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ARTICLE

Pelagic Nekton Abundance and Distribution in the Northern Sacramento–San Joaquin Delta, California

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Abstract
Knowledge of the habitats occupied by species is fundamental for the development of effective conservation and management actions. The collapse of pelagic fish species in the Sacramento–San Joaquin Delta, California, has triggered a need to better understand factors that drive their distribution and abundance. A study was conducted in summer–fall 2014 in an attempt to identify physical and biological habitat conditions that drive the abundance and distribution of pelagic species in the northern region of the system. The study was conducted in the three largest channels in the northern Sacramento–San Joaquin Delta by dimension, volume, and flow capacity. The pelagic community was dominated by three nonnative species, Siberian prawn *Exopalaemon modestus*, which comprised 56% of the total number of organisms, and two fish species, Threadfin Shad *Dorosoma petenense* and Mississippi Silversides *Menidia audens*, which together comprised 43% of the total number of organisms. Total fish and total shrimp abundance were sensitive to the most extreme values of turbidity and temperature encountered and positively associated with total zooplankton biomass. The results suggested that habitat conditions in terminal channels, historically a common feature on the landscape, support higher abundances of pelagic species and zooplankton than open-ended channels. These results provide resource managers with useful information on the habitat associations of pelagic species and on how the future distribution and abundance of pelagic species will likely change in response to climate or other ecological factors.

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Knowledge of the habitats occupied by species is fundamental for the development of effective conservation and management actions. In the broadest sense, habitat can be defined as the physical and biological attributes required to support healthy populations. Diverse spatiotemporal variability in physical and biological habitat attributes, such as those expressed in river deltas and other dynamic lotic aquatic ecosystems, typically generates heterogeneous distributions of nekton species (e.g., fish and invertebrates). Thus, understanding species–habitat relationships is a fundamental component for the study of population dynamics and for effective resource management.

River systems typically exhibit multiple scales of species–habitat relationships. Across large scales, fish assemblages in river systems generally change from the headwaters to the downstream regions as a result of species additions or replacements in response to gradients in habitat features, such as water temperature, velocity, channel morphology, and productivity (Mathews 1998). Across smaller scales, spatiotemporal variability in habitat features drives species distributions within particular regions (Converse et al. 1998; Pettit et al. 2013). This is especially true in the case of large river-dominated estuaries, where fishes and other organisms have evolved a range of physiological adaptations and life histories in order to occupy habitats that vary along the salinity gradient between riverine freshwater and oceanic salt water (Allen et al. 2006; Feyrer et al. 2015). There is a strong need to better understand species–habitat relationships in these transitional habitats in order to develop conservation and management actions to ameliorate worldwide declines in the production and yield of estuarine biota (Houde and Rutherford 1993).

The goal of this study was to examine the role of physical (water quality parameters) and biological (food supply) habitat features driving the distribution of pelagic nekton in a tidal river system. The study was conducted during the warm summer–fall period in the northern Sacramento–San Joaquin Delta, California (Figure 1). The collapse of pelagic fish populations in the system (Sommer et al. 2007; Thomson et al. 2010) has triggered a need to better understand factors that drive pelagic fish distribution and abundance. Several studies have retrospectively examined the role of selected physical and biological factors on the interannual abundance of pelagic fishes (Mac Nally et al. 2010; Thomson et al. 2010) or the physical habitat associations of pelagic fishes (Feyrer et al. 2007, 2013; Kimmerer et al. 2009; Bennett and Burau 2014). This study examined together the role of both physical and biological habitat features on pelagic fish distribution in the system. A better understanding of fish–habitat relationships in the system is needed to improve management and conservation actions because the system has been highly modified and is dominated by nonnative species. The specific hypothesis tested was that the abundance of pelagic nekton was independent of physical (water quality parameters) and biological (food supply) habitat features.

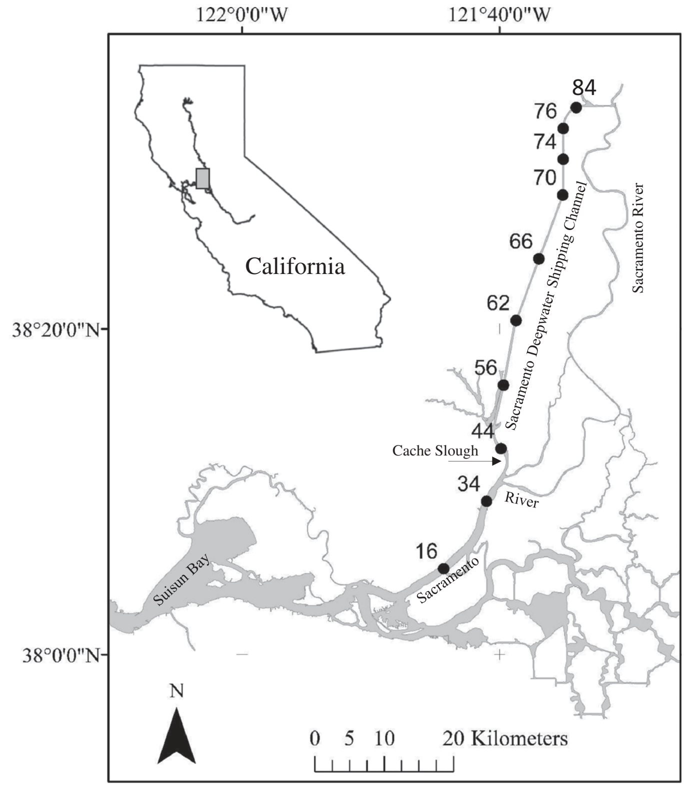

FIGURE 1. Map showing the locations of the sites (black circles) in the northern Sacramento–San Joaquin Delta where pelagic nekton and habitat conditions were assessed in summer–fall 2014. The numbered site labels refer to U.S. Coast Guard navigational markers.

METHODS

Study area.—The study was conducted along an approximately 70-km-long longitudinal transect of main channels in the northern Sacramento–San Joaquin Delta (Figure 1). The Sacramento–San Joaquin Delta is formed at the confluence of the Sacramento and San Joaquin rivers, California's two largest rivers. The two rivers drain the watershed of California's Central Valley into the Sacramento–San Joaquin Delta, leading to San Francisco Bay and ultimately the Pacific Ocean. Sampling sites were positioned along the transect such that the representative habitats ranged from slightly brackish water to freshwater near the upstream extent of tidal influence. Specific sampling sites were positioned at midchannel in the Sacramento River, Cache Slough, and the Sacramento Deepwater Shipping Channel (SDWSC) at U.S. Coast Guard navigation markers 16, 34, 44, 56, 62, 66, 70, 74, 76, 84 (Figure 1). These are the largest channels in the northern Sacramento–San Joaquin Delta by dimension, volume, and flow capacity. The SDWSC is an artificial channel that was built to connect the Sacramento River (via a short stretch [~7 km] of Cache Slough) near the city of Rio Vista to the Port of Sacramento near the city of Sacramento with a straight shipping lane for seagoing vessels. It was opened to seagoing vessel traffic in 1963. It is 42 km long and uniformly ~130 m wide. The center of the SDWSC is approximately 9 m deep and is flanked by relatively narrow, shallow (1–2 m) shoals; sampling sites within Cache Slough and the Sacramento River similarly exhibited a deep center channel flanked by relatively narrow, shallow shoals. While the downstream end of the SDWSC connects broadly to Cache Slough and ultimately the Sacramento River, the upstream end of the SDWSC is isolated from the Sacramento River at the Port of Sacramento by artificial channel gates and a large volume of sediment that has accumulated around them. Thus, the SDWSC functions ecologically as a terminal channel or "dead-end slough." Such habitats are presently rare in the Sacramento–San Joaquin Delta but were a common habitat feature in the historical landscape prior to substantial physical habitat modifications (Whipple et al. 2012).

Semidiurnal tides propagate completely through the Sacramento River, the Cache Slough, and the SDWSC. The maximum tidal range is approximately 1.5 m, and tidal velocities are typically greater than net downstream velocity except during extreme winter–spring flow events. Data for a representative subsample of the sampling sites shows that both maximum and average tidal velocities per tidal period were greatest in the downstream sites in the Sacramento River, Cache Slough, and lower SDWSC and decreased with distance upstream into the terminal SDWSC (Figure 2).

Data collection.—Field sampling was conducted August 25–29 and October 20–24, 2014, targeting age-0 fish. All sampling took place at the center channel at the navigational markers noted above. The sampling method generally followed Feyrer et al. (2013). A midwater trawl affixed with a video camera cod end (VCC; termed the SmeltCam by Feyrer et al. 2013) was towed obliquely through the water column from near bed to the surface for 12 min at each site. The VCC functioned as an open-ended system that automatically collected information on the number and species of organisms that passed freely through the trawled net without handling. It was employed in this study specifically to minimize incidental mortality of the imperiled Delta Smelt *Hypomesus transpacificus* associated with handling stress caused by traditional closed cod end sampling methods. Delta Smelt was listed as a threatened species under both the California and Federal Endangered Species Acts in 1993; its listing status was changed to endangered by California in 2009.

The VCC was attached to a midwater trawl net that was 17.6 m long with a square mouth opening of 3.6 m in width and height, with nine tapered panels of stretch mesh from 14.7 cm near the mouth to 1.3 cm near the cod end. Water volume filtered by the trawl was determined using data from a mechanical flowmeter (model 2030R, General Oceanics) suspended off the side of the vessel during each tow. Processing of the images obtained by the VCC followed the procedures outlined in Feyrer et al. (2013). Images were manually reviewed for accuracy and each species identification was given a relatively subjective human-assigned level of confidence; only species identifications with an assigned confidence level ≥ 75% were included in data analyses, which amounted to 88% of the total number or organisms observed. In total, all sites were sampled seven times except that sites 16 and 66 were sampled eight times.

Physical (water quality parameters) and biological (food supply) habitat features measured at each site included water temperature (°C), specific conductance (μS/cm), turbidity (NTU), and total zooplankton biomass density (μg dry weight/L). At the time of each trawl, water temperature and specific conductance measurements were made using a YSI Model 30 handheld digital meter and turbidity measurements were made using a Hach 2100 handheld turbidity meter. Complementary water quality sampling conducted by the Bureau of Reclamation found that the water column was well mixed (E. Van Nieuwenhuyse, Bureau of Reclamation, unpublished data); thus, all measurements retained for analysis were obtained within 1 m of the surface. Zooplankton density was measured at each site on six separate occasions during the same time frame but separately (nonsynoptically) from the fish and water quality measurements: June 24, July 30, August 28, and October 7, 21, and 23. On each date, zooplankton density was measured at each site via a vertical, integrated net tow starting just above the bed and ending at the water surface. The net had a mouth opening of 30.5 cm, had a mesh size of 125 microns, and was raised through the water column at a rate of approximately 0.3 m/s. Zooplankton sample processing followed the methods of Beaver et al. (2014).

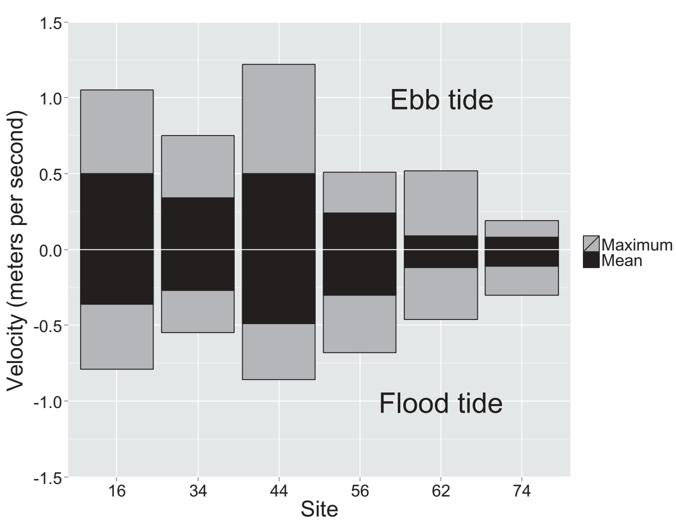

FIGURE 2. Maximum and mean tidal velocities at a representative subset of six sites from Figure 1. Ebb tides are depicted as positive values and represent water movement in a downstream direction. Flood tides are depicted as negative values and represent water movement in an upstream direction.

Data analysis.—Relationships between total fish or total shrimp abundance and habitat variables were developed using generalized additive models (GAM) implemented with the mgcv package in the R statistical programming language (Wood 2006). The GAMs are nonparametric extensions of generalized linear models useful for describing nonlinear relationships between variables. They are data driven and do not presuppose a particular functional relationship between variables; smoothers characterize the empirical relationships between explanatory and response variables. Response variables were total counts of fish or shrimp, with the volume of water sampled included as an offset. Turbidity, temperature, and total zooplankton biomass were included as predictor variables. Specific conductance was not included as a predictor variable because salinity values were uniformly less than 1 psu, except for a few samples collected at the downstream-most station. Thus, there was insufficient variability in the range of specific conductance values for inclusion in the modeling. Tidal excursions were greater than the distance between adjacent sites, which eliminated site as a predictor variable in the models. Zooplankton data included in the models were summarized as the average total biomass at each site for the three zooplankton sampling events nearest in time to the fish sampling events. Models were fit using a Poisson distribution with cubic regression spline smoothing functions. Model fits were evaluated by interpreting both deviance explained and Akaike information criterion (AIC) values. The AIC simultaneously quantifies goodness of fit, as defined by the likelihood of the data, and model complexity (as measured by k), and models with the smallest AIC values are considered preferable. Relationships between predictor variables and response variables are shown graphically in separate plots depicting response curves of the relative influence of the predictor variable. Response curves are based on partial residuals, plotted on a log scale, and standardized to have an average value of 0 (Wood 2006).

RESULTS

Nekton Community

A total of 12,962 individual organisms were observed during the midwater trawl sampling (Table 1). Overall, the community was dominated by crustaceans, namely the Siberian prawn *Exopalaemon modestus*, which comprised 56% of the total number of organisms and 99% of the crustaceans. Jellyfish, most likely *Maeotias marginata* based upon Osborn and Civiello (2013), was the second most abundant invertebrate and comprised 1% of the total number of organisms. Nine fish species were observed. Threadfin Shad *Dorosoma petenense* and Mississippi Silversides *Menidia audens* were the most abundant and together comprised 43% of the total number of organisms. No other individual species comprised > 1% of the total number of organisms. Seven individual Delta Smelt and one individual juvenile Chinook Salmon *Oncorhynchus tshawytscha* were the only native fish species observed during the study. In general, the density of Siberian prawn and the full ensemble of fish species was highest in the mid to upper reaches of the SDWSC (Figure 3). Average Siberian prawn density peaked at about 542 individuals per 10,000 m^3 of water filtered while average total fish density peaked at about 357 individuals per 10,000 m^3 of water filtered. Average jellyfish density peaked at about 11 individuals per 10,000 m^3 of water filtered at the downstream-most site.

TABLE 1. Total numbers of organisms observed in summer–fall 2014. Only Delta Smelt and Chinook Salmon are native species. Jellyfish are most likely *Maeotias marginata* based upon Osborn and Civiello (2013). Gobiidae is comprised of Yellowfin Goby *Acanthogobius flavimanus* and Shimofuri Goby *Tridentiger bifasciatus*.

Taxa	Number	Percent of total (%)
Siberian prawn *Exopalaemon modestus*	7,665	56
Threadfin Shad *Dorosoma petenense*	5,093	38
Mississippi Silversides *Menidia audens*	617	5
Jellyfish	79	<1
Striped Bass *Morone saxatilis*	73	<1
Gobiidae	26	<1
American Shad *Alosa sapidissima*	13	<1
Delta Smelt *Hypomesus transpacificus*	7	<1
Unidentified mysid shrimp	4	<1
Chinook Salmon *Oncorhynchus tshawytscha*	1	<1
Wakasagi *Hypomesus nipponensis*	1	<1

Physical and Biological Habitat Features

The observed habitat conditions (Figure 3) were consistent with those generally expected for the system during the study period. Temperature averaged 21°C and was slightly warmer at the upstream-most sites (Figure 3). Specific conductance was highest at the downstream-most site, where it averaged about 2,000 µS/cm, reflecting salinity of about 3–4 psu. The remaining sites all exhibited low specific conductance values representing salinity values less than 1 psu; it should be noted that specific conductance exhibited a slight gradual increase upstream, likely due to evaporation or other unknown factors. Turbidity peaked in the middle of the SDWSC at about 38 NTU on average and gradually decreased in either direction, except for a smaller peak of about 15 NTU at the downstream-most site (Figure 3). Total zooplankton biomass density was lowest at the downstream-most site, where it averaged 14.6 µg dry weight/L, and gradually increased upstream, where it ultimately reached 46.2 µg dry weight/L (Figure 3). The vast

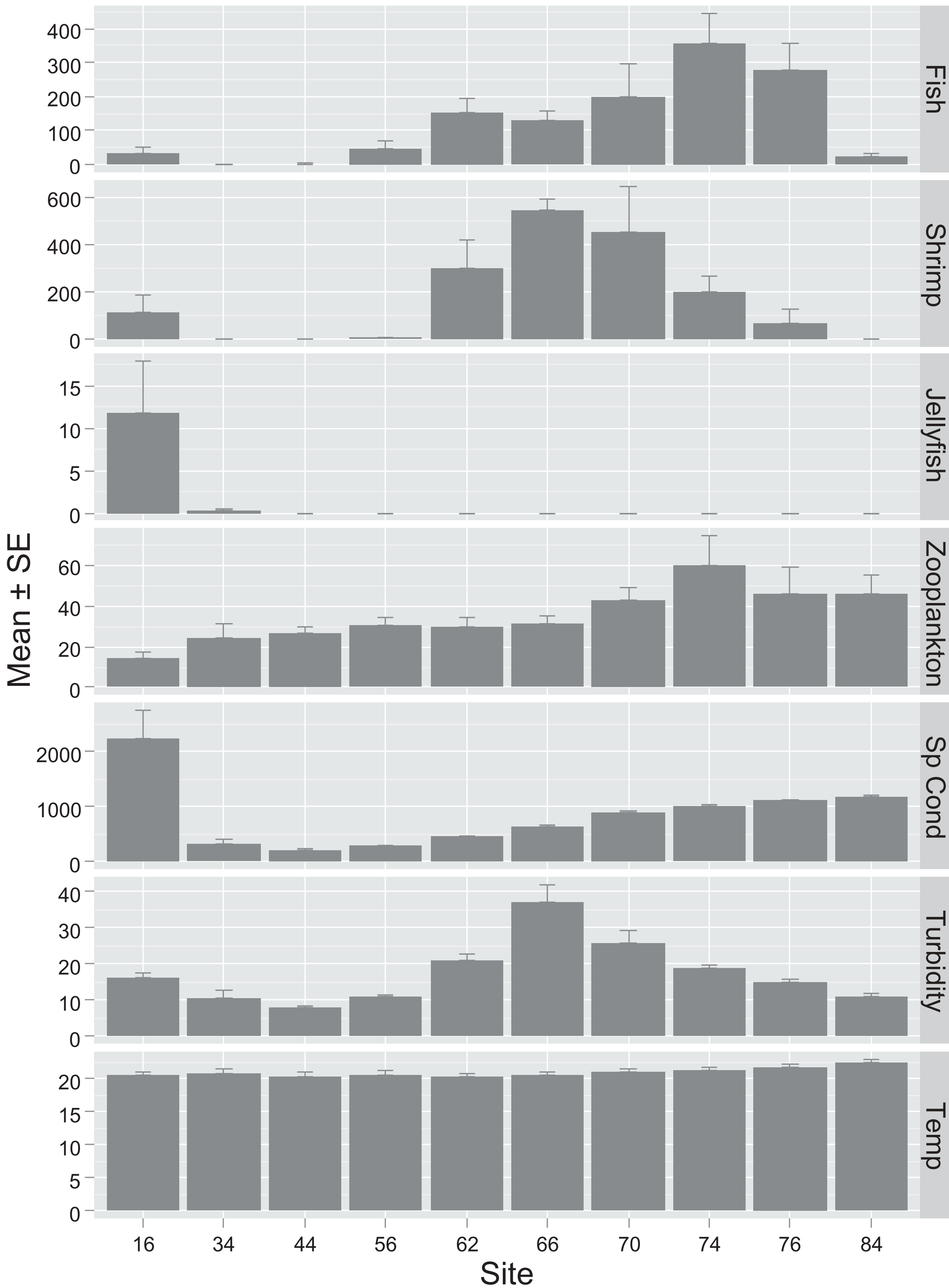

FIGURE 3. Mean ± standard error organism density and habitat conditions at 10 sites in the northern Sacramento–San Joaquin Delta in summer–fall 2014. From top to bottom the panels are as follows: total fish density (number of individuals per 10,000 m^3 of water filtered), comprised primarily of Threadfin Shad and Mississippi Silversides; total shrimp density (number of individuals per 10,000 m^3 of water filtered), comprised primarily of Siberian prawn; total jellyfish density (number of individuals per 10,000 m^3 of water filtered), most likely *Maeotias marginata*; total zooplankton biomass density (µg dry weight/L); specific conductance (Sp cond, µS/cm); turbidity (NTU); and temperature (°C).

TABLE 2. Deviance and AIC values generated from generalized additive models fit to examine the relationship between total fish or shrimp abundance and smooth functions (indicated by an "s") of predictor variables in the northern Sacramento–San Joaquin Delta. Total fish abundance is comprised predominantly by Threadfin Shad but also includes small numbers of the other fish species shown in Table 1. Total shrimp abundance is comprised predominantly by Siberian prawn but also includes small numbers of mysids.

Model	Deviance	AIC
Fish ~ s(turbidity)	36.6	5,711
Fish ~ s(turbidity) + s(temperature)	72.2	2,707
Fish ~ s(turbidity) + s(temperature) + s(zooplankton)	81.3	1,953
Shrimp ~ s(turbidity)	59.2	7,262
Shrimp ~ s(turbidity) + s(temperature)	74.9	4,585
Shrimp ~ s(turbidity) + s(temperature) + s(zooplankton)	81.7	3,435

majority of zooplankton biomass (>96%) was comprised of calanoid copepods and cladocerans, which are important food of pelagic fishes.

Relationships Between Habitat and Fish and Shrimp Abundance

Turbidity, temperature, and zooplankton biomass were all meaningful predictors of total fish or total shrimp abundance. The AIC values indicated that GAMs that included all three predictor variables were the best fitting models for total fish abundance or total shrimp abundance (Table 2). The full GAMs fitted with all three predictor variables explained 81.3% of the deviance of total fish abundance and 81.7% of the deviance of total shrimp abundance (Table 2). Relationships between total fish or shrimp density varied among the three predictor variables (Figure 4). In general, total fish or total shrimp abundance was variably sensitive to the most extreme values of temperature and turbidity. Total fish abundance exhibited a variable relationship to turbidity in that it was lowest at low and intermediate turbidity values. Total fish abundance exhibited somewhat of a noisy unimodal relationship with temperature. Total fish abundance was positively associated with zooplankton biomass. Total shrimp abundance increased sharply from 0 to 10 NTU at which point it became asymptotic and was then relatively insensitive to higher levels of turbidity. Total shrimp abundance was relatively insensitive to temperature until it dropped sharply at the upper end of the range at about 23°C. Total shrimp abundance was generally positively associated with zooplankton biomass, although abundance ultimately declined at the highest zooplankton biomass values.

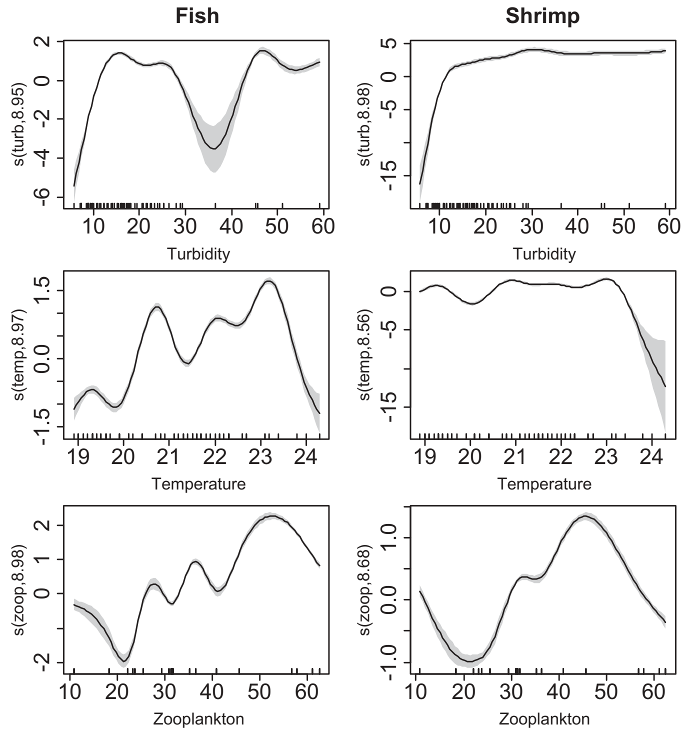

FIGURE 4. Plots showing habitat associations of total fish and total shrimp abundance by turbidity (NTU), temperature (°C), and total zooplankton biomass density (μg dry weight/L). Plots are fitted smooths and shaded 95% confidence intervals for partial responses from generalized additive models. Response curves are based on partial residuals, plotted on a log scale, and standardized to have an average value of 0. Tick marks along the *x*-axes represent observations.

DISCUSSION

Nekton Community

This study demonstrated that the pelagic nekton community of the northern Sacramento–San Joaquin Delta was dominated by a few nonnative species. The overall dominance of nonnative species is consistent with observations from the greater Sacramento–San Joaquin Delta (Feyrer and Healey 2003; Nobriga et al. 2005) and broader San Francisco Estuary, which is considered the most invaded estuary on the planet (Cohen and Carlton 1998). The proliferation of nonnative species is, at least in part, attributable to wholesale alterations to the physical habitat, hydrodynamics, and hydrology of the system (Nichols et al. 1986).

The most abundant species observed in this study, Siberian prawn, is a relatively recent invader of the Sacramento–San Joaquin Delta. It is native to freshwater areas of eastern Asia, from the Amur and Ussuri basins in Siberia, through Korea, China, and Taiwan (Holthius 1980). It was first observed in the Sacramento–San Joaquin Delta in 2000 and has since become the most common shrimp species in freshwater areas of the system (Brown and Hieb 2014). Moreover, the results of this study indicate that Siberian prawn is numerically the most abundant organism overall, at least for the northern region of the system and also probably in other relatively turbid freshwater areas. While it is an important food item of Striped Bass (Nobriga and Feyrer 2008), the ecological role of the Siberian prawn in the Sacramento–San Joaquin Delta is poorly understood and should be studied because of its prevalence in the environment and food web.

The general absence of native fishes observed in this study was somewhat surprising given that the habitat of the northern Sacramento–San Joaquin Delta resembles the historical landscape more so than other areas (Whipple et al. 2012) and that native fishes such as Delta Smelt have been relatively frequently observed in the region (Sommer et al. 2001; Sommer and Mejia 2013). Overall abundance of Delta Smelt in 2014, as recorded by the California Department of Fish and Wildlife's Fall Midwater Trawl Survey, was the lowest ever recorded (http://www.dfg.ca.gov/delta/data/fmwt/indices.asp) and likely contributed to the low number of Delta Smelt observed in this study.

Drivers of Nekton Abundance and Distribution

The study results did not support the hypothesis that the abundance of pelagic nekton was independent of physical (water quality parameters) and biological (food supply) habitat features. Rather, physical and biological habitat features played a prominent role in driving total fish and shrimp abundance. For fishes, the results largely reflect the habitat associations of Threadfin Shad since it was the dominant species in the samples. It is unfortunate that there were insufficient observations to develop models for individual native species. However, extending inferences in this study to native species such as Delta Smelt is plausible because of the generally similar ecological role of Threadfin Shad and Delta Smelt in the system as small pelagic zooplanktivorous fishes with similar habitats and diets (Feyrer et al. 2003). A key result of this study was the observation that food abundance was an important driver of fish and shrimp abundance on a local scale. This result substantiates previously demonstrated population-level effects of food availability on the abundance of pelagic fishes at interannual and decadal scales (Kimmerer 2002; Mac Nally et al. 2010; Thomson et al. 2010).

This was the first study to examine the specific habitat associations of Siberian prawn at a local scale in the system. The overall spatial distribution and specific habitat associations of Siberian prawn together indicate that it is associated with relatively turbid, low-velocity habitats, which were prevalent in the middle reach of the SDWSC. The association with turbidity might be linked to predator avoidance or other ecological or physical factors.

Conservation and Management Implications

Water diverted from the Sacramento–San Joaquin Delta supports over 22 million people and a multibillion dollar agricultural industry. Thus, water management, habitat restoration, and species conservation in the system are of national importance. The improved understanding of the habitats occupied by pelagic nekton generated by this study is fundamental to the development of effective conservation and management actions as well as future habitat investigations. Foremost, the results of this study suggest that future fish research and monitoring efforts should consider measuring appropriately scaled biological components of habitat (e.g., zooplankton biomass at sampling sites) in addition to the water quality parameters that have been traditionally measured in the system. Although the idea was not explicitly tested, the results of this study suggest that habitat conditions in terminal channels likely support higher densities of zooplankton and pelagic nekton species compared with adjacent open channels and therefore should be considered for future habitat restoration actions. Mechanisms underlying this observation require further study to be fully understood and are probably linked at some scale to lower water velocity in the terminal channels (e.g., Figure 2), which can potentially lead to increased residence time and opportunities for higher productivity under certain circumstances. It should be noted that within the study area the reach of the terminal channel (SDWSC) was longer, extended further upstream, and had more sampling sites than the open channel (Sacramento River). However, this likely did not bias the results because the observation of higher abundances of pelagic organisms in terminal channels is consistent with other fish community studies in the system (Matern et al. 2002) and studies on the habitat of native fishes, such as Delta Smelt (Bever et al. 2016).

This study expands upon the work of Feyrer et al. (2013), demonstrating the utility of new technology to address key questions and uncertainties in conservation biology, and shows that imperiled fish species can be studied with relatively little harm. Feyrer et al. (2013) found that the VCC improved the survival of the imperiled Delta Smelt by 72% over traditional sampling methods. In this study, no Delta Smelt were observed entangled in the net or trapped in the VCC. Thus, the application of the VCC in this study appears to have facilitated 100% survival of individual Delta Smelt. The development and application of new technology, such as the VCC, provides many new opportunities for the study of imperiled species, such as Delta Smelt, and can be readily applied to other species and systems.

More broadly, the results of this study provide resource managers with useful information for anticipating long-term challenges to the management of nekton populations in the face of global climate change and other ecological processes. Large rivers feeding estuaries are especially vulnerable to the effects of global climate change because of the diversity of ways in which climate affects them. Projections with downscaled global climate models indicate that local biota is likely to be subjected to increased water temperature, elevated salinity and sea level, and decreased precipitation and freshwater outflow (Cloern et al. 2011; Feyrer et al. 2011; Brown et al. 2013). The results of this study suggest that the future abundance and distribution of pelagic nekton will likely change correspondingly with changes in temperature, salinity, turbidity, and food supply.

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