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LARVAL DELTA SMELT DIET COMPOSITION AND FEEDING INCIDENCE: ENVIRONMENTAL AND ONTOGENETIC INFLUENCES

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I examined the feeding ecology of larval delta smelt, *Hypomesus transpacificus*, a threatened fish endemic to the upper San Francisco Estuary (SFE). The larvae were collected during California Department of Fish and Game ichthyoplankton surveys during spring 1992-1994. The study objectives were (1) compare current diet composition to limited historical data; (2) describe seasonal and ontogenetic influences on the diet; and (3) determine whether feeding success varied interannually, and if so, in association with what factors. In most months, historically important prey, (cyclopid copepods and the calanoid copepod *Eurytemora affinis*) dominated the diet. The calanoid copepod *Pseudodiaptomus forbesi*, introduced to the SFE in 1987, was an important prey in late spring. Electivity analysis indicated use of the aforementioned copepods was related to their abundance, but changes in the abundance of other zooplankton were not reflected in the diet. Ontogenetic changes in the size of prey ingested were apparent; the smallest feeding larvae ate mostly subadult copepods, whereas larvae ≥ 13 mm ate mostly adult copepods. Feeding incidence (FI), the presence or absence of food in the gut, increased with larval length, but for certain length groups varied up to 30% among years. A Separate Slopes Analysis of Covariance (ANCOVA) indicated larval length was positively correlated with Principal Components scores representing a gradient in calanoid copepod abundance. The ANCOVA also demonstrated that on average, feeding larvae were collected in association with higher calanoid copepod abundance than equivalently sized non-feeding larvae. Overall these results suggest (1) larval delta smelt are primarily dependent on three prey taxa, two of which have undergone a long-term decline in abundance, and (2) larval delta smelt feeding success is related to prey abundance. I conclude that well-documented ecological changes in the SFE have probably been detrimental to larval delta smelt, but that linking long-term or interannual food web variability to recruitment will require further research.

INTRODUCTION

Delta smelt, *Hypomesus transpacificus*, is a small, pelagic, estuarine-dependent

fish endemic to the upper San Francisco Estuary including the Sacramento-San Joaquin Delta (Moyle et al. 1992). Delta smelt is a State and federally listed threatened species, which underwent a substantial population decline beginning in the early 1980s (Sweetnam 1999). Although its adult abundance has recovered somewhat in recent years, it continues to show depressed juvenile abundances relative to abundance levels recorded in the 1970s. The factors affecting delta smelt recruitment are not well understood, but estuarine hydrology, water diversions, food web alterations, exotic species, and contaminants have all been implicated (Bennett and Moyle 1996).

The low salinity zone (LSZ) of the upper estuary has historically been an important rearing area for several fishes, including delta smelt (Moyle et al. 1992; Bennett and Moyle 1996). Long-term declines in productivity at several trophic levels have occurred in the approximately 0.5‰-6.0‰ LSZ (Lehman 1992; Kimmerer and Orsi 1996; Kimmerer et al. 2000). In addition to long-term declines in productivity, substantial changes to the LSZ ecosystem occurred following the introduction of a filter-feeding clam *Potamocorbula amurensis* in 1986 (Nichols et al. 1990). The establishment of *P. amurensis* was associated with substantial declines in phytoplankton (Alpine and Cloern 1992), the calanoid copepod, *Eurytemora affinis*, (Kimmerer et al. 1994) and the mysid *Neomysis mercedis* (Orsi and Mecum 1996). Spatial and temporal changes in plankton dynamics also occurred following the *P. amurensis* introduction. The abundance maxima of diatoms (Lehman 2000) and *E. affinis* (Kimmerer and Orsi 1996), which historically occurred in the LSZ, shifted into tidal fresh water regions. In addition, *E. affinis*, which historically was abundant through the summer, has been replaced system-wide each May or June by *Pseudodiaptomus forbesi*, a calanoid copepod introduced in 1987 (Kimmerer and Orsi 1996). These changes in LSZ plankton dynamics have been considered detrimental to young striped bass, *Morone saxatilis* (Meng and Orsi 1991; Kimmerer et al. 2001). They may also have been detrimental to delta smelt since limited historical diet data indicate *E. affinis* was the principal prey (Moyle et al. 1992).

Lack of detailed diet data for larval delta smelt, and information on other aspects of its feeding ecology limit current understanding of the potential impacts of food web alterations. This study investigates the feeding ecology of larval delta smelt in years following the *P. amurensis* introduction through exploratory analysis of 3 years of larval fish, zooplankton, and physical monitoring data. Specifically, I focused on three questions. (1) Has the diet changed since the latter 1970s? (2) What are the seasonal and ontogenetic influences on diet composition? (3) Does feeding success vary interannually, and if so, can environmental influences on feeding success be discerned?

METHODS

Field Methods For Collection Of Larval Fish And Zooplankton

Larval delta smelt were collected during 1992-1994 by the California Department of Fish and Game (CDFG) Egg and Larval Survey (ELS). The ELS was developed to

concurrently monitor the distribution and abundance of larval striped bass and zooplankton (CDFG[1] 1987), but larval delta smelt were commonly collected incidentally. The ELS samples were taken every 2-4 days at 60-80 stations throughout Suisun Bay and the Sacramento-San Joaquin Delta (Wang[2] 1991). Sampling encompassed most of the known range of delta smelt. The ELS samples were collected with a 505-μm mesh plankton net (0.5 m^2 mouth) mounted on a sled and towed obliquely from bottom to surface for 10 minutes at each station. Most samples were collected between sunrise and early afternoon. The volume of water that passed through the net was estimated with a General Oceanics™ flow meter. Zooplankton was usually sampled simultaneously with a 154-μm mesh Clarke-Bumpus (CB) net attached to the sled above the ELS net. A second General Oceanics™ flow meter estimated the volume of water that passed through the CB net. Water temperature (°C), surface specific conductance (microsiemens/cm), and water clarity (Secchi disk depth, m) were also recorded at each station. All samples were preserved in 5% buffered formalin. Larval delta smelt and zooplankton were identified in the laboratory by CDFG staff. This dataset contrasted a year of above average freshwater flow conditions (1993), with 2 years of below average flow conditions (1992 and 1994) (California Department of Water Resources[3] unpublished data for 1906-1999). Hereafter, 1993 is referred to as 'wet' and 1992 and 1994 are referred to as 'dry'.

Gut Contents Analysis

Larval delta smelt collected during April and May 1992 (n = 208) and March through June, 1993-1994 (n = 529 and 737, respectively) were randomly subsampled from ELS collections for gut content analysis. Standard length (SL) of each larva was measured to the nearest 0.1 mm using a dissecting microscope with an ocular micrometer. The definition of larva in this paper corresponds to the prolarva through prejuvenile stages of Wang[2] (1991). The maximum SL included in the analysis was 20.4 mm. For larvae collected in 1994, mouth widths were measured to the nearest 0.1 mm and related to SL using linear regression. The contents of the entire digestive tracts were identified and counted. Whenever possible, I identified all post-naupliar copepods and non-copepod zooplankton to genus. Because most copepod genera are

[1]CDFG (California Department of Fish and Game). 1987. Factors affecting striped bass abundance in the Sacramento-San Joaquin River system, Exhibit 25, entered by the California Department of Fish and Game for the State Water Resources Control Board 1987 Water Quality/Water Rights Proceeding on the San Francisco Bay and Sacramento-San Joaquin Delta. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Technical Report 20.

[2]Wang, J.C.S. 1991. Early life stages and early life history of the delta smelt, *Hypomesus transpacificus*, in the Sacramento-San Joaquin Estuary, with comparison of early life stages of the longfin smelt, *Spirinchus thaleichthys*. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary Technical Report 28.

[3]CDWR (California Department of Water Resources). Raw data are available at http://cdec.water.ca.gov/cgi-progs/iodir/wsihist

monospecific in the freshwater and low salinity habitats of the upper estuary (Kimmerer and Orsi 1996), identifications to genus refer to particular species and are reported as such in this paper. The zooplankton collected in the CB samples were identified according to a slightly different protocol. In the CB samples, only adult copepods were identified to genus. Sub-adult copepodite stages were identified to order (Calanoida, Cyclopoida, or Harpacticoida). Zooplankton and physical environment data, taken concurrently with smelt larvae, were available for 1,021 (69%) of the larvae examined for gut contents.

DATA ANALYSIS

All diet composition data reported in this paper were summarized as percentages of prey occurrence by number (%N). To allow differentiation between seasonal and ontogenetic influences on the diet, I summarized larval SL and %N in two ways. In the first, I calculated mean SL and %N for each month each year. In the second, I calculated %N for each 1 mm SL increment between 5 and 20 mm. The latter summary was based on combined data for all 3 years.

To assess prey use versus potential prey availability, I calculated Vanderploeg-Scavia electivity indices (Lechowicz 1982) for each fish meeting the following criteria: (1) the fish was collected with a concurrent CB zooplankton sample, and (2) the fish had eaten only prey taxa that were quantitatively sampled with the CB net. A total of 301 larvae met these criteria. The index was calculated as:

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

where

$$W_i = (r_i/p_i)/(\Sigma r_i/p_i)$$

and

r_i = relative abundance of a prey category in the diet

p_i = relative abundance of a prey category in the environment

n = number of prey categories considered.

Electivity indices are problematic when used on field data because they assume all prey types were present in every sample (Lechowicz 1982). When each prey type is not present, the index for that prey type has a mathematically nonsensical denominator of zero. Of the 301 fish included in the analysis, only 3 had eaten a prey type that was not observed in the simultaneous environment sample. These fish were excluded from further analysis. In cases where a prey item was not found in either the gut contents or the environment, the electivity index was set to zero and the fish were included in subsequent analyses because zero electivity was expected at zero abundance.

Appropriate diet data were grouped into six prey categories for the electivity analysis (Table 1). After calculating an electivity index for each larva for each prey category, I paired each electivity index for each prey category with its concurrent abundance estimate (number/m^3) from the field. Then I ranked the pairs lowest to highest based on the field abundance estimates. Next each pair was assigned to one

Table 1. Prey taxa and their ranges of abundance (organisms/m^3) in each abundance bin used in the analysis of larval delta smelt electivity.

Prey Taxon	Bin 1 (n = 100)	Bin 2 (n = 99)	Bin 3 (n = 99)
Total cyclopidae	0 – 149	149 – 528	534 – 16,612
Cal. copepodites	0 – 1,482	1,482 – 3,415	3,415 – 17,448
E. affinis adults	0 – 216	216 – 999	999 – 3,415
P. forbesi adults	0 – 103	107 – 649	649 – 10,702
S. doerri adults	0 – 234	244 – 640	640 – 6,581
Total cladocera	0 – 141	141 – 980	980 – 84,871

of three bins of approximately equal sample size (Table 1). I tested the null hypotheses that there were no differences in electivity between abundance bins for each of the six prey categories using Kruskal-Wallis nonparametric analyses of variance. To correct for the increased possibility of type I errors given six hypothesis tests, I used a Dunn-Sidak adjusted *P*-value to support or refute the null hypotheses (Sokal and Rohlf 1995). The adjusted $\propto$ needed to reject the null hypotheses was 0.009.

I used feeding incidence (FI), the presence or absence of food items in the gut, as an index of larval feeding success (Dauvin and Dodson 1990). Based on studies of other larval fishes (Hunter 1981; Gerking 1994; Bremigan and Stein 1997), I expected FI to vary with size of the larvae and with environmental conditions. As an initial assessment of these assumptions, I assigned each larva that had a simultaneous environment sample (n = 1,021) to 1 of 5 bins of approximately equal sample size (n = 204-205) based on SL. The number of bins was arbitrary, but designed to balance between retaining large sample sizes and not masking trends by being overly inclusive. Based on a qualitative examination of FI among years and SL bins, statistical examination of environmental conditions and their interaction with SL was warranted.

Since FI is a binary variable, I used a logistic regression approach (generalized linear model with binomial distribution and logit link function) to test for factors that contributed significantly to FI. The aforementioned SL bins were used as a categorical variable in the logistic analysis. In addition, I natural log transformed and standardized the physical environment data and the abundance data for zooplankton taxa that had shown a significant electivity response. These data were summarized using Principal Components Analysis (PCA) to produce a reduced number of independent variables. The constant 10 was added to each zooplankton abundance estimate before natural log transformation to avoid taking a log of zero. The logistic model comprised a Separate Slopes Analysis of Covariance (ANCOVA); [FI = (SL bin X PC1 scores) + (SL bin X PC2 scores) + SL bin]. Model coefficients were considered statistically significant at $\propto$ = 0.05.

RESULTS

In each year, the mean SL of the delta smelt larvae increased throughout the spring

Table 2. Monthly summaries of sample sizes used for diet analysis of larval delta smelt, monthly means and standard deviations of delta smelt standard length, and monthly diet composition as percent numeric contribution, 1992-1994.

	1992		1993				1994			
	April	May	March	April	May	June	March	April	May	June
# guts examined	114	94	132	146	237	14	143	481	90	23
mean standard length (mm)	6.8	11.2	5.9	7.3	8.6	11.3	5.6	7.1	11.3	15.6
Std. Dev. of SL (mm)	2.7	4.3	1.2	2.2	4.2	3.9	0.6	2.1	4.5	3.6
Diet composition										
Total Copepoda	97.8	95.3	85.5	95.8	97.9	92.6	97.5	98.4	100	100
Copepod nauplii	22.2	6.0	53.2	11.5	12.6	56.9	60.0	35.2	12.3	0
Harpacticoida	4.4	0	0	0	0	0	5.0	5.1	1.5	0
Cyclopoida										
Cyclopidae	15.6	1.3	29.0	54.2	8.5	6.5	25.0	14.3	3.6	0.8
Oithonidae	0	0	0	0	0	0	0	0.2	0	0
Calanoida										
Eurytemora affinis										
adults	4.4	6.0	1.6	2.7	43.2	0	0	6.4	52.8	20.8
copepodites	0	5.3	0	21.4	25.4	0	0	9.2	11.8	0
Pseudodiaptomus forbesi										
adults	0	42.7	0	0	0.8	11.4	0	0	5.1	59.2
copepodites	0	6.0	0	0	1.9	14.6	0	0	1.0	18.3

Sinocalanus doerrii										
adults	0	2.7	0	1.1	0.3	0	0	0	2.6	0
copepodites	0	0	0	0.4	0	0	0	0.2	0.5	0.8
Osphranticum labronectum	0	0	0	0	0	0	0	0.2	0	0
Diaptomus spp.	0	0	1.6	0.4	0	0	0	0	0	0
unidentified calanoid copepods[a]	51.1	25.3	0	4.2	5.2	3.3	7.5	27.8	8.7	0
Non-copepod zooplankton										
cladocera	0	0.7	0	1.1	0.5	4.1	0	0.5	0	0
rotifera	2.2	4.0	14.5	3.1	1.6	3.3	2.5	0.9	0	0
chironomid larvae	0	0	0	0	0	0	0	0.2	0	0
Estimated contributions[b]										
Cyclopidae + *E. affinis* all life stages	77.0	18.0	81.2	92.9	93.5	16.8	65.0	73.7	85.4	21.6
cyclopidae + *E. affinis* + *P. forbesi* all life stages	77.0	89.6	81.3	92.9	96.8	87.5	65.0	73.7	93.1	99.1

[a]represents both early copepodite stages that could not be identified to genus and, rarely, later copepodite and adult stages of individuals that were digested beyond recognition.
[b]estimates based on assumption that nauplii and unidentified calanoids had the same taxonomic composition as the identified copepods, cyclopidae, *E. affinis* and *P. forbesi,* respectively.

(Table 2). Copepods of various life stages predominated in the diet in all months, always accounting for > 85% of the gut contents. The most commonly eaten copepods represented different life stages of three taxa; cyclopidae, *Eurytemora affinis* and *Pseudodiaptomus forbesi*. Collectively, these taxa represented an estimated 65% to 99% of monthly diet composition. The prey category 'nauplii' included the larval stages of both calanoid and cyclopid copepods, but the proportions of each were not determined. The prey category 'unidentified calanoids' included individuals which were badly digested, but more often, it represented morphologically similar early copepodite stages that were difficult to differentiate. Since virtually all of the calanoid copepodites that could be identified to genus or species were *E. affinis* or *P. forbesi*, most of the unidentified calanoids were probably *E. affinis* and *P. forbesi* as well.

Seasonal shifts in diet were apparent (Table 2). Cyclopids were most commonly eaten in March-April, whereas *E. affinis* was most commonly eaten in April-May, and *P. forbesi* in May-June. Interannual differences in diet composition were also apparent. *P. forbesi* contributed to the diet more in 1992 than the other years. Similarly, cyclopids were more important in 1993 than other years. Other apparent seasonal shifts in diet (e.g., nauplii) were due to ontogenetic changes in the size of prey consumed rather than to season per se (Fig. 1). Nauplii, which are the small larval stages of copepods, and other small zooplankters such as harpacticoid and oithonid copepods, and rotifers were principally eaten by the smallest feeding larvae (5-8 mm). In contrast, the larger adult copepods were principally eaten by delta smelt ≥ 13 mm.

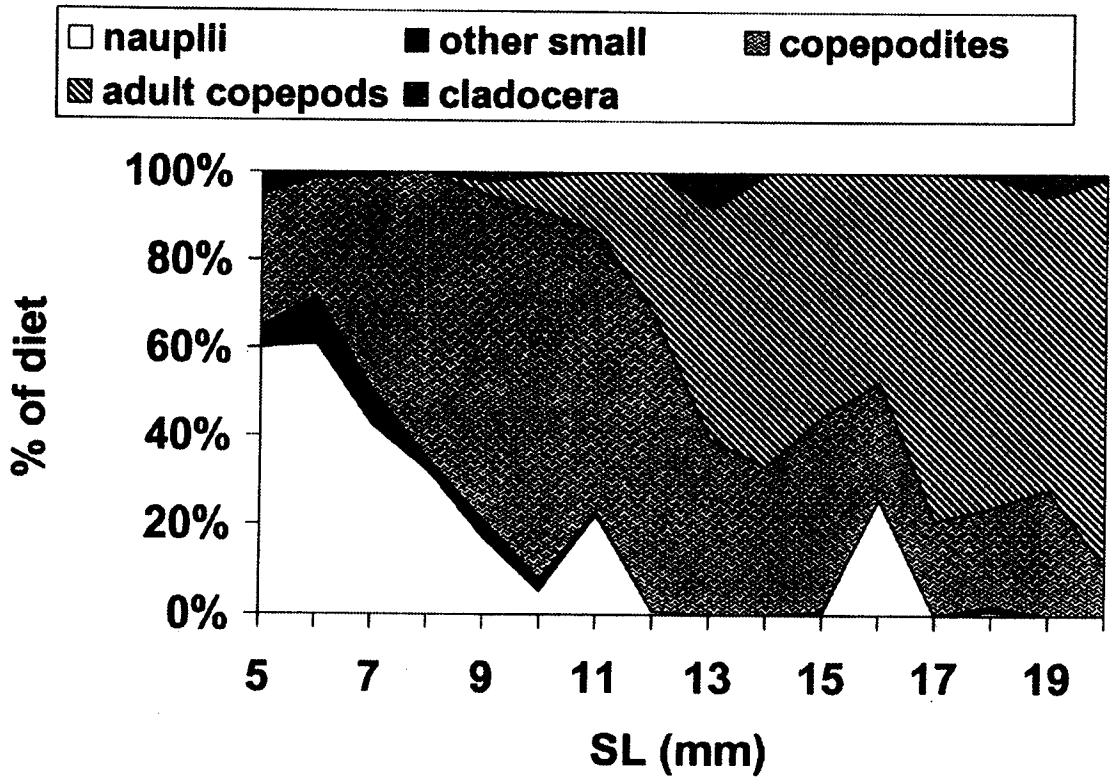

Figure 1. Larval delta smelt diet composition (% by number of occurrences) versus larval delta smelt standard length for each 1 mm length group between 5 and 20 mm.

The increase in prey size with length was consistent with a gradual increase in mouth width as SL increased [mouth width = 0.082(SL) + 0.0016; $r^2 = 0.89$; $P < 0.001$; df = 595].

The electivity analysis indicated larval delta smelt feed on a subset of potentially available prey types, and that prey use was influenced by changes in prey abundance (Fig. 2). Larval delta smelt significantly increased their use of cyclopids, calanoid

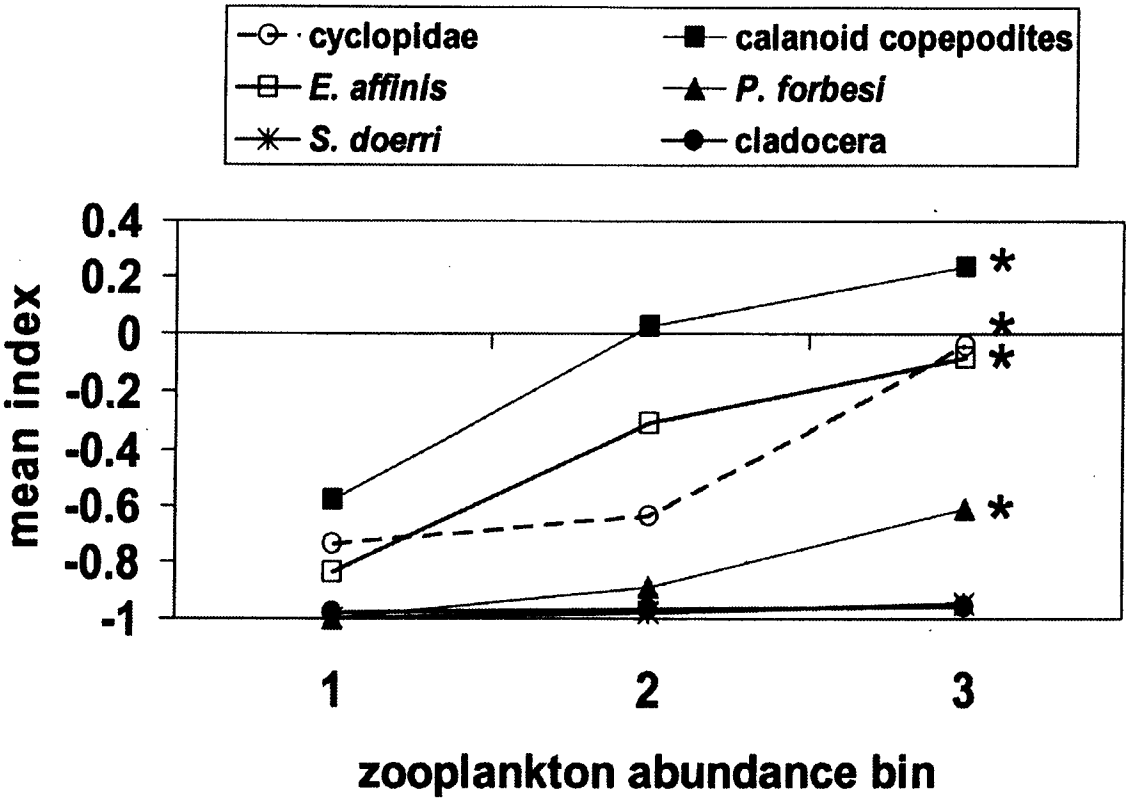

Figure 2. Relationship between bins of zooplankton abundance (number/m^3) and mean electivity for each zooplankton group shown by concurrently collected larval delta smelt. Bin 1 included the lowest 100 abundance estimates, bin 2 the intermediate 99 abundance estimates, and bin 3 the highest 99 abundance estimates for each zooplankton group. The asterisks denote changes in mean electivity that Kruskal-Wallis analyses of variance indicated were statistically significant at a Dunn-Sidak adjusted significance level of $\propto < 0.009$.

copepodites, and adult *E. affinis* and *P. forbesi* as the abundance of these prey increased (all $P < 0.0001$). In contrast, use of *S. doerri* ($P > 0.07$) and cladocerans ($P > 0.37$) did not increase in accordance with abundance in the environment.

Larval delta smelt FI varied with both SL and year of collection (Fig. 3). Overall, SL had a much larger influence than year of collection. However, interannual differences in FI were substantial (up to about 30%) within SL bins 3 and 4 (6.1 to 9.8 mm larvae) suggesting variation in environmental conditions can substantially affect feeding success of larvae shortly after the onset of exogenous feeding. Between 1992 and 1994, the ELS recorded a considerable range of environmental conditions (Table

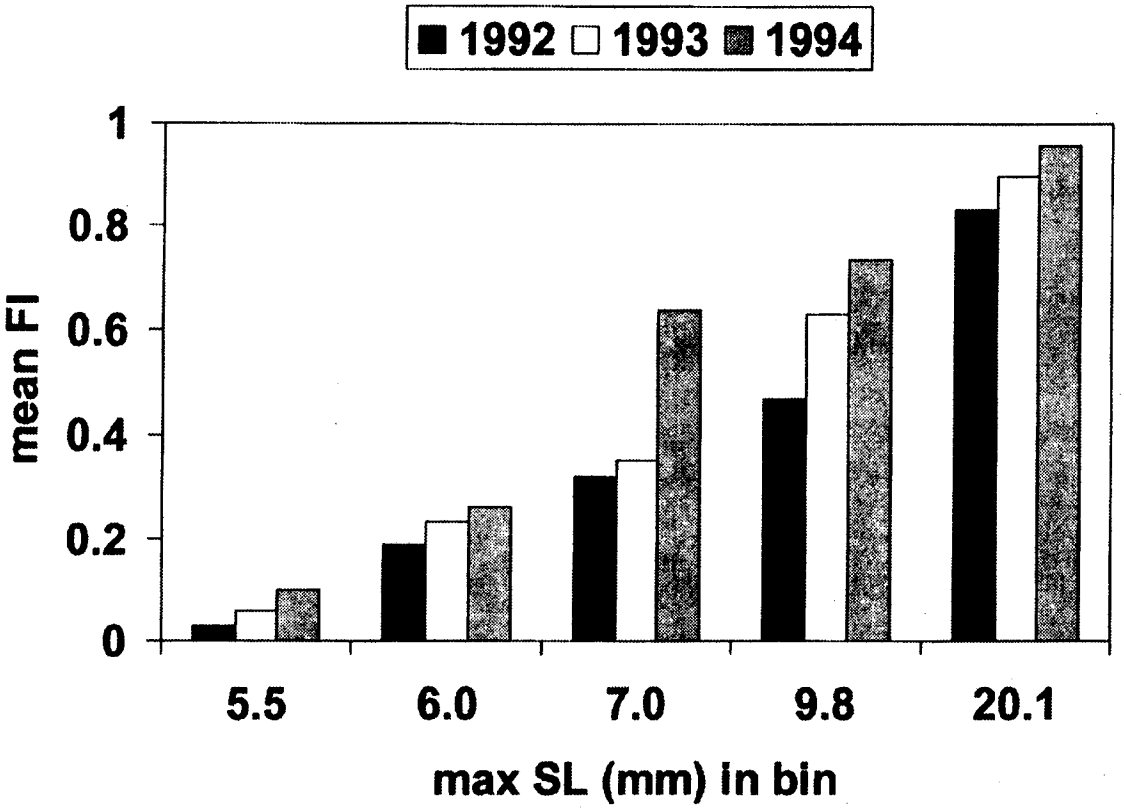

Figure 3. Larval delta smelt feeding incidence (FI; the proportion of larvae with food in their gut) versus standard length (mm), 1992-1994. Each SL bin included 204-205 fish. The minimum length in bin 1 was 4.0 mm.

Table 3. Means and ranges of environmental variables measured during the California Department of Fish and Game Egg and Larval Survey (ELS), means and ranges of ELS environmental variables for the subset of ELS data based on measurements taken concurrently with larval delta smelt collections April-May 1992 and March-June 1993-1994, and Principal Components Analysis loadings of the ln-transformed and standardized ELS environmental variables taken concurrently with larval delta smelt collections. PC1 had an eigenvalue of 3.99 and explained 50% of the variance in environmental conditions. PC2 had an eigenvalue of 1.32 and explained 16% of the variance in environmental conditions.

Environmental variable	ELS mean (range)	Smelt mean (range)	PC1	PC2
Water temperature (°C)	17.6 (10.3 - 27.2)	16.8 (10.6 - 23.3)	0.63	-0.37
Secchi disk depth (m)	0.51 (0.05 - 1.6)	0.55 (0.15 - 1.5)	0.03	-0.92
Surf. conductivity (µs/cm)	1,901 (72 - 27,088)	454 (82 - 7,913)	0.63	0.55
Copepod nauplii (#/m^3)	622 (0 - 50,207)	644 (0 - 31,246)	0.84	0.04
Cyclopid copepodites (#/m^3)	531 (0 - 36,609)	605 (0 - 12,484)	-0.57	0.20
Calanoid copepodites (#/m^3)	1,627 (0 - 30,698)	1,684 (0 - 17,448)	0.89	-0.02
E. affinis adults (#/m^3)	191 (0 - 6,008)	321 (0 - 3,414)	0.84	0.002
P. forbesi adults (#/m^3)	721 (0 - 40,214)	432 (0 - 10,702)	0.82	0.01

3). For the most part, larval delta smelt were collected over much of the range of, and under similar mean conditions to, those recorded for the entire survey. Notable exceptions were that on average larval delta smelt were collected from locations where specific conductance was an order of magnitude lower than the average for the entire survey. In addition, maximum water temperature and copepod abundances for the entire survey were somewhat higher than the maxima where delta smelt larvae were collected.

The PCA produced two principal components (PC) with eigenvalues > 1 (Table 3); the first PC explained 50% of the variation in the environmental variables, and the second PC explained an additional 16% of the variation. The PC1 represented a gradient in calanoid copepod abundance because nauplii, calanoid copepodites, *E. affinis* adults, and *P. forbesi* adults all had loadings onto PC1 that were > 0.80. Surface specific conductance and water temperature also loaded onto PC1, but less strongly than the correlated calanoid copepod variables. A fifth copepod abundance variable, total cyclopidae, contrasted somewhat with the other copepod variables. The PC2 primarily represented a gradient in Secchi disk depth that separated wet year conditions (positive PC2 scores) from the dry year conditions (negative PC2 scores).

In the ANCOVA, the SL bin and SL bin X PC1 terms were significantly positively correlated with FI (Table 4). The SL X PC2 term was not correlated with FI. Larger larvae co-occurred with higher abundances of calanoid copepods than smaller larvae (Fig. 4). However, feeding larvae in each SL bin were collected in association with higher calanoid copepod abundance than equivalent sized non-feeding larvae.

DISCUSSION

In general, the principal prey taxa of larval delta smelt have probably changed very

Table 4. Results of a Separate Slopes Analysis of Covariance testing for ontogenetic and environmental influences on feeding incidence of larval delta smelt. Feeding incidence was defined as the presence or absence of food in the gut (Dauvin and Dodson 1990). The explanatory variables included in the analysis were larval standard length (SL) as a categorical variable in bins of approximately equal sample size (n = 204-205 fish/bin) and the interaction of SL with two continuous variables; principal components scores (PC1 and PC2) summarizing physical and biological variables taken concurrently with each larva. PC1 primarily represented a gradient in calanoid copepod abundance. PC2 represented a gradient in water clarity (Secchi disk depth) that separated a wet year (1993) from two dry years (1992 and 1994).

Explanatory variable	df	Wald statistic	*P*-value
SL bin	4	69.36	< 0.000001
SL bin X PC1	5	55.68	< 0.000001
SL bin X PC2	5	5.767	0.33

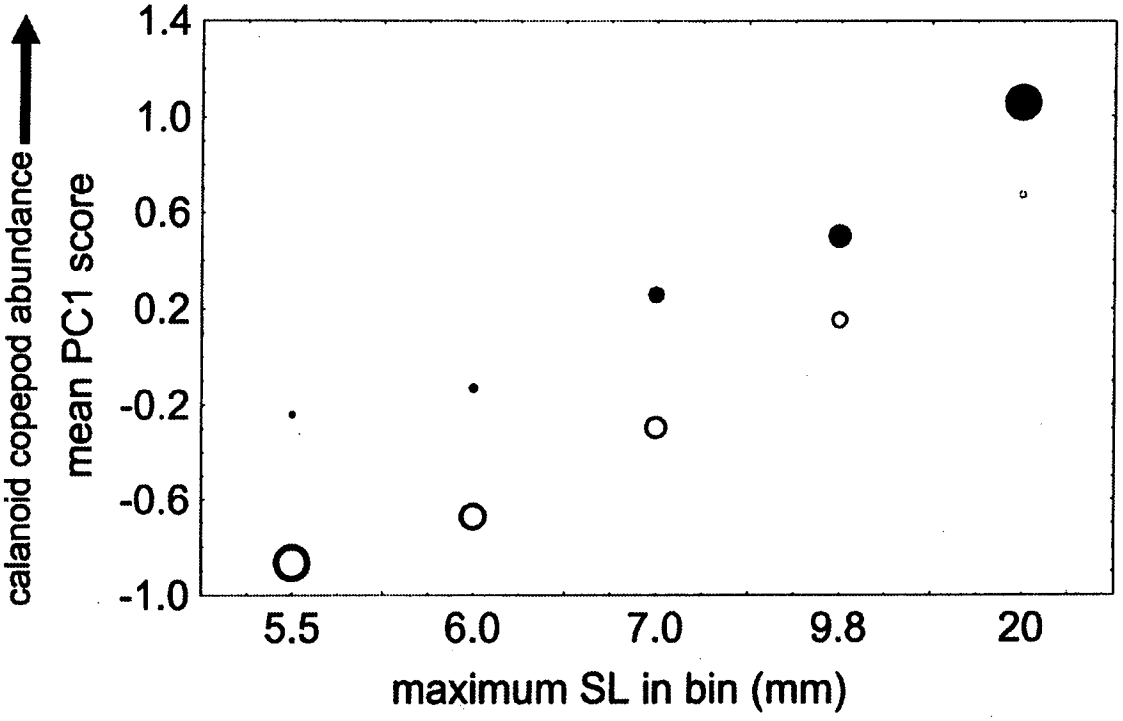

Figure 4. Interactive influences of larval delta smelt standard length (mm) and calanoid copepod abundance on larval delta smelt feeding incidence (FI; the proportion of larvae with food in their gut). The larvae collected with food in their gut are represented by solid circles and larvae collected with empty guts are represented by open circles. The calanoid copepod abundance values are scores from the first principal component of a Principal Components Analysis of physical and biological data collected concurrently with each larval delta smelt. Four copepod abundance variables (nauplii, calanoid copepodites, adult *Eurytemora affinis*, and adult *Pseudodiaptomus forbesi*) loaded strongly (loading of each > 0.80) onto PC1, with abundance of each increasing in a positive direction. Each SL bin on the x-axis represents 204-205 fish and the size of the datapoints represents the proportion of fish in each SL bin with and without food in their guts.

little since the latter 1970s. Moyle et al. (1992) presented the only historical diet data for larval delta smelt. Their results were based on a sample of only 24 larvae collected in 1977. This small sample had a diet that was 100% copepods, 99% of which was *E. affinis* and cyclopidae. Given much larger sample sizes, I found other copepods and non-copepod zooplankton are occasionally eaten as well. However, despite higher diet diversity than previously reported, both the diet composition (Table 2) and electivity results (Fig. 2) suggest larval delta smelt remain heavily dependent on *E. affinis* and cyclopids as prey. Because both *E. affinis* (Kimmerer and Orsi 1996) and cyclopids (Obrebski et al.[4] 1992) have declined in abundance since the 1970s, it follows that prey abundance for larval delta smelt has declined.

P. forbesi, introduced in 1987 (Orsi and Walter 1991), was important in the diet

[4]Obrebski, S., J.J. Orsi, and W.J. Kimmerer. 1992. Long-term trends in zooplankton distribution and abundance in the Sacramento-San Joaquin Estuary. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary Technical Report 32.

in 1992 and in June of the other years (Table 2). *P. forbesi* abundance increases in late spring (Kimmerer and Orsi 1996). Meng and Orsi (1991) concluded *P. forbesi* bloom timing would result in temporal mismatch with the emergence of striped bass larvae in the San Francisco Estuary. The low delta smelt FI in 1992 (Fig. 3) and the typically low occurrence of *P. forbesi* in the delta smelt diet until early summer (Table 2), are evidence that *P. forbesi* also is of limited use to delta smelt larvae even though it is the predominant prey for older delta smelt collected in summer and fall (Moyle et al. 1992; Lott[5] 1998).

The Vanderploeg-Scavia electivity index is awkward to interpret because it is asymmetrical around its random feeding value of zero (Lechowicz 1982). The minimum value of the index is always -1, but the maximum value increases depending on how many prey are considered for analysis. Since I used six prey categories, the maximum index value possible was 0.7. This asymmetry was the likely reason mean electivity was negative for most prey types (Fig. 2). Despite this limitation, Lechowicz (1982) recommended the Vanderploeg-Scavia index because, unlike many other commonly used electivity indices, it was stable under changes in relative abundance of prey types.

Because the smallest delta smelt larvae had usually eaten copepod nauplii and other small prey (Fig. 1) that were not sampled quantitatively by the CB net, the electivity analysis also under represented the prey selection of the smallest larvae with the lowest FI. However, the analysis was sufficient to demonstrate that larval delta smelt capture a subset of the potentially available zooplankton with which they co-occur. Clearly, *S. doerri* and cladocera were rare in the diet for reasons other than low abundance (Table 1; Fig. 2). A study of native and introduced copepods of the San Francisco Estuary demonstrated *S. doerri* has a well developed escape response that made it difficult for larval striped bass to capture (Meng and Orsi 1991). Presumably, the lack of an electivity response to *S. doerri* indicates it is also difficult for larval delta smelt to capture. Larval delta smelt also showed no electivity response to cladocera, which are commonly used in larval fish feeding experiments (Bremigan and Stein 1994; 1997) and are therefore probably not difficult to capture. Cladocera were eaten in low numbers throughout the larval period, indicating size biased predation was also not the reason for lack of use.

As in many larval fishes (Siefert 1972; Hunter 1981), prey size increased as the delta smelt grew. Ontogenetic diet shifts are important for maximizing energy intake during a period of rapid growth (Tsai 1991) and are generally made possible by morphological development resulting in increased mouth gape, fin ray development, and air bladder inflation. Delta smelt mouth width increased continuously throughout the larval period, allowing for ingestion of larger prey. Delta smelt develop fin rays at about 13 mm total length (Wang[2] 1991). It is possible the final diet shift to adult copepods, which occurs at a similar size (Fig. 1), is facilitated by fin ray development.

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[5]Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin river estuary. IEP Newsletter (Interagency Ecological Program for the San Francisco Estuary) 11(1):14-19.

The analyses of FI also provided important insights into larval delta smelt feeding ecology (discussed below). FI was a coarse, but appropriate metric of feeding success. Because 50% of the larvae examined did not have food in their gut, FI encompassed much of the variability in larval delta smelt feeding success. Although it is likely some larvae evacuated their gut contents upon capture, the larvae were collected using the same techniques and protocols each year. Furthermore, 1994 FI > 1993 FI > 1992 FI was true throughout the larval period (Fig. 3), which is a non-random pattern.

The interannual variability in feeding success at size (Fig. 3), suggests larval food supply may be limiting in some years. Moyle et al. (1992) hypothesized larval delta smelt feeding success would be enhanced in years of high freshwater flow into the estuary because the flows would facilitate seaward movement toward, and subsequent retention in, the LSZ where copepod abundance maxima historically occurred. However, feeding success did not appear to be enhanced in the wet year relative to the dry years (Fig. 3). Following the introduction of *P. amurensis*, copepod abundance maxima shifted up-estuary into less saline water (Kimmerer and Orsi 1996), possibly altering a historical benefit of the LSZ for larval delta smelt. In addition, the abundance of copepods commonly eaten by larval delta smelt does not appear to be related to freshwater flow into the estuary during spring (Jassby et al. 1995; Kimmerer and Orsi 1996). Therefore, the available evidence suggests prey abundance does not consistently differ among years of higher and lower spring outflow.

Larval delta smelt feeding success was influenced by interactions of ontogenetic and environmental influences. If the entire larval period is considered, ontogeny (size of the fish) exerted the largest influence on feeding success (Fig. 3). This is consistent with studies of other larval fishes, which have demonstrated feeding success typically increases with size and experience (Hunter 1981; Gerking 1994). However, differences in FI among years indicate environmental influences were important, particularly once exogenous feeding was fully initiated (Fig. 3). It appears that larval delta smelt feeding success was related directly to prey abundance because (1) the PC1 represented a calanoid copepod abundance gradient, and (2) PC1 scores of feeding larvae were consistently higher than PC1 scores of equivalent sized nonfeeding larvae (Fig. 4). Although a link between food abundance and feeding success is intuitive, it has not been previously demonstrated for any larval fish in the San Francisco Estuary, and it suggests long-term declines in copepod abundance have likely impacted larval delta smelt feeding success.

Overall, the findings of this study are consistent with the hypothesis that long-term declines in copepod abundance and changes in copepod species composition have had a negative impact on delta smelt. Although evidence for starvation due to food limitation is rare in larval fishes, reductions in prey availability can affect larval fish survival indirectly by reducing growth rates (Houde 1987). Reduced growth rate increases the duration of the larval stage, which can result in lower survival through

[6]Bodega Marine Laboratory, 2099 Westside Rd., P.O. Box 247, Bodega Bay, CA 94923, personal communication via electronic mail on October 18, 2002.

the larval stage. Determining whether or not there is a link between larval feeding success, larval growth rates, and survival is an obvious next step. This research is currently underway (William Bennett[6], personal communication). Clearly, a fuller understanding of direct and indirect effects of food web alteration on delta smelt recruitment is needed for effective management toward recovery.

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LITERATURE CITED

Alpine, A.E. and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

Bennett, W.A. and P.B. Moyle. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin Estuary. Pages 519-542. *in* J.T. Hollibaugh, editor. San Francisco Bay: the ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco, California, USA.

Bremigan, M.T. and R.A. Stein. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51:913-922.

Bremigan, M.T. and R.A. Stein. 1997. Experimental assessment of the influence of zooplankton size and density on gizzard shad recruitment. Transactions of the American Fisheries Society 126:622-637.

Dauvin, J.C. and J.J. Dodson. 1990. Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary. Marine Ecology Progress Series 60:1-12.

Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego, CA, USA.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17-29.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. Pages 33-77. *in* R. Lasker, editor. Marine fish larvae: morphology, ecology, and relation to fisheries. University of Washington Press, Seattle, Washington, USA.

Jassby, A.D., W.J. Kimmerer, S.G. Monismith, C. Armor, J.E. Cloern, T.M. Powell, J.R. Schubel, and T.J. Vedlinkski. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecological Applications 5:272-289.

Kimmerer, W.J., J.H. Cowan, Jr., L.W. Miller, and K.A. Rose. 2000. Analysis of an estuarine

striped bass (*Morone saxatilis*) population: influence of density-dependent mortality between metamorphosis and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 57:478-486.

Kimmerer, W.J., J.H. Cowan, Jr., L.W. Miller, and K.A. Rose. 2001. Analysis of an estuarine striped bass population: effects of environmental conditions during early life. Estuaries 24:557-575.

Kimmerer, W.J., E. Gartside, and J.J. Orsi. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

Kimmerer, W.J. and J.J. Orsi. 1996. Changes in the zooplankton of the San Francisco Bay Estuary since the introduction of the clam *Potamocorbula amurensis*. Pages 403-424. *in* J.T. Hollibaugh, editor. San Francisco Bay: the ecosystem. Pacific Division of the American Association for the Advancement of Science. San Francisco, California, USA.

Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22-30.

Lehman, P.W. 1992. Environmental factors associated with long-term changes in chlorophyll concentration in the Sacramento-San Joaquin Delta and Suisun Bay, California. Estuaries 15: 335-348.

Lehman, P.W. 2000. Phytoplankton biomass, cell diameter, and species composition in the low salinity zone of northern San Francisco Bay Estuary. Estuaries 23:216-230.

Meng, L. and J.J. Orsi. 1991. Selective predation by larval striped bass on native and introduced copepods. Transactions of the American Fisheries Society 120:187-192.

Moyle, P.B., B. Herbold, D.E. Stevens, and L.W. Miller. 1992. Life history and status of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.

Nichols, F.H. J.K. Thompson and L.E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam Potamocorbula amurensis 2. displacement of a former community. Marine Ecology Progress Series 66:95-101.

Orsi, J.J. and W.L. Mecum. 1996. Food limitation as the probable cause of a long-term decline in the abundance of Neomysis mercedis the opossum shrimp in the Sacramento-San Joaquin estuary. Pages 375-401. *in* J.T. Hollibaugh, editor. San Francisco Bay: the ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco, California, USA.

Orsi, J.J. and T.C. Walter. 1991. Pseudodiaptomus forbesi and P. marinus (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin Estuary. Bulletin of the Plankton Society of Japan Special Volume (1991):553-562.

Siefert, R.E. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. Transactions of the American Fisheries Society 101:219-225.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry 3rd ed. W.H. Freeman and Company, New York, NY, USA.

Sweetnam, D.A. 1999. Status of delta smelt in the Sacramento-San Joaquin Estuary. California Fish and Game 85:22-27.

Tsai, C-F. 1991. Prey density requirements of the striped bass, Morone saxatilis (Walbaum), larvae. Estuaries 14:207-217.

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