

Diet composition in San Francisco Estuary striped bass: does trophic adaptability have its limits?

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Abstract Trophic adaptability is a term used to describe feeding flexibility in fishes. Though a useful conceptual starting point, fishes often face constraints on their ability to switch prey that could limit feeding success even when prey switching is observed. We compared striped bass diet compositions summarized from previously published studies in California's Sacramento-San Joaquin Delta during two time periods (1963–1964 and 2001–2003), which allowed us to evaluate trophic adaptability in San Francisco Estuary striped bass at multiple time scales, ranging from intra-annual to multidecadal. The Delta is the landward region of the San Francisco Estuary; over time between the study periods, the Delta underwent substantial changes in potential prey availability for striped bass. We found evidence for trophic adaptability in San Francisco Estuary (SFE) striped bass at all temporal scales examined. Despite this ability to adapt to changes in prey availability, the relative abundance and carrying capacity of young striped

bass have declined. This decline has previously been associated with substantial declines in their dominant historical prey—mysid shrimp. Our results, coupled with these previous findings, indicate that trophic adaptability may have limited usefulness as a conceptual model to predict foraging success when other food web constraints are not considered. We speculate that this is particularly true in highly invaded ecosystems like the San Francisco Estuary because invading species often introduce substantial and permanent changes into food webs, decreasing the likelihood that a predator will find prey assemblages that fully replace historical prey assemblages.

Keywords Striped bass · *Morone saxatilis* · Diet composition · Trophic adaptability · Invasive species · San Francisco Estuary

Introduction

Gerking (1994) used the term trophic adaptability to characterize long-recognized feeding flexibility in fishes. It is well established that most fishes can exhibit opportunistic feeding habits; some fishes have been observed to 'shift gears' when confronted with shortages of their typical prey (Robertson 1987) or transient hyper-abundances of novel prey (Johnson and Dropkin 1992). The large sizes and gapes of many predatory fishes allow for the potential capture

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of both large and small prey (Mittelbach and Persson 1998), suggesting high potential for trophic adaptability. However, even the ability of large-gaped fishes to detect and catch different prey is constrained by several factors including prey behavior (Buckel and Stoner 2004), prey morphology (Reimchen 2000), and group effects (e.g., forms of interference competition, Buckel and Stoner 2004, or predator facilitation, Rahel and Stein 1988).

The striped bass *Morone saxatilis* is a trophically flexible predator that, due to its recreational importance, has been studied extensively in both its native Atlantic coast habitats (Walter et al. 2003) and in Pacific coast habitats where it was introduced in the latter nineteenth century (Moyle 2002). On both coasts, striped bass tend to feed on copepods during the larval and early juvenile periods, then switch to larger crustaceans (mainly mysids, amphipods, and decapods) and fishes when they reach the juvenile and adult stages. Despite these generalities, seasonal, interannual, and location-specific diet variation is common (Hartman and Brandt 1995; Feyrer et al. 2003; Jordan et al. 2003). For instance, on the Atlantic coast, northerly distributed striped bass often are less piscivorous than more southerly distributed individuals (Walter et al. 2003). One peculiarity of striped bass diets in California's San Francisco Estuary was the high degree of cannibalism reported historically (Stevens 1966). Thus, the available data suggest that striped bass, like most generalized predatory fishes, exhibit considerable trophic adaptability and are a suitable model to explore the utility and the limits of trophic adaptability as a conceptual model to predict fish feeding success.

The San Francisco Estuary, California, USA (Fig. 1) provides a unique opportunity to evaluate striped bass trophic adaptability because the prey spectrum available to striped bass has dramatically changed during the past several decades (Figs. 2 and 3; Feyrer et al. 2003; Bryant and Arnold 2007). Between 1962 and 2001, several potential forage fishes and the Siberian prawn *Exopalaemon modestus* invaded the estuary and became prominent members of its biotic community. These introductions may have enhanced forage opportunities for juvenile and adult striped bass. However, the invasion of the overbite clam *Corbula amurensis* (first detected in 1986, well established by 1987) diverted the majority of pelagic phytoplankton production into the benthos (Alpine and Cloern

1992). This abruptly decreased the abundance of crustacean zooplankters like mysid shrimp (Orsi and Mecum 1996; Fig. 2) that had historically been the primary prey of age-0 San Francisco Estuary striped bass (Stevens 1966; Feyrer et al. 2003). The overbite clam invasion also abruptly decreased the abundance of several pelagic fishes (Kimmerer 2006; Sommer et al. 2007), which are potential forage fish for older striped bass.

Here we compare the diet composition of striped bass collected from the Sacramento-San Joaquin Delta, the highly altered landward region of the San Francisco Estuary for two time periods, 1963–1964 and 2001–2003. This comparison allowed us to evaluate trophic adaptability in San Francisco Estuary striped bass at multiple time scales, ranging from intra-annual to multidecadal. Because the data collections occurred four decades apart, we could evaluate the cumulative, long-term effect of multiple species

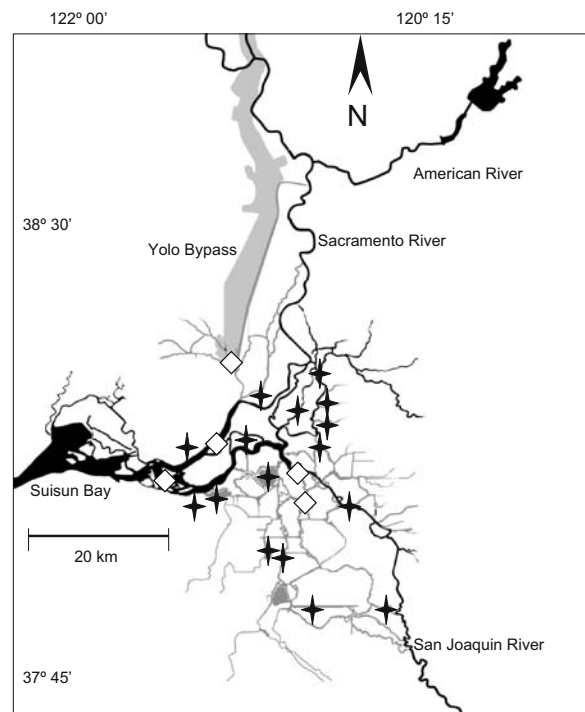


Fig. 1 Map of the Sacramento-San Joaquin Delta, California, USA showing the 16 sites sampled by Stevens (1966) and the five sites sampled by Nobriga et al. (2005) and Nobriga and Feyrer (2007). Note that Clifton Court Forebay, and the State Water Project diversions shown adjacent to the forebay, did not exist during Stevens' study. Likewise, two sites sampled by Nobriga et al. (2005; Mildred Island and Liberty Island) were terrestrial habitat (agricultural plots) at the time of Stevens' study

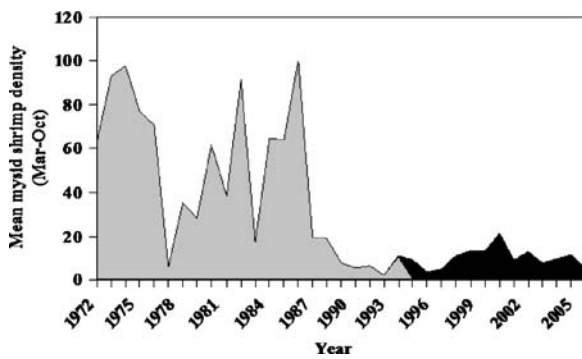


Fig. 2 Time series of mysid shrimp relative abundance in the northern San Francisco Estuary, USA. The data are mean March–October densities (number/cubic meter) of *Neomysis mercedis* (gray) and *Acanthomysis bowmani* (black) based on plankton trawling, 1972–2006. The former is a native species, the latter was first reported from the estuary in 1992. The interested reader is referred to Orsi and Mecum (1996) for a description of the sampling methods

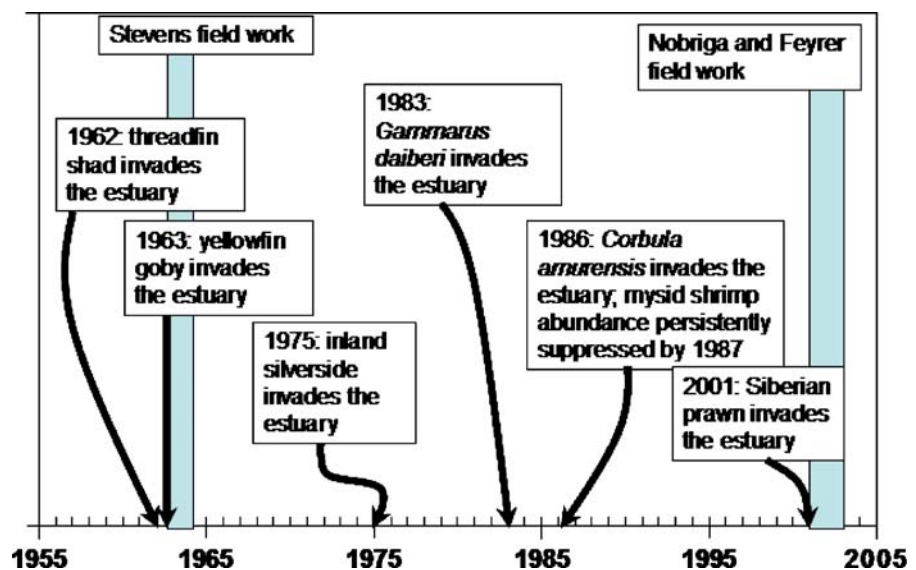
introductions on striped bass diet composition. Because newly introduced species were invading the study area during both periods of data collection, we could evaluate striped bass trophic adaptability at an intermediate time scale of 1–2 years following these introductions of new prey. Lastly, the Sacramento-San Joaquin Delta is a large area (about 27,000 ha) in a Mediterranean climatic region. Thus, it has substantial diversity in habitats and prey species compositions both spatially and seasonally. We used selected prey

density data collected concurrently with the striped bass diet data in 2001 and 2003 to evaluate striped bass trophic adaptability at intra-annual time scales. We used these assessments to address two study questions. Have San Francisco Estuary striped bass adapted their diet to changing prey availability, if so, over which time scales? What are some apparent constraints on trophic adaptability in San Francisco Estuary striped bass?

Study area

The Sacramento-San Joaquin Delta (Delta) is formed by the confluence of the Sacramento and San Joaquin rivers (Fig. 1). The Sacramento and San Joaquin rivers drain about 40% of California’s surface area and their inflows strongly affect the salinity distribution of the San Francisco Estuary (Kimmerer 2002). Sacramento and San Joaquin river inflows are highly regulated by numerous dams in the watershed. The Delta is maintained as a permanently freshwater environment (but still under tidal influence) to support regional agriculture and the export of large quantities of fresh water for agricultural and municipal users to the south and west. The largest export diversions are located in the San Joaquin River basin (Fig. 1), but most of the export is supported by reservoir releases from the Sacramento River basin, which receives considerably more precipitation. Major hydrodynamic changes resulted from water project development in

Fig. 3 Timeline of species introductions relevant to striped bass diet composition in the present study. The timing of the field work for the Stevens (1966) and Nobriga and Feyrer (2007) studies is depicted by the vertical gray bars



the upper estuary in between the diet studies used in this paper. The most significant change was the completion of the State Water Project, including its southern Delta water export diversions (1968) and Clifton Court Forebay, a reservoir in front of the State Water Project diversions (1974). There have been other notable long-term changes in the Delta ecosystem including increased rock reinforcement of levees, increased freshwater exports, increased autumn salinity intrusion, increased species invasion rates, decreased pelagic productivity, increased water clarity, proliferation of submerged macrophytes, and decreased native fish abundance (Sommer et al. 2007 and references therein).

Methods

We used the diet composition data from two previously published studies of striped bass food habits in the Sacramento-San Joaquin Delta (Stevens 1966; Nobriga and Feyrer 2007; Table 1). Stevens (1966) collected diet data on 8,624 striped bass from 16 sites (Fig. 1) using a combination of trawling and gill nets (Table 1) as part of a comprehensive ecological study of the Delta. He described the diet compositions of four age-groups of striped bass collected over the duration of his study: the 1963, 1962, 1961, and collectively, the 1960 and earlier year-classes. These fish ranged in size from

50 mm to more than 380 mm fork length (FL) when the study began in September 1963. They were 120 mm to more than 480 mm when the study ended in August 1964. The diet composition data were summarized as the percentage of stomachs that contained prey categories for four seasons (fall 1963, winter 1963–1964, spring 1964, and summer 1964). Because stomachs often contained more than one prey type, these frequencies of occurrence can sum to more than 100%. Note that we did not include the winter data ($n=2119$ fish) in our analysis because Nobriga and Feyrer (2007) did not sample during winter.

Nobriga and Feyrer (2007) examined the stomach contents of 569 striped bass collected from five sites (Fig. 1) during March–October 2001 and 2003. The purpose of the Nobriga and Feyrer (2007) study was to compare multi-species piscivore–prey dynamics in nearshore habitats of the Delta. Their striped bass were collected using 30×1.5 m beach seines with 3.2 mm mesh and 60×2.4 m gill nets with 50–100 mm mesh in randomly varying panels. The beach seines also collected potential prey fish and decapod shrimp. The beach seining was effective at collecting fish and shrimp of about 25–200 mm in fork or total length. The gill nets were effective at collecting striped bass about 200–400 mm fork length. Unlike Stevens (1966), we did not collect striped bass based on age-groups. Rather, we collected striped bass that were potentially large enough (~80 mm FL and larger;

Table 1 Comparison of field sampling of striped bass for stomach contents analysis and stomach contents analysis methods between Stevens (1966) and Nobriga and Feyrer (2007)

	Stevens (1966)	Nobriga and Feyrer (2007)
Sampling dates	September 1963–August 1964	March–October 2001 and March–October 2003
Collection gears	Midwater trawl, otter trawl, gill net (midchannel collection bias)	Beach seine, gill net (nearshore collection bias)
Number of stomachs examined	8,628	569
Stomach content evaluation	The stomach contents were not preserved; the evaluations were performed on the collection vessels whenever possible	The stomach contents were preserved in 10–15% formaldehyde; all evaluations were performed in the laboratory
Stomach content summary	Frequency of occurrence and estimated volumetric displacement ^a	Frequency of occurrence and prey weight to the nearest 0.01 g ^b in 2003

^a The volumetric data were not used in this paper.

^b In 2003, stomach contents were also blotted dry and, when possible, individual prey taxa were weighed to the nearest 0.01 g using an electronic balance.

Feyrer et al. 2003) to feed on post-larval prey fishes. We sampled up to ten striped bass per gear type, per sampling site, per month. Despite the methodological differences (detailed in Table 1), both studies evaluated qualitatively similar size distributions of striped bass, dominated by individuals about 100–250 mm in fork length, but also containing some smaller and larger fish. Note that in addition to collecting prey frequency data, in 2003 we blotted stomach contents dry, and when possible, weighed individual prey taxa to the nearest 0.01 g using an electronic balance.

We used the diet summaries to document striped bass trophic adaptability at the multi-decadal time scale (diet changes between the two studies) and the intermediate time scale (use of threadfin shad and Siberian prawn as prey 0–2 years following their introductions). We used logistic regression to evaluate striped bass trophic adaptability at shorter time scales. Specifically, we paired $n=202$ striped bass containing stomach contents in 2001 and $n=154$ striped bass with stomach contents in 2003 with concurrent estimates of prey densities. This allowed us to test whether striped bass diets reflected the prey density variation that was observed among the five sampling sites (Fig. 1) during $n=76$ individual site visits between March–October of those years.

We included both prey density (\log_{10} -transformed beach seine density as number $\times 10,000 \text{ m}^3$ seined; Nobriga et al. 2005) and striped bass fork length as explanatory variables in the logistic regression models to simultaneously test for ontogenetic and prey density effects on striped bass feeding responses. The response variables were presence or absence of inland silverside, threadfin shad (indexed as clupeid fish because 93% of the clupeid fishes identified to species were threadfin shad), and decapod shrimp. The latter was dominated by catches of Siberian prawn *Exopalaemon modestus*. We chose these taxa to evaluate intra-annual feeding responses by striped bass because they were important prey and were effectively sampled by beach seining. Inland silverside and threadfin shad dominated the beach seine catches (54% and 23%, respectively), so variation in their density was likely indexed well. Decapod shrimp were the only macroinvertebrate collected by beach seining that was commonly eaten by striped bass. We acknowledge that beach seine efficiency for decapod shrimp may be lower than it was for small, open-water fishes like inland silverside and threadfin shad.

Each prey species was modeled separately and only striped bass that had prey in their stomachs were tested. For each model, the stomach content was coded as 1 (prey present) if the tested prey taxon was reported among the stomach contents and 0 (absent) if it was not. Thus, in these analyses, zeroes do not indicate empty stomachs, but rather stomachs from which we did not confirm the presence of the tested prey taxon.

Results

There was some consistency in striped bass diet composition among time periods. For instance, mysid shrimp and corophiid amphipods were frequently occurring prey in both studies, though they did not account for much of the total prey weight in 2003 (Table 2). Mysids were notably less important in the latter time period, occurring in 24–39% fewer stomachs; the frequencies of corophiid amphipods were similar among time periods. However, striped bass showed evidence for trophic adaptability at all three time scales. Several fish and invertebrates introduced in the intervening 40 years between studies were prominent in striped bass stomach contents in 2001 and 2003 (Fig. 3; Table 2). The prominence of threadfin shad in striped bass diets during 1963–1964 demonstrated that striped bass could effectively incorporate new prey into their diet at an intermediate time scale of about 1–2 years. With a frequency of occurrence of 8% in 1963–1964 (1–2 years following its introduction), threadfin shad was a close second in importance to cannibalized striped bass as a prey fish, and it occurred at similar frequencies in striped bass stomachs 40 years later. Note that threadfin shad dominated the diet by weight contribution in 2003. Similarly, Siberian prawn occurrence increased from 14% in 2001 (the year it was introduced) to 26% in 2003, demonstrating a strong striped bass feeding response over a similar 1–2 year time scale. Due to their frequency as prey and their large size (up to about 60 mm), decapod shrimp dominated the invertebrate fraction of the diet based on weight in 2003 and most of the decapod shrimp we identified were Siberian prawn.

The logistic regression models for the three prey taxa tested showed their presence–absence in striped bass stomachs was significantly affected by both prey density and predator length (Fig. 4; all $P < 0.05$). The probabil-

Table 2 Diet compositions as percentages of San Francisco Estuary striped bass stomachs containing each prey taxon for September–November 1963, March–August 1964, March–October 2001 and March–October 2003

Prey Taxon	1963–1964 (n=4,087)	2001 (n=202)	2003 (n=154)	Wt (g)
Annelids	–	0.5	14	0.5
Bivalves	–	1.0	1.3	1.8
Copepods/Cladocerans	0.8	2.0	2.6	–
Corophiid amphipods	35	31	48	3.5
Gammarid amphipods	NP	35	43	3.3
Mysidae	63	39	24	3.9
Isopods	–	3.5	5.2	–
Decapod shrimp ^a	–	14	26	9.9
Chinese mitten crab				
<i>Eriocheir sinensis</i>	NP	0.5	0	0
Crayfish	–	0.5	0	0
Insects				
Diptera	4.0	3.5	1.9	–
Odonata	0	2.5	1.9	–
Other insects	–	1.0	1.0	0
American shad				
<i>Alosa sapidissima</i>	0.9	0	1.3	6.0
Threadfin shad				
<i>Dorosoma petenense</i>	8.0	8.0	8.4	30
Unspecified shad	–	4.5	5.8	2.8
<i>Tridentiger</i> spp.	NP	1.0	2.6	0.9
Yellowfin goby				
<i>Acanthogobius flavimanus</i>	0	6.4	3.2	10.5
Unspecified goby	0	0	1.3	0.4
Inland silverside				
<i>Menidia beryllina</i>	NP	7.4	3.9	4.3
Chinook salmon				
<i>Oncorhynchus tshawytscha</i>	0.4	0.5	0	0
Delta smelt				
<i>Hypomesus transpacificus</i>	0.4	0	0	0
Largemouth bass				
<i>Micropterus salmoides</i>	0	0.5	0	0
<i>Lepomis</i> spp.	–	0	1.3	0.3
Prickly sculpin				
<i>Cottus asper</i>	0	0.5	0	0
Splittail				
<i>Pogonichthys macrolepidotus</i>	0	0.5	0	0
Stary flounder				
<i>Platyichthys stellatus</i>	–	0	0.7	–
Striped bass				
<i>Morone saxatilis</i>	8.9	2.5	0.7	–
Tule perch				
<i>Hysterocarpus traski</i>	0	0	0.7	0.7
Cyprinodontiformes	1.0	0	0	0
Unspecified fish	5.2	17	10	1.5
Sardine/anchovy “bait” ^b	2.0	0	0	0

For 2003, total weight of prey items is also included. Sample sizes represent the number of fish with prey in their stomachs.

NP Taxa that did not occur in the estuary in 1964; “–” trace amounting to <0.25% of frequency of occurrence or weight contribution to diet composition

^a Twenty-five of 40 occurrences were identified as Siberian prawn *Exopalaemon modestus*; 3 of 40 were identified as Crangonidae; the remaining 12 were not specified.

^b Stevens (1966) found a fairly high frequency of what he identified as pieces of sardine or anchovy bait stolen from fishermen.

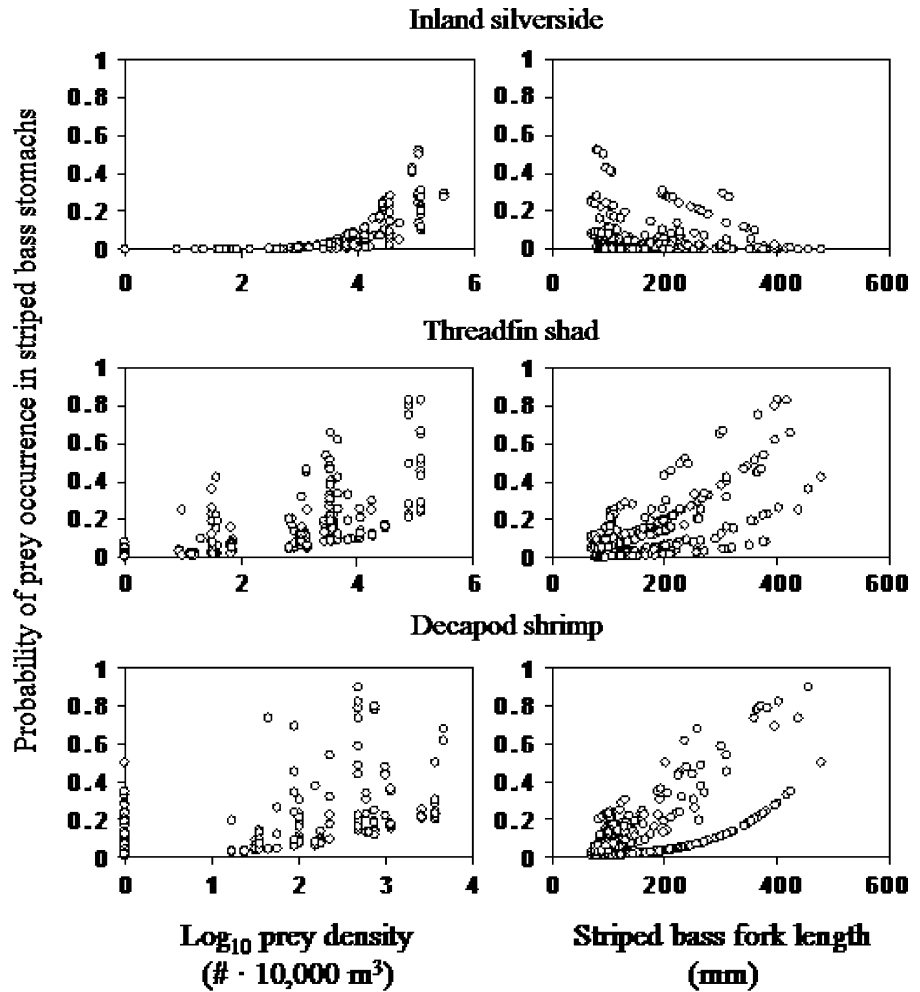
ity that striped bass were collected with inland silverside, threadfin shad, and decapod shrimp among their stomach contents increased as functions of the density of these prey. The use of inland silverside as prey tended to decrease with increasing striped bass size; striped bass more than about 400 mm fork length were not found to consume inland silverside. In contrast, the probability that striped bass stomachs contained threadfin shad or decapod shrimp increased as functions of striped bass length.

Discussion

We found that San Francisco Estuary (SFE) striped bass have exhibited, and continue to exhibit, considerable trophic adaptability. Striped bass have adapted by incorporating certain prey into their diet as they

were introduced and rose to prominence in the estuary’s faunal assemblage. This finding is consistent with Bryant and Arnold (2007), who found that younger SFE striped bass (mostly 20–60 mm FL) had likewise shown considerable diet plasticity over a 30-year period of continuous diet monitoring. Despite this trophic adaptability, the abundance of juvenile SFE striped bass has plummeted (Stevens et al. 1985; Kimmerer et al. 2000; Sommer et al. 2007). It is possible the changed SFE food web supporting juvenile striped bass production may have little to do with their decline; other factors such as excessive entrainment in water diversions (Stevens et al. 1985), exposure to toxic chemicals (Bennett et al. 1995), or declining abiotic habitat suitability (Feyrer et al. 2007) may have collectively had greater impacts. Alternatively, the extreme alteration of the SFE food web may have strongly impacted juvenile striped bass

Fig. 4 Scatterplots of prey densities (number of organisms $\times 10,000 \text{ m}^3$ beach seined) and predator (striped bass *Morone saxatilis*) fork lengths versus probability of prey occurrence in striped bass stomachs based on predictions from logistic regression models. Data were from March to October 2001 and 2003



production despite an inherent and demonstrated ability of juvenile striped bass to switch prey. As described below, there is considerable evidence for the latter. Thus, we speculate that trophic adaptability is too limited a concept to anticipate effects on populations of predators.

Striped bass and mysid shrimp often form a predator–prey association in estuaries (Feyrer et al. 2003; Walter et al. 2003), and there is evidence to suggest that SFE striped bass productivity has declined in part because mysid productivity has declined (Fig. 2). Kimmerer et al. (2000) found evidence that the carrying capacity for SFE striped bass has declined. This imparts density-dependence on the population sometime between the first summer of life and age-3, a period when mysids were the primary historical prey (Stevens 1966; Feyrer et al. 2003). Note that most of the diet data presented here came from striped bass that were between their first summer of life and age-3. The decline in carrying capacity is correlated with the declining abundance of mysids (Kimmerer et al. 2000). Similarly, Sommer et al. (2007) showed that the relative abundance of age-0 SFE striped bass by their first autumn of life was uniformly low, and stopped responding to variation in estuarine inflows, following the overbite clam invasion, which affected many organisms including mysids (Orsi and Mecum 1996). Feyrer et al. (2003) also showed that the striped bass decline matched the decline of mysids in their diet. Thus, it is likely that suppressed prey production has contributed to the lower striped bass carrying capacity.

It is noteworthy that there are data which suggest striped bass and mysid predator–prey linkages may be facultative rather than obligate. For instance, age-0 striped bass in the Hudson River did not feed on mysids at all during a recent 5-year study (Jordan et al. 2003). Rather, the diets were dominated by gammarid amphipods (frequency of occurrence varied between 27% and 81% among years) and crabs (frequency of occurrence varied between 4% and 31% among years). The Hudson River striped bass population has recently rebounded (Daniels et al. 2005), causing concern about predation pressure on Atlantic menhaden *Brevoortia tyrannus* stocks, which affects both human harvest potential (Hartman and Margraf 2003) and striped bass health (Uphoff 2003). Thus, a lack of mysid prey in the Hudson River does not appear to limit the resilience of its striped bass population.

We speculate that trophic adaptability may be too limited a concept to anticipate the effects of food web changes on predator population dynamics because an ability to switch prey does not ensure that a predator gets enough to eat. For instance, there can be growth consequences for northern pike *Esox lucius* when they have to switch to invertebrate prey (Venturelli and Tonn 2006). In systems where food webs have not been dramatically altered, prey density reductions are temporary. The densities of predators and prey also may be tightly linked such that predator and prey populations oscillate due to bottom–up and top–down influences on each other (Mittelbach et al. 1995). However, species invasions often permanently disrupt established food webs (Vanderploeg et al. 2002; Baxter et al. 2004), as they have in the SFE (Feyrer et al. 2003). Thus, prey switching in invaded systems may require new prey that fully, and permanently, replace historical prey. Permanent prey replacement involves many dimensions including approximate caloric equivalency (or at least energy content per handling time), palatability, and catchability. As described above, food web changes have likely already had population dynamic consequences for SFE striped bass. We speculate that as continued species introductions push the SFE food web further away from a pre-existing state, it is increasingly unlikely that striped bass will find a suite of invading ‘alternate prey’ that can fully replace their established historical prey.

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