

RESEARCH

The Effect of Submersed Aquatic Vegetation on Invertebrates Important in Diets of Juvenile Largemouth Bass, *Micropterus salmoides*

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ABSTRACT

A suite of submersed aquatic vegetation (SAV) species, and especially Brazilian Waterweed (*Egeria densa*), has proliferated rapidly in California's Sacramento–San Joaquin Delta. This expansion is concurrent with population declines in native fish species and increases in many non-native fish species, including Largemouth Bass *Micropterus salmoides*. In this study, we investigated the effect of SAV species composition and *E. densa* specifically on macroinvertebrate communities and juvenile Largemouth Bass diets. Invertebrate communities differed across sites in the Delta, driven primarily by

changes in abundance of the amphipod *Hyaella* sp., oligochaetes, ostracods, and insect larvae of the family Chironomidae. Juvenile Largemouth Bass consistently consumed SAV-associated invertebrates, and preferentially consumed larger taxa, when available. Gut fullness of juvenile Largemouth Bass was lowest in sites dominated by *E. densa*, although there was no clear mechanism for this difference. However, SAV species composition had little effect on abundance of *Hyaella* sp., chironomid larvae, or damselfly naiads, prey items commonly consumed by juvenile Largemouth Bass. Our results suggest that *E. densa* does not provide a qualitative increase in macroinvertebrate food for fishes compared to other SAV species.

KEY WORDS

Submersed aquatic vegetation, non-native species, aquatic macroinvertebrates,

INTRODUCTION

The establishment of non-native species in new locations has long been recognized as a fundamental threat to aquatic biodiversity (Elton 1958; Dudgeon et al. 2006). These introductions are widespread and in some areas accelerating (Cohen and Carlton 1998). Introduced species from disparate native ranges result in novel ecosystems that are intrinsically different

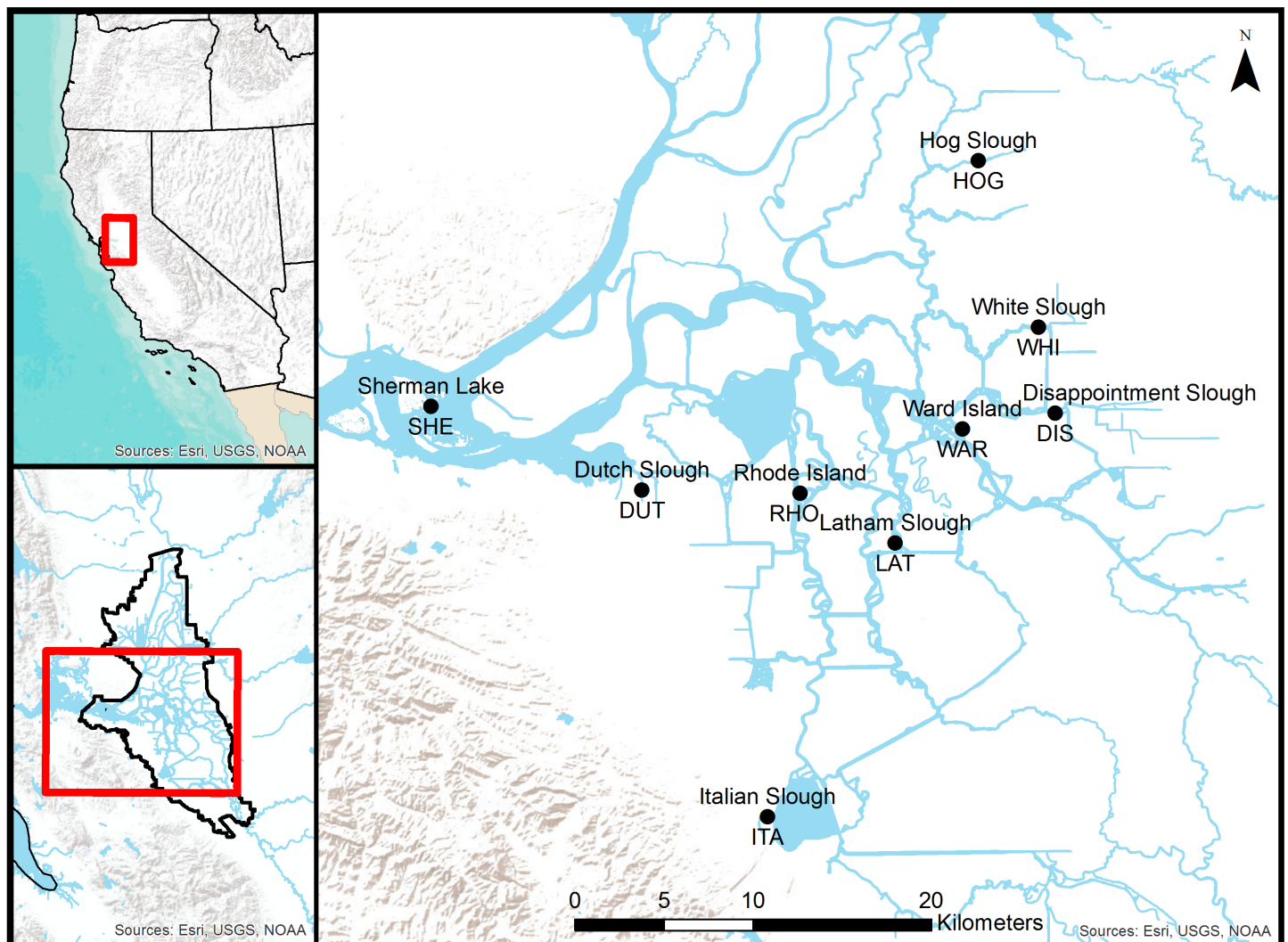


Figure 1 Site map. Points represent sampling locations with both site name and three-letter code. Location within the Sacramento–San Joaquin Delta is shown in inset.

from the original systems, pre-introduction, both for introduced species and natives (Hobbs 2006; Moyle 2014). In these highly invaded ecosystems, interactions among species that share a limited evolutionary history are often difficult to predict (Crooks 2002; Bruno et al. 2005). Native and non-native species may have negative (e.g., Ross et al. 2004), neutral (e.g., Johnson et al. 2009), or even facilitative interactions with each other (Grosholz 2005). Resource and conservation managers therefore find it difficult to react to undesirable changes in species distribution and abundance that could be related to multiple non-native species (Brown 2003).

The Sacramento–San Joaquin Delta (Delta) is the freshwater tidal extent of the San Francisco Estuary (Figure 1), a highly invaded water body (Cohen and Carlton 1995). Non-native fishes, macroinvertebrates, zooplankton, and plants have powerfully affected various components of the system (Nichols et al. 1986; Kimmerer et al. 1994; Matern et al. 2002; and Santos et al. 2011a). These changes to the flora and fauna, coupled with changes to the Delta's aquatic habitats from wetland reclamation and water diversions, have resulted in an ecosystem that bears little resemblance to the Delta that existed before the 1850s (Whipple et al. 2012). One of these non-native invaders, Largemouth Bass (*Micropterus salmoides*),

is a species of particular interest because it is highly predatory and can have myriad effects on systems into which it is introduced (Jackson 2002).

Largemouth Bass were first introduced to California in 1891, and persisted at relatively low levels in the Delta until recent decades; the Delta now supports a world-class recreational fishery (Frantzich 2013). This increase is recent, dramatic, and correlated with other changes that are part of a major ecological shift in the Delta ecosystem (Moyle and Bennett 2008), including native species declines (Brown and Michniuk 2007) and increases in submersed aquatic vegetation (SAV; Conrad et al. 2016). The expansion of non-native SAV into new locales can affect physical, chemical, and biotic aspects of the environment (Carpenter and Lodge 1986; Hershner and Havens 2008; Schultz and Dibble 2012). The most widespread and rapidly-proliferating species in the Delta is Brazilian waterweed (*Egeria densa*), a noted ecosystem engineer (Yarrow et al. 2009). *E. densa* comprises 85% of SAV biomass in the Delta, and has been known to expand its areal coverage by 10% in 1 year (Hestir 2010). The expansion of *E. densa* has led to changes in fish assemblage composition elsewhere (Parsons et al. 2009), and is thought to have facilitated increased populations of many non-native fish species in the Delta, including Largemouth Bass (Brown and Michniuk 2007; Conrad et al. 2016).

SAV can affect fish populations in a variety of ways, including altering food availability, fish foraging behavior and success, refuge availability, and spawning habitat (Carpenter and Lodge 1986; Rozas and Odum 1988); however, the precise mechanisms behind an *E. densa*-mediated population increase in Largemouth Bass are unclear. SAV can be an important nursery habitat for juvenile Largemouth Bass by supporting macroinvertebrates (Durocher et al. 1984; Hoyer and Canfield 1996; Miranda and Pugh 1997), the principal food of juvenile Largemouth Bass in the Delta (Grimaldo et al. 2009) and elsewhere (Miranda and Pugh 1997). This is especially true in summer months, when fishes are small and SAV density and macroinvertebrate production is typically high. Despite the rapid and extensive proliferation of *E. densa*, little is known about Delta SAV-associated macroinvertebrate

communities, and how these macroinvertebrate communities affect juvenile Largemouth Bass.

In this study, we address the following study questions:

1. *What are SAV-associated invertebrate communities in the Delta, and do they differ by region and SAV community?*
2. *How do these communities relate to diets of juvenile Largemouth Bass during the summer growth period?*
3. *Are invertebrate species important in the diets of juvenile Largemouth Bass differentially associated with individual SAV species?*

Answering these questions will allow for a more nuanced understanding of SAV-mediated trophic effects on non-native juvenile fishes.

MATERIALS AND METHODS

Sample Collection and Processing

We collected field samples in August 2010 from nine sites (Figure 1). We sampled in August because juvenile Largemouth Bass are abundant and are actively foraging and growing then, compared to cooler winter and spring months. Using existing data (Conrad et al. 2016), we selected sites prioritized in order of anticipated juvenile Largemouth Bass presence, by a range of moderate-to-high SAV densities, and by variable SAV species composition at the site level (Table 1). Selected SAV beds were large, either extending continuously for kilometers along the shoreline in sampled channels, or widespread for hundreds of meters in sampled shoals. We thus chose invertebrate and SAV sampling locations within each site along a transect that followed the dominant direction of the SAV bed.

We collected fish during the day by boat electrofishing (Smith-Root 18-foot Extra Heavy Duty [EHD] vessel equipped with a 5.0-Generator-Powered Pulsator [GPP] generator) at a constant 7 ± 1 amps along 300-meter transects consistent with the methodology used by Conrad et al. (2016). These electrofishing transects were adjacent, but not overlapping, our invertebrate and SAV sampling locations. The first 40 individual juvenile Largemouth

Table 1 Mean and standard error biomass density of submerged aquatic vegetation by site, and percent composition of different SAV species. EGDE=*Egeria densa*, CEDE=*Ceratophyllum demersum*, ELCA=*Elodea canadensis*, MYSP=*Myriophyllum spicatum*, POCR=*Potamogeton crispus*, Other=*Cabomba caroliniana*, *Potamogeton nodosus*, *Stuckenia* sp.

Site	Density (g m ⁻²)	EGDE	CEDE	ELCA	MYSP	POCR	Other
DIS	541.6 ± 389	90.9 ± 5%	8 ± 4%	0 ± 0%	0 ± 0%	1.2 ± 1%	0 ± 0%
DUT	373.5 ± 118	12.4 ± 8%	21.4 ± 10%	52.8 ± 12%	1.7 ± 1%	11.7 ± 8%	0 ± 0%
HOG	2735.3 ± 646	92.6 ± 7%	7.4 ± 7%	0 ± 0%	0 ± 0%	0 ± 0%	0 ± 0%
ITA	1149.2 ± 383	99.1 ± 0%	0.9 ± 0%	0 ± 0%	0 ± 0%	0 ± 0%	0 ± 0%
LAT	887.6 ± 118	58.7 ± 16%	19.9 ± 13%	4.7 ± 3%	16.7 ± 14%	0 ± 0%	0 ± 0%
RHO	620.5 ± 107	5.6 ± 5%	43 ± 10%	34.9 ± 10%	4.9 ± 4%	11.6 ± 7%	0 ± 0%
SHE	1779.6 ± 718	79.2 ± 11%	0 ± 0%	0 ± 0%	12.1 ± 7%	3.4 ± 3%	5.3 ± 5%
WAR	404.4 ± 92	99.5 ± 0%	0 ± 0%	0 ± 0%	0 ± 0%	0.5 ± 0%	0 ± 0%
WHI	1102.3 ± 466	78.4 ± 11%	21.6 ± 11%	0 ± 0%	0 ± 0%	0 ± 0%	0 ± 0%

Bass were euthanized, preserved on ice, and brought back to the laboratory and frozen immediately. We validated the ages of all fish using sagittal otoliths, keeping only young-of-year fish for analysis (for sample sizes see [Table 2](#)).

After electrofishing, we allowed the area to recover for 1 hour before we collected invertebrate samples. We collected nine invertebrate samples along each transect, spaced 30m apart. These samples were taken using a Marklund (2000) sampler ([Figure 2](#)), which was designed to sample a volume of water and the vegetation and invertebrates contained therein. We

modified the original design by extending the arms to facilitate deployment over the side of a boat. The mouth of the sampler was constructed of sharpened polyvinyl chloride with a diameter of 203 mm, and a gap of 178 mm, which therefore consistently sampled a volume of 5.76L. The mesh size on the sampler was 500 µm. The sampler was slowly lowered into a stand of SAV to minimize disturbance, and closed when a depth of 1 meter was reached and a stand of SAV was within the sampler's mouth. The sharpened edges of the cylinders that held the nets allowed SAV stems to be cut as the sampler closed. Although disturbance of the SAV before the sampler closed may have

Table 2 Mean and standard error of water quality parameters, sample size of collected juvenile largemouth bass, and mean and standard error of juvenile largemouth bass fork length (FL) and fullness score.

Site	Turbidity (NTU)	Temperature (°C)	Specific conductance (µS)	Dissolved oxygen (mg L ⁻¹)	LMB (N)	LMB (FL)	Fullness score
DIS	3.36 ± 0.5	23.75 ± 0.02	391.6 ± 0.2	7.48 ± 0.01	26	66.3 ± 2.5	3 ± 0.2
DUT	8.33 ± 0.81	24.55 ± 0.13	721.2 ± 11.4	9.67 ± 0.01	22	65.3 ± 2.9	3.6 ± 0.2
HOG	8.83 ± 0.3	24.37 ± 0.04	626.9 ± 0.3	8.58 ± 0.01	7	65 ± 9.6	2.4 ± 0.4
ITA	13.26 ± 0.59	20.96 ± 0.02	415.7 ± 0.4	8.1 ± 0.01	32	54.1 ± 2.2	1.9 ± 0.2
LAT	4.24 ± 0.37	23.46 ± 0.03	378.4 ± 1	8.41 ± 0.02	30	60.4 ± 2.4	2.6 ± 0.2
RHO	11.48 ± 0.48	21.79 ± 0.12	443.6 ± 11	9.58 ± 0.01	30	71.1 ± 3.3	3.2 ± 0.2
SHE	23.08 ± 2.3	19.06 ± 0.04	1629.4 ± 6.1	7.08 ± 0.02	4	67 ± 5.6	2.3 ± 0.3
WAR	4.56 ± 0.4	23.28 ± 0.04	336.9 ± 0.4	8.37 ± 0.02	27	64.3 ± 2.7	2.4 ± 0.2
WHI	3.29 ± 0.46	23.18 ± 0.01	331.6 ± 0.4	7.89 ± 0.01	33	56.1 ± 2	2.3 ± 0.3

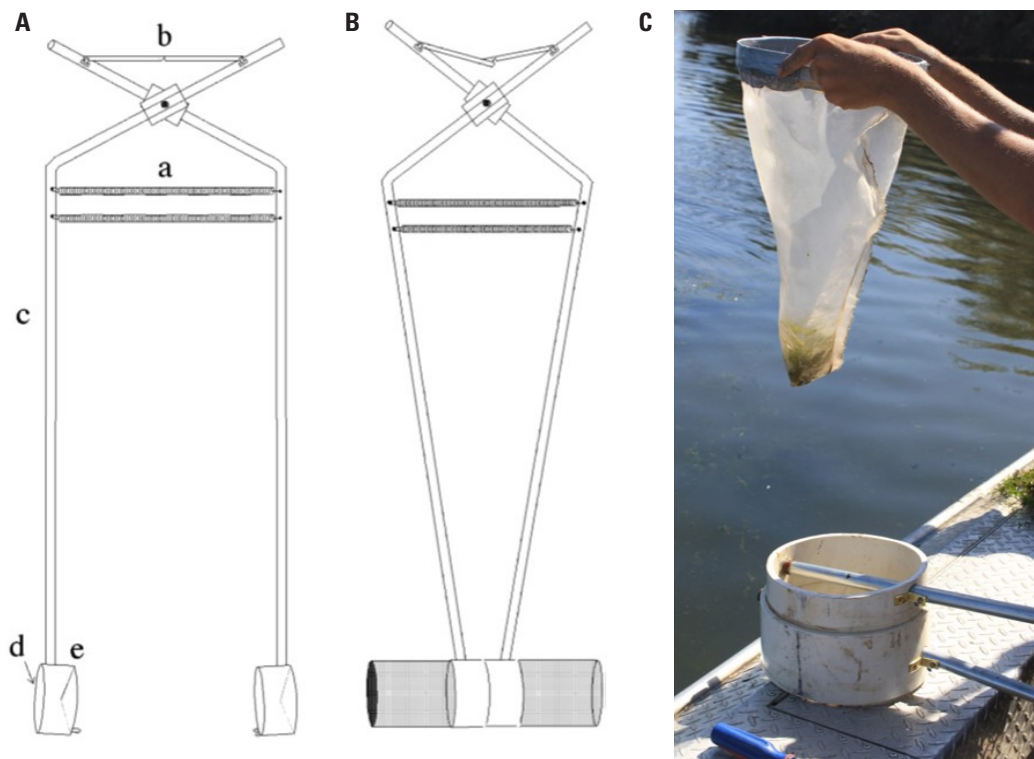


Figure 2 Modified Marklund sampler; image modified from Marklund (2000). **(A)** shows the device prior to closing. Springs (a) cause the device to close quickly, while a brace (b) holds the arms (c) of the device open during positioning. Tucked inside of the sharpened polyvinyl chloride (PVC) hoops at the bottom (e) is a pair of 500 μ m mesh nets (d). **(B, C)** shows the device after it has closed around the vegetation. Springs (a) cause the device to close quickly.

caused some more mobile invertebrates to flee, the presence of small fish (e.g., juvenile Largemouth Bass, Rainwater Killifish *Lucania parva*, Western Mosquitofish *Gambusia affinis*, and Bluegill Sunfish *Lepomis macrochirus*) in many of the samples suggested that disturbance was minimal.

Immediately after collecting the invertebrate sample, we sampled the SAV directly adjacent to each invertebrate sample. We collected this sample using a 16-foot collapsible thatch rake marked for depth. The rake was lowered straight down to the bottom, rotated 360 degrees, and then brought to the surface while being rotated constantly (Kenow et al. 2007). We recorded the depth for each sample, then bagged SAV samples and brought them back to the laboratory where we separated them by species and weighed them. In the field, we preserved all invertebrates and SAV from the Marklund sample in 95% ethanol. We standardized all invertebrate counts by grams of total SAV dry weight in the Marklund

sample. We used the rake sample to identify the SAV community associated with each invertebrate sample.

In the laboratory, we dissected the Largemouth Bass collected in the field, and removed stomachs from all fish. To evaluate stomach fullness, we assigned a category of 0 to 4 that corresponded to percent stomach fullness (0=0%, 1=1–25%, 2=26–50%, 3=51–75%, or 4=76–100%), which we estimated visually. We identified all invertebrates in stomach contents and from the Marklund sample to the lowest practical taxonomic level (Berg et al. 2008; Light 2007), and then enumerated and weighed them. After we obtained wet weights for invertebrates, we dried all samples in an oven for 24 hours at 60°C and weighed them again. We then separated the collected SAV biomass by species and obtained wet and dry weights.

Statistical Analyses

Question 1—What are the Dominant SAV-Associated Invertebrates within the Delta?

Before statistical analysis, we standardized invertebrate abundances by the dry weight of SAV collected in the Marklund sample. To test for community differences across sites, we used a one-factor permutational multivariate analysis of variance (PERMANOVA) with site as a factor; to look for community differences across different vegetation species, we used a PERMANOVA with vegetation type (described below) as a factor and site as a blocking variable (Anderson 2001). Because mono-specific SAV samples were impossible to identify from the surface, we identified dominant vegetation type—two categories: either *E. densa* or Other; defined as whether *E. densa* or a different SAV species had the highest biomass in each sample—in the PERMANOVA analysis. In effect, this tested differences in community composition in samples that were dominated by *E. densa* and those dominated by other species, while taking into account site differences. Using Bray–Curtis dissimilarity coefficients between pairs of samples, PERMANOVA uses all the permutations of the raw dissimilarity coefficients to test for differences in community structure based on a treatment variable. This analysis makes no assumptions about any underlying distribution of the data, and is thus not bound by parametric assumptions. The result is a “pseudo-F statistic” similar in interpretation to a parametric analysis of variance (ANOVA) analyses.

To identify organisms that drove inter-site differences, we used a similarity of percentages (SIMPER) analysis. SIMPER identifies the individual taxa that contribute most to dissimilarity between samples (Clarke 1993). Before running the PERMANOVA and SIMPER analyses, we square-root transformed invertebrate densities to reduce the influence of dominant taxa. All analyses used the package “vegan” in Program R (Oksanen 2015; R Core Team 2015).

Question 2—What are the diets of juvenile Largemouth Bass, and how do they relate to prey availability?

To identify SAV-associated invertebrates that were important in the diets of juvenile Largemouth Bass

across sites, we calculated the percent Prey-Specific Index of Relative Importance (% PSIRI; Brown et al. 2012; Equation 1):

$$\%PSIRI = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2} \quad (1)$$

where %FO equals frequency of occurrence in fish stomachs of prey species *i*, %PN is the numerical abundance divided by the number of stomach samples in which it occurs standardized to 100%, and %PW is the weight divided by the number of stomach samples in which it occurs standardized to 100%. This metric is considered an improvement over conventional IRI for two reasons: (1) %PSIRI does not over-emphasize abundant prey items; and (2), PSIRI is additive over taxonomic levels (Brown 2012). That is, the %PSIRI of a family or prey category will be equivalent to the sum of the %PSIRI of the species within that family. Using habitat associations from Berg et al. (2008) and Light (2007), we categorized invertebrates by broad taxonomic group and into SAV-associated or other (Appendix A). We compared correlations between gut fullness and dominant vegetation species at a site using a Pearson product-moment correlation coefficient and subsequent test for significance corrected using a Bonferroni correction.

To evaluate diet in relation to prey availability for abundant taxa, we used an index of electivity (Ivlev 1964; Equation 2):

$$E_i = \frac{r_i - n_i}{r_i + n_i} \quad (2)$$

where E_i is the electivity of invertebrate species *i*, r_i is the proportion of species *i* in the diet, and n_i is the proportion of species *i* in the environment. Electivity values range from -1 (consumption of species *i* is zero, and the species is present in the environment) to 1 (species *i* was consumed, and it was not sampled in the environment). Electivity calculations excluded copepods and cladocerans because those taxa were poorly sampled by the invertebrate sampler. We choose this particular electivity index because of its simplicity and usefulness in making rank order comparisons within multi-species samples (Lechowicz 1982).

This allowed us to identify species with relatively positive, neutral, and negative electivities for subsequent modeling.

Question 3—Do different species of SAV support different densities of invertebrates important in the diets of juvenile Largemouth Bass?

To address associations of invertebrate taxa with individual SAV species, we identified invertebrate taxa that were common in Largemouth Bass diets and abundant in our samples. Because of inter-site variation in invertebrate abundance, we needed to include this inter-site variability and isolate the effect of different SAV species. We modeled the abundance of each invertebrate taxon as a function of the presence of individual SAV species using a varying intercept generalized linear mixed model (GLMM), which allows for the incorporation of nested groups (or random effects) related to consistent clusters of data (Zuur et al. 2007). In this case, we used site as our random effect, which allowed us to include variation associated with spatial auto-correlation (i.e., invertebrate abundances differed across sites). We included dry weight of SAV sampled as an offset variable, accounting for the amount of vegetation sampled as a measure of effort. Model outcomes are, therefore, in terms of individuals per biomass SAV. The model included dummy variables that corresponded to the presence or absence of each SAV species as predictors (Equation 3). Because the goal of these models was to generate predictions of invertebrate abundance for each individual SAV species, only one SAV species was present in each model, and we included no continuous predictors in this model. The outcome is, thus, in the form of comparative slopes for each dummy variable nested within the random effect (site). This allows us to generate predictions from the model that are based on each dummy variable/SAV species.

$$\text{Invertebrate Abundance} \sim \text{Poisson}(\lambda_i)$$

$$\log \lambda_i = \log(\text{Dry Weight SAV}) + \alpha + \alpha_{\text{Site}[i]} + \beta_1 \text{SAVsp}_i + \beta_2 \text{CEDE}_i + \beta_3 \text{EDGE}_i + \beta_4 \text{ELCA}_i + \beta_5 \text{MYSP}_i + \beta_6 \text{POCR}_i + \beta_7 \text{STSPP}_i \quad (3)$$

We generated predictions for each invertebrate taxon by first simulating a matrix of varying intercepts based on the modeled posterior distribution of our site variable (McElreath 2016). We then used this

matrix of simulated intercepts to generate 2,000 posterior predictions of invertebrate density for each species of SAV. Thus, our predictions are not based on the nine sites we sampled, but instead are averaged over the variation among those sites. We then plotted and compared these posterior predictions using pairwise Tukey honestly significant difference (HSD) tests that used a Bonferroni correction. We ran these models using Hamiltonian Monte Carlo with the package ‘rethinking’ (McElreath 2015) in programs R and Stan (Carpenter et al. 2017). We specified a Poisson distribution, which is commonly used for count data, with a log link (McElreath 2016). All models were computed over 10,000 iterations with a warm-up of 5,000 iterations.

RESULTS

Question 1—SAV-Associated Invertebrate Communities

Seven of nine sites were dominated (>75% biomass; Table 1) by *E. densa*, and the other two sites were dominated by the native species *Elodea canadensis* and *Ceratophyllum demersum*. *C. demersum* was consistently present in sites dominated by *E. densa*, and mono-specific samples other than *E. densa* were rare (6% of collected samples). Water quality across all sites was generally similar, except for Sherman Lake (SHE), which exhibited higher turbidity, lower temperature, and higher specific conductance (Table 2). Total invertebrate densities ranged from 150.6 to 1,762.5 individuals/g SAV (Appendix B). Invertebrate communities across sites were significantly different based on the PERMANOVA analysis (Pseudo- $F_{1,8}=4.159$, P -value <0.001). Invertebrate communities also differed across the two categories of dominant vegetation type, after incorporating site as a blocking factor (*E. densa* and other; Pseudo- $F_{5,63}=1.813$, P -value=0.0074). However, these differences were driven primarily by sites that differed in abundance of a few dominant taxa. The dominant taxon at most locations, both numerically and by weight, was the amphipod *Hyalella* sp. (see Appendix B). The only exception to this was at Sherman Lake (SHE), where oligochaetes of the genus *Stylaria* were numerically dominant. Ostracods were the second-most abundant taxon but were entirely absent at Rhode Island (RHO) and Sherman Lake. For insects, damselflies in the family

Table 3 Similarity percentage (SIMPER) results showing taxa which contributed to inter-site community differences. There were 9 sites compared and thus a total of 36 pairwise comparisons. Table shows mean percent dissimilarities across all pairwise comparisons where contribution was significant, with standard deviation and the number of pairwise differences. Table is organized by decreasing mean percent dissimilarity.

Taxa	Mean	SD	N
<i>Hyalella</i> sp.	18.7%	4.4%	36
Ostracoda	16.6%	5.5%	33
<i>Stylaria lacustris</i>	14.9%	5.8%	36
Chironomidae (L)	11.6%	6.5%	27
Hydrozoa	9.1%	2.9%	16
Turbellaria	7.8%	2.0%	27
Ancyliidae	6.9%	0.8%	2
Acarina	6.5%	1.0%	9
Planorbidae	6.4%	1.0%	13
Physidae	5.6%	0.5%	4
Coenagrionidae (N)	5.2%	0.2%	2

Coenagrionidae (Order Zygoptera) were dominant by weight, while flies in the family Chironomidae were dominant numerically. Ward Island (WAR) and Dutch Slough (DUT) had relatively high densities of insect larvae (Chironomidae and Trichoptera) and naiads (Zygoptera and Ephemeroptera). Sherman Lake, our furthest west and most saline site, had low abundance of primarily freshwater insect naiads (Zygoptera, Ephemeroptera) and *Hyalella* sp. These *E. densa*-dominated sites exhibited higher densities of aquatic arachnids (Acarina and Araneae), turbellarians and hirudineans. Caddisfly (Trichoptera) densities were higher in sites dominated by other SAV species. The SIMPER analysis identified eleven invertebrate taxa as contributing to dissimilarities across dominant sites (Table 3); major contributors were: *Hyalella* sp. (19% average dissimilarity across sites), ostracods (17%), *S. lacustris* (an oligochaete, 15%), chironomid larvae (12%), and snails (Physidae 6% and Planorbidae 6%).

Question 2—Juvenile Largemouth Bass Diets

We collected 211 Largemouth Bass across all nine sites (Table 2). As a result of digestion, most diet contents were not identifiable to the same level as the invertebrate samples. Diet analysis showed

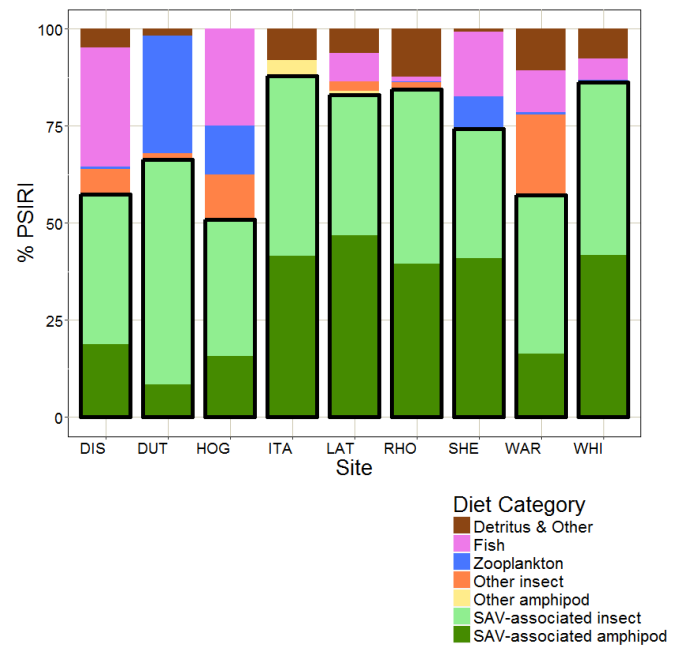


Figure 3 Percentages of major items in the diet of juvenile Largemouth Bass by site, expressed as percent prey-specific index of relative importance (%PSIRI). SAV-associated invertebrates are denoted by a thick border. See Figure 1 for site abbreviations and Appendix B for explanation of diet categories.

that SAV-associated amphipods and zygopteran naiads (primarily the family Coenagrionidae) were overwhelmingly important diet items across all sites, regardless of dominant vegetation species (Figure 3; Appendix C). In all sites in which zygopterans occurred in gut contents, they were greater than 16% PSIRI. Sherman Lake was the only site at which zygopterans did not occur in fish diets, and invertebrate sampling at this site revealed extremely low densities of zygopterans in SAV stands. *Hyalella* sp., a native SAV-associated amphipod, was greater than 8% PSIRI at all sites, reaching as high as 41% PSIRI at Sherman Lake. *Gammarus daiberi*, a non-native amphipod, comprised 21.5% PSIRI at Latham Slough and 14.7% PSIRI at Rhode Island. Fish were consumed at seven sites, and contributed more than 10% PSIRI at four sites (Disappointment Slough: 30.7%, Hog Slough: 25%, Sherman Lake: 16.7%, Ward Island: 10.8%). Largemouth Bass and *Lepomis* sp. were the most important fish prey items consumed. Smaller prey items (i.e., copepods and cladocerans) were important contributors at Dutch

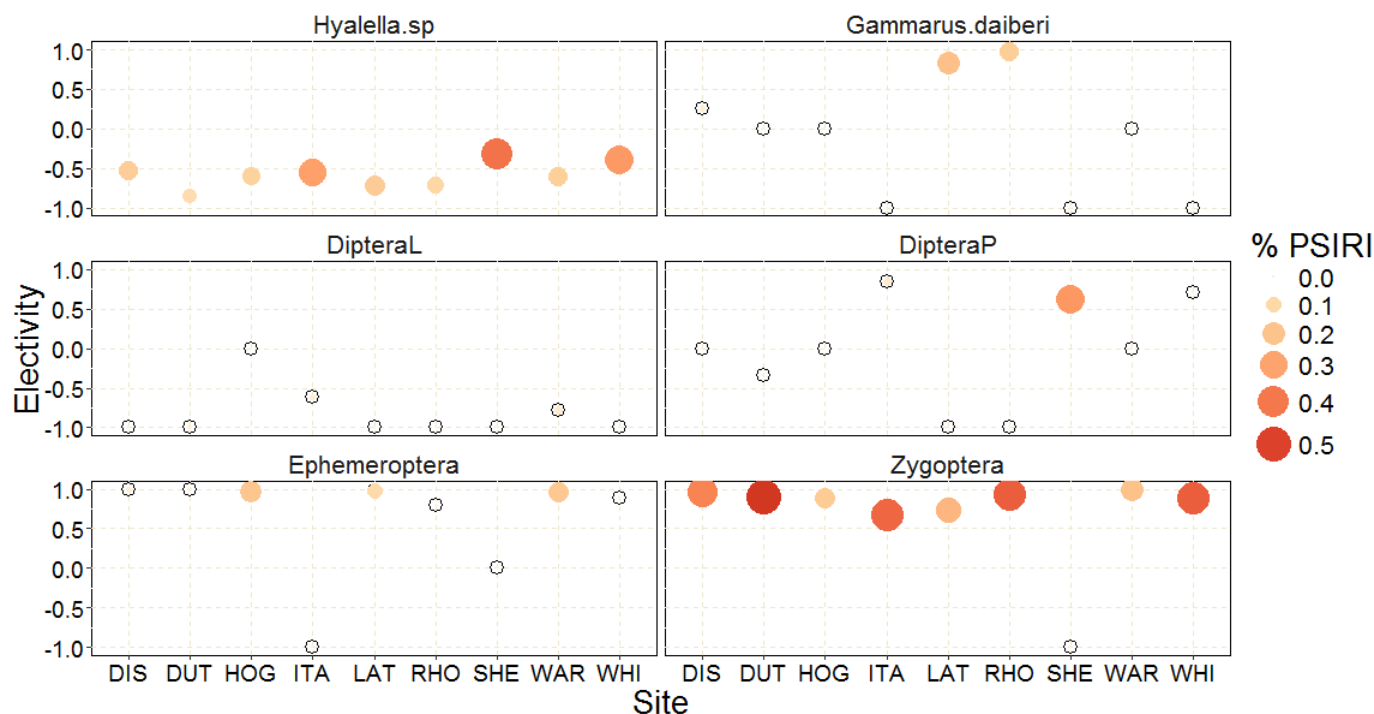


Figure 4 Electivity for common diet items of juvenile Largemouth Bass. Positive values denote consumption in higher proportion than sampled in invertebrate samples, negative values denote consumption in lower proportion. The size of the point is scaled to %PSIRI. Black circles surround points which are less than 5% of PSIRI.

Slough (cladocerans: 34%), Hog Slough (cladocerans: 17%), and Sherman Lake (copepods: 11%).

Electivity results showed that juvenile Largemouth Bass selectively consumed large-bodied insect naiads (Zygoptera and Ephemeroptera) at all sites where they were abundant (Figure 4). Larger amphipod species (*G. daiberi* and *A. spinicorne*) were sampled in low abundance, but were typically preferred when present. *Hyalella* sp. was generally consumed less frequently than expected, given its abundance in the environment, although it was still an important component of the diet. Both larval and pupal stages of Diptera (including chironomids) were consumed less frequently than expected, given environmental abundance. The primary exception to these trends was at Sherman Lake, where *Hyalella* sp. and Diptera pupae dominated diets. In general, electivities were consistent across sites, with larger prey items consumed more frequently than expected.

Gut fullness of juvenile Largemouth Bass varied across sites, although all but one site had fullness indices averaging two or higher (meaning >50%

fullness; Table 2). Dutch Slough and Rhode Island had the highest fullness indices (3.6 ± 0.2 and 3.2 ± 0.2 , respectively); Italian Slough had the lowest (1.9 ± 0.3 ; Table 3; Appendix C). Dutch Slough and Rhode Island, both sites characterized by diverse SAV communities that were not dominated by *E. densa* (<20% biomass), had the highest fullness indices. Across all sites, average gut fullness was negatively correlated with percent biomass of *E. densa* (P -value = 1.16×10^{-6} ; Appendix C), and positively correlated with percent biomass of *C. demersum* (P -value = 1.4×10^{-4}) and *E. canadensis* (P -value = 1.47×10^{-6} ; Appendix C) but not total SAV biomass (P -value = 0.07).

Question 3 – SAV Species and Largemouth Bass Diet Items

We identified three invertebrate taxa that were both important in juvenile Largemouth Bass diets (>25% PSIRI at any one site) and environmentally abundant (present in greater than 80% of samples). These three taxa were *Hyalella* sp., coenagrionid naiads (Zygoptera), and various life stages of the

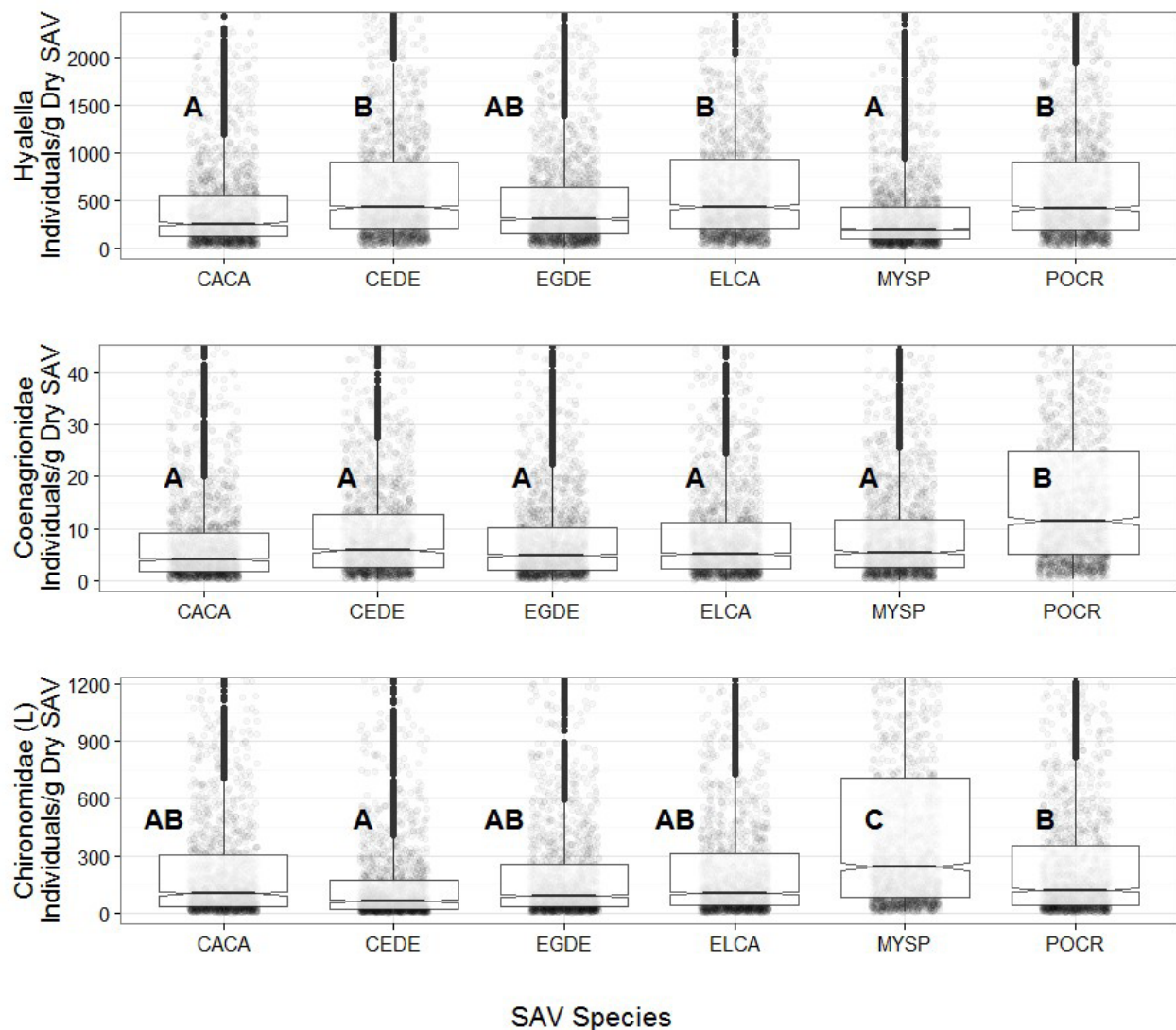


Figure 5 Points represent 2000 predicted densities of invertebrate taxa based on GLMM results. Predicted densities include inter-site variability, hence the wide range. Boxplots denote medians and 25% and 75% interquartile ranges. Letters show the results of pairwise Tukey HSD tests, with letters corresponding to differences between group means. Note high similarity among most SAV species. CACA = *Cabomba caroliniana*, CEDE = *Ceratophyllum demersum*, EGDE = *Egeria densa*, ELCA = *Elodea canadensis*, MYSP = *Myriophyllum spicatum*, POCR = *Potamogeton crispus*.

family Chironomidae. Predicted densities of each invertebrate taxon differed significantly across only a few vegetation species (Figure 5). *Hyalella* sp. densities were lowest in *Cabomba caroliniana* (median predicted density 310.1 individuals/g dry weight) and *M. spicatum* (224.2 ind./g), and did not differ significantly across other vegetation species. Predicted coenagrionid (Zygoptera) densities were highest in *P. crispus* (13.2 ind./g), with no significant differences between other species.

Predicted chironomid larvae densities were lowest in *C. demersum* (63.4 ind./g) and highest in *M. spicatum* (265.8 ind./g). Most SAV species did not exhibit significantly different predicted invertebrate densities. This suggests that the species of vegetation does not much affect the abundance of invertebrates that are important in the diets of Largemouth Bass.

DISCUSSION

Despite the rapid proliferation of SAV and SAV-associated littoral fishes (Brown and Michniuk 2007; Conrad et al. 2016), little is known about mechanisms by which SAV may affect those fishes. In this study, we demonstrate that juvenile Largemouth Bass consume primarily SAV-associated invertebrates, suggesting that SAV is high-value foraging habitat. However, different SAV species minimally affect the abundance of invertebrates common in the diets of juvenile Largemouth Bass.

Invertebrate Communities

SAV-associated invertebrate communities were dominated by non-insect invertebrates, consistent with other studies of littoral invertebrate communities in the Sacramento–San Joaquin Delta (Toft et al. 2003) and other tidal freshwater deltas (Chaplin and Valentine 2009). Invertebrate communities differed across sites, although many of these inter-site differences were driven by the rarity at a subset of sites of a few otherwise dominant taxa. The variation of these taxa likely reflect existing estuarine gradients in salinity, because salinity variation can influence tidal macroinvertebrate communities (Strayer 2007).

Based on PERMANOVA results, invertebrate communities also responded to differences in dominant vegetation type. Community changes across vegetation species are common, although the underlying causes can be varied. For example, differences in plant complexity (e.g., leaf shape, fractal dimension) are often associated with differences in invertebrate biomass and diversity (Krecker 1939; Cheruvilil et al. 2002; Taniguchi et al. 2003; Chaplin and Valentine 2008). Sampled SAV species have documented structural differences in leaf shape and fractal dimension, with *E. densa* more structurally complex than *M. spicatum* (Dibble et al. 1996) and less complex than *C. demersum* (Ferreiro et al. 2011); thus, different community composition is not unexpected.

One element of variability not taken into account in this study is the possible effect of SAV patches directly adjacent to sampling locations. Community variations can occur on multiple scales, including

within an individual habitat patch, across patches, and across sites (Dibble et al. 2006; Santos et al. 2011). For example, in addition to structural differences between SAV species, these invertebrate community differences may reflect the propensity of *E. densa* to grow in high densities and in larger, more continuous patches than other sampled SAV species (Santos et al. 2012). Total biomass and patch size have been shown to have a large influence on invertebrate communities (invertebrates and seagrass, Attrill et al. 2000; amphipods on marine algae, Russo 1990; freshwater submersed macrophytes, Cyr and Downing 1988a, 1988b).

Fish Diets and Fullness

Macroinvertebrates dominated the diets of juvenile Largemouth Bass across all sites. This is consistent with other studies in the Delta (Grimaldo et al. 2009; Kelly Wienersmith unpublished data) and elsewhere (Moyle 2002). When available, juvenile Largemouth Bass preferred larger prey items, as evinced by the positive electivity values for insect naiads. Although diets and electivities were relatively consistent across sites with differing dominant SAV species, gut fullness varied inversely with the abundance of *E. densa*. This suggests that *E. densa* may provide lower-quality foraging habitat for SAV-associated fishes compared to other SAV species. *E. densa* grows in high natural densities relative to other SAV species, particularly the native *E. canadensis* and *C. demersum* (Louise Conrad, unpublished data), a trait associated with decreased foraging success in other centrarchids (Dionne and Folt 1991) and adult Largemouth Bass (Ferrari et al. 2014). Other studies have documented a decline in foraging success of Largemouth Bass and other centrarchid fishes with increases in SAV density because the accessibility of prey items declines (Heck and Crowder 1991; Valley and Bremigan 2002; Chaplin and Valentine 2009), suggesting that this difference in growth habit may be associated with decreased gut fullness in juvenile Largemouth Bass sampled in *E. densa*-dominated sites.

Gut fullness observed in this study may possibly reflect diel feeding cycles, because Largemouth Bass and other predatory fishes typically exhibit consistent crepuscular feeding cycles. However, diurnal feeding is more common in juvenile Largemouth Bass (Eliot

1976), suggesting that a time-of-day effect would be less pronounced for juveniles. It is important to note that gut fullness for juvenile Largemouth Bass across all sites was above 50%, regardless of dominant SAV species or time of day. This suggests that, despite the lower gut fullness, *E. densa* still provides plenty of food resources for foraging juvenile fishes, and thus differences across different SAV species may not be ecologically meaningful.

The proliferation of *E. densa* has made it the dominant foraging habitat in the Delta. This resultant abundance may provide a more consistent – if less accessible – food source, supporting large populations of invertebrates and allowing for increased overwintering survival of juvenile Largemouth Bass (Miranda and Pugh 1997). Also, the same mechanism that presumably limits juvenile Largemouth Bass foraging (i.e., dense cover) also likely limits predation on juvenile Largemouth Bass by adults. Predation rates on juvenile Largemouth Bass decline as SAV density increases (Ferrari et al. 2014), suggesting that this high-density SAV will reduce cannibalism and result in higher survival rates for juvenile Largemouth Bass.

SAV Support of Diet Items

Despite observed variability in SAV biomass, SAV species composition, and invertebrate assemblages across sites, we observed only minor variation in abundance of invertebrate taxa that were generally important in Largemouth Bass diets. This was unexpected, given morphological differences across the different SAV species, and given that there are differences in the abundance of other invertebrate taxa across different floating aquatic vegetation species (Toft et al. 2003). This may reflect multi-scale invertebrate community dynamics, where adjacent patches modify our sampled community. Unlike floating aquatic vegetation in the Delta, monospecific SAV stands are rare to absent, and, instead, multiple species are found in relatively close proximity (i.e., less than 10 meters), and thus it is impossible to completely rule out the effect of other SAV species.

It is also important to note that this study only looked at late-summer fish diets and invertebrates; the relationship between SAV and invertebrates may change seasonally as a result of a variety of

factors. Senescing SAV may decrease stand density, thus increasing accessibility and foraging success, or reflect invertebrate population changes, thus altering food availability for juvenile Largemouth Bass. Further seasonal shifts in local invertebrate abundance may result from other environmental factors such as seasonal salinity intrusion (Chadwick and Feminella 2001; Howe et al., 2014) and invertebrate population dynamics (Cooper 1965).

However, based on this study, *E. densa* does not seem to provide fundamentally different habitat for invertebrates important in fish diets during summer growth periods. These summer growth periods support lipid accrual that is crucial to juvenile Largemouth Bass overwintering survival (Ludsin and DeVries 1997), particularly in environments with an abundance of piscivorous predators, including adult Largemouth Bass (Garvey et al. 1998). This suggests the possibility that, even as the SAV assemblage changes on spatial and annual scales (Boyer and Sutula 2015), different SAV species may be functionally equivalent in their support of juvenile Largemouth Bass and other fishes reliant on the same prey items during the key summer growth period.

CONCLUSIONS

SAV, Food Webs, and Restoration

The recent expansion of SAV provides large standing stocks of SAV biomass, presumably supporting SAV-associated prey items and increasing the availability of SAV-based foraging areas. This habitat expansion currently supports a food web that likely functions differently than in previous periods along the Delta's historic trajectory. Although it is difficult to quantify the difference between current and past Delta littoral food webs, littoral productivity is currently substantial (Grimaldo et al. 2009; Young 2016). The freshwater Delta's littoral zone has increasingly come to resemble a novel ecosystem (*sensu* Hobbs 2006) in which non-native species of vegetation support large populations of native invertebrates, which in turn support populations of native and non-native fishes, including Largemouth Bass. Many additional species, including Bluegill Sunfish, Golden Shiner *Notemigonus crysoleucas*, Tule Perch *Hysterocarpus traski*, and Prickly Sculpin *Cottus asper*, are highly dependent on littoral and SAV-associated insects,

amphipods, and other epibenthic invertebrates (Feyrer et al. 2003; Toft et al. 2003; Nobriga and Feyrer 2007; Grimaldo et al. 2009; Howe et al. 2014; Young 2016). Many of these species exhibit healthy populations, with non-native littoral fishes (e.g., Bluegill Sunfish and Golden Shiner) expanding in the south, east, and central Delta (Brown and Michniuk 2007), and native littoral fish populations (e.g., Tule Perch and Prickly Sculpin) maintaining populations in the Delta's western and northern extents (Moyle et al. 2012; Young et al. 2015)— all densely vegetated areas.

The success of these littoral fishes probably relates to increased food availability and habitat availability. The degree to which this is comparable to productivity associated with emergent wetland vegetation or pelagic phytoplankton is unclear, and necessitates explicit comparisons of productivity associated with non-native SAV and productivity associated with emergent wetland vegetation and other sources. Additionally, a great deal of uncertainty surrounds the effects of seasonally senescing SAV in the Delta, and what that may mean for SAV-associated macroinvertebrates and the fishes that rely on them. To identify the value of different vegetation types to fishes and restoration efforts, further studies that quantify invertebrate production in SAV and other types of vegetation across different seasons are important.

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