RESPONSE OF EELGRASS (*ZOSTERA MARINA*) TO AN ADJACENT OLYMPIA OYSTER RESTORATION PROJECT

A Thesis

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By

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ABSTRACT

Recent restoration efforts for the native Olympia oyster, *Ostrea lurida*, are commonly motivated by potential return of ecosystem services, including increased water filtration. The impact of this service on another species of restoration concern, eelgrass *Zostera marina*, is unclear, but is hypothesized to be positive if oyster filter feeding behavior increases light penetration to eelgrass. For two years after installation of a constructed oyster bed, I assessed eelgrass response in an adjacent eelgrass bed and control eelgrass bed by monitoring changes in water column light intensity, eelgrass shoot density, biomass, leaf morphometrics and epiphyte load. I found no evidence that the constructed oyster bed impacted water column light intensity, overall eelgrass bed structure (total above-ground biomass and shoot density) or eelgrass epiphyte load. However, eelgrass below-ground biomass significantly declined by 54 % the first year after the construction of the oyster bed, and remained 38 % lower than pre-construction levels after 2 year, though values were never lower than the control. Individual shoot characteristics also showed evidence of impact in the first year only through increases in leaf width (17 % increase) and shoot biomass (78 % increase), though it is unclear whether this is a positive impact or a temporary adaptive response by the eelgrass to short-term stresses associated with oyster bed construction activities. Nonetheless, these findings support the potential coexistence of constructed Olympia oyster beds and eelgrass, which is relevant to the design of future restoration efforts for both species.

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CHAPTER 1

INTRODUCTION

Large declines in historic Olympia oyster, *Ostrea lurida*, populations to the point of ecological extinction (Beck et al. 2011) have promoted a recent interest in oyster restoration on the west coast of the United States. In addition to increasing local abundances of the native oysters, restoration practitioners are motivated by the potential recovery of ecosystem services that the oyster may provide. On the east coast of the United States, the native eastern oyster, *Crassostrea virginica*, can increase habitat complexity and community diversity, improve water clarity, cycle nutrients, and stabilize sediments (Coen et al. 1999, Grabowski and Peterson 2007, Newell et al. 2005, Meyer et al. 1997). West coast oyster restoration practitioners base estimates of the ecosystem services of *Ostrea lurida* on the eastern oyster, though the provision of these services by *O. lurida* is rarely evaluated.

Ostrea lurida habitat has been associated with eelgrass, *Zostera marina*, historically and, to some extent, more recently. Pleistocene fossil deposits from northern California containing both species (Miller and Morrison 1988) support the historical association between eelgrass and the Olympia oyster, and researchers recently found Olympia oysters in small abundances within eelgrass beds in San Diego Bay, CA (Reed and Hovel 2006). Elsewhere in southern California, we have observed some evidence of overlap in *O. lurida* and *Z. marina* distributions, but more commonly Olympia oysters are found at a higher tidal elevation, with eelgrass occurring in the lower intertidal to shallow subtidal zone (personal observation, D. Zacherl, personal communication). Since both species can inhabit the lower intertidal zone, at least in some locations, there is a high potential for native oysters to live within or near eelgrass beds. As Olympia oyster restoration efforts increase in number and size, the potential for these two species to interact also increases.

Many oyster restoration practitioners commonly cite the potential benefits to water quality by other oyster species on eelgrass (Newell and Koch 2004, Coen et al. 2007), though this impact by *Ostrea lurida* has rarely been tested. Seagrass species have some of the largest light requirements of all plants, requiring almost 25% incident radiation, compared to about 1% for most angiosperms (Dennison et al 2003), which makes eelgrass productivity closely tied to water clarity. Oysters may improve water quality dramatically, both through their filtration activity and via their creation of additional three-dimensional structure. By removing phytoplankton and suspended sediments out of the water column through filter feeding, light available to eelgrass blades for photosynthesis increases (Nelson et al. 2004, see review in Dame 1996) and can translate into increased seagrass growth (Wall et al. 2008, Wall et al. 2011). The complex structure of oyster beds as an aggregate of both adult oysters and vacated oyster shell can also improve water clarity for eelgrass growth through physical stabilization of the sediment (Meyer et al. 1997, Newell and Koch 2004, Smith et al. 2009). The structure of an oyster bed can prevent fine particles that would decrease light penetration to eelgrass from becoming re-suspended in the water.

Bivalves may additionally improve light penetration to eelgrass by altering the light reaching the eelgrass leaf surface through reductions in epiphytic load. Epiphytes, organisms that grow upon or are attached to the eelgrass blades, act as an additional barrier to eelgrass in attaining light requirements for photosynthesis, as less surface area of the leaf blade is exposed to light. High epiphytic loads can also weigh leaf blades down to the benthos where they eventually are buried by sediment. Oysters may decrease eelgrass epiphytic loads by increasing the amount of habitat complexity available as predation refuge to epiphyte grazers (Peterson and Heck 2001a, b). The presence of additional epiphyte grazers may decrease the coverage of epiphytic organisms and allow more light penetration for increased eelgrass growth. Eelgrass epiphytic load may also decrease as oysters remove nutrients from the water column and deposit them to the sediment, which otherwise would have fueled algal growth on the eelgrass leaf surface.

Despite evidence of benefits of bivalves on eelgrass, there is also some evidence to suspect a negative impact associated with higher densities of oysters. Increased oyster densities have led to a decline in eelgrass cover, plant size, biomass, and growth, likely due to space competition as well as build-up of toxic sulfide levels from enriched oyster bio-deposits (Kelly and Volpe 2007, Archer 2008, Booth and Heck 2009, Wagner et al. 2012).

It is unclear whether *Ostrea lurida* shows the same impact on eelgrass as previously studied oyster species due to its much smaller size, bed structure, and lower water filtering capabilities than the larger oyster species more commonly studied (zu Ermgassen et al. 2013). In addition, prior studies of an interaction were almost exclusively done by placing high densities of oysters directly within eelgrass beds, which does not accurately reflect natural spatial arrangements of the two species, at least in southern California, or the arrangement typically used in restoration projects. It is unclear whether the benefits remain and negative impacts are diminished when native Olympia oysters are added adjacent to, rather than within, existing eelgrass beds.

Eelgrass is also a target of restoration and conservation focus along the west coast of the United States due to substantial population declines and provision of many critical ecosystem services (Orth et al. 2006). Eelgrass provide many similar ecosystem services as oyster beds, including habitat provision (Beck et al. 2001), nursery ground function (Beck et al. 2001, Heck et al. 2003) and sediment stabilization (Newell et al. 1986, Posey et al. 1993). In addition, eelgrass is also a major primary producer (Zieman and Wetzel 1990, Duarte and Chiscano 1999) and a large contributor of carbon to detrital pathways (Duarte et al. 2005). Eelgrass canopies can additionally increase sedimentation of suspended particles and improve water clarity by altering water flow through the resistance of the blades (Hemminga and Duarte 2000). The conservation and protection of valuable eelgrass habitat is a priority for natural resource managers and the National Oceanic and Atmospheric Association identified eelgrass habitat as a Habitat Area of Particular Concern (HAPC) and an Essential Fish Habitat (EFH). As such, it is important for future oyster restoration efforts to prevent any damage to existing eelgrass beds, but also to document any benefits of restoring the two species in close association, which may be used to increase the restoration success of both species.

An Olympia oyster restoration project constructed shoreward of an existing eelgrass bed offered an opportunity to begin to clarify the impact of Olympia oyster restoration on eelgrass. The objective of this study was to better elucidate the impact of not only *Ostrea lurida*, but also the construction of oyster bed, on an adjacent eelgrass bed. I examined the impacts of this restoration project on light intensity and eelgrass shoot density, biomass, leaf morphology and epiphyte load over a two-year period following bed construction.

CHAPTER 2

METHODS

Study Site and Species

This study took place in Alamitos Bay, a highly urbanized and developed bay in the city of Long Beach, in Los Angeles County, California. Although historically an estuary with tidal marshes and mudflats at the mouth of the San Gabriel River, development of Alamitos Bay into a small-vessel harbor began in the early 1900s (LSA Associates 2009). Alamitos Bay has a surface area of approximately 1.2 km^2 (285 acres) (CSWRCB et al. 1998) and a tidal prism of approximately 1.96 X 10^6 m^3 (IRC 1981). The physical conditions in the Bay are largely driven by the presence of the AES Alamitos Generating Station. Cooling water uptake by the power plants in the upper portion of Alamitos Bay creates a net transport of ocean water into the bay and a mean water residence time of approximately one day (IRC 1981). This improved flushing rate and higher current velocity may improve water quality in the bay. Because of minimal seasonal freshwater inputs, Alamitos Bay is effectively a marine environment, with salinities ranging from 30 – 35 PSU, however temperatures can range from 13º C in the winter and up to 25º C in the summer (Allen and Horn 1975, IRC 1981).

Eelgrass (*Zostera marina*) beds grow on sand and mud substrates throughout the bay (Coastal Resources Management 2009). Both intertidal and subtidal populations are present at elevations between approximately 0 m and -2.6 m MLLW (Coastal Resources

Management, 2009). Native Olympia oyster, *Ostrea lurida*, beds were documented in Alamitos Bay in the early 1900's (Bonnot 1935, Reish 1961), but current densities of the oyster are extremely low throughout the bay (bay-wide mean: 3.88 ± 0.96 (±SE) individuals m^{-2}, Tronske et al., CSU Fullerton, unpublished data, 2012). The native oyster occurs on hard substrata in the lower intertidal to shallow subtidal, with historic extreme limits for the species observed at 2 m above and 10 m below MLLW (Baker 1995), although the current lower depth limit is unclear. Because natural hard substrata are limited in the highly developed Alamitos Bay, oysters are primarily limited to man-made substrata.

Oyster Habitat Restoration Details

To return missing oyster bed habitat back to Alamitos Bay, a collaborative group composed of scientists and non-profit organizers from California State University, Fullerton, California State University Long Beach, KZO Education and Orange County Coastkeeper initiated an Olympia oyster restoration project in Jack Dunster Marine Reserve (JDMR) (33°45'43.98"N, 118° 7'10.74"W, Fig. 1) in June 2012. The reserve itself is a mitigated wetland restoration area encompassing 1.5 acres of land and 1.2 acres of shallow water created in 2004. Because of a lack of suitable oyster habitat, restoration involved supplementing clean empty oyster (*Crassostrea gigas*) shell to the mudflat to increase the recruitment of planktonic oyster larvae. Shells were originally added in one long rectangular shape parallel to shore (30 m by 2 m) up to 0.12 meters thick at an elevation of approximately +0.33 m MLLW. Within six months of construction, however, the oyster shell bed experienced significant shell loss (72%), most likely a result of significant sediment deposition. Oyster larval settlement occurred and adults were present, but at a very low density within the first year (June 2013: 2.29 ± 15.50 individuals m^{-2}, Fuentes et al., CSU Fullerton, unpublished data). In June 2013, after collecting all 1-year post-restoration samples, more shell was added to the mudflat to ameliorate shell loss at a lower intertidal height of +0.22 m MLLW. In addition, the band of oyster shell was separated into several sections to allow water flow channels in an attempt to prevent sediment deposition onto the shell bed. The adaptive management strategy maintained high shell percent cover through the end of the study and supported much higher densities of oysters (300 - 400 individuals m^{-2}) by June 2014 (Fuentes et al., CSU Fullerton, unpublished data).

Experimental Design

A large pre-existing eelgrass bed is found throughout Jack Dunster Marine Reserve (JDMR) immediately seaward of the constructed oyster bed. The initial oyster bed was located approximately 9 meters (m) above the existing eelgrass bed. To assess the impact of oyster restoration on eelgrass, I conducted a classical Before-After-Control-Impact (BACI) design, by monitoring two portions of a pre-existing eelgrass bed before and throughout the two years after construction of the restored oyster bed. I monitored a 30 m by 3 m portion of the eelgrass bed directly seaward of the constructed oyster bed as the impact eelgrass bed where the greatest impact, if any, was expected. An adjacent 30 m by 3 m portion of the eelgrass bed seaward of an un-manipulated mudflat was monitored as the control eelgrass bed (Fig. 1). Although not an ideal control because of the proximity to the oyster bed, monitoring this eelgrass bed facilitated the best comparison between eelgrass with and without a shoreward oyster bed. The lack of replication of both “treatment” and control replicates is a common issue in the evaluation of restoration projects, as well as environmental impacts, though there are designs which may help alleviate this issue (reviewed in Michener 1997). Underwood (1991, 1992, 1994) described a “beyond BACI” design which incorporates multiple control sites to compare with the impact site. Similarly, I monitored two additional eelgrass beds of the same size and tidal height outside of JDMR to improve understanding of reference eelgrass conditions not impacted by oyster restoration (Fig. 2). The first reference eelgrass bed (Reference 1) is a large eelgrass bed present on the inside of a residential boat dock located across the Los Cerritos Channel from JDMR. The second reference eelgrass bed (Reference 2) is located just southwest of the Appian Way Bridge and unprotected from currents and boat wakes, unlike the other eelgrass beds.

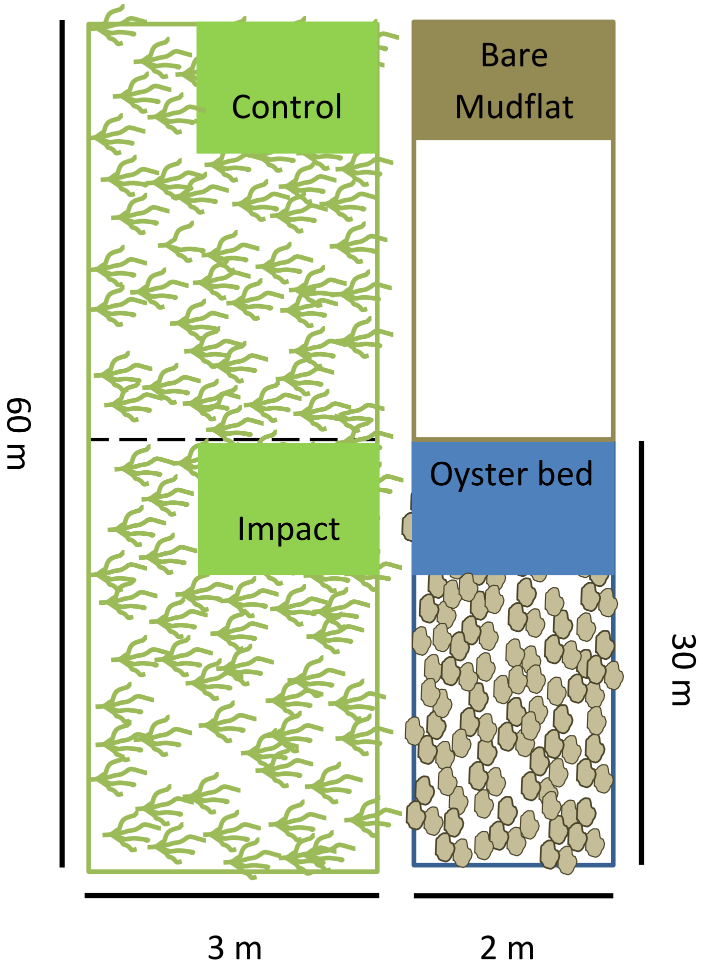


Figure 1. Impact and control beds in relation to constructed oyster bed within Jack Dunster Marine Reserve (JDMR). Distance between the oyster and eelgrass bed (9 m) not drawn to scale.

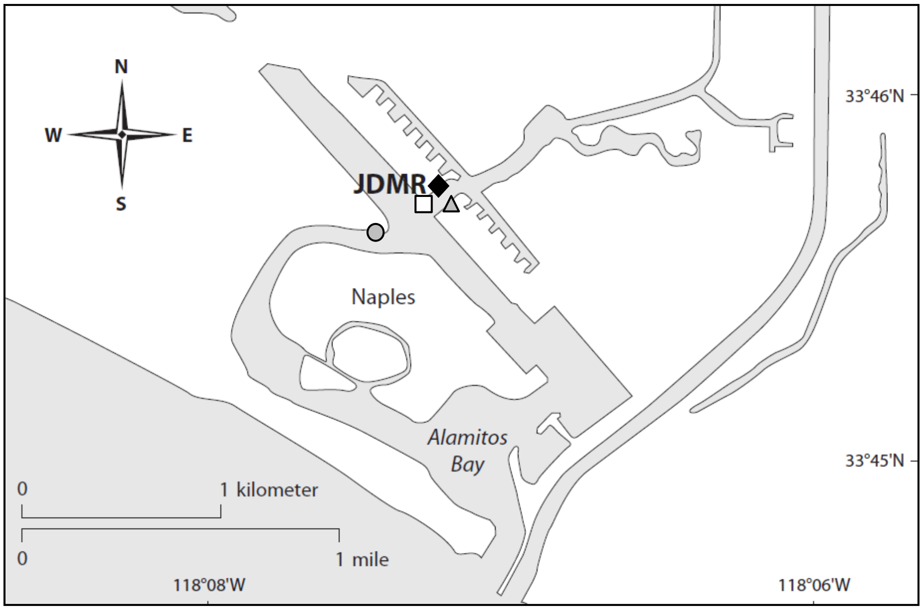


Figure 2. Impact (♦) and control beds (□) within JDMR in relation to Reference eelgrass beds 1 (▲) and 2 (●) in Alamitos Bay, Long Beach, CA.

Constructed Oyster Bed Impact on Light Intensity

I measured underwater light intensity using HOBO Pendant® Temperature and Light Data Loggers deployed within each eelgrass bed before and after oyster restoration. Light meters attached to the tops of floatable buoys were suspended at a fixed height above the eelgrass canopy at a depth of 0.3 m below mean lower low water (MLLW). The height of the meters off the sediment varied slightly between survey periods (0.6 to 0.9 m), but was consistent between the sites within the same survey periods. I placed two replicate meters at the seaward edge of each bed approximately 0.5 m apart. Light meters were deployed quarterly through the first year following oyster bed construction: June –

July 2012 (Summer 2012), August – September 2012 (Fall 2012), December 2012 – February 2013 (Winter 2013), March – May 2013 (Spring 2013), June – July 2013 (Summer 2013) and annually through two years after restoration, June – July 2014 (Summer 2014). Light meter surfaces were cleaned using a soft brush every 3 days. Due to high sedimentation rates onto the sensors, I used only the dates immediately following cleaning (n = 10 in each season) in analysis. The HOBO loggers collected light measurements every 5 minutes. I used the maximum light value between the 2 replicate light meters at each time period in analysis to eliminate instances of shading on one of the loggers, and then calculated mean daily light value for each site and season by averaging the maximum light values between the hours of 10:00 and 14:00, when the sun is most directly overhead. Since the HOBO loggers measure light intensity rather than photosynthetically active radiation (PAR), data retrieved from the HOBO loggers allow relative comparisons between sites rather than indicating the total amount of light energy available for photosynthesis. However, prior studies found that light intensity values collected with HOBO Loggers and PAR are highly correlated (Park et al. 2009, Wall et al. 2011), such that high light intensity values would suggest high PAR values.

Eelgrass Response to the Constructed Oyster Bed

Eelgrass Biomass

To measure impacts to eelgrass biomass, I collected eelgrass above-ground and below-ground samples (n = 7 of each) before initiation of the restoration project (June

2012) and each year after for two years (June 2013, June 2014). All shoots within a 15.24 cm diameter circular frame were cut at the sediment surface, preserved in a 4% formalin seawater solution and returned to the laboratory. Samples were then rinsed with DI water and preserved in 70% ethanol until further processing occurred. To determine the weight of the eelgrass above-ground material and epiphyte material separately, I dried samples in a lyophilizer to remove epiphytes from the eelgrass blades with the least amount of damage to the eelgrass blades (as described in Penhale 1977). I selected this method because the dominant epiphytes were calcareous algal epiphytes, which were difficult to remove using other physical methods. Samples were stored in a -80°C freezer and then lyophilized for 12 – 24 hours, depending on sample size, before epiphytes were gently scraped from each leaf using a stiff paintbrush. Cleaned above-ground samples and separate epiphyte samples were then transferred to a 60°C drying oven until constant mass was achieved.

I collected below-ground material, approximately beneath each above-ground sample, using PVC cores of the same diameter (15.24 cm) to a depth of 21 cm below the sediment surface. In the laboratory, I rinsed the samples with deionized water over a 0.5 mm sieve to remove sediment and preserved them in 70% ethanol until further processing. Using a dissecting microscope, I removed non-root or rhizome material (including snails, worms, other plant material, and pebbles) from each sample. Remaining root and rhizome material was rinsed with freshwater and dried to a constant mass (to the nearest 0.01 g) at 60ºC. I calculated shoot biomass for each sample as the total above-ground biomass of the sample divided by the total number of eelgrass shoots in that sample.

Eelgrass leaf morphometrics

In the laboratory, I measured the number of leaves, leaf length, and leaf width from all harvested shoots. Leaf length of both broken and entire leaves was measured from the base (ligule) to the tip of each leaf to the nearest mm. Leaf width was measured to the nearest 0.05 mm at half the total length of each leaf. In analysis, I used only the length of the longest leaf of each shoot (maximum leaf length), averaged over all the shoots in a sample. For leaf width analysis, I determined the mean leaf width of all leaves in a shoot, averaged over all the shoots in a sample.

Eelgrass shoot density

I monitored shoot density on SCUBA quarterly by counting the number of shoots within 20 quadrats (0.50 m x 0.25 m) in each site before oyster bed construction (June 2012) and approximately every 3 months after for 2 years (through June 2014). A 30 m transect was placed within each eelgrass bed approximately 1 to 1.5 meters from the shallow edge of the eelgrass bed parallel to shore in approximately the same location during each survey period. I generated coordinates for each quadrat location randomly using a random number generator (Excel), but I occasionally replaced with other random numbers to ensure that quadrats were spread across the length of the bed and that quadrats were not overlapping. Densities were converted to the number of shoots per square meter and averaged for each site and survey period.

Eelgrass Epiphyte Response to Constructed Oyster Bed

To determine impacts to the epiphytic load on each eelgrass bed, I measured epiphyte biomass and percent cover before (June 2012) and every year after initial oyster bed construction (June 2013, June 2014). I determined epiphyte biomass as the material removed from the lyophilized above-ground material, as described above in eelgrass above-ground biomass methods. Epiphyte biomass was normalized to the total above-ground eelgrass (epiphyte load). Epiphyte percent cover was determined using the oldest portion (the first 8 cm from blade tip) of the two oldest blades from 1 - 3 shoots per sample (n = 4 - 7 samples per bed per season). I overlaid a transparent rectangular grid (1 mm by 5 mm) on each 8 cm portion and identified the functional group occupying over 50% of each point-intercept using a dissecting microscope. Functional groups identified included calcareous encrusting alga, filamentous alga, foliose alga, sediment tube, serpulid worm, encrusting bryozoan, tunicate, egg mass and hydroid. I combined the front and back of each 8 cm portion into a single percent cover value for that leaf and I averaged the data from the two leaves of each shoot. For each sample, I calculated the average percent cover over all the shoots within the sample.

Statistical Analyses

Data were examined visually and checked for assumptions of normality and homogeneity using the Shapiro-Wilk and Bartlett’s tests respectively. I transformed data using a log-transformation to meet these assumptions when necessary. In the case where heteroscedastic data could not be improved through transformation, I proceeded with a parametric ANOVA because of its robustness to small deviations from homoscedasticity (Boneau, 1960).

Over the study period, I observed substantial differences between the eelgrass beds within Jack Dunster Marine Reserve (JDMR) and the reference sites outside of the reserve. Specifically, Reference 2 experienced a complete population collapse within 6 months of study initiation, and Reference 1 experienced substantial declines 6 months before study completion. These differences were likely due to larger differences between the sites, rather than the oyster restoration project itself. The sites within the reserve were afforded more protection from all human activities, whereas the reference sites were more accessible to the public. The JDMR sites and Reference 1 were also more protected from erosive currents by a floating breakwater (JDMR) and dock (Reference 1), whereas Reference 2 was completely exposed to the channel currents. To remove the confounding effect of site differences unrelated to oyster bed construction from analysis, I conducted two-way ANOVAs between the impact and control sites only.

Although quarterly data were collected in light intensity and shoot density parameters, I only used summer values in analysis, to remove confounding effects of seasonal variation in the data.

I determined the effect of the constructed oyster bed on 1) light intensity, 2) eelgrass shoot density, 3) above-ground biomass, 4) below-ground biomass, 5) shoot biomass, 6) above- to below-ground biomass ratio, 7) leaf length, 8) leaf width, 9) epiphyte load and 10) epiphyte percent cover using separate 2-way ANOVAs on each response variable with site (impact or control), year (before construction, 1 and 2 years after construction) and their interaction as predictors. I considered a significant impact of the constructed oyster bed when I obtained a significant interaction of site and year from the ANOVA ($p < 0.05$), indicating a differential response between the impact and control sites over time. I then explored the interaction further by conducting separate one-way ANOVAs and Tukey’s HSD post-hoc tests within each site among years. Additionally, I compared means for each year separately between the impact and control sites using a 2-tailed t-test. Probabilities were adjusted (by the Bonferroni method) to compensate for multiple comparisons of the same means (Underwood 1994).

CHAPTER 3

RESULTS

Constructed Oyster Bed Impact on Light Intensity

Light intensity in each eelgrass bed varied similarly across seasons during the first year of restoration, with maximum values in Spring 2013 and lowest values in Fall and Winter 2012 (Fig. 3A). When I restricted analysis to the three summer time periods following oyster bed construction (Summer 2012, Summer 2013, and Summer 2014), the summer mean daily light intensity did not vary between the sites or years, or with the construction of the oyster bed (2-way ANOVA, Site: $p = 0.532$; Year: $p = 0.227$; Site × Year interaction: $p = 0.698$; Table 1; Fig. 3B).

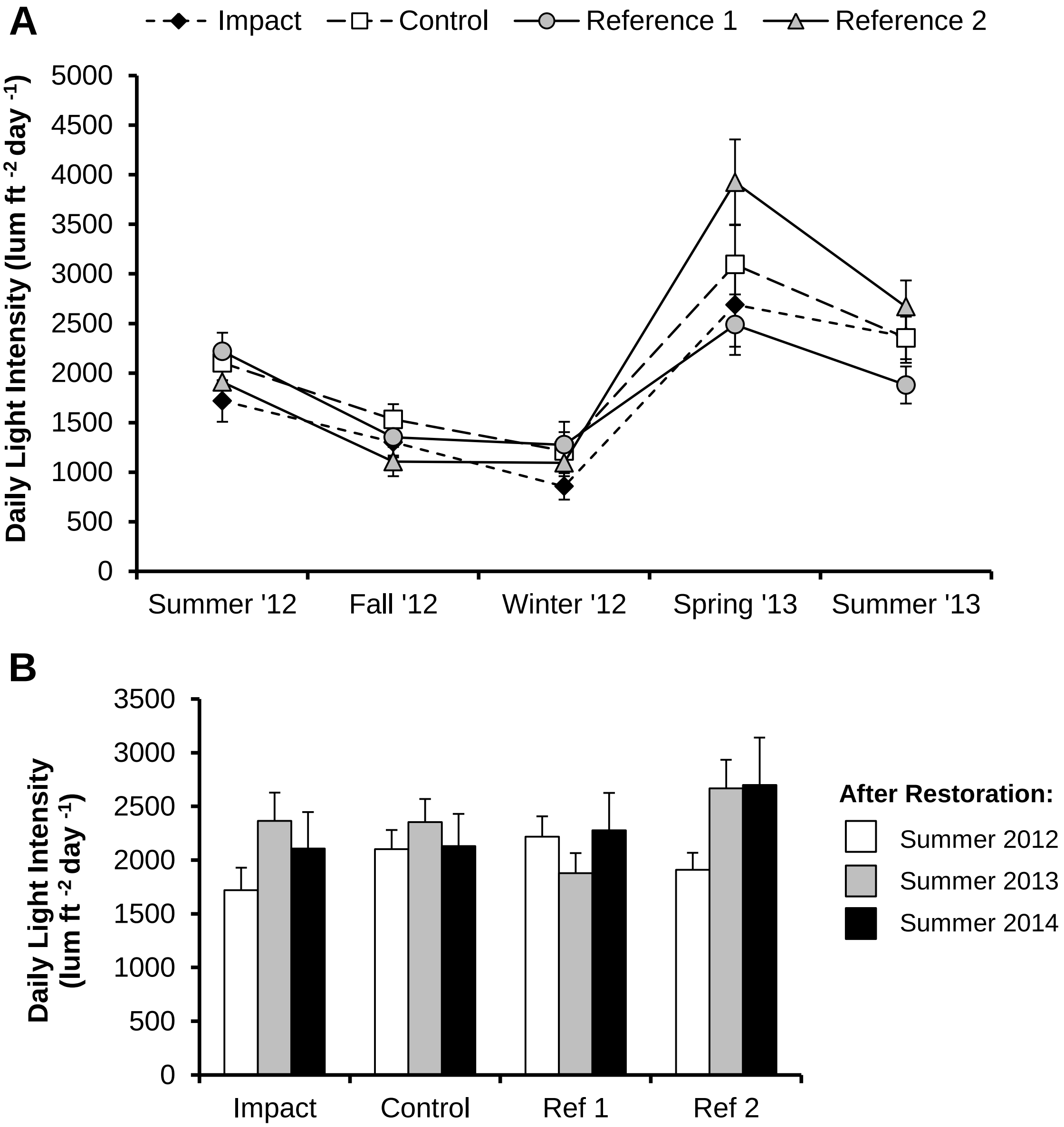


Figure 3. Mean daily light intensity (± SE) at each site A) each season during the first year following oyster bed construction prior to measurements in Summer 2012 (n = 10 days season^{-1} site^{-1}) and B) each summer following oyster bed construction (n = 10 days season^{-1} site^{-1}). Reference eelgrass beds, while not included in analysis, are included for comparison. Reference eelgrass beds are denoted with a solid line; impact and control eelgrass beds within JDMR denoted with dashed lines.

Table 1. Test statistics from ANOVAs examining the effects of oyster bed treatment and time on each measured response variable. *P* values < 0.05 are shown in bold.

	Df	SS	F	*P*
Light				
Site	1	261237	0.40	0.5320
Year	2	2017425	1.53	0.2270
Site × Year	2	479120	0.36	0.6980
Error	54	35707608		
Shoot Density				
Site	1	106364	10.98	**0.0012**
Year	2	32173	1.66	0.1948
Site × Year	2	27957	1.44	0.2407
Error	113	1095133		
Above-ground biomass				
Site	1	0	0.00	0.9952
Year	2	17916	6.34	**0.0062**
Site × Year	2	396	0.14	0.8700
Error	24	33907		
Below-ground biomass				
Site	1	80	0.52	0.4767
Year	2	204	0.66	0.5249
Site × Year	2	1280	4.13	**0.0243**
Error	36	5583		
Shoot Biomass				
Site	1	0.002	0.86	0.3628
Year	2	0.025	5.45	**0.0112**
Site × Year	2	0.532	11.42	**0.0003**
Error	24	0.056		
Above:Below-ground biomass***ǂ**				
Site	1	1.769	4.43	0.0514
Year	1	5.011	12.55	**0.0027**
Site × Year	1	0.000	0.00	0.9730
Error	16	6.387		

Maximum leaf length				
Site	1	82.200	1.40	0.2450
Year	2	2689.200	22.88	**< 0.0001**
Site × Year	2	499.600	4.25	**0.0220**
Error	36	2116.000		
Leaf Width				
Site	1	0.019	0.14	0.7113
Year	2	2.570	9.23	**0.0006**
Site × Year	2	2.097	7.53	**0.0019**
Error	36	5.015		
Epiphyte Percent Cover*				
Site	1	1.226	4.38	**0.0436**
Year	2	9.566	17.07	**< 0.0001**
Site × Year	2	1.519	2.71	0.0801
Error	36	10.088		
Epiphyte Load*				
Site	1	0.673	0.90	0.3520
Year	2	10.118	12.55	**0.0001**
Site × Year	2	0.308	0.41	0.6671
Error	24	0.747		

* Data log-transformed

ǂ Only 2013 and 2014 used in ANOVA due to sampling error in 2012

Table 2. Test statistics from one-way ANOVAs and Tukey's HSD tests for measures with a significant Site × Year interaction, for differences among years within each site. *P* values < 0.05 shown in bold.

	df	F	*P*	Tukey's HSD
Below-ground biomass				
Impact	2, 18	9.50	**0.0015**	2012 > 2013 = 2014
Control	2, 18	0.81	0.4600	2012 = 2013 = 2014
Shoot biomass				
Impact	2, 12	5.86	**0.0168**	2013 > 2012 = 2014
Control	2, 12	10.27	**0.0025**	2012 > 2013 = 2014
Maximum leaf length				
Impact	2, 18	4.27	**0.0305**	2012 = 2013 > 2014
Control	2, 18	27.16	**< 0.0001**	2012 > 2013 > 2014
Leaf width				
Impact	2, 18	6.22	**0.0089**	2013 > 2012 = 2014
Control	2, 18	9.99	**0.0012**	2012 > 2014

Before construction: 2012; after construction: 2013, 2014

Table 3. Test statistics from post-hoc 2-tailed t-tests between sites for each year on measures with a significant Site × Year interaction.

	2012	2013	2014
Below-ground Biomass	ns	ns	ns
Shoot biomass	C > I	ns	ns
Maximum leaf length	C > I	ns	ns
Leaf width	C > I	ns	ns

Before construction: 2012; after construction: 2013, 2014

I = impact, C = control; ns = no significant difference between means at p = 0.01 (p = 0.05 Bonferroni adjustment for multiple comparison of 5 means)

Eelgrass Response to Constructed Oyster Bed

Shoot Density

Eelgrass shoot density varied greatly between all locations and seasons, including a population collapse of Reference 2 within 6 months of study initiation (Fig. 4A). Restricting analysis to the three summer periods before and after oyster bed construction (June 2012, June 2013, and June 2014), I found that the shoot density was higher in the control site than in the impact site, however this effect had no relation to time and there was no interaction effect (2-way ANOVA, Site: $p = 0.001$, Year: $p = 0.195$, Site × Year interaction: $p = 0.241$, Table 1, Fig. 4B).

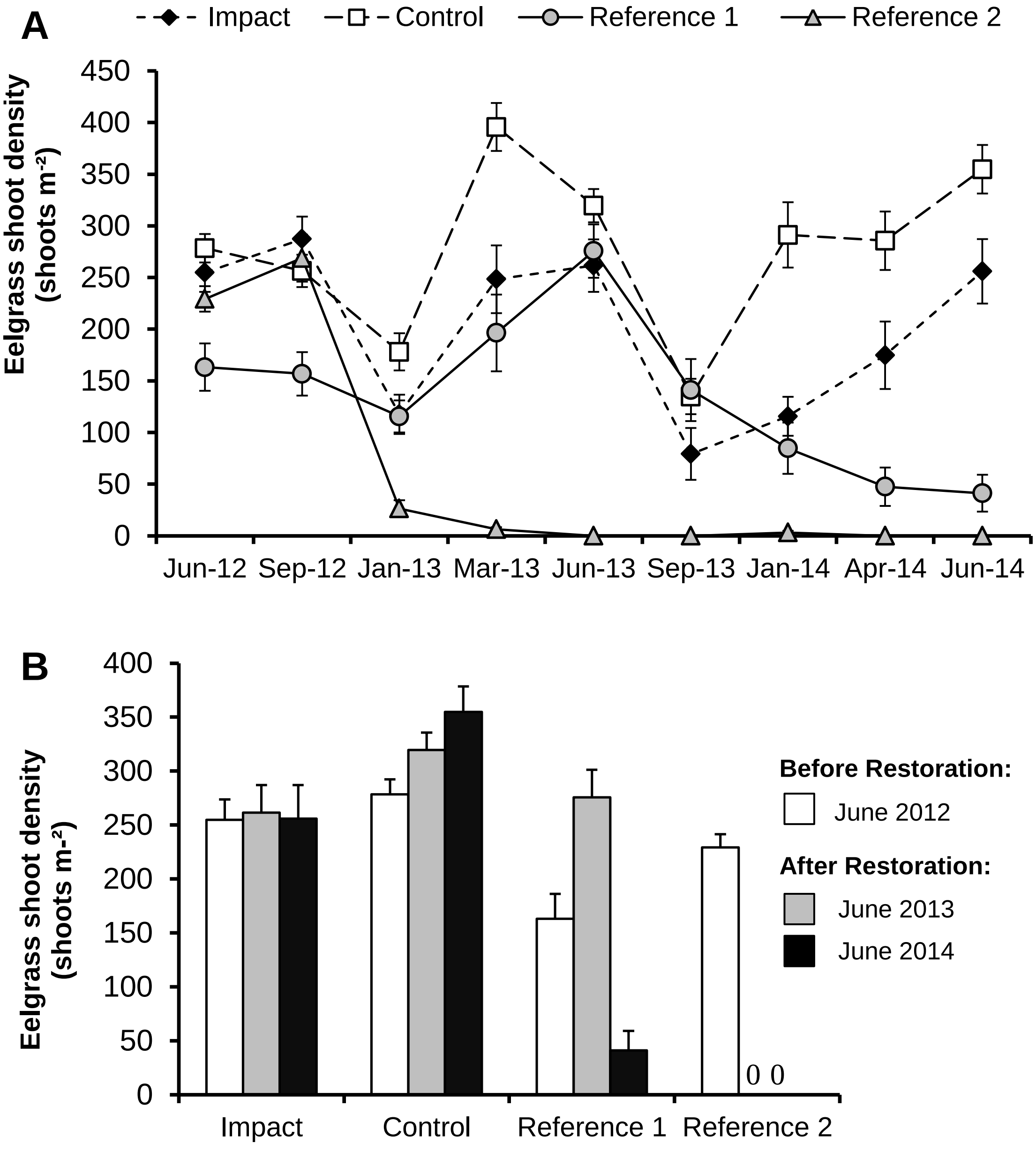


Figure 4. Mean eelgrass shoot density (± SE) before and after oyster shell beds were added after June 2012 and June 2013 eelgrass surveys. Reference eelgrass beds, while not included in analysis, are included for comparison. A) Seasonal monitoring, n = 20 per site per year. Reference eelgrass beds denoted with a solid line; impact and control eelgrass beds within JDMR denoted with dashed lines. B) June counts used in analysis, n = 20 per site per year.

Biomass

Above-ground biomass remained stable at both the impact and control sites after one year, but declined at both sites two years after oyster bed construction (2-way ANOVA, Year: $p = 0.006$, Site: $p = 0.995$, Site × Year interaction: $p = 0.867$, Table 1, Fig. 5A).

However, individual shoot biomass in the impact bed, responded differently than the control bed after oyster bed construction (2-way ANOVA, Site × Year interaction: $p = 0.0003$; Table 1, Fig. 5B), with shoot biomass increasing by 78% in the impact bed one year after oyster bed construction, but returning back to pre-construction levels after 2 years (Tukey's HSD, $p < 0.05$; Table 2). In the control bed however, I observed a 42% decline in shoot biomass one year after the oyster bed was added, with shoot biomass stabilizing thereafter (Tukey's HSD, $p < 0.05$; Table 2). Further post-hoc comparisons of the impact and control bed during each year revealed that starting shoot biomasses were approximately two times higher in the control bed, but did not significantly differ between the sites after construction (Bonferroni-corrected t-tests, $p < 0.05$; Table 3).

Below-ground biomass declined in the impact site after construction of the oyster bed, but not in the control site (2-way ANOVA, Site × Year interaction: $p = 0.024$; Table 1, Fig. 5C). While below-ground biomass in the control site did not significantly change over time (Tukey's HSD $p > 0.05$, Table 2), below-ground biomass in the impact bed declined by 54 % in the first year after construction, and remained 38 % lower two years after construction compared to pre-construction levels (Tukey’s HSD $p < 0.05$; Table 2). Despite this decline within the impact bed over time, below-ground biomass values in the impact bed were never significantly lower than values observed in the control site (Bonferroni-corrected t-tests, $p < 0.05$; Table 3).

Due to sampling errors, June 2012 above- to below-ground biomass ratios could only be calculated as the ratio of the mean above-ground value to the mean below-ground value (i.e., with no replication). However, comparisons of pre- and post-restoration values in each site reveal slightly different trends. In the impact bed, the average above- to below-ground biomass ratio increased to nearly 3 times the pre-restoration ratio after the first year of construction; this was not observed in the control site. This increase one year after construction in the impact site and decline in the control site mirrors the responses seen in the shoot biomass data as well. However, when I analyzed the post-construction data only, due to the sampling errors noted above, the above- to below-ground ratios in the control and impact sites both showed a similar decline 2 years after restoration, but did not differ from each other (Year: $p = 0.003$, Site: 0.051, Site × Year interaction: $p = 0.973$; Table 1; Fig. 5D).

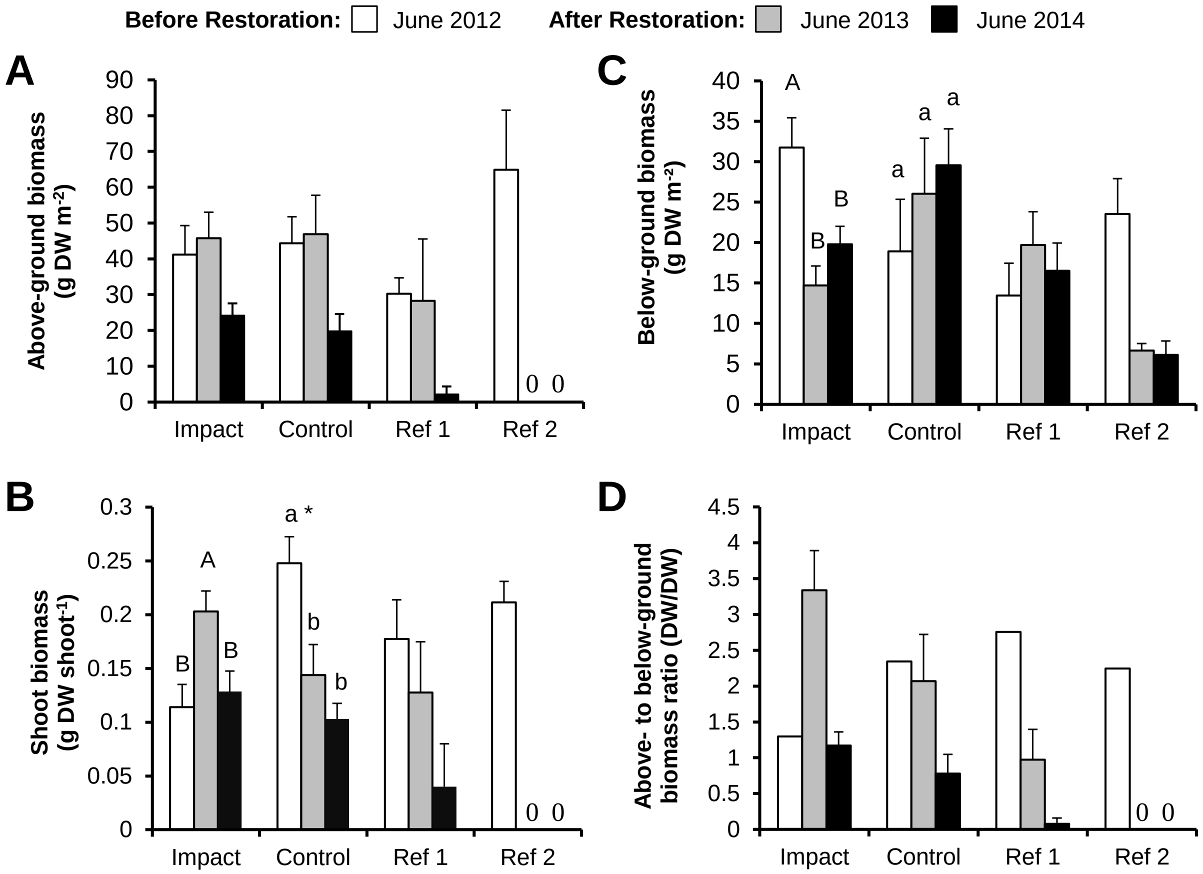


Figure 5. Mean eelgrass biomass (+SE) over time. A) Above-ground biomass, n = 5; B) shoot biomass, n = 5; C) below-ground biomass, n = 7; D) above- to below-ground biomass ratio. Reference beds were not included in analysis, but are shown for comparison. Differing letters show significant differences within each site over time (impact site = upper case; control site = lower case) (Tukey's HSD $p < 0.05$), * shows significant differences between the 2 sites within each year (Bonferroni-corrected t-tests $p < 0.05$).

Leaf Morphometrics

Eelgrass leaf morphometrics in the impact bed responded differently than the control bed to oyster bed construction (2-way ANOVA, Site × Year interaction: length $p = 0.022$; width $p = 0.002$, Table 1, Figs. 6A, B). Leaf length in the control bed declined by 28 % the first year after construction and by 53 % two years after construction of the oyster bed, whereas the leaf length in the impact bed did not decline until 2 years after construction (30 % decline) (Tukey's HSD, $p < 0.05$; Table 2; Fig. 6A). Leaf width in the impact bed increased by 17 % one year after oyster bed construction, but returned back to preconstruction levels after 2 years (Tukey HSD $p < 0.05$; Table 2), whereas the control bed declined 11 % the first year after construction and was 25 % lower by 2 years after construction (Tukey HSD $p < 0.05$; Table 2; Fig. 6B). Although both leaf length and width were initially higher in the control bed relative the impact bed, leaf length and width did not differ between sites in the years following construction (Bonferroni-corrected t-tests, $p < 0.05$; Table 3). This temporary increase in width in only the impact bed after the first year of restoration mirrors trends observed in both shoot biomass and the above- to below-ground biomass ratio.

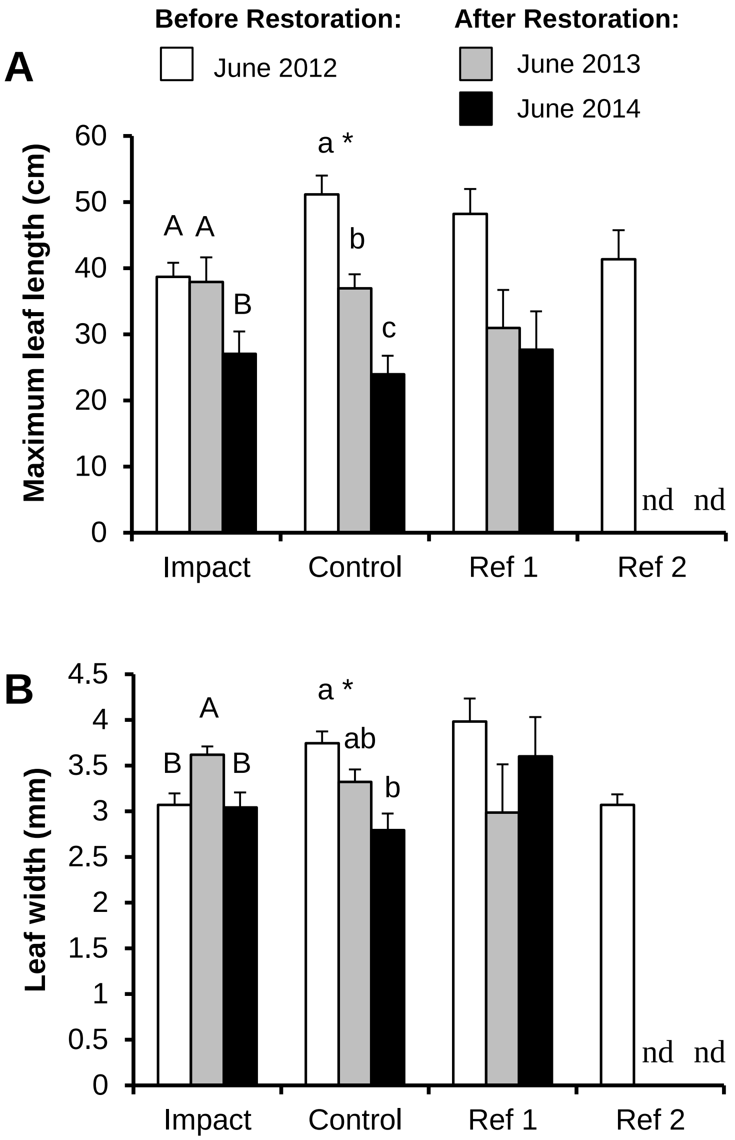


Figure 6. Mean leaf morphometrics (+SE) before, 1 year after and 2 years after oyster bed construction. A) Maximum leaf length, n = 4 – 7 samples; B) leaf width, n = 4 – 7 samples; Reference eelgrass beds were not included in analysis, but are included here for comparison. Differing letters show significant differences within each site over time (impact site = upper case; control site = lower case) (Tukey’s HSD $p < 0.05$), * shows significant differences between the 2 sites within each year (Bonferroni-corrected t-tests $p < 0.05$).

Eelgrass Epiphyte Response to Oyster Bed Construction

Eelgrass epiphyte load was highest the first year after construction in both the impact and control sites, but did not differ between the sites or show a significant interaction (2-way ANOVA, Year: $p = 0.0001$, Site: $p = 0.35$, Site × Year interaction: $p = 0.67$; Table 1; Fig. 7A). Similar trends were observed in the epiphyte load as the epiphyte percent cover. Eelgrass epiphyte percent cover was highest one year after construction and differed between the impact and control sites, but there was no interaction (2-way ANOVA, Year: $p < 0.0001$, Site: $p = 0.04$, Site × Year interaction: $p = 0.08$; Table 1; Fig. 7B).

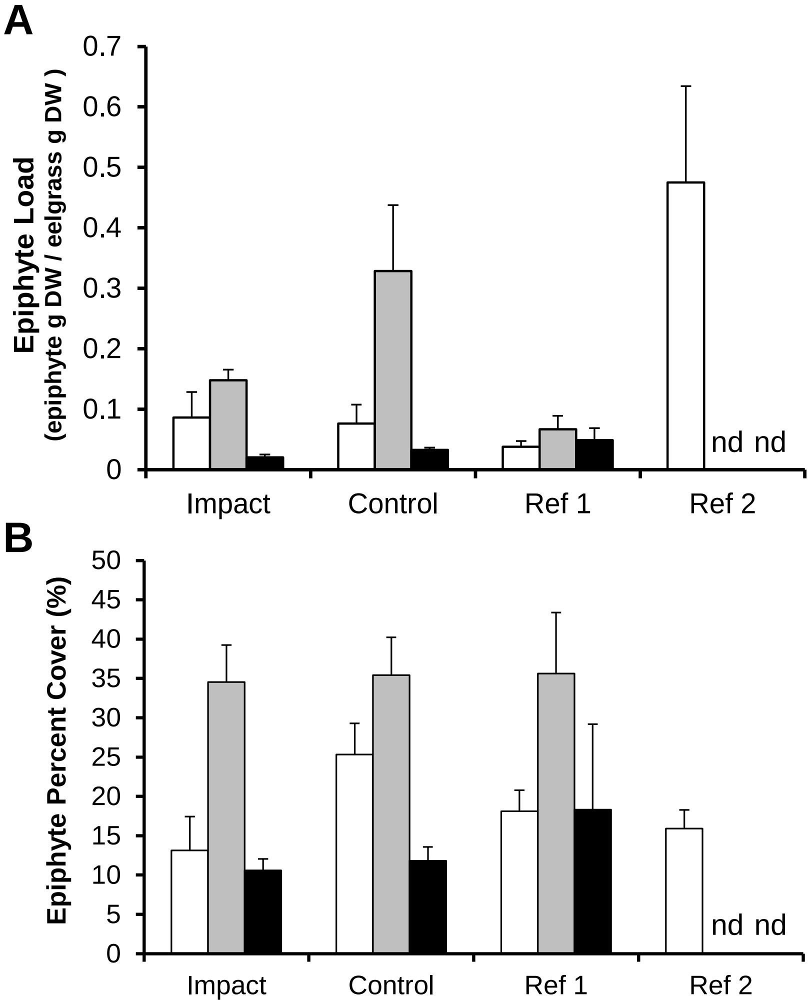


Figure 7. Mean (+SE) epiphyte load (A) and percent cover (B) in each site over time. Reference eelgrass beds were not included in analysis, but are included here for comparison. nd = No Data.

CHAPTER 4

DISCUSSION

Although I did not observe any impact of the constructed oyster bed on light intensity, I did detect significant differences in below-ground biomass and above-ground plant morphology between the eelgrass adjacent to the constructed oyster bed and the control eelgrass bed. These impacts diminished by the second year after construction, when oysters had recruited in the highest densities to the shell bed (300 - 400 individuals m^{-2}, Fuentes et al., CSU Fullerton, unpublished data). In contrast, eelgrass shoot density, total above-ground biomass, epiphyte load and epiphyte percent cover were not significantly impacted by the constructed oyster bed, even during the first year following construction.

Below-ground biomass in the impact bed declined after oyster bed construction, declining 54% one year after construction, with a slight recovery to 38% below pre-construction levels by 2 years after construction. Trends for below-ground biomass reductions did not translate into lower above-ground biomass. Total above-ground biomass was not significantly different between the two beds over time. However, shoot biomass and leaf width increased one year after construction in the impact bed. Mean shoot biomass (g DW $shoot^{-1}$) in the impact bed significantly increased one year after construction, whereas in the control bed there was a significant decrease. Leaf widths followed the same pattern with an increase after the first year of construction, which was not shared by the control bed. This trend is similar to the above- to below-ground biomass ratio, which shows evidence of an increase in the first year after construction in the impact bed, a pattern not shared by the control bed. In leaf width, shoot biomass and the above- to below-ground biomass ratio, values returned to pre-construction levels 2 years after construction, suggesting that the impact was temporary, likely caused by oyster bed construction. I am unable to tease apart whether this increase in width and shoot biomass is due to an alteration in individual plant growth or due to a shift towards a greater proportion of older and more mature shoots. The latter may be supported by lower below-ground biomass occurring at the same time in the impact bed, as new shoots are added asexually when the below-ground rhizome elongates. A shift to larger, older shoots with fewer new shoots may be symptomatic of the concurrent decline in below-ground biomass. Regardless of the cause, there was a shift in the mean leaf width and shoot biomass in the impact bed one year after construction, which is indicative of an impact.

I can hypothesize several potential mechanisms causing these impacts to the below-ground biomass and plant morphology. First, there is the potential that the construction of the oyster bed caused a temporary increase in turbidity and degraded finer-scale light conditions (too fine-scale to be detected by my light meters) within the first year of construction in the impact eelgrass bed. The light values detected in my study were not significantly different between the impact and control sites over time, but may not have captured finer-scale changes in the light condition caused by the oyster bed for several reasons. Since light was only measured at one location at each site, which, in the impact eelgrass bed, happened to be the edge farthest away from the constructed oyster bed, these light values may not reflect changes experienced in other parts of the eelgrass bed, particularly the portion of the impact eelgrass bed closest to the oyster bed. In addition, pulsed increases in turbidity not detected in mean light values or not occurring during the days monitored may greatly affect eelgrass (Zimmerman et al. 1991, Moore et al. 1997).

A large proportion of below-ground tissue becomes burdensome during times of low light, when meeting oxygen and photosynthate requirements of the roots and rhizome through photosynthesis in the above-ground leaves becomes even more strained (Hemminga 1998). Short-term reductions in light conditions resulting from construction of the oyster bed may have prevented plants in the impact bed from overcoming larger respiration costs of the large amount of below-ground biomass present before restoration. Perhaps as a result, a decline of below-ground biomass was observed following construction. Declines in below-ground biomass in reduced light conditions have been observed previously in *Zostera marina* (Biber et al. 2009); however declines in below-ground biomass are usually paired with declines in above-ground biomass as well, which were not observed in this study.

To adapt to declines in light, many *Zostera* species may alter plant size and increase allocation to photosynthetic tissues (above-ground biomass) to maximize light interception to support respiration demands of the below-ground biomass (Moore and Short 2006). In this study, I observed increases in leaf width, shoot biomass and above- to below-ground biomass allocation in the first year of the study that might support such a shift. Increasing above- to below-ground biomass ratios is a pattern observed in *Zostera* species with increasing depth, largely driven by declines in light (McKenzie 1994, Peralta et al 2002, Sultana and Komatsu 2002, Brun et al. 2003). Alterations in leaf size in response to light conditions, however, have been inconsistent among seagrass species (Ralph et al. 2007). Increases in leaf width with declines in light, have been found in *Posionia* to maximize light absorption (Via et al.1998). In contrast, the reverse response of decreased width with decreasing light has also been observed, likely to reduce respiratory demand of the leaves under low light conditions (Lee and Dunton 1997). Therefore using leaf width alone to infer light conditions may be problematic, as a universal response to decreased light in leaf width is unclear. In fact, Ochieng et al. (2010) found that *Zostera marina* leaf width increased logarithmically with increasing light, suggesting that the short-term shifts in leaf width in my study may not represent a response to decreased light.

A second potential mechanism causing these morphological changes could be tied to alterations of sediment characteristics, and subsequently the nutrient pool, caused by the construction of the oyster bed. Through the addition of a large shell bed on the mudflat, sediment characteristics may have been altered as the bed increased sedimentation of small nutrient rich sediment particles in the impact eelgrass bed. Nutrient-enriched mud substrata have been shown to contain seagrass meadows with fewer shoots, wider leaves and greater shoot biomass (Short 1983). Sediment samples collected in the impact and control eelgrass beds in 2013 found that sediment in the impact eelgrass bed showed a lower percentage of sand and a trend for increased organic material compared to the control eelgrass bed (Champieux and Whitcraft, CSU Long Beach, unpublished data). Nutrient enrichments caused by bivalve presence in seagrass beds have been experienced elsewhere and have led to increased leaf growth rate (Booth and Heck 2009, Reusch and Williams 1998, Peterson and Heck 2001a) and leaf length and width increases (Peterson and Heck 2001a). Increased nutrient content may have led to declines in the below-ground biomass either through a detrimental effect from sulfide accumulation (Terrados et al. 1999), which has been a hypothesized effect in other bivalve-seagrass impact studies (Booth and Heck 2009, Kelly and Volpe 2008), or a reduced need for absorptive surfaces as nutrient supplies were no longer limited (Short 1983). However, it is unclear why plant biomass and leaf widths returned to pre-restoration levels in the impact bed in 2014, when presumably nutrient enrichment would be the greatest, as oyster densities did not reach significant abundances until after June 2013.

Regardless of the potential mechanisms causing the impacts observed, overall eelgrass bed characteristics, such as shoot density and above-ground biomass, were not impacted by the oyster restoration project, with the exception of below-ground biomass. Although the below-ground biomass declined in the impact site after construction, impact below-ground biomass did not differ from control biomass after construction. Individual plant characteristics such as shoot biomass and leaf width, however, showed evidence of impact by the constructed oyster bed. These variations may highlight the ability of eelgrass to adapt to minor environmental changes, such as changes in light or nutrient availability, but still persist. The fact that these impacts to individual plant characteristics were seen only in the first year after oyster bed construction may suggest an impact caused by the construction phase rather than the recovery of the oysters themselves, as oyster densities were very low in the first year after construction. As oyster densities increased, this impact diminished, and, if studied over a longer time period, may have reversed. These results provide some evidence that the construction of an Olympia oyster restoration project does not cause a substantial or lasting impact to an existing eelgrass bed.

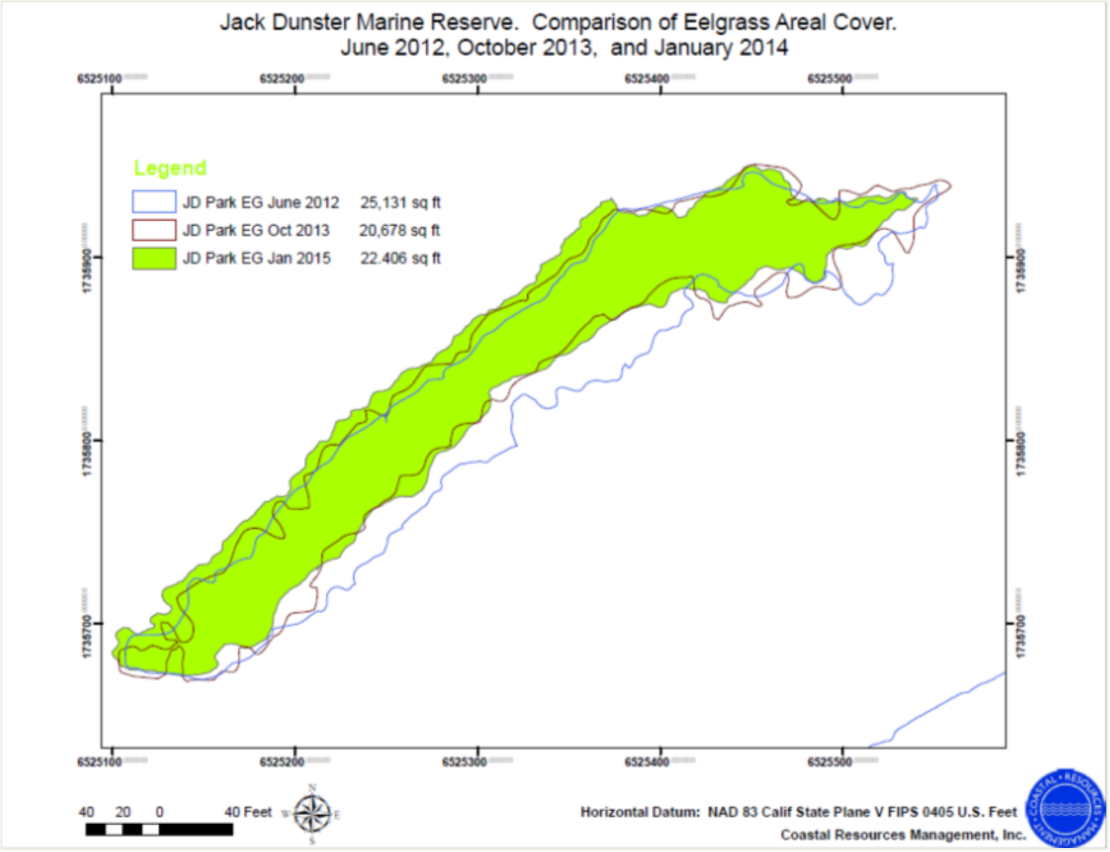
Because of a lack of impact to overall eelgrass above-ground meadow characteristics, it is difficult to classify this response to the constructed oyster bed as positive or negative. The minor impacts of oysters on eelgrass observed in our study may be a result of an already high flushing rate present at the restoration site. Because of the substantial intake of water by the Alamitos Generating Station, the residence time of Alamitos Bay has been estimated at only 1 day (IRC 1981). This low water residence time may not provide the oysters enough time to clear the water column and so may limit the oysters’ potential ability to improve water quality in Alamitos Bay. In addition, the potential impact of *Ostrea lurida* on water quality may be constrained by a lower filtration rate than other oyster species (zu Ermgassen et al. 2013), on which the benefits of oysters on water quality have been based. The separation between the species at different tidal heights may also dampen any potential impact. Prior studies typically assessed impacts by placing bivalves directly on top of seagrass beds (e.g. Peterson and Heck 2001a, 2001b, Archer 2008, Booth and Heck 2009), which is not a viable option for larger scale oyster restoration designs, nor is it representative of the distribution seen currently among remaining populations. Separating the two species at different tidal heights may limit the potential benefits that have been observed in prior studies, but it may also limit negative effects associated with higher densities of bivalves as well (Peterson and Heck 2001a, 2001b, Archer 2008, Booth and Heck 2009). The density of oysters on the shell bed after 2 years (300 - 400 individuals m^{-2}) was well above the densities previously documented to have negative effects when placed directly on seagrasses (150 individuals m^{-2}: Booth and Heck 2009). While separation may maximize densities of both species and minimize negative impacts, fewer benefits to the eelgrass may be returned.

As interest in native Olympia oyster restoration expands to areas near existing eelgrass beds, more research is necessary to better understand the interaction of *Ostrea* *lurida* and *Zostera marina* to improve restoration planning and return of larger ecosystem services. Exploring the impact of eelgrass on the Olympia oyster, which was not possible in this study, may also prove helpful to native oyster restoration planning and has only begun to be addressed by researchers (Boyer, San Francisco State University). In addition, the impact of the construction phase itself should also be considered, as we found evidence of a differential impact caused by the construction phase versus the oysters themselves. Determining the optimal arrangement of the two species that maximizes the benefits and minimizes negative impacts on each may be an important next step to inform the restoration and conservation of both species.

APPENDIX A

JDMR EELGRASS AREA

The total area of the eelgrass bed was measured by divers using GPS survey techniques in consultation with Rick Ware (Coastal Resources Management) prior to construction (June 2012) and after construction (October 2013, January 2015).



APPENDIX B

WATER TEMPERATURE

Table 1. Maximum daily water temperature ± SE collected from HOBO Loggers at each site in the summers of 2012, 2013 and 2014.

	Summer 2012 (°F)	Summer 2013 (°F)	Summer 2014 (°F)
Impact	70.88 ± 0.26	72.60 ± 0.22	73.80 ± 0.39
Control	70.76 ± 0.25	72.44 ± 0.20	73.50 ± 0.41
Ref 1	70.58 ± 0.27	72.43 ± 0.30	73.56 ± 0.30
Ref 2	70.91 ± 0.27	73.11 ± 0.24	73.98 ± 0.45

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