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UNIVERSITY OF SAN DIEGO

San Diego, California

The Distribution and Demography of the Invasive Pacific Oyster, *Crassostrea*
gigas, and Native Olympia Oyster, *Ostrea lurida*, in the San Diego River

A thesis submitted in partial satisfaction of the requirements for the degree of
Master of Science in Environmental and Ocean Sciences

By Jason Langevin

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DEDICATION

To my wife Christine and two daughters, Maya and Nina, who provided the encouragement and emotional support required for me to finish my research.

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I would like to thank my thesis chair, Dr. Jeff Crooks, who spent countless hours in person, over the phone, and through emails working on this project with me, and I have been proud to have him as my mentor and friend. I would also like to thank the rest of my committee for their help with the project and suggestions for improving the research and paper, as well as their patience through the research. Special thanks go to my wife and daughters, who have provided the emotional support required to get through the tough times of self-doubt. The University of San Diego provided the materials and supplies required to perform my research, as well as an additional grant for materials. I would also like to thank both Keith Fink and Eric Cathcart for their help using tools and knowledge during this project.

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ABSTRACT

Even though the introduction of the Pacific Oyster, *Crassostrea gigas*, to the west coast of North America, happened roughly a century ago, it has only been in the past 15 to 20 years that *C. gigas* has started to become an established and conspicuous species along Southern California's coast. The establishment of *C. gigas* in Southern California has the potential to heavily influence many native species, as it has done globally. In Southern California, this invasion is particularly relevant for the native Olympia Oyster, *Ostrea lurida*. The Olympia oyster has both historical and present-day threats to its population, due to overfishing, pollution, and exotic species introductions. Understanding the distribution and demography of both species at the relatively early stage of *C. gigas* establishment is important for future management of both species.

In order to address this, sampling was conducted along the rip rap of the San Diego River, near its connection with the Pacific Ocean. Transects were laid down at the high, mid and low intertidal, and quadrats along these transects were sampled quarterly for one year. Densities, biomass, Condition Index, length frequencies, and Von Bertalanffy growth constants were used to look at the growth of the two species over this time period. For *C. gigas*, growth lines were also used as a tool to estimate age and growth. This work demonstrated that *O. lurida* densities were in fact much greater than those of *C. gigas*, but that these native oysters had greater numbers in the low intertidal and diminished as tidal height increased. *Crassostrea gigas* numbers also decreased with increase tidal height, although less dramatically than *O. lurida*. Even though there is a large size

difference between the two species, growth rate constants found using the Von Bertalanffy growth model (k) in the low- and mid-intertidal combined were found to be very similar, indicating similar growth rates. Further analysis of growth rates of *C. gigas* across tidal zones, using growth lines, demonstrated that the growth rate decreased as tidal elevation increased.

This study on the demography on native and invasive oysters in San Diego provides a foundation of baseline scientific information against which future change can be assessed, and can also inform future research directions, such as investigations of how each species interacts independently with their environment and with one another.

CHAPTER 1: INTRODUCTION

The invasion of non-native species represents a fundamental way in which humans alter the integrity of marine ecosystems. In San Diego County's marine waters alone, it is estimated that there are well over 100 established non-native species (Crooks et al. 2016). Among the most conspicuous of these is the Pacific oyster, *Crassostrea gigas*, which is native to Asia. This invasion appears to have occurred within the last 20 years, and has the potential to impact coastal ecosystems (Crooks et al., 2015). One species, the Pacific oyster likely will influence the smaller, native Olympia oyster, *Ostrea lurida*. Recent work in San Diego Bay, the largest embayment in Southern California, has indicated zonation of the two oyster species, with *C. gigas* being found at higher elevations than the native (Tronske et al. 2016).

This study examines demographic characteristics of both *C. gigas* and *O. lurida* across tidal zones in the San Diego River estuary. This system is characteristic of many estuaries in the region, as tidal influence is muted by an intertidal sill at the mouth. Over the course of one year, the density, biomass, size and growth of the two oyster species were tracked (Chapter 1). Additional information on shell morphology (Appendix 1) and length / weight relationships were also gathered (Appendix 2). This provides a foundation of basic scientific information, and can also inform future research directions for these two species (Chapter 3).

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CHAPTER 2: DEMOGRAPHY OF *CRASSOSTREA GIGAS* AND *OSTREA LURIDA*

2.1 Introduction

Oysters represent some of the most ecologically and economically important marine invertebrates. They modify habitats by providing protective structure, increase settling substrate for sessile organisms, filter water, and provide coastal barriers and “living shorelines” (Crooks and Turner 1990; Newell and Koch 2004; Swann 2008; Padilla 2010; Troost 2010). Along the Pacific coast of the United States and Canada, there is only one native oyster species, the Olympia oyster, *Ostrea lurida*. Individuals have been recorded living from Sitka, Alaska, down to Cabo San Lucas, Baja California Sur, Mexico (Carson 2010; Polson and Zacherl 2009). *Ostrea lurida* has been found in shell middens in San Diego dating back thousands of years (Baker 1995; Carson 2010). However, a fishery for *O. lurida* developed in the 19th century along the west coast of the United States but collapsed due to heavy overfishing (Polson and Zacherl 2009; Trimble et al. 2009). Thus, there is currently a focus on major restoration efforts of *O. lurida* along the west coast (Brumbaugh and Coen 2009; Groth and Rumrill 2009; Polson et al. 2009, M. Almeida et al. 1998.).

Due to dwindling *O. lurida* populations and a desire for new, larger species for the commercial market, the Japanese oyster, *Crassostrea gigas*, also known as the Pacific or Miyagi oyster, was introduced to the west coast of the United States (Carlton 1979). Native to Japan and Southeast Asia, *C. gigas* is currently established in at least seventeen countries and has been introduced in

over sixty-five (Ruesink et al. 2005, Harris 2008). The first shipments of Japanese oysters into North America began in the early 1900's, with occasional introductions into Southern California from the 1930's to the 1980's (Carlton 1979, Crooks et al. 2015). There was no indication that *C. gigas* had established itself in San Diego California in the 20th century. However, in the early 2000's, reports of *C. gigas* in San Diego region began, possibly related to an aquaculture operation that began in northern San Diego County developed in the late 1990's (Crooks et al. 2015). Currently, *C. gigas* has been observed throughout San Diego County, including the Tijuana River Estuary, San Diego Bay, Mission Bay, Oceanside Harbor, Los Penasquitos Lagoon, and the San Diego River (Crooks et al. 2015; Merkel and Associates Inc, 2015; Tronske 2018). Many of these locations are also habitats for the native *O. lurida* (Carson 2010), and it has been reported that differences in tidal zonation between the two species are common, with *O. lurida* to inhabiting a lower tidal elevation than *C. gigas* (Merkel and Associates Inc, 2015, Tronske 2018).

Both species have been well-studied along the northwest coast of North America, where *C. gigas* considered to be “naturalized”, but spread of *C. gigas* in Southern California is relatively recent and thus our understanding of this species' population dynamics and ecosystem effects in the region are only beginning to be realized (Crooks et al. 2015; Tronske et al. 2018). In other regions, *C. gigas* outcompetes native bivalve species for space and food (Troost 2008, 2010), and this could present a problem for San Diego's much smaller native oyster (*O. lurida*) when both species are present. The main goal of this research is to

improve our understanding of the basic population biology and potential community interactions of *C. gigas* at the mouth of an urban river during its early spread throughout Southern California. This goal was met by addressing two objectives: (1) documenting the distribution and demography of both species in Southern California, and (2) identifying tidal differences between the two species' distributions in the San Diego River, as reported elsewhere (Tronske et al. 2018). By understanding the tidal distribution and demography of both species' in a semi-arid, urbanized river in San Diego, comparisons can be made to other regions of the world, and a foundation can be established for future assessments of potential interactions between the two species.

2.2 METHODS

2.2.1 Study site

The San Diego River originates in the Cuyamaca Mountains and flows west, draining into the Pacific Ocean in San Diego, California. Once connected to both Mission Bay and the San Diego Bay, the San Diego River is now isolated from both systems (Canada 2006). The first major alteration to the lower San Diego River occurred in the mid-1800's when "Derby's Dike" was created, as an attempt to prevent unwanted sediment from entering the port at San Diego Bay by diverting the river into Mission Bay (Pryde 2002). This initial dike failed, but additional construction resulted in a redirected San Diego River by 1876 (Papageorge 1971). The next major alteration came with the completion of the San Diego River flood control channel in 1953 (Papageorge 1971). The rip-rap

levees and jetties now force the San Diego River to bypass both San Diego Bay and Mission Bay and instead flow directly into the ocean (Fig. 2.1A and 2.1B).

2.2.2 Field sampling

A 50-meter distance along the San Diego River was chosen to examine the demography of *O. lurida* and *C. gigas*, where both species are commonly found. During the first sampling season, October 2016, two tidal zones were examined, one representing the highest zone where oysters were observed and the other in the mid-intertidal (approximately 0.95 and 1.16 m NAVD88). During subsequent samplings, which occurred three months starting on October 19th, 2016, followed by samplings on January 9th, 2017, April 22nd, 2017, July 24th, 2017 and September 20th. In January 2017 an additional zone in the low-intertidal, at approximately 0.68 m NAVD88, was added to the sampling design due to the observations of large numbers of oysters in the low intertidal zone. Elevation of the zones was determined by using RTK GPS (although some variability existed within each transect due to the large, three-dimensional nature of the rip rap surface).

At the 50-m long sampling site, the high-, mid- and low-tidal zones were divided into five 10-m long transects. In each of these 10-m transects, 0.5 x 0.5m quadrats were randomly selected for oyster assessments. Each quadrat was randomly assigned a number, 0-4, which represented the time sampling would occur. At each sampling, all oysters in the designated quadrat were removed by hand or with use of a chisel and hammer. Oysters were placed in plastic bags,

brought back to the University of San Diego, and frozen for at least 48hrs at -80°C.

2.2.3 Laboratory processing

In the laboratory, oysters were processed to assess shell characteristics, determine species identity, remove tissue for biomass assessments, and prepare *C. gigas* shells for growth ring analysis. Before dissection, oysters were removed from the freezer and placed in a refrigerator to allow easy shell access. Thawed oysters were then cleaned using a small scrub brush to remove any mud and organisms (other than oysters) growing on the shell. Total weight was measured to the nearest tenth of a gram. Length was measured from the hinge to the most distant point on the shell. After shell measurements, each individual oyster was opened, and the soft tissue was removed and placed into a glass beaker and wet weight of the soft tissue was taken. The soft tissue was then placed in an oven at 65° C for 48 hours to obtain dry tissue weights. Shell weight was measured for each individual oyster after drying for 24 hours. Species identifications were made by both examining the size of the individual (*C. gigas* attains much larger sizes than *O. lurida*), as well as examining shells for the presence of chomata near the hinge, which is only present in *O. lurida* (Fig. 2.2).

2.2.4 Data analyses

Abundance, oyster length, and biomass data were used to assess demography across species and tidal zones. Paired t-tests across dates were used

to examine differences in density and biomass across time, and following recent American Statistical Association guidance, P-values are reported but no assessments of significance are made based on fixed alphas (Wasserstein et al. 2019). Length-frequency distributions were created for low- and mid-intertidal sites combined, this was done to increase sample sizes. The high intertidal was not included in the length frequency distribution because of small sampling sizes. Condition Indices, representing the ratio of dry flesh weight (x 1000) to shell weight (Mann and Glomb 1978) were also calculated for combined low- and mid-intertidal samples.

For both species oyster growth was determined by calculating the growth rate constant, K, in the Von Bertalanffy Growth Function (VBGF), using TropFishR. This R package is based on ELEFAN (ELectronic LEngth Frequency Analysis), (Pauly 1987, Schwaborn et. al, 2019), and calculates parameters of the VBGF, including K (the rate at which a species approaches average asymptotic size, L_{inf}). The “Optimise” Response Surface Analysis method of ELEFAN was used, which provides best fits of both K and L_{inf} .

Growth of *C. gigas* was also assessed using growth lines. Growth lines found in cross sections of bivalves have been used to estimate the age of oysters, including *C. gigas* (Harding and Mann 2006). *Ostrea lurida* was not known to have growth lines, and this is confirmed in preliminary work for this study. After species identification, a total of 236 *C. gigas* oysters were selected for growth line counts, spanning the size range between the smallest and largest individuals. Cross sections were performed using a diamond table saw at the

University of San Diego (Fig. 2.3). According to the criteria of Harding and Mann (2006), to be considered for growth ring analysis, a straight line from the end of the shell to the umbo should pass through the adductor scar. However, in this study, there were only 19 oysters that met this requirement. Therefore, all 236 selected oysters were considered for this work. Once cut, shells were dried, and lines were counted using a compound microscope. Following the methods of Harding and Mann (2006), growth lines were categorized as thick grey lines originating at the umbo continuing through the cross section to an ending point at the outer edge of the shell (Fig. 2.3).

Growth rates in each tidal zone were calculated as the slope of the line of size vs. age (inferred as the number of lines). This was conducted for oysters with up to three growth lines (the maximum number in the high-intertidal), and all oysters within quadrats and across times were pooled (i.e., treated as independent observations) to statistically compare slopes across tide zones.

2.3 RESULTS

2.3.1 Densities

Ostrea lurida was the more prevalent oyster species in two of the three sampled tidal heights but decreased more dramatically in abundance with increasing elevation than *C. gigas*. Out of all 512 oysters sampled in the low-intertidal, 75% were *O. lurida* and 25% were *C. gigas* (Fig. 2.4). Densities of *O. lurida* were approximately twice that of *C. gigas* in the low-intertidal, although there was relatively high variability within plots (paired t-test: $t_3=2.33$, $P=0.10$)

(Fig. 2.5). As tidal height increased from the low- to mid-intertidal, the average density (across time) of *O. lurida* decreased 83% (paired t-test: $t_3=8.97$, $P=0.003$). The decrease of *C. gigas* from the low- to mid-intertidal was less pronounced (paired t-test: $t_3=1.82$, $P=0.17$), and during one sampling season (April 2017), mid-intertidal densities exceeded those in the low-intertidal. The densities of the two species were more comparable in the mid-intertidal (Figs. 2.4 and 2.5) (paired t-test: $t_4=0.57$, $P=0.60$). In the high-intertidal zone, few *C. gigas* were found and *O. lurida* were completely absent (Figs. 2.4 and 2.5).

2.3.2 Biomass

Differences in biomass, both in terms of dry flesh weight and total (dry flesh + shell) weight tended to be much more pronounced than differences in densities, driven by the larger sizes of *C. gigas*. The largest *C. gigas* collected was 227 mm, while the largest *O. lurida* was 80 mm. The average total weight of *C. gigas* per quadrat was 14 times larger than *O. lurida* in the low-intertidal (paired t-test: $t_3=5.88$, $P=0.01$), and 40 times larger in the mid-intertidal (paired t-test: $t_4=3.05$, $P=0.04$) (Fig. 2.6). Dry tissue biomass of *C. gigas* in the low-intertidal was 15 times larger than *O. lurida* in the same zone (paired t-test: $t_3=7.38$, $P=0.005$) (Fig. 2.7). In the mid-intertidal, the average difference was a factor of 30, but there was considerable variability, driven by very high biomass in April 2017 (paired t-test: $t_4=1.68$, $P=0.17$) (Fig. 2.7). With *O. lurida* being absent from the high intertidal and so few *C. gigas*, a paired t-test was not performed between the species for either total or dry weight biomass in the high-intertidal zone. For

both species, dry and total biomass weight tended to increase leading up to the spring, followed by a decrease during the summer and fall, with the one exception being *C. gigas* in the low-intertidal (Figs. 2.6 and 2.7).

2.3.3 Condition Index

Despite large differences in size and biomass, condition indices (representing the ratio of flesh weight (x 1000) to shell weight) for the two species tended to be comparable for the low- and mid-intertidal sites, ranging from 23 to 60 (Fig. 2.8). Also, there appeared to be some temporal differences in condition for *C. gigas* in the low- and mid-intertidal and *O. lurida* in the low-intertidal. In both cases, condition indices peaked in April 2017. Condition indices were much more variable for *O. lurida* in the mid-intertidal, although the species was less common there in the early seasons and absent from the last two sampling dates.

2.3.4 Length-frequency distributions and growth rates

The length-frequency histograms for combined low and mid-intertidal sites suggest some size structure in the populations and the appearance of distinct cohorts of different sizes. These are represented by peaks in the histograms (Fig. 2.9). The size of the smallest individuals found was similar for both species, with *C. gigas* at 7 mm and *O. lurida* at 6 mm. For *C. gigas*, individuals in the smallest size were found throughout the year (Fig. 2.9), suggesting the possibility of some continued recruitment. *Ostrea lurida*, on the other hand, had relatively few individuals in the smaller size class (Fig. 2.9).

Length-frequency distributions for the two species were analyzed using the ELEFAN (ELEctronic LENgth FREquency ANALysis) function of TropFishR to estimate two parameters of the Von Bertalanffy Growth Function (VBGF): the growth rate constant, K , and asymptotic size. The Response Surface Analyses (Fig. 2.10 A and B) provided comparable growth rate estimates for the two species, with *O. lurida* having a value of 0.66 yr^{-1} and *C. gigas*, 0.67 yr^{-1} (Fig. 2.10 A and B). There was a large distinction between asymptotic sizes (which should be interpreted differently than absolute maximum size, which is the max size of sampled organisms; Mildenerger et al. 2019), with *O. lurida* at 47 mm and *C. gigas* 144 mm (Fig. 2.10 A and B).

2.3.5 *Crassostrea gigas* growth lines

Growth lines in *C. gigas* were apparent, with a maximum number of 8 lines recorded in the low-intertidal sites, 7 in the mid-intertidal, but only 3 in the high-intertidal. Assuming that lines are laid down annually, as has been determined for other species elsewhere (Richardson et al. 1993a; 1993b; Kirby et al. 1998;), this suggests that *C. gigas* in the high-intertidal did not live longer than three years, while those in lower tidal zones had maximum lifespans of more than twice as long. Oyster size as a function of age, inferred as the number of lines (Fig. 2.11), also suggest differences in growth across zones, especially for young oysters. The rate of increase of size from 1-yr olds to 3-yr olds, compared as slopes of lines of size vs. age, decreased from the low to high-intertidal ($F_{2,159} = 6.67$, $P = 0.0017$). In the high-intertidal zone, the rate of increase was 17.5 ± 3.2

mm / yr (N = 17), which was lower than the growth rate in the mid-intertidal of 28.4 ± 7.4 mm / yr (N = 76). Oysters in the low-intertidal had the highest early growth rate, 40.5 ± 3.165 mm / yr (N = 72).

2.4 Discussion

Two oyster species, the native *Ostrea lurida* and invasive *Crassostrea gigas*, are the most conspicuous invertebrates on the rock banks of the San Diego River. The density of these oyster species in the mid- and low-intertidal in this area (Fig. 2.5) resemble those of other populations found in Southern California (Newport Bay, Alamitos Bay, Huntington Harbour, Los Angeles Harbor, Mission Bay and San Diego Bay) (Polson and Zacherl 2009; Tronske 2009). However, compared to other locations along the west coast of the United States, densities were lower for both species. For example, *O. lurida* densities in San Francisco Bay ranged from 140 oysters/m² to 960 oysters/m² (Polson and Zacherl 2009; Wasson et al. 2015), while in Puget Sound *C. gigas* were found at 352 oysters/m² (Valdez et al. 2016). Globally density is variable depending on location. In Scandinavia, densities in Sweden ranged between 0.64 oysters/m² to 505 oysters/m², while in Denmark densities only reached 1.43 oysters/m² to 15.30 oysters/m² (Wrange et al. 2009). In Australia, densities ranged between less than 4 oysters/ m² to 300 oysters/m², depending on substrate (Krassoi et al. 2008; Bishop et al. 2010). When first introduced in an area, *C. gigas* settlement often occurs on the shells of dead native bivalve species, such as mussel beds and other oyster species (Wehrmann et al. 2000; Diederich et al. 2004; Troost 2010). In

many cases, these reefs develop into *C. gigas* / mussel reefs, with the mussels and oysters living together (Troost 2010).

A clear pattern of zonation between *C. gigas* and *O. lurida* was present in the San Diego River, as has been observed in other local embayment's.

Crassostrea gigas favors the higher intertidal zone, while *O. lurida* the lower (Merkel and Associates Inc, 2015. Tronske et al. 2018). *Crassostrea gigas* in the San Diego River displayed comparable zonation patterns to that found in Puget Sound (Valdez et al. 2016), where five tidal elevations were examined and *C. gigas* densities increased with tidal elevation. Little is known about the cause of zonation between *C. gigas* and *O. lurida*. For *O. lurida* in Washington state (Puget Sound), higher recruitment has been documented at lower tidal elevations (Baker 1995, White et al. 2009a). Krassoi et al. (2008) suggest that competitive dominance and difference in abiotic factors (desiccation) could be a strong influence. Due to their larger size, *C. gigas* could be less prone to desiccation than *O. lurida* in the San Diego River at higher tide levels as seen with other bivalve species (Krassoi et al. 2008).

Crassostrea gigas is considered one of the largest living oyster species, with maximum sizes reported greater than 400 mm (Torigoe 1981). Although *C. gigas* in the San Diego River did not reach this size, they were still relatively large, with 227 mm as the maximum length. The largest *O. lurida* individual was 80 mm, which was closer to the maximum size reported for the species of, 80-100 mm (Arakawa 1990; Peter-Contesse and Peabody 2005; Pritchard 2015). Because of the greater lengths of *C. gigas* compared to *O. lurida*, the overall (dry and total)

biomass per quadrat of *C. gigas* was roughly 15 to 40 times larger than *O. lurida*, even though *O. lurida* densities tended to be higher than that of *C. gigas* in the low-intertidal. From a global perspective, the large, calcium-rich shells of oysters (like those created by *C. gigas*) act as potentially large organic carbon pools. For the reef-building *C. virginica* one dense reef has the potential to store over 400 million Mg carbon over a course of 300 years (Fodrie et al. 2017).

Analysis of length-frequency data throughout the sampling period provides some indication of timing of recruitment of both species. *Crassostrea gigas* had a peak in recruitment in April 2017 (Fig. 2.9). This coincided with the highest Condition Indices for the species (Figure 2.10), indicating increases in soft tissue biomass relative to shell size, possibly due to an increase in reproductive tissue. There was also constant recruitment occurring throughout the year for *C. gigas*, with individuals in the smallest size class collected during every time period. In other parts of the world, *Crassostrea gigas* have been shown to have variable reproductive periods. For example, on the South Island of New Zealand, individuals reproduce only once in the early spring, while on the North Island they have two or more spawns within a year (Dinamani 1987). Compared to *C. gigas*, *O. lurida* did not display a major recruitment period during the study although small individuals were found from October 2016 to April 2017. The cause of this low recruitment for *O. lurida* remains unknown.

Changing length-frequency distributions were also used to calculate and compare growth rates of *C. gigas* and *O. lurida*, expressed as a constant in the Von Bertalanffy Growth Function. Despite being different in size, the two species

had similar K constants, indicating comparable rates at which the species approached asymptotic size. The growth constant (K) for *C. gigas* in the San Diego River was comparable to measurements in the Wadden Sea and parts of Europe (Van Der Veer 2006; Schmidt et al. 2008), ranging between 0.300 to 0.999 yr⁻¹. In other parts of Europe, the English Channel and along the Atlantic Coast of France, growth constants were between 0.365 yr⁻¹ to 1.304 yr⁻¹ (Lartaud et al. 2010), while rates from China were between 0.02yr⁻¹ to 0.33yr⁻¹ (Harding and Mann 2006). For *O. lurida*, this is one of the very first studies to calculate the growth constant (K) of *O. lurida* using the Von Bertalanffy growth model. While some potential problems with the VBGF are recognized (Newkirk 1981, Pardo et al. 2013), such as lack of ability to account for inter-annual variations in growth rates, it is a widely-used method that allows basic growth parameters to be compared (Katsanevakis and Maravelius 2008).

Like growth lines of a tree, growth lines in bivalve species have been used as a measurement of age (Richardson et al. 1993; Peharda et al. 2002; Harding and Mann 2006). Although *C. gigas* lived higher in the intertidal, analyses of growth lines demonstrate decreasing growth rates with increasing elevations. This could be due to the environmental stress (e.g. desiccation) as well as more limited time for feeding with increasing elevations (Borrero 1987; Bartol et al. 1999, Montalto and Drago 2003). For these analyses, it was assumed that growth lines represented annual growth marks, and this assumption is supported from work done elsewhere (Richardson et al. 1993a; 1993b; Kirby et al. 1998; Harding and Mann 2006). *Crassostrea gigas* found in the mid- and low-intertidal in the San

Diego River shared similar relationships between growth lines and mean sizes lengths to individuals found in Washington, Oregon, California and China (Langdon and Robinson 1998; Harding and Mann 2006). Individuals with one growth line were between the range of 31-50mm, two growth lines between 85-90 mm, and three between 102-113 mm (Fig. 2.11). However, they are dwarfed by oysters in Korea, where *C. gigas* reached 70 mm within their first growth year (Mondol et al. 2016). *Crassostrea gigas* in Portugal and Mexico on the other hand, averaged smaller lengths resembling those found in the high tide zone of the San Diego River reaching size of 20-30 mm in their first year and 60-70 mm within their second growth year (Arizpe 1996; Almeida et al. 1998).

It is important to note that even though it was assumed that growth lines were laid down annually in the San Diego River, comparison of *C. gigas* growth in different zones would be valid if rings are laid at comparable times across zones (e.g., in association with events such as El Niños, Rollins et al. 1987). In this case, growth would be relative rather than annual. Due to the ecological and economic importance of *C. gigas*, and the potential for growth lines to provide valuable information about the species, more work is needed on growth rings both locally and in other regions. Since there has been very little work using rings to analyze age in *C. gigas*, along with the difficulty of reading them, more research should be conducted. For example, in many of the oysters examined in this study, large amounts of dirt were found within the matrix of the shell, indicating that the layers had to be laid down relatively quickly for the mud not to get washed away.

Alternative ways of measuring growth should also be attempted through mark and recapture, or chemical marking.

The goal of this research was to increase understanding of the current population and growth of *C. gigas* and *O. lurida* in Southern California. Despite a highly urbanized river mouth with muted tidal flushing, actual tidal zonation range of both species was similar to other areas with well flushed systems. Even though *C. gigas* tended to have higher densities in the higher tidal zones, they still had a decrease in growth rate compared to *C. gigas* growing in the lower tidal zones. Growth rates of both species were found to be very similar, even though *C. gigas* tends to grow to a much larger size than *O. lurida*.

The hope is to lay a foundation of baseline scientific information against which future change can be assessed and to inform future research directions, such as a focus on how each species interacts independently with their environment and with one another. Throughout the study, there were many unmeasured factors that could influence the densities and growth of both species, like temperature, salinity and pH. For example, in previous studies done in Spain, temperature was a strong influence on gametogenesis and recruitment success for *C. gigas* (Ruiz et al. 1992). Understanding recruitment and substrate preference for each species is important for both oyster restoration and management. During this study it was observed that many of the *O. lurida* collected were found residing on the shells of larger *C. gigas* (both alive and dead). This is not uncommon, as *C. gigas* shells provide hard substrate for other native species (Troost 2010). They have even been used as a recruitment tool for *O. lurida*, in

Washington State. For example, White et al. (2009) found there was no significant difference in *O. lurida* settlement preference between *C. gigas* shells (crushed and whole) and *O. lurida* shells (crushed and alive). Through this research and the methods used to measure the growth and distribution of both species, there is now a clearer picture of these ecologically and economically important species in Southern California.

A)

B)

Figure 2.1. A) Map of study site (red dot) in the San Diego River, and B) photograph of transect along rip-rap bank of the San Diego River channel, facing upstream.

A)

B

No Chomata

Figure 2.2. A) Detail of the chomata (grooves near umbo) found in *Ostrea lurida*.

(B) Umbo of *Crassostrea gigas*, with the absence of chomata.

Figure 2.3. Cross section of *Crassostrea gigas*, displaying grey growth lines running through the interior of the shell.

Figure 2.4. Percentages of *Ostrea lurida* and *Crassostrea gigas* in the high-, mid- and low-intertidal zones in the San Diego River.

A)

B)

Figure 2.5. Mean densities of A) *Ostrea lurida* and B) *Crassostrea gigas* in the San Diego River.

Figure 2.6. Mean total biomass (shell weight plus dry tissue weight) of A) *Ostrea lurida* and B) *Crassostrea gigas* in the San Diego River.

A)

B)

Figure 2.7. Mean dry weights (tissue) of A) *Ostrea lurida* and B) *Crassostrea gigas* in the San Diego River.

Figure 2.8. Mean Condition Index ($1000 \times$ dry tissue weight / shell weight) for A) *Ostrea lurida* and B) *Crassostrea gigas* in the San Diego River.

Figure 2.9. Length frequency distributions for *Ostrea lurida* and *Crassostrea gigas* in the San Diego River. N = total number of individuals.

A)

B)

Figure 2.10. Response Surface Analysis using ELEFAN to calculate growth rates (K) and asymptotic size (L_{inf}) of the Van Bertalanffy Growth Function for A) *Ostrea lurida* and (B) *Crassostrea gigas*.

Figure 2.11. Mean length vs. number of growth lines for *Crassostrea gigas* in the high-, mid-, and low-intertidal.

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3. CONCLUSIONS

This study on native and invasive oysters in the San Diego River demonstrated that although *Crassostrea gigas* had invaded this system, *Ostrea lurida* was found in higher abundances. Relative growth rates of the two species were similar, but because of the much larger size of *C. gigas*, its total biomass in the intertidal was much higher. Both species decreased in abundance with tidal height, but *C. gigas* decreased less dramatically and was found at higher elevations. These results demonstrate that although native oysters are persisting despite the Pacific oyster invasion, although there is the potential for negative interactions in zones of overlap in the intertidal.

These results provide a foundation of baseline information that can help inform future research on these two species. Potential topics could include:

- Longer-term tracking of these two species, especially since the invasion of *C. gigas* is relatively recent.
- Using other methodologies to assess growth rates, such as chemical tagging and mark / recapture techniques.
- Assessing spawning and recruitment patterns for the two species
- Characterizing the role of physical parameters, such as temperature and salinity, on oyster demography.
- Observational and experimental studies of competition between *C. gigas* and *O. lurida*.

Continued research such as this should further enhance our ability to understand and potentially manage these shellfish in San Diego's coastal waters.

APPENDIX 1. SHELL MORPHOLOGY

Summary of morphological characteristics of *Crassostrea gigas* and *Ostrea lurida* from the San Diego River. Measurements were made for shell height (SH), shell width (SW), and shell inflation (depth) (SI). Ranges for each measurement are presented, as well as the ratio between SH:SW and SH:SI and their standard error (SE).

Tidal Height	Species	n	SH Range (mm)	SW Range (mm)	SI Range (mm)	Average SH-SW Ratio (SE)	Average SH-SI Ratio (SE)
High	<i>C. gigas</i>	17	18-82	15-52	None	1.31 (0.09)	None
High intertidal	<i>O. lurida</i>	0	None	None	None	None	None
Mid intertidal	<i>C. gigas</i>	148	9-213	7-99	3-73	1.67 (0.03)	4.08 (0.02)
Mid intertidal	<i>O. lurida</i>	125	6-44	6-32	2-13	1.39 (0.03)	3.84 (0.01)
Low intertidal	<i>C. gigas</i>	208	9-227	7-124	2-68	1.60 (0.03)	3.55 (0.01)
Low intertidal	<i>O. lurida</i>	385	8-80	6-41	2-25	1.46 (0.02)	3.82 (0.01)

APPENDIX 2. LENGTH-WEIGHT RELATIONSHIPS

Linear regressions of length and dry weight relationships at each tidal height.

C. gigas High Intertidal Length and Dry Weight Relationship over a Year Period

C. gigas Mid Intertidal Length and Dry Weight Relationship over a Year Period

C. gigas Low Intertidal Length and Dry Weight Relationship over a Year Period