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Crassostrea gigas Invasion in Southern California: Macrofaunal Diversity and Local Community Impacts of Ecosystem Engineers on Estuarine Habitats

Noah Jansen-Yee

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Crassostrea gigas Invasion in Southern California: Macrofaunal Diversity and Local Community Impacts of Ecosystem Engineers on Estuarine Habitats

A thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science in Environmental and Ocean Sciences

By

Noah Jansen-Yee

Thesis Committee:

Jeff Crooks, Ph.D., Chair

Drew Talley, Ph.D.

Theresa Talley, Ph.D.

The Thesis of Noah Jansen-Yee is approved by:

Jeff Crooks, Ph.D., Chair

Drew Talley, Ph.D.,

Theresa Talley, Ph.D.

Dedication

To my late mother, whom I dedicate the body of this work and through the completion of this work I fulfill a final promise from a child to a parent.

Acknowledgments

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Abstract/Summary

Many marine ecosystems are facing the growing threat of biological invasions. These invasions can have a variety of different impacts on ecosystems and their inhabitants. The Pacific oyster, *Crassostrea gigas,* is currently in the relatively early stages of invasion in San Diego estuaries. *Crassostrea gigas* is a large, filter-feeding bivalve that forms dense oyster beds on hard substrate. These oysters are known to outcompete native counterparts and drastically alter habitats where they are present. *Crassostrea gigas* is an ecosystem engineer that, through shell creation and formation of a dense oyster matrix, impacts ecosystems in a variety of direct and indirect ways. However, the impacts of this ecosystem engineer at an early stage of invasion are not well-understood. To investigate the effects of *C. gigas* in a relatively recently-invaded site, this study examined the relationships between oyster beds and macrofaunal assemblages in Los Peñasquitos Lagoon, San Diego, California, USA. Mudflat areas with oyster beds had markedly higher total abundance, species richness, and biomass of resident macrofauna, with bivalves (not counting the oysters themselves), amphipods, and decapods tending to have higher densities and biomass in oyster beds. Interestingly, for the range of oyster beds examined here, there were minimal associations between the amount of actual shell material present and macrofaunal properties, suggesting that there may be a threshold associated with bed impacts. Overall, the findings of this study align with similar conclusions of other global studies in suggesting that *C. gigas* as invaders and ecosystem engineers have potentially large impacts on the biodiversity, and that this should be an important

consideration in considering management of this non-native bivalve and coastal ecosystems.

Chapter 1: Introduction

Biological invasions represent the arrival of a species into an area in which it did not exist in historical time. Although the movement of species to new habitats is a natural phenomenon, the breaking of natural geographic barriers, distance of species movements, and rates of invasions as propagated by human activity makes the current state of biological invasions distinctly different from natural species spreading (Carlton and Geller 1993, Crooks and Suarez 2006). For example, it is estimated that thousands of species are likely on the move at any point in time associated with ship traffic on the world's oceans (Carlton 1999). It has also been suggested that most countries have numbers of invasive species on the order of 10^2-10^4, and that this will only increase as time passes (Lodge 1993). A typical invasion can generally be characterized in to four distinct stages, and these generally include: transport, establishment, spread, and integration (Marchetti *et al*. 2004). Transport, or introduction, often occurs as a result of human activity and is characterized by the initial import of the non-native species. Successful invaders will then establish self-sustaining populations, spread geographically, and eventually become integrated as part of the ecosystem. Most studies tend to focus on these latter stages of invasion, when the invader is conspicuous and impacts evident (Kriticos et al. 2003, Crooks 2005).

Anthropogenic biological invasions represent a critical threat to coastlines and natural resources, with potentially widespread economic and ecological impacts (Pimentel et al. 2005). Understanding biological invasions in their full scale and scope can be very challenging and is always context-dependent; however understanding is critically important as these invasions may impact individual species, ecosystem functions, and habitat management. Furthermore, the role invasive species play in a recipient habitat is often complex. Invasive species do not necessarily replace potential native counterparts, but can play novel roles in ecosystems and make fundamental changes to habitats (Crooks 2002). These habitat modifiers, or ecosystem engineers, impact interactions within local communities and have effects that can cascade throughout the ecosystem (Levin and Crooks 2011). One such invasive species that is known to alter its recipient habitat in this manner is the Pacific oyster, *Crassostrea gigas* (Reusink et al. 2005, Padilla 2010). This invasive ecosystem engineer is currently at a relatively early stage of invasive in the estuarine waters of San Diego, California, USA (Crooks et al. 2015).

The Pacific oyster has been found forming small beds formations in the tidal channels of Los Peñasquitos Lagoon, San Diego. This study sought to examine the characteristics of the macrofaunal communities in Los Peñasquitos Lagoon in response to *C. gigas* beds. In addition, this study compared the allometric relationship of *C. gigas* found in Los Peñasquitos Lagoon to another recent study in the San Diego River estuary. The goal of this research is to provide the first assessment of the impact of *C. gigas* on local macrofauna, and in so doing provide a strong foundation to further research and inform management decisions being made for the health and integrity of San Diego estuaries.

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Chapter 2: Effects of *Crassostrea gigas* in Los Peñasquitos Lagoon

2.1 *Introduction*

2.1.1 Biological invasions

As concern for conservation and management of ecosystems grows, awareness of the many threats to ecosystems is a topic of increasing interest at many levels of society. Biological invasions are among the most important threats that need to be better understood and addressed. Biological invasions by non-native species have potentially huge ecological and economic impacts. Pimentel et al. (2005) estimated the total cost of invasive species to the United States to be roughly $120 billion per year, and considering the age of this study and the continual increase in biological invasions, this cost can only be expected to rise. Additionally, Ruiz et al. (2000) hypothesized that the rate of marine invasions is increasing over time. Invasive species, themselves, need to be understood to properly assess their impacts and the scope of their potential influence on habitats.

Though the consequences of invasions are not always entirely understood in their full scope and are context-dependent, understanding the impacts of invasions is extremely important. Biological invasions can have large-scale ecosystem impacts, leading to consequences for individual species, ecosystem function, and habitat management. Through competition, predation, and altering of food webs in recipient habitats, invasive species can deplete populations of native organisms, even to the point of local extinction. Invasive species do not always simply replace their native counterparts, but also can change habitats and interactions within local communities. The influence of these habitat-altering invasive species can have impacts that cascade through the ecosystem.

2.1.2 The Pacific Oyster - Crassostrea gigas

The Pacific oyster, *Crassostrea gigas*, is one of the most widespread invasive species globally. Although there has been a recent proposal to change the genus name to *Magallana*, this study retains the use of *Crassostrea*, due to lack of supportive evidence to elicit such a taxonomic change (Bayne et al., 2021). *Crassostrea gigas* occurs naturally in the western Pacific (~30-48°N, Troost 2010). A review of oyster invasions in 2005 (Ruesink et al., 2005) noted that of the 168 recorded introductions of oysters, *C. gigas* represents the most widely introduced species (66 introductions). Oysters are introduced most commonly through aquaculture, chosen for their economic value. These introductions became widespread in the 1950's, usually introduced to replace failing native oyster populations. Initially, intentional introductions of *C. gigas* were not seen as threatening, as it was thought that water temperature would be unsuitable for reproduction. However, it was soon found the oysters were able to reproduce and establish populations (Troost 2010). Outside of Asia, *C. gigas* represents much of oyster production, including European, African, and North American oyster markets (Ruesink 2005).

Intentional introduction of non-native oysters in California waters began as early at the 19th century. *Crassostrea gigas* was first introduced to California in the 1920's, followed by introductions in Newport Bay in the 1930's, the Salton Sea in the 1950's, and San Diego Bay and Catalina Island in the 1960's (Carlton

1979). *Crassostrea gigas* was again introduced into San Diego Bay the 1980's as juveniles to be used as bioindicators of toxic effects of tributytin (Smith et al. 1987). Despite these earlier introductions, self-sustaining populations of *C. gigas* did not become established until recently, representing a lag in the establishment phase of invasion (Crooks 2011, Crooks et al. 2015). This oyster is now seen in large numbers in San Diego waters and is believed to be in the early stages of an invasion.

Crassostrea gigas are bivalves that feed on planktonic organisms and detritus in the surrounding water. Compared to other species of oyster, particularly the west coast native oyster, *Ostrea lurida*, *C. gigas* is much more robust. Pacific oysters can grow over 250 mm in shell length, and maturity is reached when shell size reaches ~50 mm (Pauley et al. 1988, Troost 2010). Pacific oysters are oviparous and typically release gametes when waters start to warm in the spring and summer, which typically can be detected by decreases in tissue weight relative to shell weight (Langevin 2019). Oyster larvae settle on available hard substrate, even other oyster and bivalve shells. *Crassostrea gigas* have a broad temperature tolerance (5-25 °C, Troost 2010). The size of *C. gigas* also contributes to its ability to filter water at a much greater rate than most oysters, and Wilkie et al. (2013) found *C. gigas* to have a filtration rate nearly double that of its southeastern Australian native counterpart *Saccostrea glomerata*, (mean ± SE = 1.09±0.08 and 0.46±0.05 L/h, respectively). Planktonic organisms are filtered through the gills, bound in mucus, carried to the labial palps, and sorted for consumption or rejected (Pauley et al. 1988). Individual oysters can rapidly filter water, and oyster beds formed from many individuals (e.g., those formed by *C. virginica*) can alter water turbidity, sediment composition, nutrient cycling, and composition of planktonic organisms (Crooks 2009).

2.1.3 Habitat alteration and ecosystem engineering

The primary impacts of the Pacific oyster arise from its role as an ecosystem engineer. Ecosystem engineers affect other biota by altering the abiotic characteristics of their environment - they create, destroy or modify habitat. This habitat modification impacts resources and stressors in the environment, which then, in turn, impact other organisms (Crooks 2009). At its core, ecosystem engineering comprises two parts: alteration of abiotic aspects of the environment, and a subsequent response of other organisms to these alterations. Alteration of physical/chemical characteristics can be defined as autogenic or allogenic. Autogenic changes occur as a result of the engineer's physical body itself, whereas allogenic changes occur from the physical or chemical processes carried out by the engineering organism (Jones et al. 1994). Ecosystem engineers can be autogenic, allogenic, or both, as in the case of the Pacific oyster. Bivalves, such as *C. gigas*, autogenically change the habitat by the physical structure of their shells as individuals and by creation of oyster beds, which can change local water flow and provide new three-dimensional habitat. Allogenically, oysters suspension feed, which lowers turbidity and changes the geochemical environment (Crooks 2009).

Considering the potential impact of *Crassostrea gigas* as an invader and ecosystem engineer, it is important to understand the role this bivalve may play in an ecosystem in which it has newly established. One of the most critical factors to examine during an invasion by *C. gigas* is the impact these bivalves have on the community of local macrofauna, in terms of abundance, diversity, and composition. The importance of understanding the potential "rippling" impacts of *C. gigas* as an ecosystem engineer and invader are compounded when taking into context the various financial, recreational, and fishery value many coastal waters have.

Currently, *C. gigas* is at an early stage of invasion in the estuary waters of San Diego, California, USA. This study elucidates some of the impacts *C. gigas* has an ecosystem engineer on communities of macrofauna in the greater context of understanding their role as an invader in the Southern California lagoonal ecosystem, Los Peñasquitos Lagoon. It also compares allometric properties (length-weight relationships) of *C. gigas* in Los Peñasquitos Lagoon in 2015 to oysters sampled in a study by Langevin (2019) in the San Diego River estuary in 2016 and 2017.

2.2 *Methods*

2.2.1 Study site

The field sampling and observations of this study were conducted in the tidal channels of Los Peñasquitos Lagoon, San Diego, California, United States of America (32º55'52.165 N, 117º15'31.571 W). Sampling occurred at low tide during summer 2015 at 10 sampling locations at various points in the lagoon (Figure 2.1). Los Peñasquitos Lagoon is primarily characterized by sandy/silty substrate with minimal hard substrate, with extensive mid-marsh habitat characterized by pickleweed (*Salicornia pacifica*). *Crassostrea gigas* is typically associated with the limited hard substrate (rocks and pebbles) in the lagoon, and obvious "clumps" or beds of oysters were targeted for sampling.

2.2.2 Field sampling

Ten sampling locations were identified in the unvegetated intertidal, along channel banks. At each sampling location, a sample was taken comprised of the *C. gigas* matrix, including oyster shells (both living and dead), sediment, rocks, accumulated plant material, and associated biota (Figure 2.2). An adjacent control sample on bare sediment was taken, approximately 1-meter away from the oyster sample. Depth relative to water level at the time sampling, number of oysters, percent oyster cover, time, and latitude/longitude data were collected at each site (Appendix 4). Each sample was collected via a sediment core using a modified bucket (26.25cm diameter) to a depth of 10cm. All samples were sieved (1000 µm mesh) and all biotic material, including animals and detritus, was stored in 100% ethanol.

2.2.3 Laboratory analysis

Macrofauna samples were analyzed for biomass, abundance, and taxa richness. Organisms were counted and identified to the lowest recognizable taxonomic unit (RTU) possible. This method has been shown to be an effective tool for the analysis of invertebrate field samples when making estimates of biodiversity (Oliver and Beattie, 1993). In order to help place macroinvertebrates into the RTU's, field guides (e.g., McLean (1978) and Coan *et al* (2000)) and web-based resources were used. All remaining plant material present after sieving and sorting was kept and allowed to air dry in a fume hood for 24 hours, then weighed. Rinsed oysters from the samples were first stored in a freezer (approx. 0º C), after which their volume, shell length, total wet weight, shell-less wet weight, and shell-less dry weight were recorded. Displaced volume was measured by placing the entire intact oyster body into a volumetric flask of water of known volume and measuring the change. To dry the oyster bodies, the "wet" body was placed in a pocket of aluminum foil of known weight and then placed into a drying oven at approximately 60ºC for 24 hours (Schreck and Moyle, 1990).

2.2.4 Data analysis

To compare macrofaunal properties (abundance, taxa richness, biomass) in the presence and absence of *C. gigas* beds, Randomized Complete Block ANOVAs were used. In order to examine multiplicative rather than arithmetic effects, data were logarithmically-transformed prior to analyses, and back-transformed means and standard errors are presented. Total number of individuals (abundance), total biomass, taxa richness, and amount of plant material were assessed. When analyzing macrofaunal properties with and without oysters, *C. gigas* were not included as part of the data set. Although p-values are reported, recent guidance from the American Statistical Association suggests that no alpha value be set and assertions of significance and non-significance be avoided (Wasserstein et al. 2019).

To assess if macrofaunal in areas with oysters changed as a function of the amount of oyster shell in plots, total displacement of volume of oysters were compared to macrofaunal metrics on a plot-by-plot basis, using linear regression. Also, to evaluate allometric properties (shell length-dry weight) of *C. gigas* oysters themselves, characteristic of the *C. gigas* sampled in the San Diego River by Langevin (2019) were compared to *C. gigas* in Los Peñasquitos Lagoon. This was done using both linear regression modeling, and direct comparison of low-tidal *C. gigas* shell weight and shell-less dry-weight data for oysters sampled in Los Peñasquitos Lagoon in 2015 and oysters sampled in the San Diego River in 2016 and 2017. For the direct comparison of *C. gigas* low-tide data, condition indices (Mann and Glomb 1978), representing the ratio of dry flesh (x 1000) to shell weight were also calculated.

2.3 ***Results***

2.3.1 Overall trends in macrofaunal community

Benthic communities inside and outside of *C. gigas* beds were markedly different. Across the 10 sampling locations, a grand total of 2280 macrofaunal individuals and 26 taxa were counted across all samples, with 1386 individuals and 24 taxa in oyster bed locations and 894 individuals and 24 taxa in the controls (Appendix 1). Average abundance (back-transformed) in areas with oysters was over 50% higher than in areas without oysters (Figure 2.3), and there was also a distinct difference attributed to location (Randomized Complete Block ANOVA; Treatment P= 0.0568, Block P = 0.009). Average taxa richness of the macrofauna community, measured as a count of unique RTU, was also higher in oyster beds (Figure 2.3, Appendix 2), with 35% more taxa (P=0.0083). Again, there was also a block effect (P=0.0148). Average total biomass of the macrofauna community showed the greatest difference in areas with and without oysters (Figure 2.3, Appendix 2), and was 375% higher in the former (Treatment P=0.0026). For biomass, the block effect appeared modest (P=0.26). Also, there was approximately twice as much plant material that accrued due to the presence of the beds (Randomized Complete Block ANOVA: P= 0.0108) (Figure 2.3, Appendix 2).

2.3.2 Trends among groups of macrofauna

Among the differing taxonomic groups of macrofauna, trends in abundance, influenced by the presence or absence of the oyster beds, were observed (Figure 2.4, Appendices 1 and 2). The presence of *C. gigas* oyster beds were associated with an increase in the abundance in most taxa, including bivalves (not counting *C. gigas*), amphipods, and decapods (Randomized Complete Block ANOVAs: P= 0.02, 0.07, and 0.01, respectively) (Figure 2.4). Among the bivalves, the invasive Asian bivalves, *Musculista senhousia* and *Venerupis philippinarum* were 3.6 and 5.8 times more abundant in oyster beds compared to outside. The invasive Asian amphipod, *Grandidierella japonica,* was one of the most abundant of all organisms in the study, and it accounted for 652 of the 750 amphipods identified within the oyster samples and 353 of the 425 amphipods within the control samples (a 1.8-fold increase in the presence of oysters). The amphipods *Monocorophium acherusicum* (another invader), *Ampithoe pollex*, and *Elasmopus bampo* were all also at least twice as abundant in oyster beds. Across all taxa, the striped shore crab *Pachygrapsus crassipes* and yellow shore crab *Hemigrapsus oregonensis* showed the greatest relative differences, with 14-times and 8.6-times higher abundances (respectively) in the presence of oysters. Only four taxa showed higher abundances outside beds, including nemerteans (2.2-times more abundant) and the small gastropod *Acteocina* sp. (2.8-times more abundant)(Appendix 1).

Similarly, the presence of oyster beds showed pronounced trends influencing the biomass of bivalves, gastropods, and decapods (Randomized Complete Block ANOVA: P= 0.02, 0.06, and 0.02 respectively) (Fig. 2.5, Appendices 1 and 2). For large-bodied organisms, these tended to magnify differences seen in abundance. For example, the bivalves *M. senousia* and *V. philippinarum* had 4.9- and 5.9-times greater biomass with oysters, while the biomass of the crab *P. crassipes* was 75-times greater with oysters than without them. Biomass differences in gastropods were driven by the horn snail *Cerithideopsis calificornica*, mud snail *Nassarius tegula*, purple olive snail *Olivella biplicata*, and bubble snail *Bulla gouldiana* (ranging from 2.1- to 8.4-times more biomass with oysters).

2.3.3 Characteristics of oyster beds, and relationships to macrofaunal community

On average, plots with oysters contained 7.1 (±1.05) *C. gigas*, with an average shell length of 109.9mm (± 6.22). Although oysters were not included in the analyses of the macrofaunal communities with and without oysters, the characteristics of the beds in oyster plots in the form of shell displacement volume was analyzed to examine if characteristics of the individual beds influenced macrofaunal metrics (Fig. 2.6-2.8). Within oyster plots, there was an approximately fifteen-fold difference in the displacement volume of shells from the plots with the least amount of oyster material to the most (Fig 2.6-2.8, Appendix 4). Despite this, displacement volume correlated weakly with total abundance ($R^2 = 0.20$), taxa richness ($R^2 = 0.10$), and biomass ($R^2 = 0.03$).

2.3.4 *Comparison of allometric relationships of* Crassostrea gigas *in Los Peñasquitos Lagoon and the San Diego River Estuary*

Comparisons of *C. gigas* in Los Peñasquitos Lagoon to those in the San Diego River (Figure 2.9) reveal that the size range of oysters in Los Peñasquitos was larger than that in the San Diego River. However, a linear regression model of *C. gigas* shell-less dry weight and shell length showed that for a given size, oysters in Los Peñasquitos tended have lower tissue biomass than those over in the San Diego River. When considering the Condition Indices (representing the ratio of flesh weight (x 1000) to shell weight) for *C. gigas* samples taken all at low tide, there is noticeable variability in the shell to flesh ratio between the oysters found in the San Diego River found in 2016 with a mean Condition Index of 34.1 (±9.3), those found in the San Diego River in 2017 with a mean Condition Index of 45.1 (±8.6), and those found in Los Peñasquitos Lagoon in the summer of 2015 with a mean condition index of 16.2 (±2.0).

2.4 *Discussion*

2.4.1 Patterns of Crassostrea gigas *impact*

As an invader, *C. gigas* dramatically changes the ecosystem of intertidal mudflats of Los Peñasquitos Lagoon, San Diego. Oyster beds created by *C. gigas* add complex habitat that would otherwise not exist, as there is no analogous bed/reef-forming species that is native to this region (Crooks et al. 2015). The changes resulting from this have a variety of consequences, including increases in biomass, abundance, and taxonomic richness of resident macrofauna. Biomass showed the largest relative differences in areas with and without oysters, which also reflect differences in abundance (Fig. 2.3). Taxa richness showed lower relative differences, both at the plot scale (Fig. 2.3) but also comparing the total number of species found with oysters to the total number without (24 taxa in both cases). This may be tied to the early stage of invasion in San Diego estuaries, as it is possible that changes in the taxa composition of the macrofaunal community may incur a lag of sorts (Crooks 2011) and this pattern could change if oyster beds continue to expand, as they have in other invaded parts of the world.

Crassostrea gigas also has been found to alter the local communities of organisms in invaded ecosystems from across the globe (Table 2.1). In most cases, results elsewhere tend to align with what was found in Los Peñasquitos Lagoon, with increased abundances and species richness associated with oyster beds. For example, Lejart and Hily (2011) found *C. gigas* beds in the Bay of Brest, France, to increase species richness and abundance of macrofauna both within the bed and surrounding the bed. This effect was found in beds on both rock and mud substrate. Furthermore, the beds were found to change the relative abundance of each functional trophic group, though these effects are likely to vary between geographic location. Markert et al. (2009) compared changes in macrofauna in beds of *C. gigas* to those formed by the mussel *Mytilus edulis* in the Wadden Sea of Lower Saxony, southern German Bight, in which the non-native *C. gigas* has been invading since 1998, and found higher values for species richness, abundance, biomass, and diversity in beds composed of *C. gigas*. The oyster beds studied showed increases in anthozoans, sessile suspension feeders, epibionts, epibenthic predators (such as crabs), and, most of all, infauna. This was attributed to the increased habitat complexity and available hard substrate created by the oysters. Several studies have compared the benthic communities found associated with native bivalves to those with the non-native *C. gigas*, and found there to be little evidence to suggest differences in relative impact (Norling *et al*. 2015, Zwerschke *et al* 2016).

Beyond sampling of natural populations, manipulated beds of oysters have also been shown to be a useful tool to investigate the effects of oysters as ecosystem engineers. Experimentally-placed *C. virginica* oyster beds have been used to demonstrate the effect of beds on hydrodynamics, as refuge from environmental stress, and how degradation of beds impacts communities of invertebrates and fish (Lenihan and Peterson 1998, Lenihan 1999, Lenihan et al. 2001). Lenihan and Peterson (1998) also demonstrated the use of coupling an artificial bivalve bed with sampling of naturally occurring beds to investigate the effects of bivalves as ecosystem engineers. Wilkie et al. (2013) used artificial arrangements of *C. gigas* and found that density and arrangement of these oysters influenced settlement of the native oyster *Saccostrea glomerata*. Artificial *C. gigas* beds have also been utilized to demonstrate how the added habitat complexity of beds can influence the trophic interactions between oysters, toadfish, and mud crabs (Grabowski 2004). Importantly, Norling *et al* (2015)'s experimental study used both live and post-mortem shells and found comparable patterns, suggesting a prominent role of the presence of physical structure itself.

2.4.2 Mechanisms of oyster impact

A wide variety of different drivers (e.g., provision of refugia, amelioration of environmental conditions, and behavioral attraction to structure) can lead to increases in abundance and richness typically associated with habitat-forming engineers (Crooks, 2002). However, since these mechanisms often operate simultaneously, it can be difficult to tease apart the relative importance of each (Levin and Crooks 2011, Crooks et al. 2016). Nonetheless, it is possible to identify a broad suite of mechanisms likely to be important in shaping faunal communities associated with *C. gigas* beds in Los Peñasquitos Lagoon. These include creation of living space through structure (shell) creation, alteration of hydrodynamic conditions, and biofiltration / biodeposition (Crooks 2009).

Arguably the most important engineering effect of oyster beds is the use of the structure as living space for other organisms. At low tide especially, the bed can provide shelter from physical stressors like heat and desiccation, which can be important factors in many tidal areas where organisms must deal with large changes in temperature and moisture (Gutierrez et al. 2003, Troost 2010). The structure of the beds also provides refuge from predation. This allows prey to escape predators like birds or fishes, which are less able to access prey. The shells of the bivalve beds provide physical refuge both in empty (dead) shell cavities and between shells within interstitial space (Gutierrez et al. 2003), and dead shells can have many of the same effects as living oysters (Norling et al. 2015). The habitat complexity created by the oyster bed structure has been shown to disrupt predator-prey interactions, by providing prey with physical refuge (Grabowski 2004). In Los Peñasquitos Lagoon, shore crabs were more abundant within the areas located in and around the oyster beds, and this group is well-known for its positive responses to large structure on tidal flats (e.g., Markert et al. 2009). It is important to note that although structure may often be used by an organism in response to particular stimulus, such as threat of predation, the use of complex structure and its association with higher animal abundances is not necessarily tied to the nature of the physical structure itself, nor does it require an immediate driver, such as the presence of a predator (Crooks *et al*. 2016).

Formation of relatively high-relief structure on tidal flats and its interaction with the hydrodynamic environment is another important aspect of *C. gigas* as an ecosystem engineer. Oyster beds alter the flow of water near the surface of the bed in a manner that causes water to flow over the bed rather than through it at high oyster densities (i.e., skimming flow, Nowell and Jumars 1984, Gutierrez et al. 2003). The complex structure of the bed can also serve to catch materials within it. This study found that a greater amount of plant material accrued within the oyster bed samples than the control samples (Fig 2.3), likely related to the presence of physical structure and changing patterns of flow associated with oyster beds in Los Peñasquitos Lagoon .

Shell height, density, and abundance can determine the size and structure of the oyster beds, which in turn can have been shown to be an important factor for altering hydrodynamics near *C. virginica* beds (Lenihan 1999). In Los Peñasquitos Lagoon, the weak linear regressions between displacement volume and macrofaunal community metrics (Figs. 2.6 – 2.8) indicate that for the range of beds sampled here, amount of material was relatively unimportant. Given the clear differences between areas with and without oysters (Fig 2.3), however, it is likely that there is a threshold below which amount of material will make a difference, and above which it might have little effect. More research is needed on this topic to fully understand relationships between *C. gigas* bed characteristics and macrofaunal responses.

Crassostrea gigas impacts the water column through filtration, especially when in dense beds. Oysters remove particulates from the water column by filtering the water, and increase sedimentation by biodeposition and disrupting flow. The additional sediments in the benthos from deposition by the oysters during filtration and sediment catching in the beds means that there is more sediment available to benefit organisms favoring sediments (Crooks and Khim 1999, Gutierrez et al. 2003, Crooks 2009, Troost 2010). Biodeposition by oysters also creates a greater flux of nutrients in the form of organic matter into the sediments, altering availability in a direct manner (Lu and Grant 2008). This accumulation of material within oyster beds (including plant material) could help explain the increased abundance of surface feeders such as amphipods, such as was seen with mats of the smaller invasive mussel *M. senhousia* in nearby Mission Bay (Crooks, 1998; Crooks and Khim 1999).

One potentially negative consequence of filtration is the impact on organisms with planktonic larvae trying to settle in *C. gigas* beds. However, increased abundances of bivalves with planktonic larval stages, such as *M. senhousia* and *V. phillipinarum* within the Los Peñasquitos beds suggests that organisms with these larval modes still benefit from oyster beds. Similar lack of inhibition of planktonic developers was seen for *M. senhousia* mats in Mission Bay (Crooks 1998, Crooks and Khim 1999).

2.4.3 Crassostrea gigas *in San Diego* waters

This research on the impacts of the *C. gigas* invasion in Los Peñasquitos Lagoon is critical considering the far-reaching implications which may be brought on by the Pacific oyster, but to date there has been relatively little ecological work on *C. gigas* in the estuaries of San Diego. In 2021, Burge *et al*. documented the detection of a novel osHV-1 Ostreid herpesvirus microvariant in juvenile *C. gigas* found within a shellfish aquaculture nursery system in San Diego, California. Additionally, two studies were recently conducted that investigated the possible implications of *C. gigas* and chemical contaminant concentrations as they relate to risk assessment and consumption in San Diego Bay (Nguyen, 2019, Talley et al. 2021). This study found no significant associations between the oysters and mercury as it relates to risk and consumption, but there are many implications which *C. gigas'* invasion could have for human health in the Southern California area.

One notable pattern that has been documented, however, is the tendency of the native oyster, *O. lurida*, to grow lower in the intertidal than the invasive *C. gigas* (Tronske et al. 2018, Langevin, 2019). Langevin (2019) also examined growth rates and allometric relationships of *C. gigas* at different tidal levels in the San Diego River Estuary. When compared to *C. gigas* sampled in the San Diego River, Los Peñasquitos oysters demonstrate noticeable differences, based upon the regressions shell length to tissue weight and the comparisons of the low-tide Condition Indices. The oysters sampled in Los Peñasquitos had a tighter regression fit of shell-less dry weight vs shell length, likely indicative of the fact that the samples taken from the San Diego River were taken at a variety of tidal heights over the course of several seasons. The San Diego River oysters showed peak in the slope of the regression lines and Condition Indices in the spring, and lower values in the summer, likely related to pre- and post-spawning conditions (Langevin 2019). Oysters from Los Peñasquitos Lagoon came from the summer before these other samples were taken, and had a much lower ratio of flesh to shell weight compared to their San Diego River counterparts. This was true even for summer samples, although it remains unclear whether samples collected during the same time period would have produced similar results. Further study would be necessary to determine the relative importance of spatial and temporal factors in affecting oyster condition.

2.4.4 Significance and implications

Despite the potentially “positive” trends found in this study and others, the domino effect of impacts – where positive effects cascade throughout the ecosystems - is not necessarily so cut and dry. For example, this study was able to show the pronounced impact the presence of *C. gigas* beds had on the abundance and biomass of groups such as bivalves, gastropods, and decapods. These organisms may be showing increases in abundance and biomass due to the added habitat complexity created by the oyster beds that would otherwise not be present. This habitat has the potential to protect from desiccation and other environmental effects, but it also may be protecting from predation, which could potentially have negative effects further up the food chain (Crooks 2002).

This study also represented a unique opportunity to look at the early stages (establishment) of an invasion, which may provide valuable information for management decisions. In most cases, biological invasions are not studied until later stages when the species becomes prevalent enough to be widely conspicuous. Capitalizing on this opportunity to study this invasion during its early stages has provided insights on this biological invasion, and could be especially important to local ecosystem management. For example, there is currently an initiative in San Diego Bay to create “living” shorelines by placing structure on the mudflats to recruit native oysters. These structures are to be made of a mixture of concrete, local sand, and shell aggregate. The responses observed in Los Peñasquitos Lagoon suggests that the local macrofaunal community in San Diego Bay associated with these novel structures may experience changes in abundance, biomass, and taxa richness within a relatively short period of time.

The changes induced by *C. gigas* could have important consequences on ecosystem services in San Diego, such as aquaculture, recreational harvest, other recreational uses, and use as a “natural” habitat. San Diego estuaries serve many important functions, and biological invasions have the potential to alter the functionality of these waters. Informed management decisions require detailed research to provide the necessary information encompassing the impacts of a biological invasion.

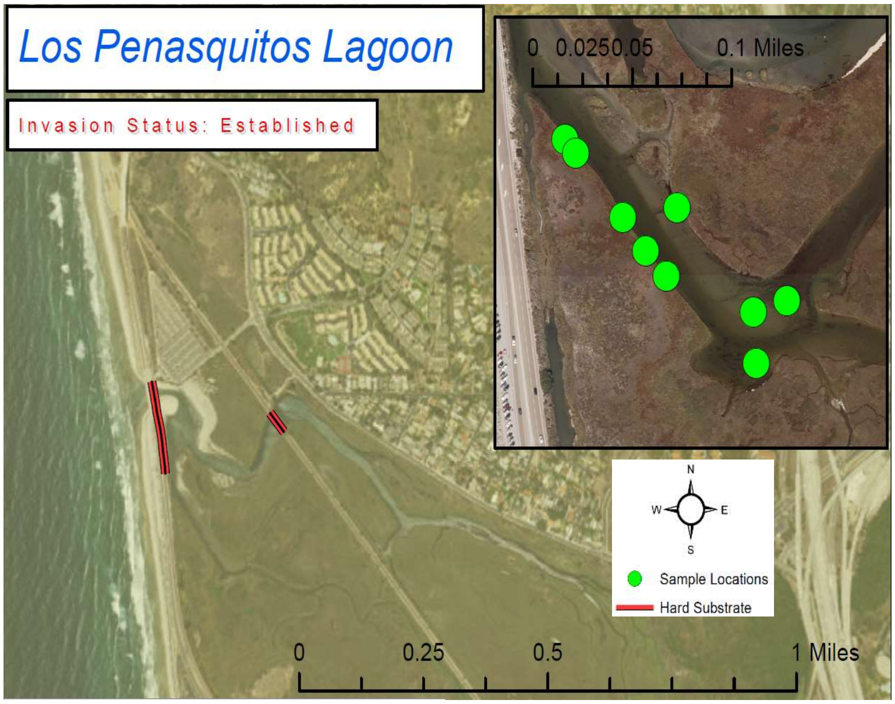

Figure 2.1. The study site, Los Peñasquitos Lagoon, San Diego, CA, USA. Green dots indicate sample locations while areas. Areas of artificial hard substrate, which were likely areas for initial establishment of *Crassostrea gigas*, are highlighted in red.

Figure 2.2. An example of a bucket core sample of taken from one of the *Crassostrea gigas* sampling locations in Los Peñasquitos Lagoon.

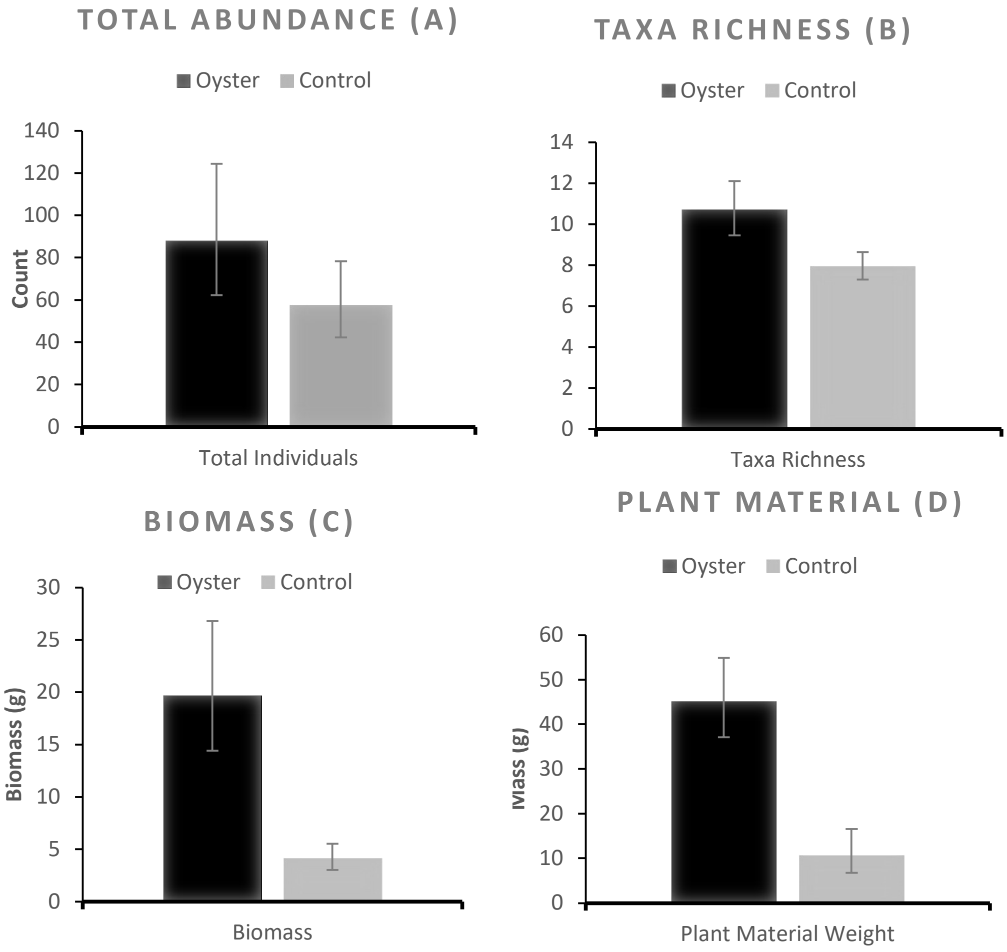

Figure 2.3. Comparisons of back-transformed (A) mean total abundance, (B) taxa richness (as measured by number of taxa), (C) biomass, and (D) amount of plant material in *Crassostrea gigas* oyster bed samples and controls, for all 10 sampling location (±SE).

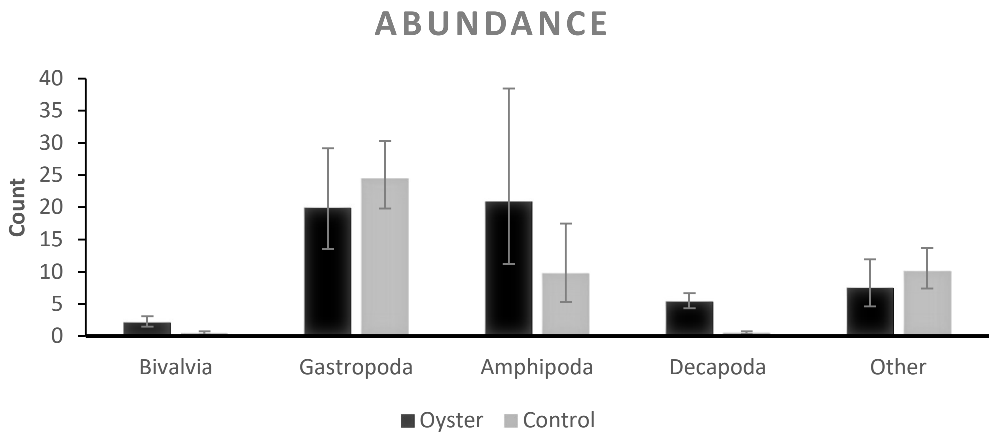

Figure 2.4 Taxonomically-grouped comparisons of back-transformed mean total abundance in *Crassostrea gigas* oyster bed samples and controls, for all 10 sampling locations (±SE).

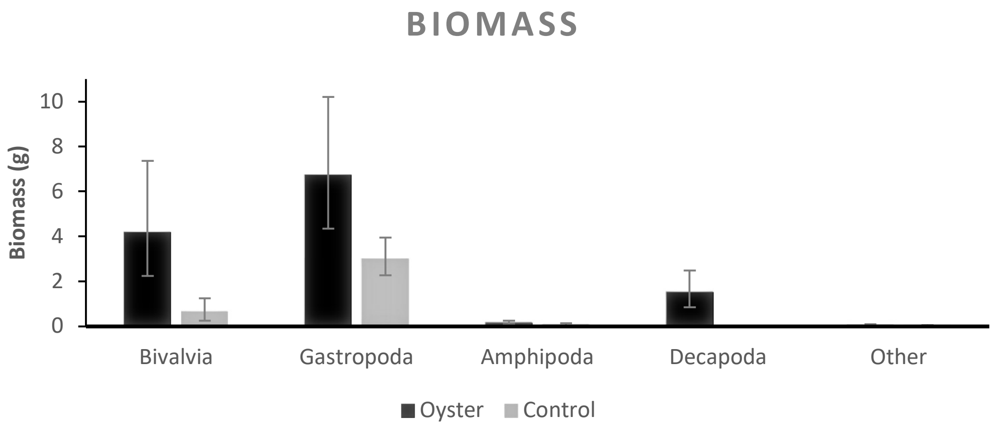

Figure 2.5 Taxonomically-grouped comparison of back-transformed mean total biomass in *Crassostrea gigas* oyster bed samples and controls, for all 10 sampling locations (±SE).

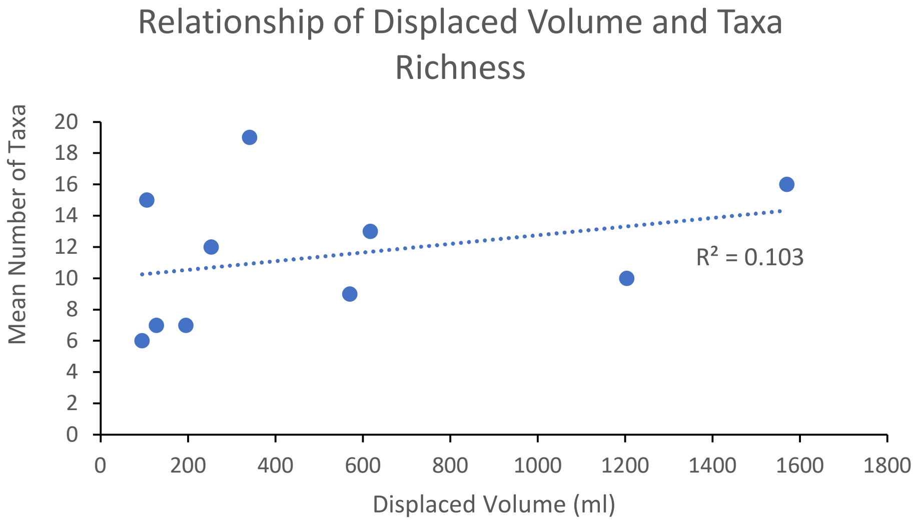

Figure 2.6 Relationship between mean displaced volume (ml) for each *Crassostrea gigas* oyster sampling location vs. mean total macrofauna number of taxa for each sampling location (10 sampling locations total), with a linear regression model.

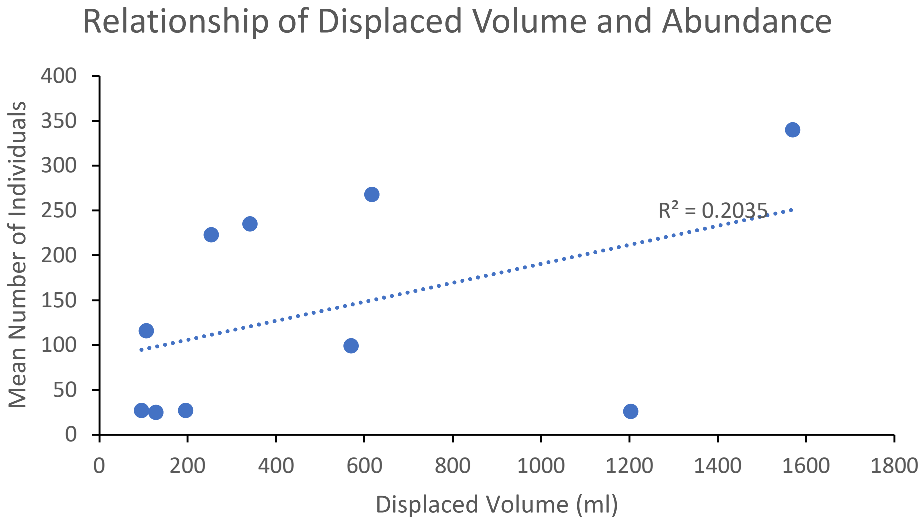

Figure 2.7 Relationship between mean displaced volume (ml) for each *Crassostrea gigas* oyster sampling location vs. the mean total macrofauna number of individuals for each sampling location (10 sampling locations total), with a linear regression model.

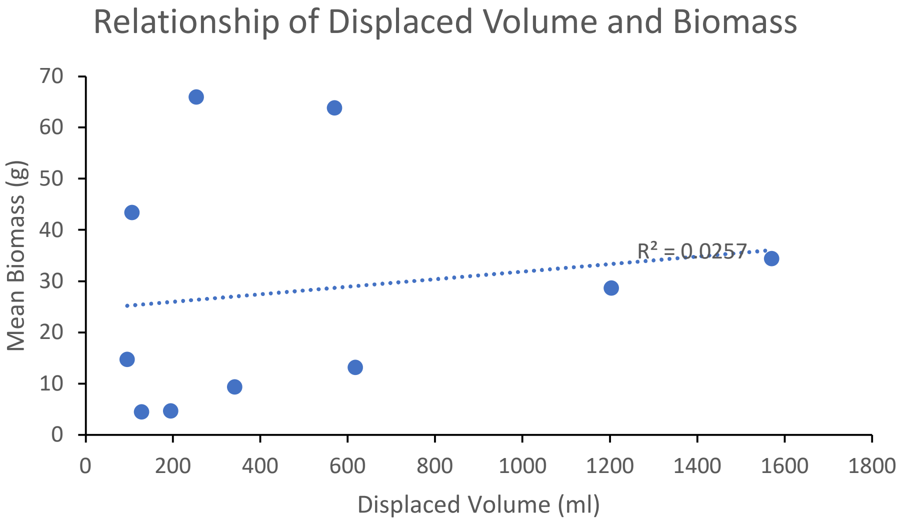

Figure 2.8 Relationship between mean displaced volume (ml) for each *Crassostrea gigas* oyster sampling location vs. the mean total macrofauna biomass (g) for each sampling location (10 sampling locations total), with a linear regression model.

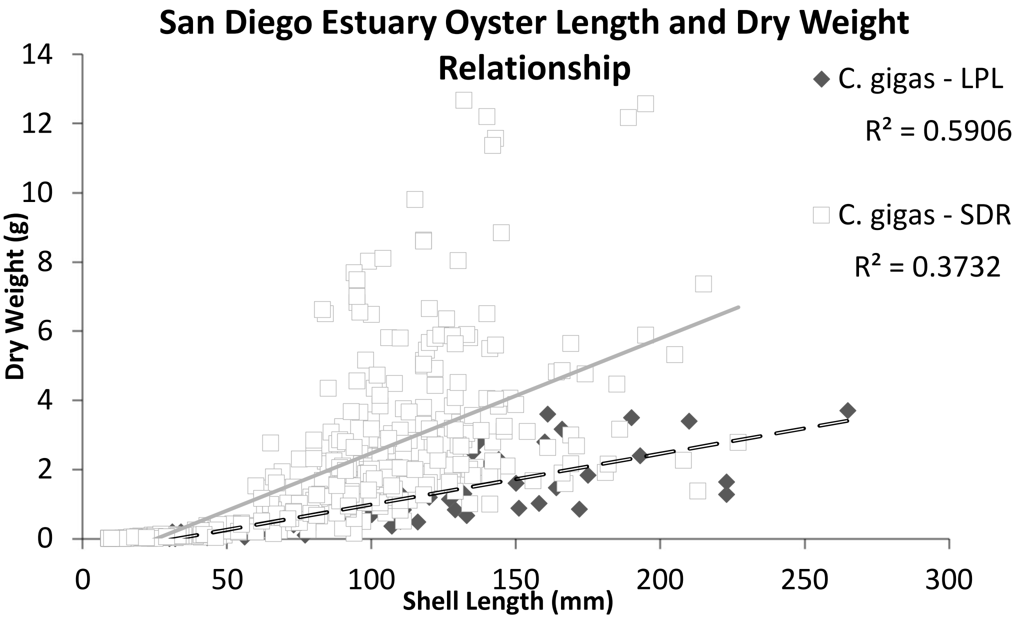

Figure 2.9 Relationship of *Crassostrea gigas* shell length and dry weight for *C. gigas* sampled in this study in Los Penasquitos Lagoon (LPL) and in another study by Langevin (2019) in the San Diego River (SDR).

Table 2.1 Summary table of peer-reviewed scientific studies which examined the Pacific oyster, *Crassostrea gigas*, as a global invader and ecosystem engineer.

Species Examined	**Habitat Location**	**Habitats compared**	**Community Examined**	**Density**	**Diversity**	**Comments**	**Reference**
C. gigas	Oostershelde Estuary, Netherlands	Oyster beds vs. adjacent mudflats	Oyster bed and Mudflat epifauna and infauna	+	+	Oyster bed infauna was found to be at maximum diversity and species richness in the transition zones of the beds (bed edges).	Van Broekhoven 2005
C. gigas and Eelgrass *Zostera marina l.*	Cortes Island, British Columbia, Canada	Adjacent-Below-Oyster beds and Eelgrass beds	Epibenthic macrofauna and macroalgae	+	+	Below-oyster beds and eelgrass communities varied significantly in community composition	Kelly et al 2008
C. gigas culture adjacent areas and Eelgrass *Zostera marina* areas	Bahia Falsa, Baja California	Eelgrass beds and areas adjacent to Oyster cultures	Macrobenthic community	NA	-	Oyster cultures changed location and density in the bay several times during the study. Detritus feeders associated with areas adjacent to oyster cultures	Villareal 1995
C. gigas and Blue mussel *M. planulatis*	Subtidal Longline Farms, Tasmania, Australia	Various Longline farms of different compositions of Pacific Oyster and Blue Mussel	Benthic Macrofauna Community	+	+	The farm that was mostly mussels has less total number of species and less mean number of individuals than the oyster dominated farms	Crawford et al 2005
C. gigas and native oyster O. *edulis*	Ballyhenry Bay, Strangford Lough, Northern Ireland	Intertidal and subtidal beds of *C. gigas, O. edulis*, and mixed	Benthic assemblages	=	=	No significant differences found in assemblage structure and species diversity between the two oyster species, however it appears C. Gigas may be able to outgrow and outcompete native oysters.	Zwerschke et al 2016

C. gigas and green algae U*lva* sp.	Bay of Mont Saint-Michel, France	*Sabellaria alveolata* (L.) biogenic Intertidal beds of low-density oyster, high-density oyster, mixed beds of algae and oyster. green algae, control with no algae or oyster,	*Sabellaria alveolata* (L.) biogenic beds community Assemblages	+	+	Higher species richness and diversity in all bed types with oysters than those without.	Dubois et al 2006
C. gigas	Bay of Brest, Brittany, France	Oyster beds on hard substrate and mud and controls of each (rock free of oysters and mud free of oysters)	Intertidal Benthic Macrofauna	+	+	In oyster beds, increased biomass of carnivores followed by deposit feeders colonizing substrate between oysters and low biomass of suspension feeders (not counting oysters themselves).	Lejart and Hilly 2011
C. gigas and Native Oyster *M. edulis*	Wadden Sea of Lower Saxony, Southern German Bight, North Sea	Sand flat (control) vs *M. edulis* beds and adjacent control vs *C. gigas* and adjacent control	Macrofaunal communities associated with oyster beds	+	+	*C. gigas* beds had higher abundances and biomass of vagile epizoic species like shore crabs and periwinkles. Higher abundances of deposit feeders were also observed in the *c. gigas* beds. *C. gigas* beds also favored sessile organisms like anthozoans, hydrozoans, and barnacles	Markert et al 2010
C. gigas and Native Oyster M. *edulis*	Lough Swilly, County Donegal, Ireland	Variations of *c. gigas* density on *m. edulis* beds on hard substrata and variations of *C. gigas* density on cleared mud flats	Epiflora and fauna as well as physical and chemical factors	NA	+	C. *gigas* increased biodiversity across the board in mudflats but at 100% density in *m. edulis* beds there was an overall decrease in biodiversity.	Green et al 2013

Table 2.1 (continued)

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Chapter 3: Conclusions and Next Steps

The non-native Pacific oyster, *Crassostrea gigas*, is becoming one of the most conspicuous invertebrates in the bays and lagoons of Southern California (Crooks et al. 2015). Some studies have begun to document the distribution and characteristics of *C. gigas* populations here (e.g. Tronske 2018, Langevin 2019), but this work is the first of its kind to investigate the relationship of the invasive ecosystem engineer to the resident community of macrofauna. This was done at a relatively early stage of invasion, and thus may provide valuable information for management. This work also offers a foundation for future research on one of the most successful and transformative of marine invaders.

As an ecosystem engineer, the impacts of this invader reach beyond its function as a single organism and extend to how it functions on ecosystem-level consequences (Crooks 2002). In Los Peñasquitos Lagoon, the presence of *C. gigas* corresponded to greater average macrofaunal abundances, taxa richness, and biomass. In addition, specific groups of taxa in particular, such as shore crabs, showed greater responses in these categories than others, such as small gastropod. However, some caution is warranted in interpretation that the oyster is having an overall "positive" effect in Los Peñasqitos Lagoon, and impacts need to be more fully evaluated to be properly understood in the greater context of the whole ecosystem. For example, it is possible that some of the organisms with higher abundances within the oysters beds where escaping from predation, which could have effects further up the food chain (Crooks 2002). Such impacts, including on trophic dynamics, were not considered here, but would be a fruitful avenue for future research. At smaller scales, this study observed positive responses from many species which are not native to Southern California, a case where one invader potentially facilitates another (e.g. Simberloff et al. 1999; Wonham et al. 2005). Additional research could focus on the differences between the responses of native and non-native species of macrofauna.

The patterns of higher richness, densities, and biomass observed in this study (Fig. 2.3) were likely driven by a variety of processes associated with the addition of novel complex physical structure. This corresponds with patterns seen with Pacific oyster invasions elsewhere (Table 3.1), and more generally with structure-producing bivalves (Gutierrez et al. 2003). However, because many different individual drivers can lead to increases in abundance and richness typically associated with habitat-forming engineers, such as refuge from predation and amelioration of environmental conditions (Crooks, 2002), it is difficult to know the relative importance of each (Crooks et al. 2016). Experimental manipulations, such as comparing the effects of living oysters to dead shells, can help elucidate some mechanisms (e.g. Wagner et al. 2012, McAfee and Bishop 2019). Also, although there were marked differences in macrofaunal communities with and without oysters, for the range of oyster beds examined here, there was little relationship between the amount of actual shell material present and macrofaunal properties (Figs 2.6 – 2.8), suggesting that there may be a threshold associated with bed impacts. Further work could examine potential density-dependent relationships, perhaps using experimental outplanting of oysters (e.g. Wagner et al. 2012).

Understanding how *C. gigas* impacts local communities across varying densities is extremely important to understanding the potential consequences of an invasion in an area. Specifically, this understanding is important to the estuaries of San Diego, which are undergoing an invasion by *C. gigas*. The study of invasive organisms, both in this study and in future studies, can produce a wide array of benefits to informed management for the communities in which they focus, as well as shed insights into fundamental ecological issues. In the case of this research, the study of *C. gigas* has yielded information which is directly applicable to how the estuarine waters surrounding San Diego are/can be managed. Understanding the potential impacts that can cascade from changing shoreline structure, such as the responses of the macrofaunal community to the addition of three-dimensional habitat as provided by *C. gigas*, can help to inform associated management decisions. In addition, the insights gained from this study have provided a better understanding of these ecosystem engineers as invaders, uniquely during an early stage of invasion. This in turn, has provided greater understanding of how these ecological processes work in the greater context of invasions, paving the way for future research. Further research is required to better understand the critical thresholds of the community of organisms and how they relate to the changes induced by an ecosystem engineer such as *Crassostrea gigas*.

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Appendices

Appendix 1: Summary Statistics Table.

Summary table of the logarithmic means and respective standard errors, and p-values associated with treatment effects and block effects yielded from randomized complete block test (two-way ANOVA without replication). P-values below 0.05 become more blue and above more red.

					P-value	
			Logarithmetic Mean	**Loagarithmetic S.E.**	**Treatment Effect**	**Block Effect**
	Total Individuals	**Oyster**	1.949450572	0.14855676	0.056800324	0.000903982
		Control	1.768058321	0.131008335		
	Species Richness	**Oyster**	1.068834099	0.049084617	0.00832137	0.01482256
		Control	0.951746607	0.032734459		
	Biomass	**Oyster**	1.316181634	0.12806515	0.002559102	0.264010973
		Control	0.71103314	0.104419947		
	Plant Material Weight	**Oyster**	1.664183406	0.083126978	0.010764663	0.387048573
		Control	1.066897043	0.177838698		
Number of Individuals	Bivalvia	**Oyster**	0.504372371	0.109017121	0.020828389	0.295835028
		Control	0.173239376	0.072528486		
	Gastropoda	**Oyster**	1.321549258	0.158304402	0.519366401	0.058701929
		Control	1.407467217	0.088153646		
	Amphipoda	**Oyster**	1.341548093	0.254828507	0.069809742	0.001186576
		Control	1.033571788	0.233646448		
	Decapoda	**Oyster**	0.805391763	0.078627169	0.000884439	0.960630635
		Control	0.180617997	0.066560236		
	Other	**Oyster**	0.931827121	0.180201769	0.396577482	0.015166536
		Control	1.045970021	0.12054703		
Species Richness	Bivalvia	**Oyster**	0.358972626	0.066108022	0.017903208	0.505193988
		Control	0.120411998	0.049157992		
	Gastropoda	**Oyster**	0.581157501	0.046219496	0.85827025	0.000950632
		Control	0.576581752	0.036719396		
	Amphipoda	**Oyster**	0.560552052	0.055083673	0.007490227	0.00707035
		Control	0.396454247	0.069877045		
	Decapoda	**Oyster**	0.461775498	0.03908659	0.004703501	0.446645057
		Control	0.180617997	0.066560236		
	Other	**Oyster**	0.4413635	0.063008908	0.242541098	0.582218301
		Control	0.527096749	0.02040241		
Biomass	Bivalvia	**Oyster**	0.716272089	0.205759523	0.02272706	0.083292464
		Control	0.224109625	0.126558193		
	Gastropoda	**Oyster**	0.888674652	0.160993757	0.052767483	0.05019751
		Control	0.603974678	0.090142836		
	Amphipoda	**Oyster**	0.067424747	0.028789292	0.238282763	0.048402939
		Control	0.036202457	0.021427327		
	Decapoda	**Oyster**	0.404881268	0.137231855	0.018276888	0.520967049
		Control	0.006408273	0.003907355		
	Other	**Oyster**	0.025474374	0.011073643	0.465866464	0.277521117
		Control	0.016698476	0.006591743		

Appendix 2: *Crassostrea gigas* Field Sampling Data Summary Table

A summary composite of oyster field sampling conditions collected from the oyster bed sites for all 10 sampling locations in Los Penasquitos Lagoon San Diego.

Sample #:	Date:	Longitude	Latitude	Time (PST)	Depth Below Water Level	Number of Oysters	% Oyster Cover
1	7/2/2015	117°15'32.84" W	32°55'53.00" N	7:40:00 AM	-12cm	6	15-20%
2	7/9/2015	117°15'31.30" W	32°55'52.97" N	10:45:00 AM	-9cm	12	50%
3	7/9/2015	117°15'32.12" W	32°55'51.98" N	10:45:00 AM	-1cm	3	20%
4	8/6/2015	117°15'31.58" W	32°55'51.41" N	9:40:00 AM	-1cm	8	40%
5	8/6/2015	117°15'29.23" W	32°55'49.40" N	10:16:00 AM	-1cm	11	60%
6	8/30/2015	117°15'34.24" W	32°55'54.53" N	4:40:00 PM	-8cm	5	35%
7	8/30/2015	117°15'33.95" W	32°55'54.22" N	5:06:00 PM	-16cm	3	20%
8	8/31/2015	117°15'32.73" W	32°55'52.74" N	4:50:00 AM	20cm	9	50%
9	8/31/2015	117°15'29.30" W	32°55'50.57" N	5:11:00 AM	-2cm	5	30%
10	8/31/2015	117°15'28.42" W	32°55'50.83" N	5:31:00 AM	-18cm	9	35%