ESSAY

Did a Shifting Ecological Baseline Mask the Predatory Effect of Striped Bass on Delta Smelt?

Matthew L. Nobriga, William E. Smith

ABSTRACT

Striped Bass, *Morone saxatilis*, has been an established member of the San Francisco Estuary's (estuary's) aquatic community for nearly a century and a half. As a predator, it has the potential to shape community composition through top-down control of lower trophic species, including the endangered Delta Smelt, *Hypomesus transpacificus*. Invasive predators can be particularly disruptive to native communities because they present novel dangers to naïve populations, but, as a long-established member of the aquatic community, Striped Bass has not previously been considered to limit the Delta Smelt population. Here, we develop an argument that Striped Bass are important to controlling Delta Smelt. We support this argument by reviewing historical data which suggests that declines in Delta Smelt before the current-day monitoring program were driven by the invasion of Striped Bass into the estuary. We describe this phenomenon as the 'phantom predator' hypothesis in the context of an analog to the shifting baseline syndrome previously described for marine fisheries. A deeper understanding of how well studied (and rapidly changing) bottom-up drivers of the estuary food web interact with poorly understood (but also rapidly changing) controls at the top of the food web could prove very important to the conservation of other declining native fishes and possible future attempts to re-introduce captive-reared Delta Smelt to the estuary.

INTRODUCTION

By sitting at or near the top of aquatic food webs, piscivorous fishes can influence the population dynamics of co-occurring fish at multiple trophic levels via direct consumption or by changing the behavior and habitat use of potential prey (Kitchell et al. 1994; Pine et al. 2009). This is well established for cases where the consequences of an introduced piscivore were monitored as the species invaded a receiving ecosystem. In the San Francisco Estuary (the estuary; Figure 1), however, the introduction of Striped Bass, *Morone saxatilis*, preceded routine monitoring of estuary
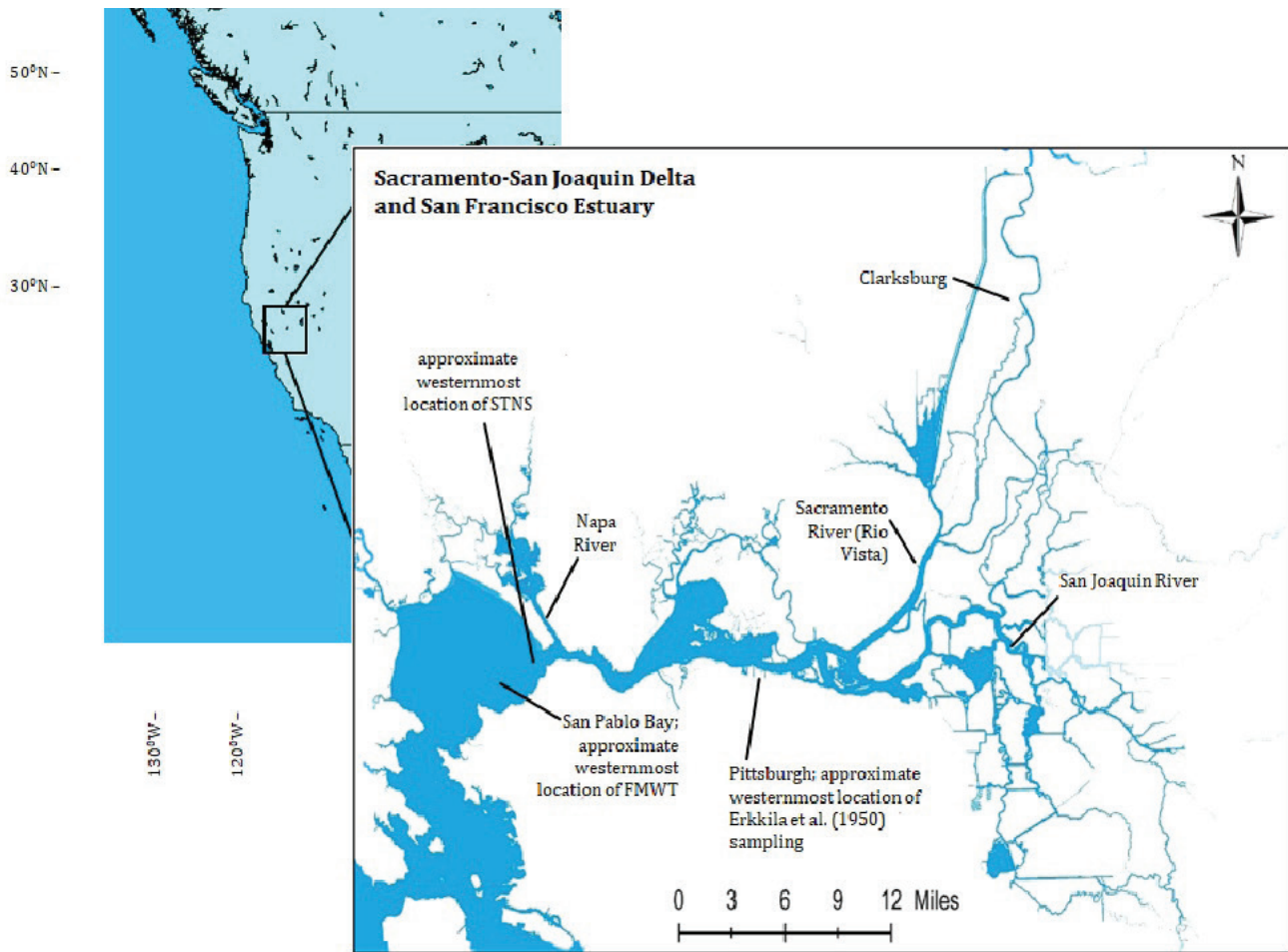
Figure 1   Map of the San Francisco Estuary including key geographic locations and river systems described in the text of this essay

fishes by 8 or more decades, leaving the potential for a substantial knowledge gap about how this and other early species introductions affected native aquatic communities (Moyle 2002).

The Striped Bass was introduced to the estuary from the U.S. east coast in 1879 and 1882, and it quickly became the estuary's top piscine predator. The Striped Bass introduction was remarkably successful from the perspective of establishing a fishery; commercial fishing started in the latter 1880s, and yields appear to have peaked between 1908 and 1915 at about 3.7 million kg · yr^{-1} (Scofield and Bryant 1926). Commercial fishing for Striped Bass was terminated in 1935, not because the population had been overfished, but because of growing conflict between sport and commercial fishers (Stevens et al. 1987). In

the estuary, Striped Bass mature at 3 to 4 years of age, and few live longer than 6 to 8 years. The contemporary population of Striped Bass still supports a popular sport fishery despite substantial apparent declines in age-0 production (Thomson et al. 2010), and the population was recently estimated to have an annual demand for prey fish that exceeded 25 million kg (Loboschefsky et al. 2012).

The estuary's native fish fauna has experienced only one extinction (Thicktail Chub *Gila crassicauda*) and one extirpation (Sacramento Perch *Archoplites interruptus*), both brackish-water-tolerant freshwater fishes (Moyle 2002). Although no additional species losses have occurred since Sacramento Perch, additional native species, including Delta Smelt, are

nearing extinction (Moyle et al. 2016; 2018; Hobbs et al. 2017). The Delta Smelt is an annual forage fish that has been listed under the U.S. and California Endangered Species Acts since 1993. Its legal status has fostered substantial increases in monitoring and research, motivated by a search for its major population drivers and viable conservation actions (e.g., Bennett 2005; Moyle et al. 2016). Delta Smelt were considered to have been abundant until the early 1980s, when relatively large and prolonged declines in available abundance indices were first observed (Moyle et al. 1992; 2016). Delta Smelt abundance indices declined abruptly again in the early 2000s; the latter resulting in a nearly continual decline to its contemporary nearly extirpated status (Thomson et al. 2010; Polansky et al. 2019).

This scenario has the implicit assumptions that the Delta Smelt population was stable before its decline in the early 1980s, and the decline was driven by an ecosystem shift associated with this time-period. The numerous quantitative models that have been developed in the last decade to evaluate drivers of Delta Smelt population dynamics have focused on concurrent potential drivers (Mac Nally et al. 2010; Thomson et al. 2010; Maunder and Deriso 2011; Miller et al. 2012; Rose et al. 2013; Hamilton and Murphy 2018; Kimmerer and Rose 2018). However, an alternative assumption is that the Delta Smelt decline had *already* occurred when the first fish monitoring program began in 1959 (Figure 2). Under this alternative assumption, the largest effects from drivers of Delta Smelt's decline may have been missed, and may no longer be as apparent as they would have been, had monitoring data been available earlier.

This phenomenon of hidden or past effects has been described as a shifting baseline syndrome by Pauly (1995). Pauly (1995) described a shifting baseline syndrome for marine fisheries in which humans fail to fully recognize the effects of their fishing efforts because the scale of ancestral fish biomass has been lost to history. As a consequence, the magnitude of decline and associated ecosystem change are not fully appreciated. An analog of the shifting baseline

syndrome has occurred in the estuary because the ancestral biomass of native fishes has similarly been lost to history. As a result, contemporary information may be mistaken for evidence that Striped Bass and native fishes have previously—and still can—successfully coexist. This may not be the case, and the current effects of Striped Bass may be significant as well as being a major driver of native species decline before the monitoring programs of today.

Furthermore, an unappreciated significance of Striped Bass on current Delta Smelt abundance may occur through small changes in juvenile prey fish survival rates, because small changes in juvenile fish survival can result in large changes in population-dynamic outcomes. For instance, Pine et al. (2009) reviewed several examples of intentional fisheries management interventions which had outcomes that went opposite to *a priori* expectations. They called these responses "counter-intuitive," and related their case study examples to small changes in per capita rates of predation and competition on juvenile fish populations. A similar dynamic might involve Striped Bass. The high mobility (Scofield and Bryant 1926; Sabal et al. 2019) and diverse diet compositions (Nobriga and Feyrer 2008; Zeug et al. 2017) of Striped Bass suggest they have limited reliance on individual prey taxa once they survive their first few months of life. Striped Bass can opportunistically switch prey based on the composition of the available prey field; thus, Striped Bass can be a source of minor per capita changes in predation rates on multiple prey populations that might result in substantial changes in juvenile survival rates, and unanticipated population consequences for prey populations.

In this essay, we combine literature review with basic summaries of widely used California Department of Fish and Wildlife fish monitoring data to provide evidence for a 'phantom predator' hypothesis: that ephemeral but persistent predation by Striped Bass helped to marginalize Delta Smelt *before* the estuary was routinely biologically monitored (Figure 2 and see Sidebar 1). Further, we hypothesize that an
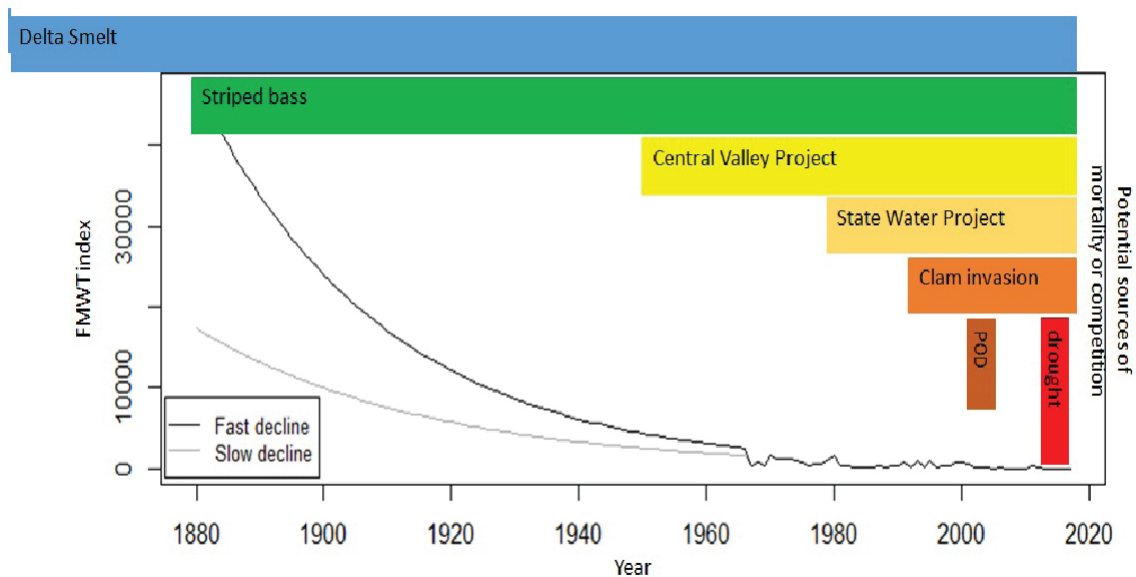
Figure 2 Conceptual depiction of the phantom predator hypothesis in the context of a shifting ecological baseline affecting Delta Smelt. Delta Smelt are hypothesized to have been much more abundant before the introduction of Striped Bass, after which abundance began declining. Initial abundances and rates of decline are hypothetical, but comparable to Fall Midwater Trawl indices recorded for more abundant co-occurring species such as age-0 Striped Bass and Longfin Smelt in the latter 1960s. Where the *smooth decline lines* begin to show variation, empirical abundance index data replace the hypothetical abundance decline. The timing of Striped Bass and other possible effects are shown as *colored bars* along the top of the graphic.

analog to the shifting baseline syndrome has led to a misinterpretation that Striped Bass had little contemporary effect on Delta Smelt. We contend that the Delta Smelt population has declined steadily since Striped Bass were introduced to the estuary, and that has masked a substantial predatory effect of Striped Bass on Delta Smelt.

This essay is divided into three parts.

- Part 1 presents evidence that the estuary's invasion by Striped Bass has occurred in the context of a long-term shifting baseline.

- Part 2 proposes that Delta Smelt abundance has been low over the entire monitoring program history, and sets the hypothesis of a continuing decline associated with accumulating changes to the estuary ecosystem. The approach is to compare Delta Smelt information to that for other small pelagic fishes, with a focus on comparison to age-0 Striped Bass.

- Part 3 discusses the feasibility that observed variation in Delta Smelt abundance indices reflects contemporary evidence that Striped Bass had a substantial influence at times.

PART 1—REVIEW OF ECOSYSTEM CHANGES THAT SHIFTED THE BASELINE FOR DELTA SMELT

Landscape Modification, Sediment Pollution, and Establishment of Non-Native Fisheries (1850–1920)

The era from 1850 to 1920 was characterized by large-scale wetland conversion, predominantly to leveed farmland, and by major additions to the estuary of hydraulic mining sediment (Nichols et al. 1986; Schoellhamer 2011; Whipple et al. 2012; Gross et al. 2018). The main effect of wetland conversion would have been to limit the connectivity between water and the estuary's once-expansive marsh–floodplain habitats (Whipple et al. 2012; Andrews et al. 2017). Mining sediments made parts of the Sacramento River and the estuary shallower, and resulted in

SIDEBAR 1: DETAILS, EXPLANATIONS, AND DEFINITIONS OF KEY CONCEPTS

This essay uses several phrases to convey concepts differently than they were originally proposed or as shorthand for new concepts.

Shifting baseline syndrome: This phrase was originally coined by Pauly (1995) to describe the circumstance in which the original biomass of a commercially harvested fish stock had been lost to history because the onset of fishing pre-dated data collection. The consequence was a failure of fishery managers to understand how much stocks had been depleted because they only had contemporary abundance information to rely upon. Here, we use the phrase shifting baseline in an analogous manner; the original population sizes or biomass of native fishes were not recorded before ecosystem alterations had likely decreased them considerably. We suggest this has led to a misperception by scientists and natural resource managers in the Bay-Delta regarding how much the Delta Smelt population may have already declined when information first started being collected in 1948 or monitoring was first sustained beginning in 1959.

Phantom predator: We use this phrase to describe the under-appreciated predatory impact that we hypothesize Striped Bass had on Delta Smelt once the former was introduced to the ecosystem in the latter 19th century. The use of the word 'phantom' is intended to convey the hypothesis that a significant predator and population limiter of Delta Smelt has been hiding in plain sight because the most numerically obvious impact of Striped Bass predation on Delta Smelt had already occurred by the time consistent monitoring data streams were available.

Ephemeral predatory impact: In this essay, we demonstrate that Striped Bass has substantially outnumbered Delta Smelt for many decades. When a predator population has a biomass that exceeds that of its prey, small changes in its predation rate on the prey population can result in large changes in prey abundance (Pine et al. 2009). We hypothesize this would happen in the San Francisco Estuary because the Striped Bass population, like any predator population, has to consume more than its own weight in food to persist (Loboschefsky et al. 2012). The low biomass of the Delta Smelt population relative to that of the Striped Bass population means that mathematically, predation by Striped Bass could very quickly lower the biomass of any year's Delta Smelt cohort—potentially even if Delta Smelt appeared to be a minor prey when considered across a season or a year.

Density-dependent prey consumption: We use this phrase as shorthand to convey the concept that the prey eaten by Striped Bass will shift through time (and vary across locations) based on the density of particular prey in the environment and perhaps their density relative to other potential prey. Thus, density-dependent predation is analogous to a Type-III functional response (Nobriga et al. 2013). Prey choices by Striped Bass in the San Francisco Estuary have previously been shown to be [prey] density-dependent (Nobriga and Feyrer 2008; Zeug et al. 2017).

mercury contamination (Hornberger et al. 1999; Bouse et al. 2010). This was also an era in which other forms of water pollution first occurred (e.g., sewage problems: Scofield and Bryant 1926), and waterways were first contaminated with industrial byproducts such as metals (Hornberger et al. 1999). For instance, Scofield and Bryant (1926) reported a decline of Striped Bass in San Pablo Bay which they attributed to a combination of water pollution and siltation from dredging that "almost entirely killed the diatoms and other plant life which form the basis of the food supply of fishes."

The estuary's native fish fauna had two major marine to mesohaline pelagic forage fishes: the Northern Anchovy *Engraulis mordax* and the Pacific Herring *Clupea pallasii* (Armor and Herrgesell 1985). It also included the facultatively anadromous Longfin Smelt *Spirinchus thaleichthys*, and the freshwater- to low-salinity-affiliated Delta Smelt (Moyle 2002). There were abundant populations of semi-pelagic forage fishes like Jacksmelt *Atherinopsis californiensis* that were at one time commercially fished (Skinner 1962). There is no known information on the historical abundance of these fishes. Contemporary information suggests that the native forage fish assemblage had evolved some degree of resource partitioning along the estuary salinity gradient (Feyrer et al. 2015). We assume that, as is the case today, the species with access to more productive marine waters outnumbered species such as the Delta Smelt, which lacked that access.

The period from 1850 to 1920 included the first non-native fish introductions to the estuary and its watershed (Moyle 2002). The first of these was American Shad *Alosa sapidissima* in 1871. The introduction quickly established this anadromous species as a member of the estuary's pelagic fish assemblage. American Shad was already being fished commercially by 1879 when the first Striped Bass introductions occurred (Stevens et al. 1987). The commercial fishery for American Shad persisted until 1957 when it was ended over concerns about Striped Bass bycatch. Striped Bass similarly reached commercial viability shortly after its introduction, so that by the latter 19th century, the estuary's pelagic fish assemblage had two prominent new members, including its new anadromous top predator. In summary, major ecosystem changes that were likely detrimental to estuarine fish production had occurred by 1920, but were apparently not sufficient to preclude the development and ongoing success of commercial fisheries for Striped Bass, American Shad, and other species.

American Shad and Striped Bass life-history characteristics likely helped them become established and thrive in the estuary, despite massive wetland conversion and potentially substantial water pollution. First, these species are anadromous, often spawning upstream of the tides, then rearing from the river systems in which they were spawned seaward throughout the estuary, and having an opportunity to move into the Pacific Ocean (Scofield and Bryant 1926; Stevens et al. 1987). Thus, although Striped Bass and American Shad typically rely on the estuary for part of their life cycle, they can use riverine and marine habitats that may help them obtain food web opportunities and reduce contaminant body burdens. In contrast, Delta Smelt are confined to the estuary (specifically its northern reach), which limits their habitat options (Moyle et al. 1992). Second, American Shad and Striped Bass are long-lived (Moyle 2002). This provides variable age-structure within their populations that buffers against poor conditions in individual years. The Delta Smelt population, with its predominantly annual turnover, does not have this temporal buffer against poor conditions. The

Delta Smelt population was possibly already in severe decline by 1920, but there are no data to determine whether this was the case.

Initial Large-Scale Hydrodynamic Alteration (1920–1950)

The period from 1920 to 1950 ushered in the first major modifications to the timing and duration of the estuary's freshwater flow regime (Hutton et al. 2017; 2018); freshwater inflow magnitude had begun to be affected in the previous era (Gross et al. 2018). This second era of change began with historic drought and culminated with Central Valley Project rim dams on the Sacramento and San Joaquin rivers. Water storage capacity in the estuary watershed grew from about 4 million acre-feet (maf) to almost 20 maf (Cloern and Jassby 2012). In addition, the loss of flood capacity in floodplains and wetlands during the previous era necessitated deeper channels to convey floodwaters through the Delta. Channelization not only increased flood conveyance, but improved trans-oceanic shipping to ports in Sacramento and Stockton (Andrews et al. 2017). The combination of greater reservoir storage and deeper channels began to change the Delta's inflow and outflow hydrographs, and increased salinity intrusion (Andrews et al. 2017; Hutton et al. 2017; Gross et al. 2018). In addition, legacy contaminants such as DDT and PCBs were entering the estuary for the first time, and these chemicals continue to bioaccumulate in the estuarine food web (Hornberger et al. 2000; Greenfield et al. 2005; Gobas and Arnot 2010). As mentioned above, legislative action in 1935 terminated commercial sale of Striped Bass, which ended its commercial fishery (Stevens et al. 1987).

During this second era of ecosystem change, the estuary's fish assemblages were haphazardly monitored. For instance, Scofield and Bryant (1926) and Scofield (1931) provided extensive reviews of what was known about Striped Bass and its fishery. Scofield (1931) also provided extensive age and growth information about Striped Bass. Both of these early reviews provided only anecdotal information about Striped Bass food habits. Scofield (1931) mentioned "smelt" as prey, but without time or location details it is not

clear whether he is referring to Osmerid fishes or marine Atherinids such as Jacksmelt, which were often reported as "smelt" by commercial fishers (see Skinner 1962). Hatton (1940) provided the first documentation of Osmerid fishes (Delta Smelt and/or Longfin Smelt) as prey for Striped Bass, reporting that about one-third of the "adult" Striped Bass stomachs he examined from collections "near Pittsburgh" had prey fish remains. Of those, 5% of identifiable prey fish were identified as Osmerids, but he was only able to identify about half of the prey fish observed into a taxonomic group (Table 1).

Near the end of this era of initial large-scale hydrodynamic modification, the first quantitative information about the relative abundance of Delta Smelt was collected. During 1948 and 1949, Erkkila et al. (1950) used trawl nets and deployment methods similar to those used in the Summer Tow Net Survey (https://www.wildlife.ca.gov/Conservation/Delta/Townet-Survey/Diagram) to sample fishes at up to 26 fixed sites in the Delta (Figure 1). The authors reported survey-specific catch and mean length data for Striped Bass, American Shad, Chinook Salmon *Oncorhynchus tshawytscha*, and "pond smelt," now recognized to be Delta Smelt (Moyle 2002). We extracted data on the catch of age-0 individuals for three of the four species listed above. We excluded Chinook Salmon because they had mostly migrated to sea by the summer months when catches of the other species peaked. We used equations provided by Kimmerer et al. (2005) to convert mean fork lengths (FL) into mean weight estimates, and then multiplied each species' catch by the mean weight to develop biomass estimates (kg), which represented the total annual sampled biomass of each species (Table 2).

The numbers and biomass of Striped Bass and American Shad were higher than Delta Smelt in both 1948 and 1949 (Table 2). Catches of all three species were higher in 1949 despite a shorter sampling season. Given this study's westernmost sampling site at Chipps Island, the higher catches might have been a result of these fish having a more landward distribution in 1949 (a dry water year) than 1948 (a below-normal water year),

but this is speculative. Nonetheless, these data show that Delta Smelt was less abundant than Striped Bass and American Shad before the onset of water exports from the Delta. Throughout the following era, water exports were considered the principal limiting factor for all three of these fish species through the entrainment of young fish and their food web, and through constriction of low-salinity zone nursery habitat into the bathymetrically simple shipping channels of the western Delta (Stevens et al. 1985; Moyle et al. 1992).

Rapid Hydrodynamic Change (1951–1986)

The period from 1951 to 1986 was the era of most rapid hydrodynamic change for the estuary (Hutton et al. 2017; 2018). Cumulative water storage capacity in the watershed rose at its fastest rate, and reached nearly contemporary levels that exceeded 50 maf by the early 1980s (Cloern and Jassby 2012). Also during this era the Delta became a freshwater transfer point for the U.S. government's Central Valley Project (CVP; since 1951) and the State of California's State Water Project (SWP; since 1968), both of which deliver Sacramento River basin water into the Delta for 'export' to more arid regions of the state. Recent change attribution papers indicate that much of the change to estuary hydrodynamics occurring during this era resulted from construction and operation of the CVP and SWP (Hutton et al. 2017; 2018).

The passage of the Clean Water Act in 1972 decreased many point sources of pollution into the estuary, but concerns remained over legacy contaminants from this and earlier eras (e.g., mercury and PCBs; Gobas and Arnot 2010; Gehrke et al. 2011). In addition, non-point run-off of agricultural pesticides emerged as a Striped Bass management concern (Cashman et al. 1992; Bailey et al. 1994), though population-dynamic consequences were not apparent (Bennett et al. 1995; Kimmerer et al. 2000). From a biological standpoint, the period from 1951 to 1986 saw several new species introductions, including non-native fishes invading the estuary from upstream lakes and reservoirs (e.g., Threadfin Shad *Dorosoma petenense*, Mississippi Silverside

Table 1 Summary of historical reports of Striped Bass predation on Delta Smelt in California's San Francisco Estuary. See Figure 1 for locations of studies reviewed in this table. All Delta Smelt diet fractions are reported as they were by the original authors, so the number of significant digits varies. Delta Smelt was once thought to be a population of Pond Smelt *Hypomesus olidus*. This is reflected where applicable. For brevity, Striped Bass diet information for times and places where Delta Smelt were not observed as prey are not included in the "Details" column of this table.

Source	Time and Location of Study	Striped Bass Life Stage(s)	Number of Stomachs Examined	Details
Hatton (1940)	March 13 to May 4, 1939 "near Pittsburgh"	"Adults"	224 with 57% reported as empty.	34% of stomachs contained fish prey. Of those,18.74% of bass had "Unidentifiable fish or remains of fish present." 4.9% had "Identifiable osmerids present." Osmerid fishes were the largest fraction of identified fish remains in this study. These could have been a combination of Delta Smelt and Longfin Smelt.
Stevens (1963)	May–September, 1962, November 1962, and February–April, 1963 in the Sacramento River from Freeport downstream to its confluence with Three-Mile Slough. Most 1962 collections were from the vicinity of Paintersville Bridge, and most 1963 collections were from the vicinity of Rio Vista	Juveniles and adults, but mostly juveniles. Mean size was reported as 305 mm (about age-2); size range was 203–826 mm.	598 with 63% reported as empty.	Delta Smelt were identified as "pond smelt" or "freshwater smelt" (*H. olidus*). June 1962: 24 Delta Smelt measuring 73–80 mm were 11.1% of total prey volume from 119 Striped Bass stomachs that contained food, primarily from the vicinity of Paintersville Bridge. July 1962: 3 Delta Smelt were 0.7% of total prey volume from 107 Striped Bass stomachs that contained food in the vicinity of Paintersville Bridge. August 1962: 13 Delta Smelt averaging 45 mm in length were 64.9% of total prey volume from 12 Striped Bass stomachs that contained food in the vicinity of Three-Mile Slough. March 1963: 39 Delta Smelt measuring 72–84 mm in length were 81.6% of total prey volume from 12 Striped Bass stomachs that contained food in the vicinity of Rio Vista. April 1963: 5 Delta Smelt were 100% of the prey volume from 3 Striped Bass stomachs that contained food in the vicinity of Rio Vista.
Stevens (1966)	September 1963–August 1964 from 16 sites in the Delta upstream of the Sacramento–San Joaquin River confluence	age-0 through age-3+	1963 year class: n=3,843 with 8% reported as empty. 1962 year class: n=2,037 with 13% reported as empty. 1961 year class: n=1,242 with 14% reported as empty. 1960 and older year classes: n=1,502 with 7% reported as empty.	Delta Smelt were identified as "pond smelt" but by this time associated with the modern Latin name (*H. transpacificus*). 1963 Year class: "trace amounts" defined as <1% by volume of Delta Smelt during summer 1964. 1962 Year class: Delta Smelt were 3% by volume in spring 1964 and 8% by volume in the summer of 1964. 1961 Year class: "trace amounts" during autumn 1963, 1% by volume in winter 1964, 4% by volume in spring 1964. 1960 and older Year classes: "trace amounts" during winter and spring 1964.
Thomas (1967)	Sampling details are very vague in this paper. Sampling occurred from San Francisco Bay to the "upper Sacramento River" from 1957–1961. Data were summarized as 3-month seasonal averages for all years combined and, in most cases, all Striped Bass sizes combined.	The author considered 152–254 mm Striped Bass to be age-1, 279–381 mm Striped Bass to be age-2, and all fish over 406 mm to be adults, but these divisions were generally not used in the paper.		Delta Smelt were identified as "pond smelt" but associated with the modern Latin name (*H. transpacificus*). Spring (March 1–May 31): Delta Smelt were 8% by volume from 134 Striped Bass stomachs that contained food collected in the "Delta." Summer (June 1–August 31): Delta Smelt were 15.6% by volume from 173 Striped Bass stomachs that contained food collected in the "lower Sacramento River."

Table 2 Summary of catch data for Striped Bass, American Shad, and Delta Smelt reported in the catch appendices of Erkkila et al. (1950) from 33 surveys; each one of which took 1 to 2 weeks to complete. The information summarized here spanned June 16–December 16, 1948 and May 18–September 22, 1949, which encompassed the period during which age-0 individuals of these three species were being collected.

Species	1948			1949		
	Catch	Mean FL (mm)	Total biomass collected (kg)	Catch	Mean FL (mm)	Biomass (kg)
Striped Bass	8,071	13–75	5.45	20,238	13–75	12.6
American Shad	5,607	22–60	3.22	22,460	22–62	10.7
Delta Smelt	2,460	33–67	2.61	8,412	27–53	5.93

Menidia audens) (Moyle 2002), and both fishes and invertebrates introduced via ballast water from trans-oceanic shipping (Choi et al. 2005; Matern and Brown 2005). We chose to end this era at 1986 because that year marked the introduction of the overbite clam, *Potamocorbula amurensis*, which initiated a further ecological regime shift in the estuary (Brown et al. 2016).

During this era of rapid hydrodynamic change, growing concern about the ecological effects of California's water development led to new research initiatives during the latter 1950s into the mid-1960s. Some of these studies documented that adult and juvenile Delta Smelt were a common prey for Striped Bass (Table 1). For instance, adult Delta Smelt were a dominant prey species in one study of stomach contents of Striped Bass collected along the Sacramento River. During more spatially comprehensive studies of the latter 1950s through mid-1960s, adult and juvenile Delta Smelt were reported to occur as prey for Striped Bass at frequencies (or volumetric contributions) of up to 8% during the spring and 16% during the summer. Age-2 and age-3 Striped Bass appeared to be the predominant predators of Delta Smelt at the time.

The quantitative dynamics of predator–prey interactions are governed by a functional response, which affects how prey are chosen, and an aggregative response, which affects how many predators get involved (Essington and Hansson 2004). The use of individual prey species by Striped Bass reflects changes in prey abundance across multiple spatio-temporal scales (Nobriga and Feyrer 2008; Nobriga et al. 2013;

Zeug et al. 2017). It is important to view historical observations of Delta Smelt as prey in the light of this density-dependent prey consumption because it indicates that Striped Bass use of Delta Smelt as prey is related to the density of Delta Smelt and Delta Smelt's density relative to other potential prey species. For instance, the dominant fish prey of Striped Bass reported by Stevens (1966) was younger conspecifics. That year (1964), young Striped Bass comprised about 80% of the Summer Tow Net Survey raw catch; Delta Smelt were about 15% (data not shown). Thus, historical aggregations of young fishes in production 'hot spots' such as the pre-overbite clam low-salinity zone likely attracted older Striped Bass to feed in this region, which resulted in some predation of Delta Smelt even though they were not the dominant species. We suggest historical consumption of Delta Smelt by Striped Bass is evidence against Moyle et al.'s (2016) assertion that "their behavior and translucent color makes them difficult to target as a prey species."

Over time, fisheries research initiatives became monitoring programs that documented the influence of inflowing freshwater on Striped Bass production (Turner and Chadwick 1972; Stevens 1977a; Stevens et al. 1985). Then, monitoring surveys established that food web support for Striped Bass was also affected by freshwater flow variation (Cloern et al. 1983; Knutson and Orsi 1983). Next, the data were used to document a broad ecosystem response to freshwater flow variation (Jassby et al. 1995). Interestingly, Delta Smelt was not one of the species that exhibited a numeric abundance response to interannual variability in freshwater input to the estuary

(Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002), even though freshwater flow was believed to be strongly affecting them (Moyle et al. 1992). By the end of this third era, it was apparent that Delta Smelt was a species in decline (Moyle et al. 1992).

The Overbite Clam and Ecological Regime Shift (1987–Present)

The overbite clam caused major changes in the estuarine food web (Brown et al. 2016). However, as in the other eras, multiple changes occurred simultaneously; some of which may have linkages to this bivalve and others which do not. These changes have been comprehensively monitored and in many cases linked to mechanisms. Key changes include the overbite clam's effects on species composition and food web productivity (Cloern et al. 2007; Kimmerer and Thompson 2014; Brown et al. 2016) and the clam's ability to biomagnify selenium in its predators (Linville et al. 2002; Stewart et al. 2004; 2013). In addition, monitoring and research programs have documented major changes in species dominance in tidal freshwater habitats that result from the proliferation of submerged aquatic vegetation (SAV; Brown and Michniuk 2007; Grimaldo et al. 2009; Conrad et al. 2016), which by increasing water transparency (Schoellhamer 2011; Hestir et al. 2016), can quantitatively affect predator–prey outcomes (Utne–Palm 2002). There have also been changes in nutrient ratios (Glibert et al. 2016), the use of highly toxic pesticides (Connon et al. 2009), and the occurrence of cyanobacteria blooms, particularly *Microcystis aeruginosa* (Lehman et al. 2013). Some of these changes have been associated with declines in estuarine-dependent fish catches (Kimmerer 2002; Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010) and increases in littoral, predominantly freshwater fish catches in the Delta where SAV is most prevalent (Mahardja et al. 2017a; Young et al. 2018). During most of the overbite clam era, Striped Bass research and diet studies have been a lower priority than endangered species research. Visual searches of Striped Bass stomach contents did not reveal evidence of predation on Delta Smelt (Nobriga and Feyrer 2007; Zeug et al. 2017),

though DNA-based methods were able to do so (Schreier et al. 2016; Michel et al. 2018).

PART 2—REVIEW OF FISH COMMUNITY ECOLOGY WITH EMPHASIS ON STRIPED BASS AND DELTA SMELT

In Part 2, we focus on catch data for age-0 Striped Bass and Delta Smelt, but provide additional context using catch data for four additional pelagic fish species that commonly occur in the region sampled by the California Department of Fish and Wildlife's long-term monitoring programs. The two longest-running fish monitoring programs in the estuary are the Summer Tow Net Survey (STNS, *http://www.dfg. ca.gov/delta/data/townet/stations.asp*) and Fall Midwater Trawl Survey (FMWT, *http://www.dfg. ca.gov/delta/data/fmwt/stations.asp*), both of which were initiated to monitor the recruitment of age-0 Striped Bass (Stevens 1977b). Both programs sample at fixed arrays of stations located from San Pablo Bay in the west through the Delta in the east (Figure 1). These are offshore or pelagic sampling programs that employ oblique towing methods starting near the bottom of the water column and finishing near the surface. The databases housing the survey information are publicly available at *ftp://ftp.dfg.ca.gov/*.

Information on the distribution and abundance of age-0 Striped Bass relative to Delta Smelt is relevant to the phantom predator hypothesis for two reasons: (1) age-0 Striped Bass are potentially an intra-guild predator of Delta Smelt, and (2) concentrations of young fishes attract predators, which can bring predation pressure to Delta Smelt even if they are not the species causing the aggregative response. Like other co-occurring juvenile piscivorous fishes, Striped Bass begin to increase their use of fish as prey when they reach about 100 mm in length (Figure 3), a size the fastest-growing individuals can reach as early as July (Figure 4). Even if age-0 Striped Bass are relatively ineffective at capturing Delta Smelt, the threat of predation can cause substantial behavioral responses in prey populations (Kitchell et al. 1994; Peckarsky et al. 2008). Therefore,
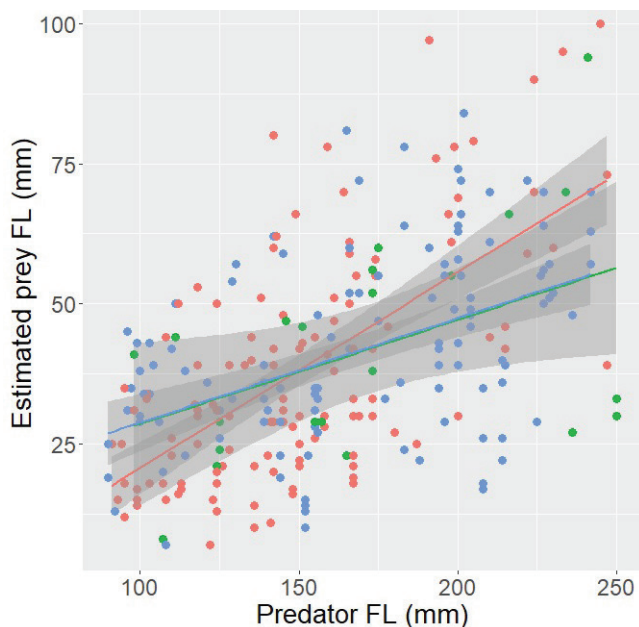
Figure 3 Scatterplot showing the estimated length of prey fish consumed by three predatory fishes as a function of predator length: *orange symbols* = Largemouth Bass, *green symbols* = Sacramento Pikeminnow, and *blue symbols* = Striped Bass. A *linear regression line* shows the predicted relationship for each species; note Striped Bass and Sacramento Pikeminnow have nearly identical predicted relationships. The *gray shading* depicts 95% confidence for where each species' regression line truly lies. The plot was made from the diet data described by Nobriga and Feyrer (2007).

Figure 4 Scatterplot of age-0 Striped Bass fork lengths for the summer and fall of 2001 comparing the California Department of Fish and Wildlife's Summer Townet Survey (*teal data points* for June–July) and Fall Midwater Trawl Survey (*teal data points* for September–October) with fork length measurements from the beach seine sampling conducted from late May through October (*orange data points*; Nobriga et al. 2005).

Delta Smelt likely adjust their distribution when larger age-0 Striped Bass are nearby.

Age-0 Striped Bass are more abundant in the STNS (Table 3) and FMWT (Table 4) than Delta Smelt. Relative to the five other most abundant concurrently sampled pelagic fishes, Delta Smelt have had higher relative abundance in the STNS (Table 3) than in the FMWT (Table 4). As we discuss in Part 3, the higher relative abundance of Delta Smelt in the STNS may relate to this survey's preceding the bulk of Striped Bass predation that has occurred by the fall, but there are other contributing reasons. One reason is the FMWT begins sampling when Delta outflow is near its annual minimum. As such, it samples a broader range of the estuarine salinity gradient than the STNS. By doing so, it overlaps more of
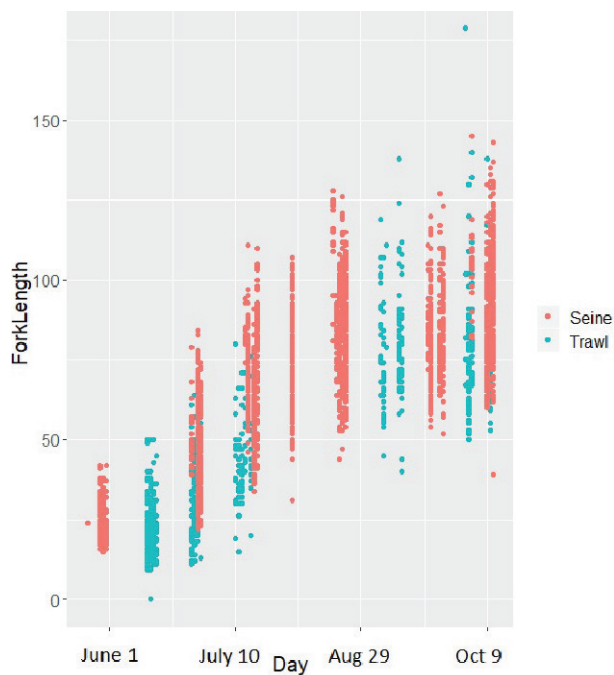
the distribution of Northern Anchovy, which is the estuary's most abundant pelagic forage fish (Kimmerer 2006; Feyrer et al. 2015). A second reason is American Shad and Threadfin Shad spawn later in the spring and summer than Delta Smelt and Striped Bass (Feyrer 2004), so the STNS under-represents shad annual production.

We summarized the distributions of Delta Smelt and the five other commonly collected pelagic fish species relative to salinity using the FMWT data divided into pre- and post-overbite clam years (Figure 5). Delta Smelt has been collected over the smallest range of salinity (about 0–20 psu). Further, Delta Smelt showed no change in its distribution along the estuarine salinity gradient after the overbite clam invasion, whereas the other five species did. After the overbite clam invasion,

Table 3 Catch summaries for six pelagic fishes commonly collected in the California Department of Fish and Wildlife's Summer Townet Survey (STNS), 1959–2017. The fork length data are median across all years of available data, and the estimated weights were developed using equations provided by Kimmerer et al. (2005).

Species	Total STNS catch (range of annual number collected)	Mean fraction of catch (standard deviation)	Median fork length (mm)	Median estimated weight (per capita; g)
Northern Anchovy *Engraulis mordax*	32,008 (16–3,102)	0.13 (0.16)	46	0.60
Longfin Smelt *Spirinchus thaleichthys*	16,871 (1–1,612)	0.057 (0.092)	36	0.28
Threadfin Shad *Dorosoma petenense*	28,212 (5–8,385)	0.11 (0.17)	30	0.33
Striped Bass *Morone saxatilis*	375,276 (164–29,020)	0.54 (0.26)	31	0.30
American Shad *Alosa sapidissima*	8,941 (1–1,131)	0.029 (0.035)	37	0.52
Delta Smelt *Hypomesus transpacificus*	56,231 (23–4,328)	0.13 (0.10)	37	0.36

Table 4 Catch summaries for the top six most commonly collected pelagic fishes in the California Department of Fish and Wildlife's Fall Midwater Trawl Survey (FMWT), 1967–2017. The fork length data are median across all years of available data (1975–1978, 1980–2017), and the estimated weights were developed using equations provided by Kimmerer et al. (2005).

Species	Total STNS catch (range of annual number collected)	Mean fraction of catch (standard deviation)	Median fork length (mm)	Median estimated weight (per capita; g)
Northern Anchovy *Engraulis mordax*	904,735 (1,257–107,448)	0.65 (0.21)	72	2.72
Longfin Smelt *Spirinchus thaleichthys*	170,317 (3–40,506)	0.083 (0.11)	62	2.06
Threadfin Shad *Engraulis mordax*	115,103 (25–10,353)	0.12 (0.13)	90	10.8
Striped Bass *Morone saxatilis*	80,362 (31–16,829)	0.055 (0.070)	88	7.70
American Shad *Alosa sapidissima*	64,641 (58–6,622)	0.070 (0.067)	92	8.66
Delta Smelt *Hypomesus transpacificus*	15,412 (2–1,276)	0.016 (0.017)	57	1.55

age-0 Striped Bass and other fishes may have spread out along the salinity gradient in search of alternative food sources, but Delta Smelt either did not or could not. This suggests that Delta Smelt's niche is a subset of the age-0 Striped Bass niche.

The STNS and FMWT were implemented to sample Striped Bass not Delta Smelt (Stevens 1977b), so these surveys possibly misrepresent the relative abundance of Delta Smelt compared to Striped Bass (e.g., Mitchell et al. 2017). To evaluate whether the long-term trawl surveys mischaracterize the relative abundance of Delta Smelt, we summarized the extensive published literature on Bay–Delta fish assemblages (Table 5). Collectively, these studies used several classes of gear types, sampled onshore and offshore habitats, and represented many years of data collection. The only gear type in which Delta Smelt has tended to outnumber Striped Bass is
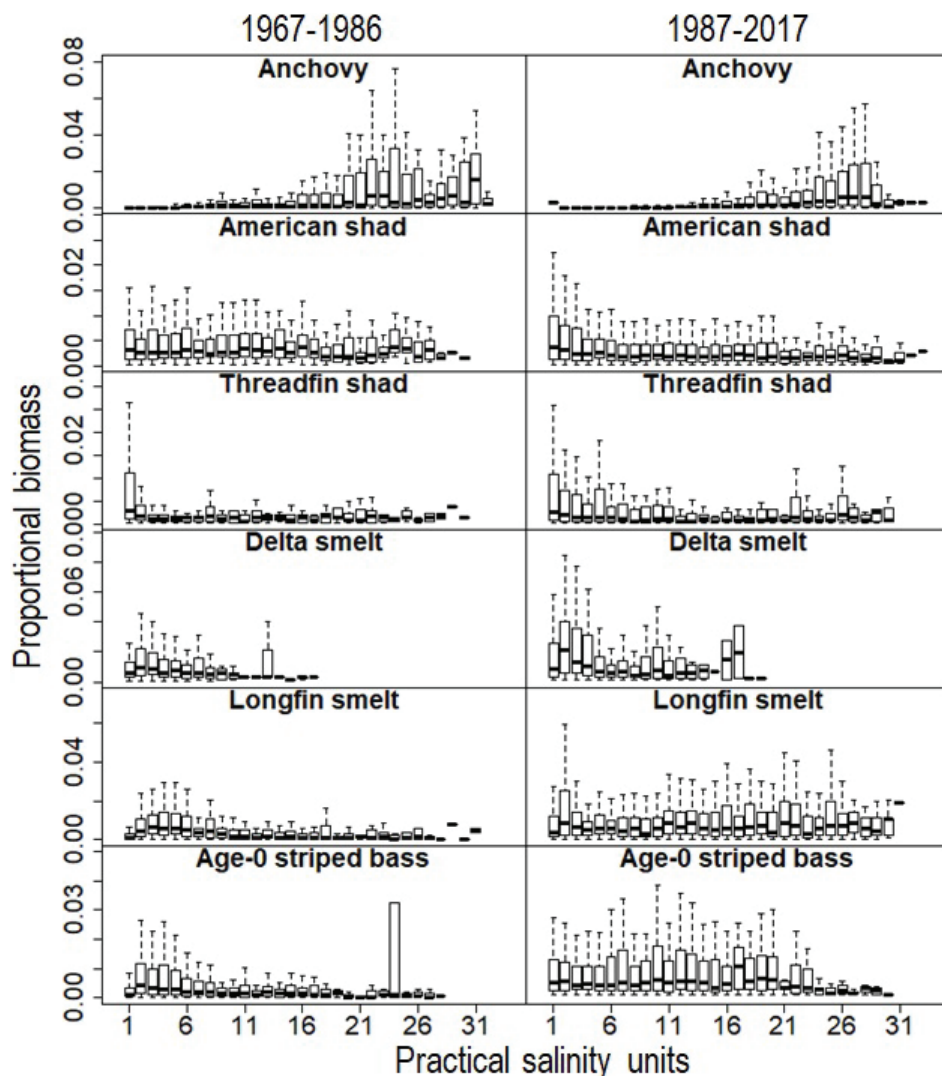
Figure 5 Salinity distributions of Fall Midwater Trawl catch for six pelagic estuary fishes, summarized by pre-overbite clam invasion years (1967–1986) and post-invasion years (1987–2017). Each Fall Midwater Trawl sample was associated with a specific conductance measurement, which was converted to practical salinity units. Annual frequencies of positive catches for each species, binned into one salinity unit increments, were divided by the total positive catch for each year–species combination, to yield proportional positive catch by salinity. Proportions represent the annual fractions of fish collected from each salinity bin. Within each salinity bin and across years, *boxplots* summarize the distributions of proportional catches lots. The boxes show the interquartile range, the *line through each box* is the median, and the *whiskers* depict 95% confidence intervals.

surface trawls (3 of 17 gear deployments). Striped Bass catches exceeded Delta Smelt catches in the remaining 14 gear deployments in ratios that ranged from about 3:1 to 1,441:1. This meta-analysis reinforces the qualitative conclusion from the trawl surveys that Striped Bass is the more abundant species and that Delta Smelt's niche is a subset of the young Striped Bass niche. Thus, we conclude from Tables 2 through 5 that there is robust evidence that age-0 Striped Bass are and have been more abundant than Delta Smelt for many decades.

PART 3—REVIEW OF DELTA SMELT POPULATION DYNAMICS THROUGH THE LENS OF THE PHANTOM PREDATOR HYPOTHESIS

Life-history theory predicts that annual fishes (opportunistic strategists; Winemiller and Rose 1992) are adapted to colonize ecotones where population dynamics are often driven by habitat conditions that vary unpredictably on small spatio-temporal scales. It also predicts that, because of their short lifespans, opportunistic strategists are adapted to high rates of predation mortality—even through adulthood. In situations where predation is a strong population regulator, density-dependent population dynamics can be expected, even when a population is not depleting its own resources (Walters and Korman 1999).

Table 5 Comparison of the numbers of Striped Bass (SB) and Delta Smelt (DS) collected from 18 fish community studies of the San Francisco Estuary. The exception is Castillo et al. (2018) who reported fish densities (number × 10⁴m³). Studies in which Delta Smelt catches outnumbered Striped Bass catches are shaded. Catch ratios are rounded to the nearest whole number of fish.

Reference	General gear type	Sampling location(s)	SB	DS	Ratio
Bennett and Burau (2015)	Surface trawl (Kodiak trawl)	Sacramento River near Rio Vista	5	707	141 DS for every 1 SB
Castillo et al. (2018)	Surface trawl (Kodiak trawl)	Spring Kodiak Trawl Survey: Napa River and sites east through the Delta	3.61	0.08	45 DS × 10⁴m⁻³ for every 1 SB × 10⁴m⁻³
Grimaldo et al. (2004)	Surface trawl (Larval net towed on from the side of a boat)	Wetlands and adjacent channels along and near the San Joaquin River Shipping Channel	88	216	3 DS for every 1 SB
Sommer et al. (2004)	Surface trawl (Larval net fished at the surface)	Yolo Bypass Toe Drain and Sacramento River at Sherwood Harbor	1,116	8	140 SB for every 1 DS
Mahardja et al. (2017a; supplemental info)	Beach seine	Delta	4,212	1,295	3 SB for every 1 DS
Bennett and Burau (2015)	Beach seine and purse seine	Sacramento River near Rio Vista	932	176	5 SB for every 1 DS
Grimaldo et al. (2012)	Beach seine and purse seine	Wetlands and adjacent channels along and near the San Joaquin River Shipping Channel	59	10	6 SB for every 1 DS
Nobriga et al. (2005)	Beach seine	Delta	5,665	553	10 SB for every 1 DS
Matern et al. (2002)	Beach seine	Suisun Marsh	5,497	69	80 SB for every 1 DS
Dege and Brown (2004)	Oblique midwater trawl	20-mm Survey: Napa River and sites east through the Delta	95,148	12,561	8 SB for every 1 DS
Mahardja et al. (2017b)	Oblique midwater trawl	20-mm Survey: Napa River and sites east through the Delta	223,004	26,823	8 SB for every 1 DS
Feyrer (2004)	Oblique midwater trawl	South Delta adjacent to the fish facilities (larval net)	3,153	74	43 SB for every 1 DS
Moyle et al. (1986)	Otter trawl (tows near the bottom)	Suisun Marsh	24,154	450	54 SB for every 1 DS
Matern et al. (2002)	Otter trawl (tows near the bottom)	Suisun Marsh	46,125	442	104 SB for every 1 DS
Gewant and Bollens (2012)	Fyke net (stationary net sampled outflowing water on ebb tides)	Remnant tidal marshes from San Pablo Bay to the Sac–San Joaquin river confluence	74	6	12 SB for every 1 DS
Sommer et al. (2004)	Rotary screw trap	Yolo Bypass Toe Drain	11,550	8	1,444 SB for every 1 DS
Brown et al. (1996)	Fish screen	Skinner Fish Facility	71.9 m	319,000	225 SB for every 1 DS

Recall, we use the term 'phantom predator' to describe potential ephemeral density-dependent regulation of the Delta Smelt population by Striped Bass.

We graphically re-analyzed trends in Delta Smelt population dynamics in the context of the phantom predator hypothesis (Figure 6A). We explored the potential for density-dependent effects on recruitment success by plotting the FMWT index versus the subsequent year's STNS index. Given Delta Smelt's primarily annual life cycle, this is in essence a spawner–recruit relationship and has been treated as such in previous studies (e.g., Moyle et al.1992; Bennett 2005; Maunder and Deriso 2011). The 1969 and 1975–1977 Delta Smelt cohorts produced

large juvenile year classes the following year (Figure 6B). These 4 strong recruitment years produced the four highest STNS indices inclusive of 1959–1965, which predate the FMWT (Figure 6A). The rest of the spawner–recruit data suggest the STNS has been a somewhat predictable function of the prior year's FMWT index, with a possible juvenile carrying capacity at an STNS index of about 20. Apart from the 4 exceptional recruitment years, the data suggest the STNS indices have declined primarily because the FMWT indices were declining; fewer juveniles in the FMWT presumably led to fewer adults, which in turn led to fewer juveniles in the following generation.
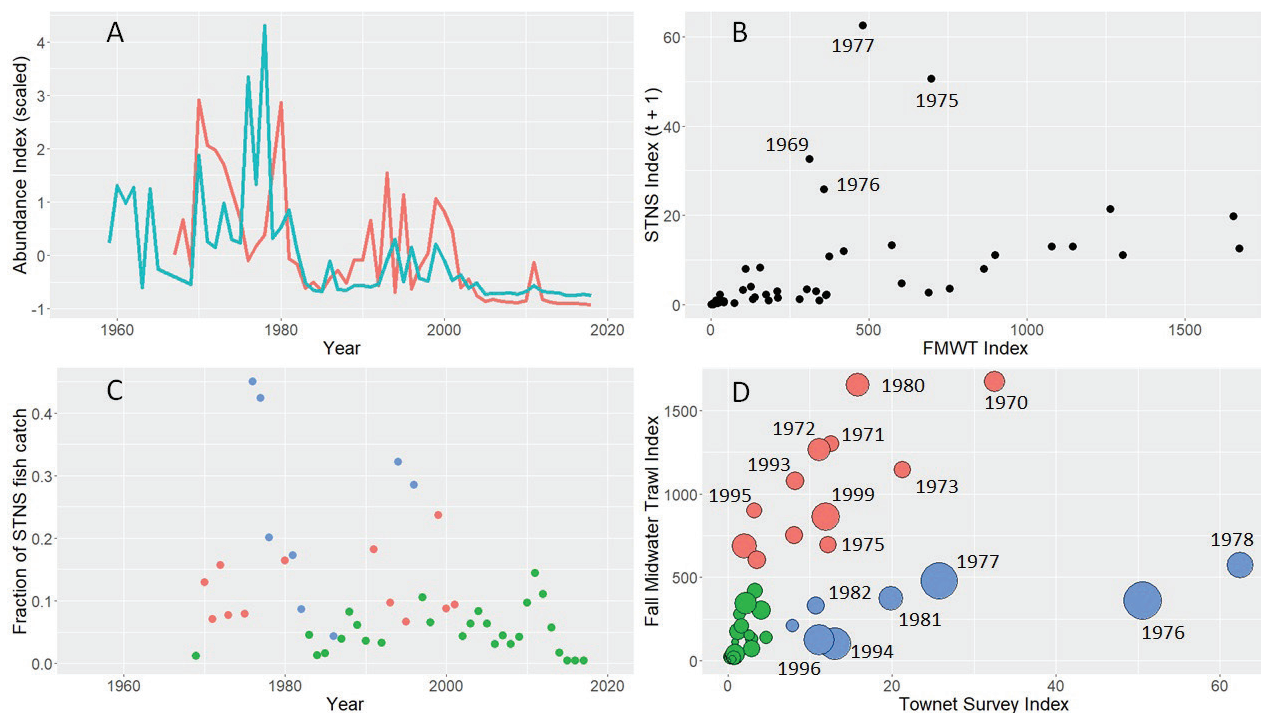

Figure 6 Population-dynamic plots for Delta Smelt: (**A**) z-scored time-series of the Summer Townet Survey (STNS; *cyan*) and Fall Midwater Trawl Survey (FMWT; *orange*) abundance indices. (**B**) Scatterplot of the FMWT versus subsequent-year STNS. Selected years are labeled, and reflect the year the FMWT sampling was conducted. The STNS is labeled $t+1$ to denote that it is data collected from the calendar year that follows the FMWT. (**C**) Time-series of Delta Smelt's fraction of the fish catch from the STNS for 1969–2015 (i.e., the years used to generate the *bubble plot* in panel **D**; 2016 and 2017 were unavailable when the database was downloaded, so these years were given the same near-zero fraction as 2015: 0.0047). (**D**) The STNS versus the next FMWT, which begins sampling 1 to 2 months after the STNS is finished. The *data points sizes* are scaled to Delta Smelt's fraction of the total fish catch in the STNS (maximum = 0.45 per panel **C**). In panels **C** and **D**, higher survival years are colored *orange*, lower survival years are colored *blue*, and years in which survival cannot be visually characterized as higher or lower are colored *green*. Selected years of higher and lower survival are labeled in panel **D**.

We explored the potential for density-dependent juvenile survival by plotting the STNS index against the subsequent FMWT index, which provides a way to evaluate the relative survival of each juvenile cohort from summer to fall (Bennett 2005; Maunder and Deriso 2011). Survival of juvenile Delta Smelt oscillated between a higher survival condition in which the indices followed an approximately linear relationship that lacked an obvious upper limit on the FMWT index, and a lower survival condition in which no matter how high the STNS index was, the subsequent FMWT index was asymptotic near a value of 600 (Figure 6D). Low survival years were not observed until 1976–1978. Unlike the strong recruitment years, which were last observed in 1978 (Figure 6B), low summer survival occurred intermittently until at least 1996 (Figure 6D). The STNS and FWMT indices have not reached high enough values to determine visually whether additional low survival years occurred after 1996, and index ratios have become increasingly unreliable as both indices declined. Low survival years often occurred when Delta Smelt comprised relatively large fractions of the STNS fish catch (20% to 45%; Figure 6C–D). We suggest that density-dependent prey consumption of Delta Smelt by Striped Bass (see Nobriga et al. 2013) may have been the ultimate mechanism for the low survival years.

Foraging arena theory (Walters and Korman 1999; Ahrens et al. 2012) is useful for understanding how predation by Striped Bass could result in ephemeral occurrence of low survival years for Delta Smelt. In foraging arena theory, fishes divide their time between foraging, which is risky but necessary for growth, and resting or hiding, which is less risky. Any factor that increases the fraction of time fish must spend foraging will in turn increase the cumulative predation risk faced by the foraging population. Previous authors have explained variation in Delta Smelt's summer survival with a variety of covariates consistent with foraging arena theory and therefore consistent with the phantom predator hypothesis. For instance, warm water temperature and low zooplankton densities have previously been linked to the summer–fall survival of Delta

Smelt (Bennett 2005; Kimmerer 2008; Maunder and Deriso 2011; Miller et al. 2012). Warm water temperatures increase the quantity of prey needed to support growth, and low zooplankton densities increase the amount of time fish need to forage to meet their caloric demands for growth, but prior studies have not recognized the bimodal nature of summer survival in the Delta Smelt data. Because of the density-dependent foraging by Striped Bass mentioned above, elevated relative abundance of Delta Smelt in the summer could have influenced how well Striped Bass were able to locate and target them as prey, particularly in years where high Delta Smelt abundance coincided with other foraging risk factors like warm water temperature or low zooplankton density. If regional densities of Delta Smelt and Striped Bass could be manipulated and Striped Bass densities controlled, the phantom predator hypothesis could be tested with field data. However, such large-scale ecosystem experiments are impractical or impossible. We mention potential ways of testing the phantom predator hypothesis using simulation models below, but it is well beyond the scope of this essay to do so.

The success of Striped Bass has been one constant throughout the long history of environmental change in the estuary. It was still being commercially fished in 1920 despite concerns about overfishing and pollution (Scofield and Bryant 1926). It was still the estuary's pre-eminent sport fish in 1950 despite concerns that the CVP would create ecological problems for it (Erkkila et al. 1950). It remained a successful sport fishery through 1986 despite ongoing concerns about increasing water exports and water pollution (Stevens et al. 1985). It adjusted to the overbite clam's food web effects with its long lifespan, flexibility in habitat use, and compensatory survival in its juvenile life stage (Kimmerer et al. 2000; 2001). At first look, it appeared that the 'pelagic organism decline' of the early 2000s might finally cause the Striped Bass population to collapse (Sommer et al. 2007; Thomson et al. 2010). But once again, that did not happen. As of 2006, the relationship between age-0 relative abundance estimates for Striped Bass and mark–recapture-based estimates of

their abundance 3 years later was growing exponentially (Figure 7), which indicates that juvenile Striped Bass were finding a way to survive that was not being reflected in the trawl surveys designed to index its early life production (see also Sommer et al. 2011; Feyrer et al. 2015). This persistent success of Striped Bass, in an estuary that increasingly cannot support macro-crustacean or pelagic fish production at levels it once could, may have changed how well native fishes such as Delta Smelt can co-exist with it.
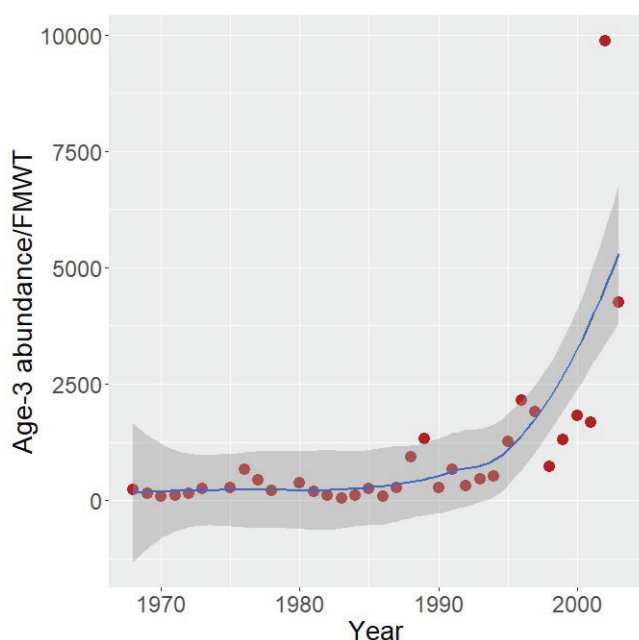
Figure 7 Time-series of the ratio of age-3 Striped Bass from mark–recapture surveys (*https://www.wildlife.ca.gov/ Conservation/Delta/Striped-Bass-Study*) to the age-0 Fall Midwater Trawl (FMWT) index from 3 years prior. The time-series begins with the 1971 age-3 abundance estimate divided by the 1968 FMWT index, and ends with the 2006 age-3 abundance estimate divided by the 2003 FMWT index. The increasing trend suggests an expanding disconnect between what recruitment appears to be based on trawling for age-0 Striped Bass and what it ends up being as they recruit to the fishery. The *blue line* is a LOESS smooth, and the *gray shading* is the standard error of the LOESS prediction.

CONCLUSION AND CONSERVATION IMPLICATIONS

The phantom predator hypothesis can be summarized as follows: (1) Striped Bass were a major predator of Delta Smelt in the past, before monitoring surveys began; (2) Striped Bass predation contributed to the historical decline of Delta Smelt; (3) when Delta Smelt abundance dropped, Striped Bass switched to other prey; and (4) when Delta Smelt would temporarily rebound, Striped Bass would target Delta Smelt again until they were no longer profitable, which maintained a persistent limit on Delta Smelt production. We think the phantom predator hypothesis provides important and previously missing context for understanding historical observations of Delta Smelt status, trend, and population dynamics. Our hypothesis borrows the notion of observation bias from its famous marine fisheries example (Pauly 1995) and couples that with the hypothesis that a major limiter of Delta Smelt production has been hiding in plain sight and has even been considered a "desirable species" from an ecosystem function and restoration perspective (Moyle et al. 2010). The phantom predator hypothesis is concordant with observations made around the world that non-native predatory fishes can cause substantial declines of native species (Kitchell et al. 1994; Jackson 2002; Côté et al. 2013), but in this case, Striped Bass was a phantom predator because most of its historical effect went unmonitored. The phantom predator hypothesis is also consistent with the case studies reviewed by Pine et al. (2009) which emphasize that even small changes to interspecies interactions can result in major changes to population and ecosystem dynamics. The phantom predator hypothesis predicts that all surveys have sampled relatively low Delta Smelt abundances compared to the ancestral stock (Figure 2); however, the Delta Smelt spawner–recruit relationship and juvenile survival relationship have retained a considerable amount of chaotic behavior that has at times appeared to be density-independent, and at other times density-dependent (Figure 6). We speculate that this switch between apparently density-independent and density-dependent recruitment was influenced by the abundance of Delta Smelt

relative to other potential forage fish, and the resulting predatory response by Striped Bass to time-varying abundance of multiple prey. Most population models on the other hand, presume simpler relationships for species population dynamics at low abundance (Rose et al. 2001; Liermann and Hilborn 2001).

The ancestral estuary likely had very high fish productivity and high abundance of predators. There were many known potential predators of fishes such as Delta Smelt (Grossman 2016). Thus, it is possible that heavy predation mortality even influenced the evolution of Delta Smelt into an annual species from its longer-lived marine cousin the Surf Smelt *Hypomesus pretiosus*. We base this speculation on fish life-history theory that predicts annual fishes (opportunistic strategists; Winemiller and Rose 1992) are adapted to absorb high rates of predation mortality—even through adulthood. Because it is unlikely that Delta Smelt evolved in an ecosystem with a limited influence of predators (e.g., predator naïve circumstances; Cox and Lima 2006), we hypothesize that changes leading to a decline in total fish production in the estuary combined with the rise of Striped Bass led to its ecological dominance in Delta Smelt habitat.

Our intent in proposing the phantom predator hypothesis is to start a scientific discussion that we think may lead to a more accurate history of what happened to the Delta Smelt, not to propose Striped Bass suppression as a conservation strategy. We note that the same review of fisheries management interventions that covered the unexpected responses we cited above (Pine et al. 2009) could apply to Striped Bass suppression. Specifically, the *a priori* expectation of some resource managers may be that Delta Smelt abundance would increase if there were fewer Striped Bass. A generalist predator like Striped Bass, however, could suppress Delta Smelt competitors in addition to Delta Smelt, leading to non-linear and counter-intuitive community dynamics. Future conservation efforts could explore alternative hypotheses about how the native estuary food web may have functioned, and how Striped Bass and other species may

have changed it. So the strong influence of salinity variation on the historical function of the estuary low-salinity zone food web (Jassby et al. 1995) can be modeled, a version of EcoPath with EcoSim is available that allows food web structures to vary with salinity (de Mutsert et al. 2012). Even if the ancestral food web cannot be reconstructed, it should be possible to construct hypothetical 1970s–1990s food webs (e.g., Kratina et al. 2014; Brown et al. 2016) to evaluate our hypothesis that the predatory effect of Striped Bass on Delta Smelt can only be understood in a multiple prey species context. It might also be possible to quantitatively evaluate this hypothesis using an end-to-end modeling approach similar to a recent model developed for California Sea Lion (*Zalophus californianus*; Fiechter et al. 2016). A deeper understanding of how well-studied (and rapidly changing) bottom-up drivers of the estuary food web interact with poorly understood (but also rapidly changing) controls at the top of the food web could prove very important to the conservation of other declining native fishes and possible future attempts to re-introduce captive-reared Delta Smelt to the San Francisco Estuary.

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