UC Berkeley
UC Berkeley Previously Published Works

Title
Tidal effects on marsh habitat use by three fishes in the San Francisco Estuary

Authors
Colombano, Denise D
Donovan, John M
Ayers, David E
et al.

Peer reviewed

Tidal effects on marsh habitat use by three fishes in the San Francisco Estuary

Denise D. Colombano, John M. Donovan, David E. Ayers, Teejay A. O'Rear & Peter B. Moyle

ONLINE FIRST

Springer

Springer

Tidal effects on marsh habitat use by three fishes in the San Francisco Estuary

Denise D. Colombano · John M. Donovan ·
David E. Ayers · Teejay A. O'Rear · Peter B. Moyle

Abstract Little is known about the ecological importance of low-order tidal marsh channels to fishes in the San Francisco Estuary, California. We conducted a passive mark-recapture study to compare residency, site fidelity, and movement patterns of fishes in a small intertidal channel (0.1 km^2) in a large tidal marsh reserve (4.25 km^2). We coupled continuous, high-frequency data on movements of fish tagged with Passive Integrated Transponder (PIT) tags and abiotic conditions from a PIT-detector and datasonde, respectively. Novel insights were gained by employing *TidalTrend*, a software program that characterizes tidal time-series data for ecological interpretation. Overall, we found that fishes exhibited different patterns of intertidal habitat use: the resident species, tule perch (*Hysterocarpus traski*), consistently spent more time per visit, per day, and per season using the intertidal channel, except during the reproductive window in spring; the transient species, Sacramento splittail (*Pogonichthys macrolepidotus*) and striped bass (*Morone saxatilis*), were more opportunistic and exhibited higher individual variation in movement patterns. Generalized additive mixed models indicated that tide height, rate of change in tide height, tidal inequality, time of day, lunar phase, and water temperature better predicted fish detections than other variables, but their effects varied across species. Based on our findings, we posit that time, through tides, allows habitat partitioning among fish species and individuals with different life-history types. Furthermore, functional connectivity between subtidal and intertidal channels in tidal marshes is a feature of the estuarine mosaic that should be integrated into habitat restoration designs in the San Francisco Estuary.

Keywords Tidal marsh · Fish · Tide · Movement · PIT tag

D. D. Colombano (✉) · T. A. O'Rear · P. B. Moyle
Center for Watershed Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA
e-mail: dpdecarion@ucdavis.edu

D. D. Colombano · D. E. Ayers · T. A. O'Rear · P. B. Moyle
Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA

J. M. Donovan · D. E. Ayers
California Water Science Center, United States Geological Survey, Placer Hall, 6000 J Street, Sacramento, CA 95819, USA

Introduction

Fish movement patterns within seascape mosaics have intrigued ecologists for decades (Boesch and Turner 1984; Kneib 1997; Beck et al. 2001). One question in particular has driven much of that curiosity: how do tides influence fish movements? Although ecologists have tackled that question with an ever-growing number of studies (see Hering et al. 2010; McNatt et al. 2016; Boswell et al. 2019), complexity of tidal systems has hindered improved understanding of how tides affect

fish movements. For example, tides create diverse habitats with varying levels of functional connectivity, in part by occurring on several time scales [semidiurnal (12.4 h), diurnal (24.8 h), spring-neap (14.8 d), and lunar (29.6 d)]. Rapid changes in other abiotic factors (e.g. water temperature or light intensity) also tend to obscure relationships between tides and fish movements. Thus, discerning how fishes use tidal systems requires fine-scale observation data concomitant with measurements of many abiotic variables over long periods coupled with hierarchical modeling.

Ecologists have, nevertheless, discerned some patterns between tides and fish movements over short periods (Hering et al. 2010; Becker et al. 2016; Boswell et al. 2019). Oftentimes, tides are thought to influence resource use. In saltmarsh habitats, for example, tidal flooding of intertidal channels may allow small fish access to the vegetated marsh plain/ edges, which provides increased opportunities for food and cover; conversely, as the tide ebbs, water draining back into subtidal channels may allow predatory fishes to ambush prey upon exit (Kneib 1997). Studies of fish have highlighted diverse strategies exhibited by fishes in seascapes, such as in relation to instantaneous tide height (Bretsch and Allen 2006; Rypel et al. 2007), flood-ebb cycles (Kimball and Able 2012; Boswell et al. 2019), hydroperiod (Minello et al. 2012), water velocity (Næsje et al. 2012; Becker et al. 2016; Viehman and Zydlewski 2017), and lunar phase and disk illumination (Milardi et al. 2018).

Recently, novel technologies have quickly advanced the ability to monitor fine-scale fish movements that would have previously been difficult to detect. Researchers can now collect continuous fish data over relatively long periods using various autonomous approaches including Radio Frequency Identification tags and detectors (Hering et al. 2010; Bass et al. 2012; McNatt et al. 2016), acoustic transmitters and receivers (Sakabe and Lyle 2010; Gannon et al. 2015; Grant et al. 2017), and imaging systems (Ellis and Bell 2008; Kimball and Able 2012; Boswell et al. 2019). Fine-scale fish movement studies are now catching up with the longstanding ability of physical scientists to effectively monitor rapid changes in hydrodynamics and water quality in estuaries [e.g. the National Oceanographic and Atmospheric Administration (NOAA) National Estuarine Research Reserve (NERR) System-Wide Monitoring Program (SWMP), Wenner and Geist 2001]. Since time, through tides, controls access to

resources (Wiens 1989), we examined responses by fishes to tidal dynamics using continuous, high-frequency observations of fish movements collected over multiple years.

We conducted our study in a tidal marsh channel network, a classic model system that has yielded important insights on life-history diversity of marine fishes (Beck et al. 2001; Nagelkerken et al. 2015). Our first question was, Do species or individuals show variation in residency (duration of habitat use) in or site fidelity (number of repeat visits) to intertidal channels? We anticipated that resident and transient fishes would show distinct patterns of residency and site fidelity. For example, we hypothesized that resident species, or those that complete their entire life history within a given region or habitat and tolerate rapidly shifting conditions within smaller home ranges, would display high residency and site fidelity. Conversely, we hypothesized that transient species, or those that inhabit a given region or habitat during certain life stages or times, would occupy marshes for shorter periods, reflecting daily, seasonal, or ontogenetic patterns of resource use. To answer this question, we compared several series of passive mark-recapture data in a small intertidal channel draining into a larger subtidal channel.

Next we asked, Do tides, time of day, or other abiotic factors influence fish movements? We hypothesized that because tides affect functional connectivity across the marsh plain and intertidal and subtidal channels, fishes would display non-random patterns of movement related to tides, reflecting behavioral adaptations to these periodic and predictable habitat fluctuations. Further, we anticipated that species would have different relationships to tides and other abiotic factors. To test this hypothesis, we compared the effects of tidal variables to temperature, salinity, dissolved oxygen, turbidity, time of day, lunar phase, and month on fish detections. Lastly, we modeled detections in relation to the proportion of time per day that the intertidal study channel was either inundated, completely dewatered, or overtopped (resulting in a flooded marsh plain).

Materials and methods

Study system

The San Francisco Estuary (SFE) is a temperate drowned river valley estuary on the US West Coast that

receives its fresh water from rivers draining into the Central Valley of California, which combine to form the Sacramento-San Joaquin Delta ("Delta"), the freshwater portion of the SFE. Suisun Marsh is a 470 km^2 brackish marsh located downstream of the Delta and 80 km upstream from the Golden Gate strait (Moyle et al. 2014; Whitcraft et al. 2011). The SFE has mixed, semidiurnal tides, with two high and two low tides of unequal value repeating each 24.8-h lunar day, and thus timing of tidal peaks and troughs advance approximately 1 h each successive 24-h solar day (Walters et al. 1985). The tides vary on several scales. First, the range in tidal amplitudes alternates weekly: "spring" tides have larger tidal amplitudes, whereas "neap" tides have smaller tidal amplitudes. Second, high-amplitude "king" tides occur near winter and summer solstices, with the highest tides during the daytime in winter and the nighttime in summer. When flood tides overtop subtidal and intertidal channel banks, water inundates the vegetated marsh plain until the subsequent ebb tide drains waters back into subtidal channels through intertidal channels (Enright et al. 2013). These types of periodic fluctuations also co-occur with seasonal changes in daylight (length and intensity), atmospheric pressure, and storm surges, further contributing to the challenge of isolating the effects of tides.

Suisun Marsh's channels are generally turbid, on the fresher side of brackish (average salinity ~4 ppt), have small patches of *Stuckenia* spp. and soft-bottom sediments, and have varying channel shapes based on management history (O'Rear et al. 2019). Though Suisun Marsh is primarily diked, there is a large swath of undiked tidal marsh located in Rush Ranch (hereafter, "the reserve"), an 8.38 km^2 part of the San Francisco Bay NERR system that is managed by the Solano Land Trust. The reserve's tidal marsh consists of meandering dendritic channels, fringed mainly by tules (*Schoenoplectus* spp.) and cattails (*Typha* spp.) atop natural berms, that transect an extensive marsh plain. The marsh plain boasts many native and endemic plants (Vasey et al. 2012) and transitions to upland grasslands and a seasonal freshwater creek (Whitcraft et al. 2011). Due to its extensive marsh plain, branching channel networks, and variable tidal dynamics, which is a rare combination of features in the contemporary estuary, the reserve serves as a reference site for historical tidal marsh geomorphology (Enright et al. 2013).

Within the reserve, Spring Branch is a relatively shallow, broad, dead-end, reticulate channel network,

with the main channel measuring ~2.4 km from mouth to terminus and containing several patches of *Stuckenia* spp. Numerous low-order channels dissect the marsh plain. Our study focused on a 0.1 km^2 intertidal channel draining into the main subtidal channel of Spring Branch (Figs. 1 and 2).

Focal species

The University of California, Davis, Suisun Marsh Fish Study (1979-present) conducts monthly surveys on fishes and invertebrates using otter trawls and seines following methods established by Moyle et al. (1986). For four decades, the program has demonstrated that Suisun Marsh remains a regional stronghold for California native fishes and supports coexistence with nonnative fishes (Palaima 2012). Sacramento splittail (hereafter: "splittail"; *Pogonichthys macrolepidotus*) and tule perch (*Hysterocarpus traski*) are native fishes that commonly co-occur in Suisun Marsh yet exhibit divergent life-history strategies (Table 1). The splittail is a highly mobile large-bodied minnow (Cyprinidae) that has a unique semi-anadromous life history, whereby adults migrate from brackish waters (e.g. Suisun Marsh) to spawn on riverine floodplains (e.g., the Yolo Bypass next to the Sacramento River) in winter/early spring (Moyle et al. 2004). Often found in shallow (<1.5 m), turbid tidal channels, splittail are the most abundant native fish in otter trawls in the reserve, accounting for 15% of total otter trawl survey catch in Spring Branch since 1979 (Moyle, UCD, unpubl. data). The tule perch is a resident surfperch (Embiotocidae) that gives birth to live young and is associated with emergent and submerged aquatic vegetation in freshwater and brackish marshes and streams (Moyle 2002). It is also abundant in the reserve, representing 12% of total otter trawl survey catch in Spring Branch since 1979 (Moyle, UCD, unpubl. data). The most abundant species in Suisun Marsh and the reserve site, according to otter trawl surveys, is the nonnative striped bass (*Morone saxatilis*; Moronidae), representing 42% of total survey catch in Spring Branch since 1979 (Moyle, UCD, unpubl. data). The striped bass is a highly mobile predator native to the Atlantic Coast that has become naturalized in the SFE since its original introduction in 1879 (Scofield 1931). It is anadromous and spawns primarily in the Sacramento River and its tributaries; juveniles rear along shorelines of the estuary's low-salinity zone and
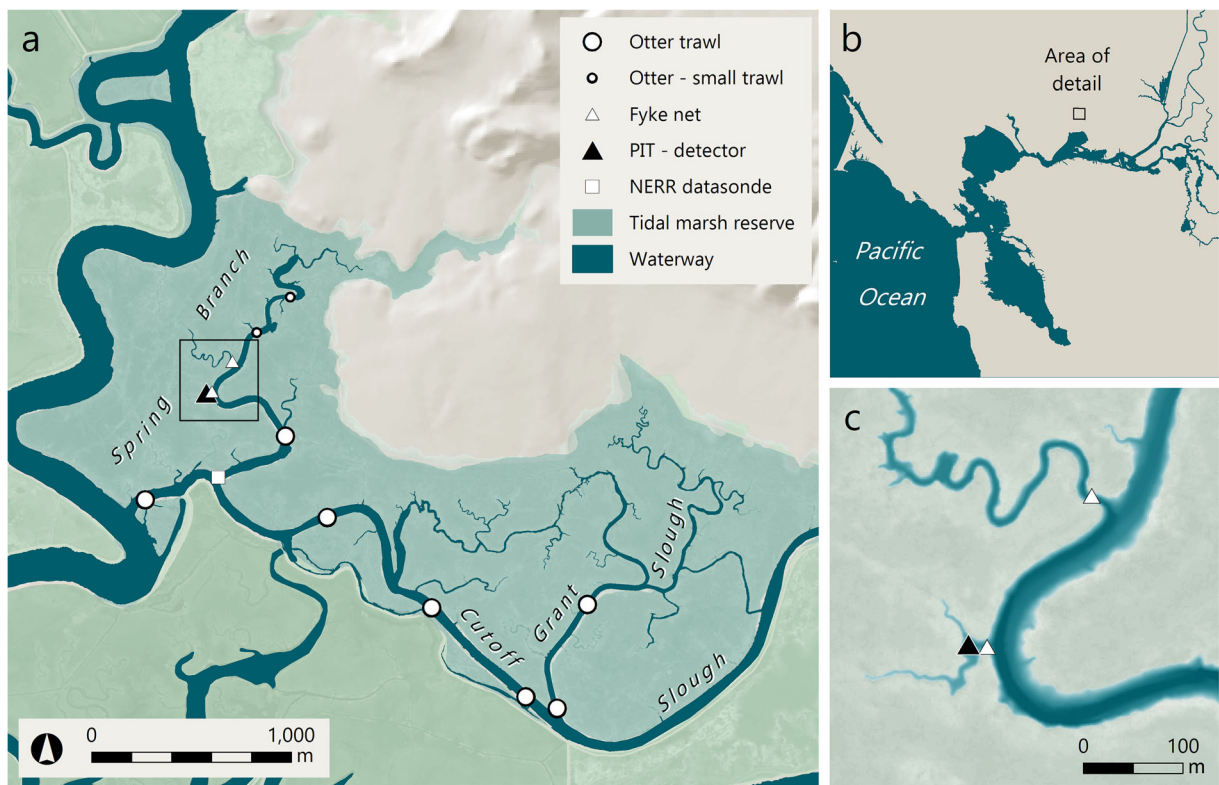
Fig. 1 a Rush Ranch is a component of the San Francisco Bay National Estuarine Research Reserve (NERR) system that encompasses 4.25km² of historic tidal marsh habitat (dark gray). **b** Location of the Rush Ranch tidal marsh reserve in the San Francisco Estuary, California. **c** Channel bathymetry and location of the PIT-detector used to monitor fine-scale movements of tagged fish; grayscale color gradient represents channel depth (dark: deep; light: shallow). Data source: Department of Water Resources Atlas (2018), Gesch et al. (2002), San Francisco Estuary Institute (2012), US Geological Survey (2004). Image credit: Amber Manfree
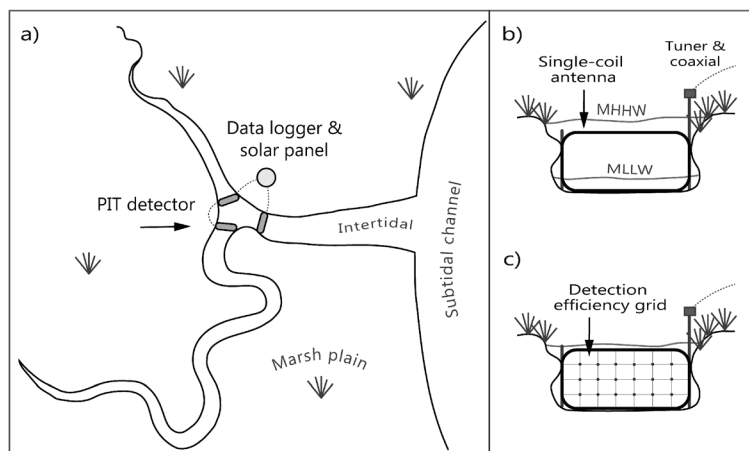
Fig. 2 a Three-antenna PIT-detector system installed in the dead-end intertidal study channel. Antennas (dark gray) connect to the on-shore data logger and solar panel system (light gray) via coaxial cables (dashed lines). **b** Cross-section of the study channel showing the PIT tag antenna setup with respect to mean higher high water (MHHW) and mean lower low water (MLLW) levels. **c** A grid system to estimate percent detection efficiency of each PIT tag antenna through time. Handheld tags were manually passed through each node around the grid (including the frame) and the binary outcome (success vs. failure) was recorded; using the total number of successes and failures from the antennas, we estimated percent efficiency of the entire PIT-detector system

Table 1 Focal species: Species code, names, life-history type, salinity range, habitat association, native vs. nonnative status (Moyle 2002)

Species code	Common name	Latin name	Life history	Salinity range	Habitat assoc.	N/NN
STB	Striped bass	*Morone saxatilis*	Transient (anadromous)	Euryhaline	Pelagic	NN
SPT	Sacramento splittail	*Pogonichthys macrolepidotus*	Transient (semi-anadromous)	Euryhaline	Benthic	N
TUP	Tule perch	*Hysterocarpus traski*	Resident	Freshwater - mesohaline	Benthic	N

then disperse throughout the estuary and along the coast as adults (Moyle 2002).

Otter trawl surveys have documented broad seasonal patterns in habitat use that vary with species and life stage. Young-of-the-year (YOY) striped bass are highly abundant during the recruitment window (late spring to autumn) whereas sub-adults are present throughout the year; larger striped bass are inadequately sampled by otter trawl but are caught year-round by hook-and-line (O'Rear, UCD, unpubl. data). Splittail YOY are highly abundant in summer after migrating to brackish waters from upstream floodplains; larger fish are commonly found in Suisun Marsh throughout the year except when adults leave the system during the spawning window in winter/spring. Overall, striped bass and splittail are strongly associated with Suisun Marsh in earlier life stages, whereas tule perch and splittail of all size classes are year-round residents and reproduce locally (Colombano et al. 2020).

Fish tagging and detection equipment

Fine-scale movements of striped bass, splittail, and tule perch were examined using a Full Duplex Passive Integrated Transponder (PIT) tag detection system (hereafter, "PIT-detector") following methods developed by Hering et al. (2010). PIT tags are small, electronic microchips encased in bio-stable glass that last the lifetime of the individual because they operate without a battery (Gibbons and Andrews 2004). Using PIT tags to passively track animal movements began in fresh water (e.g. salmonids; Prentice et al. 1985), but only recently were methods developed for brackish systems (Hering et al. 2010; Bass et al. 2012; Barbour et al. 2012).

From May 2013 to December 2014, 968 fish were collected from the reserve for tagging using several gear types as part of the Suisun Marsh Fish Study (Table 2). Trawling occurred in Spring Branch, Grant Slough, and Cutoff Slough (Fig. 1). A medium-sized (4.3-m diameter) otter-trawl net was towed by a 6.4-m aluminum boat at each main-channel trawl station for 5 min, except at the confluence of Grant and Cutoff sloughs, where it was towed for 10 min (Fig. 1). In intertidal channels, a small (2.4-m diameter) otter trawl was towed by a 4.3-m jonboat, which permitted access to shallow and narrow reaches. Fyke nets (0.7-m·1.0-m opening) were also periodically deployed in intertidal channels at high tide and subsequently retrieved at low tide to sample fishes

Table 2 Summary of individuals tagged and released and subsequently recaptured in nets or detected by the autonomous PIT-detector within Rush Ranch, a tidal marsh reserve in the San Francisco Bay National Estuarine Research Reserve (NERR) system

Species code	Tagging period	Monitoring days	No. tagged	No. recaps nets	No. detected	% Days detected	Total detections	Median daily detections
STB	May 2013 - Nov 2014	500	149	5	11	20	468	3
SPT	May 2013 - Dec 2014	500	687	7	39	36	973	3
TUP	Nov 2013 - Nov 2014	449	132	2	13	35	1110	7

A "detection event" was defined as the presence of a single individual detected within a 1-min interval. Median daily detections are calculated for days where a species was detected at least once

returning to the main channel. All methods were used to either collect fish to PIT tag or recapture previously tagged fish to measure growth rates.

Upon capture, fish were identified to species and their standard length ("SL"; mm) was measured. The minimum size of tagging for all species was 70 mm SL to minimize impacts to small fish; this threshold was developed during preliminary field observations of fish recovery in response to tagging. Fish were anesthetized in a peppermint oil solution (1,10 mixture of peppermint oil and ethanol with 4 mL per gallon water), and a 12-mm·2.1-mm·0.1-g BioMark PIT tag was sub-gastrically implanted using a syringe tag injector and a sanitized steel needle. Each PIT-tagged fish was held in an aerated water bath and released after determining full recovery was achieved based on strong swimming. Tule perch and splittail generally needed less recovery time (~5 min) than striped bass (~10 min). All tagged fish were released into Spring Branch, the main subtidal slough network, to improve the probability of detection at the PIT-detector in the nearby intertidal channel.

Fish were detected with an autonomous PIT-detector system anchored in the study channel network (Fig. 2). The configuration was designed with three single-coil non-multiplexed pass-through PIT antennas (3-m·1-m) and tuners connected with coaxial cable to an on-shore control unit with transceivers, a data logger, and a standard security disk (SD) card. The system was powered by a 24-V battery setup that was charged with solar panels during adequate daylight conditions. Each PIT-tagged fish that swam through the PIT-detector system had its tag activated by the electromagnetic field of the transceiver, which then transmitted the fish's unique code to the data logger. The PIT-detector system continuously recorded detection events, power status (on or off), and voltage with the associated date and time on the SD card. During site visits (approximately every 2 weeks), a laptop, serial cable, and PuTTY v0.63 software were used to interface with the data logger and download data.

To maintain and test the detection efficiency of the transceivers, which are subject to amperage drift over time, we manually tuned them during every site visit and conducted grid testing with handheld PIT tags to identify "dead zones" where fish may have passed through the center of the antennas without detection. We also checked efficiency in air and water (i.e. low and high tide, respectively) and found no difference. To describe the detection efficiency of the system, we then developed two metrics to include in our models: (1) percent efficiency of the entire PIT-detector system (e.g. amperage drift or saltwater corrosion affecting antenna coils in summer; Table S1 in Online Resource), and (2) the number of minutes during the 15-min sampling interval that system power was temporarily off (e.g. battery charging affected by cloud cover in winter).

Water quality, twilight, and lunar phase data

Environmental data were obtained from the NERR SWMP portal (NOAA 2019). All data collection and QA/QC methods followed national SWMP standards. The water-quality datasonde (Yellow Springs International, Inc. 6600 instrument) in Spring Branch (known in the NERR as "First Mallard Branch") was affixed to a large wooden piling at the mouth of the main subtidal channel, which was approximately one channel kilometer downstream from the PIT-detector. The datasonde probes were positioned 0.5 m above the substrate and recorded water temperature (°C), specific conductivity (microSiemens, uS/cm), salinity (practical salinity units, psu), dissolved oxygen (mg/L), tide height (m) from a non-vented sensor corrected for changes in barometric pressure, and turbidity (nephelometric turbidity units, NTU). Environmental data collection occurred every 15 min; consequently, we analyzed fish movement data grouped by 15-min intervals to match the environmental dataset. Data collected by the Suisun Marsh Fish Study at the NERR datasonde and at the intertidal channel mouth where the PIT-detector was located have shown little difference in water quality (O'Rear, UCD, unpubl. data), and thus we considered it appropriate for our analyses.

To evaluate the effects of diel and lunar phases on fish detections, we obtained "astronomical twilight" data to determine the timing and duration of dawn, sunrise, daytime, dusk, and nighttime for each day in the study period (Time and Date 2019). Dawn and sunrise and sunset and dusk were grouped to capture transitional periods between day and night. "Dawn" was defined as the period from the beginning of twilight (i.e. the moment when the geometric center of the sun is 18° below the horizon in the morning) to sunrise. "Sunrise" included the hour after sunrise; similarly, "sunset" included the hour preceding sunset. "Dusk" was defined as the period after sunset until the end of twilight (i.e. when the geometric center of the sun is 18° below the

horizon in the evening). We also obtained daily data on lunar phase (four categories: new, waxing, full, waning; eight-categories: new, waxing crescent, first quarter, waxing gibbous, full, waning gibbous, third quarter, waning crescent) and percent illumination of the moon (hereafter: "% disk illumination") using the package "lunar" (Lazaridis 2014) in Program R v3.6.1 (R Core Team 2019). Each 15-min interval in the dataset was assigned a time of day and lunar phase category.

Tide data and *TidalTrend* software

In this study, we used a newly developed software program (soon to be open source), *TidalTrend*, that implements algorithms to contextualize tide height (or water velocity) time-series data occurring on seasonal, spring-neap, daily, and tidal time scales to aid in ecological interpretation (Donovan and Ayers 2019). The following examples demonstrate *TidalTrend* output using a time series of tide heights (i.e. water depths; Fig. 3). To assign increasing or decreasing tidal limbs to a time series of depth data, the algorithm makes a pass through the time series to identify the highest and lowest values of each 12.4-h semidiurnal tidal cycle. Next it uses these minima and maxima to normalize the tidal signal, which shifts and scales each 12.4-h cycle so that the lows are assigned values of 0 and the highs are assigned values of 1, while preserving the original shape of the curve. Using the normalized signal, the algorithm then identifies whether the depth at a given time is trending higher or lower and assigns a discrete numeric value to each category; 1 for increasing stage limb and − 1 for decreasing stage limb). This contextual information is then used to assign each data point a continuous numeric value (0 to 1) to represent where it is located between the lowest and highest (increasing stage limb) or highest and lowest (decreasing stage limb) point on each stage limb. To quantify spring-neap variability, an algorithm makes a pass through the data to identify the highest and lowest values of each 24.8-h diurnal tidal cycle. Next it subtracts tidal low values from the tidal high values and smooths the resulting time series using a 24.8-h moving average. Spring tides are represented as peaks and neap tides are represented as troughs in the resulting signal. Finally, it uses the minima and maxima of this output to normalize the tidal signal, which shifts and scales each spring-neap cycle so that neaps are assigned values of 0 and springs are assigned values of 1, while preserving the original signal shape. In total,

TidalTrend quantifies tide direction, tidal range, tidal low, tidal high, tidal inequality, and rate of change in tide height (for definitions see Table 3). Our subsequent analyses represent the first documented case study linking continuous, high-frequency fish movement data to *TidalTrend* variables.

Modeling

To evaluate the relative effects of season, tides, water quality, time of day, lunar phase, and intertidal inundation period on fish detections, we constructed varying intercept generalized additive mixed models (GAMMs) following methods in Pedersen et al. 2019. GAMMs are flexible hierarchical non-linear regression functions that allow smooth relationships between predictor and response variables to vary among groups (Wood 2017). To understand trends in fish detections, we modeled the number of fish detections at the PIT-detector. We measured a single "detection" event as the presence of a single PIT-tagged fish recorded by the PIT-detector system in a single minute, which assumes that one-minute intervals are the minimum ecologically important period for fish habitat use. Detection events were then summed by individual over a 15-min interval (maximum number of detections = 15) to match environmental data. Detections of an individual on the same day of tagging were excluded from the analysis.

Model variables (Table 3) included main effects such as tide height and temperature and were z-score transformed (mean = 0, sd = 1) by month to adjust for natural seasonal fluctuations observed in environmental variables. Standardization of *TidalTrend* variables is a built-in process within the algorithms, and therefore we mean-centered (mean = 0) the variables instead of further transforming them. Month was specified as a random-effect grouping variable. In addition, we specified PIT-tag ID as a random-effect grouping variable to adjust for repeat sampling of individual fish and to estimate the effects of individual variation. The total number of days an individual fish was tagged and available for detection was log-transformed and included as an offset variable to adjust for differences in individual detection effort. Percent efficiency of the PIT-detector and number of minutes that the detector was operational during a 15-min interval were also included as log-transformed offset variables to account for differences in detection efficiency throughout the time series and to model zero-generating processes in the dataset. We used
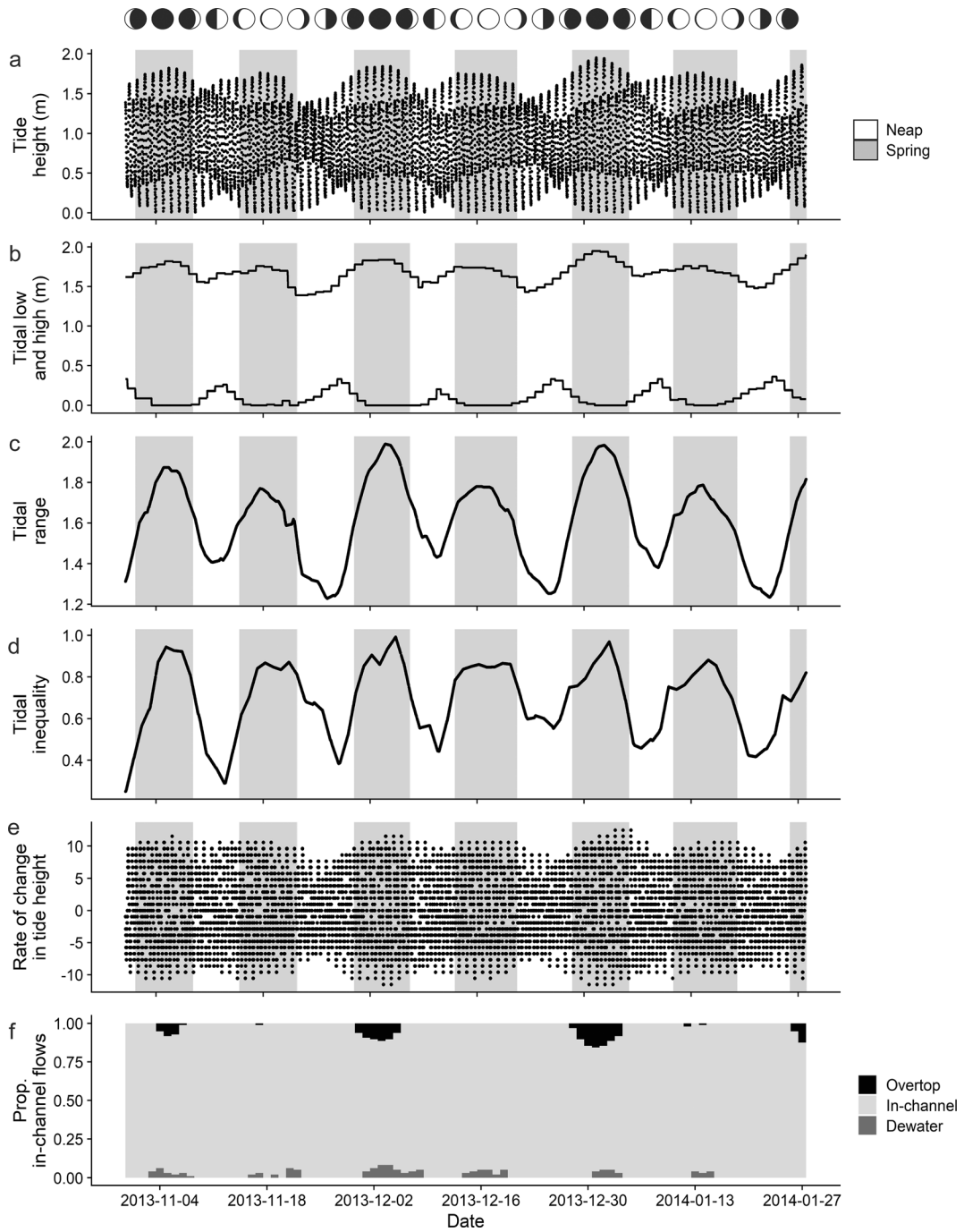
Fig. 3 **a** Example time-series of tide heights (water depths) recorded at the NERR long-term water quality monitoring station. **b-e** *TidalTrend* variables. Alternating background colors represent spring and neap tide categories derived from tidal range. **f** The proportion of time in a given day that flows overtop the marsh, remain in-channel, or dewater. Moon phases are superimposed on the time-series; new and full moons coincide with the highest observed tidal range values (i.e. "spring" tides) over a ~29.6-d lunar cycle

a zero-inflated Poisson distribution with a log-link function to adjust for skew towards small counts observed in

the detection data. Thin plate regression splines (TPRS) and cubic regression splines (CRS) were used as

Table 3 Predictor variables used in generalized additive mixed models (GAMMs)

Predictor variable	Definition	Type
Tag Days	Number of days an individual fish was PIT-tagged	Numeric
Power	Number of minutes during a 15-min interval that the PIT-detector was powered on	Numeric
Efficiency	Percent estimated efficiency of the PIT-detector system	Numeric
PIT Tag ID	Unique identifier for a PIT-tagged fish	Categorical
Month	Month of the year (1–12)	Categorical
Tide height/ water depth	Instantaneous water depth (m) measured by datasonde	Numeric
Hour of day	Hour of the solar day (0–23)	Numeric
Day-night-twilight	Time of day (dawn, day, dusk, night)	Categorical
Tide4	Increasing, high slack, decreasing, low slack	Categorical
Tide8	Increasing low, increasing mid, increasing high, high slack, decreasing high, decreasing mid, decreasing low, low slack	Categorical
Tidal high	Highest water depth value over a diurnal (24.8-h) period	Numeric
Tidal low	Lowest water depth value over a diurnal (24.8-h) period	Numeric
Tidal range	Difference between tidal high and tidal low; tidal amplitude	Numeric
Spring-neap	Spring tide (high amplitude) or neap tide (low amplitude) series	Categorical
Tidal inequality	Difference between the ranges of the two semidiurnal cycles in each tidal day	Numeric
Rate of change in tide height	Rate of change in tide height/ water depth	Numeric
Lunar phase4	New, waxing, full, waning	Categorical
Lunar phase8	New, waxing crescent, first quarter, waxing gibbous, full, waning gibbous, last quarter, waning crescent	Categorical
% Disk illumination	Percent of disk illuminated according to lunar phase	Numeric
Temperature	Water temperature (degrees C) measured by datasonde	Numeric
Salinity	Specific conductivity (uS) measured by datasonde	Numeric
D.O.	Dissolved oxygen (mg/L) measured by datasonde	Numeric
Turbidity	Turbidity (NTU) measured by datasonde	Numeric
% Day in-channel	Percent of time in each day that water inundated the channel	Numeric
% Day dewatered	Percent of time in each day that the channel was dewatered	Numeric
% Day overtop	Percent of time in each day that water exceeded bankfull conditions	Numeric

general-purpose splines that smooth the relationship between predictor and response variables and can smooth circular predictors with matching ends (e.g. hours 0–23; Wood 2003, 2017). We fit all models using the No-U-Turn Sampler (NUTS) extension of Hamiltonian Monte Carlo (Hoffman and Gelman 2014) with the packages "brms" (Bürkner 2017, 2018) and "RStan" (Stan Development Team 2018). Based on the "get_prior()" function in brms, we specified weakly informative priors with normal distributions for the mean and variance terms and logistic distributions for the offset terms. We then performed model checking procedures with "bayesplot" (Gabry et al. 2018). All analyses were conducted in Program R v3.6.1 (R Core Team 2019).

We compared models using Pareto smoothed importance sampling leave-one-out (PSIS-LOO) cross-validation methods with the package "loo" (Vehtari et al. 2018). Models with problematic observations as diagnosed by Pareto k values exceeding a 0.7 threshold were refit to compute the expected log-predictive density (hereafter: "elpd") for the problematic observations directly. Next, model weights calculated via Bayesian model stacking that exceeded a 5% threshold and had low elpd difference ("elpd diff") estimates were identified as top-ranked models; model coefficients were used to evaluate effect sizes and uncertainty among parameter estimates from the posterior prediction intervals.

Due to the large amount of environmental data collected on 15-min intervals over the study duration,

fitting models with all available data points (>40,000) was not feasible. To improve computation time, we ran model scripts using 32 vCPUs and parallel processing through a virtual computer on Amazon Elastic Compute Cloud (Amazon EC2). We also generated a random subsample of representative environmental data by using the "sample_n()" function in the package "dplyr" (Wickham et al. 2019) in Program R to query 65 random samples grouped by month and year in the data frame, which yielded 1300 observations that were then added to the detection data frames for each species (Fig. S1). For example, the data frame for striped bass contained a total of 1610 rows with 1300 subsampled data points and 310 data points where PIT-tagged fish were detected at least once. We then compared the model output to one using a random subsample of 2400 observations and determined that 1300 observations provided comparable results and thus were adequate for computation time and model interpretation.

Results

Size ranges of detected fish

Tagged fish were monitored in the study channel for a total of 449–500 d (Table 2) from June 2013 to March 2015, which spanned a multiyear drought in California (Luo et al. 2017). The mean and standard deviation SLs of tagged striped bass, splittail, and tule perch were 164 ± 86, 157 ± 60, and 125 ± 14 mm, respectively. Seven percent of tagged striped bass were detected ($n = 11$), which yielded the fewest total number of detections ($n = 468$) among species. Striped bass detections occurred on only 20% of days in the study. Most detected individuals were juveniles or sub-adults (201 ± 27 mm SL) despite tagging fish as large as 720 mm SL; a majority were originally captured in otter trawls towed in main channels in the reserve ($n = 7$). Six percent of tagged splittail ($n = 39$) were subsequently detected in the intertidal channel during 36% of days in the study period; of the detected splittail, the mean and standard deviation SL was 178 ± 27 mm at time-of-capture and the majority was originally captured in main-channel otter trawls ($n = 34$). Tule perch yielded the greatest number of detection events ($n = 1110$) despite having the fewest PIT-tagged individuals ($n = 132$) of all three species. Of the 13 adult tule perch detected ($\sim$10% of total tagged; 128 ± 4 mm SL), six were

originally captured in main channels whereas seven were originally captured in intertidal channels by fyke net ($n = 5$) or small trawl ($n = 2$). Physical recapture of PIT-tagged fish in nets was rare and thus we were unable to estimate growth rates.

Seasonal detections

Striped bass showed a seasonal pattern of detections across spring (11%), summer (44%), autumn (44%), and winter (1%; Fig. 4). Splittail detections indicated more year-round use of the channel [i.e. spring 23%, summer 25%, autumn 43%, winter 9%]. Tule perch detections occurred regularly in summer (38%), autumn (28%), and winter (34%), but not in spring [i.e., 0% during the reproductive window: late March and April ($n = 3$) through May and early June ($n = 0$)]. Peak tule perch detections occurred during the transition from summer to autumn (September), whereas striped bass detections peaked in October and splittail detections peaked from October to November.

Daily detections and times-at-large

Seven striped bass were detected on more than 1 day in the study, ranging from four to 74 d per individual [median = 5.5 d; interquartile range (IQR) = 1.75–6]. The average time-at-large, or time elapsed between detections, ranged from 1.4 d to 42 d, and encounters spanned from regular detections over 1 week to sporadic detections over 7 months. The most commonly encountered striped bass was detected for an average of 5 min per day every 1.4 d for 4 months during late summer and autumn 2014. Among detected striped bass, the median number of minutes detected per day ranged from 1.5–6 among individuals and reached a maximum of 17 min total in a single day. [Examples of different individual detection histories are available in Fig. S2].

Seventy-two percent of detected splittail occupied the intertidal channel on more than one separate occasion (median = 2.5, IQR = 1.25–6.75). Eight individuals were detected using the channel on multiple days, ranging from one detection per day over two consecutive days to 840 detections over 144 d. On a per-day basis, the median number of minutes detected per individual ranged from 1 to 5.5, and the maximum reached was 43 min total. Individuals exhibited differences in usage of the intertidal channel; for example, the most commonly encountered individual splittail used the channel

Fig. 4 Seasonal detections (%) among species. Total number of detections are in red text. Striped bass and splittail were monitored for 500 d; tule perch were monitored for 449 d
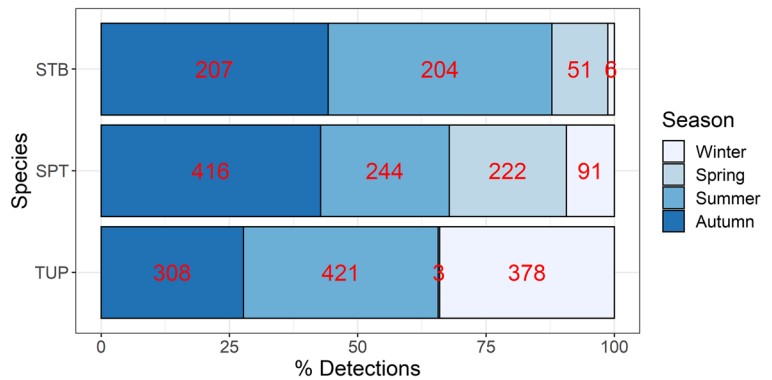
approximately every 2 days throughout the study period, except when it was absent for 61 d in winter 2013–2014 and then again for 83 d in the spring of 2014, after which it returned to using the channel on a regular basis. Another individual also used the channel approximately every 2 days during 1 month in spring 2014. In contrast, several individuals were detected a few times with large periods between detections (i.e. 135, 162, 343 and 472 d-at-large). [Examples of different individual detection histories are available in Fig. S3.]

The median number of daily detection events for tule perch was seven per day, which was more than two times greater than that of both striped bass and splittail (median = 3 per day). Eighty-five percent of detected tule perch occupied the channel on more than one occasion. Fifty percent of individuals were detected on multiple days, whereby detections ranged from 26 detections over two consecutive days to 554 detections over 130 d (median = 3 detections, IQR = 2–5). Notably, all repeatedly encountered individuals visited the intertidal channel every 1–2 d, on average, throughout their detection histories. Two commonly encountered individuals were absent for 2–4 weeks in winter 2014–2015 before returning to the channel again on a regular basis. [Examples of different individual detection histories are available in Fig. S4.]

Model comparison and selection

Striped bass model comparisons yielded six models that had stacked weights >5% and comprised 98% of total assigned stacked weights. Tide height, tidal low, tidal inequality, time of day (i.e. day, night, dawn, dusk), and/or temperature were important main effects and month was an important random effect (see Table 4 for a summary; full results are in Table S2). Specifically,

smoothed relationships from the GAMMs indicated that median predicted detections decreased with increasing tide height and tidal inequality values; in addition, estimates were positive at average tidal low values and slightly negative at average temperature values (with high uncertainty at extreme values of both metrics). Median predicted detections were highest at nighttime, lowest at dawn, and moderate at daytime and dusk (Fig. 5). Tide height (model 3; weight = 26%) yielded the top-ranked model whereby it had both the lowest elpd estimates and the highest stacked model weight. The second-highest-ranked model was model 2 (weight = 22%), the random-effect month model that showed a strong effect of and high variance in month (i.e. seasonality). Model comparisons also showed that there was considerable uncertainty in elpd estimates as measured by the standard errors, which may reflect the sensitivity of PSIS-LOO to high variance and/or insufficient detections.

Splittail model comparisons yielded six models that had both >5% stacked model weights and low elpd differences, and comprised 57% of the total assigned model weights (Table 4). Top-ranked models suggested that splittail detections were related to lunar phase, time of day, and/or tidal low values. Specifically, smoothed relationships from the GAMMs indicated that detections increased with higher percent disk illumination, and day, dusk, and nighttime categories; detections decreased with increasing lower-tidal-low and higher-tidal-low values (Fig. 6). In addition, the random effect, PIT-tag ID, had a relatively strong effect and high variance (model 1; weight = 13%), highlighting the importance of individual fish identity on observed detection patterns.

Notably, splittail models yielded elpd estimates and standard errors that indicated substantial uncertainty in

Table 4 Summary of selected GAMMs from the PSIS-LOO analysis

Species	Model Equation	Stacked Weight (%)	elpd diff	se diff	elpd loo	se elpd loo
Striped bass	Tag Days + Power + Efficiency + PIT ID + Month + Tide Height	26	0.0	0.0	−419.1	24.8
	Tag Days + Power + Efficiency + PIT ID + Month	22	−0.2	0.9	−419.3	24.9
	Tag Days + Power + Efficiency + PIT ID + Tidal Low	18	−0.3	1.1	−419.4	24.8
	Tag Days + Power + Efficiency + PIT ID + Tidal Inequality	13	−0.4	1.3	−419.4	24.8
	Tag Days + Power + Efficiency + PIT ID + Month + Day-Night-Twilight	10	−0.5	1.3	−419.5	24.8
	Tag Days + Power + Efficiency + PIT ID + Month + Temperature	9	−0.3	0.9	−419.4	24.9
Sacramento splittail	Tag Days + Power + Efficiency + PIT ID + Month + Lunar Phase8	26	−0.6	2.3	−842.9	33.1
	Tag Days + Power + Efficiency + PIT ID + Month + Day-Night-Twilight	16	−0.2	1.9	−842.5	33.3
	Tag Days + Power + Efficiency + PIT ID + Month + % Disk Illumination	9	0.0	0.0	−842.3	33.2
	Tag Days + Power + Efficiency + PIT ID + Month + Lunar Phase4	6	−0.1	1.0	−842.4	33.2
Tule perch	Tag Days + Power + Efficiency + PIT ID + Month	30	−0.3	1.2	−983.3	29.2
	Tag Days + Power + Efficiency + PIT ID + Rate of Change in Tide Height	26	0.0	0.0	−983.0	29.0
	Tag Days + Power + Efficiency + PIT ID + Month + Tide Height	22	0.0	1.2	−983.0	29.2
	Tag Days + Power + Efficiency + PIT ID + Month + Temperature	16	−0.5	1.4	−983.5	29.3

Stacked weight, calculated using Bayesian model stacking, is the Akaike weight for each model and can be 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, pp. 199). Model rank is based on stacked weight, which is thought to be superior in assigning weights to very similar models (Vehtari et al. 2018), and the difference in elpd estimates. The elpd value is the expected log predictive density and is an estimate of predictive accuracy; SE is the standard error of the elpd estimate

the PSIS-LOO analysis and did not align with stacked model weight assignments. For example, the lowest elpd estimates were assigned to the percent disk illumination model, while the highest stacked model weight was assigned to the eight-category lunar phase model. Model comparison based on both stacked weight and differences in elpd estimates yielded agreement among lunar phase, disk illumination, and time-of-day models, which were subsequently selected for interpretation (Fig. 6).

Tule perch model comparisons yielded four models that had stacked model weights >5% and totaled 94% of assigned model weights. The top-ranked models included the variables month, tide height, rate of change in tide height, and/or temperature. The models predicted that tule perch detections decreased at average rates of change in tide height, average-to-high tide heights, and average-to-high temperatures (with higher uncertainty at extreme, low, and low values, respectively; Fig. 7);

additionally, the high stacked weight of the random-effect month model (model 2; weight = 30%) indicated seasonal effects. Similar to the other species, model comparisons yielded considerable uncertainty in the elpd estimates and standard errors (Table 4).

Discussion

Our passive mark-recapture study showed that estuarine fishes repeatedly used a low-order intertidal channel in the largest remaining tidal marsh in Suisun Marsh. Main findings of our study include the following: (1) patterns of residency and site fidelity varied among species and individuals with different life-history types; (2) fishes responded to various tidal, diel, lunar, and seasonal cycles; and (3) *TidalTrend* generated useful derived parameters from tide height data, particularly, the variables tidal inequality and rate of change in tide height,

Fig. 5 Smoothed relationships for striped bass detections and **a** tide height, **b** temperature, **c** tidal low, and **d** tidal inequality from top-ranked GAMMs. Black lines represent predicted smoothed relationships; ribbons indicate 95% (light blue), 80% (medium blue), and 50% (dark blue) credible intervals and include random-effect variance. Knots (k) for thin plate regression splines (TPRS) specified on the y-axis. Red dashed lines at the zero y-intercept provide a reference point for no relationship between response and predictor variables. **e** Median predicted detections at different times of the day; intervals represent median estimates (circles) and 50% credible intervals (dark blue lines). Model weights (%) were estimated via Bayesian model stacking
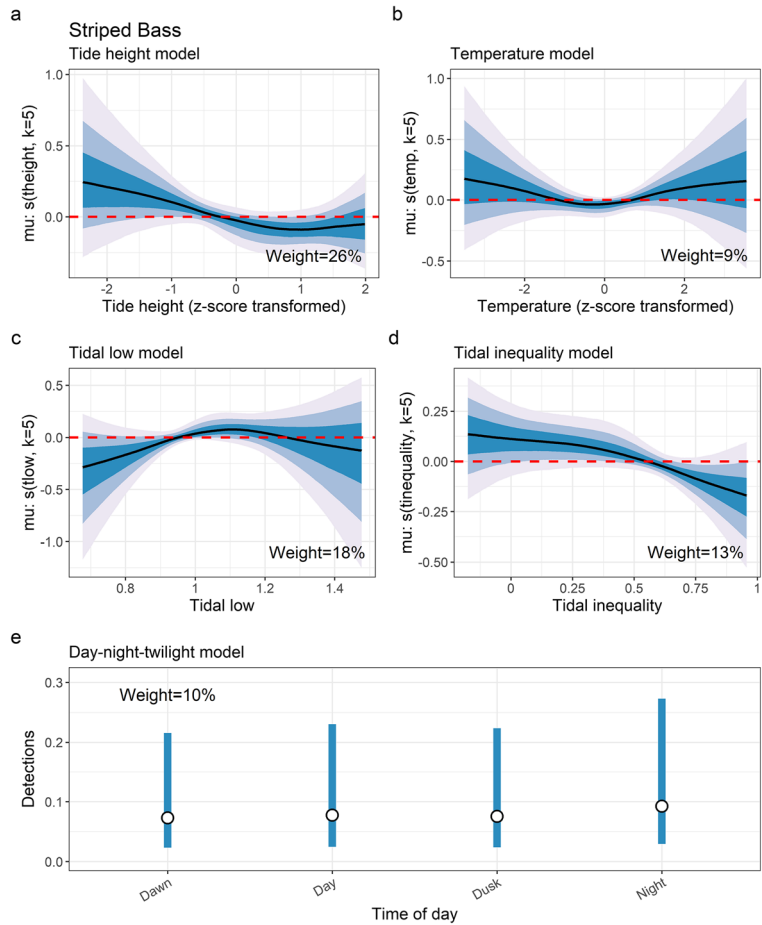
which provided insight into the different aspects of tides and scales to which estuarine fish respond. Our case study builds on previous studies of fish movements in tidal marsh channels (Hering et al. 2010; McNatt et al. 2016; Boswell et al. 2019) by documenting behavioral diversity among and within species and mechanisms for temporal habitat partitioning of the fish assemblage. In addition, it provides an instructive framework for analyzing continuous, high-frequency fish movement data in relation to complex, co-occurring changes in tidal environments over long periods.

Patterns of residency and site fidelity

Our findings generally corroborate previous studies that have examined life-history strategies and habitat use of striped bass, splittail, and tule perch in the SFE and other systems where they occur (Table 1; Moyle 2002). In addition, our passive mark-recapture study demonstrated the ecological importance of the intertidal channel to

individual fish of different species throughout their lives. In doing so, we documented both interspecific and intraspecific variation in fish movement patterns, which is a finer scale of resolution of fish movement than has been previously assessed in tidal marsh habitat in this region (but see flow responses of *Lavinia exilicauda* and *Catostomus occidentalis*; Jeffres et al. 2006). Future studies could scale up this approach using PIT or acoustic tags to compare residency and site fidelity within and among various fish species and habitat types (e.g. intertidal and subtidal channels, managed tidal ponds, submersed macrophyte beds, freshwater creeks, open bays) throughout the estuarine mosaic.

In this study, juvenile and sub-adult striped bass exhibited seasonal patterns of habitat use, which is consistent with the observation that smaller fish depend on shallow tidal marsh habitat in Suisun Marsh before emigrating to other estuarine habitats (Colombano et al. 2020). However, our study revealed that striped bass movement into a low-order intertidal channel, which

Fig. 6 Top ranked GAMMs: Median predicted detections of splittail according to **a** lunar phase, and **b** time of the day, where intervals represent median estimates (circles) and 50% credible intervals (dark blue lines); **c** smoothed relationships for detections as a function of percent disk illumination. Black lines represent predicted smoothed relationships; ribbons indicate 95% (light blue), 80% (medium blue), and 50% (dark blue) credible intervals and include random-effect variance. Knots (k) for thin plate regression splines (TPRS) specified on the y-axis. Red dashed lines at the zero y-intercept provide a reference point for no relationship between response and predictor variables. Model weights (%) were estimated via Bayesian model stacking
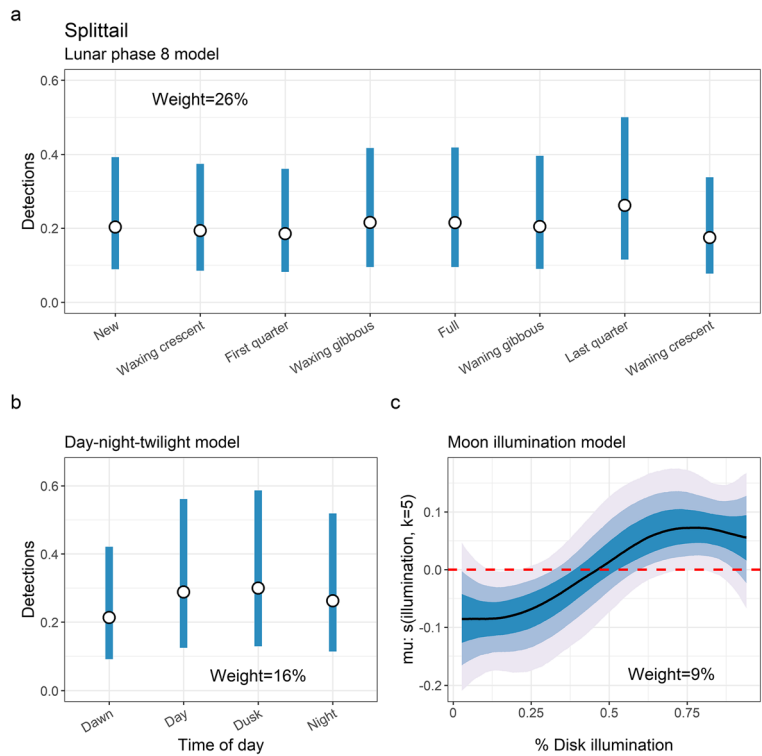
laterally connects subtidal channels to the vegetated marsh plain, is opportunistic and likely reflects their highly mobile, transient life-history. Notably, some individuals periodically revisited the study channel during summer and autumn, suggesting that while they may have a larger home range, they may exhibit ontogenetic or seasonal site fidelity to certain habitat mosaics within the seascape. Additionally, striped bass had a greater percentage of detections that co-occurred with detections of the other focal species, which, despite the low overall sample size, may reflect higher encounter rates of this piscivore with other species in tidal marshes (Fig. S2).

Splittail also exhibited patterns of habitat use reflecting a highly mobile transient life-history; however, splittail resided in the study channel for longer periods per visit compared to striped bass, suggesting a
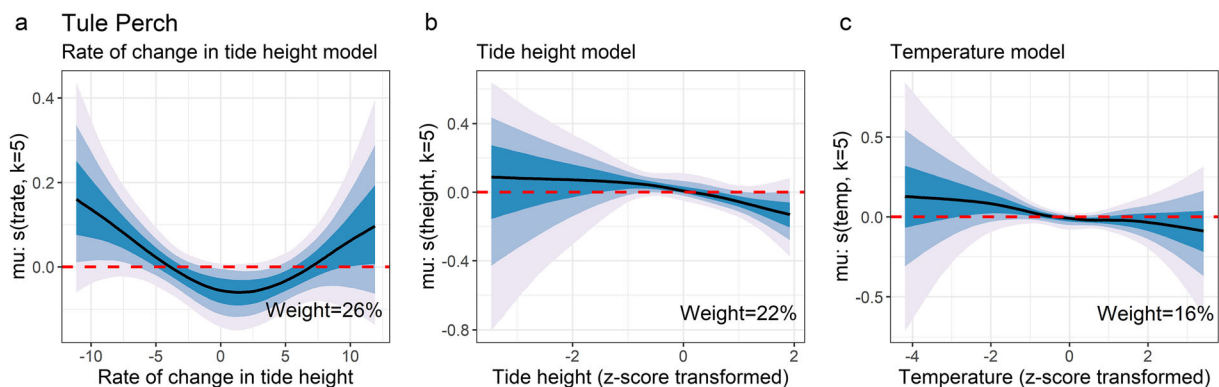
Fig. 7 Smoothed relationships for tule perch detections and **a** rate of change in tide height, **b** tide height, and **c** temperature from top-ranked GAMMs. Black lines represent predicted smoothed relationships; ribbons indicate 95% (light blue), 80% (medium blue), and 50% (dark blue) credible intervals and include random-effect variance. Knots (k) for thin plate regression splines (TPRS) specified on the y-axis. Red dashed lines at the zero y-intercept provide a reference point for no relationship between response and predictor variables. Model weights (%) were estimated via Bayesian model stacking

different mechanism of resource use such as methodical grazing for invertebrates along the benthos or hiding from predators. Site fidelity was also apparent; for example, one noteworthy individual was consistently present throughout the duration of the study except during the late winter and spring reproductive window when adult splittail typically migrate to floodplains in the upper estuary (Splittail #139; Fig. S3; Moyle et al. 2004). A broad interpretation is that they are seasonal residents of both tidal marshes and floodplains.

Consistent with previous research in Suisun Marsh (Baltz and Moyle 1982), tule perch exhibited a resident life-history characterized by frequent and consistent detections among individuals in the study channel. Tule perch displayed a high degree of residency and site fidelity with the highest number of overall detections, detections per day, and detections in summer, autumn, and winter; their extensive use of the intertidal channel was further supported by the relatively high proportion of detected individuals that were initially captured in intertidal habitat prior to tagging (Fig. S6). Tule perch were not detected in the study channel during the spring reproductive window when pregnant females typically seek out dense cover, such as patches of *Stuckenia* spp. (Moyle, UCD, unpublished data), signaling that soft-bottom intertidal channels may not be suitable for large adult females during gestation or release of live young.

Time as an influence of intertidal habitat partitioning

In coastal and estuarine environments, time may have an important influence on habitat partitioning among fish communities (Munsch et al. 2016). Our study highlights the diverse temporal scales by which estuarine fishes may use intertidal marsh and suggests several potential mechanisms for temporal habitat partitioning. Overall, the observed patterns in fish movement were consistent with previous studies showing differences over semidiurnal tidal cycles (12.4 h; Hering et al. 2010), diurnal tidal cycles (24.8 h; Kleypas and Dean 1983) and lunar cycles (29.6 d; Hampel et al. 2003; Milardi et al. 2018) in intertidal channels. In addition, the observed patterns in fish movement were consistent with differences among resident and transient fishes in other tidal marsh systems (Bretsch and Allen 2006; Kimball and Able 2012). There was no direct model support, however, for effects of flood-ebb categories on fish detections in the intertidal channel, suggesting that these estuarine fishes were well-adapted to changes in tidal direction.

Furthermore, there was no direct model support that focal species responded to the proportion of time per day that tides overtopped the marsh plain, likely because they remained in the intertidal channel and did not move onto the adjacent marsh plain as has been observed in other systems (e.g. *Fundulus heteroclitis*; McIvor and Odum 1988; Rozas et al. 1988; Kneib 1997).

Specifically, striped bass detections were related to tide height, tidal low, tidal inequality, time of day, and season. Striped bass detections declined with increasing tide height, indicating a preference for shallower depths for the smaller individuals detected in this study. This finding is consistent with previous studies showing that water depth affected fish movements (Bretsch and Allen 2006; Rypel et al. 2007; Hering et al. 2010) and that both predator and prey densities were higher in shallower depths at the confluence of an intertidal and subtidal channel (Boswell et al. 2019). However, there was also evidence of non-linear effects of *TidalTrend* metrics derived from tide height; for example, models indicated a preference for days with average low tide heights and/or smaller tidal amplitudes. After adjusting for seasonal fluctuations, temperature effects were more consistent at average values and highly variable at upper and lower values. Additionally, there was some evidence of higher striped bass detections at nighttime and daytime compared to dawn and dusk. Overall, these relationships indicate that smaller striped bass cue into shallow yet predictably stable water levels when actively searching for prey in intertidal habitat. In contrast, based on the absence of larger tagged striped bass from the PIT-detector time series, adults may remain in subtidal areas where depths are more stable and/or while waiting for prey to exit shallow intertidal habitats.

Alternatively, splittail detections varied as a function of lunar cycles, which have varying nocturnal light levels and tidal amplitudes. For example, models indicated that detections were highest 1 week after the full moon (i.e. the last quarter moon) when 50% of the moon's disk was illuminated and tidal amplitudes were muted (i.e. neap tides). Days when the moon's disk illumination was 50% or greater were also related to higher splittail detections; these findings complement that of Milardi et al. (2018), which documented effects of disk illumination and moon phase on catches of benthic fishes in a brackish lagoon. Foraging behaviors in response to light intensity may further explain the observed movement patterns. For example,

Drolet and Barbeau (2009) documented diel and lunar periodicity in the swimming activity of a benthic amphipod, *Corophium volutator*, in an intertidal mudflat in the Bay of Fundy, Canada. Alternatively, light intensity may simply increase visibility of prey in turbid benthic habitats (Mussen and Cech 2013). Collectively, the results build on studies of splittail habitat use of shallow tidal marsh habitats in the SFE (Moyle et al. 2014; Colombano et al. 2020) by showing that splittail inhabited the channel in a wide range of tide heights (Fig. S9) and responded to light-driven fluctuations that occurred on daily and lunar scales.

Tule perch detections varied as a function of tide height, rate of change in tide height, temperature, and/or season. Interestingly, models indicated that higher detections were related to higher rates of change in tide height, which occur halfway through flood and ebb tides, and likely reflect the onset of higher in-channel velocities (Becker et al. 2016). There was also model support for higher detections of tule perch in shallower depths and cooler waters. The resident tule perch is a surfperch species, which typically use their pectoral fins to swim at low to intermediate speeds and then transition to burst-and-coast propulsion to swim at higher speeds (Drucker and Jensen 1996). This unique behavior may explain the increased detections observed during peak rates of change in tide height in the tidal cycle (i.e. to reduce bio-energetic demands of swimming against the current). Tule perch may also cue into rate of change in tide height when awaiting return to intertidal or subtidal habitat after tidal flooding or draining, respectively, to continue foraging and/or hiding from predators.

Coupling behavioral observations with *TidalTrend* variables

Coupling PIT-detector technology with *TidalTrend* variables allowed us to understand the relative effects of complex and rapidly changing environmental conditions on tagged fish movements in a shallow and challenging-to-sample intertidal habitat. Notably, *TidalTrend* algorithms generated ecologically relevant derived parameters from tide height data and therein provided novel insights into species-specific behavioral adaptations to intertidal habitat. While the role of tide height in structuring fish movement patterns is well-established in the literature (Bretsch and Allen 2006; Rypel et al. 2007; Hering et al. 2010), the behavioral observations in the present study, which encompass a

diversity of life-history types over a long period, provide alternative tide-derived relationships. Specific examples include the apparent effects of tidal low, tidal inequality, and rate of change in tide height on fish detections in the study channel; such metrics revealed potential adaptations to tidal amplitude and in-channel water velocity, which would not have been apparent from absolute tide height data alone. Collectively, the use of *TidalTrend* as a tool to examine ecological relationships with respect to tides is a promising avenue that can be applied to various ecological data sets, and this case study illustrates a small subset of the types of questions that it can help to answer.

Intertidal channels as fish habitat

We observed that individuals of three estuarine fish species regularly occupied a 0.1 km^2 intertidal channel in a 4.25 km^2 tidal marsh reserve in Suisun Marsh. While previous studies have demonstrated the ecological importance of shallow, dead-end tidal marsh channels as fish habitat in Suisun Marsh (Colombano et al. 2020), tidal movements of fishes had yet to be investigated in this region. Our study indicated that fishes with different life-histories responded to predictable but rapidly shifting cycles that occur on various time scales. We posit that estuarine fishes use low-order intertidal channels for food, cover, and/or to access marsh plain edges. While the focal species in this study did not appear to use overtopping as a cue to move onto the marsh plain, seasonal flooding during wet winters and springs may provide prolonged access to marsh plain pools and ponds that could be important habitat for fish. We recommend that future studies focus on foraging behaviors and predator-prey interactions in subtidal-intertidal channel networks in relation to tides and water years to better understand such mechanisms.

Connectivity between subtidal and intertidal channels has largely been lost in the estuary due to extensive diking of shorelines in the early twentieth Century; in the present-day ecosystem, only ~5% of the historic areal coverage of undiked tidal marshes remains intact (Nichols et al. 1986). As a result, the historical importance of tidal marsh to California fishes has been debated (Brown 2003; Herbold et al. 2014). Although the percentage of detected fish in our study was small, individuals among all three focal species regularly used a single intertidal channel that represented only ~2% of available habitat in the Rush Ranch tidal marsh reserve.

The pre-European settlement extent of tidal marsh, which spanned fresh, brackish, and salt water habitats throughout the SFE, presumably provided diverse habitat opportunities for fishes. Moreover, transient species likely benefitted from such habitat heterogeneity if it permitted them to use tidal marshes to forage, avoid predators, or seek structured shelter in response to extreme conditions (e.g. high freshwater flows). Future conservation actions aimed to enhance fish habitat and life history diversity in the SFE should incorporate functional connectivity between subtidal and intertidal channels into tidal marsh restoration designs.

References

Baltz DM, Moyle PB (1982) Life history characteristics of tule perch (Hysterocarpus traski) populations in contrasting environments. Environ Biol Fish 7(3):229–242. https://doi.org/10.1007/BF00002498

Barbour AB, Adams AJ, Yess T, Behringer DC, Wolfe RK (2012) Comparison and cost-benefit analysis of PIT tag antennae resighting and seine-net recapture techniques for survival analysis of an estuarine-dependent fish. Fish Res 121–122:153–160. https://doi.org/10.1016/j.fishres.2012.01.013

Bass AL, Giannico GR, Brooks GT (2012) Performance of a full-duplex passive integrated transponder (PIT) antenna system in estuarine channels. Mar Coast Fish 4(1):145–155. https://doi.org/10.1080/19425120.2012.676384

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, … Weinstein MP (2001) The identification, conservation, and Management of Estuarine and Marine Nurseries for fish and invertebrates. BioScience 51(8), 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Becker A, Whitfield AK, Cowley PD, Cole VJ, Taylor MD (2016) Tidal amplitude and fish abundance in the mouth region of a small estuary. J Fish Biol 89(3):1851–1856. https://doi.org/10.1111/jfb.13056

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7(4):460. https://doi.org/10.2307/1351627

Boswell KM, Kimball ME, Rieucau G, Martin JGA, Jacques DA, Correa D, Allen DM (2019) Tidal stage mediates periodic asynchrony between predator and prey nekton in salt marsh creeks. Estuar Coasts 42(5):1342–1352. https://doi.org/10.1007/s12237-019-00553-x

Bretsch K, Allen DM (2006) Tidal migrations of nekton in salt marsh intertidal creeks. Estuar Coasts 29(3):474–486. https://doi.org/10.1007/BF02784995

Brown LR (2003) Will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary Watershed Science, 1(1). https://escholarship.org/uc/item/2cp4d8wk

Bürkner P (2017) Brms: an R package for Bayesian multilevel models using Stan. J Stat Softw 80(1):1–28

Bürkner P (2018) Advanced Bayesian multilevel modeling with the R package brms. R J 10(1):395–411

Colombano DD, Manfree AD, O'Rear TA, Durand JR, Moyle PB (2020) Estuarine-terrestrial habitat gradients enhance nursery function for resident and transient fishes in the San Francisco estuary. Mar Ecol Prog Ser 637:141–157

Department of Water Resources Atlas: highways, roads, California state boundary, LiDAR, bathymetry. State of California. http://atlas-dwr.opendata.arcgis.com/ (accessed January 2018)

Donovan, J. & Ayers, D. (2019). TidalTrend software technical report, US Geological Survey Dept of Interior

Drolet D, Barbeau MA (2009) Diel and semi-lunar cycles in the swimming activity of the intertidal, benthic amphipod Corophium volutator in the upper bay of Fundy, Canada. J Crustac Biol 29(1):51–56

Drucker E, Jensen J (1996) Pectoral fin locomotion in the striped surfperch. I Kinematic effects of swimming speed and body size. J Exp Biol 199(10):2235–2242

Ellis WL, Bell SS (2008) Tidal influence on a fringing mangrove intertidal fish community as observed by in situ video recording: implications for studies of tidally migrating nekton. Mar Ecol Prog Ser 370:207–219. https://doi.org/10.3354/meps07567

Enright C, Culberson SD, Burau JR (2013) Broad timescale forcing and geomorphic mediation of tidal marsh flow and temperature dynamics. Estuar Coasts 36(6):1319–1339. https://doi.org/10.1007/s12237-013-9639-7

Gabry J, Mahr T, Bürkner P, Modrák M, Barrett M (2018) Bayesplot: plotting for Bayesian models. http://mc-stan.org/bayesplot

Gannon R, Payne NL, Suthers IM, Gray CA, van der Meulen DE, Taylor MD (2015) Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid. Environ Biol Fish 98(6):1599–1608. https://doi.org/10.1007/s10641-015-0385-5

Gesch D, Oimoen M, Greenlee S, Nelson C, Steuck M, Tyler D (2002) The National Elevation Dataset. Photogramm Eng Remote Sens 68(1):5–11

Gibbons WJ, Andrews KM (2004) PIT tagging: simple Technology at its Best. BioScience 54(5):447–454. https://doi.org/10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2

Grant GN, Cowley PD, Bennett RH, Murray TS, Whitfield AK (2017) Space use by Rhabdosargus holubi in a southern African estuary, with emphasis on fish movements and ecosystem connectivity. Afr J Mar Sci 39(2):135–143. https://doi.org/10.2989/1814232X.2017.1327887

Hampel H, Cattrijsse A, Vincx M (2003) Tidal, diel and semi-lunar changes in the faunal assemblage of an intertidal salt marsh creek. Estuar Coast Shelf Sci 56(3):795–805. https://doi.org/10.1016/S0272-7714(02)00296-2

Herbold B, Baltz DM, Brown L, Grossinger R, Kimmerer W, Lehman P, … Nobriga M (2014) The role of tidal marsh restoration in fish Management in the san Francisco Estuary. San Francisco Estuary and Watershed Science, 12(1). https://escholarship.org/uc/item/1147j4nz

Hering DK, Bottom DL, Prentice EF, Jones KK, Fleming IA (2010) Tidal movements and residency of subyearling Chinook salmon (Oncorhynchus tshawytscha) in an Oregon salt marsh channel. Can J Fish Aquat Sci 67(3):524–533. https://doi.org/10.1139/F10-003

Hoffman MD, Gelman A (2014) The no-U-turn sampler: adaptively setting path lengths in Hamiltonian Monte Carlo. J Mach Learn Res 15(1):1593–1623

Jeffres CA, Klimley AP, Merz JE, Cech JJ (2006) Movement of Sacramento sucker, Catostomus occidentalis, and hitch, Lavinia exilicauda, during a spring release of water from Camanche dam in the Mokelumne River, California. Environ Biol Fish 75(4):365–373

Kimball ME, Able KW (2012) Tidal migrations of intertidal salt Marsh Creek nekton examined with underwater video. Northeast Nat 19(3):475–486. https://doi.org/10.1656/045.019.0309

Kleypas J, Dean JM (1983) Migration and feeding of the predatory fish, Bairdiella chrysura Lacépède, in an intertidal creek. J Exp Mar Biol Ecol 72(3):199–209. https://doi.org/10.1016/0022-0981(83)90106-5

Kneib R (1997) The role of tidal marshes in the ecology of estuarine nekton. Oceanography and Marine Biology: An Annual Review. http://www.vliz.be/en/imis?refid=490

Lazaridis E (2014) Lunar: lunar phase & distance, seasons and other environmental factors (version 0.1-04). Available from http://statistics.lazaridis.eu

Luo L, Apps D, Arcand S, Xu H, Pan M, Hoerling M (2017) Contribution of temperature and precipitation anomalies to the California drought during 2012–2015. Geophys Res Lett 44(7):3184–3192

McElreath R (2018) Statistical rethinking: a Bayesian course with examples in R and Stan. CRC Press

McIvor CC, Odum WE (1988) Food, predation risk, and micro-habitat selection in a marsh fish assemblage. Ecology 69(5):1341–1351. https://doi.org/10.2307/1941632

McNatt RA, Bottom DL, Hinton SA (2016) Residency and movement of juvenile Chinook Salmon at multiple spatial scales in a tidal marsh of the Columbia River estuary. Trans Am Fish Soc 145(4):774–785. https://doi.org/10.1080/00028487.2016.1172509

Milardi M, Lanzoni M, Gavioli A, Fano EA, Castaldelli G (2018) Tides and moon drive fish movements in a brackish lagoon. Estuar Coast Shelf Sci 215:207–214. https://doi.org/10.1016/j.ecss.2018.09.016

Minello TJ, Rozas LP, Baker R (2012) Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. Estuar Coasts 35(2):501–514. https://doi.org/10.1007/s12237-011-9463-x

Moyle PB (2002) Inland Fishes of California: revised and expanded. University of California Press

Moyle PB, Daniels RA, Herbold B, Baltz DM (1986) Patterns in distribution and abundance of a non-coevolved assemblage of estuarine fishes in California. Fish Bull 84:105–117

Moyle PB, Baxter RD, Sommer T, Foin TC, Matern SA (2004) Biology and population dynamics of Sacramento Splittail (Pogonichthys macrolepidotus) in the San Francisco estuary: a review. San Francisco Estuary and Watershed Science, 2(2). https://escholarship.org/uc/item/61r48686

Moyle PB, Manfree AD, Fiedler PL (2014) Suisun marsh: ecological history and possible futures. Univ of California Press

Munsch SH, Cordell JR, Toft JD (2016) Fine-scale habitat use and behavior of a nearshore fish community: nursery functions, predation avoidance, and spatiotemporal habitat partitioning. Mar Ecol Prog Ser 557:1–15. https://doi.org/10.3354/meps11862

Mussen TD, Cech JJ (2013). The roles of vision and the lateral-line system in Sacramento splittail's fish-screen avoidance behaviors: evaluating vibrating screens as potential fish deterrents. Environmental Biology of Fishes, 96(8), 971-980.

Næsje TF, Cowley PD, Diserud OH, Childs AR, Kerwath SE, Thorstad EB (2012) Riding the tide: estuarine movements of a sciaenid fish, Argyrosomus japonicus. Mar Ecol Prog Ser 460:221–232. https://doi.org/10.3354/meps09780

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish 16(2):362–371. https://doi.org/10.1111/faf.12057

Nichols FH, Cloern JE, Luoma SN, Peterson DH (1986) The modification of an estuary. Science, 231(4738), 567-573.

NOAA (2019) National Oceanic and Atmospheric Administration. US Dept of Commerce. Data accessed from the NOAA NERRS Centralized Data Management Office website: http://www.nerrsdata.org/

O'Rear TA, Moyle PB, Durand JR (2019) Trends in fish and invertebrate populations in Suisun marsh January 2018 – December 2018. California, California Department of Water Resources. https://watershed.ucdavis.edu/library/suisun-marsh-fish-study-trends-fishand-invertebrate-populations-suisun-marsh-january-2017

Palaima A (2012) Ecology, conservation, and restoration of tidal marshes: The San Francisco estuary. University of California Press

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876. https://doi.org/10.7717/peerj.6876

Prentice EP, Sims CW, Park DL (1985) A study to determine the biological feasibility of a new fish tagging system. Report (contract DEA179-83BP11982, project 83-19) to Bonneville Power Administration, Portland, Oregon.

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org/

Rozas LP, McIvor CC, Odum WE (1988) Intertidal rivulets and creekbanks: corridors between tidal creeks and marshes. Mar Ecol Prog Ser 47(3):303–307

Rypel AL, Layman CA, Arrington DA (2007) Water depth modifies relative predation risk for a motile fish taxon in Bahamian tidal creeks. Estuar Coasts 30(3):518–525. https://doi.org/10.1007/BF03036517

Sakabe R, Lyle JM (2010) The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish Acanthopagrus butcheri. J Fish Biol 77(3):643–660. https://doi.org/10.1111/j.1095-8649.2010.02703.x

San Francisco Estuary Institute (2012) Bay Area EcoAtlas. Modern baylands. Data accessed from website: http://www.sfei.org/ecoatlas/

Scofield EC (1931) The life history of striped bass. California Department of Fish and Game. Fish Bull 29:26–60

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.18.2. http://mc-stan.org/

Time and Date (2019) Antioch, California data accessed from the Time and Date website: https://www.timeanddate.com/sun/usa/antioch

US Geological Survey (2004) National Hydrography Dataset. US Department of the Interior, US Geological Survey. Reston, Virginia. Data accessed from website: https://www.usgs.gov/core-science-systems/ngp/national-hydrography/national-hydrography-dataset

Vasey MC, Parker VT, Callaway JC, Herbert ER, Schile LM (2012) Tidal wetland vegetation in the San Francisco Bay-Delta estuary. San Francisco Estuary and Watershed Science 10(2). https://escholarship.org/uc/item/44z5v7xf

Vehtari A, Buerkner P, Gabry J (2018) Leave-one-out cross-validation for non-factorizable models. http://mc-stan.org/loo/articles/loo2-non-factorizable

Viehman HA, Zydlewski GB (2017) Multi-scale temporal patterns in fish presence in a high-velocity tidal channel. PLoS One 12(5):e0176405. https://doi.org/10.1371/journal.pone.0176405

Walters RA, Cheng RT, Conomos TJ (1985) Time scales of circulation and mixing processes of San Francisco Bay waters. Hydrobiologia 129(1):13–36. https://doi.org/10.1007/BF00048685

Wenner EL, Geist M (2001) The National Estuarine Research Reserves program to monitor and preserve estuarine waters. Coast Manag 29(1):1–17

Whitcraft CR, Grewell BJ, Baye PR (2011) Estuarine vegetation at rush ranch open space preserve, san Franciso Bay National Estuarine Research Reserve, California. San Francisco Estuary and Watershed Science 9(3). https://escholarship.org/uc/item/6j89531r

Wickham H, François R, Henry L, Müller K (2019) dplyr: A Grammar of Data Manipulation. R package version 0.8.1. https://CRAN.Rproject.org/package=dplyr

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3(4):385–397. https://doi.org/10.2307/2389612

Wood SN (2003) Thin plate regression splines. J R Stat Soc Ser B (Stat Methodol) 65(1):95–114

Wood SN (2017) Generalized additive models: an introduction with R. Chapman and Hall/CRC