MORPHOLOGICAL VARIATION OF *PISASTER OCHRACEUS* IN RESPONSE TO WAVE EXPOSURE

by

ALYSSA BJORKQUIST

A THESIS

Presented to the Department of Biology
and the Robert D. Clark Honors College
in partial fulfillment of the requirements for the degree of
Bachelor of Science

June 2016

An Abstract of the Thesis of

Alyssa Bjorkquist for the degree of Bachelor of Science
in the Department of Biology to be taken June 2016

Title: Morphological Variation of *Pisaster ochraceus* in Response to Wave Exposure

Approved: Richard Emlet

Dr. Richard Emlet

Pisaster ochraceus (the Ochre Sea Star) is a keystone predator in the NE Pacific that regulates intertidal diversity through consumption of space-competing organisms. Individuals inhabit a broad range of habitats ranging from sheltered coves to exposed cliffs and experience large temporal and spatial variability in water flow throughout their lifetime. However, it is largely unknown how sea star body shape changes between wave-exposed and wave-sheltered environments throughout an organism's lifetime. Wave exposure was measured at sites near Charleston, OR using dissimilar metal dissolution and intertidal zonation of sessile organisms. At these same sites, I measured shapes and sizes of *Pisaster* juveniles and adults and analyzed how morphology changed as a function of wave exposure.

Average zinc anode mass loss differed significantly between sites during seasonal trials ($p < 0.001$). Mean upper intertidal zone limits were significantly higher at the Middle Cove and OIMB Boathouse sites for *Balanus glandula* ($p < 0.01$), *Mytilus* spp. ($p < 0.01$), *Neorhodomela oregona* ($p < 0.001$), and *Saccharina sessilis* ($p < 0.05$). Adult sea star populations the Middle Cove site had longer, narrower arms ($p < 0.001$) and smaller central discs ($p < 0.001$) than individuals from the OIMB Boathouse or Bastendorff Jetty sites for a given weight. Juveniles appeared to exhibit similar morphological trends to respective adult populations but results were inconclusive. The lack of a significant relationship between wave exposure and *Pisaster* morphology is likely due to errors in measurements of exposure and demonstrates that exposure alone does not determine body shape.

Acknowledgements

The journey towards completing my honors thesis has been incredibly rewarding and would have never been possible without support from mentors, faculty, staff, friends, and family at the University of Oregon and beyond.

I would first like to extend my sincerest appreciation to my primary thesis advisor, Dr. Richard Emlet, for his wisdom, generosity, and guidance during every step of this thesis. I owe Dr. Emlet many thanks for his patience and creativity when cultivating the foundations of my scientific research skills. His enthusiasm for studying marine invertebrates is inspiring and I hope to carry on this passion to my future schooling and career opportunities.

I would also like to thank my thesis committee members, Dr. Kelly Sutherland and Dr. Craig Young for helping me with consultations about the thesis process and future directions this project could take. Dr. Brian Bingham provided invaluable statistics support and advice about future careers in ecology. Thanks are needed to the Robert D. Clark Honors College and the University of Oregon's Department of Biology for creating a superb learning environment in which I strive to learn more about my world.

My field-intensive project could not have been completed without the unwavering support of my friends and peers. They were all willing to assist me when I needed it most whether in the form of data collection, writing consultation, moral support, or cookies. Kaitlin Brown, Shannon Brown, Sandra Dorning, and Katalin Plummer need special recognition for their patience and resourcefulness in the field and laboratory. They endured many adventures in the field at all hours without complaint and facilitated my success throughout the entire research process. I am also grateful for the additional efforts of Natalie Carrigan, Rebecca Fletcher, Zena Jensvold, Joel Kraski, Julia Metzler, Sage Riddick, Eli Rodda, Madison Wright, and Emily Zwier in helping my thesis thrive both in Charleston and Eugene, OR.

The Oregon Institute of Marine Biology was a fantastic setting for nurturing my academic interests in marine biology and scientific research. The entire OIMB faculty and staff lent incredible support in their administrative, mechanical, kitchen, and housekeeping efforts during my nine months in Charleston, OR. The staff at Englund's Marine Supply provided the materials necessary for my zinc dissolution experiment, and I welcomed their enthusiastic assistance at every visit to their store.

Lastly, I would like to thank my parents, Ted and Karen Bjorkquist, for always supporting me on this journey. My thesis was not without its challenges and my parents never gave up on me during any stage of this project. My dad spent his Thanksgiving helping me with difficult field research at night and helped me test new methods to make the process easier in the future. My mom lent invaluable advice during a particularly rough patch and always encouraged me to be brave and inquisitive. Their genuine enthusiasm for this project's success and patience in many thesis-oriented discussions provided the backbone from which I built my support network.

This thesis was supported by an Undergraduate Research Opportunities Program Mini-Grant from the University of Oregon Office of the Vice President for Research and Innovation. It was also partially funded through an NSG grant awarded to my primary advisor, Dr. Emlet.

Table of Contents

List of Figures

List of Tables

Introduction

Study Organism: *Pisaster ochraceus*

Pisaster ochraceus (Echinodermata: Asteroidea), the Ochre Sea Star, is a keystone predator commonly found along rocky intertidal coastlines of the Northeastern Pacific Ocean (Paine 1969, Robles 2013). Species distribution ranges from Cedros Island, Baja California to Prince William Sound, Alaska and *P. ochraceus* (referred to hereafter as *Pisaster*) inhabits sites with variable topographical features such as sheltered coves, exposed cliffs, or marinas and docks (Frontana-Uribe at al. 2008; Hayne 2011; Robles 2013). The interaction between biotic and abiotic factors produces cumulative effects on the ecological success of *Pisaster* by testing its food capture efficiency, metabolism rates, and reproductive fitness.

Pisaster is one of the largest mobile organisms in the intertidal and thrives as a keystone predator (Paine 1969, 1974). Power et al. (1996, p. 609) define a keystone species as, "one whose effect is large, and disproportionately large relative to its abundance." *Pisaster* uses intermediate environmental disturbance for maximizing predation and homeostatic regulation within intertidal zones of *Mytilus californianus* or *Mytilus trossulus* (Lawrence 2013; Robles 2013). Regulating colonization for space-competing species benefits intertidal communities by preventing over-competition and providing space for other organisms to settle and proliferate. When *Pisaster* is not present in large numbers, intertidal diversity declines and mussel populations extend downward into algal habitation zones (Paine 1969; Feder 1970). Tube feet help adhere *Pisaster* to hard substrata in an exposed intertidal environment and facilitate breaking open hard bivalve shells of its prey (Santos et al. 2005, Hennebert et al. 2010; Hayne 2011). Adaptations such as tube foot tenacity and body shape plasticity allow *Pisaster* to be a dominant intertidal predator that actively influences intertidal community composition (Hennebert et al. 2010).

Sea Star Wasting Disease (SSWD) has recently devastated *Pisaster* populations and will likely have far-reaching effects on larval recruitment and sea star habitation. A nationwide collaboration of marine and medical scientists recently identified a densovirus as the likely cause behind these cyclic mass fatality events (Hewson et al. 2014, Fuess et al. 2015). SSWD is a rapidly debilitating disease that causes infected individual body structures to degrade rapidly from lesions and massive tissue death in the arms and central body disc (Hewson et al. 2014). *Pisaster* demonstrated greater infection intensity and disease prevalence under the following conditions: shelter from wave exposure, infection taking hold in summer months, or higher-than-normal water temperatures (Bates et al. 2009, Eisenlord 2016). Rate of disease progression appears to be seasonally dependent in *Pisaster*, but much is still largely unknown about the virus is transferred or how the host reacts to infection (Fuess et al. 2015). As these intertidal communities rebuild along the Northeast Pacific shorelines after the 2014-2015 SSWD outbreak, it is critical to understand how these organisms change over time and how they function in challenging environments (Sanford 1999, Feder 1970, Monaco et al. 2015).

Consequences of Intertidal Conditions on *Pisaster* Morphology

The NE Pacific intertidal induces some of the most physiologically stressful environments in the Pacific Ocean (Carefoot 1977, Hayne 2011), requiring *Pisaster* to demonstrate adaptability to its environment (Denny 1988). Rocky intertidal habitats have diverse topographical features that affect water flow and subsequently impact sheltering, attachment, and predatory behaviors of adult and juvenile sea stars. Sea stars such as *Pisaster* must avoid dislodgement from waves by developing plastic anatomy in tube feet, planar area, and body shape. Optimal body structure is necessary for ensuring resistance to high drag and lift forces, particularly in wave-exposed locations (Denny 1988, Hayne 2011). Physical conditions, genetic predispositions, or ecological factors could influence developmental tracks or the degree of ecotypical plasticity that ultimately allow *Pisaster* to flourish in a wide array of environments.

Hayne's research on adult *Pisaster* morphological plasticity showed that wave exposure is highly correlated with body shape and is likely a phenotypic response to hydrodynamic forces in the intertidal (2011). Sea stars from exposed sites in British Columbia, Canada had significantly higher morphology aspect ratios relating arm width to length than those from sheltered sites. Transplanting individuals between wave-exposed to wave-sheltered sites revealed morphological variation in favor of prevailing site-specific seasonal wave exposure. Morphological plasticity was reciprocal in that *Pisaster* relocating from exposed to sheltered sites developed smaller aspect ratios and vice versa for sea stars transplanted from sheltered to exposed sites. Furthermore, Hayne found that larger aspect ratios were correlated with reduced lateral and planar areas that would consequently reduce drag and lift forces in high water flux (2011). Hayne's research confirmed body shape plasticity through experimental manipulation and related ecotypical adaptability to physical water flow forces in the intertidal. This work provides the experimental foundation for this thesis and justifies comparison of morphology aspect ratios between adult and juvenile populations at sites with differential wave exposure.

Pisaster must balance morphology with thermal regulation during emersion as sea stars with higher aspect ratios are at greater risk for overheating (Helmuth 1998). Asteroid water vascular systems are responsible for tube foot attachment and internal temperature management outside of intertidal water flux. Tube foot tenacity allows sea stars to have selective adhesion to hard substrata and manipulate hard shells of prey in the intertidal (Lawrence 2013). *Pisaster* redirects cooler water towards critical central disc tissue through coelomic cavity space in order to prevent internal temperatures from rising to lethal levels (Pincebourde et al. 2009, Pincebourde et al. 2013). Furthermore, episodic upwelling traditionally associated with El Niño-Southern Oscillations (ENSO) events and climate change trends negatively affect *Pisaster* feeding behavior and intertidal health by decreasing sea star fitness through allocation of energy reserves towards metabolism instead of reproductive fitness (Sanford 1999, Sanford 2002c, Hayne 2011, Fly et al. 2002, Pia et al. 2012).

Wave Exposure: Zinc Dissolution

Wave exposure is a primary abiotic factor involved in shaping intertidal community composition and diversity (Harley & Helmuth 2003). Denny (1988) defines wave exposure as an environmental determinant of an animal's body structure integrity. In addition, intermediate levels of disturbance via wave exposure are believed to stabilize and shape marine communities by limiting organism distribution and competitive exclusion (Kilar & McLachlan 1989). *Pisaster* fits into this model as a dominant predatory species with high adaptability to environmental variation in complex habitats. Acute emersion or short cyclic exposure to 9 and 12ºC seawater positively affects growth, feeding performance, and gonad production (Sanford 1999, Sanford 2002b, Sanford 2002c). *Pisaster*'s ability to navigate complex habitats and regulate the lower distribution and abundance of space-competitive organisms requires tenacity in light of environmental stressors.

Wave exposure encompasses tidal activity as well as water flux – the bulk movement of water past a point or through an area around physical barriers (Denny 1988; Harley & Helmuth 2003). Wave exposure introduces hydrodynamic complexity into an environment through currents, eddies, vortices and forces organisms to account for resulting drag and lift in their body plan (McGhee 1998, Boizard & DeWreede 2006). Marine scientists have developed various methods for quantifying water flux and wave exposure but these are often unreliable, difficult to calibrate, or impractical for comparing multiple sites in the same time range (Gaylord 1999). Bell and Denny (1994) noted that measuring rate of mass loss by a soluble material provides researchers a numerical measure of the overall water flux at a particular location in a study site. However, dissolution cannot provide instantaneous data about water flux magnitude, turbulence, or level of disturbance in a community (Gaylord 1999). Scientists employ dissolution to capitalize upon gathering data between sites and sample periods while reducing the cost of materials and resources.

Measuring the weight loss of a given material before and after wave exposure can serve as an indicator of flux between and within sites of interest (Jokiel and Morrissey 2006). The most commonly cited techniques for measuring water flux involving using dissolution of a solid material such as quartz, sucrose, or plaster of Paris over time (Boizard & DeWreede 2006). Plaster of Paris is a commonly cited in studies using dissolution as a measure of water activity because of its versatility and tolerance for 3-5 days of immersion (Palumbi 1984, Boizard & DeWreede 2006). However, plaster of Paris dissolves at a non-linear rate after it loses one-third of its mass and structural integrity is not consistent between batches or units (Palumbi 1984). Dissimilar metal corrosion can take place over a longer time scale than plaster of Paris (14 days versus 3-5 days, respectively) while maintaining a linear dissolution rate in the intertidal (Boizard & DeWreede 2006).

McGehee (1998) pioneered using corrosion rates of dissimilar metals for a measure of water flux, thereby functioning as a substitute material for plaster of Paris dissolution experiments. Two metals from opposite ends of the Noble Scale in contact with one another in the presence of an electrolyte will induce galvanic corrosion; ions from the anode flow out into the electrolyte and collect into a deposit on the cathode (Dexter & LeFontaine 1998, McGehee 1998). In this study, zinc and copper (anode and cathode, respectively) interacted with saltwater to induce electrolysis during wave exposure or water immersion in 13-day trials. Average percent change in zinc anode mass prior to and after intertidal deployment represents the total wave exposure at a selected site. Dissimilar metal dissolution serves as a long-term physical indicator of wave exposure and provides a snapshot of the environmental conditions *Pisaster* endures in their intertidal zone.

Wave Exposure: Intertidal Zonation

Distinct vertical bands of organisms at rocky intertidal habitats arise from of an organism's tolerance to environmental and biological stressors (Carefoot 1977, Raimondi 1988, Chapman & Underwood 1990, Gaylord 1999). Species abundance and zone distribution are influenced by desiccation and a lack of consistent water flow (Palumbi 1984, Raimondi 1988, Gaylord 1999). Ecological pressures such as space competition and predation work to shape lower zonation limits, particularly for mollusk species that are subject to ecological community engineering by *Pisaster* predation (Hutchins 1947, Jones & Demetropoulous 1968, Paine 1969, Carefoot 1977, Sanford 1999).

Grosberg (1982) asserts that vertical limits for intertidal zonation result from the following biological factors: (1) non-selective larval settlement, (2) substrata recognition at different intertidal heights by settling larvae, (3) mobile migrating adults, and (4) larval stratification in the water column resulting in larvae naturally settling at different heights. Although *Pisaster* is a mobile predator as an adult, these factors are important for initial site settlement when free-swimming brachiolaria enter into intertidal waters after swimming freely in the water column for up to eight months (Robles 2013). The biological and physical factors in play during wave exposure affects settlement, mortality, and proliferation in the intertidal and ultimately results in a stratified and diverse ecosystem (Harley & Helmuth 2003).

Morphologic plasticity facilitates efficient metabolic processes and reproductive fitness while imposing its own set of challenges in thermal regulation. Increased internal temperatures tend to occur at the upper limits of tolerance zones in wave-exposed sites. *Pisaster* that migrate too high above average exposure zones do not consistently receive enough cool water to compensate for thermal symptoms of desiccation despite having body shape adaptability to water flux. Conversely, sea stars in wave-sheltered environments can regulate their physiological responses to thermal and water variability via water uptake through the madreporite, yet are at greater risk for dislodgment in occasionally high water flux events (Hayne 2011). Chronic exposure to sublethal environmental conditions significantly reduces *Pisaster* feeding performance and imposes higher metabolic costs on the organism throughout its lifetime (Feder 1970, Sanford 2002c, Pincebourde et al. 2008, Fly et al. 2012, Lawrence 2013). Over time, this may result in the sea star not reaching sexual maturity or reducing fitness as a consequence of death or poor energy reserve storage in the pyloric caeca (Sanford & Menge 2007, Robles 2013).

Many intertidal species have developed special body forms and physiological processes that allow them to compensate for wave-induced drag and lift within their biological zone (Friedland & Denny 1995, Hurd 2000). Macroalgal species that form characteristic zonation patterns have been shown in lab and field studies to reduce drag, acceleration, and lift forces by maximizing upon their volume and developing narrower, flatter blades (Friendland & Denny 1995, Hurd 2000). Barnacles and mussels will alter their body structures by reforming shells to better accommodate water flow, strengthening podia attachment to substrata, or increasing byssal thread quantity (Carefoot 1977, Hayne 2011, Lawrence 2013).

General distribution of organisms in the littoral and intertidal zones can serve as a comparison of water activity across sites of interest (Jones & Demetropoulos 1968, Harley & Helmuth 2003). Harley and Helmuth (2003) detail that wave exposure drives intertidal communities along a vertical plane by balancing tolerances to water emersion and immersion. Habitats with upper zone limits set higher above mean low low water

(MLLW) can be categorized as being more wave-exposed than those environments sheltered from season flux with narrower ranges and upper zone limits closer to MLLW. Studying the mechanisms and outcomes of wave exposure is critical for understanding the intersection between biological and physical factors that shape intertidal diversity and ecology.

Experimental Hypotheses

In my thesis, I built upon ecotypical plasticity research conducted by Hayne (2011) by exploring how wave exposure affects juvenile and adult *Pisaster* population morphology along an environmental gradient of exposure. Aspect ratios relating radial length and arm width measured arm morphology and ratios comparing arm length to central disc diameter served as a body shape measure. Dissimilar metal dissolution and intertidal zonation described cumulative wave exposure. Together, these experiments provided a basis for a correlation and subsequent physiological response of *Pisaster* morphology to temporal and spatial changes in average wave exposure.

Intertidal zonation and dissimilar metal dissolution techniques independently measured the biological and physical factors associated with wave exposure. I hypothesized that upper limits of biological zones and percent change in zinc mass would be greater in environments experiencing more water flux. Consequently, *Pisaster* would have higher aspect and body shape ratios when populations inhabited habitats with greater average wave exposure. I further posited that there would be no significant difference in body shapes of adult and juvenile *Pisaster* populations because of exposure to similar environments after larval settlement.

Materials and Methods

Study Sites

Field surveys of *Pisaster* body sizes and shapes were performed in three locations near Charleston, OR from June – August 2015 (Figure 1): Middle Cove at Cape Arago (43º 18’13.93” N, 124º24’1.78” W), the South Jetty on Bastendorff Beach (43º21’8.73” N, 124º20’52.95” W), and the OIMB Boathouse Dock (43º20’54.44” N, 124º19’48.53” W). Middle Cove (MC), Bastendorff Beach (BA), and the OIMB Boathouse (OB) were selected to represent environments where *Pisaster* were exposed to different degrees of wave activity. Juvenile (N = 232) and adult (N = 128) sea stars were sampled in a variety of microhabitats including wave-exposed cliff faces, mussel beds, rocky crevices, and dock pilings (at OB only). Tidal heights were noted during each site visit from Charleston Marina Tide Table 2015 and 2016 records (http://www.charlestonmarina.com/tide.htm).

Wave Exposure: Zinc Dissolution

Wave exposure via dissimilar metal dissolution was measured at each site using methods adapted from previous literature (McGhee 1998, Boizard and DeWreede 2006). Dissimilar metals were deployed simultaneously at each site for 13-day trials during summer (August 15-28, 2015), fall (November 13-26, 2015), and winter (January 9-22, 2016) seasons. Poor weather conditions and logistical constraints prevented dissolution units from being deployed at BA in fall or winter trials, although data were collected at BA in the summer trial. Zinc anodes (length: 6.5 cm, diameter: 1.0 cm) and copper pipe segments (length: 5 cm, diameter: 1.6 cm) were used due to their availability and gradual dissolution rate within the Cape Arago environment. Dissolution units (Figure 2) comprised of two zinc/copper pairs were positioned in opposite directions and secured with thin strips of surgical tubing on PVC pipe (length: 13 cm, diameter: 2.2 cm). In addition, cement pads prepared prior to dissolution unit deployment with a mixture of 1 L freshwater and 10 g Speed-Crete Blue Line held bolt anchors and dissolution units in place throughout each trial.

In order to facilitate the retrieval of the dissolution units at night during the winter trial, PVC pipes were painted with one coat of Krylon® Special Purpose Fluorescent spray paint (Red Glowing Orange and Glowing Lemon Yellow). One half of the pipe was painted with Red Glowing Orange spray paint and the other half with Glowing Lemon Yellow paint to maximize color contrast against the variable surfaces in the intertidal. Krylon® Crystal Clear Acrylic Coating was applied on top of the colored spray paint layers to preserve their integrity during water immersion. Two fluorescent orange and yellow zip ties were then attached next to the metal rod pairs once the paint dried for six hours. The paints and zip ties fluoresced under application of an ultraviolet flashlight, thereby significantly decreasing dissolution unit retrieval time while minimizing impact on metal dissolution rates.

Zinc anodes and copper pipes were weighed separately with a Mettler PM400 scale before and after deployment in order to calculate the total percent loss of mass due to wave exposure. Although six cement pads were built at each site, only 4 – 10 dissolution units were measured due to cement pad degradation or unit disappearance during deployment in the field. Following their retrieval, dissolution units were dried in a constant laboratory environment for at least 3 hours after being rinsed with freshwater and separated into individual parts. Wave exposure was quantified through the average percent of zinc anode mass (g) lost via electrolysis-mediated dissolution. A 2-way ANOVA was used to compare dissolution between season and site of deployment.

Corrosion of dissimilar metals provides a long-term measure (weeks) of wave exposure in a particular space compared to other materials that are better suited for short-term measures (minutes to days), such as plaster of Paris, gypsum, or sucrose. Comparing water activity between sample sites and seasons allows for a year-round characterization of exposure that juvenile and adult *Pisaster* experience. For example, if there is a greater change in zinc mass dissolution at MC compared to OB after simultaneous deployment then *Pisaster* at MC likely experienced more wave exposure than those at OB in the same period.

Wave Exposure: Intertidal Zonation

Site-specific intertidal zonation was calculated separately from zinc dissolution as a biological measure of wave exposure. A site level was used to measure the upper limits of an organism's zones relative to average water level during data collection in August 2015. Mean upper zonation limits and water levels were corrected to account for tide chart data published in Charleston Marina Tide Table 2015 records (http://www.charlestonmarina.com/tide.htm). Distribution of selected invertebrate (*Balanus glandula* and *Mytilus* spp.) and algal species (*Saccharina sessilis* and *Neorhodomela oregona*) found at all three sites were used as references of wave exposure in separate 1-way ANOVA tests.

Pisaster Morphology

Sea stars that appeared healthy and had all five arms of similar sizes were haphazardly selected in the field for morphology measurements at MC, OB, and BA. *Pisaster* were collected from different locations within each site to prevent repeated measures of individuals. During each sampling period, sea stars were removed from rocks and allowed to rest in approximately two gallons of fresh seawater for 5 – 15 minutes until their bodies flattened against the container. This process ensured that sea star arms maximized lateral extension of arms prior to body size and shape measurements. Each individual was then placed on a flat surface and the planar side was photographed with a Pentax Optio WG-3 digital camera. *Pisaster* were returned to their approximate capture locations after photographs and wet weight (g) from an American Weigh ZX-600 g Digital Pocket Scale was recorded.

Wet weight measurements allow for size differences among individuals to be factored in morphology data analysis and provide a basis for distinguishing juveniles from adults. Size designations for *Pisaster* followed those outlined in Robles (2013) such that 70 g served as the break between juveniles and adults. Sexual maturity in *Pisaster* has been recorded in sea stars with a minimum wet weight of 70 g (Robles 2013). In this thesis, juveniles were defined as having a wet weight less than 70 g and adult sea stars as weighing 70 g or more.

Three aspects of *Pisaster* morphology were calculated in the laboratory using image analysis software on 72 dpi photographs of *Pisaster* body shape and size (Figure 3). Radial length (RL) was defined as the distance from the central point of the central disc to the tip of an arm. The central disc's radius—the distance from the central point to the base of each arm—was used to calculate the disc diameter (DD). Lastly, the width of each arm (AW) was measured where the arm joined the central disc. RL, AW, and DD were averaged across all five arms to give arm and body shape ratios that represented different measures of *Pisaster* morphology. Analysis of covariance tests (ANCOVA) were used to compare mean RL/AW or RL/DD ratios to wet weight of juveniles and adults between sites.

Software Programs

All data from morphological measurements and water flux experiments were compiled and organized in Microsoft Excel 2010. Google Earth 2015 was used to map the locations of each *Pisaster* sampling zone and dissolution unit deployment. *Pisaster* morphological measurements were made with ImageJ 1.49 software. All graphs were produced from SigmaPlot 12.5 and tables were made on Microsoft Word 2010. Statistical tests for each experiment were processed using RStudio Version 0.99.467.

Results

Wave Exposure: Zinc Dissolution

Zinc anode dissolution changed significantly between seasons and sites as a function of wave exposure (Table 1: $F_{1,30} = 11.39$, $p < 0.001$, $\eta^2 = 0.43$), however these results are likely altered due to methodology errors. The mean percent zinc loss during a trial increased at OB and decreased at MC from summer to winter (Figure 4A). Furthermore, the greatest differences in zinc dissolution between sites occurred during summer and winter trials. Similar proportions in zinc dissolution were measured at MC and OB during the fall trial. Overall, there was no significant difference in the mean zinc dissolution between sites over different seasons (Figure 4B). Although dissolution units were initially deployed at BA during the summer, hazardous environmental conditions prevented the site from being included in subsequent data collection or statistical analyses. A Tukey's HSD test revealed that there was not a significant difference in the mean percent of zinc dissolved at BA compared to MC or OB.

Wave Exposure: Intertidal Zonation

The upper boundaries of intertidal zones were measured for four species found near *Pisaster* at all three study sites (Figure 5). Space-competing species such as *B. glandula* and *Mytilus* spp. lived higher above MLLW than alga. Species' zone limits were significantly higher at MC and OB than at BA on average, suggesting that wave exposure produces significant differences in zone heights (Table 2). *B. glandula* (Table 3A: $F_{2,17} = 9.35$, $p < 0.01$, $\eta^2 = 0.52$), *Mytilus* spp. (Table 3B: $F_{2,7} = 1.54$, $p < 0.01$, $\eta^2 = 0.76$), *N. oregona* (Table 3C: $F_{2,12} = 21.28$, $p < 0.001$, $\eta^2 = 0.78$), and *S. sessilis* (Table

3D: $F_{2,15} = 5.7$, $p = 0.014$, $\eta^2 = 0.44$) were shown through 1-way ANOVA tests to live in zones with significantly different vertical distribution limits between sites. Tukey's HSD tests revealed that *N. oregona* was the only species in which zone limits were significantly higher at OB than at MC. Intertidal zonation appears to show that organisms at MC and OB experience more annual wave exposure than those at BA as seen by elevated upper habitation zone ranges relative to MLLW. However, there were no significant differences in exposure between OB and MC.

***Pisaster* Morphology**

Sea stars measured in sites with variable wave exposure exhibited significant differences in morphology aspect ratios (Table 4). Adult *Pisaster* from MC had significantly higher average RL/AW and RL/DD ratios than those from BA or OB. There were no significant differences in adult *Pisaster* morphological ratios for measured at BA and OB when adjusted for size differences. However, juvenile sea stars at OB had significantly higher mean aspect ratios than those at BA (Figures 6C and 6D). Individuals from MC can be therefore be characterized as having narrower arms and smaller central discs relative to arm length than stars of a similar size from OB or BA (Figures 6A and 6B).

Body shape ratios increased at a faster rate relative to body size in juveniles than in adults (Figures 7A and C). Juvenile *Pisaster* experienced the most rapid change in morphology until they reached sizes associated with sexual maturity (70-150 g wet weight); ratios began to plateau in individuals above 150 g wet weight. No juvenile *Pisaster* were found at MC during this study so it was not possible to demonstrate morphological convergence with other populations in the Cape Arago region. However, these data show that morphological variations in Pisaster populations arise after larval metamorphosis based on the degree of wave exposure in their habitat.

Increasing wave exposure was correlated with adult *Pisaster* morphological aspect ratios. Individuals from MC had higher aspect ratios for arm morphology (Table 5A: $F_{2,124} = 66.30$, $p < 0.001$) and overall body shape (Table 5B: $F_{2,120} = 47.10$, $p < 0.001$) relative to sea stars of a similar size at OB or BA. Site had a greater effect on observed variations in aspect ratios between sites than body size alone, explaining 97% of arm morphology and 44% of disc size to arm length, respectively. Lack of a significant interaction between site and body size suggests that wave exposure plays a greater role than age in determining how morphology is affected by water flux.

Juvenile sea stars exhibited similar morphological patterns similar to adults of their respective population in that aspect ratios were significantly higher at sites with more wave exposure (Figures 6C and 6D). Site of settlement ($F_{1,229} = 5.78$, $p = 0.017$, $\eta_p^2 = 0.025$) and body size via wet weight ($F_{1,229} = 4.42$, $p = 0.037$, $\eta_p^2 = 0.019$) had significantly affected population differences between OB and BA in arm morphology (Table 5C). Aspect ratios comparing RL and DD were also significantly affected by wave exposure (Table 5D; $F_{1,229} = 8.02$, $p < 0.01$, $\eta_p^2 = 0.034$), but not wet weight ($F_{1,229} = 3.29$, $p = 0.071$, $\eta_p^2 = 0.014$). Despite OB being exposed relative to BA from the perspective of juvenile morphology, it is likely that both sites are sheltered. Average aspect ratios for juveniles are below or meet those of their respective adult populations and no juvenile morphology data is available from MC to compare wave exposure throughout an organism's lifetime between all sites.

Discussion

Wave Exposure: Zinc Dissolution

Changes in wave exposure at MC and OB across common time periods were cumulatively measured using corrosion of dissimilar metals. Although there was statistical significance suggesting that wave exposure differed between sites across seasons; however, this significant interaction does not accurately portray flux conditions during this experiment. Errors in methodology and lack of control for mean intertidal height relative to chart datum likely skewed results from expected conditions, making it difficult to assert that exposure at MC and OB follows the patterns depicted in Figure 4. Dissolution at BA was not considered in statistical analysis due to environmental hazards during data collection and non-significant differences with OB during one season confirmed with Tukey's HSD test. Simultaneous water immersion of dissolution units at MC and OB allows for comparison of total wave exposure during trial periods and a physical foundation from which to correlate observed differences in *Pisaster* morphology.

More variability in the proportion of dissolved zinc was observed during the winter trial, a period characterized by annual averages of 6-8 m waves in the Cape Arago region (Fos and Davis 1978; Tilloston and Komar 1997). McGhee (1998) warned that areas with faster flow often result in a wider range of zinc weight loss. The dissolution data reflected this phenomenon as sites with more water exposure were associated with greater percent changes in zinc mass. OB saw an increasing trend in wave exposure intensity as seasons transitioned from summer to winter, whereas the proportion of zinc dissolved at MC decreased slightly. This demonstrates that *Pisaster* at OB may experience more seasonal variation in wave exposure and *Pisaster* at MC live in more consistent hydrodynamic conditions throughout the year sampled in this experiment.

Other environmental factors may have contributed to variable zinc dissolution at MC and OB throughout the study. Sand scour resulting from motion of sand particles across the surface of a dissolution pair during fall and winter trials would introduce an additional physical erosion factor into catalysts of dissolution. Increased freshwater runoff from storms with high levels of rainfall could have altered the amount of saltwater available for facilitating electrolysis in that less zinc would dissolve during winter trials. However, zinc anodes at OB dissolved more after winter trials than in the summer or fall so altered electrolyte salinity was not a significant factor behind these skewed results. Changes in overall water temperature across the Cape Arago region are also unlikely to be a large source of variation as MC and OB would have seen similar changes to mean zinc percent mass loss.

Changes in wind or swell direction during meteorological events could have induced abnormally high volumes of water movement past dissolution units during trials, potentially compromising the sheltering aspects of a habitat for intertidal organisms. Historical data from a Charleston, OR NOAA Tide and Current Station (Station ID: 9432780) show that wind directions changed from Southern to Northern winds during fall and winter trials (http://tidesandcurrents.noaa.gov/stationhome.html?-id=9432780&units=metric#info). OB's orientation to Coos Bay would result in greater prevailing exposure relative to normal conditions and likely increase dissolution unit immersion. Furthermore, predominately South and West-directed wind patterns during the summer trial would expose deployed dissolution units to increased bulk water movement into MC habitats. McGhee (1998) confirmed that the rate of dissimilar metal corrosion changes proportionally with the degree of water flux around dissimilar metal pairs, as measured by weighing the metals prior to and after immersion. Other studies examining dissolution of soluble material as an indication of water motion have also qualified that sites with higher wave motion or water flow are often associated with the highest proportions of mass lost after submersion (Palumbi 1984; Bell and Denny 1994; Boizard and DeWreede 2006).

Zinc dissolution served as a viable method for characterizing cumulative wave exposure in the field for a longer period of time with its many benefits outweighing its disadvantages. Many materials cited in the literature as tools for measuring water flux cannot maintain structural integrity in similar environmental conditions for the same time period that zinc and copper can. Dissolution of gypsum, plaster of Paris, and dynamometers take more immediate measurements of water flow (e.g. minutes or hours). This would require researchers to invest more materials, money, and effort to deploy and recapture devices in more trials before enough data can be collected to characterize a site as exposed or sheltered. Dissimilar metals such as zinc and copper largely retained their shape after approximately two week trials in Oregon intertidal habitats across a wide range of environmental exposure, allowing them to capture long-term summaries of water conditions that *Pisaster* experienced during the trial. Since *Pisaster* is a long-lived species, data recorded over a longer period provides more information about the conditions a typical sea star endures throughout the year at a particular site.

While this method provides useful data for longer measures of water flux, the mechanisms of its construction and deployment can be refined in future studies to prevent potential sources of error. The dissolution units were anchored onto a cement pad at different locations between and within sites with the assumption that they were as close to the same vertical height as possible. Failing to include this step in my methodology can potentially confound zinc dissolution by providing differential exposure times and variability in percent zinc corrosion within sites. It is critical that the dissolution units are immersed at the same time so that comparisons of zinc loss during a particular time frame can be made between sites. Using a site level to measure locations for cement pad construction (see Methods – Wave Exposure: Intertidal Zonation) in future experiments can ensure that dissolution units will be deployed at the same height and subsequently exposed to water motion simultaneously at all study sites.

Furthermore, some of the cement pad structures experienced slight erosion throughout the study and subsequently altered the stability of dissolution unit anchors from their original construction. It is possible that units may have rotated under high water motion during wave exposure, resulting in potentially more zinc dissolving than what would be expected than if the unit were stationary. These effects would be exaggerated in high water flux conditions, potentially resulting in inflated values, greater variability, and/or reduced validity of results in samples. The disappearance of cement pads or dissolution units during a trial could also serve as another source of error and variability. A poor cement mixture or compromised pad-rock settlement failure is likely the reason for degraded quality cement pads outside of environmental exposure. Similarly, poor anchoring technique for dissolution metal pairs to PVC pipes or dissolution units to the cement pads likely compromised dissimilar metal pair stability during trials, ultimately resulting in lost data points.

Corrosion of dissimilar metals in the presence of salt water could prove to be a reliable measure of water flux over time once flaws in methodology are controlled for. This method could be employed in a variety of habitats due to its cost-effective and low-maintenance nature. Zinc anodes never lost more than 15% of their total mass from water immersion and should subsequently dissolve at a relatively linear rate compared to plaster of Paris, which has been observed to lose more than 60% of its structure during a similar trial period (Jokiel and Morrissey 1993). These researchers warned that the rate of weight loss takes on an exponential decline at two weeks in the field. Although mass dissolution with zinc and copper are not as appropriate for short-term water flux measures like plaster of Paris, their durability allows them to withstand greater environmental pressures over a longer time scale while dissolving at a relatively constant rate. Future experiments utilizing this dissimilar metal corrosion method should increase their sample size (the amount of dissolution units deployed at each site) and the timescale of their measurements in order to gain more statistical power and a more confident assertion of the degree of water flux between targeted locations. Zinc dissolution appears to be a significant physical measure for comparison of cumulative wave exposure in environments inhabited by *Pisaster*.

Wave Exposure: Intertidal Zonation

Intertidal zonation functioned as a biological comparison of wave exposure between sites by relating the upper boundaries of vertical organism distribution to differences in water immersion. The average upper limits of *B. glandula*, *Mytilus* spp., *N. oregona*, and *S. sessilis* were higher at MC and OB than at BA, demonstrating that broader vertical zones of environmental tolerance are associated with increased annual wave exposure. Site location explained 44-78% of variation in observed zone limits for each species (Tukey's HSD tests, Tables 3A-3D). Furthermore, barnacles and mussels inhabited separate zones higher above MLLW than measured for algal species at all sites. With the exception of *N. oregona*, there were no significant differences between organism settlement above MLLW at MC and OB. Although this result contradicted my original hypothesis, small sample sizes and lack of replication likely contribute to the observed results. These data demonstrate a gradient of intertidal wave exposure between more wave-exposed sites such as MC and OB and wave-sheltered BA.

Pisaster's role as a keystone predator must balance physical and biological environmental factors as they regulate distribution of space-competing organisms and thermal tolerance. The physical interface between air and water at zonation boundaries affects how intertidal species balance homeostatic and reproductive requirements necessary for species proliferation (Carefoot 1977; Harley and Helmuth 2003). According to Sanford, intertidal zones shift vertically to accommodate changes in air and water temperature (2002a). Intertidal consumers such as *Pisaster* alter lower zone boundary predation on *Mytilus* spp. during upwelling events when they directly internalize declining sea temperature through their water vascular system (Sanford

2002a). Increasing wave exposure will drive intertidal communities upward from MLLW because of a decreased risk for desiccation and will likely change between seasons. Interactions between the biological and physical consequences of wave exposure provide the basis for food availability that *Pisaster* relies upon as an ecological engineer.

Climate events or experimental design may explain why there were no significant differences between intertidal zone upper limits at MC and OB for *B. glandula*, *Mytilus* spp., *N. oregona*, and *S. sessilis*. Small samples of zone limits for each species may have caused data to not be as representative of a species' true distribution at all sites. Intertidal communities in the Northeast Pacific intertidal were subject to an El Niño-South Oscillation (ENSO) event, the effects of which include inhibited offshore upwelling and nutrient availability deficiencies for primary producers (Glynn 1988; Wootton et al. 1996). The 2015 ENSO event may have diminished intertidal zone heights compared to a typical year or influenced the degree to which a site exposed or sheltered inhabitants from wave activity. Future studies utilizing intertidal zonation could test how zone upper limits change between seasons to better reflect annual variation in wave exposure at a site.

Intertidal zonation served as a biological indicator of wave exposure and complemented results obtained from physical flux measures with dissimilar metal dissolution. Both methodologies demonstrated that MC was a wave-exposed site on average through greater percent zinc mass lost during immersion and higher intertidal zones. Species at MC can live higher above MLLW without negatively impacting survival or reproductive fitness compared to more wave-sheltered locations such as OB or BA. Zinc dissolution and intertidal zonation confirmed variability in exposure at OB during the course of the study, and more research is needed to confirm the extent to which OB is sheltered from wave activity.

***Pisaster* Morphology**

Adult and juvenile *Pisaster* exhibited morphological differences among sites in the Cape Arago region. Adult sea stars from MC populations had higher arm and central disc body shape ratios on average compared to those of a similar size measured in OB and BA. Juveniles also showed significant variance in body morphology between sites but results were inconclusive due to absence of juvenile body size and shape data from an exposed population for comparison, such as *Pisaster* from MC. Poor larval recruitment, unfavorable environmental conditions for post-metamorphosis development, or an ENSO event likely factored into why juvenile *Pisaster* were not present at MC during this study. *Pisaster* are long-lived species and distinct aspects of morphology between separate populations show that their bodies average wave exposure across their lifetime.

Differences in *Pisaster* morphology could arise from distinct genetic pools or phenotypic plasticity driven by changes in the environment. If body plan were derived at the molecular level, morphological differences between populations at high- and low-exposure sites could develop as a result of reduced larval recruitment, increased mortality of stars with unfavorable body shapes, or selective juvenile recruitment into particular sites (Hayne 2011). However, *Pisaster* is panmictic despite relatively low population diversity from high proliferation of a homozygous lethal intron polymorphism (Pankey and Wares 2008). Free spawning distributes long-lived larvae larva that can spend up to eight months in the water column (Strathmann 1978) across large distances, so larval recruitment is unlikely to be the root cause of differences in body shape or size. The interaction between physical and biological factors at a site necessitates plasticity after larval settlement in order to adapt to spatial and temporal variation in wave exposure.

Pisaster appears to derive necessary morphology from their environment beginning after larval metamorphosis. Adults reached a maximum size after reaching sexual maturity and juvenile morphology changed rapidly with development (Figures 7A and 7B). *Pisaster* body shape ratios were significantly different between populations in sexually mature sea stars; however, morphology was nearly equal when juveniles were as small as 1.0 g. These data demonstrate that distinct morphologies arise after larval metamorphosis and that body shape adaptability is likely a consequence of environment or wave exposure. Juveniles tend to seek shelter from water flux by taking refuge in rock cracks or crevices until their tube foot tenacity can overcomes drag and lift forces (Feder 1970). Post-metamorphosis *Pisaster* may experience an accelerated growth rate to compensate for increased effects of wave exposure, thermal regulation, and metabolism requirements at a small size.

Research into *Pisaster* morphology could be expanded to incorporate experimental manipulations of phenotypic plasticity within an individual or their environment. Although aspect ratios for adult *Pisaster* were significantly higher at a MC, the nature of sea star plasticity could be tested through a transplant-recapture study utilizing methods implemented by Hayne and Palmer (2013). *Pisaster* transplanted from wave-exposed to wave-sheltered environments developed lower aspect ratios, and vice versa for sea stars transplanted from sheltered to exposed sites (Hayne and Palmer 2013). Future studies could also track how morphology changes for sea stars between seasons, particularly in sites with high water flux where environmental conditions can reduce mobility, reproductive fitness, or the amount of food available.

Conclusions

Dissimilar metals were shown to be reliable and durable materials for comparing long-term measurements of water activity between sites over a common time period.. Intertidal zonation served as a biological indicator of wave exposure by correlating upper settlement limits with average water immersion at a site. Distinct habitation zones arose between species within a site; however, there were no significant differences between MC and OB despite differences in observed sea star morphology between the two sites. Methodology issues and environmental conditions made it difficult to define study sites by quantified exposure or attribute regional variation in *Pisaster* body shape to wave exposure alone. Adult *Pisaster* from MC had longer, narrower arms and smaller central discs relative to other individuals of given weight from OB or BA. Although no juveniles were measured at MC during the course of this experiment, the data suggest that water flux is not the primary factor affecting morphological development after larval metamorphosis.

This thesis provides valuable insight into the mechanisms of environmental adaptability of a keystone species. By allocating resources towards changing body shape, *Pisaster* can maximize predation on space-competing organisms while reducing risk for dislodgement with a physically efficient body shape for its size. Diversity in *Pisaster* morphology both among and between populations has far-reaching effects on community composition and a species' reproductive fitness. Understanding how keystone organisms respond to environmental change is critical towards developing effective conservation strategies for the species and their subsequent habitats.

Figures

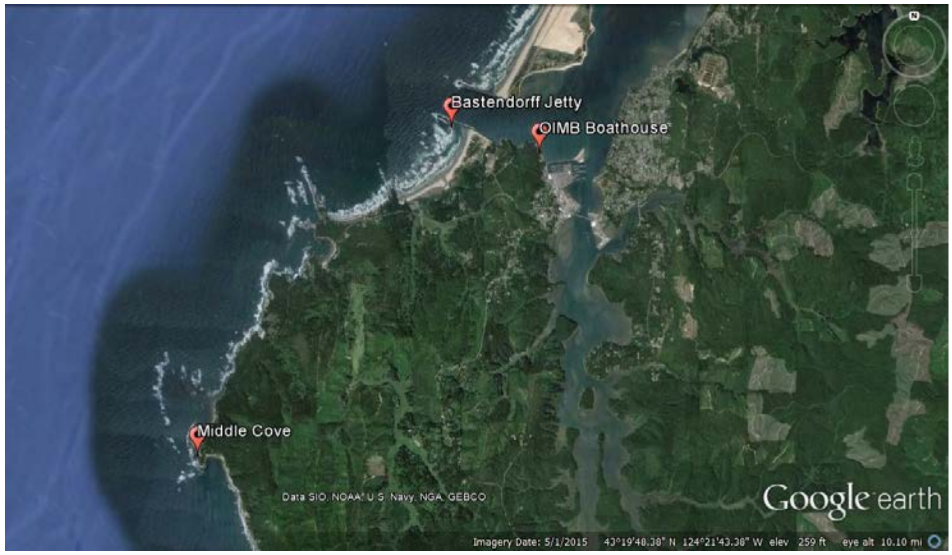

Figure 1. Study Site Locations.

Middle Cove (MC), Bastendorff Beach (BA), and OIMB Boathouse (OB) ranged in the degree of wave exposure near Charleston, OR in Cape Arago.

Figure 2. Dissolution Unit *In Situ*

Dissolution units consisting of dissimilar metal pairs and PVC pipe were anchored onto cement pads at MC and OB intertidal habitats to measure long-term wave exposure. Dissolution data were not collected at BA in fall or winter trials.

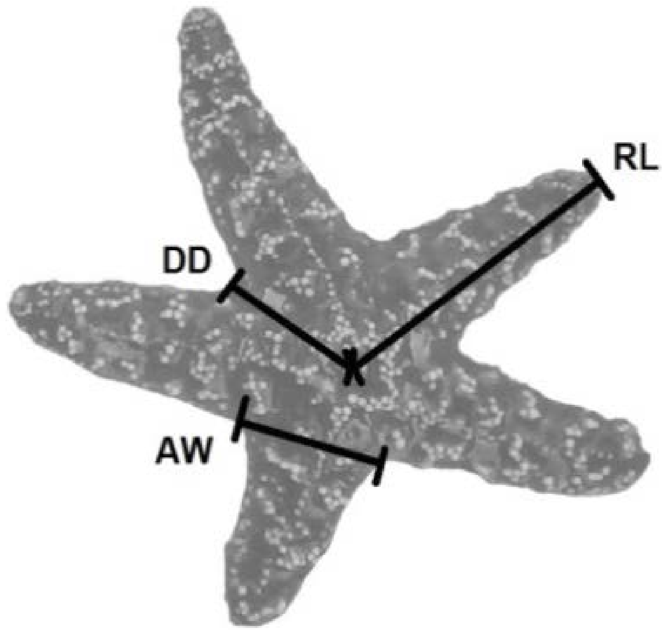

Figure 3. *Pisaster* Morphology: Body Shape Ratio Components

Each *Pisaster* was measured for radial length (RL), disc diameter (DD), and arm width (AW) on all five arms with imaging software to generate morphology ratios.

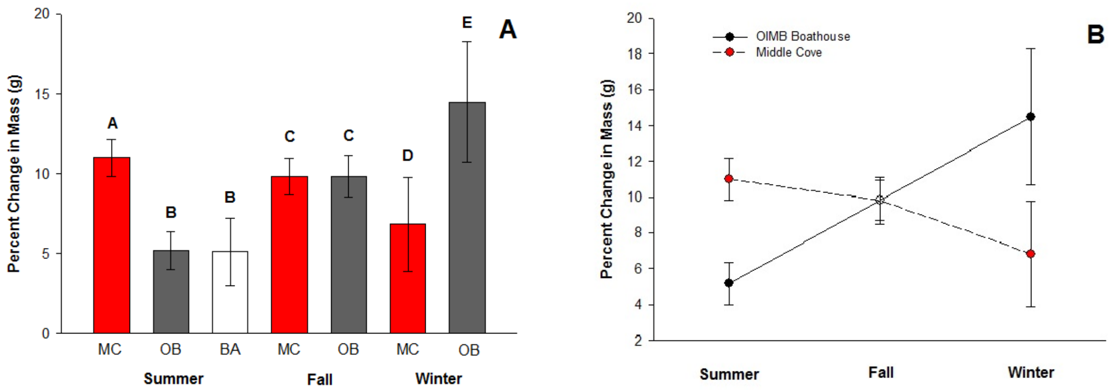

Figure 4. Wave Exposure: Zinc Dissolution

4A: The average percent change in zinc mass deployed differed significantly at each site between seasons.

4B: Seasonal variability in water flux conditions played a significant role on the change in observed zinc mass during a trial at each sample site.

Bars indicate ± Standard Error

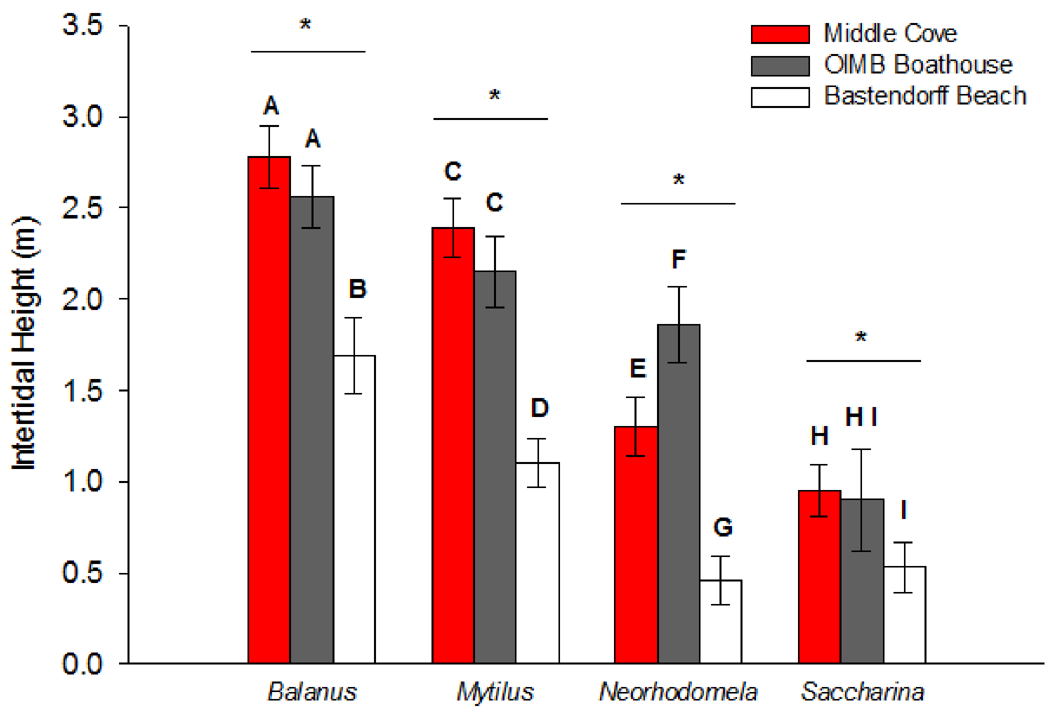

Figure 5. Wave Exposure: Intertidal Zonation

Upper limits of intertidal zonation heights differed significantly between study site and species. On average, organisms at MC and OB had higher upper limits on their habitable zones than at BA.

Bars indicate ± Standard Error

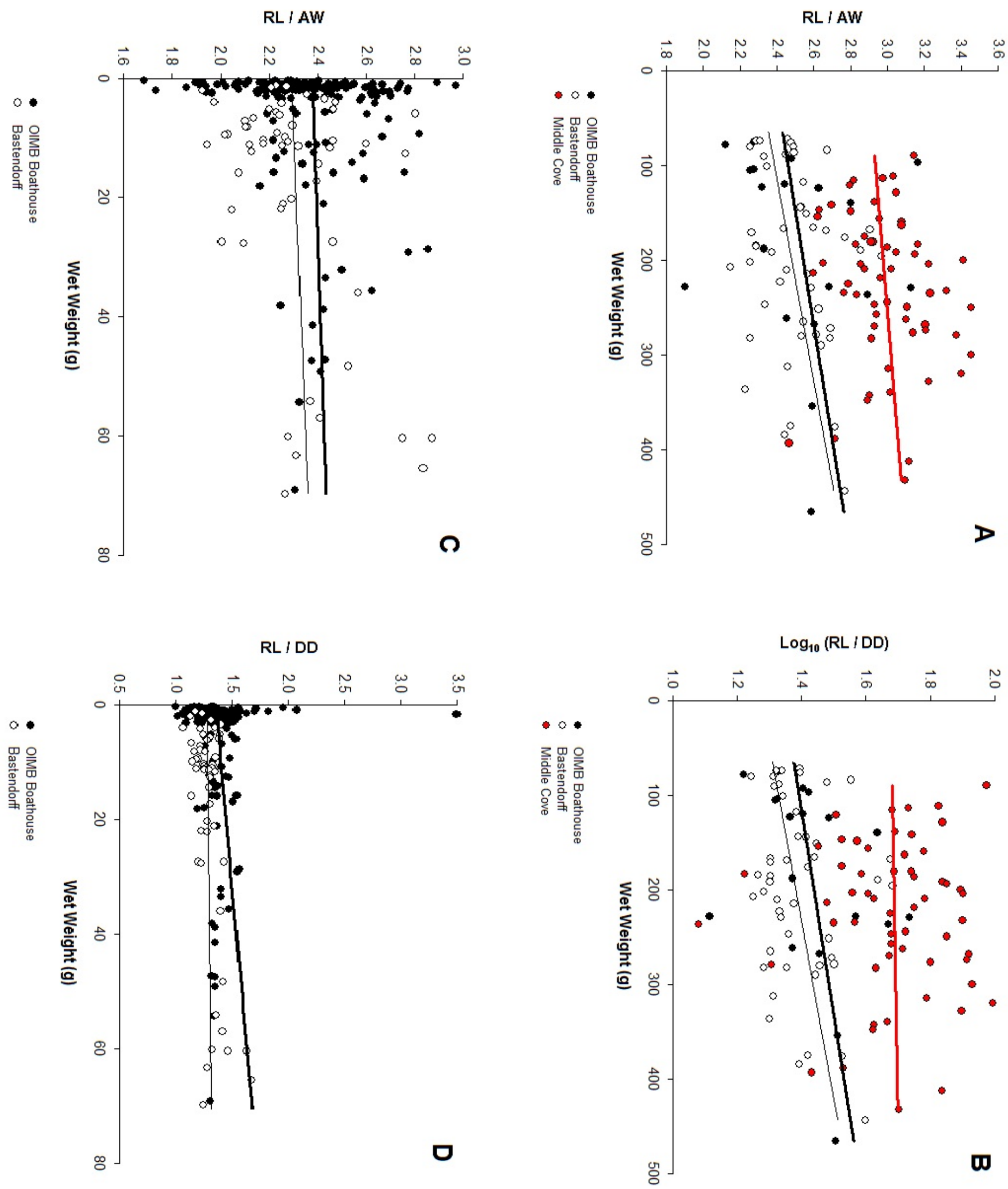

Figure 6. *Pisaster* Morphology: Body shape Ratios by Wet Weight (g)

6A, 6B: Adult *Pisaster* from MC had significantly higher body shape ratios on average than those from OB or BA.

6C, 6D: Juvenile sea stars from OB had higher ratios than those from BA. No juvenile *Pisaster* were found at MC during the sampling period.

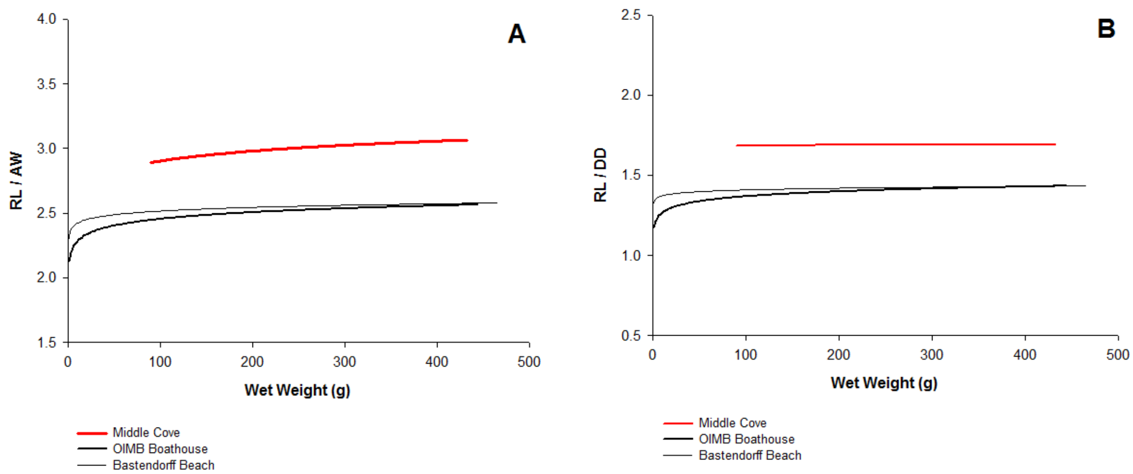

Figure 7. *Pisaster* Morphology: All Juveniles and Adults

7A: Sea stars appear to respond to wave exposure post-metamorphosis.
7B: *Pisaster* body shape development may be affected by wave exposure but more sampling from exposed sights is needed. Outlier not included in this graph.

Tables

Factor	df	Sum Sq	F-value	p-value	η^2
Site	1	13.58	1.21	0.28	0.039
Season	2	55.07	2.44	0.10	0.1
Site : Season	2	256.21	11.39	< 0.001	0.43
Residuals	30	337.36			

Table 1. 2-way ANOVA for Zinc Dissolution

The mean percent loss of zinc mass at each site changes with seasonality of wave exposure.

Species	Mean Upper Zone Limit (m) ± SE		
	MC	OB	BA
Balanus glandula	2.78 ± 0.17	2.56 ± 0.17	1.69 ± 0.20
Mytilus spp.	2.39 ± 0.16	2.15 ± 0.20	1.10 ± 0.13
Neorhodomela oregona	1.30 ± 0.16	1.86 ± 0.20	0.46 ± 0.13
Saccharina sessilis	0.95 ± 0.14	0.90 ± 0.28	0.53 ± 0.14

Table 2. Mean Intertidal Upper Zone Limits

Intertidal zone boundaries for four species found at MC, OB, and BA changed with wave exposure. Selected invertebrate species could tolerate more water emersion than alga, as evidenced by higher mean limits relative to MLLW.

SE = Standard Error

A

Factor	df	Sum Sq	F-statistic	p-value	η^2
Site	2	4.18	9.35	< 0.01	0.52
Residuals	17	3.79			

B

Factor	df	Sum Sq	F-statistic	p-value	η^2
Site	2	3.08	1.54	< 0.01	0.76
Residuals	7	0.95			

C

Factor	df	Sum Sq	F-statistic	p-value	η^2
Site	2	4.07	21.28	< 0.001	0.78
Residuals	12	1.15			

D

Factor	df	Sum Sq	F-statistic	p-value	η^2
Site	2	1.04	5.79	0.014	0.44
Residuals	15	1.34			

Table 3. 1-way ANOVAs for Intertidal Zonation Species

3A: *Balanus glandula*

3B: *Mytilus* spp.

3C: *Neorhodomela oregona*

3**D**: *Saccharina sessilis*

There were significant differences between upper limits of zones for each species tested, indicating that wave exposure plays an important role in vertical intertidal species distribution.

Aspect Ratio	Population	Mean Body Shape Ratio ± SE	
		Juvenile	Adult
RL / AW	MC	−	2.99 ± 0.22
	OB	2.39 ± 0.046	2.59 ± 0.30
	BA	2.26 ± 0.024	2.54 ± 0.20
RL / DD	MC	−	1.68 ± 0.020 **
	OB	1.35 ± 0.028	1.43 ± 0.036 **
	BA	1.26 ± 0.015	1.39 ± 0.023 **

Table 4. Mean Morphology Body Shape Ratios

Mean shape ratios in juveniles and adults appeared to increase with wave exposure.

**Transformed by $\log_{10}$ to account for violation of normality assumption required for ANCOVA.

SE = Standard Error

A

Factor	df	Sum Sq	F-value	p-value	η_p^2
Intercept	1	93.45	1868.55	< 0.001	0.94
Site	2	6.63	66.30	< 0.001	0.97
Weight	1	0.20	4.01	0.048	0.031
Residuals	124	6.20			

B

Factor	df	Sum Sq	F-value	p-value	η_p^2
Intercept	1	0.27	139.08	< 0.001	0.54
Site	2	0.18	47.10	< 0.001	0.44
Weight	1	0.0038	1.96	0.16	0.016
Residuals	120	0.23			

C

Factor	df	Sum Sq	F-value	p-value	η_p^2
Intercept	1	187.59	1842.43	< 0.001	0.89
Site	1	0.59	5.78	0.017	0.025
Weight	1	0.45	4.42	0.037	0.019
Residuals	229	23.32			

D

Factor	df	Sum Sq	F-value	p-value	η_p^2
Intercept	1	58.14	1467.01	< 0.001	0.86
Site	1	0.32	8.02	< 0.01	0.034
Weight	1	0.13	3.29	0.071	0.014
Residuals	229	9.08			

Table 5. ANCOVAs for Sea Star Body Shape Ratios by Wet Weight (g)

5A: Adult RL/AW

5B: Adult RL/DD**

5C: Juvenile RL/AW

5**D**: Juvenile RL/DD

**Transformed by $\log_{10}$ to account for violation of normality assumption.

Type III Sums of Squares Performed

Differences in wave exposure at each site were associated with significantly higher body shape ratios in juvenile and adult *Pisaster*.

Bibliography

Bates AE, Hilton BJ, Harley CDG (2009) Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. Dis Aquat Organ 86: 245-251.

Bell EC, Denny MW (1994) Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. J Exp Mar Biol Ecol 181: 9-29.

Boizard SD, DeWreede RE (2006) Inexpensive water motion measurement devices and techniques and their utility in macroalgal ecology: a review. ScienceAsia 32: 43-49.

Carefoot T (1977) Pacific seashores: a guide to intertidal ecology. University of Washington Press, Seattle, WA.

Chapman ARO, Underwood AJ (1990) Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192: 21-33.

Denny MW (1988) Biology and Mechanics of the Wave-Swept Environment. Princeton University Press, Princeton, NJ.

Dexter SC, LaFontaine JP (1998) Effect of natural marine biofilms on galvanic corrosion. Corrosion 54: 851-861.

Eisenlord ME, Groner ML, Yohioka RM, Elliot J, Maynard J, Fradkin S, Turner M, Pyne K, Rivlin N, van Hooidonk R, Harvell CD (2016) Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. Philos T Roy Soc B 371: 20150212.

Feder HM (1970) Growth and predation by the ochre sea star, Pisaster ochraceus (Brandt), in Monterey Bay, California. Ophelia 8: 161-185.

Friedland MT, Denny MW (1995) Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). J Exp Mar Biol Ecol 190: 109-133.

Frontana-Uribe S, de la Rosa-Vélez J, Enriquez-Paredes L, Ladah LB, Sanvicente-Añorve L (2008) Lack of genetic evidence for the subspeciation of *Pisaster ochraceus* (Echinodermata: Asteroidea) in the north-eastern Pacific Ocean. J Mar Biol Assoc U.K. 88: 395-400.

Fuess LE, Eisenlord ME, Closek CJ, Tracy AM, Mauntz R, Gignoux-Wolfsohn S, Moritsch MM, Yoshioka R, Burge CA, Harvell CD, Friedman CS, Hewson I, Hershberger PK, Roberts SB (2015) Up in arms: immune and nervous system response to Sea Star Wasting Disease. PLoS ONE10: e0133053.

Gaylord B (1999) Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. J Exp Mar Biol Ecol 239: 85-124.

Glynn PW (1988) El Niño-Southern Oscillation 1982-1983: Nearshore population, community, and ecosystem responses. Annu Rev Ecol Evol Syst19: 309-345.

Grosberg RK (1982) Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. Ecology 63: 894-899.

Harley CDG, Helmuth BST (2003) Local- and regional-scale patterns of wave exposure, thermal stress, and absolute effective shore level on patterns of intertidal zonation. Limnol Oceanogr 48: 1498-1508.

Hayne KR (2011) Plastic phenotypic responses of the sea star *Pisaster ochraceus* to spatial and temporal variation in wave exposure. Dissertation, University of Alberta, Edmonton, Alberta.

Hayne KR, Palmer AR (2013) Intertidal sea stars (*Pisaster ochraceus*) alter body shape in response to wave action. J Exp Biol 216: 1717-1725.

Hennebert E, Haesaerts D, Dubois P, Flammang P (2010) Evaluation of the different forces brought into play during tube foot activities in sea stars. J Exp Biol 21: 1162-1174.

Hewson I, Button JB, Gudenkauf BM, Miner B, Newton AL, Gaydos JK, Wynne J, Groves CL, Hendler G, Murray M, Fradkin S, Breitbart M, Fahsbender E, Laffert KD, Kilpatrick AM, Miner CM, Raimondi R, Lahner L, Friedman CS, Daniels S, Haulena M, Marliave J, Burge CA, Eisenlord ME, Harvell CD (2014) Densovirus associated with sea-star wasting disease and mass mortality. P Natl Acad Sci USA 111:17278-17283.

Hurd, CL (2000) Water motion, marine macroalgal physiology, and production. J Phycol 36: 453-472.

Hutchins LW (1947) The Bases for Temperature Zonation in Geographical Distribution. Ecol Monogr 17: 325-335.

Jones WE, Demetropoulos A (1968) Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey. J Exp Mar Biol Ecol 2: 46-63.

Jokiel PL, Morrissey JI (1993) Water motion on coral reefs: evaluation of the ‘clod card’ technique. Mar Ecol Prog Ser 93:175-181.

Kilar JA, McLachlan J (1989) Effects of wave exposure on the community structure of a plant-dominated, fringing-reef platform: Intermediate disturbance and disturbance-mediated competition. Mar Ecol Prog Ser 54: 265-276.

Lawrence JM (2013) Starfish: biology and ecology of the Asteroidea. The Johns Hopkins University Press, Baltimore, MD.

McGhee MA (1998) Comparisons of water motion in coral reefs by measuring corrosion rates of dissimilar metals. Caribb J Sci 239: 286-297.

Monaco CJ, Wethey DS, Gulledge S, Helmuth B (2015) Shore-level size gradients and thermal refuge use in the predatory sea star *Pisaster ochraceus*: the role of environmental stressors. Mar Ecol Prog Ser 539:191-205.

Paine RT (1969) The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50: 950-961.

Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal provider. Oecologia 15: 93-120.

Palumbi SR (1984) Measuring intertidal wave forces. J Exp Mar Biol Ecol 81: 171-179.

Pankey MS, Wares JP (2008) Overdominant maintenance of diversity in the sea star *Pisaster ochraceus*. J Evolutionary Biol 22: 80-87.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills S, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. BioScience 46: 609-620.

Pia TS, Johnson T, George SB (2012) Salinity-induced morphological changes in *Pisaster ochraceus* (Echinodermata: Asteroidea) larvae. J Plankton Res 0: 1-12.

Pincebourde S, Sanford E, Helmuth B (2009) An intertidal sea star adjust thermal inertia to avoid extreme body temperature. Am Nat 174: 890-897.

Raimondi PT (1988) Settlement cues and determination of the vertical limit of an intertidal barnacle. Ecology 69: 400-407.

Robles C (2013) Pisaster ochraceus. In: Lawrence JM (ed) Starfish: biology and ecology of the Asteroidea. The Johns Hopkins University Press, Baltimore, MD, p 161-173.

Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. Science 283: 2095-2097.

Sanford E (2002a) Community responses to climate change: Links between temperature and keystone predation in a rocky intertidal system. In: Schneider SH, Root TL (ed) Wildlife response to climate change: North American case studies. Island Press, Washington D.C., p 165-200.

Sanford E (2002b) The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. J Exp Mar Biol Ecol 273: 199-218.

Sanford E (2002c) Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. Integr Comp Biol 42: 881-891.

Sanford E, Menge BA (2007) Reproductive output and consistency of source populations in the sea star *Pisaster ochraceus*. Mar Ecol Prog Ser 349: 1-12.

Santos R, Gorb S, Jamar V, Flammang P (2005) Adhesion of echinoderm tube feet to rough surfaces. J Exp Biol 208: 2555-2567.

Strathmann R (1978) Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. J Exp Mar Biol Ecol 34: 23-27.

Tilloston K, Komar PD (1997) The wave climate of the Pacific Northwest (Oregon and Washington): a comparison of data sources. J Coastal Res 13: 440-452.

Wootton JT, Power ME, Paine RT, Pfister CA (1996) Effects of productivity, consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal community. P Natl Acad Sci USA 93: 13855-13858.