Bay-wide abundance estimates of native (*Ostrea lurida*) and non-native (*Magallana gigas*) oysters in San Diego Bay, CA

Final Report

- Prepared for –

Merkel & Associates, Inc.

and

Port of San Diego

- Prepared by -

Bryce Perog, Chelsea Bowers-Doerning, Marah Wolfe, and Dr. Danielle Zacherl

California State University Fullerton

June 2022

ABSTRACT

Urbanization and resource exploitation have resulted in drastic declines of native estuarine species impacting critical ecosystem services. Simultaneously, non-indigenous species (NIS) have established populations in areas outside of their native distribution, sometimes becoming invasive. Long-term monitoring of native species and NIS is necessary to identify trends between their population dynamics and changes in distribution caused by climate change and human-induced impacts. In 2020, we developed abundance estimates for native oysters, *Ostrea lurida,* and NIS, *Magallana gigas,* for the Port of San Diego by extrapolating densities measured on different habitat types to the total habitat available in San Diego Bay, assayed by using Google Earth imagery. We later determined that pier piling habitat was severely under-sampled, so in 2021, we aimed to provide a more accurate bay-wide abundance estimate for both oyster species by surveying additional pier piling habitat. In addition, we examined whether densities and percent cover of oysters vary across sites and tidal elevations and if densities differed between oyster species and across habitat types. In 2021, we sampled pier pilings across 10 sites, both above floating docks and below stationary docks as available. We found that pier pilings below stationary docks are a critical habitat for *O. lurida*, allowing them to achieve a broader and higher tidal distribution and significantly greater densities compared to other habitats. By sampling this habitat, our *O. lurida* bay-wide abundance estimate was 52% higher in 2021 versus our 2020 estimate, while our *M. gigas* abundance estimate increased by 6%. *O. lurida* are numerically dominant in San Diego Bay, but *M. gigas* still dominate in percent cover across all habitats. The bay-wide estimated abundance for *O. lurida* was 76,115,266 oysters and for *M. gigas* was 30,288,069 for a total of 106,403,335 oysters bay-wide. Our baseline abundance estimates will provide a benchmark against which to compare future changes in the population demographics of both oyster species.

INTRODUCTION

Estuaries and bays provide important habitat for a broad array of fish, bird, and invertebrate species. Urbanization, resource use, and commercialization have resulted in drastic declines of native estuarine species abundances through habitat reduction and modifications to the natural hydrology (Lotze et al., 2006; Van Dyke & Wasson, 2005). Shoreline armoring is one form of modification used to protect the thousands of structures in the U.S threatened by the effects of climate change (NOAA Fisheries, 2020), however breakwaters, jetties, and seawalls can fragment or eliminate natural habitats (Goodsell et al., 2007) and accelerate erosion (Gittman et al., 2015). Reductions in native species through anthropogenic modifications can also impact critical ecosystem services, leaving these habitats at risk for poor water quality and invasions by non-indigenous species (Lotze et al., 2006, Wells et al., 2019).

Non-indigenous species (NIS) have established populations in areas outside of their native distribution, typically as a result of deliberate or accidental human activity. NIS may become invasive if they have adverse economic or ecological consequences, including the reduction in native species richness or abundance (Blum et al., 2007). Estuaries are highly invaded relative to the open coast (Ruiz et al., 1997), and anthropogenic structures may favor the settlement of NIS (Airoldi et al., 2015; Bulleri & Chapman, 2010; Tyrrell & Byers, 2007). Long-term monitoring of NIS is necessary to identify trends between their population dynamics and changes in distribution versus long-term factors including climate change and habitat transformation (Pyšek et al., 2020).

Understanding the relative densities and abundances of both native species and NIS can provide a clearer picture of the state of their populations that can be tracked through time. Density is defined as the number of individuals per unit area, while abundance is the overall number of individuals in an area. Density can be used to extrapolate the abundance of individuals in an area, but sites and habitats are highly variable in the number and diversity of animals they can support. Abundance estimates can expose areas with low numbers of individuals of the species of interest that can be targeted for restoration. Abundances can be estimated through various methods, including line transects, mark-recapture, and statistical modeling. Abundance estimate methods are well-established for mobile species including harbor porpoises (Hiby & Lovell, 1998), lake fish larvae (McKenna Jr. & Johnson, 2009), endangered vaquitas (Jaramillo-Legorreta et al., 1999), rare blue whales (Williams et al., 2011), and economically important blue crabs (Zohar et al., 2008). Remote sensing via satellite imagery has been used to opportunistically estimate abundances of congregating species (Moxley et al., 2017), marine macro-debris on the shoreline (Kataoka et al., 2018), and intertidal algae and subtidal kelp beds (Mora-Soto et al., 2020). Plant abundance has been estimated by extrapolating percent cover values of woody plants (Cornwell & Ackerly, 2010), and may be applied to sessile animals. The habitats for organisms targeted for abundance estimates are often homogenous, but some habitats (e.g., intertidal habitats) are heterogenous. Estuarine intertidal habitat can be highly variable, especially with the increase in shoreline armoring (see example of California counties in Griggs & Patsch, 2019). Challenges with estimating abundance of organisms in heterogenous environments have been addressed for invasive oyster drills (Buhle & Ruesink, 2009), horseshoe crabs hibernating in winter (Liang et al., 2017), and salamanders (Dodd Jr & Dorazio, 2004), but estimates of these species have the added complexity of difficulty of detection. Defeo & Rueda (2002) have advised using models instead of extrapolating density measurements for heterogenous environments that yield patchy distributions of intertidal swash-zone species, however, sessile mussel abundances have been successfully estimated using randomly-placed quadrats along transect to determine density, which, when multiplied by habitat area, can provide abundance estimates (Bodkin et al., 2018; Pooler & Smith, 2005). Oysters are another group of species occupying heterogenous estuarine environments and although changes in oyster abundance have been studied over time using harvest amounts and reef size (when present) as proxies for abundances (Zu Ermgassen et al., 2012; Zu Ermgassen et al., 2016), commonly-found remnant oysters settled upon habitats outside of oyster grounds have typically not been considered. Currently, oysters on the U.S. west coast rarely form high-density oyster grounds but they can be common members of diverse intertidal assemblages, so methods applied to mussel abundance estimates can be used to help establish new baseline abundance estimates of remnant oyster populations.

The native Olympia oyster, *Ostrea lurida,* is distributed from British Columbia to Baja California (Polson & Zacherl, 2009). It was historically abundant along its range, and wild *O. lurida* populations were used for aquaculture until their reefs were depleted at which point non-indigenous Pacific oysters, *Magallana* (formerly *Crassostrea*) *gigas*, were imported from Japan and implanted into the estuaries to supplement the industry (Barrett, 1963). In San Diego Bay, native oyster reefs were present but not abundant enough to support harvest by as early as the 1930s due to pollution in the bay (Bonnot, 1935). Today, *M. gigas* are well-established in multiple locations within the *O. lurida* geographic range (Kornbluth et al., 2022, Polson & Zacherl, 2009), including in Puget Sound, Washington and in San Diego Bay (Crooks et al., 2015; Tronske et al., 2018), California. *M. gigas* may have a facultative or detrimental (Buhle & Ruesink, 2009; Trimble et al., 2009) role in *O. lurida* recovery, so it is critical to establish a baseline of the two species' abundance where their distributions overlap.

The bay mussel, *Mytilus galloprovincialis*, is another non-native bivalve that is established on the west coast of North America (Fofonoff et al., 2018). Its native range is the Mediterranean, but its invasive range is not fully defined partly because *M. galloprovincialis* is a morphologically cryptic species in a species complex with four other *Mytilus sp*. (Fofonoff et al., 2018). *M. galloprovincialis* was introduced to supplement native *M. trossulus* aquaculture on the west coast of North America, including in Agua Hedionda Lagoon in San Diego County (Shaw, 1997), but its mechanism of spread to other areas in California is largely unknown (Fofonoff et al., 2018). *M. galloprovincialis* was first detected in San Diego in 1987 by molecular analysis (McDonald & Koehn, 1988) and has since hybridized with the native *M. trossulus* (Braby & Somero, 2006). *M. galloprovincialis* can cause reduced growth and survival of native mussels (Shinen & Morgan, 2009). Recent mussel surveys in Newport and San Diego Bays have yielded only *M. galloprovincialis*, among which there may be cryptic hybrids (Garcia, Walter, and Zacherl, unpublished data, 2018).

O. lurida, *M. gigas*, and *M. galloprovincialis* co-occur within estuarine intertidal habitat. Their adult densities overlap but are partly separated by tidal elevation, where *M. gigas* is found at upper intertidal elevations, *O. lurida* is found at lower intertidal to shallow subtidal elevations, and *M. galloprovincialis* is found between and among the two oyster species (Figure 1). Bivalves provide important ecosystem services (see review, Padilla, 2010). For example, oysters, as foundation species, increase ecosystem productivity (Peterson & Heck Jr., 1999), provide water filtration, improve water quality, and enhance available habitat (Coen et al., 2007). Oysters sequester carbon when they deposit carbon-rich seston into the sediment and facilitate the expansion of other carbon sinks (Fodrie et al., 2017) and contribute to bioremediation (Dalrymple & Carmichael, 2015).

Figure 1. Example zonation of three bivalve species on a pier piling below a dock at Tom Ham's Lighthouse, San Diego, CA, in 2021. *M. gigas* is at the highest elevation, *M. galloprovincialis* is in the middle, and *O. lurida* is within and below the band of mussels.

San Diego Bay has the highest percentage of hard armored shoreline among counties in California (Griggs & Patsch, 2019). The San Diego Bay Integrated Natural Resources Management Plan has reviewed the negative environmental impacts to the bay from armored shorelines and has goals to reduce their impact and improve estuarine ecosystem health. Of the intertidal habitat in the bay, 74% has been armored since 1859 (USDN/NFECS & Port of San Diego, 2013). Although the habitat in the intertidal has changed dramatically, the artificial hard habitat is still utilized by intertidal organisms, including oysters and mussels. The Port of San Diego was interested in establishing baseline abundance estimates of native *O. lurida*, non-indigenous *M. gigas*, and non-indigenous *M. galloprovincialis* in San Diego Bay and monitoring them over time to inform aquaculture and blue technology opportunities in the bay.

In 2020, we developed abundance estimates for *O. lurida* and *M. gigas* by extrapolating densities measured on different habitat types to the total habitat available in San Diego Bay, assayed by using Google Earth imagery. We completed surveys before understanding the dominant substrate types, and later determined that pier piling habitat was severely under-sampled in our surveys (we sampled 0.002% of total estimated pier piling habitat available in the bay). In 2021, we aimed to provide a more accurate bay-wide abundance estimate for both oyster species by surveying additional pier piling habitat.

STUDY OBJECTIVE

Conduct follow-up field surveys during summer 2021 specifically targeting pier pilings throughout San Diego Bay to assay bay-wide intertidal oyster abundance and density.

STUDY QUESTIONS

1. The 2021 field studies addressed the following primary question:
   What is the refined total estimated bay-wide abundance of native Olympia oysters, *Ostrea lurida* and Pacific oysters, *Magallana gigas*?

2. In addition, outside of the scope of the contract work, we explored density and percent cover of *O. lurida*, *M. gigas*, and *M. galloprovincialis* (percent cover only) on pier pilings and compared oyster densities across sites, habitat types and tidal elevations:
   a. Do densities and percent cover of oysters vary across sites and tidal elevations?
   b. Do densities differ between oyster species and across habitat types?

STUDY DESIGN & METHODS

Field Surveys

We surveyed *Ostrea lurida* and *Magallana gigas* density, percent cover, bay-wide abundance, and substrate availability at 11 sites spanning the perimeter of the bay on diverse substrata in 2020, and an additional 10 sites were selected to survey pier pilings under docks and attached to floating docks in 2021. These sites were selected based on accessibility and were distributed throughout the entire bay (Figure 2). All sites were sampled during the summers of 2020 and 2021 between the months of June and July (Table 1).

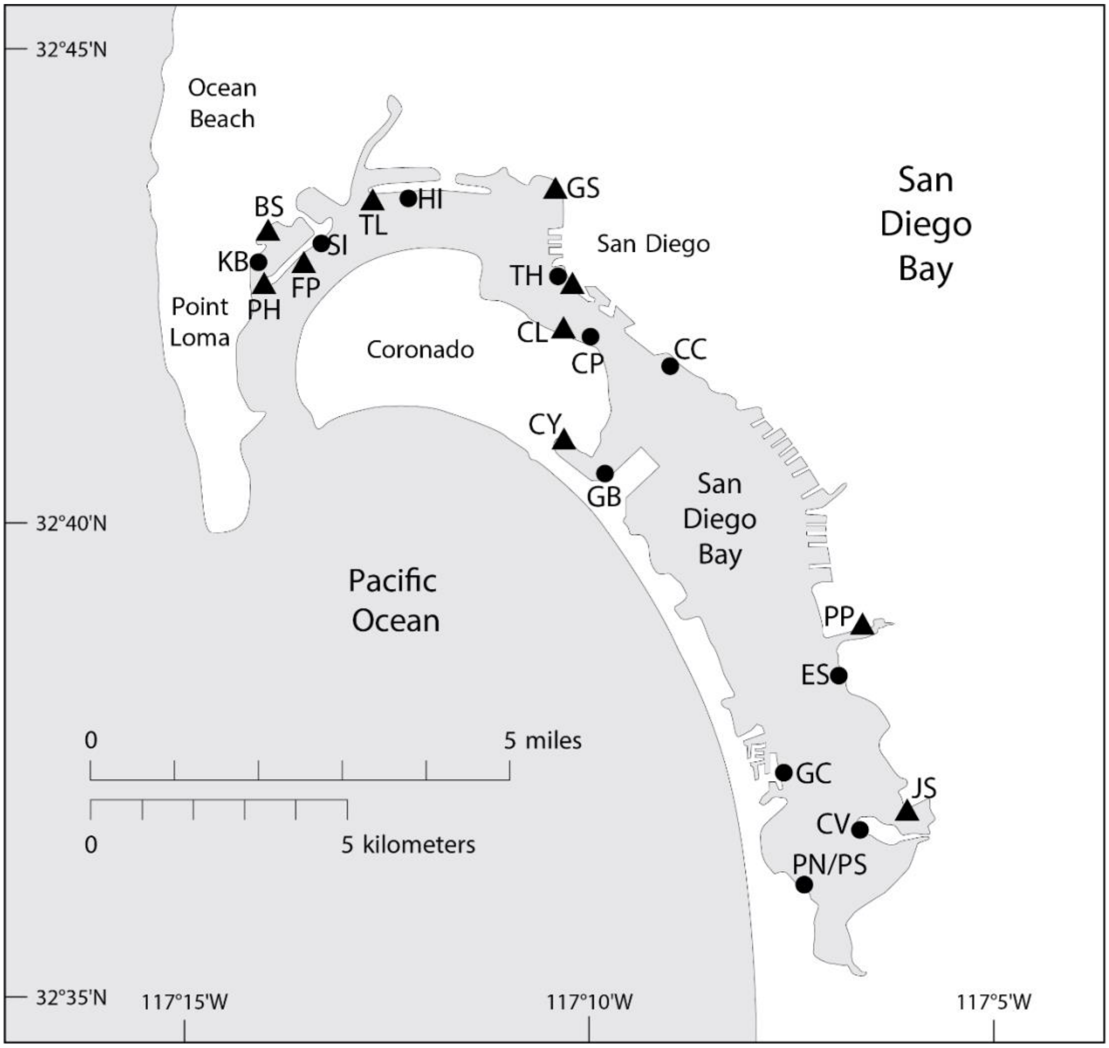

Figure 2. Oyster and mussel field survey locations in San Diego Bay, CA, in 2020 (circles) and 2021 (triangles).

Table 1. Site, tidal elevation range, oyster abundance estimate, and oyster and mussel densities and percent cover in San Diego Bay, CA from surveys performed in 2020 – 2021. *M. gallo* = *Mytilus galloprovincialis*. Note that sites are in order of increasing distance to the mouth of the bay.

Site	Code	Date of survey	Latitude, Longitude	Habitat types	Tidal elevation range sampled (m MLLW)	Abundance estimate		*M. gigas*/m^2 (SE, n)	*O. lurida*/m^2 (SE, n)	% cover *M. gigas* (SE, n)	% cover *O. lurida* (SE, n)	% cover *M. gallo* (SE, n)
						M. gigas	*O. lurida*					
Police Harbor Dock	PH	6/26/21	32.7093, -117.2350	Pier piling (above)	0.16 to 0.98	3,852	2,975	80 (14.4,39)	50.0 (13.2, 39)	15.1 (2.2, 39)	0.9 (0.4, 39)	14.0 (3.5, 39)
Kellogg Beach	KB	6/22/20 & 6/25/20	32.7114, -117.2367	Pipe, riprap, seawall, soft	-0.11 to 0.98	103,334	120,198	159.4 (16.9, 89)	144.2 (30.8, 89)	26.0 (2.6, 89)	4.5 (1, 89)	6.5 (1.0, 89)
Shelter Island Fishing Pier	FP	7/24/20	32.7115, -117.2281	Pier piling (below)	-0.1 to 0.98	12,730	56,024	115.6 (24.8, 27)	411.9 (98.5, 27)	11.5 (2.6, 27)	5.5 (1.6, 27)	30.4 (3.7, 27)
Bessemer	BS	6/27/21	32.7182, -117.2328	Pier piling (below)	-0.18 to 1.02	465	22,420	9.3 (4.8, 20)	613.3 (130.3, 20)	4.6 (2.0, 20)	20.8 (4.2, 20)	6.9 (1.6, 20)
Shelter Island	SI	7/24/20	32.7159, -117.2230	Riprap	-0.06 to 1.26	18,298	22,660	78.1 (10.3, 44)	94.8 (21.0, 44)	8.3 (1.2, 44)	0.8 (0.2, 44)	0.0 (0.0, 44)
Tom Ham's Lighthouse	TL	6/25/21	32.7213, -117.2134	Pier piling (below)	-0.31 to 0.91	12,752	79,135	172.6 (56.9, 19)	835.1 (250.0, 19)	15.5 (5.2, 19)	10.5 (4.0, 19)	14.2 (3.3, 19)
Harbor Island Park	HI	7/21/20	32.7247, -117.2076	Riprap	0.05 to 1.51	438,354	2,654,950	45.0 (6.2, 36)	126.0 (38.7, 36)	2.3 (0.7, 36)	0.4 (0.2, 36)	0.2 (0.1, 36)
Grape Street	GS	7/25/21	32.7247, -117.2076	Pier piling (below)	-0.09 to 1.48	85,586	205,787	285.3 (52.7, 33)	438.8 (153.7, 33)	22.1 (4.2, 33)	4.8 (1.8, 33)	1.7 (1.0, 33)

Site	Code	Date of survey	Latitude, Longitude	Habitat types	Tidal elevation range sampled (m MLLW)	Abundance estimate		*M. gigas*/m² (SE, n)	*O. lurida*/m² (SE, n)	% cover *M. gigas* (SE, n)	% cover *O. lurida* (SE, n)	% cover *M. gallo* (SE, n)
						M. gigas	*O. lurida*					
Tuna Harbor Pier Pilings	TH (P)	6/24/21	32.7110, -117.1744	Pier piling (above)	0.17 to 1.54	3,735	2,393	23.5 (7.6, 57)	8.5 (3.9, 57)	2.5 (0.9, 57)	0.3 (0.2, 57)	0.3 (0.3, 57)
Tuna Harbor Rip Rap	TH (R)	6/24/20	32.7118, -117.1746	Riprap	0.05 to 1.24	80,301	3,154	64.6 (7.3, 45)	2.0 (0.9, 45)	10.1 (1.2, 45)	0.6 (0.4, 45)	0.0 (0.0, 45)
Centennial Park	CP	7/23/20	32.6698, -117.1711	Riprap, seawall, soft	-0.11 to 1.35	65,680	102,505	62.0 (13.5, 45)	62.4 (25.3, 45)	4.8 (1.2, 45)	1.5 (0.6, 45)	0.1 (0.1, 45)
Cesar Chavez Park	CC	7/22/20	32.6961, -117.1511	Cobble, pier piling (below), seawall, soft	0.08 to 1.35	9,903	32,572	61.5 (19.0, 39)	99.3 (38.9, 39)	9.4 (2.4, 39)	2.4 (1.1, 39)	0.5 (0.3, 39)
Coronado Ferry Landing	CL	6/23/21	32.6995, -117.1698	Pier piling (below)	-0.31 to 1.15	10,552	109,505	127.0 (39.5, 21)	1089.5 (298.7, 21)	16.9 (5.1, 21)	25.9 (4.5, 21)	5.0 (1.3, 21)
Glorietta Bay	GB	6/10/20	32.6751, -117.1674	Chain Link Fence	0.08 to 1.2	4,144	2,764	225.5 (31.5, 34)	143.5 (38.2, 34)	32.6 (4.0, 34)	5.9 (2.0, 34)	0.0 (0.0, 34)
Coronado Yacht Club	CY	7/23/21	32.6818, -117.1742	Pier piling (above)	0 to 0.93	2,809	6,030	19.9 (9.4, 30)	30.2 (12.0, 30)	4.1 (1.9, 30)	0.9 (0.4, 30)	0.0 (0.0, 30)
Pepper Park (Below)	PP (B)	7/26/21	32.6493, -117.1123	Pier piling (below)	0.2 to 1.26	8,024	7,989	320.0 (64.0, 16)	343.3 (109.6, 16)	37.2 (6.7, 16)	6.0 (1.9, 16)	0.0 (0.0, 16)
Pepper Park (Above)	PP (A)	7/26/21	32.6496, -117.1106	Pier piling (above)	0.22 to 0.92	440	533	48.0 (30.5, 10)	56.0 (29.1, 10)	8.7 (5.3, 10)	5.3 (2.8, 10)	0.0 (0.0, 10)

Site	Code	Date of survey	Latitude, Longitude	Habitat types	Tidal elevation range sampled (m MLLW)	Abundance estimate		*M. gigas*/m² (SE, n)	*O. lurida*/m² (SE, n)	% cover *M. gigas* (SE, n)	% cover *O. lurida* (SE, n)	% cover *M. gallo* (SE, n)
						M. gigas	*O. lurida*					
Grand Caribe	GC	6/9/20	32.6263, -117.1297	Riprap, seawall, soft	-0.04 to 1.26	25,121	5,627	51.6 (9.3, 91)	18.1 (5.2, 91)	8.9 (1.6, 91)	1.0 (0.4, 91)	0.0 (0.0, 91)
E Street	ES	6/26/21	32.6332, -117.1076	Soft	-0.16 to 1.34	0	0	0.0 (0.0, 46)	0.0 (0.0, 46)	0.0 (0.0, 46)	0.0 (0.0, 46)	0.0 (0.0, 46)
J Street	JS	7/24/21	32.6244, -117.1055	Pier piling (below)	-0.17 to 1.14	2,286	43,009	8.6 (5.5, 28)	155.6 (44.4, 28)	3.6 (1.8, 28)	4.1 (1.1, 28)	0.0 (0.0, 34)
Chula Vista Wildlife Reserve	CV	6/8/20	32.6143, -117.1138	Cobble	-0.22 to 1.79	177,667	101,167	33.8 (6.5, 42)	15.1 (3.8, 42)	3.5 (1.0, 42)	0.4 (0.1, 42)	0.0 (0.0, 34)
Pond 11 North	PN	6/23/20	32.6027, -117.1178	Cobble	-0.26 to 1.01	35,693	23,509	12.9 (4.1, 43)	5.3 (1.9, 43)	2.5 (0.9, 43)	0.1 (0.1, 43)	0.0 (0.0, 43)

Field Point Contact and Density Surveys

Pier pilings in San Diego Bay are attached to floating docks as well as underneath stationary docks. Floating docks had rollers on a subset of the sides of pilings that stabilized the floating docks relative to the pilings and also acted to scrape portions of the pilings, thus the pier pilings associated with floating docks had various combinations of scraped and unscraped sides. In summer 2021, we quantified oysters on pier pilings below stationary docks at 10 sites and on floating dock pier pilings at 4 sites. Paddleboards were used to access sites with pier pilings in deep water that were otherwise inaccessible during low tides. Methods for surveys on rip rap, seawall, soft, cobble, pipe, and chain-link fence habitat were detailed in Perog et al. (2021). Substrate availability on pier piling was determined using a point-contact technique with modified gridded quadrats that contained 15 – 21 points depending upon the width of the pier piling. Quadrats wrapped around a small subset of pier pilings that were round. We randomly selected specific pier pilings to be sampled, as well as tidal elevation of the quadrat, and sides of the pier pilings that were surveyed. We recorded the cardinal direction of each quadrat because we hypothesized that exposure to the sun has an impact on oyster distribution. Correlations between cardinal direction and oyster density are not explored in this report but are available upon request. Pier pilings were each surveyed with only a single quadrat except at one site, Coronado Ferry Landing, that had limited accessible pilings.

To understand the percent cover of organisms on the pier pilings via the point-contact technique, we identified the substrate first encountered with our probe at each point. Canopy alga and bryozoan points were only counted if the probe hit the attachment site of the organism onto the pier piling. Otherwise, the algal or bryozoan canopy was moved to reveal the substrate beneath. Mobile organisms were removed and the substrate beneath was counted.

Once percent cover was quantified, we replaced the gridded quadrat with an open quadrat to collect oyster density data. Other epifaunal species such as sponges, tunicates, and dead oysters were removed as-needed to expose deeper layers of oysters. Oysters whose shells were at least halfway into the quadrat were identified and counted. We identified all live oysters by external examination of the shell based on presence/absence of shell foliations (*O. lurida* lacks foliations) or by internal identification of the presence/absence of chomata (*Ostrea* genus has chomata present; identification techniques from Polson et al., 2009; Raith 2013). A subset of oysters were measured for maximal length (mm) at each site. Data on shell lengths are available upon request.

Since pier pilings were partially submerged during the time of surveys, tidal elevation of quadrats were calculated by measuring the distance from the water to the middle of the quadrat and adding the measurement to the predicted tidal elevation by NOAA (Station ID: 9410170) at time of census. Table 1 reports the tidal elevation range for each site. A tidal elevation of 0.30 m MLLW was used as the cutoff for “high” and “low” tidal elevations for statistical and qualitative comparisons because it is the zone where *M. gigas* lower distributional limits and *O. lurida* upper distributional limits generally overlap (Tronske et al., 2018).

Bay-wide Habitat Estimates

We used Google Earth, an open-access database of satellite imagery, to determine substrate type along the entire shoreline of San Diego Bay (Perog et al., 2021). We gathered estimates for the number of pier pilings in 2020, but in 2021 we further categorized pier pilings into three groups, those above floating docks, below stationary docks, and unattached to docks. A combination of satellite imaging and in-person photos (when available) of the areas were used to identify and measure the distance (in meters) of various habitat types. We assume the number of pier pilings are underestimated due to the lack of adequate satellite and/or in-person images provided by Google Earth. Combined habitat types observed in Google Earth (i.e., sparse cobble on a sandy beach) were divided equally into each habitat category. Habitat below buildings that had obstructed views on Google Earth was hypothesized to be riprap and/or seawall from field observations of similar areas, so they were treated as combined habitat.

Habitat Type per Quadrat

For multiple sites, habitat type varied by tidal elevation such that we surveyed many different habitat types within a site. We determined the habitat type for each quadrat by assigning the hard habitat type to quadrats with at least 20% cover of hard habitat (i.e., riprap and sand are both habitat types at Grand Caribe, so a quadrat with ≥ 20% hard cover of rip rap would be classified as riprap). This 20% cutoff was established because previous survey data revealed that oysters increased in density notably at approximately 20% cover of hard habitat, so it was chosen as the cutoff between hard and soft habitat. Habitat types classified by this method are displayed in Table 1. We excluded habitat types that were profoundly under-sampled at sites (e.g., < 3 quadrats), such as boulder/riprap at Cesar Chavez Park, Pond 11 North, and Chula Vista Wildlife Reserve. Percent of habitat sampled compared to total habitat available is reported in Table 2 and was calculated by dividing the sum of all quadrat lengths per habitat type sampled by total perimeter of each habitat type bay-wide. In Perog et al. (2021), we overestimated the amount of habitat sampled by including the perimeter of the entire site sampled, but in this report, we included perimeter of quadrats sampled within sites. For pier pilings, we generally limited sampling to one quadrat per pier piling, so percent of habitat sampled was calculated by dividing number of quadrats by total number of pilings. Coronado Ferry Landing had limited pilings and 9 pilings were sampled twice, so the percent of pier pilings below stationary docks sampled was adjusted accordingly.

Abundance estimate

Bay-wide abundances of *M. gigas* and *O. lurida* were estimated by first determining the average oyster density by site, tidal elevation, and habitat type. Pier pilings were estimated to have a 1.33 m average circumference (i.e., along-shore "length"), by calculating a weighted mean average of the circumference of pier pilings found at 30 sites in San Diego Bay on maintenance construction drawings provided by the San Diego Unified Port District (T. Barrett, personal communication, 2021). The height (i.e., "width"), per elevational range was estimated for pier piling, seawall, and chain-link fence by finding the difference between the tidal elevation cutoff (0.3 m MLLW) and the lowest and highest tidal elevation. Length and width of other habitat types were estimated using the measure tool on Google Earth. We estimated site-wide abundances by multiplying average oyster density by the habitat length, width, and number pier pilings (where appropriate). Habitat dimensions and species densities were different above and below 0.3 m MLLW, so we calculated the abundance of the oysters per habitat type and tidal elevation. Abundance was calculated by multiplying the average oyster density across sites sampled by bay-wide habitat perimeter estimate and average habitat type height. Then, we summed the abundance estimates to find oyster densities per habitat type in the bay. Lastly, we summed all abundances across all habitat types to produce a bay-wide abundance estimate for each oyster species.

Data analysis

Differences in densities and percent cover of *M. gigas* and *O. lurida* were assessed (separately per species) as a function of site, tidal elevation, and their interaction using two-way ANOVAs. We also evaluated whether there were differences in density as a function of species and habitat type and their interaction using two-way ANOVAs.

Qualitatively, we observed that oysters appeared to achieve broader tidal distributions and higher densities on pier pilings below stationary docks relative to other habitat types we sampled, especially relative to “similar” vertical substrata such as concrete seawalls. Since we used oyster density on seawalls as a proxy for oyster density on pier pilings in our 2020 abundance estimates, this apparent observed difference in density seemed especially relevant to explore. To determine if these differences in density were significant, we compared densities on vertical substrata (seawalls versus pier pilings below stationary docks) as a function of tidal elevation, and their interactions using two-way ANOVAs for each species separately.

Heteroscedasticity was checked by visually examining residuals in predicted, studentized and normal quantile plots for all ANOVAs. Data that did not meet the assumptions of the ANOVA were log or square root transformed (Table A1). If main effects or interaction effects were present, then post-hoc Tukey tests were used to determine the differences among response factors. All analyses were completed in JMP version 14. Post hoc analyses can be visualized in Table A2.

RESULTS

Qualitative Observations - Pier Pilings

Oyster densities on pier pilings above floating docks and below stationary docks were vastly different, with highest densities of oysters found on pilings below stationary docks (Figure 3).

Floating dock oyster densities were negatively impacted by the presence of stabilizing elements of varying effectiveness that often scraped the pier pilings clean as the docks floated up and down with the changing tides (Figure 3A). Oyster densities were approximately 5 times higher on unscraped surfaces of floating dock pier pilings relative to scraped surfaces (Figure A1). Based upon our qualitative observations, the effectiveness of the rollers as “scrapers” and responding community assemblages varied.

Pier pilings below stationary docks had relatively very high densities of oysters forming thick clusters, with multiple layers of oysters mixed with other animals (Figure 3B). We observed fouling organisms (sponges, tunicates, and bryozoans) dominating the surface layer at lower tidal elevations on these pier pilings and thus our oyster detection efficiency may have been reduced in percent cover surveys, resulting in conservative estimates of percent cover, even when we detected high densities of oysters in excavated samples.

Intertidal habitats below stationary docks were not explicitly surveyed, but there we also observed extremely high densities of both oyster species, even occasionally forming reef assemblages that were otherwise rare in San Diego Bay (Figure 4).

Figure 3. Qualitative difference in dock community assemblages on pier pilings above floating docks (A) versus below stationary docks (B) in San Diego Bay, CA during 2021 surveys. (A) Pier pilings above dock with stabilizing roller at Coronado Yacht Club. (B) High density of oysters and other foulers at Bessemer.

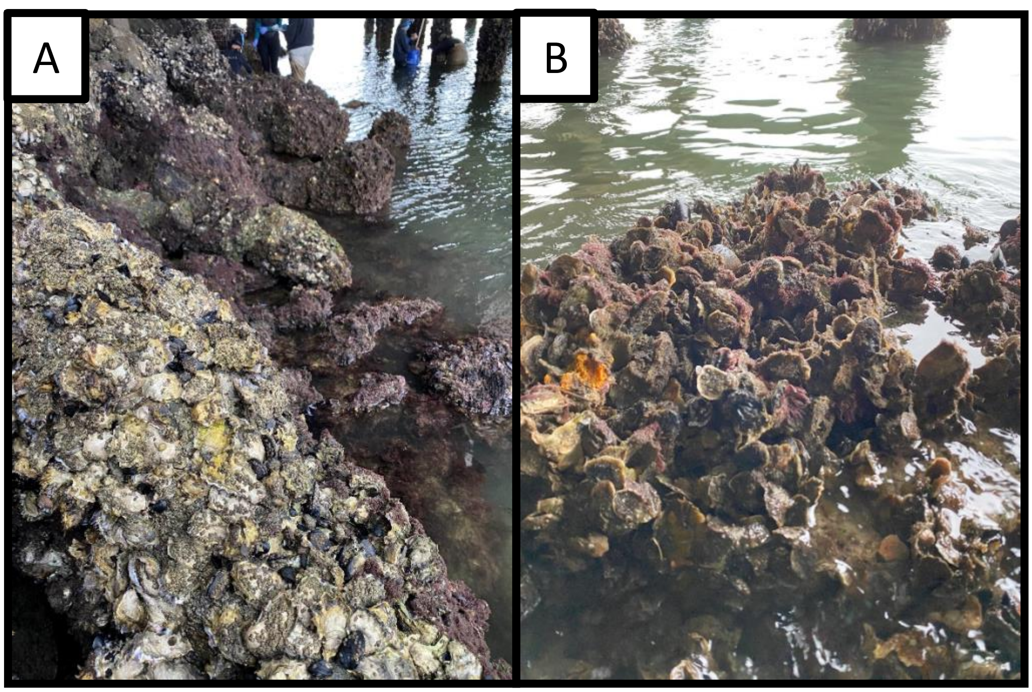

Figure 4. Patches of oyster reefs on the shoreline at Tom Ham's Lighthouse, San Diego Bay, CA, below a stationary dock in 2021. (A) *M. gigas* dominating the cover of riprap at higher tidal elevations and (B) *O. lurida* growing in a patch reef on the benthos at lower tidal elevations.

Oyster Densities and Percent Cover Across Sites and Tidal Elevation

Across all sites surveyed in 2020 and 2021 *M. gigas* average densities ranged from 0.0 to 115.7 ± 26.9 (SE) oysters/m^2 at the lower tidal elevations (< 0.3 m MLLW), and from 0.0 to 391.8 ± 63.4 oysters/m^2 at the higher tidal elevations (> 0.3 m MLLW). *M. gigas* generally achieved greater densities at high tidal elevations (Figure 5, 2-way ANOVA, 2-way interaction, site*tidal elevation, p<0.0001, Table A1a, Table A2). Average *M. gigas* densities were highest at the site PP(B) at 391.8 ± 63.4 oysters/m^2, followed by GS and TL (324.6 ± 56.1 oysters/m^2 and 271.5 ± 85.4 oysters/m^2, respectively).

Across all sites surveyed in 2020 and 2021 at the lower tidal elevations (< 0.3 m MLLW), *O. lurida* average densities ranged from 0.0 ± 0.0 to 1,723.4 ± 411.3 oysters/m^2 and at the higher tidal elevations (> 0.3 m MLLW) ranged from 0.0 ± 0.0 to 847.6 ± 316.8 oysters/m^2. *O. lurida* were generally in greatest densities below 0.3 m MLLW (Figure 5, 2-way ANOVA, 2-way interaction, site*tidal elevation, p<0.0001, Table A1b, Table A2). The greatest densities of *O. lurida* were found on pier pilings below stationary docks at TL with an average of 1,723.4 ± 411.3 oysters/m^2, followed by CL and GS (1573.3 ± 631.5 oysters/m^2 and 1,460.0 ± 760.8 oysters/m^2, respectively). At higher tidal elevations, average *O. lurida* densities were greatest on pier pilings (below) at CL (847.6 ± 316.8 oysters/m^2), followed by two sites that also had the greatest *M. gigas* densities, PP(B) and GS (365.1 ± 134.2 oysters/m^2 and 297.9 ± 127.7 oysters/m^2, respectively).

O. lurida were present in generally greater densities compared to *M. gigas*, but *M. gigas* dominated the space in percent cover, especially above 0.3 m MLLW. Percent cover of *M. gigas* across all sites surveyed in 2020 and 2021 below 0.3 m MLLW ranged from an average of 0.0 to 18.0 ± 4.2% cover and above 0.3 m MLLW ranged from an average of 0.0 to 45.1 ± 6.4% cover. Percent cover of *M. gigas* was generally greatest above 0.3 m MLLW (Figure 6, 2-way ANOVA, 2-way interaction, site*tidal elevation, p<0.0001, Table A1c-d). In addition to density of oysters, *M. gigas* percent cover was also highest at PP(B) at 45.1 ± 6.4% cover; second and third highest percent cover of *M. gigas* were found at GB and KB (37.0 ± 3.9% cover and 27.3 ± 3.0% cover, respectively).

Percent cover of *O. lurida* across all sites surveyed in 2020 and 2021 below 0.3 m MLLW ranged from 0.0 to 35.0 ± 3.7% cover and above 0.3 m MLLW ranged from 0.0 to 22.5 ± 5.7% cover. Percent cover of *O. lurida* was generally greatest below 0.3 m MLLW (Figure 6, 2-way ANOVA, 2-way interaction, site*tidal elevation, p<0.0001, Table A1c-d, Table A2). Even though BS did not have the highest densities of *O. lurida* across sites (Figure 5), highest average percent cover of *O. lurida* was found at this site (35.0 ± 3.7% cover). Five sites that achieved the highest percent cover of *O. lurida* were pier piling sites, and all but one were below stationary docks (BS, CL, TL, PP (A), GS). Above 0.3 m MLLW, the highest percent cover of *O. lurida* was found at the same site as where it was in greatest density (CL, 22.5 ± 5.7% cover).

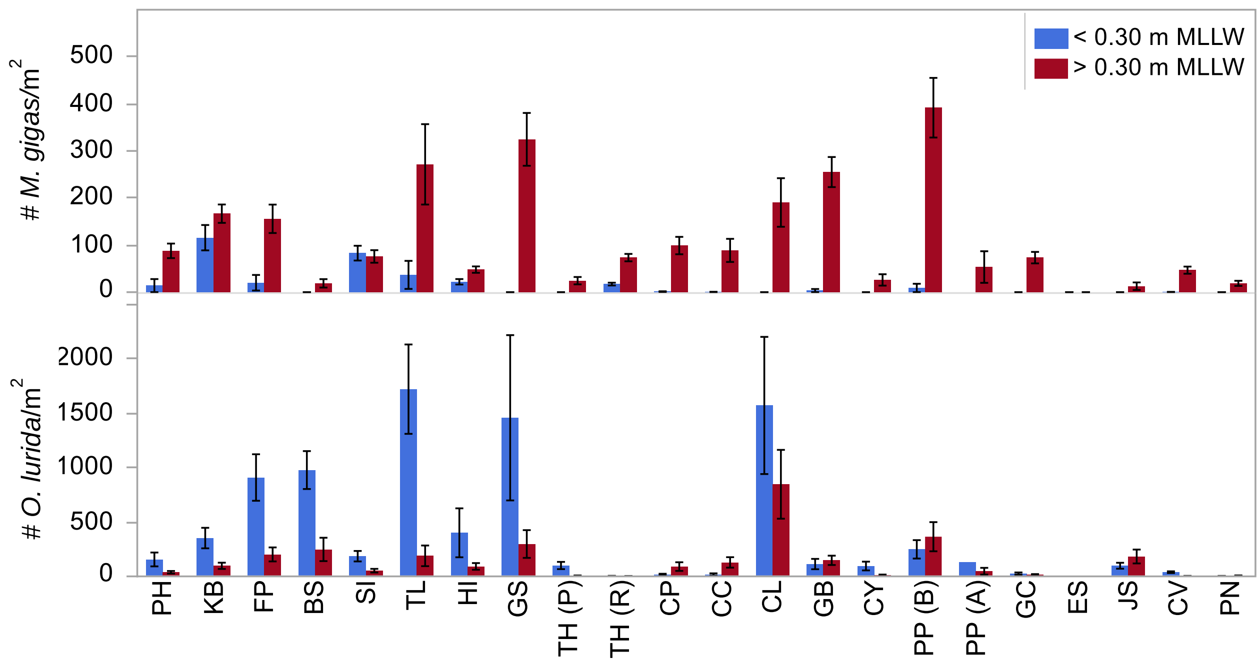

Figure 5. *M. gigas* and *O. lurida* densities below and above 0.30 m MLLW across sites in San Diego Bay in 2020 and 2021. Error bars are ± 1 SE. Site codes are identified in Table 1.

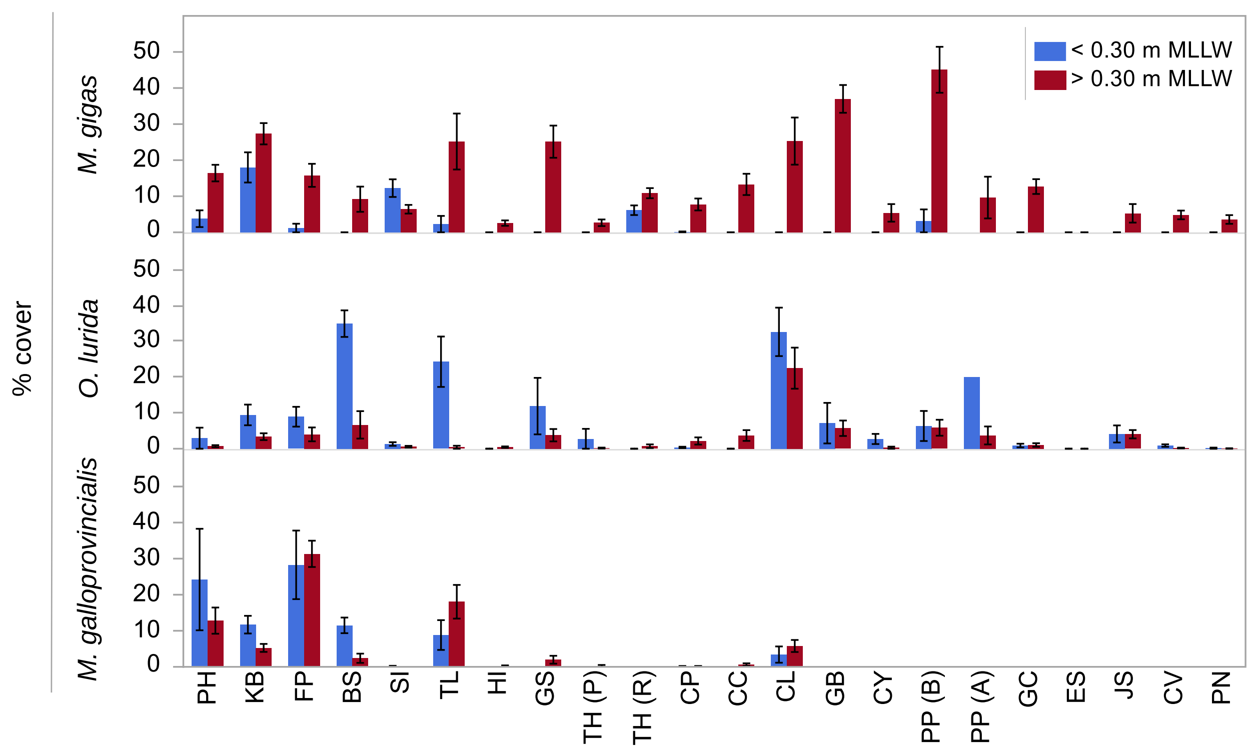

Figure 6. *M. gigas*, *O. lurida*, and *M. galloprovincialis* percent cover below and above 0.30 m MLLW across sites in San Diego Bay in 2020 and 2021. Error bars are ± 1 SE. Site codes are identified in Table 1.

Oyster Densities and Percent Cover across Habitat Type

Across all sites, both oyster species experienced their lowest densities on the only natural habitats in the bay, cobble and soft sediment. On hard substrates across all tidal elevations, average *M. gigas* densities ranged from 24.2 ± 4.1 oysters/m^2 to 285.5 ± 48.4 oysters/m^2, while average *O. lurida* densities ranged from 11.3 ± 2.2 oysters/m^2 to 518.8 ± 63.0 oysters/m^2. *O. lurida* occurred in significantly greater densities on pier pilings below stationary docks compared to *M. gigas*, while *M. gigas* occurred in significantly greater densities on riprap and seawall compared to *O. lurida* (Figure 7, 2-way ANOVA, 2-way interaction, oyster species*habitat type, $p<0.0001$, Table A1e, Table A2). *M. gigas* and *O. lurida* densities were similar on chain link fence and pipe habitats.

Across all sites, average percent cover across all tidal elevations of *M. gigas* ranged from 3.1 ± 0.7% to 34.8 ± 6.1% cover on hard substrate, while densities of *O. lurida* ranged from 0.2 ± 0.1% to 12.9 ± 3.1% cover on hard substrate. *M. gigas* had greater cover than *O. lurida* on all hard substrates except for pier piling (Figure 8, 2-way ANOVA, 2-way interaction, oyster species*habitat type, $p<0.0001$, Table A1f, Table A2).

When comparing oyster densities on pier pilings under stationary docks to seawall across all tidal elevations, pier pilings had relatively high *M. gigas* densities across a larger tidal range that expanded higher in the intertidal, where oyster distribution extended to a maximum of ~1.5 m MLLW compared to seawall at ~1.2 m MLLW (Figure 9). *M. gigas* density was greatest at higher elevations on both habitat types though the effect was stronger on pier pilings, and density on pier pilings was significantly greater than on seawall but only at the highest elevations (Figure 9, 2-way ANOVA, habitat type*tidal elevation interaction, $p=0.0006$, Table A1g, Table A2). Also see Figures A2 – A4 for depictions of these data converted into ft MLLW, in their transformed states, and binned by 1 ft tidal elevation bins, respectively.

O. lurida densities were greater on pier pilings compared to seawall across all elevations, and varied inversely with elevation (Figure 9, 2-way ANOVA, habitat type $p<0.0001$, tidal elevation $p<0.000$, Table A1h, Table A2), but also were distributed across a larger tidal range than that found on seawall, reaching a maximum of ~1.2 m MLLW compared to seawall at ~1.1 m MLLW. Also see Figures A2 – A4 for depictions of these data converted into ft MLLW, in their transformed states, and binned by 1 ft tidal elevation bins, respectively. We were able to sample lower tidal elevations for pier pilings than seawall (which typically do not extend as deeply into the lower intertidal as a habitat type) and that correlated with higher densities of *O. lurida.*

Importantly, when comparing binned mean densities across species on pier pilings versus seawalls (Figure A4), *O. lurida* density far exceeds that of *M. gigas* in the 1 – 2 ft MLLW tidal range on pier pilings, while their densities were roughly equivalent on seawalls. Further, the two species' densities are equivalent in the 2 – 3 ft MLLW tidal range on pier pilings, while, on seawalls, *M. gigas* far outpaced *O. lurida*.

Mussel Density and Percent Cover

While we did not quantify mussel density in our open quadrats, density was exceedingly low bay-wide**.** *M. galloprovincialis* occupied an average of 0.0 to 23.8 ± 9.5% cover below 0.3 m MLLW and 0.0 to 31.3 ± 3.6 m MLLW above 0.3 m MLLW across all sites surveyed in 2020 and 2021 (Figure 6). Although they were detected in percent cover measurements at 12 of the 23 sites, they exceeded an average of 10% cover at just 3 of the sites (Table 1). Average *M. galloprovincialis* percent cover ranged from 0.0 to 15.6 ± 2.9% cover across habitat types and was highest on pipe and pier piling (Figure 8).

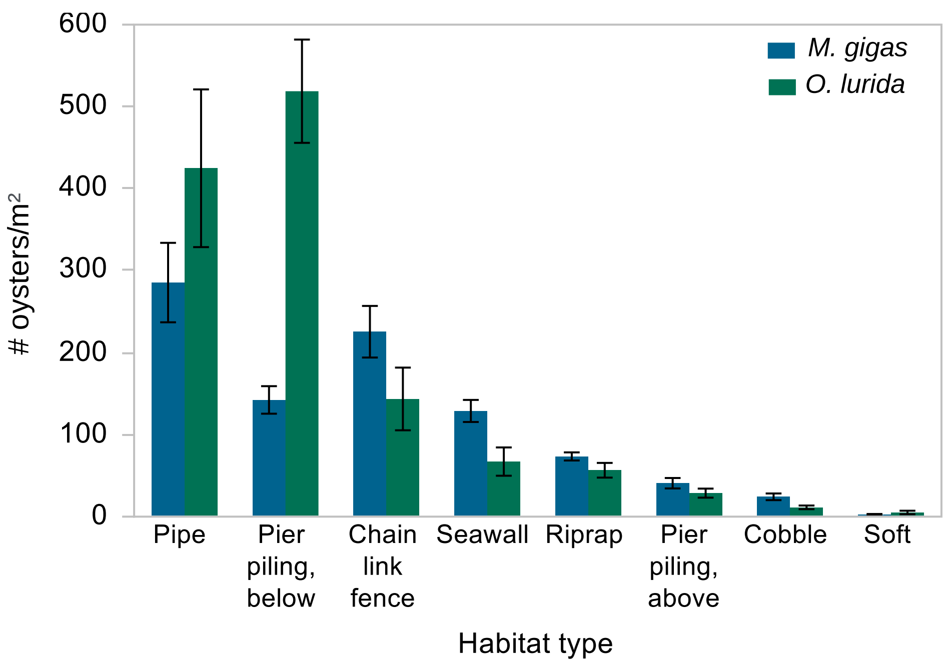

Figure 7. *O. lurida* and *M. gigas* density across habitat types in San Diego Bay, CA in 2020 and 2021. Error bars=1 SE. Note that habitat types are arranged along the X-axis in decreasing number of oysters.

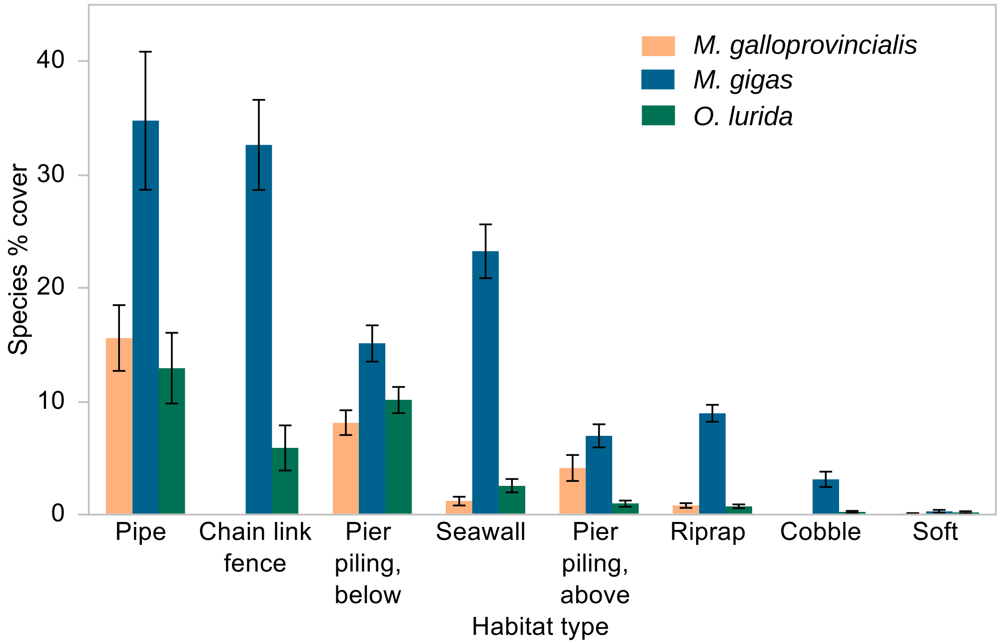

Figure 8. Percent cover of *M. galloprovincialis, M. gigas* and *O. lurida* across habitat types in San Diego Bay, CA in 2020 and 2021. Error bars=1 SE. *M. galloprovincialis* percent cover is displayed but was not included in statistical analysis. Note that habitat types are in decreasing number of oysters in the same order as Figure 7.

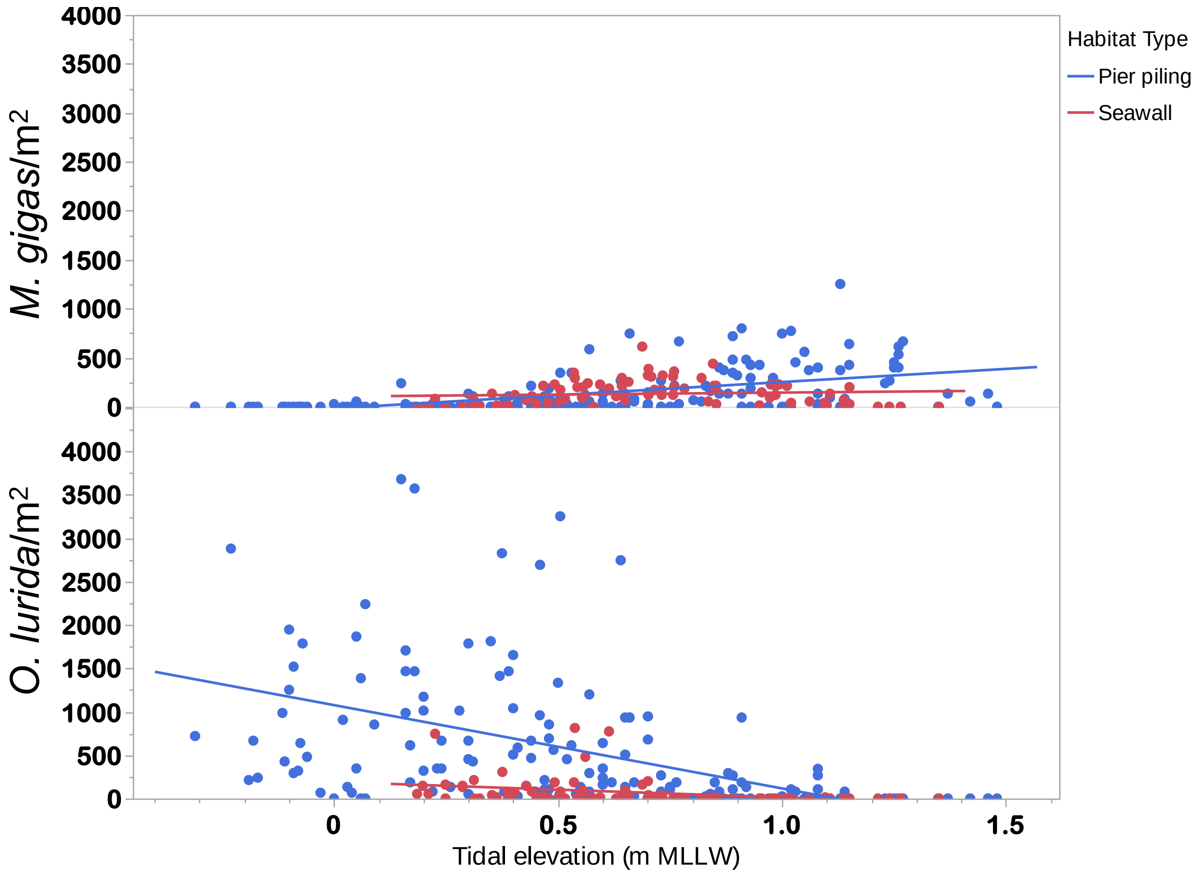

Figure 9. *M. gigas* and *O. lurida* densities on pier pilings below stationary docks and on seawall across tidal elevations in San Diego Bay, CA during 2020 – 2021. Lines of best fit shown with 95% confidence intervals.

Perimeter and Abundance Estimates

Across sites, estimated *M. gigas* and *O. lurida* abundances were highest at HI (438,354 *M. gigas* and 2,654,950 *O. lurida*) and lowest at PP (A) (440 *M. gigas* and 553 *O. lurida*) and ES (no oysters were detected in quadrats) (Table 1).

Visual surveys using Google Earth revealed that the perimeter of San Diego Bay is comprised of mostly hard substrates (81.7% comprised of rip rap, seawall, cobble, chain link fence, pipe, boat launch, outfall; Table 2) that may facilitate oyster recruitment. Most of this is human-introduced substrate, including riprap and seawalls upon which *M. gigas* densities and percent cover were higher than other substrates (Figure 7, Figure 8). Both oyster species were present on each type of hard substrate but at exceedingly low densities on the soft substrate that comprises 18.3% of the bay perimeter. Construction drawings and visual estimates of pier pilings from docks, piers, and other structures revealed an estimated 64,559 pier pilings, that included guide pier pilings attached to floating docks ("above"), below stationary docks ("below"), and unattached to a dock, used as markers or offshore sites for boat parking ("unattached"). Most of the pier pilings were below stationary docks (90.1%) which provides additional available habitat for *M. galloprovincialis* and both oyster species, especially *O. lurida* (Figure 7). Pier pilings varied in size and material, but limitations in Google Earth prevented further categorization. Pipes and chain link fence jutting into the bay added additional oyster habitat to the perimeter of the bay (113 m, or 0.1% of perimeter), while boat launches and outfalls do not provide habitat for oysters (254 m, or 0.3% of perimeter).

The estimated bay-wide abundance for *O. lurida* is 76,115,266 and is about 2.5 times greater than *M. gigas*, which is estimated at 30,288,069 oysters (Table 2). Pier pilings added an additional 85,863 m of habitat “perimeter” for intertidal species and allowed *O. lurida* to outnumber *M. gigas* in abundance by 45,827,198 oysters. *M. gigas* were in highest abundance on riprap (46.5% of total oysters) followed by below pier pilings (33.4% of total oysters), while *O. lurida* were in highest abundance on pier pilings below stationary docks (61.3% of oysters) followed by riprap (29.4% of total oysters).

Pier piling abundance estimate 2020 vs 2021

Using seawall as a proxy for oyster densities on pier pilings profoundly underestimated the bay-wide abundance of *O. lurida* (11,867,854 estimated in 2020 versus 47,007,449 estimated in 2021) but was more accurate for the *M. gigas* abundance estimate (9,324,493 estimated in 2020 versus 10,457,203 estimated in 2021) on these structures.

Table 2. Habitat type, total perimeter (m), percentage of total perimeter, number of pier pilings, percent of habitat sampled, *M. gigas* and *O. lurida* abundances (# of individuals), and percent of total for each species for shoreline habitats in San Diego Bay, CA from surveys performed in 2020 – 2021. Note that rows are in order of descending percent of perimeter, then decreasing number of pier pilings. The “Other” category is combined habitats that include pipe, chain link fence, boat launch, and outfall.

							Abundance		% of total	
Habitat type	Perimeter (m)	% of perimeter	# of pier pilings	Sum length (m) of quadrats	n quadrats	% habitat sampled	*M. gigas*	*O. lurida*	*M. gigas*	*O. lurida*
Riprap	44,625	43.7%		96.5	193	0.2%	14,081,893	22,363,431	46.5%	29.4%
Seawall	32,797	32.1%		42.0	84	0.1%	4,447,990	4,321,643	14.7%	5.7%
Soft	18,727	18.3%		65.5	131	0.3%	619,832	1,803,941	2.0%	2.4%
Cobble	5,687	5.6%		41.0	82	0.7%	655,412	588,019	2.2%	0.8%
Other	367	0.4%		28.0	56	7.6%	25,738	30,784	0.1%	0.0%
# Below			48,382	44.2	172	0.3%	10,113,099	46,655,065	33.4%	61.3%
# Above			6,315	29.6	136	2.2%	323,307	333,096	1.1%	0.4%
# Unattached			251	0.0	0	0.0%	20,798	19,287	0.1%	0.0%
Grand total	**102,203**	**100.0%**	**64,559**	**347**	**854**	**0.3%**	**30,288,069**	**76,115,266**	**100.0%**	**100.0%**
Hard shoreline	**83,476**	**81.7%**								

DISCUSSION

Pier pilings below stationary docks are a critical habitat for native oysters. By sampling this habitat, our *O. lurida* bay-wide abundance estimate was 52% higher this year compared to last year, while *M. gigas* abundance estimate only increased by 6%. *O. lurida* are numerically dominant in San Diego Bay, but *M. gigas* still dominate in percent cover across all habitats.

We found that pier pilings under stationary docks allow both *O. lurida* and *M. gigas* to have dense aggregations higher in the intertidal than what is found on any other habitat in San Diego Bay. Pier pilings below stationary docks provide a unique habitat compared to other habitats in the bay. Their cylindrical surfaces likely allow water to flow more quickly around them, but the rugosity provided by the high density of sessile bivalves and other benthic fauna causes the water to slow in the crevices such that larvae can be retained (Abelson & Denny, 1997), causing a self-reinforcing reef to form. Further, multiple animal species have been observed to settle in higher abundances in shaded compared to exposed environments (Glasby, 1999; Blockley & Chapman, 2006). Surveys in Los Angeles and Long Beach Harbors have also found that epifauna are in higher species abundance, percent cover, and density on pier pilings compared to riprap (Stolzenbach et al., 2021). Extremely high densities of oysters on pier pilings below docks may have a spillover effect on the surrounding environment, such as onto the oyster reef observed below Tom Ham's Lighthouse (Figure 4). The pier piling habitat under stationary docks may be analogous to the interior habitat provided by reef balls, a new living shorelines strategy in San Diego Bay that was recently deployed to restore *O. lurida* while protecting the shoreline from erosion.

Our data on shoreline armoring indicate an increase of 7.7% in armored shorelines since 2013 – approximately 81.7% of San Diego Bay's shoreline is now armored with human-introduced habitat compared to 74% reported in 2013. It is unclear whether the former estimate classified cobble as human-introduced armor, as we did here (K. Merkel, personal communication, 2020). Regardless, if cobble was not included in the total for armored shorelines, 76.1% of the shoreline has hard armor, which is a 2.1% increase, or 2,146 m of additional hardened shorelines.

We found that contextualizing our data could produce different conclusions. For example, tidal elevation was a critical factor for oyster distribution. Site-wide abundance estimates for oysters did not show the same trends as bay-wide abundances for *M. gigas* and *O. lurida* likely because of the site size and amount of habitat available as a function of tidal elevation. Although pier pilings below stationary docks had the highest densities of *O. lurida*, sites with this habitat did not correspond to the highest abundance of the species. Conversely, *O. lurida* were in lowest densities on riprap, but site-wide abundances showed HI with the highest abundance for both *O. lurida* and *M. gigas*, due to the relatively large size of the site. Bay-wide, there are a lot of pier pilings, so they contributed greatly to the high density estimate of *O. lurida* in the bay.

Density comparisons between oyster species showed different results than percent cover because of the growth patterns of the oysters. *M. gigas* have a much larger adult size than *O. lurida* (Figure A5) and often grow flat on surfaces at high tidal elevations (Figure 4) where there are fewer fouling species.

While we refined our baseline estimate of oyster abundances in San Diego Bay, we still have additional sources of error that can be addressed in future studies. Perog et al. (2021) suggested sampling a minimum of 0.5% of each habitat available in San Diego Bay, but here, we achieved that sampling goal in just 3 of 8 available habitats (Table 2). We should specifically sample two habitats more intensively in future studies: shaded seawalls and subtidal habitats, including floating docks. There is a considerable amount of seawall under stationary docks alongside pier pilings that may experience high densities of oysters. We only surveyed one such seawall at Cesar Chavez Park, and while its densities were comparable to other seawall habitat, we should increase our sample size in the future. Sampling subtidal habitat will provide a more refined abundance estimate for oysters, especially *O. lurida*. Figure 9 suggests that *O. lurida's* highest densities may be lower than -0.5 m MLLW. *O. lurida* settle in substantial densities as low as -3 to -6 m (-10 to -20 ft) MLLW (Frantz, Zacherl, and Merkel, unpublished data, 2021). Understanding subtidal population demographics will increase our abundance estimate for *O. lurida* since subtidal habitats are not represented in our current abundance estimate.

Continuing to ground-truth our perimeter estimates and correctly categorizing habitat types that are in the intertidal zone (i.e., seawall was often found very high in the intertidal zone, but was still factored into the perimeter estimate) would better correct our abundance estimate and likely overestimated *M. gigas* abundance.

Oyster densities near the front of the bay were not surveyed, but the habitat was factored into the abundance estimate. The closest site to the mouth of the bay that we surveyed was ~2.5 km (1.6 miles) away and had some of the highest densities of oysters (Police Harbor Dock). Although permission to complete a full protocol survey in sites near the mouth of the bay was not pursued due to naval activities, we may be able to perform kayak or walking surveys in the future to understand the relative densities of oysters in the area.

ACKNOWLEDGEMENTS

Thanks to the Southern California Ecosystems Research Program scholars from CSUF who aided in data collection and data recording during summers 2020 and 2021. The San Diego Unified Port District and Merkel & Associates, Inc. provided funding and facilitated much-appreciated access to field sites.

REFERENCES

Airoldi, L., Turon, X., Perkol-Finkel, S., & Rius, M. (2015). Corridors for aliens but not for natives: Effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, *21*(7), 755–768.

Barrett, E. M. (1963). *The California oyster industry* (Vol. 123). Resources Agency of California, Department of Fish and Game.

Blockley, D., & Chapman, M. (2006). Recruitment determines differences between assemblages on shaded or unshaded seawalls. *Marine Ecology Progress Series, 327*, 27–36. https://doi.org/10.3354/meps327027

Blum, J. C., Chang, A. L., Liljesthröm, M., Schenk, M. E., Steinberg, M. K., & Ruiz, G. M. (2007). The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. *Journal of Experimental Marine Biology and Ecology*, *342*(1), 5–14.

Bodkin, J. L., Coletti, H. A., Ballachey, B. E., Monson, D. H., Esler, D., & Dean, T. A. (2018). Variation in abundance of Pacific blue mussel (*Mytilus trossulus*) in the Northern Gulf of Alaska, 2006–2015. *Deep Sea Research Part II: Topical Studies in Oceanography*, *147*, 87–97.

Bonnot, P. (1935). The California oyster industry. *California Fish and Game*, *21*(1), 65–80.

Braby, C. E., & Somero, G. N. (2006). Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. *Marine Biology*, *148*(6), 1249–1262.

Buhle, E. R., & Ruesink, J. L. (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.

Bulleri, F., & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology*, *47*(1), 26–35.

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., & Tolley, S. G. (2007). Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, *341*, 303–307.

Cornwell, W. K., & Ackerly, D. D. (2010). A link between plant traits and abundance: Evidence from coastal California woody plants. *Journal of Ecology*, *98*(4), 814–821.

Crooks, J. A., Crooks, K. R., & Crooks, A. J. (2015). Observations of the non-native Pacific oyster (*Crassostrea gigas*) in San Diego County, California. *California Fish and Game*, *101*(2), 101–107.

Dalrymple, D. J., & Carmichael, R. H. (2015). Effects of age class on N removal capacity of oysters and implications for bioremediation. *Marine Ecology Progress Series*, *528*, 205–220.

Defeo, O., & Rueda, M. (2002). Spatial structure, sampling design and abundance estimates in sandy beach macroinfauna: Some warnings and new perspectives. *Marine Biology*, *140*(6), 1215–1225.

Diederich, S., Nehls, G., van Beusekom, J. E. E., & Reise, K. (2005). Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: Invasion accelerated by warm summers? *Helgoland Marine Research, 59*(2), 97–106. https://doi.org/10.1007/s10152-004-0195-1

Dodd Jr, C. K., & Dorazio, R. M. (2004). Using counts to simultaneously estimate abundance and detection probabilities in a salamander community. *Herpetologica*, *60*(4), 468–478.

Fodrie, F. J., Rodriguez, A. B., Gittman, R. K., Grabowski, J. H., Lindquist, Niels. L., Peterson, C. H., Piehler, M. F., & Ridge, J. T. (2017). Oyster reefs as carbon sources and sinks. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20170891.

Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). *NEMESIS Database Species Summary*. National Exotic Marine and Estuarine Species Information System. http://invasions.si.edu/nemesis/

Gittman, R. K., Fodrie, F. J., Popowich, A. M., Keller, D. A., Bruno, J. F., Currin, C. A., Peterson, C. H., & Piehler, M. F. (2015). Engineering away our natural defenses: An analysis of shoreline hardening in the US. *Frontiers in Ecology and the Environment*, *13*(6), 301–307.

Glasby, T. M. (1999). Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. *Marine Ecology Progress Series*, *190*, 113–124.

Goodsell, P. J., Chapman, M. G., & Underwood, A. J. (2007). Differences between biota in anthropogenically fragmented habitats and in naturally patchy habitats. *Marine Ecology Progress Series*, *351*, 15–23.

Griggs, G., & Patsch, K. (2019). The protection/hardening of California's coast: Times are changing. *Journal of Coastal Research*, *35*(5), 1051–1061.

Hiby, L., & Lovell, P. (1998). Using aircraft in tandem formation to estimate abundance of harbour porpoise. *Biometrics*, 1280–1289.

Jaramillo-Legorreta, A. M., Rojas-Bracho, L., & Gerrodette, T. (1999). A new abundance estimate for vaquitas: First step for recovery 1. *Marine Mammal Science*, *15*(4), 957–973.

Kataoka, T., Murray, C. C., & Isobe, A. (2018). Quantification of marine macro-debris abundance around Vancouver Island, Canada, based on archived aerial photographs processed by projective transformation. *Marine Pollution Bulletin*, *132*, 44–51.

Kornbluth, A., Perog, B. D., Crippen, S., Zacherl, D., Quintana, B., Grosholz, E. D., & Wasson, K. (2022). Mapping oysters on the Pacific coast of North America: A coast-wide collaboration to inform enhanced conservation. *PloS One, 17*(3), e0263998. https://doi.org/10.1371/journal.pone.0263998

Liang, D., Nesslage, G., Wilberg, M., & Miller, T. (2017). Bayesian calibration of blue crab (*Callinectes sapidus*) abundance indices based on probability surveys. *Journal of Agricultural, Biological and Environmental Statistics*, *22*(4), 481–497.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., & Jackson, J. B. C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*(5781), 1806–1809.

McDonald, J. H., & Koehn, R. K. (1988). The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America. *Marine Biology*, *99*(1), 111–118.

McKenna Jr., J. E., & Johnson, J. H. (2009). Spatial and temporal variation in distribution of larval lake whitefish in eastern Lake Ontario: Signs of recovery? *Journal of Great Lakes Research*, *35*(1), 94–100.

Mora-Soto, A., Palacios, M., Macaya, E. C., Gómez, I., Huovinen, P., Pérez-Matus, A., Young, M., Golding, N., Toro, M., Yaqub, M., & Macias-Fauria, M. (2020). A high-resolution global map of giant kelp (*Macrocystis pyrifera*) forests and intertidal green algae (*Ulvophyceae*) with Sentinel-2 imagery. *Remote Sensing*, *12*(4), 694.

Moxley, J. H., Bogomolni, A., Hammill, M. O., Moore, K. M. T., Polito, M. J., Sette, L., Sharp, W. B., Waring, G. T., Gilbert, J. R., Halpin, P. N., & Johnston, D. W. (2017). Google haul out: Earth observation imagery and digital aerial surveys in coastal wildlife management and abundance estimation. *BioScience*, *67*(8), 760–768.

Nehls, G., Diederich, S., Thieltges, D. W., & Strasser, M. (2006). Wadden Sea mussel beds invaded by oysters and slipper limpets: Competition or climate control? *Helgoland Marine Research, 60*(2), 135–143. https://doi.org/10.1007/s10152-006-0032-9

NOAA Fisheries. (2020). *Understanding Living Shorelines | NOAA Fisheries* (National). NOAA. https://www.fisheries.noaa.gov/insight/understanding-living-shorelines

Padilla, D. K. (2010). Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. *Integrative and Comparative Biology*, *50*(2), 213–225.

Peterson, B. J., & Heck Jr, K. L. (1999). The potential for suspension feeding bivalves to increase seagrass productivity. *Journal of Experimental Marine Biology and Ecology*, *240*(1), 37–52.

Polson, M. P., & Zacherl, D. C. (2009). Geographic distribution and intertidal population status for the Olympia oyster, *Ostrea lurida* Carpenter 1864, from Alaska to Baja. *Journal of Shellfish Research*, *28*(1), 69–77.

Pooler, P. S., & Smith, D. R. (2005). Optimal sampling design for estimating spatial distribution and abundance of a freshwater mussel population. *Journal of the North American Benthological Society*, *24*(3), 525–537.

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534.

Ruiz, G. M., Carlton, J. T., Grosholz, E. D., & Hines, A. H. (1997). Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist*, *37*(6), 621–632.

Shaw, W. N. (1997). The shellfish industry of California—Past, present and future. *NOAA Tech. Rep. NMFS*, *128*, 57–74.

Shinen, J. S., & Morgan, S. G. (2009). Mechanisms of invasion resistance: Competition among intertidal mussels promotes establishment of invasive species and displacement of native species. *Marine Ecology Progress Series*, *383*, 187–197.

Stolzenbach, K., Johnson, T., Stransky, C., Rudolph, Isham, B., Merkel, K., Stidum, B., Gonzales, C., Wood, V., Prickett, K., McPherson, R., Centeno, C., & Luedy, J. (2021). 2018 Biological Surveys—Los Angeles and Long Beach Harbors. 381.

Trimble, A. C., Ruesink, J. L., & Dumbauld, B. R. (2009). Factors preventing the recovery of a historically overexploited shellfish species, *Ostrea lurida* Carpenter 1864. *Journal of Shellfish Research*, *28*(1), 97–106.

Tronske, N. B., Parker, T. A., Henderson, H. D., Burnaford, J. L., & Zacherl, D. C. (2018). Densities and zonation patterns of native and non-indigenous oysters in southern California Bays. *Wetlands*, *38*(6), 1313–1326.

Tyrrell, M. C., & Byers, J. E. (2007). Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology*, *342*(1), 54–60.

USDN/NFECS (U.S. Department of the Navy, Naval Facilities Engineering Command Southwest) & Port of San Diego. (2013). *San Diego Bay Integrated Natural Resources Management Plan, Final September 2013*.

Williams, R. O. B., Hedley, S. L., Branch, T. A., Bravington, M. V., Zerbini, A. N., & Findlay, K. P. (2011). Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. *Conservation Biology*, *25*(3), 526–535.

Wrange, A.L., Valero, J., Harkestad, L. S., Strand, Ø., Lindegarth, S., Christensen, H. T., Dolmer, P., Kristensen, P. S., & Mortensen, S. (2010). Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions, 12*(5), 1145–1152.

Van Dyke, E., & Wasson, K. (2005). Historical ecology of a central California estuary: 150 years of habitat change. *Estuaries*, *28*(2), 173–189.

Wells, S. R., Wing, L. C., Smith, A. M., & Smith, I. W. G. (2019). Historical changes in bivalve growth rates indicate ecological consequences of human occupation in estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(9), 1452–1465.

Zohar, Y., Hines, A. H., Zmora, O., Johnson, E. G., Lipcius, R. N., Seitz, R. D., Eggleston, D. B., Place, A. R., Schott, E. J., Stubblefield, J. D., & Chung, J. S. (2008). The Chesapeake Bay Blue crab (*Callinectes sapidus*): A Multidisciplinary Approach to Responsible Stock Replenishment. *Reviews in Fisheries Science*, *16*(1–3), 24–34.

Zu Ermgassen, Philine S. E., Spalding, M. D., Blake, B., Coen, L. D., Dumbauld, B., Geiger, S., Grabowski, J. H., Grizzle, R., Luckenbach, M., McGraw, K., Rodney, W., Ruesink, J. L., Powers, S. P., & Brumbaugh, R. (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.

Zu Ermgassen, P.S.E., Hancock, B., DeAngelis, B., Greene, J., Schuster, E., Spalding, M., & Brumbaugh, R. (2016). Setting objectives for oyster habitat restoration using ecosystem services: A manager's guide. *The Nature Conservancy: Arlington, VA, USA*.

APPENDIX

Table A1. Two-way ANOVA test statistics for effects of site, tidal elevation, habitat type per quadrat, and oyster species on density and percent cover of *M. gigas* and *O. lurida* and density and percent cover of oysters surveyed on various habitats in 2020 - 2021 in San Diego Bay, CA. Bold indicates significant difference. Tide = tidal elevation.

Table #	Response Variable	Transformation	Source	DF	Sum squares	F ratio	P
1a	# *M. gigas*	Log (x+1)	Site	21	912.13	16.17	**<0.0001**
			< or > 0.30 m MLLW	1	447.73	166.72	**<0.0001**
			Site*< or > 0.30 m MLLW	21	316.81	5.62	**<0.0001**
			Error	818	2196.75		
			Total	861	4686.03		
1b	# *O. lurida*	Log (x+1)	Site	21	1573.84	19.03	**<0.0001**
			< or > 0.30 m MLLW	1	367.89	93.43	**<0.0001**
			Site*< or > 0.30 m MLLW	21	420.58	5.09	**<0.0001**
			Error	818	3221.13		
			Total	861	5568.65		
1c	% cover *M. gigas*	Log (x+1)	Site	21	303.53	11.29	**<0.0001**
			< or > 0.30 m MLLW	1	161.46	126.11	**<0.0001**
			Site*< or > 0.30 m MLLW	21	122.87	4.57	**<0.0001**
			Error	818	1047.31		
			Total	861	1956.05		
1d	% cover *O. lurida*	Log (x+1)	Site	21	279.70	18.62	**<0.0001**
			< or > 0.30 m MLLW	1	35.21	49.23	**<0.0001**
			Site*< or > 0.30 m MLLW	21	90.22	6.01	**<0.0001**
			Error	818	584.99		
			Total	861	981.20		
1e	# oysters	Log (x+1)	Habitat type/quadrat	7	2301.66	76.06	**<0.0001**
			Species	1	134.41	31.09	**<0.0001**

			Habitat type/quadrat*Species	7	544.45	17.99	**<0.0001**
			Error	1714	7409.39		
			Total	1729	10363.48		
1f	% cover oysters	Log (x+1)	Habitat type/quadrat	7	565.50	63.72	**<0.0001**
			Species	1	287.39	226.69	**<0.0001**
			Habitat type/quadrat*Species	7	190.63	21.48	**<0.0001**
			Error	1714	2172.91		
			Total	1729	3264.04		
1g	# *M. gigas*	Square root	SeawallvsPierPile	1	78.74	1.62	0.2048
			Tide	1	1324.91	27.19	**<0.0001**
			SeawallvsPierPile*Tide	1	592.01	12.15	**0.0006**
			Error	255	12425.06		
			Total	258	17489.94		
1h	# *O. lurida*	Log (x+1)	SeawallvsPierPile	1	133.25	29.65	**<0.0001**
			Tide	1	516.10	114.83	**<0.0001**
			SeawallvsPierPile*Tide	1	0.06	0.01	0.9057
			Error	255	1146.05		
			Total	258	2228.98		

Table A2. Results of Post-hoc Tukey comparisons for all statistical tests where appropriate. Groups that share a common letter within each test are statistically the same. Viewable via link: https://www.dropbox.com/s/ke56xyu7saqga3q/5.%20TABLE%20A2%20Post%20hoc%20analyses%20with%20filter.xlsx?dl=0

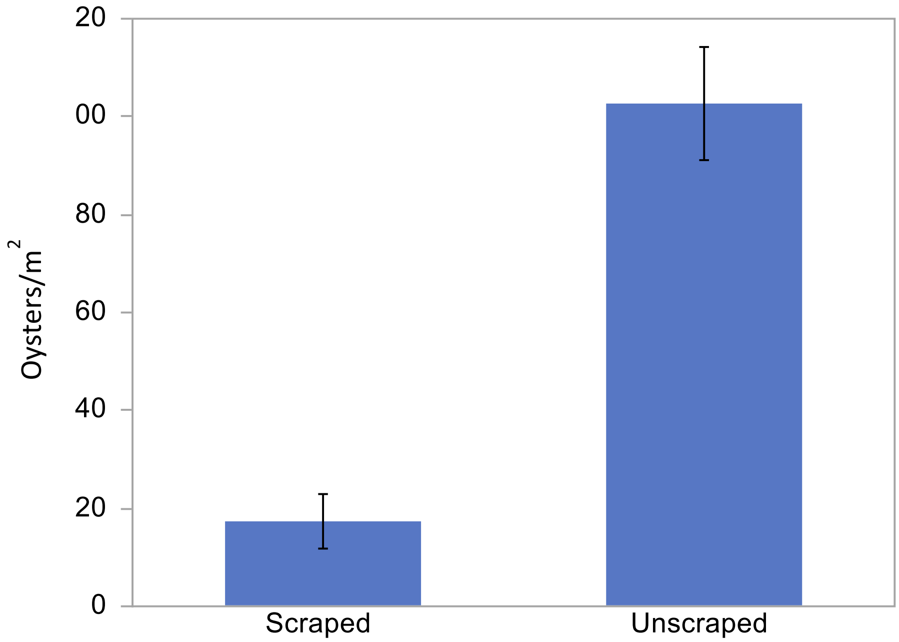

Figure A1. Oysters/m^2 on scraped and unscraped pier pilings attached to floating docks surveyed in 2021 in San Diego Bay, CA. Error bars are ± 1 SE.

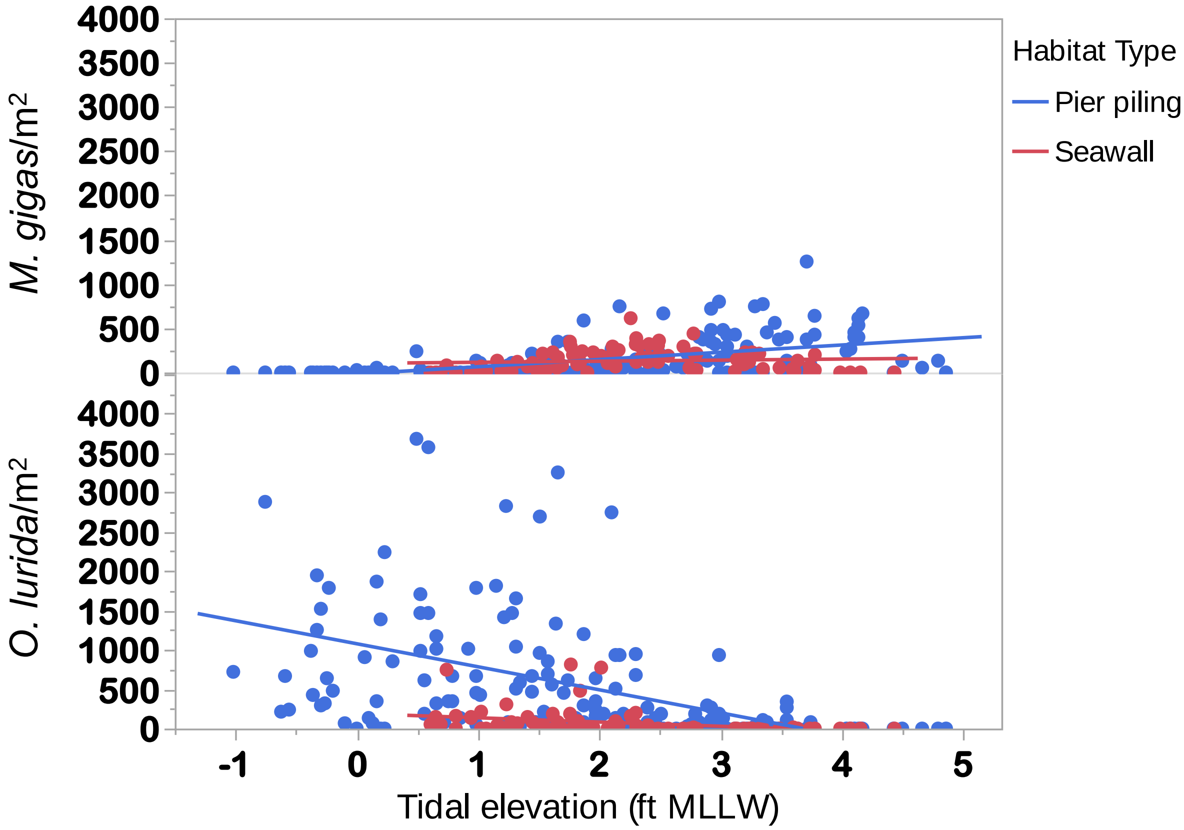

Figure A2. *M. gigas* and *O. lurida* densities on pier piling and seawall across tidal elevations (ft MLLW). Line of best fit shown.

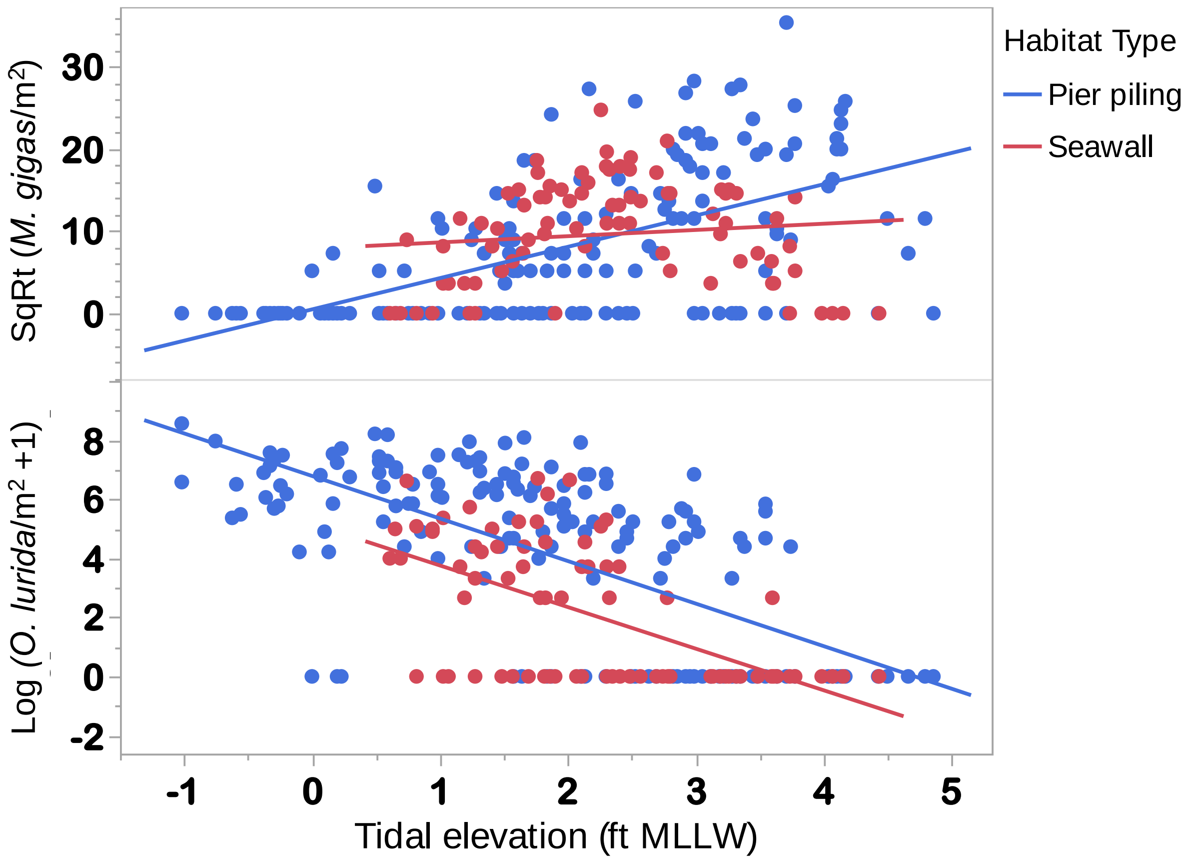

Figure A3. *M. gigas* and *O. lurida* densities on pier piling and seawall across tidal elevations (ft MLLW). Data are transformed in respect to the ANCOVA. Line of best fit shown.

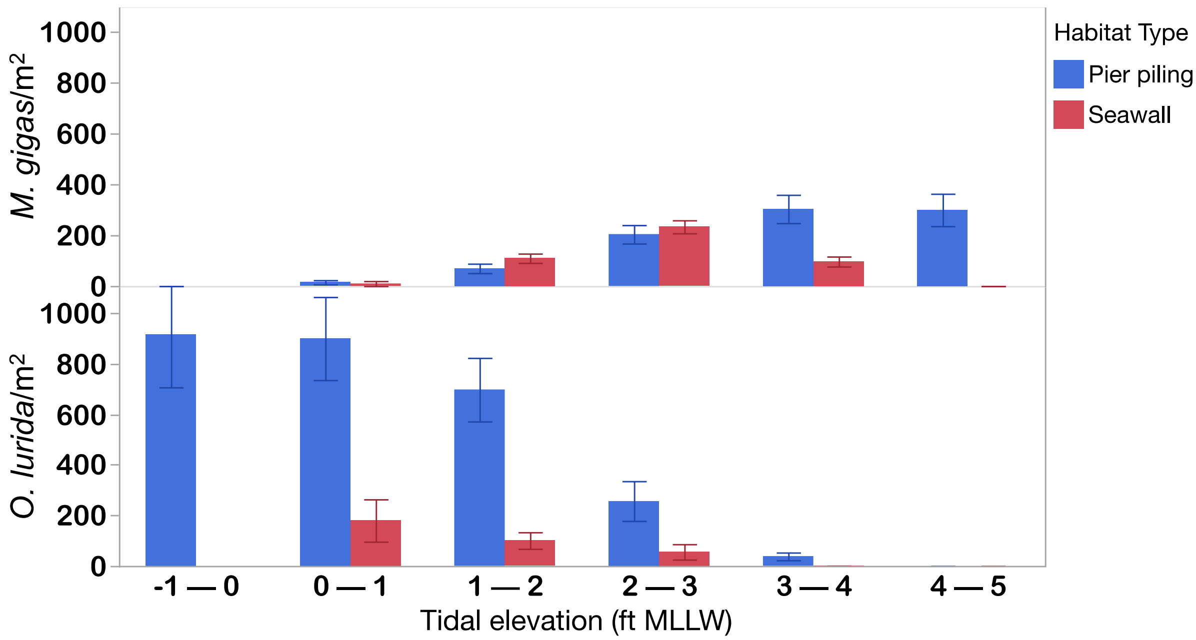

Figure A4. *M. gigas* and *O. lurida* densities (#/m^2) on pier piling and seawall habitats across binned tidal elevations (ft MLLW) in San Diego Bay, CA, 2021-2022. Error bars = 1 SE.

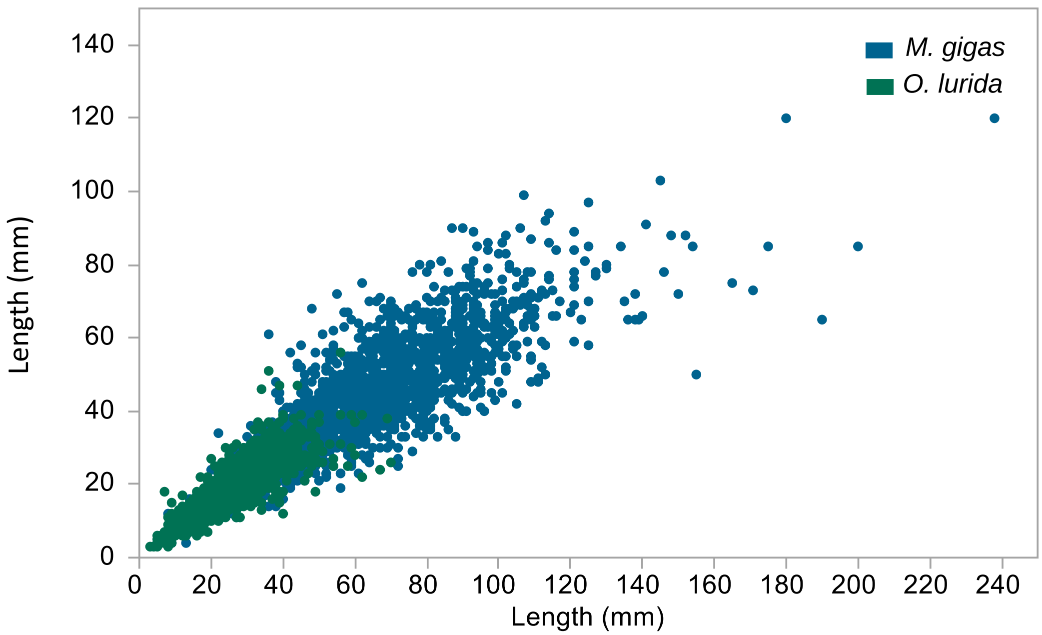

Figure A5. Maximum length (mm) of oysters, *M. gigas* and *O. lurida*, surveyed across multiple habitat types and locations in San Diego Bay, CA during 2020 – 2021.