



Fish-Habitat Relationships Along the Estuarine Gradient of the Sacramento-San Joaquin Delta, California: Implications for Habitat Restoration

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Abstract

Estuaries are highly variable environments where fish are subjected to a diverse suite of habitat features (e.g., water quality gradients, physical structure) that filter local assemblages from a broader, regional species pool. Tidal, climatological, and oceanographic phenomena drive water quality gradients and, ultimately, expose individuals to other habitat features (e.g., stationary physical or biological elements, such as bathymetry or vegetation). Relationships between fish abundances, water quality gradients, and other habitat features in the Sacramento-San Joaquin Delta were examined as a case example to learn how habitat features serve as filters to structure local assemblages in large river-dominated estuaries. Fish communities were sampled in four tidal lakes along the estuarine gradient during summer-fall 2010 and 2011 and relationships with habitat features explored using ordination and generalized linear mixed models (GLMMs). Based on ordination results, landscape-level gradients in salinity, turbidity, and elevation were associated with distinct fish assemblages among tidal lakes. Native fishes were associated with increased salinity and turbidity, and decreased elevation. Within tidal lakes, GLMM results demonstrated that submersed aquatic vegetation density was the dominant driver of individual fish species densities. Both native and non-native species were associated with submersed aquatic vegetation, although native and non-native fish populations only minimally overlapped. These results help to provide a framework for predicting fish species assemblages in novel or changing habitats as they indicate that species assemblages are driven by a combination of location within the estuarine gradient and site-specific habitat features.

Keywords Fish · Habitat associations · Submersed aquatic vegetation · San Francisco Estuary

Introduction

Estuaries frequently exhibit clear gradients in environmental conditions that can act as regional filters on local fish assemblages (*sensu* Smith and Powell 1971). Direct physiological

limitation by the freshwater to marine salinity gradient is the most consistent predictor of broad estuarine fish distribution (Gunter 1961; Boesch 1977). Other gradients can also impact species distributions (e.g., turbidity, Cyrus and Blaber 1987; nutrients, Underwood et al. 1998); however, these gradients can shift on daily, monthly, and seasonal timeframes due to changing tidal, climatological, or oceanographic phenomena (Rozas 1995; Feyrer et al. 2015). Estuarine nekton distribute themselves along this fluctuating salinity regime according to their physiological tolerances (Peterson 2003). Within this salinity regime, other habitat elements influence the distribution and abundance of nekton, including bathymetry (Martino and Able 2003), presence and type of vegetation (Odum 1988; Rozas and Odum 1988; Sogard and Able 1991), access to intertidal areas (McIvor and Odum 1988; Kimmerer 2004), and biotic interactions (Crain et al. 2004; Alcaraz et al. 2008). These habitat features are typically fixed and thus less variable than fluctuating gradients (Weinstein et al. 1980). For example, fish assemblages in river systems within the

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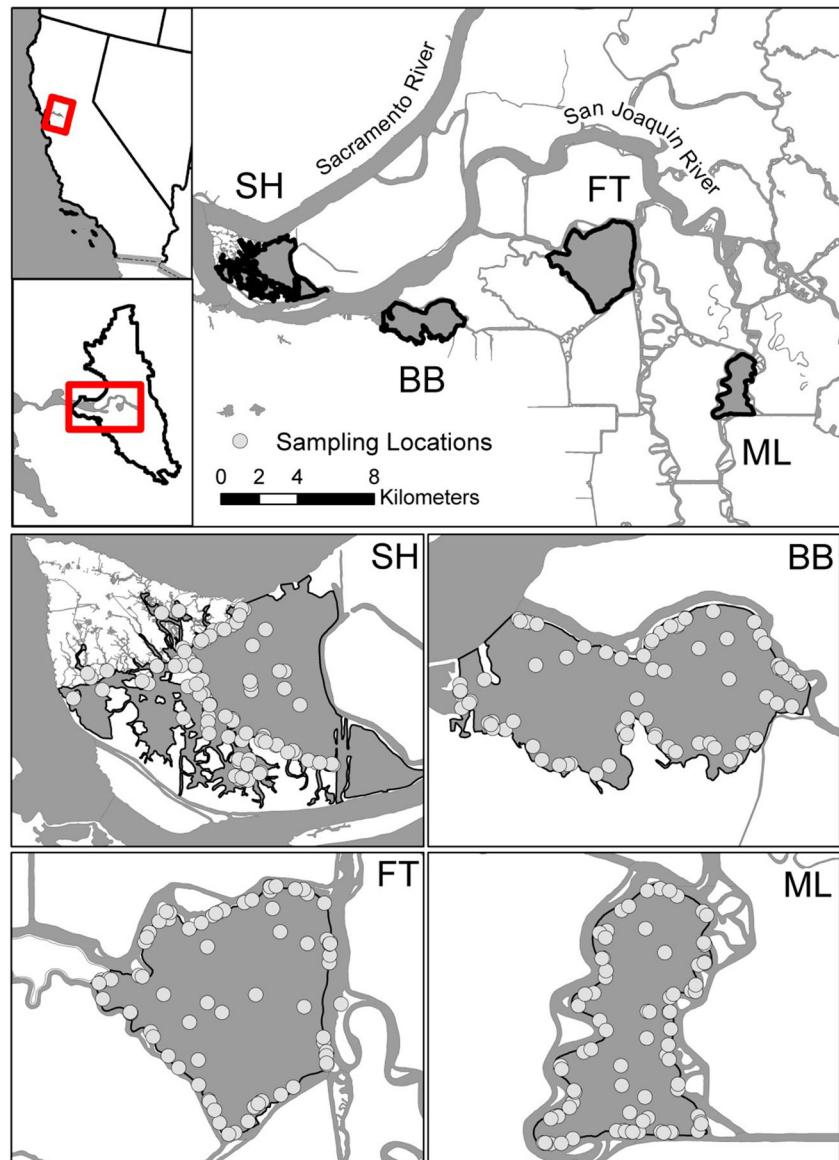
Chesapeake Bay respond primarily to salinity changes along a gradient and then to structural habitat elements within the region defined by salinity (Wagner and Austin 1999).

This structuring of habitat elements, from landscape-scale gradient to fine-scale habitat, strongly influences the distribution of fishes with respect to their environment. Each of these habitat elements acts hierarchically to “filter” fishes from the overall species pool (*sensu* Smith and Powell 1971; Peterson 2003). The variability inherent in estuaries, however, can make identification of distributional drivers across multiple spatial scales difficult. Further complicating these relationships are anthropogenic modifications to estuaries, which affect both landscape gradients and fine-scale habitat aspects. This includes channelization that affects the salinity gradient by enhancing tidal excursion and other modifications that may

alter or destroy habitats such as tidal marshes (Kennish 2001). Additionally, the introduction of non-native species, typically with unpredictable habitat associations and ecological impacts, can further obfuscate the relationships between native fishes and habitat.

The San Francisco Estuary (SFE) in California, USA, is a large, highly altered estuary where heavy anthropogenic modifications have moderated estuarine variability (Conomos et al. 1985; Monismith et al. 2002; Monsen et al. 2007). Hydrodynamic variability is constrained by year-round dam releases designed to maintain a consistent salinity gradient (Knowles 2002; Lund et al. 2008), which dampens variability in several other hydrodynamic variables including turbidity (Durand et al. 2016) and temperature (Moyle et al. 2012). In addition to a

Fig. 1 Map of major tidal lakes within the Sacramento-San Joaquin Delta. Delta boundary defined within inset. Bottom four panels are of each tidal lake, with gray circles denoting all sampling locations. SH Sherman Lake, BB Big Break, FT Franks Tract, ML Mildred Island



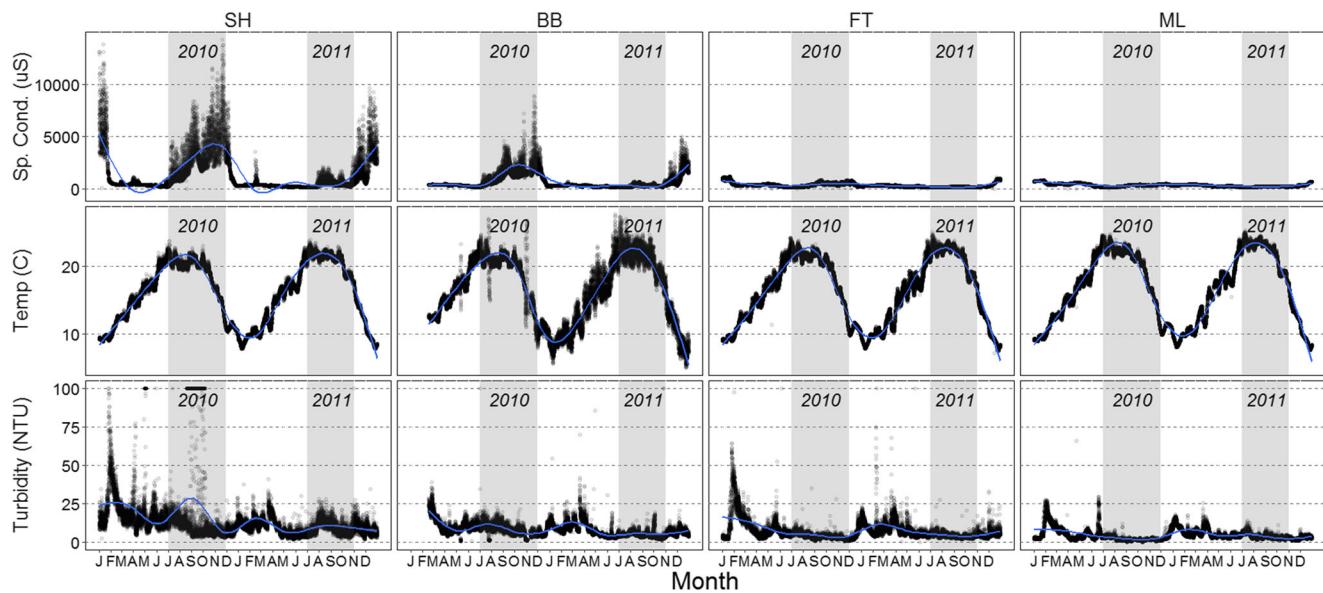


Fig. 2 Water quality variables from permanent water quality stations located adjacent to tidal lakes over the course of this study. Panels are arranged in order from west to east. Gray bars represent months when fish

data were collected. Data—cdec.water.ca.gov. CDEC stations referenced: Sherman Lake (SH – ANH), Big Break (BB – BLP), Franks Tract (FT – OSJ), Mildred Island (ML – HLT)

Fig. 3 Biplot of results from NMDS ordination. Points represent sampling events with the shape from each tidal lake. Texts are species codes. Ellipses are 95% confidence intervals. Dashed lines are fitted environmental variables. For lake codes see Fig. 1 and for species codes see Table 2

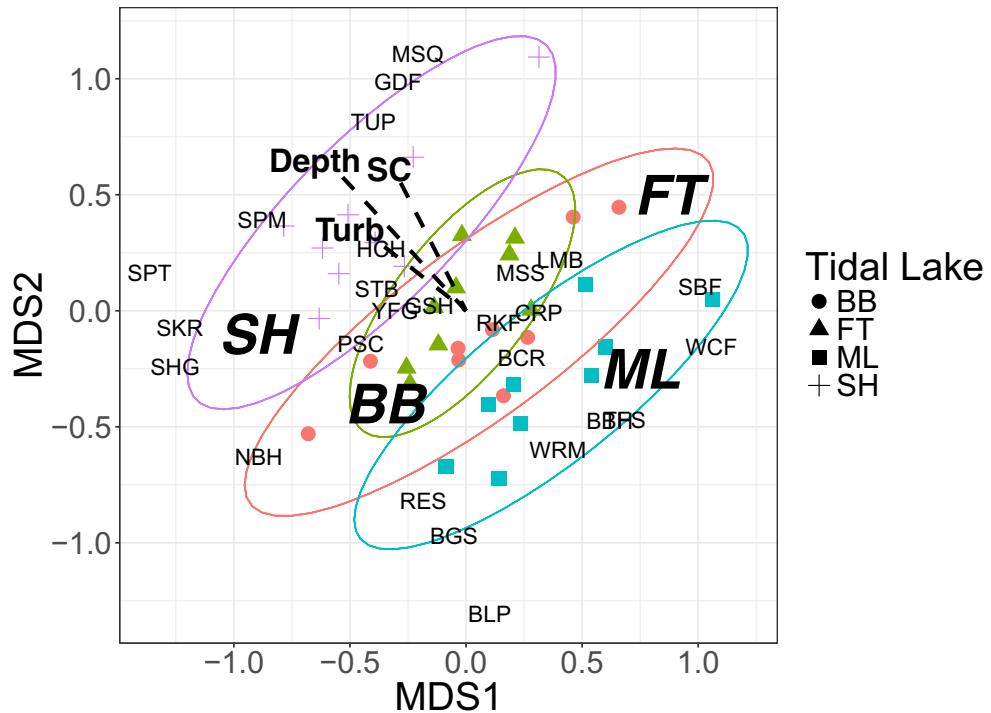


Table 1 Summary statistics of each tidal lake. Mean \pm SD is given for depth and all water quality variables, with minimum and maximum included for water quality data

Tidal lake	Area (km ²)	Elevation (m)	Distance from ocean (km)	Water quality			Prominent submersed aquatic vegetation species							
				Conductivity (µS)	Temp (°C)	Turbidity (NTU)	EGDE (%)	CEDE (%)	MYSP (%)	POCR (%)	STSPP (%)	ELCA (%)		
Sherman Lake	SH 7.43	-0.26 ± 1.27	86	1045 ± 929 (126–3457)	19.5 ± 3.9 (9.1–30.9)	5.1 ± 5.3 (0–28.4)	69	15	47	8	9	0	13	0
Big Break	BB 5.98	-0.69 ± 0.62	94	777 ± 586 (161–1977)	19.8 ± 4.3 (7.5–26.9)	2.3 ± 4.9 (0–32.0)	65	64	46	33	26	19	0	4
Franks Tract	FT 12.84	-1.54 ± 0.59	104	460 ± 344 (112–1275)	20.7 ± 3.0 (14.1–25.7)	0.9 ± 1.6 (0–8.1)	71	33	5	51	24	11	0	2
Mildred Island	ML 4.05	-3.22 ± 1.18	117	307 ± 131 (132–573)	21.6 ± 3.0 (14.1–26.5)	1.1 ± 2.3 (0–15.3)	80	60	12	19	0	4	0	0

Submersed aquatic vegetation values are the percent of sampled sites where each species made up > 10% of vegetation coverage
 CACA *Cabomba caroliniana*, CEDE *Ceratophyllum demersum*, EGDE *Egeria densa*, ELCA *Eloea canadensis*, MYSP *Myriophyllum spicatum*, POCR *Potamogeton crispus*, STSPP *Stuckenia* sp.

Table 2 Species codes and catch-per-unit-effort (fish h⁻¹) for all species sampled. Native fishes are bolded, and all species modeled with GLMMs are denoted with an asterisk. Tidal lakes are ordered from west to east

Code	Common name	Latin name	Total CPUE	SH	BB	FT	ML
LMB*	Largemouth bass	<i>Micropterus salmoides</i>	79.2	32.3	92.6	76.2	121.1
RES*	Redear sunfish	<i>Lepomis microlophus</i>	38.0	5.6	46.3	65.3	35.8
TUP*	Tule perch	<i>Hysterocarpus traskii</i>	16.5	56.5	2.2	4.0	0.4
ISS*	Mississippi silverside	<i>Menidia audens</i>	13.	7.7	15.4	10.0	22.6
GSH*	Golden shiner	<i>Notemigonus crysoleucas</i>	11.8	19.3	18.5	6.4	2.5
MSF	Misc. sunfish	<i>Lepomis</i> sp.	9.5	0.2	13.8	8.8	16.2
BGS*	Bluegill	<i>Lepomis macrochirus</i>	8.4	0.1	3.0	6.2	25.5
TFS	Threadfin shad	<i>Dorosoma petenense</i>	2.8	0.4	—	—	11.3
RKF	Rainwater killifish	<i>Lucania parva</i>	2.4	1.8	4.0	1.5	2.7
CRP	Common carp	<i>Cyprinus carpio</i>	1.8	0.4	1.9	3.2	1.8
YFG	Yellowfin goby	<i>Acanthogobius flavimanus</i>	1.3	1.2	0.6	2.6	0.5
HCH	Hitch	<i>Lavinia exilicauda</i>	1.0	2.0	0.6	1.0	0.1
BCR	Black crappie	<i>Pomoxis nigromaculatus</i>	0.9	0.1	0.6	0.9	2.1
WCF	White catfish	<i>Ameiurus catus</i>	0.8	—	0.5	0.0	2.7
SPT	Sacramento splittail	<i>Pogonichthys macrolepidotus</i>	0.7	2.8	—	—	—
STB	Striped bass	<i>Morone saxatilis</i>	0.7	1.5	0.1	0.2	0.9
WRM	Warmouth	<i>Lepomis gulosus</i>	0.6	—	0.1	0.2	2.0
PSC	Prickly sculpin	<i>Cottus asper</i>	0.5	0.4	0.5	0.8	0.3
GDF	Goldfish	<i>Carassius auratus</i>	0.4	1.1	0.2	0.2	0.1
BBH	Black bullhead	<i>Ameiurus melas</i>	0.4	1.1	0.2	0.2	0.1
SPM	Sacramento pikeminnow	<i>Ptychocheilus grandis</i>	0.3	1.0	0.2	—	—
BLP	Bigscale logperch	<i>Percina macrolepida</i>	0.2	—	—	<0.1	0.9
SKR	Sacramento sucker	<i>Catostomus occidentalis</i>	0.2	0.5	0.3	—	0.1
NBH	Brown bullhead	<i>Ameiurus nebulosus</i>	0.1	0.1	0.1	<0.1	0.2
SBF	Sacramento blackfish	<i>Orthodon microlepidotus</i>	0.1	—	0.1	0.1	0.1
MSQ	Western mosquitofish	<i>Gambusia affinis</i>	0.1	0.1	0.1	—	—
SHG	Shimofuri goby	<i>Tridentiger bifasciatus</i>	<0.1	0.1	0.1	—	—
CHN	Chinook salmon	<i>Oncorhynchus tshawytscha</i>	<0.1	—	—	—	0.1
MGB	Misc. goby	<i>Tridentiger</i> sp.	<0.1	—	0.1	—	—
		Total fish h ⁻¹	192.5	135.7	202.0	188.2	250.8
		Total hours sampled	78.9	20.8	19.0	20.4	18.6

modified hydrology, the SFE has been modified structurally (Lund et al. 2007). These alterations have resulted in the loss of many geomorphic features important for local species richness, such as tidal marsh with complex dendritic channels (Atwater et al. 1979; Whipple et al. 2012), sloughs with heterogeneous bathymetry (Meng and Matern 2001; Desmond et al. 2000; Visintainer et al. 2006), and intertidal areas dominated by emergent vegetation (Brown 2003; Whipple et al. 2012).

Additionally, the SFE has a long history of species introductions and is recognized as one of the most highly invaded estuaries in the world (Cohen and Carlton 1995, 1998). Non-native biota are particularly dominant in the upstream portion of the SFE, the Sacramento-San Joaquin Delta (Delta), where the estuarine gradient

between more saline water and freshwater is consistent across years and has a strong impact on Delta fish assemblages (Matern et al. 2002; Feyrer and Healey 2003; Nobriga et al. 2005; Moyle et al. 2012; Feyrer et al. 2015). Rapidly proliferating non-native submersed aquatic vegetation (SAV), an important structural element in many aquatic habitats (Carpenter and Lodge 1986), has contributed to altered physical structure and water quality of littoral habitats Delta-wide (Hestir 2010). The spread of SAV has been concomitant with native fish decline in littoral habitats and commensurate increases in non-native fishes (Brown and Michniuk 2007), including piscivorous largemouth bass *Micropterus salmoides* (Conrad et al. 2016). Brazilian waterweed *Egeria densa* dominates many littoral SAV

assemblages and is presumed to be the primary SAV species driving fish assemblage changes; however, the impact of SAV on local fish assemblages can differ based on the species of SAV (Rozas and Odum 1988; Grenouillet et al. 2002). These novel fish assemblages are dominated by freshwater non-native species, many of which are well-adapted to the relatively stable conditions characteristic of the contemporary Sacramento-San Joaquin Delta (Moyle et al. 2012) although they are potentially poorly adapted to historic variability.

This combination of changes to the physical structure and biotic community has led to the recognition that in many ways the Sacramento-San Joaquin Delta is a novel ecosystem (Hobbs et al. 2006; Mount et al. 2012). In this study, we evaluate fish-habitat relationships among and within regional tidal habitats in the Sacramento-San Joaquin Delta on multiple spatial scales and address the following questions: (1) How do fish assemblages and environmental variables differ among regions, and which environmental variables are related to assemblage differences? (2) What fine-scale physical habitat features, including SAV species composition, affect the density of abundant fish species? We then identify

whether native and non-native species respond differentially to broad environmental gradients, fine-scale habitat structure, or both. This study is important because it allows us to assess the relationships of novel fish assemblages to novel habitats and thus inform a framework for predicting possible fish assemblages associated with intended (e.g., habitat restoration; Herbold et al. 2014) or unintended (e.g., sea level rise, catastrophic levee failure; Mount and Twiss 2005; Moyle 2008) habitat alterations.

Methods

Study Area

The Sacramento-San Joaquin Delta (Delta) is a 2985 km² network of channels and tidal habitats comprising the freshwater extent of the tidal San Francisco Estuary (Fig. 1). The largest and most discrete of these tidal habitats are open-water regions formed when reclaimed marshlands subside below sea level due to compaction and oxidation from agriculture and are

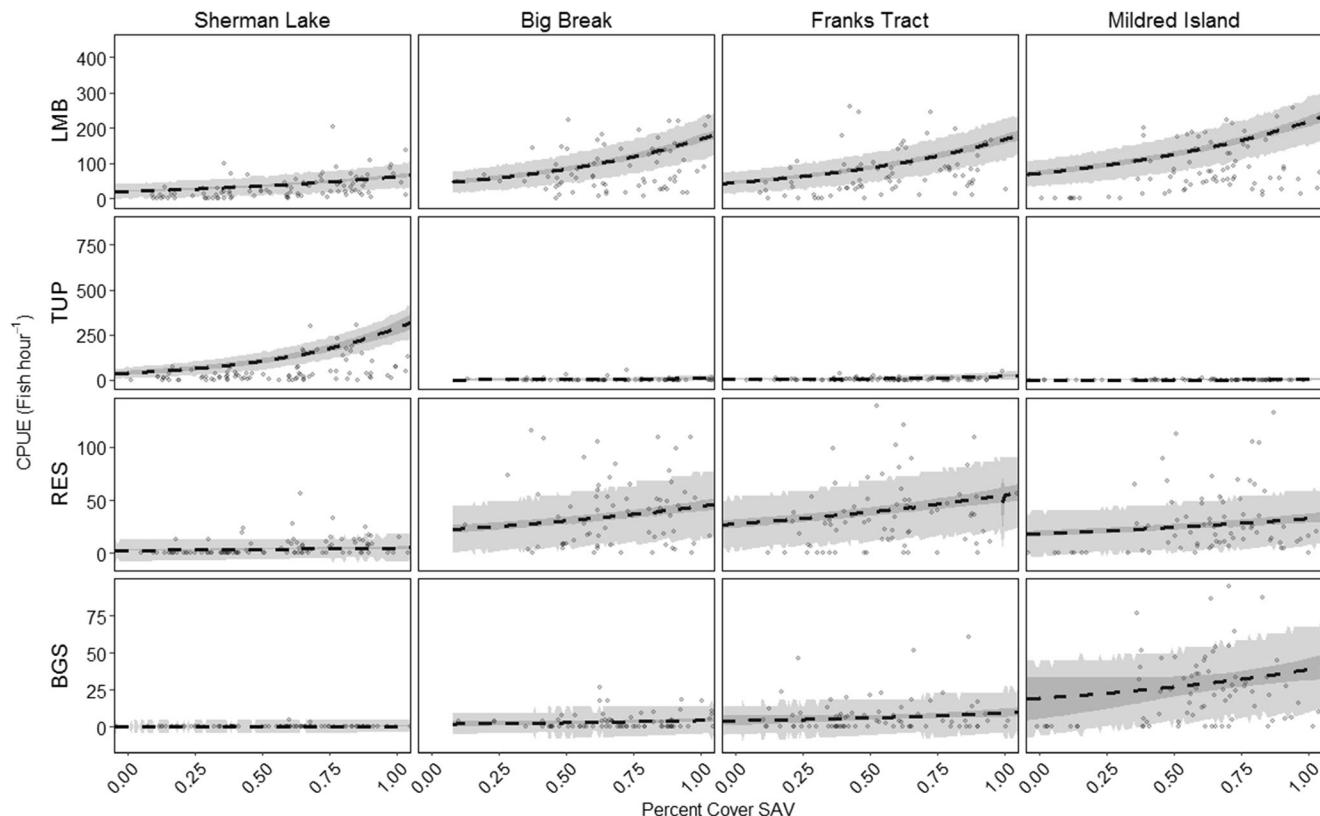


Fig. 4 Predicted CPUE of each fish species positively associated with SAV for each sampled tidal lake. Points are observed values. The dashed line is the predicted mean CPUE, the thin dark ribbon around the mean is the 95 percentile intervals for the mean, and the broader light ribbon

denotes the 95% prediction intervals for the model. The light ribbon incorporates the range of model predictions. Panels are arranged in order from west to east. Fish species codes are in Table 2

tidally reconnected to the estuary through levee failures. Most of the levees remain intact, with only a few breaches connecting these tidal lakes to the estuary. Each of these tidal lakes (or, colloquially, “flooded islands”) has distinctive physical characteristics (e.g., elevation) related to age, former land use, and location within the gradient between turbid, cooler, saltier areas closer to San Francisco Bay and clearer, warmer, fresher areas near the central Delta. We chose the four largest, longest inundated tidal lakes in the Delta, spanning a gradient of conditions, to sample in this study.

Mildred Island (ML) is the farthest east and is the most recently flooded with levee failure in 1983 (Lund et al. 2007). Due to its long history of intensive cultivation, Mildred Island exhibited substantial subsidence prior to flooding and is currently the deepest Delta tidal lake (mean elevation relative to mean sea level -3.2 ± 1.2 m). It is the smallest lake studied by area ($\sim 4 \text{ km}^2$); although due to its elevation, it is not the smallest by volume. Because it is farthest from any marine influence, Mildred Island is the warmest and freshest of the four lakes in this study (Fig. 2). The center of the lake is too deep for SAV colonization ($\sim 4\text{--}5$ m; Durand et al. 2016), with just a narrow strip of shallow, littoral habitat fringing the perimeter densely colonized by SAV.

Mildred Island is relatively isolated hydrodynamically, as its perimeter levee is breached in only a few places (Lucas et al. 2002).

Franks Tract (FT) is $\sim 13 \text{ km}^2$ and is located 10 km northwest of Mildred Island. It is bordered by distributary channels of the San Joaquin River. Franks Tract was flooded in 1938, and this shorter period of cultivation resulted in less subsidence and a relatively shallow lake (mean elevation -1.5 ± 0.6 m). The levee surrounding Franks Tract is perforated with numerous small and three relatively large (> 100 m) breaches. The center of Franks Tract is shallow enough to allow for SAV colonization, resulting in dense stands of SAV throughout the interior of the lake.

Ten kilometers west of Franks Tract is Big Break (BB; $\sim 6 \text{ km}^2$), located just upstream of the confluence of the Sacramento and San Joaquin rivers. Big Break was permanently inundated in 1928 with minimal subsidence; therefore, Big Break is shallow (mean elevation -0.7 ± 0.6 m). The entire western levee of Big Break has eroded, opening the lake to the adjacent San Joaquin River. Like Franks Tract, Big Break is shallow and has dense SAV growth throughout the lake.

Sherman Lake (SH; $\sim 7.5 \text{ km}^2$), located near the confluence of the Sacramento and San Joaquin rivers, is the

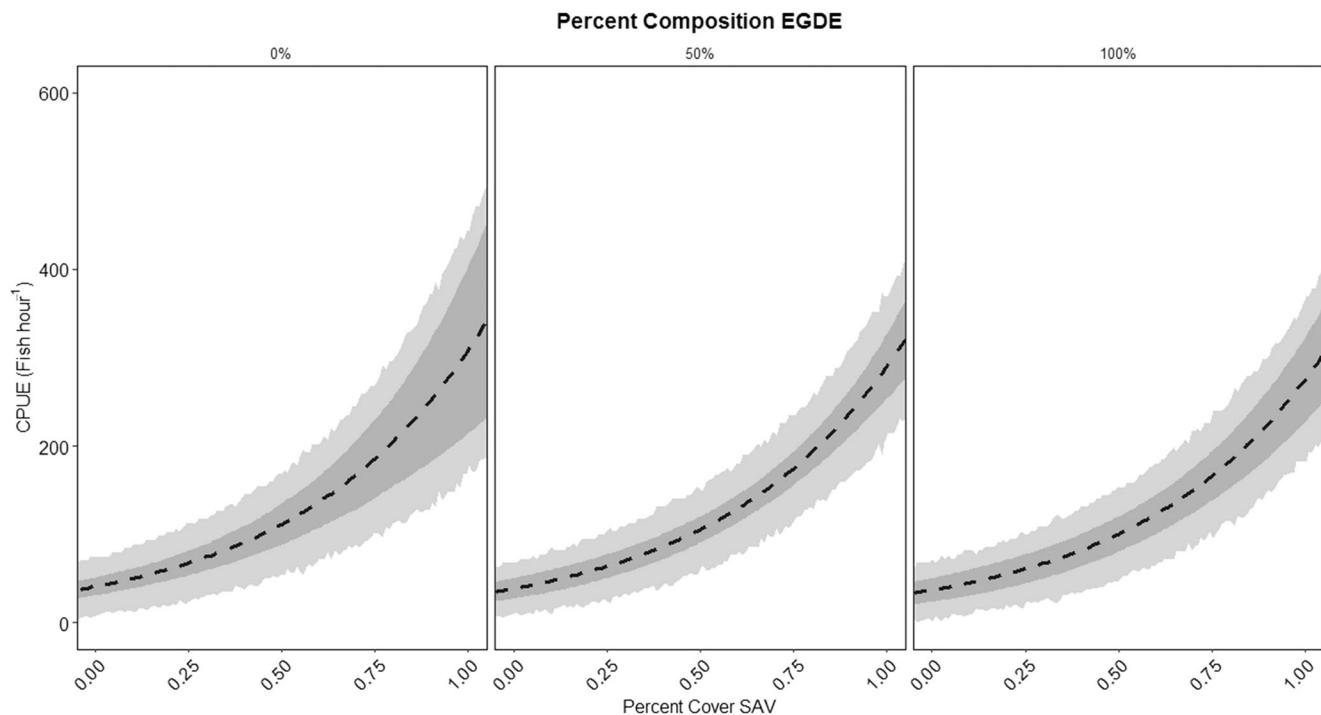


Fig. 5 Predicted CPUE of tule perch against percent composition of *Egeria densa* (EGDE). The leftmost panel shows the predicted relationship of tule perch CPUE with SAV given that 0% of the SAV is EGDE, while the rightmost is the predicted relationship if 100% of the

SAV is EGDE. The dashed line is the predicted mean CPUE, the thin dark ribbon around the mean is the 95 percentile intervals for the mean, and the broader light ribbon denotes the 95% prediction intervals for the model

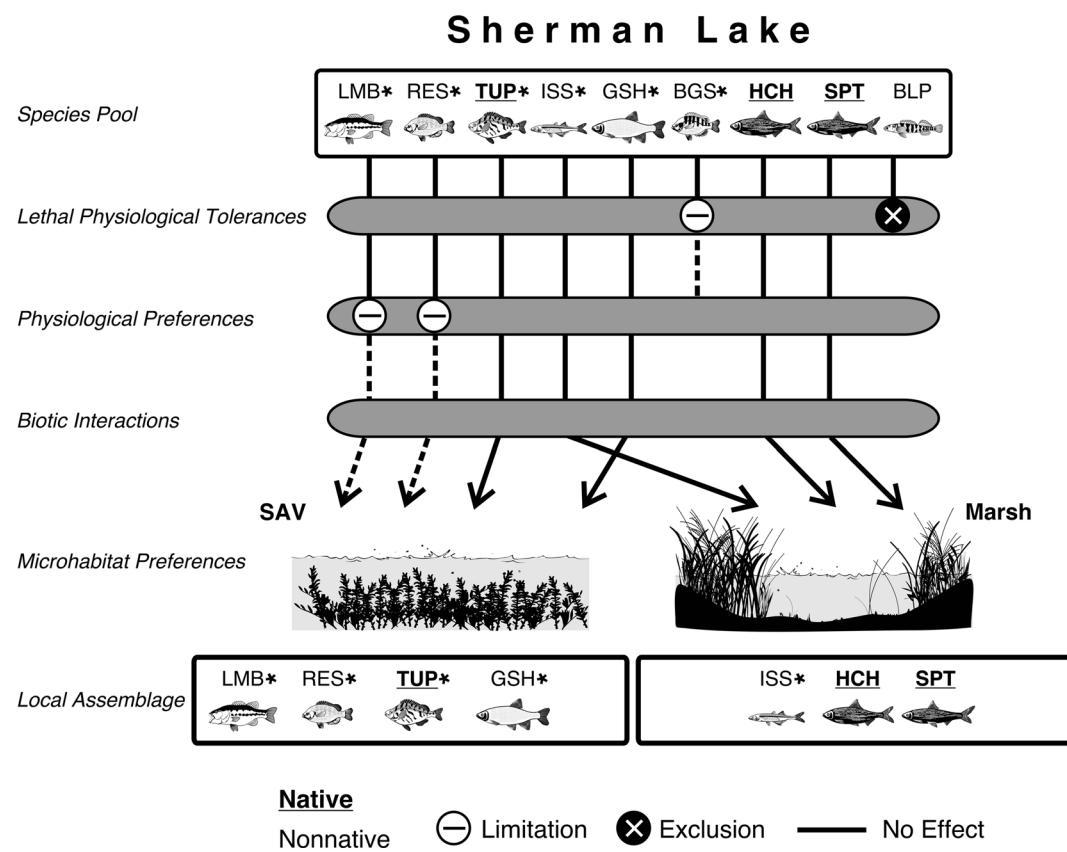
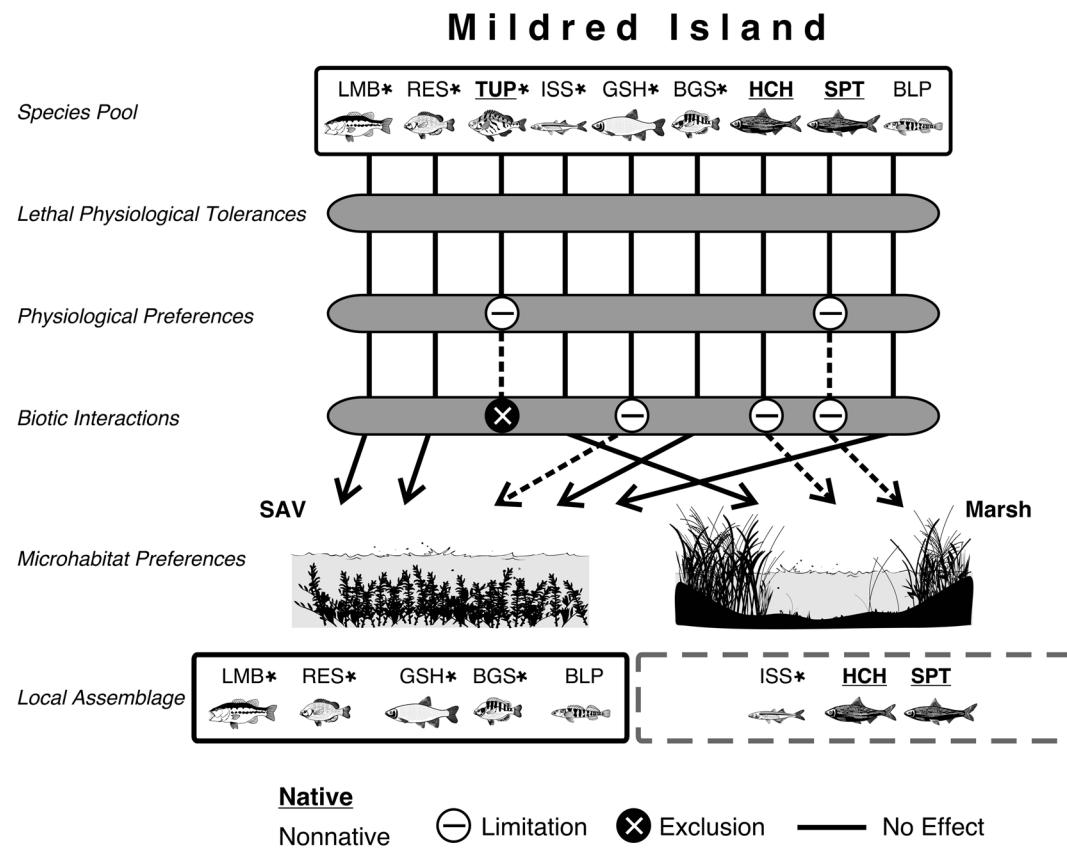


Fig. 6 A proposed application of the hierarchical filter conceptual model (based on Smith and Powell 1971) applied to fish assemblages at Sherman Lake (top) and Mildred Island (bottom). Solid lines represent individual species, and gray ovals represent “filters” which act to exclude species. Species with traits unsuitable for “passing through” these filters are limited in CPUE (−) or excluded (x) at lower levels. For each lake, two different microhabitat types are included, SAV (left) and tidal marsh (right). Species codes are in Table 2. Assignment of physiological filters based on observed salinity and temperatures and lethal and preferred values summarized in the literature (Moyle 2002)

farthest west and flooded prior to 1920 (California Department of Fish and Wildlife 2007). With many breaches in the remnant levee along both the Sacramento and San Joaquin rivers, it is heavily impacted by riverine flow. Sherman Lake is the tract nearest to San Francisco Bay and is thus most strongly affected by salinity and temperature fluctuations. Unlike the other flooded tracts, agricultural activity on Sherman Lake was minor. Instead, the tract was primarily used for deposition of dredge spoils, a practice which continued into the 1960s. This legacy of brief inundation length, minimal subsidence, and addition of substrate has resulted in a shallow tract (mean elevation -0.3 ± 1.3 m), with large areas at or above mean sea level. Sherman Lake is the second largest sampled tidal lake by area, including an extensive ~ 0.3 km² marsh complex along the western boundary of the tract (Fig. 1); however, Sherman Lake contains the least volume. Because Sherman Lake is farthest downstream, it is typically the most saline lake (Fig. 3). Similar to Franks Tract and Big Break, the open, subtidal region of Sherman Lake is colonized by SAV. Despite all of these differences between tidal lakes, pelagic primary productivity has declined and is generally low Delta-wide (< 4 µg L⁻¹; Jassby et al. 2002).

Data Collection

We sampled summer fish assemblages monthly from July through November of 2010 and July through October of 2011 by boat electrofishing. We used an 18-ft Smith-Root EHD electrofishing vessel equipped with a 5.0 GPP electrofisher, a model rated effective to specific conductivity of 5500 µS. To ensure that all sampling events were below this threshold, we measured ambient specific conductivity prior to sampling. The maximum measured specific conductivity during a sampling bout was 3457 µS (Table 1), well below the 5500 µS threshold. This method was chosen because of its success in other shallow, heavily vegetated aquatic habitats in the Delta (Brown and Michniuk 2007; Conrad et al. 2016). Electrofishing was conducted along 300-m transects oriented parallel to shore with each transect

selected by random point generation using GIS software and filtered so that each point was greater than 500 m from every other point on any given sampling day to ensure independence among samples. During each month, eight 300-m transects were sampled along the perimeter of each lake. To ensure that all habitat types in each lake were adequately sampled, an additional 2–5 transects were sampled in the marsh complex of Sherman Lake. Marsh habitats were absent in the other tidal lakes. In 2011, we sampled three additional transects within the center of each lake, each located greater than 100 m from the closest shore. These three transect types were classified as littoral, marsh, and pelagic. All fishes were netted, placed in an aerated live well until fully recovered, identified, measured to fork length (total length for species with no fork in tail), and released. Juvenile fish in the genus *Lepomis* smaller than 40 mm fork length were identified as *Lepomis* sp. Fish in this category were most abundant in July of both years. Larger leporomids (40–50 mm FL) in subsequent months were in approximate proportion to adult fishes of the same genus. Thus, for statistical analysis, all juvenile fish identified as *Lepomis* sp. were assigned a species based on the proportion of adults from the same site.

After each transect was sampled, we recorded temperature (°C), dissolved oxygen (mg L⁻¹), specific conductivity (µS), and turbidity (NTUs) using a YSI6920 sonde, and tidal phase (i.e., high, low, ebb, flood). Emergent vegetation was assessed by driving the transect in reverse and visually estimating the percent of the shoreline bordered by emergent vegetation. SAV percent areal coverage was assessed in the same fashion. SAV and emergent vegetation coverage were not measured as part of the same total (i.e., SAV + emergent did not equal 100%) because emergent vegetation assessments were based on the adjacent shoreline rather than the sampled transect. Species composition of SAV was assessed by using a garden rake to bring vegetation onto the boat and identify the proportion of species present. At high tide (depth > 1 m) and/or during periods of high turbidity (NTU > 10), the transect would be revisited at low tide to assess SAV areal coverage and species composition (9% of transects). Mean elevation relative to mean sea level for each transect was extracted from bathymetric LiDAR courtesy of the California Department of Water Resources and the United States Geological Survey (<http://baydeltaoffice.water.ca.gov/modeling/deltamodeling/modelingdata/DEM.cfm>).

Statistical Analysis

Question 1—How Do Littoral Fish Assemblages and Environmental Variables Differ Across Tidal Lakes?

To compare differences in littoral fish assemblages among tidal lakes, we compiled all of the fish data per sampling day

per lake. We then ordinated a matrix of Bray-Curtis dissimilarities using non-metric multidimensional scaling (NMDS) with the package “vegan” in Program R (Oksanen et al. 2018; R Core Team, 2016). NMDS is preferable over other ordination methods because it does not require data that are normally distributed and it is relatively robust to zero-inflated community data (Zuur et al. 2007). The stability of the ordination is measured by stress, which describes the degree to which the ordination accurately simplifies the original data. Stress values below 0.1 signify the ordination is a good fit and highly robust, values below 0.2 suggest the ordination is less robust but is still useful for interpretation, and stress values greater than 0.3 suggest the ordination is a poor fit. We used a minimum of 1000 random starts and 5000 iterations to ensure that the ordination was an accurate reflection of the data and that the ordination did not converge on a local, rather than absolute, stress minimum. A 95% confidence ellipse was projected around the centroid of the NMDS points corresponding to each tidal lake and year. Using the function envfit (R: vegan), we fit all measured environmental variables to the ordination, including temperature, specific conductivity, dissolved oxygen, pH, turbidity, elevation, percent cover SAV, and percent border emergent vegetation. Fitting these environmental variables identifies the direction within ordination space in which continuous environmental variables change most rapidly, and whether environmental variables are significantly correlated with ordination axes. We plotted both tidal lakes and fish species on the ordination biplot to identify trends in species distribution, as well as the significant environmental variables from the envfit analysis.

Question 2—What Fine-Scale Physical Habitat Features, Including SAV Species Composition, Affect the Distribution of Abundant Fish Species Within Tidal Lakes?

To assess the distribution of abundant fish species with respect to fine-scale habitat features within tidal lakes, we first identified fish species that comprised greater than 5% of sampled abundance at any single lake. For each species that met this criterion, we modeled counts of fish per transect using a series of varying intercept generalized linear mixed models (GLMMs). With these models, we used a Poisson distribution, a distribution commonly used for count data, with a log link (Eq. 1; Zuur et al. 2009). We chose this modeling approach because GLMMs allow for the incorporation of hierarchical information related to consistent clusters of data (Zuur et al. 2007). In this case, the possibility of consistent differences in fish abundance across tidal lakes, sampling years, and seasons led us to include tidal lake, year, and month as random effect variables (denoted as α , Eq. 1).

$$\text{Fish Abundance} \sim \text{Poisson}(\lambda_i) \quad (1)$$

$$\begin{aligned} \log \lambda_i = & \log(\text{Effort}(s)_i) + \alpha + \alpha_{\text{Lake}[j]} + \alpha_{\text{Year}[k]} + \alpha_{\text{Month}[l]} \\ & + \beta_p \text{TransectType}_{ijkl} + \beta_t \text{Tide}_{ijkl} + \beta_1 \text{Elevation}_{ijkl} \\ & + \beta_2 \% \text{SAV}_{ijkl} + \beta_3 \% \text{EV}_{ijkl} \end{aligned}$$

This allowed us to account for the effect of inter-lake environmental gradients, as well as inter-annual and seasonal differences and isolate fine-scale habitat variables. All random effects (Eq. 2) were assigned weakly informative priors for mean, modeled using a Gaussian distribution, and variance, modeled using a half-Cauchy distribution (Polson and Scott 2012).

$$\alpha_{\text{Lake}[j]/\text{Year}[k]/\text{Month}[l]} \sim N(\mu, \sigma) \quad (2)$$

$$\mu \sim N(0, 10)$$

$$\sigma \sim \text{cauchy}(0, 1)$$

Sampling effort was accounted for in the model by including the log of sampling time (electrofishing seconds) as an offset variable, and a modeled intercept (α). The categorical variables transect type and tide stage were coded as follows: transect type: littoral = 0, pelagic = 1, and marsh = 2; tide stage: low slack = 0, flood = 1, high slack = 2, ebb = 3. We specified weakly informative priors for all categorical variables (i.e., $\beta_p, \beta_t \sim N(0, 10)$).

Fine-scale habitat variables were included in the model (Eq. 1) as linear continuous variables with weakly informative priors (i.e., $\beta_1, 2, 3, 4, 5 \sim N(0, 10)$). This included elevation (m), temperature (C), percent cover SAV, and percent cover emergent vegetation (EV; primarily *Schoenoplectus* spp.). Because different species of SAV potentially have different impacts on fish distribution (Rozas and Odum 1988), we compared additional models for all species which exhibited a relationship with SAV. These additional models included the percent composition of four different SAV species categories: *Egeria densa*, *Ceratophyllum demersum*, non-native other, and native other. All continuous variables were z-score transformed relative to the mean value in each lake, thus identifying relative differences within a lake (e.g., transforming elevation identified “shallower” or “deeper” regions within a lake). Turbidity and conductivity were not included in the model as these variables co-varied substantially across tidal lakes and had minimal within-lake variation. Due to this co-variation, turbidity and conductivity are inherently incorporated into the models as part of the lake-specific random effects.

We ran all models using Hamiltonian Monte Carlo with the package “rethinking” (McElreath 2016) in programs R and Stan (Carpenter et al., 2017; Stan

Development Team 2017). In select instances, data for a variable were missing from a site and the model incorporated Missing Completely At Random imputation to model missing values (Little and Rubin 2002). The number of missing values for GLMMs ranged from 1 to 14 (mean = 5). We ran a parent model using all variables and refined candidate models were selected using a step-wise removal of variables until all different combinations were tested. We compared model performance using the Weighted Akaike Information Criterion (WAIC), which is calculated by taking log-likelihood means over the posterior distribution and is used to estimate out-of-sample deviance. We used all models with a WAIC weight greater than zero to create ensemble models for simulation (McElreath 2015). In cases where no ensemble was necessary, we used the best-fitting model for simulation.

Results

Question 1—How Do Environmental Variables and Littoral Fish Assemblages Differ Among Tidal Lakes?

There was a clear gradient in water quality variables across tidal lakes (Table 1, Fig. 2). Specific conductivity, a proxy for salinity, was consistently highest in Sherman Lake and declined from west to east among the four tidal lakes, although occasionally all lakes had low conductivity. Turbidity decreased and temperature generally increased along the same gradient. Daily and seasonal variation in conductivity, turbidity, and temperature followed the same gradient, as Sherman Lake exhibited the most variation in these variables and variability decreased towards Mildred Island (Table 1). SAV coverage in all lakes was uniformly high (averaging > 50%) when elevation was appropriate (< 2–3 m below sea level). Mildred Island was the only lake where the center of the lake was too deep for SAV to grow. Although SAV coverage was consistently high, the composition of SAV communities differed across lakes. SAV in Mildred Island was dominated by *Egeria densa* and *Ceratophyllum demersum* (Table 1). Franks Tract had large stands of *Potamogeton crispus* and *Stuckenia* sp. in addition to *E. densa* and *C. demersum*. Big Break had large stands of *Myriophyllum spicatum*, as well as those species abundant in Franks Tract. Sherman Lake had high densities of *E. densa*, *C. demersum*, and *M. spicatum*, and was the only tidal lake with significant stands of *Cabomba caroliniana*.

We collected 15,176 fishes belonging to 27 species (Table 2), which were summarized as catch per unit effort

(CPUE; fish h⁻¹). Non-native fishes in the family Centrarchidae (primarily largemouth bass, redear sunfish *Lepomis microlophus*, and bluegill *Lepomis macrochirus*) comprised roughly 80% of samples from Mildred Island, Franks Tract, and Big Break, but only 28% from Sherman Lake. Largemouth bass was the most abundant species overall and was numerically dominant in Mildred Island, Franks Tract, and Big Break. Tule perch *Hysterocarpus traskii* was the third most abundant species overall and was dominant in Sherman Lake. Redear sunfish, Mississippi silverside *Menidia audens*, and golden shiner *Notemigonus crysoleucas* were abundant in each tidal lake, although densities differed across lakes. Densities of native fishes were highest in Sherman Lake (63.2 fish h⁻¹, 49% of the total) and low in other lakes (Mildred Island—1.0 fish h⁻¹, 0.4%; Franks Tract—5.9 fish h⁻¹, 3.3%; Big Break—3.8 fish h⁻¹, 2.1%).

Ordination results indicated strong differences in fish assemblages among most tidal lakes (Fig. 3). A two-dimensional ordination was sufficient to keep the ordination stress under 0.2 (stress = 0.19). Confidence ellipses for Big Break and Franks Tract overlapped extensively, suggesting high similarity in their fish assemblages, while Sherman Lake had minimal overlap with any other lake. Many native fishes, such as tule perch, hitch *Lavinia exilicauda*, Sacramento pikeminnow *Ptychocheilus grandis*, Sacramento splittail *Pogonichthys macrolepidotus*, and Sacramento sucker *Catostomus occidentalis*, were associated with Sherman Lake, while certain non-native species, such as threadfin shad *Dorosoma petenense* and white catfish *Ameiurus catus*, were associated with Mildred Island. Golden shiner, largemouth bass, and Mississippi silverside were abundant in all tidal lakes and thus plotted near the center of the ordination. There was high overlap between sampling months and years in the ordination, suggesting the assemblages were consistent over time. Turbidity, elevation, and conductivity were the environmental variables significantly associated with the ordination axes (envfit P values 0.042, 0.001, and 0.005, respectively). Sherman Lake was positively associated with increased turbidity, conductivity, and elevation. Mildred Island was oppositely associated with all three variables, while Big Break and Franks Tract were intermediate with respect to all three variables. Temperature and SAV abundance were not strongly associated with either ordination axis.

Question 2—What Fine-Scale Physical Habitat Features, Including SAV Species Composition, Affect the Distribution of Abundant Fish Species?

We identified six species that comprised greater than 5% of sampled abundance at any single lake for fine-scale modeling with GLMMs: largemouth bass, redear sunfish, tule perch, Mississippi silverside, golden shiner, and bluegill. Multiple

models for largemouth bass, tule perch, and bluegill exhibited a model weight greater than 0.01 ([Appendix 1 Table 3](#), [Appendix 2 Table 4](#)) and were thus used to create an ensemble. Other species each were simulated using a single, best model. In comparisons of model simulations against observed abundances, the models generally over-predicted fish abundance at intermediate densities and under-predicted at high densities (see [Appendix 3 Fig. 7](#)), a phenomenon common with GLMMs and other modeling methods (Zuur et al. 2009). The effect of tidal lake was highly variable and differed for each species. This can be seen in lake-specific intercept differences for several species across the east-west gradient (e.g., bluegill, tule perch; [Appendix 2 Table 4](#)) and in the posterior distribution for lake-specific intercept standard deviations ([Appendix 4 Fig. 8](#)). The variability of lake-specific posterior standard deviations limits the applicability of these models to unsampled areas without additional data and highlights the importance of including the effect of region on modeled fish abundance. Sampling year was included in the best model or ensemble for every species except for largemouth bass, although model coefficients were relatively small and frequently overlapped with zero. Sampling month was included in the best model or ensemble for every species except for Mississippi silverside. Month effects were strongest in November, when most species had negative model coefficients.

Transect type was important for each species model. Marsh habitats were only present in Sherman Lake, where tule perch, Mississippi silverside, and golden shiner were positively associated with marsh transects, while the non-native centrarchids (largemouth bass, bluegill, and redear sunfish) were more abundant in littoral transects. Fish CPUE in pelagic transects was low for all species, likely a result of sampling inefficiency. Redear sunfish and tule perch both exhibited positive relationships with low tide as compared to other tide phases. Bluegill and Mississippi silverside were the only two species to exhibit a relationship with elevation (both were positively associated with shallow water). Largemouth bass, redear sunfish, bluegill, and tule perch displayed a positive relationship with percent cover of SAV ([Fig. 4](#)), and golden shiner, redear sunfish, and tule perch displayed a positive association with emergent vegetation.

Every fish species that had a relationship with SAV exhibited a relationship with at least one individual SAV species category. These relationships reflected intra-lake distributional differences, suggesting SAV species was important. In some instances, the SAV species reinforced the existing relationship with SAV percent cover. For example, tule perch were generally associated with increased coverage of SAV, although this relationship was damped if the SAV species was *E. densa*

([Fig. 5](#); [Appendix 2 Table 4](#)). This indicates that tule perch densities in SAV increase as the percent composition of *E. densa* decreases. Redear sunfish were more positively associated with *C. demersum*. Bluegill exhibited relationships with different SAV species in the ensemble model, with a weak positive relationship with *E. densa* and negative relationships with the “native other” and “non-native other” categories. Largemouth bass were positively associated with *E. densa*. The relationships of modeled fish species to individual SAV species were similar to the tule perch example above; the net effect of SAV cover was generally positive, but differed for certain SAV species.

Discussion

Fishes in this study responded to both broad environmental gradients (i.e., salinity, turbidity, and elevation) and fine-scale intra-lake habitat differences (e.g., vegetation type and density, transect type, and relative elevation). Native fishes were broadly associated with saline, turbid conditions while non-native fishes were variable. Native and non-native fish species evinced similar relationships to certain stationary habitat variables, specifically SAV coverage, although had minimal overlap in space. This suggests that SAV presence alone does not drive the decline of native fish species, but rather raises the possibility of other, unmeasured variables as important habitat requirements. Our study included every large ($> 4 \text{ km}^2$) and long inundated ($> 25 \text{ years}$) tidal lake in the Sacramento-San Joaquin Delta; however, future levee breaches (either intentional or unintentional) would necessitate careful consideration of regional location and habitat configuration prior to making predictions of fish response to the resultant available habitat.

Fish Assemblages Across Tidal Lakes

Both native and non-native fish species responded to broad environmental gradients, with native species more abundant at higher salinity and turbidity and lower elevation. Because these factors all co-vary along the same gradient, it is difficult to identify the effects of each. However, each individual species likely responded to different environmental conditions in different ways. Sampled fishes were dominated by stenohaline freshwater species, some of which are sensitive to relatively small changes in salinity. This sensitivity is evidenced by the near-complete disappearance of less tolerant freshwater species (e.g., warmouth *Lepomis gulosus* (salinity 1–4), bigscale logperch *Percina macrolepidota* (salinity < 4); Moyle 2002) and the perseverance of other, closely related species (e.g., redear sunfish (salinity 5–

12) and largemouth bass (salinity < 16); Moyle 2002) across the conductivity gradient. Reduction in CPUE of bluegill is similar to that of intolerant stenohaline fishes, despite observations of bluegill across a wide salinity range in estuaries in which it is native (Peterson and Ross 1991; Peterson et al. 1993). This could reflect local salinity adaptation of the source population for bluegill introduction, or some other mechanisms (e.g., seasonal turbidity fluctuation, tidal dewatering of nesting sites). The general pattern of gradual species loss based on individual species tolerances is common in low-salinity zones of estuaries (Wagner and Austin 1999; Martino and Able 2003).

The influence of turbidity on fish distributions in other estuaries is inconsistent, having a strong impact in some estuaries (Cyrus and Blaber 1987), but not others (Marshall and Elliot 1998). In this and other studies, conductivity and turbidity typically co-vary, making it difficult to parse out impacts of turbidity (Cyrus and Blaber 1992). However, turbidity in the upper SFE is thought to influence the distribution and abundance of pelagic species (Latour 2016), including delta smelt *Hypomesus transpacificus* (Feyrer et al. 2007), and is included in many conceptual models of the ecosystem (Sommer et al. 2007; Moyle et al. 2012). The influence of turbidity on littoral fish distributions is likely through modification of fish behavior (e.g., predator avoidance or predation success) rather than a strict physiological limit such as that imposed by conductivity (Whitfield 1999). Visual predators, such as largemouth bass, exhibit decreased foraging success in turbid habitats in mesocosm studies (Ferrari et al. 2014) and are frequently associated with high water clarity (Moyle 2002). This may be reflected in the relatively low abundance of largemouth bass in Sherman Lake, the most turbid site.

Elevation is widely recognized as an important habitat element in tidal environments; elevation and tide combine to dictate inundation and therefore access to many habitats (Knieb and Wagner 1994). All sites sampled in this study, however, are subtidal, meaning that they are inundated throughout the entire tidal cycle and habitat accessibility was not limiting. Rather than limiting inundation, the importance of elevation for these tidal lakes is to influence total lake volume and thus moderate variability in temperature, conductivity, and other factors, as well as affect overall habitat suitability. Mildred Island has demonstrably lower exchange with the rest of the Delta than other tidal lakes (Lucas et al. 2002) and is thus a relatively stable environment, with warmer temperatures and less variability than other tidal lakes. Based on the ordination, temperature was not important to fish distribution despite a temperature

gradient across tidal lakes. The mean of summer temperatures in Sherman Lake is roughly 2 °C lower than other lakes. Although not above physiological maxima, the higher temperatures in the interior of the Delta are not preferred by many native fish species (e.g., tule perch, delta smelt; Moyle 2002), just as the cooler temperatures in Sherman Lake are relatively undesirable for many warm-water non-native fishes (e.g., largemouth bass; Moyle 2002). For many non-native species, however, this temperature variation falls within the temperature ranges they experience in their native ranges, and thus, temperature may not affect non-native distribution.

Relatedly, the inter-lake distribution of many euryhaline native fishes (e.g., Sacramento splittail and tule perch) and native fishes highly tolerant of warm temperatures (e.g., hitch, Sacramento sucker) suggests that water quality variables were not the sole distributional driver. Rather, either other aspects of the environment were unsuitable or these native fishes are excluded by non-native fishes via predation or competition rather than a direct relationship with salinity, temperature, or turbidity. Many of these non-native species, such as largemouth bass and bluegill, have been shown to negatively impact native fish communities in other regions (Jackson 2002; Maezono and Miyashita 2003).

Fish Habitat Associations Within Tidal Lakes

Aquatic vegetation is widely recognized as an important element structuring aquatic communities and habitat use (Carpenter and Lodge 1986); therefore, the importance of vegetation in our study was not surprising. Submersed aquatic vegetation coverage in the Delta has increased due to the proliferation of *E. densa* and other SAV species since the 1980s (Hestir 2010; Santos et al. 2011), commensurate with an increase in many non-native littoral fish species (Brown and Michniuk 2007). In our study, these non-native littoral fish species (e.g., largemouth bass, redear sunfish, bluegill, and golden shiner) were positively associated with SAV, a finding consistent with previously documented habitat associations for largemouth bass in the Delta (Conrad et al. 2016). The positive association of tule perch with SAV was expected given the species' affinity for emergent vegetation, overhanging riparian vegetation, and complex cover in other California ecosystems (Moyle 2002). Aquatic macrophytes are often associated with decreased catchability of fishes by electrofishing (Zalewski and Cowx 1990), and so it is unlikely that the positive association of these fish species with SAV is a result of sampling bias. Instead, since catchability was likely lower in areas of high

SAV coverage, these results are conservative estimates of habitat associations for these species.

Although each of these fish species was associated with increased SAV cover, SAV species composition had only moderate influence. *Egeria densa* is widely suspected of facilitating the spread of non-native littoral fishes; however, none of the modeled non-native fishes displayed any preference for *E. densa*. This discrepancy may reflect the density and complexity of the different SAV species, as *E. densa* has the highest density (g SAV m^{-3}) relative to other Delta macrophytes (Conrad, unpublished data). Foraging efficiency, and thus growth and survival, of both adult and juvenile fishes can decline once habitat complexity exceeds some threshold (Valley and Bremigan 2002), and therefore, thick stands of *E. densa* may provide less-than-optimal foraging habitat. Despite the similarity in response of native and non-native fishes to SAV and other fine-scale habitat variables, there was minimal overlap in distribution. Tule perch was dominant in Sherman Lake, while the sunfishes were increasingly more abundant from west to east. This pattern suggests that a primary distributional driver of some native littoral fishes is prevailing environmental gradients (e.g., salinity, turbidity) in conjunction with presence of non-native species, which can displace native fish species, rather than simply the distribution of SAV.

Conservation and Management Implications

The results of our study provide insight into the likely outcomes of intentional (or unintentional; e.g., levee failure) habitat restoration activities in the Sacramento-San Joaquin Delta. To illustrate these potential restoration outcomes, we framed our interpretations of statistical modeling results with a conceptual model of fish-habitat relationships based on Smith and Powell (1971). This conceptual model (Fig. 6) hierarchically applies physical and biological habitat features as filters to the local species pool, which here consists of fish species modeled with GLMMs and three other species which exhibited clear distributional differences based on ordination results (bigscale logperch, hitch, Sacramento splittail). Based upon this conceptual model, habitat variability and position along the estuarine salinity gradient should be a key consideration for managers evaluating habitat restoration actions. This is particularly evident at the two lakes which reflect the extremes of the estuarine gradient sampled in our study, Sherman Lake and Mildred Island. Non-native species are favored in the stable, freshwater environment of Mildred Island, while native species are favored in the brackish, dynamic environment of Sherman. In this example, we show how physiological tolerances and preferences can limit or exclude species

sensitive to salinity or temperature, how biotic interactions may plausibly limit native fish CPUE, and how microhabitat availability may limit fish distributions. For example, the native species hitch and Sacramento splittail were only found in marsh microhabitats in Sherman Lake, and that microhabitat was lacking entirely from Mildred Island.

The role of SAV in this conceptual framework and its effect on local species assemblages are of particular interest to resource managers in this system (Moyle et al. 2012). The concomitant proliferation of non-native SAV and non-native fish species has caused concern that habitat restoration actions without a non-native SAV control measure of some form will provide benefits to non-native species to the detriment of native species (Brown 2003; Herbold et al. 2014). Our study found that each sampled lake was heavily dominated by non-native SAV (primarily *E. densa*) in all areas of suitable elevation (0.5–3 m below sea level), despite position along the estuarine salinity gradient and associated environmental variability. This observation suggests that existing non-native SAV species such as *E. densa* are likely to invade virtually any permanently wetted habitat restoration project. However, there was no study-wide negative relationship between SAV and native species, suggesting that other key habitat features, either associated with the physiological tolerances of individual species or the availability of microhabitat types, can help to provide advantages to native fish species.

In summary, habitat restoration is a potentially viable tool to enhance fish populations in the Sacramento-San Joaquin Delta and other systems as well. The ecological outcomes of habitat restoration will certainly be varied and difficult to predict. Planning actions around conceptual models such as those we have developed will provide opportunities for resource managers to generate desirable results. Moreover, incorporating experimental designs within restoration projects would foster continued learning opportunities and generate information to revise and refine existing conceptual models.

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Compliance with Ethical Standards

All animals were sampled under IACUC protocol number 16617 and California Department of Fish and Wildlife scientific collecting permit number 11540.

Appendix

Table 3 Comparison of top 20 model results for each species, ranked by WAIC. Fish species codes are found in Table 2. Lk lake, Yr year, Mon month, Type transect type, Td tide phase, Elev elevation, SAV percent cover submersed aquatic vegetation, EV percent cover emergent

vegetation, EGDE percent *Egeria densa*, CEDE percent *Ceratophyllum demersum*, Othnat percent other native species, Othnonnat percent other non-native species

Species	Model no.	Rank	Equation	WAIC	pWAIC	dWAIC	Model weight	SE	dSE
RES	98	1	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + CEDE + Othnat	4491.5	300.7	0	1	547.37	NA
RES	104	2	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + CEDE	4510.3	287.8	18.8	0	548.33	48.19
RES	96	3	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + CEDE + Othnat + Othnonnat	4513.6	317.5	22	0	553.6	11.97
RES	93	4	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE + Othnat	4519	314.8	27.4	0	553.19	12.73
RES	97	5	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE	4532.7	307.5	41.2	0	557.38	44.96
RES	102	6	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + CEDE + Othnonnat	4536.7	309	45.1	0	558.93	47.71
RES	94	7	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE + Othnat	4541.8	318.9	50.2	0	556.25	53.02
RES	105	8	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + Othnat	4551.9	257.5	60.4	0	584.72	164.63
RES	7	9	Lk + Yr + Mon + Type + Td + SAV + EV	4554.8	241.1	63.2	0	581.79	166.13
RES	4	10	Lk + Yr + Type + Td + Elev + SAV + EV	4555.9	181.9	64.3	0	588.87	138.04
RES	103	11	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE	4562.9	265.5	71.4	0	582.52	134.67
RES	100	12	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + Othnat	4571.3	279.7	79.7	0	587.45	144.12
RES	2	13	Lk + Yr + Mon + Type + Td + Elev + SAV + EV	4575.3	250.5	83.7	0	587.01	166.04
RES	99	14	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + Othnat + Othnonnat	4580.5	288.7	89	0	586.39	157.51
RES	101	15	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + Othnonnat	4593.2	308	101.6	0	584.03	86.7
RES	95	16	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + Othnat + Othnonnat	4597.2	322.4	105.6	0	586.65	96.94
RES	106	17	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + Othnonnat	4610.3	279.8	118.8	0	596.55	174.58
RES	8	18	Lk + Yr + Mon + Type + Td + Elev + EV	4634.3	233.5	142.8	0	577.33	165.42
RES	17	19	Lk + Yr + Type + Elev + SAV + EV	4638.5	169.1	147	0	584.31	179.17
RES	6	20	Lk + Yr + Mon + Type + Elev + SAV + EV	4659.2	238.7	167.7	0	585.71	208.06
TUP	74	1	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE + Othnat	1840.7	144	0	0.66	205.1	NA
TUP	79	2	Lk + Yr + Mon + Type + Td + SAV + EV + Othnat	1842.6	137.5	1.9	0.26	202.92	27.02
TUP	72	3	Lk + Yr + Mon + Type + Td + SAV + EV + CEDE + Othnat	1846.3	151.7	5.6	0.04	205.49	46.73
TUP	70	4	Lk + Yr + Mon + Type + Td + SAV + EV + CEDE + Othnat + Othnonnat	1846.9	156.8	6.2	0.03	209.54	41.09
TUP	73	5	Lk + Yr + Mon + Type + Td + SAV + EV + Othnat + Othnonnat	1849.5	146.7	8.8	0.01	205.65	15.65
TUP	69	6	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE + Othnat + Othnonnat	1852.3	151.6	11.6	0	206.78	3.41
TUP	66	7	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE + CEDE + Othnat + Othnonnat	1853	164.1	12.3	0	209.27	46.95
TUP	7	8	Lk + Yr + Mon + Type + Td + SAV + EV	1853.7	134	13	0	206.58	31.01
TUP	67	9	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE + CEDE + Othnat	1855.6	158	14.9	0	209.71	37.72
TUP	78	10	Lk + Yr + Mon + Type + Td + SAV + EV + CEDE	1856	147.9	15.3	0	210.15	50.33
TUP	87	11	Lk + Yr + Mon + Type + SAV + EV + EGDE + Othnat	1858.3	137.3	17.6	0	209.88	43.98
TUP	76	12	Lk + Yr + Mon + Type + Td + SAV + EV + CEDE + Othnonnat	1861.1	155.2	20.4	0	213.8	49.22
TUP	1	13	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE + Othnat + Othnonnat	1861.3	183.9	20.6	0	216.58	60.9
TUP	77	14	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE	1861.4	143.4	20.7	0	208.97	19.4
TUP	80	15	Lk + Yr + Mon + Type + Td + SAV + EV + Othnonnat	1863.4	142.7	22.7	0	208.84	26.8
TUP	68	16	Lk + Yr + Mon + Type + Td + SAV + EV + EGDE + CEDE + Othnonnat	1863.4	162.8	22.7	0	212.87	56.71
TUP	3	17	Lk + Mon + Type + Td + Elev + SAV + EV	1866.8	150.2	26.1	0	225.85	81.43
TUP	5	18	Lk + Yr + Mon + Td + Elev + SAV + EV	1868.1	145.9	27.4	0	213.23	52.5
TUP	2	19	Lk + Yr + Mon + Type + Td + Elev + SAV + EV	1868.6	157.7	27.9	0	220.88	66.76
TUP	88	20	Lk + Yr + Mon + Type + SAV + EV + Othnat	1868.9	133.6	28.2	0	209.69	55.35
LMB	59	1	Lk + Mon + Type + SAV + EGDE	5779.1	252.8	0	0.98	1108.48	NA
LMB	49	2	Lk + Mon + Type + SAV + EGDE + CEDE + Othnat	5787.7	282.6	8.6	0.01	1138.11	50.36
LMB	48	3	Lk + Mon + Type + SAV + EGDE + CEDE + Othnat + Othnonnat	5788.2	292.3	9.1	0.01	1137.26	56.24
LMB	81	4	Lk + Yr + Mon + Type + SAV + EGDE	5793.3	267.7	14.3	0	1102.28	23.6
LMB	56	5	Lk + Mon + Type + SAV + EGDE + Othnat	5795	271.1	15.9	0	1156.9	59.66
LMB	53	6	Lk + Mon + Type + SAV + EGDE + CEDE	5796.4	272.3	17.3	0	1107.84	19.51
LMB	51	7	Lk + Mon + Type + SAV + EGDE + Othnat + Othnonnat	5797.8	279.2	18.7	0	1146.52	50.83
LMB	40	8	Lk + Mon + Type + Elev + SAV + EGDE + Othnat	5797.9	276.7	18.8	0	1157	60.29
LMB	82	9	Lk + Yr + Mon + Type + SAV + EGDE + CEDE + Othnat + Othnonnat	5799.6	315.3	20.5	0	1120.81	55.27
LMB	62	10	Lk + Mon + Type + SAV + Othnonnat	5799.9	249.3	20.8	0	1097.73	40.96
LMB	32	11	Lk + Mon + Type + Elev + SAV + EGDE + CEDE + Othnat + Othnonnat	5801.2	308	22.1	0	1143.06	60.98
LMB	57	12	Lk + Mon + Type + SAV + EGDE + Othnonnat	5801.7	264.8	22.7	0	1119.07	12.69

Table 3 (continued)

Species	Model no.	Rank	Equation	WAIC	pWAIC	dWAIC	Model weight	SE	dSE
LMB	46	13	Lk + Mon + Type + Elev + SAV + Othnonnat	5803.5	263.8	24.5	0	1095.32	42.81
LMB	39	14	Lk + Mon + Type + Elev + SAV + Othnat + Othnonnat	5806.4	275.9	27.3	0	1109.27	48.94
LMB	55	15	Lk + Mon + Type + SAV + Othnat + Othnonnat	5807.4	265.8	28.3	0	1114.06	48.18
LMB	41	16	Lk + Mon + Type + Elev + SAV + EGDE + Othnonnat	5808.8	277.7	29.7	0	1124.13	21.16
LMB	50	17	Lk + Mon + Type + SAV + EGDE + CEDE + Othnonnat	5809.9	284.5	30.8	0	1110.75	28.9
LMB	83	18	Lk + Yr + Mon + Type + SAV + EGDE + CEDE + Othnat	5810	301.3	30.9	0	1132.51	51.69
LMB	33	19	Lk + Mon + Type + Elev + SAV + EGDE + CEDE + Othnat	5810.6	300.6	31.5	0	1152.31	61.29
LMB	34	20	Lk + Mon + Type + Elev + SAV + EGDE + CEDE + Othnonnat	5812.7	296.7	33.6	0	1109.95	31.92
BGS	22	1	Lk + Mon + Type + SAV	1432	54.2	0	0.78	131.99	NA
BGS	20	2	Lk + Mon + Type + Elev + SAV	1435.4	59	3.4	0.14	136.22	10.43
BGS	25	3	Lk + Mon + Type	1438.2	42.8	6.2	0.04	139.81	22.64
BGS	64	4	Lk + Yr + Mon + Type + SAV	1441.1	60.4	9.1	0.01	134.27	3.13
BGS	63	5	Lk + Yr + Mon + Type + Elev + SAV	1441.2	63.1	9.2	0.01	137.62	11.66
BGS	62	6	Lk + Mon + Type + SAV + Othnonnat	1441.5	61	9.5	0.01	133.49	2.96
BGS	59	7	Lk + Mon + Type + SAV + EGDE	1441.7	61.2	9.7	0.01	133.89	3.01
BGS	43	8	Lk + Mon + Type + Elev + SAV + EGDE	1442.7	64.8	10.7	0	137.6	11.62
BGS	46	9	Lk + Mon + Type + Elev + SAV + Othnonnat	1443.2	64.7	11.2	0	137.43	11.54
BGS	45	10	Lk + Mon + Type + Elev + SAV + Othnat	1443.3	64.8	11.3	0	136.53	10.8
BGS	9	11	Lk + Yr + Mon + Type + Td + Elev + SAV	1443.6	66.3	11.6	0	139.03	13.77
BGS	61	12	Lk + Mon + Type + SAV + Othnat	1443.6	61.8	11.6	0	133.4	5.17
BGS	60	13	Lk + Mon + Type + SAV + CEDE	1445.1	63.6	13.1	0	134.48	4.03
BGS	44	14	Lk + Mon + Type + Elev + SAV + CEDE	1445.1	66.6	13.1	0	137.84	11.58
BGS	23	15	Lk + Yr + Mon + Type	1445.5	48.8	13.5	0	142.27	24.17
BGS	92	16	Lk + Yr + Mon + Type + SAV + Othnonnat	1447.1	65.5	15.1	0	134.74	4.3
BGS	3	17	Lk + Mon + Type + Td + Elev + SAV + EV	1448	74.8	16	0	138.92	18.08
BGS	91	18	Lk + Yr + Mon + Type + Elev + SAV + Othnonnat	1448.3	69.1	16.3	0	138.4	12.41
BGS	18	19	Lk + Mon + Type + Elev + SAV + EV	1448.3	72.6	16.3	0	138.09	15.23
BGS	57	20	Lk + Mon + Type + SAV + EGDE + Othnonnat	1449.1	67	17.1	0	134.78	4.28
GSH	47	1	Lk + Yr + Mon + Type + Elev + EV	3130.1	278.9	0	1	866.57	NA
GSH	6	2	Lk + Yr + Mon + Type + Elev + SAV + EV	3180	303.5	49.9	0	896.32	41.32
GSH	8	3	Lk + Yr + Mon + Type + Td + Elev + EV	3182.9	315.3	52.8	0	902.49	44.97
GSH	19	4	Lk + Yr + Type + Elev + EV	3196.6	206.4	66.5	0	933.82	123.34
GSH	2	5	Lk + Yr + Mon + Type + Td + Elev + SAV + EV	3202	329.8	71.9	0	904.75	45.95
GSH	21	6	Lk + Yr + Type + EV	3208.4	183	78.3	0	933.11	126.31
GSH	17	7	Lk + Yr + Type + Elev + SAV + EV	3219.2	225.8	89.2	0	944.11	114.91
GSH	7	8	Lk + Yr + Mon + Type + Td + SAV + EV	3225.2	323.3	95.1	0	912.08	79.81
GSH	5	9	Lk + Yr + Mon + Td + Elev + SAV + EV	3233	300.8	102.9	0	863.61	61.29
GSH	4	10	Lk + Yr + Type + Td + Elev + SAV + EV	3277.9	267.4	147.8	0	968.25	129.74
GSH	18	11	Lk + Mon + Type + Elev + SAV + EV	3376.9	295.1	246.8	0	1032.9	222.29
GSH	3	12	Lk + Mon + Type + Td + Elev + SAV + EV	3380.4	329.2	250.3	0	1026.63	207.57
GSH	65	13	Lk + Yr + Mon + Type + Elev	3403.1	306	273	0	952.24	155.83
GSH	23	14	Lk + Yr + Mon + Type	3409.6	288	279.5	0	948.67	177.05
GSH	1	15	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE + Othnat + Othnonnat	3415.8	469.6	285.7	0	1093.9	241.53
GSH	11	16	Lk + Yr + Mon + Type + Td + Elev	3430.1	332.4	300	0	963.2	161.05
GSH	63	17	Lk + Yr + Mon + Type + Elev + SAV	3433.5	323.7	303.4	0	959.89	162.31
GSH	64	18	Lk + Yr + Mon + Type + SAV	3447.5	308.5	317.4	0	954.38	183.21
GSH	24	19	Lk + Yr + Type	3473.3	196.7	343.2	0	987.65	218.98
GSH	9	20	Lk + Yr + Mon + Type + Td + Elev + SAV	3476.6	361.9	346.5	0	971.78	171.43
ISS	27	1	Lk + Yr + Elev	3967.6	187.9	0	1	581.14	NA
ISS	16	2	Lk + Yr + Type + Td + Elev	3990	232.6	22.5	0	595.05	62.27
ISS	19	3	Lk + Yr + Type + Elev + EV	4006.2	252	38.6	0	586.19	80.11
ISS	17	4	Lk + Yr + Type + Elev + SAV + EV	4043.6	289.3	76.1	0	598.09	89.55
ISS	4	5	Lk + Yr + Type + Td + Elev + SAV + EV	4062.1	313.8	94.5	0	605.62	97.28
ISS	65	6	Lk + Yr + Mon + Type + Elev	4111.2	329.5	143.7	0	629.37	104.25
ISS	26	7	Lk + Yr + Mon + Elev	4121.2	312.7	153.6	0	625.9	76.8
ISS	11	8	Lk + Yr + Mon + Type + Td + Elev	4127	352.3	159.4	0	635.33	116.24
ISS	63	9	Lk + Yr + Mon + Type + Elev + SAV	4138.7	359.9	171.2	0	634.32	106.89
ISS	1	10	Lk + Yr + Mon + Type + Td + Elev + SAV + EV + EGDE + CEDE + Othnat + Othnonnat	4143.4	515.7	175.9	0	612.82	166.91
ISS	9	11	Lk + Yr + Mon + Type + Td + Elev + SAV	4170.7	386.7	203.1	0	647.68	124.98
ISS	8	12	Lk + Yr + Mon + Type + Td + Elev + EV	4190.4	407.4	222.8	0	644.96	137.16
ISS	6	13	Lk + Yr + Mon + Type + Elev + SAV + EV	4193.4	413.1	225.8	0	639.31	129.34
ISS	5	14	Lk + Yr + Mon + Td + Elev + SAV + EV	4222.8	413.5	255.3	0	638.74	131.18
ISS	2	15	Lk + Yr + Mon + Type + Td + Elev + SAV + EV	4232.4	442.2	264.8	0	653.25	148.61
ISS	10	16	Lk + Type + Td + Elev + SAV + EV	4292.6	309.4	325	0	696.71	237.67
ISS	20	17	Lk + Mon + Type + Elev + SAV	4343.5	367.8	376	0	725.13	267.61
ISS	28	18	Lk + Mon + Elev	4363.9	318.5	396.4	0	713.31	259.75
ISS	18	19	Lk + Mon + Type + Elev + SAV + EV	4389.5	409.9	421.9	0	734.26	277.71
ISS	3	20	Lk + Mon + Type + Td + Elev + SAV + EV	4410.4	440.3	442.9	0	737.25	286.51

Table 4 Mean and standard deviation of model coefficients for all species, parameters, and models included in the analysis, including individual WAIC weights. Estimates for all coefficients derive from Hamiltonian Monte Carlo model output. All models where WAIC did not equal 0 were used for ensembles. Coefficients for environmental and species interactions relate to z-score transformed continuous parameters. Parameters not included in the best fitting models are denoted with dashes. For fish species codes see Table 1, lake codes see Fig. 1

Species	BGS						GSH	ISS
Model	22	20	25	64	63	62	59	47
WAIC weight	0.78	0.14	0.04	0.01	0.01	0.01	0.01	1.00
Intercept	-7.21 ± 1.37	-7.24 ± 1.32	-7.18 ± 1.36	-7.31 ± 1.41	-7.26 ± 1.40	-7.18 ± 1.31	-7.26 ± 1.34	-6.77 ± 1.39
Lake intercepts	-2.87 ± 1.68	-2.87 ± 1.37	-2.83 ± 1.39	-2.81 ± 1.36	-2.87 ± 1.35	-2.91 ± 1.34	-2.83 ± 1.38	-6.2 ± 1.21
Intercept [SH]	0.28 ± 1.35	0.28 ± 1.31	0.25 ± 1.35	0.34 ± 1.32	0.29 ± 1.31	0.24 ± 1.29	0.31 ± 1.33	-0.52 ± 0.36
Intercept [BB]	0.91 ± 1.35	0.91 ± 1.31	0.90 ± 1.35	0.98 ± 1.31	0.91 ± 1.31	0.87 ± 1.29	0.94 ± 1.33	0.94 ± 0.65
Intercept [FT]	2.42 ± 1.35	2.43 ± 1.31	2.45 ± 1.35	2.49 ± 1.31	2.43 ± 1.31	2.38 ± 1.29	2.46 ± 1.33	0.18 ± 0.36
Intercept [ML]	-	-	-	0.03 ± 0.48	0.03 ± 0.51	-	-	0.51 ± 0.36
Year	Intercept [2010]	-	-	0.02 ± 0.48	0.02 ± 0.51	-	-	-0.45 ± 1.17
Intercept [2011]	-	-	-	0.00 ± 0.24	0.00 ± 0.21	-0.05 ± 0.26	-0.06 ± 0.23	-0.33 ± 1.16
Month	Intercept [Jul]	-0.05 ± 0.25	-0.05 ± 0.24	-0.25 ± 0.24	-0.27 ± 0.22	-0.27 ± 0.26	-0.25 ± 0.23	0.77 ± 0.42
Intercept [Aug]	-0.27 ± 0.25	-0.25 ± 0.24	-0.52 ± 0.24	0.49 ± 0.21	0.53 ± 0.26	0.52 ± 0.23	0.55 ± 0.23	-0.26 ± 0.25
Intercept [Sep]	0.53 ± 0.25	0.52 ± 0.24	0.02 ± 0.24	0.06 ± 0.21	0.02 ± 0.26	0.02 ± 0.23	0.03 ± 0.23	-0.18 ± 0.43
Intercept [Oct]	0.02 ± 0.25	0.02 ± 0.24	-0.21 ± 0.25	-0.22 ± 0.22	-0.23 ± 0.27	-0.22 ± 0.24	0.04 ± 0.24	-0.01 ± 0.43
Category	Intercept [Nov]	-0.23 ± 0.26	-0.21 ± 0.25	-0.21 ± 0.25	-0.23 ± 0.22	-0.23 ± 0.27	-0.23 ± 0.24	-0.22 ± 0.25
Pelagic	-6.83 ± 2.57	-6.47 ± 2.55	-7.09 ± 2.40	-6.79 ± 2.46	-6.75 ± 2.54	-6.79 ± 2.54	-6.83 ± 2.54	-1.02 ± 0.47
Marsh	-3.40 ± 3.29	-3.41 ± 3.29	-3.60 ± 3.29	-3.40 ± 3.28	-3.39 ± 3.31	-3.47 ± 3.33	-3.38 ± 3.29	-2.25 ± 0.40
Tide	-	-	-	-	-	-	-	0.53 ± 0.14
Continuous	Elevation	0.07 ± 0.04	-	-	0.07 ± 0.04	-	-	-
SAV	0.22 ± 0.05	0.24 ± 0.05	-	0.22 ± 0.05	0.22 ± 0.05	0.23 ± 0.05	0.22 ± 0.06	0.6 ± 0.02
Tule	-	-	-	-	-	-	-	-
CEDE	-	-	-	-	-	-	-	-
EGIDE	-	-	-	-	-	-	-	-
SAV species	Other native	-	-	-	-	-	-	-
	Other nonnative	-	-	-	-	-	-	-
Species	LMB			RES		TUP		
Model	59	49	48	98	74	79	72	70
WAIC weight	0.98	0.01	0.01	1.00	0.66	0.26	0.04	0.03
Intercept	-4.09 ± 0.49	-4.10 ± 0.50	-5.04 ± 1.17	-7.78 ± 1.48	-7.77 ± 1.51	-7.81 ± 1.50	-7.75 ± 1.43	-7.81 ± 1.56
Lake intercepts	-0.77 ± 0.42	-0.78 ± 0.43	-0.79 ± 0.44	-1.52 ± 0.72	2.92 ± 1.22	2.93 ± 1.27	2.92 ± 1.22	2.97 ± 1.33
0.32 ± 0.42	0.34 ± 0.43	0.34 ± 0.44	0.70 ± 0.71	-0.34 ± 1.23	-0.33 ± 1.28	-0.28 ± 1.28	-0.28 ± 1.23	-0.32 ± 1.33
0.10 ± 0.42	0.12 ± 0.43	0.12 ± 0.44	0.81 ± 0.72	0.07 ± 1.23	0.11 ± 1.28	0.14 ± 1.27	0.11 ± 1.22	0.11 ± 1.33
0.51 ± 0.42	0.49 ± 0.43	0.44 ± 0.44	0.36 ± 0.72	-2.11 ± 1.25	-2.14 ± 1.30	-2.10 ± 1.29	-2.16 ± 1.25	-2.16 ± 1.35
Year	-	-	-0.17 ± 0.92	0.28 ± 0.81	0.24 ± 0.81	0.23 ± 0.78	0.19 ± 0.68	0.26 ± 0.72
Month	0.32 ± 0.25	0.35 ± 0.26	0.34 ± 0.24	-0.07 ± 0.15	1.17 ± 0.43	1.25 ± 0.45	-0.04 ± 0.45	-0.13 ± 0.68
	0.01 ± 0.26	0.02 ± 0.26	0.01 ± 0.24	-0.06 ± 0.15	-0.09 ± 0.43	-0.01 ± 0.47	-0.01 ± 0.51	-0.13 ± 0.72

Table 4 (continued)

	0.13 ± 0.25	0.12 ± 0.26	0.12 ± 0.24	0.02 ± 0.15	-0.33 ± 0.43	-0.33 ± 0.45	-0.33 ± 0.47	-0.30 ± 0.51	-0.31 ± 0.46
	0.19 ± 0.26	0.19 ± 0.26	0.20 ± 0.24	0.31 ± 0.15	-0.81 ± 0.44	-0.90 ± 0.45	-0.87 ± 0.48	-0.75 ± 0.51	-0.81 ± 0.46
	-0.62 ± 0.26	-0.59 ± 0.26	-0.60 ± 0.24	-0.14 ± 0.15	0.08 ± 0.44	0.08 ± 0.45	0.12 ± 0.48	0.15 ± 0.51	0.09 ± 0.46
Category	-1.45 ± 0.12	-1.49 ± 0.12	-1.42 ± 0.12	-2.12 ± 0.19	-0.03 ± 0.30	-0.16 ± 0.30	-0.13 ± 0.30	0.04 ± 0.30	-0.02 ± 0.30
	-0.63 ± 0.22	-0.52 ± 0.22	-0.50 ± 0.22	-6.01 ± 2.63	0.15 ± 0.14	0.23 ± 0.14	0.30 ± 0.14	0.10 ± 0.15	0.08 ± 0.14
	-	-	-	0.62 ± 0.05	0.67 ± 0.12	0.73 ± 0.11	0.71 ± 0.11	0.67 ± 0.11	0.71 ± 0.12
Continuous	-	-	-	-0.02 ± 0.02	-	-	-	-	-
	0.31 ± 0.02	0.31 ± 0.02	0.31 ± 0.02	0.16 ± 0.02	0.59 ± 0.04	0.54 ± 0.04	0.57 ± 0.04	0.59 ± 0.04	0.59 ± 0.04
	-	-	-	0.24 ± 0.02	0.25 ± 0.03	0.25 ± 0.03	0.26 ± 0.03	0.24 ± 0.03	0.24 ± 0.03
SAV species	0.06 ± 0.01	0.15 ± 0.03	0.19 ± 0.02	-	-	0.09 ± 0.02	0.12 ± 0.02	-	-
	0.10 ± 0.01	0.16 ± 0.02	0.29 ± 0.04	-	-0.14 ± 0.04	-	-	-	-
	-	0.09 ± 0.01	0.11 ± 0.02	-	-0.40 ± 0.09	-0.32 ± 0.08	-0.28 ± 0.08	-0.34 ± 0.09	-0.38 ± 0.09
	-	-	0.13 ± 0.03	0.14 ± 0.02	-	-	-	0.15 ± 0.04	0.11 ± 0.04

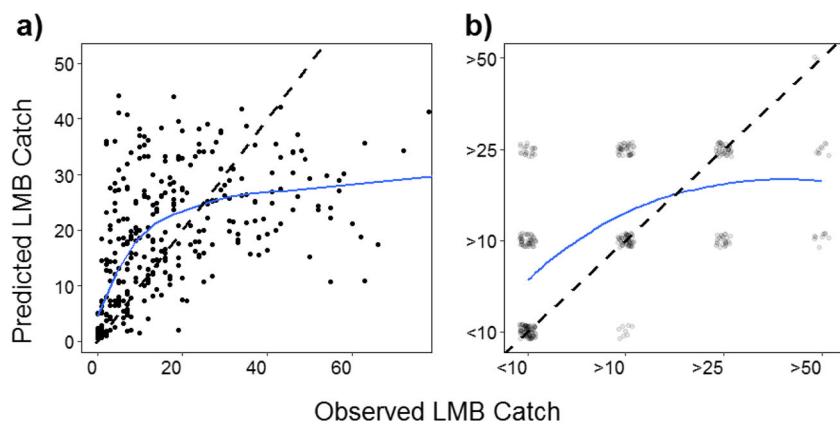


Fig. 7 Plot of predicted catch of largemouth bass (LMB) against observed catch. Dotted lines show a line of 1:1, where values would match up directly. Solid line shows loess smoothed curve of actual distribution of points. In **a**, note that predicted values are higher than expected for observed numbers below roughly 25 and lower than expected for observed numbers above 25. **b** shows the same data

binned into categories of catch to help identify broad trends. The model accurately or under-predicts all observed values greater than 25 or 50, and accurately or over-predicts most values under 25. This phenomenon is common with regression models, particularly of species which are not uniformly distributed across a given habitat. Similar trends were seen for all species

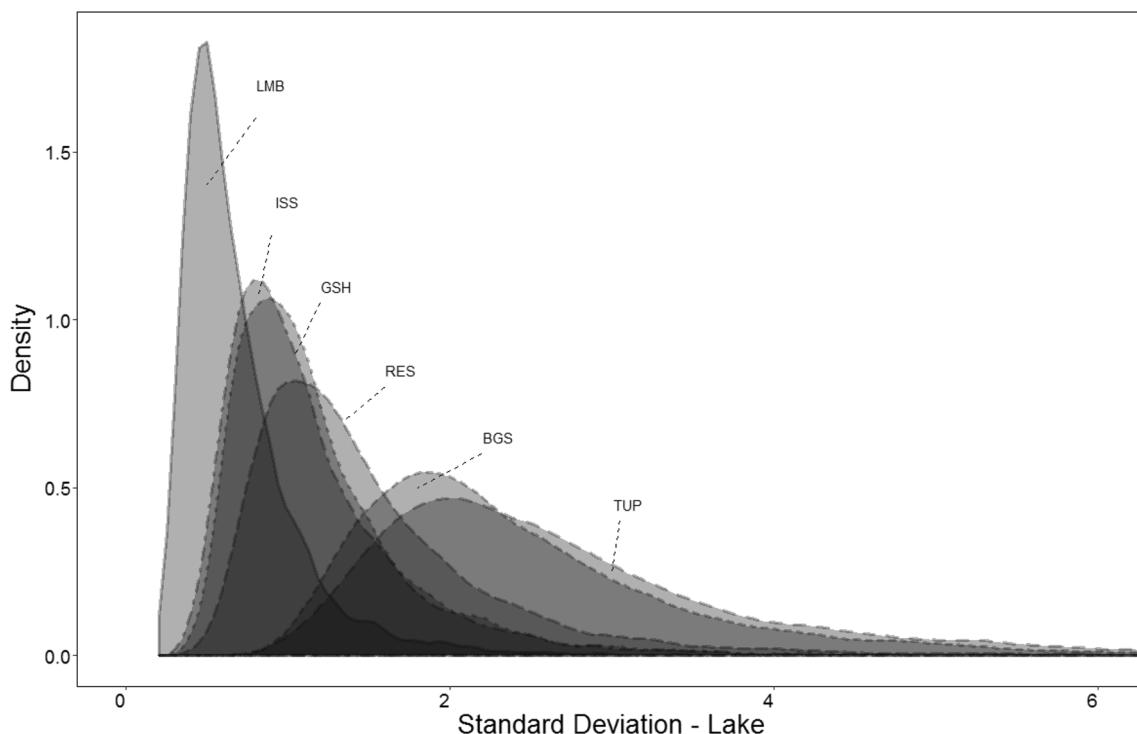


Fig. 8 Posterior distributions of the varying tidal lake standard deviations. The narrow width for largemouth bass (LMB) suggests that the variability across lakes is low for LMB, while the increased width for

bluegill (BGS) and tule perch (TUP) suggests that variability across lakes is high for these species

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