THE EFFECT OF SEDIMENTATION ON OYSTERS (OSTREA LURIDA) ADJACENT TO EELGRASS BEDS (ZOSTERA MARINA)

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A Thesis

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Master of Science

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ABSTRACT

Oyster and eelgrass beds both provide ecosystem services that may include providing complex three-dimensional habitats, refuge from predation, and shoreline resiliency by buffering erosion. California's native oyster, *Ostrea lurida*, and native eelgrass, *Zostera marina*, have declined over the past two centuries on the west coast of the United States. As part of a Living Shorelines initiative to restore these important habitats while promoting shoreline resiliency, I restored oysters and eelgrass alone and adjacent to one another. Specifically, I aimed to assess if the oyster response is affected by eelgrass due to eelgrass-induced sediment deposition. From June 2016—April 2017, four treatments were established with restored eelgrass, oyster, oyster/eelgrass, and control plots at each of four locations in Newport Bay, California. Sediment characteristics such as grain size, sediment deposition onto oyster shell, and upshore sedimentation were measured using mud cores, point-contact techniques, and sediment pins. Eelgrass and oyster responses were measured by assessing eelgrass blade density, oyster settlement, adult oyster density, and adult oyster size. After one year, both the Oyster and Oyster/Eelgrass treatments tended to have more upshore silt and clay sediments than Eelgrass and Control treatments. Similarly, six months after oyster bed construction, mud deposition on shell was higher on oyster beds restored alone than on beds restored adjacent to eelgrass, suggesting that eelgrass may filter sediments from the water column, reducing the sediment load delivered to adjacent

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oyster beds. However, after one year this "filtering effect" remained at only one of the sites, and there was no significant difference in sedimentation upshore of treatment plots. In the reproductive season following restoration, cumulative settlement onto oyster beds was not affected by the presence of eelgrass. After one year, adult oyster density was either unaffected by the presence of eelgrass or was greater where oysters were restored alone than adjacent to eelgrass. Consistent with previous studies, oyster length increased with mud deposition on shell. Collectively, my results suggest some sediment filtering by eelgrass beds, with varying effects on adjacent oysters across time and among sites. Conclusions about whether to restore oysters alone versus adjacent to eelgrass meadows may be premature given the temporal and spatial context dependency observed within the first year after restoration, warranting continued and future investigation into these processes. Ultimately my findings may direct future restoration initiatives involving oysters and eelgrass.

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CHAPTER 1

INTRODUCTION

Climate change (Schlacher et al., 2008), rising sea levels (Aagaard and
Sorensen, 2011), and habitat degradation (Gittman et al., 2016) have motivated interest
in how to protect our shorelines in the face of an uncertain future. Shoreline protection
has been a concern for hundreds of years in the United States, even pre-dating
concerns about climate change, with concrete seawall construction dating back to 1784
in Boston Harbor, Massachusetts. Armoring shorelines with seawalls has continued in
this country for over 350 years as a means of shoreline protection (Rosen and Vine,
1995), despite a growing recognition that seawalls increase wave energy from wave
reflection that can increase downshore erosion and potentially damage neighboring
habitat (Bozek and Burdick, 2005). An alternative to seawalls is the use of natural
habitats as buffers, which can both protect shorelines from erosive forces while
simultaneously enhancing neighboring ecosystems (Patrick et al., 2016). One such
initiative is referred to as a "living shoreline," which uses natural and nature-based
features to buffer erosion, typically while conserving and/or restoring coastal habitat
(Bilkovic et al., 2016).

The evidence that natural habitats can buffer erosive forces is ample and strong.
For example, remaining coral reefs along the coast of Grenada have correlated with
higher shoreline stability compared to areas without reef structures (Reguero et al.,

2018) and coastal areas of Alabama with *Spartina alterniflora* had lower wave levels than at nearby sites without vegetation (Roland and Douglass, 2003). Restored natural habitats, particularly oyster reefs, have also demonstrably increased shoreline resiliency. In Mobile Bay, Alabama, breakwater reefs were created with the use of loose oyster shell, and experimental plots mitigated shoreline retreat by more than 40% at one site (Scyphers et al., 2011). Additionally, in Dauphin Island, Alabama, breakwater reefs were deployed to restore oyster populations, resulting in sediment accretion upshore of these structures (Swann, 2008).

If restoring one habitat results in shoreline resiliency and ecosystem gains, could restoration of coupled habitats result in even greater gains? There have so far been only a couple of living shoreline initiatives aimed at exploring the benefits of restoring multiple natural habitats simultaneously that have resulted in published data, though several multi-habitat projects are underway. Some current multi-habitat projects include The City of Madeira Beach Shoreline Park project in Florida, which makes use of oyster habitat and plant species such as live oaks and cabbage plants, the Nags Head Woods Ecological Preserve Living Shorelines project in North Carolina, which uses 0.5-acre shell bags and 0.25-acre native widgeon grass, and the Coastal Marsh and Living Shorelines project on the Outer Banks, North Carolina, which makes use of 600 feet of shell bags for oyster restoration plus marsh grass (NOAA Restoration Center, 2018). These ongoing multi-habitat projects all aim to restore habitat while buffering erosion. One recent study in San Francisco Bay, California, showed that plots with both oysters and eelgrass accumulated two times as much sediment compared to a control plot one year after oyster bed construction (Latta and Boyer, 2015).

Despite limited evidence so far for the efficacy of multi-habitat living shoreline projects, there is plenty of evidence that combinations of habitat-forming species may benefit one another. For example, a rich literature exists on the relationships between bivalves and vegetative species. Mussels and cordgrass share a mutualism, and nitrification occurs at the highest rate when both mussels and cordgrass are coupled compared to alone (Bilkovic et al., 2017). The relationship between mussels (*Mytilus edulis*) and eelgrass (*Zostera marina*), clams (*Mercenaria mercenaria*) and eelgrass (*Zostera marina*), and oysters (*Crassostrea virginica*) and eelgrass (*Zostera marina*) have consistently demonstrated that bivalves lower chlorophyll *a* concentrations, and subsequent eelgrass leaf area productivity increases in plots with high bivalve density (Wall et al., 2008). Mussels (*Geukensia demissa*) experience a decline in growthand increases in mortality after loss of cordgrass (*Spartina alterniflora*) (Bertness et al., 2015), suggesting that bivalves may benefit from such a relationship. Cordgrass (*Spartina alterniflora*) may also provide predator and/or heat stress refuge for mussels (*Geukensia demissa*; Bilkovic et al., 2017). Collectively, these studies suggest that there may be greater ecosystem and restoration success gains in a living-shoreline approach that aims to restore multiple species or habitats simultaneously, though a thorough understanding of the interactions of bivalves and plant species is still lacking, particularly for some attractive target habitats in living-shorelines initiatives, such as oyster reefs.

The recognition that oyster reefs had significant value for humans beyond their value as a fishery came unfortunately after most oyster reefs declined globally. In the last 200 years, oyster habitat abundance declined 85% globally (Beck et al., 2011) due

to pollution (Sinderman, 1996, Matthews-Amos and Agenbroad, 1999), disease (Ewart and Ford, 1993), habitat destruction (Rothschild et al., 1994), and overharvesting (Blake and Zu Ermgassen, 2015). Along the west coast of the United States, oyster reefs built by the Olympia oyster, *Ostrea lurida,* are now classified as "functionally extinct," and are critically reduced compared to their historic numbers (Beck et al., 2011, zu Ermgassen et al., 2012).

Prior to their collapse, oysters had significant ecological (MacKenzie, 1997) and economic (Humphreys, 2014) impacts on estuaries. As foundation species, oysters have a disproportionate effect on their associated ecosystem (Gedan et al., 2014), providing complex, three-dimensional habitat upon which many species live and grow (Shipley and Kiesling, 1994). The reef offers shelter to a variety of species and protects organisms from predation (Grabowski and Peterson, 2007). Additionally, oysters are filter feeders, removing phytoplankton from the water column (Gedan et al., 2014). This decreases the chance of harmful algal blooms (HABs), which can negatively impact human health as well as ecosystem health (NOAA, 2001). Ecosystem services associated with oyster reefs are valued between $2,225 - $40,064/acre annually (Grabowski et al., 2012).

Eelgrass (*Zostera marina*) is a plant species also targeted for living-shorelines initiatives that has historically co-occurred with oysters on the west coast of the United States (Miller & Morrison, 1988). This habitat has also declined dramatically, with a 58% decline in their abundance since the 1900s (Waycott et al., 2009), primarily due to wasting disease, which is caused by the slime mold *Labyrinthula zosterae* (Short et al., 1986). Wasting disease caused a 90% decline in eelgrass in the Atlantic Ocean in the

1930s (Muehlstein, 1989), and the Pacific Coast was similarly affected in the 2010s (Short, 2014). Nutrient influx has also contributed to the decline in eelgrass abundance (Dennison et. al., 1993). The largest culprit for eutrophication has been nitrogen, which pours into estuaries and bays due to groundwater contamination from septic systems (Valiela et al., 1990). Nitrogen stimulates phytoplankton growth that then acts as a photosynthetic competitor to eelgrass, and additionally blocks sunlight from penetrating down to eelgrass (Short and Burdick, 1996). Increased nutrients have been observed in bays and estuaries in the United States since the 1960s and 1970s (Golden et. al., 2010).

Like oysters, eelgrass is also a foundation species, and has a disproportionate impact on the ecosystems in which it resides (Leber and Greening, 1980). *Zostera marina* is a highly productive component of an estuary ecosystem, and provides a large amount of primary productivity and nutrient deposition (Peterson and Heck, 2001). Eelgrass slows wave action in an estuary and allows for habitats to form around its shoots (Davis and Short, 1997). Additionally, eelgrass can be used as a substrate upon which other organisms live, such as epiphytes and scallops. These organisms depend on eelgrass for survival and have declined due to eelgrass decline (NOAA, 2014). Economically, the ecosystem services associated with eelgrass meadows are estimated to be greater than $46,960/acre annually (Costanza et al., 1994), making them the third most valuable ecosystem per unit area in the world.

Projects that simultaneously restore both oysters and eelgrass are underway in central and southern California (e.g., Latta and Boyer, 2016, K. Nichols personal communication, Orange County Coastkeeper). Oysters and eelgrass both provide

three-dimensional habitat for a variety of species (Tolley and Volety, 2005, Short et al., 2000), offer protection from predators (Fonseca and Kenworthy, 1987, Grabowski and Peterson, 2007) and provide a buffer against wave action along coastlines (Manis et al., 2014). With sea levels rising, restoring both oysters and eelgrass together in living-shorelines initiatives could help to increase resiliency to large coastal disturbances.

It is still an open question whether these specific species and their associated communities benefit from simultaneous restoration. Many researchers have explored the effect of oysters on eelgrass, with contradictory outcomes. Oysters may stimulate the growth of eelgrass through nutrient deposition (Wall et al., 2008), increase mortality of eelgrass due to space competition (Wagner et al., 2012), or have limited or ecologically non-significant impact to eelgrass (Briley et al., 2015). However, sedimentation from eelgrass beds, while attractive as a shoreline resiliency outcome, has been hypothesized to negatively impact nearby oysters (Valdez et al., 2017). A well-known attribute of eelgrass beds is its ability to decrease water velocities within the bed (Worcester, 1995). These lower velocities result in increased sedimentation throughout the eelgrass bed (Fonseca and Kenworthy, 1987).

Sedimentation causes gill clogging in oysters which can result in oyster mortality. Generally, when sedimentation increases in an oyster bed it smothers the organism and makes it difficult to obtain oxygen and food (NOAA, 2007). Sedimentation can increase mortality in oyster larvae because they are more sensitive to suspended sediments than adults (Soletchnik et al., 2007). Additionally, larval oysters are unlikely to settle on soft sediment (Saoud et al., 2000). Sedimentation stress in *O. lurida* may be particularly significant. This species is thought to have the highest sensitivity and exposure

response to sedimentation compared to any other stressor (Wasson et al., 2015). Although burial tolerances are not established for *O. lurida,* it may be more sensitive compared to other oyster species because of its relatively small size. Although this sensitivity can be mitigated with the addition of hard substrata for settling (Latta and Boyer, 2015), exposure to sedimentation is also high, with 71% of west coast embayments experiencing moderate to high sedimentation according to resource users of west coast bays and estuaries (Wasson et al., 2015). Sedimentation is thought to be the only threat to *O. lurida* that has a combined high sensitivity and exposure index, making it potentially the most lethal influence on *O. lurida* (Wasson et al., 2015). An ongoing restoration project in Newport Bay, California, that is simultaneously restoring both oysters and eelgrass, combined and in isolation from one another, provides an excellent opportunity to study the effects of sedimentation by eelgrass on oysters.

<div align="center">Purpose and Hypothesis</div>

The purpose of my project is to determine (1) how oysters respond to eelgrass in adjacent restoration plots relative to plots in isolation, and (2) if oyster response is affected by eelgrass due to increased sedimentation caused by eelgrass. My hypothesis is that the increase in sedimentation that occurs within eelgrass beds will increase sedimentation adjacent to the eelgrass meadows, and thus decrease density of adult oysters.

CHAPTER 2

METHODS

<u>Study Site and Experimental Set-up</u>

Beginning in June 2016, collaborators from Orange County Coastkeeper (Katie Nichols, Restoration Coordinator), CSU Long Beach (Dr. Christine Whitcraft, Associate Professor), and Dr. Danielle Zacherl (CSU Fullerton, Professor) constructed four Living Shoreline Blocks (110 m X 12 m) in Upper Newport Bay, California. The Living Shoreline blocks were at Deanza Peninsula (33°37'13.18" N, 117°53'54.81" W, hereafter Deanza), Pacific Coast Highway (33°37'9.55" N, 117°54'17.41" W, hereafter PCH), Shellmaker Beach (33°37'21.60" N, 117°53'32.19" W, hereafter Shellmaker), and Westcliff Beach (33°37'16.81" N, 117°54'7.29" W, hereafter Westcliff) in Upper Newport Bay (Fig. 1; for aerial photos of sites see Appendix A1). These locations were chosen because they were thought to have similar erosive impacts from waves, nearby oyster and eelgrass restoration projects have been successful, and environmental conditions such as water quality, depth, and sediment were thought to be consistent among sites. Within each of these blocks there are four treatments: 1) a constructed oyster shell bed (20 X 1.5 m), hereafter Oyster, 2) a transplanted eelgrass bed (20 X 8 m), hereafter Eelgrass, 3) a constructed oyster shell bed directly upshore from a transplanted eelgrass bed with a 2 to 3 m buffer zone between habitats, hereafter Oyster/Eelgrass, and 4) a control treatment left un-manipulated, hereafter Control (Fig. 2). Each of these treatments were constructed 10 m apart from one another to reduce influences of

treatments on one another, with each treatment aligned parallel to the shore. Eelgrass

restoration occurred in June-July 2016, and oyster bed construction was completed in

April 2017.
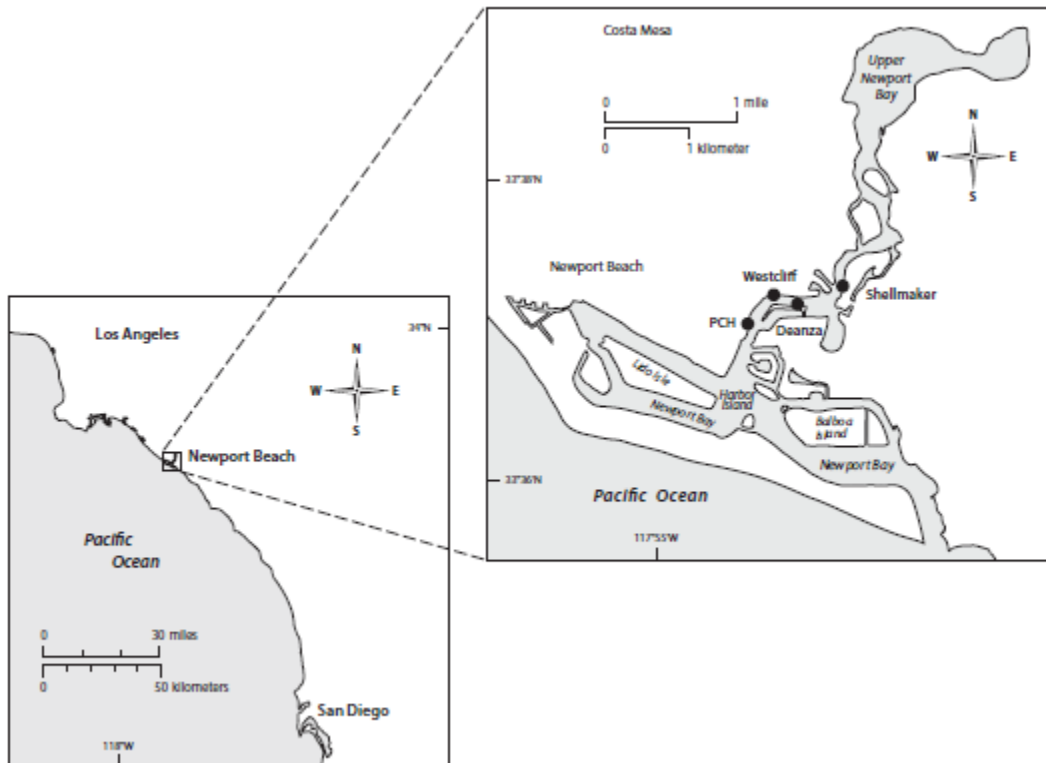
Figure 1. The four locations (PCH, Westcliff, Deanza, and Shellmaker) in Upper
Newport Bay, CA, that each contain oyster and eelgrass beds restored together and in
isolation as well as an un-manipulated control plot. Eelgrass restoration occurred in
June-July 2016, and oyster bed construction occurred in April 2017.

From April 2016 to May 2018 a team of researchers from CSUF monitored oyster

settlement, recruitment, density, and size following guidelines provided by The Nature

Conservancy's *Oyster Habitat Restoration Monitoring and Assessment Handbook*

(Baggett, 2014).

Eelgrass Response

A team of collaborators from Orange County Coastkeeper, CSULB and CSUF assessed eelgrass density non-destructively in August 2017 and May 2018 via SCUBA along 6 transects per treatment, with 4 quadrats per transect (n=24 total quadrats per treatment per site).
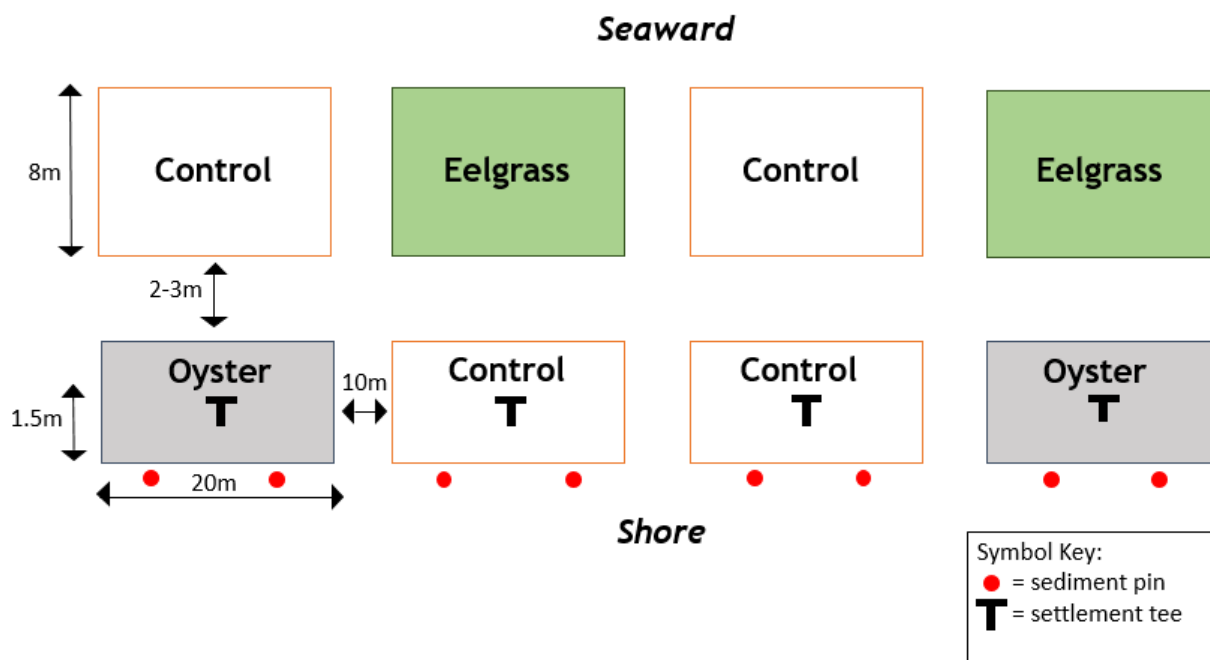
Figure 2. The restoration treatment layout at each of four sites in Newport Bay, CA, followed this general schematic (not drawn to scale). Each of these treatments (Oyster, Eelgrass, Oyster/Eelgrass, and Control) were present at each of the four locations (Deanza, PCH, Shellmaker, and Westcliff) with randomized arrangement of treatments along the shoreline at each of the four sites. Symbols have been provided to assess approximate sediment pin and settlement tee location.

Upshore Sedimentation and Grain Size

I calculated sedimentation upshore of each treatment plot using sedimentation pins (US Geological Survey, 2012). Two sedimentation pins were hammered into the

sediment at every treatment, located at the 5 m mark and at the 15 m mark across the 20 m total treatment width at 0.85 m upshore of each treatment area (Fig. 2). Sedimentation pins were 1.5 m tall, with 0.9 m hammered into the sediment, and 0.6 m of pin exposed. Every month, a team of technicians from CSUF measured changes in elevation in sediment height (in mm) on each sedimentation pin on the north, south, east, and west side and the height of pins were averaged together to get a representation of sedimentation occurring throughout the upshore area of each treatment plot (US Geological Survey, 2012). Upstream and downstream sediment pin effects were also visually inspected to ensure averaging sediment pins was appropriate. There was no detectable upstream or downstream effect on sedimentation among pins within treatments via visual inspection and therefore sedimentation was averaged across the two sediment pins at each treatment.

I assessed grain size at each treatment plot across all sites prior to oyster bed construction (March-April 2017), and twelve months (May 2018) after construction. Grain size measurements were taken 0.85 m upshore of each treatment and centered at the 10 m. Each representative core was 3 cm deep within a 10 X 10 cm area.

In addition to the univariate analyses, multivariate analyses were also used to provide a global assessment of whole-site and across-treatment percent grain size characteristics (sand, silt, and clay) prior to oyster bed construction (March 2017) and twelve months post-oyster bed construction (May 2018) using non-metric multidimensional scaling (nMDS). Percent grain size results were first transformed to LOG (x+1) to ensure values were of the same magnitude among grain size categories. All major grain size categories (sand, silt, and clay) were used to test for significant

differences among sites and treatments by using a two-way analysis of similarity (ANOSIM). All multivariate responses were produced using PRIMER statistical software (Version 7.0.13).

<center>Percent Mud Coverage and Mud Deposition on Hard Substrata</center>

Percent substratum cover measurements were taken within each treatment plot using 10 randomly-placed 0.5 X 0.5 m gridded quadrats pre-oyster bed construction (January 2017), six months (November 2017), and twelve months post-oyster bed construction (May 2018) using point-contact techniques (n=49 points per quadrat). At each point, technicians at CSUF used a probe to assess not only the substratum but also mud or sand burial upon it. If the mud/sand depth was >9 mm at a representative point, then the substratum was scored as mud or sand.

The hard substratum was recorded as well as the depth of mud (or sand) when <9 mm of sediment was measured upon the hard substratum. Indicating the potential burial height of our shell beds is a crucial factor in oyster mortality as survival decreases significantly once an oyster's body is 90% covered by sediment (Colden and Lipcius, 2015). The point contact technique, therefore, allowed us to simultaneously track the conversion of shell habitat back into mud (i.e., changes in % mud cover over time) while also scoring the extent of sedimentation occurring on habitat that we continued to score as "shell".

<center>Oyster Settlement and Recruitment</center>

Oyster settlement is defined as the event when oyster larvae settle out of the water column, metamorphose, and attach to a substratum, and oyster recruitment is the continued survival of settled oysters over a given time period (arbitrarily defined, but

generally at least one to two months post-settlement; Zajac et. al., 1989). Oyster settlement and recruitment were both measured separately using ceramic tiles (0.0225 m^2 area) suspended from polyvinyl chloride (PVC) tees 10 cm above the substratum in the middle of each treatment at -0.15 m MLLW. Technicians from CSUF retrieved settlement tiles bimonthly from April to September, in both 2016 and 2017, and monthly from September to April of each year.

Recruitment tiles were left in the field for the entirety of the summer spawning season (April to September 2016, and March to September 2017) and retrieved and analyzed in September 2016 and September 2017. Oyster recruits and settlers were counted on the underside of the tile, where they prefer to settle (Hopkins, 1935). Using a dissecting microscope, technicians from CSUF identified oysters to species based on their morphology, particularly the shape of the umbo on the larval shell (Loosanoff et al., 1966). Settlement of *Ostrea lurida*/tile over each representative year (2016, 2017) and for each treatment at each site was summed to measure cumulative settlement for ease of statistical analyses (Zacherl et al., 2015). To additionally assay seasonal variation in oyster settlement, *Ostrea lurida*/m^2/day was averaged by treatment per sampling period from 2016 to 2017.

<p style="text-align:center"><u>Adult Density</u></p>

Mean oyster density measurements (*O. lurida/*m^2) were taken within each treatment plot using 10 randomly located (0.5 m^2 area) quadrats along the 20 m length and 1.5 m width of each treatment at twelve months (May 2018) post-oyster bed construction. Surface shell within each quadrat was excavated into a 1 ga Zip-Loc bag for lab processing. All oysters within the quadrat were identified and counted within a 1

mm sieve. Density measurements were used to assess the changes in density of *O. lurida* in each treatment over time.

Oyster Size

Oyster size measurements were taken of each oyster from each excavated quadrat at twelve months (May 2018) post-oyster bed construction. Oyster size (length) was estimated using Vernier calipers by measuring, in millimeters, the distance from the umbo to the longest point.

Synthesis of Data Collection

For a summary of all response factors and time-periods measured, please refer to Table 1.

Table 1. All response factors listed and their data collection time period (filled in gray) during this study in Upper Newport Bay, CA.

	2016									2017												2018				
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Eelgrass Density																	■									■
Upshore Sedimentation												■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Percent Mud Coverage										■										■						■
Mud Deposition on Hard Substratum																				■						■
Grain Size												■	■													■
Oyster Settlement	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						
Oyster Recruitment						■												■								
Adult Oyster Density																										■
Oyster Size																										■

Statistical Analyses

Each response factor (eelgrass density, shell sedimentation, upshore sedimentation, percent shell cover, grain size, cumulative settlement, recruitment, and density) was analyzed statistically using ANOVA for the effects of treatment with sites as block, and, when possible, for the interaction between treatment and site. In some instances (sedimentation pins, change in percent grain size concentration, cumulative settlement, and recruitment), we did not have enough within-treatment replication to allow analysis of interaction effects. Prior to each analysis, I checked to ensure that the assumptions of ANOVA were met by testing for unequal variances (O'Brien, Brown-Forsythe, Levene, and Bartlett Test) and normality of distribution (Shapiro-Wilk W Test). When these assumptions were not met, data was either log-transformed (e.g., eelgrass density) to achieve equal variance and normality of distribution or ranked (e.g., mud deposition on shell, change in percent grain size concentration, cumulative settlement, recruitment, and adult oyster density) to allow ANOVA tests of effects to proceed. All ANOVA analyses were produced using JMP statistical software (Version 13). Statistical differences among and between sites and treatments were then assessed using post-hoc Tukey HSD when appropriate.

Post-hoc Pearson correlation analyses were also performed to assess the relationship between mud deposition on oyster shells (mm) and oyster size (mm), and the relationship between eelgrass density (m^2) and oyster density (m^2) from data collected one year post-oyster bed construction (May 2018). My primary goal was to look for relationships between eelgrass, mud deposition, and oyster success, and while the lack of eelgrass success at Shellmaker (see below) prevented inclusion of the site in

ANOVA analyses if organized by treatment, Shellmaker data *were* used in regression

analyses because eelgrass (or lack thereof) would still be expected to affect the

response factors. Prior to searching for correlations between eelgrass density and

oyster density, I log-transformed oyster density because visual inspection of the

relationship indicated a potentially exponential relationship. Correlation analyses were

performed using JMP statistical software (Version 13).

CHAPTER 3

RESULTS

<u>Eelgrass Density</u>

In August 2017, approximately one year after eelgrass restoration and four

months following oyster bed construction, eelgrass density ranged from a mean of 0

stipes/m^2 to 133.67 ± 15.07 stipes/m^2 (Fig. 3). Eelgrass was well-established on

Eelgrass and Oyster/Eelgrass treatments with the exception of at Shellmaker (Fig. 3). At

Shellmaker, there was no detectable difference in eelgrass stipe density among any of

the treatments while at all other sites, there was significantly more eelgrass on the

Eelgrass and Oyster/Eelgrass treatments compared to Control and Oyster treatments

(two-way ANOVA, treatment*site $p<0.0001$, Table 2, Fig. 3). In May 2018, eelgrass

density ranged from a mean of 0 stipes/m^2 to 260.0 ± 10.46 stipes/m^2. In May 2018,

eelgrass continued to be well-established on Eelgrass and Oyster/Eelgrass treatments

at all sites with the exception of Shellmaker (Fig. 4). Unlike in August 2017, eelgrass

stipe density at Shellmaker in the Eelgrass treatment was significantly higher than on

the Oyster and Control treatments (Table 3, Fig. 4); however, it was substantially lower

than other Eelgrass and Oyster/Eelgrass treatments at other sites. In addition, the

occupancy rate of eelgrass stipes at Shellmaker was ≤25% in August 2017 (Fig. A2,

Appendix), compared to >66% on all other eelgrass beds, and ≤50% by May 2018,

compared to >83% on all other eelgrass beds (Fig. A3, Appendix); qualitatively, the

eelgrass beds on each treatment at Shellmaker only covered half of each treatment,

with the other half eelgrass-free, compared to the eelgrass beds at all other sites that

contained nearly continuous coverage of eelgrass with only occasional small patches

($<$1-2 m^2) of unoccupied areas within the beds. Because of the substantial lack of

eelgrass in August 2017, when young recruit oysters would have been smallest and

most susceptible to sedimentation stress, and because of the limited eelgrass in May

2018, Shellmaker was excluded from all further ANOVA analyses because I believe that

the experimental design has not been maintained adequately enough to expect a

detectable effect on sedimentation and subsequently on oysters (Fig. 4). The main

purpose of my study was to measure the differences between oyster treatments with

and without adjacent eelgrass; without significant eelgrass presence at the Shellmaker

Oyster/Eelgrass treatment, this treatment could not be expected to exert the treatment

effect intended.

Table 2. Two-way ANOVA results for effects of site, treatment, and their interactions on eelgrass density four months after oyster bed construction, August 2017, in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Site	129151.17	3	43050.39	32.23	**<0.0001**
Treatment	530929.83	3	176976.61	132.49	**<0.0001**
Treatment*Site	220758.83	9	24528.76	18.36	**<0.0001**
Model	880839.80	15	58722.70	43.96	**<0.0001**
Error	491576.00	368	1335.80		
Total	1372415.8	383			
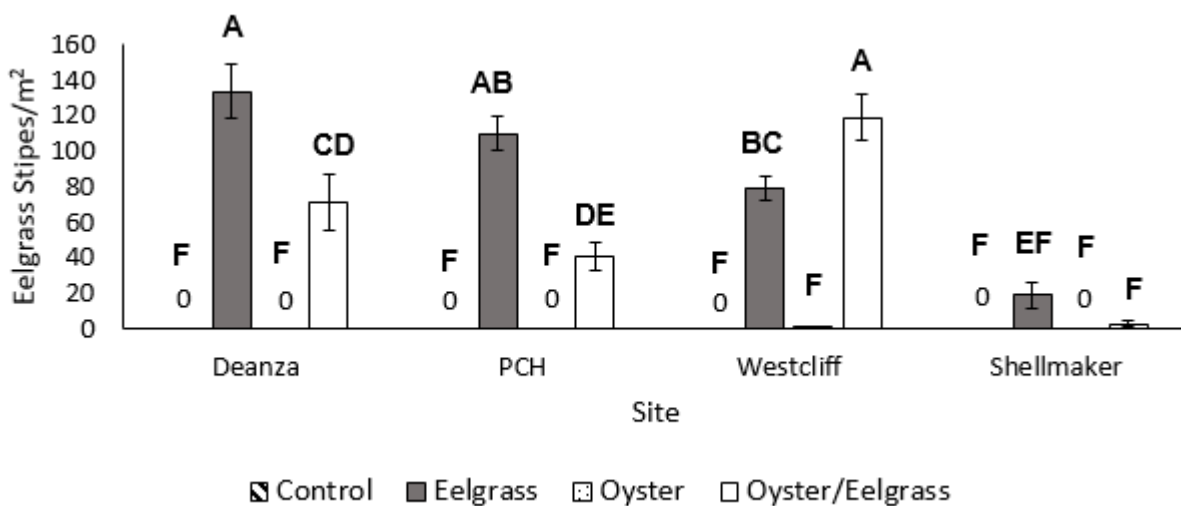
Figure 3. Eelgrass density per treatment per site (n=24 quadrats per treatment) in August 2017. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences based upon post-hoc Tukey HSD.
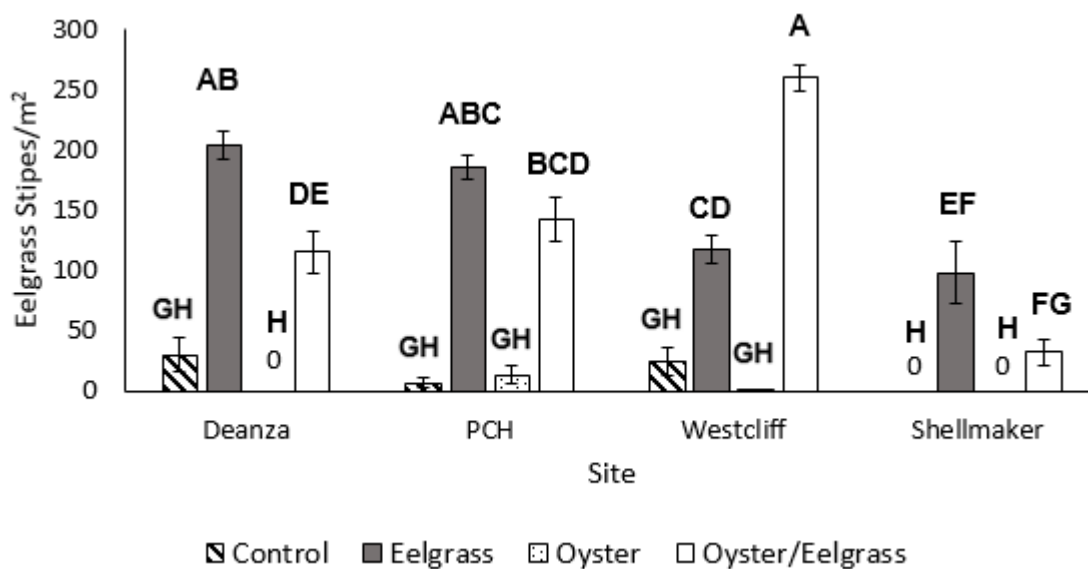
Figure 4. Eelgrass density per treatment per site (n=24 quadrats per treatment) in May 2018. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences based upon post-hoc Tukey HSD.

Table 3. Two-way ANOVA test statistics for effects of site, treatment, and their interactions on eelgrass density twelve months after oyster bed construction in Newport Bay, CA, in May 2018. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	2219775.90	3	739925.30	223.62	**<0.0001**
Site	339759.20	3	113253.07	34.23	**<0.0001**
Treatment*Site	364379.10	9	40486.57	12.24	**<0.0001**
Model	2918132.00	15	194542	58.79	**<0.0001**
Error	1230902.50	372	3308.88		
Total	4149034.50	387			

<u>Upshore Sedimentation</u>

In May 2018, approximately one year after oyster bed construction, upshore sedimentation ranged from a mean of -0.30 ± 0.53 cm to 1.67 ± 0.72 cm (Fig. 5). Negative values indicate erosion and positive values indicate deposition. A year after the oyster beds were constructed, in May 2018, sedimentation did not differ by site or up-shore of treatment (two-way ANOVA, treatment p=0.0865, site p=0.3726, Figs. 5 & 6, Table 4). There was, however, a trend towards net sedimentation upshore of the Oyster, Oyster/Eelgrass, and Eelgrass treatments compared to the erosional Control treatments.
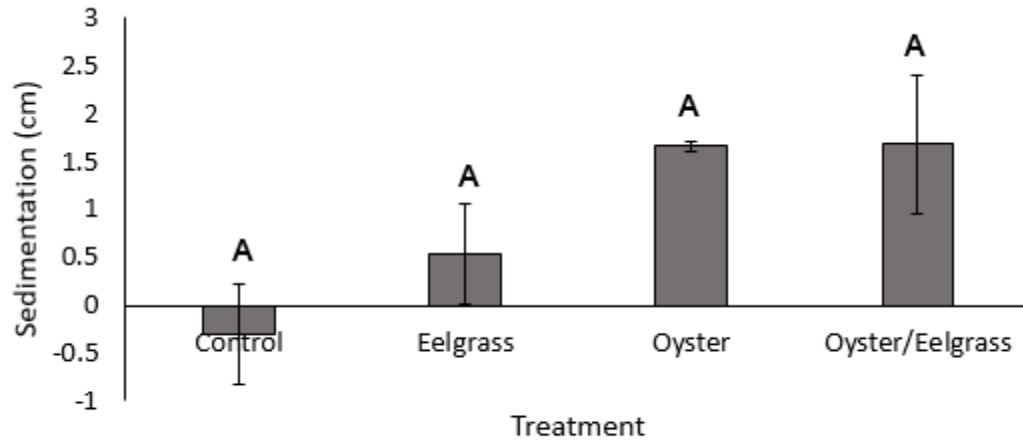
Figure 5. Total sedimentation (cm) per treatment across sites (n=3) in May 2018 after twelve months of experimental data collection. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences based upon post-hoc Tukey HSD.

Figure 6. Total sedimentation (cm) per treatment across treatments (n=4) in May 2018 after twelve months of experimental data collection. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences based upon post-hoc Tukey HSD.

Table 4. Two-way ANOVA test statistics for effects of site, and treatment on upshore sedimentation measured with sediment pins twelve months after oyster bed construction in Newport Bay, CA, in May 2018. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Site	1.79	2	0.90	1.17	0.3726
Treatment	8.22	3	2.74	3.57	0.0865
Model	10.02	5	2.00	2.61	0.1372
Error	4.61	6	0.77		
Total	14.62	11			

<u>Percent Mud Coverage</u>

During pre-oyster bed construction in January 2017, mud coverage was more than 90% at all treatments, ranging from a mean of 90.20 ± 3.47% to 100 ± 0% (Fig. 7). The Oyster/Eelgrass treatment had higher mud coverage than the Oyster treatment at Deanza, most likely due to scatterings of cobble and stone noted during pre-restoration conditions. There was no significant difference in mud coverage at the Oyster and Oyster/Eelgrass treatments at Westcliff and PCH (two-way ANOVA, treatment $p<0.0001$, site $p<0.0001$, treatment*site $p<0.0001$; Fig. 7, Table 5).

Six months post-oyster bed construction in November 2017, mud coverage on Oyster and Oyster/Eelgrass treatment dropped precipitously relative to pre-restoration because of the placement of 100% cover of dead oyster shell during oyster bed construction. Nonetheless, some mud deposited onto the oyster beds in subsequent months, slightly reducing shell cover and returning a small percentage of the constructed oyster bed habitat back into mud habitat. Mud cover ranged from a mean of 2.24 ± 0.83% to 13.47 ± 3.51% (Fig. 8) on constructed oyster bed treatments while the Control and Eelgrass treatments ranged from a mean of 92.65 ± 1.56% to 99.59 ± 0.27%. There was no significant difference in mud coverage at the Oyster and

Oyster/Eelgrass treatments at all sites (two-way ANOVA, treatment $p<0.0001$, site

$p=0.0407$, treatment*site $p=0.0011$; Fig. 8, Table 6).

Twelve months post-oyster bed construction in May 2018, mud coverage ranged

from a mean of $3.88 \pm 1.76\%$ to $40.0 \pm 4.71\%$ at Oyster and Oyster/Eelgrass treatments

and ranged from a mean of $91.22 \pm 1.52\%$ to $99.79 \pm 0.20\%$ at Control and Eelgrass

treatments (Fig. 9). Percent mud coverage was significantly higher at the Oyster

treatment than the Oyster/Eelgrass treatment at PCH and Westcliff, but no difference in

percent mud coverage at Deanza between the Oyster and Oyster/Eelgrass treatment

(two-way ANOVA, treatment $p<0.0001$, site $p=0.0092$, treatment*site $p<0.0001$) (Fig. 9,

Table 7). Results for percent mud coverage from April 2017—May 2018 collectively are

given in Fig. 10. Mud coverage on all constructed oyster beds (a proxy for conversion

back to mudflat habitat) was below 17% except on the PCH Oyster treatment.
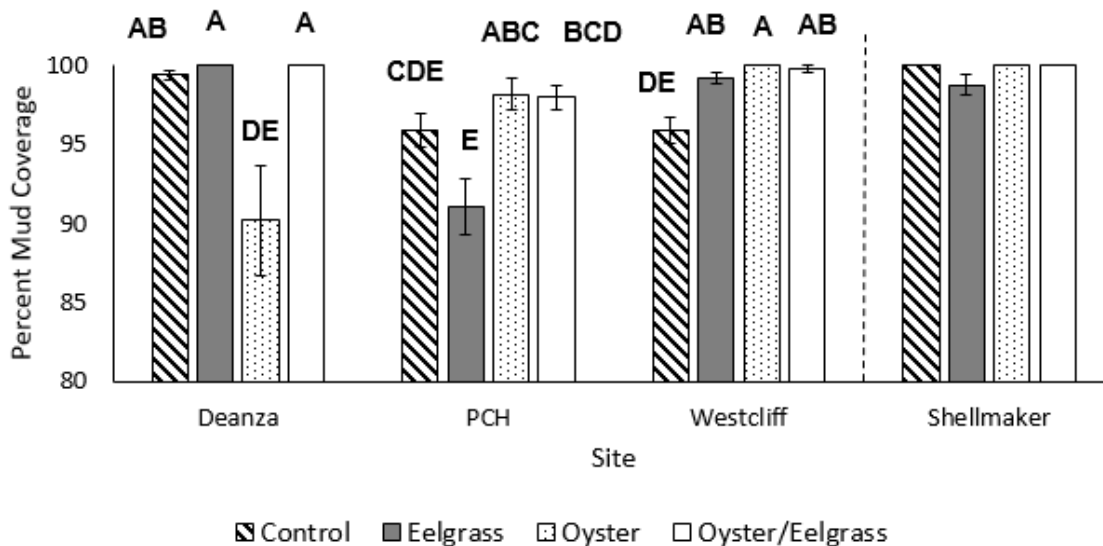
Figure 7. Percent mud coverage per treatment per site (n=3) in January 2017, during pre-oyster bed conclusion. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments and sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.
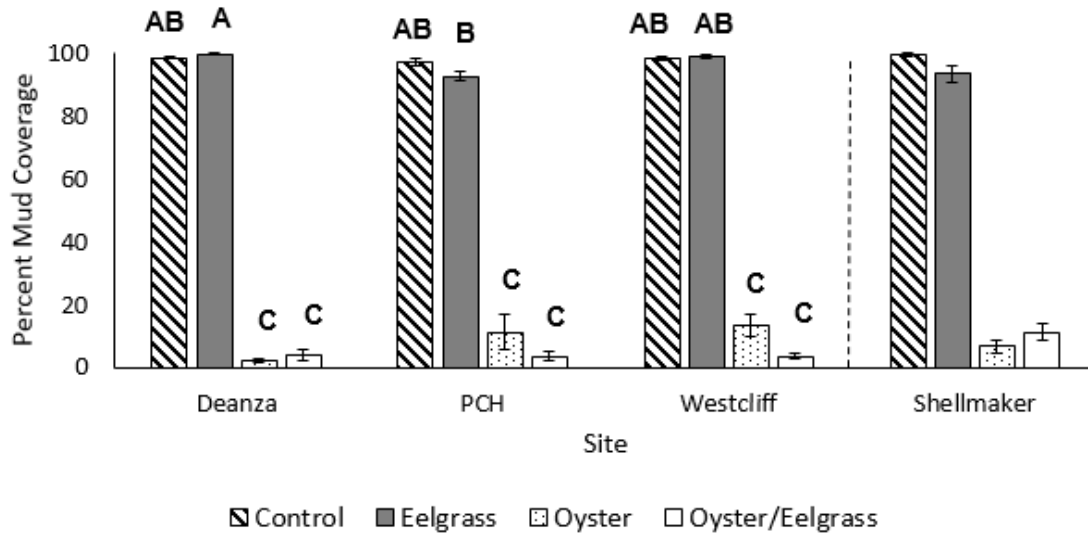
Figure 8. Percent mud coverage per treatment per site (n=3) in November 2017, six months post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments and sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.
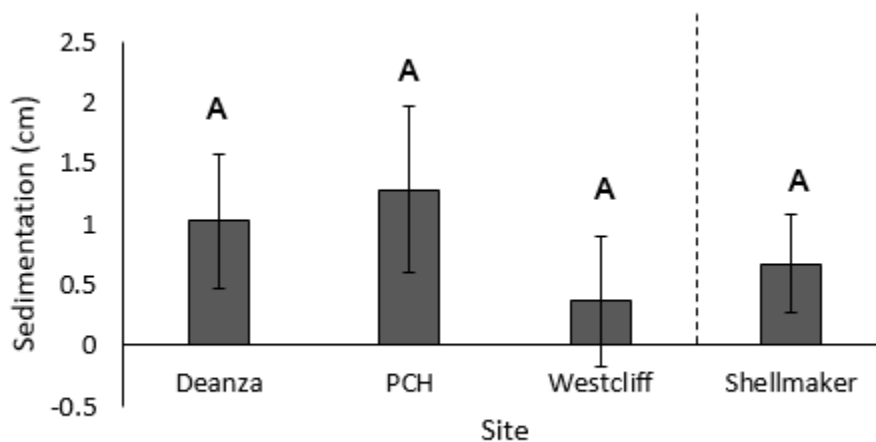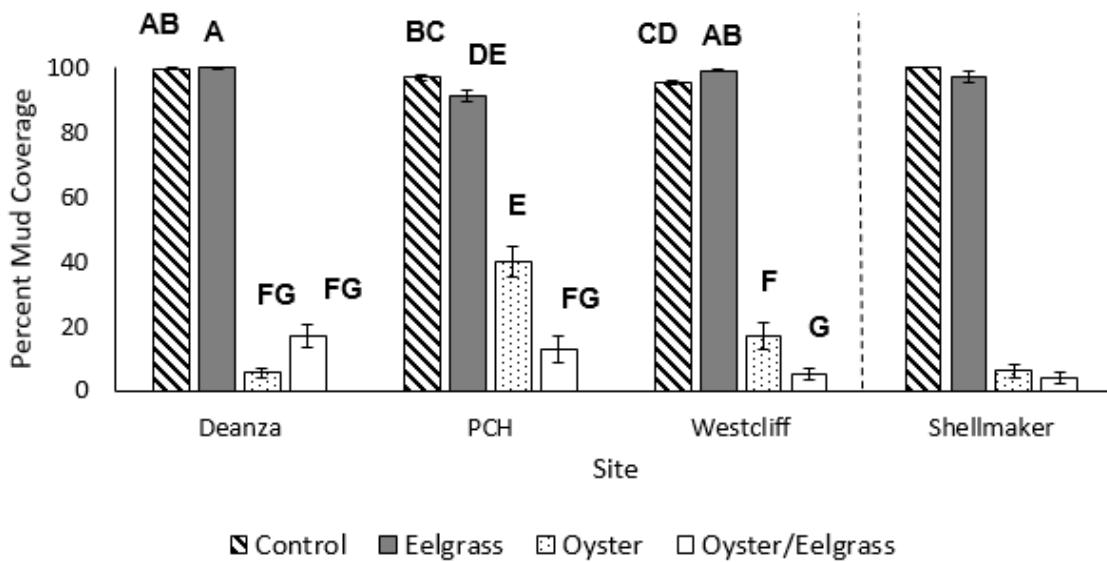

Figure 9. Percent mud coverage per treatment per site (n=3) in May 2018, twelve months post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments and sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Figure 10. Percent mud coverage in April 2017 (during oyster bed construction), November 2017 (six months after oyster bed construction), and May 2018 (one year after oyster bed construction) at Oyster and Oyster/Eelgrass treatments. For ease of graphing, DA = Deanza, PCH = PCH, WC = Westcliff, and O = Oyster, OE = Oyster/Eelgrass. Gray color correlates to Oyster/Eelgrass treatments, and black color correlates to Oyster treatments. Same sites have the same line design in dash pattern. Deanza is represented by triangles, PCH is represented by squares, and Westcliff is represented by circles.

Table 5. Two-way ANOVA test statistics for effects of site, treatment and their interaction on percent mud coverage in January 2017, during pre-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	11556.85	3	3852.28	8.79	**<0.0001**
Site	17419.14	2	8709.57	19.88	**<0.0001**
Treatment*Site	43757.96	6	7293.00	16.64	**<0.0001**
Model	72733.95	11	6612.18	15.09	**<0.0001**
Error	47325.05	108	438.19		
Total	120059.00	119			

Table 6. Two-way ANOVA test statistics for effects of site, treatment and their interaction on percent mud coverage in November 2017, six months post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	108757.68	3	36252.56	156.14	**<0.0001**
Site	1531.95	2	765.98	3.31	**0.0407**
Treatment*Site	5626.72	6	937.79	4.04	**0.0011**
Model	115916.35	11	10537.90	45.39	**<0.0001**
Error	25074.65	108	232.2		
Total	140991.00	119			

Table 7. Two-way ANOVA test statistics for effects of site, treatment and their interaction on percent mud coverage in May 2018, twelve months post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	109307.42	3	3645.81	275.59	**<0.0001**
Site	1294.96	2	647.48	4.91	**0.0092**
Treatment*Site	17224.07	6	2870.68	21.71	**<0.0001**
Model	127826.25	11	11620.60	87.91	**<0.0001**
Error	14278.55	108	132.2		
Total	142105.00	119			

Mud Deposition on Shell

Six months post-oyster bed construction, sediment deposition onto hard substrata (including coir, rock, and shells) on oyster beds ranged from 2.27 ± 0.18 mm to 3.07 ± 0.53 mm and was significantly higher on the Oyster treatments than at Oyster/Eelgrass treatments (two-way ANOVA, treatment p=0.0450, site p=0.7494, treatment*site p=0.7911; Fig. 11, Table 8).
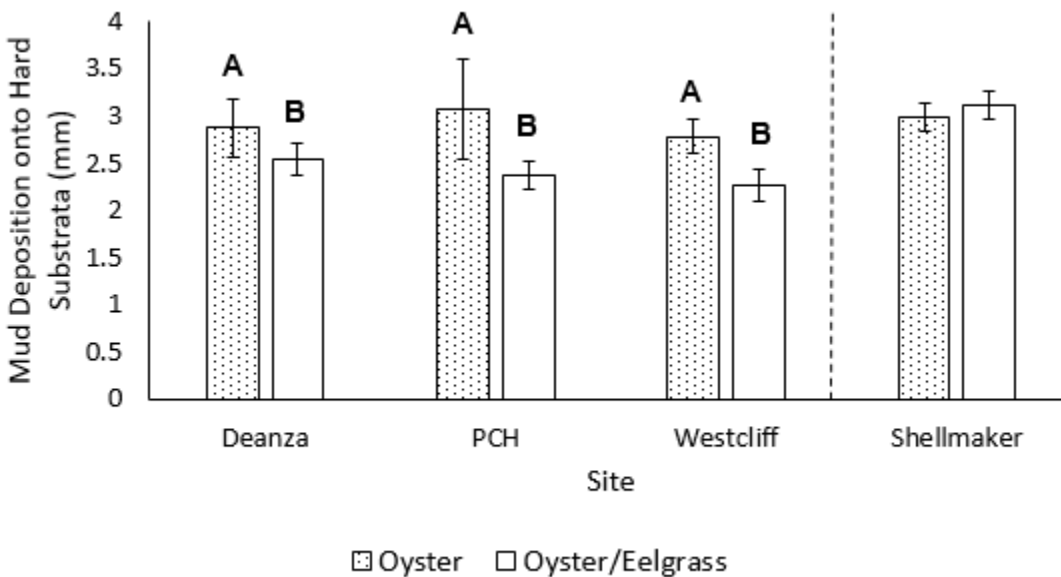
Figure 11. Mud deposition (mm) onto hard substrata on oyster bed treatments in November 2017, six months after oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.
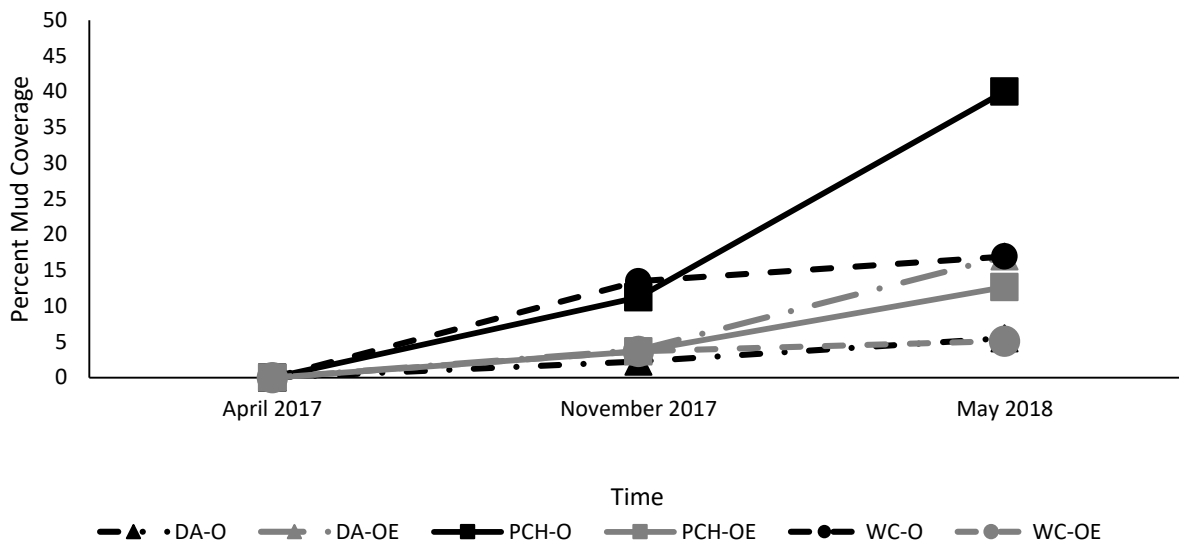
Table 8. Two-way ANOVA test statistics for effects of site, treatment and their interactions on average millimeter of mud measurements taken on oyster shell six months after oyster bed construction in Newport Bay, CA, in November 2017. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Site	176.03	2	88.01	0.29	0.7494
Treatment	1278.82	1	1278.82	4.21	**0.0450**
Site*Treatment	142.86	2	71.43	0.24	0.7911
Model	1597.70	5	319.54	1.05	0.3967
Error	16390.30	54	303.52		
Total	17988.00	59			

Twelve months post-oyster bed construction, sediment deposition onto hard substrata (including coir, rock, and shells) on the oyster beds ranged from 1.96 ± 0.24 mm to 3.98 ± 0.18 mm and remained significantly higher on Oyster treatments compared to Oyster/Eelgrass treatments only at PCH, with no differences in

sedimentation detected at other sites among treatments (two-way ANOVA, treatment

p=0.0003, site p=0.1492, treatment*site p<0.0001; Fig. 12, Table 9).
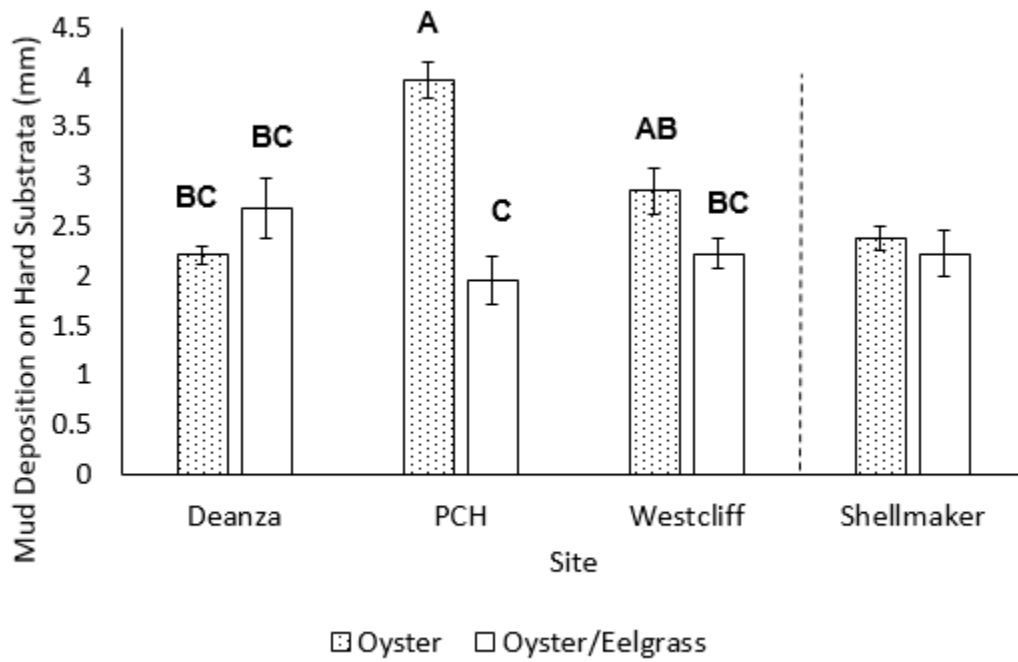
Figure 12. Mud deposition (mm) on hard substrata per treatment per site in May 2018, twelve months after oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 9. Two-way ANOVA test statistics for effects of site, treatment and their interactions on sediment deposition onto oyster shells twelve months after oyster bed construction in Newport Bay, CA, in May 2018. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Site	676.30	2	338.15	1.97	0.1492
Treatment	2574.15	1	2574.15	15.00	**0.0003**
Treatment*Site	5476.80	2	2738.40	15.96	**<0.0001**
Model	8727.25	5	1745.45	10.17	**<0.0001**
Error	9265.25	54	171.58		
Total	17992.50	59			

Grain Size

Changes in percent clay ranged from -2.26 to +1.67%, changes in percent silt ranged from -7.43 to +11.20%, and changes in percent sand ranged from -12.91 to +8.72% twelve months post-oyster bed construction and were not significantly different among treatments (Clay treatment p=0.7020, Table 10, Silt treatment p=0.1630, Table 11, and Sand treatment p=0.1817, Table 12). There were, however, site effects. PCH had significantly higher change in percent clay concentration than at Deanza and Westcliff (site p=0.0417, Fig. 13, Table 10), and significantly higher change in percent silt concentration than at Deanza. Deanza had significantly higher change in percent silt concentration than at Westcliff (site p=0.0033, Fig. 14, Table 11). Westcliff and Deanza both had significantly higher change in percent sand concentration than at PCH (site p=0.0035, Fig. 15, Table 12). A breakdown of overall percent grain size composition per treatment pre-restoration, six months after oyster restoration, and twelve months after oyster restoration is given in Fig. 16.

In March 2017, during pre-oyster bed construction conditions, sites showed significantly different grain size characteristics (ANOSIM, site p=0.015, Rho=0.657, treatment p =0.126, Rho=0.417, Fig. 17). Westcliff was characterized by relatively high percent silt, while PCH was more sandy. In May 2018, one year post-oyster bed construction, representative treatments were more similar to one another in grain size characteristics than site-level characteristics, with a marginally non-significant treatment effect (ANOSIM, treatment p=0.055, Rho=0.41, site p=0.276, Rho=0.25, Fig. 18). In general, Oyster and Oyster/Eelgrass treatments were characterized by higher

percentages of silt and clay, while Eelgrass and Control treatments had higher % sand.

The reliability of both nMDS plots was very good (stress=0.0). Results of a multivariate

analysis of grain size characteristics, including Shellmaker during pre-oyster bed

conditions (March 2017) and twelve months post-oyster bed conditions (May 2018), are

in Figs. A4 and A5.

Figure 13. Change in percent clay concentration per site (n=4) from pre-survey
conditions to post-oyster bed construction twelve months. Error bars are ±1 SE.
Variations in bold letters above bars indicate statistically significant differences among
sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses
but is included in graph for reference.
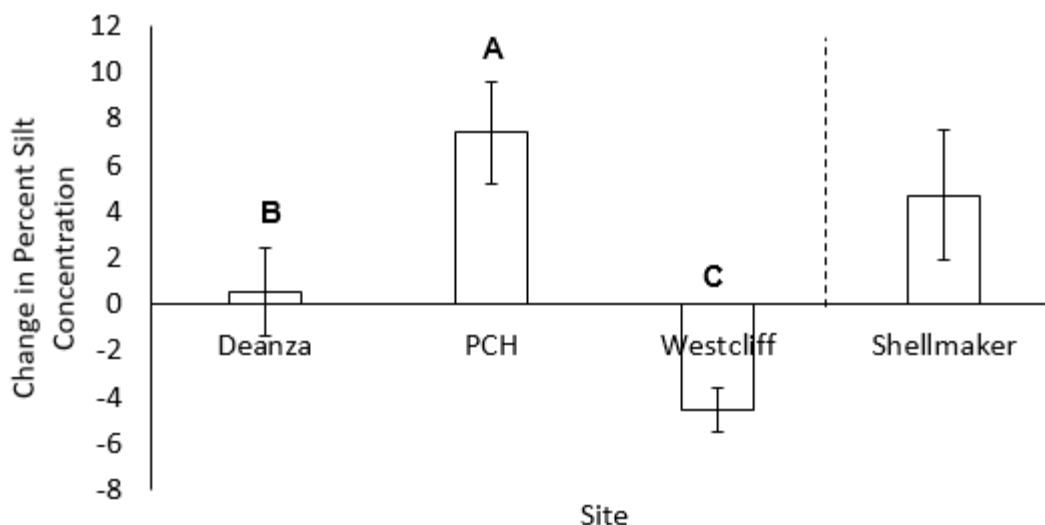
Figure 14. Change in percent silt concentration per site (n=4) from pre-restoration to post-oyster bed construction twelve months. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

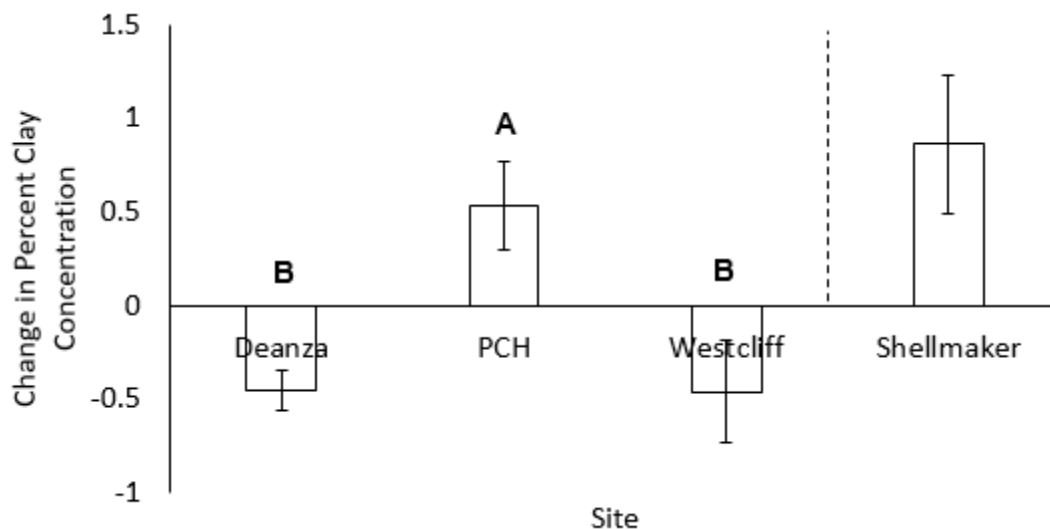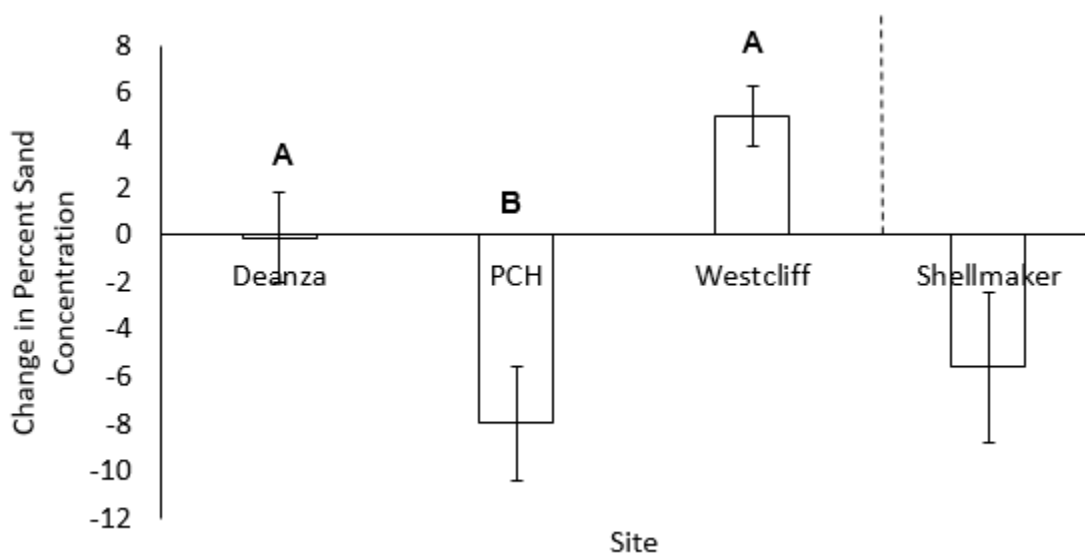*Figure 15.* Change in percent sand concentration per site (n=4) from pre-restoration to post-oyster bed construction twelve months. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 10. Two-way ANOVA test statistics for effects of site, and treatment on change in percent clay concentration from pre-restoration to twelve months after oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	0.34	3	0.11	0.49	0.7020
Site	5.65	2	2.83	5.65	**0.0417**
Model	2.93	5	0.59	1.56	0.3012
Error	1.39	6	0.23		
Total	4.34	11			

Table 11. Two-way ANOVA test statistics for effects of site, and treatment on change in percent silt concentration from pre-restoration to twelve months after oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	61.67	3	20.56	2.43	0.1630
Site	288.32	2	144.16	17.06	**0.0033**
Model	768.11	5	153.62	13.53	**0.0032**
Error	50.69	6	8.45		
Total	400.67	11			

Table 12. Two-way ANOVA test statistics for effects of site, and treatment on change in percent sand concentration from pre-restoration to twelve months after oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	69.34	3	23.11	2.26	0.1817
Site	341.63	2	170.82	16.71	**0.0035**
Model	123.67	5	24.73	7.68	**0.0138**
Error	22.17	6	3.69		
Total	143.00	11			
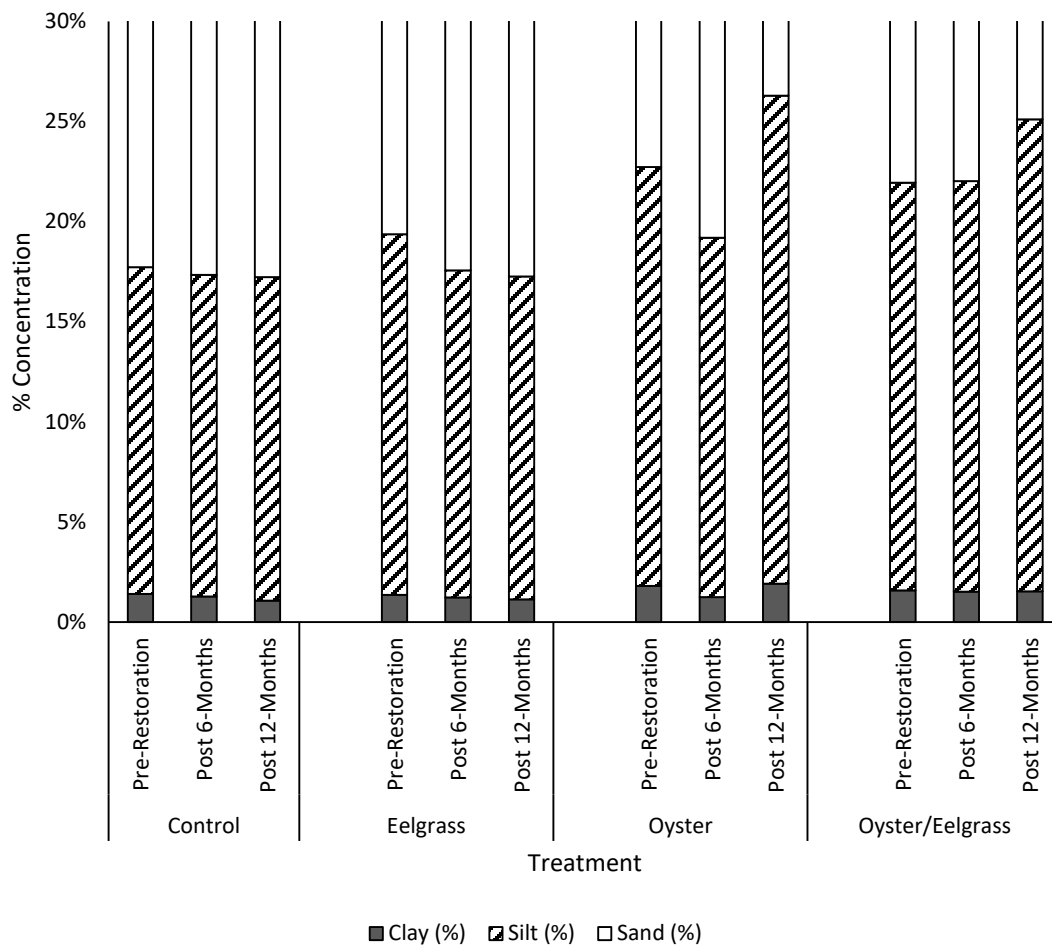
Figure 16. Mean grain size by treatment (n=3) pre-restoration, six months after oyster bed construction, and twelve months after oyster bed construction in Newport Bay, CA.
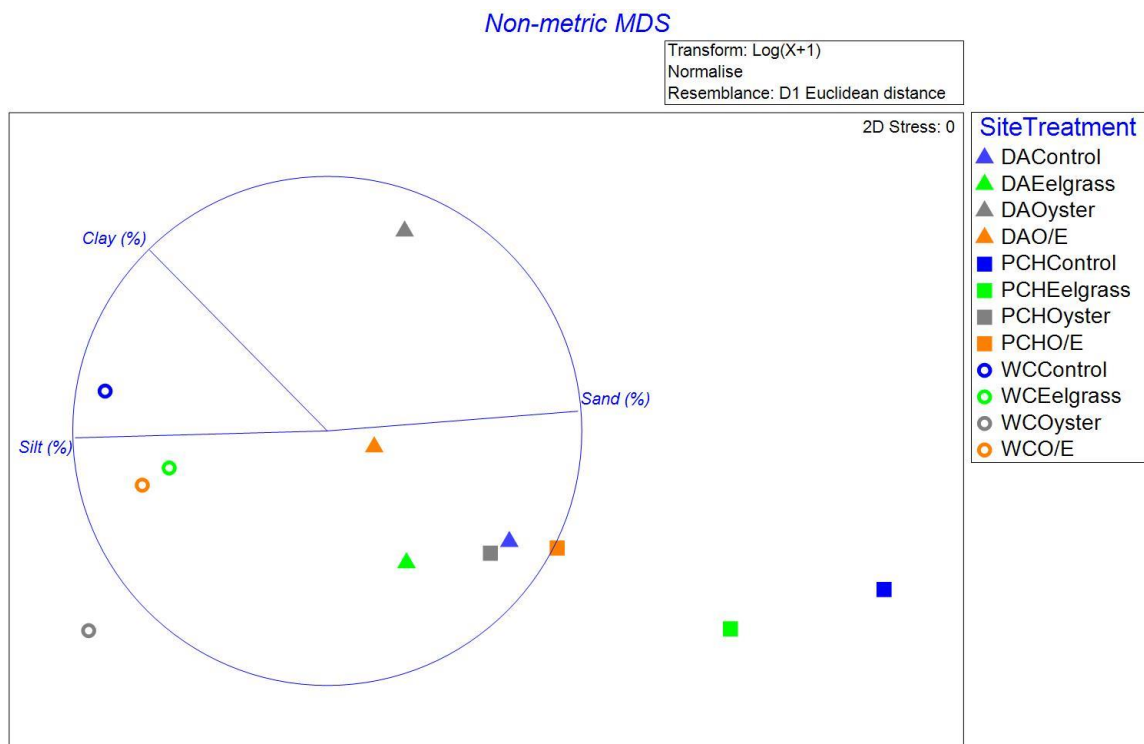
Figure 17. Non-metric multidimensional scaling (nDMS) plot of grain size characteristics (sand, silt, and clay) by treatment per site in March 2017, pre-restoration in Newport Bay, CA. For ease of graphing, DA = Deanza, PCH = PCH, WC = Westcliff, and O/E = Oyster/Eelgrass.
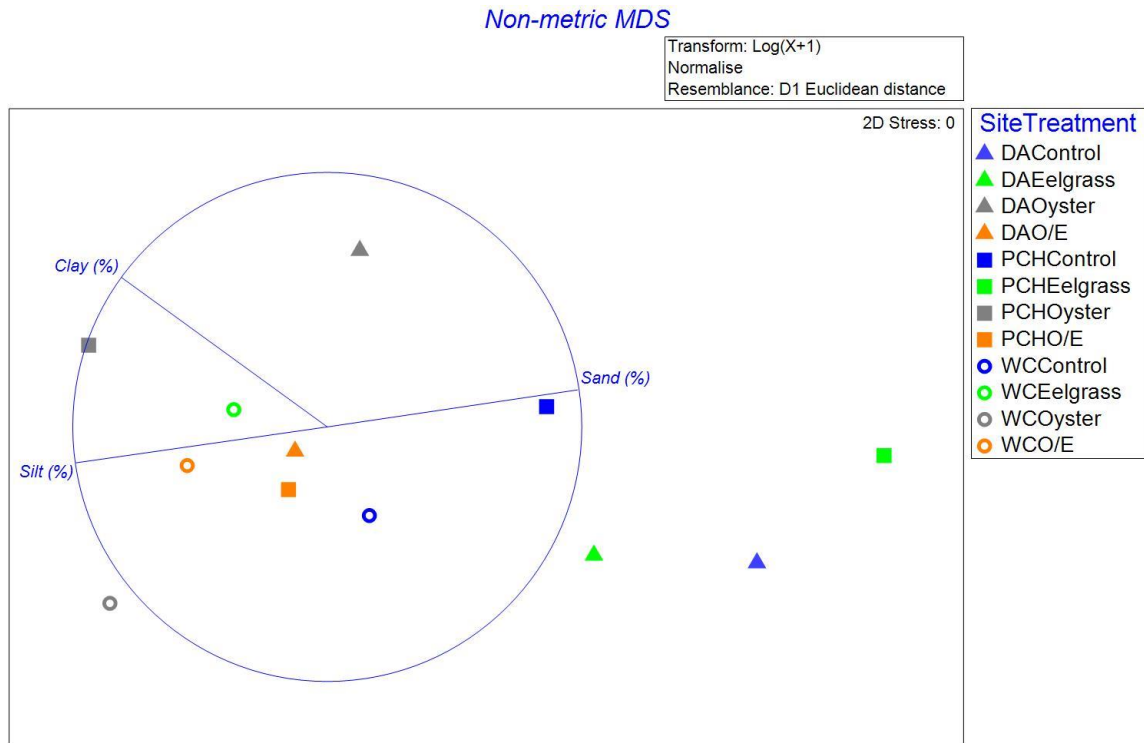
Figure 18. Non-metric multidimensional scaling (nMDS) plot of grain size characteristics (sand, silt, and clay) by treatment per site in May 2018, one year post-oyster bed construction in Newport Bay, CA. For ease of graphing, DA = Deanza, PCH = PCH, WC = Westcliff, and O/E = Oyster/Eelgrass.

Cumulative Settlement

In 2016, cumulative settlement ranged from a total of 37 oysters/tile to 396 oysters/tile. Before oyster bed construction in 2016, cumulative settlement (oysters/tile) of *Ostrea lurida* did not vary significantly among treatments (two-way ANOVA, treatment p=0.2414, Fig. 19, Table 13), but PCH and Deanza received more cumulative settlement than Westcliff (two-way ANOVA, site p=0.0059, Fig. 20, Table 13). After oyster bed construction in 2017, cumulative settlement ranged from a total of 8 oysters/tile to 172 oysters/tile, showing a large decline in overall cumulative oyster settlement/tile compared to 2016. In 2017, cumulative settlement of *Ostrea lurida* was significantly greater on Oyster tiles than on Eelgrass tiles (two-way ANOVA, treatment

p=0.0073, site p=0.0288, Fig. 21, Table 14), and cumulative settlement continued to vary by site (PCH received more cumulative settlement than Westcliff, and Deanza received the same amount of cumulative settlement as PCH and Westcliff, Fig. 22). Seasonal differences in oyster settlement per treatment, expressed in per m^2 per day to allow for across study comparisons, are reported in Figs. 23 and 24. Overall, most oysters settled during summer months (July—September) in both 2016 and 2017, with few or no oysters settling during the colder/wetter months (October—June) when water temperatures dip below 16 degrees Celsius, the critical reproductive temperature threshold for the Olympia oyster (Coe, 1931).
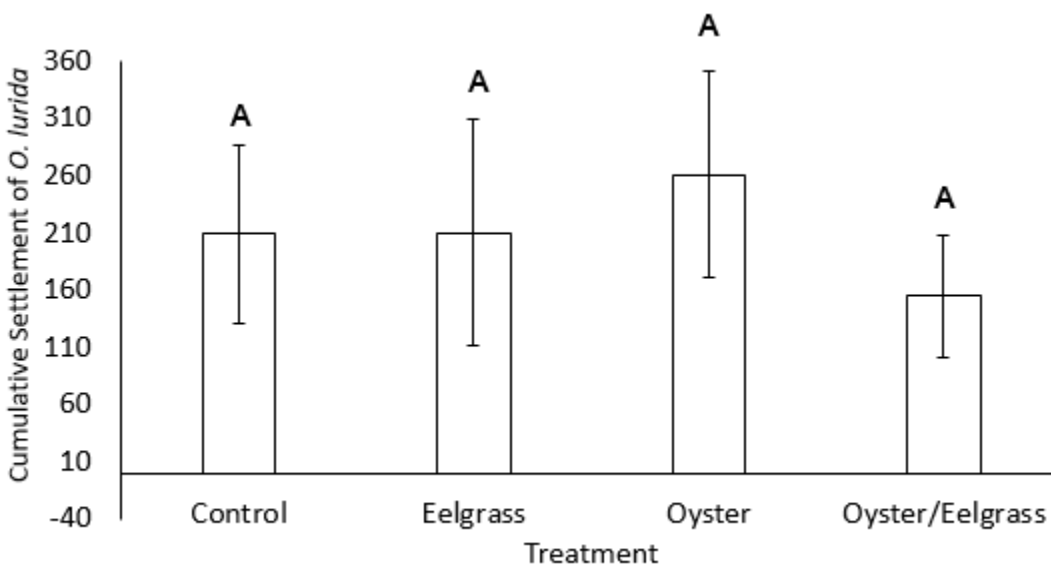
Figure 19. Mean *Ostrea lurida* cumulative settlement per tile per treatment in 2016. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD.

Figure 20. Total cumulative settlement of *Ostrea lurida* per site in 2016. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Figure 21. Total cumulative settlement of *Ostrea lurida* per treatment in 2017. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD.

Figure 22. Total cumulative settlement of *Ostrea lurida* per site in 2017. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 13. Two-way ANOVA test statistics for effects of site, and treatment on cumulative oyster settlement in 2016 pre-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	20.33	3	6.78	1.83	0.2414
Site	100.50	2	50.25	13.60	**0.0059**
Model	120.83	5	24.17	6.54	**0.0203**
Error	22.17	6	3.69		
Total	143.00	11			

Table 14. Two-way ANOVA test statistics for effects of site, and treatment on cumulative oyster settlement in 2017 post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	53.67	3	17.89	6.19	**0.0288**
Site	72.00	2	36.00	12.46	**0.0073**
Model	125.67	5	25.13	8.70	**0.0101**
Error	17.33	6	2.89		
Total	143.00	11			
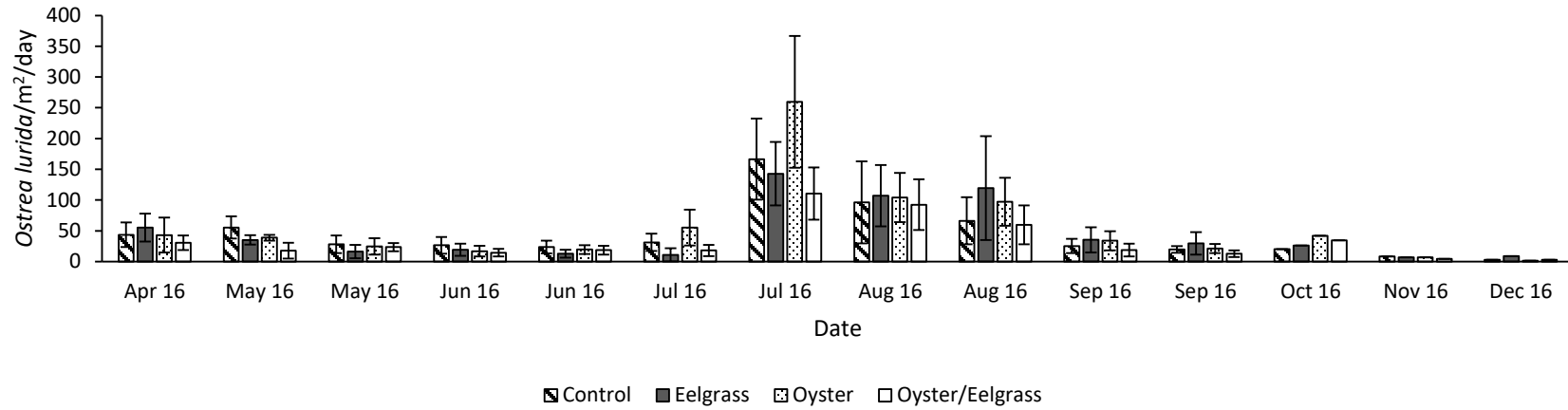
Figure 23. Daily settlement of *Ostrea lurida* (oysters/m²/day) from April 2016-December 2016 by treatment in Newport Bay, CA. Error bars are ±1 SE.
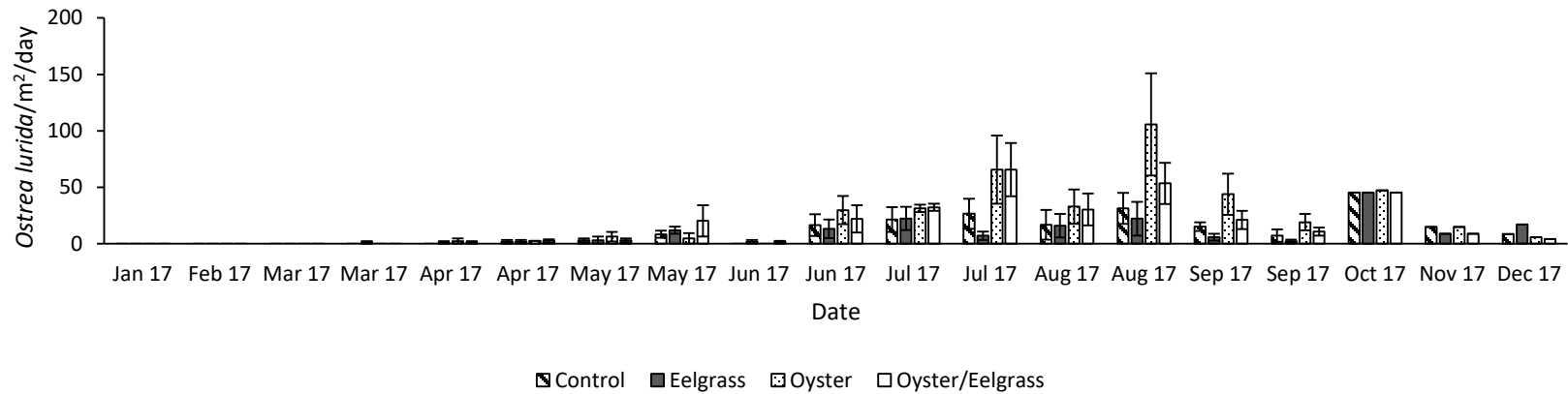
Figure 24. Daily settlement of *Ostrea lurida* (oysters/m²/day) from January 2017-December 2017 by treatment in Newport Bay, CA.

Recruitment

Before oyster bed construction in 2016, *Ostrea lurida* recruitment ranged from a total of 5 oysters/tile to 68 oysters/tile and did not vary significantly among treatments (two-way ANOVA, treatment $p=0.4927$, Fig. 25, Table 15). Recruitment differed among sites, however: recruitment was higher at Deanza than at PCH and Westcliff, and was higher at PCH than at WC (two-way ANOVA, site $p=0.0015$, Fig. 26). After oyster bed construction in 2017, *Ostrea lurida* recruitment ranged from a total of 3 oysters/tile to 36 oysters/tile and was significantly greater on the Oyster treatment than the Control treatment (two-way ANOVA, treatment $p=0.0167$, Fig. 27, Table 16), and did not vary significantly among sites (site $p=0.0784$, Fig. 28).
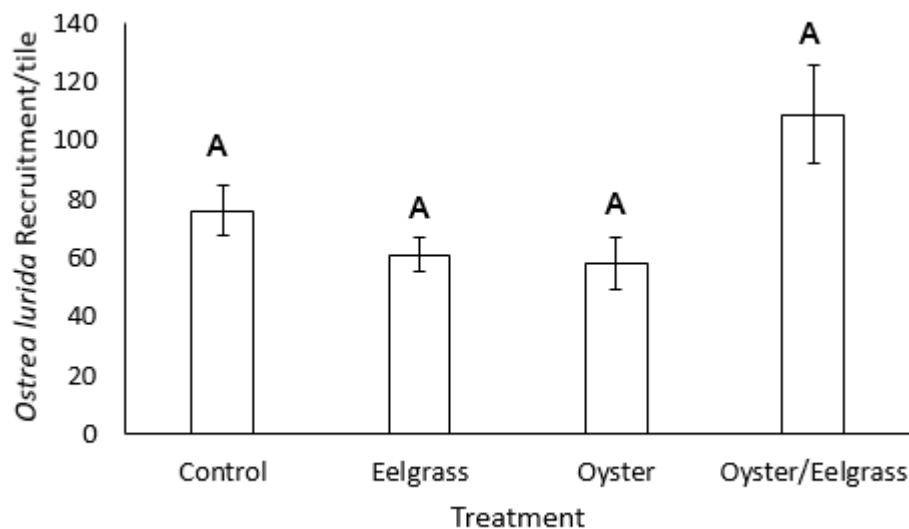
Figure 25. Recruitment of *Ostrea lurida* per tile per treatment in 2016, pre-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD.
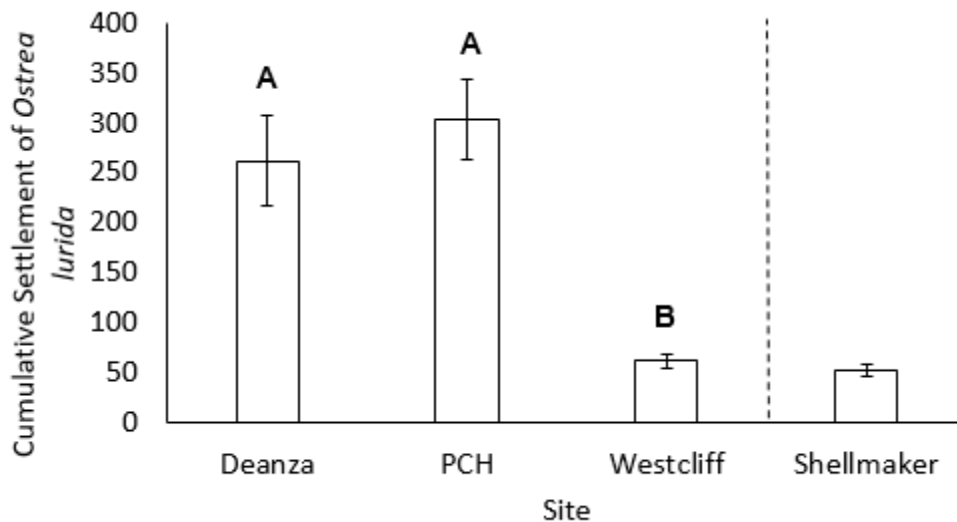
Figure 26. Recruitment of *Ostrea lurida* per tile per site in 2016, pre-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.
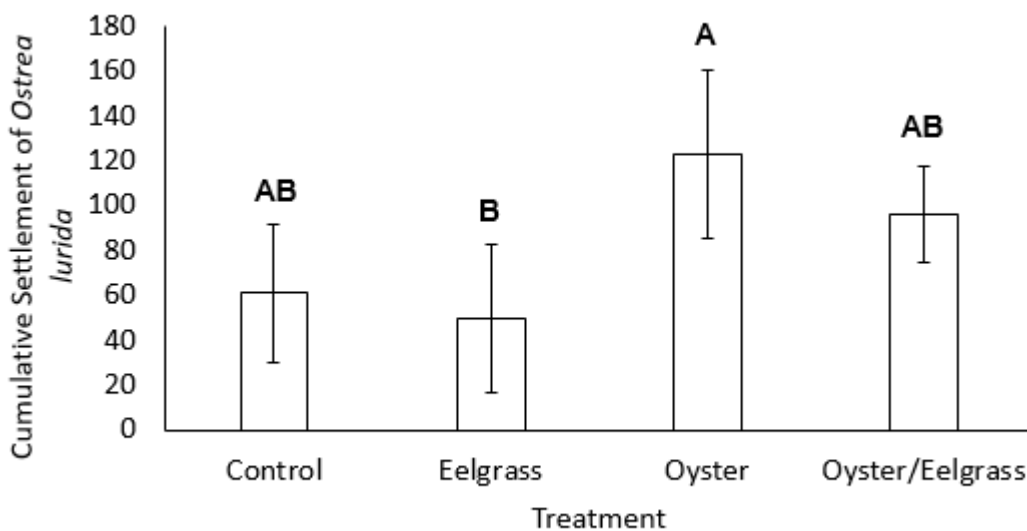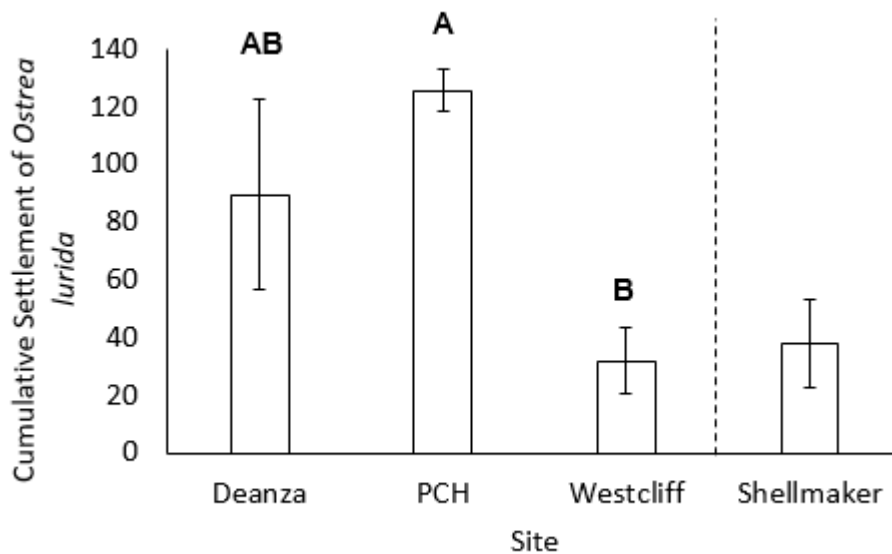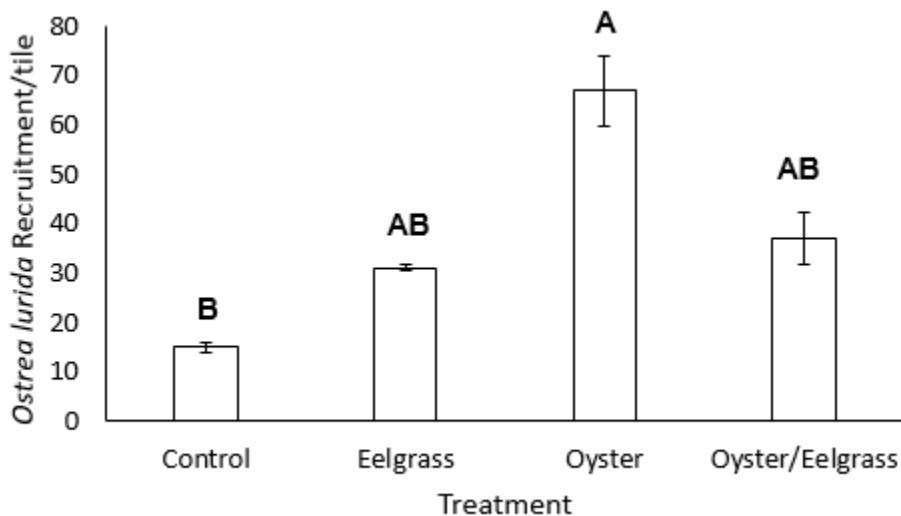

Figure 27. Total recruitment of *Ostrea lurida* per tile per treatment in 2017, post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD.
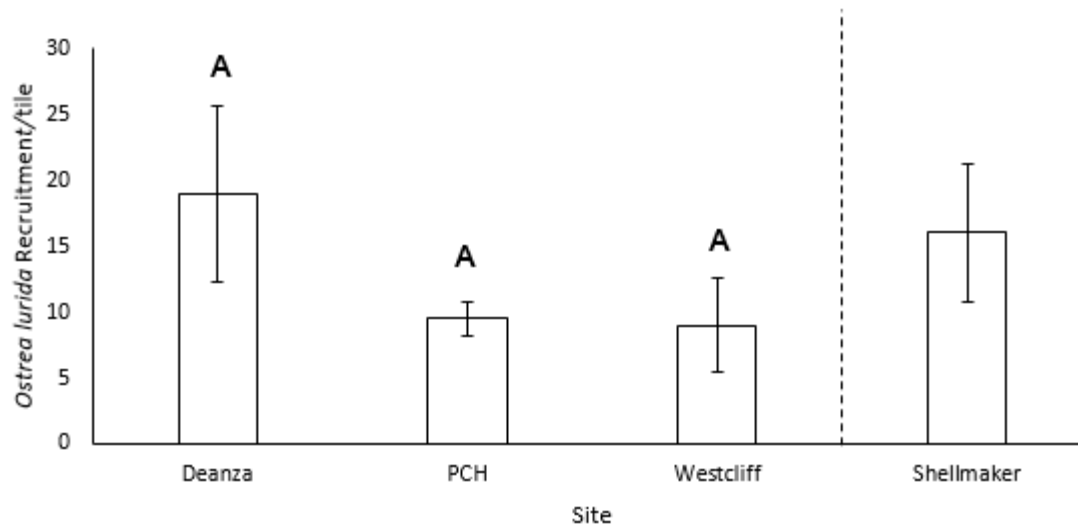
Figure 28. Total recruitment of *Ostrea lurida* per tile per site in 2017, post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 15. Two-way ANOVA test statistics for effects of site, and treatment on oyster recruitment in 2016 pre-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	7.00	3	2.33	0.90	0.4927
Site	120.50	2	60.25	23.32	**0.0015**
Model	127.50	5	25.50	9.87	**0.0074**
Error	15.50	6	2.58		
Total	143.00	11			

Table 16. Two-way ANOVA test statistics for effects of site, and treatment on oyster recruitment in 2017 post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	88.83	3	2.33	7.88	**0.0167**
Site	30.13	2	60.25	4.01	0.0784
Model	118.96	5	23.79	6.33	**0.0219**
Error	22.54	6	2.58		
Total	141.50	11			

Adult Density

Twelve months after oyster bed construction in May 2018, adult density of

Ostrea lurida ranged from 41.60 ± 12.67 oysters/m^2 to 238.4 ± 49.49 oysters/m^2.

At two of three sites, there was no significant difference between Oyster and

Oyster/Eelgrass but density was significantly greater on the Oyster treatment

compared to Oyster/Eelgrass treatment at Deanza, and the same trend toward

higher densities on the Oyster treatments was apparent at all sites. The Control

and Eelgrass treatment had significantly lower densities than both the Oyster and

Oyster/Eelgrass treatment at all sites (two-way ANOVA, treatment p<0.0001, site

p=0.0003, treatment*site p=0.0033 Fig. 29, Table 17).
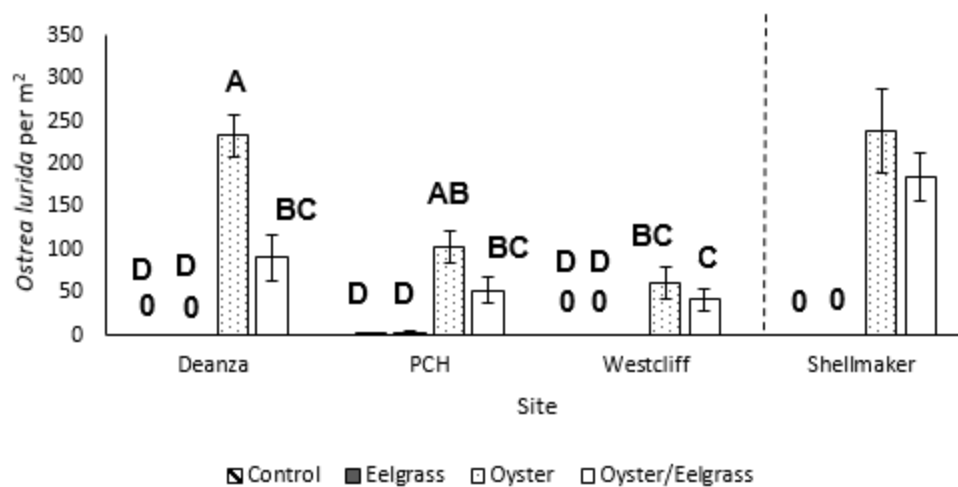
Figure 29. Ostrea lurida (per m^2) per site and treatment (n=10) in May 2018, twelve months post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant difference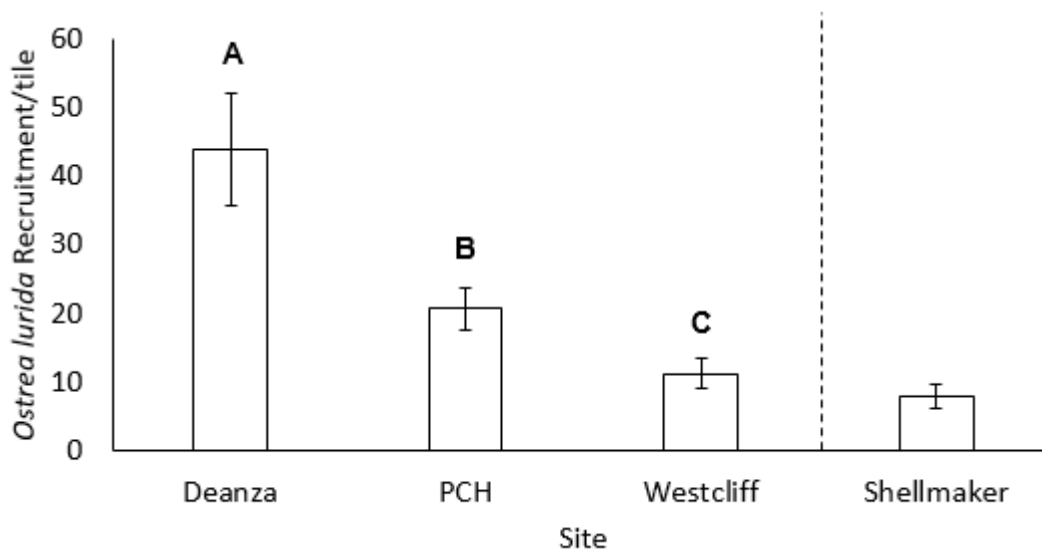s among treatments and sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 17. Two-way ANOVA results for effects of site, treatment, and their interaction on adult oyster density in May 2018, one year post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	85644.05	3	28548.02	104.57	**<0.0001**
Site	4201.14	2	2100.57	7.69	**0.0003**
Treatment*Site	5052.31	6	842.05	3.49	**0.0033**
Model	94897.50	11	8627.05	35.73	**<0.0001**
Error	26071.50	108	241.40		
Total	120969.00	119			

<u>Size</u>

Twelve months after oyster bed construction in May 2018, *Ostrea lurida* length ranged from 30.29 ± 4.72 mm to 34.54 ± 5.64 mm. There was no difference in oyster length among treatments at twelve months post-oyster bed construction (Fig. 30), but oysters were 9.9% larger at PCH compared to Deanza (two-way ANOVA, treatment p=0.2115, site p=0.0382, treatment*site p=0.3978, Fig. 31, Table 18).
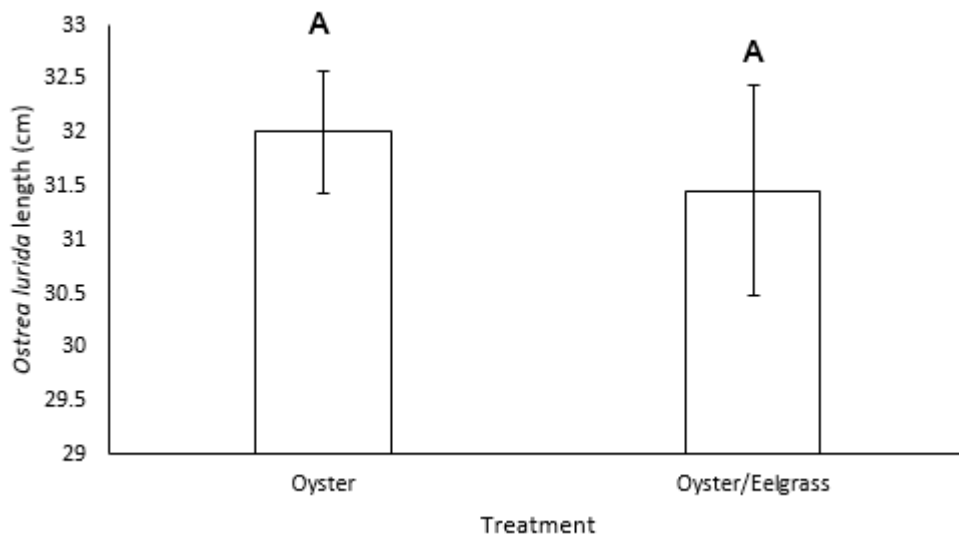
Figure 30. Length of *Ostrea lurida* (mm) by treatments containing oysters in May 2018, one year post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among treatments based upon post-hoc Tukey HSD.
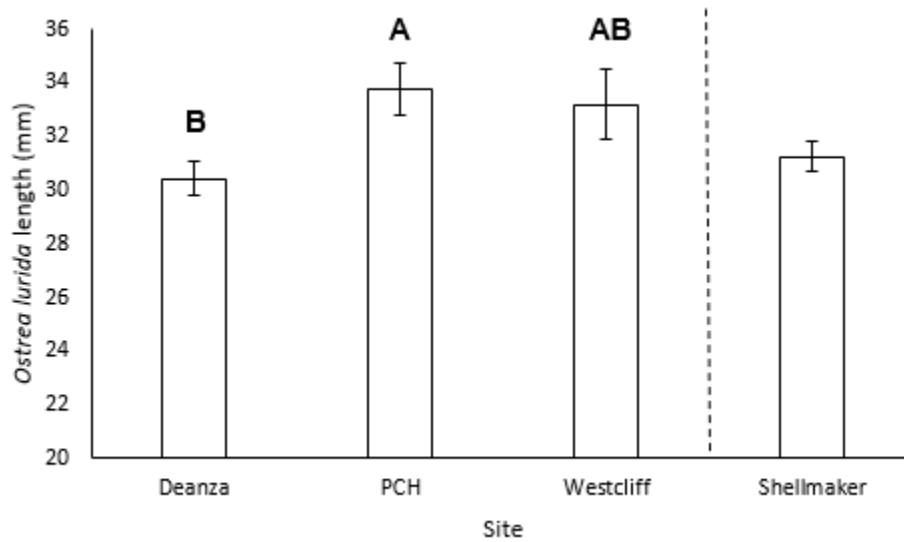
Figure 31. Length of *Ostrea lurida* (mm) per site in May 2018, one year post-oyster bed construction. Error bars are ±1 SE. Variations in bold letters above bars indicate statistically significant differences among sites based upon post-hoc Tukey HSD. Shellmaker is excluded from statistical analyses but is included in graph for reference.

Table 18. Two-way ANOVA results for effects of site, treatment, and their interaction on oyster length size (mm) in May 2018, one year post-oyster bed construction in Newport Bay, CA. Bold indicates statistical significance.

Source	SS	DF	MS	F ratio	Prob > F
Treatment	138.11	1	138.11	1.57	0.2115
Site	580.77	2	290.39	3.29	**0.0382**
Treatment*Site	167.48	2	83.74	0.95	0.3878
Model	1118.55	5	223.71	2.54	**0.0283**
Error	31826.32	361	88.16		
Total	32944.86	366			

<u>Size vs. Mud Deposition on Hard Substrata</u>

Twelve months after oyster bed construction in May 2018, mean oyster length was positively correlated with mean mud deposition on hard substrata on oyster beds across all eight oyster beds (Pearson correlation, r=0.7144, p=0.0465, Fig. 32).
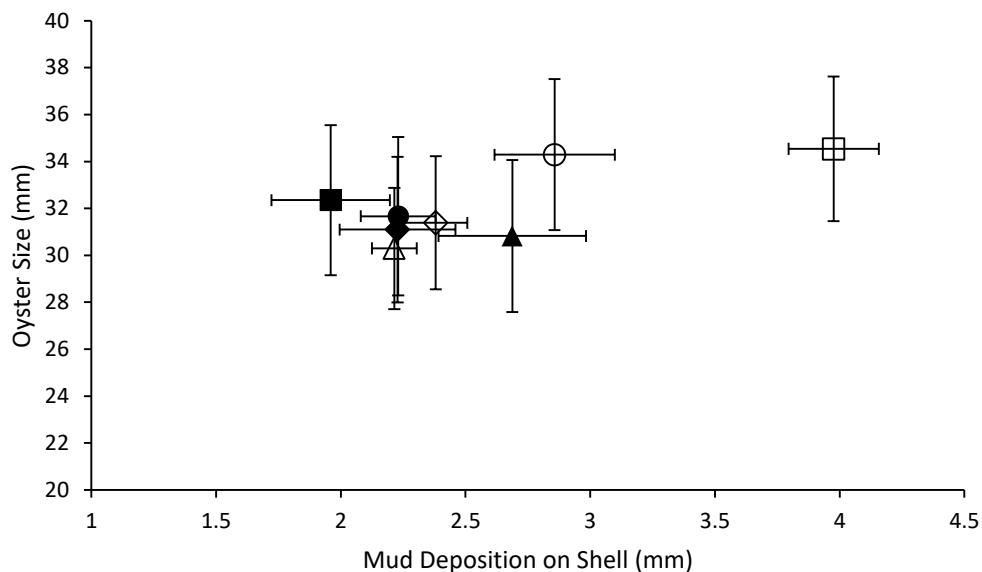
Figure 32. Relationship between mean *Ostrea lurida* length and mean mud deposition onto hard substrata on oyster beds in May 2018, twelve months post-oyster bed construction in Upper Newport Bay, CA. Beds were located across four sites. Error bars are ±1 SE. Triangles represent Deanza, circles represent Westcliff, squares represent PCH, and diamonds represent Shellmaker. Unfilled symbols are Oyster treatments and filled symbols are Oyster/Eelgrass treatments.

Oyster vs. Eelgrass Density

Twelve months after oyster bed construction in May 2018, adult oyster density/m^2 was negatively correlated with eelgrass density/m^2 across all eight oyster beds (Pearson correlation, r=-0.7252, p=0.0418, Fig. 33). Oyster density values were log transformed prior to statistical analysis, thus the significant correlation indicates a negative exponential relationship between eelgrass density and oyster density.
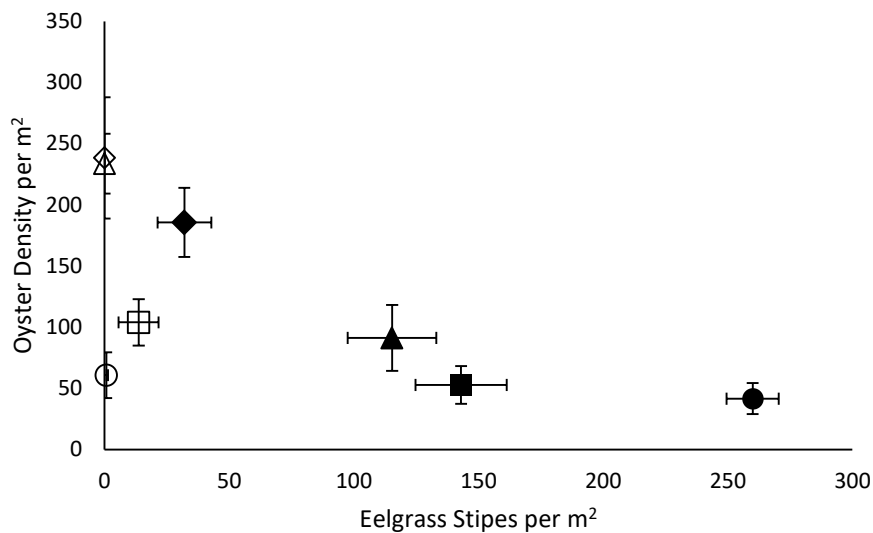
Figure 33. Relationship between mean density of adult *Ostrea lurida* as a function of mean eelgrass density in May 2018, twelve months post-oyster bed construction in Upper Newport Bay, CA. Beds were located across four sites. Error bars are ±1 SE. Triangles represent Deanza, circles represent Westcliff, squares represent PCH, and diamonds represent Shellmaker. Unfilled symbols are Oyster treatments and filled symbols are Oyster/Eelgrass treatments.

CHAPTER 4

DISCUSSION

Collectively, my data recorded in the first year following construction of

oyster beds across four sites in Upper Newport Bay, California, suggest that

oyster beds restored adjacent to eelgrass beds may have lower oyster densities

and receive less sedimentation than oyster beds restored alone. However, these

results were inconsistent over time and across sites, suggesting that the effects

of eelgrass beds on oysters is context-dependent, and that any broad

conclusions about these effects may be premature.

<u>Context Dependency</u>

My findings suggest that the interaction between oysters and eelgrass,

including those mediated by sedimentation, may be context-dependent; the

strength of this interaction changed and may continue to change across time and

space due to factors that remain unidentified. For example, Kimbro et al. (2014)

assessed predator-prey interactions on an oyster (*Crassostrea virginica*) reef and

found that although predation on consumers remained consistent across all sites

on the reef, the effects of predators on behavior varied across sites and

environmental gradients. It is essential to note that one year of experimental data

cannot draw the same conclusions that a longer-term or broader-scale study

could make, because responses may shift over temporal and spatial scales

(Berlow, 1997, Menge et. al., 1994). In a study comparing various substrata used

to recruit *O. lurida* oysters in San Francisco, California, oysters significantly preferred one of five possible substrata after the first year, but this effect disappeared two years post-construction (Latta and Boyer, 2015). Additionally, the strength of effects can also be mediated by seasonal scales (Prasad and Sukumar, 2010), but my study was not designed to assess seasonal differences.

Although I observed a trend of less sedimentation on oysters adjacent to eelgrass beds, it is not clear if this finding is driven by the eelgrass or if the effect will be the same a year or two in the future (Chamberlain et al., 2014). It is also possible that, over time, the difference in oyster densities between the Oyster and Oyster/Eelgrass treatments may become more apparent at the remaining research sites. Therefore, I cannot conclude that densities of adult oysters are consistently higher or lower on Oyster versus Oyster/Eelgrass treatments, although I did detect an inverse exponential correlation of lower adult oyster densities in the presence of eelgrass. The cause of this trend, however, may be different than originally hypothesized.

<u>Filtering Effect of Eelgrass</u>

I initially hypothesized that the difference in adult oyster density between Oyster and Oyster/Eelgrass treatments would be related to higher amounts of sedimentation on Oyster/Eelgrass treatments compared to Oyster treatments. Although, to my knowledge, I am the first to measure sedimentation *adjacent to* eelgrass beds, other studies have shown increased sediment accretion *within* eelgrass beds (Valdez et. al., 2016, Fonseca and Kenworthy, 1987). I originally thought that eelgrass might increase sedimentation on *adjacent* oyster beds, via

a "shadow effect". My data support the opposite effect, i.e., eelgrass potentially "filtering" sediments out of the water column entirely within the eelgrass bed, and thus reducing sedimentation on adjacent oyster beds at six months post-oyster restoration, although this effect of reduced sedimentation on the Oyster/Eelgrass treatment was weakened by twelve months post-oyster restoration. Nonetheless it is clear that I can reject my hypothesis that there is higher sedimentation on oysters restored adjacent to eelgrass compared to oyster-only treatments.

Interestingly enough, this potential filtering effect could be detrimental to oyster survival (assuming that adult density can be used as a proxy for survival), as indicated by the overall significant negative relationship between oyster density and eelgrass density across all sites. Oysters depend on free-floating phytoplankton as a food source and, if eelgrass filters out sediments, it may also serve to filter out phytoplankton. Thus, the oysters restored adjacent to eelgrass may be limited by food availability. My oyster length data lend credence to this hypothesis with a trend toward lengthier oysters on the Oyster treatments compared to Oyster/Eelgrass treatments. Additionally, and *importantly*, *O. lurida* larvae, which spend between 21 days (Baker, 1995) to eight weeks (Breese, 1953) in the plankton before settling out of the water column, may also be filtered out by eelgrass. This filtering effect on larvae is consistent with my cumulative settlement findings at all sites, where there was more settlement at the Oyster treatment compared to the Eelgrass treatment.

Alternately, the oysters on the Oyster treatments may have been lengthier due to efforts to escape sediment stress. In my study, *Ostrea lurida* size was

correlated with mud deposition onto the shell beds they resided upon, and thus agree with other findings (Housego and Rosman, 2016) that oysters must grow faster than the rate of sedimentation to avoid burial.

An interesting test of these competing hypotheses for differences in oyster length between Oyster and Oyster/Eelgrass treatments would be to test for the condition index of oysters (Lawrence and Scott, 1982, Mercado-Silva, 2005) on the two treatment types – if faster growth were the result of greater food availability, I would expect the condition of oysters on the Oyster treatment to be better than on the Oyster/Eelgrass treatments. Alternately, if faster growth resulted from sedimentation stress, the condition of oysters on the Oyster treatment would be worse than on the Oyster/Eelgrass treatments. It may be very misleading to use oyster density as a metric for success (e.g., Zacherl et al. 2015, Saoud et al. 2000, Scyphers et al., 2011, Swann, 2008) if oysters, in fact, are more stressed when restored in isolation. It is possible that oyster size and density are reduced in the presence of eelgrass, but that individual oysters themselves are heathier, plumper per unit length, and thus more reproductively successful. This is a critically important venue for future studies on oyster restoration in the context of Living Shorelines.

<u>Impacts to Oyster Communities</u>

The fact that I found increases in oyster settlement as a function of treatment post-oyster bed construction reinforce the findings of Zacherl et al., (2015) that oyster shell habitat can increase total cumulative settlement. Oysters

are known to use chemotaxis to navigate toward oyster shell (Kingsford et al. 2002).

The non-native Pacific oyster, *Crassostrea gigas*, is invading shores on virtually every continent, but was barely detected in my study (a single individual was observed in 2018, representing 0.16% of the oysters found). It was not found on any settlement tiles in 2016 and 2017, and only one individual was recorded on a recruitment tile in 2017. I attribute the scarcity of *C. gigas* to the tidal elevation at my restoration sites (-0.15 m MLLW). *Crassostrea gigas* in southern California is seldom observed below -0.2 m MLLW and achieves maximum density at +0.4 m MLLW, whereas *O. lurida* achieves its maximum density at or below +0.2 m MLLW (Tronske et al., 2018). Given that invasive species are on the minds of all resource managers, a restoration project that can greatly increase native oysters while not providing habitat for invasive species is of definite interest.

<u>Living Shoreline Implications</u>

My grain size results corroborate other findings (Warrick et al., 2009) that structures that slow wave velocity, such as living shoreline blocks, cause decreases in grain size. Increases in percent silt/clay concentrations impact oyster beds more profoundly compared to oyster beds with larger grain size characteristics, indicating that oysters may be influenced by smaller grain sizes more profoundly than larger ones (Wall et. al., 2005), potentially due to issues with filtration such as gill clogging. Uchio and Uchio (1962) reported that grain sizes varied significantly by location along the Shinano River, Japan, with finer

grain sizes closer along the shoreline where there was less wave energy. During pre-oyster bed construction, sites differed in their grain size characteristics, with Westcliff having the smallest grain sizes, implying the slowest velocity, and PCH and Deanza having largest grain sizes, potentially implying faster water velocities. However, at one year post-oyster bed construction, site effects were ameliorated by a treatment effect, with living shoreline structures (Eelgrass, Oyster, and Oyster/Eelgrass treatments) tending to decrease grain size compared to Control treatments.

Both constructed oyster beds and eelgrass beds in my study appear to perform as living shorelines structures through net sedimentation upshore of treatments. After one year, restored beds tended to have more sedimentation upshore than Control treatments, which were erosive. Because sedimentation is a slow process that may not be apparent for decades (US Geological Survey, 2012), it is encouraging that I observed trends toward the predicted treatment effects after only a single year. Future monitoring efforts are expected to clarify the effects of living shoreline structures on sedimentation upshore.

Oyster and eelgrass restoration projects are of utmost importance as both habitats have declined dramatically, could provide substantial ecosystem services if restored, and can help increase shoreline resiliency. Conclusions about whether to restore oysters alone versus adjacent to eelgrass meadows are preliminary based upon a single year of post-restoration monitoring, especially in light of the temporal and spatial context dependency I observed, suggesting that

additional monitoring of recovery is warranted. Ultimately my findings may direct

future restoration initiatives involving oysters and eelgrass.

APPENDIX
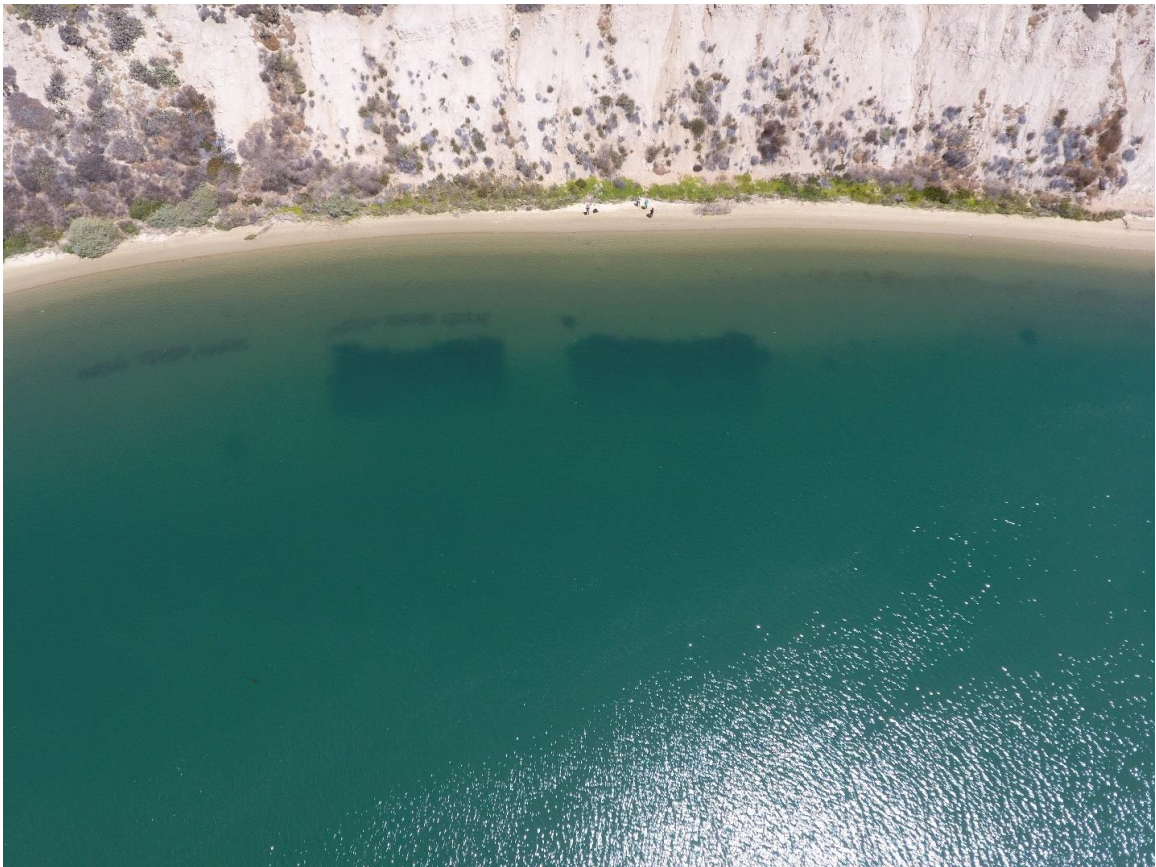
Figure A1. Aerial photo of all treatments at Westcliff during high tide. Treatments from left to right of photo are Oyster, Oyster/Eelgrass, Eelgrass, and Control.
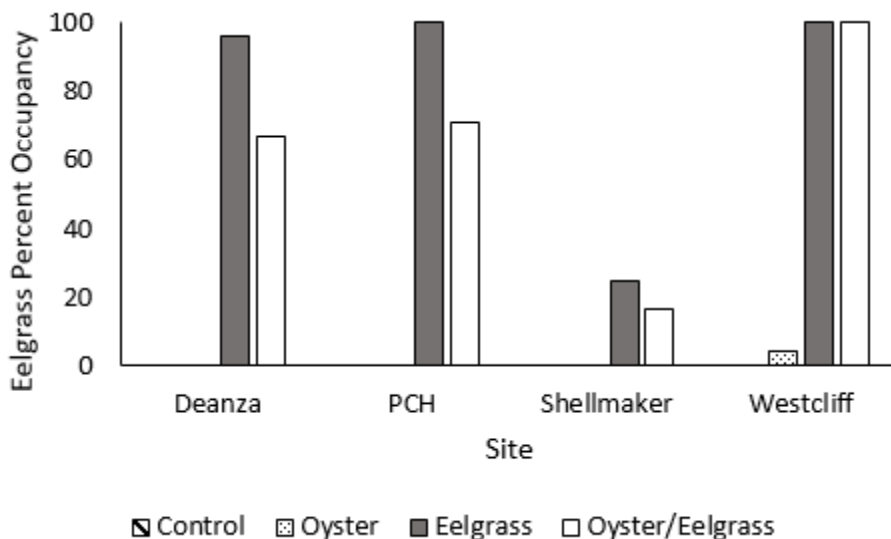
Figure A2. Eelgrass percent occupancy per treatment per site (n=24) in August 2017, approximately one year after eelgrass restoration and four months following oyster bed construction.
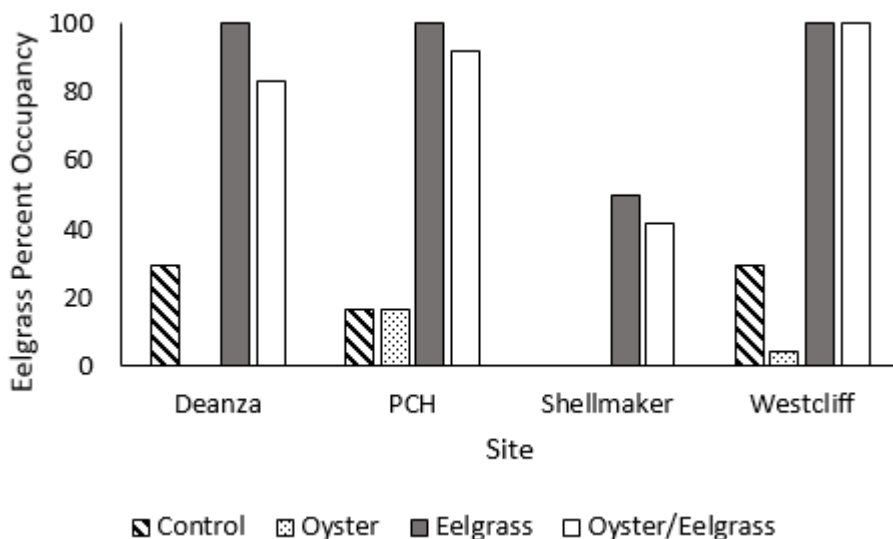
Figure A3. Eelgrass percent occupancy per treatment per site (n=24) in May 2018, approximately two year after eelgrass restoration and one year following oyster bed construction.
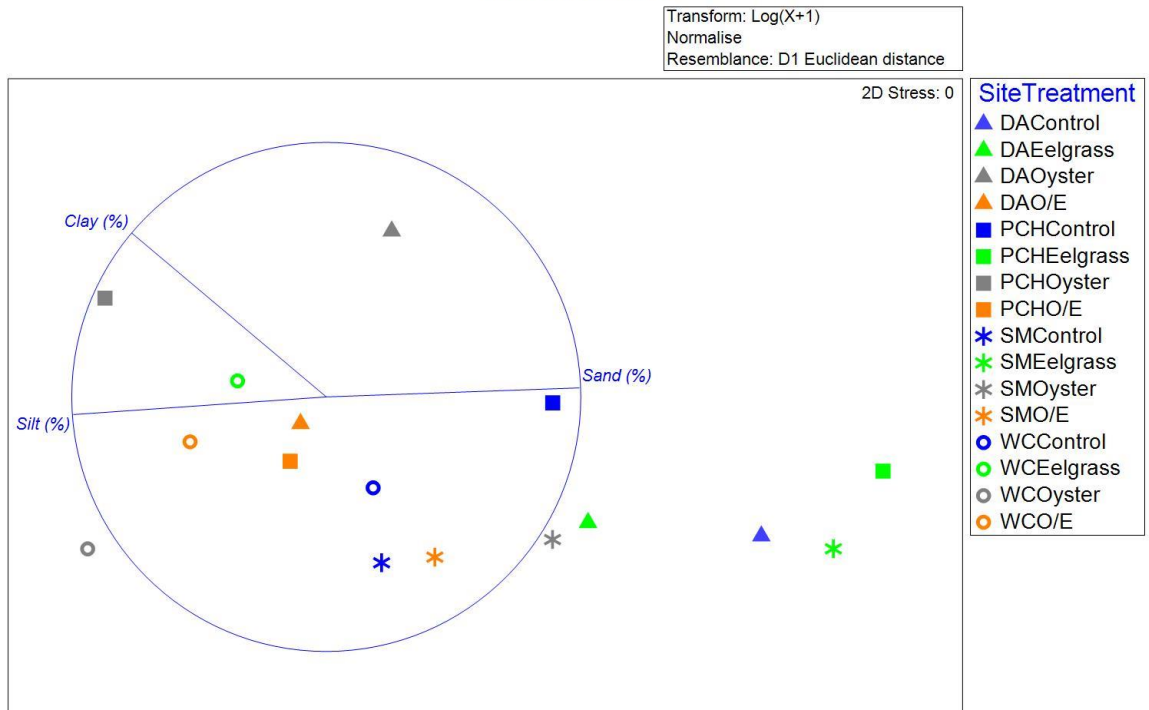
Figure A4. Non-metric multidimensional scaling of grain size characteristics (sand, silt, and clay) per treatment per all sites (including Shellmaker) in March 2017, pre-restoration in Newport Bay, CA. For ease of graphing, DA = Deanza, PCH = PCH, WC = Westcliff, SM = Shellmaker, and O/E = Oyster/Eelgrass.
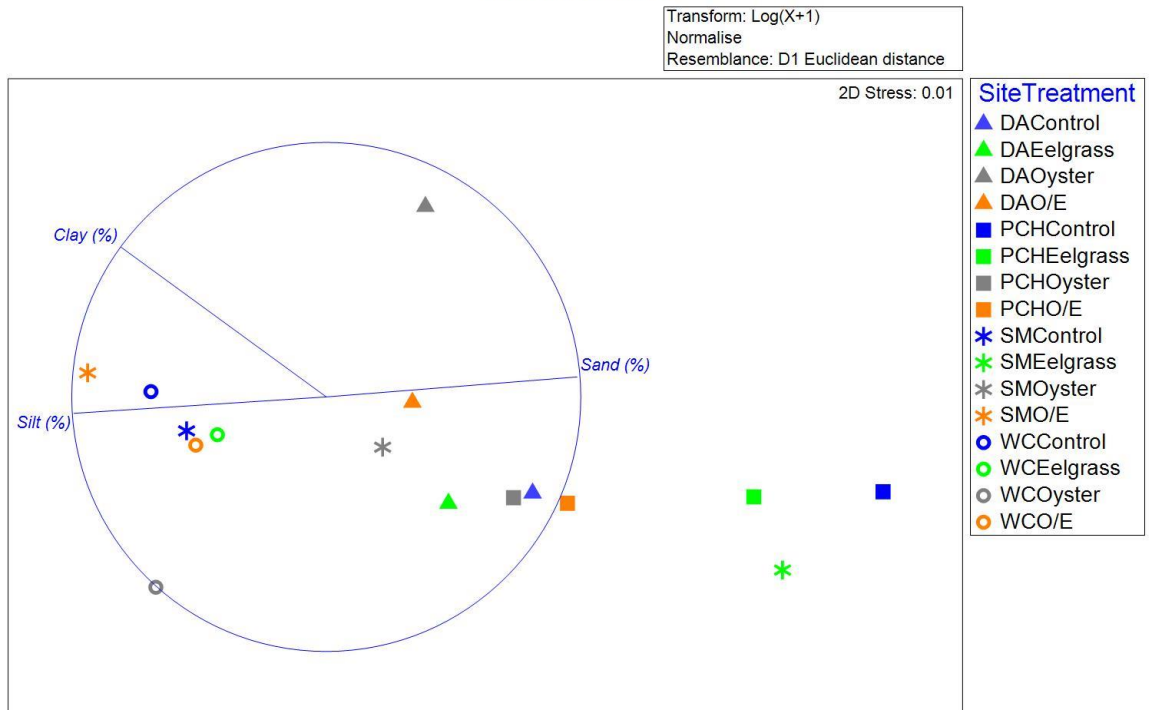
Figure A5. Non-metric multidimensional scaling of grain size characteristics (sand, silt, and clay) per treatment per all sites (including Shellmaker) in May 2018, twelve months after oyster-bed construction in Newport Bay, CA. For ease of graphing, DA = Deanza, PCH = PCH, WC = Westcliff, SM = Shellmaker, and O/E = Oyster/Eelgrass.

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