

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

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## 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 and 2021, 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. In 2025-2026, we repeated surveys at most locations to provide updated population demographic data and abundance estimates. We sampled multiple habitat types across sites for a total of 20 sampling dates. At each survey location we examined whether densities and percent cover of oysters and the mussel, *Mytilus galloprovincialis,* varied across tidal elevations and sites and if densities and percent cover varied significantly across sampling periods (2020-21 versus 2025-26). *O. lurida* remain 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 57,217,109 oysters and for *M. gigas* was 29,226,304. While a comparison with abundance estimates from 2020-21 indicates a 24.8% decline in *O. lurida* and a 3.43% decline for *M. gigas*, the baseline abundance estimates from 2020-21 fit within the margin of error for both species. The estimated bay-wide abundance for *M. galloprovincialis* was 50,124,070. All three species were most abundant on pier piling habitat (61.3% of *O. lurida*, 41.3% of *M. gigas* and 96.9% of *M. galloprovincialis*). Statistical tests of variation in oyster density across time revealed little to no change, but trends in the data indicating declines in density for *O. lurida* and in cover for both *O. lurida* and the bay mussel, *M. galloprovincialis,* while density and cover trended towards gains for *M. gigas.* Our abundance estimates across a 5-year period will provide temporal and spatial benchmarks against which to compare future changes in the population demographics of both oyster species as well as the bay mussel.

## 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), often via shoreline armoring. Shoreline armoring is used to protect the thousands of structures in the U.S threatened by wave energy, shoreline erosion, and the effects of climate change (NOAA Fisheries, 2020), however breakwaters, jetties, and seawalls can fragment or eliminate natural habitats (Goodsell et al., 2007) and, perversely, accelerate erosion (Gittman et al., 2015). Reductions in native species through anthropogenic modifications can also impact critical ecosystem services, leaving estuaries and bays 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 because 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 helps 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 can be used to extrapolate the abundance of individuals in an area, and the resultant estimates can reveal areas with low numbers of individuals of the species of interest that can be targeted for restoration. Estuarine intertidal habitat can be highly variable, especially with the increase in shoreline armoring (see example of California counties in Griggs & Patsch, 2019), which can make abundance estimation a challenging endeavor. These challenges associated 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); these species have the added complexity of being difficult to detect. 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 currently distributed from British Columbia to Baja California (Polson & Zacherl, 2009). It was historically abundant along its range, and wild *O. lurida* populations were a harvested fishery 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 deemed 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). It 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 (Tronske et al., 2018), 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 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), and our visual surveys using Google Earth in 2020-21 revealed that 81.7% of the perimeter of San Diego Bay is now comprised of hard substrate (e.g., rip rap, seawall, cobble, chain link fence, pipe, boat launch). Although the habitat in the intertidal has changed dramatically, the artificial hard habitat is still used 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, so in 2020-21, we developed baseline 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. In 2025-2026, we repeated surveys to update the estimates of oyster density and bay-wide abundance, and to investigate if any changes occurred across the 5-year period between sampling events.

## STUDY OBJECTIVE

Conduct follow-up field surveys during 2025-2026 throughout San Diego Bay to assay bay-wide intertidal oyster and mussel abundance and density and assess whether densities and/or abundances changed across time.

## STUDY QUESTIONS

1. The 2025-2026 field studies addressed the following primary question:
   What is the estimated bay-wide abundance of native Olympia oysters, *Ostrea lurida,* Pacific oysters, *Magallana gigas,* and bay mussels*, Mytilus galloprovincialis*?

2. In addition, we determined density and percent cover of *O. lurida*, *M. gigas*, and *M. galloprovincialis* to address the following question: do bivalve densities vary across sites, habitat types and tidal elevations?

## STUDY DESIGN & METHODS

### Field Surveys

We surveyed *Ostrea lurida*, *Magallana gigas, and Mytilus galloprovincialis* density, percent cover, at 17 sites spanning the perimeter of the bay on diverse substrata between June 2025 and May 2026. These sites were accessible, were initially sampled in 2020-21 (with a few exceptions), and were distributed throughout the entire bay (Table 1, Figure 2).

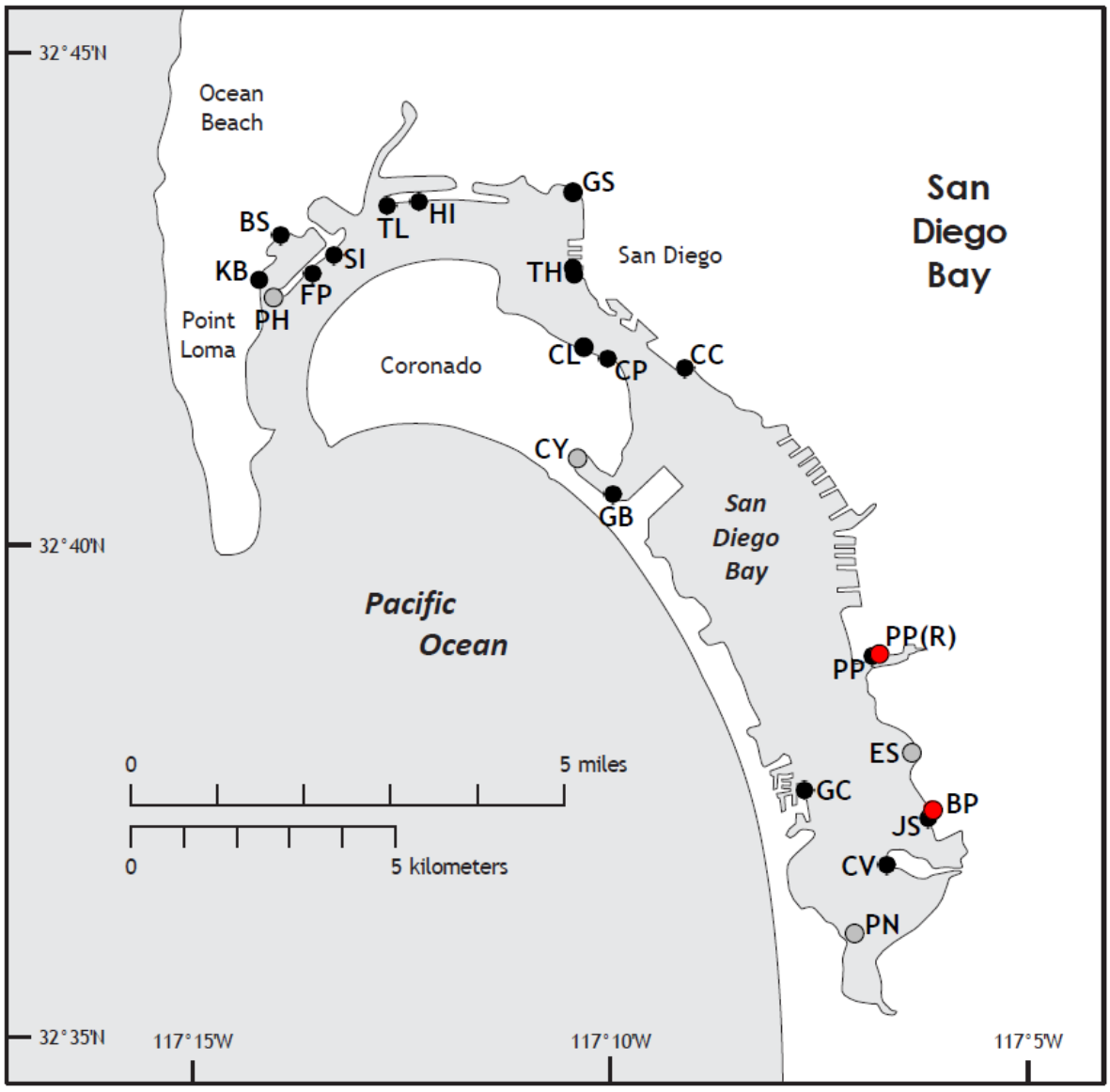



**Figure 2**. Oyster and mussel field survey locations in San Diego Bay, CA, across both sampling years in 2020-21 and 2025-26 (black dots). Survey locations PH, CY, ES and PN were sampled only in 2020-21, while the newly added survey locations PP(R) and BP in 2025-26 are labeled with red dots.

**Table 1.** Site, tidal elevation range, oyster and mussel site-wide abundance estimate, and oyster and mussel densities and percent cover in San Diego Bay, CA from surveys performed in 2020 – 2021 and 2025 – 2026. *M. gallo* = *Mytilus galloprovincialis*. Note that sites are in order of increasing distance to the mouth of the bay. Abundance estimates and densities for *M. gallo* were not captured in the 2020 - 2021 surveys. Values with 0.0 show undetected presence of oysters or mussels, and zero values with an asterisk (0.0*) indicate presence of oysters or mussels, but with density or cover averages <0.045.

| Site | Code | Latitude, Longitude | Habitat type | Date of survey | Tidal elevation range sampled (m MLLW) | Abundance estimate | | | *M. gigas*/m² (SE, n) | *O. lurida*/m² (SE, n) | *M. gallo*/m² (SE, n) | % cover *M. gigas* (SE, n) | % cover *O. lurida* (SE, n) | % cover *M. gallo* (SE, n) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *M. gigas* | *O. lurida* | *M. gallo* | | | | | | |
| Police Harbor Dock | PH | 32.7093, -117.2350 | Pier piling (above) | 6/26/2021 | 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 | 32.7114, -117.2367 | Pipe, riprap, seawall, soft | 6/22/20 & 6/25/20 | -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) |
| | | | | 6/25/2025 & 6/26/2025 | -0.16 to 1.06 | 21,934 | 18,566 | 8,242 | 215.9 (34.9, 89) | 243.3 (57.5, 89) | 119.0 (28.0, 89) | 26.8 (3.0, 89) | 1.7 (0.5, 89) | 1.3 (0.3, 89) |
| Shelter Island Fishing Pier | FP | 32.7115, -117.2281 | Pier piling (below) | 7/24/2020 | -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) |
| | | | | 6/12/2025 | 0.04 to 1.24 | 12,470 | 14,334 | 260,914 | 94.0 (16.2, 42) | 115.0 (20.0, 42) | 2116.8 (321.9, 42) | 0.1 (0.0, 42) | 0.0* (0.0, 42) | 0.3 (0.0, 42) |
| Bessemer | BS | 32.7182, -117.2328 | Pier piling (below) | 6/27/2021 | -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) |
| | | | | 6/15/2025 | -0.01 to 0.87 | 705 | 9,892 | 6,976 | 21.1 (9.3, 19) | 339.6 (93.8, 19) | 227.4 (80.4, 19) | 3.5 (1.6, 19) | 6.0 (1.2, 19) | 12.0 (3.7, 19) |
| Shelter Island | SI | 32.7159, -117.2230 | Riprap | 7/24/2020 | -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) |
| | | | | 7/25/2025 | -0.26 to 0.94 | 4,168 | 2,292 | 16 | 44.5 (5.4, 47) | 25.8 (5.1, 47) | 0.2 (0.1, 47) | 0.1 (0.0, 47) | 0.0* (0.0, 47) | 0.0 (0.0, 47) |
| Tom Ham's Lighthouse | TL | 32.7213, -117.2134 | Pier piling (below) | 6/25/2021 | -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) |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 6/14/2025 | -0.04 to 1.35 | 10,837 | 54,488 | 159,454 | 107.8 (26.3, 24) | 585.6 (122.0, 24) | 1,600.0 (361.3, 24) | 0.1 (0.0, 24) | 0.0* (0.0, 24) | 0.2 (0.0, 24) |
| Harbor Island Park | HI | 32.7247, -117.2076 | Riprap | 7/21/2020 | 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) |
| | | | | 7/24/2025 | -0.17 to 1.51 | 125,059 | 282,222 | 49,226 | 34.5 (6.8, 45) | 62.2 (11.0, 45) | 12.8 (4.6, 45) | 0.0* (0.0, 45) | 0.0* (0.0, 45) | 0.0* (0.0, 45) |
| Grape Street | GS | 32.7247, -117.2076 | Pier piling (below) | 7/25/2021 | -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) |
| | | | | 6/13/2025 | 0.01 to 1.42 | 113,765 | 161,525 | 177,066 | 390.9 (66.5, 50) | 472.5 (82.0, 50) | 603.7 (148.0, 50) | 0.3 (0.0, 50) | 0.0* (0.0, 50) | 0.17 (0.03, 50) |
| Tuna Harbor | TH (P) | 32.7110, -117.1744 | Pier piling (above) | 6/24/2021 | 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) |
| | TH (R) | 32.7118, -117.1746 | Riprap | 6/24/2020 | 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) |
| | | | | 7/26/2025 | -0.04 to 1.31 | 8,595 | 12,392 | 0 | 11.1 (2.8, 47) | 21.7 (3.5, 47) | 0.0 (0.0, 47) | 0.0 (0.0, 47) | 0.0 (0.0, 47) | 0.0 (0.0, 47) |
| Centennial Park | CP | 32.6698, -117.1711 | Riprap, seawall, soft | 7/23/2020 | -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) |
| | | | | 6/24/2025 & 6/28/25 | 0.01 to 1.21 | 26,413 | 23,551 | 1,322 | 121.3 (18.5, 20) | 73.3 (28.1, 20) | 9.3 (4.6, 20) | 13.6 (2.6, 20) | 2.3 (1.2, 20) | 0.2 (0.1, 20) |
| Cesar Chavez Park | CC | 32.6961, -117.1511 | Cobble, pier piling (below), seawall, soft | 7/22/2020 | 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) |
| | | | | 6/27/2025 & 5/19/2026 & 5/22/2026 | -0.11 to 1.21 | 227,556 | 642,729 | 25,709 | 154.6 (28.1, 92) | 381.3 (75.6, 92) | 13.8 (4.9, 92) | 10.7 (1.8, 92) | 5.0 (1.0, 92) | 1.2 (0.8, 92) |
| Coronado Ferry Landing | CL | 32.6995, -117.1698 | Pier piling (below) | 6/23/2021 | -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) |
| | | | | 6/24/2025 & 6/28/25 | 0.09 to 1.24 | 18,224 | 67,997 | 47,127 | 191.5 (70.8, 23) | 958.8 (188.1, 23) | 517.6 (179.2, 23) | 17.5 (5.0, 23) | 7.1 (2.3, 23) | 9.1 (3.9, 23) |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Glorietta Bay | GB | 32.6751, -117.1674 | Chain Link Fence | 6/10/2020 | 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) |
| | | | | 3/27/2026 | -0.13 to 1.0 | 5,782 | 618 | 19 | 348.2 (42.7, 30) | 21.8 (6.9, 30) | 1.3 (1.0, 30) | 1.0 (0.1, 30) | 0.0* (0.0, 30) | 0.0* (0.0, 30) |
| Coronado Yacht Club | CY | 32.6818, -117.1742 | Pier piling (above) | 7/23/2021 | 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 | PP (B) | 32.6493, -117.1123 | Pier piling (below) | 7/26/2021 | 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) |
| | PP (A) | 32.6496, -117.1106 | Pier piling (above) | 7/26/2021 | 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) |
| | PP (P) | 32.6493, -117.1123 | Pier piling (below) | 5/30/2025 | -0.06 to 1.08 | 5,242 | 10,690 | 116 | 214.3 (43.4, 28) | 440.0 (101.3, 28) | 4.8 (2.4, 28) | 19.3 (3.3, 28) | 5.6 (1.3, 28) | 0.0* (0.0, 28) |
| | PP (R) | 32.6495, -117.1122 | Rip Rap | 5/29/2025 | -0.29 to 0.99 | 14,884 | 6,612 | 201 | 49.7 (12.4, 40) | 21.7 (5.2, 40) | 0.7 (0.4, 40) | 6.7 (1.3, 40) | 0.2 (0.1, 40) | 0.0* (0.0, 40) |
| Grand Caribe | GC | 32.6263, -117.1297 | Riprap, seawall, soft | 6/9/2020 | -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) |
| | | | | 7/23/2025 | 0.22 to 1.35 | 24,467 | 4,284 | 71 | 55.6 (6.7, 52) | 10.8 (2.9, 52) | 0.2 (0.2, 52) | 10.2 (1.4, 52) | 0.1 (0.1, 52) | 0.0* (0.0, 52) |
| Bayside Park | BP | 32.6254, -117.1046 | Riprap | 5/27/2025 | -0.41 to 1.30 | 3,074 | 931 | 0 | 4.8 (1.6, 40) | 1.8 (0.90, 40) | 0.0 (0.0, 40) | 0.02 (0.00, 40) | 0.0 (0.0, 40) | 0.0* (0.0, 40) |
| E Street | ES | 32.6332, -117.1076 | Soft | 6/26/2021 | -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 | 32.6244, -117.1055 | Pier piling (below) | 7/24/2021 | -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) |
| | | | | 5/31/2025 | 0.02 to 1.34 | 4,921 | 31,100 | 0 | 13.3 (10.6, 28) | 107.6 (23.6, 28) | 0.0 (0.0, 28) | 0.0* (0.0, 28) | 0.0* (0.0, 28) | 0.0 (0.0, 28) |
| Chula Vista | CV | 32.6143, -117.1138 | Cobble | 6/8/2020 | -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) |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wildlife Reserve | | | | 5/28/2025 & 1/18/2026 | -0.41 to 1.21 | 22,122 | 30,021 | 107 | 30.5 (3.7, 80) | 30.1 (5.1, 80) | 0.2 (0.1, 80) | 4.0 (0.5, 80) | 0.4 (0.1, 80) | 0.0* (0.0, 80) |
| Pond 11 North | PN | 32.6027, -117.1178 | Cobble | 6/23/2020 | -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

At each site, we surveyed the tidal range from the waterline of the lower low tide to the highest evidence of living or dead oyster. At sites with cobble, riprap, and mud and sand, 1-3 50 m transects were laid out to divide the habitat into equal sections to capture the density of oysters across the available tidal range. Sites with pier piling, pipe, chain-link fence, or seawall habitat were surveyed using a single 12 – 30 m transect placed above the visible oyster zone. X and Y-values were randomized for the placement of quadrats (n = 19-89 per site, n = 14-80 within each habitat type).

Quadrat size varied relative to sampling habitat. For cobble, riprap, and sand, quadrat size was 0.5-m length x 0.5-m length (0.25 $m^2$). For sites with pipe, chain-link fence, or seawall habitat, we reduced the quadrat size to 0.5-m length x 0.15-m height (0.075 $m^2$) quadrats to constrain each individual quadrat to more specific tidal elevations. For pier piling, quadrat size was 0.25-m length x 0.15-m height (0.0375 $m^2$).

We quantified oysters and mussels on pier pilings below stationary docks at 8 sites. Paddleboards were used to access sites with pier pilings in deep water that were otherwise inaccessible during low tides. 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.

To determine substratum availability within the habitats we employed a point contact technique, using a gridded quadrat with 35-49 points based on the quadrat size and habitat type. At each point we identified the substratum first encountered with our probe. Alga and eelgrass (*Zostera marina*) points were only counted if the probe hit the holdfast. Otherwise, the alga or eelgrass cover was moved to reveal the substratum beneath. Mobile organisms were removed and the substrate beneath was counted. Hard substrate types encountered included wall, fence, gravel, small rock, medium rock, large rock, boulder, concrete, pier piling, wood, terracotta, live and dead *O. lurida*, live and dead *M. gigas,* live and dead barnacles, live and dead *Musculista senhousia*, tunicates, sponge, bryozoan, and live and dead *Mytilus galloprovincialis.* Soft substrates included mud and sand. These data were used to assign each quadrat to a habitat type (Table 1).

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 contained within 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.

To capture the tidal elevation at each site we used a Laser Mark LM-30 rotary laser by calculating the difference in height from an established watermark at a specific time and

using predicted NOAA tidal elevations (Station ID: 9410170). We estimated the tidal elevation for each quadrat (see Table 1 for tidal elevation range for each site). 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.

Oyster density data were converted to per $m^2$ and then combined with data we generated on bay-wide habitat availability (see below) to estimate bay-wide abundances for the three bivalve species. We calculated density above and below 0.3 m MLLW within each site on several habitat types including seawall, rip rap, pier pilings, cobble, soft sediment, pipe, and chain-link fence, and then generated average densities across sites per habitat type and tidal elevation. 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).

Pier pilings associated with floating docks and unattached pier pilings were not sampled in 2025-26 because they comprised only approximately 1.2% and 0.4% of *M. gigas* and *O. lurida* abundances respectively (based upon the 2020-21 surveys) and thus the sampling effort was deemed too large relative to the importance of the habitat for supporting bivalves; instead, we used estimates of those habitats from the 2020-21 effort.

**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). 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. Percent of habitat

sampled compared to total habitat available is reported in Table 3 and was calculated by dividing the sum of all quadrat lengths per habitat type sampled by total perimeter of each habitat type bay-wide.

**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 per habitat separately for the high and low tidal elevations (above and below 0.3 m MLLW), by first calculating average bivalve density across sites with the same habitat sampled and then multiplying the averages by bay-wide habitat perimeter estimates and average habitat type heights. We also used 95% confidence intervals per habitat and tidal elevation density measure so that we could calculate low and high estimates of abundance per habitat type and elevation. Then, we summed the abundance estimates to find oyster abundances per habitat type in the bay, with high and low abundance estimates as well. Lastly, we summed all abundances across all habitat types to produce a bay-wide abundance estimate, with high and low estimates also calculated to provide a margin of error for bay-wide abundance of each bivalve species.

**Data analysis**

To test whether density (*M. gigas, O. lurida*) and percent cover (*M. gigas, O. lurida, M. galloprovincialis)* changed across the two sampling periods (2020-21 versus 2025-26) and whether they varied among sites, plus their interactions, we employed two-way ANOVAs in JMP edition 18. Since the variation in density and cover among habitats was quite large at both upper (Fig. 7) and lower (Fig. 8) elevations, we analyzed data divided into three separate habitat type categories (cobble/riprap, pier pile/pipe, and fence/seawall) and by tidal elevation. At the lower elevation, seawall and chain link fence habitat had replication less than n=5 for at least one year at all sites (or the habitat did not exist at the lower elevation) and thus those data were not analyzed statistically. Further, we did not compare density across time for *M. galloprovincialis* since in 2020-21 we only recorded cover for this species.

To assess whether data conformed to the assumptions of ANOVA, they were visually inspected using residual by predicted, studentized residual and residual by normal

quantile plots. If they did not conform, then they were log or square root transformed, and when they still did not conform, data were rank-transformed (non-parametric) before proceeding with the two-way ANOVA. If significant effects of time or site were found, we followed the ANOVA with post-hoc Tukey comparisons.

To provide a synopsis of change in oyster density and cover across time and across tidal elevations (above or below 0.3 m MLLW) and categorical habitat types (pier pile/pipe, riprap/cobble, and seawall/fence), we calculated log response ratios (LRR). The LRR is a widely used statistical metric in marine ecology (Hedges et al 1999, Benedetti-Cecchi et al. 2024) and has specifically been used in oyster ecological studies (e.g., Smith and Castorani 2023) that quantifies the proportional change between two conditions – in this case between 2020-21 and 2025-26. We used the formulas: LRR = ln (mean density$_{25\text{-}26}$/mean density$_{20\text{-}21}$) and LRR = ln (mean cover$_{25\text{-}26}$/mean cover$_{20\text{-}21}$). LRRs offer several advantages – they are easily interpretable (LRR=0 indicates no change, + values indicate growth and – values indicate decline) and scaled proportionally (i.e., ideal for providing a synopsis of change in situations where there is significant variability across habitats and elevations).

## RESULTS

### Density trends across elevations, sites, space, and habitats during 2025-2026

All three bivalve species had densities that varied across tidal range (Figure 3). Both *M. gigas* and *M. galloprovincialis* generally averaged greater densities at and above 0.3 ft MLLW, while *O. lurida* generally averaged similar or greater densities below 0.3 m MLLW. Across all sites surveyed, *Magallana gigas* ranged from averages of 0 to 160.00 ± 108.87 oysters per m² below 0.3 ft MLLW and 9.33 ± 2.84 to 454.57 ± 72.84 per m² at and above 0.3 ft MLLW, *Ostrea lurida* ranging from 3.00 ± 1.64 to 1140.00 ± 335.83 per m² below 0.3 ft MLLW and 0.67 ± 0.67 to 855.24 ± 229.93 per m² at and above 0.3 ft MLLW, and *M. galloprovincialis* ranging from 0 to 576.00 ± 524.30 per m² below 0.3 ft MLLW and 0 to 2325.05 ± 345.96 per m²at and above 0.3 ft MLLW.

In terms of spatial variation (Figure 3), all three species' densities also varied across sites and across the bay. The south bay supported lower densities of all three species, particularly *M. galloprovincialis*, which averaged exceedingly low densities at GB and sites further south bay, and which were not detected at BP and JS.

When grouped by habitat surveyed (Figure 4), it was evident that cobble and rip rap habitats supported much lower densities of all three bivalve species relative to more vertical structures such as pier piles and seawalls. Mussels were only supported in any great number on pier piles located in the northern and central portions of the bay and at the pipe at Kellogg Beach.

Relative to one another across all sites within San Diego Bay (Figure 3), *O. lurida* generally achieved higher densities than both other bivalve species. *O. lurida* averaged

23 times greater density relative to *M. gigas* below 0.3 m MLLW, and 1.8 times greater density above 0.3 m MLLW. Considering only the sites where mussels were present, *M. galloprovincialis* averaged 5.5 greater densities below 0.3 m MLLW and 3.7 times greater densities above 0.3 m MLLW compared to *M. gigas,* and compared to *O. lurida*, it was 99 times and 18 times lower densities at the lower and higher elevations respectively, except at two key locations, FP and TL, both pier pile only site, where its average density was about 4 times higher than *O. lurida* at tidal elevations above 0.3 m MLLW.

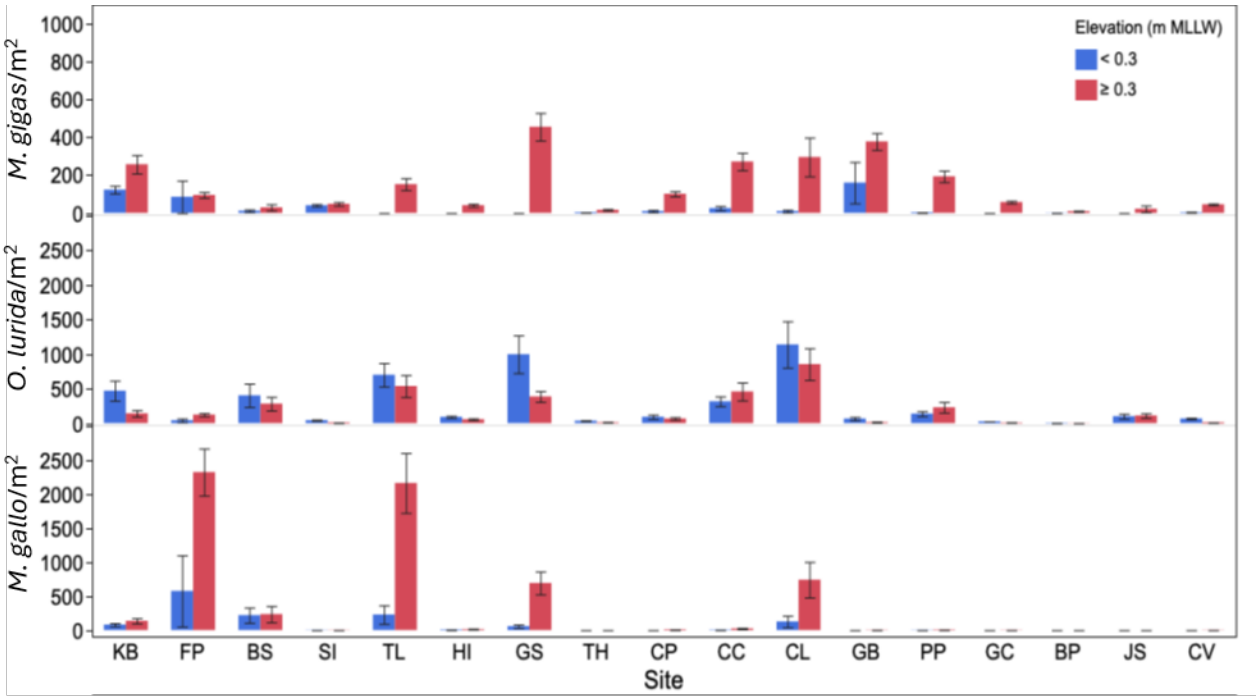



Figure 3. Density of oysters and mussels at two tidal elevations from sites throughout San Diego Bay, CA from surveys conducted during May 2025 through June 2026. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. *M. gallo* = *Mytilus galloprovincialis*. Note difference in scale on the Y axis.

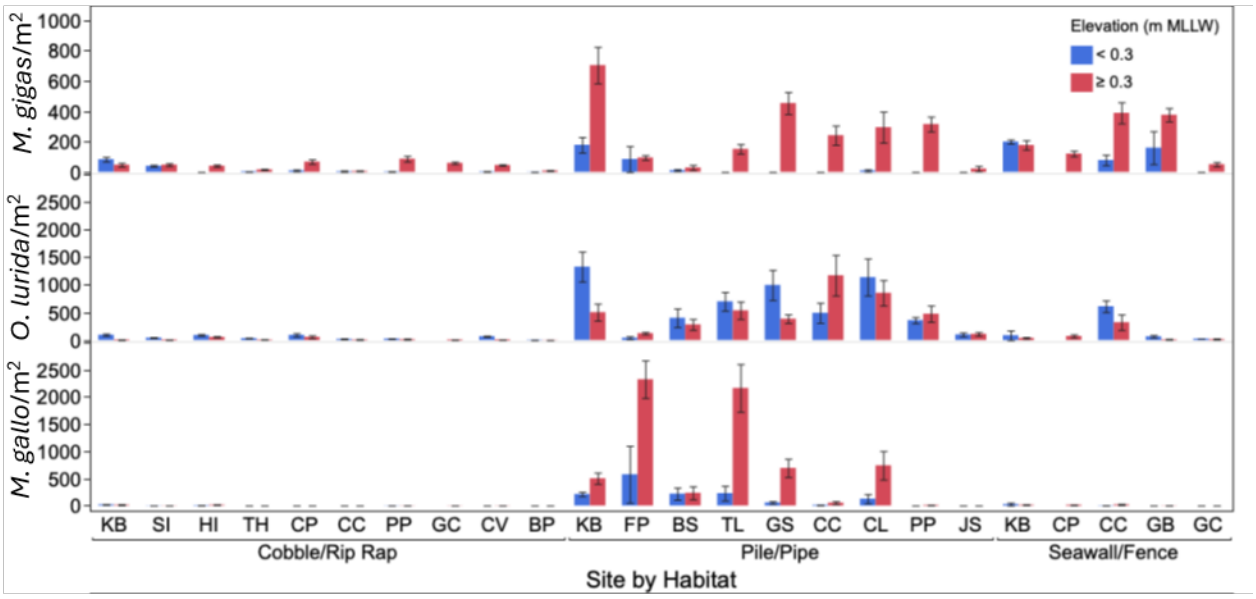



Figure 4. Density of oysters and mussels at two tidal elevations from sites throughout San Diego Bay, CA grouped by habitat type from surveys conducted during May 2025 through June 2026. Error bars are +/- 1 SE. Site abbreviations and specific habitats are as in Table 1. *M. gallo* = *Mytilus galloprovincialis*. Note difference in scale on the Y axis.

## Percent cover trends across elevations, sites, space, and habitats during 2025-2026

As with density, percent cover of all three species varied across sites and tidal elevations (Figure 5), with *M. gigas* ranging from 0 to 36.4 ± 18.8 % below 0.3 ft MLLW and 2.9 ± 0.6 to 58.2 ± 5.0 % at and above 0.3 ft MLLW, *O. lurida* ranging from 0 to 8.1 ± 3.6 % below 0.3 ft MLLW and 0 to 6.5 ± 3.0% at and above 0.3 ft MLLW, and *M. galloprovincialis* ranging from 0 to 13.6 ± 6.1% below 0.3 ft MLLW and 0 to 32.7 ± 4.0% at and above 0.3 ft MLLW. The same pattern of cover across elevations was evident; *M. gigas* and *M. galloprovincialis* generally averaged greater cover at and above 0.3 ft MLLW, while *O. lurida* generally averaged similar or greater cover below 0.3 m MLLW. The south bay supported lower percent cover of all three species, particularly *M. galloprovincialis.*

When grouped by habitat surveyed (Figure 6), it was again evident that cobble and rip rap habitats supported much lower cover of all three bivalve species relative to more vertical structures such as pier piles and seawalls. Mussel cover was notable only on pier piles and the pipe at Kellogg Beach.

Notably, while *O. lurida* and *M. galloprovincialis* densities were greater compared to *M. gigas* (see above), the pattern was reversed for percent cover, with the much larger individually-sized *M. gigas* generally occupying at least twice as much space as *O. lurida* or *M. galloprovincialis*.

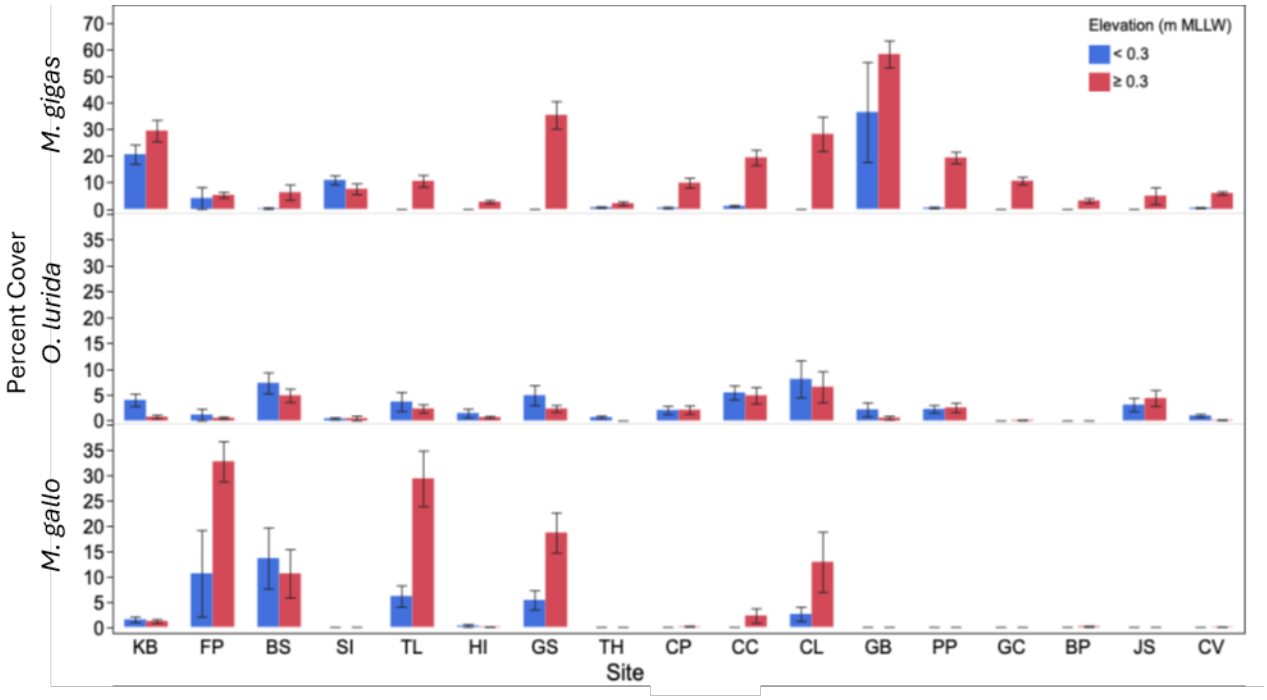



Figure 5. Percent cover of oysters and mussels at two tidal elevations from sites throughout San Diego Bay, CA from surveys conducted during May 2025 through June 2026. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. *M. gallo* = *Mytilus galloprovincialis*. Note difference in scale on the Y axis.

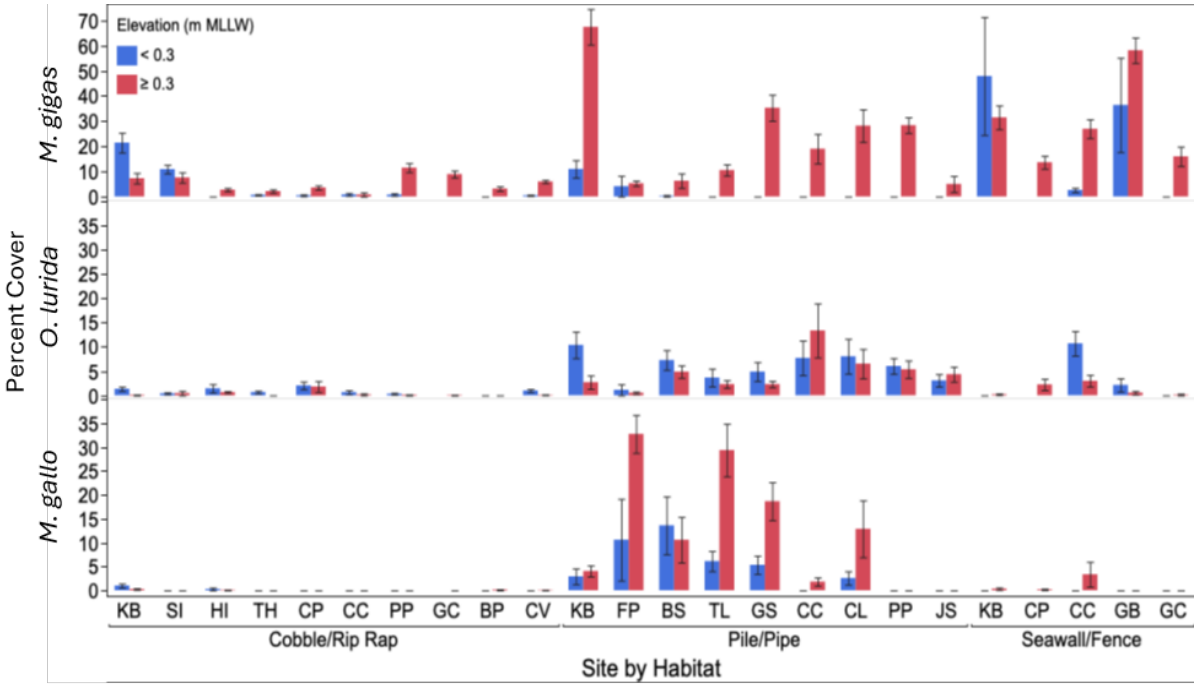



Figure 6. Percent cover of oysters and mussels at two tidal elevations from sites throughout San Diego Bay, CA grouped by habitat type from surveys conducted during May 2025 through June 2026. Error bars are +/- 1 SE. Site abbreviations and specific habitats are as in Table 1. *M. gallo* = *Mytilus galloprovincialis*. Note difference in scale on the Y axis.

## Variation in Density across time (2020-21 versus 2025-26)

As a reminder, since the variation in density among habitats was quite large at both upper and lower elevations (Figures 7, 8), we analyzed data across time by dividing the data into three separate habitat type categories (cobble/riprap, pier pile/pipe, and fence/seawall) and by tidal elevation. At the lower elevation, seawall and chain link fence habitat had replication less than n=5 for at least one year at all sites (or the habitat did not exist at the lower elevation) and thus those data were not analyzed statistically. Further, we did not compare density across time for *M. galloprovincialis* since in 2020-21 we only recorded cover for this species.

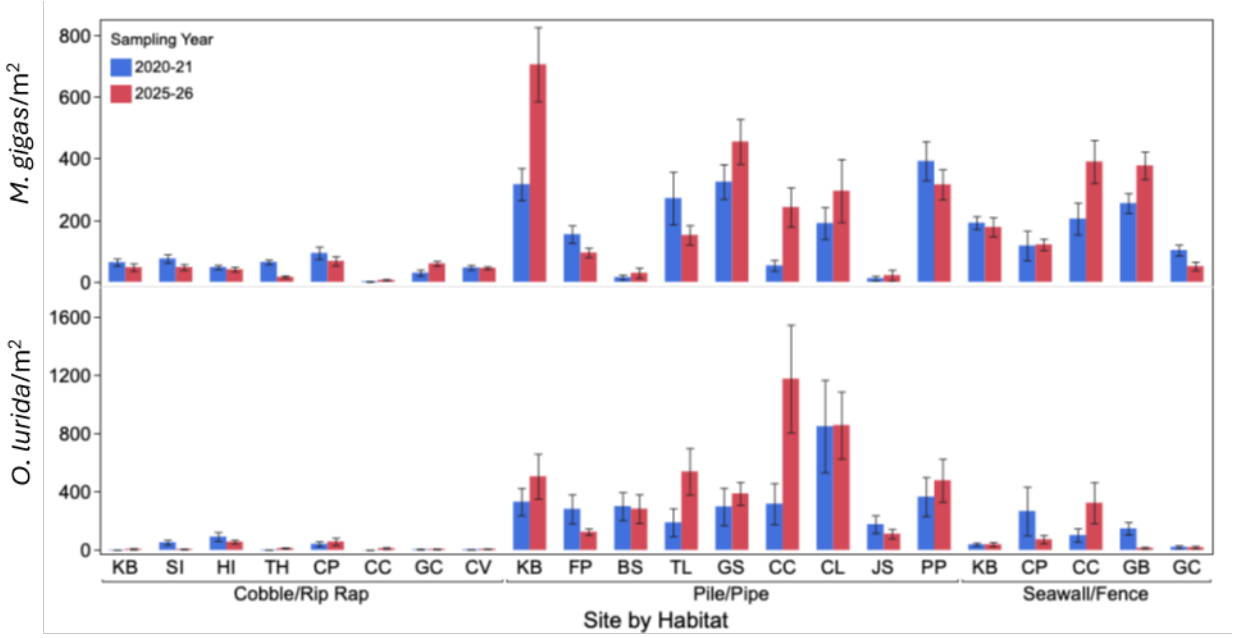



Figure 7. Density of oysters across sampling years and habitats from tidal elevations 0.3 m MLLW and greater at sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Note difference in scale on the Y axis.

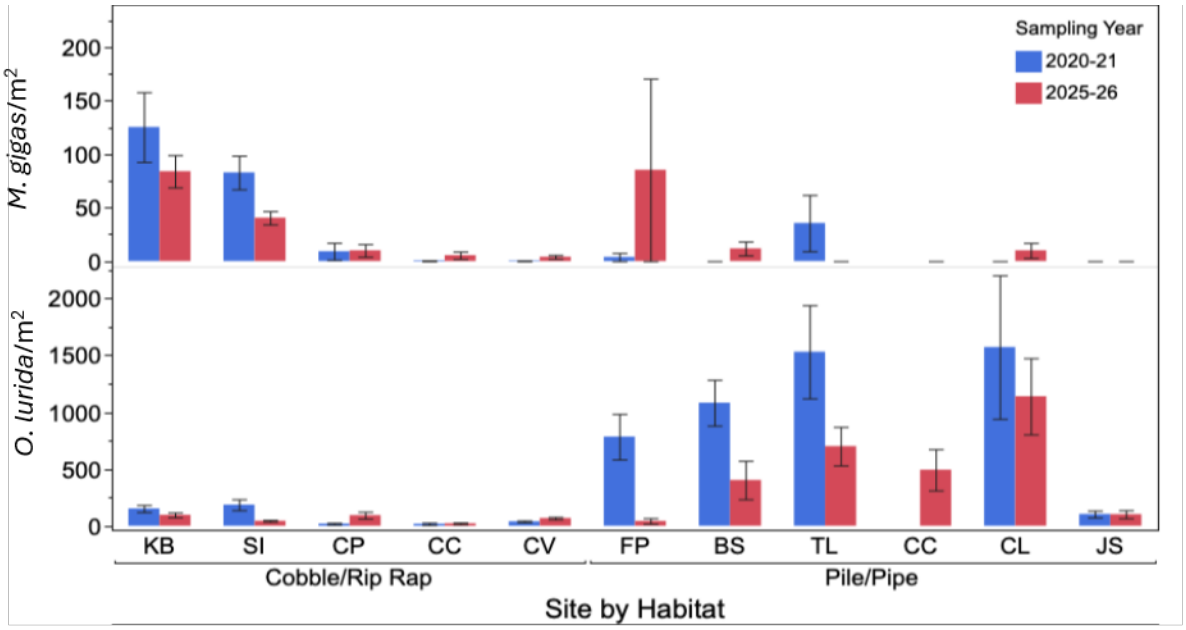



Figure 8. Density of oysters across sampling years and habitats from tidal elevations lower than 0.3 m MLLW at sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Note that seawall and chain link fence sites had replication less than n=5 for at least one year and thus are not displayed. CC pier pilings were only sampled in 2025-26. Note difference in scale on the Y axis.

### Change in density across time on pier pile and pipe habitat

*M. gigas*: On pier pile and pipe habitat above 0.3 m MLLW, *M. gigas* density did not change across time, nor did time interact with site, but there was a significant difference in densities across sites, with Kellogg Beach pipe supporting the highest densities of *M. gigas* at 474.17 ± 66.17 oysters per m2, which were 17-22 times greater than at BS and JS, which supported the lowest densities at 21.82 ± 8.53 and 16.58 ± 8.85 respectively. (Figure 9 left panel, Table 3, Two-way ANOVA, site $p<0.0001$). Below 0.3 m MLLW, time interacted with site (Figure 10 left panel, Table 4, Two-way ANOVA, time*site interaction $p<0.0464$), with trends towards increases in density at FP and declines at TL, however post-hoc Tukey tests could not pull out any significant differences at all across years or sites, and measurement error was high. Thus, there was no overarching change in density across time on pier pile or pipe habitat at either upper or lower elevations for *M. gigas*.

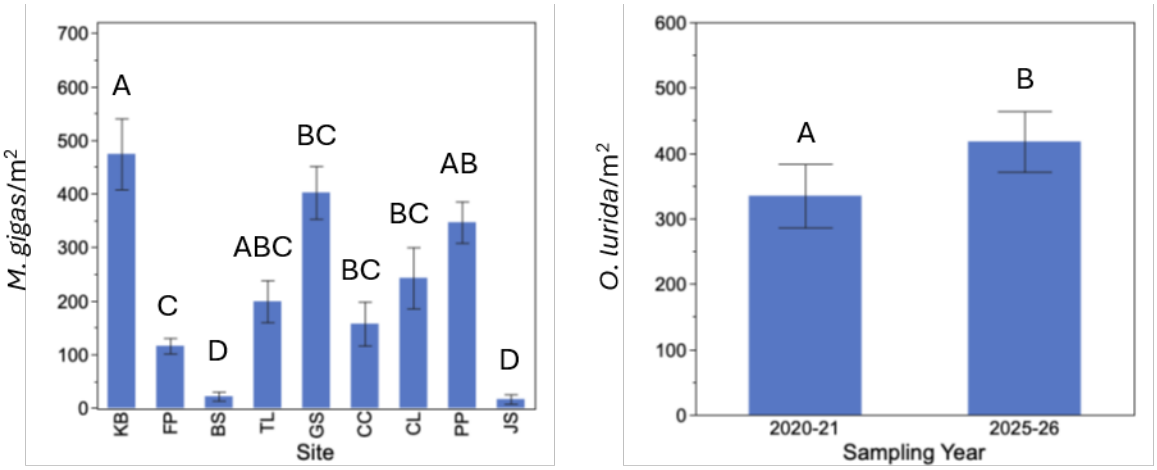



Figure 9. Density of oysters across sampling years at tidal elevations 0.3 m MLLW and greater from pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Left panel: *M. gigas* density across pier pile and pipe sites. Right panel: *O. lurida* density on pier piles and pipe between sampling periods. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

**Table 3.** Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas and O.lurida density data collected from tidal elevations 0.3 m MLLW and greater at pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded.**

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | p-value |
|---|---|---|---|---|---|---|
| *M. gigas*/m$^2$ | Rank-transformed | Site | 8 | 12764381 | 20.3068 | **<.0001** |
| | | Year | 1 | 24211 | 0.3081 | 0.5792 |
| | | Site *Year | 8 | 999477 | 1.5901 | 0.1269 |
| | | Model | 17 | 13611459 | 10.1903 | **<.0001** |
| | | Error | 310 | 24357321 | | |
| | | Total | 327 | 37968780 | | |
| *O. lurida*/m$^2$ | Rank-transformed | Site | 8 | 1161446 | 1.6403 | 0.1127 |
| | | Year | 1 | 391736 | 4.4259 | **0.0362** |
| | | Site *Year | 8 | 235204 | 0.3322 | 0.9532 |
| | | Model | 17 | 1661604 | 1.1043 | 0.3482 |
| | | Error | 310 | 27437927 | | |
| | | Total | 327 | 29099530 | | |

*O. lurida*: On pier pile and pipe habitat above 0.3 m MLLW, *O. lurida* density increased about 25% from 2020-21 to 2025-26, from 334.84 ± 48.62 to 417.83 ± 46.31 oysters per m2 (Figure 9 right panel, Table 3, Two-way ANOVA, time p = 0.0362). There were no significant differences among sites nor was there any interaction. Below 0.3 m MLLW, *O. lurida* density declined significantly, but only at two sites, FP and BS (Figure 10, Table 4, Two-way ANOVA, time*site interaction p=0.009).

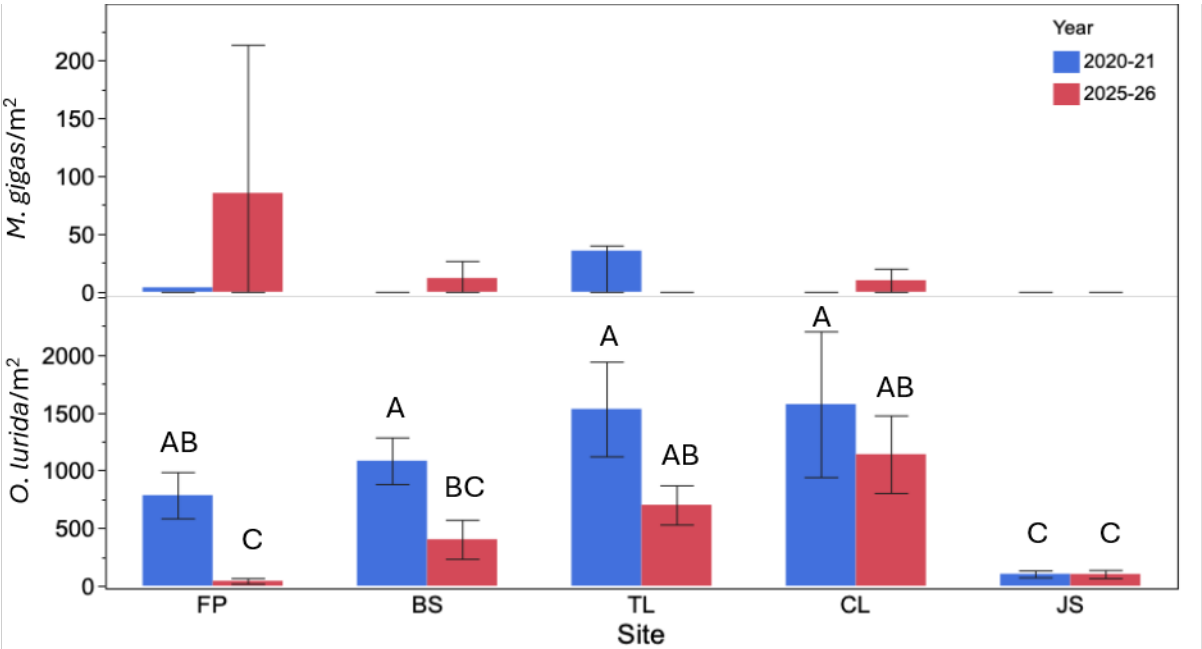



Figure 10. Density of oysters across sampling years at tidal elevations lower than 0.3 m MLLW from pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Top panel: *M. gigas* density across pier pile and pipe sites. Bottom panel: *O. lurida* density on pier piles and pipe between sampling periods. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 4. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas and O. lurida density data collected from tidal elevations lower than 0.3 m MLLW at pier piling and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | p-value |
|---|---|---|---|---|---|---|
| *M. gigas*/m$^2$ | Rank-transformed | Year | 1 | 141.1821 | 0.6827 | 0.4115 |
| | | Site | 4 | 745.6133 | 0.9014 | 0.4681 |
| | | Site *Year | 4 | 2114.0106 | 2.5556 | **0.0464** |
| | | Model | 9 | 3105.852 | 1.6687 | 0.1135 |
| | | Error | 69 | 14269.503 | | |
| | | Total | 78 | 17375.354 | | |
| *O. lurida*/m$^2$ | Rank-transformed | Year | 1 | 5874.97 | 18.1673 | **<.0001** |
| | | Site | 4 | 20735.587 | 16.0303 | **<.0001** |
| | | Site *Year | 4 | 4758.665 | 3.6788 | **0.009** |
| | | Model | 9 | 30405.677 | 10.4471 | **<.0001** |
| | | Error | 69 | 22313.292 | | |
| | | Total | 78 | 52718.968 | | |

## Change in density across time on riprap and cobble habitat

*M. gigas*: On riprap and cobble habitat above 0.3 m MLLW, *M. gigas* density did not evidence an overall pattern, but rather density declined at TH and rose at GC, but was otherwise stable across time (Figure 11, Table 5, time*site interaction, $p < 0.001$). Density generally did not vary across sites except that it was significantly lower during both time periods at CC relative to many other sites. Below 0.3 m MLLW, there were a couple of sites (HI, TH) that lacked sufficient replication of quadrats at the lower elevation during one or the other time period, precluding an ability to compare across years. In addition, GC completely lacks the habitat type of riprap/cobble below 0.3 m MLLW and so it was also eliminated from analysis. For the remaining 5 sites with sufficient habitat and replication, there was a significant difference in *M. gigas* density across sites but not across time (Figure 12, Table 6, site, $p < 0.001$), with KB and SI supporting densities of M. gigas that were 9 to 14 times higher in 2020-21 compared to CP, with no *M. gigas* detected within the quadrats at CC and CV below 0.3 m MLLW, and 4 to 20 times higher in 2025-26 compared to CP, CC and CV. Notably, *M. gigas* was detectable at the lower elevation at both CC and CV in 2025-26, with both sites supporting densities of 4-5 *M. gigas*/$m^2$. Overall, as with pier pile and pipe habitat, there was no overarching change in density across time at either upper or lower elevations for *M. gigas,* though the detection of *M. gigas* at lower elevations than detected previously at two sites is notable.

*O. lurida*: On riprap and cobble habitat above 0.3 m MLLW, *O. lurida* density, as *with M. gigas*, did not show any overall pattern of change across time. However, differences among sites did vary across the two time periods, with KB, TH and CV showing lower density compared to other sites in 2020-21 but not during 2025-26 (Figure 11, Table 5, Two-way ANOVA, time*site interaction $p =0.0046$). Below 0.3 m MLLW, time and site also interacted (Figure 12, Table 6, Two-way ANOVA, time*site interaction $p<0.001$) but there was no overarching pattern of change across time, with density declining at SI and increasing at CP, but otherwise stable at the remaining sites. Overall, as with *M. gigas*, there was no consistent pattern of change across time at either elevation on riprap and cobble habitat.

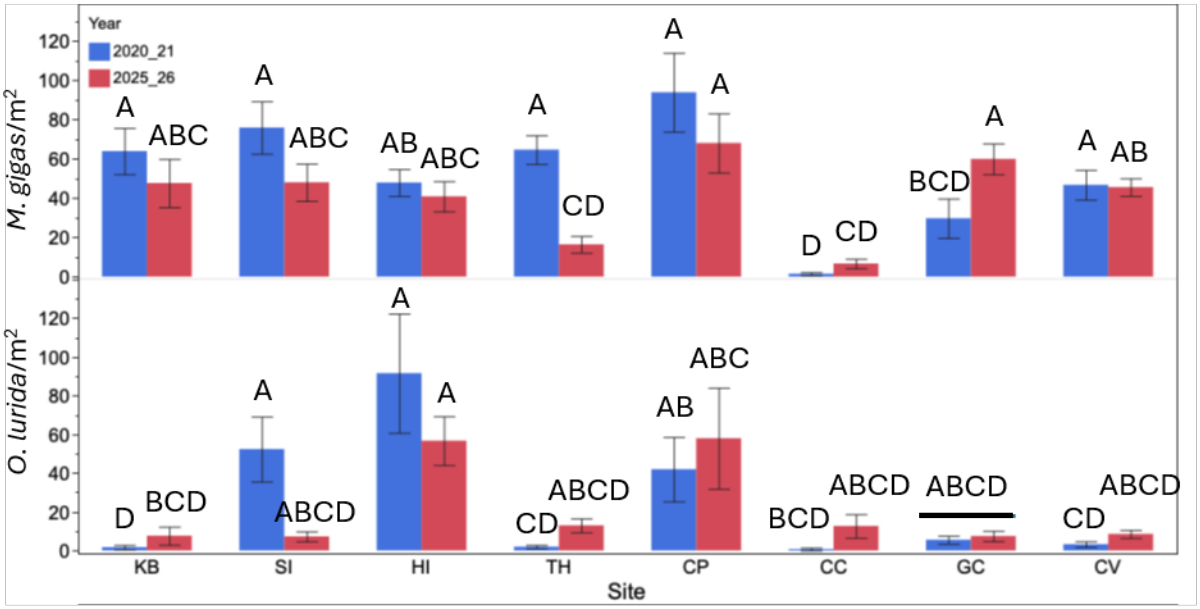



Figure 11. Density of oysters across sampling years at tidal elevations 0.3 m MLLW and greater from riprap and cobble throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Top panel: *M. gigas* density across riprap and cobble sites. Right panel: *O. lurida* density on riprap and cobble sites. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 5. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas and O. lurida density data collected from tidal elevations 0.3 m MLLW and greater at rip rap and cobble sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | p-value |
|---|---|---|---|---|---|---|
| *M. gigas*/m$^2$ | Rank-transformed | | | | | |
| | | Site | 7 | 740879 | 7.464 | **<.0001** |
| | | Year | 1 | 8206 | 0.5787 | 0.4472 |
| | | Site *Year | 7 | 698347 | 7.0355 | **<.0001** |
| | | Model | 15 | 1448973 | 6.8123 | **<.0001** |
| | | Error | 435 | 6168322 | | |
| | | Total | 450 | 7617295 | | |
| *O. lurida*/m$^2$ | Rank-transformed | | | | | |
| | | Site | 7 | 716551 | 8.8012 | **<.0001** |
| | | Year | 1 | 50946 | 4.3803 | **0.0369** |
| | | Site *Year | 7 | 242530 | 2.9789 | **0.0046** |
| | | Model | 15 | 1095357 | 6.2785 | **<.0001** |
| | | Error | 435 | 5059384 | | |
| | | Total | 450 | 6154741 | | |

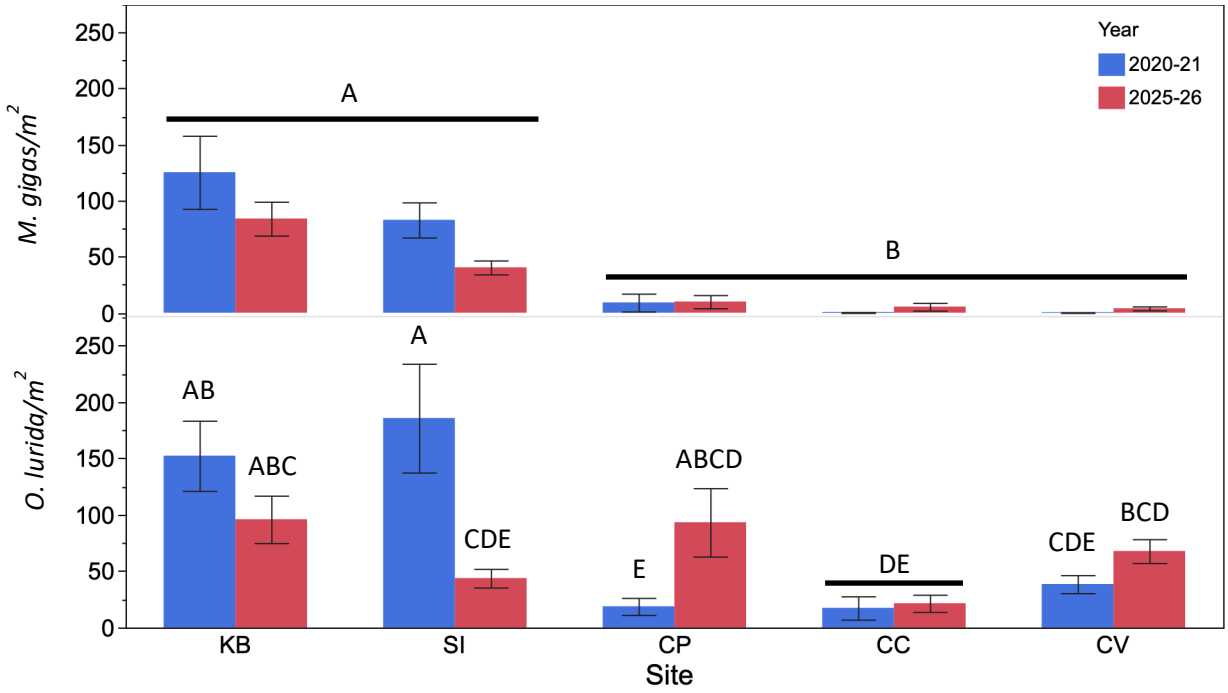



Figure 12. Density of oysters across sampling years at tidal elevations lower than 0.3 m MLLW from riprap and cobble sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Top panel: *M. gigas* density across riprap and cobble sites. Bottom panel: *O. lurida* density on riprap and cobble between sampling periods. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 6. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas and square root-transformed O. lurida density data collected from tidal elevations lower than 0.3 m MLLW at riprap and cobble sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | p-value |
|---|---|---|---|---|---|---|
| *M. gigas*/m$^2$ | Rank-transformed | Year | 1 | 295.62 | 0.3629 | 0.5478 |
| | | Site | 4 | 186542.69 | 57.2492 | **<.0001** |
| | | Site *Year | 4 | 5562.53 | 1.7071 | 0.1512 |
| | | Model | 9 | 190857.37 | 26.0326 | **<.0001** |
| | | Error | 154 | 125449.63 | | |
| | | Total | 163 | 316307 | | |
| *O. lurida*/m$^2$ | Square root | Year | 1 | 2.49732 | 0.1362 | 0.7126 |
| | | Site | 4 | 900.67227 | 12.2811 | **<.0001** |
| | | Site *Year | 4 | 632.89584 | 8.6299 | **<.0001** |

| | | | | |
|---|---|---|---|---|
| Model | 9 | 1462.5314 | 8.8633 | **<.0001** |
| Error | 154 | 2823.5106 | | |
| Total | 163 | 4286.042 | | |

## Change in density across time on seawall and chain-link fence

*M. gigas*: On seawall and chain link fence habitat above 0.3 m MLLW, *M. gigas* density varied across sites but there was no density change across time, nor did time and site interact (Figure 13, Table 7, Two-way ANOVA, site p <0.0001). Densities at CC and GB were X to Y times higher compared to CP and GC.

*O. lurida*: On seawall and chain link fence habitat above 0.3 m MLLW, *O. lurida* density did not change across time and did not vary across sites. (Figure 13, Table 7, Two-way ANOVA, all factors p >0.05).

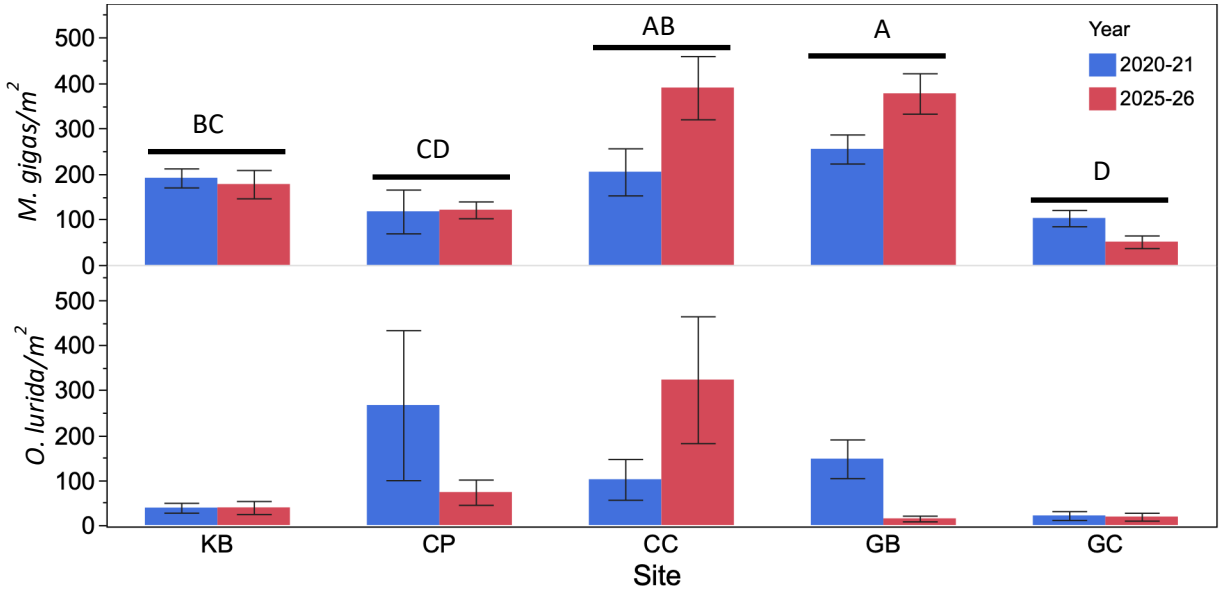



Figure 13. Density of oysters across sampling years at tidal elevations 0.3 m MLLW and greater from seawall and chain link fence throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Top panel: *M. gigas* density across seawall and chain link fence sites. Right panel: *O. lurida* density on seawall and chain link fence. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 7. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas and O. lurida density data collected from tidal elevations 0.3 m MLLW and greater at seawall and chain link fence sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | p-value |
|---|---|---|---|---|---|---|
| *M. gigas*/m$^2$ | Rank-transformed | Site | 4 | 188361 | 18.0573 | **<.0001** |
| | | Year | 1 | 2502 | 0.9594 | 0.3285 |
| | | Site *Year | 4 | 22689 | 2.1751 | 0.0732 |
| | | Model | 9 | 232935 | 9.9246 | **<.0001** |
| | | Error | 198 | 516348 | | |
| | | Total | 207 | 749283 | | |
| *O. lurida*/m$^2$ | Rank-transformed | Site | 4 | 13635 | 1.2026 | 0.311 |
| | | Year | 1 | 3047 | 1.075 | 0.3011 |
| | | Site *Year | 4 | 24403 | 2.1523 | 0.0758 |
| | | Model | 9 | 54954 | 2.1541 | **0.0268** |
| | | Error | 198 | 561238 | | |
| | | Total | 207 | 616192 | | |

## Variation in percent cover across time (2020-21 versus 2025-26)

As with density, since the variation in cover among habitats was quite large at both upper and lower elevations (Figures 14, 15) we analyzed data across time by dividing the data into three separate habitat type categories (cobble and riprap, pier pilings and pipe, and seawall and chain-link fence) and by tidal elevation. At the lower elevation, seawall and chain link fence habitat had replication less than n=5 for at least one year at all sites, or the habitat did not exist at the lower elevation, thus those data were not analyzed statistically. Unlike density, percent cover across time was evaluated for *M. galloprovincialis*, as cover data were recorded during both sampling intervals.

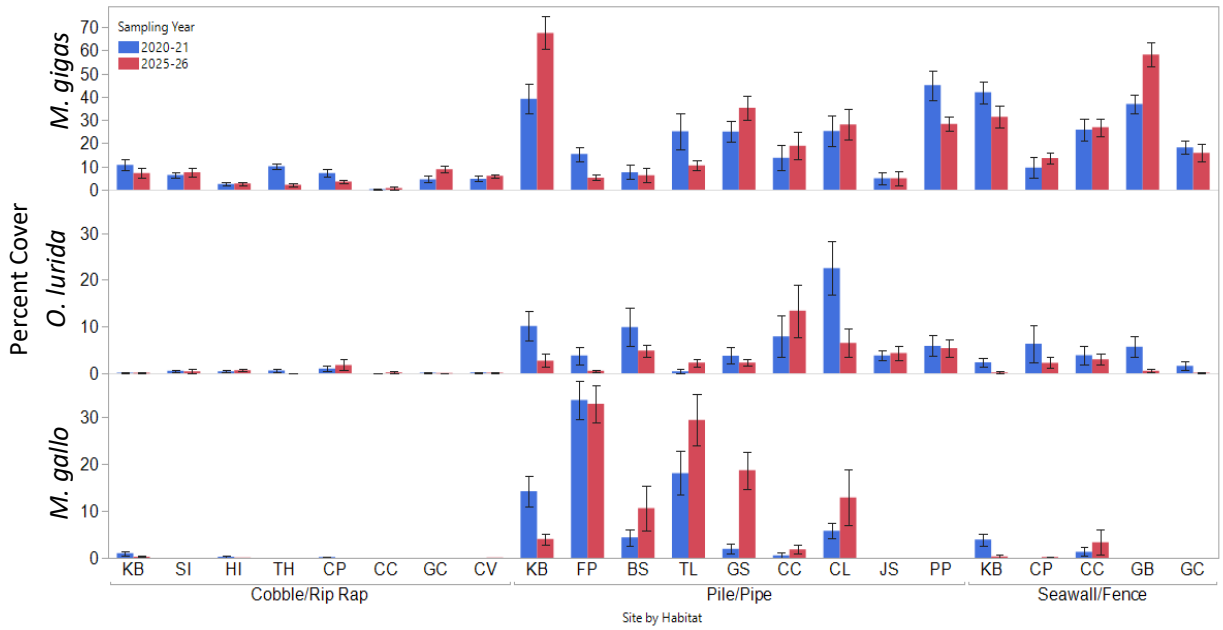



Figure 14. Percent cover of bivalves across sampling years and habitat type categories from tidal elevations 0.3 m and greater at sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. *M. gallo* = *Mytilus galloprovincialis*. Note difference in scale on the Y axis.

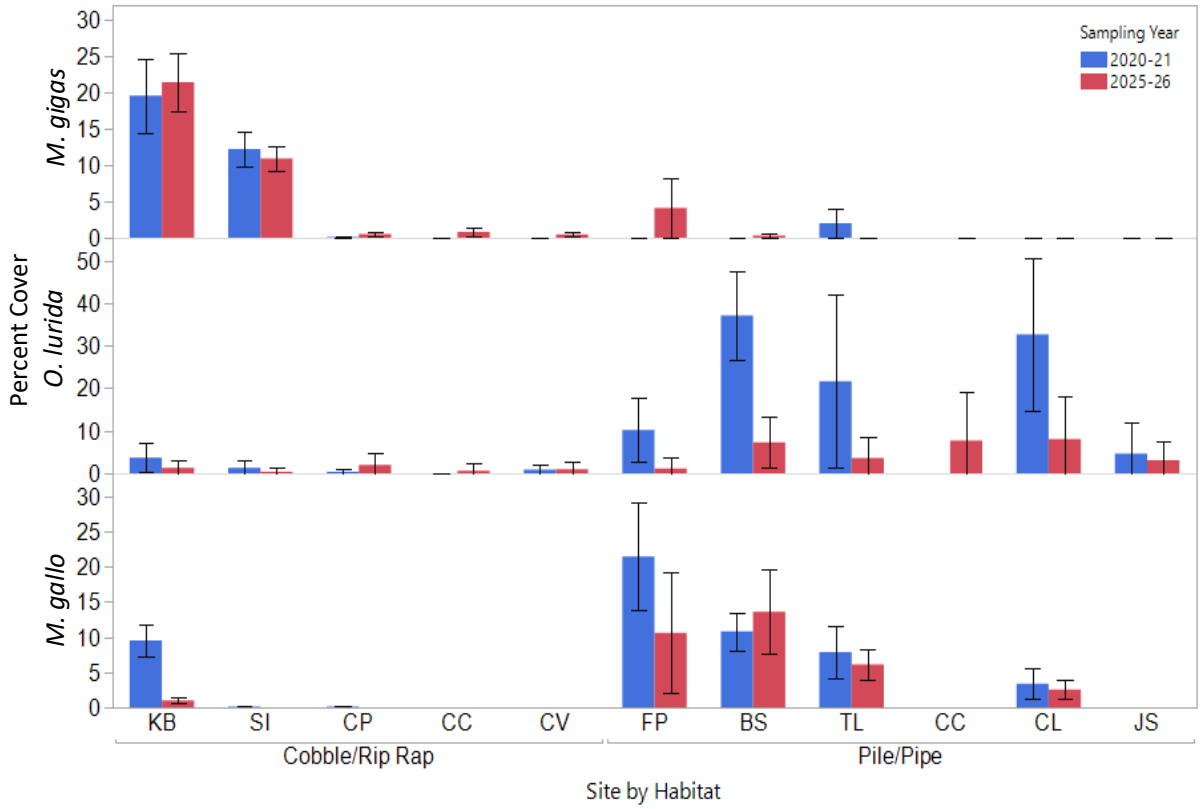



Figure 15. Percent cover of bivalves across sampling years and habitat type categories from tidal elevations <0.3 m MLLW at sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. *M. gallo* = *Mytilus galloprovincialis.* Note difference in scale on the Y axis.

## Change in percent cover across time on pier pile and pipe habitat

*M. gigas*: On pier pile and pipe habitat at and above 0.3 m MLLW, *M. gigas* percent cover did not change across time but there was a significant interaction between sampling periods and site (Figure 16 top panel, Table 8, Two-way ANOVA, year*site $p < 0.0299$). Percent cover of *M. gigas* trended towards an increase at KB from 39.2 ± 6.46% in 2020-21 to 67.5 ± 7.09% in 2025-26 with trends towards decreases in cover at TL and PP, however post-hoc Tukey tests could not pull out any significant differences. Below 0.3 m MLLW, *M. gigas* percent cover did not change across time, nor did individual sites differ significantly, and there was no interaction between year and site (Figure 17 top panel, Table 9, Two-way ANOVA, $p>0.05$, all factors). Thus, we conclude there was no overarching change in percent cover across time on pier pile or pipe habitats at either upper or lower elevations for *M. gigas*.

*O. lurida*: On pier pile and pipe habitat at and above 0.3 m MLLW, there was a significant interaction between time and site for *O. lurida* percent cover (Figure 16 middle panel, Table 8, Two-way ANOVA, time*site interaction $p = 0.0324$). There was a trend toward decreasing cover across sampling periods 2020-21 to 2025-26 at sites KB from 10.1 ± 3.11% to 2.71 ± 1.38% and CL from 22.5 ± 5.74% to 6.53 ± 3.02%, though post-hoc Tukey tests did not

reveal any site-level cover shifts across time, likely due to high within-site variance. Below 0.3 m MLLW, percent cover of *O. lurida* on pier pile and pipe habitats significantly decreased by 16.37% between sampling years, dropping from an initial baseline of 21.25 ± 2.93% in 2020-21 down to 4.88 ± 1.02% in 2025-26 (Figure 18 left panel, Table 9, Two-way ANOVA, year $p < 0.0001$). Across sites, post-hoc Tukey comparisons revealed that sites BS and CL supported the highest overall cover of *O. lurida*, which were significantly greater than cover at FP and JS, which supported the lowest (Figure 18 right panel, Table 9, Two-way ANOVA, site $p < 0.0001$). There was no significant interaction between year and site ($p = 0.0682$). Overall, at high and low elevations across time we conclude that cover of *O. lurida* declined at pier pile and pipe sites.

*M. galloprovincialis*: On pier pile and pipe habitat above 0.3 m MLLW, *M. galloprovincialis* percent cover did significantly interact between sampling periods and site with an increase in cover only at GS from 1.97 ± 1.1% in 2020-21 up to 18.7 ± 3.96% in 2025-26 (Figure 16 bottom panel, Table 8, Two-way ANOVA, site $p < 0.0117$). FP had the highest cover of *M. galloprovincialis*, while JS and PP supported the lowest cover, both relatively 0%. Below 0.3 m MLLW, *M. galloprovincialis* percent cover did not change across time, nor did time interact with site, but there was a significant difference across individual sites (Figure 17 bottom panel, Table 9, Two-way ANOVA, site $p < 0.0001$). Post-hoc Tukey comparisons revealed FP, BS and TL supported the highest overall cover, whereas JS supported the lowest, where zero percent cover was recorded across both sampling years.

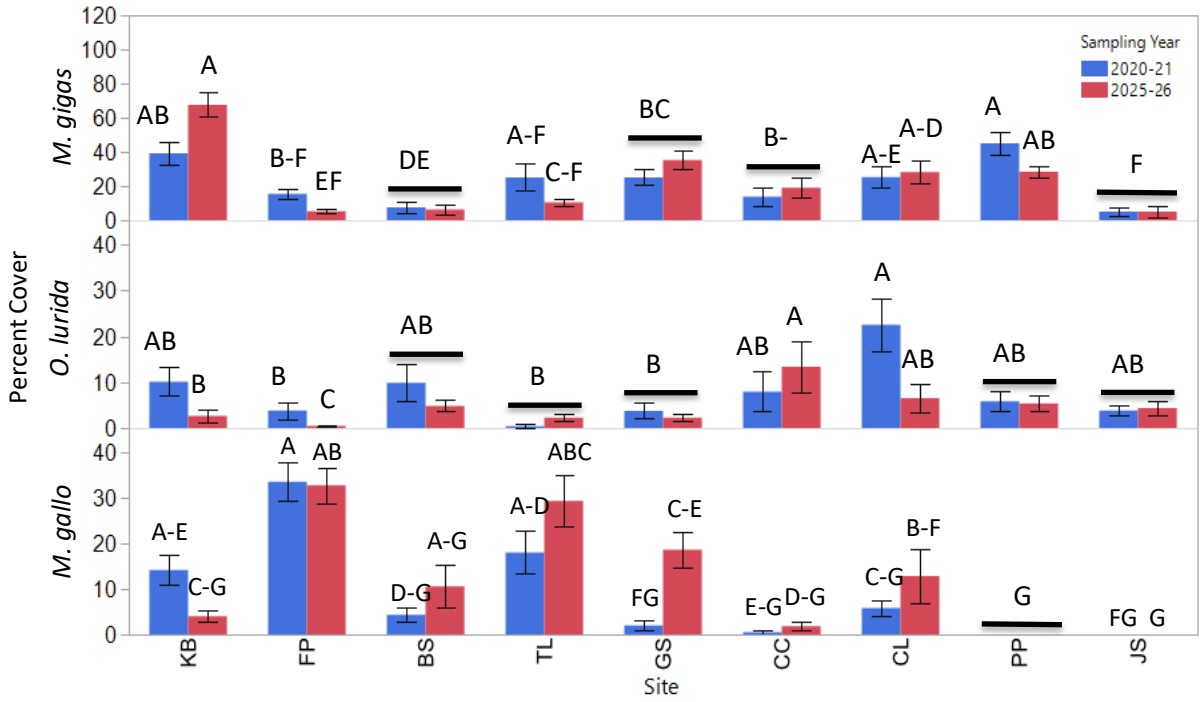



Figure 16. Percent cover of bivalves across sampling years at tidal elevations 0.3 m MLLW and greater from pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 8. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed *M. gigas, O. lurida* and *M. gallo* (*Mytilus galloprovincialis*) percent cover data collected from tidal elevations 0.3 m MLLW and greater at pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | P |
|---|---|---|---|---|---|---|
| % Cover *M. gigas* | Rank-transformed | Year | 1 | 186.62 | 0.0308 | 0.8608 |
| | | Site | 8 | 844097.24 | 17.4141 | **<.0001** |
| | | Year* Site | 8 | 104984.2 | 2.1659 | **0.0299** |
| | | Model | 17 | 971277.1 | 9.4296 | **<.0001** |
| | | Error | 309 | 1872235.4 | | |
| | | Total | 326 | 2843512.5 | | |
| % Cover *O. lurida* | Rank-transformed | Year | 1 | 3784.17 | 0.632 | 0.4272 |
| | | Site | 8 | 246731.54 | 5.151 | **<.0001** |
| | | Year* Site | 8 | 102278.41 | 2.1352 | **0.0324** |
| | | Model | 17 | 376205.1 | 3.696 | **<.0001** |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | Error | 310 | 1856128.9 | | |
| | | Total | 327 | 2232334 | | |
| % Cover | | | | | | |
| *M. gallo* | Rank-transformed | Year | 1 | 13122.9 | 2.9928 | 0.0846 |
| | | Site | 8 | 975919.69 | 27.8209 | **<.0001** |
| | | Year* Site | 8 | 88088.71 | 2.5112 | **0.0117** |
| | | Model | 9 | 60300.49 | 15.0102 | **<.0001** |
| | | Error | 154 | 42563.01 | | |
| | | Total | 163 | 102863.5 | | |

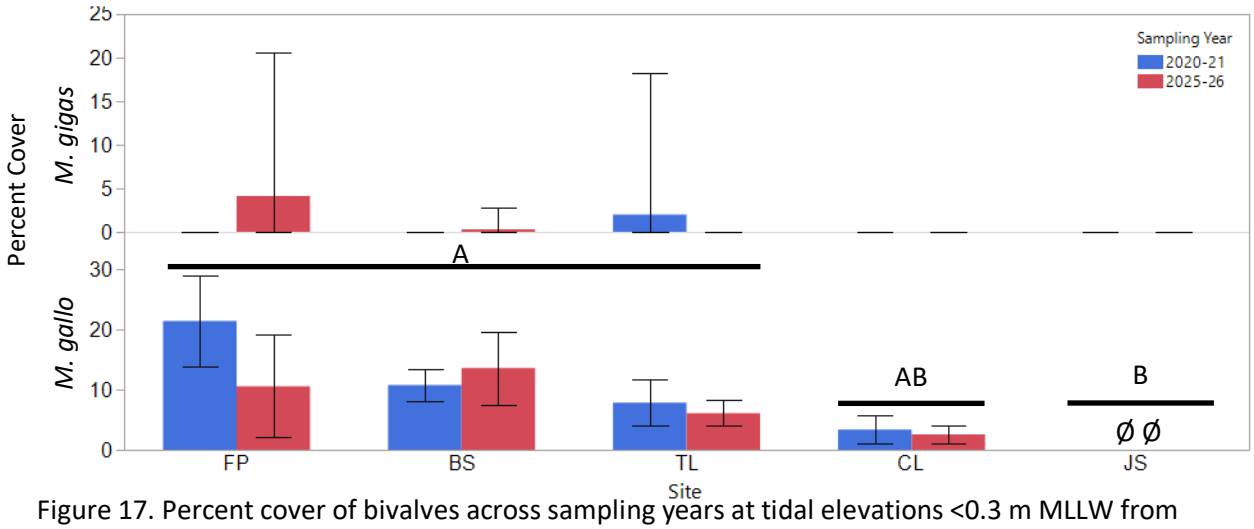



Figure 17. Percent cover of bivalves across sampling years at tidal elevations <0.3 m MLLW from pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

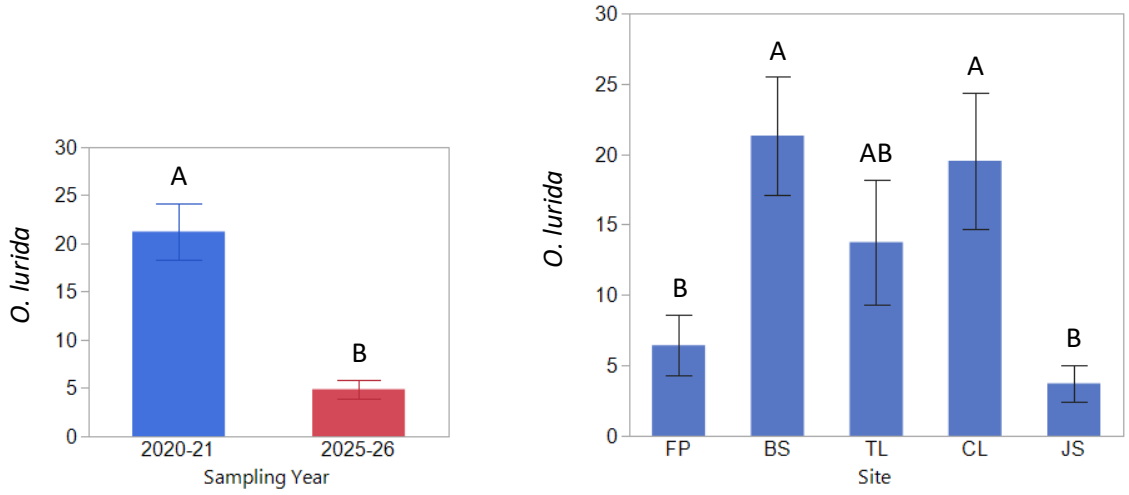



Figure 18. Percent cover of *O. lurida* between sampling years (left panel) and individual sites (right panel) at tidal elevations <0.3 m MLLW from pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 9. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed *M. gigas* and *M. gallo* (*Mytilus galloprovincialis*), and Log(x+1) transformed *O. lurida* percent cover data collected from tidal elevations <0.3 m MLLW at pier pile and pipe sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | P |
|---|---|---|---|---|---|---|
| % Cover *M. gigas* | Rank transformed | Year | 1 | 48.47134 | 0.8327 | 0.3647 |
| | | Site | 4 | 165.63479 | 0.7113 | 0.587 |
| | | Year* Site | 4 | 313.95416 | 1.3483 | 0.261 |
| | | Model | 9 | 488.3556 | 0.9321 | 0.5033 |
| | | Error | 69 | 4016.6444 | | |
| | | Total | 78 | 4505 | | |
| % Cover *O. lurida* | Log (x+1) | Year | 1 | 38.016564 | 30.6772 | **<.0001** |
| | | Site | 4 | 36.191493 | 7.3011 | **<.0001** |
| | | Year* Site | 4 | 11.370587 | 2.2939 | 0.068 |
| | | Model | 9 | 80.31144 | 7.2008 | **<.0001** |
| | | Error | 69 | 85.50776 | | |
| | | Total | 78 | 165.8192 | | |
| % Cover *M. gallo* | Rank transformed | Year | 1 | 433.2856 | 1.3669 | 0.2464 |
| | | Site | 4 | 9729.2384 | 7.673 | **<.0001** |
| | | Year* Site | 4 | 1048.244 | 0.8267 | 0.5127 |
| | | Model | 9 | 11606.397 | 4.0682 | **0.0003** |
| | | Error | 69 | 21872.603 | | |
| | | Total | 78 | 33479 | | |

## Change in percent cover across time on riprap and cobble habitat

*M. gigas*: On cobble and riprap habitat above 0.3 m MLLW, M. gigas percent cover did change across time, but there was a highly significant interaction between year and site (Figure 19 top panel, Table 10, Two-way ANOVA, year*site interaction $p < 0.0001$). This interaction was driven by a decline in cover over time at only TH, dropping from 10.1 ± 1.23% in 2020-21 to 2.18 ± 0.66% in 2025-26. Below 0.3 m MLLW, the three sites lacking sufficient habitat or quadrat replication (HI, TH, and GC) were excluded from analysis. For the remaining five sites, *M. gigas* percent cover did not vary significantly across sampling years, nor was there an interaction effect, but it differed regionally among sites (Figure 20 top panel, Table 11, Two-way ANOVA, Site $p < 0.0001$). Overall, *M. gigas* percent cover showed no consistent shift across time at either elevation on riprap and cobble habitat.

*O. lurida:* On riprap and cobble habitat at 0.3 m MLLW and greater, *O. lurida* percent cover did not show an overarching pattern of change across time, nor was there a significant interaction effect, but it varied significantly by site (Figure 19 middle panel, Table 10, Two-way ANOVA, site $p = 0.0001$). CP supported the highest overall cover, while the remaining sites remained uniformly low and statistically indistinguishable from one another. Below 0.3 m MLLW, year and site interacted significantly to influence *O. lurida* percent cover (Figure 20 middle panel, Table 11, Two-way ANOVA, year*site $p = 0.0283$). This interaction may have reflected opposing localized trajectories with percent cover dropping from 2020–21 to 2025–26 at KB from 3.74 ± 1.03% to 1.35 ± 0.42% but increasing over the same time period at CP from 0.36 ± 0.19% to 2.04 ± 0.79%, however post-hoc Tukey tests could not pull out any significant differences across time by sites. Overall, *O. lurida* percent cover on cobble and riprap remained stable but uniformly low at the upper tidal elevation, whereas the lower elevation experienced a trend defined by opposing, site-specific increases and decreases across time.

*M. galloprovincialis*: On riprap and cobble habitat at and above 0.3 m MLLW, *M. galloprovincialis* percent cover did not change over time, nor was there an interaction between year and site, but percent cover differed significantly across sites (Figure 19 bottom panel, Table 10, Two-way ANOVA, Site $p < 0.0001$). Post-hoc comparisons pulled out KB, HI, CP, and CV as supporting low (<1%) but detectable cover, while *M. galloprovincialis* went entirely undetected across both sampling years at SI, TH, CC, and GC. Below 0.3 m MLLW there was a highly significant interaction between year and site (Figure 20 bottom panel, Table 11, Two-way ANOVA, year*site interaction $p < 0.0001$). This strong interaction was driven entirely by a decline at KB, where percent cover fell from a site maximum of 9.52 ± 2.32% in 2020–21 to 0.99 ± 0.41 in 2025–26. In contrast, cover at the remaining analyzed sites SI, CP, CC, and CV remained consistently minimal or undetected during both survey intervals. Thus, outside of a significant decline at KB at the lower elevation, there was no uniform, bay-wide shift in *M. galloprovincialis* percent cover across time on riprap and cobble structures.

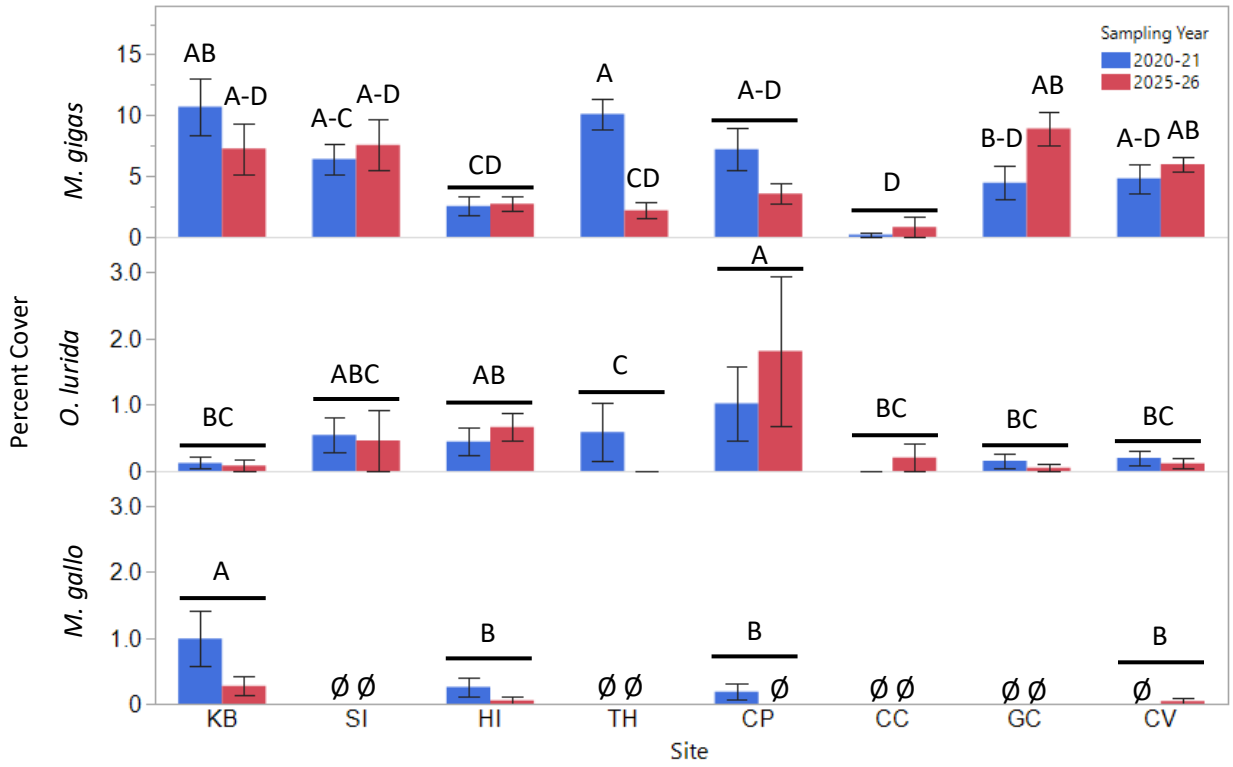



Figure 19. Percent cover of bivalves across sampling years at tidal elevations 0.3 m and greater cobble and riprap sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 10. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed M. gigas, O. lurida, and M. gallo (Mytilus galloprovincialis) percent cover data collected from tidal elevations 0.3 m and greater at cobble and riprap sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | P |
|---|---|---|---|---|---|---|
| % Cover *M. gigas* | Rank transformed | Year | 1 | 14890.28 | 1.0776 | 0.2998 |
| | | Site | 7 | 651983.34 | 6.7403 | **<.0001** |
| | | Year* Site | 7 | 647384.64 | 6.6927 | **<.0001** |
| | | Model | 15 | 1430288.4 | 6.9003 | **<.0001** |
| | | Error | 438 | 6052509.1 | | |
| | | Total | 453 | 7482797.5 | | |
| % Cover *O. lurida* | Rank transformed | Year | 1 | 442.1 | 0.0983 | 0.7541 |
| | | Site | 7 | 136332.26 | 4.3294 | **0.0001** |
| | | Year* Site | 7 | 24703.97 | 0.7845 | 0.6006 |
| | | Model | 15 | 167259.1 | 2.4787 | **0.0016** |
| | | Error | 438 | 1970385.4 | | |
| | | Total | 453 | 2137644.5 | | |
| % Cover *M. gallo* | Rank transformed | Year | 1 | 3814.104 | 2.2188 | 0.1371 |
| | | Site | 7 | 69882.948 | 5.8076 | **<.0001** |
| | | Year* Site | 7 | 9847.611 | 0.8184 | 0.5723 |
| | | Model | 15 | 90643.46 | 3.5153 | **<.0001** |
| | | Error | 438 | 752927.04 | | |
| | | Total | 453 | 843570.5 | | |

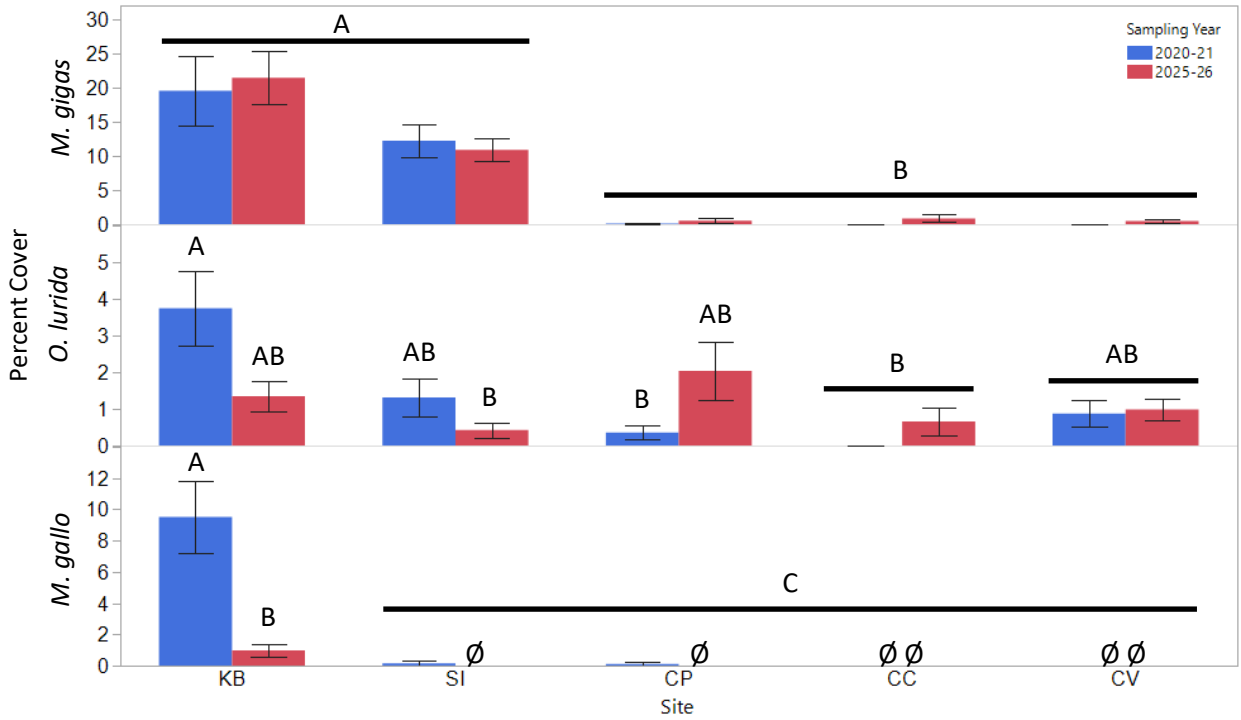



Figure 20. Percent cover of bivalves across sampling years at tidal elevations <0.3 m MLLW from cobble and riprap sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 11. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed *M. gigas*, *O. lurida* and *M. gallo* (*Mytilus galloprovincialis*) percent cover data collected from tidal elevations <0.3 m MLLW at cobble and riprap sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | P |
|---|---|---|---|---|---|---|
| % Cover *M. gigas* | Rank transformed | Year | 1 | 1393.7 | 2.211 | 0.1391 |
| | | Site | 4 | 188159.65 | 74.6262 | **<.0001** |
| | | Year* Site | 4 | 1593.4 | 0.632 | 0.6404 |
| | | Model | 9 | 194412.08 | 34.2693 | **<.0001** |
| | | Error | 154 | 97072.42 | | |
| | | Total | 163 | 291484.5 | | |
| % Cover *O. lurida* | Rank transformed | Year | 1 | 132.079 | 0.0975 | 0.7552 |
| | | Site | 4 | 24444.528 | 4.5127 | **0.0018** |
| | | Year* Site | 4 | 15119.084 | 2.7911 | **0.0283** |
| | | Model | 9 | 38475.47 | 0.0016 | **0.0016** |
| | | Error | 154 | 208548.03 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | Total | 163 | 247023.5 | | |
| % Cover | | | | | | |
| *M. gallo* | Rank transformed | Year | 1 | 4273.132 | 15.4609 | **0.0001** |
| | | Site | 4 | 50059.397 | 45.2808 | **<.0001** |
| | | Year* Site | 4 | 9186.162 | 8.3093 | **<.0001** |
| | | Model | 9 | 60300.49 | 24.2419 | **<.0001** |
| | | Error | 154 | 42563.01 | | |
| | | Total | 163 | 102863.5 | | |

### Change in percent cover across time on seawall and chain-link fence

*M. gigas*: On seawall and chain-link fence habitat at and above 0.3m MLLW, there was a significant interaction between sampling year and site for *M. gigas* percent cover (Figure 21 top panel, Table 12, Two-way ANOVA, year*site interaction p = 0.0436). This interaction was primarily driven by an increase in cover across time at GB from 37.0 ± 3.85% in 2020-21 to 58.2 ± 5.04% in 2025-26, while the remaining sites stayed relatively stable.

*O. lurida*: On seawall and chain-link fence habitat 0.3m MLLW and greater, *O. lurida* percent cover changed significantly across time (Figure 21 middle panel, Table 12, Two-way ANOVA, year p = 0.0361), but did not vary significantly among sites nor was there evidence of an interaction effect between sampling year and site. Thus, we conclude there was an overarching regional reduction in *O. lurida* percent cover on seawall and fence structures over the five-year interval.

*M. galloprovincialis*: On seawall and chain-link fence habitat 0.3m MLLW and greater, there was a highly significant interaction between sampling year and site for *M. galloprovincialis* percent cover (Figure 21 bottom panel, Table 12, Two-way ANOVA, year*site interaction p = 0.0009). This interaction was driven by a decline at KB, where percent cover dropped from 3.90 ± 1.24% in 2020–21 to 0.34 ± 0.25% in 2025–26 while at the remaining sites there was no detectable change in cover through time.

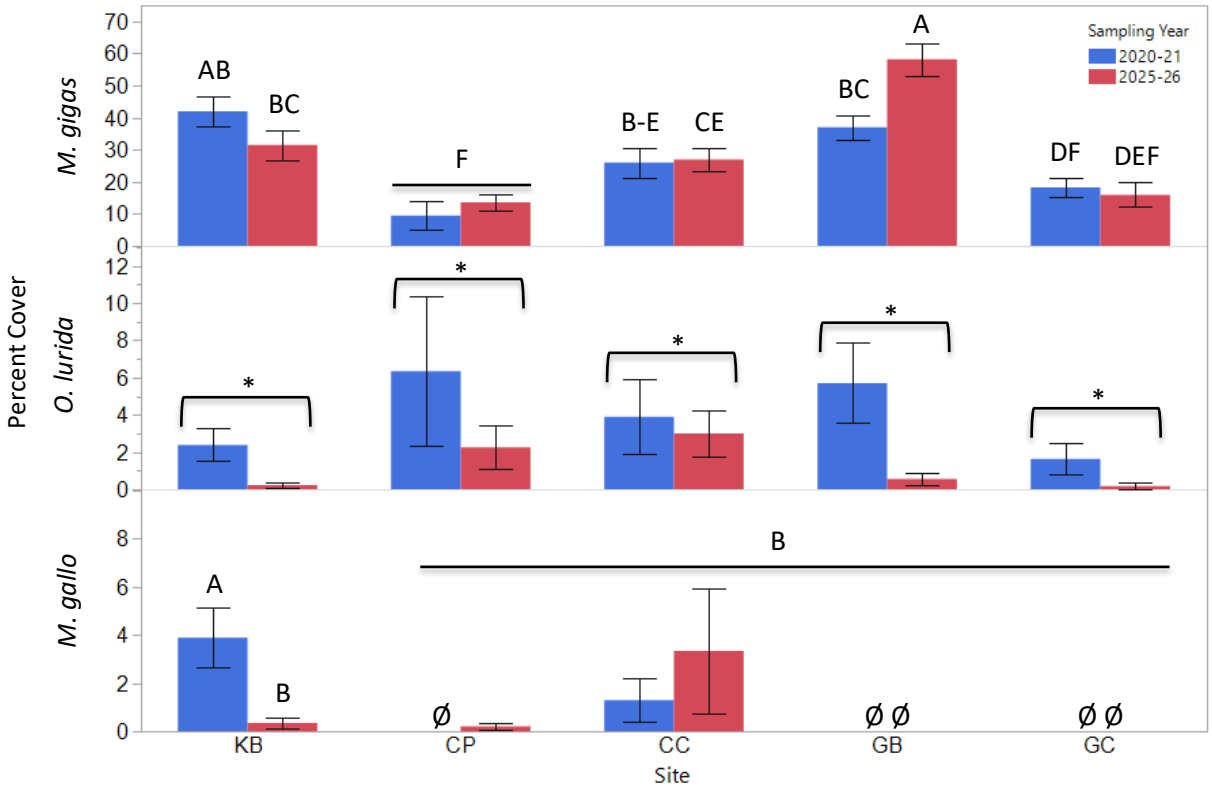



Figure 21. Percent cover of bivalves across sampling years at tidal elevations 0.3 m and greater seawall and chain-link fence sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Error bars are +/- 1 SE. Site abbreviations are as in Table 1. Differing letters or asterisk (*) above bars indicate statistically significant differences based upon Tukey post-hoc comparisons.

Table 12. Two-way ANOVA test statistics for effects of site and year and their interaction on rank-transformed *M. gigas*, *O. lurida*, and *M. gallo* (*Mytilus galloprovincialis*) percent cover data collected from tidal elevations 0.3 m and greater at seawall and chainlink fence sites throughout San Diego Bay, CA from surveys conducted during 2020-21 and 2025-26. Significant p values are **bolded**.

| Response Variable | Transformation | Source | DF | Sum squares | F Ratio | P |
|---|---|---|---|---|---|---|
| % Cover *M. gigas* | Rank transformed | Year | 1 | 713.11 | 0.2781 | 0.5985 |
| | | Site | 4 | 192929.32 | 18.8094 | **<.0001** |
| | | Year* Site | 4 | 25676.99 | 2.5033 | **0.0436** |
| | | Model | 9 | 240881.16 | 10.4375 | **<.0001** |
| | | Error | 198 | 507724.84 | | |
| | | Total | 207 | 748606 | | |
| % Cover *O. lurida* | Rank transformed | Year | 1 | 8386.063 | 4.4505 | **0.0361** |
| | | Site | 4 | 11452.353 | 1.5195 | 0.1979 |
| | | Year* Site | 4 | 1893.024 | 0.2512 | 0.9087 |
| | | Model | 9 | 22410.66 | 1.3215 | 0.2276 |
| | | Error | 198 | 373088.34 | | |
| | | Total | 207 | 395499 | | |
| % Cover *M. gallo* | Rank transformed | Year | 1 | 2389.462 | 3.295 | 0.071 |
| | | Site | 4 | 29604.483 | 10.206 | **<.0001** |
| | | Year* Site | 4 | 14238.304 | 4.9086 | **0.0009** |
| | | Model | 9 | 52535.27 | 8.0495 | **<.0001** |
| | | Error | 198 | 143584.23 | | |
| | | Total | 207 | 196119.5 | | |

## Summary – bivalve change in density and percent cover across time

Log response ratios of change across time for density and cover (Figure 22) were largely consistent with our more granular statistical comparisons within each categorial habitat type and elevation presented above but in aggregate allow us to see trends otherwise lost in the details or not captured by the statistical comparisons. For example, while statistical comparisons of *M. gigas* and *O. lurida* across time largely revealed non-significant change in density and cover, *M. gigas* density and cover are clearly trending in a positive direction across many habitat types while *O. lurida* cover, in particular, trends lower (Figure 22), and with statistically significant declines at some sites (Figures 18, 21). As with the statistical comparisons, trends in *O. lurida* density were more equivocal (Figure 22) with both significant declines (Figures 10, 12) and gains (Figures 9, 12) across habitats and sites. *M. galloprovincialis* cover also trends lower (Figure 22), and with statistically significant declines at some sites (Figures 20, 21).

| Habitat Type | *M. gigas* | | *O. lurida* | |
|---|---|---|---|---|
| | <0.3 m MLLW | >0.3 m MLLW | <0.3 m MLLW | >0.3 m MLLW |
| Pier pile/pipe | 3.11 | 0.34 | -1.00 * | 0.22 * |
| Riprap/cobble | 0.86 | -0.05 * | 0.09 * | 0.67 |
| Seawall/fence | | 0.06 | | -0.51 |

| Habitat Type | *M. gigas* | | *O. lurida* | | *M. galloprovincialis* | |
|---|---|---|---|---|---|---|
| | <0.3 m MLLW | >0.3 m MLLW | <0.3 m MLLW | >0.3 m MLLW | <0.3 m MLLW | >0.3 m MLLW |
| Pier pile/pipe | 0.51 | -0.14 | -1.34 * | -0.38 | -0.63 | 0.62 |
| Riprap/cobble | 0.47 | 0.00 * | -0.07 | -0.19 | -2.27 * | -1.42 |
| Seawall/fence | | 0.09 | | -1.65 * | | -0.75 * |

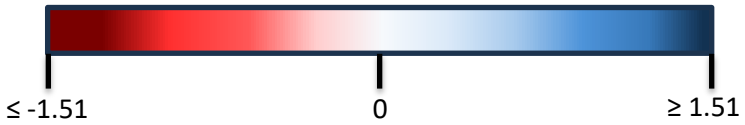



Figure 22. Log response ratio of density (top) and percent cover (bottom) of bivalves compared across sampling years 2020-21 and 2025-26 at tidal elevations >0.3 m and <0.3 m MLLW from categorical habitat types throughout San Diego Bay, CA. Shades of blue indicate positive change across time and shades of red indicate decline over time. Log response ratios with asterisks (*) indicate statistically significant change in the direction indicated for at least one site, while log response ratios with no asterisks indicate non-significant trends.

## Abundance Estimates

From 2025-26, across sites, estimated *M. gigas* and *O. lurida* abundances were highest at CC (227,556 *M. gigas* and 642,729 *O. lurida*), while highest abundance for *M. galloprovincialis* was at FP (260,914) (Table 1). Estimated abundances were lowest at BS for *M. gigas* (705) and GB for *O. lurida* (618) *M. galloprovincialis'* lowest abundance was 0 (not detected within quadrats) at three sites – BP, JS and TH).

The estimated bay-wide abundance for *O. lurida* is 57,217,109 and was about 2 times greater than *M. gigas*, which is estimated at 29,226,304 oysters (Table 3). While a comparison with abundance estimates from 2020-21 (Table 2) indicates a 24.8% decline in *O. lurida* and a 3.43% decline for *M. gigas*, the baseline abundance estimates from 2020-21 fit well within the margin of error for both species. For example, the 2025-26 range of estimates for *O. lurida* (built using the 95% confidence intervals around the density estimates per habitat) were from 23.5 million on the low end to 92.6 million oysters on the high end, fully encompassing the 2020-21 estimate of 76 million oysters.

Both species of oysters were in highest abundance on pier pilings followed by rip rap (61.3% on pier pilings, 29.4% on rip rap for *O. lurida* and 41.3% on pier pilings, 26.8% on rip rap for *M. gigas*). The bay mussel, *M. galloprovincialis* was found almost exclusively on pier pilings (96.9% of abundance) within San Diego Bay.

**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 | Peri-meter (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 | 64,348 | | 48,382 | 44.2 | 172 | 0.1% | 10,113,099 | 46,655,065 | 33.4% | 61.3% |
| # Above | 8,399 | | 6,315 | 29.6 | 136 | 0.4% | 323,307 | 333,096 | 1.1% | 0.4% |
| # Unattached | 334 | | 251 | 0.0 | 0 | 0.0% | 20,798 | 19,287 | 0.1% | 0.0% |
| **Grand total habitat perimeter** | **175,284** | | **64,559** | **347** | **854** | **0.2%** | **30,288,069** | **76,115,266** | **100.0%** | **100.0%** |
| **Grand total shoreline perimeter** | **102,203** | **100.0%** | | | | | | | | |
| **Hard shoreline perimeter** | **83,476** | **81.7%** | | | | | | | | |

**Table 3.** 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 2025 – 2026. 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. The abundance estimate range is a margin of error metric built around our abundance estimates that was calculated using the 95% confidence intervals of per-habitat and tidal elevation densities. *M. gallo* = *Mytilus galloprovincialis*

| | | | | | | | Abundance | | | % of Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat type | Peri-meter (m) | % of perimeter | # of pier pilings | Sum length (m) of quadrats | (n) quadrats | % habitat sampled | *M. gigas* | *O. lurida* | *M. gallo* | *M. gigas* | *O. lurida* | *M. gallo* |
| Riprap | 44,625 | 43.7% | | 146.0 | 292 | 0.3% | 7,827,092 | 9,315,541 | 914,022 | 26.8% | 16.3% | 1.8% |
| Seawall | 32,797 | 32.1% | | 45.0 | 90 | 0.1% | 6,207,314 | 4,964,637 | 392,559 | 21.2% | 8.7% | 0.8% |
| Soft | 18,727 | 18.3% | | 17.0 | 34 | 0.1% | 1,912,982 | 2,230,374 | 210,367 | 6.5% | 3.9% | 0.4% |
| Cobble | 5,687 | 5.6% | | 48.5 | 97 | 0.9% | 837,801 | 1,422,819 | 3,234 | 2.9% | 2.5% | 0.0% |
| Other | 367 | 0.4% | | 25.0 | 50 | 6.8% | 44,521 | 32,370 | 14,044 | 0.2% | 0.1% | 0.0% |
| # Below | 64,348 | | 48,382 | 58.5 | 234 | 0.1% | 12,073,288 | 38,918272 | 48,589,844 | 41.3% | 68.0% | 96.9% |
| # Above | 8,399 | | 6,315 | 29.6 | 136 | 0.4% | 323,307 | 333,096 | | 1.1% | 0.6% | 0.0% |
| # Unattached | 334 | | 251 | 0.0 | 0 | 0.0% | 20,798 | 19,287 | | 0.1% | 0.0% | 0.0% |
| **Grand total habitat perimeter** | **175,284** | | **64,559** | **370.0** | **933** | **0.2%** | **29,226,304** | **57,217,109** | **50,124,070** | **100.0%** | **100.0%** | **100.0%** |
| **Grand total shoreline perimeter** | **102,203** | **100.0%** | | | | | Abundance Estimate Range | | | | | |
| | | | | | | | 10,668,125 – 49,500,849 | 23,485,750 – 92,594,886 | 7,322,950 – 93,539,748 | | | |
| **Hard shoreline perimeter** | **83,476** | **81.7%** | | | | | | | | | | |

## DISCUSSION

While our statistical tests of variation in oyster density across time revealed little to no change, there were clearly trends in the data indicating declines in density for *O. lurida* and in cover for both *O. lurida* and the bay mussel, *M. galloprovincialis,* while density and cover trended towards gains for *M. gigas*, consistent with the increases in density of *M. gigas* within San Diego Bay measured across the decade from 2010-2020 (Wolfe et al. 2024). Notably, our oyster recruitment data from Grand Caribe from 2020-2024 reveal a trend of increasing *M. gigas* recruitment versus declining *O. lurida* recruitment (Zacherl 2026). The 2023-2024 El Nino event brought warming sea surface temperatures and may have set up a particularly strong recruitment event for *M. gigas* in 2024. *M. gigas* larval growth and settlement are positively impacted by warming water (Kheder et al. 2010). The increasing trend for *M. gigas* density and cover that occurred during a period when warming waters may have positive impacted their reproduction is also consistent with global increases in *M. gigas* during periods of warming summer seawater temperatures (e.g., Schmidt et al. 2008). An important caveat to the above discussion is that our statistical tests of change in *M. gigas* and cover were largely non-significant, but the concordance in trends across habitats and elevations underscores the importance of continued semi-decadal surveys to assess whether *M. gigas* continues to make gains within San Diego Bay.

Despite the potential ~ 25% decline in *O. lurida* abundance between 2020-21 and 2025-26, *O. lurida* remain the numerically dominant bivalve in San Diego Bay, even compared to bay mussels, *M. galloprovincialis*, but *M. gigas* still dominate in percent cover across all habitats. *M. gigas* are likely able to dominate cover via their much larger adult body size and biomass, and the fact that that they often grow in a flattened configuration at high tidal elevations where there are many fewer fouling species, including *O. lurida*. However, even at elevations below 0.3 m MLLW, cover of *M. gigas* is now trending towards increases while *O. lurida* cover trends toward declines. Whether *M. gigas* is successfully shifting its distribution lower, possibly in response to global climate change, remains to be determined.

A strength of this round of surveys was the addition of a margin of error to our abundance estimates using the 95% confidence intervals on our density calculations. This exercise revealed how sensitive the abundance estimate is to an accurate density measure. Oysters are patchy and, even on the same habitat within San Diego Bay (e.g., riprap), can vary substantially depending upon factors such as solar aspect and location within the bay. Regional and site-level differences in seawater quality parameters such as salinity, temperature, wave energy, and seawater exchange rates may greatly impact bivalve densities and likely contributed to large variation in our population metrics across sites. This patchiness elevates the importance of sampling effort, which still hovered around 0.2% of total habitat sampled. Given how little habitat was sampled and the variation in density across even the same habitat, it is not surprising that our range of estimated abundances was quite high. 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 2 of 8 available habitats (Table 3). If we want to achieve a

narrower margin of error for the abundance estimates, we would need to greatly increase the number of sites sampled per habitat, which would directly reduce the 95% confidence interval values. Constraints in funding or time may preclude this outcome.

As noted in the last Bay-wide Final report, we are likely underestimating total abundance because we do not sample subtidal habitats, including floating docks, subtidal pier pilings, and any existing subtidal hard structured habitat. *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), thus significant subtidal abundances may exist. Understanding subtidal population demographics will increase our abundance estimate for *O. lurida* since subtidal habitats are not represented in our current abundance estimate. Pier pilings below stationary docks remain a critical habitat for native oysters and have become the habitat supporting the highest abundance of Pacific oysters and bay mussels as well. As was noted in our previous reports, 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. That reef-like structure is likely also able to form and is reinforced by the shaded environment provided by the overhead piers; many other marine species also settle in higher abundances in shaded compared to exposed environments (Glasby, 1999; Blockley & Chapman, 2006). Our qualitative observations suggest that these vertical reefs on pier pilings are among the few observed instances in San Diego Bay where reef-like complexity is achieved for oysters. The only other circumstance where reef-like aggregates of oysters were observed was at Kellogg Beach on and around the riprap and rock present onsite, providing the only circumstance of an exposed and horizontal reef-like aggregate of oysters. These dense aggregates of oysters, whether horizontal or vertical, could provide an important benchmark when setting objectives for future restoration.

Establishing a bay-wide estimate of native and non-native oysters remains especially important in San Diego Bay because the Port of San Diego may introduce aquaculture practices of *M. gigas* in the bay. Anticipated warmer summer seawater temperatures due to climate change may benefit *M. gigas* which is known to increase recruitment during warm summers (Diederich et al., 2005; Nehls et al., 2006; Wrange et al., 2009), so this kind of study is relevant to aquaculture operations if viable *M. gigas* are cultured within the bay. Our baseline abundance estimates will provide a benchmark against which to compare future changes in the population demographics of both oyster species as well as the bay mussel.

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