

**DO PURPLE SEA URCHINS ALTER THEIR MORPHOLOGY IN
RESPONSE TO VARIATION IN PREDATOR ABUNDANCE AND
RESOURCE AVAILABILITY?**

A THESIS

Presented to

The Faculty of the Environmental Studies Program

The Colorado College

In Partial Fulfillment of the Requirements for the Degree

Bachelor of Arts in Environmental Science

By

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May 2020



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Abstract

Predators can trigger defensive traits in their prey through a variety of mechanisms. We studied whether predators stimulate inducible defenses of sea urchins in temperate kelp forests in the Northern Channel Islands of Southern California. We hypothesized that inside of Marine Protected Areas (MPAs), where fishing is completely restricted or limited, urchins would be better defended than in fished areas due to the recovery of predators in the MPAs. We collected urchins from four management zones that varied in predator and resource abundance and measured variation in three defensive traits: load resistance, spine length, and test thickness. While we did not find strong differences in load resistance or test thickness between management zones, we did document significant variation in spine length. However, this variation was attributed to resource abundance but not predator abundance, suggesting that resource availability may interact with urchin behavior to influence this trait. Urchins develop longer spines when resource abundance is minimal because they must be exposed while searching for food, placing them at higher risk of predation even when predator abundance is low. Urchins also showed energetic trade-offs between distinct defensive traits and between defensive traits and reproduction, further suggesting that different habitat types impact how urchins allocate resources towards their morphology. Lastly, we found strong variation in gonadosomatic index and spine lengths between sampling zones directly adjacent to one another, demonstrating the plasticity and lack of mobility of purple urchins. Our findings suggest that the morphological responses of purple urchins to changing environments reflect the plasticity of these animals, and therefore, the challenges present in kelp forest community returning to natural states without direct human-management techniques.

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Abstract

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Acknowledgements

I am incredibly grateful for everyone who has helped me throughout this process. I would like to acknowledge Dr. Rebecca Barnes for not only supporting me for the duration of my Colorado College career, but also for the entirety of this project in a topic that was completely new to her. Dr. Barnes has instilled a confidence in myself as a scientist and a person, and has provided me with the skills I need to move forward.

I would also like to thank my REU program at the University of California, Santa Barbara this past summer for providing me with this research experience. I am grateful for Dr. Jenn Caselle who including me in her lab and provided me with such an impactful learning experience. I am appreciative of all the members of the Caselle Lab for welcoming me into their community and assisting in field collection and data processing for hours on end. Within the Caselle Lab, I would especially like to thank Katie Davis Koehn for guiding me throughout this project. She aided in improving my comprehension of the scientific method, introduced me to programming in R, challenged me to think deeper about our findings, and has continued to assist in the creation of this thesis following our summers work.

I would like to continue to send my appreciations to my family and friends for always encouraging me to study science and continuously providing me with the support I need to hopefully succeed as an environmental steward in my future. Lastly, thank you to the National Science Foundation for funding this research.

I. Introduction

Marine biodiversity has declined globally, requiring the development of ecosystem-based management strategies to confront widespread ecological degradation and its subsequent impact on ecosystem services (Fraschetti et al., 2011). To address the impacts of human-induced stressors throughout marine ecosystems around the world, different countries have a long history of implementing Marine Protected Areas (MPAs). MPAs are an ecosystem-based management approach that create stricter fishing regulations or completely prohibit fishing in designated geographical regions (Fox et al., 2013). Rather than conserving individual marine species, MPAs incorporate precautionary resource and ecosystem management principles to protect entire ecological systems with the goal of returning them to their natural functional states (Williams, 1998). This holistic management approach allows for the integration of fisheries management and conservation goals. The restoration of fish stocks within MPAs has the potential to enhance fisheries outside of their borders. MPAs allow humans to continue to utilize economic and social resources from the world's oceans while simultaneously sustaining marine systems for future use (Williams, 1998).

Many protocols and treaties exist worldwide to address marine degradation caused by anthropogenic mechanisms such as fisheries, water pollution, and shipping (Kelleher & Kenchington, 1991). The initial legal framework for MPAs came from the United Nations Conference between 1973 and 1977 on the Law of the Sea (Kelleher & Kenchington, 1991). Currently, over 26,000,000 km² or 7.43% of the world's oceans are designated MPAs (UNEP-WCMC and IUCN, 2020). On the Pacific Coast of the United States, MPAs have been used as a management tool for the past century (Gleason et al., 2013). Currently, over 16% of California's

coastal waters are protected via the Marine Life Protection Act (MLPA), which connects all of California's MPAs under the same management network (Fox et al., 2013; Obegi, 2005).

MPAs have been implemented on the Pacific Coast of the United States to address continued human exploitation of available marine resources. The degradation of the coastline has resulted in cascading effects on ecosystem structures, transforming numerous marine ecosystems to undesirable states (Gleason et al., 2013). In particular, the overfishing of predators in these temperate rocky reef communities has led to trophic cascades, the most common of which shifts rocky reefs from kelp forest communities to urchin barrens (Paine & Vadas, 1969; Harrold & Reed, 1985; Schiel & Foster, 1986; Estes et al, 1998; Sala et al., 1998; Tegner & Dayton, 2000; Behrens & Lafferty, 2004). MPAs are one of the tools that coastal managers have implemented to minimize these fishing pressures and allow ecosystems to return to their pre-fishing or natural states.

In the Channel Islands of southern California, MPAs have been used to address the degradation of healthy ecosystem interactions in kelp forest communities. Giant Kelp (*Macrocystis pyrifera*) is the foundational species on which much coastal biodiversity depends. Herbivores, like purple urchins (*Strongylocentrotus purpuratus*), regulate kelp abundance and in excess they can overgraze the kelp (Tegner & Dayton, 2000). Predators like California spiny lobster (*Panulirus interruptus*) and California sheephead (*Semicossyphus pulcher*) indirectly sustain giant kelp by regulating purple urchin populations (Behrens & Lafferty, 2004; Caselle et al., 2018). The removal of these predators through fishing can lead to an influx of purple urchins, consequently

depleting the kelp population which results in the loss of a major ecological niche (Ling et al., 2015; Graham, 2004).

Ecosystem hysteresis helps stabilize communities in alternative states after a disturbance-induced shift. In kelp forests, the shifts between states are path-dependent, meaning that the direction in which changes occur impacts how these changes transpire (Scheffer et al., 2001). In the case of kelp forest communities, overfishing results in cascading effects which promote the ecosystem to move from kelp forest dominated to urchin dominated rocky-reef systems. These shifts from kelp forest to urchin barren reinforce themselves through positive feedbacks. In temperate rocky reef systems in Australia, an influx of urchin grazing resulting from the overfishing of top-predators prompts catastrophic shifts from kelp beds to urchin barrens. When urchins overgraze kelp beds, ecosystem feedbacks result in continued macroalgal depletion, further challenging the ability of the ecosystem to revert to a kelp forest state (Ling et al., 2015). Drastic measures must be taken to shift urchin barrens back to abundant kelp forests.

Kelp forest communities provide many ecosystem services and thus must be conserved. Kelp provides economic value via fisheries and recreation, and it may sequester impactful sums of carbon (Vásquez et al., 2014). Kelp beds are a crucial habitat for many marine invertebrates and fish and without these habitats, biodiversity will be lost. The deforestation of giant kelp from the effects of trophic cascades results in a shift in the primary producers towards ephemeral algae, which impacts all trophic levels that rely-upon the macroalgae structure (Graham, 2004). Consequently, measures taken to sustain kelp forest communities have far-reaching implications for humans and the biodiversity of rocky-reef ecosystems.

MPAs have aided in developing more resilient kelp forest communities (Caselle et al., 2018; Behrens & Lafferty, 2004). The Channel Island MPAs, implemented in 2003, was the first network to be established in California and included one historical protected area dating back to 1978. In some regions of the Channel Islands, the top-down effects of fishing increased urchin populations and depleted kelp forests (Behrens & Lafferty, 2004; Hamilton & Caselle, 2015; Caselle et al., 2018). The use of the Channel Island's MPA network may result in more resilient kelp forests than those in fished regions. For example, in the Northern Channel Islands, removing fishing pressure in MPAs resulted in larger sheephead populations and thus healthier and more resilient kelp forests (Hamilton & Caselle, 2015; Eisaguirre et al 2020). Caselle et al. (2018) also found that ecosystems protected by older MPAs were more resilient to the invasive species than the newer MPAs, illustrating the power of long-lasting MPAs to sustain kelp forests, even in an area with severe human impacts (Caselle et al., 2018; Eisaguirre et al. 2020).

The direct and indirect impacts of altered predation threat and resource availability caused by differing management strategies impacts both urchin behavior and physiology. Understanding the effect of altered community structure on urchin behavior and physiology is pivotal for comprehending the implications of differing management strategies. The return of top-predators like spiny lobsters and California sheephead directly regulates urchin populations, which indirectly recovers kelp beds (Behrens & Lafferty, 2004). Furthermore, an increase in top-predators also indirectly impacts the behavior and physiology of purple urchins by altering food availability, hiding spaces, and overall responses to predation threat (Selden et al., 2009; Matassa, 2010; Haag et al., 2016). Consequently, the addition of MPAs is crucial to the stability

of kelp forest communities in regions where fishing has created cascading effects because of the direct and indirect effects predators invoke on all trophic levels in these communities (Behrens & Lafferty, 2004).

The availability of macroalgae indirectly alters how purple urchins graze. Macroalgae consist of fronds that are discarded to the ocean floor as they age. Fronds decompose into pieces that either become benthic detritus or float through the water column as drift. Urchins can sedentarily feed rather than actively graze on kelp in the form of drift or benthic detritus that is captured in cracks and crevices on the reef (Harrold and Reed, 1985). Within MPAs where predation threat is high and food is abundant, purple urchins can hide from predators and sedentarily feed on drift kelp to survive (Nichols et al., 2015). This cryptic change in urchin behavior within MPAs further supports more resilient kelp forests because the urchins do not actively graze on the living kelp.

The increased abundance of predators inside of MPAs could also indirectly change purple urchin feeding behavior due to risk aversion. Matassa (2010) conducted an experiment which showed that urchins exposed to higher abundances of spiny lobsters responded by decreasing their feeding rates. However, studies examining urchin feeding response to predator presence have mixed results. One study showed that when predators are prevalent, urchins remain cryptic in pits rather than actively foraging for food (Haag et al. 2016), while a similar study showed that urchins under increased predation risk prioritized consuming kelp over protecting themselves (Green, 2012). Each of these studies were conducted in a lab, but differ in how they manipulated the presence of predators. Haag (2016) and colleagues physically exposed urchins to spiny lobsters, while Green (2012) cut the spines of the urchins to induce conspecific stress cues

associated with predation. These contrasting results suggest that purple urchins show variability in their behavior depending on the type of predation threat and food availability in their respective ecosystems (Haag et al., 2016; Green 2012)

Predation threat and food availability not only influence the behavior of purple urchins, but also impact their physiology. Urchin skeletons consist of calcite plates that connect to one another at the sutures via ligaments (Selden et al., 2009). These echinoderms change in structure on a spectrum of rigidity throughout their life depending on the thickness of their skeletal walls and the strength of their connective ligaments. To grow, urchins accrete calcite on the edges of existing plates or grow new plates. The structural strength of an urchin is dependent on both the strength of the binding of the suture ligaments and the physical thickness of each individual plate (Ellers et al., 1998). Springing from their skeleton plates, urchins have an additional defense: calcite spines (Tegner & Levin, 1983). Thus, measuring spine length, test thickness, and the physical strength of the test can inform about the morphological defenses of purple urchins. Purple urchins are known to show phenotypic plasticity in the face of environmental stresses such as limited food availability (Russell, 1987), potentially resulting in differences in urchin physiology between habitat types. Habitat types differ based on factors such as the availability of food and the potential threat of predators. In environments where urchins are food-stressed, they adapt to consume as much food as possible, sometimes changing their method of grazing. Thus, food availability and predation threats affect how urchins allocate their energy. For example, urchins in food-limited habitats have been shown to allocate their resources towards developing larger jaws to promote better food consumption capabilities (Edwards & Ebert, 1991; Selden et al., 2009). Similarly, food-limited urchins with spine damage increase energy allocation towards

their tests rather than their spines (Edwards & Ebert, 1991). These morphological differences represent how variation in habitat type influence the physical responses of urchins, potentially impacting predator-prey dynamics and food web structures.

Another aspect of urchin physiology which can be impacted by habitat and food availability is reproductive potential. The energy-rich gonads, which are sought by potential predators, are where urchins store gametes and nutritive phagocyte cells throughout the multistep process of gametogenesis (Dodge & Edwards, 2012; Moehrlin and Juliano, 1998; Wade and Jones, 2004). The process includes the buildup of nutrients in the nutritive phagocyte cells, which then are transferred into the gamete cells. Once gametes reach maturity, they are spawned through the gonadopores, and the entire process restarts (Chatlynne, 1969). The stage of gametogenesis determines how much energy urchins must allocate to their reproductive cycle. Furthermore, both the quantity and quality of food impacts an urchin's gonad mass (Dodge and Edwards, 2012). Consequently, the morphology of purple urchins depends on both their physical protective needs (ie. their tests and spines) and their reproductive needs. Thus, by measuring purple urchin gonads as a comparison to their body mass or size, one can infer how urchins are allocating their resources.

The behavioral and physiological responses of purple urchins to differences in habitats inside and outside of MPAs may impact the health of the respective ecosystems. Thus, research analyzing how urchins respond to differences in predation threat and food availability may better inform kelp forest management practices. A study conducted in New Zealand examined the influence of food stress and predation threat on the inducible defenses of New Zealand sea

urchins (*Evechinus chloroticus*) and determined that while greater predation risk did induce a response (stronger tests) the physiological effect of variation in food availability was much larger than the effect of predation risk (Spyksma et al., 2017). This suggests that urchins within MPAs are better able to resist predation than urchins from outside of MPAs because the greater availability of food allows for a plastic response in organisms to allocate more resources towards their defenses.

This study seeks to understand how purple urchins alter their inducible defenses between differing management zones around Anacapa Island in the northern Channel Islands of California. Variability in urchin morphology and behavior in different management zones has implications for shifts between urchin barrens and kelp forest environments. Evaluating differences in urchin morphology between management zones aids in comprehending the efficacy of MPAs in instilling healthier kelp forest environments. Urchins within the MPAs are hypothesized to better resist predation due to the increased abundance of predators inside MPAs. The ample abundance predators in MPAs is expected to directly select out weaker urchins, stimulate urchins to allocate energy towards their defenses for protection, and indirectly provide food for urchins to allocate towards their defenses. Comprehending how different management techniques impact the morphology of purple urchins is informative for deciphering the optimal ways to protect kelp forest communities.

II. Methods

Participants

I conducted this research with members of the Dr. Jennifer Caselle Lab at the Marine Science Institute at University of California, Santa Barbara in the summer of 2019. The participants consisted of both divers who collected samples, and lab scientists who assisted with processing in the lab.

Study Location

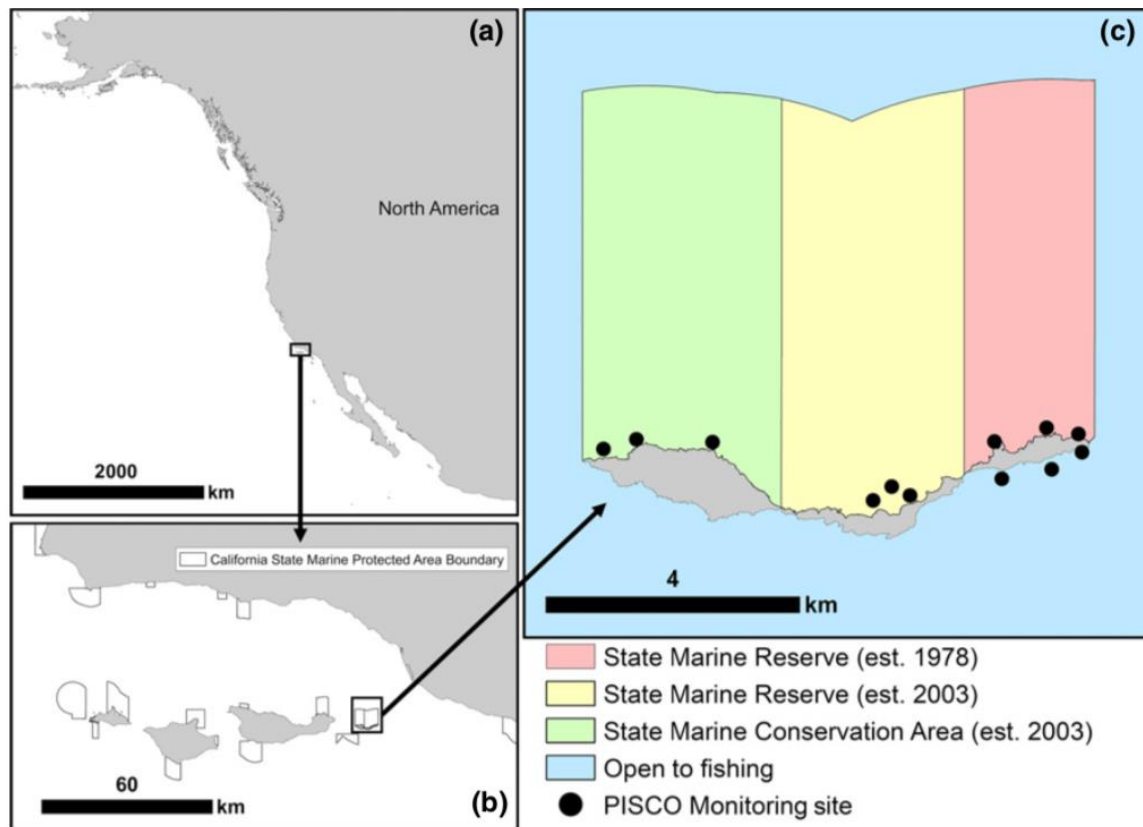


Figure 1: Maps of Anacapa Island in the Channel Islands (Caselle et al., 2018). State Marine Reserve (est. 1978) is referred to as Old SMR in this paper. State Marine Reserve (est. 2003) is referred to as New SMR in this study. State Marine Conservation is referred to as SMCA in this study. Open to Fishing is referred to as Fished Area in this study.

To investigate differences in the inducible defenses of purple urchins inside and outside of MPAs, we collected samples at five locations within four management zones around Anacapa

Island, the easternmost island of the northern Channel Islands in the Santa Barbara Channel, California (Fig. 1). The island has four different management zones: one State Marine Conservation Area, two State Marine Reserves of different ages, and a reference or fished zone. The State Marine Conservation Area (SMCA), established in 2003, allows for commercial and recreational fishing of California spiny lobsters and recreational fishing of pelagic finfish. The State Marine Reserves include the Old Reserve (Old SMR) established in 1978 and the New Reserve (New SMR) established in 2003. Each of the SMRs are no-take zones meaning no fishing or resource extraction is permitted. The fished Area is open to commercial and recreational fishing subject to California fishing regulations. Samples and data were collected at five sites from around Anacapa: the SMCA, the Old SMR, the New SMR, a kelp dominated area in the fished area, and an urchin barren area of the fished area (Fig. 1). These five sites provide a range of habitat types, fishing pressures, and community structures to examine how varying food web dynamics might influence urchin morphology.

Field Collection

Purple urchin collections occurred in the five zones around Anacapa Island throughout July and August of 2019. At each site, a team of divers collected 20 urchins (a total of 100 urchins were collected) from a depth of approximately 6-10 meters. All urchins ranged from 3 to 6 cm in diameter, with a range of size classes collected from each management zone. In the field, divers recorded the sample ID, date, time, protection status, latitude and longitude, collection depth, and detailed habitat notes (ie. habitat type and urchin behavior). After collection, we bagged urchins individually, placed them on ice and transported them to the UCSB Marine Science Institute. Urchins were stored in a cold room overnight prior to measurements the following day.

Urchin Morphological Analyses

We used several metrics to investigate urchin defensive traits including: (1) body size and morphometrics, (2) load resistance of the tests using a force meter instrument, and (3) spine length and test thickness. We also dissected urchins to access and measure gonads and gut contents. . Finally, we analyzed a long time series of kelp forest data, collected as part of a long term kelp forest monitoring program (described below), to understand predation pressure and food abundance in each study location.

Body Size - The day after collection, in the lab, we measured several aspects of urchin body size that are indicative of defense traits. Specifically, we measured each urchin's test diameter (0.1 mm), total diameter (0.1 mm) including spine canopy, and test height (0.1 mm) using calipers, and we also recorded total wet weight (0.001 g). We photographed each urchin for future reference.

Load Resistance - To test the physical strength of each urchin's test, we placed urchins on a machine that tests load resistance, simulating the force needed for a predator to crack into an urchin's test (Spyksma et al., 2017). We performed load resistance tests in UC Santa Barbara's Mechanical Engineering Test Lab using the lab's Force Machine, a micro-stepper motor controlled machine that applies a load down onto the object at a specified rate (in this case 1 mm per minute), recording the resulting force (N), the displacement (mm), over time (minutes). We calibrated the Force Machine prior to each use to maintain consistency across sampling periods.

This experiment required calibrating the machine to a 320N load cell with an attached 38mm weighted cylinder foot. The machine was applied onto the oral-aboral axis of each urchin.

To prepare the urchins to sit flat on the instrument, we removed spines from the oral and aboral surfaces using a Dremel tool without nicking the body. We began the experiment with the machine applying a force onto each urchin at 1mm/min. We ran the experiment until the force applied onto the urchin reached a peak and consistently declined following this peak. This was when the machine had clearly cracked into the urchin (verified in many cases by an audible cracking sound). After running the experiment, we recorded the crack type for each urchin (i.e. whether the test cracked along a seam in the side of the urchin, or the crown of the urchin caved in), which may provide insight into how various types of predators would successfully prey on urchins. Further exploration of urchin strength was conducted by comparing the slopes of load resistance versus displacement prior to the maximum load to understand how urchins resisted the load machine. Slope was calculated from the load versus displacement plots for the 30 seconds prior to the maximum load.

Spine Length and Test Thickness - To characterize spine length, we plucked ten of the longest spines (assessed visually), fully intact, from each urchin using forceps (prior to spine removal for the load resistance machine) and measured each one to the closest 0.1 mm using calipers. We used five spots along the top of the test and five spots along the bottom of the test to measure the thickness of the test using calipers.

Gonads and gut contents - Following strength tests, we dissected urchins to access and measure internal structures. We weighed the gut content and gonads to the nearest 0.001g with a lab balance. We also recorded gonad color and photographed gonads for future reference.

Kelp Forest Community Structure - We utilized long-term kelp forest monitoring data from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) to analyze how the kelp forest community structure in the four different management zones around Anacapa Island have changed over time. These comprehensive time-series includes annual abundances of species relevant to this study, including California spiny lobster density, California sheephead biomass, sea urchin density, and kelp density.

Data Analysis and Statistics

To analyze whether inducible defenses varied by management zone, we tested the differences between a) maximum load resistance relative to body size, b) average spine lengths, and c) test thickness using ANOVA with Tukey Family comparisons. To understand how food availability might influence the way urchins allocate their resources, we compared gonad weights relative to total wet body weight using ANOVA Tukey Family comparisons across management zones. We used Pearson's Correlation to describe relationships between (a) maximum load resistance and spine length, (b) test thickness and spine length, (c) Gonadosomatic Index (GSI) and spine length, (d) GSI and maximum load, (e) GSI and test thickness, providing information on the significance of energy allocation relationships. Relationships were considered significant at $p < 0.05$. I used the computer software program R Version 1.1.463 for all data analysis in this study (RStudio, Inc., 2016).

III. Results

Inducible Defenses

Urchin strength was compared by examining maximum load from urchins in all five zones around Anacapa Island. When comparing load resistance of urchins from all five zones there was a positive relationship between urchin size and load resistance (Fig. 2). Thus, maximum load for each urchin was normalized to its respective test diameter to remove the effect of size of the animal in the analyses for differences among zones. Within all five zones (including barrens and kelp areas in the fished area) a significant relationship between maximum load and test diameter ($p < 0.05$; Fig. 2) existed. However, only urchins from the New SMR had significantly larger ratios of maximum load to test diameter than urchins from the fished area ($p = 0.0007$, F -value=5.209, $df=3$; Fig. 2). Maximum load and ratio of maximum load to test diameter of urchins from the five zones was highly variable, ranging from 75 N to 372 N for max load and from 1.23 N/mm to 4.63N/mm for max load to test diameter.

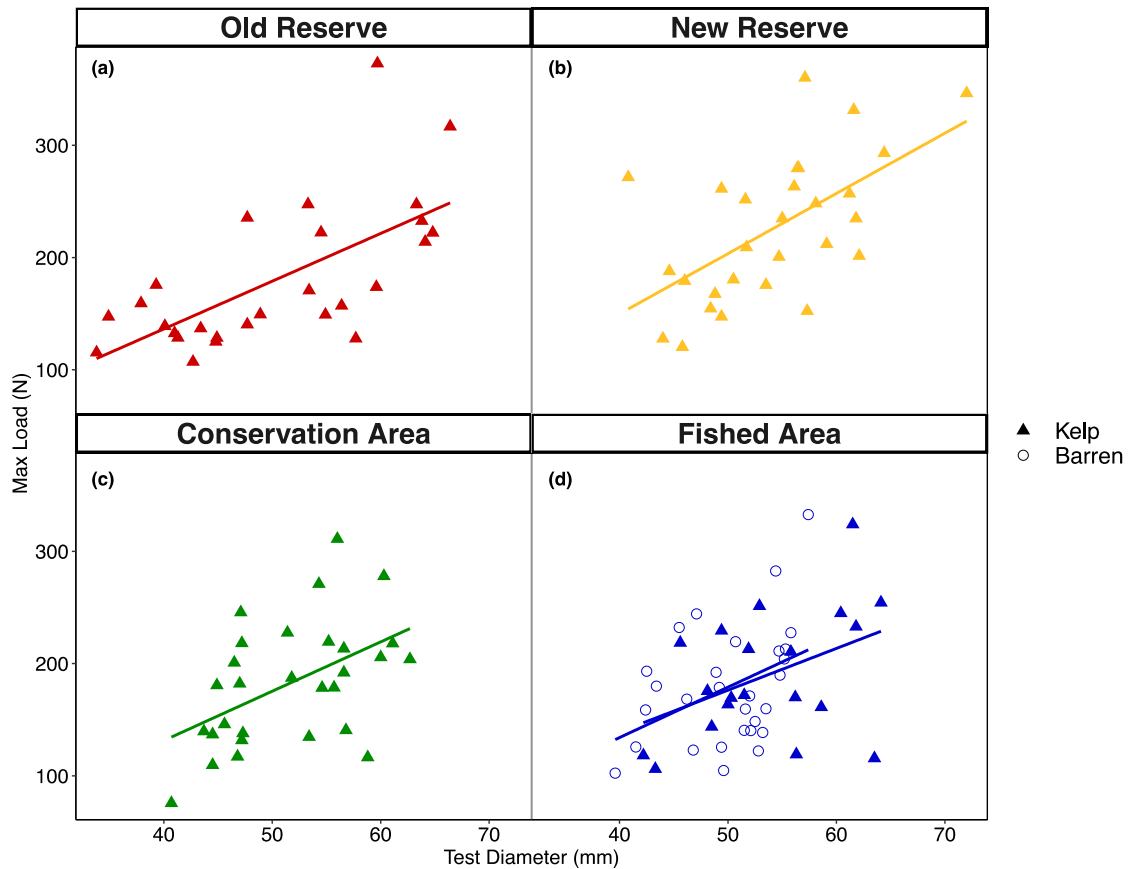


Figure 2: A comparison of urchin's test diameter to maximum load required to break the urchin's test. This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Filled in triangles represent kelp dominated reefs, while empty circles represent urchin barren reefs.

A positive relationship between the slope of load versus displacement for the 30 seconds prior to maximum load and test diameter is present in all five zones (Fig. 3). There is a significant relationship between slope and test diameter when samples are grouped together for all zones with kelp ($p = 0.0085$, $F\text{-value} = 7.201$, $df = 102$; Fig. 3), but no significant relationships exist in any of these individual study sites, nor for the barren site.

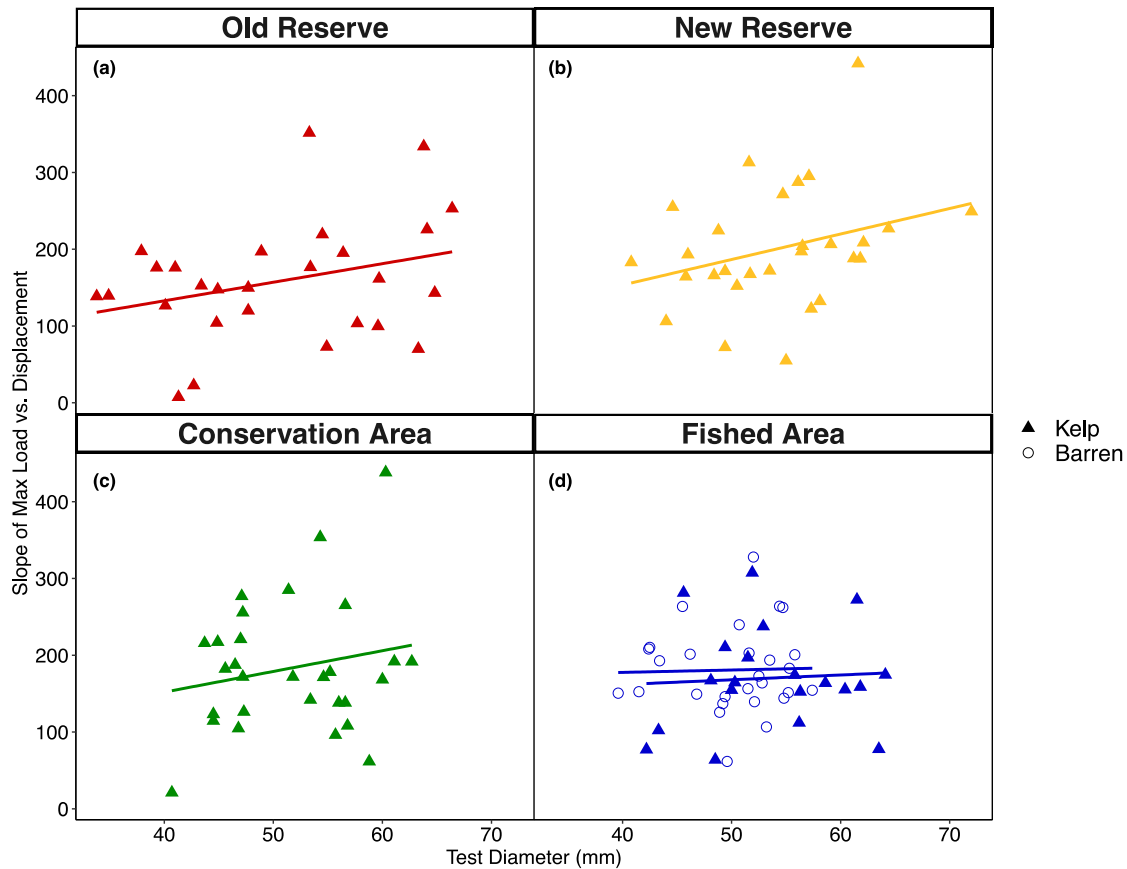


Figure 3: A comparison of urchin’s test diameter to the slope of maximum load versus displacement 30 seconds prior to reaching the maximum force required to break the urchin’s test. This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Filled in triangles represent kelp dominated reefs, while empty circles represent urchin barren reefs.

Spine lengths of each urchin were normalized to body size, as larger urchin have longer spines, and then compared among zones (Fig. 4). Urchins from the barren region of the fished zone had significantly longer spines than urchins from the Old SMR, New SMR, and the SMCA grouped together ($p= 0.04179$, <0.00001 , and 0.00002 , respectively. $F\text{-value}=13.14$, $df=3$; Fig. 4).

Similarly, average test thickness of each urchin was compared between the five zones. Urchins in the New SMR and the SMCA had significantly thicker tests than those from the reference zone ($p= 0.000987$ and $p= 0.0280019$, respectively. $F\text{-value}=7.219$, $df=3$). No significant differences between test thickness exist between any other zones.

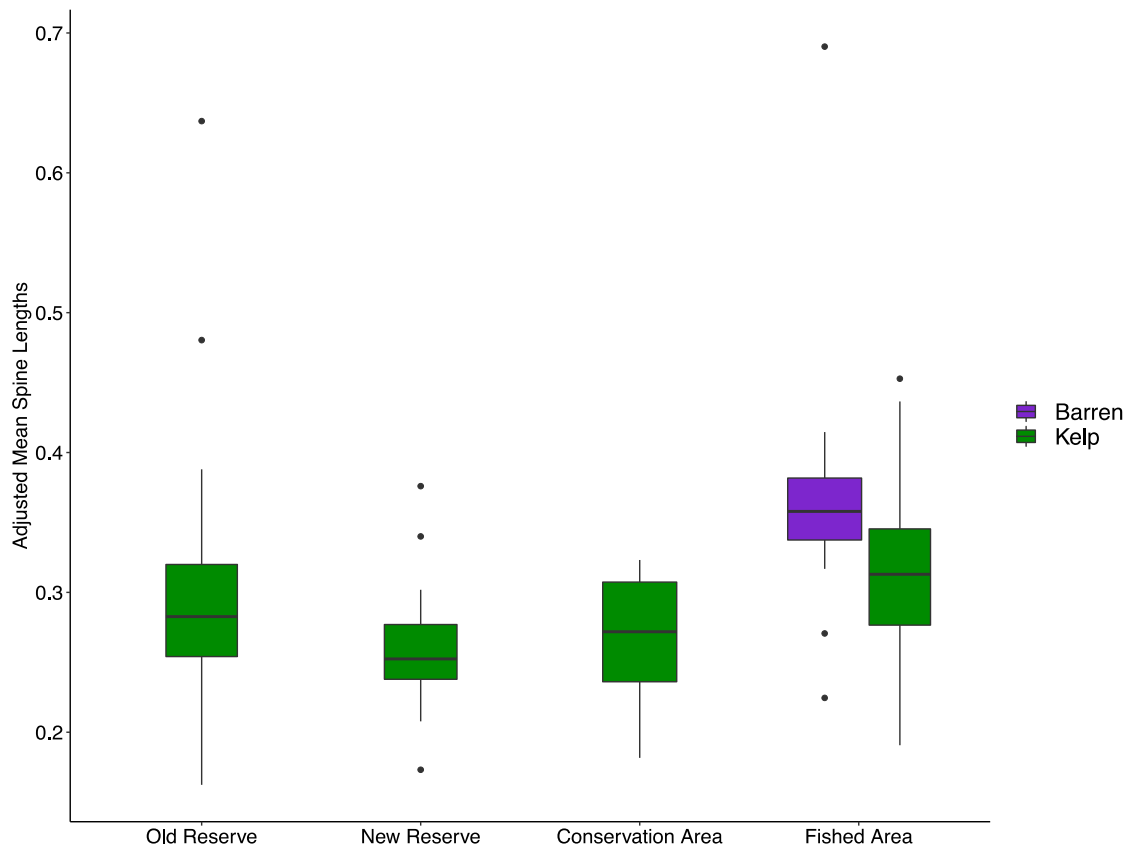


Figure 4: A comparison of the adjusted mean spine lengths between all five zones with mean and standard error bars and dots representing outliers. Adjusted mean spine length is a measure of the longest spine relative to the size of each urchin's body (test diameter). This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Green represents kelp dominated reefs, while purple represents urchin barren reefs.

Energy Allocation Trade-Offs

To understand potential energy trade-offs in urchins' defenses, spine length was compared to both maximum load (Fig. 5) and test thickness (Fig. 6). In all four zones with kelp, there was a significant negative relationship between maximum load and average spine length ($p= 0.000926$, $F\text{-value}=11.64$, $df=102$; Fig. 5). However, the barren site did not have a significant relationship between maximum load and average maximum spine length ($p= 0.2042$, $F\text{-value}=1.693$, $df=27$;

Fig. 5). Similarly, in all four kelp zones, there was a significant negative relationship between maximum load and test thickness ($p= 7.172e-06$, $F\text{-value}=22.39$, $df=102$, Fig. 6), while again, the barren zone did not have a significant relationship between these two variables ($p=0.47488$, $F\text{-value}=7.28$, $df=27$, Fig. 6).

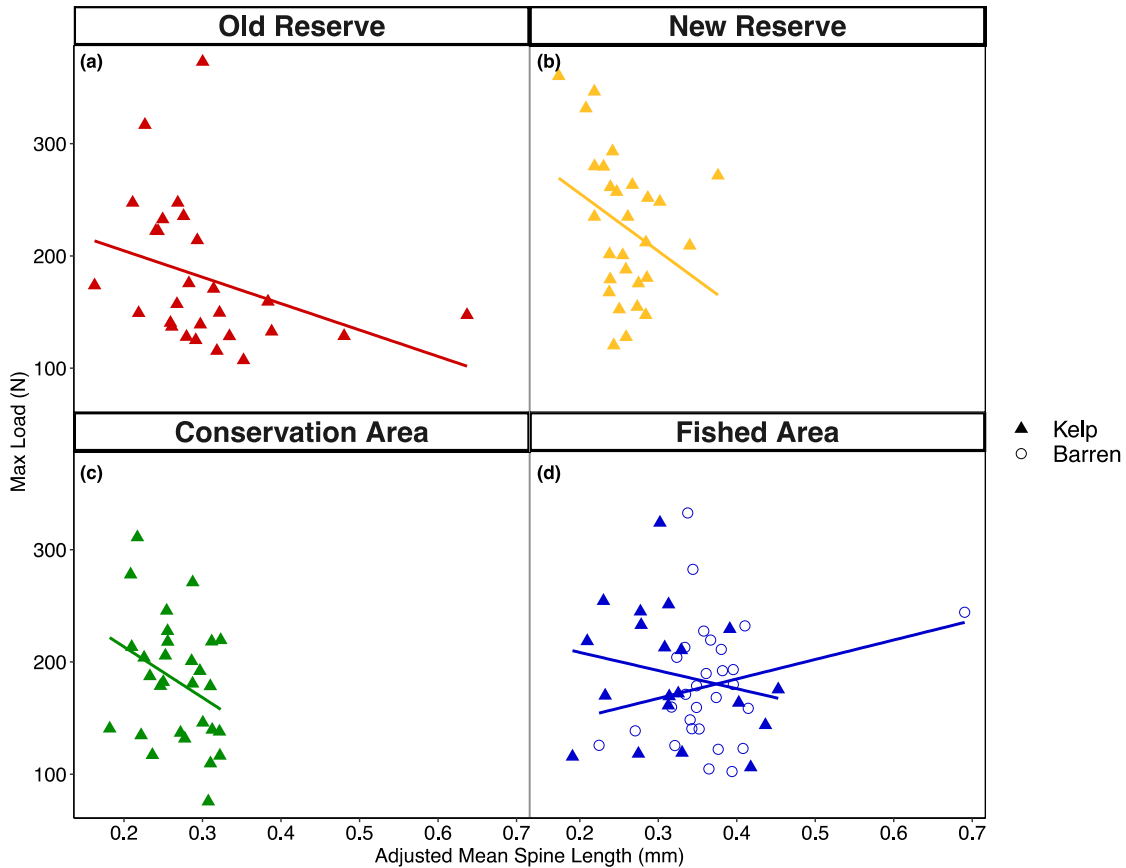


Figure 5: A comparison of urchin's adjusted mean spine length to the maximum load required to break the urchin's test. This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Filled in triangles represent kelp dominated reefs, while empty circles represent urchin barren reefs.

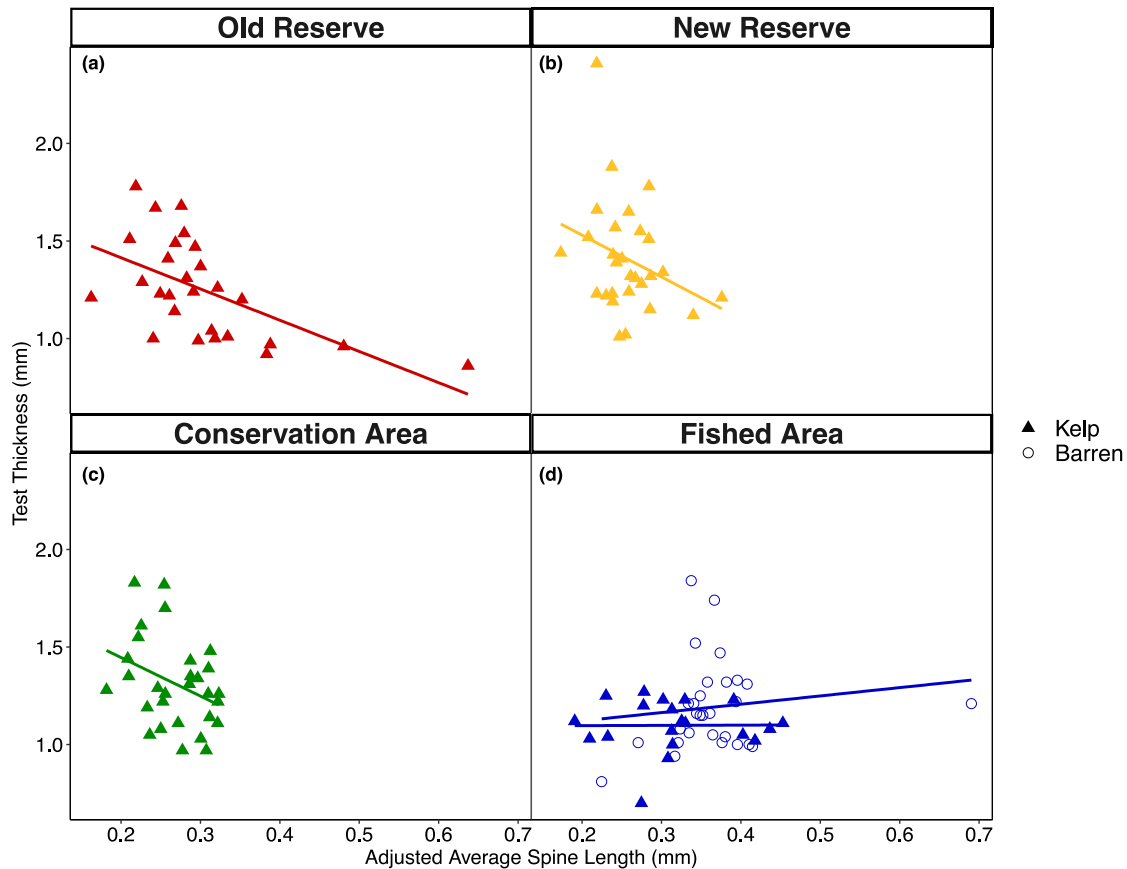


Figure 6: A comparison of adjusted average spine length to the test thickness of each urchin. This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Filled in triangles represent kelp dominated reefs, while empty circles represent urchin barren reefs.

To test for a tradeoff in energy allocation between defense and reproduction, we compared the gonadosomatic index (GSI, gonad weight divided by the total wet weight of each animal) across zones. Urchins from the barren site of the fished zone had significantly lower GSI than urchins from all four kelp regions (Fig. 7). Moreover, urchins from the barren area within the fished zone had significantly smaller GSI than urchins from the kelp site within that same zone, at a location roughly 20 meters away ($p= 3.24e-06$; $F\text{-value}=23.66$, $df=1$; Fig. 7). GSI was compared to spine length, load resistance, and test thickness to evaluate potential energy trade-offs. The relationship

between GSI and average spine length normalized by body size was significant in the reference zone ($p=0.007821$, $F\text{-value}=0.4725$, $df=47$), and across all zones ($p=0.0201$, $F\text{-value}=0.6699$, $df=102$). No significant relationship exists between GSI and maximum load, nor GSI and test thickness.

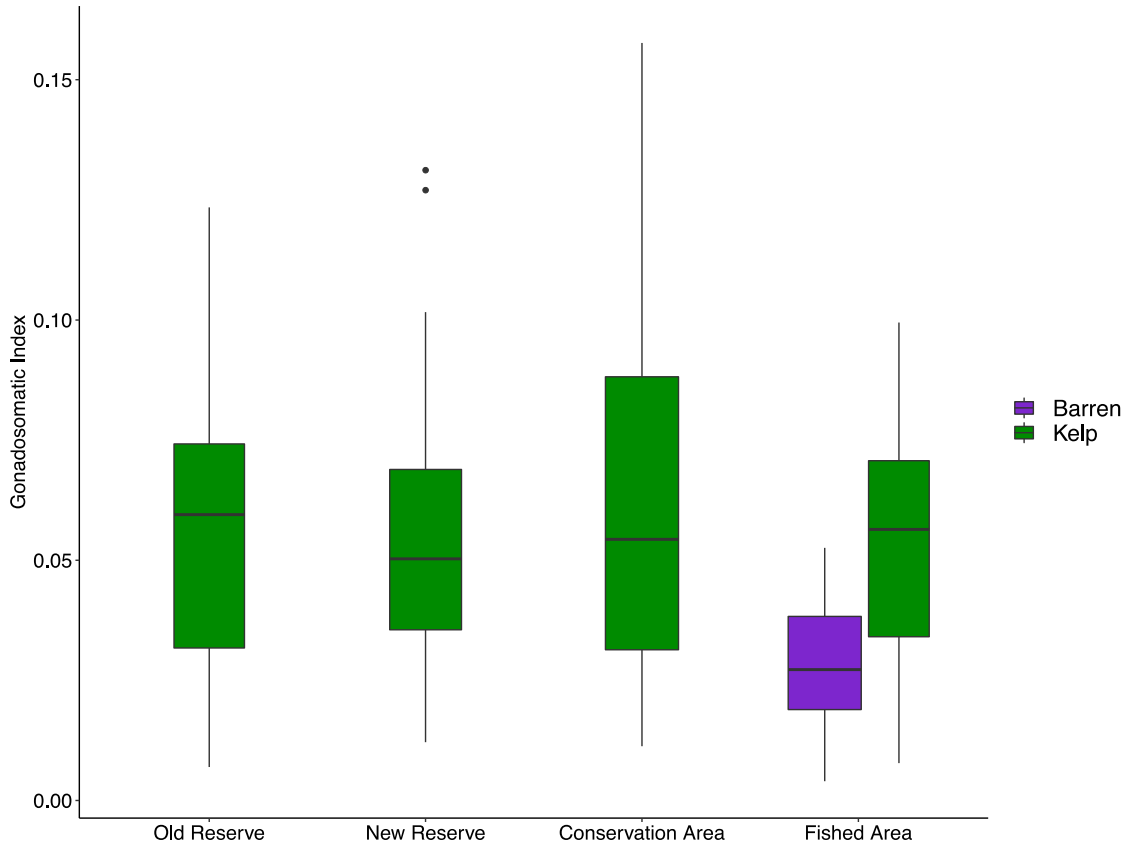


Figure 7: A comparison of gonadosomatic index of each urchin between all five zones with mean and standard error bars and dots representing outliers. Gonadosomatic index is a measure of the total gonad weight divided by the total wet weight of each urchin. This comparison is represented within all five study sites: Old Reserve, New Reserve, Conservation Area, Fished Area (Kelp), Fished Area (Barren). Green represents kelp dominated reefs, while purple represents urchin barren reefs.

Kelp Forest Community Structure Analysis

The predators in the three different MPAs around Anacapa Island have increased in numbers over time (Figs. 8; 9). Lobster density has increased in the Old Reserve and New Reserve while

it has stayed the same and at low levels in the Conservation Area and fished zone where lobsters are fished (Fig. 8). Sheephead biomass has increased in all three MPA zones but stayed the same overall in the fished zone (Fig. 9). Urchin density has remained consistently low in the Old Reserve (Fig. 10). Meanwhile, in the New Reserve and Conservation Area, urchin density has decreased over time to the current low levels. In the fished area, urchin density has also slightly decreased, but this area still contains the highest densities of urchins. Kelp density has increased in all the MPA zones and has remained low in the fished zone (Fig. 11). Currently, in the Old and New Reserves sheephead, spiny lobsters and kelp are abundant, and urchins are scarce. In the Conservation Area, sheephead and kelp are abundant, and urchins and spiny lobsters are scarce. In the fished area, urchins are abundant, and kelp, sheephead and spiny lobsters are scarce.

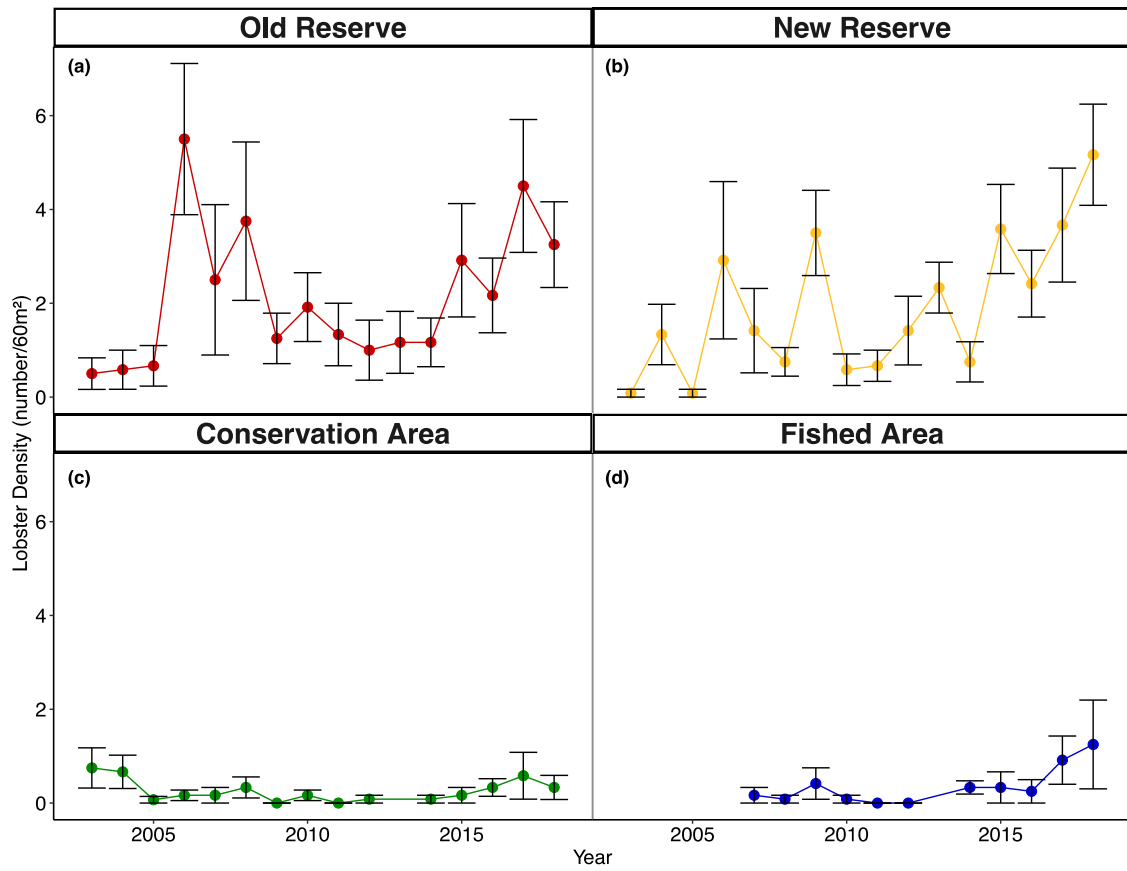


Figure 8: A time-series of lobster (*Panulirus interruptus*) density calculated from counts of lobsters along transects from 2003 to 2018 in all four different manage zones around Anacapa Island.

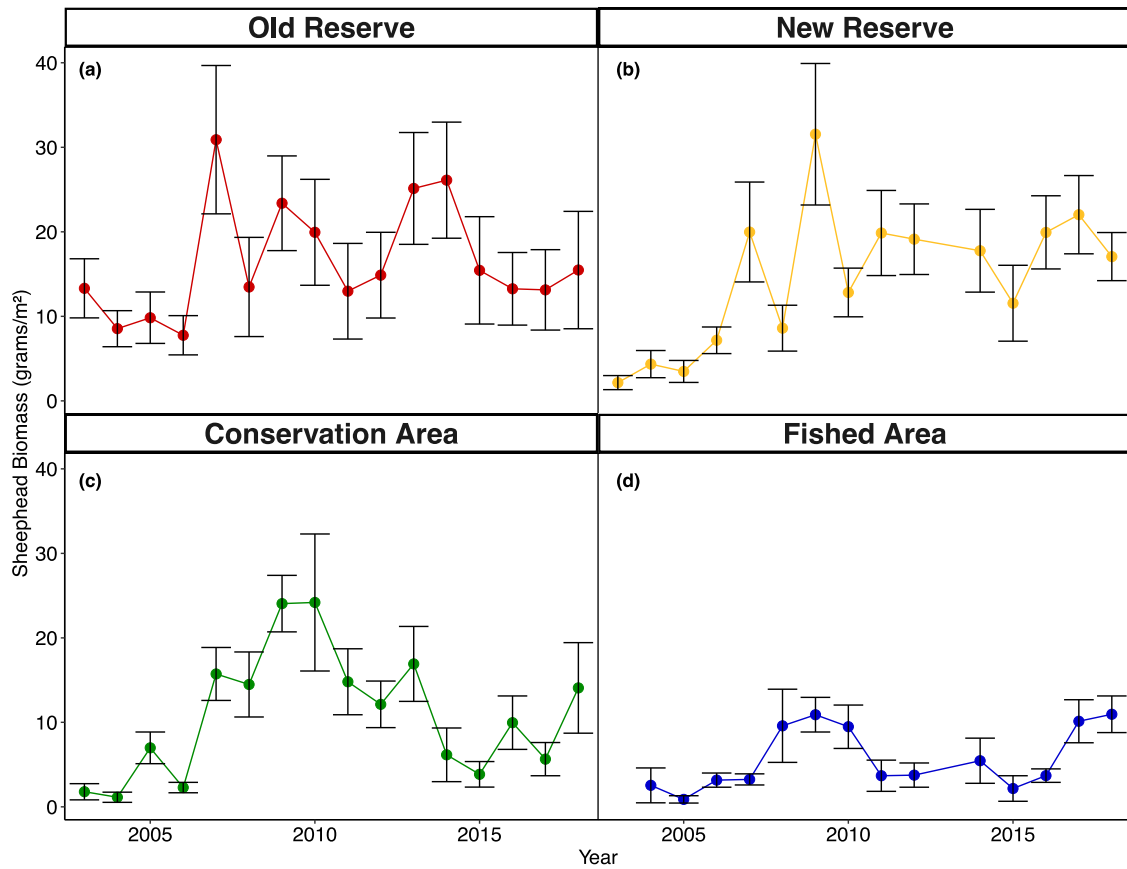


Figure 9: A time-series of sheephead (*Semicossyphus pulcher*) biomass calculated from counts of sheepheads multiplied by their respective body sizes along transects from 2003 to 2018 in all four different manage zones around Anacapa Island.

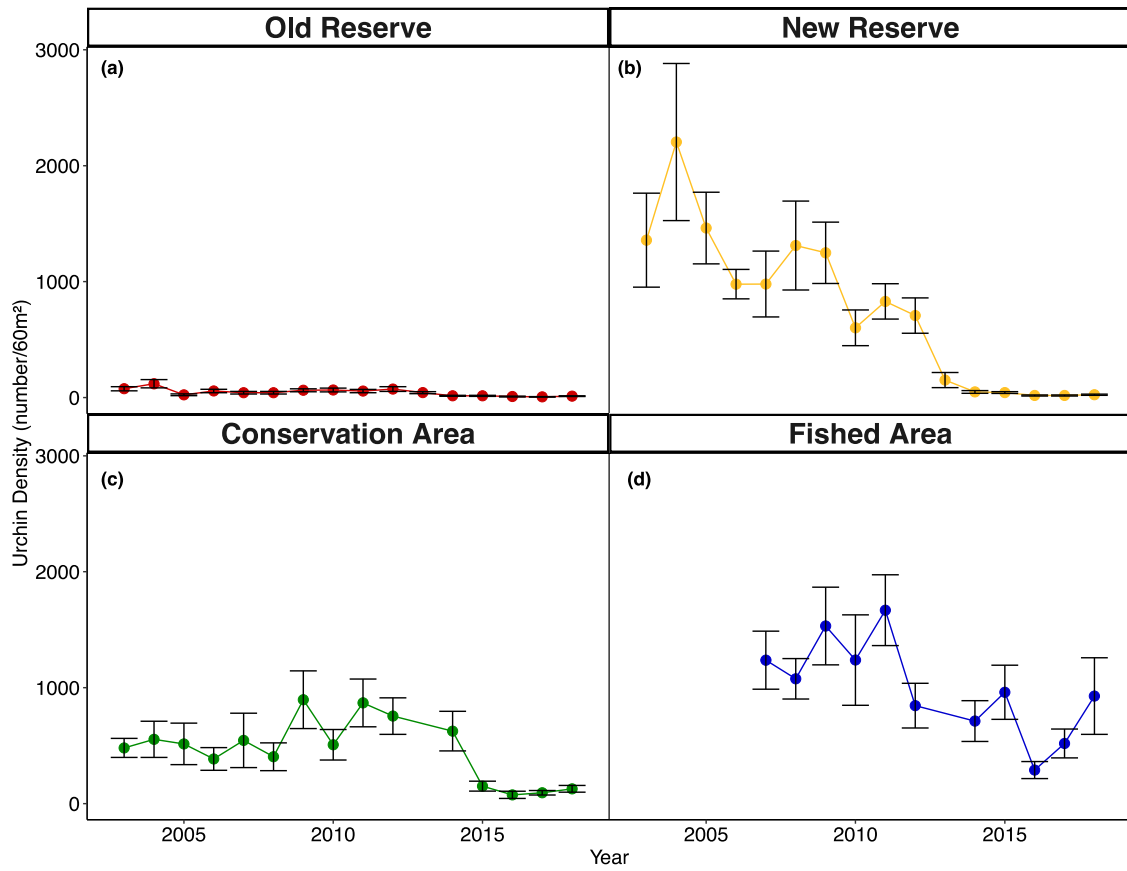


Figure 10: A time-series of purple urchin (*Strongylocentrotus purpuratus*) density calculated from counts of urchins along transects from 2003 to 2018 in all four different manage zones around Anacapa Island.

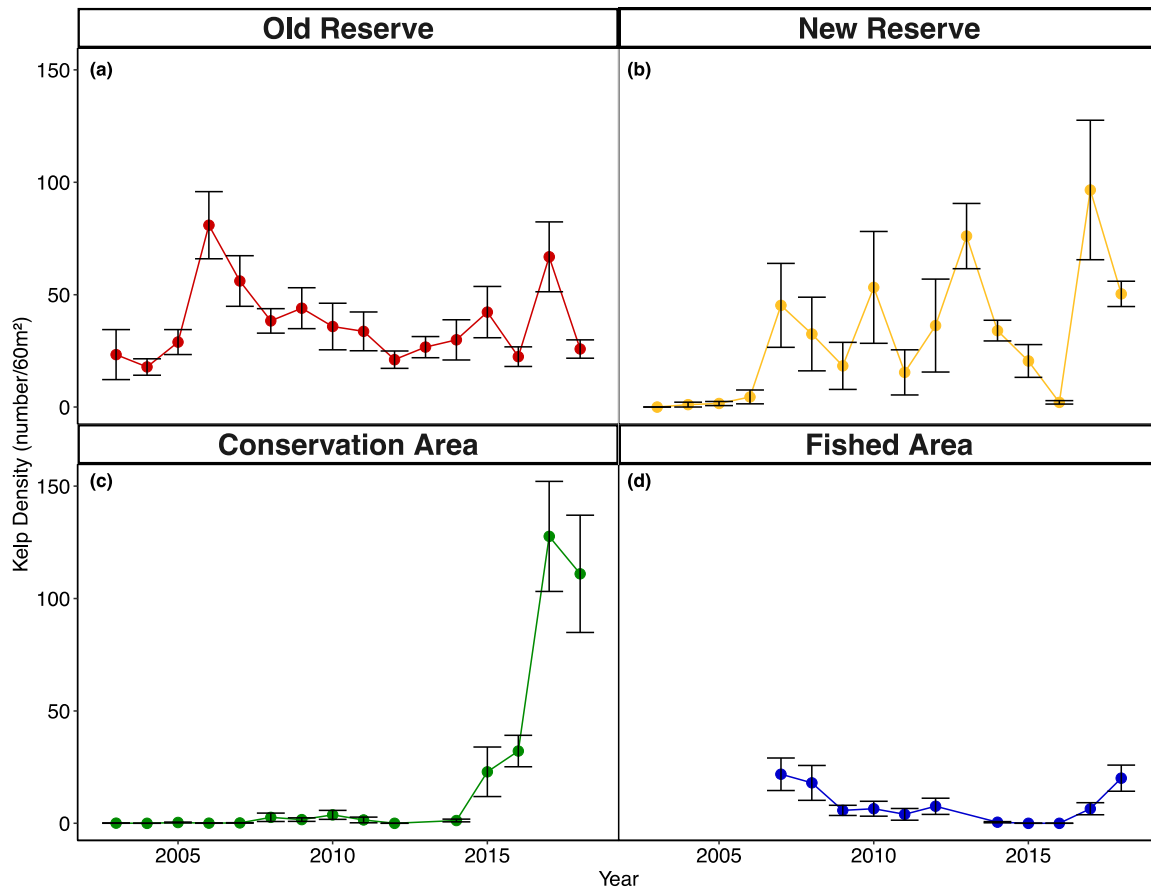


Figure 11: A time-series of giant kelp (*Macrocystis pyrifera*) density calculated from stipe counts along transects from 2003 to 2018 in all four different manage zones around Anacapa Island.

IV. Discussion

The results from our study provide insight into factors that managers must consider when designing effective kelp forest community conservation strategies. Specifically, our results suggest that the physical and behavioral responses of purple urchins to changes in food web structure are likely important in determining how coastal communities shift between urchin barrens and kelp forests. We initially hypothesized that urchins inside of the MPAs would be more able to resist predation because of increased predator presence and greater food availability; however, findings suggest urchins from the fished area were likely better defended. These results demonstrate that along with predation threat, habitat type and thus urchin foraging behavior may impact their morphology.

Our findings comparing differences in inducible defenses of purple urchins inside and outside of MPAs around Anacapa Island suggest that urchin morphology may be dependent on predation risk. However, predation risk is not only contingent on predator abundance, but also the indirect effect that predators have on habitat type (ie. kelp forest structure) and urchin behavior (ie. crypticity). Results from this study suggest that the lack of kelp forces a behavioral change in urchins to forage out in the open, which may make them more vulnerable and necessitate better defenses. This informs the need for MPAs to induce changes in urchin strength and allow kelp forest structures to propagate. Furthermore, the presence of both energy trade-offs between distinct defenses and between defenses and reproduction, along with the evidence for small-scale spatial differences in urchin physiology between barren and kelp sites show the plasticity of this species and may indicate limitations in mobility.

1. Urchins outside of MPAs are better apt to resist predation.

An assessment of urchin resistance to predation based on defensive traits demonstrated urchins outside of MPAs to be better defended. The load resistance experiments showed a positive relationship between the size of an urchin and its ability to resist predation (Fig. 2). Urchins from the New SMR were significantly stronger than urchins from all of the other zones, however, this result is difficult to interpret in that this zone had similar resources and predator abundances as the other MPA zones. This finding aligns with the results from a similar study in New Zealand showing that urchins were stronger in zones with more food (Spyksma et al., 2017). Overall, little difference existed between urchins' test strength across the five zones, which does not support our initial hypothesis that urchins from the MPAs are stronger, nor is it consistent with the findings of Spyksma et al. (2017). The lack of variation in strength between urchins could result from an insufficient consideration for each urchins' variation in growth rate. Urchins grow at differing rates based on predation threat and food availability, which may have impacted impact their strength at the point in time this study was conducted (Ellers, 1998; Grupe, 2006).

Food limitation impacts urchin ability to allocate resources towards both reproductive structures and defenses. However, it is likely that the first stage of food limitation would result in a reduction in resources towards gametogenesis rather than growing physical defenses (Dodge & Edwards, 2012; Wade & Jones, 2004). Urchin feeding rates and energy allocation are also known to vary seasonally (Dodge & Edwards, 2012), with reproductive season for purple urchins generally peaking in the winter months. A more in-depth analysis of seasonality and gametogenesis needs to be considered in how reproduction and seasonality impacts each urchin's

ability to allocate energy to strengthen their tests. In future studies, it could be valuable to conduct similar work over multiple seasons to account for the reproductive timing of purple urchins. However, our results of a strong decrease in the GSI of urchins from the barren area relative to kelp areas even outside of the peak reproductive season is notable.

Changing ocean conditions due to climate change may also affect urchin morphology.

Specifically, ocean acidification, a process where ocean pH decreases as the ocean absorbs more CO₂, greatly alter the carbonate chemistry of the world's oceans (Doney et al., 2009). Recent research on ocean acidification and urchin morphology suggests that the skeletal growth of urchins early on in their development is impacted by changing ocean acidity (LaVigne et al., 2013). Even though this study controlled for body size differences, it did not consider potential age variation in the urchins relative to water pH. Consequently, more analysis of pH relative to early development of each urchin could help in analyzing strength differences and may help explain a lack of differentiation between urchins of all zones and all ages.

Study methods used here were a significant improvement on past load resistance measurements (Spyksma et al., 2017), however there were still some potential limitations of load resistance measurements that may have impacted results in this study. Despite attempting to flatten the basal and dorsal surfaces of the urchin to allow solid contact with the instrument base, future studies might design a base that can align with a rounded urchin for more precise comparisons. Because urchins varied in shape, it was somewhat challenging to properly apply the foot of the loading machine down onto the urchin. It also could be useful to use a penetrating pointed tool rather than the larger diameter foot when applying force down onto each urchin. This would

provide a more specific place of contact and possibly mimic predation in the field more accurately by simulating a sheephead tooth or lobster leg. Lastly, implementing more engineering knowledge into the analysis of the data could be valuable to develop a greater understanding of how to compare strengths between urchins from different zones. These improved techniques may be helpful in forming a better analysis in differences of urchin strength between management zones.

Even though no meaningful differences were found between the strengths of urchins from around Anacapa Island, we did observe significant variation in spine lengths between zones (Fig. 4). Spines, another form of defense for purple urchins, protect the body of the animal from the bite of a predator. Urchins from the barren site of the fished zone had significantly longer spines than urchins from the other kelp zones, partially supporting the hypothesis that urchins from outside of the MPAs would be better apt to resist predation (Fig. 4). These differences in spine length between the five zones may be a result of differences in food availability. The variability in food abundance results from the indirect effect that predators have on macroalgae presence. During collections for this study, all urchins from the fished area were found to be out in the open whereas all the urchins from inside the MPAs were cryptic. These differences reflect the behavioral trade-off decisions made by urchins to minimize risk and maximize resource availability (Lima & Dill, 1990; Beckerman et al., 1997). Differences in urchin behavior between the five zones result from both the direct and indirect effects of predators, who act as a strong selective pressure on the population of prey and who alter how the prey interacts with its environment (Beckerman et al., 1997). Urchins prioritize the decision that will ensure the highest fitness (Lima & Dill, 1990), which in this study is contingent upon food availability. Urchins in

the fished area must openly search for food. Meanwhile, urchins in the MPAs may remain cryptic and rely upon drift for food.

A study that examined the effects of predator risk on food webs between spiders and grasshoppers concluded the behavioral responses caused by predators on their prey is more pertinent in explaining trophic cascades than direct mortality via predation (Schmitz, 1998). This concept of predator-mediated behavioral responses can be applied to the trophic cascades in California kelp forests. Predators may directly impact urchin behavior by forcing them to hide. Inside of the MPAs, where both spiny lobster and California sheephead populations are high (Behrens & Lafferty, 2004; Hamilton and Caselle, 2015; Caselle et al, 2018; Eisaguirre et al, 2020) urchins may prioritize protection rather than grazing. Both cues released by predators in the water column and the existence of crushed conspecifics generates a response by urchins to prioritize staying hidden rather than foraging for food (Haag et al., 2016). Spiny lobsters have been shown to reduce grazing rates of purple urchins by an average of 43-44% when present in nearby areas (Matassa, 2010). Within the MPAs, where fishing is restricted, predator abundances are high, which may invoke this cryptic behavior in urchins to protect themselves from predation (Figs. 12; 13). In this situation, urchins are prioritizing minimizing risk, which could put them at a loss of gaining more energy through foraging, however, this antipredator behavior protects them from being eaten (Lima & Dill, 1990). Meanwhile, outside of MPAs, where fishing pressure is high, there are fewer predators to induce this direct behavioral response, resulting in urchins that continue to forage as normal. This aligns with the availability of urchins in each zone of this study: all urchins within the MPAs were cryptic, meanwhile, all urchins in the fished zones were not hidden and exposed on the reef.

Predators can also indirectly impact urchin behavior by increasing food availability through trophic cascades. Within MPAs, the indirect cascading effect that increased predators have on amplifying macroalgae can lead to more food available for the primary grazers in the system (Behrens & Lafferty, 2004). Furthermore, urchins do not need to actively graze on food and instead rely upon sedentary feeding of drift algae (Harrold & Reed, 1985). In areas with higher densities of kelp, drift algae is more prominent, which further increases their cryptic response because they can rely upon drift algae for food. Therefore, the increase in the amount of food allows urchins to be more cryptic as they can remain as sedentary drift feeders rather than active grazers (Nichols et al., 2015). Meanwhile, outside of MPAs, there is less algal coverage to provide hiding places, and there is less food to provide drift algae for sedentary feeding. These urchins respond by actively grazing on macroalgae, requiring them to expose themselves to an increased risk of predation.

These differences in urchin behavior may induce variation in urchin morphology. Urchins inside of the reserves are physically protected by their hiding places. Meanwhile, urchins outside of the reserves are actively grazing in the open. Crevices and rocks that urchins live under reduce the need for urchins to grow defenses, and physically reduce urchin's capability of growing longer spines. When comparing the growth of urchins that reside inside (pit urchins) versus outside (non-pit urchins) of pits, non-pit urchins grow significantly larger tests and longer spines (Grupe, 2006). Non-pit urchins also grow faster than pit urchins because non-pit urchins are not restricted by their habitat.

Inside of the MPAs, where urchins are cryptic, crevices may be restricting urchins from growing to the same capacity as urchins in the barren that are in the open. Green urchins (*Strongylocentrotus droebachiensis*), another species of urchins, react differently to predators based on size. Smaller green urchins, who are cryptic in the presence of predators, are slower to develop long spines and thick tests compared to larger urchins who remain in the open in the presence of predators (Selden et al., 2009). The same process could be occurring in purple urchins where the cryptic response of urchins to an abundance of predators results in a slowed growth rate, which explicates why urchins inside of the MPAs have shorter spines than those in the fished area. The MPA urchins because of their antipredation response to remain cryptic, may be physically restricted by their habitat, and therefore, grow slower.

2. Energy trade-offs suggest that habitat types impact urchin morphology.

Energy trade-offs found between distinct defensive traits and between defensive traits and reproduction, suggest that different habitat types impact how urchins allocate resources to a variety of aspects of their morphology.

Energy trade-offs exist because urchins exhibit morphological plasticity, meaning that differences in urchin morphology are often due to phenotypic adaptations rather than variance in genetic make-up (Russell, 1987). Specifically, urchins from regions that vary in both predator and food abundance show different traits because of phenotypic plasticity, meaning they can actively adapt to their environment for survival (Russell, 1987). Urchins must adapt to changing environments, meaning they must allocate energy to the needs that will increase fitness. For example, when urchins are food limited, they allocate energy towards developing larger jaws,

allowing them to eat more and/or different things such as algal crusts. Therefore, they can consume more food to be able to allocate towards other traits (Edwards & Ebert, 1991).

Results illustrate that urchins allocate energy to separate defenses based on their needs. The significant negative relationship between maximum load and spine length (Fig. 5) and the significant negative relationship between spine length and test thickness were prevalent in the kelp areas (Fig. 6). These two relationships show that urchins either prioritize growing longer spines or developing stronger tests.

In the barren site, urchins are food limited and thus allocated their resources differently. Trophic cascades in the Santa Barbara Channel have led to less kelp but more urchins (Hamilton and Caselle, 2015; Behrens & Lafferty, 2004) in some locations. In barren area of this study, where urchins actively forage for food, they most likely prioritize developing longer spines that can both protect them from predation and help them catch drift kelp.

Urchins in the kelp areas show energetic trade-offs between developing longer spines and allocating resources towards stronger bodies. However given their cryptic behavior (i.e. they are physically restricted by their habitat) their spines can only be so long. Often when urchins' spines break, they react by developing stronger tests (Edwards & Ebert, 1991). Since long spines may physically break against rocks or other hard surfaces, urchins may or may not allocate resources towards growing longer spines depending on whether they are cryptic and the size of crevice spaces. These trade-offs are possible because these urchins have prevalent drift algae to feed them, allowing them to prioritize different types of fitness.

Purple urchins in this study also showed energetic trade-offs between defenses and reproduction (Figs. 9, 10, 11). These negative relationships between GSI and defenses were prevalent in every zone. Urchins emphasize reproductive development as they age, meaning that older urchins allocate fewer resources to defenses and more to their reproductive cycle to ensure fecundity (Lord & Shanks, 2012). These energy trade-offs occurred between urchins of all sizes, showing that urchins must allocate energy differently depending on predation risk and habitat type. When animals assess a high risk of predation, they may alter their reproductive efforts by allocating energy towards their defenses (Lima & Dill, 1990). In barren areas, if urchins feel threatened by predators due to their need to feed in the open, they may allocate resources to their defenses over their reproductive health to be able to fend off predators (Dodge & Edwards, 2012). However, in kelp areas, urchins may allocate more resources to their reproductive success because their habitats protect them from predation, allowing them to prioritize successful reproduction. These trade-offs provide more insight into how habitat influences the morphology of urchins. It is not just about urchin's placing energy into their defenses, it is also about urchins allocating towards their reproduction. The clarity of these energy-tradeoffs in this study represent how behavioral differences caused by human-induced top-down changes in trophic structure prompts trade-offs in how urchins grow and reproduce.

3. Small Scale spatial differences demonstrate the plasticity of purple urchins and their lack of mobility.

One intriguing result from this study was the discovery of small-scale spatial differences in urchin morphology. The differences in defenses and gonadosomatic index in urchins within the

same management zone, from sites just 20 meters away from one another (Fig. 4) illustrates the plasticity of these animals, and a lack of mobility.

The differences in gonadosomatic index found between these two nearby sites, the barren and kelp zones of the fished area, align with previous studies on urchin gametogenesis. These results are especially striking considering that these urchins were sampled during the summertime when they are not spawning. When purple urchins have a limited food source, they have smaller gonad mass (Dodge & Edwards, 2012). This corresponds with findings here that food limited urchins in the barren area had smaller gonads than urchins in the kelp zones. Urchins are also found to eat more quickly when they are food deprived to fill their need for quicker nutrient absorption which fuels their reproductive cycle. However, this is more prevalent earlier on in their reproductive cycle (Dodge & Edwards, 2012). Urchins that are food limited later in their reproductive cycle can still reproduce successfully, showing adaptability in urchin reproduction in times of starvation (Dodge & Edwards, 2012). Urchins from the barren area may still reproduce successfully as long as they can obtain the proper nutrients early on in their reproductive cycle. Therefore, later in their reproductive cycle they may prioritize allocating resources to their defenses as they remain in the open foraging for food.

Because urchins show phenotypic plasticity as the trait for differences between nearby zones rather than predisposed genetic distinctions, it is evident that urchins in these two areas within the fished zone are adapting to their respective habitats (Russell, 1987). However, it is interesting that urchins in the barren area that are starving do not attempt to move to the kelp bed 20 meters away. A study on a different urchin species (*Paracentrotus lividus*) showed that urchins have

quite limited mobility (Hereu, 2005). Based on the small-scale differences found in this study, this same theory may be applied to purple urchins, meaning that instead of moving to an area that would provide more food, they adapt to their local habitats.

V. Conclusion

Our findings suggest that the morphological responses of purple urchins to changing environments reflect the plasticity of these animals, and therefore, the challenges present in kelp forests returning to natural states without direct human-management techniques. The implementation of MPAs can minimize fishing pressure, resulting in less-defended urchins, and potentially improve the ability for kelp to revitalize on rocky-reef structures. It is likely that these feedbacks of decreased urchin strength and increased kelp abundance will reinforce themselves as management remains in place. Furthermore, the lack of significant differences in urchin morphology between MPAs suggests that timing is not crucial to the success of promoting less defended urchins. Therefore, minimizing fishing pressure is likely to quickly induce changes in urchin behavior and physiology, which will ultimately create relatively quick shifts from urchin barrens to kelp forest structures. To experience shifts back to the valuable kelp forests, we must make a continued effort to effectively implement MPAs in coastal regions that require assistance, which will provide many benefits for humanity (increased biodiversity, recreation, carbon sequestration, etc.). Our study illustrates the necessity to continue to implement and maintain MPAs for the success of kelp forest communities.

VI. References

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