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## SPECIAL ISSUE: THE STATE OF BAY–DELTA SCIENCE 2016, PART 1

# Predation on Fishes in the Sacramento–San Joaquin Delta: Current Knowledge and Future Directions

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**Volume 14, Issue 2 | Article 8**
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Several small errors have been discovered in Table 2 of *Predation on Fishes in the Sacramento–San Joaquin Delta: Current Knowledge and Future Directions*, published in *Volume 14, Issue 2* of the online journal *San Francisco Estuary and Watershed Science*. These errors do not affect any conclusions made in the paper and are as follows: for predatory Sacramento Pikeminnow the prey classification of Longfin Smelt should go from C to M, and for Mississippi Silversides, Smallmouth Bass, and Threadfin Shad the prey classification should be reduced from M to O. For predatory Largemouth Bass, the classifications of both Smallmouth Bass and Sacramento Pikeminnow should switch from C to M. For predatory Smallmouth bass the prey classification of Chinook Salmon should be lowered from C to M and finally, predatory White Catfish consumed Smallmouth Bass with a frequency of O rather than M.

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## ABSTRACT

The Sacramento–San Joaquin Delta (Delta) is a heterogeneous, highly modified aquatic system. I reviewed relevant predator–prey theory, and described extant data on predator–prey relationships of Delta fishes. I ranked predator consumption rates as occasional, moderate, and common, based on frequency-of-occurrence data, and evaluated the frequency, and hypothesized the effects of predation on native and invasive species. I identified 32 different predator categories and 41 different prey categories. Most predators were occasional consumers of individual prey species, although I also observed moderate and common consumption of some prey types. My analysis yielded few generalizations regarding predator–prey interactions for Delta fishes; most predators consumed a variety of both native and invasive fishes. The only evidence for predator specialization on either native or invasive fishes occurred in Prickly Sculpin which, when it consumed fishes, ate mostly native species. Both Striped and Largemouth Bass exhibited wide dietary breadth, preying upon 32 and 28 categories of fish prey respectively. Sacramento Pikeminnow, a native predator, also displayed wide dietary breadth of piscine prey, with 14 different prey categories consumed. Data for reptilian, avian, and mammalian predators were sparse; however, these predators may be significant fish predators in altered habitats or when hatchery salmonids are released. The database for predators and their fish prey was not strong, and I recommend long-term dietary studies combined with prey availability and behavioral and experimental studies to establish predator preferences and anti-predator behaviors, rather than just consumption. The behavioral effects of contaminants on prey species also warrant further examination. Although it has been suggested that a reduction in the Striped Bass population be implemented to reduce predation mortality of Chinook Salmon, the large number of salmon predators in the Delta make it unlikely that this effort will significantly affect salmon mortality.

## KEY WORDS

Delta Smelt, Longfin Smelt, Chinook Salmon, Rainbow Trout, Striped Bass, Largemouth Bass, Pikeminnow, predator–prey interactions

## INTRODUCTION

The Sacramento–San Joaquin Delta (the Delta) is the eastern portion of the largest estuarine system on the West Coast of the Americas (San Francisco Estuary), encompassing an area of 3,238 $km^2$ (Whipple et al. 2012). This system provides critical habitat for plants and animals with over 700 species recorded, as well as providing irrigation water to farms in the highly productive Sacramento and San Joaquin valleys. In the last 150 years, human effects on the Delta include a variety of environmental changes (DSC 2013; Wiens et al. 2016) including:

1. physical (channelization, flow control, water export),
2. chemical (discharge of toxins, nutrients), and
3. biological (species invasions, conversion of floodplain to agriculture) characteristics, most of which have produced declines in habitat quality for native species.

These decreases in habitat quality in concert with the effects of introduced species, are linked to major declines in formerly abundant native species such as Chinook Salmon (*Oncorhynchus tshawytscha*), Steelhead (*Oncorhynchus mykiss*), Delta Smelt and Longfin Smelt (*Hypomesus transpacificus* and *Spirinchus thaleichthys*, respectively), the extinction of the Thicktail Chub (*Gila crassicauda*), and the local extinction of the Sacramento Perch (*Archoplites interruptus*). Population declines have not just occurred in native species; both Striped Bass (*Morone saxatilis*) and Threadfin Shad (*Dorosoma petenense*) display recent decreases in abundance (Sommer et al. 2007).

There are few data on either the historic or current effects of predators on the abundance, size, structure, and dynamics of Delta fish populations. Nonetheless, it is clear that native and invasive (I use the term invasive because it accurately represents the fact that these species have invaded a habitat) prey species run a gauntlet of potential predators including invasive predatory fishes (Striped Bass, centrarchids, percids and ictalurids), native and introduced snakes and amphibians (garter snakes and bullfrogs), mammals (North American river otter *Lontra canadensis*), and birds (herons, egrets, terns and gulls) (Draulans 1988). Because the Delta is a heterogeneous, highly modified aquatic system (Kimmerer et al. 2008; Dettinger et al., submitted; *Luoma et al. 2015*), it is a challenge to quantify the true effect of predation on fishes, given the ubiquity of co-varying factors (e.g., habitat degradation) capable of negatively affecting fish populations (Grossman et al. 2013; Wiens et al 2016). In this paper, I describe relevant predator–prey theory, and potential predator–prey interactions among resident predators and fish prey. Unfortunately, there is scant information on the interactions between predators and prey in the Delta; consequently, my main source of information comes from dietary studies of predatory fishes. This information includes the published scientific and selected gray literature references, as well as presentations at the 2013 Fish Predation Workshop (*http://www.dfg.ca.gov/erp/predation.asp*) and 2015 Interagency Ecological Program Workshop (*http://www.water.ca.gov/iep/activities/workshop_events.cfm*).

## THE DYNAMICS OF PREDATION ON FISH POPULATIONS

How predation effects a fish population may be examined at varying levels of resolution, ranging from quantification of the frequencies, numbers, masses or volumes of prey species in gut contents, to estimates of the number of prey consumed per predator per day, to estimates of the proportion of the prey population consumed by each predator over a given time interval (day, month, season). The level of precision required to quantify predator effects depends on the question being posed. At the most basic level, gut content information tells us that a given predator consumes a given prey species, but yields limited information on the effects of predation on the prey species. Alternatively, lab experiments with a single predator and prey species yield information on the behavioral interactions of the species pair, but cannot tell us how the predator will behave in the presence of alternate prey or in “natural habitats.” The most detailed level of predator-prey studies involves quantification of the effects of a given predator on prey abundance and survivorship and requires measurement of multiple factors including: (1) the amount of predation mortality experienced by a prey population over time, (2) ultimate and proximate causes of mortality, and (3) assessment of the role of predation in the regulation of prey abundance. Grossman et al. (2013) discuss the potential methods for approaching predation-effect studies for fish predators and salmonid prey that inhabit the Delta.

Despite the difficulty of the task, scientists and managers may require information on how predators affect fish populations, which, in addition to the factors listed above, requires: (1) accurate and precise estimates of predator and prey abundance, and (2) numerical and proportional estimates of predation mortality on the prey population or for a particular life-history stage (e.g., eggs, fry, and juveniles). Quantifying these parameters is both logistically and methodologically difficult, and obtaining estimates with reasonable accuracy and precision requires replication in space and time. For example, providing accurate data for step two requires experiments quantifying the functional and numerical responses of important predators on fish, coupled with annual and seasonal estimates of prey abundance and productivity (Grossman et al. 2013). Although this will produce an estimate of mortality attributable to predation, the estimate then must be compared to other sources of mortality (e.g., disease) to determine whether predators contribute significantly to population mortality through time. In the Delta, mortality from predation is just one of many potential sources of mortality, including: entrainment by water abstraction facilities, physiological stress, contaminants, food limitation, disease, and parasites, all of which may interact. Finally, mortality may be compensatory such that an increase in predation mortality may be offset by a decrease in disease mortality, with the overall mortality rate remaining constant. Because of the presence of compensatory processes in many fish populations (Grossman et al. 2006, 2012), quantifying the direct effects of predation on the total mortality rate of a population is difficult, at best (Kerfoot and Sih 1987).

The ultimate goal of predation studies is to quantify the importance of predator–prey relationships on both the dynamics of populations and the behavior of individuals. However, predation may be either the proximate or the ultimate cause of individual mortality, and identifying which of these two processes is operating may be problematical. In the Delta, decreased and altered timing of freshwater inputs, combined with water abstraction may alter flow patterns, especially in the east and south Delta (Kimmerer et al. 2008; Dettinger et al., submitted; *Luoma et al. 2015*). This may confuse prey species and shift their movements and migratory pathways in a manner that keeps them in greater contact with potential predators (Winder et al. 2011; Cloern and Jassby 2012). In this case, predation may be the proximate cause of mortality, whereas altered flow regimes are the ultimate cause. Clearly, the classification of mechanisms as either ultimate or proximate causes of mortality is an over-simplification, and the point at which a process moves from merely being an “influence” to a proximate cause, and, finally, an ultimate cause of mortality is typically unknown and, even when known, frequently subject to debate.

It is reasonable to assume, however, that some anthropogenic factors, especially contaminants known to affect fish behavior, are likely to be the ultimate cause of a significant amount of predation mortality for Delta fishes. Much more research is needed on the behavioral effects of contaminants on Delta fishes, because little is known about these effects (but see Connon et al. 2009, 2011; McIntyre et al. 2008, 2012). There are some extant data for other related species and these likely can be use to gain insights on predator–prey interactions of Delta fishes. The contaminant load of the Delta is likely substantial and includes the following potentially bioactive agents: pesticides, pharmaceuticals and personal care products (e.g., psychcoactive drugs and triclosan), estrogen disruptors, ammonia, metalloids such as selenium, and heavy metals such as mercury, copper, and aluminum. These contaminants are all are present in concentrations that could affect fish behavior (Sloman and Wilcox 2006; Connon et al. 2011; Brooks et al 2012; Fong et al., submitted). Aluminum, in particular, affects physiological homeostasis as well as learning and behavioral performance in Atlantic Salmon (*Salmo salar*, Grassie et al. 2013). Similarly, Sandahl et al. (2007) demonstrates that copper concentrations commonly found in Delta waters can produce abnormal anti-predator behaviors in Coho Salmon (*Oncorhynchus kisutch*). Their video (*http://pubs.acs.org/doi/suppl/10.1021/es062287r*; see page 2) shows control salmon ceasing movement and dropping to the bottom of the tank when exposed to a fright stimulus, whereas fish exposed to copper continue moving around the tank in an agitated and highly visible manner, that almost certainly renders them more susceptible to predation.

Sloman and Wilcox (2006) reviewed the literature on the relationship between chemical contaminants and behavior of both prey and predator, and concluded that chemicals significantly impaired anti-predator behavior of multiple prey species including salmonids, cyprinids, cyprinodontids, poeciliids and gasterosteids; findings supported by more recent studies that examined European perch (*Perca fluviatilis*, Brodin et al. 2013) coho salmon (*Oncorhynchus kisutch*, McIntire et al. 2008, 2012) and fathead minnows (*Pimephales promelas*, Fritsch et al. 2013). Consequently, it seems clear that contaminants can be the ultimate cause of mortality for prey fishes in the Delta, although this conclusion is complicated by the fact that some of the same compounds that disorient prey also inhibit the foraging behavior of predators (Sloman and Wilcox 2006). Finally, McGourty et al. (2009) found that Longjaw Mudsuckers (*Gillichthys mirabilis*) from San Francisco Bay displayed higher contaminant burdens and mortality rates, lower growth rates, and lower adult abundances, than individuals of the same species from the relatively contaminant-free Tomales Bay. The current status of contaminants in the Delta is reviewed in Fong et al. (submitted) and Schoellhamer et al. (submitted).

## Components of the Predation Process

The act of predation may be broken into several component rates, including search and encounter, pursuit and attack, capture and handling, and consumption, and these components are affected by a variety of changes that have occurred in the Delta (Figure 1). In unmodified environments, these components are affected by factors such as prey abundance and availability, spatial and temporal overlap of predator and prey, habitat complexity, turbidity, behavior, physiology, and morphological adaptations that facilitate (predator) or inhibit (prey) the predation process. Although most fish predators are opportunistic feeders (Gerking 1994), differences in prey characteristics (e.g., morphology, behavior, and energy content) also affect prey choice (Moyle and Cech 2004). All else being equal, foraging theory predicts that predators will choose prey that maximize their net energy gain (Grossman 2014), although this can be achieved through a variety of methods. It is likely that Delta predators prefer fish prey that are energy-rich (Hartman and Brandt 1995), easily handled and consumed (i.e., small, soft-rayed and fusiform) and naïve to invasive predators (Kuehne and Olden 2012; Carthey and Banks 2014). Several authors document the importance of behavioral naiveté to predation mortality by demonstrating that invasive Lake Trout and Northern Pike feed disproportionately on salmonids despite the apparently higher abundance of native catostomid prey (Johnson and Martinez 2000; Johnson et al. 2002; Lepak et al. 2012). Given that the majority of fish predators in the Delta are invasives (Table 1), native fishes in the Delta may suffer increased predation because a lack of shared evolutionary history could produce predator naiveté in prey species (reviewed by Carthy and Banks 2014). Nonetheless, it is also true that some invasive predators have

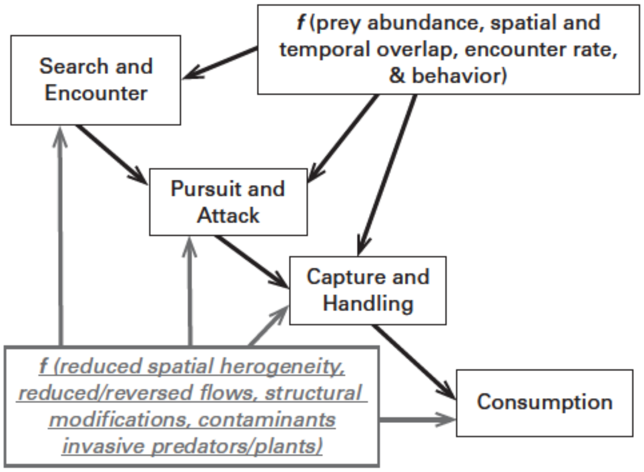

**Figure 1** A schematic depicting the components of predation and factors that affect predation in the Delta. "Search and Encounter" refers to the activities involved in locating prey, "Pursuit and Attack" to drawing close to the prey and initiating capture, "Capture" to the physical capture of the prey, and "Handling" to the physical act of manipulating the prey for consumption. The factors in the black boxes represent factors in unmodified environments that affect the predation process. The factors in underlined gray italics represent anthropogenic environmental changes in the Delta that increase predation rates on fishes.

**Table 1** Native and invasive fishes in the Sacramento–San Joaquin Delta system. Uncommon species are included, although primary marine and estuarine fishes that occasionally enter the Delta are not. Piscivores are marked in bold and the names of predators that may prey on fishes for some portion of their lifespan or when periodically available are underlined.

| Native species common name | Scientific name | Invasive species common name | Scientific name |
|---|---|---|---|
| **Chinook Salmon** | ***Oncorhynchus tshawytscha*** | American Shad | *Alosa sapidissima* |
| Delta Smelt | *Hypomesus transpacificus* | Bigscale Logperch | *Percina macrocephalus* |
| **Green Sturgeon** | ***Acipenser medirostris*** | **Black Bullhead** | ***Ameiurus melas*** |
| Hardhead | *Mylopharodon conocephalus* | **Black Crappie** | ***Pomoxis nigromaculatus*** |
| Longfin Smelt | *Spirinchus thaleichthys* | **Blue Catfish** | ***Ictalurus furcatus*** |
| **Pacific Lamprey** | ***Entosphenus tridentatus*** | Bluegill | *Lepomis macrochirus* |
| Prickly Sculpin | *Cottus asper* | **Brown Bullhead** | ***Ameiurus nebulosus*** |
| **River Lamprey** | ***Lampetra ayresi*** | Common Carp | *Cyprinus carpio* |
| **Steelhead** | ***Oncorhynchus mykiss*** | **Channel Catfish** | ***Ictalurus punctatus*** |
| Sacramento Hitch | *Lavinia exilicauda* | Fathead Minnow | *Pimephales promelas* |
| Sacramento Splittail | *Pogonichthys macrolepidotus* | **Green Sunfish** | ***Lepomis cyanellus*** |
| **Sacramento Pikeminnow** | ***Ptychocheilus grandis*** | Goldfish | *Carassius aurata* |
| Sacramento Blackfish | *Orthodon microlepidotus* | Golden Shiner | *Notemogonis chrysoleucus* |
| **Sacramento Perch**[a] | ***Archoplites interruptus*** | **Largemouth Bass** | ***Micropterus salmoides*** |
| Threespine Stickleback | *Gasterosteus aculeatus* | **Mississippi Silverside** | ***Menidia beryllina*** |
| Tule Perch | *Hysterocarpus traskii* | Rainwater Killifish | *Lucania parva* |
| **White Sturgeon** | ***Acipenser transmontanus*** | Red Shiner | *Cyprinella lutrensis* |
| | | Redear Sunfish | *Lepomis microlophus* |
| | | **Redeye Bass** | ***Micropterus coosae*** |
| | | **Smallmouth Bass** | ***Micropterus dolomieu*** |
| | | Shimofuri Goby | *Tridentiger bifasciatus* |
| | | Shokihaze Goby | *Tridentiger barbatus* |
| | | **Spotted Bass** | ***Micropterus punctulatus*** |
| | | **Striped Bass** | ***Morone saxatilis*** |
| | | Threadfin Shad | *Dorosoma petense* |
| | | Wakasagi | *Hypomesus nipponensis* |
| | | **Warmouth** | ***Lepomis gulosus*** |
| | | Western Mosquitofish | *Gambusia affinis* |
| | | **White Catfish** | ***Ameiurus catus*** |
| | | **White Crappie** | ***Pomoxis annularis*** |
| | | Yellowfin Goby | *Acanthagobius flavimanus* |

a. Effectively extinct from the Delta.

been established in the Delta for over 100 years (e.g., Striped Bass) and it is possible that prey species have had sufficient time to develop behavioral adaptations to these predators.

The effects of both contaminants and invasive species may be magnified by environmental changes that have occurred in the Delta over the last 100 years including: (1) species invasions that alter physical habitat structure, (2) alterations of hydrologic regimes, temperature regimes and turbidity levels, (3) wetland loss, and (4) anthropogenic changes in physical structure (levees, canals, and abstraction facilities), coupled with changes in climate (Cloern and Jassby 2012; Dettinger et al., submitted). Predation on Delta fishes also is affected by ecosystem-level effects of invasives, such as the shift in the food web produced by the non-predatory overbite clam (*Corbula amurensis*, Cloern and Jassby 2012, Brown et al., forthcoming) or changes in the structural complexity of littoral habitats produced by invasive submerged aquatic macrophytes such as *Egeria* (Brown et al. 2016, forthcoming; Conrad et al. 2016). The increase in littoral structural complexity favors invasive species that currently inhabit the Delta, although it may also provide refuge for some prey species. Figure 2 illustrates the complexity of predator-fish prey interactions as potentially affected by invasions from introduced macrophytes where increases in vegetation have different effects on prey and predator, as well as different effects on roving predators (i.e., Striped Bass) versus ambush predators (i.e., Largemouth Bass).

The study of predator–prey dynamics in fishes is complicated by the fact that almost all fishes display ontogenetic dietary niches. The majority of fishes are micro-carnivores when young and then may transition through the macro-invertivore and finally to the piscivore stage. In addition, even herbivores may be sufficiently opportunistic to take advantage of periodically abundant high-energy prey, such as fish eggs or fry, and the population-level effects of this predation are largely unknown. If a predator is piscivorous, however, its effect on prey may be sublethal or indirect. For example, introduced Largemouth Bass almost extirpated cyprinids from Wisconsin lakes, by forcing cyprinids to shift from high-quality littoral areas to low-quality pelagic microhabitats with high temperatures, low food abundance, and abundant avian predators (Carpenter and Kitchell 1993). In other cases, behavioral avoidance of multiple predators may produce multiplicative effects, where the effect of one predator enhances the efficiency of a second predator (Hixon and Carr 1997). An hypothetical but not unlikely example for the Delta involves Striped Bass preying on native species such as hitch (*Lavinia exilicauda*) or Sacramento Blackfish (*Orthodon microlepidotus*) in open water habitats. To avoid

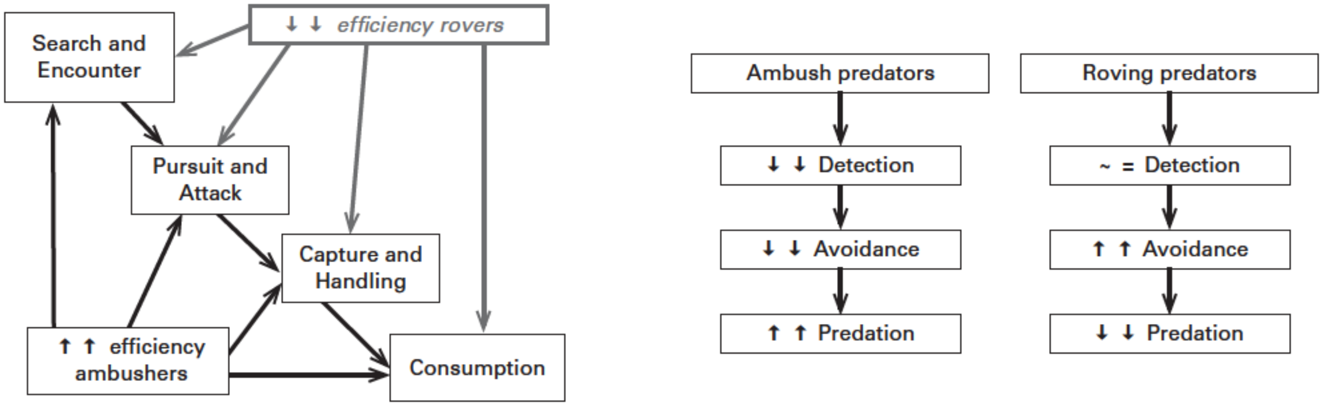

**Figure 2** Figure 2 illustrates the potential complexity of how predators and prey respond behaviorally to environmental changes (e.g., submerged aquatic vegetation, SAV) in the Delta. **(A)** illustrates potential effects on ambush (Largemouth Bass) and roving (Striped Bass) predators and their ability to capture prey. **(B)** displays the potential effects of how prey respond to ambush and roving predators and their mortality rate. Components in gray italics represent processes that will decrease predation in the presence of SAV, whereas those in black will increase predation in the presence of SAV.

Striped Bass, an individual of these species might find refuge in submerged aquatic vegetation (SAV), the preferred habitat of centrarchids and ictalurids, and then be eaten by one of these invasives.

Estimating the effects of predators on prey populations generally requires quantification of functional and numerical responses of predators to prey. The functional response describes the per-capita feeding rate of predators, usually as a function of prey density. An example of a functional response would be measurement of how the per capita predation rate of striped or Largemouth Bass on Chinook Salmon changed as the abundance of smolts changed during the outmigration. Most predatory fishes display a Type III functional response, which is "s" shaped and allows for both learning and compensatory responses to predation. However, if a functional response becomes asymptotic as prey density increases (e.g., a Type II functional response) depensatory mortality and population instability may occur (Essington and Hansson 2004). The numerical response details how changes in prey abundance affect predator abundance. Using the previous example, if we quantified the numerical response for Striped Bass and Chinook Salmon smolts, we would determine how changes in smolt abundance affected the numerical abundance of Striped Bass. When per-capita predator feeding rates are affected by predator abundance (e.g., numerical response, intra- or inter-specific interference competition) or when only a fraction of prey are vulnerable to predators, then predation rates may be relatively insensitive to fluctuations in predator abundance (DeAngelis et al. 1975; Ahrens et al. 2012). For example, the abundance of Atlantic Cod (*Gadus morhua*) in the Baltic Sea is not strongly related to changes in their major prey juvenile herring (*Clupea harengus*, Essington and Hansson 2004) and vice versa. In addition, meaningful quantification of the functional and numerical responses for abundant predators on Central Valley Chinook Salmon populations is complicated by the fact that the energetic contribution of this prey to Delta predators is so low that predator abundance is more likely influenced by the abundances of alternate prey than by Chinook Salmon abundance.

## The Context-Dependency of Predation

Predation is almost always context-dependent; meaning the effects of predators on both individual prey and their populations vary based on the spatial and temporal context of the interaction. For example, predator–prey relationships in the Delta likely differ substantially in drought versus high-flow years. Linking context-dependency to spatial heterogeneity in the Delta means simply that the predation rate of Least Terns on Delta Smelt in the Sacramento River channel will likely differ from the predation rate of the same predator and prey at the same abundances in Franks Tract. An additional aspect of spatial context-dependency in the Delta involves the presence of predation hot spots where physical conditions combine to make predation much more likely than in unaltered habitats. Grossman et al. (2013) identified 13 predation hot-spots in the Delta based on data from the Bay–Delta Conservation Plan (BDCP 2013) and the California Fish and Wildlife Fish Predation Workshop (2013), (i.e., mortality data from tagged fish and flow alterations that likely would shift fish out of their normal migration path into low-quality habitat). Grossman et al. (2013) identified the following hot spots:

1. the junction of the Sacramento River and Sutter Slough,
2. Georgiana Slough,
3. Delta Cross Channel Canal,
4. Franks Tract,
5. Mildred Island,
6. Stockton Ship Channel,
7. Clifton Court Forebay,
8. Borden Highway Bridge,
9. head of Old River,
10. head of Old River Barrier (HORB),
11. Old River near Tracy,
12. pumping plant salvage release sites, and
13. the Red Bluff Diversion Dam.

In addition, a recent study (Sabal et al. 2016), demonstrated that the Woodbridge Irrigation

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District Dam on the Mokelumne River also may be a predation hot spot, as well as the Tuolomne River below Don Pedro Dam (FISHBIO 2013).

Many other factors will induce variation into predator–prey relationships including: (1) the presence and type of shelter (e.g., SAV or woody debris) (Conrad 2016), (2) the ratio of prey size to predator size, (3) seasonal changes in abundance of the prey array, (4) defensive morphological (e.g., spines) or behavioral adaptations (Mittelbach and Persson 1998; Scharf et al. 2000), and (5) seasonal changes in habitat quality for prey, such as those produced by influxes of contaminants during winter–spring high flows or high water temperatures during summer and fall. Most predators are gape limited, which means that larger individuals and species are exposed to fewer predators than smaller individuals and species. Hence, environmental conditions that increase growth rates of prey such as favorable water temperatures, and increases in habitat and food quantity and quality, have a direct effect on predation rates. Predator foraging tactics also change depending on the array of prey available; hence, predator–prey relationships cannot be viewed as static entities.

The context dependency of predator–prey interactions combined with the high environmental, temporal, and spatial variability of the Delta environment undoubtedly will make quantifying the population-level effects of predation on fish populations very difficult.

## Predator Control Case Studies

I will review the history of predator control studies because substantial concerns have been raised that predation by both native and invasive predators has contributed to declines in salmonid populations in the Sacramento–San Joaquin Delta (CDFW 2011; Grossman et al. 2013). This has led some members of the public to call for control measures on some predatory fishes, such as Striped Bass (Grossman et al. 2013, *www.youtube.com/watch?v=eEB3dnDmsBc*). Control of invasive fishes is not an uncommon fishery management strategy (Kolar et al. 2010) but it has not had a high success rate. At present, several large-scale predator removal programs are underway in North America to aid in the recovery of native and sport fishes. The following case studies illustrate the breadth of approaches and their efficacy in controlling predatory fishes.

One of the most widespread and effective predator control programs has been directed at Sea Lamprey *Petromyzon marinus* in the Great Lakes (Smith and Tibbles 1980; Larson et al. 2003). Application of the highly selective lampricide TFM (3-trifluoromethyl-4-nitrophenol) in rearing streams has been effective at reducing Sea Lamprey populations by 90% in most areas (Adair and Sullivan 2013) at a cost of about $16 million per year (MDNR 2013). Lamprey control probably has been successful because lampreys have a vulnerable life-history stage (ammocoete) that occupies a restricted habitat (burrows in soft sediment in streams) which limits their ability to escape a toxin. Consequently, population reduction via toxicant application is logistically feasible and effective. However, because of the unusual characteristics of lampreys this success must be viewed as a special rather than a general case for predator control strategies.

The Northern Pikeminnow (*Ptychocheilus oregonensis*) Sport-Reward Program began in 1991 and is sponsored by Bonneville Power Administration. The program seeks to maintain a 10% to 20% exploitation rate on Northern Pikeminnow throughout the Columbia River by paying anglers $4 to $8 to harvest fish >228 mm TL (Porter 2010). The program removed over 2.2 million fish during 1998–2009 and is believed to have reduced predation on juvenile salmonids; nonetheless, concomitant increases in salmonid population abundance have been difficult to detect (Carey et al. 2012). The lack of positive population-level responses may be a result of compensatory responses by other predators such as Caspian terns (*Hydroprogne caspia*) and marine mammals such as California sea lions (*Zalophus californianus*, Carey et al. 2012). The possibility of compensatory responses by other predators illustrates a major shortcoming of predator control strategies; rarely is predation mortality a function of just one species. Although these programs are expensive—$14 million was paid out in bounties from 1998–2009 alone—angler reward systems may be more cost-effective than if agencies performed removals themselves (Carey et al. 2012).

Lake Trout have been widely introduced for sport fishing in western US lakes and reservoirs. In some systems, these fish threaten native and introduced salmonid populations (Dux et al. 2011). Commercial fishing and sport angling appear to have reduced Lake Trout abundance and allowed for kokanee recovery at Lake Pend Oreille, ID (Hansen et al. 2010). Angler incentives do not appear to have been effective at Flathead Lake, Montana (Federal Register 2012). Although commercial-scale netting has removed over 450,000 Lake Trout from Yellowstone Lake (Wyoming/Montana), this species continues to threaten native Cutthroat Trout (Syslo et al. 2011).

As part of the Upper Colorado River Endangered Fish Recovery Plan (USFWS 2012), invasive Channel Catfish (*Ictalurus punctatus*), Northern Pike (*Esox lucius*), Smallmouth Bass (*Micripterus dolomieu*) and other potential predators are being removed from critical habitat for ESA listed cyprinids and catostomids (Tyus and Sauders 2000; Johnson et al. 2008). Invasive fish control in the Upper Colorado River Basin costs over $1 million annually (Mueller 2005). Demonstrating native fish responses to removal of invasive fishes has been complicated by highly variable environmental conditions that differentially affect predators and prey. However, the available literature demonstrates that even in isolated reaches with intense removal efforts, there have been few demonstrable positive responses from native fishes (Bestgen et al. 2007; Skorupski et al. 2012).

The literature on predator removal as a management strategy for recovery of desirable species indicates there is little evidence for strong, positive, population-level responses in prey.

Predator removal, even in relatively simple systems such as reservoirs and lakes, is a difficult and costly management technique, and the lack of success illustrates the challenges inherent in functionally eliminating wild fish populations in systems with complex dynamics. Eradication generally is unlikely, except in small, isolated systems where re-invasion can be prevented (Kolar et al. 2010), and even in these systems re-introductions may occur via disgruntled members of the public. Predator suppression may sometimes facilitate increases in abundances of prey fish populations, but this requires intensive and sustained efforts at removal (Beamesderfer 2000), which is expensive. In addition, because of the generalist nature of most fish predators, a decrease in the abundance of one predator may result in increases in the abundance of competing predators, or in the abundance of competitors of the prey species; the result being a net overall negative effect on the prey population of interest. Given the dynamic and highly modified environment of the Delta, if the goal is increasing population sizes of species of concern, such as Chinook Salmon or Delta Smelt, it will take careful study before any predator removal or suppression technique should be undertaken.

## PREDATION ON DELTA FISHES

The assemblage of predatory fishes in the Delta is dominated by invasive species (Table 1) (Brown and Michniuk 2007; Nobriga and Feyrer 2007; NRC 2010; Cavallo et al. 2012; NRC 2012; Brown 2013, unreferenced, see "Notes"), although most non-piscine predators are native species. General survey data provide some estimates of abundance or relative abundance (catch-per-unit-effort) data for some predators and prey fishes at certain times and locations; however, quantitative abundance estimates for many predators and prey frequently are lacking. Nonetheless, numerous predators such as Striped Bass, Largemouth Bass, ictalurids, Mississippi Silversides, some centrarchids, and birds (e.g., ducks, herons, egrets, and terns) appear to be common in the Delta (Nobriga et al. 2002; Dege and Brown 2004; Brown and May 2006; CDFW 2013).

### Predation Studies on Delta Fishes

A variety of approaches have been used to elucidate relationships among Delta predators and prey. The vast majority of studies are dietary investigations whose main purpose was to quantify the diets of game fishes (e.g., Thomas 1967; Stevens 1966; Bryant and Arnold 2007; Nobriga and Feyrer 2007), although several more recent studies directly address consumption of prey by predatory fishes (Lindley and Mohr 2003; Cavallo et al. 2012; Loboschefsky et al. 2012; FISHBIO 2013; Nobriga et al. 2013). The landmark dietary studies in Turner and Kelly (1966) provide important information for both game and several non-game species. Nonetheless, the design of most dietary studies limits their use for quantifying how predators affect prey fish populations (see below). A majority of the strongest studies (Lindley and Mohr 2003; Loboschefsky et al. 2012; Nobriga et al. 2013) involve mathematical modeling that uses empirical data, which provide insights into the potential dynamics of Striped Bass predation on Delta fishes. However, the modeling studies still possesses shortcomings that limit their ability to predict future dynamics including: (1) lack of independent empirical verification of the dynamics modeled and predicted outcomes, (2) lack of empirical verification of model assumptions, and (3) limited empirical databases (e.g., limited temporal and spatial data as well as a lack of resolution in some data; e.g., prey categories such as "fish" rather than prey species). Nonetheless, all studies possess shortcomings, and in the absence of complete data these models serve as a starting point for management decisions and as hypothesis-generating tools for further studies.

Several recent studies address the predation issue directly, most notably Cavallo et al. (2012), Sabal et al. (2016) and Demetras et al. (2016). In an ambitious study, Cavallo et al. (2012), attempted a BACI (Before, After, Control, Intervention) assessment of how predatory fishes affected Chinook salmon juvenile survival, using boat electrofishing to remove predatory fishes from a section of the Mokelumne River. As might be expected with field experiments, the predator removal experiment was relatively short-term (slightly over 2 weeks long). Nonetheless, Chinook Salmon displayed higher survivorship in the removal section than in the unshocked control section after the first predator removal; however, the second removal did not result in increased Chinook Salmon survivorship. Unfortunately, predator densities in the treatment section *tripled* after the first removal, which underscores the importance of potential compensatory responses by other predatory species when a single predator species is removed. This phenomenon is the biggest weakness of the "predator removal" management approach (e.g., Striped Bass predation limits Chinook Salmon populations), because in the Delta there are literally 10 to 20 other predatory species that could potentially increase in abundance (and prey consumption) if a dominant predator is removed. Indeed, this may have occurred when the Northern Pikeminnow removal program was put into practice, given that both Caspian tern and sea lion predation apparently increased concomitantly with the removal program (Carey et al. 2012). Nonetheless, the finding of increased Chinook Salmon survivorship in the first removal of Cavallo et al. (2012) may be conservative, because fishes in the control section were not shocked and, therefore, likely in better condition.

Very recent published work by Sabal et al. (2016) and Demetras et al. (2016) indicate that Striped Bass predation upon juvenile Chinook Salmon could be substantial, although the amount of predation experienced by wild as opposed to hatchery fish—or those in habitats other than predation hot spots—remains unknown. In a multi-faceted study, Sabal et al. (2016) demonstrated that Striped Bass aggregated below the Woodbridge Irrigation District Dam on the Mokelumne River (a predation hot spot) and that Chinook Salmon survivorship increased when Striped Bass were removed. The Woodbridge Dam has a fish ladder, but Striped Bass do not typically ascend fish ladders; rather ,they typically aggregate below dams and fish ladders where they prey extensively on smaller fishes (Davis et al. 2012). In predation hot spots in the Delta, predators may aggregate and consume large numbers of prey that are disoriented by: (1) unnatural or reversed flow patterns, and (2) modified habitat structures such as fish ladders, water abstraction devices, modified channels, or impoundments (Davis et al. 2012; Grossman et al. 2013). Demetras et al. (2016) developed an innovative predator detection system that documented predation by Striped Bass and unidentified fish predators on tethered Chinook Salmon, and found a positive relationship between current velocity and predation rate and an inverse relationship between water column depth and predation rate. Although this highly innovative system documented predation by Striped Bass and other predators on tethered Chinook Salmon, it is difficult to extrapolate these results to estimates of predation rates throughout the Delta.

Much of the data for my analysis came via the courtesy of researchers who provided data from their unpublished studies (e.g., Barry 2015; Brandl et al. 2015; Smith et al. 2015; Young 2015; Zeug 2015, all unreferenced, see "Notes"); and these data and the work of Baerwald et al. (2013) illustrate the advantages of DNA analysis for dietary analyses.

Analyses using DNA typing allow investigators to analyze large numbers of stomachs with a high level of precision of prey identification. Unfortunately at present, they cannot be used to quantify the intensity of prey consumption, but only whether or not a given prey species has been consumed.

## The Data and Analysis

I searched the literature and contacted researchers actively working on dietary or predator–prey studies on Delta fishes and compiled a matrix of predator species and their piscine prey. Sources are listed in Table 2. Based on the frequency of prey occurrence in predator gut contents, I ranked predator consumption as occasional, moderate, or common (Table 2). I used these data to evaluate the frequency of predation on native and invasive species and their hypothesized effect on prey populations (Table 3). I also evaluated the data base of dietary and predation papers and ranked data for each species as: none, fair, good, or excellent (Table 2). In general, the data base of dietary/predation studies is fair but very weak for mammals, many carnivorous birds and some reptiles and amphibians (Table 2). In addition, the data base is biased towards highly valued game species (e.g., Striped and Largemouth Bass) and the level of prey resolution varies according to the authors' purposes (in many studies, broad prey categories were used e.g., "fish"). I recorded 32 different predator categories, although categories such as gulls, herons and egrets, and terrestrial garter snakes contained multiple predatory species (Table 2). I recorded 36 different prey species and five multi-species categories, including unidentified fishes, unidentified salmonids, unidentified shad, *Lepomis* species, and *Tridentiger* species. The data indicated that most predators only were occasional consumers of individual prey species, although moderate and common consumption also were observed, for example,

1. Moderate: Sacramento Pikeminnow consuming Longfin Smelt, Striped Bass consuming Sacramento Splittail, Largemouth Bass consuming Prickly Sculpin; and
2. Common: Striped Bass consuming Chinook Salmon, Largemouth Bass consuming Sacramento Pikeminnow, Channel Catfish consuming Largemouth Bass (see also Table 2).

My analysis yielded few generalizations regarding predator–prey interactions for Delta fishes other than the observation that most predators were unspecialized and consumed a wide variety of both native and invasive fishes. The sole exception was Prickly Sculpin which, when it consumed fish, preyed upon mostly natives (Table 2; Merz 2002b). Both Striped and Largemouth Bass exhibited broad dietary breadths, with Striped and Largemouth Bass preying upon 32 and 28 categories of prey, respectively (Table 2). These predators preyed upon a wide variety of both native and invasive fishes, and, as important game fish, had the broadest temporal and spatial coverage in dietary data (Table 2). The Sacramento Pikeminnow, a native predator, also displayed broad dietary breadth, with 14 different categories of fish prey eaten. These data reinforce the general opinion of the literature that most fish predators are generalists that consume many different prey types (Moyle and Cech 2004).

Most predators fed primarily on invasive species, which are the most abundant fishes in the Delta (Brown and Michniuk 2007). Given the generalist nature of vertebrate predators, this likely represents consumption of prey in proportion to their abundance. In addition, it is likely that some predators, such as snakes, fed primarily on invasive species because both predator and prey are found in modified habitats where invasives dominate (B. Halstead, pers. comm., to me, 2015, unreferenced, see "Notes"). The effects of avian, reptilian, amphibian, and mammalian predation on fishes in the Delta are not well known, although Caspian terns can consume high numbers of stocked Chinook Salmon (Evans et al. 2011; Andrean et al. 2012; Hostetter et al. 2015).

Several additional impediments limited my ability to reach strong conclusions about the effects of predators on the abundance of prey species. First, dietary data lacked resolution to the family or species level because predation on fish prey frequently was listed merely as "unidentified fishes." Second, there was a lack of data on direct predation as well as a lack of dietary data that included prey availability so that prey selection could be determined (also see Grossman et al. 2013). Third, although we know fish were consumed, we do not know if they were healthy, stressed, or even dead.

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**Table 2** Predator–prey interactions among Delta animals. Prey consumption by predators is ranked as O–occasional <5% by frequency of occurrence, M–moderate >5% to 49%, C–Common >50%. A question mark indicates that the predator is known to be piscivorous but no dietary data are available for the Delta.

| | PREDATOR | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sacramento Pikeminnow | Sacramento Perch | Sacramento Splittail | Steelhead | Chinook Salmon | Prickly Sculpin | Striped Bass | Largemouth Bass | Smallmouth Bass | Warmouth | Bluegill | White Crappie | Black Crappie | White Catfish | Channel Catfish | Brown Bullheads | Black Bullheads | Mississippi Silversides | Common carp | Yellowfin goby | Shimofuri goby | Caspian Tern | California Least Tern | Double-crested cormorants | Herons & Egrets | Gulls | Giant Gartersnake | Aquatic Gartersnake | Common Garteresnake et al. | Bullfrogs | Western Pond Turtles |
| **Data quality** | G | F | F | F | F | F | E | G | F | F | F | | F | F | F | F | F | F | F | | F | F | F | N | N | N | F | N | N | N | F |
| **PREY** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Native | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Bay Pipefish | | | | | | | O$^{33}$ | | | | | | | | | | | | | | | | | | | | | | | | |
| Chinook Salmon | | | | | | | O$^{1,4,25}$<br>O-C$^{22}$<br>M$^{2,8}$ C$^{7}$ | O$^{1,23,25}$<br>M$^{8}$ | C-M | | | | O$^{23}$ | O$^{25}$ | M$^{2,25}$ | | | | | | | O$^{6}$ | O-?$^{24}$ | | | | | | | | |
| Delta Smelt | | | | | | | O$^{2,4}$<br>O-C$^{19}$<br>O-M$^{22}$ | | | | | | O$^{23}$ | O$^{2}$ | | | | M-C$^{9}$<br>?$^{11}$ | | | | | | | | | | | | | |
| Hitch | | | | | | | O$^{4}$ | O$^{13}$ | | | | | | | | | | | | | | | | | | | | | | | |
| Longfin Smelt | C-M | | | | | | O$^{2}$ | | | | | | | | | | | | | | | | | | | | | | | | |
| Pacific Lamprey | | | | | | O$^{21}$ | O$^{4,33}$<br>O-M$^{22}$ | O$^{13}$ | | | | | | | | | | | | | | | | | | | | | | | |
| Prickly Sculpin | O$^{1}$ | | | | O$^{21}$ | O-M$^{21,32}$ | O$^{1,33}$ | M$^{1}$<br>O$^{13}$<br>O-M$^{32}$ | | | | | | O$^{3,a}$<br>O-M$^{32}$ | | | | | | | | | | | | | | | | | |
| Sacramento Blackfish | | | | | | | O$^{4}$ | O$^{13}$ | | | | | | | | | | | | | | | | | | | | | | | |
| Sacramento Pikeminnow | | | | | | | M$^{2}$ | C-M | | | | | | M$^{2}$ | M$^{2}$ | | | | | | | | | | | | | | | | |
| Sacramento Sucker | | | | | O$^{21}$ | O-M$^{21}$ | | | | | | | | | | | | | | | | | | | | | | | | | |
| Splittail | O$^{2}$ | | | | | | O$^{1}$<br>M$^{2,25}$<br>O-M$^{22}$ | O$^{1}$ | M$^{2}$ | | | | | M$^{2}$ | M$^{2,25}$ | | | | | | | | | | | | | | | | |
| Steelhead | | | | | | | O$^{2,25}$ | | | | | | | | M$^{25}$ | | | | | | | O$^{6}$ | | | | | | | | | |
| Threespine Stickleback$^{b}$ | | | | | | | O$^{4}$ | O$^{13}$ | | | | | | O-M$^{3,a}$ | | | | | | | | | | | | | | | | | |
| Tule Perch | O$^{1}$ | | | | | | O$^{1,33}$ | O$^{1,13}$ | | | | | | | | | | | | | | | | | | | | | | | |
| White Sturgeon | | | | | | | O$^{2,25}$ | | | | | | | | | | | | | | | | | | | | | | | | |
| Unidentified salmonids | M-C$^{10}$ | | | | | | C$^{10}$ | | | | | | | | | | | | | | | | | | O-?$^{31}$ | | | | | | |
| Cottidae | | | | | | | O$^{33}$ | | | | | | | | | | | | | | | | | | | | | | | | |
| Unidentified fishes$^{c}$ | M$^{1}$<br>M-C$^{10}$ | O-C$^{14}$ | M$^{15}$ | O-C$^{18}$ | O$^{21}$ | O$^{21}$ | M$^{1,4,8,15,22,33}$<br>M-C$^{20,33}$<br>C$^{10}$ | M$^{1,8,3,23}$ | M$^{8}$ | O$^{23}$ | O$^{23}$ | | M$^{23}$ | O$^{5}$<br>M$^{15}$ | M$^{5,25}$ | O$^{5}$ | M$^{5}$ | | O$^{15}$ | | | | O-?$^{24}$ | O-? | O-?$^{31}$ | O-? | O-?$^{26}$ | O-?$^{26,28}$ | ?$^{26,28}$ | ?$^{28,29,30}$ | O-?$^{27}$ |

a. 40% by volume.
b. Suisun Bay.
c. Includes invasive fishes.

Sources: [1]Nobriga and Feyrer 2007, [2]Brandl et al. 2015*, [3]O'Rear 2007, [4]Stevens 1966, [5]Turner 1966a, [6]Andrean et al. 2012, [7]Lindley and Mohr 2003, [8]FISHBIO 2013, [9]Baerwald et al. 2013, [10]Tucker et al. 1998, [11]Bennett 2005, [12]Bennett 1993, [13]Conrad et al. 2013*, [14]Crain and Moyle 2011, [15]Whitley and Bollens 2014, [16]Matern and Brown 2005, [17]Clark et al. 2009, [18]Merz 2002a, [19]Nobriga et al. 2013, [20]Feyrer et al 2003, [21]Merz 2002b, [22]Thomas 1967 (includes data for the entire San Francisco Bay system, only Delta prey were recorded), [23]Turner 1966b, [24]Riensche et al. 2012, [25]Smith et al. 2015*, [26]Halstead et al. 2015*, [27]Bury 1986, [28]Barry 2015*, [29]Wylie et al. 2003, [30]Corse and Metter 1980, [31]Kushlan and Hancock 2005, [32]Young 2015*, Zeug et al. 2015*. An asterisk indicates the data are unpublished.

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**Table 2** (*Continued*) Predator-prey interactions among Delta animals. Prey consumption by predators is ranked as O–occasional <5% by frequency of occurrence, M–moderate >5% to 49%, C–Common >50%. A question mark indicates that the predator is known to be piscivorous but no dietary data are available for the Delta.

| | PREDATOR | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sacramento Pikeminnow | Sacramento Perch | Sacramento Splittail | Steelhead | Chinook Salmon | Prickly Sculpin | Striped Bass | Largemouth Bass | Smallmouth Bass | Warmouth | Bluegill | White Crappie | Black Crappie | White Catfish | Channel Catfish | Brown Bullheads | Black Bullheads | Mississippi Silversides | Common carp | Yellowfin goby | Shimofuri goby | Caspian Tern | California Least Tern | Double-crested cormorants | Herons & Egrets | Gulls | Giant Gartersnake | Aquatic Gartersnake | Common Garteresnake et al. | Bullfrogs | Western Pond Turtles |
| **Data quality** | G | F | F | F | F | F | E | G | F | F | F | | F | F | F | F | F | F | F | | F | F | F | N | N | N | F | N | N | N | F |
| **INVASIVE** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| American Shad | O[1,33] | | | | | | O[1,4]<br>O-M[22] | | | | | | O[23] | | | | | | | | | | | | | | | | | | |
| Bigscale Logperch | O[1] | | | | | | O[1] | O[1]<br>O[13] | | | | | | ?[5]<br>O-M[32] | | | | | | | | | | | | | | | | | |
| Black Bullhead | | | | | | | | | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Black Crappie | | | | | | | O[4] | O[13]<br>M[23] | | | | | | | | | | | | | | | | | | | | | | | |
| Bluegill | | | | | | | O[4] | O[13]<br>M[23] | | O[23] | | | | ?[5] | | | | | | | | | | | | | O-?[26] | | | | |
| Clupeidae | | | | | | | O[33] | | | | | | | | | | | | | | | | | | | | | | | | |
| Common Carp | | | | | | | O[4]<br>O-M[22] | O[13] | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Fathead Minnow | | | | | | | | | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Gobiidae | | | | | | | O[33] | | | | | | | | | | | | | | | | | | | | | | | | |
| Golden Shiner | O[1] | | | | | | O[4] | O[1,13]<br>O-M[32] | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| *Hypomesus* spp. | | | | | | | O[33] | | | | | | | | | | | | | | | | | | | | | | | | |
| Green Sunfish | | | | | | | M[22] | | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Largemouth Bass | O[25] | | | | | | O[1,2]<br>M[25] | O[1,13] | | | | | | M[2]<br>C[25] | M[2]<br>C[25] | | | | | | | | | | | | O-?[26] | | | | |
| *Lepomis* spp. | | | | | | ?[21] | | M[1]<br>O[13] | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Mississippi Silverside | M-O | | | | | | O[33]<br>M[2] | O[13]<br>O-M[32]<br>M[1]<br>M[2] | | | | | O[32] | M[2] | M[2] | | | | | O[32] | | | | | | | O-?[26] | | | | |
| Rainwater Killifish | | | | | | | | O[1,13] | | | | | | | | | | | | | | | | | | | | | | | |
| Red Shiner | | | | | | | | | | | | | | | | | | | | | | | | | | | O-?[26] | | | | |
| Redear Sunfish | | | | | | | | O[13] | | | | | | | | | | | | | | | | | | | | | | | |
| Smallmouth Bass | M-O | | | | | | O[2] | C-M | | | | | | M[2] | M[2] | | | | | | | | | | | | | | | | |
| Striped Bass | O[1]<br>C[2] | | | | | | O[1,22]<br>M[4] | O[1,13]<br>C[2] | C[2] | | | M[32] | M[23] | M-O | M[2]<br>C[25] | | | ?[12] | | | | | | | | | | | | | |
| Threadfin Shad | M-O | | | | | | O[25,33]<br>O-M[32]<br>M[1,2,4] | O[1,13]<br>O-M[32]<br>M[2,23] | | | | | O-M[23] | ?[5]<br>O[25]<br>M[2] | O[25]<br>M[2] | | | | | | | | | | | | | | | | |
| *Tridentiger* spp. | O[1] | | | | | | O[1,33] | O[1,13] | | | | | | O[3,a] | | | | | | | | | | | | | | | | | |
| Unidentified Shad | M[1] | | | | | | M[1] | M[1] | | | | | | | | | | | | | O-M[16] | | | | | | | | | | |
| Yellowfin Goby | O[33]<br>M[1] | | | | | | O[33]<br>M[1] | M[1]<br>O[13] | | | | | | | | | | | | | | | | | | | | | | | |
| Wakasagi | | | | | | | O[2,33] | | | | | | | | | | | | | | | | | | | | | | | | |
| White Catfish | | | | | | | | | | O-M[23] | | | | | | | | | | | | | | | | | | | | O-?[26,29] | |
| Western Mosquitofish | O[1] | | | | | | O-M[32] | O[1,13] | | | | | | | | | | | | | | | | | | | | | O-?[28] | | |
| Warmouth | | | | | | | | O[13] | | | | | | | | | | | | | | | | | | | | | | | |

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**Table 3** Hypothesized effects of predators on Delta fish populations based on Table 2. If a citation is not given, the entry is based on the author's personal observation. A "U" in a category means that only unidentified fishes were listed as fish prey. Scientific names listed only when not previously mentioned.

| Species | Abundance (since 1980) | % Native fish in diet (frequency of occurrence) | % Invasive fish in diet (frequency of occurrence) | Hypothesized predator effect on prey population |
|---|---|---|---|---|
| **Native predators** | | | | |
| Sacramento Pikeminnow | Likely decreasing[a] | 30 | 70 | Unlikely, except in predation hot spots |
| Thicktail Chub, *Gila crassicauda* | Extinct | None | None | None |
| Sacramento Perch | Functionally extinct | None | None | none |
| Sacramento Splittail | Common | U | U | Unlikely |
| Steelhead | Declining | U | U | Unlikely |
| Chinook Salmon | Declining | 100 | 0 | Unlikely |
| Prickly Sculpin | Common | 75 | 25 | Unlikely, low % of fish in diet |
| Caspian tern | Common[b] | 100[c] | Unknown | Possibly on stocked salmonids |
| River otter | Increasing[d] | Piscivorous | Piscivorous | Possibly in isolated habitats or hot spots |
| Giant garter snake, *Thamnophis gigas* | Threatened | Largely piscivorous | Largely piscivorous | Unlikely to be significant |
| Herons and egrets, *Ardea* and *Nycticorax* spp. | Common | Largely piscivorous | Largely piscivorous | Unlikely to be significant |
| Mergansers, *Mergus* spp. | Uncommon | U | U | Possibly in isolated habitats or hot spots |
| Double-crested cormorant *Phalacrocorax auritus* | Common and increasing[e] | Largely piscivorous | Largely piscivorous | Possibly in isolated habitats or hot spots |
| Western grebe *Aechmophorus occidentalis* | Common | Largely piscivorous | Largely piscivorous | Possibly in isolated habitats or hot spots |
| Western pond turtles *Actinemys marmorata* | Common | U | U | ? |
| California least tern *Sternulla antillarum browni* | Increasing | 100 | 0 | ? |
| Gulls | ? | U | U | ? |
| Aquatic garter snake *Thamnophis atratus* | ? | U | U | ? |
| Commom garter snake *Thamnophis sirtalis* | ? | 0 | 100 | ? |
| **Invasive predators** | | | | |
| Largemouth Bass | Increasing[f] | 33 | 67 | Possibly |
| Striped Bass | (¯ age-0 in pelagic surveys, or stable for sub-adults, ¯ for adults)[g] | 47 | 53 | Possibly |
| Smallmouth Bass | ? | 6 | 33 | ? |
| Mississippi Silverside | Abundant | 50 | 50 | Possibly for eggs, larvae, juveniles |
| White Catfish | Common | 40 | 60 | ? |
| Channel Catfish | Common | 50 | 50 | ? |
| Warmouth | Common[h] | 0 | 100 | ? |
| Black crappie | Common[h] | 40 | 60 | ? |
| Bluegill | Common | U | U | ? |
| Brown bullheads | Common | U | U | ? |
| Black Bullheads | Common | U | U | ? |
| Common Carp | Common | U | U | ? |
| Shimofuri Goby | Common | 0 | 100 | ? |
| Bullfrog *Lithobates catesbiana* | Common | Piscivorous | Piscivorous | Possibly in isolated habitats or hot spots |

a. FISHBIO 2013; Nobriga and Feyrer 2007.
b. Evans et al. 2011; Andrean et al 2012.
c. Only dietary data from recovered tags of stocked salmonids.
d. P. Moyle, pers. comm., 2015, unreferenced, see "Notes."
e. Adkins et al. 2014.
f. Salvage data from the State Water Project and Central Valley Project in the Sacramento-San Joaquin Delta (*http://www.delta.dfg.ca.gov/Data/Salvage/*), Brown and Michniuk 2007; Nobriga and Feyrer 2007; Cavallo et al. 2012; Conrad 2013, unreferenced, see "Notes"; FISHBIO 2013.
g. Nobriga and Feyrer 2007; Cavallo et al. 2012; CDFW 2013; Grossman et al. 2013; FISHBIO 2013.
h. Turner and Kelly 1966.

The high numbers of Chinook Salmon and the occasional Steelhead eaten by Channel Catfish suggest that these prey may have been stressed or dead when consumed, especially because genetic analysis rather than visual inspection determined their frequency of consumption (Smith et al. 2015). Fourth, my conclusions were limited by the fact that frequency-of-occurrence data are not necessarily correlated with predation intensity. For example, a frequency of occurrence of 100% is obtained when each individual of a predatory species consumes just one individual of a given prey species. However, the same value is obtained if each predator consumes 25 individuals of a given species. Consequently, Tables 2 and 3 are rudimentary estimates of predator–prey interactions for Delta fishes. Fifth, many of the dietary studies were limited in their spatial and temporal coverage, which may result in over-estimation of the intensity of predator–prey interactions if data were collected during a period when the predator fed intensively on a prey that only was temporarily abundant. Conversely, the data may under-estimate these relationships if samples were lacking for multiple days within a season, or seasons within a single year, or multiple years. Sixth, it is well known that even non-predatory fishes will consume both fish eggs and larvae, yet these resources typically are only available for weeks or a month, and are frequently missed in dietary studies. It is possible that some species such as Mississippi Silversides may prey significantly on eggs or larvae of species such as Delta Smelt (Baerwald et al. 2012). Finally, recent DNA analyses of stomach contents of Delta fish predators may allow a species' diet to be quantified accurately and quickly (Baerwald et al. 2012; Brandl et al. 2015, unreferenced, see "Notes"; Smith et al. 2015), but cannot quantify the energetic importance of a given prey to the predator, and, concomitantly, the number of prey eaten by an individual predator.

Although it is beyond the scope of this study, Grossman et al. (2013) described a variety of potential methods for quantifying the effects of piscine predators on salmonid populations in the Delta, including modeling, bioenergetics, direct experimentation, and prey tagging studies. These methods apply equally well to other predator–prey interactions. Lindley and Mohr (2003) and Hendrix (2013, unreferenced, see "Notes") provide useful examples of modeling approaches to predator–prey dynamics, Loboschefsky et al. (2013) of bioenergetic modeling, and Cavallo et al. (2012) and Ferrari et al. (2014) of direct experimentation. Not surprisingly, there is a trade-off between logistical ease and realism, with indirect approaches such as population or bioenergetic modeling producing results that may be consistent with predator limitation, but typically cannot exclude alternative agents of mortality. Hence, their conclusions must be considered correlative rather than causal. Conversely, predator removal experiments are logistically difficult and may have limited realism (e.g. exclusions of pelagic roving predators), but may directly address whether predators depress prey populations on a local scale (Cavallo et al. 2012; Grossman et al. 2013). It will take a combination of methods that focus on direct experimentation, population modeling, and dietary and behavioral studies to yield further insights into the effects of predation on Delta fishes. Given the difficulty of separating ultimate from proximate causes of mortality, and the widespread distribution of bioactive contaminants on fishes throughout the Delta (Fong et al., submitted), it will be very difficult to untangle the ultimate from proximate causes of predation mortality for prey fish populations.

## CONCLUSIONS

An understanding of any important ecological system requires extensive study of the abiotic and biotic relationships driving the system. The Sacramento–San Joaquin Delta supports a biological stew of native and invasive predators and prey whose ingredients are likely to change over time as new invasions occur and climate change progresses (Dettinger et al., submitted; Wiens et al., this volume). Unfortunately this means the biological conclusions drawn from the Delta of today may not be relevant a decade from now (e.g., trophic web shift caused by overbite clams), especially as invasions continue. Nonetheless, the invasive and the few remaining native fish predators in the Delta are generalists that likely consume whichever fish prey are locally available. Given that invasives are the most abundant fish species in the Delta, predators appear to prey most heavily on these species—as expected of generalist predators. However, the predator-fish prey database

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is not strong, and I would urge future efforts to undertake long-term dietary studies combined ,with attempts to establish predator preferences, rather than just consumption. This will be particularly important given the highly fluctuating environmental conditions typical of the Delta and the likely changes that global climate change will produce, including: (1) increases in sea-level; (2) shifts in the variability, timing, and amount of precipitation; and (3) increased temperatures, which may facilitate future species invasions (Moyle et al. 2013; Dettinger et al., submitted). If the Delta experiences more drought and increased water exports, fishes may be concentrated in small patches of suitable habitat, which could alter predator–prey relationships and render prey species more susceptible to predation not only by fishes but also by birds, reptiles, and mammals. Although the data base is not extensive, it is clear that predation on fishes in the Delta is a common phenomenon that warrants further investigation. Hopefully future investigations will elucidate the effects of this phenomenon on both native and invasive fishes in the Delta.

Finally, it has recently been proposed that Striped Bass populations be significantly reduced to facilitate recovery of endangered Central Valley Chinook Salmon (*http://www.youtube.com/watch?v=eEB3dnDmsBc*). Although from a scientific standpoint it is always interesting to see how removal of an abundant species affects community structure and ecosystem processes, unless a removal study is conducted under rigorous experimental conditions (controls, monitoring of other predators, demonstration of direct predation and predator per-capita effects), it is unlikely to yield conclusive information on the relationship between predation and Chinook Salmon survival. As mentioned previously, the most likely outcome of Striped Bass removal is that a competing predator will increase in abundance and there will be little reduction in predation mortality for Chinook Salmon. It is likely that the most productive management strategy for decreasing predation on Chinook Salmon and other Delta fishes is to restore natural habitat and flows, especially in predation hot spots.

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