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Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary

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Synopsis

We compared dietary patterns within a temperate estuarine fish assemblage (Suisun Marsh, CA, U.S.A.) during a period of high mysid shrimp abundance and after a major decline in mysid abundance caused by the invasion of the overbite clam *Potamocorbula amurensis*. Prior to the invasion, high dietary overlap, high stomach fullness, and low niche breadth occurred among the fishes in spring when mysid populations were high. Dietary overlaps decreased and niche breadth increased for all species but the endemic splittail *Pogonichthys macrolepidotus* in fall when mysid populations were low. Eight native species exhibited lower overall collective overlaps and fuller stomachs than five alien species, suggesting more efficient resource partitioning. After mysid abundance declined, only alien striped bass *Morone saxatilis* preyed upon mysids in greater than trace amounts. An alien mysid became an important prey for small striped bass, but striped bass also switched to piscivory at a smaller size than when mysids were abundant. Eight of 13 species exhibited significant declines in abundance during the study period, which were concordant with the original importance of mysids in their diets. Our results suggest that altered lower food web dynamics in the San Francisco Estuary caused by the invasion of the overbite clam changed fish diets and have contributed to declines in fish abundance.

Introduction

Estuaries are complex and highly variable environments in good part because river and tidal inflow contributes to large-scale seasonal and annual fluctuations in temperature, salinity, and other factors. Urbanized estuaries, such as the San Francisco Estuary, have become even more variable due to human-caused habitat and hydrodynamic manipulations (Nichols et al. 1986) and a continuing influx of alien species (Cohen & Carlton 1995). Alien species have become established at every trophic level and have irreversibly altered the estuary's food web (Cohen & Carlton 1995, Kimmerer et al. 1994, Orsi & Mecum 1996). These and

other interactive factors have contributed to dramatic declines in fish abundance in the estuary (Herbold et al. 1992, Bennett & Moyle 1996).

Estuarine fishes often exhibit strong trophic adaptability (Gerking 1994) as a mechanism to cope with their dynamic environment. In estuaries throughout the world, this often takes the form of feeding guilds centered on seasonally abundant food resources such as mysid shrimps (Herbold 1987, Hostens & Mees 1999). The opossum shrimp *Neomysis mercedis* (Mysidae) has historically been an important food for fish in the San Francisco Estuary (Turner & Kelly 1966, Herbold 1987). Historically, the abundance of this mysid shrimp varied from year to year but its seasonal

pattern of abundance consistently reached a peak in April and a low in October (Moyle et al. 1986).

A major decline in the abundance of most planktonic invertebrates occurred in the San Francisco Estuary following invasion of the overbite clam *Potamocorbula amurensis*. Peak abundance of *N. mercedis* decreased by up to 90% (Kimmerer & Orsi 1996) and was attributed to food limitation (Orsi & Mecum 1996). Kimmerer et al. (2000) found a significant positive relationship between the abundance of mysids and the abundance of juvenile striped bass *Morone saxatilis*, suggesting that the extended period of low mysid populations may have contributed to poor survival of juvenile striped bass.

Suisun Marsh is one of the largest remaining estuarine marshes on the west coast of North America and still exhibits habitat complexity lost from much of the San Francisco Estuary as a result of human activities. However, many fish species that characterized the marsh in the late 1970s and early 1980s have undergone severe declines (Meng et al. 1994, Matern et al. 2002). The simultaneous decline in mysid abundance suggested that fish declines may have been tied to the altered estuarine food web (Herbold et al. 1992, Meng et al. 1994).

In this paper, we asked the following questions: (1) Did historic fish diets differ between seasons of high and low mysid abundance, and if so, were there different patterns among the native and alien fish species? We hypothesized that diets would differ between seasons because such has been demonstrated in many regions including North America (Van Snik Gray et al. 1997), the neotropics (Winemiller 1989), Asia (Xie et al. 2000), Europe (Thorman 1982), and the Arctic (Willette et al. 1999). (2) Did the mysid abundance crash affect fish diets? The year-round abundance of mysids is presently lower than during the historic seasons of low abundance (Kimmerer & Orsi 1996); therefore we hypothesized that current diet patterns would be similar to those present during the historic seasons of low mysid abundance. (3) Were declines in fish abundance related to changes in diet? We hypothesized that fishes depending most on mysids would exhibit the most severe declines in abundance.

Methods

Study site

Together with Suisun and Grizzly Bays, Suisun Marsh (Figure 1) forms the primary nursery area for many

juvenile fishes in the San Francisco Estuary. The marsh covers an area of 34 000 ha, 33% of which comprise tidally influenced sloughs. Sloughs are typically 2–3 m deep, 10–100 m wide, and lined with tules (*Scirpus* spp.) and reeds (*Phragmites communis*). Physical conditions in the marsh are highly seasonal and vary strongly from year to year. Salinity in the marsh ranges from 0 to 16 ppt and is negatively correlated with river flow; lower salinities occur in winter and spring when river inflow is greatest (Moyle et al. 1986, Meng et al. 1994, Matern et al. 2002). Water temperature ranges from 5°C to 25°C and varies seasonally like salinity.

Field and laboratory methods

We have conducted monthly otter trawl sampling in Suisun Marsh since 1979 to monitor the abundance and distribution of fishes (Moyle et al. 1986, Meng et al. 1994, Matern et al. 2002). A four-seam otter trawl (1 × 2.5 m at opening, 5.3 m in length, and mesh sizes of 35 mm in the body to 6 mm in the codend) has been towed at fixed stations throughout the marsh each month over the course of the study (Figure 1). Matern et al. (2002) provide further details on the sampling program and fish abundance and distribution trends in the marsh.

Fishes were retained for dietary analysis during two time periods, August 1979 to May 1983 and April 1998 to January 1999. During the first study period, when possible, at least ten individuals of the most common species (Moyle et al. 1986; Table 1) were randomly retained per month from the otter trawl samples. Declines in fish abundance throughout Suisun Marsh (Matern et al. 2002) before the second sampling period constrained us to fewer species and smaller numbers than were available from the first study period. Fish were retained quarterly during the second sampling period. Upon collection, all fishes were immediately preserved in 10% formalin and the body cavities of fishes > 100 mm standard length (SL) were opened to ensure the preservation of items in the digestive tract.

In the laboratory, fish were measured to the nearest mm (SL) and weighed wet to the nearest 0.1 g. Stomach contents were removed, enumerated to the lowest practical taxon with the aid of a dissecting microscope, and weighed to the nearest 0.0001 g. Gut contents of splittail *Pogonichthys macrolepidotus* and yellowfin gobies *Acanthogobius flavimanus*, which lack true stomachs, were examined to the first 180° bend in the digestive tract.

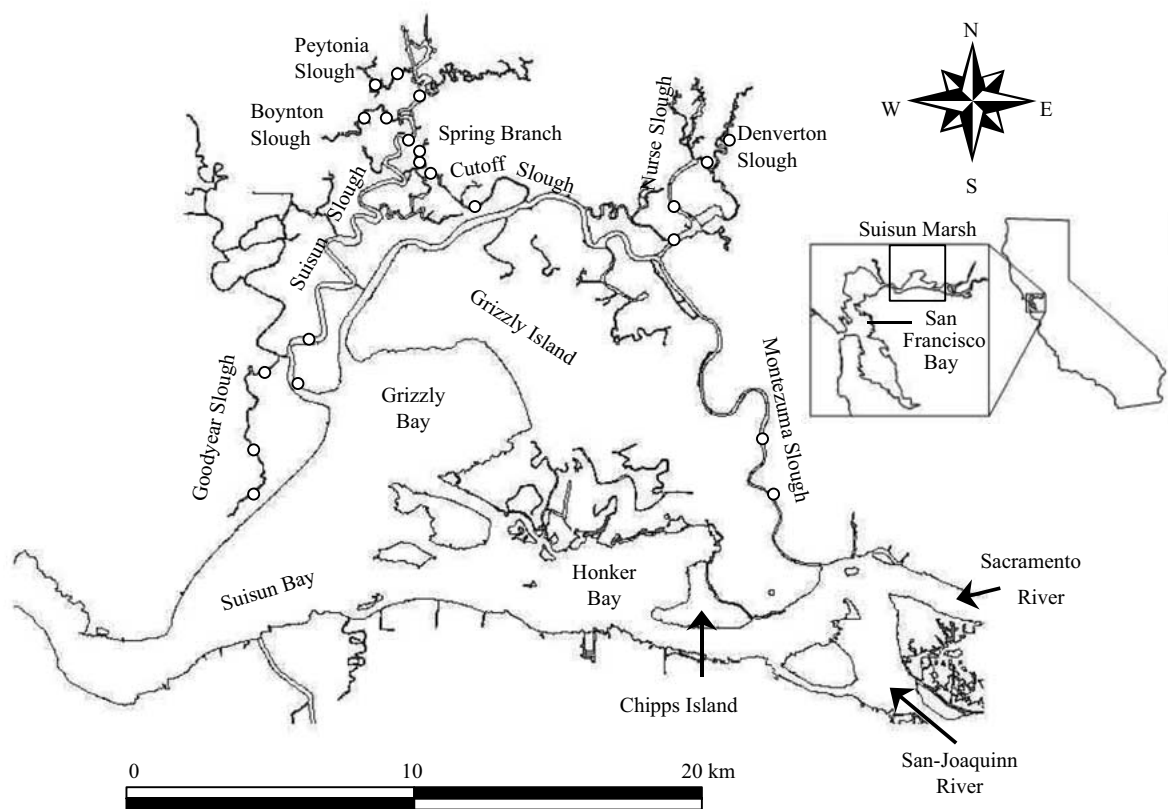


Figure 1. Fish sampling locations (circles) within Suisun Marsh in the San Francisco Estuary.

Data analysis

Data were grouped into three periods: (A1) data from the spring (February–June) sampling period, before establishment of the overbite clam, (A2) data from the fall (August–December) sampling period, before the establishment of the overbite clam, and (B) data from 1998 to 1999. Small sample size and low abundance of mysids precluded partitioning the data into seasons over the later sampling period. Our analyses focused on overall population and community diet trends; therefore, data are mostly summarized over all size ranges of each species and across the full time span of each season or sampling period. Prior to data analyses, we excluded fish with empty stomachs (Table 2) and ensured normality of SL distributions for each species in each sampling period by removing outliers and using the Anderson–Darling test.

We summarized the importance of prey items as percent of total prey mass (%M). Pope et al. (2001)

found %M was correlated with mean caloric contribution of stomach contents and Liao et al. (2001) found %M was correlated with % occurrence, % number and the compound index of relative importance. For data analyses, prey items were grouped into 17 categories (Appendix A).

We estimated stomach fullness following the methods of Herbold (1986). For each species, maximum observed gut content mass for each length of fish was used to estimate the degree of fullness for each individual of that length. This procedure permits the scaling of gut content mass of each fish to the maximum gut content mass expected for a fish of that size, regardless of non-linearities in changes of gut volume to fish size.

We calculated niche breadth (NB) for each individual with the Shannon diversity index:

$$NB = - \sum \frac{n_i}{N} \left(\log \frac{n_i}{N} \right)$$

Table 1. Fish taxa (asterisk indicates native species), code, and sample size of fishes retained for dietary analysis during each sampling period.

Taxon	Period			
	Code	A1	A2	B
Cyprinidae				
Splittail <i>P. macrolepidotus</i> *	ST	386 (145 ± 40)	112 (136 ± 50)	70 (164 ± 63)
Common carp <i>C. carpio</i>	CP	24 (177 ± 50)	34 (140 ± 85)	
Catostomidae				
Sacramento sucker <i>Catostomus occidentalis</i> *	SS	53 (151 ± 79)	22 (134 ± 34)	
Osmeridae				
Longfin smelt <i>Spirinchus thaleichthys</i>	LS	40 (71 ± 14)	48 (61 ± 10)	
Delta smelt <i>Hypomesus transpacificus</i> *	DS	33 (60 ± 8)	10 (67 ± 16)	
Clupeidae				
Threadfin shad <i>Dorosoma pentense</i>	TS	15 (63 ± 16)	17 (63 ± 25)	
American shad <i>Alosa sapidissima</i>	AS	9 (111 ± 13)	22 (92 ± 16)	
Embiotocidae				
Tule perch <i>Hysterocarpus traski</i> *	TP	113 (101 ± 23)	91 (84 ± 19)	44 (100 ± 22)
Cottidae				
Prickly sculpin <i>Cottus asper</i> *	PS	439 (47 ± 24)	26 (74 ± 16)	51 (59 ± 20)
Staghorn sculpin <i>Leptocottus armatus</i> *	SC	371 (54 ± 18)	14 (113 ± 20)	
Gobiidae				
Yellowfin goby <i>Acanthogobius flavimanus</i>	YG	65 (110 ± 40)	94 (112 ± 24)	37 (102 ± 27)
Moronidae				
Striped bass <i>M. saxatilis</i>	SB	154 (114 ± 79)	95 (83 ± 55)	113 (124 ± 41)
Plueronectidae				
Starry flounder <i>Platichthys stellatus</i> *	SF	36 (94 ± 24)	36 (60 ± 29)	11 (147 ± 55)

Mean standard length and one standard deviation are given in parentheses. A1 = spring season during pre-clam period, A2 = fall season during pre-clam period, B = post-clam period.

Table 2. Percentage of empty stomachs encountered during each study period.

Species	Period		
	A1 (%)	A2 (%)	B (%)
Splittail	13	17	16
Common carp	46	0	—
Sacramento sucker	49	23	—
Longfin smelt	13	21	—
Delta smelt	9	0	—
Threadfin shad	0	6	—
American shad	0	9	—
Tule perch	31	48	32
Prickly sculpin	15	15	2
Staghorn sculpin	5	7	—
Yellowfin goby	12	6	3
Striped bass	10	18	8
Starry flounder	3	22	9

where n_i is the mass proportion of resource i and N is the total mass of all resources. We used a generalized linear model procedure to assess differences in stomach fullness and niche breadth among seasons and sampling period.

We calculated dietary overlap (Φ) for pairwise species comparisons with the symmetric niche coefficient (Pianka 1974):

$$\Phi_{ij} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where P_{ij} is the proportion of prey category i in the diet of fish j and P_{ik} is the proportion of prey category i in the diet of fish k . Following Winemiller & Pianka (1990), we used the geometric mean (g_i) of p_i and consumer electivity (e) in place of p_i in the calculation of Φ . Consumer electivity (e) is the p_i value

standardized by resource availability (R_i): $e = p_i/R_i$. The availability of each prey category was estimated as the relative proportion of the p_i column sums from the original community diet matrix (Winemiller 1989). Winemiller & Pianka (1990) demonstrated that g_i is less biased than either p_i or e_i because it is not overly influenced by either overly abundant or rare resources. For each species during the two seasons of mysid abundance in the first sampling period, we summed all Φ values with the other species to calculate collective e -based dietary overlap. Previous investigators have used collective overlap as a method to estimate diffuse competition (Pianka 1974, Winemiller 1989).

We used cluster analysis with Ward's linkage method and Euclidean distance to elucidate functional feeding groups among fishes during each season of mysid abundance in the pre-clam period. Ward's linkage method calculates the distance between two clusters as the sum of squared deviation from points to centroids, essentially minimizing sums of squares. We used e -based resource matrices for this analysis.

We sought to determine if the mysid abundance pattern in Suisun Marsh followed that described for the entire San Francisco Estuary (Kimmerer & Orsi 1996, Orsi & Mecum 1996). We obtained mysid abundance data from the California Department of Fish and Game (CDFG) and compared the estuary-wide indices with indices calculated solely for Suisun Marsh from 1979 to 1999, a time span encompassing our entire study period (J.J. Orsi, CDFG, Central Valley Bay-Delta Branch, Stockton, CA, U.S.A., written communication). We plotted the two data series and used Pearson product-moment correlation to quantify their relationship.

To determine if mysid abundance changes were reflected in fish diets, we compared fish diets of the post-clam period (B) to the two pre-clam periods (A1 and A2) with Pianka's (1974) symmetric niche coefficient (Φ). We used non- e -based resources matrices for this analysis because of the few species examined during post-clam period. The dietary importance of mysids for each fish species during the post-clam period was compared to the two pre-clam periods by χ^2 analysis with Yates correction for continuity (Zar 1999). We examined how changes in mysid prey availability may have influenced fish diets by comparing the ontogenetic pattern of fish consumption by striped bass between the two study periods. We focused on striped bass because it has been previously demonstrated in this system that striped bass exhibit a marked switch from mysids to fish prey as they grow larger (Feyrer 1999).

We examined fish abundance trends before and after the mysid abundance crash by comparing mean annual abundance (catch per minute [CPUE], Matern et al. 2002) of each species during 1980–1986 versus 1988–1999 with two-sample t-tests. For species that exhibited significant declines in abundance ($P < 0.05$), we used rank correlation analysis to examine the relationship between CPUE change and dietary importance of mysids during the first study period.

Results

Fish diets

We collected 2685 fishes (9 families, 12 species) for diet analysis (Table 1). The relative abundance of fishes in our samples generally reflected their relative abundance in the environment as measured by otter trawl catches (Matern et al. 2002). All fishes preyed heavily on mysids during the spring pre-clam period (data summary appears in Appendix A). During this time, mysids ranked either first or second in dietary importance for 12 of 13 species. For the single disparate species, prickly sculpin, mysids ranked third in importance out of 13 prey items. Detritus was the prevalent item found in the guts of splittail; mysids, however, were the most important non-detrital item. Only copepods (cyclopoids and calanoids) were more important than mysids in the diet of delta smelt and threadfin shad. The two species that relied the least on mysids, prickly sculpin and tule perch, fed primarily on amphipods (*Corophium* and *Gammarus*).

During the fall season of lowered mysid abundance (A2), only striped bass, American shad, starry flounder, and longfin smelt continued to exploit mysids as their primary food item, albeit with a decrease in importance compared to spring. Only striped bass continued to prey almost exclusively on mysids while longfin smelt and American shad relied more heavily on copepods and starry flounder more on amphipods. For the remaining species, alternative prey items increased in importance to compensate for lowered mysid availability; splittail consumed more detritus, staghorn sculpin consumed more fish and caridean shrimp, yellowfin gobies consumed more amphipods, and common carp *Cyprinus carpio* consumed more harpacticoid copepods and insects. The conspicuous lack of detritus in the diet of carp stems from this prey category not being fully differentiated from unidentified debris for this

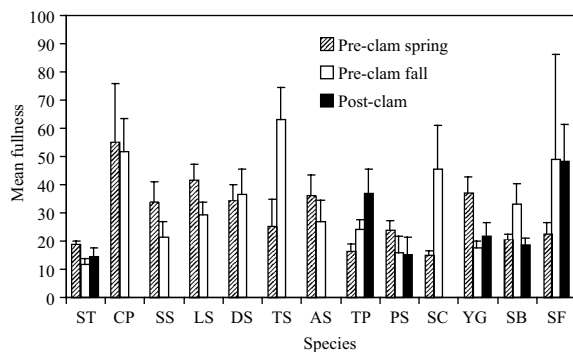


Figure 2. Mean percent of maximum stomach fullness of fishes in each study period. Error bars represent one standard error and species codes are as in Table 1.

species during laboratory work. We acknowledge this as a potential source of bias because our analyses may somewhat under- or overestimate carp's diet similarity with other species based upon the degree of detritivory. Diets of delta smelt, threadfin shad, tule perch, and prickly sculpin did not greatly change.

During the post-clam period, only striped bass continued to consume mysids as a primary food item, albeit with a substantial decrease in overall dietary importance. Amphipods were the most important prey items for tule perch, prickly sculpin, and yellowfin gobies, while annelids and amphipods were for starry flounder, and splittail continued to rely heavily on detritus.

Stomach fullness

During the pre-clam period, stomach fullness was significantly lower during fall for splittail and yellowfin goby, and significantly lower during spring for threadfin shad and staghorn sculpin ($P < 0.05$; Figure 2). Stomach fullness was significantly higher during the post-clam period compared to spring of the pre-clam period for tule perch. For striped bass, pre-clam fullness was significantly higher in fall compared to the post-clam period ($p < 0.05$).

Niche breadth

On average, every species except splittail exhibited greater NB during fall of the pre-clam period compared to spring (Figure 3). Sacramento sucker and longfin smelt were the only species for which this difference was statistically significant ($p < 0.05$). NB for splittail was significantly higher during spring ($p < 0.05$). NB for striped bass during the post-clam period was

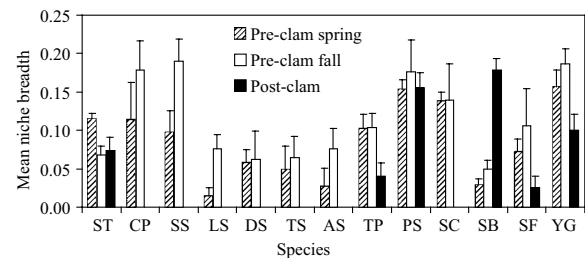


Figure 3. Mean niche breadth, calculated with the Shannon diversity index, for fishes in each study period. Error bars represent one standard error and species codes are as in Table 1.

significantly higher than either pre-clam season, while for yellowfin goby NB was significantly higher during spring of the pre-clam period compared to the post-clam period ($p < 0.05$).

Collective dietary overlap

On average, collective dietary overlap was higher during the spring pre-clam period (mean = 4.26) than during fall (mean = 3.61), reflecting the high overall reliance of the fish assemblage on mysids during spring. Among native species, average collective overlap was higher in spring (2.28) than fall (1.50). Alien species exhibited an opposite pattern where average collective overlap was higher in fall (1.47) than spring (1.39).

Feeding groups

Cluster analysis identified distinct feeding groups among species during the pre-clam seasons (Figure 4). In general, diets of each group were similar however, group membership shifted based upon how individual species changed diet across seasons.

Five major groupings were apparent during spring – A1 (Figure 4). Group one consisted of species (delta smelt and threadfin shad) that preyed very heavily on pelagic copepods. Group two consisted solely of common carp, which ate mainly bivalves and caridean shrimp. Group three consisted of species (Sacramento sucker and splittail) which relied on harpacticoid copepods. Group four consisted of species (prickly sculpin, tule perch, staghorn sculpin, and yellowfin goby) which were primarily amphipod feeders, while group five consisted of species (American shad, longfin smelt, starry flounder, and striped bass) which were primarily mysid feeders.

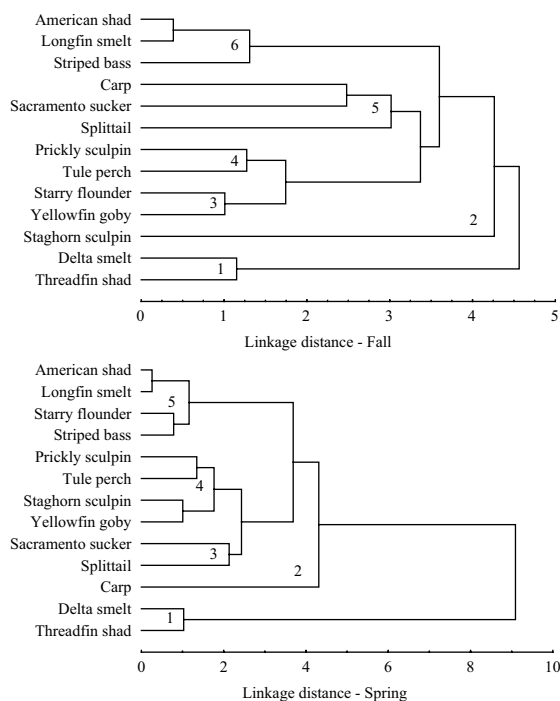


Figure 4. Dendrograms of cluster analysis using Bray's linkage method and Euclidean distance on e-based resource matrices for fish species in the spring (bottom) and fall (top) seasons of the pre-clam period. Numbers within the dendrograms identify feeding groups that are referred to in the text.

Six major groupings were apparent during fall – A2 (Figure 4). Group one, just as during spring, consisted of species (delta smelt and threadfin shad) that preyed heavily on pelagic copepods. Group two consisted solely of staghorn sculpin, which ate mainly fish and caridean shrimp. Group three consisted of species (yellowfin goby and starry flounder) that exhibited a higher than average use of annelids. Group four consisted of species (prickly sculpin and tule perch) that relied heavily on benthic invertebrates such as amphipods, isopods, and gastropods. Group five consisted of species (common carp, Sacramento sucker, and splittail) that showed a higher than average use of harpacticoid copepods, while group six consisted of species (American shad, longfin smelt, and striped bass) which were primarily mysid feeders.

Mysid abundance and consumption

Annual estuary-wide indices of mysid abundance were highly correlated with indices calculated solely for Suisun Marsh ($r = 0.91$, $p < 0.01$; Figure 5). Both

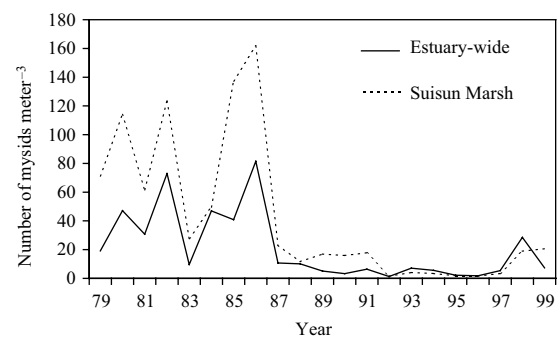


Figure 5. Annual estuary-wide mysid densities plotted with densities calculated solely for Suisun Marsh. The two data series are significantly correlated ($r = 0.91$). Data were obtained from the California Department of Fish and Game.

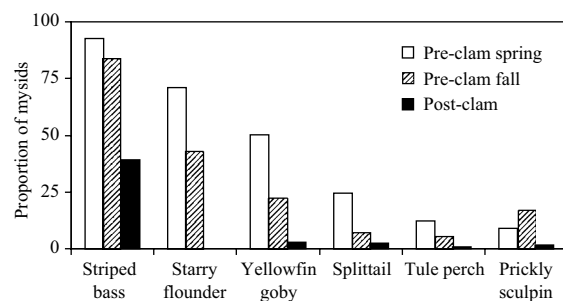


Figure 6. Dietary importance of mysids in each study period. For every species, the importance of mysids in the post-clam period is significantly lower than during each season of the pre-clam period ($p < 0.05$).

data series showed a sharp decline in mysid abundance in 1987 that persisted through 1999.

Except for tule perch and prickly sculpin, two amphipod feeders, diets of fishes during the post-clam period were more similar to the fall pre-clam period rather than spring. However, for every species, dietary importance of mysids during the post-clam period was significantly lower than either pre-clam season ($p < 0.05$; Figure 6). Pooled dietary importance of mysids for each study period was as follows: pre-clam spring – 43%, pre-clam fall – 30%, and post-clam – 8%. Striped bass was the only species for which mysids represented >3% of diet during the post-clam period.

The ontogenetic pattern of fish consumption by striped bass differed between study periods (Figure 7). During the pre-clam period, striped bass shifted to fish at about 140 mm. However during the post-clam period, the shift to fish occurred at about 80 mm and the percentage of fish in the diet was highly variable

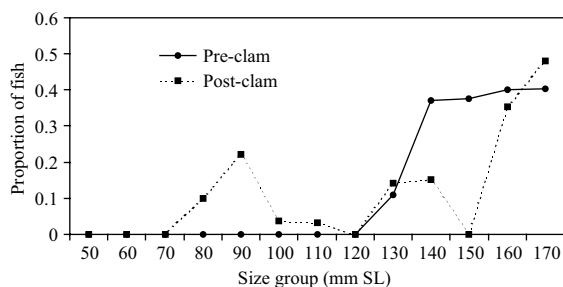


Figure 7. Ontogenetic patterns of fish consumption by striped bass during the pre- and post-clam periods. Values are expressed as the average importance for all individuals falling into each length grouping.

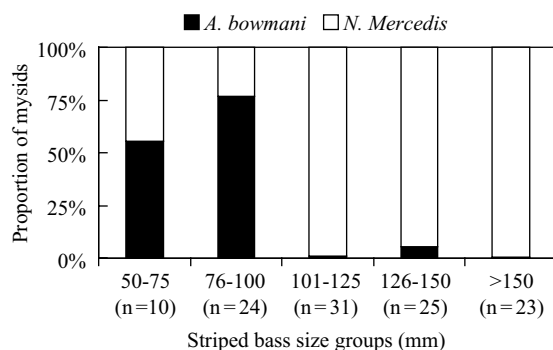


Figure 8. Ontogenetic pattern of mysid species consumption by striped bass during the post-clam period.

thereafter. Striped bass also exhibited an ontogenetic trend in mysid species consumption during the post-clam period where fish up to 100 mm SL preyed mostly on the alien mysid *Acanthomysis bowmani* while larger fish preyed almost exclusively on the native *N. mercedis* (Figure 8).

Fish abundance

Abundance of all but five species (delta smelt, stary flounder, American shad, yellowfin goby, and staghorn sculpin) was significantly lower during 1988–1999 compared to 1980–1986 ($p < 0.05$). Decrease in CPUEs ranged from 51% to 78%. CPUE declines were significantly concordant with dietary importance of mysids during the first study period ($P < 0.005$, Figure 9), indicating a strong relationship between fish abundance declines and their historic reliance on mysid prey.

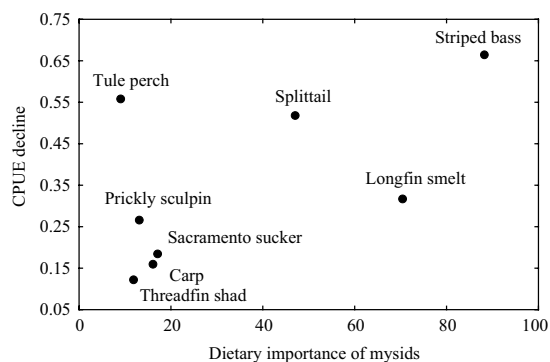


Figure 9. The historical dietary importance of mysids plotted against the decline in CPUE for fishes that exhibited significant declines during 1988–1999 compared to 1980–1986.

Discussion

Our hypothesis that historical fish diets would differ across mysid abundance seasons held true. In general, fishes took advantage of highly abundant mysids during spring. During fall, mysids decreased in dietary importance and niche breadth increased. Only the endemic splittail did not increase niche breadth during fall. For other species, increased niche breadth during fall indicates a more generalized feeding strategy, consistent with the theory of trophic adaptability (Gerking 1994). Fuller stomachs and lower collective overlap of natives compared to aliens during fall suggests natives were more efficient at partitioning resources.

The single alien species that exhibited significantly greater stomach fullness in fall, threadfin shad, was conspicuous because it had very similar diet patterns to endemic and threatened delta smelt. Nearly identical diet composition, niche breadth, and stomach fullness patterns suggest significant resource overlap between these species. Although similarity in resource use does not imply competition, these data suggest that threadfin shad is the most likely alien species in the group studied to compete with delta smelt.

Splittail was the sole native species that was significantly less full in fall. Despite an accompanying lower NB and a substantial increase in dietary importance of detritus, mysids remained the primary non-detrital food item for splittail in fall, suggesting a strong preference for this prey item. The decline in stomach fullness in splittail due to presumed fidelity to mysid prey is similar to observations of Matthews et al. (1988) for striped bass and their preferred prey in an Oklahoma (U.S.A.) reservoir. They observed that prey fidelity

caused striped bass starvation because alternative prey were not exploited during conditions of low preferred prey abundance.

Our observation that collective overlaps were lower during the season of low prey abundance is consistent with Pianka's (1974) niche overlap hypothesis. Similar to our observations, Thorman (1982) found decreased collective overlaps during low food abundance seasons in an estuary on the Swedish west coast. Low collective overlap was observed in the Venezuelan ilanos during the transition season, which was characterized by high fish densities and low invertebrate prey availability (Winemiller 1989). Van Snik Gray et al. (1997) observed greater food resource partitioning linked primarily through size dimensions during lean seasons by a diverse darter community in a stream in the eastern United States.

Our hypothesis that the mysid abundance crash would impact fish diets held true. Each species exhibited a significant decline in dietary importance of mysids and only striped bass consumed greater than trace amounts during the post-clam period. The fact that overall diets during the post-clam period were more similar to those of the fall pre-clam period, and that all species but striped bass rarely fed on mysids during the post-clam period, suggests that the historic seasonality in diets centering around mysids was dampened or eliminated after mysid abundance decreased.

Striped bass, one of the most abundant fish in the estuary, showed a strong ontogenetic shift in diet following the mysid abundance decline. The switch from mysids to fish at a much smaller size may have been triggered by lowered overall mysid availability, size-selective predation on mysids, or a combination of these and other factors. Optimal foraging theory (Pyke 1984) suggests that striped bass would have shifted from mysids to fish at a smaller size if mysids were so scarce that fish prey were energetically favorable. The ontogenetic pattern of mysid species consumption by striped bass also follow what would be expected under optimal foraging theory in terms of size-selective predation because the presently common alien mysid *A. bowmani*, consumed by smaller striped bass, is smaller in size than the native *N. mercedis*. In a review of the ontogeny of piscivory, Mittlebach & Persson (1998) found that species which became piscivorous at younger ages or smaller sizes tended to be larger at the end of their first year and that this size difference carried on to later ages. We have not determined if striped bass have increased in size by age-1 since the early

1980s, but the question is particularly intriguing given that Kimmerer et al. (2000) have documented density dependence for striped bass prior to recruitment to the fishery at age-3 in this system.

Splittail diet was largely composed of detritus and bivalves (including the overbite clam) during the post-clam period. A diet increasingly focused on bivalves, especially the overbite clam, has potential to negatively influence the reproductive biology of splittail and other fishes because of the overbite clam's role as a pathway for transferring high concentrations of selenium to upper trophic levels (R. Stewart, U.S. Geological Survey, Menlo Park, CA, U.S.A., personal communication). Feyrer and Baxter (1998) documented lowered fecundity of splittail during the late 1990s compared to the early 1980s, suggesting this hypothesis merits further investigation.

Although we believe this may be the first documented case of an invading bivalve significantly altering fish diets in a large estuary, similar phenomena have been observed in lentic systems. Pothaven et al. (2001) documented a diet shift with decreased body condition and length at age in lake whitefish *Coregonus clupeaformis* associated with changes in prey availability caused by invading zebra mussels *Dreissena polymorpha* in Lake Michigan. Thayer et al. (1997) showed experimentally that invading zebra mussels indirectly affected diet and growth of yellow perch *Perca flavescens* through changes in prey availability. The significance of these examples together with our results indicate that indirect impacts of alien species can be profound.

Our hypothesis that fishes most dependent on mysids would suffer the most severe declines in abundance appeared to hold true. Clearly, many interacting factors have contributed to declines in fish abundance in the San Francisco Estuary (Bennett & Moyle 1996). Meng et al. (1994) associated declines in fish abundance and diversity in Suisun Marsh to decreased freshwater flow and increasing salinity. The results of our study suggest that food web alterations stemming from the overbite clam have likely played a significant role in fish abundance declines in Suisun Marsh. Kimmerer (2002) found little support for trophic linkages to early life stage abundance or survival of several fish species in the San Francisco Estuary. Our results and those of Kimmerer et al. (2000) suggest that a trophic linkage may exist at older life stages when mysids should be an important food item for fishes. Kimmerer et al. (2000) provided evidence that a decline in carrying capacity has resulted in density-dependant survival of striped

bass between young-of-year and age-3. They reasoned that food limitation was the most likely factor because the decline in carrying capacity paralleled the decline in food resources, and they showed a positive correlation between striped bass and mysid abundance. Our results showing significantly decreased mysid consumption, an earlier onset of piscivory, and a significant decline in abundance for juvenile striped bass is consistent with the food limitation hypothesis of Kimmerer et al. (2000).

Overall, it appears that the native fish fauna of Suisun Marsh lived in a highly variable but predictable environment, to which they responded by exploiting seasonally abundant prey and then changing their diets to maintain stomach fullness and to minimize dietary overlap during seasons when food was less abundant. The introduction of alien fishes had little apparent influence on the diets of most native fishes because most species continued to heavily exploit *N. mercedis*, which was apparently so abundant that it was not a limiting resource for fishes. However, alien species were generally less able to maintain stomach fullness during seasons of low mysid abundance. When mysid populations collapsed to a low level year-round, populations of both native and alien species that had relied upon it exhibited diet shifts and abundance declines. It is worth noting that while most fishes were in decline, a new alien species, shimofuri goby *Tridentiger bifasciatus*, invaded the marsh and exploded in numbers. One reason for the success of this fish is its ability to feed on novel prey, mainly alien invertebrates not fed upon by other fishes (Matern 1999). Our study demonstrates how a single invader, the overbite clam, can change an entire food web through cascading impacts on phytoplankton, zooplankton, mysids, and fish and make it more difficult to undertake management actions that can benefit native fishes. Our results strongly support efforts to prevent further introductions into aquatic ecosystems.

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Appendix A. (Continued)

Species	Period	Mys	Cor	Cop	Ins	Gam	Ann	Cla	Har	Pla	Fis	Iso	Pal	Cra	Biv	Dec	Gas	Det
TP	A1	12	60	2	8	8	1	3	1	2					1	1		
	A2	6	44	8	10	3		2		7		9	2					10
	B	1	48			20	9	18				4						
PS	A1	9	34		3	33	7				7	3		1		3		
	A2	17	39	1	4	16					5	6	5	1		2		4
	B	2	23			59					5	11						
SC	A1	41	18		8	15	7			1	4	5	1	1				
	A2	22	4							10	19		18	23		4		
YG	A1	50	14		9	7	4		1	6	1		6					
	A2	22	23	11	3	6	5	2	4	13		4	1	3	3	1		
	B	5	32		4	44	11			1		4						
SB	A1	93	3		1	1	0	1			2							
	A2	84	2	2			1		4		7							
	B	43	11			16	5	8			14	3	1					
SF	A1	71	13		1	6	6								3			
	A2	43	39		3	2	8			6								
	B		1			11	89											

Values are expressed as the average dietary importance of each prey item for each species and are rounded to the nearest whole number. Species and period codes are given in Table 1. Prey items are given in order by the number of fish species that consumed them; Mys = Mysidae, Cor = *Corophium* amphipods, Cop = Copepoda (cyclopoids and calanoids), Ins = Insecta, Gam = *Gammarus* amphipods, Ann = Annelida, Cla = Cladocera, Har = Harpacticoida, Pla = plant material, Fis = fish, Iso = Isopoda, Pal = *Palaemon macrodactylus*, Cra = *Crangon franciscorum*, Biv = Bivalve, Dec = Decapoda, Gas = Gastropoda, Det = detritus.