

MODELING HABITAT COVARIATES FOR ATLANTIC OYSTER DRILLS IN
RICHARDSON BAY, CALIFORNIA

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In

Geography: Resource Management and Environmental Planning

by

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August 2019

CERTIFICATION OF APPROVAL

I certify that I have read *Modeling Habitat Covariates for Atlantic Oyster Drills in Richardson Bay, California* by Jeffrey Gregor Blumenthal, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirement for the degree Master of Arts in Geography: Resource Management and Environmental Planning at San Francisco State University.

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The Atlantic oyster drill *Urosalpinx cinerea* is an introduced muricid whelk in San Francisco Bay that has posed significant challenges to Olympia oyster restoration projects on the United States West Coast. Atlantic oyster drills have a patchy spatial pattern of presence and absence in San Francisco Bay and occur in a range of abundances where they are present. This project incorporated substrate composition, elevation, water temperature, salinity, inundation, and drill abundance data that I collected from summer 2017 to summer 2018 at eight sites in Richardson Bay, an embayment of San Francisco Bay, to model the significance of key abiotic habitat factors. Using generalized linear mixed effects models with logistic and negative binomial distributions, I determined that amount of coarse substrate cover and elevation above mean lower low water are significant environmental factors associated with drill abundance. Consequently, the absence of Atlantic drills from parts of Richardson Bay is not due to a lack of coarse substrate cover at significant elevations. My hope is that these model results will contribute to appropriate site selection of Olympia oyster restoration projects.

I certify that the Abstract is a correct representation of the content of this thesis.

Chair, Thesis Committee

Date

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1. Introduction

1.1 San Francisco Bay management goals and Atlantic oyster drills

Natural resource managers have listed restoration of native biodiversity in San Francisco Bay (SFB) as a long-term habitat management goal (Subtidal Goals Project 2010). That goal includes limiting the negative impact of an introduced muricid whelk (predatory sea snail), the Atlantic oyster drill (*Urosalpinx cinerea*, Atlantic drill) on population recovery projects for native Olympia oysters (*Ostrea lurida*) as part of a living shorelines approach to climate change adaptation. Living shorelines refers to a coastal management strategy that simultaneously supports healthy ecosystems and protects shorelines from erosion and sea level rise (Restore America's Estuaries 2015). In parts of SFB where Atlantic drills are abundant, these whelks have hindered investigations into the possible benefits of Olympia oyster restoration to living shorelines projects (Boyer et al. 2017). In other parts of SFB, however, Atlantic drills are scarce or have never been observed. The reasons for the patchy spatial distribution of Atlantic drill populations in the region are not fully understood, and this knowledge gap has posed a challenge to ecologists hoping to predict the potential impact of Atlantic drills on oyster restoration projects (Wasson et al. 2015). An improved understanding of the environmental drivers of spatial distribution patterns of Atlantic drill populations around SFB could improve restoration site selection and inform efforts to control Atlantic drill populations (Zabin et al. 2010), in support of both oyster restoration and living shorelines projects.

I investigated the possibility that the distribution of Atlantic drills in Richardson Bay can be explained by a combination of their dispersal history and the environmental

variations related to their ecological niche – the biotic and abiotic parameters that define an organism’s potential habitat (Hutchinson 1957). The goal of this project was to analytically characterize the major environmental covariates of Atlantic drill habitat, namely, substrate, elevation, water temperature, salinity, and inundation, by relating drill abundance data to environmental data that I collected over a 12-month period from summer 2017 to summer 2018. My hope is that a better understanding of how these habitat factors relate to drill distribution will help natural resource managers understand the potential impacts of this invasive predator and better mitigate their impact.

1.2 Ecological niche theory

The hypothesis that Atlantic drill abundance is related to habitat parameters is derived from the concept of the ecological niche -- the set of biotic and abiotic conditions that relate the distribution or abundance of an organism or community to its environment (Guisan, Thuiller, and Zimmermann 2017; Hirzel and Le Lay 2008). Ecological niche theory holds that a certain combination of physical habitat factors and living community interactions specific to each species are required for its subsistence (Guisan, Thuiller, and Zimmermann 2017). These conditions are defined by a theoretical multidimensional space defined by abiotic factors and by the *in situ* living environment that it occupies (Hutchinson 1957, Soberon 2007; Hirzel and Lay 2008). This project modeled the importance of several key abiotic components of the Atlantic drill’s ecological niche based on field measurements of drill abundance and physical conditions using an iterative process of biota surveys, environmental monitoring, and statistical modeling.

1.3 Importance of Olympia oysters and Atlantic drills

Natural resource managers have targeted Olympia oysters for restoration due to their role as a foundational species (Grosholz et al. 2007). Oysters support biodiversity and ecosystem functioning by providing habitat and food for other organisms (Kimbrow and Grosholz 2006) and by filtering water (Ermgassen et al. 2013). Additionally, as the only oyster species endemic to the west coast of North America, Olympia oysters are a unique element of the region's natural landscape and cultural heritage and were an important source of food for the region's original human inhabitants (Postel 1988, Ingram 1998, Zu Ermgassen et al. 2012).

Atlantic drills have negatively impacted Olympia oyster restoration projects in California and Washington by feeding on juvenile oysters, which has resulted in oyster populations that are fewer in number and smaller in average size (Boyer et al. 2017, Wasson et al. 2015). Atlantic drills can also harm Olympia oysters indirectly by altering food webs that allow Olympia oysters and native drills to coexist (Kimbrow et al. 2009, Cheng 2014). Anticipating the potential impacts of Atlantic drills, therefore, is an important element in oyster restoration project planning on the West Coast (Wasson et al. 2015, Zabin et al. 2010, Subtidal Goals Project 2010). Although the presence or absence of Atlantic drills at a site is an obvious consideration, population density (abundance) is also important (Wasson et al. 2015). For example, the predation rate of Atlantic drills and survival rate of oysters can vary according to drill abundance, and adult oysters are more

resistant to predation by drills than juvenile oysters. (Buhle and Ruesink 2009, Kimbro et al. 2009, Cheng and Grosholz 2016).

1.4 Natural history of Atlantic drills

1.4.1 Biogeography

The Atlantic oyster drill feeds on oysters, mussels, barnacles, and other encrusted sessile organisms by using a radula (a tongue-like spiked organ) to bore a hole into its prey's shell and consume the soft tissue inside (Puglisi 2008). The native range of Atlantic drills includes portions of the east coast of North America from Florida to Massachusetts (Carriker 1955). Atlantic drills undergo very little natural dispersal over their lifetime (Federighi 1931; Buhle and Ruesink 2009): they lay their egg cases on hard substrate where the egg cases remain attached until juveniles emerge and crawl away as fully-formed individuals that never migrate across broad distances, such as by latitude (Carriker 1955). Nevertheless, Atlantic drills are now found on the west coast of the United States, in southern England, and in parts of the Gulf of Mexico, largely transported by humans via shipments of eastern oyster (*Crassostrea virginica*) seed for aquaculture, as well as in ballast water (Puglisi 2008).

Atlantic drills were accidentally introduced to SFB in the 1870s as stowaways in railroad shipments of eastern oysters from the Atlantic and Gulf coasts destined for San Francisco's burgeoning commercial oyster industry (Barrett 1963). By that time, the natural Olympia oyster population in SFB had largely collapsed, in part due to overharvesting associated with the population boom of the California Gold Rush (Postel

1988). Although local commercial oyster production ceased by the early 20th century, present-day occurrences of Atlantic drills in SFB roughly correspond to areas where eastern oysters were cultivated, in particular south SFB, although some subsequent dispersal has taken place (California Academy of Sciences 2017, Barrett 1963, Fig. 1). As a result, Atlantic drills are unevenly distributed in SFB, both in terms of presence and absence as well as the relative abundance of drills at geographically separated populations (Boyer et al. 2017, Wasson et al. 2015). Whether Atlantic drill range expansion in SFB has been more limited by dispersal history or habitat suitability has not been closely studied, although ecological niche theory suggests that both play a role, and ecologists have expressed the need to identify the factors that influence Atlantic drill abundance (Subtidal Goals Project 2010).

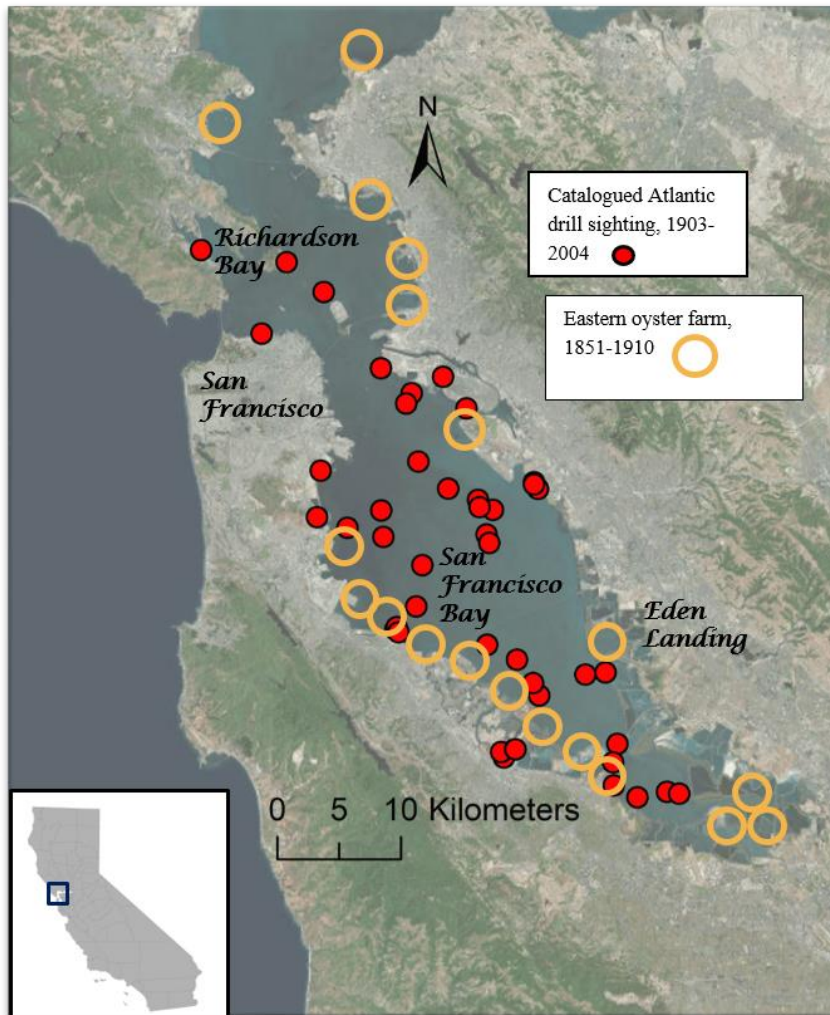


Figure 1: Presence of Atlantic drills in San Francisco Bay (California Academy of Sciences 2017) and former locations of eastern oyster farms (Barrett 1963). Locations of Atlantic drills and oyster farms frequently overlap.

Although recent research has improved our understanding of the functional role of Atlantic drill invasions in California and Washington (e.g. Cheng 2014), questions remain about their population dynamics within invaded areas. For example, at small spatial scales (e.g. distances of 1-2 km between sites), why are drills relatively abundant in some areas but relatively scarce in others? There is speculation that the spatial

variation in Atlantic drill abundance corresponds to geographical gradients in environmental niche factors (C. Zabin, personal communication, 22 May 2017), and there is a need to investigate associations between abundance and environmental factors (Zabin et al. 2010, Subtidal Goals Project 2010).

1.4.2 Atlantic drill habitat factors

Experimental and observational studies have indicated that elevation, water temperature, salinity, inundation, and substrate composition are important environmental niche factors in the Atlantic drill lifecycle, although interactions among these factors are likely more important to drill populations than any individual variable (Carriker 1955). Atlantic drills are highly adaptable to their environment (Carriker 1955; Cheng, Komoroske, and Grosholz 2017), as evidenced by their distribution across a broad latitudinal range spanning widely varying conditions (Cheng 2014). Many field studies simply note ambient salinity and water temperature conditions without evaluating the suitability of these conditions (e.g. Franz 1971). Moreover, some laboratory experiments on populations from varying locations have elicited slightly different responses to environmental change (e.g. Federighi 1931; Manzi 1970; Franz 1971; Zachary and Haven 1973; Cheng, Komoroske, and Grosholz 2017), while others have found remarkable consistency across native and introduced ranges (Blum 2012) making it difficult to predict the response of Atlantic drill populations from Richardson Bay to habitat variations *in situ*. Nevertheless, there is enough commonality among study results to

establish a frame of reference for key Atlantic drill environmental niche factors. A summary of drill responses to water temperature and salinity is given in Table 1.

Controlled laboratory studies have identified favorable water temperatures for survival, feeding, and reproduction in both East Coast Atlantic drill populations (e.g. Federighi 1931, Ganaros 1958, Manzi 1970) and West Coast populations (e.g. Lord 2014; Cheng, Komoroske, and Grosholz 2017). These studies generally agree on 15-25°C as a comfortable zone for Atlantic drill feeding and reproduction. At water temperatures over 20°C, drill reproduction and feeding increase as water temperature increases (Ganaros 1958; Lord 2014). Cheng, Komoroske, and Grosholz (2017) measured optimal growth performance at around 26.5°C, above which growth performance declined until a death point of 37.6°C. Conversely, when the water temperature drops below 10°C, Atlantic drill activity slows or ceases (Federighi 1931, Carriker 1955, Lord 2014).

Atlantic drill response to salinity variation in laboratory experiments is similar to their response to water temperature variation: drills are more active in terms of feeding and reproduction at higher salinities, and a decline in salinity leads to a corresponding decline in activity (Manzi 1970) and, at a certain low level, to death, although specific salinity thresholds for Atlantic drills vary from different geographies. Historical records of Atlantic drills in Chesapeake Bay indicated a preferred salinity of greater than 15 ppt and a minimum salinity of 9-12 ppt (Harding and Mann 2016). In laboratory experiments, Federighi (1931) observed a salinity death point of 12.5 ppt in Atlantic drill populations from Hampton Roads, NC. In the same study, Atlantic drills from Beaufort, NC, where

Table 1: Summary of temperature and salinity limits for Atlantic oyster drills.

<i>Environmental covariate</i>	<i>Death point</i>	<i>Lower limit of normal activity</i>	<i>Comfortable zone for feeding and reproduction</i>	<i>Optimum for growth performance</i>	<i>Critical threshold</i>	<i>Population origin</i>	<i>Notes</i>	<i>Source</i>
Temperature (°C)				26.5	37.6	Tomales Bay, CA	Critical threshold defined as 50% probability of mortality	1.
Temperature (°C)		10	15-25			East Coast, USA		2., 3., 4.
Temperature (°C)			15-25			West Coast, USA		1., 2., 4.
Salinity (ppt)		9-12	>15			Chesapeake Bay, MD		5.
Salinity (ppt)	12.5					Hampton Roads, NC		2.
Salinity (ppt)	15.6					Beaufort, NC		2.
Salinity (psu)	7.5					Tomales Bay, CA	Death point defined as 50% mortality over 4 days	1.
Salinity (ppt)	9.2					James River, VA	52% mortality over 5 days	6.

1. Cheng, Komoroske, and Grosholz (2017)

2. Federighi (1931)

3. Carriker (1955)

4. Lord (2014)

5. Harding and Mann (2016)

6. Zachary and Haven (1973)

summer salinity averages >30 ppt, exhibited a salinity death point of 15.6 ppt, suggesting that Atlantic drills salinity tolerances vary according to their environment.

Manzi (1970) experimentally tested the combined effects of water temperature and salinity on activity and survival of Atlantic drills from Long Island Sound near Norwalk, CT, where the average summer water temperature was 22.2°C, and the average summer salinity was 27 ppt. At various water temperature and salinity combinations between 15-25°C and 12.5-26.5 ppt, these drills were more active at higher water temperature-salinity combinations. Mortality, however, was highest at high water temperatures and low salinity and was lowest at low water temperatures and high salinity. Testing Atlantic drills from Tomales Bay, CA, Cheng, Kormoroske, and Grosholz (2017) experimentally observed low-salinity mortality starting at 12 psu and determined a critical minimum salinity of 7.5 psu over four days of exposure. This 50 percent mortality point is close to the 9.2 ppt critical minimum salinity over five days observed by Zachary and Haven (1973) in Atlantic drills from James River, VA, although mortality among that population was observed in a small percent of animals over a 20-30 day period at salinity values of approximately 13-15 ppt.

Atlantic drills require habitat with enough sizeable hard substrate to support their sessile prey and to provide attachment surfaces for drill egg cases (Puglisi 2008). In Richardson Bay, hard substrate refers to cobble and boulder, both natural and remnants of old seawalls or other structures. Atlantic drills are rarely found in open mud flats, which are prevalent near the lower low water mark in Richardson Bay, although drills will

venture into open mud to feed on prey on isolated islands of hard substrate (personal observations, Buhle and Ruesink 2009).

In terms of elevation, Atlantic drills are typically observed low in the intertidal zone, near the lower low water mark. Boyer et al (2017) found that Atlantic drill predation on juvenile oysters was highest at elevations close to mean lower low water (MLLW). In response, the spatial distribution of oysters shifted to higher elevations where drill abundance was lower but where conditions are less favorable for both oysters and drills due to desiccation and heat stress. Previous studies have shown that if hard substrate is present, Atlantic drill abundance is greater at elevations near MLLW than at higher elevations near the upper edge of the rocky intertidal zone (Boyer et al. 2017, Wasson et al. 2015).

Although there are multiple interpretations of the role of inundation (periods of high tide when habitat is submerged) on drill activity, it is a relevant environmental factor that facilitates their feeding process (Person et al. 1967, Carriker 1957). Submersion in water is a requirement for both prey chemoreception as well as for drilling. Thus, more time spent under water could positively affect drills' ability to feed and, therefore, their abundance.

1.5 Research goal and study questions

The goal of this research was to model the relationship between Atlantic drill abundance and key habitat covariates by comparing the presence and absence of drills and their abundance at 10 sites to variations in abiotic environmental conditions between

those sites. Specifically, I investigated the following question: Is there a significant relationship between Atlantic drill abundance and fine-scale differences in abiotic habitat characteristics in Richardson Bay? I anticipated that Atlantic drills would be more abundant at sites that have greater availability of hard substrate at relatively low elevations, experience higher average water temperatures and fewer extreme or sub-optimal water temperature events (below 10 °C and above 26.5°C), and experience higher average salinities and fewer low salinity (<10 ppt) periods.

2. Methods

To answer my study question, I employed an iterative process of data collection, statistical exploration and analysis, and model building. I sampled drill abundance and environmental conditions along the shoreline of Richardson Bay, CA between the towns of Sausalito and Tiburon (Fig. 2) from June 2017 to July 2018. After exploring statistical relationships among the resulting data, I fit and compared multiple models that expressed Atlantic drill abundance as a function of abiotic habitat covariates.

2.1 Study area

The study area was a 16-km discontinuous band of intertidal shoreline in Richardson Bay, an approximately 4 km² sub-embayment along the western edge of SFB, approximately 10 km north of the Golden Gate (Fig. 2). In Richardson Bay, Atlantic drills inhabit the rocky intertidal zone, a narrow band of shoreline about 1-3 m wide and vertically situated between the mean lower low water (MLLW) mark and about one meter above MLLW, referenced to tide predictions for Sausalito, CA. I surveyed for Olympia oyster and Atlantic drill abundance and monitored environmental conditions at 10 sites in Richardson Bay. These 10 sites were intended to represent the range of the area's biological and environmental diversity. At two of those sites (Aramburu Treatment and Lani's Beach), an Atlantic drill removal experiment was ongoing; therefore, data from those two sites were excluded from statistical analysis, but have been included in charts of my results.

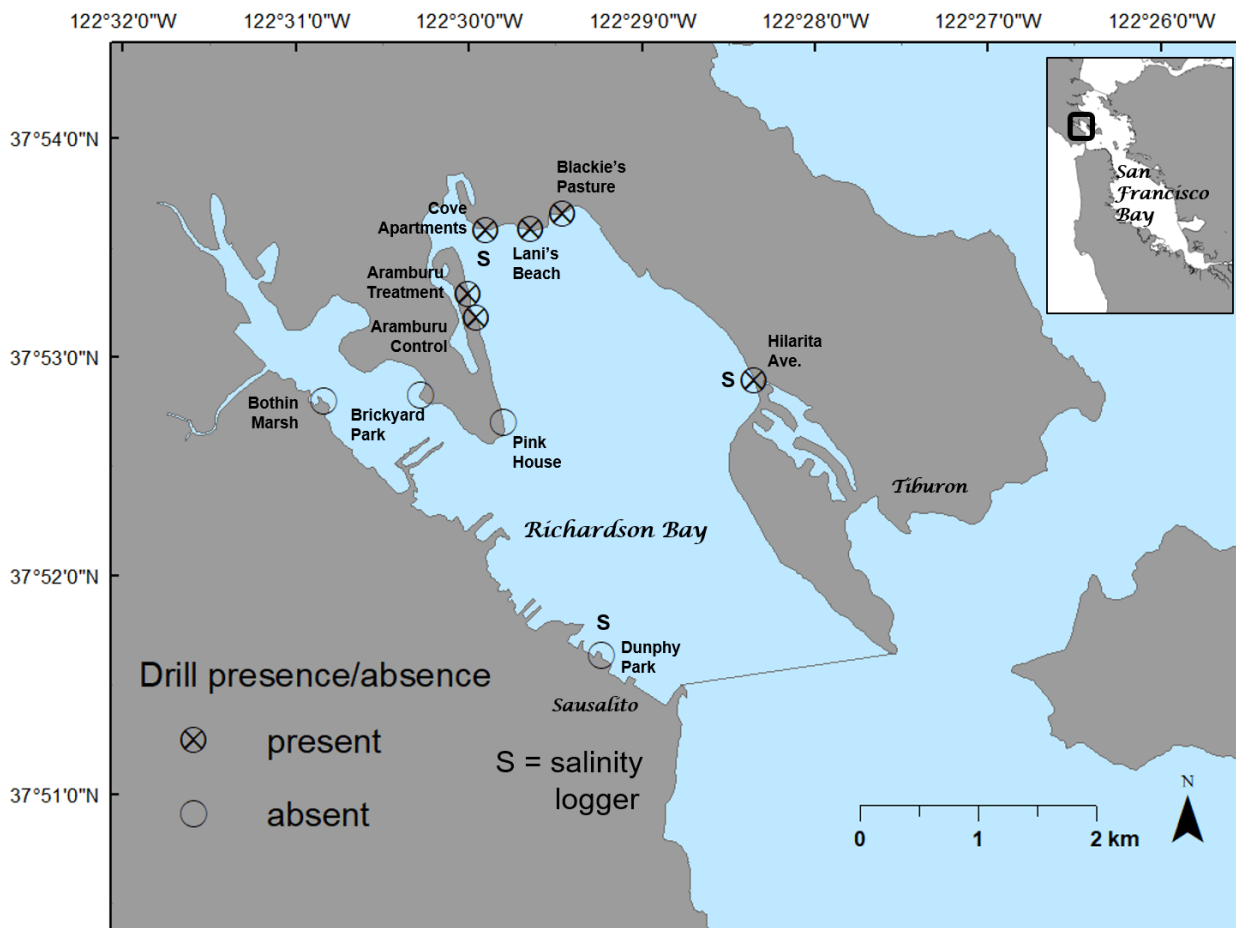


Figure 2: Study area. Map indicates the location of the 10 study sites in Richardson Bay, a sub-embayment of San Francisco Bay, CA (inset). Atlantic oyster drills are present in the north and east sides of Richardson Bay at varying levels of abundance, but they are absent in the south and west sides. Aramburu Control and Aramburu Treatment are located on Aramburu Island.

Richardson Bay is of particular interest with respect to *Olympia* oysters and Atlantic drills because there appears to be a biogeographic gradient along the shoreline: in the northeast half of Richardson Bay, Atlantic drills are present, but oysters are absent, whereas in the southwest half of Richardson Bay, oysters are present, but drills are absent (Fig. 2). At one site roughly in the middle, Aramburu Island, both drills and oysters have been observed. In the area where drills are present, they are found at a range of densities,

from relatively scarce (e.g. < 5 drills per square meter) to relatively abundant (> 50 drills per square meter). I hypothesized, therefore, that there might be an environmental gradient of habitat conditions corresponding to this biogeographic gradient. It is possible that drills are absent from half of Richardson Bay because they were only introduced through oyster farming or other cause along the northeastern edge of Richardson Bay and never migrated to the southwestern half. Records of oyster farming in SFB do not clearly indicate the exact location in Richardson Bay or variety of outplanted oysters that may have introduced Atlantic drills to Richardson Bay (Townsend 1893; Barrett 1963), leaving the reasons for the patchy distribution of Atlantic drills in Richardson Bay in question.

2.2 Data collection

In addition to drill abundance, I measured five environmental factors that are important to the life history of Atlantic drills as well as practicable for data collection within the logistical constraints of the project: elevation, substrate, water temperature, inundation, and salinity. Data were collected at three tidal elevations: 15 cm (0.5 ft), 46 cm (1.5 ft), and 76 cm (2.5 ft) above MLLW (hereafter, +15 cm, +46 cm, and +76 cm). These elevations correspond to lower, middle, and upper elevations within the intertidal zone of available habitat throughout most of Richardson Bay.

Drill abundance surveys were conducted quarterly at each site: summer (June 1 through August 31) 2017, fall (September 1 through November 30) 2017, winter (December 1 - February 28) 2017-18, and summer 2018. Surveys were conducted at each

of the three elevations (+15 cm, +46 cm, and +76 cm) where rocky substrate was present. I sampled drill abundance by placing a 0.5 x 0.5 m PVC quadrat at five randomly chosen points along each side of a 30-m shore-parallel transect, resulting in ten quadrat samples per transect. The quadrat was searched exhaustively for Atlantic drills, Atlantic drill egg cases, and Atlantic drill prey (oysters, mussels, and barnacles). Based on opportunistic sample observations that found no drills in the broad mud flats, which lack rocky substrate, that characterized some sites at +15 cm and +46 cm, I assumed that drill abundance in those places was zero.

Tidal elevation was estimated using tide level predictions for Sausalito, CA from the National Oceanographic and Atmospheric Administration (www.tidesandcurrents.noaa.gov) and Tide Graph for Android mobile device application (Brainware, Long Beach, CA). At each study site, a stake was deployed at the water's edge at the time that the tidal elevation was predicted to be +15 cm, +46 cm, and +76 cm. These stakes were left in place and used as transect start and end points for repeated visits to each site.

Substrate composition was measured using a modified Wentworth scale that recognized five grain size classes: boulder (≥ 250 mm), cobble (≥ 65 mm and < 250 mm), pebble (≥ 2.5 mm and < 65 mm), sand (< 2.5 mm), or mud (saturated clay or clay-dominant mixture) (Bunte and Abt 2001). I used a 0.5 x 0.5 m PVC quadrat threaded with twine to make a 5 x 5 grid with 36 intersecting points and recorded substrate composition along each transect using the point-intercept method. The quadrat was placed ten times at three-meter intervals on alternating sides of the transect, and the point

on the beach immediately beneath each intersection in the 5 x 5 grid was classified as boulder, cobble, pebble, sand, or mud. I represented coarse substrate cover as the average amount of cobble or boulder per quadrat, as measured by *psi* (Ψ), the product of the sum of the number of points of boulder or cobble per quadrat and a multiplier, the base-two log of the average grain size of the boulder and cobble grain size classes, respectively (Bunte and Abt 2001). The grain size multiplier accounts for the three-dimensional aspect of usable rocky surface per quadrat.

HOBO UA-002-64 Pendant Temperature/Light loggers (Onset Computer Corp., Bourne, MA) were deployed at each site on metal or PVC stakes at +15 cm, +46 cm, and +76 cm from June 2017 until July 2018. These loggers recorded ambient air and water temperature at 15-minute intervals. Air and water temperatures were later separated using water level data from NOAA Tides and Currents (www.tidesandcurrents.noaa.gov). I summarized water temperature differences by comparing seasonal water temperature averages as well as the percent of water temperature measurements above the biologically significant thresholds of 26.5°C and 37.6°C and below 10°C (Table 1).

Inundation was defined as the amount of time any given elevation at a study site was submerged by the tide. Inundation was measured at each site from July 2017 until December 2017 using a HOBO U20-001-01 (Onset Computer Corp., Bourne, MA) water level logger deployed at +15 cm taking absolute pressure readings at 15-minute intervals. Inundation was calculated using HOBOWare Pro 3.7 software, which converts absolute pressure readings to water depth factoring for atmospheric pressure data, which was downloaded from NOAA Tides & Currents.

Salinity was measured at three sites (Dunphy Park, Cove Apartments, and Hilarita Ave., Fig. 2) from December 2017 until May 2018 using Odyssey conductivity and temperature loggers (Dataflow Systems Ltd, Christchurch, NZ) deployed at +15 cm. The deployment sites were chosen as most likely to represent a potential salinity gradient within Richardson Bay based on their position at the upstream (Hilarita Ave.) and downstream (Dunphy Park) ends of the mouth of Richardson Bay and the inner edge (Cove Apartments) of Richardson Bay. Conductivity was converted from specific conductance (SC, mS/cm) to practical salinity units (psu) using the following formula (Wagner et al. 2006):

$$psu = 0.012 + (-0.2174 * (SC/53.087)^{0.5}) + (25.3283 * (SC/53.087)) + (13.7714 * (SC / 53.087)^{1.5}) + (-6.4788 * (SC / 53.087)^2) + (2.5842 * (SC / 53.087)^{2.5})$$

Finally, in the resulting environmental datasets, I assumed that some temperature and water level data could be shared between Cove Apartments and Lani's Beach and between the two Aramburu sites in order to fill in gaps due to logger failure in the temperature and water level time series data.

2.3 Habitat covariate modeling

I took a correlative modeling approach to approximating fine-scale difference in Atlantic drill habitat suitability. This approach stands in contrast to a mechanistic approach by excluding physiological process measurements (e.g. energy expenditure) and focusing only on statistical relationships (parameter estimation) between the target species and its environment (Kearney 2006; Dormann et al. 2012). The correlative

approach can be useful when the target species has not been widely studied, or, in the case of Atlantic drills, has not been widely studied *in situ* (Kearney and Porter 2009).

I visually checked for collinearity among independent variables by plotting related environmental factors: water temperature and elevation, temperature and salinity, and substrate and elevation. No significant co-linearity was evident. Next, I plotted univariate relationships of drill abundance and the individual environmental factors and checked for simple linear relationships.

I used two types of generalized linear mixed effects model (GLMM) to compare environmental data to drill abundance data: GLMM with a binomial distribution (i.e. logistic regression) to model the overall presence and absence of drills between sites; and GLMM with a negative binomial distribution to compare variations in drill abundance at sites where drills were present. GLMMs account for both fixed and random effects on the response variable and are suitable for analyzing data, like those in this study, that contain repeated measurements over time and exhibit spatial correlation (Bolker et al. 2009, Zuur et al. 2009). Models were developed in R (version 3.6.1: R Core Team 2019) using the `glmmTMB` package (Brooks et al. 2017). I used a manual backwards stepwise model-selection approach that sequentially excluded variables from a baseline model that included all possible fixed effects and compared outcomes using the Akaike information criterion (AIC). The best-fitting model was defined as the one with the lowest the AIC (Zuur et al. 2009). Any model that resulted in a convergence problem warning was eliminated (Brooks et al. 2019).

For logistic regressions, I characterized sites by the presence or absence of drills based on whether drills were ever observed there during any survey, regardless of elevation or season. Fixed effects included a site-level average of coarse substrate across all elevations and overall averages of water temperature, inundation, and salinity. Site was a random effect in logistic regressions.

Negative binomial GLMM variations used quarterly drill abundance survey results and the temporally corresponding seasonal averages of water temperature, salinity, and inundation, as well as elevation and each elevation's associated coarse substrate observation as fixed effects. Site and season were random effects in these models. Only models using elevation, coarse substrate, and temperature as fixed effects could temporally incorporate all drill surveys, from summer 2017 – summer 2018, so I considered this model the baseline. Because of the heterogenous temporal and spatial range of the inundation and salinity datasets, I generated separate sets of models for these two factors. Because of these differing parameters, I did not consider the resulting AICs to be comparable to the baseline model AIC. Negative binomial GLMMs were iterated with and without a zero-inflation term to account for multiple possible sources of zero counts (e.g. zeroes resulting from the absence of drills as well as zeroes resulting from instances where drills were present but were not observed). I also modeled interactions between fixed effects and nesting within random effects.

3. Results

3.1 Atlantic drill abundance survey results

As in the pre-study exploratory surveys, no drills were found at the sites along the southwestern portion of the Richardson Bay shoreline (from Dunphy Park to Pink House). Drills were still present at the rest of the sites along the northeastern portion of the study area (from Aramburu Control to Hilarita Ave). Drill abundance was highest at Cove Apartments, $12.92 \pm \text{SE}$ drills per quadrat on average, well above the drill abundance at all other sites, which ranged from $0.82 \pm \text{SE}$ drills per quadrat at Blackie's Pasture to $3.04 \pm \text{SE}$ drills per quadrat at the Aramburu Control site (Fig. 3).

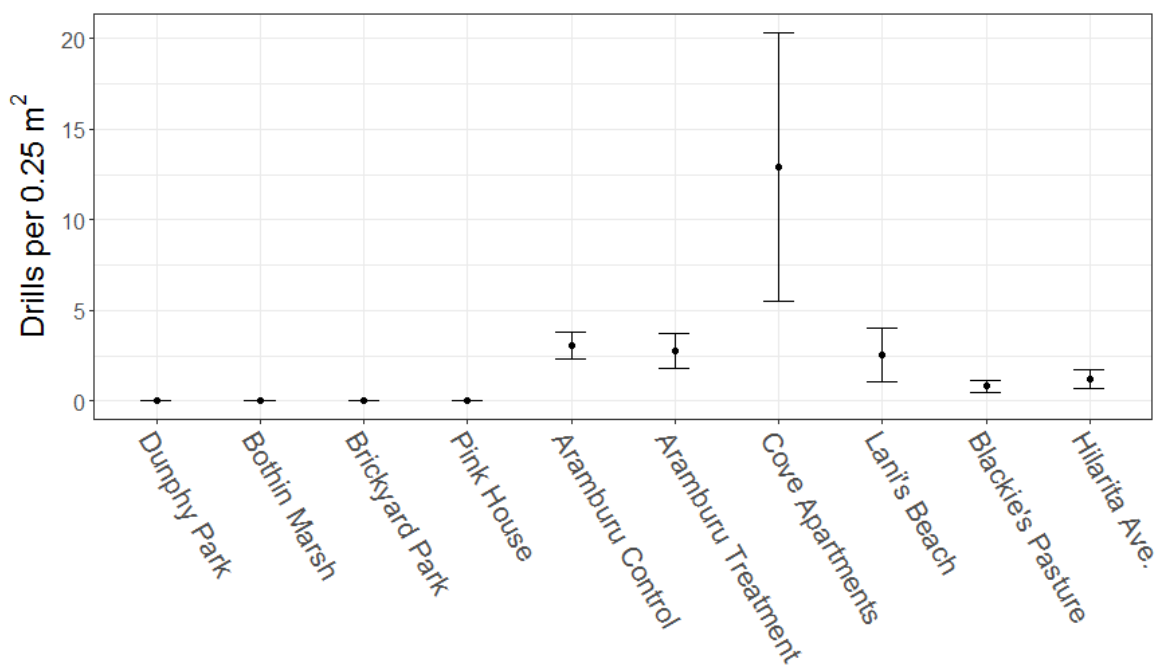


Figure 3: Atlantic oyster drill abundance per 0.25 m^2 at all 10 study sites in Richardson Bay, CA, surveyed quarterly from summer 2017 to summer 2018. Each point represents the average of all seasonal survey per-quadrat averages at all elevations. Error bars are standard error. The order of the sites from left to right corresponds to clockwise around Richardson Bay from southwest, Aramburu Island, to northeast, Hilarita Ave.

The dramatic difference between drill abundance at Cove Apartments and the other sites was driven by an extreme outlier, the fall 2017 survey at +46 cm in which I observed over 300 drills in one quadrat at the middle elevation and seven of the nine highest drill counts per quadrat of the entire project (Fig. 4). Differences in drill abundance where drills were present were significant, except for at Blackie's Pasture and Aramburu Treatment, a drill removal site (Table 2).

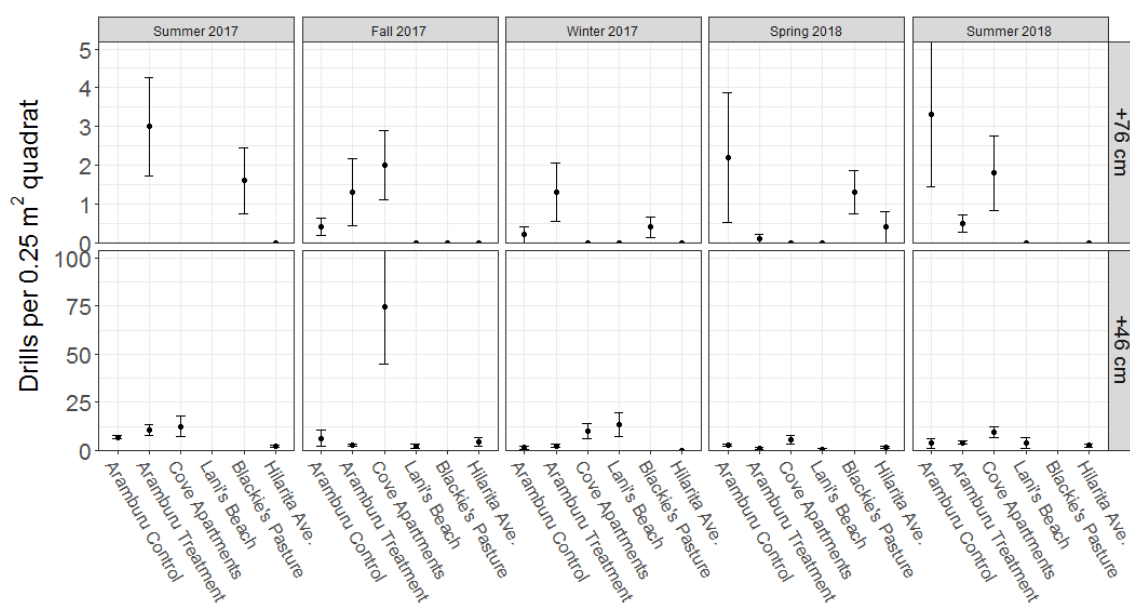


Figure 4: Atlantic oyster drill abundance by season and elevation above mean lower low water at the six sites in Richardson Bay, CA where Atlantic drills were present. Surveys were not conducted at the lowest elevation, +15 cm, where coarse substrate was not present. Y-axes are different scales. Missing data points indicate that surveys were not conducted because the site became inundated by the rising tide. The order of the sites from left to right corresponds to clockwise around Richardson Bay from southwest, Aramburu Island, to northeast, Hilarita Ave.

Table 2: GLMM results of differences in drill abundance between sites. Statistics are relative to Aramburu Control.

<i>Effect</i>	<i>Site</i>	<i>Estimate</i>	<i>Standard error</i>	<i>Z-statistic</i>	<i>P-value</i>
fixed	Aramburu Treatment	-0.3	0.3	-0.99	0.32
fixed	Cove Apartments	0.61	0.31	1.96	0.05
fixed	Lani's Beach	-0.82	0.34	-2.45	0.01
fixed	Blackie's Pasture	0.22	0.38	0.58	0.56
fixed	Hilarita Ave.	-1.67	0.34	-4.97	<0.001
random	season	0.28	NA	NA	NA
random	elevation	1.12	NA	NA	NA

Over 70 percent of drill counts per quadrat in the project were zero; quadrats containing drills were the exception regardless of site, season, or location. This pattern of drill count results followed a zero-inflated, negative binomial distribution (Fig. 5).

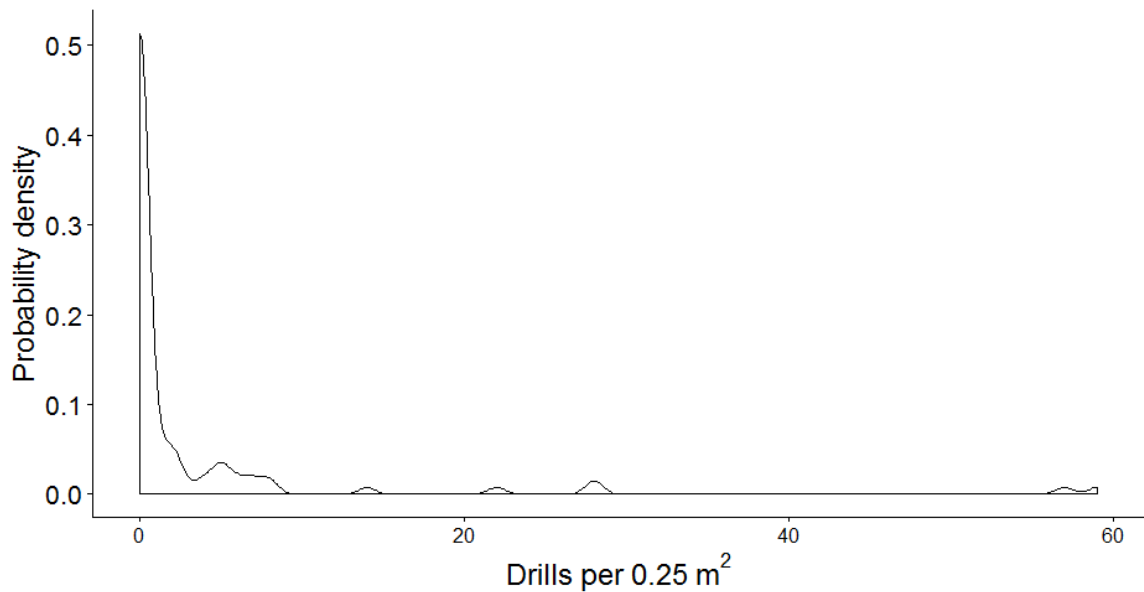


Figure 5: Probability density plot of drill abundance survey results. Sample size = 100. Area fits a zero-inflated negative binomial distribution.

3.2 Environmental covariate results

The presence of hard substrate indicated potential drill habitat and dictated at which elevations we conducted surveys (Table 3). The only sites at which hard substrate was present at +15 cm were along the southwestern shore of Richardson Bay where drills were not present: Dunphy Park, Brickyard Park, and Pink House. At all other sites, +15 cm consisted entirely of deep mud (Fig. 6). Bothin Marsh and Blackie's Pasture were the only sites at which hard substrate was only present at one elevation (+76 cm) with only deep mud at the other elevations.

Table 3: Elevations where surveys were conducted, by site. Surveys were conducted where hard substrate was present.

<i>Site</i>	<i>Elevation where surveys were conducted (X)</i>		
	+15 cm	+46 cm	+76 cm
Dunphy Park	X	X	X
Bothin Marsh			X
Brickyard Park	X	X	X
Pink House	X	X	X
Aramburu Control		X	X
Aramburu Treatment		X	X
Cove Apartments		X	X
Lani's Beach		X	X
Blackies Pasture			X
Hilarita Ave.		X	X

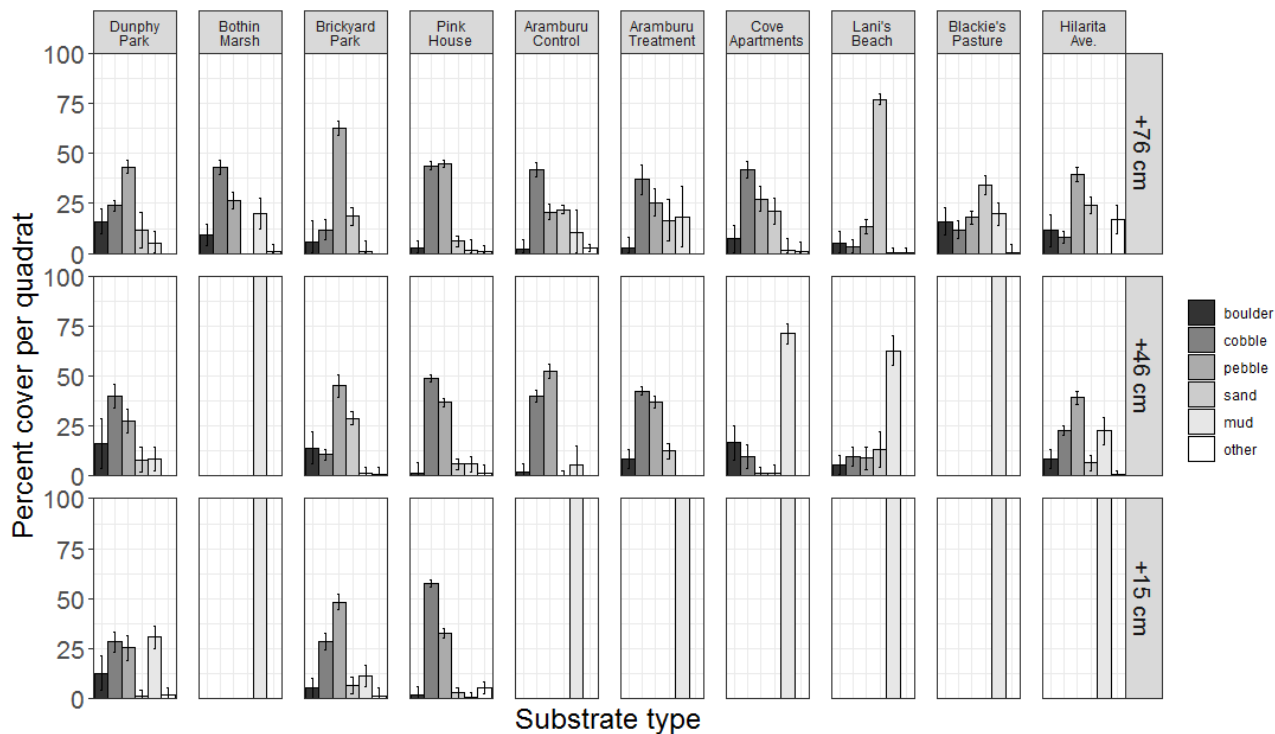


Figure 6: Substrate profile of each study site in Richardson Bay, CA, by elevation. The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.).

A generalized view of the substrate data that aggregates fine substrate material (mud, sand, and pebble) and coarse substrate material (cobble and boulder) revealed that in most cases fine material was more abundant than coarse material at all sites and elevations (Fig. 7).

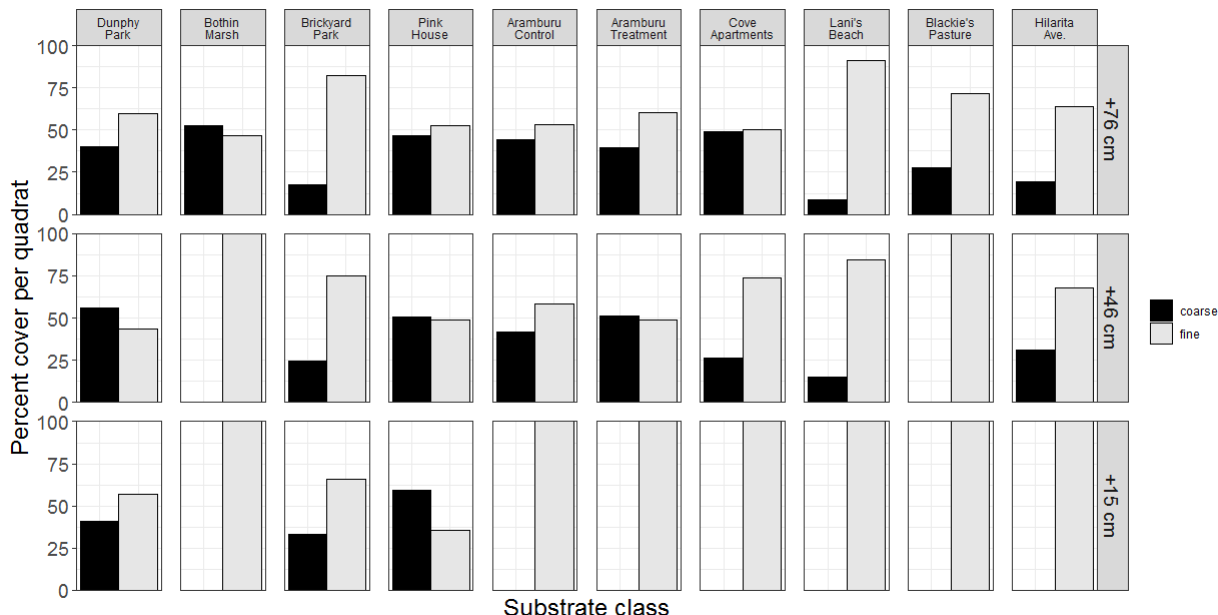


Figure 7: Generalized substrate profile of each study site in Richardson Bay, CA, by elevation. Grain size data has been categorized as coarse (boulder or cobble) or fine (pebble, sand, or mud). The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.).

Water temperature data were inspected for spatial and temporal patterns between sites, across seasons, and across the three study elevations. The average water temperature between sites ranged from a low of 11.5°C at Bothin Marsh during the 2017-2018 winter and a high of 22.0°C at Cove Apartments during the summer of 2018. During spring and summer, sites were increasingly warmer on average as distance from the edges of Richardson Bay (Dunphy Park and Hilarita Ave.) increased towards the back of Richardson Bay (Cove Apartments and Lani's Beach, Fig. 8). This pattern was not evident, however, during the winter and fall when there was less variation in average water temperatures between sites. Concurrently, the southwestern side of Richardson

Bay, where drills were absent, was generally cooler than the northeastern side, where drills were present (logistic regression, $Z = 64.51$, $P < 0.001$).

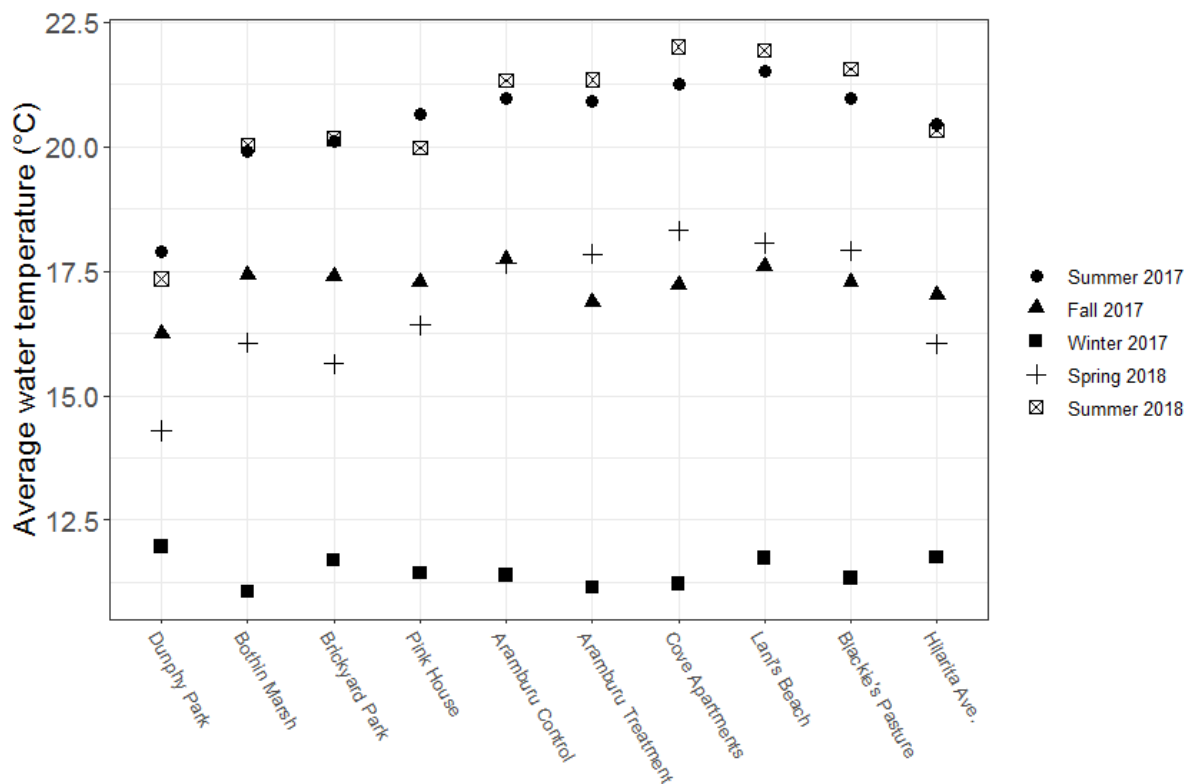


Figure 8: Average water temperature for each study site by season, summer 2017 to summer 2018. The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.).

I also assessed water temperature differences based on the percentage of logger readings above and below hot (26.5°C) and cold (10°C) thresholds, respectively. These temperatures represent points above and below which Atlantic drill activity (e.g. feeding and movement) decreases with increased exposure over time (Cheng, Komoroske, and Grosholz 2017). By this measure, the same spatial gradient was evident during hot periods: almost four times more water temperature readings above 26.5°C per site were

recorded from Aramburu Island to Blackie's Pasture (the inner portion of northeast Richardson Bay, where drills are present) than from Dunphy Park to Pink House (the southwest portion of Richardson Bay). Hilarita Ave. was outlier as a cooler site at the edge of the northeastern part of Richardson Bay, and Bothin Marsh was an outlier as a warmer site in the southeastern part of Richardson Bay (Fig. 9). During cold periods, there was a similar spatial gradient (Fig. 10). With the exceptions of Bothin Marsh and Hilarita Ave., sites on the northeastern side of Richardson Bay experienced a greater proportion of hot periods than sites on the southwestern side. There were no trends evident in water temperature across sites by elevation.

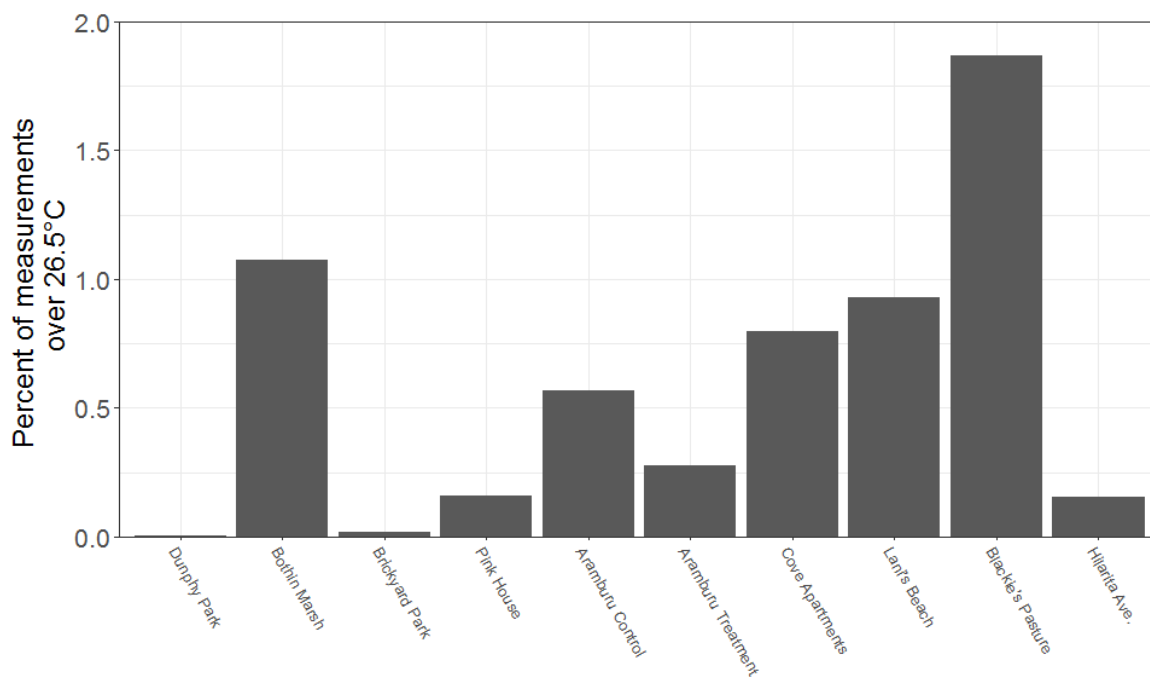


Figure 9: Percent of water temperature readings over 26.5°C recorded over all seasons, from summer 2017 to summer 2018. The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.).

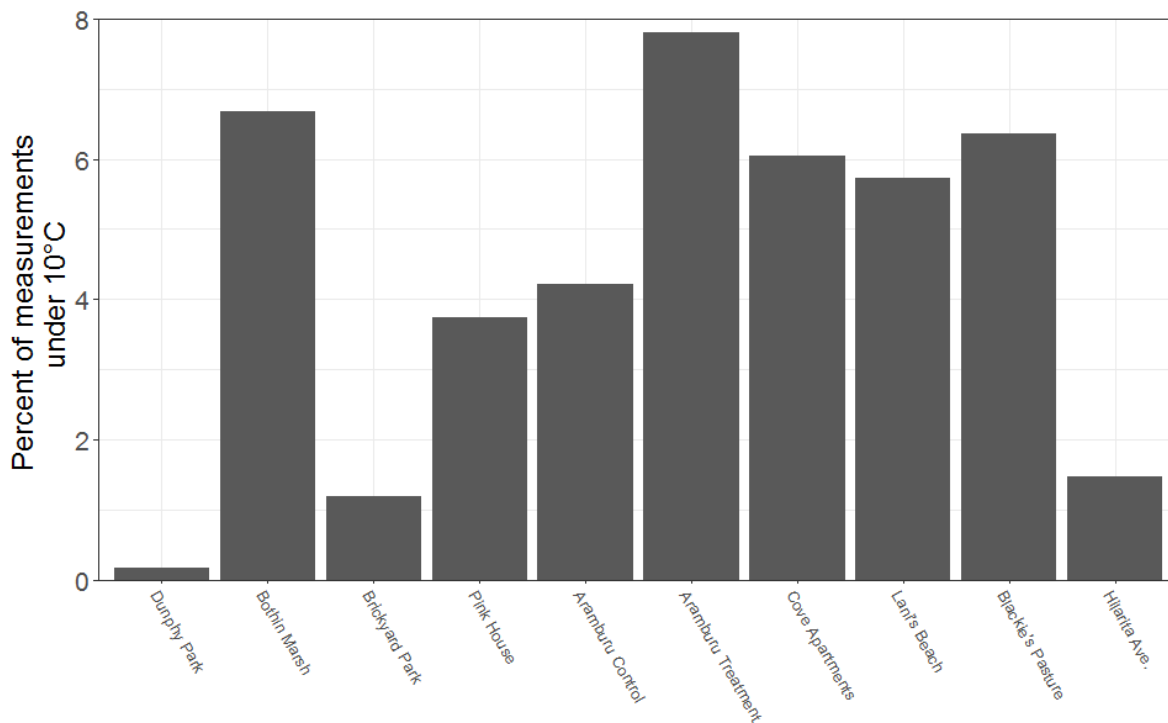


Figure 10: Percent of water temperature readings below 10°C recorded from summer 2017 to fall 2018 at each study site in Richardson Bay, CA. The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.).

I consistently observed higher water levels at sites along the southwestern shore of Richardson Bay (Dunphy to Brickyard Parks) than along the northeastern shore (Aramburu Island to Hilarita Ave.), where inundation was 0.21 meters lower on average (Fig. 11). Unfortunately, numerous water level loggers failed due to damage or battery age. As a result, I was not able to recover any data from one of the sites (Pink House), and of the seven months during which I collected data (June – December 2017), there were too few timepoints during which all loggers were functioning simultaneously to

include the dataset in the baseline drill abundance models. Temporally, inundation levels changed very little from summer to fall 2017 and declined slightly in December 2017.

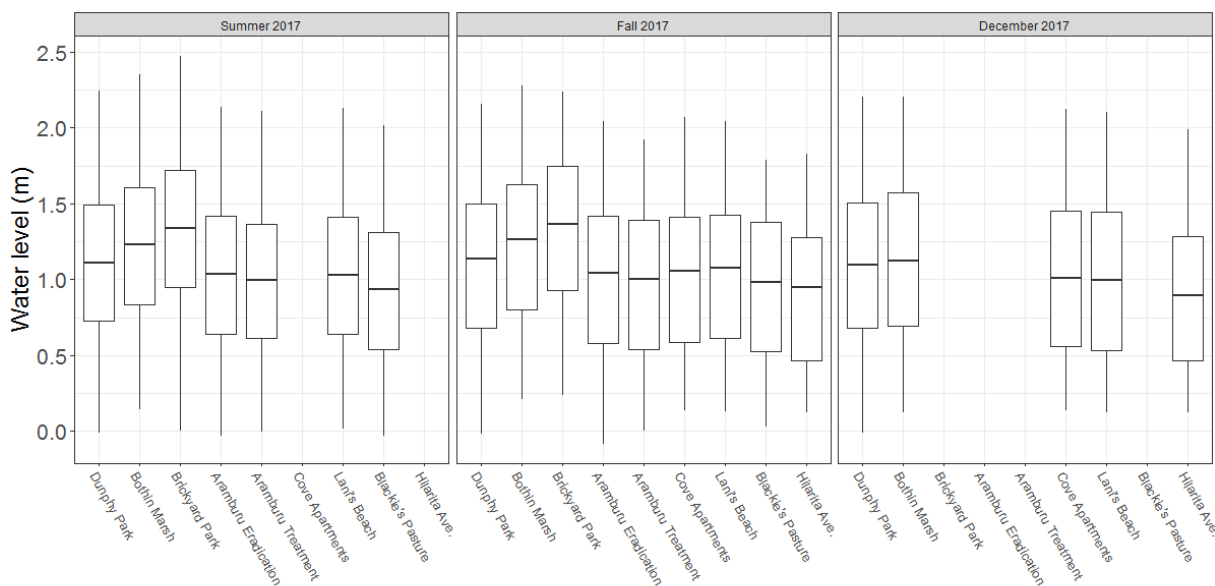


Figure 11: Inundation from June – December 2017 at each study site in Richardson Bay, CA, by season. Inundation was measured by water level in meters. The order of the sites moving from left to right corresponds to moving clockwise around Richardson Bay starting at the southwestern-most point (Dunphy Park) and moving to the northeastern-most point (Hilarita Ave.). Gaps in the dataset correspond to logger failures.

The salinity data I collected from December 23, 2017 – June 30, 2018 ranged from a high of 34.18 psu at Cove Apartments to a low of 11.23 psu at Hilarita Ave. during a rain event (Fig. 12). The 11 psu readings, however, are outliers and only represent approximately one hour of exposure and at relatively warm water temperatures, around 20°C. Excluding these outliers, the low end of the salinity range was approximately 15 psu, putting the overall salinity range within the tolerance range of Atlantic drills (Table 2). Salinity values tended to remain within 3-6 psu of each other

across sites at any given time point with Cove Apartments typically registering the highest salinity and Hilarita Ave. typically registering the lowest.

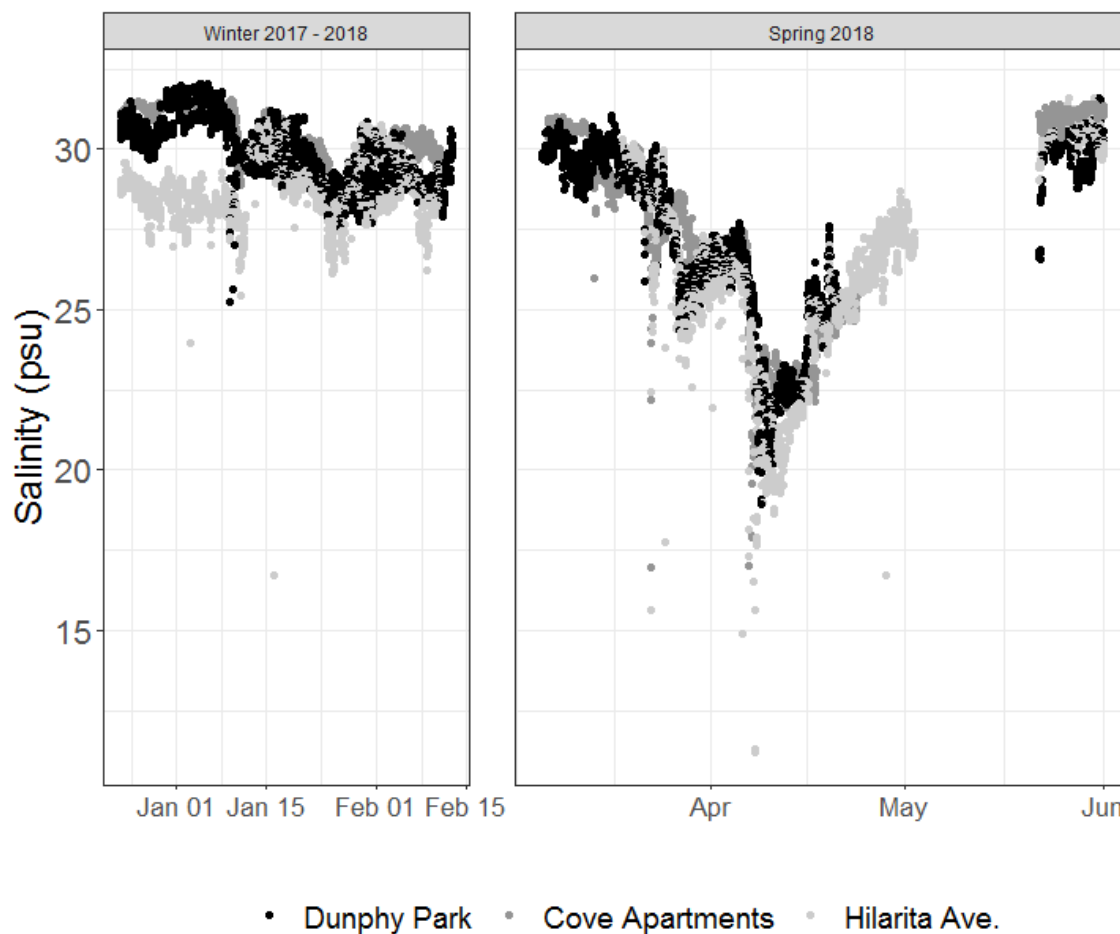


Figure 12: Salinity reading time series in practical salinity units (psu) at three study sites in Richardson Bay, CA from December 23, 2017 – June 30, 2018. Gaps indicate periods when loggers were not deployed.

3.3 Modeling results

According to the logistic model results, none of the environmental factors that I measured were significantly related to the presence or absence of drills (Table 4).

Table 4: Logistic model results. No environmental covariates were significant.

<i>Fixed effect</i>	<i>AIC</i>	<i>Significant factors (P < 0.05)</i>
Salinity	4.0	-
Water temperature	11.2	-
Inundation	12.1	-
Coarse substrate + water temperature	12.9	-
Coarse substrate	14.7	-

The best-fitting variation of the negative binomial GLMM baseline model indicated that elevation and coarse substrate were significantly related to drill abundance (Table 5). The marginal contributions of elevation and coarse substrate to the best fitting model are pictured in Fig. 13 and Fig. 14, which illustrate that the model predicted greater drill abundance at +46 cm than at +76 cm and a positive relationship with coarse substrate cover. There were no model permutations in which water temperature was significant, whether by average water temperature or by the percentage of readings above or below biologically important thresholds. Removing water temperature from the model always lowered the AIC, so it was dropped from all models. Nesting variables or including variable interactions resulted in a model convergence warning, suggesting that insufficient replication was available to use such model constructions; therefore, neither were used. Including a zero-inflation term yielded identical results in terms of significant

factors, but the standard errors were too high (on the order of 1×10^4) to be considered a good fit for the data. The best fitting model for the available data, therefore, incorporated coarse substrate and elevation as fixed effects with site and season as random effects and did not include a zero-inflation term, nesting, or interactions.

Table 5: Results of variations on the baseline negative binomial GLMM, which incorporated water temperature, coarse substrate, and elevation. Datasets cover all 12 months and all eight sites. Models are ranked in terms of AIC in ascending order. A lower AIC score indicates a better fitting model.

<i>Fixed effects</i>	<i>AIC</i>	<i>Significant factors (P < 0.05)</i>
Coarse substrate + elevation	151.3	Coarse substrate, elevation
Coarse substrate + elevation + water temperature	152.5	Coarse substrate, elevation
Elevation	159.8	Elevation
Coarse substrate	167.9	Coarse substrate

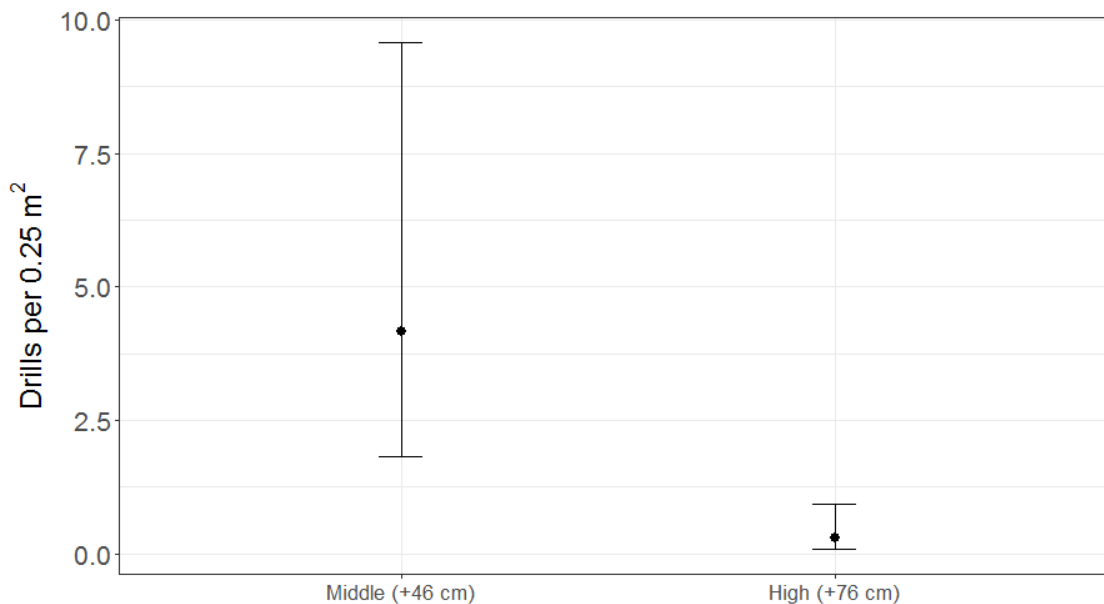


Figure 13: Marginal effects plot of elevation from the GLMM incorporating elevation and coarse substrate as fixed effects and all seasons of drill abundance data.

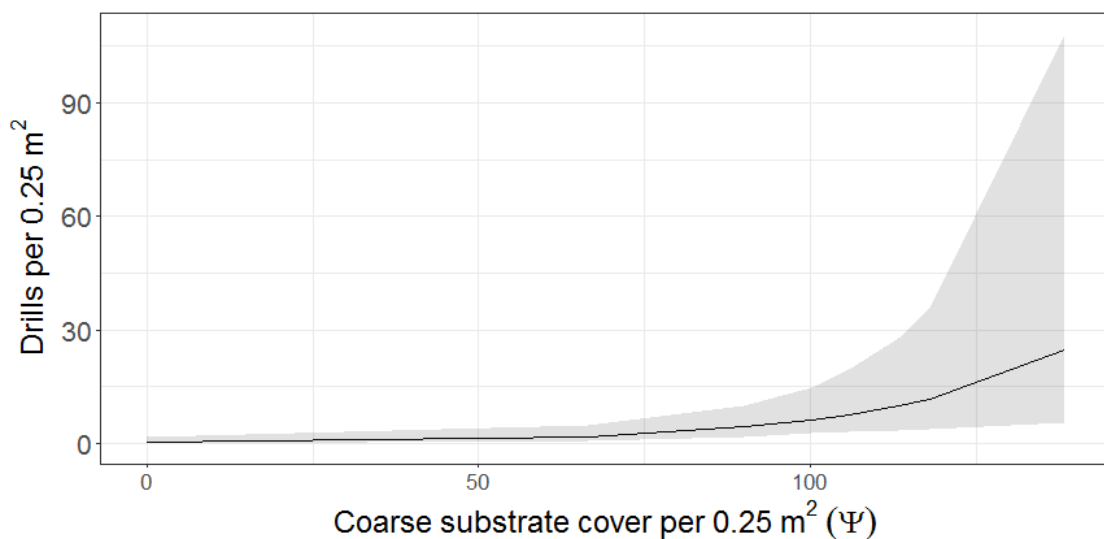


Figure 14: Marginal effects plot of coarse substrate (boulder and cobble) from the GLMM incorporating elevation and coarse substrate as fixed effects and all seasons of drill abundance data. The solid line indicates the predicted count of drills per quadrat and the shaded area is the 95% confidence interval.

Negative binomial GLMM variations including the salinity dataset covered six months (December 2017 – May 2018) and the three sites where salinity loggers were deployed. Salinity was not significant in either of these model variations (Table 6). Models of salinity alone, salinity and coarse substrate, or any variations including temperature or inundation did not converge or yield AIC or *P* values. Because the spatial and temporal parameters of the salinity dataset were different than those of the baseline model, I did not consider the AIC score to be comparable to the baseline model. The model did not indicate that salinity was a significant factor.

Table 6: Negative binomial GLMM results incorporating salinity. Dataset covers six months and three sites. Models are ranked in terms of AIC in ascending order. A lower AIC score indicates a better fitting model. A Model of salinity alone, salinity and coarse substrate, and models including temperature did not converge and no AIC or *P*-values were generated.

<i>Fixed effects</i>	<i>AIC</i>	<i>Significant factors (P < 0.05)</i>
Salinity + elevation	34.0	Elevation
Salinity + coarse substrate + elevation	35.6	none

Model variations incorporating the inundation dataset covered seven months (July 2017 – December 2017), and elevation was the only significant factor in the best fitting model (Table 7). Although inundation was significant when modeled independently, it had the highest AIC score, suggesting it was the poorest fitting model. Models including temperature did not converge and did not converge or yield an AIC or *P*-values. For glmmTMB to generate results for any model incorporating inundation, however, I had to add dummy data indicating zero drill abundance at +15 cm (i.e. in the mud flat where I

assumed there were no resident drills) in order to avoid a model convergence warning. Because of these dummy data, and because the temporal parameters of the dataset were different those of the baseline model, I did not consider the AIC score to be comparable to the baseline model.

Table 7: Negative binomial GLMM results of variations of the model incorporating inundation. Dataset covers seven months a. Models including temperature did not converge and no AIC or P-values were produced.

<i>Fixed effects</i>	<i>AIC</i>	<i>Significant factors (P < 0.05)</i>
Inundation + coarse substrate + elevation	82.7	Elevation
Inundation + coarse substrate	89.7	Coarse substrate
Inundation	98.5	Inundation

Although all loggers were deployed simultaneously in December 2017, models for only that time period resulted in convergence warnings, possibly due to the small size of that dataset.

4. Discussion

4.1 Modeling implications

My models suggest two broad conclusions: 1) Some factor or combination of factors other than habitat suitability related to the environmental factors that I measured is responsible for the lack of drills in the southwest half of Richardson Bay; and 2) Elevation and coarse substrate cover are significant factors that influence spatial variations in Atlantic drill abundance in Richardson Bay. These factors could be used to inform oyster restoration project site selection and design by suggesting ways for projects to work around the presence of Atlantic drills at a site or by avoiding sites that have environmental conditions that would support high densities of drills.

There were no patterns in the environmental data that suggested that the southwestern part of Richardson Bay is unsuitable for Atlantic drills. If ample coarse substrate at +46 cm favors higher drill populations, one would expect Dunphy Park and Brickyard Park to be highly suitable for drills, yet drills were not present at those two sites. It is, therefore, likely that their absence is due to some other cause, such as different environmental or ecological factors or simply a lack of dispersal of drills to those locations.

One notable difference between these two sites, Dunphy Park and Brickyard Park, and the sites where drills are present is the lack of a broad mud flat at +15 cm at Dunphy Park and Brickyard Park. There is some evidence that soft sediment serves as a refuge for drills in the winter where they enter a low-activity state of quasi-hibernation (Carriker 1955), but mud is present at +15 cm at Dunphy Park and Brickyard Park, albeit in more

limited amounts. Mechanistically, there is no documented positive connection between mud and Atlantic drill abundance, and drills are not commonly found in open tidal flats, although they may travel there to feed on prey patches before dispersing (Buhle and Ruesink 2009, authors' observations).

My finding that the positive correlation with drill abundance was stronger at +46 cm than at +76 cm is consistent with other research that suggests the upper intertidal zone may offer oysters some refuge from oyster drills (Boyer et al. 2017, Zabin et al. 2019). A similar elevational pattern was observed during an earlier oyster restoration experiment in Hayward, approximately 40 km southeast of Richardson Bay on the opposite side of San Francisco Bay. At that site, researchers observed significant drill predation of oysters on artificial substrates placed at +67 cm compared to no predation at +90 cm (Boyer et al. 2017). My study and the Hayward study covered the same vertical range (30 cm) and demonstrated a similar pattern of fewer drills at relatively higher elevation but at different absolute elevations above MLLW. This difference suggests that absolute elevation may not be the most relevant descriptor for drill habitat and that the association between drill abundance and elevation is likely influenced by other site-specific habitat factors. For example, slope, bathymetry, and a piling-up effect of water on the shore at high tide, which has been observed at Eden Landing, are all site-specific geographic factors that may affect the habitat suitability of various elevations (A. Chang, personal communication). A detailed comparison of the habitat conditions and drill abundances at Hayward and Richardson Bay sites might offer further insight into how elevation relates to other habitat factors. In addition to site-specific geography, the potential of upper

intertidal elevations as oyster habitat is limited by the more stressful conditions there for oysters due to increased exposure to heat, desiccation, and predators, such as birds.

It is not surprising that the availability of coarse substrate is positively correlated with drill abundance given our knowledge of Atlantic drill life history in which rocks and other hard surfaces play an essential role in reproduction and feeding. There does not seem to be a simple linear relationship, however, between coarse substrate and drill abundance. A plot of elevation, coarse substrate, and drill abundance suggests that there may be a threshold above which additional cobble and boulder do not bolster drill abundance, around 100 on the Ψ -scale of coarse substrate cover per quadrat (Fig. 15). A similar threshold may exist for *Olympia* oysters.

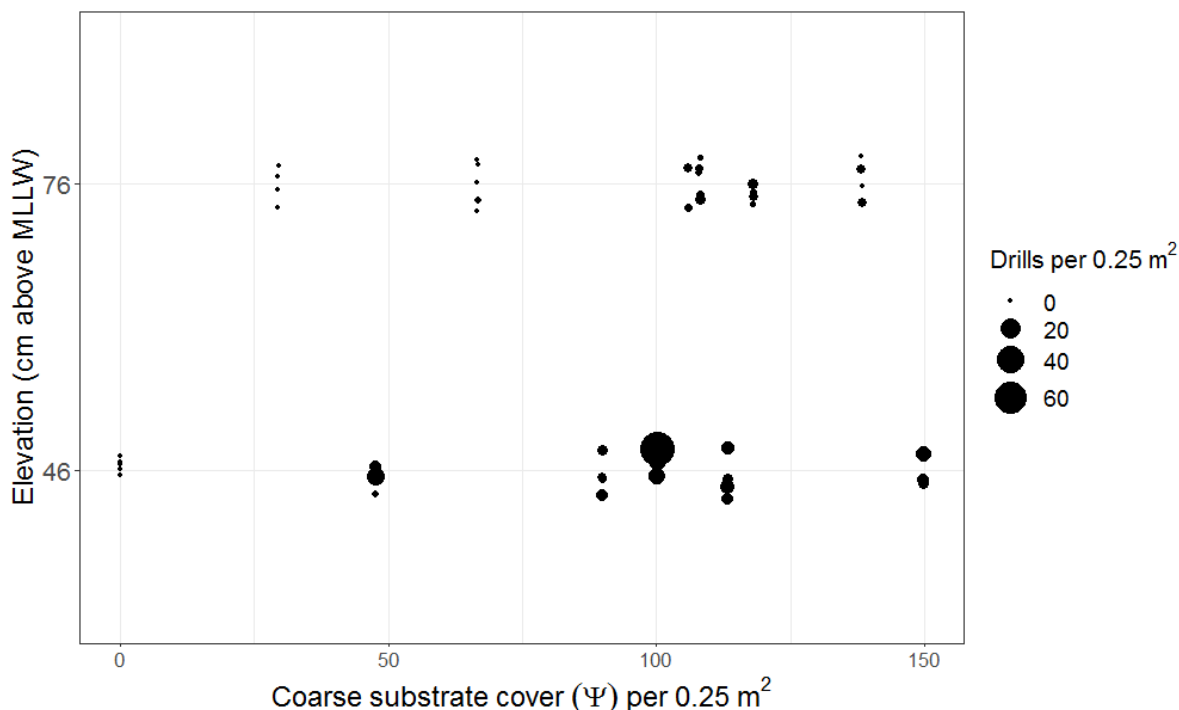


Figure 15: Drill abundance in relation to coarse substrate cover and elevation. Each point represents a transect. Only sites where drills were present are plotted. All sites and seasons are plotted together. Points are jittered for visual clarity. The highest abundance of drills occurs at +46 cm elevation around 100 (Ψ) coarse substrate.

For restorationists looking for locations that are suitable for oysters but limited in their capacity to support drill populations, an area with the minimum coverage of coarse substrate needed to support the desired oyster population but low enough to limit drill abundance might be advisable. Further analysis of the dataset, which includes oyster abundance, might reveal in quantitative terms whether such an ideal level of hard substrate availability thresholds for oysters and drills exists (Zabin et al., unpublished data). Alternatively, given drills' poor dispersal ability, a site with ample rocky substrate without drills that is isolated from nearby drill-populated areas (for example, due to surrounding mud flats) might be desirable for oyster restoration if other conditions that are favorable for oysters are present. Care would need to be taken not to introduce drills accidentally to the site. Protective measures, such as fine-mesh netting enclosures, might also be appropriate, as natural introduction of drills is a possibility, for example, during storm events that carry natural rafts, such as driftwood, and accompanying drills to new locations.

Additionally, although it is possible that the absence of oysters in the northeastern portion of Richardson Bay is due to the presence of drills (Zabin et al. 2019), there are sites throughout SFB where Olympia oysters and Atlantic oyster drills co-exist at varying levels of drill density. The potential for coexistence at sites with low drill density is particularly relevant to Olympia oyster restoration projects, where juvenile oysters are more vulnerable to predation than adults [citation needed]. In Tomales Bay, CA, Cheng and Grosholz (2016) observed oyster populations coexisting with Atlantic drill populations in the range of 1-2 drills per 0.25 m² at unspecified elevations. Both Hilarita

Ave. and Blackie's Pasture support drill populations around one drill per 0.25 m². A comparison of the environmental profiles between these two Richardson Bay locations and the study sites at Tomales Bay could offer additional insights into how broadly applicable my model results are. Hilarita Ave. and Blackie's Pasture might also be well-suited for future drill removal experiments or experiments testing the viability of Olympia oyster transplants amid a low-density drill population.

4.2 Spatial-environmental patterns

The hypothesized gradient in Richardson Bay of environmental conditions was evident in the temperature and inundation datasets but not obviously discernable in the substrate or salinity data. The higher inundation observations in the southwest portion of Richardson Bay, and to a lesser extent around Cove Apartments, could be due to water flow, eddy, and current patterns, possibly wind-driven, resulting in a piling-up effect of water on the shore. Inner-Bay (near Cove Apartments and Lani's Beach) and outer-Bay (Dunphy Park and Hilarita Ave.) differences driven by water residence time and exchange with downstream seawater or upstream Sacramento River water could have caused the observed temperature and salinity gradients. Greater proximity to the Golden Gate, and therefore more exchange with cold, saline Pacific seawater, could account for the cooler temperatures I observed in the southwest portion of the Richardson Bay during summer and spring and the periods when salinity was highest at Dunphy Park. In contrast, extreme hot and cold air temperatures have more time to transfer to water settled in the back of Richardson Bay, which in turn exhibits a greater percentage of hot (over

26.5°C) and cold (under 10°C) temperatures, which we observed from Aramburu Island to Blackie's Pasture. Resident back-Bay water could also experience more evaporation and, therefore, higher salinity than the outer-bay sites, which might account for the periods when salinity was highest at Cove Apartments. Between January and July, salinity was lowest at the Hilarita Ave. site, which is consistent with what one might expect given that this site is the furthest upstream from the Golden Gate and should experience the least mixing with ocean water.

4.3 Study limitations

Although I hope that this project improves understanding of Atlantic drill habitat and abundance, there is uncertainty and error built-in to the models based on both the study design and implementation. For example, there are biotic and abiotic factors that I did not model that potentially influence drill abundance, such as air temperature, pH, dissolved oxygen, prey availability, predation, and competition. Ecological interactions represent a key component of Atlantic drills' occupied niche and are likely embedded in the drill abundance dataset itself. As such, my results should not be taken as definitive ecological niche measurements but rather should serve as a guide to focus on two environmental factors that influence variations in Atlantic drill abundance.

I was also logistically limited in my ability to monitor salinity and water level year-round and at all sites, and logger failures resulted in further spatial and temporal patchiness in the datasets. Complete datasets that capture the full extent of environmental microheterogeneities between sites might offer more insight into whether and how

salinity and inundation contribute to drill abundance. Questions also remain regarding drill abundance at elevations in between the ones that I surveyed. Intertidal surveys are strictly time-limited, and it would have been impossible to sample the entire width of the beach, but some pilot and opportunistic surveys at +24 cm and +61 cm suggested that these elevations might also be favorable for drills. Future surveys, therefore, along shore-normal transects that incorporate elevations below and in between this projects' target elevations might help fine-tune our understanding of elevation and Atlantic drill habitat.

4.4 Recommendations

The possibility of dispersal-limited drill distribution should generate great caution for anybody traveling between parts of Richardson Bay, or SFB at-large, to avoid being a vector for drills or other potentially problematic introduced species. Thorough washing of field equipment and gear, such as boots, between site visits was an integral part my protocol and should serve as a model for other researchers and the general public.

Additionally, I recommend more surveys, both in Richardson Bay and in other parts of San Francisco Bay, to map the potentially changing distribution of Atlantic drills and the environmental conditions where drills are found. As noted above, although drill populations exhibit clear elevational preferences, these preferences can vary between locations. Broadening the reach of this habitat study to other locales could provide insight into how applicable the importance of elevation and substrate conditions are and what other factors may be driving or interacting with those conditions. This additional data could also be used to test the hypothesis that there is an ideal combination of coarse

substrate cover and elevation. To better understand the coexistence of Atlantic drills and Olympia oysters, surveys should also include counts of oysters and alternative prey, such as barnacles, as source data for incorporating ecological interactions into a habitat model.

Making these and additional environmental and abundance data spatially explicit would allow analysts to produce geographic information science (GIS)-based habitat suitability models. GIS models are well-suited for applying a fine-scale model like mine to other areas where appropriate substrate, elevation, and other environmental data exist (Guisan et al. 2000). Although broad-scale classification datasets of the SFB shoreline exist (e.g. San Francisco Estuary Institute 2017), they do not contain the fine-scale environmental attributes (e.g. substrate grain size) over a broad extent that would be required to extend my model to other areas. Using remote sensing techniques, such as aerial drone photography, for detailed environmental measurements of long reaches of intertidal shoreline could be of a great benefit to this end.

It is also important to monitor the spatial range of drills to determine if they are spreading to new areas. Monitoring whether drill range is static, expanding, or contracting is important to know when modeling habitat suitability, as these models typically assume a level of pseudo-equilibrium between a species and its environment without which the model could produce biased results (Guisan, Edwards, Hastie, 2002). More broadly, it is not currently recommended to attempt oyster restoration in Richardson Bay where drills are present (Zabin et al. 2019); understanding whether and how drill range may be changing will be crucial in assessing what constitutes a safe distance from drills in Richardson Bay and elsewhere. As living shorelines projects

incorporating Olympia oyster restoration expand in SFB and throughout the West Coast, understanding how Atlantic drills fit into these landscapes will be an important component of successful project outcomes.

5. References

- Barrett, E. M. 1963. The California Oyster Industry. *Fish Bulletin* 123. Sacramento, CA: The Resources Agency of California, Department of Fish and Game.
<http://escholarship.org/uc/item/1870g57m> (last accessed 16 December 2019).
- Blum, J. C. 2012. Temperature Sensitivity and Predation Risk Cue Detection in Native and Introduced Populations of the Atlantic Oyster Drill, *Urosalpinx cinerea*.
<http://juliablum.org/files/Blum2012-MSThesis.pdf>.
- Bolker, B. M., M. E. Brooks, C. J. Clark, and S. W. Geange. 2009. Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution. *Trends in Ecology & Evolution* 24 (3):127–135.
- Boyer, K. E., C. J. Zabin, S. De La Cruz, E. D. Grosholz, M. Orr, J. Lowe, M. Latta, J. Miller, S. Kiriakopoulos, C. Pinnell, D. Kunz, J. Moderan, K. Stockmann, G. Ayala, R. Abbott, and R. Obernolte. 2017. San Francisco Bay Living Shorelines: Restoring Eelgrass and Olympia Oysters for Habitat and Shore Protection. In *Living Shorelines: The Science and Management of Nature-Based Coastal Protection*, eds. D. M. Bilkovic, M. Mitchell, J. Toft, and M. La Peyre. Boca Raton, FL: CRC Press Marine Science Series.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R-journal* 9(2): 378-400.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2019. Troubleshooting with glmmTMB. <https://cran.r-project.org/web/packages/glmmTMB/vignettes/troubleshooting.html> (last accessed 16 December 2019).
- Buhle, E. R., and J. L. Ruesink. 2009. Impacts of invasive oyster drills on Olympia oyster (*Ostrea lurida* Carpenter 1864) recovery in Willapa Bay, Washington, United States. *Journal of Shellfish Research* 28 (1):87–96.
- Bunte, K., and S. R. Abt. 2001. Sampling Surface and Subsurface Particle-Size Distributions in Wadable Gravel- and Cobble-Bed Streams for Analyses in Sediment Transport, Hydraulics, and Streambed Monitoring. General Technical Report RMRS-GTR-74. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 428 pp.

- California Academy of Sciences. 2017. Invertebrate zoology collection database. http://researcharchive.calacademy.org/research/izg/iz_coll_db/Index.asp (last accessed 13 October 2017).
- Carriker, M. R. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Special Scientific Report: Fisheries no. 148. Washington, D.C.: US Department of the Interior, Fish and Wildlife Service. 150 pp.
- Cheng, B. S. 2014. *Climate change, invasive species, and predator-prey interactions in California estuaries* (Doctoral dissertation). Proquest Dissertations and Theses.
- Cheng, B. S., and E. D. Grosholz. 2016. Environmental stress mediates trophic cascade strength and resistance to invasion. *Ecosphere* 7 (4):1–13.
- Cheng, B. S., L. M. Komoroske, and E. D. Grosholz. 2017. Trophic sensitivity of invasive predator and native prey interactions: integrating environmental context and climate change. *Functional Ecology* 31 (3):642–652.
- Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X. Morin, C. Römermann, B. Schröder, and A. Singer. 2012. Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography* 39 (12):2119–2131.
- Ermgassen, P. S. E., M. W. Gray, C. J. Langdon, M. D. Spalding, and R. D. Brumbaugh. 2013. Quantifying the historic contribution of *Olympia* oysters to filtration in Pacific Coast (USA) estuaries and the implications for restoration objectives. *Aquatic Ecology* 47 (2):149–161.
- Ermgassen, P. S. E., M. D. Spalding, B. Blake, L. D. Coen, B. Dumbauld, S. Geiger, J. H. Grabowski, R. Grizzle, M. Luckenbach, K. McGraw, W. Rodney, J. L. Ruesink, S. P. Powers, and R. Brumbaugh. 2012. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proceedings of the Royal Society B: Biological Sciences* 279 (1742):3393–3400.
- Federighi, H. 1931. Studies on the oyster drill (*Urosalpinx cinerea*, Say). *Bulletin of the Bureau of Fisheries* 47 (4):83–115.
- Franz, D. R. 1971. Population Age Structure, Growth and Longevity of the Marine Gastropod *Urosalpinx cinerea* Say. *Biological bulletin* 140 (1):63–72.
- Ganaros, A. 1958. On development of early stages of *Urosalpinx cinerea* (Say) at constant temperatures and their tolerance to low temperatures. *Biological Bulletin* 114 (2):188–195.

- Grosholz, E. D., J. Moore, C. J. Zabin, S. Attoe, and R. Obernolte. 2007. *Planning for Native Oyster Restoration in San Francisco Bay: Final Report to California Coastal Conservancy*. Agreement # 05-134.
<http://www.des.ucdavis.edu/faculty/grosholz/people/files/grosholz/GrosholzFinalReport05-134.pdf> (last accessed 27 September 2017).
- Guisan, A., A. Guisan, N. E. Zimmermann, and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135 (2–3):147–186.
- Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. *Habitat Suitability and Distribution Models With Applications in R*. New York, NY: Cambridge University Press.
- Harding, J. M., and R. Mann. 2016. Habitat Disturbance Combined with Life History Traits Facilitate Establishment of *Rapana venosa* in the Chesapeake Bay. *Journal of Shellfish Research* 35 (4):885–910.
- Hirzel, A. H., and G. Le Lay. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45 (5):1372–1381.
- Hutchinson, G. E. 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–442.
- Kearney, M. 2006. Habitat, environment and niche: What are we modelling? *Oikos* 115 (1):186–191.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12 (4):334–350.
- Kimbro, D. L., and E. D. Grosholz. 2006. Disturbance influences oyster community richness and evenness, but not diversity. *Ecology* 87 (9):2378–2388.
- Kimbro, D. L., E. D. Grosholz, A. J. Baukus, N. J. Nesbitt, N. M. Travis, S. Attoe, and C. Coleman-Hulbert. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* 160 (3):563–575.
- Lord, J. P. 2014. Effect of Temperature Changes on Competitive and Predator-Prey Interactions in Coastal Epi- Benthic Communities.
<http://digitalcommons.uconn.edu/dissertations> (last accessed 4 April 2018).
- Manzi, J. J. 1970. Combined Effects of Salinity and Temperature on the Feeding, Reproductive, and Survival Rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Source: Biological Bulletin Biol. Bull* 138 (138):35–46.

- Person, P., A. Smarsh, S. J. . Lipson, and M. R. . Carriker. 1967. Enzymes of the Accessory Boring Organ of the Muricid Gastropod *Urosalpinx cinerea follyensis* . I. Aerobic and Related Oxidative Systems. *Biological Bulletin* 133 (2):401–410.
- Postel, M. 1988. A lost resource. *California History* 1 (67):26–41.
<http://www.jstor.org/jpllnet.sfsu.edu/stable/pdf/25158456.pdf> (last accessed 27 September 2017).
- Puglisi, M. P. 2008. *Urosalpinx cinerea*. Fort Pierce, Florida.
https://naturalhistory2.si.edu/smsfp/irlspec/Urosalpinx_cinerea.htm (last accessed 16 December 2019).
- R Core Team. 2019. R: A language and environment for statistical computing.
<https://www.r-project.org/> (last accessed 16 December 2019).
- Restore America's Estuaries. 2015. *Living Shorelines: From Barriers to Opportunities*. Arlington, VA. <https://estuaries.org/resource-library/living-shorelines-from-barriers-to-opportunities/> (last accessed 16 December 2019).
- Subtidal Goals Project. 2010. *San Francisco Bay Subtidal Habitat Goals Report*. Oakland, CA: State Coastal Conservancy. 180 pp.
- Townsend, C. H. 1893. *Report of the observations respecting the oyster resources and oyster fishery of the Pacific coast of the United States*. Washington, D.C.: US Government Printing Office.
- Wagner, R.J., R.W. Boulger, Jr., C.J. Oblinger, B.A. Smith. 2006. Guidelines and standard procedures for continuous water-quality monitors: station operation, record computation, and data reporting. USGS Techniques and Methods 1-D3. Reston, VA: US Department of the Interior, US Geological Survey. 96 pp.
- Wasson, K., C. J. Zabin, J. Bible, S. Briley, E. Ceballos, A. Chang, B. Cheng, A. Deck, T. Grosholz, A. Helms, M. Latta, B. Yednock, D. Zacherl, and M. Ferner. 2015. *A Guide to Olympia Oyster Restoration and Conservation: Environmental Conditions and sites that Support Sustainable Populations*. Elkhorn Slough National Estuarine Reserve.
- Zabin, C., A. Chang, B. Cheng, J. Blumenthal, and S. Ferner. 2019. Community-based oyster research for living shorelines design: management of a non-native predator to improve native oyster restoration success. Final report to the California State Coastal Conservancy, September 30, 2019.
- Zabin, C. J., S. Attoe, and E. D. Grosholz. 2010. Appendix 7-1 : Shellfish Conservation and Restoration in San Francisco Bay: Opportunities and Constraints. Final Report for the Subtidal Habitat Goals Committee. 107 pp.
<http://www.sfbaysubtidal.org/PDFS/Ap7-1%20Shellfish.pdf> (last accessed 16 December 2019).

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer Science+Business Media.