Exploring high intertidal refugia as an approach for the restoration of an intertidal oyster

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ABSTRACT: Marine organisms frequently inhabit intertidal zones that serve as refuges from predation and competition but are not optimal physiologically. Restoration practitioners working with intertidal species may similarly have to consider whether restoration success will be greater where conditions are more benign (usually lower in the intertidal) or where negative biotic interactions are reduced (usually higher in the intertidal). In cases where a target species has greater desiccation tolerance than its enemies, restoration may be more successful higher in the intertidal zone, despite potential performance trade-offs. In many US West Coast estuaries, non-native drill species can decimate native oyster populations, posing a challenge to restoration. Given that native Olympia oysters *Ostrea lurida* should be better able to withstand tidal emersion than the non-native Atlantic oyster drill *Urosalpinx cinerea*, we explored using the high intertidal as a refuge from predation as a potential restoration technique. Using surveys and a field experiment, we investigated the recruitment, growth, and survival of oysters as well as drill abundance and predation over 3 tidal elevations. Oysters recruited and survived equally well at +0.1, +0.5, and +0.8 m mean lower low water, but juvenile oyster growth decreased with increasing elevation. In our experiment, predation on oysters was lower at the highest elevation than at low and mid elevations, but in natural populations there was a near complete absence of *O. lurida* at any elevation where *U. cinerea* was present. This suggests that a higher tidal elevation refuge is not a viable approach for oyster restoration in our study area.

KEY WORDS: Olympia oysters · *Ostrea lurida* · *Urosalpinx cinerea* · Predation · Intertidal zonation · Refuge · Restoration

1. INTRODUCTION

"I believe that many of the results of experimental ecology suggest that marine intertidal animals do not occupy 'optimal zones'; rather, they are often confined to refuges where risk is minimized, and performance, measured on any number of criteria, is relatively poor." (Paine 1980, p. 383).

For most intertidal species, physical conditions are more benign lower in the intertidal zone where immersion times are longer (Orton 1929, Doty 1946, Connell 1961). Longer immersion time may increase the number of larvae arriving to surfaces in the low intertidal and/or early survival of new settlers (Roegner & Mann 1995, Hoffmann et al. 2012, Wang et al. 2020). For many (but not all) taxa, longer immersion may provide greater feeding opportunities and thus faster growth (Gillmor 1982, Crosby et al. 1991, Johnson & Black 2008) and higher fecundity (Borrero 1987, Harvey & Vincent 1989, McCarthy et al. 2003). However, these advantages may be offset by greater competition for space and food and/or by greater predation at lower tidal elevations (Connell 1961, Paine 1966, Menge & Sutherland 1987). The interplay of

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these various factors sets the upper and lower elevational ranges for intertidal organisms (reviewed in Tomanek & Helmuth 2002), such that many individuals may not live in the intertidal or shallow subtidal zones where physical conditions are best for growth and survival but are instead limited by ecological interactions to refugia with less-than-optimal conditions.

Habitat restoration projects seek to maximize the performance of target taxa, usually in terms of population size, density, growth, and reproduction. To achieve this goal, restoration practitioners attempt to select locations with optimal conditions for target taxa. However, it may not be possible to optimize all performance measures at a single site; for example, a location with high recruitment rates might not have high survivorship (Torok & Helm 2017, Kimbro et al. 2019). Similarly, for intertidal species, there may not be a tidal elevation that is optimal by all metrics. Many measures of performance are likely to be higher in the lower intertidal compared to higher tidal elevations, e.g. greater recruitment (Fodrie et al. 2014, Zabin et al. 2016), greater survival of transplants (Bull et al. 2004), or faster growth of recruits (Jiang et al. 2019). However, survival of target taxa can be greater at higher intertidal levels due to reduced competition (Fodrie et al. 2014, Jiang et al. 2019) and fewer predators, pests, and parasites (Johnson & Smee 2014, Carroll et al. 2021) when the target taxa have higher tolerance for desiccation or heat stress than their enemies. In fact, in some cases, the initial benefits of being in the lower intertidal have been demonstrated to decline or even reverse over time, with target taxa in the higher intertidal ultimately demonstrating equivalent adult sizes (Zabin et al. 2016), equal densities (C. J. Zabin unpubl. data), higher densities (Fodrie et al. 2014), or faster growth (Bishop & Peterson 2006). Thus, as in natural settings, species that are the focus of restoration efforts may ultimately have the greatest longer-term success in refugia where physical conditions are stressful. A decision to carry out restoration in higher intertidal refugia may mean accepting trade-offs in some fitness measures to meet a restoration goal of greater numbers of individuals (Fodrie et al. 2014, Johnson & Smee 2014).

Habitat restoration typically occurs within a subset of the locations where a species once existed (Palmer et al. 1997). Estuarine and marine habitats in particular have been enormously modified by human activities, including dredging, resource extraction, chemical pollution, shoreline hardening, climate change, and invasive species (Grosholz 2002, Lotze et al. 2006,

Halpern et al. 2015), limiting where along a shoreline restoration can proceed (Pogoda et al. 2019, Howie & Bishop 2021). The impacts of some of these new stressors might also vary with tidal elevation (Tice-Lewis et al. 2022), reducing the vertical extent over which restoration can be successful. Thus, for intertidal restoration, practitioners may increasingly need to identify both horizontal and vertical refugia within a species' historic range.

Oyster reefs are one of the most threatened marine habitats globally, having declined by >90% from historic levels in many bays and estuaries (Beck et al. 2009, Zu Ermgassen et al. 2012), and efforts to restore oysters have increased over the past several decades (Gillies et al. 2015, Bersoza Hernandez et al. 2018, Pogoda et al. 2019, Ridlon et al. 2021). The Olympia oyster *Ostrea lurida*, native to the West Coast of North America, is estimated to be at 1% of historic baseline population levels (Zu Ermgassen et al. 2012). Interest in restoring this oyster has been increasing over the past 2 decades, with more than 40 projects underway from Southern California to British Columbia (Ridlon et al. 2021). Predation on oysters is one of the top challenges to the successful restoration of Olympia oysters, with non-native gastropods such as Atlantic oyster drill *Urosalpinx cinerea* and the Japanese oyster drill *Ocinebrellus inornatus* of particular concern in locations where they are abundant (Wasson et al. 2015, Ridlon et al. 2021). Predation on native oysters by these drills has been documented in several estuaries (Buhle & Ruesink 2009, Kimbro et al. 2009, Koeppel 2011). Oyster mortality has been demonstrated to increase with increasing drill densities, with up to 90% mortality recorded at drill densities of >1 drill m^{-2} (Kimbro et al. 2009, Cheng & Grosholz 2016), and the impact of drills on oysters is expected to increase with climate change (Sanford et al. 2014, Cheng et al. 2017).

Non-native drill distribution and abundance varies within West Coast estuaries; drills are completely absent in some locations and highly abundant in others (Buhle & Ruesink 2009, Kimbro et al. 2009, Koeppel 2011). While the drivers of these patchy distributions are not completely known, drills are frequently absent in lower salinity locations (Buhle & Ruesink 2009, Cheng et al. 2017). Locating restoration projects at lower salinity sites to reduce predation and disease prevalence has been recommended as a practice for eastern oyster *Crassostrea virginica* restoration (Mann & Evans 2004, Miller et al. 2017); however, Olympia oysters are less tolerant of lower salinity (some mortality at 10 psu, death at 5 psu for >8 d; Bible et al. 2017) than eastern oysters, with

upstream populations at risk of high mortality during years of heavy rains (Cheng et al. 2016). Restoration of oysters in the more saline parts of estuaries may be increasingly important given the likelihood of more frequent low-salinity events with climate change (Cheng et al. 2016).

Here, we explored the possibility of using the high intertidal zone as a potential refuge from predation by *U. cinerea* on the Olympia oyster in San Francisco Bay (SFB), California, USA, where these drills have decimated oysters in restoration projects (Boyer et al. 2016, authors' pers. obs.). While research has supported the approach of restoring the eastern oyster higher in the tidal prism to avoid predators, including oyster drills (Fodrie et al. 2014, Johnson & Smee 2014), this method has not been investigated on the West Coast.

We expected this approach to work, given that oysters are likely better adapted than drills to withstand desiccation stress. Oysters can reduce water loss by closing their shells tightly during low tide, while oyster drills possess a siphonal canal and may not be able to seal themselves off completely from the environment. Drilling activity may also cease or slow down with aerial exposure, reducing feeding opportunities for the snails at higher tidal elevations (Koeppel 2011). Studies of *U. cinerea* in its native range indicate higher predation rates at lower tidal elevations (Chestnut & Fahy 1953, Katz 1985). An earlier field experiment in SFB using adult oysters settled on tiles (Zabin & Kiriakopolos 2015) documented high predation by drills on oysters, with 65% mortality due to drills at ca. +0.6 m mean lower low water (MLLW) and limited predation on oysters (0.5% mortality due to drills) placed at ca. +0.9 m MLLW over a 5 mo period. However, oysters failed to recruit in high numbers at any tidal elevation to that site (Boyer et al. 2016), leaving open the question of whether locating oyster restoration projects in the high intertidal zone could work, given that present restoration methods in SFB rely on natural recruitment.

While Olympia oysters have been reported to occur from as high as 2 m above MLLW in some locations (Baker 1995), in SFB, naturally occurring oysters are most abundant around 0 m MLLW (authors' pers. obs.), presumably due to both higher recruitment and higher long-term survival at this elevation. We were interested in determining whether, at sites where drills are present, it was possible to take advantage of an apparent decrease in drill predation over an increasing tidal gradient by placing restoration substrates in the high intertidal zone. We used a field experiment to determine whether predation was indeed reduced at a high intertidal elevation, and conducted surveys and experiments to examine the effects of tidal elevation on several measures of oyster fitness that might be expected to decrease with tidal elevation: recruitment, survival of young oysters, growth, and adult densities. Both decreased predation and successful recruitment and long-term survival of oysters need to be demonstrated before proceeding with restoration at higher tidal elevations.

2. MATERIALS AND METHODS

2.1. Study location

Richardson Bay is a wave-protected embayment within the north-central portion of SFB (Fig. 1). Several non-profit organizations, management agencies, and community groups have expressed interest in oyster restoration within this region (California State Coastal Conservancy 2010). However, oyster drills are present in high abundances at some locations within Richardson Bay (5—25 drills m^{-2} at 2 locations; Cheng et al. 2022), and at these sites, no live oysters had been found in recent surveys at the ca. +0.5 m MLLW tidal elevation (Cheng et al. 2022). Live oysters placed at ca. +0.5 m MLLW at 2 sites with high drill densities were rapidly killed (100% mortality) by drills, demonstrating that drill predation is at least one factor limiting oysters at these sites (Cheng et al. 2022). Drill management is thus key to the success of future oyster restoration at these sites along with natural recruitment of larvae, given that hatchery-reared spat is not currently used for oyster restoration in SFB (Ridlon et al. 2021).

During our study, both water temperature and salinity were well within ranges tolerated by both Olympia oysters and Atlantic oyster drills (Blumenthal 2019). Temperatures in the intertidal zone in Richardson Bay ranged from 11.5°C in winter to 22°C in summer, with sites near the back of the bay slightly warmer in summer and sites on the northwestern side of the bay slightly cooler on average (Blumenthal 2019). Salinity ranged between 15 and 34 psu, and sites were within 3—6 psu of each other over this period (Blumenthal 2019). For our caging experiment, we expected that oysters would experience high predation intensity during July—August when the experiment was deployed because water temperatures are greatest during this time (average: 19.3°C) and because *Urolsalpinx cinerea* predation activity increases up to 26.7°C in laboratory physiological studies (Cheng et al. 2017).
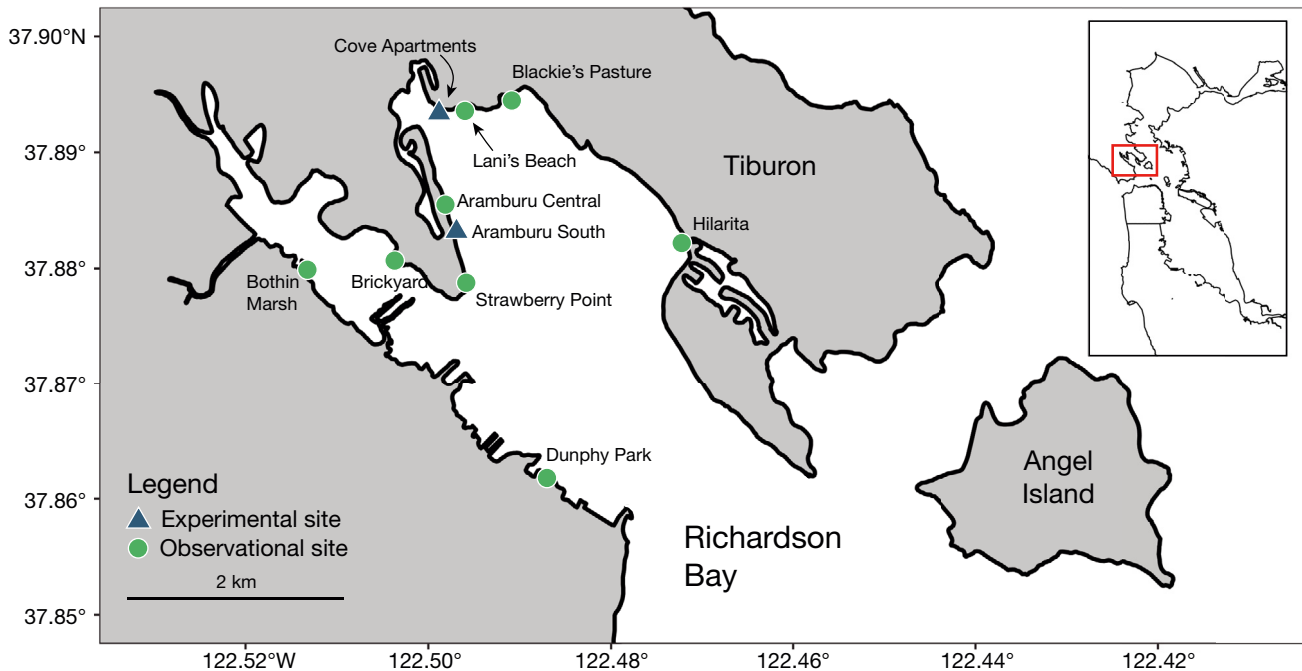
Fig. 1. Study sites within Richardson Bay, California, USA. Inset map: red rectangle indicates location of Richardson Bay within San Francisco Bay

2.2. Field experiment: effects of tidal elevation on drill predation and oyster survival and growth

To determine whether oysters have a high intertidal refuge from predation that could be used as part of a restoration strategy, in July 2018 we constructed a field experiment at 2 sites where surveys (see Section 2.4) indicated that drills were abundant: Aramburu South and Cove Apartments (Fig. 1). In this experiment, we tested for potential effects of tidal elevation on differences in drill predation as well as survival and growth of young oysters. These sites were selected because they are managed by the Richardson Bay Audubon Center & Sanctuary, which is interested in shoreline habitat enhancement, including oyster restoration. For this experiment, we used cyanoacrylate glue (Loctite Control Gel Super Glue) to attach 10 hatchery-reared oysters (Puget Sound Restoration Fund, California Department of Fish and Wildlife Permit no. 2018-5211; oyster shell height: 10–15 mm) to the unglazed side of ceramic wall tiles (Daltile model RE1544HD1P4; 10.625 × 10.625 cm). Tiles were numbered, photographed, and randomly assigned into one of 3 treatments: (1) uncaged; (2) caged; and (3) cage controls. Cages were made of sturdy aquaculture netting (Memphis Net & Twine PN3, black, 62.5 mm mesh), wrapped with plastic window screening (Phifer BetterVue Screen; 1 mm mesh

size). This mesh size was sufficient to exclude even very small (2 mm) drills. To control for cage effects, such as shading and reduction of water flow, we cut windows (ca. 2.5 × 5 cm) in the cage-control treatments, which allowed drills to access the oysters. This cage control approach has been used in several Olympia oyster studies to evaluate caging artefacts without issue (Kimbro et al. 2009, Cheng & Grosholz 2016, Cheng et al. 2022). Tiles and cages were attached with plastic cable ties to bricks, which were in turn attached to metal reinforcing bars driven into the substrate. The bricks were set on the benthos and helped to keep the cages and tiles upright and secured to the rebar. Eight replicates of each treatment type (8 × 3 = 24) were placed at each of the ca. +0.1, ca. +0.5, and ca. +0.8 m MLLW tidal elevations (elevations established as described in Section 2.4) at each site (total: 144 experimental units).

Tiles and cages were checked within 1 d of deployment. Repairs were made as needed so that all tiles had 8–10 live oysters at the start of the experiment. One month later, in August 2018, we removed all tiles from the field. Tiles and photographed and examined in the laboratory and oysters were classified as alive, dead, or missing.

To quantify the effect of tidal elevation on predation, we initially used generalized linear mixed models to measure oyster survival. In this analysis,

the binomial response variable was oyster counts that were alive or dead (e.g. 4 alive, 6 dead), with missing oysters also coded as dead individuals. We combined missing and dead oysters because missing oysters were typically found detached and immediately below experimental plots with evidence of predation (drill holes). This classification is also consistent with prior modeling approaches (Cheng & Grosholz 2016, Cheng et al. 2022). As in our past studies, the survival data exhibited 'complete separation', which occurs when the response data are perfectly predicted by the predictors (e.g. there is zero variation within a treatment). Therefore, we used Firth's bias-reduced logistic regression (Heinze & Schemper 2002), which uses a penalized maximum-likelihood estimation procedure to account for data exhibiting complete separation. For this analysis, we modeled the effects of tidal elevation, caging treatment, and their interaction as predictors of oyster survival. We then used Tukey's post-hoc tests to compare treatment groups.

While we expected survival to increase with tidal elevation, we also expected that growth might decrease with increasing elevation due to decreased inundation times. To quantify growth, for oysters that were alive at the end of the experiment, we used image analysis (ImageJ v.1.51j8; Schneider et al. 2012) to measure oyster size (area cm^2) in before and after photographs of oysters in the caged treatments to calculate growth (difference in area of shells). We restricted our growth analysis to oysters in the caged treatments only, as there were too few live oysters in the uncaged and partial cage treatments. We used a linear mixed model with tidal elevation, site, and their interaction as fixed factors and tile as a random effect to evaluate differences in oyster growth. We then performed group contrasts with Tukey's HSD tests and the Satterthwaite approximation to estimate degrees of freedom. All statistical tests were done in the R statistical computing environment (v.4.2.1; R Core Team 2022) along with the packages 'glmmTMB', 'logistf', 'car', 'emmeans', and 'tidyverse'.

2.3. Oyster recruitment and survival by tidal elevation

Oyster recruitment is essential to the success of self-sustaining restoration projects. To determine the effects of tidal elevation on oyster recruitment and longer-term (>3 mo) survival, we used settlement tiles to measure oyster recruitment and survival at 7 sites (Table 1). Although we surveyed 10 sites (see Section 2.4), permitting issues prevented deploying tiles at all sites. For these studies, we used ceramic wall tiles as described above, which were attached to PVC frames following methods used for several earlier projects in SFB (Wasson et al. 2014, Chang et al. 2016). The frames consisted of a horizontal bar and 2 vertical legs, which were attached with cable ties to rebar stakes driven into the ground. A hole was drilled in the center of each tile, and tiles were attached to the horizontal bar of the frame, oriented horizontally with the unglazed side facing down, with a stainless-steel bolt and nylon wingnut. In total, 6 tiles were attached to each frame: 3 below the horizontal bar that served as recruitment tiles and 3 above that served as survival tiles. At each site, we placed 2 frames, with the horizontal bar centered at the 3 tidal elevations described above.

Tiles were placed in the field in June 2017. For each tidal elevation, we had 6 tiles for recruitment measurements and 6 tiles for survival measurements. We retrieved recruitment tiles and replaced them with new tiles quarterly until fall 2018 (total of 5 timepoints: approximately September 2017, December 2017, March 2018, June 2018, and September 2018). The survival tiles remained in the field for the duration of the project and were photographed quarterly.

Recruitment tiles were brought into the laboratory where they were viewed under a dissecting microscope at 10× magnification. All live oysters on the tiles were counted and measured; dead oysters with top valves were also counted and drill holes were noted. For analysis, recruitment rates were calculated

Table 1. Study sites in geographical order, southwest to northeast, around Richardson Bay, California, USA (see Fig. 1). ✓: activities at each site. Transect surveys were done at all 10 sites at elevations where hard substrate was present. Recruitment and survival tiles were placed at all 3 tidal elevations at 7 of the sites

| Site | Hard substrate survey at tidal elevations | | | Recruitment tiles | Survival tiles |
	Low	Mid	High		
Dunphy Park	✓	✓	✓	✓	✓
Bothin Marsh			✓		
Brickyard Park	✓	✓	✓	✓	✓
Strawberry Point	✓	✓	✓		
Aramburu South	✓	✓	✓	✓	✓
Aramburu Central	✓	✓	✓	✓	✓
Cove Apartments		✓	✓	✓	
Lani's Beach		✓	✓	✓	
Blackies Pasture		✓			
Hilarita		✓	✓	✓	✓

from the number of recruits per unit area per day the tile had been in the field. We used a generalized linear mixed model (GLMM) with negative binomial error distribution to evaluate the relationship between mean recruitment counts and site and elevation during the recruitment tile deployment period, with site assigned as a random factor to account for repeated measures. Elevation was treated as a categorical variable, as our estimates of the exact elevation at each site were based on the National Oceanographic and Atmospheric Administration (NOAA) tide level predictions rather than observed water levels, which can deviate from predictions due to factors such as weather, storm runoff, and local topography.

To calculate survival rates, we used field photographs of tiles and assigned unique numbers to individual oysters. By comparing photographs from successive quarters, we were able to determine which oysters had survived and which had died (either missing from tile or empty shell remaining). As new oysters appeared on the tile, they were assigned numbers and their survival was tracked. For each quarter, we then calculated survival on a per-site basis by dividing the number of live oysters by the total oysters from the previous quarter, as low sample size prevented us from being able to calculate survival rates per tile. We then assessed the probability of survival of individual oysters using a logistic regression (GLMM with binomial error distribution). Individual oysters were coded as live or dead for each timepoint. Sites were classified as having drills (present) or no drills (absent). Fixed factors used in the model were drill presence at a site and elevation, with oyster ID specified as a random variable to account for repeated measures. As in the recruitment model described above, elevation was treated as a categorical variable. The interaction between drill presence and elevation was not examined, as the 2 variables were partially confounded and the interaction would have been uninformative.

2.4. Field surveys: adult oyster and drill distribution

Surveys of natural populations were carried out to determine whether and where oysters and oyster drills co-occur within our study sites and whether this varies by tidal elevation. Adult population densities are the result of the cumulative effects of settlement and survival over time, and thus provide clues for how oyster restoration projects might perform at these sites and elevations over the longer term. In June and

July 2017, we established 10 intertidal field sites in Richardson Bay (Fig. 1). Sites were selected based on previous research and/or site visits earlier that year with the goal of representing the range of both oyster and oyster drill abundances found in Richardson Bay. At each site, we established permanent 30 m transects at 3 tidal elevations: ca. +0.1, ca. +0.5, and ca. +0.8 m MLLW. These elevations were selected to represent low, mid, and high tidal elevations over which oysters might be found in Richardson Bay based on preliminary surveys. The low, mid, and high elevations were exposed to air during low tides on average approximately 5, 21, and 38% of each day, respectively. Tidal elevation was estimated using tide level predictions for Sausalito, CA, from NOAA (www.tidesandcurrents.noaa.gov/). At each study site, on a calm-weather day (little wind or wave surge) we deployed a stake at the water's edge at the time that the tidal elevation was predicted to be at our selected elevations. These stakes were left in place and used as transect start- and end-points for repeat visits to each site for the duration of the study.

Oysters require hard substrate to settle, and although oyster drills can travel across mud and are sometimes found buried in shallow mud near rocks or cobble, they tend to aggregate on hard substrates where many of their preferred prey items live (Carriker 1955, Buhle & Ruesink 2009, authors' pers. obs.). Earlier surveys on intertidal mudflats at some of our sites also revealed few if any drills (authors' unpubl. data). Therefore, we only surveyed transects that contained hard substrates. All sites had hard substrate at one or more of the target elevations, and 5 sites had no hard substrate at the lowest elevation (Table 1).

We surveyed sites at least 4 times during low tides in summer (June–July 2017), fall (September–October 2017), winter (December 2017), and spring (April–May 2018). An exception to this schedule was a site (Strawberry Point) that was first surveyed in late August due to permitting delays; the fall survey was then skipped at this location. At the 7 sites where we also monitored for recruitment and survival, we surveyed a fifth time, in July 2018. At each sampling interval, we attempted to survey sites within a single spring (extreme low) tide series; all sites were surveyed within 2 subsequent spring tide series (2 wk apart).

In each transect on hard substrate, we counted and measured oysters and oyster drills within 50 × 50 cm quadrats. Transects were placed alternately shoreward and seaward along the transect line. Quadrat locations were selected using a random number gen-

erator, with 5 numbers generated to fall between the 0 and 15.0 m marks on the transect line and 5 between 15.1 and 30 m. We made counts of all live oysters and oyster drills found within the quadrats.

3. RESULTS

3.1. Field experiment: effects of tidal elevation on drill predation and oyster survival and growth

We observed drills on the tiles at the +0.5 m tidal elevation 1 d after deployment and on the lower and higher set of tiles within 1 wk. At Aramburu South, and particularly at the lowest tidal elevation, we observed small cancrid crabs (mostly *Romaleon antennarium* and some *Metacarcinus magister*) inside the cage controls, and we observed broken oyster shells in these treatments, which suggested at least some crab predation had occurred in addition to drill predation.

Tidal elevation interacted with caging treatment to determine oyster survival in the cage experiment (Fig. 2). For oysters on uncaged tiles, survival was greatest at the highest tidal elevation tested (mean ± SE: 45.9 ± 7.1% on uncaged tiles and 25.7 ± 7.4% on partially caged tiles). Survival was intermediate at the lowest elevation (17.7 ± 6.4% on uncaged tiles and

22.2 ± 6.2% on partial cages). Survival was lowest at the mid elevation (0% uncaged tiles and 2.5 ± 1.9% partial cages). Across all tidal elevations, oysters in cages had the highest survival (86.5 ± 2.6, 89.8 ± 3.5, and 87.9 ± 2.7% at low, mid, and high elevations, respectively). The bias-reduced logistic regression indicated that survival was influenced by the main effects of elevation ($p < 0.001$), caging treatment ($p < 0.001$), and their interaction ($p < 0.001$).

Oyster growth was calculated for 375 oysters in the closed cage treatment across the 3 tidal elevations and 2 sites. Tidal elevation had an effect on oyster growth over the month that tiles were deployed (one-way ANOVA, $F = 89.98$, df = 2, $p < 0.0001$). In caged treatments, oyster growth was greatest at the lowest tidal elevation (mean final size: $3.3 ± 0.01$ cm^2), intermediate at the middle elevation ($2.7 ± 0.07$ cm^2), and smallest at the highest elevation ($1.5 ± 0.13$ cm^2). Tukey's HSD determined that these differences between tidal elevations were statistically significant. Growth was driven by both elevation ($\chi^2 = 328.5$, df = 2, $p < 0.001$), site ($\chi^2 = 15.8$, df = 1, $p < 0.001$), and their interaction ($\chi^2 = 20.9$, df = 2, $p < 0.001$). Pairwise contrasts generally revealed decreased growth with increasing tidal elevation but with some evidence for complex interactions with site (Table A1 in the Appendix). This pattern of declining growth with elevation was strongest for oysters deployed at the Cove Apartments but less so for Aramburu (Fig. 3).

3.2. Oyster recruitment and survival by tidal elevation

Some recruitment occurred at all monitored sites but was greatest overall at sites that had adult oyster populations (Fig. 4). Recruitment was not significantly correlated with elevation ($p > 0.31$ for all elevations). Relative to Aramburu Central (an arbitrarily chosen reference site with low recruitment overall at mean $0.4 ± 0.2$ oysters m^{-2}), both Brickyard and Dunphy had significantly greater recruitment across all elevations (GLMM: $z = 3.567$, $p = 0.0003$ for Brickyard with $3.1 ± 0.4$ oysters m^{-2}; $z = 3.360$, $p = 0.0008$ for Dunphy with $1.3 ± 0.2$ oysters m^{-2}). No other sites were significantly different from Aramburu Central across all timepoints.

Over time, survival of the oysters that recruited to tiles was greatest at the 2 sites without drills (Dunphy Park and Brickyard Park) (GLMM, $\chi^2 = 12.582$, $p = 0.00039$; Fig. 5). There was a trend towards higher survival at higher tidal elevations compared to the low
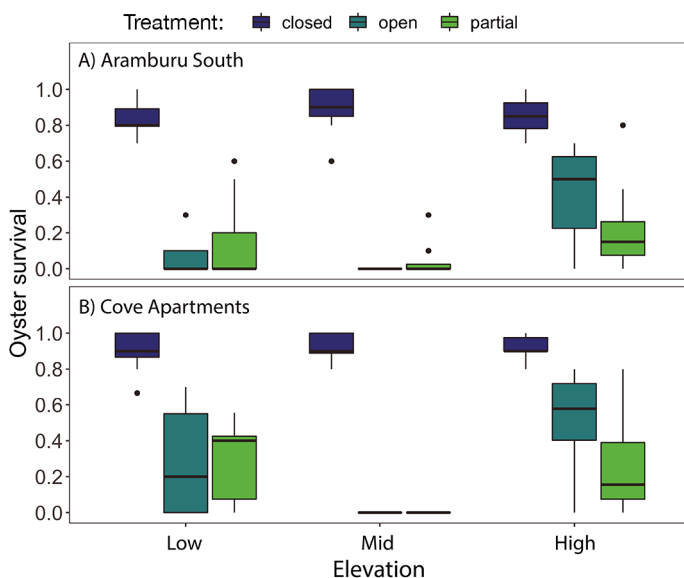

Fig. 2. Oyster survival (proportional) by tidal elevation at Aramburu Island South and Cove Apartments (Richardson Bay Audubon Center). For treatments accessible to predators, oyster survival was highest at the +0.8 m tidal elevation. Box plots — bar: median; box: interquartile range; whiskers: 1.5× interquartile range; dots: outliers
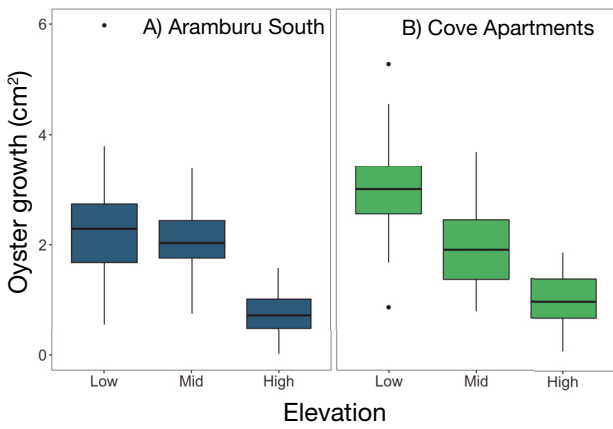
Fig. 3. Oyster growth by tidal elevation within closed treatments in the field experiment at (A) Aramburu South and (B) Cove Apartments. Boxplot parameters as in Fig. 2

elevation at some sites in some quarters, but this was not statistically significant. Oysters did not recruit to the survival tiles at Lani's Beach or Cove Apartments, or to the highest tidal elevation at any site except Brickyard Park.

3.3. Field surveys: adult oyster and drill distribution

Oysters were present in the western half of Richardson Bay across all elevations surveyed but absent from the eastern half of the bay; overall, abundance was greatest at Dunphy Park (1.1 ± 0.3, 6.8 ± 1.1, and 3.2 ± 1.1 oysters m^{-2} for high, medium, and low elevations, respectively) and Strawberry Point (0.3 ± 0.1, 2.9 ± 0.7, and 6.7 ± 1.1 oysters m^{-2} for high, medium, and low elevations, respectively; Fig. 6). Strikingly, oyster abundance was almost perfectly inversely correlated with drill presence (GLMM: $z = -3.133$, $p < 0.001$; Fig. 6); oysters and drills co-occurred only at Aramburu South. Drill density was highest at the Cove Apartments (1.0 ± 0.4 and 22.5 ± 6.9 drills m^{-2} at high and mid elevations, respectively; no drills were found at the low elevation).

Oyster abundance was greatest at mid (1.3 ± 0.2 oysters m^{-2}) and lower tidal elevations (3.1 ± 0.5 oysters m^{-2}) and lowest at the high elevation (0.2 ± 0.04 oysters m^{-2}, GLMM: $z = -4.712$, $p < 0.001$; Fig. 6). Drill abundance was highest at mid elevation
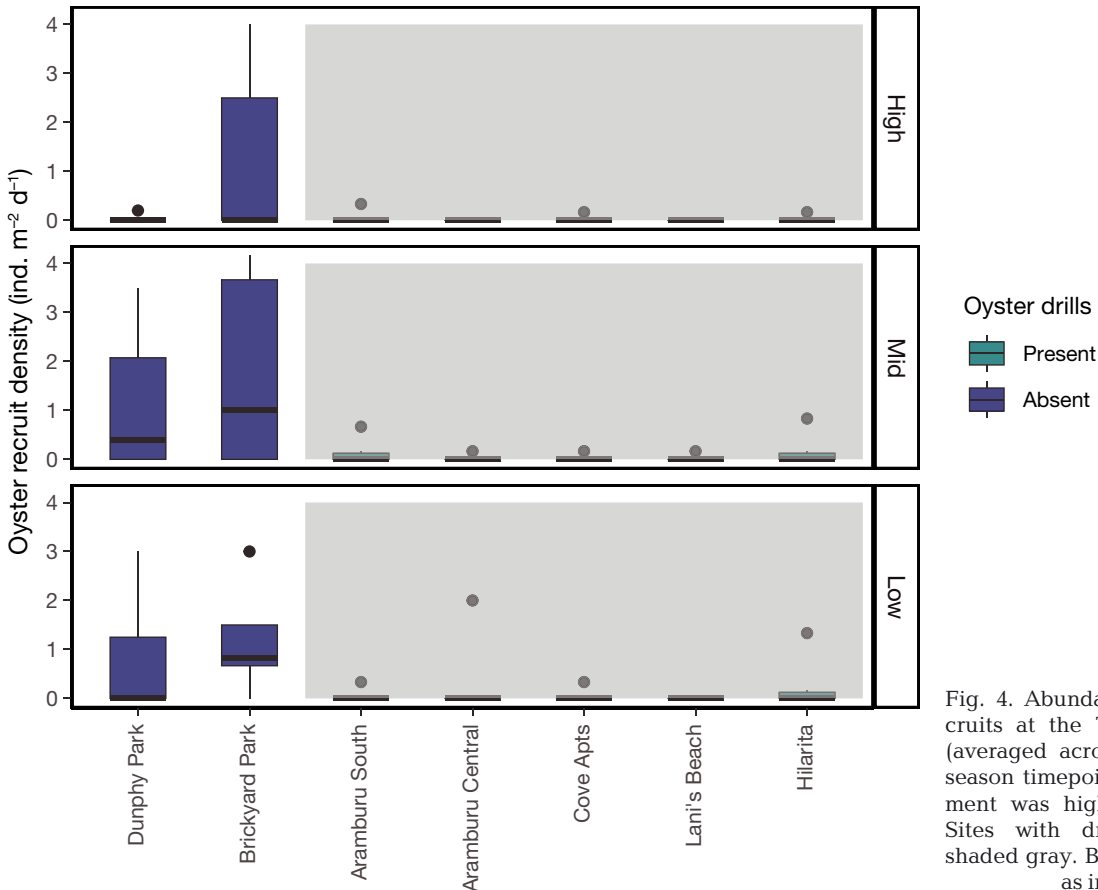

Fig. 4. Abundance of oyster recruits at the 7 sites monitored (averaged across the 2 summer season timepoints, when recruitment was highest at all sites). Sites with drills present are shaded gray. Boxplot parameters as in Fig. 2
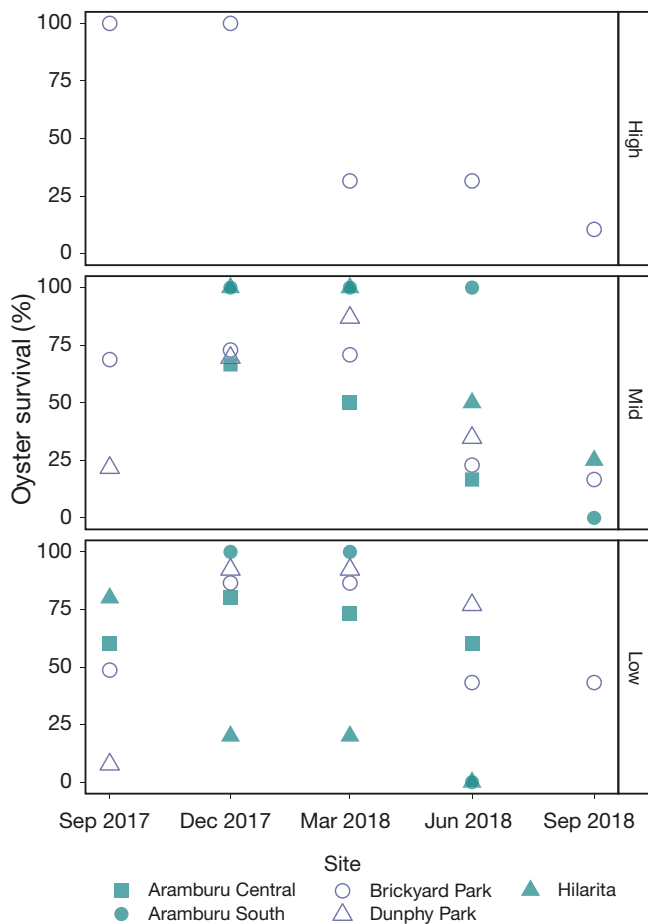
Fig. 5. Quarterly survival of naturally settled oysters on tiles that remained in place over the course of the study, across 3 tidal elevations (relative to mean lower low water). Filled shapes: sites where oyster drills were present; open shapes: sites where drills were absent. Oysters did not recruit to survival tiles at Lani's Beach or Cove Apartments or to tiles at the high elevation at any site except Brickyard Park. Overall, oyster survival was greatest at the 2 sites without oyster drills, and lower at the sites with drills

(5.1 ± 1.1 drills m^{-2} compared to 0.5 ± 0.1 and 0.8 ± 0.2 drills m^{-2} at high and low elevations, respectively; Fig. 6). Due to the lack of overlap in drill and oyster distributions across sites, there were insufficient data to assess correlations between drill and oyster abundances at different elevations in the field.

4. DISCUSSION

Intertidal restoration projects may be able to take advantage of the increase in physical stressors that occurs with higher tidal elevation when target taxa are less affected by these stressors than their competitors, predators, and parasites (Fodrie et al. 2014,

Jiang et al. 2019, Carroll et al. 2021). In such cases, locating restoration at an elevation that is highly stressful to a predator but tolerable to the target taxa might allow for the co-existence of prey and predator. However, restoration practitioners may need to balance a reduction in predation against a concurrent reduction in fitness of target taxa if the elevation is also stressful to the prey species. We demonstrated both a reduction in drill predation on oysters at our highest tidal elevation and some negative effects of increased elevation on oysters.

Our field experiment found that predation on oysters by drills was lowest at the highest tidal elevation (+0.8 m MLLW). This is consistent with the general finding from research elsewhere of decreased mortality of oysters due to drills (and other predators) at higher tidal elevations (Johnson & Smee 2014, Fodrie et al. 2014, Carroll et al. 2021) and with the results of an earlier study in SFB (Zabin & Kiriakopolos 2015). In contrast to other studies, we found that predation was highest at mid elevation (+0.5 m MLLW) and intermediate at the lowest elevation, but this is likely explained by the lack of hard substrate at the lowest elevation at our experimental sites, where drills had to cross a stretch of mudflat to reach the oyster tiles. We observed some evidence for a caging artefact at high elevations, where oyster mortality was greater in partial cage plots compared to open plots. Such an artefact most likely arose from the thermoregulatory behavior of *Urosalpinx cinerea* to reduce thermal and desiccation stress as seen in other gastropods (Chapperon & Seuront 2011, Hayford et al. 2021). At one site, we also observed some likely predation within cage controls by small cancrid crabs. However, there is little evidence that these crabs are a major source of oyster mortality in our area; indeed, in nearby Tomales Bay, oyster abundances are positively correlated with the abundance of cancrid crabs, which are effective predators on drills and ultimately benefit oysters via a trophic cascade (Kimbro et al. 2009, Cheng & Grosholz 2016).

Our experiment demonstrated that growth of young oysters that were protected from drills was inversely related to tidal elevation, suggesting that conditions are not optimal for oysters at our highest intertidal elevation. This finding is also consistent with other studies of oyster species. For example, eastern oysters in Corpus Christi Bay transplanted to the subtidal, when caged from predators, grew faster than those in the intertidal (Johnson & Smee 2014), and Olympia oyster size after 1 yr was higher at a low intertidal elevation than a higher one (Zabin et al. 2016).
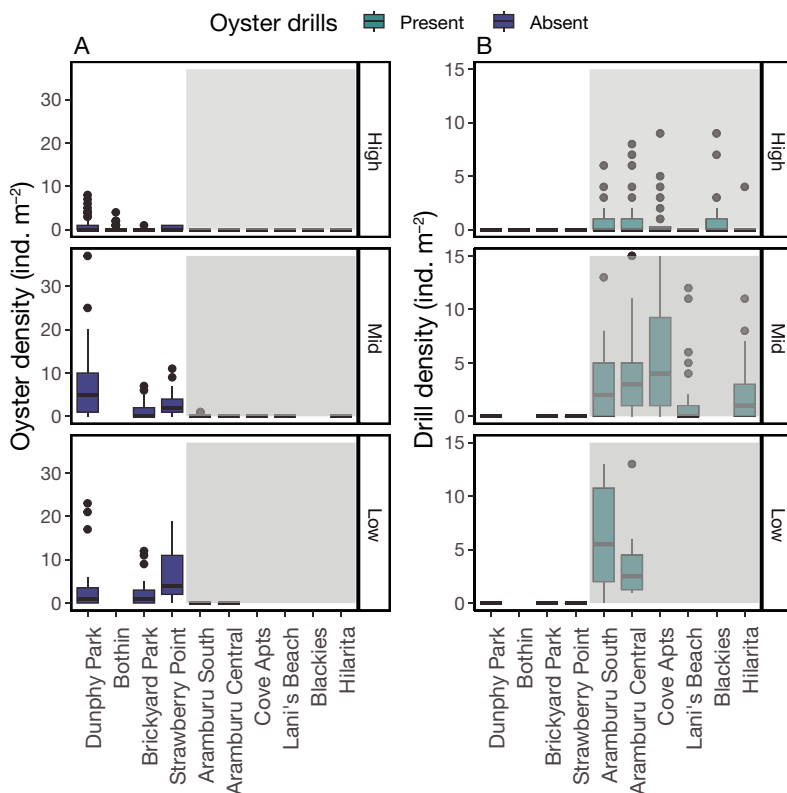
Fig. 6. (A) Oyster and (B) drill density at 10 study sites across 3 tidal elevations (relative to mean lower low water). Sites with drills present are shaded gray. All sites contained hard substrate at the high elevation, but some sites lacked hard substrate at mid and low elevations; these cases are indicated by the absence of abundance data. One outlier has been removed from the drill density panel (an observation of 74.3 drills m^{-2} in September 2017 at Cove Apartments) to present the data more clearly. Boxplot parameters as in Fig. 2

In contrast, we did not detect differences by tidal elevation in recruitment or survival of oysters >1 yr that recruited naturally to our tiles. When protected from predators in our experiment, there were also no differences in survival rates of young oysters across tidal elevations. The finding of no difference in recruitment by tidal elevation is somewhat, but not completely, surprising. While we have generally observed greater recruitment lower in the intertidal zone in SFB (authors' unpubl. data) and elsewhere (Zabin et al. 2016), this pattern does not always hold for some locations and years (Deck 2011, authors' unpubl. data). The finding of no difference in survival of young oysters (<1 yr) by tidal elevation is consistent with studies elsewhere in Central California (Deck 2011, Zabin et al. 2016). Based on our surveys of naturally occurring populations at sites without drills, however, it does appear that recruitment and/or survival are lower at the highest elevation over the long term, resulting in lower adult oyster densities. This indicates that in our area, restoration of native oysters

could be carried out from 0.0 to at least +0.8 m MLLW but that lower densities of oysters are likely over the longer term at higher elevations.

Taken together, these findings suggest that restoration could, in theory, make use of a high intertidal refuge in SFB. The approach of locating restoration above the tidal elevation that is physiologically ideal for oysters for greater long-term survival (Johnson & Smee 2014, Fodrie et al. 2014) or trying to find the tidal elevation that provides the best balance between biotic and abiotic stressors (Carroll et al. 2021) has been recommended for eastern oysters and could be considered for *Ostrea lurida* as well (Zabin et al. 2016).

However, while we did demonstrate decreased predation at the highest elevation over the month that our experiment was deployed, drills at that elevation still killed 45% of deployed oysters. This contrasts with the earlier study in SFB (Zabin & Kiriakopolos 2015) in which less than 1% of adult oysters were killed by drills at the higher of 2 tested elevations (+0.87 m compared to +0.57 m MLLW) over a 4 mo period. Two factors in addition to tidal elevation may have acted to decrease predation in the first study: oyster size and access to oysters. The oysters used in the earlier study were larger on average (23 mm; author's unpubl. data) than in the present study (12 mm), and drills appear to preferentially attack small *O. lurida* (Buhle & Ruesink 2009, Sanford et al. 2014). Additionally, in the earlier study, tiles with naturally settled oysters were deployed on a mudflat with little other hard substrate nearby and were placed above the substrate on PVC poles 7 or 37 cm tall. In the present study, tiles were in direct contact with the benthos and placed among cobbles or on the mudflats within 1–2 m of cobbles where dense aggregations of drills were present. Although *U. cinerea* readily climb PVC poles (authors' pers. obs.) and can travel across soft substrates such as mud and sand to find prey (Carriker 1955, Pratt 1977), it is possible that these factors reduced access to the experimental oysters in the earlier study. In aquaculture, oysters are often grown off the benthos on racks, which may decrease access by crawling predators such as oyster drills (T. Sawyer pers. comm.). In contrast, oyster restoration structures

are typically placed directly on the benthos (Ridlon et al. 2021); the present study thus more closely represents current restoration approaches that may give drills greater access.

Multiple other lines of evidence suggest that oyster restoration in the high intertidal within Richardson Bay is unlikely to be successful. Data from natural populations revealed that there was a nearly complete lack of live oysters on existing substrates at all surveyed tidal elevations at sites where drills were present, despite evidence that environmental conditions at these sites could still support oyster populations. In contrast, a small natural population of oysters exists on the shoreline in the high intertidal at the site where the earlier study was carried out (Wasson et al. 2014). Californian populations of introduced *U. cinerea* are also exposed to extremely long growth seasons where temperatures allow drills to forage up to 320 d yr^{-1} (seawater temperature > 10°C; Villeneuve et al. 2021), which suggests that any spatial refuge in predation is unlikely to persist over time. Additionally, Olympia oyster recruitment is extremely variable, often low in magnitude, and prone to outright failure where 0 recruits are found for an entire year (Chang et al. 2016, Wasson et al. 2016). A synthesis of oyster recruitment along the west coast of the USA revealed that 20 of 37 sites had at least 1 recruitment failure and that the average recruitment failure rate was 20% across all sites (Wasson et al. 2016). Thus, it is hard to imagine a scenario in which oyster recruitment could outpace a numerical response by drills.

For now, oyster restoration in SFB can continue to take advantage of another stressor to which oysters are more tolerant than drills: low salinity. Sites in the northern portion of SFB, which periodically receive large amounts of freshwater from 2 major river systems, are free of drills likely because of these periodic freshwater inputs. Natural populations in this part of SFB attain high densities (1000s m^{-2}; Cheng et al. 2016), and an estimated 3 million oysters recruited to a mid-size restoration project deployed there within 1 yr (Boyer et al. 2016). These sites are risky for restoration, however. Extreme freshwater input driven by atmospheric rivers, which are predicted to increase in frequency with climate change, decimate both natural oyster populations (Cheng et al. 2016) and restoration projects (Zabin et al. 2022). Unlike drills, which are direct developers, oysters can rapidly recruit back to restoration sites after flood events (Zabin et al. 2022). If fluctuating dynamic oyster populations are an acceptable outcome for restoration, these locations can be used.

Another approach is to restrict oyster restoration to the central portion of SFB, which includes Richardson Bay, and which is not as susceptible to extreme low-salinity events as areas to the north or south (Wasson et al. 2014). Our study identified 3 sites without drills, and previous work has identified other sites within the more saline waters of SFB where drills are absent (Wasson et al. 2014). However, it is not clear why these sites are drill-free, and whether they will continue to be so into the future. A habitat suitability study conducted in Richardson Bay that considered presence and size of substrate, water temperature, salinity, and inundation time indicated that all our study sites could support drill populations (Blumenthal 2019). In fact, drills have recently been recorded from Brickyard Park (A. L. Chang pers. obs.) where they had previously been absent.

Olympia oyster populations can persist in the presence of drills under some conditions. In Tomales Bay, drill populations vary in abundance and in the impacts they have on oysters; oyster densities are highest in locations where drill densities are <1 m^2 (Cheng et al. 2016). Within SFB, we have observed sites where drills and oysters co-exist and have done so for at least as long as we have been observing them (ca. 18 yr). It was thus surprising to find that the presence of drills in Richardson Bay nearly completely predicted the absence of oysters. Clearly, a better understanding of the conditions that can result in the co-existence of Olympia oysters and *U. cinerea* is needed before restoration can proceed in locations with these predators.

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Appendix.

Table A1. Pairwise contrasts in oyster growth analysis. Contrasts are considered significant at $p \leq 0.05$

Contrasts	Estimate	SE	df	t	p
Low Aramburu South × Mid Aramburu South	0.180	0.137	39.8	1.313	0.776
Low Aramburu South × High Aramburu South	1.493	0.136	39.5	10.951	<0.001
Low Aramburu South × Low Cove Apts	−0.769	0.136	39.5	−5.639	<0.001
Low Aramburu South × Mid Cove Apts	0.348	0.155	39.1	2.240	0.243
Low Aramburu South × High Cove Apts	1.223	0.141	39.2	8.688	<0.001
Mid Aramburu South × High Aramburu South	1.313	0.135	38.4	9.693	<0.001
Mid Aramburu South × Low Cove Apts	−0.949	0.136	38.3	−6.999	<0.001
Mid Aramburu South × Mid Cove Apts	0.169	0.155	38.2	1.090	0.882
Mid Aramburu South × High Cove Apts	1.044	0.140	38.1	7.456	<0.001
High Aramburu South × Low Cove Apts	−2.262	0.135	38.1	−16.737	<0.001
High Aramburu South × Mid Cove Apts	−1.145	0.154	38.0	−7.418	<0.001
High Aramburu South × High Cove Apts	−0.269	0.140	37.9	−1.931	0.400
Low Cove Apts × Mid Cove Apts	1.117	0.154	38.0	7.237	<0.001
Low Cove Apts × High Cove Apts	1.992	0.140	37.8	14.266	<0.001
Mid Cove Apts × High Cove Apts	0.875	0.158	37.9	5.529	<0.001