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ARTICLE

Novel Species Interactions in a Highly Modified Estuary: Association of Largemouth Bass with Brazilian Waterweed *Egeria densa*

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Abstract

Frequent invasions in coastal ecosystems result in novel species interactions that have unknown ecological consequences. Largemouth Bass *Micropterus salmoides* and Brazilian waterweed *Egeria densa* are introduced species in the Sacramento–San Joaquin River Delta (the Delta) of California, a highly modified estuary. In this system, Brazilian waterweed and Largemouth Bass have seen marked increases in distribution and abundance in recent decades, but their association has not been specifically studied until now. We conducted a 2-year, bimonthly electrofishing survey with simultaneous sampling of water quality and submerged aquatic vegetation (SAV) biomass at 33 locations throughout the Delta. We used generalized linear mixed models to assess the relative influences of water temperature, conductivity, Secchi depth, and SAV biomass density on the abundance of both juvenile-sized and larger Largemouth Bass. Water temperature had a positive relationship with the abundance of both size-classes, but only juvenile-sized fish had a positive association with SAV biomass density, with highest abundances at intermediate SAV densities. In contrast, larger fish were generally ubiquitous across all sampling

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conditions, even when SAV was absent or present at low densities. Our results on the Largemouth Bass–SAV relationship are consistent with those of previous studies from lake systems within the Largemouth Bass’s native range, where they interact with a different SAV species assemblage. These results are supportive of the hypothesis that the proliferation of Brazilian waterweed has expanded Largemouth Bass rearing habitat in the Delta. Finally, this study has implications for tidal wetland restoration plans for the Delta, suggesting that the larger-sized Largemouth Bass may still inhabit restored areas even if invasive SAV establishment is limited.

Estuarine ecosystems suffer frequent and rapid species invasions because they are foci of commerce and recreational activities that are vectors for invaders (Ruiz et al. 2000; Weigle et al. 2005; Wonham and Carlton 2005). This influx of introduced species results in unique species assemblages that have novel interactions with unknown ecological outcomes (Seastedt et al. 2008). In some cases, these novel species interactions are characterized by mutual facilitation, leading to “invasional meltdown” scenarios in which entire communities become dominated by invasive species (Simberloff and Von Holle 1999). Given the potential for such widespread impacts, novel species interactions need to be understood and managed, particularly in highly modified ecosystems targeted for restoration (Hobbs et al. 2009; Suding 2011; Moyle 2014).

In this study, we explored the habitat associations of an introduced top predator, Largemouth Bass *Micropterus salmoides*, in the Sacramento–San Joaquin River Delta (the Delta) of California (Figure 1), particularly with respect to Brazilian waterweed *Egeria densa*, a prolific aquatic macrophyte invader. While Largemouth Bass habitat associations have been well studied in lake systems within the species’ native range (e.g., Hoyer and Canfield 1996; Maceina and Bettoli 1998; Johnson et al. 2014), less work has been done on estuarine populations, particularly where the species is introduced and exists within a novel community. Although Largemouth Bass is typically a freshwater species, coastal populations are also common: studies from the Mobile–Tensaw Delta of Alabama (which is within their native range) suggest that Largemouth Bass can adapt to variable salinity conditions (Meador and Kelso 1990; Lowe et al. 2009; Norris et al. 2010) and that they may not move to freshwater even when salinity exceeds 10‰. However, along the Pacific coast, where Largemouth Bass are introduced, increasingly abundant, and occur in highly invaded systems within unique species assemblages, their distributions are not well studied. An understanding of their ecology in these areas is important for invasive species management, given their potential for far-reaching impacts in other systems where they are introduced (Cucherousset and Olden 2011; Maezono and Miyashita 2003).

Largemouth Bass have existed in the Delta for over 100 years (Lee 2000; Moyle 2002) but have seen a remarkable increase in abundance only in recent decades (Brown and Michniuk 2007). The Delta now supports a world-renowned recreational fishery for Largemouth Bass (Frantzich 2013). Their expansion has taken place in the context of major

ecological shifts, including an accelerating rate of species invasions, leading the Delta to become one of the most invaded estuaries in the world (Cohen and Carlton 1998). The

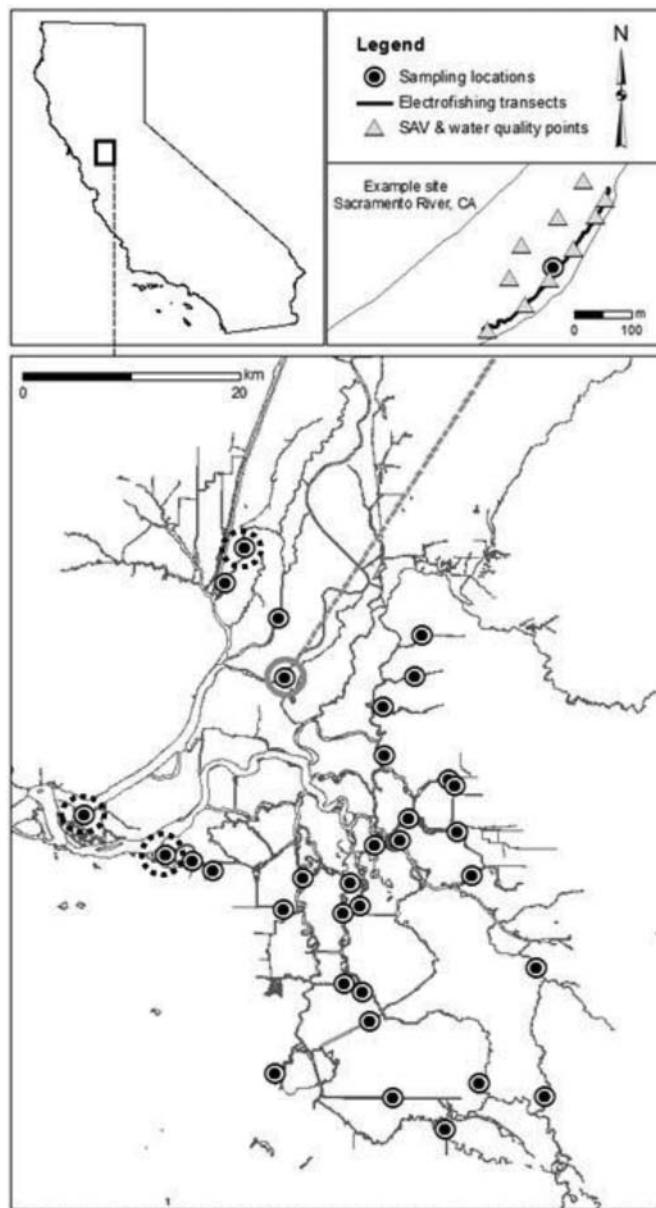


FIGURE 1. Sampling site locations in the Sacramento–San Joaquin Delta. An inset shows an example electrofishing transect with SAV and water quality sampling points. Sites encircled by dashes were added in February 2009.

Delta has tremendous socioeconomic importance, as it provides water for over 25 million Californians and irrigation for a multibillion dollar agricultural industry with international exports (Arthur et al. 1996). It is also home to a diverse assemblage of native species, some listed as threatened or endangered under the California and federal Endangered Species Acts. However, land reclamation for municipal or agricultural use has transformed the once vast tidal wetlands and floodplains into a network of leveed channels (Whipple et al. 2012). Salinity and turbidity patterns have also changed. Historically, salinity was highly variable, but the Delta is now managed for freshwater conditions in order to maintain water quality for human use (Moyle et al. 2010). Construction of upstream dams, followed by extreme flushing events, have changed the Delta from historically turbid conditions (Schoellhamer et al. 2012) to a sediment-starved state (Wright and Schoellhamer 2004; Hestir et al. 2013). Widespread expansion of invasive submerged aquatic vegetation (SAV), composed primarily of Brazilian waterweed, may have contributed to the water clearing (Hestir 2010) by reducing water velocity and limiting sediment resuspension (Mazzeo et al. 2003).

The main hypothesis for the recent Largemouth Bass population increase is that their habitat expanded with the concurrent proliferation of Brazilian waterweed (Nobriga 2009). This SAV species was established in the Delta by the 1980s (Brown and Michniuk 2007) and has since expanded its distribution, reaching a coverage in some years of 12% of the waterways (Hestir et al. 2008; Hestir 2010). Brazilian waterweed is the dominant submerged aquatic macrophyte in the Delta because it can outcompete other SAV species (Santos et al. 2012). Its relatively recent spread is a major change in shallow-water habitats because historical accounts only refer to emergent vegetation such as tules *Schoenoplectus* spp. (Whipple et al. 2012).

Despite their concurrent increase, the association of Largemouth Bass and Brazilian waterweed has not yet been quantified. Intensive invasions of aquatic plants often increase macroinvertebrate and fish densities (Schultz and Dibble 2012) because the increased biomass and surface area stimulate the food web, benefiting multiple trophic levels (Bickel and Closs 2008). However, previous work in other systems suggests that the relationship between Largemouth Bass abundance and SAV depends on Largemouth Bass age and the particular ecological system. In Florida and West Virginia lakes, age-0 abundance is generally higher where SAV coverage is higher (Hoyer and Canfield 1996; Maceina 1996; Tate et al. 2003) or reaches a peak at intermediate SAV levels (Miranda and Pugh 1997; Allen and Tugend 2002). In some cases the relationship between adult Largemouth Bass and SAV is positive (Smith and Orth 1992; Bettoli et al. 1993), but other studies report a parabolic relationship (Wiley et al. 1984; Maceina 1996) or no relationship at all (Hoyer and Canfield 1996; Allen et al. 2003).

Along with species invasions, abiotic changes in the Delta have brought about a new state of the ecosystem characterized by increased water clarity, reduced salinity variability, and

increased abundance of invasive species, including aquatic macrophytes and nearshore predators such as Largemouth Bass (Brown and Michniuk 2007; Moyle and Bennett 2008; Hestir 2010; MacNally et al. 2010). These changes make the Delta an apt system to examine how ecosystem stressors play out in novel species interactions. Furthermore, recent California legislation has established water supply reliability and ecosystem restoration as “co-equal” goals (Sacramento–San Joaquin Delta Reform Act 2009). Restoration required by this mandate aims to create favorable habitat for native species as opposed to introduced species such as Largemouth Bass, requiring an understanding of species interactions and the drivers of species’ distributions.

To understand the factors driving the distribution of Largemouth Bass in the Delta and, in particular, the relationship between Largemouth Bass and invasive SAV, we sampled the abundance of Largemouth Bass across a range of SAV biomass densities and water quality conditions over a 2-year period. An understanding of the factors associated with the current high abundance levels of Largemouth Bass in the Delta will inform the management of this introduced predator as efforts progress toward ecosystem restoration.

METHODS

Field methods.—We conducted bimonthly sampling for Largemouth Bass, SAV biomass, and water quality between December 2008 and October 2010. We selected sampling sites using a stratified random process that was based on existing maps of annual SAV distribution. The Center for Spatial Technology and Remote Sensing of the University of California–Davis created these maps every June from 2004 through 2008 using aerial hyperspectral imagery (Hestir et al. 2008). Using these maps and bathymetry data for the Delta, we created a base map in ArcGIS such that sampling locations would have the following criteria: (1) SAV was detected at least once during the 2004–2008 surveys; and (2) water depth was no greater than 3 m (2008 bathymetry data from California Department of Water Resources; <http://baydeltaoffice.water.ca.gov/modeling/deltamodeling/modelingdata/DEM.cfm>), as this was considered a limit for effectively visualizing and capturing stunned fish during electrofishing. The criterion for SAV presence ensured that we sampled in areas that were potentially SAV habitat but not that SAV would be present at the time of sampling because SAV distribution varies seasonally and interannually (Santos et al. 2012). Using these criteria, we generated a list of 50 random points as potential sampling locations. We screened these points to eliminate locations that were not logistically feasible or that were too close together, keeping a minimum distance of 1 km between locations. This screening reduced the number of sites to 30. In February 2009, we added 3 sites from the original set of random points to ensure adequate representation in the western and northern Delta areas, such that the full data set includes 33 sites (Figure 1).

We conducted surveys in all weather conditions except heavy rain or wind, which would have limited boat operability or the visibility of stunned fish; in these cases, we returned to missed sites within 2 weeks of their scheduled sampling day, although rescheduling was not possible for two sites in December 2008. We used an electrofishing boat (Smith-Root, 5.48 m long, equipped with a 5.0 generator-powered pulsator electrofisher) to sample the fish community. This method allowed us to sample a large number of sites and cover a wide range of habitats—unlike other methods like beach seining, which cannot effectively sample densely vegetated areas.

At each sampling location, we electrofished along a 300-m transect, recording the transect line in a Global Positioning System data logger (Trimble GeoXT Series; accuracy within 1 m) in order to sample the same transect at each site visit. We conducted electrofishing at 6–10 A (50–500 V, 20–80% of range). Most sites were adjacent to the shoreline; the exceptions were some locations in previously reclaimed wetland areas that have since experienced levee failure, resulting in large expanses of shallow water. Two netters captured stunned fish and placed them in an onboard live well. We measured all of the Largemouth Bass, except in seven instances when we caught an exceptionally large number and time did not permit measuring every fish. In these instances, we measured a minimum of 20% of the catch by first counting them, then returning them to the live well and haphazardly netting individual fish for measurement after agitating the water to minimize size bias in the subsample. We followed an animal handling protocol approved by the University of California–Davis Institutional Animal Care and Use Committee (accredited by the Association for Assessment and Accreditation of Laboratory Animal Care, Protocol 16617).

After electrofishing, we sampled the SAV biomass density every 60 m at six points along the transect and at four parallel points 60 m away from the transect (Figure 1). If the sampling area was less than 60 m wide, we collected these off-transect samples a minimum of 40 m away from the transect or not at all. In open-water areas, we collected a set of off-transect samples on each side of the transect. We used a 4.8-m handheld threshing rake (base width of 35 cm with fourteen 5.5-cm-long metal teeth on either side) to collect SAV samples. We lowered the rake straight down, rotated it 360° while in contact with the bottom, and then continually rotated it while raising it to the surface. This method provided a standardized area for SAV collection (0.101 m²), affording an estimation of SAV biomass density (Kenow et al. 2007). This method provided a quantitative measure of SAV density, and was unbiased—unlike visual estimates of percent cover, which are subjective and highly dependent on visibility. In the laboratory, we rinsed and separated the SAV samples by species and recorded wet weight. We calculated the dry weight of each species based on published wet : dry weight conversions (Santos et al. 2011).

We obtained vertical water quality profiles at every SAV sampling point with a YSI 6920 multiparameter sonde that

recorded temperature and conductivity every 0.5 s. Before electrofishing, we took a single Secchi depth measurement (nearest 0.1 m) at the start of the fishing transect, in the shade of adjacent trees or the boat. If the water was too shallow or densely vegetated at the transect, we took the Secchi depth at the nearest possible location. We recorded the GPS points for the samples to ensure that the sampling locations were the same at every site visit.

Data processing.—Because Largemouth Bass habitat associations are likely to vary with fish size (Hoyer and Canfield 1996), we partitioned the Largemouth Bass catch into two size-classes by visually examining length-frequency distributions. We created length-frequency distributions with 1-mm size bins for each sampling month and determined a maximum fork length (FL) for the smallest size-class (defined by the first peak in frequency), following methods in DeVries and Frie (1996). Every month of sampling had an obvious peak in frequency for the smallest fish in the sample. Fish that were below the maximum FL of this first peak were most likely young of the year; however, we do not assume a specific age because size-at-age data were not available. We refer to all fish below the maximum FL for a given month as “juvenile-sized,” while all fish above this FL are “larger” individuals. The sample size ranged from 275 to 1,593 individuals per sampling month, and the maximum FL for the juvenile-sized fish ranged from 52 mm (June 2010) to 153 mm (December 2008; see Table A.1 in the appendix). For the seven instances in which we subsampled the FL measurement, we determined the proportions of the juvenile-sized and larger size-classes for the site from the measured fish and then applied these proportions to the unmeasured fish to obtain total numbers for each size-class.

We screened the water quality data by removing all values outside of the 2.5th and 97.5th quantiles for each profile to ensure that the data did not include any values accidentally recorded while the sonde was out of the water or during sensor equilibration. We used the remaining data to calculate the mean water temperature and conductivity for each site visit.

Given the dominance of Brazilian waterweed throughout the sampling period (Figure 2), we lumped SAV biomass values for all macrophyte species and calculated the average SAV biomass density for each site visit.

Statistical analyses.—We used a series of generalized linear mixed models (GLMMs) to evaluate the relative influences of water quality, SAV biomass density, and time of year on the juvenile-sized and larger Largemouth Bass catch per transect. The GLMM approach allows nonnormal distributions and estimates parameters for both fixed effects (factors pertinent to the central study questions) and random effects (factors such as site location that describe the variability in the response to fixed effects; Bolker et al. 2009). We specified a negative binomial distribution (Hilbe 2007) in order to account for overdispersion (O’Hara and Kotze 2010), with site location as a random effect. Transect length was an “offset” variable, as there was modest variation among sites and sampling months.

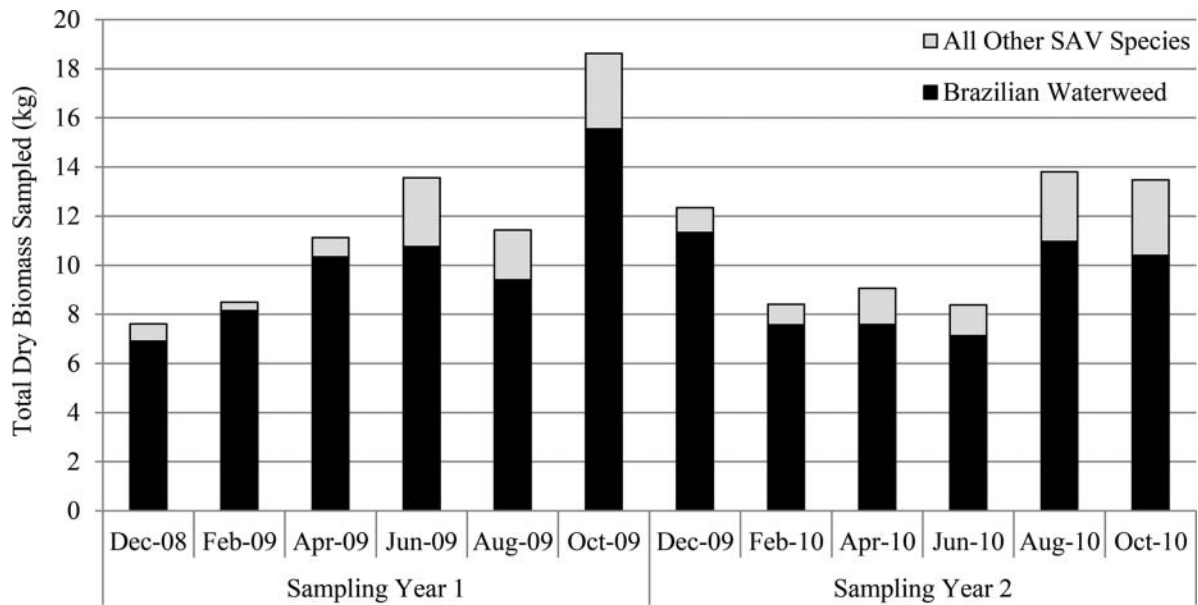


FIGURE 2. Total SAV biomass for Brazilian waterweed and all other aquatic macrophyte species sampled during each sampling month.

We included as fixed effects of sampling month (December, October, February, April, June, or August), sampling year (December 2008–October 2009 = year 1 and December 2009–October 2010 = year 2), water temperature, conductivity, Secchi depth, and SAV biomass density as linear predictors in the model. We z -score transformed water temperature, conductivity, and SAV biomass for each site visit within each sampling month in order to compare the relative influence of each variable. We prescreened all predictor variables for collinearity by calculating variance inflation factors, treating values <2.0 as indicating that variables were not collinear (Zuur et al. 2009). Given existing evidence for a parabolic relationship between SAV and Largemouth Bass abundance (Wiley et al. 1984; Miranda and Pugh 1997; Allen and Tugend 2002), we added a squared term for the effect of SAV; a positive linear (first-degree) term with a negative squared (second-degree) term indicated a maximum at intermediate SAV densities.

We ran parallel sets of 64 candidate models for each size-class that included all possible additive models for fixed effects, that is, all single-term models, all combinations of variables for two-, three-, four-, and five-term models, and the full model with all six fixed-effect variables (for the full list of models, see Table A.2). We compared candidate models with the Akaike information criterion (AIC), with the top-ranking model having the lowest AIC value (Burnham and Anderson 2002; Burnham et al. 2011). We calculated model weights, or the probability that a given model will be the best in the set of models (Burnham et al. 2011). We averaged parameter coefficients (Burnham and Anderson 2002) for models within 2 AIC points of the top-ranking model, weighting each model by its model weight. We examined 95% confidence intervals of the averaged parameter estimates for each size-class to evaluate

the strength of their effect on Largemouth Bass catch. If the confidence interval included zero, we concluded that the variable in question did not have an important influence on abundance.

We used the parameter coefficients from the averaged model set to plot the estimated relationship between Largemouth Bass abundance and environmental variables whose confidence intervals did not include zero. We plotted these relationships while holding all other variables at their standardized mean and used sampling month effect estimates from August 2009. We conducted all analyses using the package *glmmADMB* in version 3.2.2 of Program R (Fournier et al. 2012) for GLMMs.

RESULTS

Water quality and SAV biomass conditions varied seasonally and between sampling years (Table 1). Water temperatures were warmest in the months of June and August, with the maximum temperature reaching nearly 27°C in August of 2009, while the coldest temperatures occurred in December 2009 (6.9°C). Conductivity was lowest during April and June of both sampling years and highest during late October and December. Approximately 95% of the conductivity values over the entire study were less than 1,000 $\mu\text{S}/\text{cm}$, estimated to be about 1% given measured water temperatures. Thus, sampling generally occurred in fresh to low-salinity water, with conductivity values ranging from 100 to 3,725 $\mu\text{S}/\text{cm}$. Secchi depths were relatively stable, with most average monthly values hovering in the 1.0–1.5-m range (Table 1).

The SAV assemblage was made up of eight macrophyte species (Table 2). Brazilian waterweed made up 85.2% of the total

TABLE 1. Average (minima, maxima) for water quality variables, SAV biomass density, and Largemouth Bass catch for sampling years 1 and 2, by sampling month.

Month and year	SAV biomass (dry; g/m ²)	Water temperature (°C)	Conductivity (µS/cm)	Secchi depth (m)	Catch (number/transect)	
					Juvenile-sized	Larger
Sampling year 1						
Dec 2008 ^a	248 (0, 1,119)	11.4 (8.9, 13)	589 (151, 1,300)	1.5 (0.6, 3.0)	17 (0, 106)	7 (0, 29)
Feb 2009	253 (0, 1,121)	10.6 (9.5, 12.1)	609 (223, 1,336)	1.4 (0.4, 2.3)	4 (0, 45)	4 (0, 14)
Apr 2009	341 (0, 1,756)	17.3 (13.1, 22.6)	322 (136, 649)	1.1 (0.4, 1.8)	4 (0, 15)	7 (0, 24)
Jun 2009	419 (0, 2,868)	21.7 (20.1, 24.3)	317 (143, 1,044)	1.2 (0.2, 2.2)	13 (0, 215)	14 (0, 63)
Aug 2009 ^b	460 (0, 1,509)	24 (21.1, 26.7)	401 (162, 1,393)	1.3 (0.3, 2.0)	54 (0, 228)	13 (0, 52)
Oct 2009	630 (0, 2,351)	17.8 (15.6, 19.4)	525 (143, 2,420)	1.5 (0.3, 2.5)	18 (0, 66)	5 (0, 12)
Sampling year 2						
Dec 2009	426 (0, 1,320)	9.5 (6.9, 11.1)	626 (202, 3,725)	1.9 (0.3, 3.5)	7 (0, 75)	4 (0, 14)
Feb 2010	293 (0, 1,430)	12.5 (10.5, 15.1)	479 (267, 875)	0.9 (0.4, 2.4)	4 (0, 33)	7 (0, 26)
Apr 2010	303 (0, 1,313)	14.7 (12.4, 18.1)	392 (177, 746)	1.5 (0.0, 3.5)	5 (0, 24)	4 (0, 15)
Jun 2010	323 (0, 2,010)	21.6 (18.2, 25.1)	251 (100, 557)	1.2 (0.3, 2.4)	2 (0, 25)	8 (0, 23)
Aug 2010	469 (0, 1,557)	22.7 (19.1, 26)	534 (323, 1,629)	1.4 (0.3, 3.2)	18 (0, 94)	7 (0, 32)
Oct 2010 ^c	472 (6, 1,398)	20.1 (16.2, 21.9)	655 (294, 2,876)	2.0 (0.3, 4.6)	17 (0, 47)	6 (0, 17)

^aBased on 28 of 30 sites scheduled for sampling during this month. Sampling took place before the addition of three sites in February 2009 (Figure 1), and inclement weather prohibited sampling of 2 sites.

^bBased on 30 of 33 sites because the electrofishing vessel malfunctioned and could not be repaired in time for sampling.

^cBased on 32 of 33 sites because data were permanently lost for 1 site.

sampled biomass and was consistently the predominant species sampled over the entire study period (Figure 2). SAV densities exhibited high spatial and temporal variability. At individual sites, SAV ranged from being consistently absent to consistently present, but at varying densities. Site visits that recorded low SAV densities (an average of 50 g [dry weight]/m² or less) were common, but we also observed densities upwards of 1,500 g/m² (Figure 3).

TABLE 2. Percent total sampled biomass of all native (N) and introduced (I) submerged aquatic macrophyte species.

Species	Status	% Total biomass
Brazilian waterweed <i>Egeria densa</i>	I	85.2
Coontail <i>Ceratophyllum demersum</i>	N	5.8
Carolina fanwort <i>Cabomba caroliniana</i>	I	3.5
American pondweed <i>Elodea canadensis</i>	N	2.1
Curlyleaf pondweed <i>Potamogeton crispus</i>	I	1.2
Sago pondweed <i>Stuckenia</i> spp.	N	1.2
Eurasian watermilfoil <i>Myriophyllum spicatum</i>	I	1.0
Longleaf pondweed <i>Potamogeton nodosus</i>	N	<0.5

The SAV assemblage was dominated by Brazilian waterweed, except at five sites where other SAV species made up >50% of the total sampled biomass. However, SAV was relatively sparse at those five sites, with the total SAV biomass being only 8% of all SAV sampled and Brazilian waterweed generally being present, albeit not dominant. SAV densities were highest in August and October, though densities were also exceptionally high in June and December of 2009 (Figure 2).

Over the entire study period, we caught a total of 7,814 Largemouth Bass. We considered 5,106 fish to be juvenile-sized after examining length-frequency distributions. In every sampling month there were sites with zero catches of either juvenile-sized or larger fish, and maximum catch varied seasonally (Table 1).

Juvenile-Sized Largemouth Bass

Three models had AIC values within 2.0 points of the top-ranking model, and we used all four of these models (cumulative model weight = 0.741; Table 3) to derive averaged parameter coefficients. Although these models included all predictor variables, the confidence intervals for the parameter estimates for conductivity, Secchi depth, and select sampling months included zero (Table 4), indicating these variables did not have predictable influences on the abundance of this size-class. The parameter estimate for the first-degree (linear) SAV term was positive while

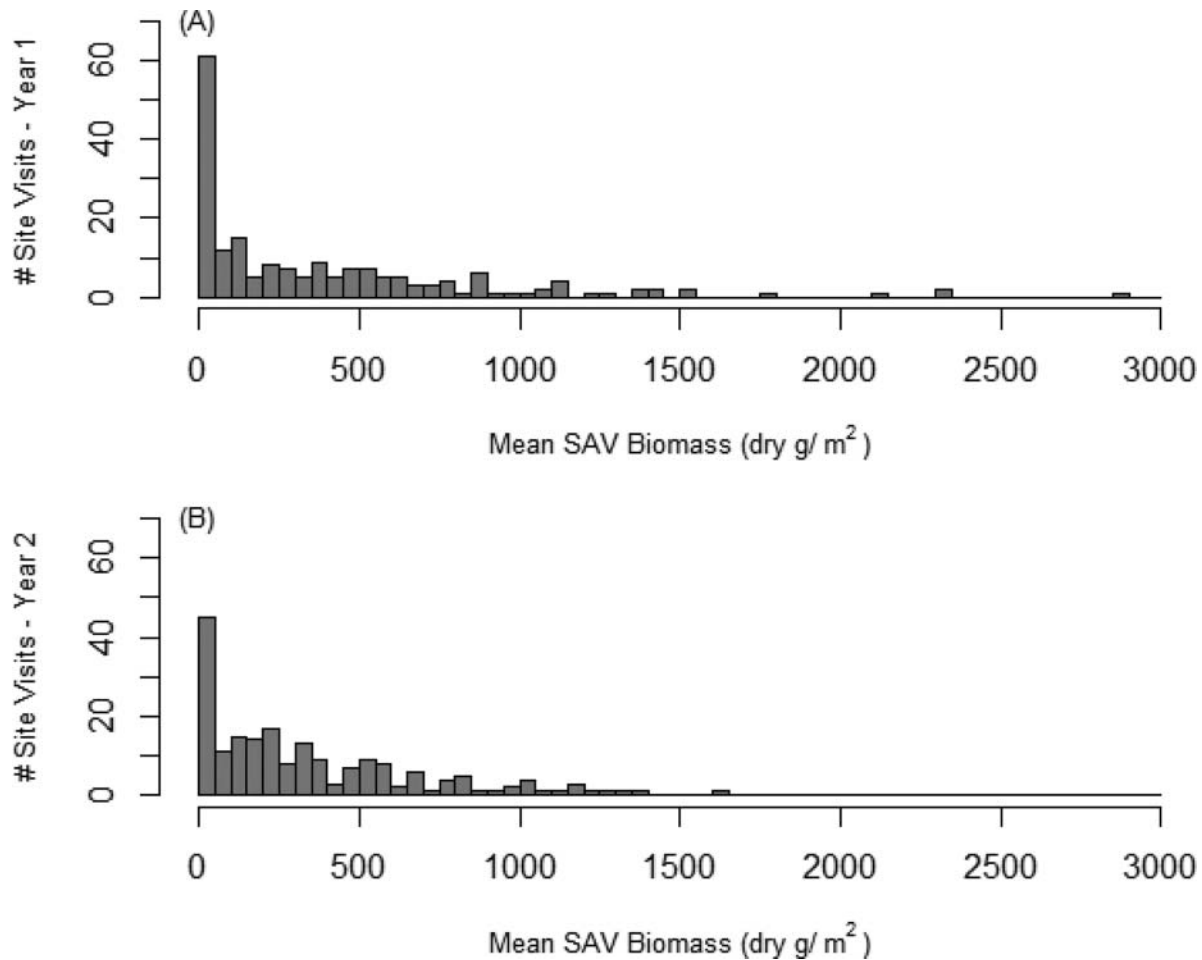


FIGURE 3. Frequency of site visits binned by mean SAV biomass density in increments of 50 g/m^2 for (A) year 1 and (B) year 2.

that for the second-degree (squared) term was negative and the confidence intervals for both terms did not include zero, indicating that the abundance of juvenile-sized fish was highest at intermediate SAV densities (Table 4; Figure 4). The abundance of juvenile-sized fish increased with water temperature (Figure 5A). The effects of sampling month indicated that the abundance of juvenile-sized fish is higher in August and October, but lower in February, relative to the reference month of April (Table 4). These results match expectations, given that there is a general period of reproduction in the late spring and early summer. The negative parameter estimate for sampling year 2 indicates that overall the abundance of juvenile-sized fish was lower during this year than in year 1.

Larger Largemouth Bass

Two models had AIC values within 2.0 points of the model with the lowest AIC value for the larger size-class of Largemouth Bass (cumulative model weight = 0.575; Table 3). These models did not include SAV biomass density; rather, they included water temperature, conductivity, Secchi depth,

sampling month, and sampling year. Only water temperature, select sampling months, and sampling year had averaged confidence intervals that did not include zero (Table 4). Abundance increased with water temperature, but the parameter estimate for the effect of temperature was only half of what it was for juvenile-sized fish (Figure 5B).

The abundance of larger-sized fish was higher in August and June than in the reference month of April, but was comparable to April in all other months (Table 4). As with juvenile-sized fish, the abundance of this size-class was lower in sampling year 2.

DISCUSSION

We describe habitat associations for an estuarine population of Largemouth Bass where it has a novel interaction with Brazilian waterweed, a highly invasive aquatic macrophyte (Yarrow et al. 2009). We know from previous work in the Delta that Largemouth Bass have dramatically increased in abundance in recent decades and this increase is often attributed to the proliferation of Brazilian waterweed (Brown and Michniuk 2007; Nobriga 2009). Our GLMM results suggest that it is

TABLE 3. The ten best GLMMs describing the variation in the abundance of juvenile-sized and larger Largemouth Bass. The models listed have the lowest AIC values of the 64 models estimated for each size-class. Submerged aquatic vegetation (SAV) is included in each model as both a linear and a squared term. Other variables are as follows: Cond = conductivity, Temp = water temperature, Mon = sampling month, and Yr = sampling year. The models in bold italics were included in model averaging to generate the average parameter coefficients and confidence intervals.

Model	df	AIC	Δ AIC	w
Juvenile-sized Largemouth Bass				
<i>SAV+Cond+Temp+Mon+Yr</i>	<i>13</i>	<i>1,768.33</i>	<i>0.000</i>	<i>0.309</i>
<i>SAV+Temp+Mon+Yr</i>	<i>12</i>	<i>1,769.51</i>	<i>1.184</i>	<i>0.171</i>
<i>SAV+Cond+Secchi+Temp+Mon</i>	<i>14</i>	<i>1,770.02</i>	<i>1.696</i>	<i>0.132</i>
<i>SAV+Cond+Temp+Mon</i>	<i>12</i>	<i>1,770.08</i>	<i>1.758</i>	<i>0.128</i>
SAV+Secchi+Temp+Mon+Yr	13	1,771.18	2.854	0.074
SAV+Temp+Mon	11	1,771.87	3.540	0.053
SAV+Cond+Secchi+Temp+Mon	13	1,771.87	3.548	0.052
SAV+Secchi+Temp+Mon	12	1,773.64	5.316	0.022
SAV+Cond+Mon+Yr	12	1,773.79	5.466	0.020
SAV+Mon+Yr	11	1,775.11	6.782	0.010
Larger Largemouth Bass				
<i>Temp+Mon+Yr</i>	<i>10</i>	<i>1,838.93</i>	<i>0.000</i>	<i>0.306</i>
<i>Secchi+Temp+Mon+Yr</i>	<i>11</i>	<i>1,840.27</i>	<i>1.342</i>	<i>0.156</i>
<i>Cond+Temp+Mon+Yr</i>	<i>11</i>	<i>1,840.93</i>	<i>1.998</i>	<i>0.113</i>
SAV+Temp+Mon+Yr	12	1,841.69	2.762	0.077
Cond+Secchi+Temp+Mon+Yr	12	1,842.27	3.338	0.058
Mon+Yr	9	1,842.61	3.680	0.049
SAV+Secchi+Temp+Mon+Yr	13	1,843.30	4.372	0.034
Temp+Mon	9	1,843.55	4.616	0.030
SAV+Secchi+Temp+Mon+Yr	13	1,843.69	4.758	0.028
Secchi+Mon+Yr	10	1,844.08	5.146	0.023

mainly the juvenile component of the Largemouth Bass population that is associated with SAV in the Delta, and Brazilian waterweed is the dominant SAV species throughout the year. Consistent with studies of Largemouth Bass in other systems (Miranda and Pugh 1997; Allen and Tugend 2002), juvenile-sized fish were most abundant at intermediate densities of SAV. The observed decline in the abundance of juvenile-sized fish at the highest SAV densities could be the result of reduced sampling efficiency (Serafy et al. 1988; Killgore et al. 1989); however, our results are comparable to those of Allen and Tugend (2002), in which age-0 Largemouth Bass were scarce at SAV biomass densities similar to the maximum densities that we observed in the Delta.

While our study does not reveal the mechanism behind the association between juvenile-sized Largemouth Bass and SAV, previous studies suggest that it is based on a trade-off between the benefit of increased protection from predators (Olson et al. 2003; Ferrari et al. 2014) and reduced feeding efficiency in dense SAV beds (Valley and Bremigan 2002). Studies from the native range of Largemouth Bass suggest that

TABLE 4. Average parameter estimates, standard error (SEs), and 2.5th and 97.5th quantiles of the confidence intervals (CIs) for the top-ranked model and all models with Δ AIC values <2.0 for juvenile-sized and larger Largemouth Bass. April and sampling year 1 are the baseline (reference) periods for the interpretation of temporal fixed effects. Variables in bold italics have CIs that do not include zero.

Variable	Estimate	SE	2.5th percentile	97.5th percentile
Juvenile-sized Largemouth Bass				
Intercept	1.31	0.30	0.73	1.89
<i>SAV (linear)</i>	<i>0.74</i>	<i>0.17</i>	<i>0.40</i>	<i>1.08</i>
<i>SAV (squared)</i>	<i>-0.27</i>	<i>0.08</i>	<i>-0.43</i>	<i>-0.11</i>
<i>Water temperature</i>	<i>0.27</i>	<i>0.10</i>	<i>0.08</i>	<i>0.46</i>
Conductivity	-0.21	0.11	-0.43	0.02
Secchi depth	0.06	0.12	-0.16	0.29
Month				
<i>August</i>	<i>1.62</i>	<i>0.27</i>	<i>1.08</i>	<i>2.15</i>
December	0.28	0.28	-0.27	0.83
<i>February</i>	<i>-0.69</i>	<i>0.28</i>	<i>-1.23</i>	<i>-0.14</i>
June	-0.08	0.28	-0.64	0.47
<i>October</i>	<i>1.20</i>	<i>0.29</i>	<i>0.63</i>	<i>1.76</i>
<i>Sampling year 2</i>	<i>-0.32</i>	<i>0.16</i>	<i>-0.64</i>	<i>-0.01</i>
Larger Largemouth Bass				
Intercept	1.40	0.19	1.03	1.76
<i>Water temperature</i>	<i>0.12</i>	<i>0.05</i>	<i>0.02</i>	<i>0.22</i>
Conductivity	0.00	0.07	-0.13	0.13
Secchi depth	0.05	0.07	-0.08	0.18
Month				
<i>August</i>	<i>0.52</i>	<i>0.16</i>	<i>0.20</i>	<i>0.83</i>
December	-0.01	0.17	-0.34	0.31
February	0.02	0.16	-0.29	0.32
<i>June</i>	<i>0.77</i>	<i>0.15</i>	<i>0.47</i>	<i>1.07</i>
October	-0.08	0.17	-0.42	0.25
<i>Sampling year 2</i>	<i>-0.24</i>	<i>0.09</i>	<i>-0.43</i>	<i>-0.06</i>

age-0 recruitment increases as SAV coverage increases (Hoyer and Canfield 1996; Tate et al. 2003; Johnson et al. 2014). Notably, these studies often relate Largemouth Bass abundance to hydrilla *Hydrilla verticillata*, which, like Brazilian waterweed, is a prolific macrophyte invader that can have profound ecosystem impacts (Sousa 2011). Likewise, our results suggest that the spread of Brazilian waterweed has expanded suitable habitat for juvenile-sized Largemouth Bass in the Delta. Interestingly, however, we observed relatively low frequencies of the intermediate SAV densities that our modeling suggests are most favorable to the juvenile-sized fish, compared with the frequency of low-SAV densities (Figure 3). These observations suggest that continued increases in SAV density in the Delta will expand the optimal habitat for juvenile-sized Largemouth Bass. However, more studies will be necessary to determine whether juvenile Largemouth Bass use of SAV beds in the Delta translates to increased survival rates,

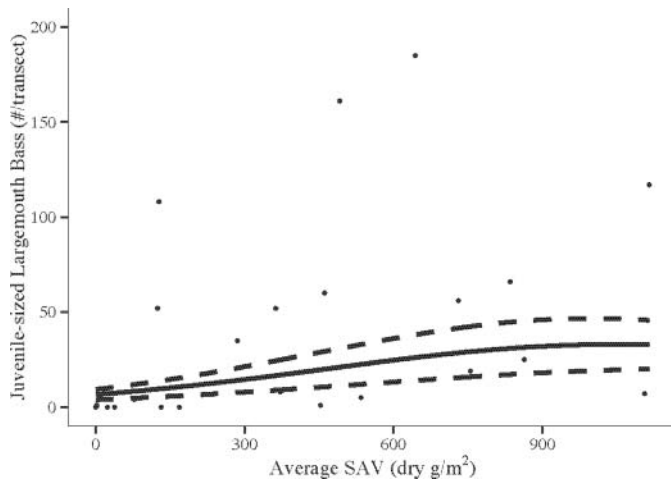


FIGURE 4. Predicted relationship (solid line, with the 95% confidence interval indicated by the dashed lines) between juvenile-sized Largemouth Bass catch and SAV biomass density, based on averaged model coefficients for the top-ranked GLMMs for juvenile-sized fish. Water temperature, conductivity, and Secchi depth were held at their mean values for August 2009. The points are observed catch numbers for August 2009, the sampling period chosen for specifying model estimates for the effects of month and year in the predicted relationship.

as has been observed with different aquatic macrophyte species within the species' native range.

Unlike with juvenile-sized fish, SAV biomass density was not an explanatory factor for the abundance of larger Largemouth Bass in the top models. This result is consistent with previous work that found no relationship between adult Largemouth Bass and SAV (Hoyer and Canfield 1996). Recent work from Florida shows that the abundance of intermediate and trophy-sized Largemouth Bass did not change after hurricanes caused widespread vegetation losses, while young-of-the-year recruitment declined (Johnson et al. 2014). In our study, the sheer ubiquity of the larger size-class was notable: of 387 site visits, larger fish were present in 335 (86%) while juveniles were present in only 253 (65%). The model results reflected this ubiquity, as water temperature was the only environmental variable with a predictable influence on the abundance of the larger size-class, with a weaker effect than it had for juvenile-sized fish. However, our grouping of larger Largemouth Bass encompassed a broad size distribution and there may be more specific habitat associations for narrower size categories within this group.

The positive relationship between water temperature and abundance for both size-classes suggests that Largemouth Bass have higher densities in Delta areas that maintain higher water temperatures than other areas. This result is not surprising given that average water temperatures, even during the warmer months of June and August, were below the optimal range of 25–30°C for Largemouth Bass growth (Coutant 1977). Water temperatures exceeded 25°C at only 11 of 387 site visits. Previous research on the movement patterns of Largemouth Bass in the Great Lakes, where temperatures are

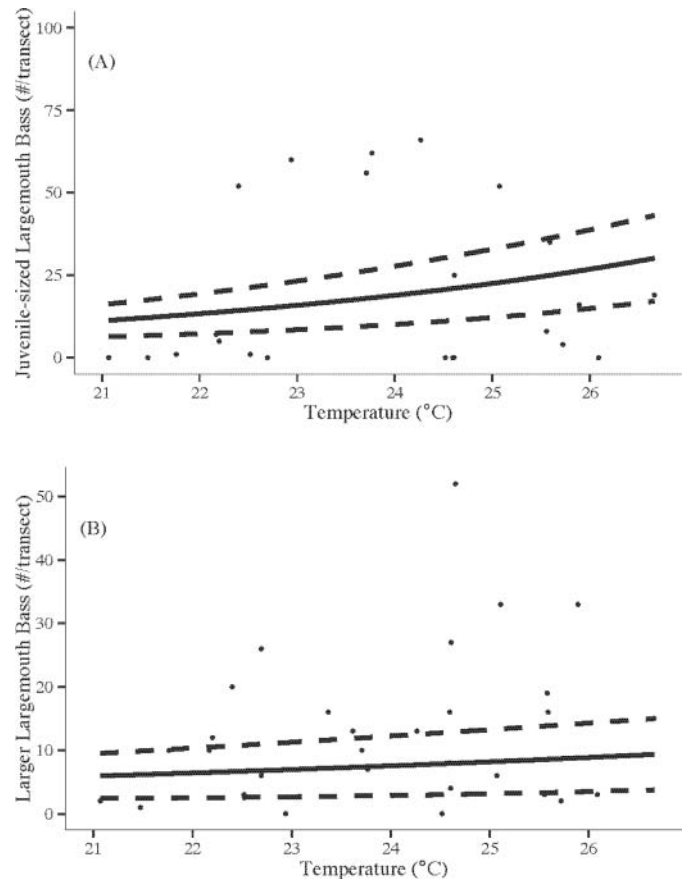


FIGURE 5. Predicted relationships between water temperature and (A) juvenile-sized and (B) larger Largemouth Bass. The predictions are based on averaged model coefficients from the top-ranked GLMMs for each size-class. All other fixed-effect variables were held at their mean values for August 2009. See Figure 4 for additional details.

also generally below the optimal range, has shown that adults seek out relatively warm areas, particularly in colder months (Carter et al. 2012).

The variation in abundance with respect to sampling month reflects changes in the abundance of juvenile-sized fish after reproductive periods and seasonal variation in electrofishing efficiency. Catches of the larger size-class were higher in August and June than in the cooler month of April, while those in December, February, and October were similar to those in April. These lower catches during these colder months may result from a general tendency for deep areas beyond the reach of electrofishing sampling gear, or from reduced electrofishing effectiveness at lower temperatures (Reynolds 1996). The abundance of both size-classes was lower in the second sampling year. The reasons for this difference are not clear, but it is notable that mean water temperatures in April were lower in the second sampling year (Table 1), suggesting the potential for a shorter spawning window in that year.

For both size-classes, there was no appreciable association between abundance and conductivity. This lack is interesting

given the results from studies in other estuarine systems. In the Chesapeake Bay there is a clear negative relationship between salinity and abundance (Love 2011), while studies from the Mobile–Tensaw Delta of Alabama suggest that Largemouth Bass can adapt to salinities up to 10‰ (Meador and Kelso 1990; Lowe et al. 2009; Norris et al. 2010). We assessed abundance over a more limited salinity range, with most values at or below 1‰. Electrofishing efficiency decreases as conductivity increases (Reynolds 1996) but is effective for Largemouth Bass even when conductivity reaches 1,700 $\mu\text{S}/\text{cm}$ (Dill and Willis 1994). Conductivity exceeded 1,700 $\mu\text{S}/\text{cm}$ only three times in our study and in these instances we still caught juvenile fish (not necessarily Largemouth Bass), which suggests that electrofishing was still reasonably efficient at that level (Reynolds 1996). Sampling over a broader geographic and salinity range with gear that is still effective at high salinities will be necessary to determine the maximum salinity thresholds for Largemouth Bass in the Delta.

Secchi depth was not an important predictor of abundance for either juvenile-sized or larger Largemouth Bass, unlike in previous work that has shown greater Largemouth Bass abundance in clearer water (where Secchi depth was predominantly below 1 m; Love 2011). The previously observed pattern is likely a result of increased feeding efficiency in clearer water (Shoup and Wahl 2009; Huenemann et al. 2012). In our study, mean Secchi depth generally exceeded 1 m, and it is possible that water clarity was generally not low enough in the conditions we sampled to compromise Largemouth Bass foraging.

Current habitat restoration plans in the Delta call for the restoration of thousands of acres of tidal wetland habitat (California Department of Water Resources 2012). While these efforts will expand the largely missing shallow-water habitat in the Delta, a major concern is that increased shallow water area will expand the habitat for Brazilian waterweed and consequently increase the abundance of Largemouth Bass, creating a predation sink for target native fishes (Brown 2003). However, our GLMM results suggest that the larger-sized Largemouth Bass (likely the most piscivorous ones) inhabit shallow-water areas even when SAV is absent or present only at low densities. As these fish were generally present across the range of water quality conditions we sampled, it may be useful to sample across a broader range of water clarity, salinity, and water temperature conditions to determine the conditions that are limiting for this size-class.

Brazilian waterweed and Largemouth Bass are species that, even when they invade ecosystems on their own, can have far-reaching impacts on the physical environment and the food web (Maezono and Miyashita 2003; Yarrow et al. 2009; Almeida et al. 2012). Despite their novel interaction in the Delta, their association seems to resemble what other studies have observed in the native range of Largemouth Bass when they interact with a different SAV species assemblage. The positive association in the Delta between juvenile-sized Largemouth Bass and Brazilian waterweed at intermediate plant densities is part of a general trend at the community scale in

the Delta. In this system, Brazilian waterweed is associated with a host of nonnative fishes that now compose the majority of the fish biomass in the system (Nobriga et al. 2005; Brown and Michniuk 2007; Nobriga and Feyrer 2007), a pattern that is consistent with the idea of an “invasional meltdown” (Simberloff and Von Holle 1999).

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Appendix: Additional Data and Model Results

TABLE A.1. Maximum FL of juvenile-sized Largemouth Bass for each sampling session (month and year of sampling).

Sampling session	FL (mm)
Oct 2008	142
Dec 2008	153
Feb 2009	142
Apr 2009	151
Jun 2009	66
Aug 2009	112
Oct 2009	140
Dec 2009	134
Feb 2010	102
Apr 2010	131
Jun 2010	52
Aug 2010	111
Oct 2010	125

TABLE A.2. Full list of candidate GLMMs describing the variation in the abundance of juvenile-sized and larger Largemouth Bass. Variables are as follows: SAV = submerged aquatic vegetation, Cond = conductivity, Temp = water temperature, Mon = Sampling month, and Yr = Sampling year. The models in bold type were included in model averaging to generate average parameter coefficients and confidence intervals.

Model	df	AIC	Δ AIC	w
Juvenile-sized Largemouth Bass				
SAV+Cond+Temp+Mon+Yr	13	1,768.326	0	0.309
SAV+Temp+Mon+Yr	12	1,769.51	1.184	0.171
SAV+Cond+Secchi+Temp+Mon+Yr	14	1,770.022	1.696	0.132
SAV+Cond+Temp+Mon	12	1,770.084	1.758	0.128
SAV+Secchi+Temp+Mon+Yr	13	1,771.18	2.854	0.074
SAV+Temp+Mon	11	1,771.866	3.54	0.053
SAV+Cond+Secchi+Temp+Mon	13	1,771.874	3.548	0.052
SAV+Secchi+Temp+Mon	12	1,773.642	5.316	0.022
SAV+Cond+Mon+Yr	12	1,773.792	5.466	0.020
SAV+Mon+Yr	11	1,775.108	6.782	0.010
SAV+Cond+Secchi+Mon+Yr	13	1,775.434	7.108	0.009
SAV+Cond+Mon	11	1,775.978	7.652	0.007
SAV+Secchi+Mon+Yr	12	1,776.736	8.41	0.005
SAV+Cond+Secchi+Mon	12	1,777.718	9.392	0.003
SAV+Mon	10	1,777.934	9.608	0.003
SAV+Secchi+Mon	11	1,779.674	11.348	0.001
Cond+Temp+Mon+Yr	11	1,782.372	14.046	<0.001
Cond+Secchi+Temp+Mon+Yr	12	1,783.37	15.044	<0.001
Temp+Mon+Yr	10	1,783.778	15.452	<0.001
Secchi+Temp+Mon+Yr	11	1,784.84	16.514	<0.001
Cond+Temp+Mon	10	1,785.342	17.016	<0.001
Cond+Secchi+Temp+Mon	11	1,786.482	18.156	<0.001
Cond+Mon+Yr	10	1,787.154	18.828	<0.001
Temp+Mon	9	1,787.552	19.226	<0.001
Cond+Secchi+Mon+Yr	11	1,788.254	19.928	<0.001
Mon+Yr	9	1,788.678	20.352	<0.001
Secchi+Temp+Mon	10	1,788.77	20.444	<0.001
Secchi+Mon+Yr	10	1,789.856	21.53	<0.001
Cond+Mon	9	1,790.444	22.118	<0.001
Cond+Secchi+Mon	10	1,791.696	23.37	<0.001
Mon	8	1,792.846	24.52	<0.001
Secchi+Mon	9	1,794.196	25.87	<0.001
SAV+Cond+Temp+Yr	8	1,842.19	73.864	<0.001
SAV+Cond+Secchi+Temp+Yr	9	1,842.778	74.452	<0.001
SAV+Cond+Temp	7	1,843.394	75.068	<0.001
SAV+Cond+Yr	7	1,843.478	75.152	<0.001
SAV+Cond+Secchi+Temp	8	1,843.934	75.608	<0.001
SAV+Cond+Secchi+Yr	8	1,844.144	75.818	<0.001
SAV+Cond	6	1,844.782	76.456	<0.001
SAV+Temp+Yr	7	1,845.218	76.892	<0.001
SAV+Cond+Secchi	7	1,845.41	77.084	<0.001
SAV+Secchi+Temp+Yr	8	1,845.678	77.352	<0.001
SAV+Temp	6	1,846.68	78.354	<0.001
SAV+Yr	6	1,846.828	78.502	<0.001
SAV+Secchi+Temp	7	1,847.086	78.76	<0.001

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TABLE A.2. Continued.

Model	df	AIC	Δ AIC	w
SAV+Secchi+Yr	7	1,847.426	79.1	<0.001
SAV	5	1,848.412	80.086	<0.001
SAV+Secchi	6	1,848.962	80.636	<0.001
Cond+Secchi+Yr	6	1,857.69	89.364	<0.001
Cond+Secchi+Temp+Yr	7	1,857.984	89.658	<0.001
Cond+Yr	5	1,858.27	89.944	<0.001
Cond+Temp+Yr	6	1,858.922	90.596	<0.001
Cond+Secchi	5	1,860.4	92.074	<0.001
Cond+Secchi+Temp	6	1,860.798	92.472	<0.001
Cond	4	1,861.268	92.942	<0.001
Secchi+Yr	5	1,861.48	93.154	<0.001
Secchi+Temp+Yr	6	1,861.654	93.328	<0.001
Yr	4	1,861.788	93.462	<0.001
Cond+Temp	5	1,862.052	93.726	<0.001
Temp+Yr	5	1,862.378	94.052	<0.001
Secchi	4	1,864.548	96.222	<0.001
Secchi+Temp	5	1,864.804	96.478	<0.001
Intercept only	3	1,865.1	96.774	<0.001
Temp	4	1,865.794	97.468	<0.001
Larger Largemouth Bass				
Temp+Mon+Yr	10	1,838.9	0.000	0.306
Secchi+Temp+Mon+Yr	11	1,840.3	1.342	0.156
Cond+Temp+Mon+Yr	11	1,840.9	1.998	0.113
SAV+Temp+Mon+Yr	12	1,841.7	2.762	0.077
Cond+Secchi+Temp+Mon+Yr	12	1,842.3	3.338	0.058
Mon+Yr	9	1,842.6	3.680	0.049
SAV+Secchi+Temp+Mon+Yr	13	1,843.3	4.372	0.034
Temp+Mon	9	1,843.5	4.616	0.030
SAV+Cond+Temp+Mon+Yr	13	1,843.7	4.758	0.028
Secchi+Mon+Yr	10	1,844.1	5.146	0.023
Cond+Mon+Yr	10	1,844.6	5.620	0.018
Secchi+Temp+Mon	10	1,845.2	6.266	0.013
SAV+Cond+Secchi+Temp+Mon+Yr	14	1,845.3	6.368	0.013
Cond+Temp+Mon	10	1,845.5	6.612	0.011
SAV+Mon+Yr	11	1,845.6	6.678	0.011
SAV+Temp+Mon	11	1,846.0	7.082	0.009
Cond+Secchi+Mon+Yr	11	1,846.0	7.094	0.009
Mon	8	1,846.5	7.532	0.007
Cond+Secchi+Temp+Mon	11	1,847.2	8.260	0.005
SAV+Secchi+Mon+Yr	12	1,847.3	8.360	0.005
SAV+Cond+Mon+Yr	12	1,847.6	8.620	0.004
SAV+Secchi+Temp+Mon	12	1,847.9	8.932	0.004
SAV+Cond+Temp+Mon	12	1,848.0	9.076	0.003
Secchi+Mon	9	1,848.2	9.262	0.003
Cond+Mon	9	1,848.4	9.482	0.003
SAV+Mon	10	1,849.2	10.256	0.002
SAV+Cond+Secchi+Mon+Yr	13	1,849.2	10.304	0.002
SAV+Cond+Secchi+Temp+Mon	13	1,849.9	10.926	0.001

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TABLE A.2. Continued.

Model	df	AIC	Δ AIC	w
Cond+Secchi+Mon	10	1,850.2	11.220	0.001
SAV+Secchi+Mon	11	1,851.1	12.146	0.001
SAV+Cond+Mon	11	1,851.1	12.206	0.001
SAV+Cond+Secchi+Mon	12	1,853.0	14.098	<0.001
Temp+Yr	5	1,877.8	38.836	<0.001
SAV+Temp+Yr	7	1,877.8	38.846	<0.001
Secchi+Temp+Yr	6	1,878.1	39.124	<0.001
SAV+Secchi+Temp+Yr	8	1,879.0	40.026	<0.001
1+Yr	4	1,879.4	40.484	<0.001
SAV+Cond+Temp+Yr	8	1,879.7	40.726	<0.001
Cond+Temp+Yr	6	1,879.7	40.768	<0.001
Secchi+Yr	5	1,879.8	40.856	<0.001
SAV+Yr	6	1,879.8	40.910	<0.001
Cond+Secchi+Temp+Yr	7	1,880.0	41.032	<0.001
SAV+Cond+Secchi+Temp+Yr	9	1,880.8	41.896	<0.001
SAV+Secchi+Yr	7	1,881.0	42.098	<0.001
Cond+Yr	5	1,881.4	42.480	<0.001
Cond+Secchi+Yr	6	1,881.8	42.850	<0.001
SAV+Cond+Yr	7	1,881.8	42.896	<0.001
SAV+Cond+Secchi+Yr	8	1,883.0	44.082	<0.001
SAV+Temp	6	1,884.4	45.428	<0.001
Temp	4	1,885.4	46.460	<0.001
SAV	5	1,885.8	46.856	<0.001
SAV+Secchi+Temp	7	1,885.9	46.954	<0.001
Secchi+Temp	5	1,886.1	47.196	<0.001
SAV+Cond+Temp	7	1,886.2	47.272	<0.001
Intercept only	3	1,886.4	47.448	<0.001
Secchi	4	1,887.2	48.262	<0.001
Cond+Temp	5	1,887.3	48.360	<0.001
SAV+Secchi	6	1,887.3	48.394	<0.001
SAV+Cond+Secchi+Temp	8	1,887.7	48.784	<0.001
SAV+Cond	6	1,887.8	48.828	<0.001
Cond+Secchi+Temp	6	1,888.0	49.066	<0.001
Cond	4	1,888.4	49.436	<0.001
Cond+Secchi	5	1,889.2	50.240	<0.001
SAV+Cond+Secchi	7	1,889.3	50.360	<0.001