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RESEARCH

Diets of Largemouth Bass (*Micropterus salmoides*) in the Sacramento–San Joaquin Delta

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ABSTRACT

Largemouth Bass (*Micropterus salmoides*) were introduced into the Sacramento-San Joaquin Delta (the Delta) over 100 years ago. In the last 2 decades, the abundance of centrarchids (including Largemouth Bass) in the littoral zone has increased, while some native fish and fish that were previously abundant in the pelagic zone have declined. Largemouth Bass are now one of the most abundant piscivores in the Delta. Understanding the ecology of this top predator—including a comprehensive understanding of what prey are important in Largemouth Bass diets—is important to understanding how this species may affect the Delta fish community. To address this need, we conducted electrofishing surveys of Largemouth Bass at 33 sites every 2 months from 2008 to 2010, measuring fish fork lengths and collecting stomachs contents at each site. We characterized diets using Percent Index of Relative Importance for 3,004 Largemouth Bass, with samples that spanned all seasons. Amphipods dominated the diets of Largemouth Bass ≤175 mm FL year-round, with dipterans, odonates, and copepods and cladocerans representing other important diet items. Non-native red swamp crayfish (*Procambarus clarkii*) were the most important prey for Largemouth Bass >175 mm FL. Non-native centrarchids (including Largemouth Bass) and amphipods were important prey items as well. Prickly Sculpin (*Cottus asper*) were the most frequently consumed native fish. Other native fish and pelagic fish species rarely occurred in Largemouth Bass diets, and we discuss trends in how the frequency of co-occurrence of these fishes with Largemouth Bass in the electrofishing surveys was associated with their frequency in Largemouth Bass diets. The Largemouth Bass in the Delta appear to be sustained largely on a diet of other non-natives that reside in the littoral zone.

KEY WORDS

Largemouth Bass, non-native predators, diet, predation, red swamp crayfish, centrarchids

INTRODUCTION

The spread of invasive species has resulted in a world in which exotic species dominate many ecosystems (Hobbs et al. 2006; Mascaro et al. 2008; Needles and Wendt 2012). One of the most invaded ecosystems in the world is the San Francisco Estuary (Cohen and Carlton 1998), which includes the Sacramento-San Joaquin Delta (the Delta, Figure 1). The Delta is the freshwater tidal region of an estuary of major socio-economic and ecological importance, because it supplies water for municipal purposes that serve over 25 million people, and provides irrigation for an internationally important agricultural region (Arthur et al. 1996; Lund et al. 2007). The Delta also provides a home for a variety of fish and wildlife, including multiple species protected by federal and California Endangered Species Acts (Emmett et al. 2000).

One introduced species that can do particular harm in the Delta is Largemouth Bass (*Micropterus salmoides*). In other systems, Largemouth Bass are keystone predators (Mittelbach et al. 1995) because they affect the entire community structure. Where they are introduced, Largemouth Bass effects vary, but can include (1) alteration of aquatic invertebrate community structure (South Africa: Weyl et al. 2010), (2) consumption of endangered native fish (Spain: Nicola et al. 1996), and (3) a reduction in species richness and diversity (Japan: Tsunoda et al. 2010).

Largemouth Bass were introduced to the Delta in the 1890s (Dill and Cordone 1997; Moyle 2002) but remained at low abundance for many decades. Between the 1980s and 2000, the abundance of Largemouth Bass and other centrarchid fishes increased substantially (Brown and Michniuk 2007; Mahardja et al. 2017). This increase in Largemouth Bass abundance coincided with the spread of Brazilian waterweed (*Egeria densa*), a submerged aquatic plant which resides in the littoral zone and was first reported in the Delta in 1946 (Light et al. 2005). Recent work has shown that juvenile Largemouth Bass are indeed associated with Brazilian waterweed-dominated habitats in the Delta littoral zone (Conrad et al. 2016; Young et al. 2018b). This increase in the Largemouth Bass population, along with their known potential for altering native fish communities, has generated interest in their diet patterns. In this paper, we describe the diet composition of Largemouth Bass in the Delta across seasons and years for two size classes of Largemouth Bass.

Within their native range, Largemouth Bass frequently consume aquatic invertebrates, sunfish species (in the genus *Lepomis*), and crayfish (Keast 1985; Olson 1996; Miranda and Pugh 1997). Notably—because Largemouth Bass, *Lepomis* species, and red swamp crayfish (*Procambarus clarkii*) are introduced species in many countries worldwide—Largemouth Bass in their introduced ranges often consume these same prey items (Hickley et al. 1994; Nicola et al. 1996; Azuma and Motomura 1998; García-Berthou 2002; Lorenzoni et al. 2002; Maezono and Miyashita 2003; Jo et al. 2016; Yasuno et al. 2016). Because Delta food webs are now highly altered and dominated by introduced species (Brown et al. 2016), we may expect Largemouth Bass diets to consist largely of other non-native species.

Given that Largemouth Bass are so abundant that they are in some cases the most common fish captured during littoral-based field surveys (Young et al. 2018b), even occasional consumption of native fish could have important implications for the Delta native fish community. Previous studies that examined Largemouth Bass diets in the Delta (Turner 1966; Nobriga and Feyrer 2007; Grimaldo et al. 2009; Grossman 2016; Young et al. 2018a) focused on particular Largemouth Bass size groups (e.g., juveniles) and habitats, or were not conducted recently. Nobriga and Feyrer (2007) sampled Largemouth Bass stomachs in 2001 and 2003 at five sites in the Delta, and found that Largemouth Bass consumed more species of native fish and likely had a greater per capita impact than did the non-native Striped Bass (*Morone saxatalis*) or the native Sacramento Pikeminnow (*Ptychocheilus grandis*) in the Delta's shallow-water habitats. Their study, however, focused on relatively unvegetated habitats that were possible to beach seine. To get a full view of Largemouth Bass diet, it is necessary to sample the full range of littoral habitats—including heavily vegetated areas—because these areas are a dominant habitat type for Largemouth Bass.

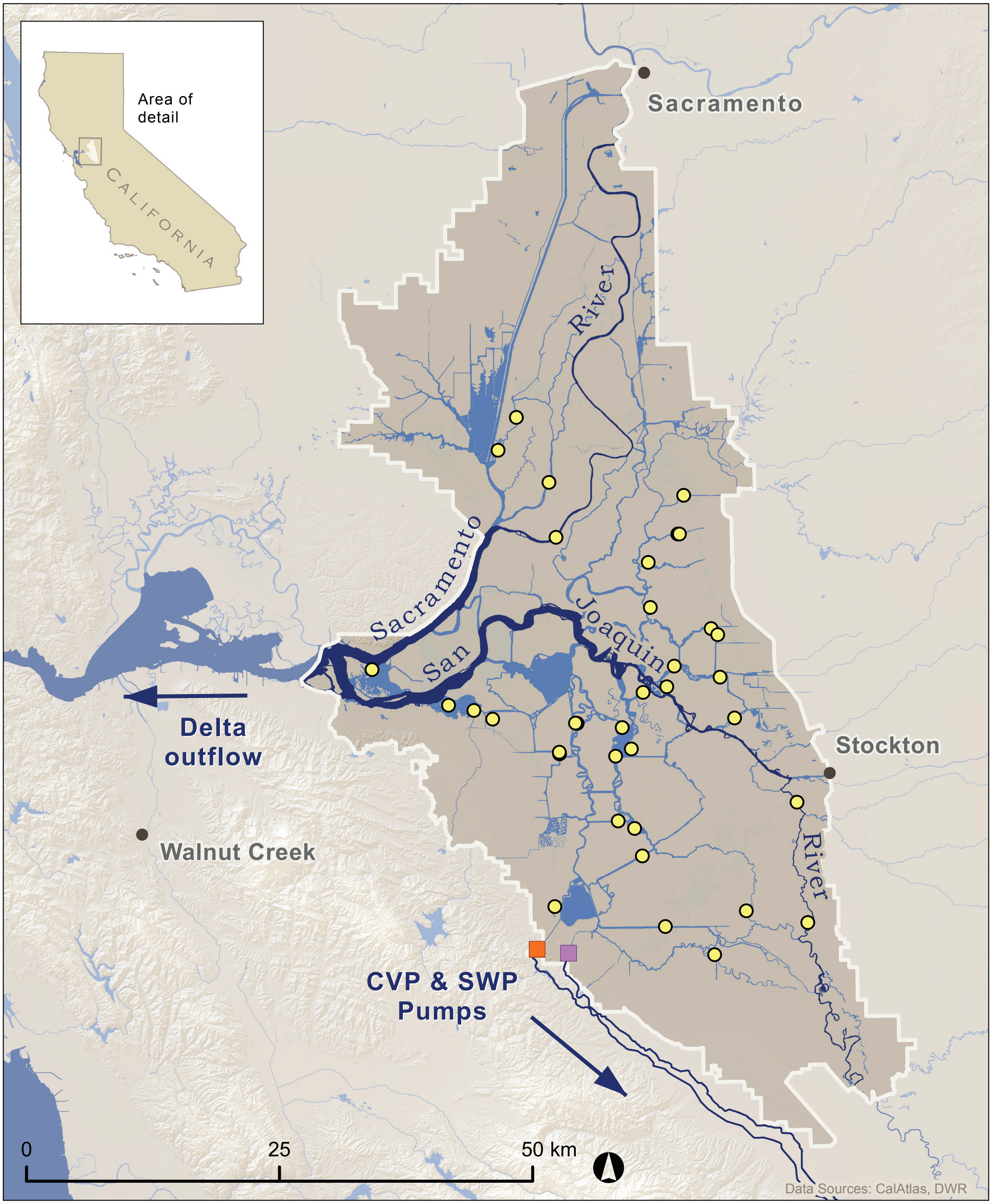

Figure 1 The Sacramento–San Joaquin Delta. The 33 study sites are indicated as yellow circles.

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A large population of Largemouth Bass could also be problematic for the fish species that reside in the Delta's pelagic zone. At the beginning of this century, after the centrarchid abundance increased in the Delta, four major pelagic fish declined precipitously, and this drop became known as the Pelagic Organism Decline, or POD (Sommer et al. 2007; MacNally et al. 2010). These four species are the native Delta Smelt (*Hypomesus transpacificus*), and Longfin Smelt (*Spirinchus thaleichthys*), and the non-native Striped Bass and Threadfin Shad (*Dorosoma petenense*). When given a choice between pelagic prey (specifically, Delta Smelt) and vegetation-associated prey in mesocosms, Largemouth Bass adults preferentially consume pelagic prey (Ferrari et al. 2014). Although Threadfin Shad and Striped Bass have been reported in the stomachs of Largemouth Bass in the Delta (Turner 1966; Nobriga and Feyrer 2007), the extent to which Largemouth Bass actually consume these fishes when they co-occur is unclear.

To address current questions about Largemouth Bass diet in the highly altered and invaded Delta, we surveyed Largemouth Bass diets throughout the Delta that spanned multiple years and seasons, multiple Delta habitats, and included all sizes of Largemouth Bass. We sampled Largemouth Bass at fixed sites across the Delta over a 2-year period, and addressed the following specific questions: (1) Are Largemouth Bass primarily consuming a diet of other non-native species? (2) To what extent do native fish contribute to the diets of Largemouth Bass? (3) To what extent do the pelagic fishes—particularly those recognized as part of the POD—contribute to the diets of Largemouth Bass?

MATERIALS AND METHODS

Collection of Field Data

We collected Largemouth Bass via electrofishing surveys (Smith-Root electrofishing boat with a 5.0 generator-powered pulsator, fishing at 6-10 A, 50-500 V, 20%-80% of range) at 33 sites throughout the Delta (Figure 1). We visited all sites on a bi-monthly basis from December 2008 to October 2010, for a total of 12 sampling sessions. Each site consisted of a 300-m transect, adjacent to the shoreline except for several open-water areas in flooded agricultural tracts. We chose sites randomly from areas that were ≤ 3 m in depth and harbored submerged aquatic vegetation (SAV) at least once from 2004 to 2008, based on annual aerial surveys conducted during this period (Hestir et al. 2008). Over the study period, SAV densities at our study sites ranged from zero (consistently and completely absent), to densities that exceeded 1,500 dry g m^2 (Conrad et al. 2016). We focused on water depths of ≤ 3 m because Brazilian waterweed and Largemouth Bass are common in these water depths, and because this is an effective working depth for electrofishing. Using these criteria, we originally picked 30 random sites. In February 2009, we added an additional three sites from the original list of random locations to increase coverage of the northern and western regions of the Delta.

At each bi-monthly site visit, we counted all stunned fish (i.e., all fish species encountered) and recorded their fork lengths (FL, mm). We collected Largemouth Bass diet samples by either preserving whole fish in 10% formalin and extracting stomach contents in the laboratory (for fish that measured ≤175 mm FL, up to 10 fish per site), or by gastric lavage (for fish that measured > 175 mm). We used 175 mm FL as the cut-off for preserving fish because our preliminary fieldwork showed this to be a reasonable minimum length for performing gastric lavage effectively and without harming the fish. When collecting diet samples using gastric lavage, we flushed the stomach of each bass twice into an aquarium net, removed visible diet items with forceps after each flush, and placed stomach contents in 10% formalin. For analyses, we partitioned the data set by the 175 mm FL cut-off, because procedures for collecting diet samples—and thus potential sampling errors—differed for fish above and below this length. The University of California Davis Institutional Animal Care and Use Committee (Protocol #16617) approved all field methods.

Diet Sample Processing

All preserved fish were held in the lab in 10% formalin for at least 1 week, and then transferred into 70% ethanol. We dissected stomachs out of whole preserved fish and identified contents to the lowest practical taxonomic category (Table 1). When possible, we used species-specific cleithrum bones

Table 1 Categories used for the analysis of Largemouth Bass stomach contents

Prey category	Types of prey included in category
Amphipods	Hyalellidae, Gammaridae, Corophiidae, and unidentified amphipods
Copepods and cladocerans	
Red swamp crayfish	*Procambarus clarkii*
Shrimp	
Unidentified decapods	
Other crustaceans	Isopoda and Mysida
Dipterans	
Odonates	Zygoptera, Anisoptera, and unidentified odonates
Hemipterans	
Other insects	Ephemeroptera, Trichoptera, Hymenoptera, Coleoptera, Lepidoptera, and unidentified insects
Other invertebrates	Arachnida, Nemertea, Oligochaeta, Megaloptera, Euhirudinea, Acarina, Turbellaria, and Corbicula
Largemouth Bass	*Micropterus salmoides*
Other centrarchids	*Lepomis macrochirus, L. microlophus, L. gulosus, Pomoxis nigromaculatus*, and unidentified centrarchids
Non-native demersal fish	*Acanthogobius flavimanus, Tridentiger bifasciatus, Percina macrolepida*, and catfish
Native demersal fish	*Cottus asper*
Unidentified demersal fish	Unidenfitied gobies and sculpins
Non-demersal native fish	*Lampetra tridentata, Hysterocarpus traskii, Orthodon microlepidotus, Lavinia exilicauda*, and *Gasterosteus aculeatus*
Pelagic Organism Decline (POD) Fish	*Morone saxatilis, Dorosoma petenense, Hypomesus transpacificus*, and *Spirinchus thaleichthys*
Other fish	*Menidia beryllina, Notemigonus crysoleucas, Gambusia affinis, Lucania parva, Cyprinus carpio*, and unidentified cyprinids
Unidentified fish	
Other vertebrates	Amphibians, reptiles, and mammals

(Hansel et al. 1988) to identify partially digested fish species. Prey in all categories were blotted with a Kim Wipe, counted and weighed, with wet weight determined to 0.001 grams. When the number of copepods and cladocerans was prohibitively high to count, we estimated their numbers by determining their total weight and dividing by the average weight of these crustaceans in counted samples. Additionally, if prey weight for a diet category was too low to register on the scale, we recorded a value of 0.0001 grams.

Quantitative Diet Description

We calculated the percent prey-specific index of relative importance (%PSIRI; Brown et al. 2012) of prey items in the diet of both size groups of Largemouth Bass. The %PSIRI metric accounts for: (1) the frequency at which a particular food type occurred in the stomachs of Largemouth Bass that had contents in their stomachs at the time of capture, (2) the relative numerical abundance of that food type in each individual's diet, and (3) the relative biomass of that food type in each individual's diet (Brown et al. 2012). We calculated prey-specific abundance (PN_i), prey-specific weight (PW_i), frequency of occurrence (FO_i), and %PSIRI as follows:

$$PN_i = \frac{\sum_{j=1}^{n} N_{ij}}{n_i},\ PW_i = \frac{\sum_{j=1}^{n} W_{ij}}{n_i},\ FO_i = \frac{n_i}{n},$$

$$\%PSIRI_i = \frac{[FO_i \times (PN_i + PW_i)] \times 100}{2},$$

where N_{ij} is the proportion of the prey count in stomach j that are prey type i, W_{ij} is the proportion of the biomass in stomach j that is of prey type i, n_i is the number of stomachs containing prey type i, and n is the number of stomachs containing at least some contents (empty stomachs are excluded from this analysis).

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We chose %PSIRI over percent index of relative importance (%IRI, Cortés 1997) because %IRI overemphasizes frequency-of-occurrence data and because %PSIRI—unlike %IRI—is additive across prey categories or taxonomic levels (Brown et al. 2012).

For analyses, June, August, and October were grouped together as "summer," and December, February, and April were grouped together as "winter." This division yielded four "seasons" for analysis: winter 2009 (December 2008, February 2009, and April 2009), summer 2009 (June 2009, August 2009, and October 2009), winter 2010 (December 2009, February 2010, and April 2010), and Summer 2010 (June 2010, August 2010, and October 2010). This approach allowed us to pool sample sizes so that the %PSIRI calculations reflected an ample number of Largemouth Bass diets over all sites for both size classes, within similar environmental conditions. We performed %PSIRI calculations in RStudio Version 1.0.143 (RStudio Inc. 2016) running R Version 3.4.0 (R Development Core Team 2017).

RESULTS

We analyzed the gut contents of 1,933 Largemouth Bass ≤175 mm FL and 1,071 Largemouth Bass >175 mm FL. Figure 2 shows fork length distributions, sample sizes, and the percent of Largemouth Bass with empty stomachs for each season. Figures 3 and 4 present %FO and %PSIRI (see Tables A1 and A2 in Appendix A). Information about the biotic and abiotic conditions during each sampling period (and information about how Largemouth Bass abundance is influenced by these conditions) is available in Conrad et al. 2016. All data on environmental characteristics of the study sites, plus Largemouth Bass fork length, weight, and diet data are available in Appendix B. R code for the %PSIRI analysis is included in Appendix A.

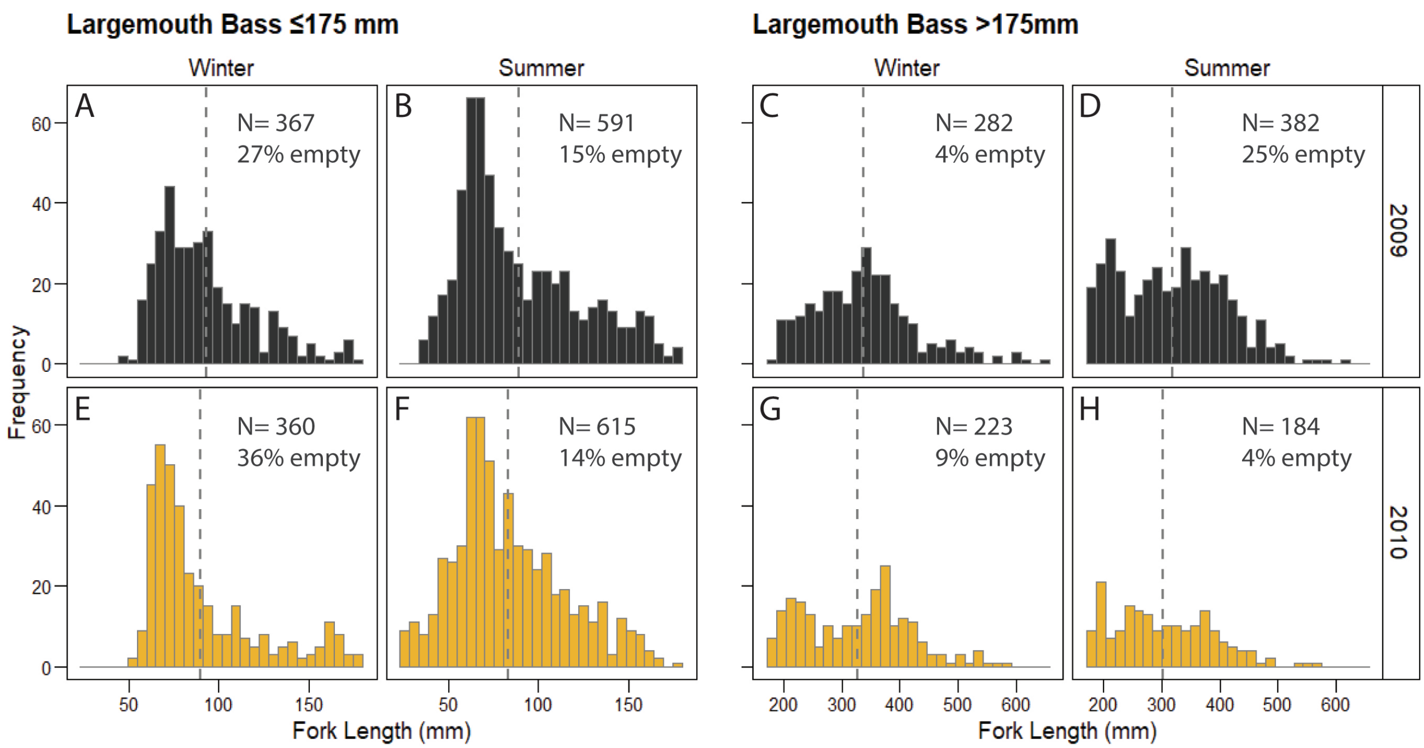

Figure 2 Length–frequency distributions for Largemouth Bass ≤175 mm FL (**A**, **B**, **E**, and **F**) and >175 mm FL (**C**, **D**, **G**, and **H**) during the winter (December, February, and April) and summer (June, August, and October) seasons in 2009 (*top row* of graphs) and 2010 (*bottom row* of graphs). Average fork lengths for each size group in each season are indicated with a *dashed line*. Sample sizes for the diet analyses and the percent of Largemouth Bass with empty stomachs in each season are indicated in the *top right corner* of each graph.

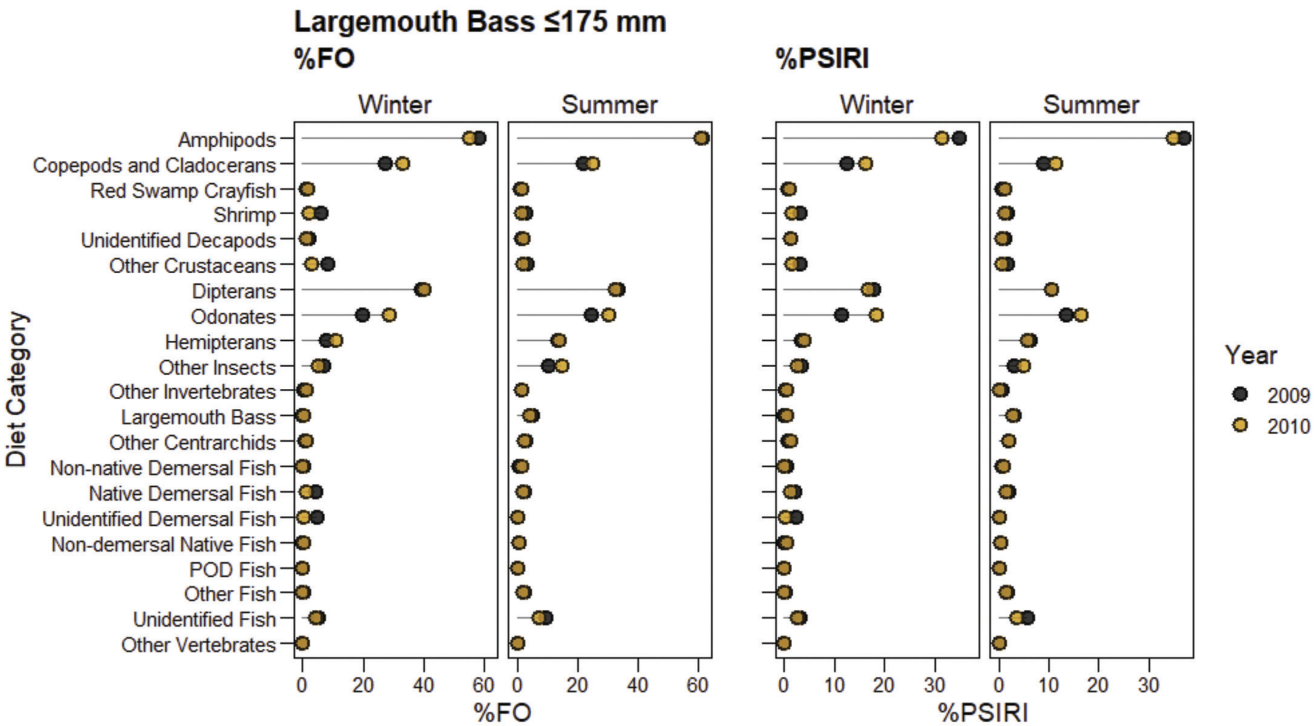

Figure 3 Percent prey-specific frequency of occurrence (%FO) and prey-specific index of relative importance (%PSIRI) for Largemouth Bass ≤175 mm FL during the winter (December, February, and April) and summer (June, August, and October) seasons in 2009 (grey circles) and 2010 (yellow circles). Table 1 contains information about which prey are included in each diet category.

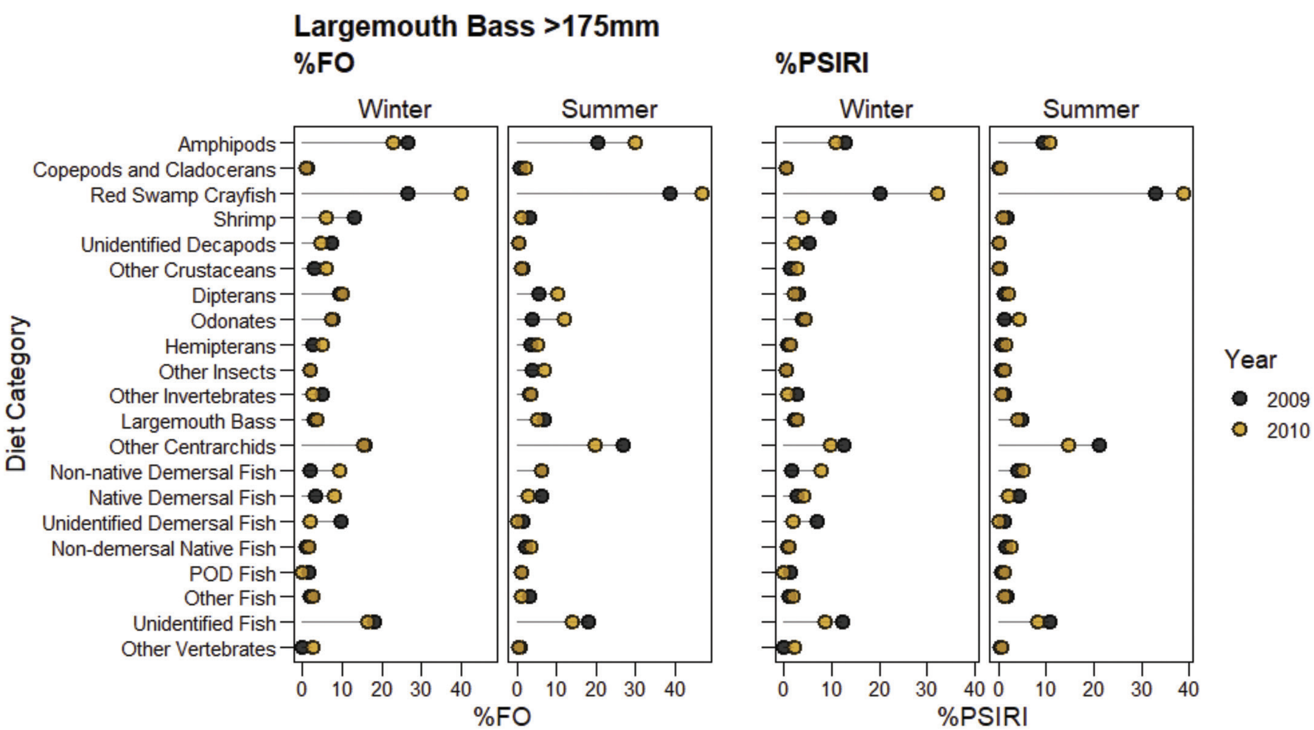

Figure 4 Percent prey-specific frequency of occurrence (%FO) and prey-specific index of relative importance (%PSIRI) for Largemouth Bass >175 mm FL during the winter (December, February, and April) and summer (June, August, and October) seasons in 2009 (grey circles) and 2010 (yellow circles). Table 1 contains information about which prey are included in each diet category.

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Diets of Largemouth Bass ≤175mm Fork Length

Across seasons and years, amphipods dominated the diets of Largemouth Bass ≤175 mm, with %PSIRI ranging from ~31%-37% across the study (Figure 3, Table A1). The next three most important diet categories ranked by %PSIRI were odonates, dipterans, or copepods and cladocerans, depending on the season and year. Although the exact ranking of these categories changed across seasons, each category exhibited a %PSIRI range of 8.9 to 18.4 (Figure 3).

In general, fish in this smaller size class consumed fewer other fishes over the entire study period. The %PSIRI for centrarchids ranged from 0.0 to 3.1 for Largemouth Bass (i.e., cannibalism), and from 0.6 to 2.0 for other centrarchids. The %PSIRI values ranged from 1.3 to 2.1 for Prickly Sculpin (*Cottus asper*, a native, demersal fish); a total of 42 were found in the stomachs of 35 fish. Non-demersal native fish never exceeded 0.4 %PSIRI, and Largemouth Bass ≤175 mm FL consumed only five fish in this category. The five fish were one Tule Perch (*Hysterocarpus traskii*), three Sacramento Blackfish (*Orthodon microlepidotus*), and one Threespine Stickleback (*Gasterosteus aculeatus*). Of the four pelagic fish species the POD comprised, only one specimen (a Threadfin Shad) was found in the guts of Largemouth Bass ≤175 mm FL over the course of the study. In the summer season, centrarchids (diet categories of Largemouth Bass and Other centrarchids) had higher %PSIRI values than native fish (native demersal fish plus non-demersal native fish categories); and in the winter season, native fish exhibited higher %PSIRI values than centrarchids. In general, piscivory by Largemouth Bass ≤175 mm FL was more frequent in summer months. This size class were more likely to have empty stomachs in winter (27% in 2009 and 36% in 2010), compared to ~14% to 15% in summer 2009 and 2010.

Diets of Largemouth Bass >175mm Fork Length

The non-native red swamp crayfish was the most important prey category for Largemouth Bass >175 mm FL across all seasons, with %PSIRI that ranged from 20.0 to 38.8 across the entire study period (Figure 4, Table A2). Across all seasons, the categories for other centrarchids, amphipods, and unidentified fish were the three next highest-ranked diet categories by %PSIRI. The percent of fish with empty stomachs was generally low (4%, 9%, and 4% in winter 2009, winter 2010, and summer 2010, respectively), though 25% of the Largemouth Bass >175 mm FL exhibited empty stomachs in summer 2009.

The %PSIRI values for Largemouth Bass (i.e., cannibalism) ranged from 2.0 to 4.8 for Largemouth Bass >175 mm FL; values for other centrarchids ranged from 9.7 to 21.1 (Figure 4). Forty-eight Largemouth Bass >175 mm FL consumed 59 Prickly Sculpin, and the %PSIRI for this diet category ranged from 2.0 to 4.2. Seventeen Largemouth Bass in this size class consumed 23 non-demersal native fish, with %PSIRI ranging from 0.6 to 2.6. Specifically, we observed two Pacific Lamprey (*Lampetra tridentata*), four Tule Perch, 11 Sacramento Blackfish, and six Hitch (*Lavinia exilicauda*) in Largemouth Bass >175 mm. We also seldom observed the four pelagic fishes that comprised the POD in the stomach contents of Largemouth Bass >175 mm: we observed only 11 of these fish (three Striped Bass and eight Threadfin Shad) in the stomachs of nine Largemouth Bass (0–1.2 %PSIRI; Figure 4).

DISCUSSION

This study provides a previously unavailable and comprehensive account of Largemouth Bass diets across seasons, years, and size classes. We show that Largemouth Bass in the Delta have fairly consistent diets across seasons, with a prevalence of amphipods, dipterans, and odonates in smaller fish, and the special importance of crayfish and other centrarchid fishes in the diets of larger fish (Figures 3 and 4). The diets of larger Largemouth Bass are of special interest to managers because they can potentially prey upon fishes with protected status such as Delta Smelt, Chinook Salmon, and Central Valley Steelhead, or upon pelagic fishes that are part of the POD. However, over a sample size of more than 1,000 fish that measured more than 175 mm, native and pelagic fishes were only a small component of the diet of predatory Largemouth Bass. Instead, Largemouth Bass >175 mm FL are a top predator of a largely non-native community of littoral fishes and invertebrates. Indeed, cannibalism occurred more frequently in this size group of Largemouth Bass than consumption of non-demersal native fish (Figure 4). As we discuss here, this result does not preclude the possibility that Largemouth Bass are important predators of native fishes in localized areas where native fishes are still relatively abundant. However, as non-native sunfish (*Lepomis* spp.) are particularly abundant in the littoral regions of the Delta (Brown and Michniuk 2007), and tend to overlap with Largemouth Bass (Young et al. 2018b), they are the fishes that contribute the most to predatory Largemouth Bass diets.

Consumption of Invertebrates (Excluding Red Swamp Crayfish)

Amphipods were an important invertebrate prey item for both size groups of Largemouth Bass (Figures 3 and 4). These results are consistent with other studies of Largemouth Bass diets in the Delta, as Grimaldo et al. (2009) and (Young et al. 2018a) found that nearshore fishes associated with SAV beds tended to consume SAV-associated amphipods (mainly *Gammarus* and *Hyalella* spp.). Largemouth Bass ≤175 mm FL also consumed many insects, chiefly Dipterans and Odonates (Figure 3). This was true in all seasons and across both years. This diet reflects the diet composition described for other non-native Largemouth Bass populations. For example, Largemouth Bass between 32 and 138 mm total length (TL) in Eastern Cape River, South Africa, consume mainly amphipods and dipterans (Wasserman et al. 2011).

Non-Native Decapods and Centrarchids

The Delta food web is now highly altered, consisting of many non-native species (Brown et al. 2016). In the Delta, Largemouth Bass, a non-native predator, consume largely non-native centrarchids (particularly *Lepomis* spp.) and non-native red swamp crayfish when the bass exceed >175 mm FL (Figure 4). Red swamp crayfish were not always the most important decapod in Largemouth Bass diets in the Delta. In 1966, Turner found that signal crayfish (*Pacifastacus leniusculus*) were the most frequently observed item in the stomachs of Largemouth Bass (Turner 1966). In later studies in the Delta, the Siberian Prawn (*Exopalaemon modestus*) was more common in Largemouth Bass stomachs than were crayfish (Nobriga and Feyrer 2007). All three of these decapods are non-native, revealing the importance of this prey type for Largemouth Bass in the Delta. The higher prevalence we observed of red swamp crayfish in Largemouth Bass diets may reflect the dense SAV habitats included in our study design that were not included in previous studies, because red swamp crayfish are generally associated with vegetation (Gutiérrez-Yurrita et al. 1998).

Interestingly, red swamp crayfish and centrarchids in the genus *Lepomis* are a common feature of non-native Largemouth Bass diets around the world. For example, Largemouth Bass diets often comprise *Lepomis* spp. or red swamp crayfish or both in countries as widespread as Kenya (Hickley et al. 1994), Korea (Jo et al. 2016), Spain (Nicola et al. 1996; García-Berthou 2002), Italy (Lorenzoni et al. 2002), and Japan (Azuma and Motomura 1998; Maezono and Miyashita 2003; Yasuno et al. 2016), highlighting the broad distribution of these non-native species around the world and the consistency of their trophic interactions.

Native Demersal Fish

Previous studies have found that Largemouth Bass in introduced populations often consume native demersal fish. For example, in the Ruidera Lakes in Spain, Largemouth Bass consume an endangered blenny (*Blennius fluviatilis*) (Nicola et al. 1996); and gobies (including *Rhinogobius* spp.) are found in the stomachs of Largemouth Bass introduced in Japan (Azuma and Motomura 1998; Maezono and Miyashita 2003; Tsunoda et al. 2010; Hossain et al. 2013; Taguchi et al. 2014). In the Delta, the native fish most commonly consumed by Largemouth Bass during our surveys was the demersal Prickly Sculpin. The record of Prickly Sculpin consumption was not related to their co-occurrence with Largemouth Bass as detected in our survey sample, possibly because demersal fishes are not well surveyed with electrofishing gear. Prickly Sculpin were also the most commonly consumed native fish in a survey of Largemouth Bass diets conducted in 2001 and 2003 (Nobriga and Feyrer 2007). The population of Prickly Sculpin in the Delta has increased from 1995 through 2015 (Mahardja et al. 2017). Given this trend, it

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appears as though Largemouth Bass predation is not sufficient to drive this native species into a decline. Also, note that the three categories of demersal fish—i.e., native demersal fish, non-native demersal fish, and unidentified demersal fish—were the most important fish prey group aside from centrarchids.

Non-Demersal Native Fish

In the 3,004 Largemouth Bass whose stomach contents were examined over the 2 years of this study, a total of 28 non-demersal native fish (2 Pacific Lamprey, 5 Tule Perch, 14 Sacramento Blackfish, 6 Hitch, and 1 Threespine Stickleback) were identified in stomach contents. The consumption of non-demersal native fish never rose above 0.4 %PSIRI for Largemouth Bass ≤175 mm FL, and never rose above 2.6 %PSIRI for Largemouth Bass >175 mm. These values of %PSIRI are small compared to other fishes, particularly other centrarchids (*Lepomis* spp. and *Pomoxis* spp.), which had values as high as 21.1 %PSIRI for Largemouth Bass >175 mm FL (Figure 4). This difference in %PSIRI is most likely a reflection of the relative abundance of centrarchid fishes compared to non-demersal native fishes: on average during the study period, catch of sunfish and crappies was ten or more times the catch of non-dermersal native fishes. Like the Prickly Sculpin, both Tule Perch and Threespine Stickleback have recently shown increasing population trends in nearshore habitats (Mahardja et al. 2017), suggesting that these species can coexist with Largemouth Bass.

Nevertheless, Largemouth Bass could still affect localized populations of native fishes within the Delta. For example, at a few sites in the North and West Delta regions, the catch of non-demersal native fishes occasionally outnumbered the catch of sunfish and crappies (the "other centrarchids" diet category). These Delta regions have shown a higher abundance of native fishes in previous studies, as well (Brown and Michniuk 2007; Young et al. 2015; Schreier et al. 2016; Young et al. 2018b). Where the fish composition included more non-demersal native fishes compared to sunfish and crappies, the Largemouth Bass diet also had a higher frequency of occurrence of non-demersal native fishes (Figure 5). Our data does not allow the effects of Largemouth Bass predation on non-demersal native fish to be assessed. However, the trend of increased frequency of predation on these native fishes in areas where they are more common is consistent with the potential to affect these localized populations of natives, and the potential historical effect of Largemouth Bass predation on native, non-demersal fishes.

Pelagic and Migratory Fishes

Four pelagic species (juvenile Striped Bass, Longfin Smelt, Delta Smelt, and Threadfin Shad) suffered dramatic declines at the turn of the century (Feyrer et al. 2007; Sommer et al. 2007; Mac Nally et al. 2010; Miller et al. 2012), and some analyses have implicated Largemouth Bass as a potential contributor to these declines (Mac Nally et al. 2010). Of these four pelagic fish species, only three Striped Bass and nine Threadfin Shad were identified in the guts of Largemouth Bass over our entire study period. This minimal consumption of pelagic fishes occurred despite moderately common co-occurrence: 443 and 354 diet samples from Largemouth Bass (>175 mm) were collected during the 78 and 63 surveys in which they co-occurred with Striped Bass and Threadfin Shad, respectively. Co-occurrence of Largemouth Bass and Delta Smelt was relatively rare during the study period but did occur twice. In both instances, the Largemouth Bass stomachs (N = 2) collected from the same surveys did not contain identifiable Delta Smelt.

In addition to the pelagic fishes, potential predation of migratory salmonids as they travel through the Delta is of interest to managers because a known source of their mortality is their predation in the Delta (Grossman 2016). In our study, Chinook Salmon were sampled in the same surveys as Largemouth Bass 13 times, and 68 diet samples were collected in these surveys from Largemouth Bass >175 mm. Chinook Salmon were never identified in Largemouth Bass stomach contents over the entire study period. Central Valley Steelhead were sampled in the same surveys as Largemouth Bass six times during our study, but also were never identified in Largemouth Bass stomach contents.

MANAGEMENT IMPLICATIONS

An understanding of Largemouth Bass diet patterns is important because shallow-water habitat may expand

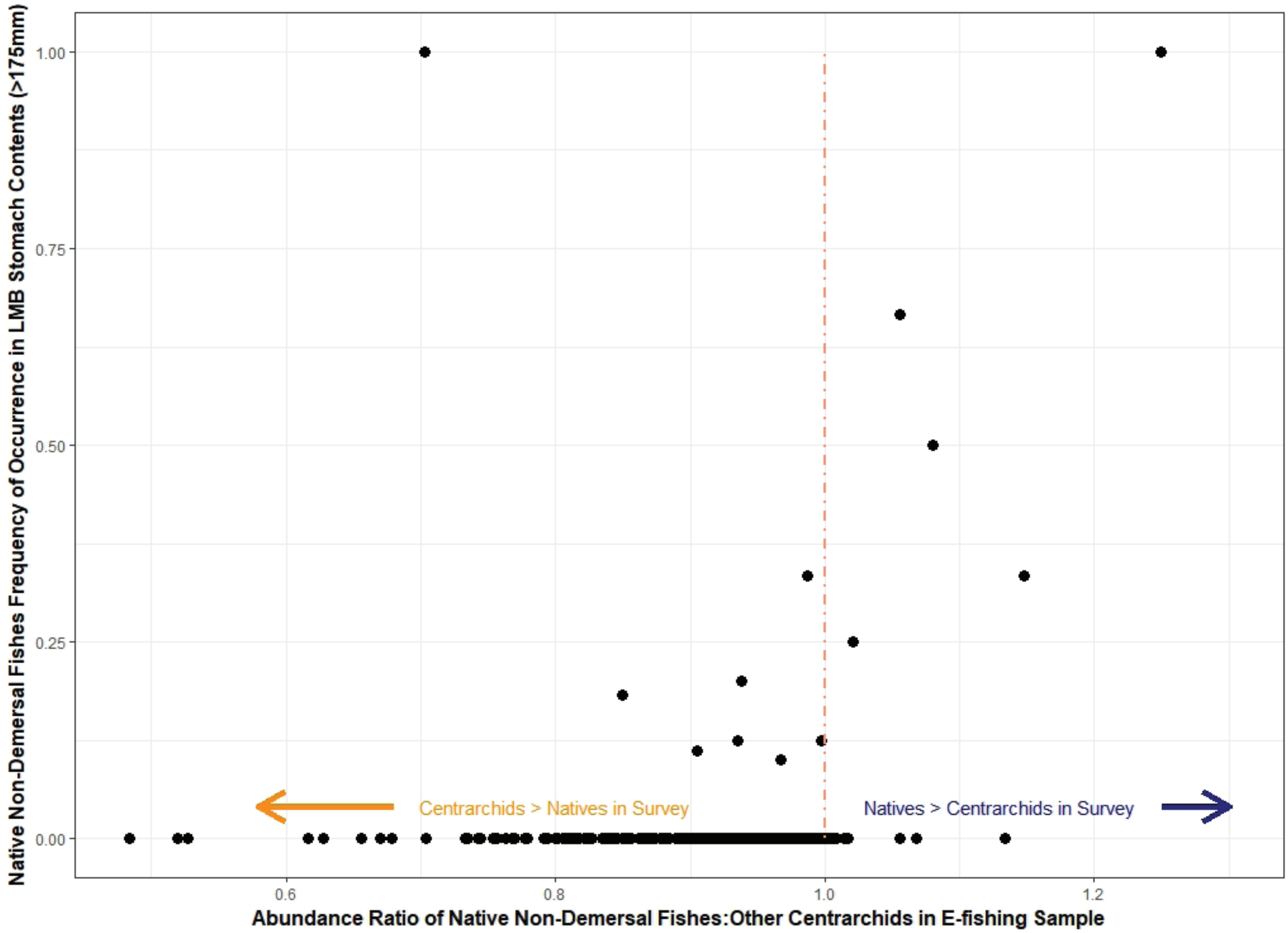

Figure 5 The frequency of occurrence of native, non-demersal fishes in Largemouth Bass (> 175 mm FL) stomach contents plotted against the ratio of the abundance of native fishes (Pacific Lamprey, Tule Perch, Sacramento Blackfish, Hitch, and Threespine Stickleback) to the abundance of other centrarchids (Bluegill, Redear Sunfish, Warmouth, and Black Crappie) in the electrofishing survey. A ratio of 1 indicates that abundance levels of the two fish groups were equivalent.

in the Delta and provide additional capacity for the Largemouth Bass population. Several management initiatives (e.g., California EcoRestore, *http://resources.ca.gov/ecorestore/*) call for the creation of thousands of acres of tidal wetland habitat to benefit native fishes and boost ecosystem processes such as planktonic productivity (Herbold et al. 2014). It seems plausible that the expansion of shallow-water habitat will result in more SAV and its associated fish assemblage in the Delta, comprising mainly Largemouth Bass and other centrarchid fishes. However, in a recent study of shallow-water fish assemblages across environmental gradients in the Delta, Young and colleagues (2018b) observed that both non-native and some native species had positive associations with SAV, and that abiotic conditions (e.g., higher salinity) better predicted the presence of native fish than SAV. The native fishes we saw consumed in this study are not the target beneficiaries of planned tidal wetland restoration projects, but these restored areas may be suitable habitat for species such as Sacramento Blackfish, Tule Perch, and Hitch. Because the Delta generally lacks tidal marsh habitat, the interaction between these species and Largemouth Bass specifically within these newly restored habitats is difficult to predict. If these species do colonize these habitats in significant

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numbers along with Largemouth Bass, the results of our study suggest that natives will indeed be preyed upon more frequently (Figure 5), but our data cannot be used to infer how this increased predation may affect the populations of native fish. Given the results of this study and those from Young et al. (2018b), the best chances for restored shallow-water habitat to serve as a refuge for native fishes such as Tule Perch may be to locate projects in Delta regions where abiotic conditions are favorable for natives. Natives are then more likely to have a competitive edge in the face of predation pressure from Largemouth Bass.

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