$). We found relatively low monthly feeding incidence in April, May, and June of 2005, when compared to later months in the year and when compared to the same months of 2006 (Table 1). Feeding incidence reached 100% in September both years, as expected given larger, mobile individuals.

Environmental Conditions

Delta outflow varied substantially from January through June of 2005 and 2006, and was much lower in 2005 than in 2006 (Figure 2). Yet even 2005 outflow levels remained well above “dry year” levels (cf. Kimmerer 2002a) during winter and spring. By July of each year, outflow declined to relatively low levels and then remained somewhat constant through November. Low-salinity habitat remained farther downstream in spring 2006 than in 2005. By June of

Table 1 Data results from the examinations of Delta Smelt gut contents done in 2005 and 2006

	2005						2006					
	Apr	May	Jun	Jul	Aug	Sep	Apr	May	Jun	Jul	Aug	Sep
Number examined	31	169	75	57	8	10	10	58	129	48	1	15
Feeding incidence	74%	64%	72%	98%	100%	100%	90%	88%	84%	94%	0%	100%
Minimum FL (mm)	5.7	4.3	13.2	11.6	38.8	38.9	7.6	7.0	12.0	22.4	53.9	40.1
Maximum FL (mm)	16.3	34.9	50.8	60.5	58.2	60.6	13.0	27.3	45.2	55.7	53.9	54.6
Mean FL (mm)	12.1	17.3	25.8	40.3	52.2	50.0	10.6	17.1	22.1	40.6	53.9	49.1

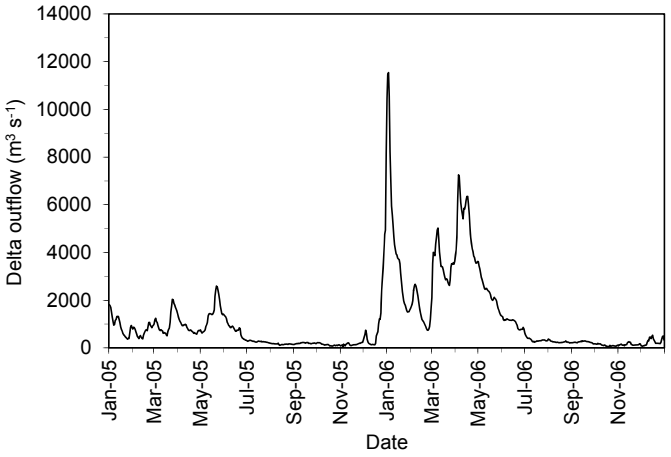

Figure 2 Daily net freshwater outflow ($m^3 s^{-1}$) at Chipps Island from the Sacramento–San Joaquin Delta in 2005 and 2006

both years, low salinity habitat began a rapid shift upstream such that by September Delta Smelt habitat was centered at the confluence of the Sacramento and San Joaquin rivers.

Regional mean water temperatures typically varied only 2 to 3 °C within spring months, but difference increased up to 6 °C as water temperatures warmed in summer months (Figure 3A). By September, mean temperatures declined and the difference across regions diminished (Figure 3A). In downstream regions (San Pablo, west Suisun Bay) during both years, temperature varied less across months than in upstream regions. Secchi depth tended to decline from upstream to downstream, with the exception of some large Secchi depths in San Pablo Bay in spring 2005 (Figure 3B). Salinity increased from upstream to downstream regions, increased across months within regions, and was lowest in late spring of both years (Figure 3C).

Diet Composition

Delta Smelt consumed a wide variety of prey types, but mostly crustaceans. Copepods comprised over 90% of their diet by number and over 85% by weight (Tables 2 and 3). In April, young larvae began their feeding by consuming nauplii and copepodite stages of calanoid (primarily *E. affinis* and *P. forbesi*) and cyclopoid copepods. By May, larvae and small juve-

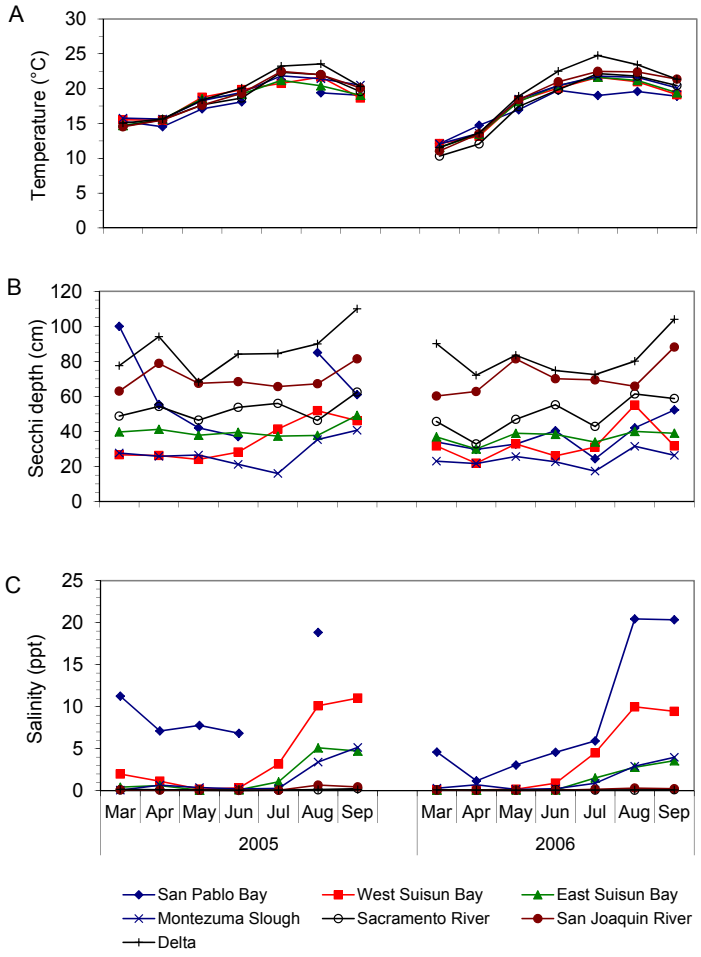

Figure 3 Mean (A) temperature, (B) Secchi depth, and (C) salinity among regions of the upper San Francisco Estuary collected by the 20-mm Survey (March to July), Summer Townet Survey (August), and Fall Midwater Trawl Survey (September) in 2005 and 2006

niles (Table 1) began consuming adult stages of both copepod groups and added cladocerans as a substantial fraction of their diet (Tables 2 and 3). By June and July, *E. affinis* dropped out of their diet and *P. forbesi* increased in importance. In addition, the primarily juvenile fish began consuming a few early-stage mysids and amphipods, as well as an expanding list of more evasive (e.g., *S. doerrii*; Meng and Orsi 1991) or more brackish-water and larger copepod species (e.g. *A. sinensis* and *Tortanus* spp.; Orsi and Ohtsuka 1999). Also starting in July, consumption increased sharply on the small, highly abun-

Table 2 Delta Smelt diet composition, April through September 2005

	APR			MAY			JUN			JUL			AUG			SEP		
Prey type	%N [a]	%W [b]	%FO [c]	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO
Copepods																		
Copepod nauplii	22.2	4.3	26.1	16.5	1.1	6.4	0.1	<0.1[d]	3.7	0	<0.1	1.8	0.2	<0.1	25.0	0	0	0
Cyclopoid copepodites	6.3	7.0	17.4	1.2	0.5	4.6	0.5	0.1	13.0	0	0	0	26.0	22.9	25.0	0.1	0.3	10.0
Acanthocyclops vernalis adults	0	0	0	0.2	0.2	0.9	0	0	0	0	0	0	0	0	0	0	0	0
Limnoithona spp. juveniles	0	0	0	0.2	0	0.9	0	0	0	0	0	0	0	0	0	0.1	<0.1	10.0
Limnoithona spp. adults	3.2	1.4	4.3	0.7	0.1	1.8	0.6	0.1	9.3	1.8	0.2	21.4	0.4	0.2	25.0	85.7	50.4	100.0
UnID [e] cyclopoid copepods	0	0	0	1.7	1.8	6.4	0.3	0.2	9.3	0.3	0.2	8.9	30.3	26.1	37.5	0.8	1.4	20.0
Calanoid copepodites	0	0	0	0.7	0.3	3.7	0.1	<0.1	1.9	0	0	0	0.4	0.4	25.0	0	0	0
Eurytemora affinis copepodites	28.6	23.2	43.5	6.8	2.0	26.6	0.1	<0.1	3.7	0	0	0	0	0	0	0	0	0
Eurytemora affinis adults	6.3	20.6	17.4	23.9	27.5	45.0	0.1	0.1	3.7	0	0	0	0	0	0	0	0	0
Pseudodiaptomus spp. nauplii	3.2	0.5	8.7	1.2	0.1	3.7	0.1	0.3	1.9	0.1	<0.1	3.6	0	0	0	0	0	0
Pseudodiaptomus spp. copepodites	23.8	26.3	43.5	8.5	3.3	25.7	11.0	3.7	51.9	2.9	0.9	39.3	2.8	2.6	50.0	0.4	0.6	20.0
Pseudodiaptomus forbesi adults	1.6	7.0	4.3	21.5	33.8	41.3	80.4	85.8	94.4	60.0	38.1	83.9	22.9	23.5	62.5	5.1	7.7	30.0
Sinocalanus doerrii nauplii	1.6	0.3	4.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinocalanus doerrii copepodites	0	0	0	0.8	0.6	3.7	0.2	0.4	3.7	0.2	0.1	7.1	0.6	0.9	50.0	0	0	0
Sinocalanus doerrii adults	0	0	0	11.5	23.3	22.0	4.6	7.1	35.2	0.8	0.8	23.2	14.4	21.4	62.5	0	0	0
Acartiella sinensis copepodites	0	0	0	0	0	0	0	0	0	0.1	0.1	5.4	0	0	0	0.2	1.6	20.0
Acartiella sinensis adults	0	0	0	0	0	0	0	0	0	25.1	31.8	51.8	0.3	0.4	25.0	3.0	10.9	80.0
Tortanus spp. copepodites	0	0	0	0	0	0	0.1	0.1	1.9	0	0	0	0	0	0	1.9	5.3	50.0
Tortanus spp. adults	0	0	0	0	0	0	0.1	0.8	1.9	5.6	16.7	41.1	0.1	0.6	25.0	0.8	13.6	30.0
Diaptomus spp. copepodites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus spp. adults	0	0	0	0.3	0.7	1.8	0.1	0.1	1.9	0	0	0	0	0	0	0	0	0
UnID [e] calanoid copepods	3.2	9.4	8.7	2.0	2.1	9.2	1.3	0.9	11.1	1.2	0.7	21.4	1.2	0.6	25.0	0.3	0.3	20.0
Harpacticoid copepods	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	12.5	1.3	2.4	50.0
Cladocerans	0	0	0	2.2	2.7	5.5	0.3	0.1	9.3	0.5	0.3	7.1	0.2	<0.1	12.5	0	0	0
Mysids																		
Hyperacanthomysis longirostris	0	0	0	0	0	0	0	0	0	0.4	5.1	3.6	0	0	0	0.1	0.5	10.0
UnID [e] mysids	0	0	0	0	0	0	0	0	0	0.2	3.0	3.6	0	0	0	0.1	0.2	10.0
Cumaceans	0	0	0	0	0	0	0	0	0	0.1	0.7	3.6	0	0	0	0	0	0
Amphipods																		
Gammarus spp.	0	0	0	0	0	0	0	0	0	0.3	0.3	12.5	0	0	0	0	0	0
Corophium spp.	0	0	0	0	0	0	0	0	0	0.1	0.1	3.6	0	0	0	0.5	4.8	10.0
Other zooplankton	0	0	0	0.2	0	0.9	0.2	0.1	3.7	0.2	1.0	7.1	0.2	0.3	25.0	0.1	0.1	10.0
UnID [e] animal material	—	—	0	—	—	0.9	—	—	0	—	—	26.8	—	—	37.5	—	—	40.0
UnID [e] plant material	—	—	0	—	—	0.9	—	—	0	—	—	7.1	—	—	12.5	—	—	10.0
Debris [e] (sand / silt / mud)	—	—	0	—	—	0	—	—	1.9	—	—	1.8	—	—	0	—	—	10.0
Total	100	100	178	100	100	212	100	100	263	100	100	386	100	100	538	100	100	540

a %N = percent number.
b %W = percent weight.
c %FO = percent frequency of occurrence.
d Trace levels at <0.1.
e UnID = unidentified. Unidentified animal material, unidentified plant material, and debris were not included in %N and %W, because enumeration of these items was not possible.

Table 3 Delta Smelt diet composition, April through September 2006

	APR			MAY			JUN			JUL			AUG			SEP		
Prey type	%N [a]	%W [b]	%FO [c]	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO
Copepods																		
Copepod nauplii	2.2	0.4	11.1	0.2	<0.1[d]	2.0	2.3	0.1	6.5	<0.1	<0.1	2.2				0	0	0
Cyclopoid copepodites	52.2	47.7	44.4	39.1	22.0	19.6	0.5	0.2	8.3	0.1	0.1	11.1				0.2	0.1	13.3
Acanthocyclops vernalis adults	0	0	0	0	0	0	0.1	<0.1	0.9	<0.1	<0.1	4.4				0.1	<0.1	6.7
Limnoithona spp. juveniles	2.2	0.1	11.1	0	0	0	0.1	<0.1	0.9	0.2	<0.1	4.4				0	0	0
Limnoithona spp. adults	0	0	0	0.7	0.2	3.9	6.9	1.0	8.3	52.7	8.2	75.6				38.7	11.5	100.0
UnID [e] cyclopoid copepods	6.5	19.3	22.2	6.0	10.6	17.6	0.4	0.4	2.8	0.1	0.1	13.3				0.3	0.7	20.0
Calanoid copepodites	2.2	2.0	11.1	0.7	0.4	5.9	0.1	<0.1	0.9	<0.1	<0.1	4.4				0	0	0
Eurytemora affinis copepodites	23.9	16.1	33.3	14.7	6.1	49.0	3.9	1.1	34.3	0	0	0				0	0	0
Eurytemora affinis adults	0	0	0	24.4	40.5	68.6	7.6	7.5	48.1	0	0	0				0	0	0
Pseudodiaptomus spp. nauplii	0	0	0	0.5	<0.1	3.9	2.2	0.1	3.7	<0.1	<0.1	6.7				0.2	0.2	20.0
Pseudodiaptomus spp. copepodites	4.3	4.0	22.2	0.9	0.5	5.9	12.5	6.9	42.6	1.4	1.7	48.9				5.8	8.0	80.0
Pseudodiaptomus forbesi adults	0	0	0	1.2	2.6	7.8	60.8	76.7	58.3	43.6	83.0	82.2				25.5	45.7	100.0
Sinocalanus doerrii nauplii	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0
Sinocalanus doerrii copepodites	2.2	3.4	11.1	0.2	0.2	2.0	0.3	0.2	1.9	<0.1	<0.1	6.7				0	0	0
Sinocalanus doerrii adults	0	0	0	0.2	0.7	2.0	0.8	1.5	6.5	0.2	0.4	22.2				0	0	0
Acartiella sinensis copepodites	0	0	0	0	0	0	0	0	0	<0.1	<0.1	6.7				0.1	<0.1	6.7
Acartiella sinensis adults	0	0	0	0	0	0	0.1	0.1	0.9	0.1	0.2	13.3				1.4	2.6	53.3
Tortanus spp. copepodites	0	0	0	0	0	0	0	0	0	<0.1	<0.1	4.4				0	0	0
Tortanus spp. adults	0	0	0	0	0	0	0	0	0	0.5	3.2	28.9				0	0	0
Diaptomus spp. copepodites	2.2	1.7	11.1	0	0	0	0	0	0	0	0	0				0	0	0
Diaptomus spp. adults	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0
UnID [e] calanoid copepods	2.2	5.3	11.1	0.9	1.4	7.8	0.8	0.8	7.4	0.6	0.8	33.3				0.9	0.8	33.3
Harpacticoid copepods	0	0	0	0	0	0	0	0	0	0.1	<0.1	11.1				25.3	22.6	86.7
Cladocerans	0	0	0	10.2	14.8	11.8	0.4	1.8	4.6	0.1	0.1	13.3				1.0	2.4	60.0
Mysids																		
Hyperacanthomysis longirostris	0	0	0	0	0	0	0.1	1.3	1.9	<0.1	<0.1	4.4				0	0	0
UnID [e] mysids	0	0	0	0	0	0	0	0	0	<0.1	<0.1	2.2				0	0	0
Cumaceans	0	0	0	0	0	0	0	0	0	0	0	0				0.2	1.6	13.3
Amphipods																		
Gammarus spp.	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0
Corophium spp.	0	0	0	0	0	0	0	0	0	0.1	2.3	8.9				0.4	3.7	26.7
Other zooplankton	0	0	0	0	0	0	0.1	0.4	1.9	0	0	0				0	0	0
UnID [e] animal material	—	—	0	—	—	5.9	—	—	6.5	—	—	13.3				—	—	40.0
UnID [e] plant material	—	—	0	—	—	0	—	—	1.9	—	—	0				—	—	0
Debris [e] (sand / silt / mud)	—	—	0	—	—	0	—	—	0	—	—	0				—	—	6.7
Total	100	100	189	100	100	214	100	100	249	100	100	422				100	100	667

a %N = percent number.
b %W = percent weight.
c %FO = percent frequency of occurrence.
d Trace levels at <0.1.
e UnID = unidentified. Unidentified animal material, unidentified plant material, and debris were not included in %N and %W, because enumeration of these items was not possible.

dant, introduced cyclopoid copepod *L. tetraspina*. In August and September, consumption continued to varying degrees on the aforementioned species, but increased on a number of small organisms and early life stages, including *L. tetraspina*, harpacticoid copepods, and copepodites of various copepod species (Tables 2 and 3).

Prey Size

Mean prey size by wet weight differed significantly between 2005 and 2006 (Figure 4; Mann–Whitney U = 37,425.5; df = 1; $P < 0.0001$). Delta Smelt consumed a higher frequency of larger prey types in 2005 than 2006 (Figure 4), which included more of the relatively large calanoid copepods *A. sinensis* and *Tortanus* spp., as well as mysids and amphipods (Tables 2 and 3). We found prey size also differed significantly among months in both 2005 (Kruskal–Wallis = 99.128; df = 5; $P < 0.0001$) and 2006 (Kruskal–Wallis = 15.126; df = 4; $P = 0.0044$). In both years, Delta Smelt larvae consumed prey of similar size in April followed by an increase in prey size through June (Figure 4). The size of prey consumed decreased from July through September of both years (Figure 4). By September 2006, the size of prey consumed by juvenile fish was no different than the size of prey consumed by larvae that year (Mann–Whitney U = 466; df = 1; $P = 0.156$).

Prey Selectivity

In April of both years, Delta Smelt exhibited little feeding selectivity, except for positively selecting *P. forbesi* in 2005 (Figure 5). By May and continuing through July, Delta Smelt generally exhibited significant positive selection for *E. affinis* and *P. forbesi* (Figure 5) when available (Figure 6), though significance varied by month and year. *E. affinis* relative abundance dropped considerably in June of both years when compared to abundance of other zooplankton (Figure 6). Delta Smelt exhibited neutral or a significant negative selection for cyclopoid copepods, other than *Limnoithona* spp., in all months except April 2006, when highly variable, but positive selection occurred. Selectivity toward *S. doerrii* varied between years but was significantly negative from May through July of 2006 (Figure 5). Larval and juvenile Delta Smelt selectivity toward cladocerans and *Limnoithona* spp. tended to be neutral or significantly negative (Figure 5). Selectivity toward *L. tetraspina* shifted from negative to neutral in July coincident with an increase in its seasonal abundance (Hennessy 2011).

Fullness

We represent maximum gut fullness at length with the relationship: $V = 0.000000531 \times L^{2.712}$ ($r^2 = 0.963$; n = 12). Our examination of fish stomach fullness at time of collection revealed that Delta Smelt fed from early low-light conditions at sunrise throughout the daylight hours and even though they exhibited a slight increase in fullness through late afternoon, the variance explained in the data remains inconsequential (y = 0.5445x + 0.9312; $r^2 = 0.0103$; n = 481; $P = 0.0259$) (Figure 7). We found no difference in stomach fullness between 2005 (mean ± SE = 1.039 ± 0.032) and 2006 (mean ± SE = 1.053 ± 0.032) (Mann–Whitney U = 29,099; df = 1; P = 0.980). Fullness differed significantly among months in both 2005 and 2006 (2005: Kruskal–Wallis = 18.041; df = 5; P = 0.00290; and 2006: Kruskal–Wallis = 18.560; df = 4; P = 0.00096). In 2005, mean fullness increased from a low in April to June, and remained flat through August (Table 4); whereas in 2006 mean fullness started high in April, decreased in May, remained flat through June, and increased in July (Table 4). Fullness declined in September of both years (Table 4). Regional monthly mean fullness was often highest in the Sacramento River and lowest in west Suisun Bay (Table 4).

Body Condition

We found that although body condition (K_n) declined slightly with increasing FL, the variance explained remained inconsequentially small, which we interpret as no influence of FL on condition (y = 1.0661 – 0.0019x; $r^2 = 0.007$; n = 564; P = 0.0481) (Figure 8). Annual body condition was significantly lower in 2005 (mean ± SE = 1.010 ± 0.016) compared to 2006 (mean ± SE = 1.039 ± 0.013) (Mann–Whitney U = 33,696; df = 1;

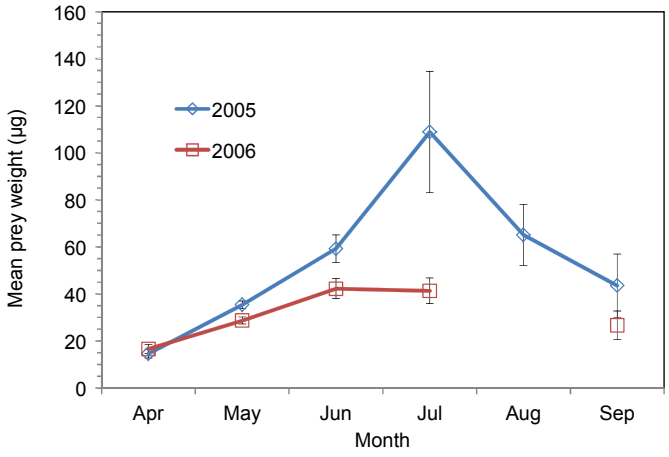

Figure 4 Mean (±SE) prey size by wet weight (µg) found in Delta Smelt from April through September in 2005 and 2006

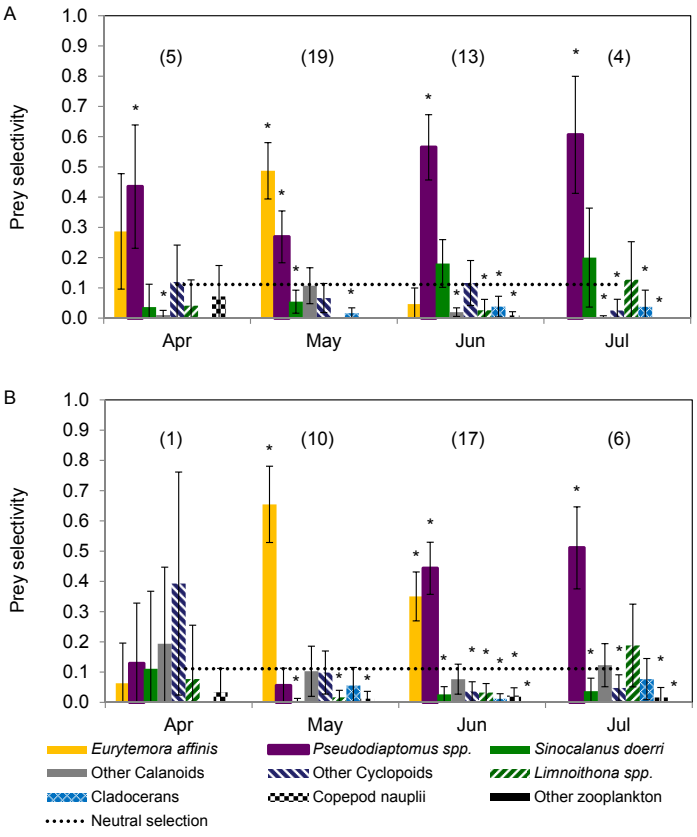

Figure 5 Mean (±95% confidence intervals) prey selectivity (Chesson's α) for Delta Smelt collected by the 20-mm Survey from April through July in (A) 2005 and (B) 2006. Number of monthly coincident fish and zooplankton station samples reported in parentheses in figure. Dotted line represents the value for neutral prey selection. Asterisks indicate significant differences from neutral selection.

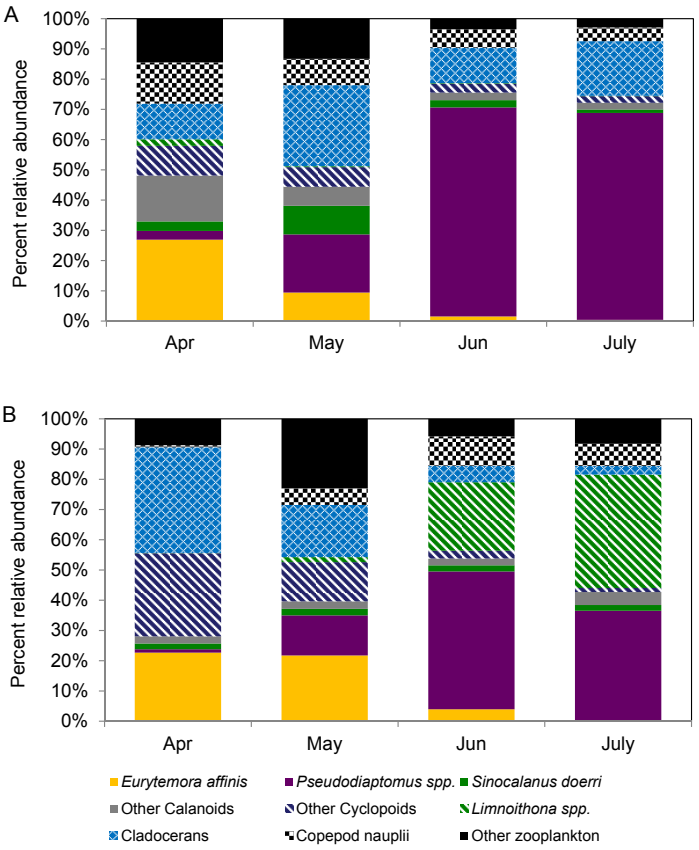

Figure 6 Percent relative abundance of crustaceans collected by the CDFW 20-mm Survey mesozooplankton net from all stations during April through July in (A) 2005 and (B) 2006

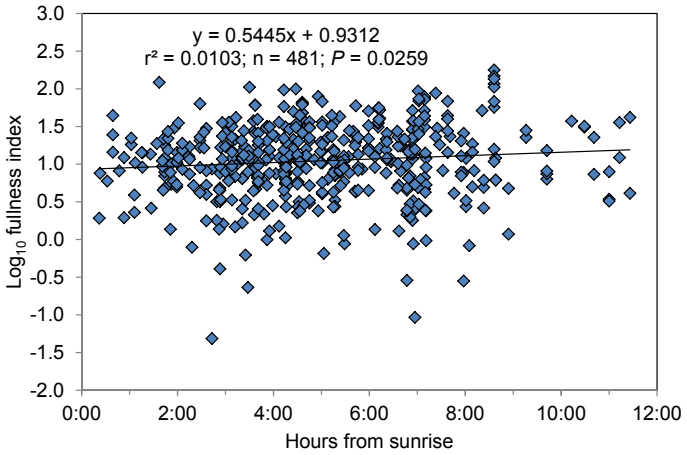

Figure 7 Relationship between $\log_{10}$ fullness index values and the number of hours between sunrise and time of collection for Delta Smelt found with food present in stomachs. The collection time of three fish was unknown.

Table 4 Fullness index values [a] for Delta Smelt among regions in the upper San Francisco Estuary from April through September, 2005 and 2006

Year	Month	San Pablo Bay	Napa River	West Suisun Bay	East Suisun Bay	Montezuma Slough	Sacramento River	San Joaquin River	Monthly Mean
2005	Apr		0.46 ± 0.16 (8)		1.01 ± 0.16 (6)	1.07 ± 0.12 (9)			0.84 ± 0.10 (23)
	May		0.94 ± 0.16 (14)	1.13 ± 0.13 (12)	0.93 ± 0.09 (21)	0.92 ± 0.07 (28)	0.92 ± 0.10 (21)	1.00 ± 0.05 (13)	0.96 ± 0.04 (109)
	Jun			1.59 ± 0.09 (13)	1.01 ± 0.13 (14)	1.00 ± 0.14 (12)	1.04 ± 0.17 (12)	1.19 ± 0.09 (3)	1.16 ± 0.07 (54)
	Jul			1.11 ± 0.91 (2)	1.14 ± 0.09 (46)		1.25 ± 0.15 (7)		1.15 ± 0.08 (55)
	Aug			0.38 ± 0.12 (2)	2.09 ± 0.00 (1)		1.33 ± 0.25 (5)		1.19 ± 0.25 (8)
	Sep			0.79 ± 0.20 (5)	1.15 ± 0.21 (3)		1.12 ± 0.25 (2)		0.96 ± 0.13 (10)
2006	Apr	1.34 ± 0.13 (9)							1.34 ± 0.13 (9)
	May		0.97 ± 0.06 (32)	0.80 ± 0.13 (5)		1.16 ± 0.12 (5)	1.29 ± 0.16 (8)		1.02 ± 0.05 (50)
	Jun		0.88 ± 0.09 (26)	0.88 ± 0.11 (16)	0.97 ± 0.07 (32)	1.12 ± 0.07 (18)	1.23 ± 0.11 (14)		1.00 ± 0.04 (106)
	Jul			0.63 ± 0.31 (7)	1.34 ± 0.10 (31)		1.45 ± 0.22 (7)		1.24 ± 0.10 (45)
	Aug								
	Sep				0.82 ± 0.12 (15)				0.82 ± 0.12 (15)
Regional Mean		1.34 ± 0.13 (9)	0.88 ± 0.05 (80)	1.03 ± 0.07 (62)	1.08 ± 0.04 (169)	1.02 ± 0.04 (72)	1.15 ± 0.06 (76)	1.03 ± 0.05 (16)	1.05 ± 0.02 (484)

a Values in table expressed as mean ± standard error (number of samples).

$P = 0.0025$). Body condition varied significantly among months for both 2005 and 2006 (2005: Kruskal–Wallis = 25.270; df = 4; $P < 0.001$, and 2006: Kruskal–Wallis = 13.071; df = 5; $P = 0.023$). In 2005, mean monthly condition started low—although highly variable—in April and increased slightly in May where it remained through June, followed by an increase in July (Table 5). Conversely, in 2006 mean monthly body condition started highest in April, declined to May, where it remained through July, before declining in August and again in September to the lowest value of the year (Table 5). These monthly patterns generally tracked those of the fullness index, but body condition appeared less variable region to region (cf. Table 4). To investigate further, we regressed body condition on the fullness index. Although a significant relationship resulted, fullness explained only 3% of the variation in body condition (y = 0.0846x + 0.9382; $r^2 = 0.031$; n = 486; $P < 0.001$) and we deemed it inconsequential. Moreover, the variation from essentially empty (fullness = 0) to full guts (fullness = 2) resulted in a

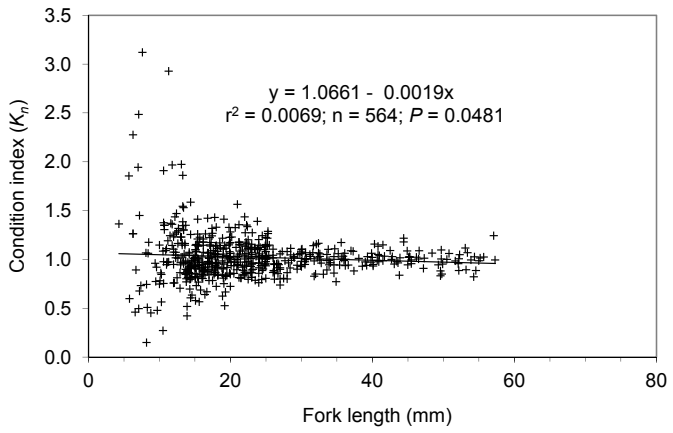

Figure 8 Relationship between allometric relative condition index values (K_n) and fork lengths (mm) for Delta Smelt (n = 564; fish preserved ≥ 8 weeks) during April through September in 2005 and 2006

Table 5 Condition index values (K_n) [a] for Delta Smelt among regions in the upper San Francisco Estuary from April through September, 2005 and 2006

Year	Month	San Pablo Bay	Napa River	West Suisun Bay	East Suisun Bay	Montezuma Slough	Sacramento River	San Joaquin River	Monthly Mean
2005	Apr		0.86 ± 0.04 (11)		0.70 ± 0.07 (10)	1.18 ± 0.18 (10)			0.91 ± 0.07 (31)
	May		0.93 ± 0.03 (16)	1.04 ± 0.06 (19)	1.04 ± 0.05 (42)	0.96 ± 0.03 (39)	1.08 ± 0.08 (32)	1.00 ± 0.06 (21)	1.02 ± 0.02 (169)
	Jun			1.05 ± 0.01 (16)	0.99 ± 0.03 (20)	1.04 ± 0.04 (15)	1.05 ± 0.04 (18)	0.92 ± 0.05 (6)	1.02 ± 0.01 (75)
	Jul			0.92 ± 0.08 (2)	1.05 ± 0.03 (18)		1.10 ± 0.06 (7)		1.05 ± 0.03 (27)
	Aug								
	Sep				1.05 ± 0.00 (1)				1.05 ± 0.00 (1)
2006	Apr	1.22 ± 0.22 (10)							1.22 ± 0.22 (10)
	May		1.00 ± 0.03 (35)	1.03 ± 0.05 (6)		1.11 ± 0.08 (7)	1.13 ± 0.11 (10)		1.04 ± 0.03 (58)
	Jun		1.09 ± 0.03 (34)	0.93 ± 0.04 (22)	1.07 ± 0.02 (38)	1.02 ± 0.03 (20)	1.02 ± 0.02 (15)		1.04 ± 0.01 (129)
	Jul			1.02 ± 0.03 (10)	1.02 ± 0.01 (31)		1.14 ± 0.04 (7)		1.04 ± 0.01 (48)
	Aug			1.00 ± 0.00 (1)					1.00 ± 0.00 (1)
	Sep				0.93 ± 0.02 (15)				0.93 ± 0.02 (15)
Regional Mean		1.22 ± 0.22 (10)	1.00 ± 0.02 (96)	1.00 ± 0.02 (76)	1.01 ± 0.02 (175)	1.02 ± 0.03 (91)	1.08 ± 0.03 (89)	0.99 ± 0.05 (27)	1.02 ± 0.01 (564)

a Values in table expressed as mean ± standard error (number of samples).

change in condition index of about 0.17, or about the typical within month variation in mean condition index across regions (Table 4). So even though variation in fullness could potentially drive much of the observed variation in body condition, it did not. No consistent regional patterns in body condition emerged (Table 5). Delta Smelt from the Sacramento River exhibited slightly better body condition than those in other regions in both years (Table 5).

DISCUSSION

Delta Smelt diet and feeding selectivity have not changed much during the past decade since the only previous comprehensive investigations (Lott 1998; Nobriga 1998, 2002), even though three new copepods—*L. tetraspina*, *A. sinensis*, and *T. dextrilobatus*—had been introduced to the upper estuary and were becoming established in the mid-1990s (Orsi and Ohtsuka 1999). A sharp decline in *E. affinis* abundance had already taken place by the early 1990s (Kimmerer et al. 1994), but thereafter it remained a very important diet constituent in spring along with cyclopoid copepods (Lott 1998; Nobriga 1998, 2002) (Tables 2 and 3). The introduced *P. forbesi* was well established in the early 1990s and an important late-spring, summer and fall diet constituent that remained very important in the mid-2000s. Our findings regarding the timing and amount *E. affinis* contributed to diets resulted in part from moderate spring flows in 2005 and better flows in 2006: such flows now tend to increase and prolong a modest spring abundance increase of *E. affinis* (Kimmerer and Orsi 1996; Kimmerer 2002b). Though *E. affinis* undoubtedly remains an important food item in all years, increasing or extending its period of abundance seemed to provide feeding (incidence and fullness)—if not condition—benefits to larval and small juvenile Delta Smelt. By summer, *P. forbesi* dominated the diet, and both *A. sinensis* and *Tortanus* spp. began showing up in stomachs, particularly in 2005 (Tables 2 and 3), in part from the expansion of juvenile Delta Smelt into brackish water and in part from Delta Smelt achieving sufficient size to consume these larger copepods (see Appendix A). Perhaps the most

striking feeding observation from the 2000s was the relatively high numerical and weight-based feeding on *L. tetraspina* from July through September (Tables 2 and 3); although sample sizes were small, we suspect a real pattern because increased consumption was observed in both years and occurred coincident with modest increases in consumption of other relatively small-sized prey, including copepodites of several species and Harpacticoid copepods (Tables 2 and 3; Appendix A). Though Lott (1998) documented some juvenile feeding on *L. tetraspina*, its numerical abundance in the system has increased substantially since the mid-1990s (Bouley and Kimmerer 2006; Baxter et al. 2010; Hennessy 2011), likely leading to greater availability. However, it's utility as food has been questioned because of its small size and its tendency to remain motionless reducing detection by predators (Bouley and Kimmerer 2006). Late larval and juvenile Delta Smelt in laboratory tests avoided *L. tetraspina* when larger *E. affinis* and *P. forbesi* were available (2012 email from L. Sullivan, San Francisco State University, to S. Slater, unreferenced, see "Notes"). Our results indicate some negative selection and that *L. tetraspina* consumption occurred during periods of high abundance in late summer and fall (Figure 6; Bouley and Kimmerer 2006; Hennessy 2011). Some *L. tetraspina* consumption may have resulted from limited availability of other prey or incidental ingestion when Delta Smelt targeted other prey. Mysids, a historically important prey type during summer and fall, did not contribute much to diets in the 2000s (Tables 2 and 3). Only the introduced mysid *H. longirostris* was found in stomachs and at very low levels. Very low densities of *H. longirostris* and nearly non-detectable densities of other mysids in the environment occurred during our study period (Hennessy 2011).

Although we didn't directly examine diet changes based on ontogeny, our monthly time steps included primarily larvae in April and May, a combination of larvae and juveniles in June, and mostly juveniles thereafter (Table 1). We interpret some of the observed dietary shifts as ontogentic shifts (cf. Tables 1–3) similar to past findings of Nobriga (1998, 2002) and Lott (1998). Feeding theory suggests that organisms should attempt to maximize the size of food items consumed in order to achieve the best return for effort (Hunter 1981; Gill 2003). Further, the size of items consumed should increase with predator size and foraging capability (Hunter 1981). These patterns were generally evident in both past and present diet studies (cf. Lott 1998; Nobriga 1998, 2002; Tables 1–3; Figure 4). During development from larvae through juvenile stages, Delta Smelt initially consumed *E. affinis* nauplii, then copepodites (note that Nobriga [2002] did not distinguish species at the nauplii and copepodite stages in all cases), followed by *E. affinis* and *P. forbesi* adults, and finally to evasive *S. doerrii*, the larger *A. sinensis* and *Tortanus* spp., and less-common mysids and amphipods (Tables 2 and 3; Figure 4). This feeding pattern was similar to that found in striped bass larvae, which exhibited a selective preference for *E. affinis* and then *P. forbesi*, and selected against *S. doerrii*, in large part because of the predator avoidance behaviors of this copepod (Meng and Orsi 1991). However, the expected increase in prey size with fish size did not continue past mid-summer. Instead, early copepod life stages and the *L. tetraspina* became very important food items in late summer and fall, particularly in 2005 when *L. tetraspina* comprised about half the diet by weight (Table 2). We interpret this shift back to small food items (Figure 4) as reflecting a regional food limitation in the west Suisun region (Table 3), and a partial mismatch of fish in Suisun Bay and prey (*P. forbesi*) primarily upstream in the Sacramento and San Joaquin rivers (results not shown). In recent years, *P. forbesi* numbers in Suisun Bay may have been subsidized from upstream Delta populations (2012 email from J. Durand, University of California, Davis, to S. Slater, unreferenced, see "Notes"). In September 2006, *L. tetraspina* and harpacticoid copepods (small and bottom oriented) together comprised about a third of the diet by weight, and though *P. forbesi* remained available, our fullness data suggested only limited rations for fish in east Suisun Bay (Table 4). Although limited, our results nonetheless support previous findings suggesting summer and fall food limitation (Feyrer et al. 2003; Bennett 2005; Miller et al. 2012).

We reported metrics to assess the availability of food (feeding incidence), the ration obtained (fullness), and

long-term feeding success (body condition). Feeding incidence, specifically the absence of food, tends to be critical for young larvae (Houde 1987) which often possess minimal energy reserves for growth and development (Hunter 1981). If a larva can survive through air bladder inflation (ca. 21 to 22 mm FL; Mager et al. 2004), it can then forage more efficiently and is more likely to develop energy reserves. Our findings from April of 2005 and 2006 reflect mostly young larval <17 mm (Table 1) and compare favorably with findings from Lott (1998) that >30% of entire digestive tracts for Delta Smelt larvae < 14 mm were empty. In addition, the frequency of empty stomachs peaked during late spring-early summer months for older larvae during metamorphosis into juveniles (ca. 20 to 24 mm FL) in both the 1990s (Lott 1998) and the 2000s (Table 1). Lott (1998) found a higher percentage of empty stomachs during the metamorphosis period (ca. 20 to 24 mm FL) than our study, in part from having processed only stomachs for fish >20 mm FL. We processed the entire digestive tract for 46% of the fish measuring 20 to 26 mm FL, because of a lack of a fully developed and "flipped" stomach, increasing our opportunity for positive detection of feeding incidence.

Metamorphosis, an energetically demanding period, proves to be a critical period in fish (Thorisson 1994; Islam and Tanaka 2006). To compound the apparent feeding problem during metamorphosis, at about the same time a transition occurs between dominant copepod prey species, *E. affinis* to *P. forbesi*. Bennett et al. (2008) identified this transition as a difficult period for Delta Smelt because of a periodic "gap" in the availability of suitable prey, particularly in the Suisun Bay regions where *E. affinis* tends to be most abundant. We observed a lower feeding incidence in both Suisun Bay regions during this transition between copepod species (May 2005, June 2006) as compared to previous and subsequent months; however, this pattern was not reflected in our indices of fullness and body condition. Instead, and then only in west Suisun Bay, gut fullness and to a lesser degree body condition did not decline until later in the summer and fall. This suggests that reduced incidence of feeding in spring may reflect more the limitations of Delta Smelt to utilize available prey at the time than a food limitation. By late summer and fall, limited food resources affected fullness and to a lesser extent body condition regionally (Table 5). Although our body-condition measures in August and September were not as extensive as those for fullness, it seems plausible that the substantially lower fullness measures for west Suisun Bay during August and September 2005 could have led to real declines in body condition for both months. This pattern if real should be detectable in other, yet to be analyzed data from future years. Our data did not show a strong relationship between fullness and time of day, in part because sampling was limited to daylight hours and Delta Smelt are known visual feeders active during the day (Baskerville–Bridges et al. 2004; Mager et al. 2004; Hobbs et al. 2006). The extreme variability in fullness through the daylight hours suggests that feeding success varies based on a large number of factors and in particular a substantial level of fullness can be achieved rapidly.

We identified three-stage allometric growth in Delta Smelt from length–weight data and applied this information to the development of an index of relative condition. Our sample collection stopped before the timing of significant gonad development, so we cannot say if another length–weight growth stanza exists for maturing or mature Delta Smelt. Indices of condition based on length–weight data have been long recognized as a means to determine the "well-being" of fish at various spatial and temporal scales (Le Cren 1951; Anderson and Neumann 1996). Effective use of such an index requires understanding and incorporation of how ontogenetic morphological changes affect weight at length, so to ensure that variation does not result from "poor fit" and can properly be interpreted as the effect of environmental factors (food supply and temperature) on fish condition (Peck et al. 2005). In the early larval growth stanza, a several-mm length interval overlap existed among fish with and without yolk-sacs and oil globules that resulted in high variability in body condition, yet relatively little change in weight with length (slope, b = 2.0123). A small amount of additional variation likely resulted from differences in moisture loss from such small larvae during the time needed to complete weighing and yet larvae were measured in

a prompt and systematic way to minimize variability between readings. As Delta Smelt entered the second stanza (post-12 mm), they possessed dorsal and caudal fin rays, and developed fin rays of paired fins and an air bladder (Mager et al. 2004), which likely accelerated their ability to acquire food, somewhat reduced energy costs and allowed more rapid weight gain (b = 4.5488). By the third stanza (≥ 28 mm), all larvae have fully transformed into juveniles (Mager et al. 2004) and the rate of weight change slowed (b = 3.3177) to one similar to those reported for other fishes (Gartz 2004; Kimmerer et al. 2005b). The particular pattern in the second stanza suggests a potential trade-off: generating mass as a hedge against food limitation or growing longer to avoid predation.

In other water bodies, researchers use body condition to track how well a fishery or fish community is doing from year to year (Anderson and Neumann 1996; Madenjian et al. 2003). In such circumstances, the ability to judge "good" condition from "bad" is based upon many years of data. Here we only provide 2 years of data: though insufficient to develop a strong baseline, this does allow for a decent contrast between years. As mentioned previously, good spring outflows occurred in both 2005 and 2006 and likely provided somewhat better feeding conditions than other recent years with mostly low spring flows. Our assessments of diet and condition remain ongoing. Incorporating body condition measures from these additional years will enable us to establish a solid baseline from which to distinguish and quantify "good" verses "bad" body condition. Along similar lines, our baseline for comparing gut fullness should improve as well. This in turn should allow for better inference about the physical habitat and their interaction with food levels that lead to good Delta Smelt condition and likely survival.

Questions remain regarding the relative effects of food and habitat on the abundance of Delta Smelt. Feyrer et al. (2007, 2011) linked Delta Smelt recruitment success (and thus abundance) to the quantity and quality of physical habitat during fall. Miller et al. (2012) argued that food remains an important missing component of the aforementioned habitat analyses. Other researchers treated food as a covariate in abundance trend analysis (Mac Nally et al. 2010; Thomson et al. 2010). In an analysis of factors that affect abundance in the long-term, Thomson et al. (2010) used a couple of Bayesian modeling techniques to identify the physical and biological covariates with the strongest association to Delta Smelt abundances, and to determine which of those covariates could explain statistical change points in the abundance trend. These authors did not find that spring or summer calanoid copepod biomass explained much of the variation in Delta Smelt abundance, and the abundance decline in the early 2000s remained unexplained by the extensive suite of variables used in the analysis. In another analysis of long-term data, Mac Nally et al. (2010) used multivariate autoregressive modeling in an effort to identify factors responsible for the decline of Delta Smelt from among 54 expert-elicited relationships built into the model. Spring and summer food variables were not among the top tier of explanatory variables, and—though calanoid copepod summer biomass was a weakly supported variable influencing Delta Smelt abundance in the fall—the authors concluded that it was important. Thompson et al. (2010) and Mac Nally et al. (2010) used June–September calanoid copepod biomass as a covariate or response variable, respectively, to search for relationships. This long period could have averaged out the short-term feeding limitations that our data suggests. More specifically, low calanoid copepod abundance in August and September appears most likely to have affected feeding and survival in our study years. Like Mac Nally et al. (2010), we believe that late summer feeding conditions can affect fall abundance. Our data suggests that in June and July Delta Smelt do not use all calanoid copepod species equally as prey. If this apparent selection persisted throughout the summer period, use of a combined calanoid copepod biomass estimate might over represent available food, and complicate examination of Delta Smelt population response. Our results indicate that in two otherwise good years for July feeding, feeding conditions appeared to decline by fall; this was particularly evident in west Suisun Bay, where gut fullness appeared substantially lower than in upstream regions. The concurrent diet shift to smaller food items in fall brings into question whether the numbers of young copepods and *L. tetraspina* ingested provided sufficient energy to meet metabolic

and growth needs. The caloric and nutritional qualities of *L. tetraspina* and the other small organisms ingested remain to be investigated. It remains unclear what affect these apparently poor feeding conditions had on the Delta Smelt population in 2005 and 2006; Delta Smelt abundance was low in both years (Baxter et al. 2010).

Although the prey field and diet of Delta Smelt remained similar between the 1990s and 2000s, we found several measures that suggest some food limitation for Delta Smelt in spring of 2005 and August and September of both study years. A large percentage of larval fish were found to have empty digestive tracts from April through June in 2005. Fullness and condition of fish declined after July, which coincided with declines in historically important mesozooplankton prey and increased consumption of small pelagic and benthic prey. Although our results remain only suggestive, we believe that they reflect actual conditions in the upper estuary and are likely to be supported by analysis of subsequent years of data.

ACKNOWLEDGMENTS

This study was supported by the Interagency Ecological Program for the San Francisco Estuary as part of the Pelagic Organism Decline special studies. We thank Julio Adib–Samii and April Hennessy for providing project data. We acknowledge CDWR's Dayflow program provided valuable environmental data. We thank numerous California Department of Fish and Wildlife staff that provided invaluable assistance during field collections and sample processing in the laboratory. We thank Jason Dubois for his considerable and detailed effort in review of this document. Lastly, we thank Gonzalo Castillo and two other reviewers who provided valuable comments that considerably improved this manuscript.

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