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Assessing Fish Distribution in Richardson Bay, California: A Preliminary Dual-Frequency Identification Sonar and Environmental Data Approach

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ABSTRACT

Estuaries provide critical habitat for many economically and ecologically valuable species that are adapted to a wide range of conditions and environmental variability, but the often turbid water presents challenges to monitoring efforts. This study explored fish habitat use in Richardson Bay, California (a sub-estuary of San Francisco Bay) at two points in time: one following a dry winter (2016) and the other following a historically wet winter (2017). Dual-frequency Identification Sonar (DIDSON) was used to record finfish and ray (>10 cm) abundance (MaxN) and size distribution, putative ray foraging pit size and abundance (MaxN), and eelgrass (*Zostera marina*) presence. We measured temperature, salinity, and dissolved oxygen (DO) at each site, and water samples at a subset of sites for nutrient analysis (urea, ammonium, nitrate, silicate, phosphate). Relationships between these data were explored using an information-theoretic modeling approach. Finfish abundance was best predicted by nutrient concentration in 2016 (–) and eelgrass presence in 2017 (–), whereas fish length was best predicted by salinity in 2016 (–) and eelgrass presence in 2017 (+). Foraging-pit abundance was strongly related to nutrient concentrations (+) in both years. This work presents a first attempt to establish relationships between fish distributions and environmental variables in Richardson Bay, and highlights the value of imaging sonar for studying fish communities in turbid estuaries.

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KEY WORDS

imaging sonar, fish community, salinity, nutrients, eelgrass, bioturbation, ray pits

INTRODUCTION

Estuaries are dynamic ecosystems inhabited by species adapted to survive in a variable environment. They are among the most productive ecosystems on the planet, providing crucial spawning and nursery grounds for fish, as well as a variety of environmental conditions and benthic substrates inhabited by diverse fauna, including both migratory and resident species (Allen et al. 2006; Vasconcelos et al. 2015). When conditions become too extreme, however, estuarine fish are forced into energetically expensive osmoregulation and relocation (Whitfield 2015), potentially altering entire estuarine communities altogether (Feyrer et al. 2015; Whitfield 2021; Gillanders et al. 2022). Thus, understanding the distributions, abundance, and habitat use of estuarine species is necessary to recognize changes, particularly in times of climatic shifts.

Richardson Bay, California, USA is a relatively turbid, shallow sub-estuary of San Francisco Bay that experiences strong seasonal and interannual variability in temperature and salinity (Figure 1). This sub-estuary has a mix of rocky and soft sediment shorelines and benthic habitat, extensive docks and hardened shoreline, and the second-largest extent of eelgrass beds (*Zostera marina*) in San Francisco Bay (~135 hectares; Merkel & Associates 2015). The latter provide important habitat, which is also frequently damaged and uprooted by boat anchors and mooring tackle (Kelly et al. 2019) and is a major target of ongoing restoration efforts (Boyer and Wyllie–Echeverria 2010; Pawlak 2012; Boyer et al. 2017; Pinnell et al. 2021). Additionally, Richardson Bay is home to more than 50 species of primarily anadromous or euryhaline finfishes that inhabit the area for at least part of their life cycle (Green 1975; Smith 1984). In particular, the state-managed Pacific Herring (*Clupea pallasii*) commercial fishery is supplied largely by the spawning and rearing that occurs within Richardson Bay (CDFW 2019). These herring, along with Northern Anchovy (*Engraulis mordax*) and other schooling fishes, are highly ecologically important species that form links between trophic levels, and they have suffered population declines since the 1980s (Spratt et al. 1992; Watters et al. 2004; Allen et al. 2006). Steelhead Trout, a threatened species at the federal level, also use the low-salinity areas of the Richardson Bay as critical spawning grounds (Smith 1984).

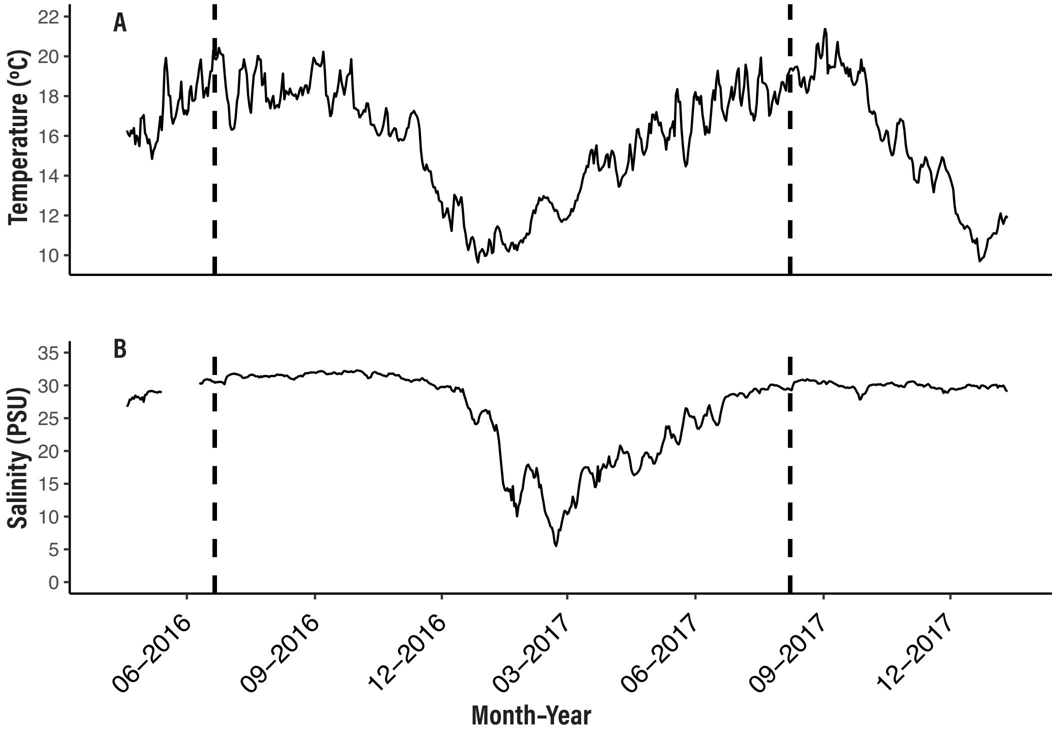

Figure 1 Daily average salinity and temperature from the Richardson Bay National Estuaries Research Reserve (NERR) sonde. During May–June 2016, the sonde returned erroneous salinity values, which were removed. *Vertical bars* indicate dates of DIDSON and nutrient sampling in Richardson Bay (June 21, 2016; August 8, 2017). Source: Data provided by the Smithsonian-led MarineGEO program in collaboration with the San Francisco Bay NERR.

Some cartilaginous fishes such as Bat Rays (*Myliobatis californica*) and Leopard Sharks (*Triakis semifasciata*) are considered residents as well (Green 1975). Both fishing pressures and extreme environmental changes (including the after-effects of oil spills and substantial drought and rainfall events) have negatively affected many of these species historically (Watters and Oda 2002; Incardona et al. 2012; Retallack et al. 2019) and their food sources (Ayala 2021), causing great declines in stocks. Despite the commercial, economic, and ecological significance of Richardson Bay, little information is available to describe the distribution of fish and associated habitat or environmental gradients in the bay.

To address the lack of information on fish distributions and associated habitat and environmental conditions, we used Dual-frequency Identification Sonar (DIDSON) to document the community of large finfish (>10 cm) and elasmobranchs in Richardson Bay. High-resolution imaging sonars such as DIDSON provide the means to study the fish community and benthic habitat in turbid estuaries such as Richardson Bay. Imaging sonars have proven effective for studying fish communities in both stationary (Martignac et al. 2015; Ogburn et al. 2017; Legett et al. 2023) and mobile (Able et al. 2013, 2014; Dunn et al. 2022; Olson et al. 2023) deployments, and can out-perform visible-light cameras when cryptic fish are present in the water column (Sibley et al. 2023). Sonar footage provides scaled images from which animal lengths can be measured (Burwen et al. 2007), and can sometimes provide species-level information when the shape or behavior of species is distinct from others in the study area (Able et al. 2013, 2014; Martignac et al. 2015). This technology can also reveal benthic habitat structures such as seagrass beds (Olson et al. 2023) and pits created by animals foraging in soft sediments, which can indicate patterns of habitat use and the likely presence of animals in the absence of other visual evidence (Thistle 1981; Cross and Curran 2004; O'Shea et al. 2012).

The primary objective of this baseline study was to provide an initial exploration of spatial variation in fish abundance, size distributions, and habitat use among variable habitat characteristics and environmental conditions using two snapshots in time from consecutive summers (2016 and 2017). Fish foraging activity—particularly bioturbation by rays to capture infaunal food—can leave behind foraging pits, or round depressions in soft benthic sediments (Gregory et al. 1979; Flowers et al. 2021) that are visible using imaging sonar. These pits provide insight on feeding activity in marine and estuarine environments even after the foraging animals have left the immediate area (Hines et al. 1997). The pits may vary in size depending on ray size, feeding intensity, and repeated use by rays and other animals for either shelter or secondary feeding, and they may indicate areas where fish foraging activity releases nutrients from sediments into the water column (Grant 1983; D'Andrea et al. 2004). Further, estuaries tend to be highly fertilized ecosystems where fish may be more abundant and larger in areas of higher nutrient concentration and more complex substrate, as a result of increased primary productivity, food availability, and options for shelter (Nixon et al. 1986; Thom et al. 1989; Josefson and Rasmussen 2000; Wilson 2002; González–Solis and Torruco 2013). Thus, we hypothesized that fish abundance, length measurements, and foraging pit size and abundance would be higher in areas of Richardson Bay with more nutrients and seagrass beds. We also posited that fish presence would be documented throughout Richardson Bay regardless of salinity, since it hosts estuarine fish associated with a wide gradient of salinity levels (Kimmerer 2002; Cloern et al. 2010; Kimmerer et al. 2013).

To address these hypotheses, we surveyed the fish community and benthic habitat using DIDSON, collected water-quality data and nutrient concentrations at DIDSON survey sites and at a data sonde deployed in Richardson Bay, and analyzed associations among the resulting faunal and environmental data. This study is one of the first to document the distribution and abundance of fish alongside relevant environmental variables in Richardson Bay and to report data from the Richardson Bay data sonde.

MATERIALS AND METHODS

Study Sites

In June 21, 2016, and August 8, 2017, we surveyed fish and habitat characteristics in Richardson Bay. We selected fifty sampling stations (Figure 2) by covering the study area with a grid, numbering each intersection of the grid, and using a random-number generator to select which intersections to sample. Of the 50 planned sampling locations, four sites in 2016 and one site in 2017 could not be sampled because water was too shallow to access by boat. We selected a subset of these sites (25 in 2016; 23 in 2017) for water collections to quantify nutrient loads since the study lacked sufficient funding to process samples for all fish survey stations. We also collected water samples at four additional sites that were of interest because of potential inputs from a nearby wastewater treatment plant, where heightened nutrient loads and wastewater treatment by-products have been measured previously (Damashek et al. 2016).

Environmental Data

On each sampling date, we measured water-quality to characterize spatial variation in environmental parameters. At each site (46 in 2016; 49 in 2017), we used a hand-held probe (YSI Pro 2030) to record water temperature,

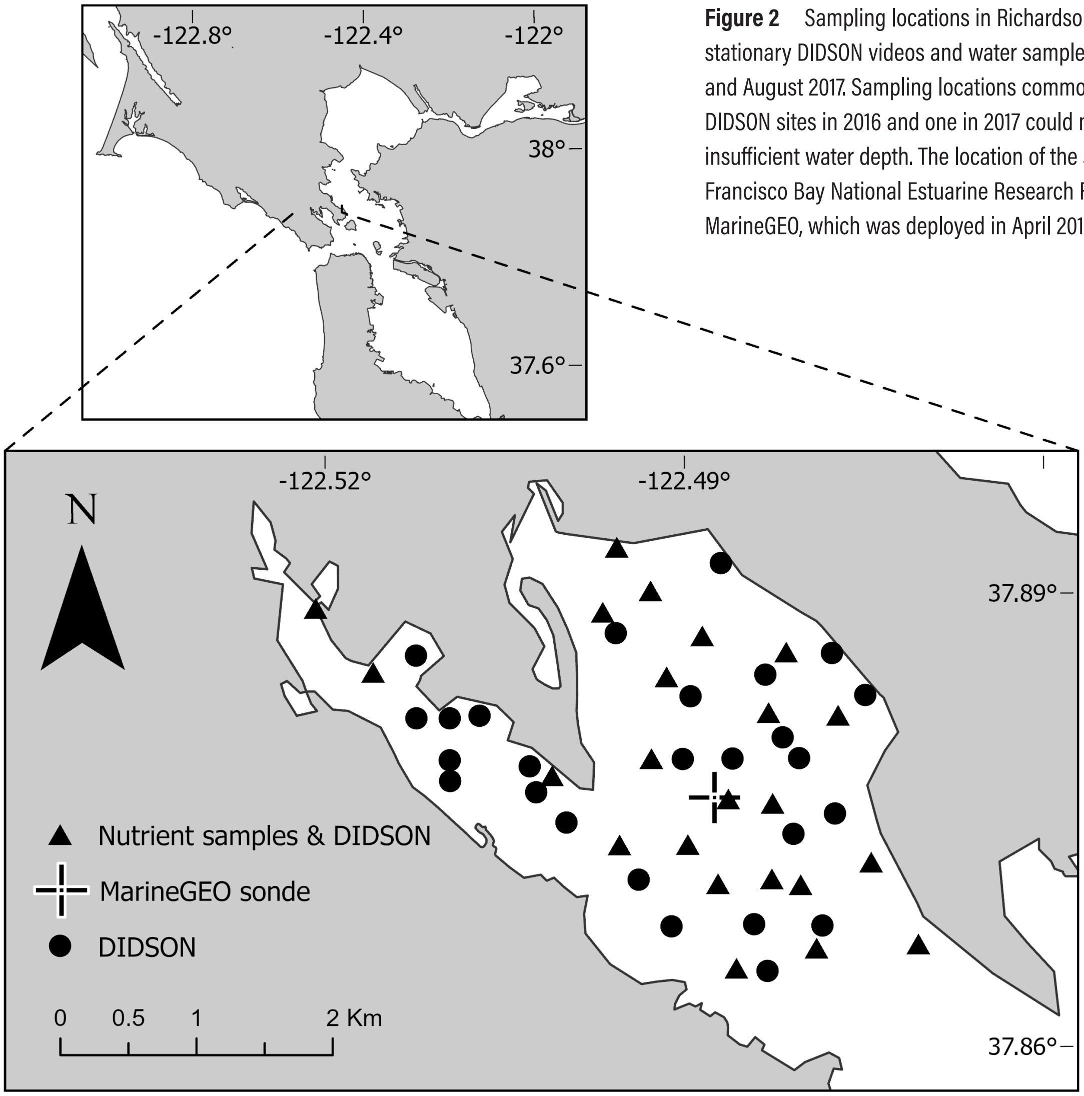

Figure 2 Sampling locations in Richardson Bay, California, where stationary DIDSON videos and water samples were collected in June 2016 and August 2017. Sampling locations common to both years shown. Four DIDSON sites in 2016 and one in 2017 could not be sampled as a result of insufficient water depth. The location of the sonde maintained by the San Francisco Bay National Estuarine Research Reserve (NERR) in support of MarineGEO, which was deployed in April 2016, is also shown (+).

salinity, and DO concentration near the surface and bottom. We collected water samples for nutrient analysis in pre-cleaned, rinsed Nalgene bottles. We gently filtered samples through pre-combusted filters (25-mm-diameter Whatman® GF/F filters), and the filtrates stored frozen (–20 °C) in pre-cleaned, rinsed 15-mL polypropylene conical tubes (Falcon®; Becton Dickinson Labware) until analysis. We thawed samples overnight at room temperature (ca. 20 °C) before analysis for nitrate plus nitrite ($NO_3^- + NO_2^-$; hereafter referred to as nitrate, or simply NO_3^-), orthophosphate (PO_4^{3-}), and silicate ($Si(OH)_4$) with a Lachat Instruments Flow Injection Analysis system (8000 series; Hach Co.) according to the Quick-Chem® colorimetric techniques (Smith and Bogren 2001; Knepel and Bogren 2002; and Wolters 2002, respectively). We filtered ammonium (NH_4^+) samples similarly into rinsed, 50-mL polypropylene centrifuge tubes (Corning®), and freshly analyzed using a Turner Trilogy fluorometer equipped with an ultraviolet (UV) colored dissolved organic matter (CDOM)/Ammonium optical insert (Turner Designs, Sunnyvale, California) following the fluorometric method of Holmes et al. (1999), whereas filtered urea samples were frozen before analysis with a spectrophotometer equipped with a 10-cm cell and following the diacetyl monoxime thiosemicarbazide technique of Price and Harrison (1987) as outlined by Cochlan et al. (2008). We recorded water depth at each site using the boat's depth finder (one measurement recorded per site). We subsequently used inverse distance weighting to create interpolations from dissolved nutrient samples and environmental (temperature, salinity, DO) samples to visualize estimated patterns throughout Richardson Bay.

Additionally, we obtained continuous environmental data from a YSI EXO Multi-Parameter Water Quality Sonde located in central Richardson Bay (37° 52′ 36.09″ N, 122° 29′ 15.23″ W) (Figures 1 and 2). This regularly calibrated device is maintained by the San Francisco Bay National Estuarine Research Reserve (NERR) in support of the Smithsonian-led MarineGEO program. Available data for this includes temperature, salinity, DO, turbidity, and chlorophyll-*a* concentration, which are collected for 4 seconds every 15 minutes and rigorously checked for quality assurance within 2 weeks of data download. We flagged any data with unusually high or low values for internal review before either adjusting or removing erroneous values.

Fish and Habitat Surveys

We conducted fish and benthic habitat surveys with a point count approach using a DIDSON imaging sonar unit set to high resolution (1.8 MHz). We surveyed the habitats by stopping the boat at each sampling station, lowering the DIDSON unit into the water, and recording a 1-minute video. The sonar unit was mounted on a fiberglass pole, held 0.5 m below the surface at the bow of the boat, and aimed horizontally with the beam angled downward so that it intersected the bottom near the middle of the viewing window (–3° to –27° angle, depending on water depth). The DIDSON window length (operational field of view) was set to 10 m, with a window start distance of 1.25 m from the sonar lens. This approach allowed us to collect images of fish in the water column and along the bottom and obtain images of the substrate surface to evaluate habitat characteristics. Maintaining a consistent distance at which the sonar beam intersected with the bottom ensured that we were evaluating a similar volume of water across sites. We visited all survey sites within 4 to 5 hours and conducted surveys around the time of high tide during spring tides to allow for maximum access to shallower areas of Richardson Bay. Changes in water level (based on NOAA station #9414290[1]) were similar on the two sampling days in 2016 (predicted low–high–low water levels of –0.22 m, 1.43 m, and 0.87 m) and 2017 (predicted low–high–low water levels of –0.08 m, 1.54 m, and 0.74 m); and sites were sampled in the same order, minimizing potential differences in depth between years as much as possible.

Imaging Sonar Processing

We processed video files in Sound Metrics DIDSON Software version 5. Within each 1-minute video file, we grouped fish by readily visible body shapes (finfish, bat rays, and sharks) and

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[1] *https://tidesandcurrents.noaa.gov/stationhome.html?id=9414290*

enumerated them using the "MaxN" method (Ellis and DeMartini 1995), whereby the maximum number of individuals visible within a single video-frame are counted to avoid counting individual fish multiple times in the video. We enumerated only fish >10-cm total length (or >10-cm disc width for bat rays), because smaller fish were near the detection limit of DIDSON and typically observed in dense schools, making it difficult to enumerate individuals. We determined length (or width) measurements of all fish >10 cm manually, using the measuring tool. We observed few rays or sharks in DIDSON videos; consequently, we excluded abundances of these species from statistical analyses. Because of the inherent difficulty of identifying species from DIDSON videos, we did not attempt to identify species for finfish.

We characterized habitat in the DIDSON recordings to determine the presence of eelgrass (*Zostera marina*) and the size and relative abundance of foraging pits (an indicator of foraging activity by rays and other species), which were the two common habitat types observed other than fairly homogenous soft sediments. By providing a record of foraging activity, foraging pit abundance may indicate relative densities of infaunal prey (Hines et al. 1997). Pit size and abundance are also metrics of benthic habitat complexity which can dictate rates of habitat use by other species (Crook et al. 2022). Eelgrass was readily visible in videos and recorded as present or absent. In some cases, especially dense eelgrass beds may have produced acoustic shadowing (blockage of sonar beams), potentially concealing fish. However, in all videos, the deployment vessel and DIDSON unit were drifting slightly during recording, thus providing a continually shifting angle to see behind eelgrass blades, and making it possible to select an image for fish counting in which all fish present were visible. Because of the wide variation we observed in pit size and abundance of foraging pits, we used two methods to quantify and measure them. First, we identified the largest pit in each video file, recorded the associated frame number, and measured the minimum and maximum diameters of the largest pit using the measuring tool in the DIDSON software. Next, within the video frame containing the largest pit, we recorded the total number of pits visible in the frame. We counted only roughly oval or circular pits to try to exclude non-biogenic depressions and provide a conservative estimate of putative foraging pits (Gregory et al. 1979).

Habitat Associations

We applied an information-theoretic approach to explore variation in the abundance and size of fish >10 cm, and abundance and size of foraging pits in relation to habitat characteristics and water-quality conditions. Considering that multiple nutrient variables were positively correlated with one another in both 2016 and 2017, we calculated an aggregate nutrient index separately by year. Observations of positively correlated nutrient concentrations urea, NH_4^+, NO_3^-, and $Si(OH)_4$ were first standardized to mean zero, standard deviation one (i.e., z-scores), and then summed by sample (Fabricius and De'ath 2004; Fabricius et al. 2005). This process alleviates multi-collinearity by collapsing individual, standardized variables into an aggregate index of nutrient concentrations wherein higher values represent higher overall nutrient concentrations, and lower index values correspond to lower total concentrations. We did not include phosphate concentrations in the nutrient index because of their negative correlations with other nutrients; nor did we include them as a model predictor, given preliminary analyses that showed a negligible relationship with all response variables. Given that nutrient samples were taken at a subset of DIDSON sites, we assembled separate year-wise model sets to assess the effects of (1) nutrient index and environmental variables (subset of sites), and (2) environmental variables (all sites) on fish and foraging pit size and abundance (Table 1).

Before model fitting, we standardized all continuous predictors to mean zero and standard deviation 0.5 (Gelman 2008). This process reduces the variability that predictors introduce on different scales and facilitates comparing how each predictor relatively affects the response variable. We fit global models containing all

Table 1 Summary of nutrient and environmental variables included in models of fish abundance, fish total length, foraging pit abundance, and foraging pit diameter. N is the number of sampling locations included in each model.

Model type	Variable
Nutrient models 2016: N = 21 2017: N = 23	Nutrient index
	Bottom temperature (°C)
	Bottom salinity
	Bottom dissolved oxygen concentration (mg L^{-1})
	Distance from shore (m)
	Eelgrass (*Z. marina*) presence/absence
	Depth (m)
Environmental models 2016: N = 46 2017: N = 49	Bottom temperature (°C)
	Bottom salinity
	Bottom dissolved oxygen concentration (mg L^{-1})
	Distance from shore (m)
	Eelgrass (*Z. marina*) presence/absence
	Depth (m)

predictors of interest using R package *glmmTMB* (Brooks et al. 2017) in R version 4.2.0 (R Core Team 2022). Model selection tables were assembled using the 'dredge' function from the *MuMIn* R package (Bartón 2022) with all models ranked by Akaike's Information Criterion for small sample sizes (AIC_c). To address potential issues arising from multi-collinearity between predictors, we assembled Pearson correlation matrices for each year and type of model (i.e., nutrient models, environmental models) (see supplementary Tables S1 and S2[2]). We used a cutoff value of $|r| > 0.7$ as criteria for mutual exclusion of correlated variables in a candidate model, because collinearity above this threshold is associated with warped parameter estimates and model predictions (Dormann et al. 2013). Only bottom temperature and surface temperature collected during 2016 nutrient sampling exhibited problematic collinearity ($r = 0.93$) (Table S1A). Thus, we specified subset conditions within the *MuMIn*::dredge() function for 2016 nutrient model selection such that bottom temperature and bottom salinity were not mutually included in any candidate model.

We determined the maximum number of predictors allowed in a single candidate model by the 1:10 rule for predictors:samples (Harrell et al. 2001). We used the natural average approach to average models within the top 10 AICc of the best-fitting model, whereby predictor coefficients are averaged across the models in which they appear and scaled according to model weights (Anderson and Burnham 2002; Bolker 2009; Tables S3A–S3D and S4A–S4D). For models in which the predictor was present across the top model set, we calculated the relative variable importance (RVI) of each predictor as the sum of model weights.

RESULTS

Environmental Data

Overall, water temperature and salinity in Richardson Bay were slightly lower during the summer of 2017 than in 2016. Bottom temperature measured at sampled points in 2016 averaged 20.0 ± 2.2 °C (mean ± SD) and salinity averaged 29.6 ± 0.6. In 2017, bottom temperature averaged 19.1 ± 1.0 °C and salinity averaged 27.5 ± 5.3 (Figure 3). These snapshots were corroborated by the continuous temperature and salinity patterns measured by the Richardson Bay sonde for the period June–August in 2016 (average temperature ± SE = 18.70 ± 0.02 °C and salinity ± SE = 31.82 ± 0.02) and 2017 (18.45 ± 0.02 °C and 28.43 ± 0.03) (Figure 1). Spatial patterns in temperature and salinity differed among years, including cooling of northwestern regions of Richardson Bay (>2 °C cooler) and freshening of the northeastern region (salinity decrease of 2-5) (Figure 3). The sonde data also revealed seasonal variation in temperature and a dramatic drop in salinity during the very wet winter between sampling events, when salinity dropped below 10 for 12 days and reached a low of 4.94 in February 2017.

Dissolved oxygen (DO) concentrations were similar for both sampling events, whereas nutrient concentrations were generally higher in 2017 samples than 2016 samples. The mean

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[2] Supplementary material can be found at *https://doi.org/10.25573/serc.27229194*.

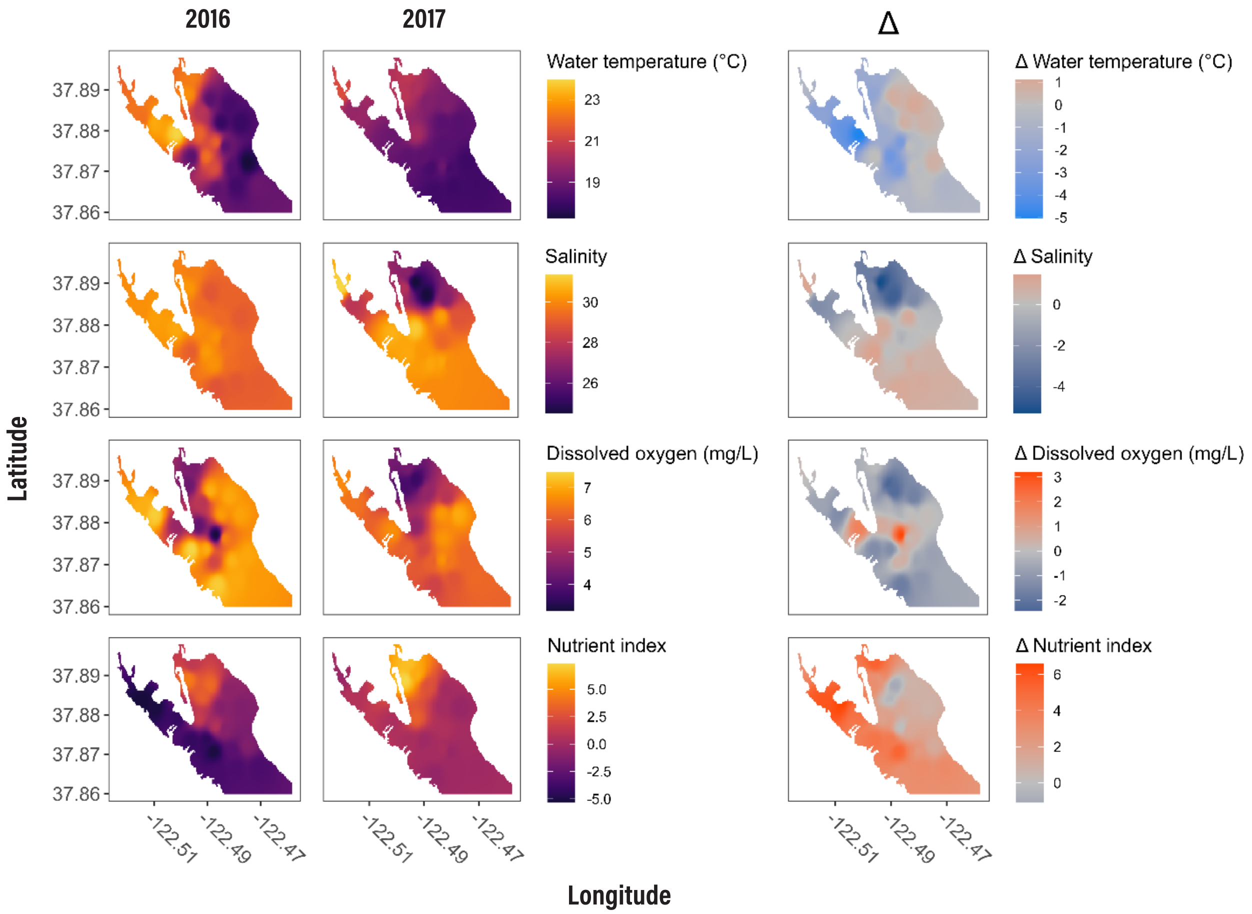

Figure 3 Interpolated distribution maps of bottom water temperature (°C), bottom salinity, bottom dissolved oxygen concentration (mg L^{-1}), and nutrient concentrations [urea, NH_4^+, NO_3^-, and $Si(OH)_4$] as represented by a standardized nutrient index. Inverse distance weighting (IDW) was used to create interpolations from dissolved nutrient samples (25 in 2016; 23 in 2017) and environmental (temperature, salinity, dissolved oxygen) samples (46 in 2016; 49 in 2017). "Δ" indicates the intensity of year–year changes in environmental variables between 2016 and 2017.

bottom DO concentration was 6.1 ± 1.6 mg L^{-1} in 2016 and 5.4 ± 1.6 mg L^{-1} in 2017 (Figure 3). A region of lower DO (<5 mg L^{-1}) occurred in the northeastern region of Richardson Bay in both years, with small differences in the location of the lowest values driving the only substantial spatial differences between the sampled points in time (Figure 3). Concentrations of NH_4^+, NO_3^-, and $Si(OH)_4$ determined from the discrete samples were greater in August 2017, leading to a higher average, across-years nutrient index (NI = 1.66 ± 2.62), compared to the index calculated for June 2016 (NI = –1.52 ± 2.91). Conversely, mean phosphate concentrations in Richardson Bay were greater in 2016 (3.1 ± 0.83 µM) compared with 2017 (2.31 ± 0.19 µM) (Table 2). Chlorophyll-*a* concentrations measured by the Richardson Bay sonde were also higher during the field sampling events in 2017 than in 2016, and they exceeded 40 µg mL^{-1} twice during the winter between the yearly sampling events (Figure S1). Similar to DO, the highest nutrient index values occurred in the northeastern region of Richardson Bay in both snapshots, whereas the nutrient index values were very low in the northwestern region in 2016 but similar to values in other areas of the bay in 2017 (Figure 3).

Mobile Fauna and Habitat Associations

Sonar videos, recorded at 46 sites in Richardson Bay in late June 2016 and 49 sites in early August 2017, revealed the presence of finfish, rays, and sharks, as well as eelgrass and foraging pits.

Table 2 Average dissolved nutrient concentrations (± SD) from surface-water samples collected in 2016 and 2017. Note that sample sizes for nutrient concentrations reflect total nutrient samples collected within Richardson Bay, a subset of which had accompanying DIDSON surveys and were included in models (Table 1).

Nutrient	2016 (N = 25)	2017 (N = 23)
Urea (µg N L^{-1})	2.83 ± 3.16	2.76 ± 2.81
NH_4^+ (µM)	3.5 ± 2.5	7.15 ± 2.16
$NO_3^- + NO_2^-$ (µM)	9.76 ± 4.93	16.23 ± 2.29
$Si(OH)_4$ (µM)	67.18 ± 32.3	89.70 ± 30.03
PO_4^{3-} (µM)	3.09 ± 0.83	2.32 ± 0.19

Across Richardson Bay, fewer finfish >10 cm were observed in 2016 (mean MaxN ± SE = 3.24 ± 0.54) than in 2017 (mean MaxN ± SE = 6.43 ± 1.19). Finfish appeared more abundant in the northwestern region of the bay in the 2016 sampling event, and in the northeastern region in the 2017 sampling event (Figure 4). Finfish total length ranged from 10.2 cm to 128.0 cm in 2016 (median = 17.4 ± 0.22 cm), and 10.0 cm to 70.4 cm in 2017 (median = 19.2 ± 0.34 cm); note that fish <10 cm were not measured because of insufficient resolution of DIDSON images. The total number of rays varied from 28 in 2016 to 68 in 2017, and rays were most common in eastern regions of the bay in both snapshots (Figure 5). Only three sharks were observed in 2016 and one in 2017. Eelgrass was observed in a similar area in each year, with somewhat lower coverage in 2016 than in 2017 (28.3% and 36.7% of sites in each respective year; Figure S2). Foraging pits were present in 91.3% of sites in 2016 and 98.0% in 2017 despite similar numbers of pits between the years (2016 mean MaxN ± SE = 6.76 ± 0.69; 2017 = 5.67 ± 0.62; Figure S3). The maximum diameter of foraging pits varied from 31 cm to 196 cm (mean 110 ± 6 cm) in 2016, and from 35 to 206 cm (mean 97 ± 6 cm) in 2017.

Finfish abundance and size were associated with different water-quality and habitat variables in the two sampling events. In 2016, finfish abundance was negatively associated with nutrient index and positively associated with salinity and temperature (Figure 6A, Table S3A). Fish total length was negatively associated with salinity and temperature (Figure 6B; Table S3B). However, in 2017, these associations disappeared, and finfish abundance was negatively associated with eelgrass presence (Figure 6A; Table S3C), whereas length was positively associated with eelgrass presence (Figure 6B; Table S3D). Neither fish abundance nor mean fish length was correlated with DO concentration.

Foraging pit size and abundance were also associated with environmental and habitat variables. Foraging pit abundance was positively associated with eelgrass presence in 2016, and with nutrient index in both years (Figure 7A; Tables S4A, S4C). In contrast, foraging-pit diameter was negatively associated with water depth in 2016 and positively associated with nutrient index in 2017 (Figure 7B; Table S4B, S4D). In 2017, bottom DO concentration had an inverse correlation with foraging pit abundance (Spearman's rho = –0.56, $p < 0.01$).

DISCUSSION

This study provides baseline surveys of fish distribution and habitat use in 2 years with contrasting rainfall patterns for Richardson Bay, a sub-estuary of the San Francisco Bay for which information on the fish community is limited. It also provides data on spatial and temporal patterns in environmental data and explores associations with the fish community and bioturbation by fish in the form of foraging pits. Overall, bat rays and finfish were distributed relatively evenly throughout Richardson Bay in both surveys, and, as we hypothesized, foraging pit presence was associated with higher nutrient loads in the water, regardless of salinity or depth. Drivers of finfish abundance and total length

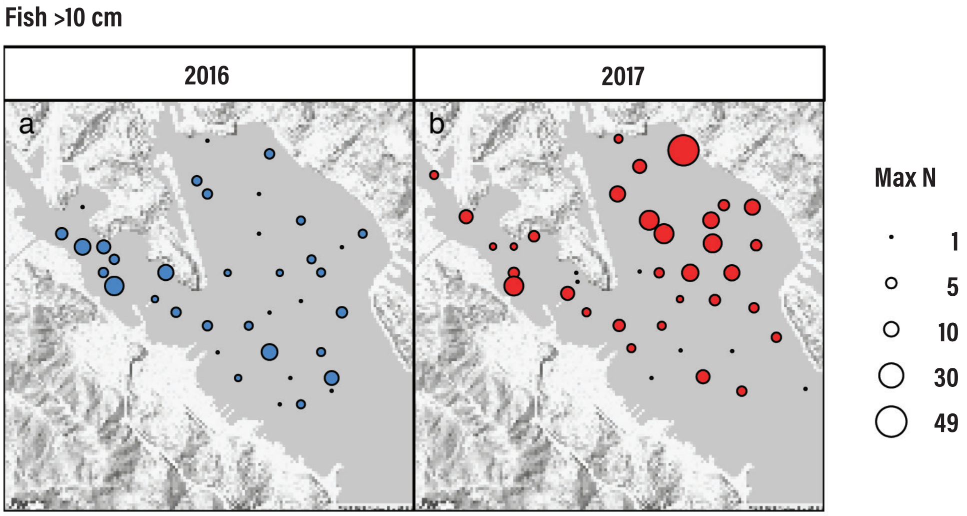

Figure 4 Finfish abundance (MaxN) from stationary DIDSON footage collected in Richardson Bay in June 2016 and August 2017. Only fish >10 cm total length (TL) were included in MaxN counts.

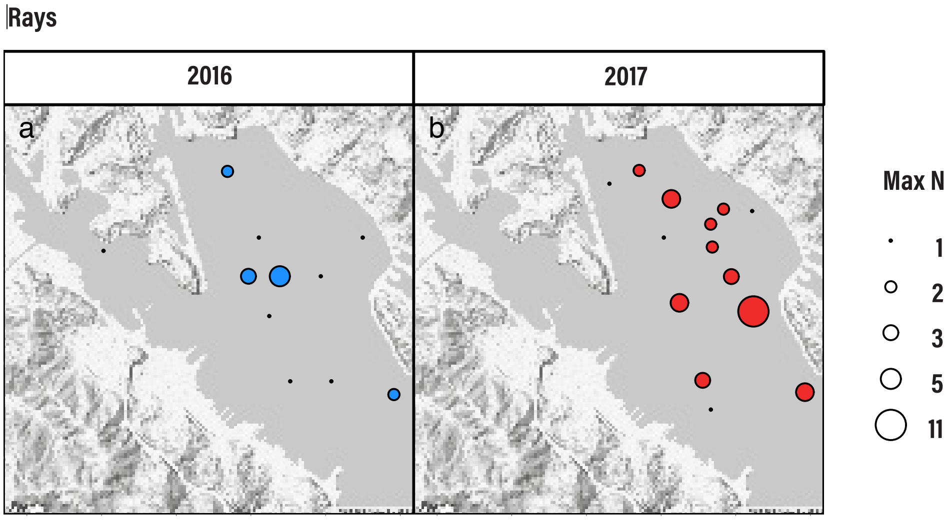

Figure 5 Ray abundance (MaxN) from stationary DIDSON footage collected in Richardson Bay in June 2016 and August 2017

differed between sampling events, such that we did not observe consistent associations with environmental or habitat variables.

Environmental Data

From 2012 to 2016, the San Francisco Bay Area experienced the most extreme drought in recorded history (Lund et al. 2018), with record-high water temperatures and salinities in 2015 (Work et al. 2017). The drought in the region ended abruptly with heavy rainfall over the winter of 2016–2017 (Wang et al. 2017), which in turn led to an extended period of low salinity, increased nutrient concentrations, and lower concentrations of DO (Wang et al. 2017; Work et al. 2017). Thus, the timing of our sampling events unexpectedly occurred near the end of the extended drought in 2016, then during the summer of 2017 following the intense rain.

Continuous monitoring by both the Richardson Bay sonde and our two sampling events captured spatial and temporal patterns in temperature and salinity that indicate several mechanisms which drive complex and dynamic salinity gradients that are commonly observed in estuaries (Cloern et al. 2017). In summer 2016, Richardson Bay was a reverse estuary, with water at the upper end of the estuary both warmer and saltier than at the connection with San Francisco Bay

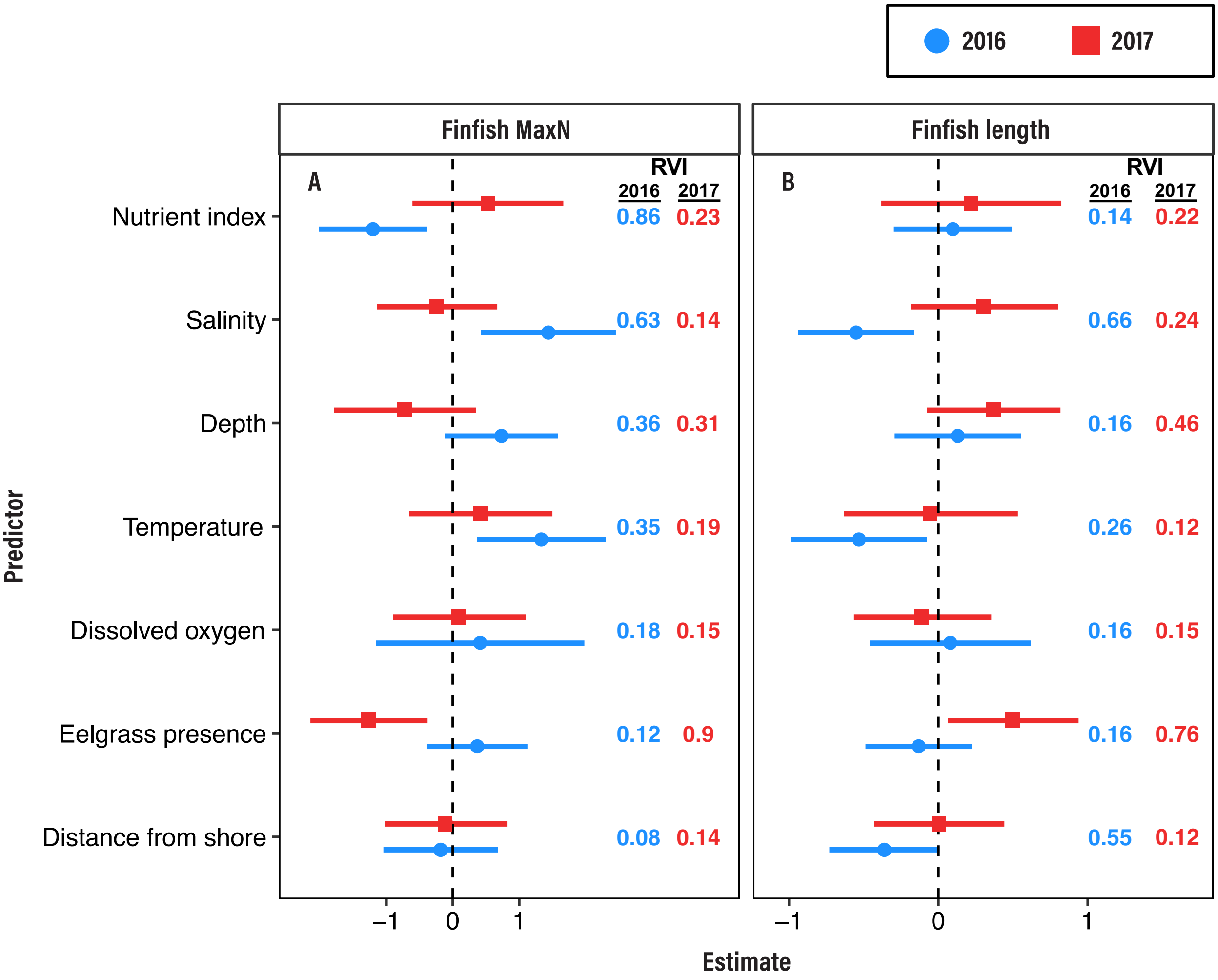

Figure 6 Model-averaged, standardized-regression-coefficient estimates and 95% confidence intervals from models of (**A**) fish abundance (MaxN) and (**B**) mean fish length from stationary DIDSON videos captured in Richardson Bay in 2016 and 2017. Relative variable importance (RVI) is the sum of Akaike weights (W_i) from models in the top model set (ΔAIC_c <10) in which a given predictor was present. Before model fitting, predictors were standardized to mean 0, standard deviation 0.5.

(Figure 3). This result indicates evaporation and potentially long retention times in this area. During the winter of 2016–2017, the extreme precipitation events drove salinity below 10 for a period of 12 days at the Richardson Bay sonde location (Figure 1). Unfortunately, the spatial pattern of salinity during the influx of freshwater was not recorded, so it is not known whether local catchments or San Francisco Bay were the dominant freshwater source during this time. By summer 2017, average salinity was only slightly lower than in 2016. However, there was a notable area of low-salinity water in the northeastern region of Richardson Bay. Because little surface water was then entering Richardson Bay (no stream gage data are available for Richardson Bay, so actual discharge is unknown), the source of the freshwater may have been groundwater. This idea is supported by discharge data from nearby Corte Madera, which was very low during both sampling events, and slightly lower in 2017 than 2016 (USGS 2019) (Figure S4).

The spatial distribution of nutrients was relatively consistent between years, but the total nutrient concentrations were higher during the August

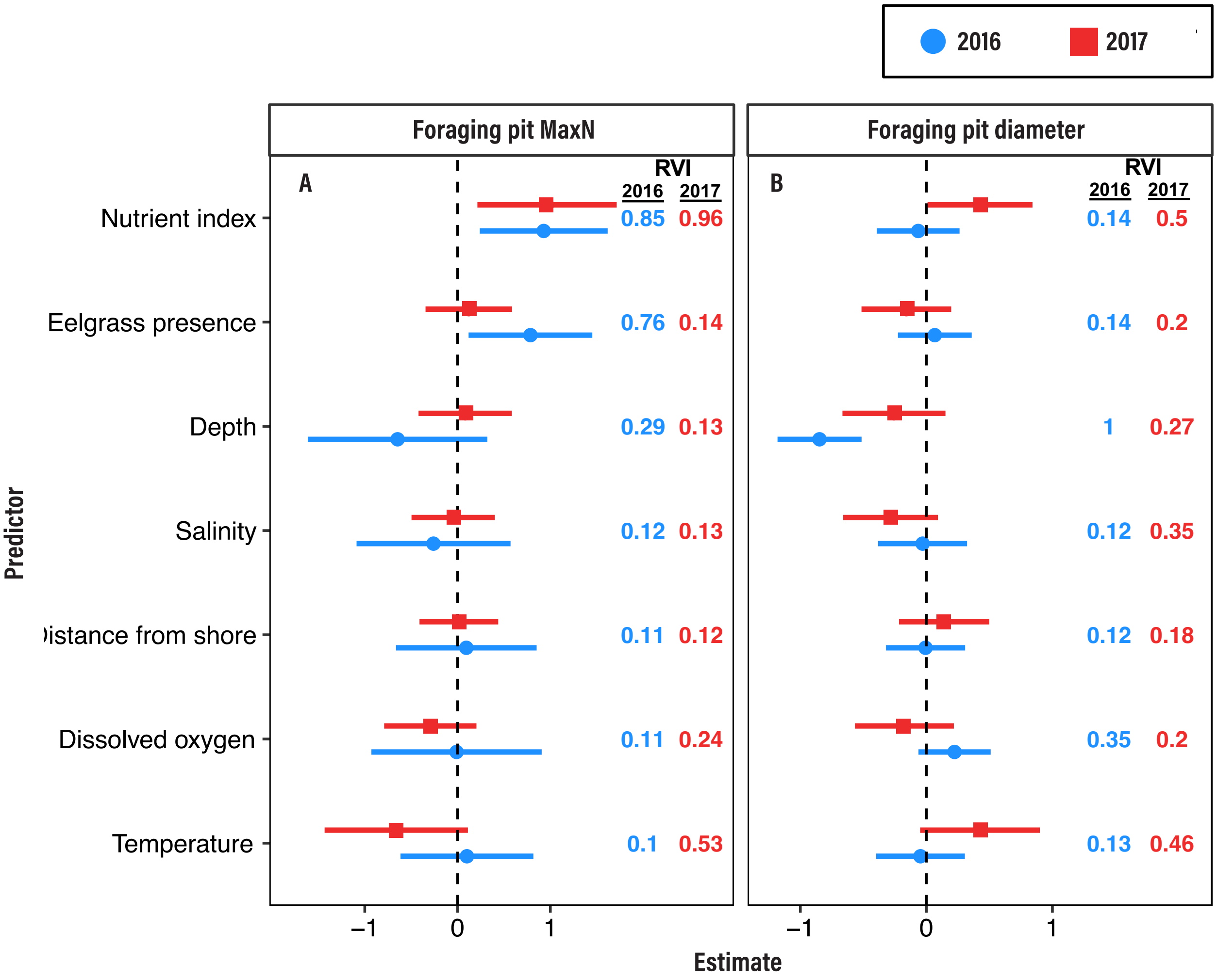

Figure 7 Model-averaged, standardized-regression-coefficient estimates and 95% confidence intervals from models of (**A**) foraging pit abundance (MaxN) and (**B**) foraging pit diameter from stationary DIDSON videos captured in Richardson Bay in 2016 and 2017. Relative variable importance (RVI) is the sum of Akaike weights (W_i) from models in the top model set (ΔAIC_c <10) in which a given predictor was present. Before model fitting, predictors were standardized to mean 0, standard deviation 0.5.

2017 sampling event following the wet winter. Ambient concentrations of urea, NH_4^+, NO_3^-, and $Si(OH)_4$ were all higher in the 2017 samples than in those from 2016, and they were found in especially high levels in the northeastern region of Richardson Bay. The source of nutrients is unclear. The closest wastewater treatment discharge is located in San Francisco Bay west of the mouth of Richardson Bay, and we did not observe high nutrient concentrations in association with this treatment facility during our study. Alternatively, nutrients could have originated from groundwater or stormwater discharging into the northeastern area of Richardson Bay, given the low salinities observed there in the 2017 samples. Further, Richardson Bay is near the northern California coast, where seasonal upwelling increases surface concentrations of NO_3^- and $Si(OH)_4$ each year (Dugdale et al. 2006). There could also be a biological source such as the large number of migratory waterfowl that overwinter in this area of Richardson Bay (Goals Project 2000; Winton et al. 2016), which could contribute to the urea levels observed in this region. In addition, bioturbation from foraging behaviors of Bat Rays and other species (forming the foraging pits assessed in this study) may contribute to re-suspension of sediment and accompanying nutrients into the water column (D'Andrea et al. 2004). Conversely, phosphate was elevated in the northwestern and northeastern areas in 2016 but was lower throughout Richardson Bay in 2017, which likely indicates an alternative or supplemental source of the nutrient. Given these nutrients' considerable effects on primary production and phytoplankton biomass (Cloern et al. 2020), further study is warranted to determine their source and influence on Richardson Bay species.

Fish and Habitat Associations

We observed fish throughout Richardson Bay during both sampling events, with higher overall numbers of fish in 2017. We observed more fish in the northern sections of the Richardson Bay in both years (Figures 3 and 4). However, while we saw more fish in the nutrient-enriched northeastern areas in 2017, abundances in 2016 were concentrated in the northwestern region of lower nutrient levels. This likely explains the negative relationship between finfish abundance and nutrient index seen in 2016, though neither abundance nor length had a significant relationship to this variable in 2017 (Figure 6). Finfish abundance and length were also significantly associated with both salinity and temperature in 2016 but not in 2017, and the direction of these relationships varied between response variables (Figure 6). Although we expected clearer relationships based on previous literature, differences in fish abundance between the two sampling events may have resulted, in part, from shifting faunal assemblages or size distributions over the course of the summer (late June vs. early August), which often happens in estuarine systems as salinity and temperatures change seasonally (Gewant and Bollens 2005, 2012). Lingering higher salinity in summer 2016 from the drought and lower salinity in 2017 following the rain—as well as Richardson Bay's increased nutrient load in 2017—may have also influenced differences in fish abundance and community composition on the two sampled dates. Mobile species with differing environmental preferences and adaptability may opportunistically enter or exit estuaries or alter their movements depending on water-quality parameters (Potter et al. 1983; Kimmerer 2002; Breitburg et al. 2009; Cloern et al. 2017), which could have been the case here. For example, Northern Anchovy in San Francisco Bay have previously been documented tolerating higher salinity ranges than usual when nutrient availability was low (Cloern et al. 2017), while Pacific Herring may utilize the region for annual spawning but suffer high egg mortality rates when water-quality parameters are poor, resulting in lower populations in subsequent years (O'Farrell and Larson 2005).

Finfish metrics were also associated with benthic habitat characteristics in the second round of sampling. In 2017, finfish abundance was negatively associated with eelgrass presence and total length was positively associated with eelgrass presence, suggesting that larger individuals were associated with eelgrass in that year. Although our ability to observe fish using DIDSON was slightly reduced in eelgrass, we do not believe this resulted in the observed relationship because fish >10 cm were readily visible in eelgrass as the boat drifted slightly during recordings. Instead, changes in species composition of the fish community (which weren't possible to assess from imaging sonar data), prey availability, or other factors could have led to the observed differences between years. Evidence of considerably different epifaunal invertebrate communities on the Richardson Bay eelgrass beds in 2016 vs. 2017 may have influenced fish community shifts as well, depending on the dietary preferences of the fish in the area (Ayala 2021). To develop a more complete understanding of drivers of fish-habitat use in Richardson Bay, future studies could consider using methods that complement imaging sonar by providing species-specific information (e.g., occasional fishing surveys to maintain a list of local and seasonal taxa), sampling more regularly to document seasonal and annual variation, and conducting targeted studies to understand the population dynamics, habitat use, and connectivity of unique species.

Bat Rays were commonly observed in northeastern areas of Richardson Bay, and higher numbers were observed in 2017 than in 2016 (Figure 5). They were also common in the southeastern region of the Richardson Bay where they may have been transiting between Richardson Bay and the mainstem of San Francisco Bay. Foraging pits, which were most likely formed by bat rays, were also similar in abundance, size, and distribution throughout Richardson Bay in both years surveyed (Figure S3). Areas of abundant foraging pits had higher nutrient concentrations on both sampling days. Foraging pits were particularly abundant and large in the northeastern region of Richardson Bay in both years, where the highest concentrations of nutrients included in the nutrient index (urea, NH_4^+, NO_3^-, and $Si(OH)_4$) and lowest DO were found (Figures 3 and 7). The co-occurrence of abundant, large foraging pits and rays in the most nutrient-rich area of the Richardson Bay was one of the most obvious patterns observed in this study. This result suggests high benthic productivity of clams, worms, or other infauna that make up their diet (Cross and Curran 2004; Flowers et al. 2021), which warrants further investigation to understand drivers of productivity in Richardson Bay. Ray feeding behaviors displace sediment into the water column both vertically and horizontally (Grant 1983; D'Andrea et al. 2004), which generally increases ambient nutrient levels. It is not known whether the elevated nutrient load in the water column in this area is driven by nutrient inputs to Richardson Bay at the time of sampling, or re-suspension of nutrients from the bioturbation activity of rays and other species that resulted in formation and maintenance of the foraging pits.

While foraging pit abundance was associated with higher nutrient load in both sampling events, as we hypothesized, as well as by higher eelgrass presence in 2016, the only significant predictor variable in determining pit size was water depth in the 2016 data. The lack of clear predictors here may be caused by the challenging nature of defining the extent of a foraging pit, because larger pits may have resulted from multiple foraging efforts and the combination of neighboring pits, while smaller pits may indicate older pits that have partially filled in, lower foraging effort, or smaller foraging animals. Further, foraging pits have relatively short lifespans before surrounding sediment refills the space (Hines et al. 1997), though this time-frame depends upon multiple factors, including substrate composition, wave and current action, and frequency of benthos reworking by aquatic creatures. Despite these challenges, recording putative foraging pit abundance and size offers some evidence of habitat usage and the activity of bioturbating fishes at these two points in time. Indeed, bat rays known to feed in Richardson Bay were observed in the areas that contained foraging pits in this study, suggesting that they were likely one of the primary organisms creating the pits (Thistle 1981; Cross and Curran 2004; O'Shea et al. 2012). To our knowledge, no alternative surveying methods currently exist to detect foraging pits in turbid environments, which is a clear benefit of sonar technology. Moreover, repeated temporal measures of the same sites (e.g., daily-to-weekly frequency) could resolve these challenges and refine quantitative estimates of pit abundance and dynamics.

CONCLUSIONS

This study, although limited in scale, establishes baseline observations of fish distributions, habitat use, and environmental variation that can inform future studies on the dynamic and ecologically important Richardson Bay, a sub-estuary of San Francisco Bay. Increased environmental variability and intensity of rainfall and droughts can alter estuarine communities as species face greater extremes and less predictable conditions, so it is more crucial than ever to develop non-destructive monitoring techniques in ecologically important areas (Swain et al. 2018; Sanford et al. 2019; Colombano et al. 2022). Here, imaging sonar effectively recorded observations of fish presence, abundance, and size in a turbid environment without requiring fish handling or destructive sampling, and it could provide information on fish behavior that was beyond the scope of this study. Although imaging sonar remains a relatively new technique in ecological research, the information gathered from our videos adds to a growing body of literature that demonstrates its value for surveying fish in estuaries, either alone or in combination with other methods. There are distinct advantages, such as the ability to record images in turbid waters, throughout the diel cycle, and in multiple habitats with little or no disturbance to fish, but also drawbacks related to a limited ability to distinguish species, short range at high frequency, and challenges distinguishing fish from benthic habitat (Able et al. 2014; Martignac et al. 2015; Olson et al. 2023; Sibley et al. 2023). This study also reported on spatial variation in environmental conditions and nutrients, revealing patterns that will help identify key inputs and drivers that can inform efforts to manage and improve water quality.

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DATA ACCESSIBILITY STATEMENT

Full supplementary material, including all supplementary tables, may be found at *https://doi.org/10.25573/serc.27229194*

Richardson Bay sonde data is in preparation for public access, and will soon be accessible at *https://doi.org/10.25573/serc.26871091*

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