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Matthew L. Nobriga, Erik Loboschefskey, and Frederick Feyrer

ARTICLE

Common Predator, Rare Prey: Exploring Juvenile Striped Bass Predation on Delta Smelt in California’s San Francisco Estuary

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15 **Abstract**

There is growing concern that predation by juvenile (ages 1–3) Striped Bass *Morone saxatilis* may negatively affect the population dynamics of Delta Smelt *Hypomesus transpacificus*, an imperiled species listed as threatened under the U.S. Endangered Species Act and endangered under the state of California’s Endangered Species Act. We explored the potential predator–prey interaction between juvenile Striped Bass and Delta Smelt in California’s San Francisco Estuary. Specifically, we addressed two study questions. (1) Is juvenile Striped Bass abundance correlated with Delta Smelt survival? (2) What is the estimated peak monthly consumption of Delta Smelt by juvenile Striped Bass during summer? We addressed the first study question using regression techniques and the second with functional responses to estimate per capita Striped Bass consumption of Delta Smelt using Delta Smelt biomass densities estimated from trawl surveys as input to the functional responses. We found no evidence for a correlation between juvenile Striped Bass abundance and Delta Smelt survival. Based upon available data, we estimated that consumption of Delta Smelt may range from a level not discernibly different from 0 g·Striped Bass⁻¹·month up to about 11 g·Striped Bass⁻¹·month⁻¹. These are the first estimates of potential Striped Bass consumption of Delta Smelt.

30 In nearshore coastal zones and estuaries, opportunistic strategist forage fishes like engraulids, atherinids, osmerids, and small clupeids often play central roles in the transfer of energy to higher trophic levels and can therefore be subjected to intense predation mortality (Gleason and Bengtson 1996; Jung and Houde 2004; Hallfredsson and Pedersen 2009). However, forage fishes are obviously adapted to predation. This is borne out of their ecological niche and their life history strategies, which tend toward rapid intrinsic rates of population increase, fueled by

rapid maturation and repeated spawns over extended spawning seasons (Winemiller and Rose 1992; Rose et al. 2001). Thus, of itself, “predation” is not expected to cause long-term declines of opportunistic strategist fishes without some additional context (e.g., habitat change, introductions of novel predators).

40 Of course, the dynamics between piscivorous fishes and their prey are subject to many context-dependent details that make generalizations about predatory impacts difficult. Examples include variation caused by food web structure (Kitchell et al. 45

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Received June 14, 2012; accepted June 18, 2013

1994), predator group dynamics (Buckel and Stoner 2004), predator responses to prey morphology and behavior (Scharf et al. 2003), ontogenetic diet shifts of the predator (Mittelbach and Persson 1998), and within- and across-system variation caused by the type, complexity, and disposition of local habitats (Eklöv and Persson 1995; Rodríguez and Lewis 1997; Perry et al. 2010). Thus, depending on context, it is possible for the consumption of individual prey species to either respond strongly or be unresponsive to variation in predator abundance (Essington and Hansson 2004; Turesson and Brönmark 2007).

There are two reasonably common generalities about piscivore–prey dynamics that are often relevant aspects of their interactions including the underlying functional response. First, piscivorous fishes tend to eat prey when they are abundant and, by extension, ignore rarer potential prey. This frequently results in prey use that conforms to positive density dependence (Buckel et al. 1999; Anderson 2001; Hallfredsson and Pedersen 2009), though we recognize that this basic density dependence of prey choice is not universal because prey vulnerability can vary considerably across species and habitats (Eklöv and Persson 1995; Turesson and Brönmark 2007; Perry et al. 2010). One emergent outcome of density-dependent prey choice in an ecosystem containing many potential prey species is that variability in how a predator responds to densities of multiple individual prey can result in strong or weak predator–prey coupling (Essington and Hansson 2004) that may not be apparent from laboratory feeding experiments (e.g., Buckel et al. 1999; Buckel and Stoner 2000).

Second, most piscivorous fishes eat prey smaller than themselves (Mittelbach and Persson 1998). This is a natural extension of gape limitation and its influence on capture efficiency (Juanes and Conover 1994), though, we recognize that the transition to piscivory has context dependence (Mittelbach and Persson 1998). The emergent outcome of ontogeny in the diets of predatory fishes is that predator–prey relationships can be strongly size-selective (Sogard 1997); as fish grow from eggs to adults, the diversity and number of predators that can effectively capture them diminishes. Major predators of the eggs and larvae of nearshore coastal and pelagic estuarine forage fishes can include invertebrates (DeBlois and Leggett 1993) and numerous small fishes not typically thought of as “piscivorous” (Johnson and Dropkin 1992), including adults of their own species (Takasuka et al. 2003). As they metamorphose into juveniles, forage fish populations can be preyed on by fewer, larger predators, with which they may form strong or weak predator–prey interactions (Essington and Hansson 2004).

In this paper, we focused on the potential influence of juvenile (ages 1–3) Striped Bass *Morone saxatilis* on the population dynamics of juvenile Delta Smelt *Hypomesus transpacificus*, an annual forage fish that is endemic to California’s San Francisco Estuary (SFE) (Moyle et al. 1992) and is listed under the U.S. federal and state of California Endangered Species Acts (ESAs). We focused on juvenile Striped Bass for four reasons. First, several studies have already concluded that there is no correlation between adult Striped Bass abundance (ages 3 and older) and

Delta Smelt abundance or survival (Thomson et al. 2010; Maun- 100
der and Deriso 2011; Miller et al. 2012). Second, Loboschefs- 105
ky et al. (2012) recently demonstrated that juvenile Striped Bass demand for prey was similar to adult Striped Bass demand for prey because juvenile abundance was much higher. Third, a 110
larger fraction of the juvenile Striped Bass population forages 115
in habitats that Delta Smelt occupy. Delta Smelt complete their life cycle within the upper SFE; their acute upper salinity tolerance is about 19 psu or roughly two-thirds seawater (Swanson et al. 2000), and the vast majority of Delta Smelt never leave a salinity range of about 0–10 psu (Dege and Brown 2004; Feyrer et al. 2007). Further, juvenile Striped Bass extensively utilize the turbid, offshore habitats where Delta Smelt most frequently occur (Feyrer et al. 2007). Thus, juvenile Striped Bass have the highest large- and small-scale habitat overlap with Delta Smelt of any major piscivorous fish in the SFE. Lastly, Delta Smelt 120
have been found in juvenile Striped Bass stomach contents. During 1963–1964, Stevens (1966) evaluated seasonal variation in the diets of juvenile Striped Bass in the Sacramento–San Joaquin Delta; only age 2 and age 3 Striped Bass contained more than trace amounts of Delta Smelt. The highest reported predation on 125
Delta Smelt was 8% of the age-2 Striped Bass diet by volume during the summer. Thomas (1967) reported on spatial variation in Striped Bass diet composition based on collections throughout the SFE and the Sacramento River above tidal influence. The field collections occurred from 1957 to 1961; data were 130
collected on age-1 and older Striped Bass but were only summarized as all ages combined. Delta Smelt accounted for 8% of the spring diet composition and about 16% of the summer diet composition of Striped Bass in the Sacramento–San Joaquin Delta. 135

We addressed two study questions. (1) Is juvenile Striped Bass abundance correlated with Delta Smelt survival? (2) What is the estimated peak monthly consumption of Delta Smelt by juvenile Striped Bass during summer? 140

STUDY AREA 145

The SFE (Figure 1) is a tidal river estuary in California that has undergone massive ecological transformation over the past 165 years (Kimmerer 2004; Cloern and Jassby 2012). The SFE is formed by the confluence of two large river systems, the Sacramento and San Joaquin rivers (Figure 1). These rivers meet in the Sacramento–San Joaquin Delta (hereafter Delta) where they begin to mix with Pacific Ocean waters. This estuarine mixing intensifies in a westward direction in the several embayments that comprise San Francisco Bay. The central region of San Francisco Bay (near the Golden Gate Bridge) is almost always a fully marine habitat, while most of the Delta, though still under tidal influence, is maintained as a freshwater habitat. The Delta is a major source of irrigation and drinking water for much of southern California and parts of the San Francisco Bay area and is a region of intense resource management conflict (Hanemann 150
and Dyckman 2009; Cloern and Jassby 2012).

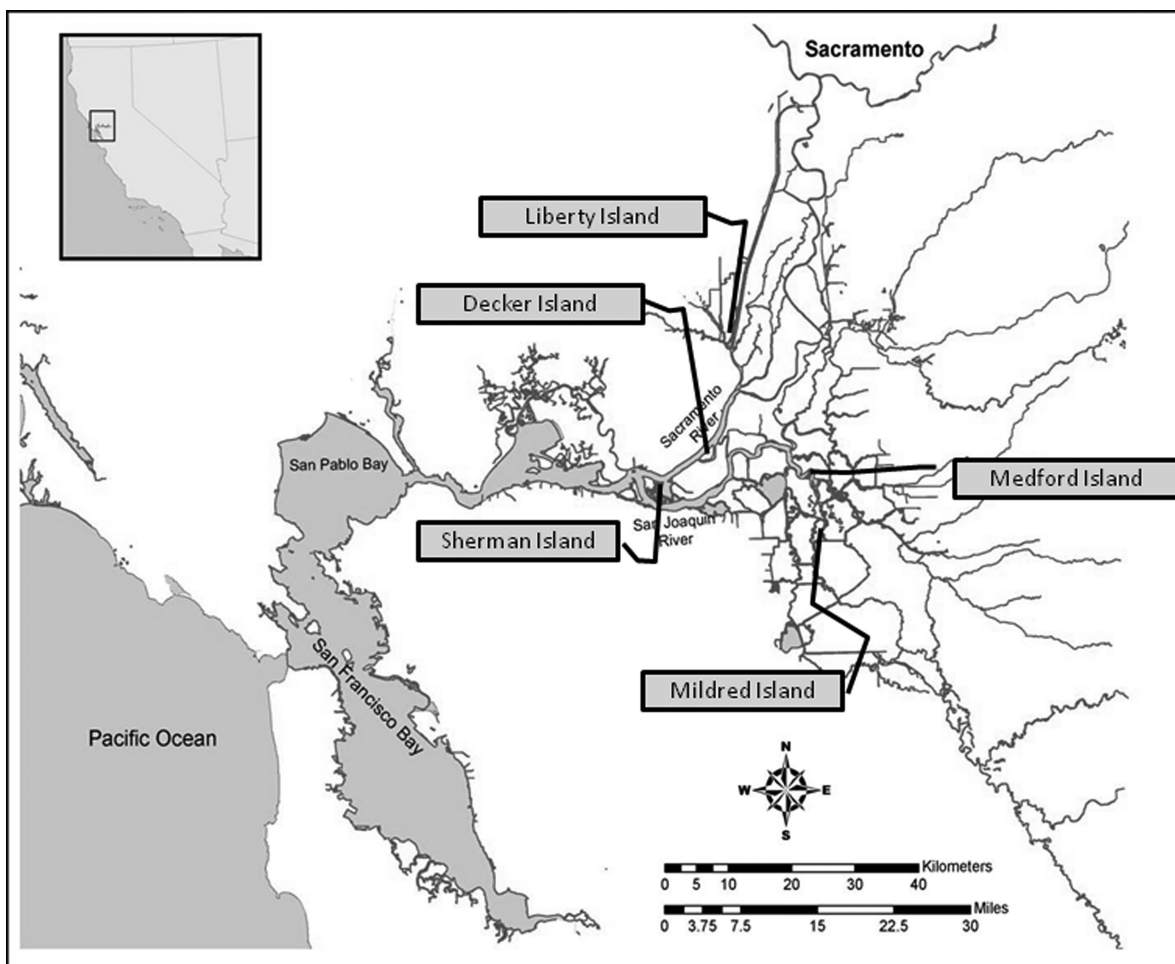


FIGURE 1. The San Francisco Estuary showing sites sampled by Nobriga et al. (2005).

Numerous fish populations that use the SFE have steadily declined for decades (e.g., winter-run Chinook Salmon *Oncorhynchus tshawytscha*, Longfin Smelt *Spirinchus thaleichthys*, Delta Smelt); additional populations including nonnative species have declined more recently (e.g., Threadfin Shad *Dorosoma petenense*) (Lindley and Mohr 2003; Thomson et al. 2010). Some of the native fish declines have resulted in listings under the federal and state ESAs with associated limits on the storage and diversion of water for human uses in the SFE and its watershed as well as major policy initiatives to restore ecosystem “health” (NRC 2011).

Between San Pablo Bay and the Delta (Figure 1), nonnative plants (Santos et al. 2009), invertebrates (Winder and Jassby 2011), and fish (Matern et al. 2002) dominate the aquatic biota. The most numerous and wide-ranging piscivore in this region is Striped Bass, a highly mobile anadromous fish that was introduced to the SFE between 1879 and 1882 (Moyle 2002). Striped Bass is an apex predator that forages on many kinds of prey in many different habitats (e.g., marine, estuarine, riverine). As such, Striped Bass can play an important role in the population dynamics of its prey; in its native habitats along the U.S.

Atlantic coast, the recent recovery of the Striped Bass fishery has led to concern regarding its predation on species of commercial or conservation interest (Hartman 2003; Uphoff 2003; Grout 2006; Tuomikoski et al. 2008), but in the SFE the scientific understanding of this potential is extremely limited (Loboschewsky et al. 2012). Nonetheless, the potential exists so there is a growing management interest in quantifying the predation mortality that Striped Bass impart on individual prey taxa, particularly fishes listed under the ESA (e.g., Lindley and Mohr 2003).

Overview of Delta Smelt Population Dynamics

Throughout its typically 1-year life cycle, Delta Smelt relative abundance is extensively monitored (Table 1; <http://www.dfg.ca.gov/delta/data/>). The relative abundance of juvenile Delta Smelt has been tracked by the two longest running sampling programs, the Summer Towntnet Survey (STNS) and the Fall Midwater Trawl (FMWT) (Moyle et al. 1992). More recently, the relative abundance of spawning adults and their progeny has also been tracked using the Spring Kodiak Trawl Survey (SKTS) and the 20-mm Survey, respectively. The

TABLE 1. Summary of trawl-based monitoring programs used to index Delta Smelt relative abundance in the San Francisco Estuary, California.

Monitoring survey	Sampling method and citation
Spring Kodiak Trawl Survey (SKTS; 2002–present)	Surface trawl targeting spawning adult Delta Smelt at up to 40 stations from the Napa River landward throughout the Delta from January to May. Sampling site map available at http://www.dfg.ca.gov/delta/data/skt/skt_stations.asp
20-mm Survey (20 mm; 1995–present)	Oblique trawl targeting late larval stage Delta Smelt at up to 54 stations from the Napa River landward throughout the Delta from March to July (Dege and Brown 2004). Sampling site map available at http://www.dfg.ca.gov/delta/data/20mm/stations.asp
Summer Towntnet Survey (STNS; 1959–present)	Oblique trawl targeting 38-mm age-0 Striped Bass at up to about 40 stations from June to August (Moyle et al. 1992). Sampling site map available at http://www.dfg.ca.gov/delta/data/towntnet/stations.asp
Fall Midwater Trawl Survey (FMWT; 1967–present)	Oblique trawl targeting age-0 Striped Bass and other pelagic fishes at up to 116 stations from September to December (Moyle et al. 1992). Sampling site map available at http://www.dfg.ca.gov/delta/data/fmwt/stations.asp

abundance indices derived from these four sampling programs have been used extensively in published evaluations of Delta Smelt population dynamics (e.g., Moyle et al. 1992; Dege and Brown 2004; Bennett 2005; Kimmerer 2008; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012). We refer the reader to these references for methodological details of the trawl surveys and indexing methods that we summarize below. Note that indices of Delta Smelt relative abundance for a given life stage can be higher than those for a prior life stage because each survey generates different unitless indices.

A stock–recruit relationship for Delta Smelt can be derived by plotting the FMWT index versus the following year’s STNS index (Bennett 2005; Figure 2a). On average, the stock–recruit relationship has been nearly linear (density independent) though compensation clearly occurred a few times during the 1970s. Thus, in general, more juvenile production alive at the end of a given year tends to translate into more production of young juveniles the following summer.

Ambiguity about density dependence in the stock–recruit relationship can be refined using the newer monitoring surveys. Though it is limited to data from the last 10 years, the relationship between the FMWT index of juveniles at the end of their first calendar year of life and the SKTS index of spawning adults the following spring is strong and essentially linear (Figure 2b). This indicates that Delta Smelt year-class strength is set by the end of the first calendar year of life and there is no obvious indication of a noteworthy source of overwinter mortality that decouples these indices. Therefore, we did not explore this life stage transition further.

In contrast, the relationship between the SKTS index of adult Delta Smelt abundance and the 20-mm Survey index of their progeny is clearly nonlinear (Figure 2c), implying there may be a carrying capacity for larval production. Because there does not appear to be much variation in adult mortality prior to spawning, the nonlinear relationship in Figure 2c most likely represents a mechanism that affects Delta Smelt eggs or larvae, which was

not the focus of our study because of the likely diversity of potential predators involved.

In contrast to the long-term stock–recruit relationship, Delta Smelt survival during the juvenile stage (summer to fall) has shown much stronger evidence for compensatory density dependence over the preceding several decades (Bennett 2005; Maunder and Deriso 2011; Figure 2d). This density dependence has been correlated with a stressful bioenergetic environment (high water temperature and declining prey density; Kimmerer 2008; Maunder and Deriso 2011; Miller et al. 2012). The relationship between the 20-mm Survey index of late stage larvae and the STNS index, which overlaps in time with the 20-mm Survey is linear and strong (Maunder and Deriso 2011; Figure 2e). Thus, these two indices appear to be redundant indicators of Delta Smelt relative abundance during early summer when the young of year (age-0 fish) begin reaching sizes at which they could become a potential focal prey species of juvenile Striped Bass (Figure 3).

The relationship between the 20-mm Survey index and the FMWT index of the same cohort of fish later in its birth year has likewise been approximately linear since the 20-mm Survey started sampling in 1995, but the relationship has been more variable (Figure 2f), suggesting that like the STNS, the 20-mm Survey index does not provide a reliable forecast of recruitment. Because juvenile Delta Smelt are large enough to be potential focal prey for juvenile Striped Bass and because of the long-term, density-dependent (Figure 2d) or density-vague (Figure 2f) survival of juvenile Delta Smelt, we focused our analysis on this life stage transition.

METHODS

Our analysis proceeded in two distinct steps that corresponded to our study questions. In step 1, we tested for an influence of juvenile Striped Bass abundance on the stock–recruit residuals from the relationships shown in panels (d) and (f) in

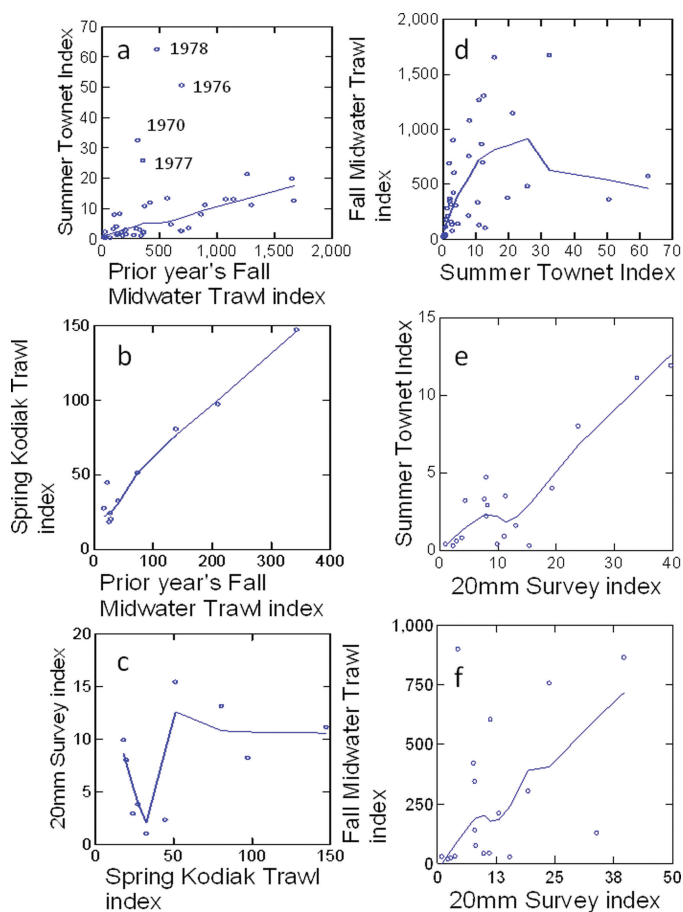


FIGURE 2. Scatterplots showing (a) stock–recruit relationship for Delta Smelt in the San Francisco Estuary based on Fall Midwater Trawl Survey and Summer Townet Survey indices of relative abundance (1969–2012), (b) relationship between juvenile Delta Smelt indices of relative abundance for the end of the first calendar year of life (Fall Midwater Trawl Survey) and indices of adult relative abundance the following year (Spring Kodiak Trawl Survey), 2003–2012, (c) stock–“pre”-recruit relationship for Delta Smelt in the San Francisco Estuary based on Spring Kodiak Trawl Survey and 20-mm Survey indices of relative abundance (2003–2012), (d) long-term summer survival relationship, Summer Townet Survey versus Fall Midwater Trawl Survey (1969–2012), (e) relationship between late larval-stage relative abundance (20-mm Survey) and summertime juvenile relative abundance (Summer Townet Survey) (1995–2012), and (f) shorter-term summer survival relationship, 20-mm Survey versus Fall Midwater Trawl Survey (1995–2012). In each panel, the spline is a LOWESS regression line with tension set to 0.75.

Figure 2. In step 2, we applied functional responses based on several nonnative juvenile Striped Bass prey other than Delta Smelt (which we describe in detail below) and used these functional responses to estimate per capita consumption of Delta Smelt by juvenile Striped Bass. We used surrogate prey to estimate the functional responses because insufficient data exist for Delta Smelt; Striped Bass diets have not been routinely monitored in the SFE and the most recent studies (Feyrer et al. 2003; Nobriga and Feyrer 2007) have not detected Delta Smelt in the stomach contents of Striped Bass. This lack of occurrence of Delta Smelt in general surveys of the stomach contents

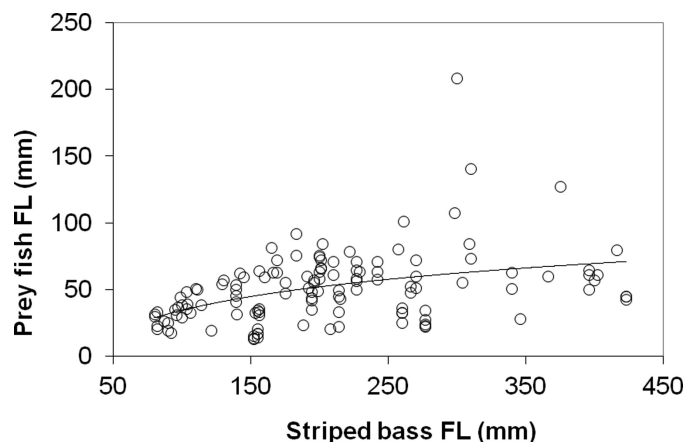


FIGURE 3. Scatterplot showing piscine prey sizes of juvenile Striped Bass in the San Francisco Estuary as a function of Striped Bass length (all prey fish species combined). See Nobriga and Feyrer (2007) for details of Striped Bass stomach contents evaluations.

of Striped Bass is probably related to the very low abundance of Delta Smelt, particularly compared with a large number of alternative prey.

Our hypothesis for step 1 was that if juvenile Striped Bass predation imparted a strong predatory limit on Delta Smelt production, then juvenile Striped Bass abundance should be inversely correlated with the residuals of regression fits to the summer–fall life stage transition for Delta Smelt (i.e., Figure 2d, f). We tested this hypothesis as follows. First, we fit the following Ricker model to the data shown in Figure 2d:

$$FMWT = AS (e^{-BS}), \quad (1)$$

where A and B are regression parameters solved using the Systat software program, and S is an estimate of “stock” or prior abundance, in this case the STNS index. We calculated the standardized residuals from equation (1) [(observed FMWT – predicted FMWT) / predicted FMWT] and used the residuals as the response variable in a linear regression employing juvenile Striped Bass abundance (sum of age 1–3 abundance; Table 2) as the explanatory variable. Note that we calculated standardized residuals for 1969–2012, but we only had juvenile Striped Bass abundance estimates for 1981–2004 (Loboschewsky et al. 2012), so the linear regression test only used the data for 1981–2004.

As a second test of our hypothesis, we approximated the spline fit in Figure 2f by fitting a linear regression without an intercept to the relationship between the 20-mm Survey Delta Smelt indices and the FMWT Delta Smelt indices. We then calculated the standardized residuals from that relationship and used them as a response variable in a second linear regression test of potential influence of juvenile Striped Bass abundance on Delta Smelt. Note that we calculated standardized residuals for 1995–2012, but we only had juvenile Striped Bass abundance estimates for 1995–2004, so the linear regression test only used the data for 1995–2004. The use of untransformed index data

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TABLE 2. Abundance estimates (in millions) of juvenile (ages 1–3) Striped Bass in the San Francisco Estuary for 1981–2004 (taken from Loboschefskey et al. 2012) and the weighted mean age and weighted average FL during July of juvenile Striped Bass based on age-specific relative abundance.

Year	Age 1	Age 2	Age 3	Mean age (years)	Mean FL (mm)
1981	5.70	1.64	0.532	1.34	239
1982	5.02	0.621	0.822	1.35	243
1983	2.59	1.05	0.564	1.52	264
1984	8.48	1.06	0.879	1.27	231
1985	6.01	0.953	0.433	1.25	226
1986	4.92	1.12	0.551	1.34	239
1987	5.94	0.920	0.667	1.30	235
1988	3.70	0.436	0.433	1.28	233
1989	5.20	1.12	0.315	1.26	228
1990	14.4	0.617	0.358	1.09	205
1991	13.5	1.63	0.447	1.16	215
1992	5.77	0.713	0.589	1.27	230
1993	11.9	1.40	0.364	1.16	214
1994	6.15	2.53	0.617	1.40	247
1995	4.02	2.49	0.657	1.53	263
1996	7.21	2.16	0.697	1.35	240
1997	6.93	1.95	0.650	1.34	239
1998	9.33	2.63	0.604	1.31	233
1999	8.08	4.09	0.844	1.44	251
2000	7.85	4.27	1.08	1.49	258
2001	11.1	1.32	0.893	1.23	225
2002	21.1	0.826	0.702	1.10	207
2003	5.83	1.66	0.709	1.38	244
2004	4.38	0.758	1.26	1.51	267

TABLE 3. Summary of 20-mm Survey data used to estimate consumption of Delta Smelt by juvenile Striped Bass. Data are available at [http://www.dfg.ca.gov/delta/projects.asp?ProjectID = 20 mm](http://www.dfg.ca.gov/delta/projects.asp?ProjectID=20%20mm) except mean weight, which was estimated as $[0.0018(\text{FL}^{3.38})]/1000$ (Kimmerer et al. 2005). N is the number of Delta Smelt used to generate the mean FL.

Year	Survey	Sample dates	Number of sample stations	N	Mean FL (mm)	Mean weight (g)
1995	6	July 3–10	39	111	30.5	0.187
1996	7	July 8–13	38	303	30.4	0.185
1997	8	July 8–13	41	42	36.9	0.356
1998	7	June 28–July 3	41	82	33.0	0.244
1999	7	July 6–10	41	333	25.7	0.105
2000	9	July 10–15	41	332	31.4	0.206
2003	8	July 1–3	34	90	29.7	0.171
2004	8	July 6–10	39	42	36.5	0.343

developed by Loboschefskey et al. (2012). We used the BEM to estimate consumption of all Striped Bass prey on a 30-d time step, using 40 combinations of Striped Bass size (based on 325 estimated seasonal average weights for fish ages 1–6) and 10 water temperatures (8–26°C in 2°C increments), which were held constant for the duration of the simulations. We summarized the results of these 400 individual model runs using multiple linear regression to produce an easily applicable approximation 330 of consumption tailored to SFE Striped Bass:

$$C_a = 0.002103(\text{FL}) + 0.02488(T) + 1.426, \quad (3)$$

where FL is Striped Bass fork length in millimeters (converted from weight using the equation provided by Kimmerer et al. 2005 and converting weights between milligrams and grams), and T is water temperature in °C. Equation (3) captured most 335 of the variation in the original consumption estimates based on the full BEM ($R^2 = 0.96$, $P < 0.000001$). Note that equation (3) does not predict maximum consumption by SFE Striped Bass; it is tailored to fit average growth, which is estimated to reflect a proportion of maximum consumption ranging from 340 about 60–68% (E. Loboschefskey, unpublished data).

During March–October 2001 and 2003, Nobriga et al. (2005) concurrently sampled Striped Bass and their potential prey using gill nets and beach seines once per month at five nearshore sites in the Delta (Figure 1). The full methodological details 345 were provided by Nobriga et al. (2005) and Nobriga and Feyrer (2007). Those authors conducted 76 d of sampling over their 2-year study; here we term each day of sampling as a sampling event, S . Striped Bass captured using both gear types were lethally sampled for stomach contents analysis so no individuals were recaptured in subsequent sampling events. In the 350 laboratory, stomach contents were identified to lowest practicable taxon (typically species for prey fishes) and all prey taxa were blotted dry and weighed to the nearest 0.001 g using an

305 can be unreliable for linear regression, so we also repeated this analysis using \log_{10} -transformed index data to see whether our conclusion would change.

Estimating Delta Smelt consumption by Striped Bass.—The “Delta Smelt” consumption estimates produced in this study 310 were based on a simple equation that is the product of a per capita estimate for Striped Bass consumption (of all prey) and functions that provide density-dependent predictions of the fractional contribution of prey taxa to the diet composition for Striped Bass, i.e.,

$$C_{ds} = C_a \cdot D_j, \quad (2)$$

315 where C_{ds} is consumption of “Delta Smelt” in units of g-Striped Bass⁻¹·month⁻¹, C_a is consumption of all Striped Bass prey in the same units, and D_j is a predicted fraction of consumption represented by any one of the nonnative prey taxa (j) that we used as surrogates for Delta Smelt. We applied equation (2) to 320 each of 34–41 sampling stations per 20-mm Survey (Table 3).

We estimated the monthly per capita consumption of all prey taxa by Striped Bass (C_a) using the bioenergetics model (BEM)

355 electronic balance (Nobriga and Feyrer 2007). No Delta Smelt
remains were detected in the stomach contents of Striped Bass
during this study, despite the examination of several hundred
stomachs and the use of diagnostic bone reference collections
to facilitate the identification of partially digested prey fishes.

360 We attempted to develop empirical functional responses for
four prey taxa of juvenile Striped Bass (Threadfin Shad, Missis-
sippi Silverside *Menidia audens*, Yellowfin Goby *Acanthogob-
ius flavimanus*, and caridean shrimp, most commonly Siberian
prawn *Exopalaemon modestus*) using beach-seine biomass den-
365 sities, B_{jS} (g/10,000 m³) (Nobriga et al. 2005), where the sub-
script j refers to these four prey taxa and S to the sampling
event in which they were collected. Mississippi Silverside and
Threadfin Shad were the two most numerous species collected,
comprising 50% and 25% of the total catch, respectively; Yel-
370 lowfin Goby and caridean shrimp were also common Striped
Bass prey that comprised about 3% and 2% of the beach seine
catch, respectively. For comparison, Delta Smelt comprised only
0.7% of the beach-seine catch and 54% of that occurred during
one sampling event.

375 We used diet composition data (proportional contribution
by weight) from 291 Striped Bass ranging in size from 80
to 478 mm FL to generate the functional responses. We used
generalized additive models (GAMs; performed in R using the
“mgcv” package with the identity link function, which assumes
380 a normal distribution of error in the response variable and default
degrees of freedom in the smooth terms) to describe the empir-
ical relationships between prey biomass densities, Striped Bass
FLs, and prey contributions to Striped Bass diet composition. A
GAM is not constrained to predict a particular relationship; it
385 produces an empirical spline (Feyrer et al. 2007; Nobriga et al.
2008). Thus, it is important to describe what “shape” is expected
between explanatory and response variables. of each prey taxon
when its biomass density increased, and we expected to see ju-
venile Striped Bass increase their use of each prey taxon as they
Q4 390 got larger. The one exception is that we expected to see juvenile
Striped Bass decrease their use of Mississippi Silverside as they
Q5 got larger (Nobriga and Feyrer 2008). As an additional check on
the utility of the GAMs, we also generated null models for each
prey taxon; the null models (or intercept-only models) enabled
395 us to determine how well the GAMs explained juvenile Striped
Bass diet composition compared with simply calculating the
mean diet composition and treating individual prey contribu-
tions to the diet as constants.

400 We used the information-theoretic approach based on the
Akaike information criterion (AIC) (Burnham and Anderson
1998) to compare the null models to the GAMs that included ex-
planatory variables and to choose from among the following two
alternative forms of explanatory variables for each prey taxon (j).

$$D_{j,S} = B_{j,S} + FL_S, \quad (4)$$

405 and

$$D_{j,S} = B_{j,S} + FL_S, \quad (5)$$

where $D_{j,S}$ is the predicted Striped Bass diet proportion of prey
taxon j in sampling event S , FL_S is the one or more observed
Striped Bass FL in sampling event S , and $B_{j,S}$ is defined as
above. For each prey taxon (j), we examined the better fitting of
the above two model variants using scatterplots. For the GAMs
410 based on equation (5), we multiplied the two explanatory vari-
ables before performing the analysis because GAMs do not
handle explicit interaction terms effectively the way that lin-
ear regression techniques do ([http://ecology.msu.montana.edu/
labdsv/R/labs/lab5/lab5.html](http://ecology.msu.montana.edu/labdsv/R/labs/lab5/lab5.html)). 415

We used the GAMs developed for caridean shrimp, Threadfin
Shad, and Mississippi Silverside to estimate what would be
the predicted consumption by Striped Bass for each of these
functional response models at observed Delta Smelt biomass
densities, i.e., after we developed the functional responses we
420 used Delta Smelt biomass densities as inputs to the GAMs and
used the mgcv package in R to make new predictions based on
those inputs. We calculated Delta Smelt biomass densities from
the 8 years of 20-mm Surveys for which sampling occurred
during the first week or so of July; 34–41 stations from the
425 Delta seaward to the Napa River were sampled in each survey
(Table 3). We converted the numeric CPUEs reported by the
California Department of Fish and Wildlife into biomass den-
sities (g/10,000 m³) using the mean Delta Smelt lengths reported
in Table 3 and the length–weight conversion in Kimmerer et al.
430 (2005).

No data existed to determine a mean FL of Striped Bass for
every 20-mm Survey sample. The mean FL of Striped Bass of
ages 1, 2, and 3 during July is about 193, 317, and 491 mm, re-
435 spectively (E. Loboschefskey, unpublished data). Thus, we used
a weighted mean Striped Bass FL that varied annually but was
assumed to be the same across sampling stations for a given
year. Specifically, we calculated average July Striped Bass FLs
weighted by the relative abundance of each of the three age-
440 classes (Table 2) to use as GAM inputs to estimate “Delta Smelt”
fractional contributions to the diet of juvenile Striped Bass and
as inputs to equation (3). Our rationale for choosing July as a
reference condition was that it is usually the month with the
warmest water temperatures in the SFE (Kimmerer 2004) and
445 thus the month in which juvenile Striped Bass demand for prey
is expected to peak.

We summarized the Delta Smelt consumption estimates
(equation 2) based on the Threadfin Shad and caridean shrimp
GAMs as bootstrapped means and 95% CIs. Predicted estimates
of consumption by Striped Bass using these two surrogate prey
450 models were summarized in two ways: the first summarized the
predictions “as is.” However, both of these GAMs had nonzero
intercepts, meaning that they predicted some prey consumption
even when prey biomass density was zero. Therefore, we set the
GAM predictions to zero when prey (Delta Smelt) biomass den-
455 sity was zero in a second set of bootstrap estimates to see how
much difference this made in the predictions. Bootstrapping was
not needed to summarize the results based on the Mississippi
Silverside GAM (see Results).

460 **RESULTS**

The parameters of the Ricker model fit to the STNS and FMWT data were $A = 112.6$ and $B = -0.04292$ ($r^2 = 0.42$, $n = 42$). The standardized residuals from the Ricker model were not related to juvenile Striped Bass abundance ($P = 0.37$, $r^2 = 0.036$, $n = 24$). The slope of the untransformed linear regression model depicting the relationship between (untransformed) 20-mm Survey and FMWT indices for Delta Smelt was 18.03. Due to the lack of an intercept, the relationship was statistically significant ($P = 0.0005$, $r^2 = 0.52$, $n = 18$), but the standardized residuals from this linear regression were also not related to juvenile Striped Bass abundance ($P = 0.48$, $r^2 = 0.065$, $n = 10$). The \log_{10} -transformed 20-mm Survey and FMWT indices were significantly related ($P = 0.02$, $r^2 = 0.29$, $n = 18$), but once again the standardized residuals were not related to juvenile Striped Bass abundance ($P = 0.99$, $r^2 = 0.00001$, $n = 10$). We also examined scatterplots of these relationships to make sure that we were not misrepresenting the results using linear regression. None of the scatterplots showed any indication of a linear or nonlinear correlation, so we found no evidence that juvenile Striped Bass abundance can predict Delta Smelt survival during the time of year during which water temperature and juvenile Striped Bass demand for prey peaks.

All eight variations of the GAMs that related prey biomass density and Striped Bass FL to the proportional contribution of prey to juvenile Striped Bass diet composition were highly statistically significant, as were the null models (Table 4). However, all eight GAMs that included terms to predict Striped Bass diet composition outperformed the null models according to the AIC calculations. Both the percentage of null deviance explained by these models and their AIC scores suggested that the interaction term model (equation 5) provided the best prediction

of caridean shrimp and Threadfin Shad contribution to juvenile Striped Bass diet composition. In contrast, the separate-terms model (equation 4) provided the best prediction of Mississippi Silverside and Yellowfin Goby contribution to juvenile Striped Bass diet composition.

For caridean shrimp and Threadfin Shad, the GAM predictions suggested prey switching above a threshold value of the biomass density–Striped Bass FL interaction term (Figure 4), which is an indication that the fractional contribution of these prey taxa to juvenile Striped Bass diets is density dependent because it increases (in part) as a function of their density. Caridean shrimp appeared to be more vulnerable to predation by juvenile Striped Bass as evidenced by the lower value of the interaction term that was associated with prey switching (x-axis value of about 7 for shrimp and about 10 for Threadfin Shad) and the faster rise in the spline for shrimp, which reached an estimated 100% fractional contribution to Striped Bass diet near an interaction term of 9.5.

The fractional contribution of Mississippi Silverside to juvenile Striped Bass diet composition was similarly density dependent (Figure 5a). However, its proportional contribution peaked at about 0.4 and then dropped off, indicating that Mississippi Silverside was less vulnerable to predation by juvenile Striped Bass than were caridean shrimp or Threadfin Shad. We consider the decline in use of Mississippi Silverside as prey that was predicted at the highest biomass densities to be an artifact of having few observations rather than an indication that juvenile Striped Bass avoid Mississippi Silverside when their density peaks. The GAM also predicted that Mississippi Silverside's fractional contribution to Striped Bass diet composition declines as Striped Bass grow larger (Figure 5b), which caused some of the GAM predictions to be negative.

TABLE 4. Results of generalized additive models (GAMs) used to predict juvenile Striped Bass diet composition (proportional prey contribution by weight) from prey biomass density ($\text{g}/10,000 \text{ m}^3$) and Striped Bass FL (mm). The null models test the explanatory value of the mean (i.e., a model with no shape). The results shaded in gray highlight the better fitting model variant for each of the four prey taxa listed in the table. P -value refers to the probability of the intercept in the null models. See text for details of equations (4) and (5).

Prey taxon	GAM model	P -value (prey density term)	Deviance explained (%)	AIC score
Caridean shrimp	Null model	8×10^{-9}	0	111.7
	Equation (4)	2×10^{-16}	38	-6.508
	Equation (5)	2×10^{-16}	44	-44.41
Threadfin Shad	Null model	3×10^{-7}	0	70.84
	Equation (4)	2×10^{-6}	19	26.69
	Equation (5)	4×10^{-13}	22	8.691
Yellowfin Goby	Null model	2×10^{-4}	0	-81.02
	Equation (4)	7×10^{-3}	14	-106.4
	Equation (5)	2×10^{-3}	5	-91.92
Mississippi Silverside	Null model	6×10^{-5}	0	-84.44
	Equation (4)	5×10^{-11}	23	-142.0
	Equation (5)	3×10^{-6}	13	-114.8

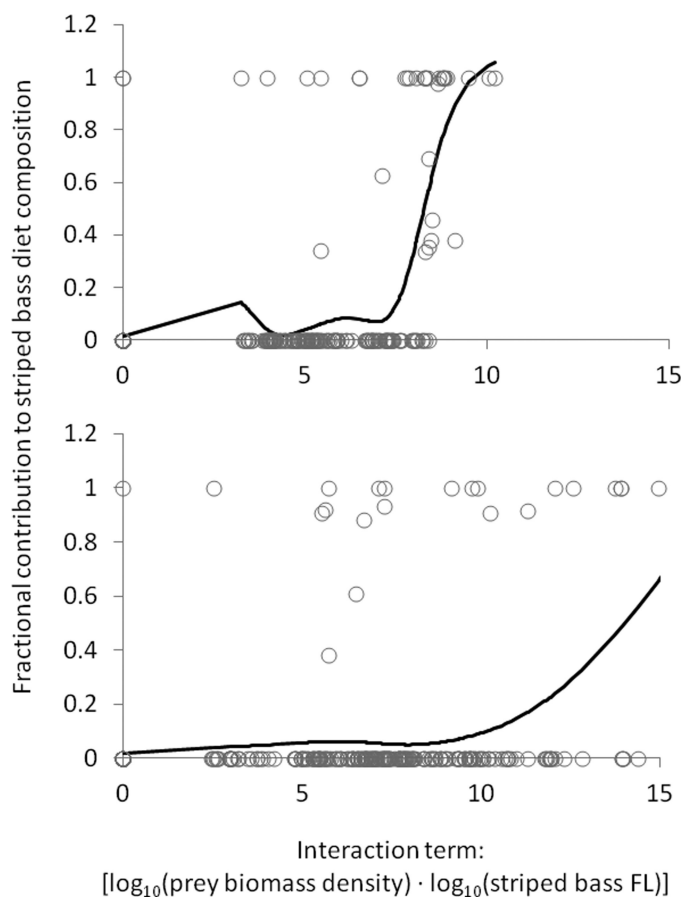


FIGURE 4. Scatterplots showing interaction terms between prey biomass density ($\text{g}/10,000 \text{ m}^3$) \cdot Striped Bass length (mm) versus the observed proportional weight of the prey in Striped Bass stomachs (open circles) and generalized additive model predictions of the proportional weight contribution of each prey taxon to Striped Bass diet composition (solid lines) for (top panel) caridean shrimp and (bottom panel) Threadfin Shad.

The GAM predictions for Yellowfin Goby had lower predictive capacity than those of the other prey taxa (Table 4) and did not generate predictions that were consistent with our expectations (Figure 5c, d), so we did not use them further.

The “Delta Smelt” D_j predictions (equation 2) generated by inputting Delta Smelt biomass densities from the 20-mm Survey into the Mississippi Silverside GAM predicted diet contributions that were always represented by negative numbers; thus, using this functional response, the per capita consumption of Delta Smelt by Striped Bass was not discernibly different from zero. The “Delta Smelt” consumption predictions based on the Threadfin Shad and caridean shrimp functional responses ranged from a low of 4.45 $\text{g}\cdot\text{Striped Bass}^{-1}\cdot\text{month}^{-1}$ in 1998 (95% CI = 3.85–4.76), using the Threadfin Shad model, to a high of 8.74 $\text{g}\cdot\text{Striped Bass}^{-1}\cdot\text{month}^{-1}$ in 1996 (95% CI = 6.15–10.6) using the caridean shrimp model (Table 5). Forcing the predictions to equal zero at a prey biomass density of zero had the obvious effect of lowering the mean values, but increasing the relative size of the confidence intervals.

DISCUSSION

We did not find evidence for a strong predator–prey interaction between juvenile Striped Bass and Delta Smelt, which means the evidence indicates that Delta Smelt survival declines when juvenile Striped Bass abundance increases (sensu Essington and Hansson 2004). This finding is similar to other recent studies that found no evidence for a strong interaction between adult Striped Bass and Delta Smelt (Thomson et al. 2010; Maun-der and Deriso 2011; Miller et al. 2012). Thus, our analyses and those of others have found no evidence that variation in Striped Bass abundance has measurably contributed to variation in juvenile Delta Smelt survival.

TABLE 5. Estimated per capita consumption of Delta Smelt by Striped Bass during the month of July ($\text{g}\cdot\text{Striped Bass}^{-1}\cdot\text{month}^{-1}$) for each year listed using Delta Smelt biomass densities as inputs to generalized additive models (GAMs) depicting the relationship between Threadfin Shad or caridean shrimp biomass density and the fractional contribution of these prey to Striped Bass diet. Value in parentheses represents 95% CI of estimate. The GAMs had nonzero intercepts; consumption estimates based on the GAM predictions “as is” and estimates in which consumption was assumed to equal zero when no Delta Smelt were detected by the 20-mm Survey are both provided.

Year	Consumption based on Threadfin Shad GAM	Consumption based on Threadfin Shad GAM with zero intercept	Consumption based on caridean shrimp GAM	Consumption based on caridean shrimp GAM with zero intercept
1995	5.90 (5.65–6.04)	2.59 (1.02–3.24)	6.96 (5.69–8.01)	4.08 (1.83–5.49)
1996	5.85 (5.53–6.02)	2.68 (1.29–3.45)	8.74 (6.15–10.6)	5.97 (2.41–8.34)
1997	5.37 (5.13–5.51)	1.89 (0.900–2.57)	6.04 (5.09–6.69)	3.01 (1.43–4.15)
1998	4.45 (3.85–4.76)	1.81 (0.779–2.46)	5.26 (4.02–6.15)	2.97 (1.10–4.11)
1999	6.04 (5.82–6.19)	3.00 (1.52–3.67)	8.03 (6.17–9.25)	5.38 (2.75–7.06)
2000	5.98 (5.67–6.16)	2.37 (1.18–3.10)	8.27 (5.88–10.3)	5.12 (1.99–7.42)
2003	5.87 (5.65–5.97)	2.60 (1.23–3.32)	6.85 (5.64–7.63)	4.01 (1.84–5.30)
2004	6.25 (5.92–6.40)	2.05 (0.783–2.73)	6.89 (5.87–7.82)	3.23 (1.26–4.63)

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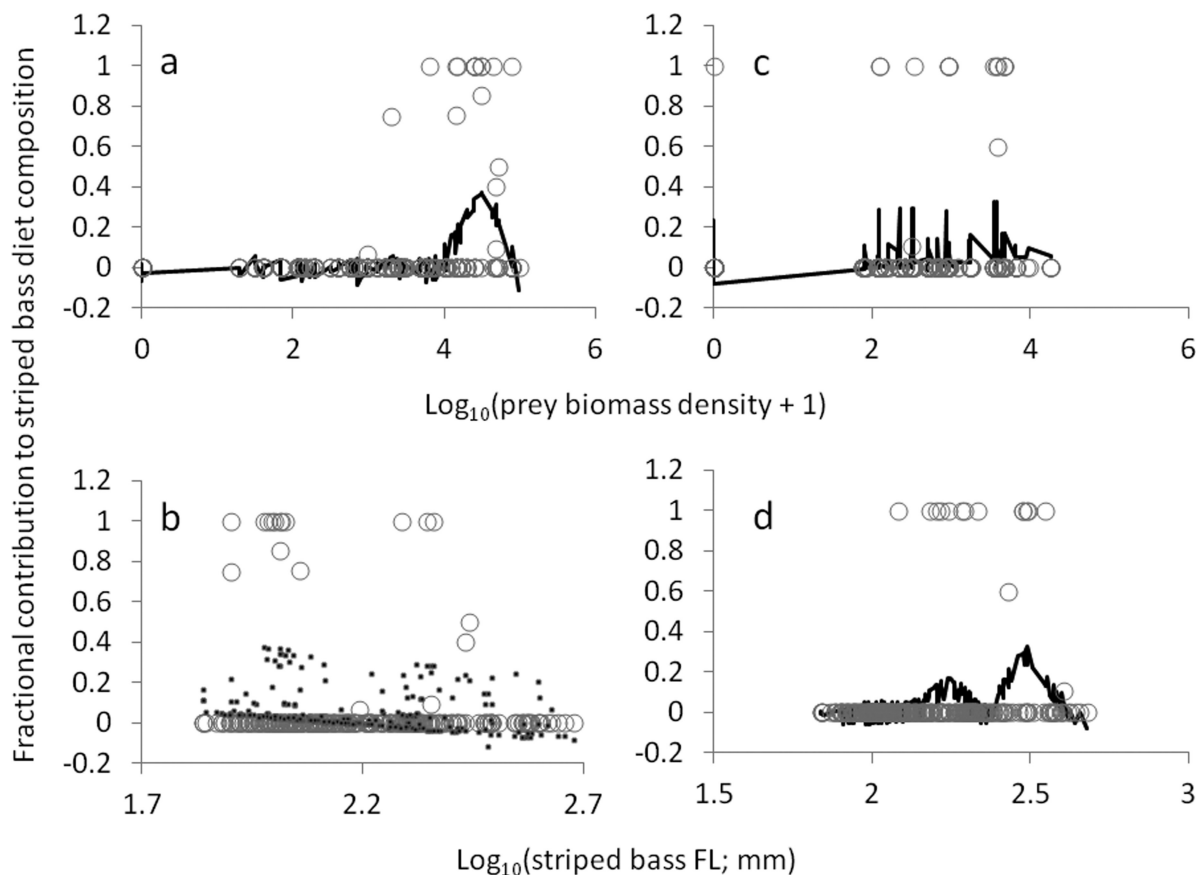


FIGURE 5. Scatterplots of relationships between prey biomass density ($\text{g}/10,000 \text{ m}^3$) (panels a and c) and Striped Bass length (mm) (panels b and d) versus the observed proportional weight of the prey in Striped Bass stomachs (open circles) and generalized additive model predictions of proportional weight contribution of each prey to Striped Bass diet composition (solid lines) for (a, b) Mississippi Silverside and (c, d) Yellowfin Goby. The jaggedness in the prediction lines in panels a, c, and d and the scatter in the solid symbols in panel b reflect the variability caused by the other term in each prey species' model.

555 We confirmed our prior finding (Nobriga and Feyrer 2008)
 560 that juvenile Striped Bass prey choice is frequently density dependent and consistent with type-III prey switching (Figures 4, 5), though we could not confirm this for a fourth prey taxon (Yellowfin Goby). This may be because some juvenile Striped Bass prey taxa are highly vulnerable such that they can be efficiently captured across a wide range of densities; but more likely, this result reflected limited efficacy of beach seining to depict the spatial-temporal variation in Yellowfin Goby density. Lastly, we used empirical functional responses to derive the first estimates of Striped Bass predation rate on Delta Smelt using functional responses for several surrogate prey taxa with widely divergent vulnerability to juvenile Striped Bass. We discuss the implications of this below.

570 Abrams and Ginzburg (2000) called for increased research into predator functional responses in the field, and several fisheries researchers have recently responded to this request (Anderson 2001; Essington and Hansson 2004; Rindorf and Gislason 2005; Hallfredsson and Pedersen 2009). Contemporary functional response equations have both predator- and prey-dependent terms (Abrams and Ginzburg 2000; Essington and

Hansson 2004). The prey-dependent component of functional responses is the influence of prey density on its own predation rate and this influence generally follows one of three basic models, type I, II, or III (Holling 1959). In a type I response, the consumption of a prey item increases linearly with its density. In type II, the consumption of a prey item has an asymptotic relationship to its density because the predator can be satiated when prey density is sufficiently high. In type III, the relationship between the density and consumption of a prey taxon is sigmoidal. In a laboratory setting, type III responses are caused by a predator switching between prey taxa as relative prey density changes.

585 All three functional response forms have been reported for piscivorous fishes based on field studies. Essington and Hansson (2004) found the type I relationship was best supported in their study of Atlantic Cod *Gadus morhua* in the Baltic Sea. In contrast, Rindorf and Gislason (2005) found the type II or III relationship was best supported in their study of Whiting *Merlangius merlangus* in the North Sea. Buckel et al. (1999) hypothesized a type III response for juvenile Bluefish *Pomatomus saltatrix* based on observed prey switching in New York's

Hudson River. However, when this phenomenon was tested in large laboratory enclosures, the Bluefish functional response to two prey taxa alone or in combination was best described as type I or II (Buckel and Stoner 2000). These authors hypothesized that prey refuging had led to prey switching by juvenile Bluefish in the wild. Our field-derived functional responses for juvenile Striped Bass were most consistent with the type III model; i.e., prey had to reach certain densities to become the focal prey of juvenile Striped Bass. Below these thresholds, predation occurs, but at a lower background level (Figures 4, 5).

Early functional response equations were explicitly prey dependent because they assumed the per capita consumption of a prey taxon by a predator was a predictable function of prey density unaffected by the presence of additional predators. Predictions based on prey-dependent functional response equations always predict that prey consumption increases with predator abundance (Essington and Hansson 2004). However, strictly prey-dependent functional responses are unlikely to be common in nature (Abrams and Ginzburg 2000). Strong predator dependence in a functional response can override the prey (density) dependence and decouple prey mortality from variation in predator abundance (Essington and Hansson 2004). The data do not currently exist to test explicitly for predator dependence in juvenile Striped Bass functional responses in the SFE. However, the lack of correlation between juvenile or adult Striped Bass abundance and Delta Smelt survival may be indirect evidence for predator dependence that results in the apparently weak food web linkage between these species.

Essington and Hansson's (2004) review of the literature on factors that can lead to predator dependence in functional responses included predator interference; high densities of Striped Bass have been shown experimentally to reduce their per capita feeding rate (Buckel and Stoner 2004). Other factors mentioned by those authors that may be relevant to the Striped Bass-Delta Smelt interaction in the SFE include spatial heterogeneity in predation risk and size-based predation risk. We clearly found evidence for the latter for common prey of juvenile Striped Bass (Figures 4, 5), which is not surprising given that most predation on fishes is strongly influenced by sizes of predators and prey (Sogard 1997; Mittelbach and Persson 1998).

Delta Smelt biomass densities were much lower than the beach-seine-based densities of the surrogate prey taxa. We do not think this is a sampling artifact; Delta Smelt densities are higher in the offshore environment than they are nearshore (Nobriga et al. 2004), which is why trawl-based surveys historically collected Delta Smelt in high numbers (Moyle et al. 1992) and remain the method of choice for targeting this species (Table 1). Thus, we can state with fair certainty that Delta Smelt is a dilute potential prey for juvenile Striped Bass that, on average, occurs at densities well below those expected to cause Striped Bass to focus on them.

We estimated that per capita juvenile Striped Bass summertime predation rates on Delta Smelt are from about 0 to 11 g-Striped Bass⁻¹.month⁻¹, a range of estimates that is driven

mainly by choice of surrogate functional response because different prey have very different apparent vulnerability to predation by juvenile Striped Bass (Mississippi Silverside, comparatively low; Threadfin Shad, intermediate; caridean shrimp, comparatively high). The upper end of the range of consumption estimates translates into as many as 23 Delta Smelt, 40 mm in length, or 62 Delta Smelt, 30 mm in length, eaten per Striped Bass per month (Kimmerer et al. 2005). However, there are two important caveats to this estimate: (1) they are the maxima from the upper CI limit of the highest vulnerability functional response (caridean shrimp); most estimates that were discernable from zero were less than half of this maximum (Table 5); and (2) they are translations of biomass into numbers of Delta Smelt at sizes representing early July. By the end of summer (e.g., September), many Delta Smelt exceed 50 mm in length, which translates into a weight of about 1 g each. This means that by the end of summer most of our (nonzero) consumption estimates would translate into fewer than 10 Delta Smelt consumed per Striped Bass per month.

Juvenile Striped Bass is a common predator and Delta Smelt is a rare prey; population estimates for juvenile Striped Bass in the SFE have frequently exceeded 10 million fish (Table 2). Thus, if every juvenile Striped Bass were preying on Delta Smelt, that would represent losses of up to 10⁷-10⁸ fish to predation by Striped Bass each July. There are no robust population estimates for Delta Smelt, but all of the numeric trawl-survey densities have been expanded by one or more authors. Expansions of Delta Smelt catches from the 20-mm Survey and STNS give estimates in the 10⁶-10⁷ range (Bennett 2005); this is not enough fish to support our higher estimates if every juvenile Striped Bass was a potential predator. Expansions of the FMWT catches suggest the juvenile Delta Smelt population has only ranged from 10⁴-10⁶ fish (Bennett 2005; Newman 2008), but these values are known to be biased low because SKTS estimates range from 10⁵-10⁶ (Kimmerer 2008). Either way, if 10-20 million Striped Bass preyed on Delta Smelt for several months during the summer and early fall, that would represent a major source of mortality that should be highly apparent in population dynamic assessments. As stated above, neither we nor other authors (Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012) have found Striped Bass abundance estimates to be a significant predictor of Delta Smelt survival.

There are two possible explanations for the above paradox and discerning among them is an important next step for research. The first possibility is that the number of juvenile Striped Bass actually overlapping the distribution of Delta Smelt during the summer and fall is much lower than the whole-system abundance estimates. Many juvenile Striped Bass occupy habitats seaward of Delta Smelt's spatial distribution (Moyle 2002) and many also occupy the southern Delta during the summer and fall (Feyrer and Healey 2003; Nobriga et al. 2005) when Delta Smelt do not (Feyrer et al. 2007; Nobriga et al. 2008). Thus, it is likely that the number of Striped Bass overlapping Delta Smelt's distribution is much lower than the whole-system population

705 estimates generated by Loboschefskey et al. (2012) and reported
 in Table 2. The second possibility is that the abundance of
 Striped Bass is always high enough to suppress the growth rate
 of the Delta Smelt population, such that correlations between
 Striped Bass abundance and Delta Smelt population dynamic
 710 indicators do not emerge, even though Striped Bass is a major
 contributor to total mortality. This is also clearly possible if the
 biomass of Striped Bass available to forage on Delta Smelt is as
 large, or larger, than the biomass of the Delta Smelt population.
 Discerning among these two possibilities is of critical impor-
 715 tance to management because Delta Smelt have had a long-term
 negative population growth rate (Bennett 2005; Thomson et al.
 2010) and thus, even low levels of predation will contribute fur-
 ther to that negative population growth rate (Lindley and Mohr
 2003). However, the opposite side of this argument, as Lindley
 and Mohr (2003) showed using simulations for winter-run Chi-
 720 nook Salmon, is that if Striped Bass predation is not the major
 limit to population growth, then even complete removal of the
 predator (if it were technologically feasible) would not solve the
 species' underlying conservation problem.

725 Our results are the first estimates of potential Striped Bass
 consumption of Delta Smelt, and important next research steps
 to put our estimates into a population context will be to deter-
 mine (1) how many juvenile Striped Bass closely overlap
 the distribution of juvenile Delta Smelt during the summer and
 730 early fall, and (2) the biomass of juvenile Delta Smelt during
 the summer and fall.

ACKNOWLEDGMENTS

This study emerged from work done by the authors for the
 Bay-Delta Conservation Plan. The viewpoints expressed are
 735 those of the authors and do not necessarily reflect the opin-
 ions of the U.S. Department of the Interior, the U.S. Fish and
 Wildlife Service, the U.S. Bureau of Reclamation, or the Cali-
 fornia Department of Water Resources. We thank K. Newman
 for statistical advice. The manuscript was greatly improved by
 740 the helpful comments of several anonymous reviewers.

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