



Estuarine–terrestrial habitat gradients enhance nursery function for resident and transient fishes in the San Francisco Estuary

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ABSTRACT: Nursery functions of US West Coast drowned river valley estuaries are not well understood. Using long-term fish-monitoring data (1995–2017) in Suisun Marsh, San Francisco Estuary, California, USA, we examined spatial and temporal trends in abundance and apparent growth of fishes with diverse life-history types. Focal species were Sacramento splittail *Pogonichthys macrolepidotus*, striped bass *Morone saxatilis*, tule perch *Hysterocarpus traski*, and starry flounder *Platichthys stellatus*, which collectively represented 55 % of total catch (n = 140 092). We identified keystone habitat patches that functioned as nursery hotspots during the peak young-of-the-year recruitment window. Deep, flow-through sloughs close to the open estuary were important nursery habitats for the marine transient starry flounder. In contrast, splittail and striped bass mostly migrated through such corridors to rear in shallow, dead-end sloughs transecting tidal marsh plains, managed tidal ponds, and uplands. Tule perch were concentrated in shallow, interior sloughs, reflecting their resident life-history type and adaptations to variable conditions in a small home range. Interactions among freshwater flows and stationary habitat features (e.g. channel depth, land-to-open-water ratio) were related to fish abundance; however, species and age classes differed in their relationships to these interactions, suggesting a mechanism for habitat partitioning in space and time. Overall, we inferred that habitat connectivity—longitudinal, lateral, and vertical—along the estuarine–terrestrial gradient was a driver of fish species diversity and productivity. Consideration of seascape–landscape dynamics across multiple spatial and temporal scales in estuaries should help maintain or increase fish populations and ecological resilience in the face of rising sea levels and other environmental stressors.

KEY WORDS: Fishes · Habitat gradients · Land–water interactions · Seascape nursery

1. INTRODUCTION

Understanding the drivers of nursery function for nekton is a central goal in marine ecology (Beck et al. 2001). Recent research proposes that nursery function is driven by environmental variability, hydrodynamics, trophic coupling, ontogenetic movements, and differential use of habitat patches and corridors

(Litvin et al. 2018). The notion is that complex, connected, and productive shallow-water habitats improve survival of juveniles because they allow movement among habitats that differ in food, predation refuge, or water quality or flow conditions (Beck et al. 2001, Nagelkerken et al. 2015). Understanding the natural history of juvenile fishes (e.g. ontogenetic shifts in habitat use) and how species with different

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life histories leverage variable conditions across space and time are thus essential to developing management strategies for coastal and estuarine environments (Munsch et al. 2016).

Ecologists have historically described nurseries as areas that support substantial numbers of economically, recreationally, or ecologically significant species that depend on nearshore habitats as juveniles and then recruit to offshore marine fisheries as adults (Hay 1905, Gunter 1967, Boesch & Turner 1984). Beck et al. (2001) developed a conceptual framework that defined nurseries as habitat patches that contribute disproportionately to the density, biomass, growth, and/or survival of juveniles to adult populations. Some examples of well-recognized nursery habitats are salt marshes, seagrass meadows, mangrove forests, and coral reefs. This seminal concept inspired ecosystem-based fishery management through protection of high-value nursery habitats similar to that of offshore marine protected areas. However, the concept does not explicitly integrate many of the dynamic processes of coastal and estuarine ecosystems (Litvin et al. 2018).

The recently proposed 'seascape nursery' concept (Nagelkerken et al. 2015) posits that nurseries encompass mosaics of coastal and estuarine habitats that are functionally linked physically and ecologically. An important advancement is that this concept explicitly incorporates dynamic patterns and processes in heterogeneous marine environments; however, critical transition zones along the land–water interface require closer investigation (Boström et al. 2011, Oleson et al. 2017). This is especially true in topographically diverse systems that have received less attention in the literature, such as drowned river valley estuaries on the US West Coast (Hughes et al. 2014). Tidal marshes are model systems for studying ecological gradients because they are complex mosaics of connected habitats and corridors that occur along a gradient of estuarine and terrestrial influences; the gradient can structure ontogenetic habitat use by juvenile nekton (Rountree & Able 2007, Weinstein et al. 2014). To better understand drivers of nursery function using a systems approach *sensu* Nagelkerken et al. (2015), we related long-term fish-monitoring data to flows, water-quality conditions, and stationary habitat features in a large brackish wetland, located in a major drowned river valley estuary in California.

Our first question was: Do species exhibit temporal shifts in abundance, distribution, or growth over ontogeny? Recent research on a nearshore fish assemblage has shown that different fish types can

partition habitat in both space and time (Munsch et al. 2016). Resident species, which typically spend their entire life in a given habitat/area, are adapted to frequent shifts in habitat quality in smaller home ranges, whereas transient species are highly mobile and frequently move among habitat patches in search of resources (Rountree & Able 2007). Trade-offs in food availability and predation risk may also play an important role in habitat selection (McIvor & Odum 1988, Munsch et al. 2016). For example, nearshore habitats often have a lot of food; however, the need for transient juveniles to grow may be offset by their need to occupy habitats less accessible to predators (Lankford & Targett 1994, Sogard 1997, Dahlgren & Eggleston 2000, Grol et al. 2011). Nevertheless, growing rapidly in risky habitats may be advantageous if it allows individuals to recruit to the next size class quickly. Larger fish may have a 'refuge in size' from predation, allowing them to occupy habitats with more food (Sogard 1997). To determine how fishes with different life histories exhibit such spatial and temporal habitat partitioning over ontogeny, we evaluated seasonal and annual trends in abundance, distribution, and apparent growth using hierarchical non-linear models.

Next, we asked: What are the relative effects of stationary habitat features, freshwater flows, and water-quality conditions on habitat use? Specifically, do land–water interactions influence nursery function? To answer these questions, we used a seascape ecology approach to characterize structural patterns among sloughs. We then used a combination of non-metric multidimensional scaling and hierarchical linear models to compare the effects of stationary habitat variables, flows, and water quality on fish distribution and abundance. We anticipated such relationships because freshwater flows affect fish assemblages in brackish zones and because temperate estuaries exhibit seasonal shifts in prevailing environmental conditions while individuals grow. Based on these expectations, we hypothesized that species with different life histories, all of which evolved under dynamic estuarine conditions yet have different environmental tolerances/preferences, would exhibit distinct habitat associations along the estuarine–terrestrial gradient. We also looked for evidence of marsh dependence in early stages of ontogeny. We hypothesized that because juveniles must balance tradeoffs between foraging and predator avoidance, and because marshes can provide refuges from predators (Kneib 1997) while supplying food (Robertson & Duke 1990), early life-history stages of fishes rely on marshes or other terrestrial-influenced habitats.

2. MATERIALS AND METHODS

2.1. Study system

Surveys were conducted in Suisun Marsh, San Francisco Estuary, California, USA (Fig. 1), a 470 km² brackish wetland ecosystem located approximately 80 km upstream of the Golden Gate of San Francisco Bay and west of the Sacramento–San Joaquin Delta ('Delta'; Whitcraft et al. 2011). Approximately two-thirds of the landscape is diked wetlands, which are managed primarily as tidal ponds for waterfowl; the remaining one-third is a network of subtidal and intertidal sloughs featuring varying levels of channel realignment, diking, infill, and ditching for mosquito control (Moyle et al. 2014). Low- to moderate-relief grasslands are hydrologically connected to Suisun

Marsh's sloughs by perennial and seasonal creeks and seeps, intermittent overland flow, groundwater discharge, and/or marsh pore-water exchange with tides. In addition, several freshwater creeks (e.g. Spring Branch, Green Valley, Ledgewood, Denver-ton) drain into Suisun Marsh.

Suisun Marsh consists of large, flow-through sloughs that connect the estuary to networks of small, dead-end sloughs that transect tidal marsh plains and managed tidal ponds. In these large and small sloughs, bottom substrates comprise either compacted or loose sediments, respectively (Baumsteiger et al. 2017). Sloughs are either flanked by gradually sloping berms formed by tides or by riprap/peat levees constructed to prevent unmanaged flooding and are lined with emergent vegetation such as tules (*Schoenoplectus* spp.), cattails (*Typha* spp.), and common reed *Phragmites*

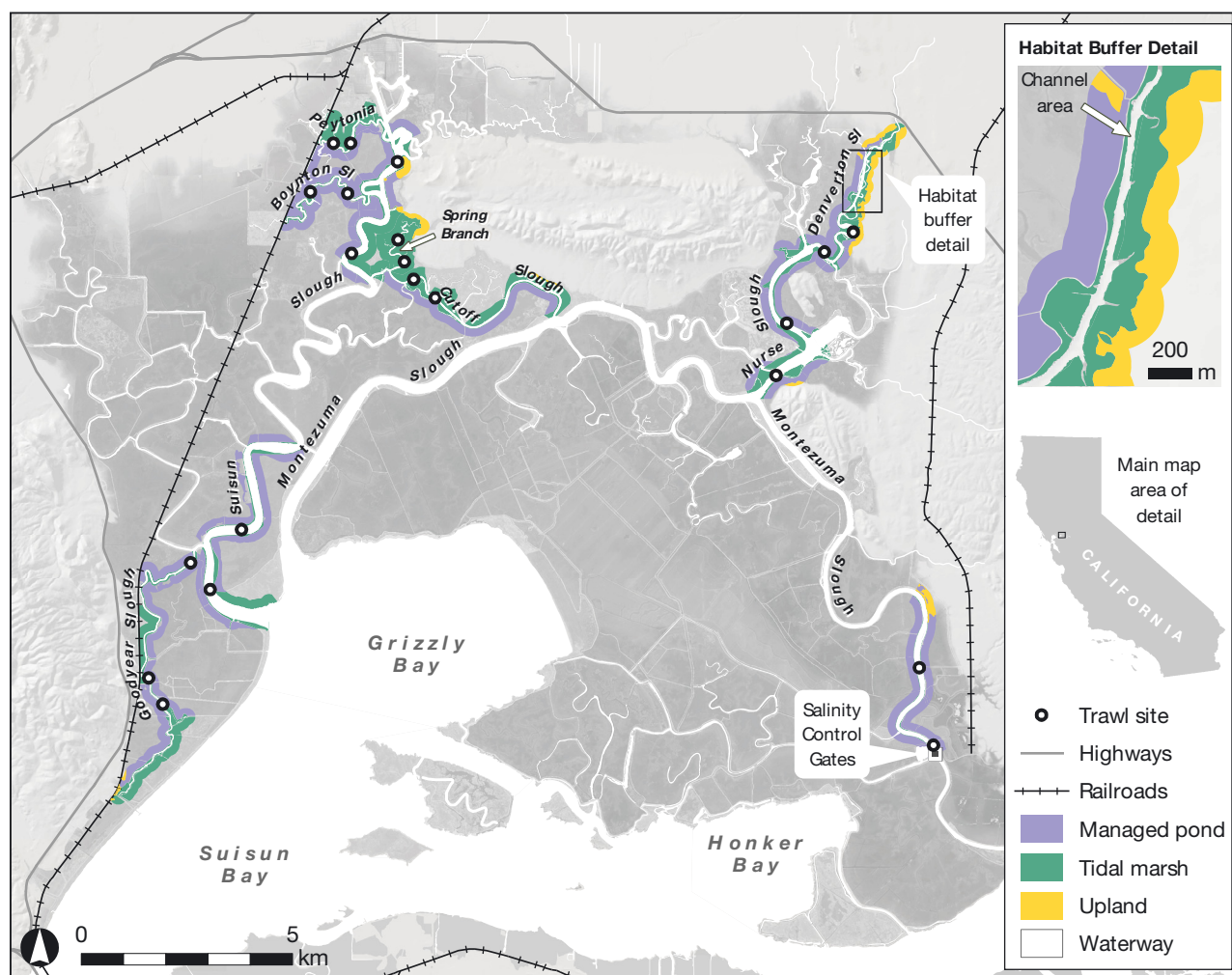


Fig. 1. Long-term trawl survey sites and adjacent land cover buffers calculated in Suisun Marsh, a large brackish wetland complex in the San Francisco Estuary, California, USA. Data: CalAtlas (2012), Department of Water Resources Atlas (2018, <http://atlas-dwr.opendata.arcgis.com>), Gesch et al. (2002), San Francisco Estuary Institute (2012), US Geological Survey (2004)

australis. Submersed macrophytes (e.g. *Stuckenia* spp.) are patchily distributed along some shallow depositional banks, but they are not abundant, likely due to high turbidity limiting light (Moyle et al. 2014). A tidal marsh reserve (Rush Ranch National Estuarine Research Reserve) with reticulate slough networks and natural marsh-plain flooding of pools and ponds represents the largest remaining undiked tidal marsh in Suisun Marsh (4.24 km²; <1% of total Suisun Marsh area; Whitcraft et al. 2011, Enright et al. 2013).

The Mediterranean climate drives annual and seasonal variability in freshwater flows from 2 major rivers, the Sacramento and San Joaquin, which drain California's Central Valley, flowing through the Delta and then into Suisun Marsh and San Pablo Bay. River regulation from dams has dampened seasonal variability, especially in the wet season from winter and spring. However, precipitation patterns, ranging from prolonged droughts to extreme wet years, remain the primary driver of estuary-wide hydrology, and Delta flows have substantial impacts on water quality in Suisun Marsh. Semidiurnal tides transport salt water from the Pacific Ocean up the axis of the estuary twice a day. From autumn to spring during dry periods, a large salinity control structure in eastern Montezuma Slough restricts flow of saltier waters from the estuary on flood tides and subsequently traps inflows from the fresher Delta on ebb tides. This results in a net movement of lower-salinity water from east to west through Suisun Marsh. The gates are operated by law to create favorable conditions for freshwater vascular plants, widely viewed as the preferred food of wild ducks and geese, in managed tidal ponds (Moyle et al. 2014).

Managed tidal ponds are typically located between sloughs or at their ends. During the waterfowl-hunting season (October to February), tidal waters are slowly circulated through gated culverts and water

levels are maintained with flashboards. In winter and spring, punctuated flood-and-drain events occur in the ponds to remove salts from pond soils to encourage desired plant growth. Over the summer season, dry ponds subside as peat soils oxidize (Moyle et al. 2014). This water management schedule modestly overlaps with the young-of-the-year (YOY) fish recruitment window (i.e. spring to autumn).

2.2. Surveys

The UC Davis Suisun Marsh Fish Study is a fish-monitoring program that was started to document fish population trends in tidal sloughs (Meng et al. 1994) and is commonly used to examine long-term change in the ecosystem relative to other changes in the San Francisco Estuary. We analyzed data from monthly otter-trawl surveys conducted from 1995 to 2017 in 9 sloughs, which is the program's longest comprehensive time series across Suisun Marsh. Otter-trawl surveys were conducted during daylight and across all tides permitting boat access. Nets were towed along the channel bottom for 5 min in small sloughs or 10 min in large sloughs, during which bottom depths (m) were averaged among 1 or 2 min intervals, respectively, from a transom-mounted transducer. Fish were identified to species, measured in standard length (SL, mm), and released. Temperature (°C), specific conductivity (µS), salinity (ppt), dissolved oxygen (µg l⁻¹), and Secchi depth (cm) were recorded at each trawl site with a Yellow Springs Instrument 85 or Pro 2030 device and a 20 cm white disk.

Focal species selected for this study were 4 common fishes that have historically dominated YOY catch in otter-trawl surveys, and which represent diverse life-history strategies (Table 1). The Sacramento splittail *Pogonichthys macrolepidotus* is a large-bodied, benthic-oriented minnow. Sexually

Table 1. Focal species, including species code, common name, binomial, life-history strategy, salinity range, and spawning habitat type (Moyle 2002). All species are native to the San Francisco Estuary except for the naturalized striped bass

Code	Common name	Binomial	Life history	Salinity range	Spawning habitat
SPT	Sacramento splittail	<i>Pogonichthys macrolepidotus</i>	Transient (semi-anadromous)	Euryhaline	Riverine floodplain
STB	Striped bass	<i>Morone saxatilis</i>	Transient (anadromous)	Euryhaline	Riverine
TUP	Tule perch	<i>Hysterocarpus traski</i>	Resident	Freshwater–mesohaline	Estuarine/riverine
STAFLO	Starry flounder	<i>Platichthys stellatus</i>	Transient (marine)	Euryhaline	Coastal/estuarine

mature adults migrate to fresh water to spawn on floodplains in winter and spring, after which YOY migrate to the low-salinity zone to rear in tidal marshes, including those of Suisun Marsh (Moyle et al. 2004). The striped bass *Morone saxatilis* is a large, predatory, anadromous species that was introduced to California in 1879 (Scofield 1931) and also rears in nearshore habitats in the low-salinity zone (Sommer et al. 2011). The tule perch *Hysterothys traski* is a native live-bearing resident associated with vegetation in freshwater and brackish environments (Baltz & Moyle 1982). The starry flounder *Platichthys stellatus* is a native marine transient species that makes seasonal migrations into shallow coastal or estuarine habitats (Kimmerer et al. 2009). Collectively, these species represented 55% of the total trawl catch ($n = 140\,092$).

2.3. Analyses

2.3.1. Stationary habitat features along the estuarine–terrestrial gradient

We calculated stationary habitat variables by using heads-up digitizing and aerial photographs from 2015, in which polygons were drawn to represent channel edges and delineate wetland habitats at 1:3000 scale or better. First, slough polygons surrounding otter-trawl transects were identified and channel areas were calculated. Second, we identified land cover types (i.e. emergent marsh, managed tidal pond, upland) and calculated their respective areas within 10 to 200 m buffers directly surrounding channel polygons. The 200 m buffers were selected for the analysis to capture the greatest diversity of land

cover types and zone of terrestrial influence around sampled sloughs. Buffers >200 m were deemed too large due to overlap among sites. The marsh to open water (OW) ratio was calculated as the emergent marsh polygon area divided by the channel polygon area (m^2 ; Shafer & Streever 2000). The metric was intended to characterize the extent of biogenic habitat (i.e. vegetated structure that governs the exchange of nutrients and organisms across the land–water interface) that may influence nursery function in tidal marshes (Boström et al. 2011, Litvin et al. 2018). Due to the importance of marsh to OW ratios to fish in previous studies (Weinstein et al. 2001, Teal & Weinstein 2002, Litvin et al. 2018, Hammock et al. 2019), we replicated the approach for the other hydrologically connected land cover types (i.e. managed tidal pond and upland) to characterize estuarine–terrestrial gradients among sampled sloughs; the resulting variables are hereafter referred to as ‘Marsh:OW,’ ‘Pond:OW,’ and ‘Upland:OW.’ The sums of these metrics are ‘Wetland:OW,’ which includes tidal marsh and managed tidal ponds, and ‘Land:OW,’ which includes all 3 land cover types (i.e. tidal marsh, managed tidal pond, upland). Recorded depths from trawl surveys were used to calculate means and standard deviations of channel depths. Lastly, sinuosity (S), defined as the ratio of meander intrinsic length (L_s) along the channel axis and its Cartesian length (L_x) (Marani et al. 2006), was estimated in each slough as a measure of channel complexity. The resulting stationary habitat variables (Table 2) were then plotted to examine variances and correlations. Regions were delineated as ‘east’ and ‘west,’ and Suisun Slough was separated into upper and lower sections based on Matern et al. (2002), which yielded a total of 10 study sloughs.

Table 2. Stationary habitat features of sampled sloughs. Ratios of land cover area to open water (OW) area were calculated using 200 m buffers surrounding slough polygons. Wetland:OW is the sum of marsh and pond areas divided by open water area. Land:OW is the sum of marsh, pond, and upland areas divided by open water area. FW: freshwater; WWTP: waste-water treatment plant. Depths were measured in meters

Slough	Region	Marsh: OW	Pond: OW	Upland: OW	Land: OW	Wetland: OW	Sinuosity (S)	Depth mean (SD)	Local FW creek/input	Channel type
Boynton	West	2.20	7.70	0.00	9.90	9.90	1.97	3.1 (1.0)	WWTP	Dead-end
Cutoff	West	5.55	3.91	0.13	9.59	9.46	1.47	2.3 (0.6)	Overland	Flow-through
Denverton	East	3.27	3.07	2.20	8.54	6.34	1.62	3.1 (1.1)	Seasonal	Dead-end
Goodyear	West	7.04	9.18	0.17	16.38	16.21	1.46	2.3 (1.0)	Overland	Dead-end
Montezuma	East	0.26	3.18	0.26	3.71	3.45	1.23	6.2 (2.3)	Overland	Flow-through
Nurse	East	1.45	1.95	0.04	3.45	3.41	1.42	5.3 (2.4)	Overland	Flow-through
Peytonia	West	8.00	5.08	0.00	13.08	13.08	1.92	2.8 (0.9)	Perennial	Dead-end
Spring Branch	West	14.25	0.00	2.24	16.49	14.25	2.00	1.7 (0.6)	Seasonal	Dead-end
Suisun Lower	West	0.68	1.26	0.00	1.94	1.94	1.87	4.0 (1.8)	Overland	Flow-through
Suisun Upper	West	0.90	1.18	0.15	2.22	2.08	1.40	5.8 (2.1)	Overland	Flow-through

2.3.2. Annual and seasonal abundance, distribution, and apparent growth

To evaluate spatial and temporal shifts among fish species and life stages, we used estimated age classes established in a previous analysis of length-frequency histograms (Manfree 2014). Three distinct groups (likely YOY, age-1, and age-2+) were identified for Sacramento splittail, striped bass, and starry flounder. Two distinct groups (likely YOY and age-1+) were identified for tule perch. Due to very small catches of age-2+ starry flounder, we pooled catches for age-1 and age-2+ to create an age-1+ grouping.

To understand annual trends in the abundance and age-class structure of each species across the 22 yr study duration, we used generalized additive mixed models (GAMMs). GAMMs are flexible hierarchical non-linear regression functions that allow smooth relationships between predictor and response variables to vary between groups and are commonly used to model time-series data (Pedersen et al. 2019). Specifically, we modeled annual species catches with year as a main effect with smoothness that was allowed to vary as a function of estimated age class. Trawl site (i.e. repeat visits to each sampling location) was included as a random-effect grouping variable. The year parameter included a thin plate regression spline (TPRS), a general-purpose spline that smooths the relationship between predictor and response variables (Wood 2003). The number of trawl minutes was log-transformed and included as an offset variable to adjust for differences in sampling effort (i.e. 5 or 10 min trawls). We used a Poisson distribution to adjust for skew towards smaller catches observed in the raw data and specified weakly informative priors with a normal distribution for the mean and a half-Cauchy distribution for the variance (McElreath 2018).

Next we examined seasonal dynamics of YOY fish abundance and apparent growth by slough. We modeled YOY fish abundance using a TPRS smoother as described above; in this version, we specified month as a main effect with smoothness that was allowed to vary as a function of slough. Random-effect grouping variables included year, trawl site, and trawl minutes adjusted for sampling effort. A zero-inflated Poisson distribution adjusted the models for excess zeros present in the monthly dataset (i.e. May to November, the YOY recruitment window).

To evaluate apparent growth through time, defined as the average change in the population's size structure (i.e. measured SL, mm) across sampling months, we specified month as a main effect that was allowed

to vary as a function of slough and the random-effect grouping variables year and trawl site. We used a Gaussian distribution and specified weakly informative Student's *t*-distribution for normally distributed data. We fit all models using the 'No-U-Turn Sampler' (NUTS) extension of Hamiltonian Monte Carlo (Hoffman & Gelman 2014) with the packages 'brms' (Bürkner 2017, 2018) and 'RStan' (Stan Development Team 2018). We then performed model checking procedures with 'bayesplot' (Gabry & Mahr 2019) in Program R v3.5.0 (R Core Team 2018).

2.3.3. Species–habitat relationships

We evaluated physical habitat effects on species and age-class distributions via non-metric multidimensional scaling (NMDS) using the package 'vegan' v2.4-6 (Oksanen et al. 2018) in Program R v3.5.0 (R Core Team 2018). First, we constructed a Bray-Curtis dissimilarity matrix describing annual CPUE for each species, age class, and slough combination. Next, we fit stationary habitat features (Table 2) and water-quality variables to the ordination. Missing values for monthly water-quality variables were imputed using predictive mean matching in the package 'mice' (Buuren & Groothuis-Oudshoorn 2011), and then mean annual specific conductivity, temperature, and Secchi depth were calculated for each slough. Species, age classes, and sloughs were plotted along with fitted environmental variables. In addition, we termed sloughs that had ratios of land to open water >4 within their 200 m polygon buffers as 'land-dominated' and the others as 'open-water-dominated,' then projected their mean NMDS values as ellipses on the ordination biplot to look for broader, seascape-scale differences in species and age-class distributions across the estuarine–terrestrial gradient.

2.3.4. Land–water interactions

We also tested for effects of land–water interactions on nursery function by modeling YOY and age-1+ abundances using generalized linear mixed models (GLMMs; McElreath 2018). We used season, year, and trawl site as random-effect grouping variables for each species and age-class combination (Table 3). The number of trawl minutes was log-transformed and included as an offset variable to adjust for differences in sampling effort. Net Delta outflow, an estimate of daily average outflow from

Table 3. Definitions of predictor variables used in generalized linear mixed models

Variable	Definition	Type
Effort	Number of minutes trawled	Numeric
Site	Trawl survey location	Categorical
Year (Yr)	Year that trawl survey occurred	Categorical
Season (Sn)	Season that trawl survey occurred	Categorical
Depth	Average water depth of trawl site	Numeric
Land:OW (LOW)	Ratio of land (marsh, pond, upland) area to open water area	Numeric
Wetland:OW (WOW)	Ratio of wetland (marsh, pond) area to open water area	Numeric
Marsh:OW (MOW)	Ratio of marsh area to open water area	Numeric
Pond:OW (POW)	Ratio of pond area to open water area	Numeric
Upland:OW (UOW)	Ratio of upland area to open water area	Numeric
Sinuosity (S)	Ratio of meander intrinsic length along the channel axis and its Cartesian length	Numeric
Outflow	Net delta outflow	Numeric

the upstream Delta (<https://data.cnra.ca.gov/dataset/dayflow>), was averaged by season and year and z-score transformed (mean = 0, SD = 1) to attribute seasonal and annual differences to the season and year categorical variables (Zuur et al. 2009). All stationary habitat variables were mean centered (mean = 0; see Table 3). Next, we examined the standardized variables for multicollinearity by calculating variance inflation factors in the package 'car' (Fox & Weisberg 2018) and selected combinations of variables that yielded values below 2 (Zuur et al. 2009). Because we anticipated that freshwater flows would strongly influence the abundance of focal species (Meng & Matern 2001, Matern et al. 2002), we chose to examine both additive and 2-way interaction effects among Delta outflow and each stationary habitat variable to see which combinations improved model predictions. To do so, we constructed varying-intercept GLMMs with a Poisson distribution and specified weakly informative priors with a normal distribution for the mean and a half-Cauchy distribution for the variance, respectively (mean prior: 0,10; variance prior: 0,1; McElreath 2018). We fit all models and conducted posterior predictive checks using the same Program R packages as described in the GAMM analysis. Then we compared model results using leave-one-out cross-validation with the package 'loo' (Vehtari et al. 2018). The leave-one-out cross-validation information criterion (looic) was calculated by taking averages of log-likelihood over the posterior distribution. Model (Akaike) weights for each model were interpreted as 'an estimate of the probability that the model will make the best predictions on new data, conditional on the set of models considered' (McElreath 2018, p. 199).

3. RESULTS

3.1. Overall patterns in Suisun Marsh

Survey data showed that focal species exhibited resident or transient life-history strategies (Table 1), corroborating literature within the San Francisco Estuary and other estuaries where the species occur (Moyle 2002). Tule perch were present in Suisun Marsh year-round and thus were the only true resident in the present study. Splittail were also present throughout the year, but we did not consider them strictly resident, because most sexually mature adults make spawning migrations upriver in winter months (Moyle et al. 2004) and most YOY in Suisun Marsh come from floodplains (e.g. Yolo Bypass; Sommer et al. 1997, Feyrer et al. 2010). Striped bass and starry flounder were found in Suisun Marsh primarily as YOY in summer and autumn, after which recruits likely dispersed throughout the estuary. Large fish of both species were likely inadequately captured by otter trawl because they are better able to avoid or escape the net, so they may have been more abundant than the data indicated. However, large striped bass are caught year-round by anglers in Suisun Marsh (T. A. O'Rear unpubl. data).

GAMM predictions indicated that species exhibited wide interannual variability in abundance. Across the entire dataset, striped bass yielded the highest predicted CPUE, followed by Sacramento splittail and tule perch; starry flounder were periodically present in Suisun Marsh but in relatively low numbers (Fig. 2). YOY were numerically dominant compared to older age classes for striped bass and starry flounder but not for splittail or tule perch, which also had high numbers of older age classes.

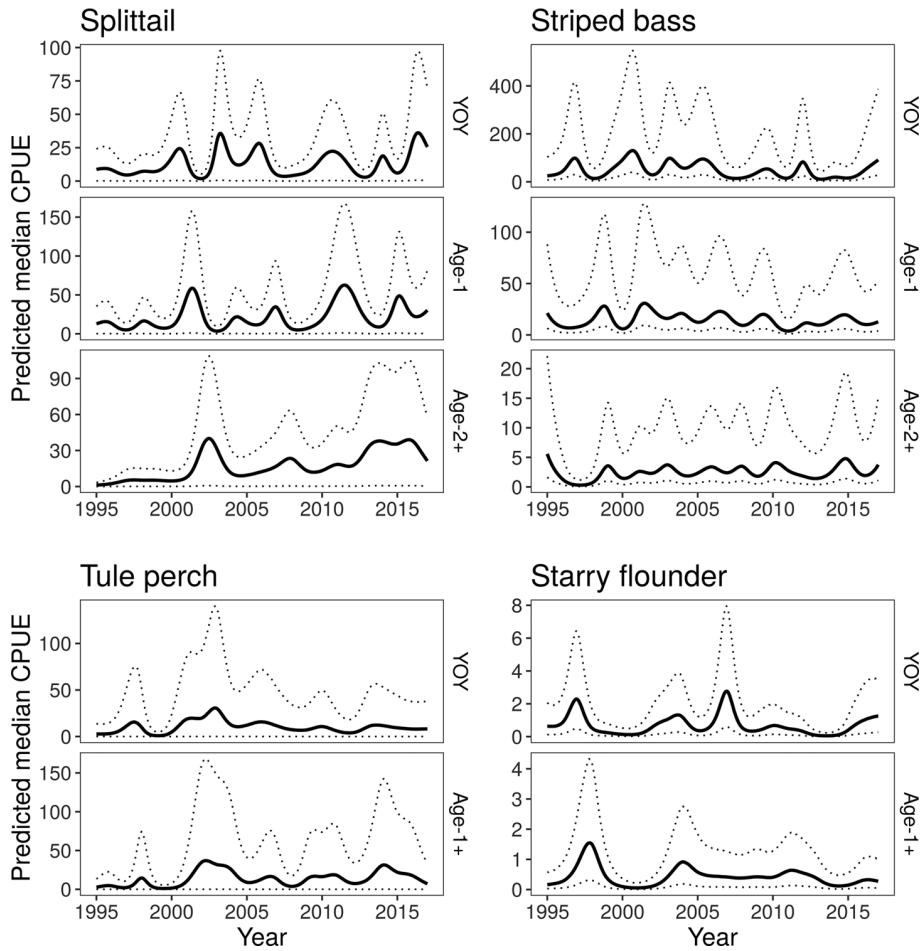


Fig. 2. Annual catch-per-unit-effort (CPUE) trends of focal species and age classes monitored in Suisun Marsh. Black lines indicate predicted median estimates from generalized additive mixed models; dotted lines indicate 95% credible intervals around the median

Timing of recruitment into Suisun Marsh from downstream saltwater habitats (starry flounder), upstream freshwater habitats (Sacramento splittail and striped bass), or local reproduction within Suisun Marsh itself (tule perch) generally peaked in summer (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m637p141_supp.pdf). Across Suisun Marsh, predicted CPUE of YOY striped bass peaked earlier in the season (May to June). Conversely, YOY starry flounder peaked in July and August, and both YOY tule perch and splittail peaked in August. Predicted CPUE of all species subsequently declined as months progressed.

3.2. Fine-scale spatial and temporal patterns of YOY fish

According to the YOY GAMM results, fine-scale temporal and spatial variation occurred among species with respect to abundance; however, there was little evidence for differences in apparent growth

rate except for tule perch in summer (Fig. 3). For splittail, the predicted YOY CPUE was greatest overall in western dead-end sloughs (Spring Branch and Goodyear), where it peaked earlier in summer (June and July), whereas eastern sloughs (Nurse and Denver-ton) became relatively more important from late summer to autumn. Predicted body size and apparent growth rate followed similar trajectories over time but showed variability among sloughs in June and July, during the peak recruitment period, when young splittail were moving into Suisun Marsh from upstream floodplain habitats (median SL: 32–44 mm). Notably, during this period, sloughs with the highest predicted abundance only had average predicted apparent growth rates (change in median predicted SL: $\sim 14 \text{ mm mo}^{-1}$).

For striped bass models, predicted YOY CPUE was disproportionately greater in the dead-end slough Spring Branch from May to June. The initial predicted body sizes in May and June were 6 and 18 mm, respectively, reflecting the movement and settlement of larval and post-larval fish into Suisun Marsh from late

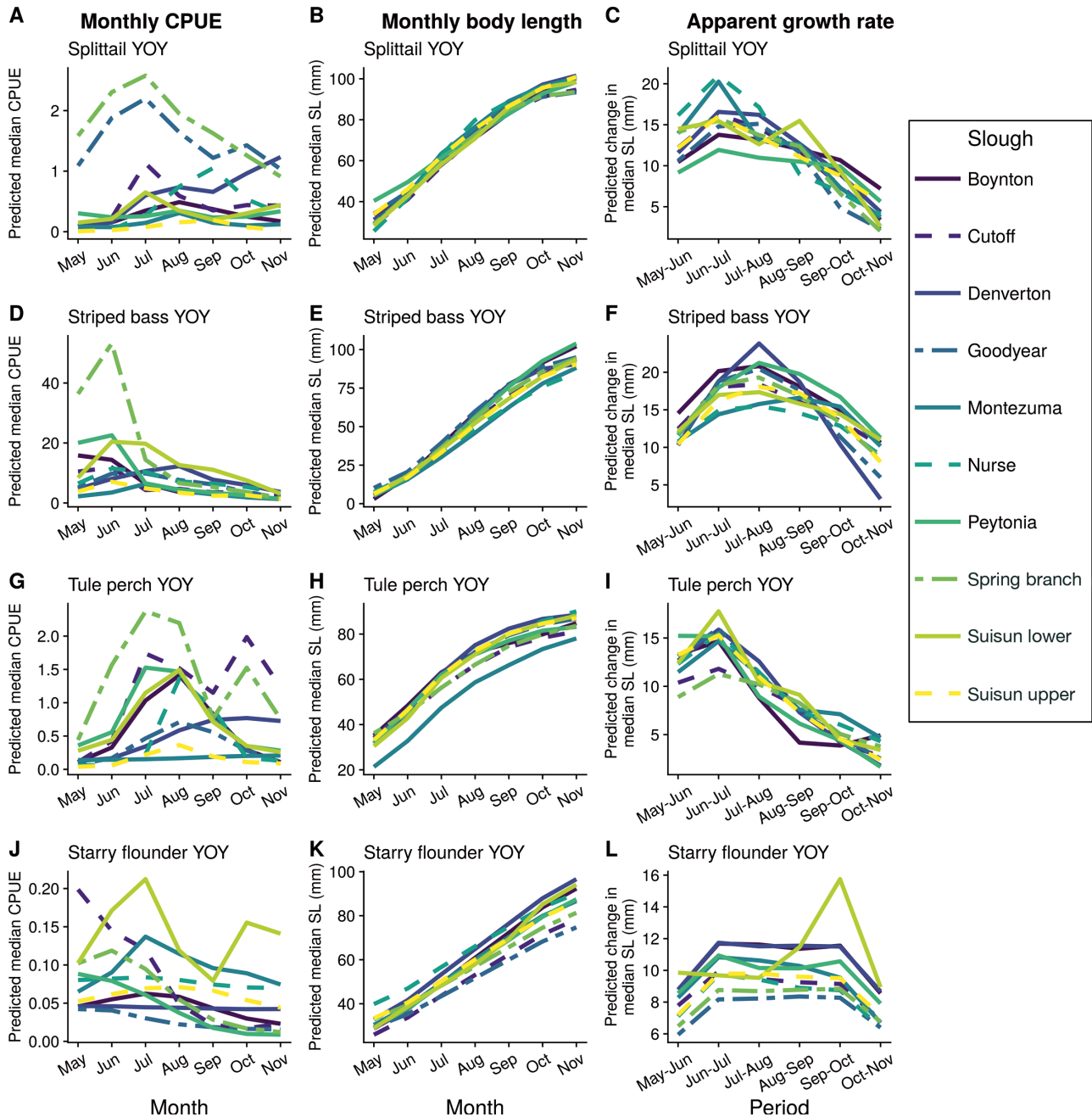


Fig. 3. Seasonal dynamics for predicted young-of-the-year (YOY) catch-per-unit-effort (CPUE), body length (standard length, SL), and growth rates in Suisun Marsh. Lines indicate predicted median estimates from generalized additive mixed models and colors and line types represent sloughs. Panels represent model predictions for focal species: (A–C) Sacramento splittail, (D–F) striped bass, (G–I) tule perch, and (J–L) starry flounder

spring to early summer (Fig. 3). The predicted apparent growth rates were also similar among sloughs during this time. However, other sloughs yielded higher predicted CPUE across seasons (Denverton and lower Suisun sloughs; Figs. S2 & S3).

Model predictions for YOY tule perch indicated that various sloughs yielded higher CPUE on a

seasonal basis; for example, the dead-end slough Spring Branch yielded disproportionately greater predicted CPUE in summer (June to August), which coincided with the smallest predicted apparent growth rates among sloughs; similarly, Cutoff Slough, a flow-through slough draining Spring Branch, yielded the greatest predicted CPUE in

autumn and also had relatively low predicted apparent growth rates (Fig. 3). Eastern dead-end sloughs (e.g. Denverton) also had higher predicted CPUE in autumn compared to spring and summer. Overall, predicted CPUE was relatively high in other sloughs throughout Suisun Marsh (e.g. Nurse, lower Suisun, Boynton, and Peytonia; Fig. S2). Predicted body sizes of YOY tule perch, which are released as live young by pregnant females, ranged from a median estimate of 32 to 44 mm in May and June, respectively.

While total sample sizes were relatively low for starry flounder, models clearly indicated that large flow-through sloughs closest to the open estuary (Montezuma and lower Suisun Sloughs) yielded the highest predicted YOY CPUE across the study period. However, Cutoff Slough, a flow-through slough draining Spring Branch, yielded higher CPUE in early summer months, which coincided with the smallest predicted body sizes (Fig. 3). Overall, predicted median body sizes ranged from 31 to 86 mm from May to November, respectively, and predicted apparent growth rates peaked across all sites in mid-summer months, except for lower Suisun Slough, where they peaked in autumn.

3.3. Stationary habitat features

Each sampled slough had a different combination of values for the land to OW variables (Table 2). Ratio estimates yielded Marsh:OW > 0 for all sloughs, Pond:OW > 0 for 9 of 10 sloughs, and Upland:OW > 0 for 6 of 10 sloughs, reflecting geographic, geomorphic, and management differences across Suisun Marsh. The western dead-end slough, Spring Branch, which is located in the large tidal marsh reserve, represented the highest Marsh:OW and Upland:OW ratios and sinuosity, and the lowest Pond:OW ratio and channel depth. Despite differences in land cover type and areas, several sloughs had similarities between the more general Land:OW and Wetland:OW values. For example, the western dead-end sloughs Spring Branch and Goodyear had different proportions of marsh and pond areas, but when these values were pooled, both sloughs yielded the highest observed Land:OW and Wetland:OW values (>14). In contrast, the largest and deepest flow-through sloughs sampled in the study (lower Suisun, upper Suisun, Montezuma, and Nurse) yielded the lowest Land:OW and Wetland:OW values (<4) and were categorized as 'open-water-dominated.'

3.4. Freshwater flows and water-quality conditions

Delta outflow data indicated that over the 22 yr study duration, 8 years were designated as 'wet' and 8 were designated as 'dry' or 'critically dry,' reflecting California's variable hydrologic conditions, which feature extreme wet years and multi-year droughts (Figs. S4–S7). For example, the time series started out with consecutive wet years (water years 1995–1998) and ended with a 4 yr drought (water years 2012–2015) and the highest water-year on record (2017). Within Suisun Marsh, water quality was variable on regional and local scales. Consistent with the literature, there was a regional salinity gradient from east to west, illustrating a transition from fresher to saltier conditions as a function of the distance from the Sacramento–San Joaquin Delta to the east and San Francisco Bay to the west. For example, Montezuma, Nurse, and Denverton sloughs in eastern Suisun Marsh were more freshwater-influenced, averaging 3 ppt and ranging from 0–12.4 ppt. In contrast, Suisun and Goodyear sloughs in southwest Suisun Marsh were consistently the saltiest, averaging 6 ppt and ranging from 0–16.8 ppt.

Temperature ranges also varied across sloughs and were related to channel depth. For example, Montezuma, a deep flow-through slough that connects Suisun Marsh to the main axis of the estuary, had the lowest recorded summer temperature maximum (23.9°C), whereas the shallowest dead-end slough (Spring Branch) had the highest recorded summer temperature maximum (32.1°C) throughout the time series. Water clarity, as measured by Secchi depth, was generally higher and more variable in open-water-dominated sloughs. Seasonal and annual differences drove these patterns, whereby autumn months with low flows were on average clearer, especially in larger sloughs.

3.5. Species–habitat relationships over ontogeny

The ordination indicated that the focal species were distributed across the estuarine–terrestrial gradient, whereby YOY striped bass, splittail, and tule perch were more associated with shallower sloughs with higher Land:OW ratios (Fig. 4). Results from a 2-dimensional NMDS analysis yielded a stress level <0.2 (stress = 0.14) and fitted environmental variables yielded significant results for depth, Marsh:OW, Upland:OW, and Land:OW ratios, and salinity at a <0.05 level, and Pond:OW and temperature at a <0.1 level. To visualize relationships among species

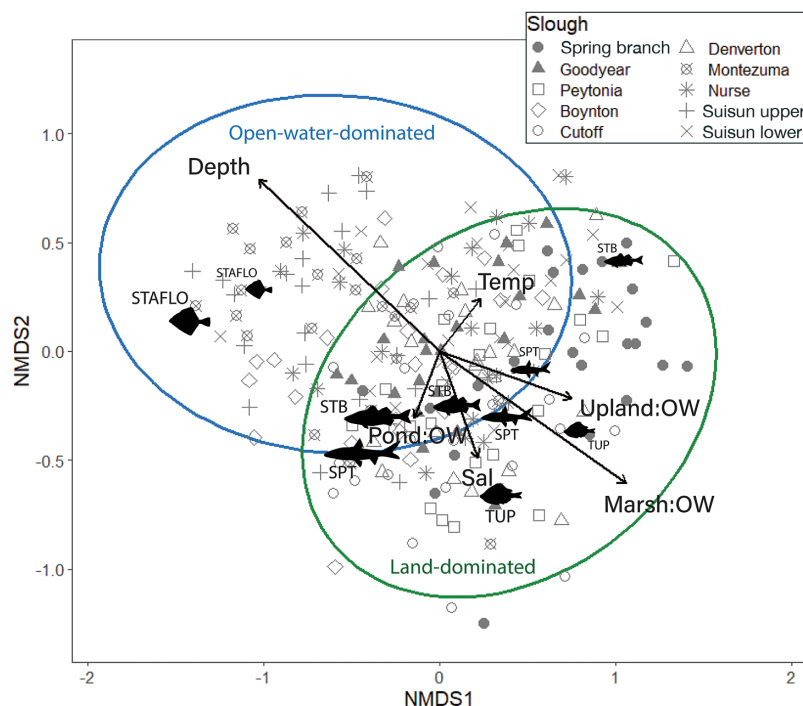


Fig. 4. Non-metric multidimensional scaling (NMDS) biplot results. Points represent sampling events pooled by year and slough. Text and symbols represent species codes (see Table 1) and age classes are represented by small (YOY), medium (age-1), or large (age-1+ / age-2+) symbols. Ellipses represent mean NMDS values grouped by open-water (OW)-dominated habitat (blue) or land-dominated habitat (green). Arrows are fitted environmental variables

with respect to the estuarine-terrestrial gradient, Land:OW was depicted as a categorical factor in ordination space (i.e. 'land-dominated' = Land:OW >4 and 'open-water-dominated' = Land:OW <4), where mean NMDS values for each category were projected as ellipses.

Species and age classes varied in their use of open-water-dominated and land-dominated sloughs. YOY striped bass were positively related to shallow, warm, land-dominated sloughs and negatively related to managed tidal ponds; age-1 striped bass were closer to the center of the ordination, whereas age-2+ were more associated with ponds and cooler temperatures. Sacramento splittail had a similar distribution as striped bass, but the strengths of the relationships were weaker. YOY tulle perch were associated with shallower depths, marshes, and uplands, and age-1+ tulle perch had similar associations except that they were also associated with saltier water and ponds. While YOY striped bass, YOY tulle perch, and age-1+ tulle perch were strongly associated with land-dominated sloughs, the NMDS ellipses indicated that splittail and older age classes of striped bass were associated with both land- and open-water-dominated sloughs. Conversely, YOY and age-1+ starry flounder

were strongly associated with deeper, open-water-dominated sloughs, and drove major observed differences in the focal community.

3.6. Land-water interactions and nursery function

Modeled relationships of fish abundance as a function of stationary habitat features and flow conditions varied by species and estimated age class. In general, models tended to slightly under-predict zeros and over-predict intermediate fish counts (Figs. S8 & S9). The random-effect grouping variables year, trawl site, and season were important in all models. In particular, the year variable had a strong but highly variable effect for the focal transient species, likely due to inter-annual variability in reproduction success and/or prevailing environmental conditions affecting transient species in the estuary, river, or ocean. Season was similarly strong, indicating that summer yielded strong associations

with YOY abundances. Model coefficients for the trawl site term were highly variable and indicated relatively strong effects for all estimated age classes of tulle perch and older splittail (Table 4, Fig. 5).

Overall, the sizes of interaction effects were smaller than random effects, which captured the high variability in temporal and spatial trends in the dataset. Outflow was an important predictor for all species and, as hypothesized, its effect was dependent on the effect of stationary habitat variables as indicated by smaller 'loo' values for models specifying 2-way interaction effects (Table 4, Fig. 5). Interestingly, YOY splittail, striped bass, and tulle perch abundances were best predicted by the interaction of freshwater flows and depth, whereby splittail and striped bass were positively related to higher flows and shallower water. Notably, tulle perch showed the inverse relationship, whereby they were positively related to lower flows (i.e. drought conditions) and shallower water. Channel depth was correlated with several other metrics, including Marsh:OW and Land:OW ratios and sinuosity, but provided better predictions as indicated by 'looics,' out-of-sample deviances, and model weights (see Table 4 for a summary; Table S1 for full model comparisons). Shared

Table 4. Summary of top-ranked models for each species (see Table 1) and age class; looic: estimated out-of-sample deviance; ploo: estimated effective number of parameters; SE: standard error of the looic estimate. See Section 2.3.4 for details. Random-effect grouping variables included season, year, and site (i.e. revisited trawl location in the long-term monitoring study). '+' and 'x' indicate additive and interaction effects, respectively. Model selections were based on a combination of model weights and prediction performance. See Table S1 in the Supplement for full model comparisons

Species code	Age class	Model no.	Rank	Equation	looic	ploo	Model weight	SE
SPT	YOY	24	1	Effort + Site + Year + Season + Outflow × Depth	7515.4	429.6	1.00	516.19
SPT	Age-1+	26	1	Effort + Site + Year + Season + Outflow × Sinuosity	14635.3	532.4	1.00	745.92
STB	YOY	24	1	Effort + Site + Year + Season + Outflow × Depth	39388.4	1972.5	1.00	3362.50
STB	Age-1+	26	1	Effort + Site + Year + Season + Outflow × Sinuosity	17831.0	872.9	1.00	1675.22
TUP	YOY	24	1	Effort + Site + Year + Season + Outflow × Depth	7916.2	441.3	1.00	509.22
TUP	Age-1+	22	1	Effort + Site + Year + Season + Outflow × Upland:OW	7053.9	272.5	0.90	326.86
STAFLO	YOY	14	1	Effort + Site + Year + Season + Outflow × Land:OW	1912.4	102.8	0.35	128.72

model weights among YOY starry flounder indicated that the 2-way interaction effects of outflow with Land:OW, Marsh:OW, or Wetland:OW ratios all performed similarly, reflecting their relationship to open-water-dominated sloughs. Abundances of larger splittail and striped bass were best predicted by the interaction effect of outflow and sinuosity, whereas larger tule perch were best predicted by the Upland:OW ratio. Larger starry flounder were excluded from the analysis due to unreliable model estimates as indicated by the HMC sampler.

4. DISCUSSION

Our study shows that Suisun Marsh is an important seascape nursery for 4 fish species with diverse life histories, a condition that likely relates to other fishes using the area. Our major findings include the following: (1) there are geographic locations that function as YOY hotspots within the seascape nursery; (2) the focal species have diverse life-history adaptations, including seasonal and ontogenetic habitat shifts by transient species; and (3) land–water interactions are likely drivers of nekton diversity and productivity in this nearshore ecosystem. Our study underscores the benefits of long-term datasets in understanding how estuarine habitat mosaics are functionally linked by complex physical and ecological processes. The implication of this study is that cultivating habitat complexity along an estuarine–terrestrial gradient, particularly in drowned river valley estuaries, can promote fish species persistence. Specifically, our study highlights process-based nursery functions of slough networks connecting migratory corridors to hotspots, which represent a habitat continuum at the seascape–landscape interface.

4.1. Fish use of the seascape nursery

Our observation that YOY splittail, striped bass, and tule perch were consistently abundant in dead-end, shallow sloughs across regions of Suisun Marsh (e.g. Spring Branch, Goodyear, Denverton sloughs) suggests that there are 'keystone habitats' within mosaics of connected and interacting habitat patches (Hitchman et al. 2018). Seasonal and ontogenetic habitat shifts by YOY splittail and striped bass seem to drive population connectivity and persistence, and are consistent with previous studies on these species' use of shallow marshes and shorelines in other parts of the estuary (Feyrer et al. 2005, Sommer et al. 2011). Differences in YOY abundance and distribution were clearer than differences in apparent growth. For resident tule perch, lower apparent growth rates in nursery areas early in ontogeny (Cutoff and Spring Branch sloughs from May to July) are suggestive of density-dependent processes, whereby individuals may have spent more time hiding from predators than foraging/growing during this sensitive life stage. Aging and microchemistry studies of calcified structures (e.g. otoliths) would help quantify growth and emigration/immigration rates and should be considered for future studies.

Variation in habitat use among years was also apparent. For example, YOY tule perch were more abundant in interior sloughs during low-flow years, reflecting their adaptations as year-round residents to locally fluctuating conditions (e.g. salinity; Rountree & Able 2007). Tule perch may also have been responding to increased submersed macrophyte growth during clearer, low-flow years, which may have provided increased localized cover for pregnant females and for their newly released young (Baltz & Moyle 1982, Moyle 2002, Young et al. 2018). Differ-

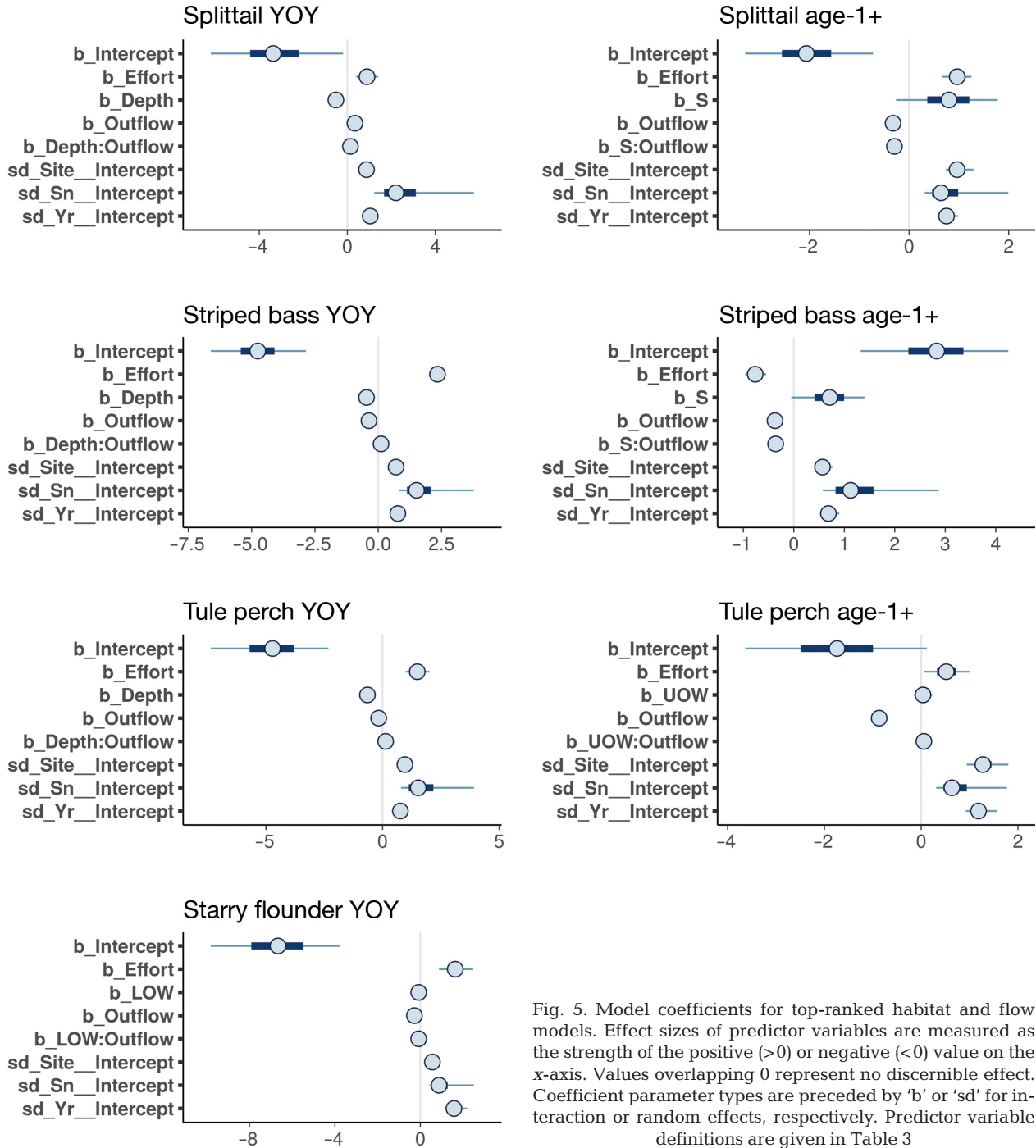


Fig. 5. Model coefficients for top-ranked habitat and flow models. Effect sizes of predictor variables are measured as the strength of the positive (>0) or negative (<0) value on the x-axis. Values overlapping 0 represent no discernible effect. Coefficient parameter types are preceded by 'b' or 'sd' for interaction or random effects, respectively. Predictor variable definitions are given in Table 3

ences in the timing of peak abundance among YOY with different life histories was suggestive of fine-scale temporal habitat partitioning and may have prevented density-dependent growth where multiple species' hotspots spatially overlapped. On a seascape scale, the redundancy of keystone habitats, each with different physical characteristics, may have played an important role in the persistence of

these species throughout the study duration and across variable hydrologic conditions; if true, redundancy may further explain why Suisun Marsh, a large brackish wetland system with more intact habitat area and complexity compared to other areas in the upper estuary, functioned as a nursery area when conditions were considered unfavorable or unproductive in nearby bays and rivers.

4.2. The estuarine–terrestrial gradient in three dimensions

In Suisun Marsh, the transition from open-water-dominated to land-dominated sloughs propagates in longitudinal, lateral, and vertical dimensions. In the longitudinal dimension, Suisun Marsh features brackish conditions that result from mixing of oceanic waters from San Francisco Bay with fresh water from the Sacramento–San Joaquin Delta in large slough networks formed by fluvial and tidal processes (Moyle et al. 2014). In the lateral dimension, sloughs are connected to a variety of historic and anthropogenic habitats, including shallow vegetated intertidal zones and managed tidal ponds, respectively. In the vertical dimension, fluvial processes connect uplands to tidal marshes, ponds, and sloughs, and, in some cases, form perennial or seasonal freshwater creeks. Based on our observations, we infer that the high degree of complexity within each of these 3 dimensions of Suisun Marsh represents a seascape–landscape interface that, as a whole, supports beneficial conditions for juveniles of a variety of species and life histories.

Channel depth and ratio of marsh to open water were correlated, and highly important, measures of nursery function for native species such as Sacramento splittail and tule perch, and the non-native striped bass. These trends were driven mostly by high YOY catches in Spring Branch, a dead-end slough in the large tidal marsh reserve. Fish may have benefitted from numerous co-occurring physical and ecological processes, which may explain the apparent marsh dependence of small-sized YOY in late spring and summer. Examples of these processes include increased physical access to the marsh plain with increasing length of marsh edge and decreasing stream order (Rozas et al. 1988, Kneib 1997, Visintainer et al. 2006) and tidal exchange of nutrients, sediment, and organisms across the land–water interface (Levin et al. 2001). Shallow depths likely provide small YOY with refuge from large-bodied predatory fishes, which has been documented in other near-shore nurseries (Munsch et al. 2016), and loose sediments likely preclude establishment of invasive clams (e.g. *Potamocorbula amurensis*; Baumsteiger et al. 2017), which alter pelagic food webs by filtering phytoplankton at high rates. The combination of high densities of zooplankton (Montgomery 2017) and high areal coverage of emergent vegetation in shallow dead-end sloughs likely supports survival and growth of young transient fish by reducing competition for food and space. Also, where fluvial and tidal processes intersect at high marsh elevations, diverse

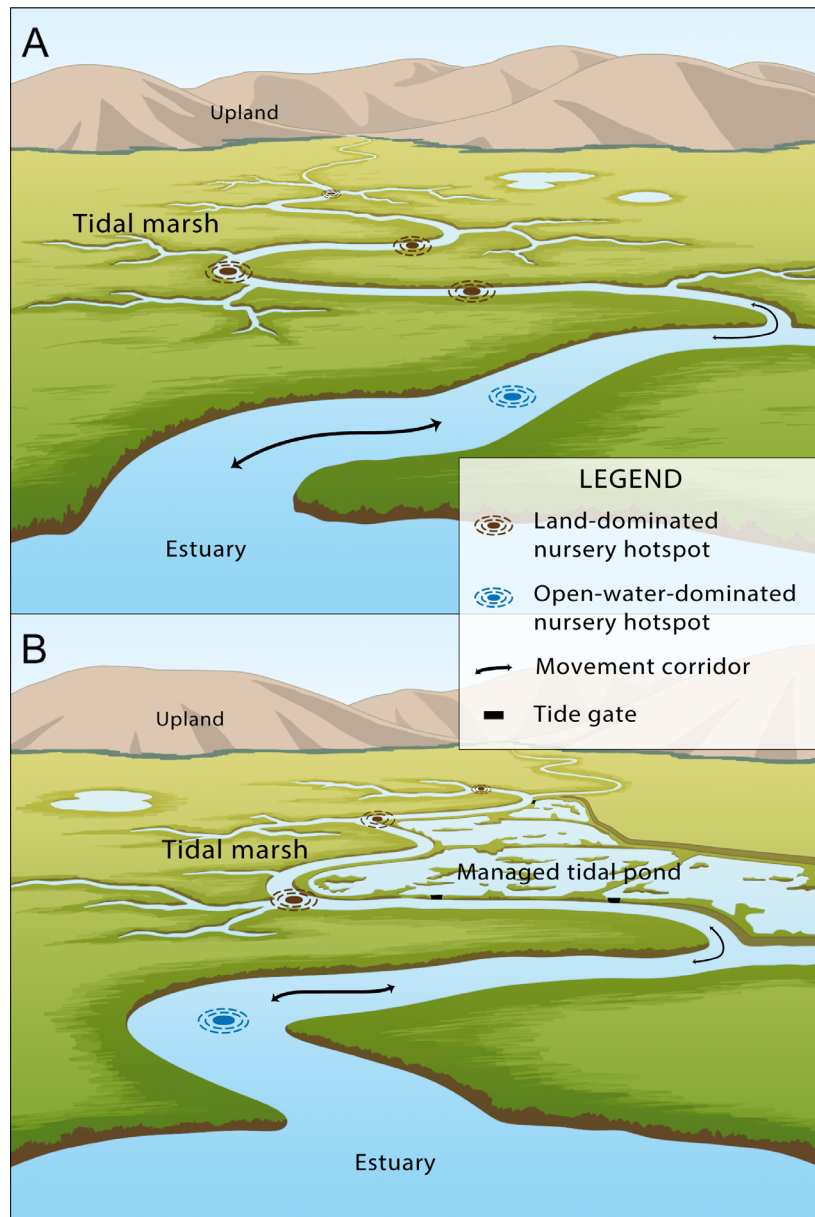
sources of organic matter may contribute to aquatic food webs that include juvenile fish (Odum 1984, Simenstad et al. 2011). Uplands can provide local sources of sediment, nutrients, or fresh water from creeks, seeps, or groundwater, and contribute to both habitat variability and self-sustaining processes such as marsh accretion (Schile et al. 2014, Goals Project 2015). As sea-level rise gradually moves marshes into adjacent uplands (Fagherazzi et al. 2019), sites possessing a marsh–upland transition zone should continue to support both terrestrial and aquatic communities, as well as species persistence and ecological resilience (Weinstein & Kreeger 2000, Goals Project 2015, Kirwan et al. 2016, Beller et al. 2019).

4.3. Restoring habitat at the land–water interface

Re-creating dynamic conditions favorable to small fish in Suisun Marsh now and into the future requires restoration of large swaths of tidal marsh drained by shallow meandering channels that connect to transitional vegetation and grasslands (Fig. 6A). Ideally, such restoration will maintain or even increase juvenile fish abundance and population resilience, and enhance survival during migrations to and from the greater estuary. In scenarios where marsh-upland restoration is not feasible due to dredged channels, leveed banks, lack of sediment, newly introduced noxious species, and/or ongoing land-use practices (e.g. managing ponds for waterfowl), managers may prefer to adopt a reconciliation ecology approach to maintain biodiversity in these human-dominated landscapes (Rosenzweig 2003, Moyle 2014). For example, tidal ponds managed intensively for waterfowl are novel habitats that may function similarly to historic tidal marsh ponds and pools, at least on a seasonal basis, when they are flooded and tidal waters are exchanged with adjacent sloughs. Even if the ponds are not directly occupied, it is possible that fish can benefit from managed tidal pond production when the water is exported to adjacent sloughs (i.e. food subsidies; Weinstein & Kreeger 2000, Litvin & Weinstein 2003, 2004, Weinstein et al. 2005), especially where ponds are embedded in marshes (e.g. Goodyear or Denverton sloughs; Fig. 6B).

Overall, our study shows that tidal marsh habitats in the San Francisco Estuary, California, can be important nursery areas for fishes with diverse life histories, and that the most productive and resilient habitats have physically and ecologically complex characteristics and are hydrologically connected to adjacent terrestrial habitats. Our findings may apply

Fig. 6. Conceptual model of the Suisun Marsh estuarine–terrestrial gradient, which facilitates diverse physical and ecological processes at the seascape–landscape interface and supports nursery hotspots for fishes with different life histories. The transition from open-water-dominated to land-dominated habitats, including deep and shallow sloughs, tidal marshes, managed tidal ponds, and uplands, represents a habitat continuum that provides abundant opportunities for foraging and refuge across a range of environmental and flow conditions. (A) Historic tidal marsh–upland gradients consistently function as nursery hotspots and serve as idealized models for habitat restoration. (B) Novel tidal marsh–pond–upland gradients are also nursery hotspots and offer alternative models aimed to enhance fish recruitment in altered landscapes/seascapes. Image credit: Emily Damstra



to ecological gradients in other marine systems, but their application is most appropriate for drowned river valley estuaries with topographic heterogeneity and small upland watersheds draining into marshes. Conservation and management of estuarine fishes will depend on improved understanding of these ecosystems, and on synthesis of long-term data that track responses of fish assemblages to natural and anthropogenic stressors and to restoration of habitat heterogeneity within the estuarine habitat mosaic.

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