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Santa Barbara

Interspecific differences in the feeding ecology, metabolism, and trophic impact of the sea urchins *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution, and Marine Biology

by

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March 2025

The dissertation of Katrina D. Malakhoff is approved.

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ABSTRACT

Interspecific differences in the feeding ecology, metabolism, and trophic impact of the sea urchins *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*

by

Katrina D. Malakhoff

Sea urchins are voracious omnivorous grazers that are capable of dramatically altering coastal marine ecosystems worldwide, including kelp forests. Changes in urchin grazing patterns due to their abundances, behavior, or food availability can result in transitions between lush, biodiverse kelp forests and urchin barrens denuded of macroalgae. In the Santa Barbara Channel, two species of sea urchins predominate: the red urchin *Mesocentrotus franciscanus* and the purple urchin *Strongylocentrotus purpuratus*. To date, the majority of ecological research in this region has focused on a single urchin species or aggregated both. However, these two species differ in many ways that are highly relevant to their ecological role, including in their morphology, distribution, competitive ability, and vulnerability to predation and harvest. I used an extensive long-term population dataset to assess how these two major grazers are differentially influenced by management (chapter 1) and the environment (chapter 2). I also combined laboratory studies of foraging rates on common understory algae species with long-term data on kelp forest community structure to evaluate the ecological implications of these differences (chapter 3). Lastly, I contextualized

the results of my feeding study by quantifying the interspecific differences in metabolism between red and purple urchins fed different algal diets (chapter 4).

My results demonstrate that species identity cannot be discounted when assessing the management and impact of these key ecosystem engineers. While red urchin populations have increased inside some marine reserves where they are protected from fishing pressure, purple urchin populations displayed no reserve effect; rather, they were associated with heat wave events and declines in kelp density. Purple urchins also had significantly higher foraging rates than red urchins proportional to their size, indicating the potential ecological impact of these populations on the understory algae community could exceed that of red urchin dominated systems. This work lays the foundation for more accurately parameterized models of urchin populations, allowing us to make better predictions of urchin grazing and the factors affecting urchin barren formation and recovery.

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Abstract

In marine ecosystems, fishing often targets predators, which can drive direct and indirect effects on entire food webs. Marine reserves can induce trophic cascades by increasing predator density and body size, thereby increasing predation pressure on populations of herbivores, such as sea urchins. In California's northern Channel Islands, two species of sea urchins are abundant: the red urchin *Mesocentrotus franciscanus*, which is targeted by an economically valuable fishery, and the virtually unfished purple urchin *Strongylocentrotus purpuratus*. I hypothesized that urchin populations inside marine reserves would be depressed by higher predation, but that red urchins would be less affected due to fishing outside reserves. Instead, my analyses revealed that purple urchin populations were unaffected by reserves, and red urchin biomass significantly increased in response to protection. Therefore, urchin biomass overall has increased inside reserves, and I found no evidence that giant kelp is positively affected by reserves. My results reveal the overwhelming direct effect of protecting fished species in marine reserves over indirect effects that are often predicted but seldom clearly documented. Indirect effects due to marine reserves may eventually occur in some cases, but very effective predators, large reserves, or extended time periods may be needed to induce them.

Introduction

Without fishing, there are more and bigger fish. This simple axiom has been confirmed by many studies of marine protected areas over the last thirty years (Molloy et al., 2009; Lester et al., 2009; Sciberras et al., 2013), supporting the use of spatial reserves as a conservation tool. Beyond these direct effects on fished species, however, ecological theory and models predict deeper indirect ecological effects of marine reserves, particularly since fished species are often top predators within interacting communities and food webs (Baskett et al., 2007). Trophic cascades are a prominent example: top predators increase in reserves resulting in decreases in their herbivore prey and subsequent increases in primary producers, particularly foundational species like macroalgae and corals that characterize community states (Shears & Babcock, 2002; Salomon et al., 2009; Ripple et al., 2016).

Trophic cascades and the relative importance of top-down (consumer-driven) and bottom-up (producer-driven) processes in the structuring of ecological communities have long captured the interest of ecologists (Ripple et al., 2016; Hairston et al., 1960). Many early examples of trophic cascades came from freshwater and marine ecosystems, which may have stronger cascades than terrestrial ecosystems (Strong, 1992; Shears & Babcock, 2002; Shurin, 2002; Shurin & Seabloom, 2005). Marine reserves have been at the forefront of this research, as they represent large-scale manipulations of predator density, providing a milieu in which to investigate the effects of predation on marine ecosystems (Madin et al., 2016; Palumbi et al., 2003) at more realistic spatial and temporal scales than permitted by manipulative experiments (Shears & Babcock, 2002). Despite predictions of widespread top-down trophic cascades in marine reserves (Pinnegar et al., 2000), however, evidence for

their occurrence is equivocal (Sala et al., 1998; Shears, Babcock, & Salomon, 2008; Sciberras et al., 2013; Bruno, Côté, & Toth, 2019) and controversial (Schiel, 2013).

Although predicted by food web theory (Barbier & Loreau, 2018), there are many reasons why trophic cascades may not be apparent in natural ecosystems such as marine reserves. Detecting indirect effects may be hampered by study design, particularly spatial comparisons that rely on a few sites, which can be inevitable given that the number of reserves to work in is often limited to only one in a region (Sale et al., 2005). Indirect effects of predators on the ecosystem can be confounded by stronger effects of environmental gradients, habitat, other impacts besides fishing, and other factors (Sala et al., 1998; Shears, Babcock, & Salomon, 2008). The effect of reserves on predators may not be strong enough to induce a trophic cascade, due to small reserve sizes compared to predator home ranges (Parnell et al., 2006), insufficient time since reserve establishment (Molloy et al., 2009), or lack of enforcement of reserve protection. The pathways of indirect effects may not manifest as expected; for example, predators may prefer other prey than hypothesized or shift their feeding behavior depending on the suite of available prey (Berriman et al., 2015), or species interactions such as competition between fished and unfished species may obscure indirect effects (Shears et al., 2012). Finally, the complexity of the food web and intrinsic characteristics of the species involved, such as body size ratios, life history characteristics, and productivity, may affect the strength of trophic cascades (Strong, 1992; Shurin & Seabloom, 2005).

To tease apart the effects of direct versus indirect effects of reserves, it would be ideal to examine pairs of ecologically similar species that are fished and unfished, but both subject to predation by the same fished species. In southern California we have a situation

that approximates this, with two species of coexisting sea urchin, the red urchin *Mesocentrotus franciscanus*, the target of one of California's top five most valuable fisheries, and the virtually unfished purple urchin, *Strongylocentrotus purpuratus*. Both urchin species consume macroalgae, including the giant kelp *Macrocystis pyrifera*, and when densely populated can create so-called urchin barrens that are more or less devoid of macroalgae (Graham, 2004). Both species are preyed on by sheephead fish, *Semicossyphus pulcher*, and California spiny lobster, *Palinurus interruptus*, which are important fisheries species themselves, as well as by the sea star *Pycnopodia helianthoides*. The sea otter *Enhydra lutens*, an iconic urchin predator (Estes & Palmisano, 1974), was historically present but has not successfully recolonized the region. Greater abundances and body sizes of sheephead and spiny lobster have been documented in marine reserves in the northern Channel Islands (Kay et al., 2012; Hamilton & Caselle, 2015) and have been hypothesized to control urchin populations in the reserves (Eurich, Selden, & Warner, 2014; Selden et al. 2017). Most studies, however, have focused on only one of the two urchin species, or all urchins in aggregate.

Channel Islands National Park (CINP) has maintained one of the longest-running time series subtidal surveys in the eastern Pacific since 1982 (Kushner et al., 2013). In 2003, a network of marine protected areas, including eight no-take marine reserves, was established in the islands. Four of these reserves had been monitored since the early 1990's by CINP. Here I used Before-After-Control-Impact (BACI) analysis of this exceptional ecological time-series dataset to examine how the establishment of marine reserves has affected populations, biomass and demography of the two dominant sea urchin species. I found that biomass of the fished red urchin has responded positively to reserve protection,

while purple urchins have not responded to reserves. Overall, the biomass of urchins responded positively to reserve protection. Positive responses of urchin predators were strongest at the reserves with the largest increases in urchin biomass. I found no evidence of trophic cascades due to reserves.

Methods

Diver surveys

The National Parks Service's Kelp Forest Monitoring Program (KFM) has been annually collecting data at 33 sites throughout the Channel Islands, with 16 original sites established between 1981 and 1986. Divers collected data annually on the density and sizes of sea urchins – along with metrics on many other species – on a 100-meter permanent transect line at each site. Beginning with an initial random sampling point between 0-7 m, a pair of 1 m^2 quadrats were laid out on either side of the transect line at 8.33 meter intervals. A total of 12 quadrat pairs were sampled for counts of 25 target species, including *M. franciscanus* and *S. purpuratus*. The first 200 urchins of each species, or all individuals if less than 200, were sampled along the transect line and test diameter measured to the nearest millimeter using calipers. In this analysis, we also used data collected by KFM on *Semicossyphus pulcher* (California sheephead), *Pycnopodia helianthoides* (sunflower star), and *Panulirus interruptus* (California spiny lobster). Sunflower stars and spiny lobsters were counted along twelve 3 x 20 m (60 m^2) transects. Lobster were found infrequently and size information was not collected. For California sheephead, divers surveyed fish communities visually on four 3 x 2 x 50 m transects. Starting in 2007, estimated total length of fish was also collected to the nearest 5 cm for large fish (>15 cm) and 1 cm for small fish. Giant kelp

(*Macrocystis pyrifera*) was surveyed along the 100 m permanent transect lines by counting the number of kelp stipes at 1m above the bottom in 40 5 m^2 quadrats that covered the entire span of the transect line on each side.

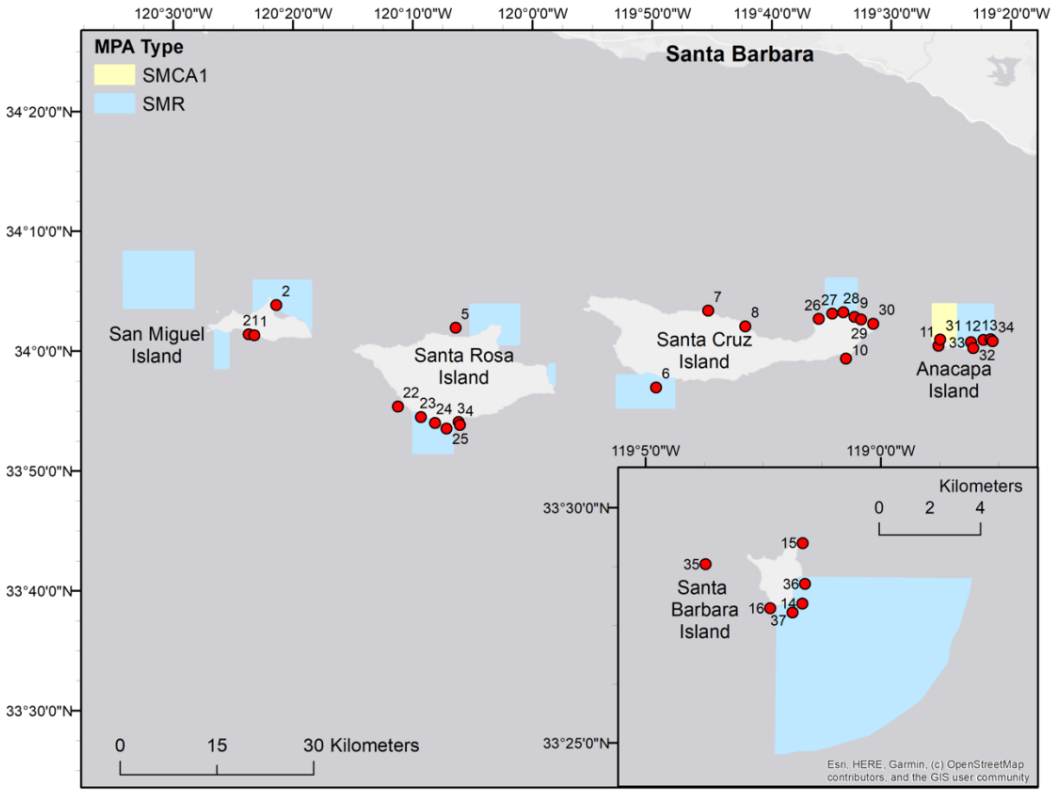

Figure 1.1: Map of Kelp Forest Monitoring sites used in this analysis. Blue polygons represent the boundaries of State Marine Reserves (SMR) and the yellow polygon represents the boundaries of a State Marine Conservation Area (SMCA1). No fishing of any kind is allowed in marine reserves, while the conservation area allows for the recreational take of spiny lobster and pelagic finfish, and commercial take of spiny lobsters.

Before-After Control-Impact analyses

All data analysis was performed in R (R Core Team 2019). For the BACI analysis, I only considered the continuous dataset for KFM sites 1-11 and 14-16 from 1991-2019. These sites were the first set of sites to be surveyed, whereas newer sites were not surveyed until after the establishment of marine reserves in 2004. Sites 12 and 13 were excluded

because they were located in the Anacapa Marine Reserve, which is a much older reserve (established 1978). Urchin test diameters were converted to wet mass (g) with the following formulas (Reed et al., 2016):

$$M = 5.9 * 10^{-4} * L^{2.917} \qquad \textit{Mesocentrotus franciscanus}$$

$$M = 5.9 * 10^{-4} * L^{2.870} \qquad \textit{Strongylocentrotus purpuratus}$$

Total species-specific biomass in g m^{-2} was calculated by multiplying the average wet mass of the species at a site by the average density of individuals at that site.

All analyses were performed in R following methods from Underwood (1993) and Schwarz (2015). Sites 2 (San Miguel Island), 6 (Santa Cruz Island, South), 9 (Santa Cruz Island, North), and 14 (Santa Barbara Island) transitioned from non-reserve to reserve sites in 2004. These sites were considered impact sites, whereas the other 10 sites were control sites.

The linear mixed effects model to evaluate effects of marine reserve protection on sea urchin populations was formulated as follows:

$$y_i = \mu + \beta_1 x_{1,i} + \beta_2 x_{2,i} + (\beta_1 \beta_2)_{ij} + b_{0,j[i]} + b_{1,j[i]} x_{1,i} + b_{2,j[i]} x_{2,i} + e_i$$

where μ is the mean urchin biomass (g m^{-2}), x_1 and x_2 are categorical reserve status variables [x_1: 0 indicates before the impact (before 2004) and 1 indicates after impact, x_2: 0

indicates control site (not a marine reserve) and 1 indicates an impact site (marine reserve)], $(\beta_1\beta_2)_{ij}$ is the interaction between time period (before or after) and location (reserve or non-reserve), β_k characterizes the fixed effects, $b_{k,j[i]}$ characterizes the group-level effects, $j[i]$ denotes the group (site ID) of observation i, and e_i is the error term. Since ACF (autocorrelation function) and pACF (partial autocorrelation function) plots indicated short lags in the data, I added an AR(1) correltation term to account for temporal autocorrelation. Models were fit using the lme4 package in R (Bates et al. 2015). After model diagnostics (residuals plots and QQ plots) and selection via AICc (Akaike Information Criterion with correction for small sample sizes), I used a two-way repeated measures ANOVA to compare results. The BACI contrast (effect size) was estimated using the emmeans package in R (Lenth 2020).

I used separate BACI models to evaluate reserve effects on total urchin biomass, on the two sea urchin species separately, and on densities of kelp stipes. In the total urchin biomass model, I used urchin species as a grouping factor in the error structure to account for heterogeneity of variance. The response variable (urchin biomass) was log transformed to normalize residuals in all models. For each species, I also grouped urchins into size classes following Selden et al. (2017) using test diameters (small < 35 mm, medium 35-50 mm, large 50-70 mm, very large 70+ mm) to estimate the biomass occupied by each class and construct BACI models on small urchins only. Due to low densities of urchin predators in the surveys, there were not enough data to perform a statistically rigorous BACI analysis and these values were presented graphically.

Results

Urchin biomass

There was a significant interaction (p=0.0126) between treatment (control or reserve) and time (before or after establishment of marine reserves) in the linear mixed-effects model of total urchin biomass. The interaction term for this full model was positive, indicating increases in urchin biomass in reserve sites over fished sites after 2004, and the BACI contrast (using estimated marginal means on the log scale) was significant for reserve sites (p=0.0002), reflecting the significant increase in urchin biomass at reserve sites after protection began in 2004 (Fig.1.2) The difference between the change in biomass at fished versus reserve sites was -55.00 g m^{-2} yr^{-1} with a standard error of 36.85 g m^{-2} yr^{-1}. Thus, on average, urchin biomass increased nearly three times more in reserve sites than in fished sites after the network of marine reserves was established.

This change in urchin biomass was driven primarily by red urchins. A separate model for red urchins alone had a significant positive interaction term (p=0.0004), meaning that control (fished) sites had a significantly smaller increase in red urchins than marine reserve sites after marine reserve establishment. On average, red urchin biomass density increased by 266 g m^{-2} at sites that became marine reserves, nearly quadrupling (397% increase) compared to the decrease of 89 g m^{-2} at fished sites. Two out of the four reserve sites, Gull Island and Hare Rock, had the largest increases in red urchin biomass, although in recent years red urchin biomass has declined at Hare Rock (Fig. 1.3). The BACI model for purple urchins had no significant terms, indicating that purple urchins did not change significantly between control and reserve sites or before and after 2004, nor was there an interaction between time and reserve status.

On average, biomass of both purple and red urchins was higher inside marine reserves than non-reserve sites after the network was established in 2004, although red urchins initially increased more rapidly than purple urchins, and only red urchins had a significant difference in biomass ($p=0.0020$). Purple urchin biomass increased over time outside marine reserves, however, while red urchins decreased in biomass outside reserves (Fig. 1.2)

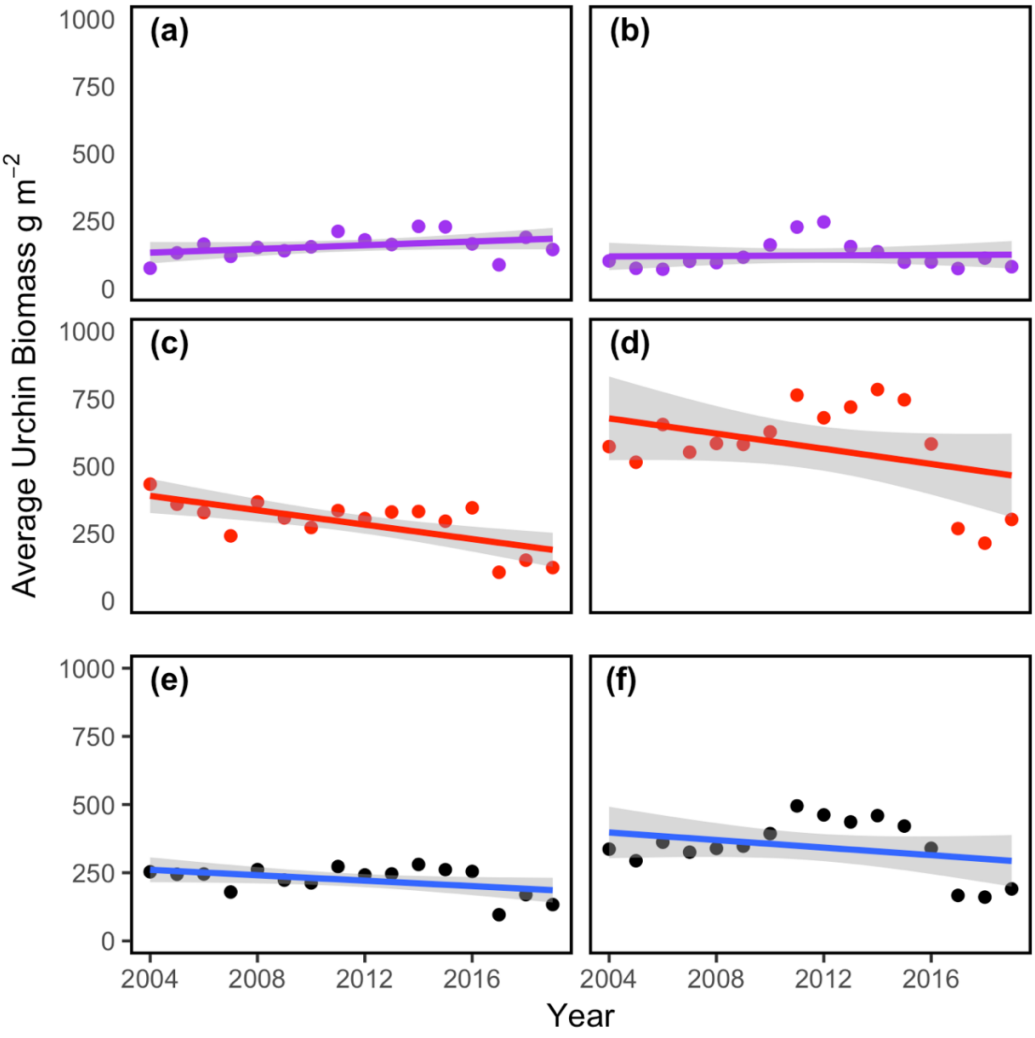

Figure 1.2: Changes in average total biomass (g m^{-2}) after 2004 for *S. purpuratus* in (a) all fished sites and (b) all reserve sites, and for *M. franciscanus* in (c) all fished sites and (d) all reserve sites. The bottom panes represent the average biomass for both species in (e) all fished sites and (f) all reserve sites.

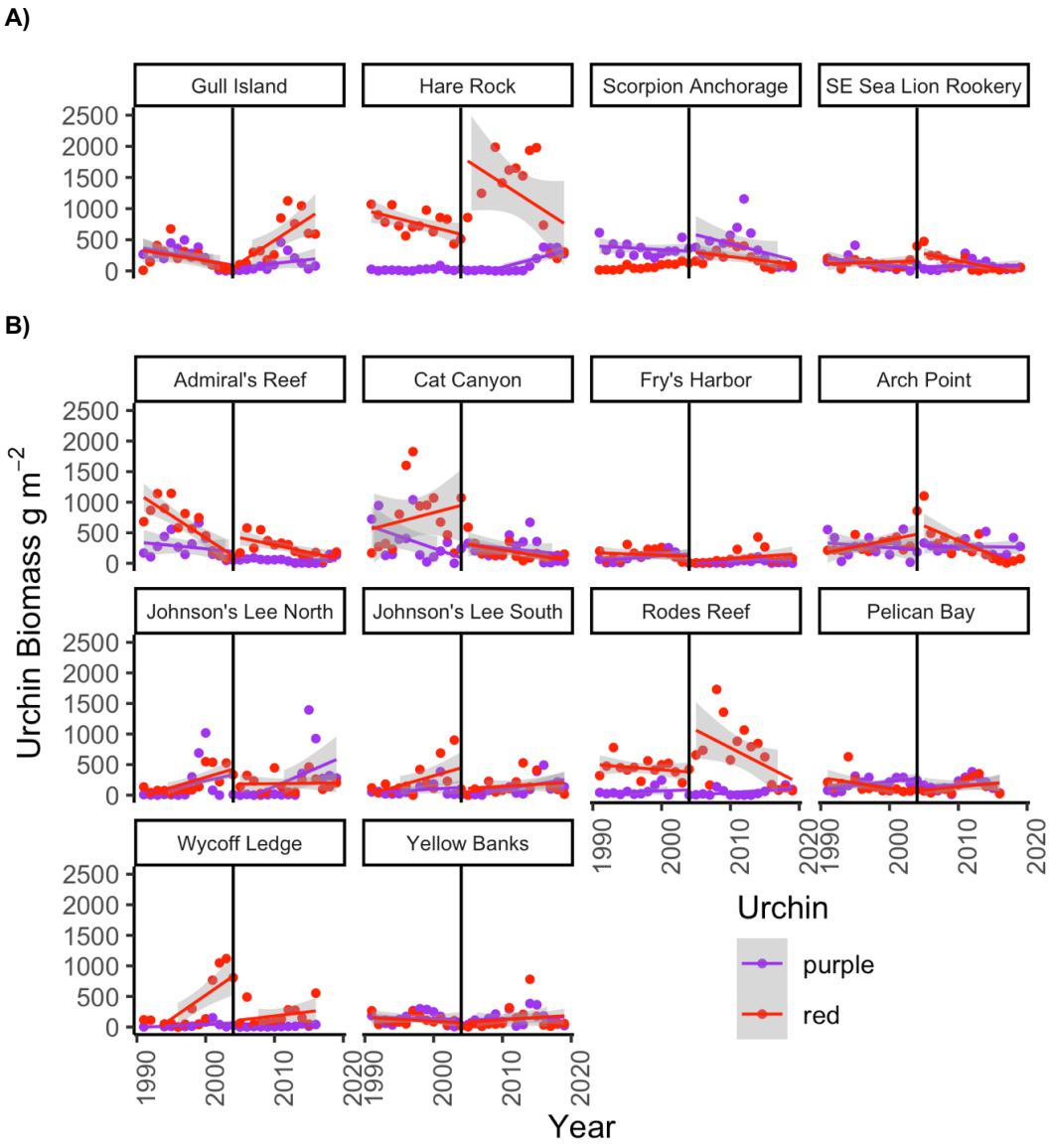

Figure 1.3: Changes in urchin biomass over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical line) at reserve (a) and control (b) sites. Titles are site names.

Urchin size distributions

Since smaller urchins are typically more vulnerable to predation, abundance of small urchins may be a more sensitive indicator of changes in predation pressure on urchin

populations due to reserve protection of their predators. Nevertheless, we found a similar pattern in small urchins to that for urchin populations as a whole. The value for the interaction term in a BACI model for small red urchin biomass was significant (p=0.0444) and positive (b=.1701), indicating that on average small red urchin biomass increased inside reserves compared to outside (Fig. A1.1). There was no significant interaction term for small purple urchins, and when this term was dropped from the model, time period was significant (p=0.0024) but reserve status was not (p=0.6406). Biomass of small purple urchins was not significantly different between reserve and fished sites, but the negative estimate for time period (b=-0.3596) indicates a slight decline in small purple urchin biomass both inside and outside reserves after the reserves were established. The majority of red urchin biomass was distributed across large size classes (Fig. A1.7), while the majority of purple urchin biomass was distributed across small and medium size classes (Fig. A1.8).

Kelp density

No significant effect of reserve status (p=0.0940) or time period (p=0.4653) or the interaction between status and time (p=0.1514) was evident for kelp stipe density (Fig. S2). In the mixed effects model with both urchin species grouped together, time period and average urchin biomass did not have a significant effect on mean stipe density. All the available data from KFM sites across all years showed no significant relationship between urchin densities and kelp stipe densities, and the correlation for red sea urchins was in fact weakly positive (Fig. A1.9).

Urchin predators

I planned to use BACI analyses to test whether marine reserves were effectively increasing predator densities. However, because the densities of urchin predators were low,

inconsistently measured, did not meet statistical assumptions for parametric tests, and were not all sized to yield biomass estimates, these analyses were not possible. Qualitatively, plots of these data show dramatic differences between sites that are not always consistent with reserve effects (Figs A1.4-A1.6). These data show, however, that Gull Island and Hare Rock reserves, where urchins had the strongest positive response to reserve establishment, also had relatively high predator densities compared to the other two reserves (although similar to some fished sites). Hare Rock reserve, which showed the greatest urchin response, also had the highest densities of sheephead and sunflower stars among the 4 reserve sites (although data from the Scorpion Anchorage reserve was sparse).

Anacapa Island urchin biomass

Anacapa Island was considered separately because it is uniquely old, and no data were available there prior to the establishment of the marine reserve in 1978. However, three sites there have been continuously monitored since 1981, two within and one outside the marine reserve. ANOVA revealed a significant difference in red urchin biomass between the reserves and the fished site ($p=2.45 \times 10^{-7}$), and ANCOVA yielded a significant reserve ($p=2.15 \times 10^{-8}$) and time effect (6.94×10^{-5}) but not an interaction between the two. In general, red urchin biomass decreased at all Anacapa sites, but the highest rate of decrease *and* the lowest overall red urchin biomass was at the fished site. For purple urchins, there was a significant interaction between reserve status and time ($p=1.5 \times 10^{-6}$); purple urchins had higher biomass at the fished site compared to the reserves in the 1990's, but decreased sharply and by the early 2000's onward, populations have been as low or lower at the fished site than the reserve sites (Fig A1.2).

Discussion

In temperate marine ecosystems, including the California Channel Islands, protection of top predators inside marine reserves has been widely predicted to cause trophic cascades – decreases in herbivore biomass, often sea urchins, and corresponding increases in kelp, along with increased biodiversity associated with kelp forests (Byrnes et al., 2006; Kalvass & Hendrix, 1997). I found no evidence, however, of strengthened trophic cascades in response to 15 years of marine reserve protection in the Channel Islands. On the contrary, total sea urchin biomass density *increased* on average inside marine reserves. Rather than suppressing urchin populations, marine reserves have led to population recovery of fished red sea urchins (*Mesocentrotus franciscanus*), while populations of unfished purple urchins (*Strongylocentrotus purpuratus*) were unaffected. Two of the reserves I examined, Gull Island (at Santa Cruz Island) and Hare Rock (San Miguel Island), are in areas of historically high sea urchin catches (Kalvass & Hendrix, 1997) and showed particularly dramatic increases in red sea urchin biomass (Fig. 1.3), despite having some of the highest counts of urchin predators after reserve establishment (Figs. A1.4-A1.6). This suggests that the benefits of release from fishing pressure far outweighed any effect of increases in predators on sea urchins inside the reserves.

Increases in predator density and biomass inside reserves don't necessarily translate to rapid effects on prey populations. For example, if small individuals are favored by predators, as is the case with both purple and red sea urchins (Hamilton & Caselle, 2015; Selden et al., 2017), the effects of increased predation would take time to propagate through the prey population as new recruits suffer higher mortality, but larger size classes remain unaffected. For this reason, I examined juvenile urchin populations separately, and found a

similar pattern to overall population biomass – red urchin juveniles increased inside reserves, while purple juveniles were unaffected. Therefore, the lack of a trophic cascade effect on urchin populations was apparently not due to a time lag caused by a holdover of large predation-resistant urchins predating reserve establishment (Salomon et al., 2009). In fact, increases in red urchins in response to fishing protection were evident after only 6 years of marine reserve protection (Teck et al. 2017). Reserve protection, moreover, appears to have increased local recruitment of fished red sea urchin populations, suggesting that retention of sea urchin larvae may be occurring on the scale of the reserves.

Another possible effect of increased predation inside reserves is altered behavior of prey and consequent changes in their ecological impacts in a "landscape of fear" (Laundré, Hernándex, & Ripple, 2010). In areas with abundant predators, herbivores may flee or take shelter and spend less time actively grazing (Lima, 1998). Such a trait-mediated indirect interaction, rather than direct predation, can be the dominant cause of a trophic cascade (Schmitz, Krivan, & Ovadia, 2004). Sea urchins may spend less time grazing in the presence of predators (Freeman, 2005), and this pattern has been suggested to occur in the Channel Islands (Teck et al., 2017). If marine reserves were causing such indirect effects, primary producers, in this case giant kelp, would be expected to increase in abundance. Yet the density of giant kelp, which is grazed by sea urchins, was unaffected by reserve protection in the Channel Islands. My results demonstrate no evidence, therefore, that increases in predators inside Channel Islands marine protected areas are causing, either through direct or indirect effects, a trophic cascade leading to positive effects on kelp forests via decreased sea urchin biomass and grazing.

Although data on the density of urchin predators were not available for all sites and years, there is clearly a high degree of variability in predator populations across space and time (A1.4-A1.6). This variability, combined with the lack of data on predator body size and biomass, limits the conclusions I can draw about the effect of the reserves on predators. However, other studies have shown positive effects of Channel Islands reserves on population density and body size of urchin predators including sheephead (Hamilton & Caselle, 2015) and lobster (Kay et al., 2012). The unfished sea star *Pycnopodia helianthoides* is a voracious predator of *S. purpuratus* in particular, so even a few individuals could have a large impact on urchin populations (Herrlinger, 1983). Fluctuations in its density due to disease and other factors may have affected some of the site-specific temporal patterns in urchin abundance. In addition, urchin populations that are abundant due to release from predation or other factors may be reduced by density-dependent disease outbreaks (Lafferty, 2004). Any effect of these processes on urchin populations, however, did not appear to vary with reserve status.

Why have increased predator populations inside reserves apparently not affected urchin populations and led to trophic cascades? There are two obvious possibilities. First, predator populations and sizes have not yet, after 15 years, rebounded to the extent necessary for cascades to occur. Second, purported urchin predators do not rely on urchins as prey with enough frequency to significantly affect their populations. These two explanations could be related, in that predator populations might be expected to exploit all prey once a density-dependent threshold is reached. In the following paragraphs, I discuss the evidence for each of these two possible explanations.

The main predators of sea urchins in our region at present are considered to be sheephead fish (*Semicossyphus pulcher*), spiny lobster (*Palinurus interruptus*), and the sunflower star (*Pycnopodia helianthoides*), which is unfished and not considered further here. A decade after reserve establishment, Hamilton and Caselle (2015) found positive effects on both density and biomass of sheephead, with the strongest effects on densities of large individuals and total biomass at Santa Cruz and Santa Rosa Islands. Mean total length of sheephead inside reserves at all five islands was larger than the approximately 25 cm that Selden et al. (2017) observed as the size at which sheephead become effective predators of small urchins, and was much larger at some islands – the average total length in Santa Rosa marine reserves was greater than 40 cm. Densities Hamilton and Caselle reported were comparable, albeit somewhat lower, to those in an unfished population at San Nicholas Island (Cowen, 1983), and large individuals were likely more abundant in the historic populations (Hamilton & Caselle, 2015). On transects across the northern Channel Islands in reserve and non-reserve sites, Hamilton and Caselle (2015) found a negative relationship between sheephead biomass and urchin density (both species combined). However, no overall effects of reserve status on urchin biomass or kelp abundance were found.

Spiny lobster exhibited a very strong positive response to reserve protection in the Channel Islands, increasing 4-6 times in density at the reserves in this study after only six years of protection (Kay et al., 2012). Since then, surveys in two of the reserves, Gull Island and Scorpion Anchorage, showed that 15 years after reserve protection lobsters have continued to increase, reaching approximately 20 times the biomass of pre-reserve populations (Fitzgerald, 2019). Spiny lobsters presented with relatively unpalatable prey, the

sea hare *Aplysia californica*, only attacked them inside reserves throughout southern California, suggesting food limitation due to higher densities (Berriman et al., 2015).

Based on a comparative analysis of monitoring data, Babcock et al. (2010) estimated that indirect effects should take longer to detect than direct effects (13.1 years vs. 5.13 years, respectively). Overall, the evidence suggests that, after 15 years of protection from fishing, predator populations have rebounded in the reserves to an extent that would be expected to affect urchin prey populations. Although it is still possible that urchin numbers will be affected as predator populations continue to grow in the reserves, this suggests that the presumed predator species are not heavily reliant on sea urchins for prey. Studies of sheephead diet have shown that it is highly variable, often including urchins but to varying degrees (Cowen, 1986). Larger fish tend to rely more on sea urchins as food (Hamilton, Newsom, & Caselle, 2014; Hamilton & Caselle, 2015), and are more effective sea urchin predators (Selden et al., 2017). *In situ* observations showed highly variable feeding by sheephead on urchins, but also demonstrated that sheephead could cause high urchin mortality at small scales (Dunn & Hovel, 2019). Although aquarium experiments have shown that lobster will consume urchins (Tegner & Levin, 1983), evidence from nature on the importance of urchins in spiny lobster diets is sparse. A study of spiny lobster gut contents in Baja California showed that gastropods were most important, and no echinoderms were detected (Diaz-Arredondo & Guzmán-de-Próo, 1995). Off San Diego, lobster gut contents were mostly made up of mollusks and crustaceans, although urchins were also frequently consumed, particularly in deeper rocky habitats (Winget, 1968). More information on spiny lobster feeding habits and their reliance on sea urchins is needed.

Complex food webs have been thought to weaken the strength of top-down control in terrestrial ecosystems, potentially explaining why many examples of trophic cascades are aquatic (Strong, 1992; Shurin, 2002). Like many marine ecosystems, however, giant kelp forests are highly diverse (Schiel & Foster, 2015), with greater than 8,700 trophic links identified in a California giant kelp forest food web, not including parasites (Morton, 2020). Byrnes et al. (2006) identified 39 kelp forest species that serve as prey for sheephead and 25 species that serve as prey for spiny lobster, and a more recent food web found that sheephead had the widest diet breadth of any kelp forest species, consuming 129 genera (Morton, 2020). Increased predator diversity can also dampen the impact of predation on herbivores, as different predator species feed on each other and on shared prey species, weakening potential cascades (Hart, 2002; Finke & Denno, 2004). Post-settlement movement of mobile predators outside reserves could also act to dilute their impact, allowing for increases of both predators and fished prey (Jiao, Pilyugin, & Osenberg, 2016).

Around the world, but particularly along the west coast of North America, top-down control and resulting trophic cascades have often been cited as maintaining kelp forests that would otherwise collapse under pressure of sea urchin grazing (Estes, Duggins, & Rathbun, 1989; Jackson et al., 2001), although this view has not been universal (Foster & Schiel, 2010; Foster, 1990). Urchin grazing, however, is affected by multiple factors, including recruitment, disease, and physical disturbance, and the spatial scale of its impact varies widely (Filbee-Dexter & Scheibling, 2014). In the northwest Atlantic, an early paradigm that lobster predation on urchins drove top-down control of urchin barrens has not been supported by empirical or experimental evidence (Scheibling, 1996), although historically high abundances of groundfish may have driven trophic cascades in the past (Steneck et al.,

2002). Trophic cascades have been documented in northeastern New Zealand, but their strength depends on environmental context (Shear, Babcock, & Salomon, 2008), and other factors are more important in structuring kelp forests across much of New Zealand (Schiel, 2013). In Tasmania, increasing recruitment of urchins due to changes in oceanographic patterns and warming have interacted with lower predation due to lobster overfishing to reduce resiliency of kelp forests to urchin grazing (Ling et al. 2009). In other regions, kelp forest ecosystems are mainly structured by non-trophic factors. In the northeast Atlantic, ocean climatic patterns drive kelp forest community structure, and urchin grazing plays a minor role (Smale et al., 2013; Smale & Moore, 2017). In Chile, South Africa, and southwestern Australia, although sea urchin densities vary greatly, they depend on drift algae as food (as Californian urchins often do), and have not been associated with large-scale kelp deforestation (Castilla & Morena, 1982; Santelices & Ojeda, 1984; Vanderklift & Kendrick, 2005). Overall, this suggests that the widespread depiction of kelp forests and urchin barrens as alternative stable states controlled by predation is an unwarranted paradigm.

Trophic cascades are sometimes considered dominant forces in ecosystems, controlling their entire structure (Terborgh & Estes, 2010). Cascades are considered more common in marine ecosystems (Strong, 1992; Shurin, 2002), where most examples involve echinoderms, particularly sea urchins, as key herbivores (Salomon et al., 2009). My results demonstrate, however, that trophic cascades are not always prevalent in marine ecosystems, and that fishing bans in marine reserves will not necessarily result in clear trophic cascades. In part, this reflects the fact that humans are often the ultimate predator, and direct effects of protection from us dominates community patterns (Trites, Christensen, & Pauly, 2006) in

conjunction with pervasive environmental effects (Lamy et al. 2020). In addition, only certain marine predators may be effective enough to drive cascades, and many ecosystems may lack such species due to biogeography or past extirpations. In southern California, kelp forest trophic cascades may never be realized until sea otters return in significant numbers, if that ever occurs. Until then, we have much to learn about the true ecological effects of marine reserves and their value for testing hypotheses about ecological interactions on large spatial and temporal scales. My study demonstrates the value of studying marine reserves even as the results fail to support the paradigmatic view that marine reserves will result in lush, resilient kelp forests through predator-mediated trophic cascades.

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Appendix

Supplementary Figures

A)

B)

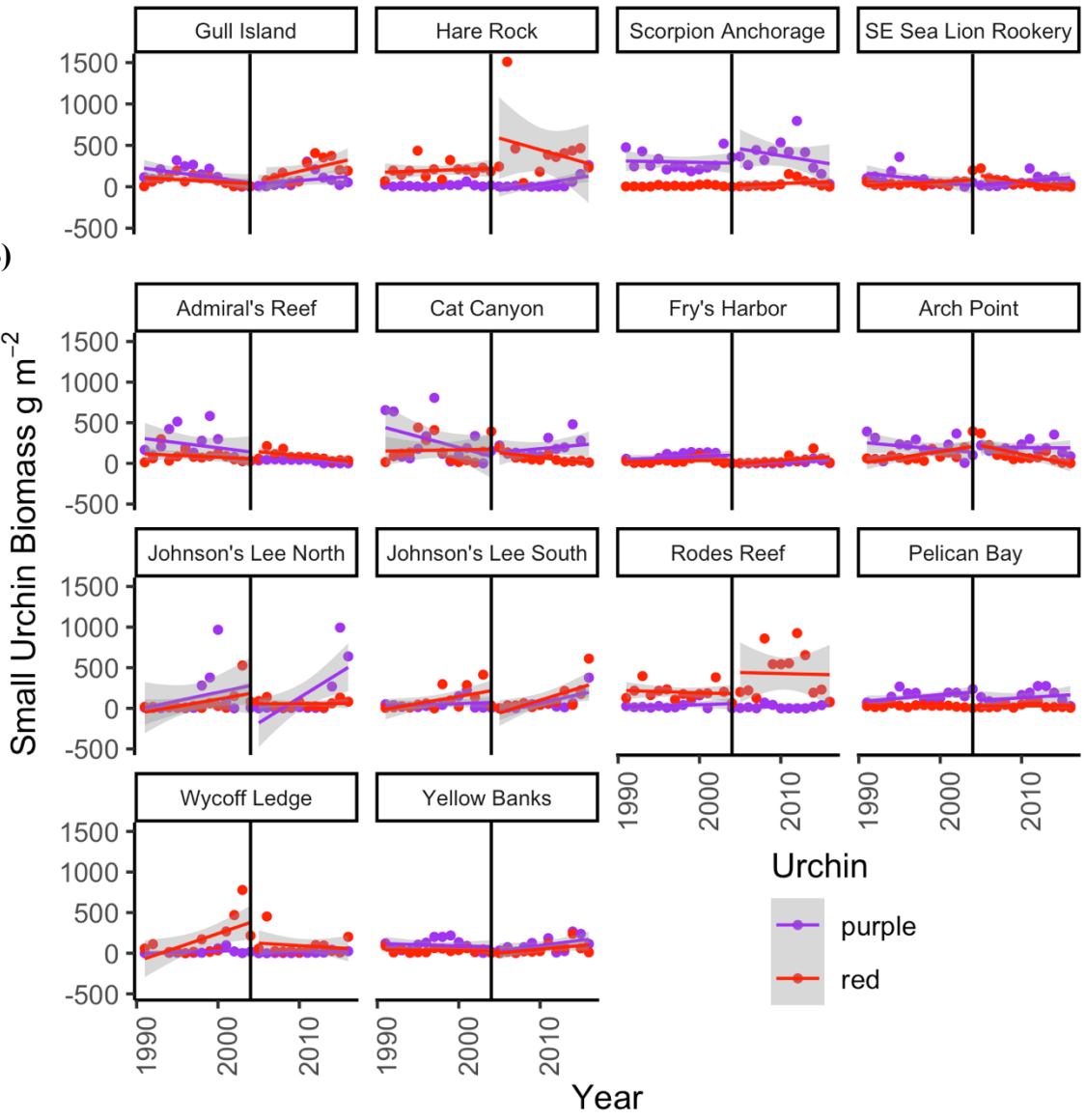

Figure A1.1 Changes in average small (<35 mm test diameter) urchin biomass over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical line) at reserve (**A**) and control (**B**) sites.

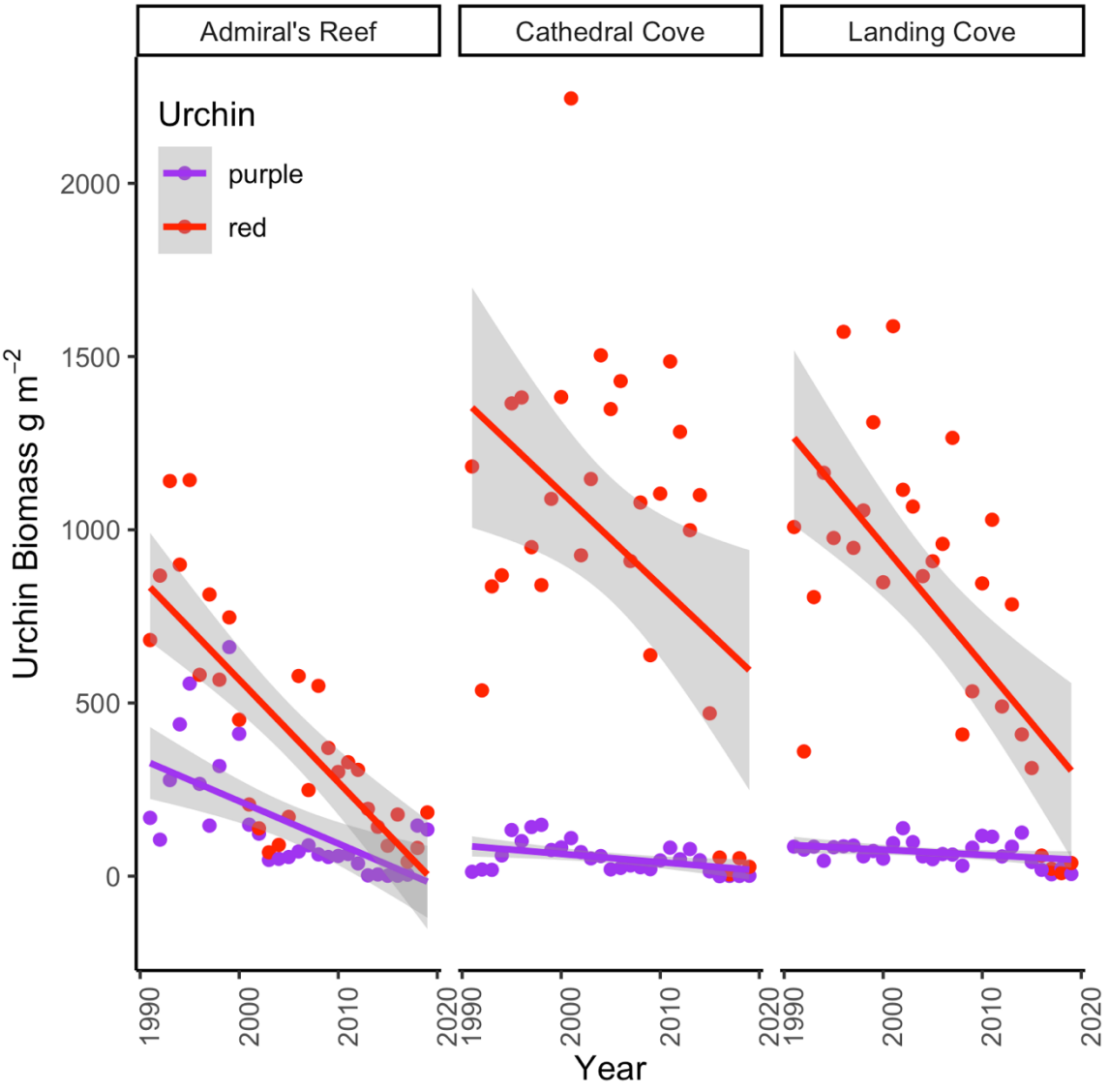

Figure A1.2. Change in urchin biomass over time at the three original Anacapa monitoring sites, with regression lines fit for red and purple urchins, respectively. Admiral's Reef is the fished site, Cathedral Cove and Landing Cove are reserve sites.

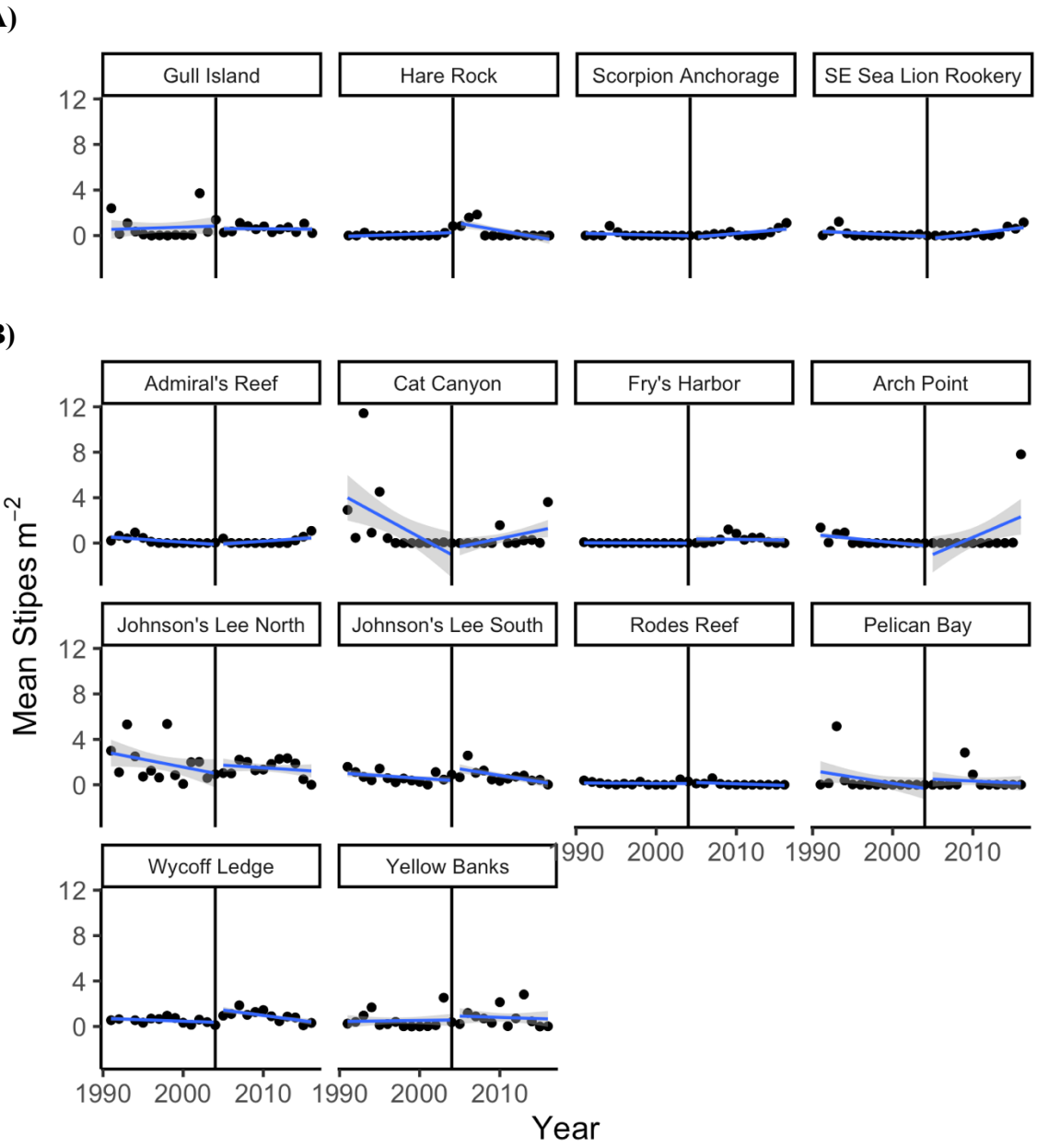

Figure A1.3. Change in kelp stipe density over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical lines) at reserve (**A**) and control (**B**) sites.

Site ID	Site Name	Island	Marine Reserve?	Date Reserve Established
1	Wycoff Ledge	San Miguel	No	
2	Hare Rock	San Miguel	Yes	2004
3	Johnson's Lee North	Santa Rosa	No	
4	Johnson's Lee South	Santa Rosa	No	
5	Rodes Reef	Santa Rosa	No	
6	Gull Island	Santa Cruz	Yes	2004
7	Fry's Harbor	Santa Cruz	No	
8	Pelican Bay	Santa Cruz	No	
9	Scorpion Anchorage	Santa Cruz	Yes	2004
10	Yellow Banks	Santa Cruz	No	
11	Admiral's Reef	Anacapa	No	
12	Cathedral Cove	Anacapa	Yes	1978
13	Landing Cove	Anacapa	Yes	1978
14	SouthEast Sea Lion Rookery	Santa Barbara	Yes	2004
15	Arch Point	Santa Barbara	No	
16	Cat Canyon	Santa Barbara	No	

Table AT1.1. List of the 16 sites used in this study, listed by site ID number according to NPS KFM. Date Reserve Established is the year when no-take regulations were put into effect.

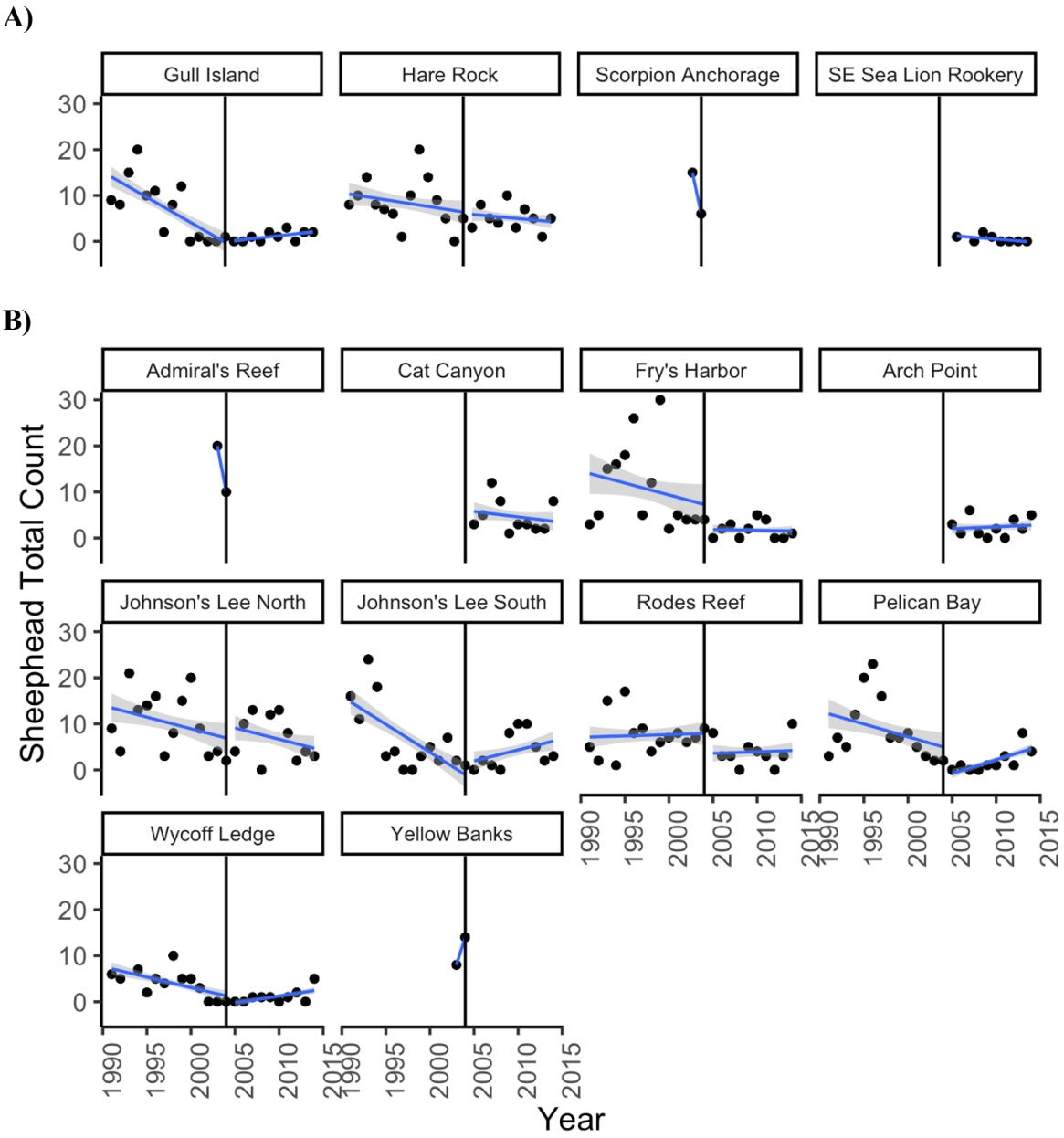

Figure A1.4. Changes in sheephead counts over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical lines) at reserve (**A**) and control (**B**) sites.

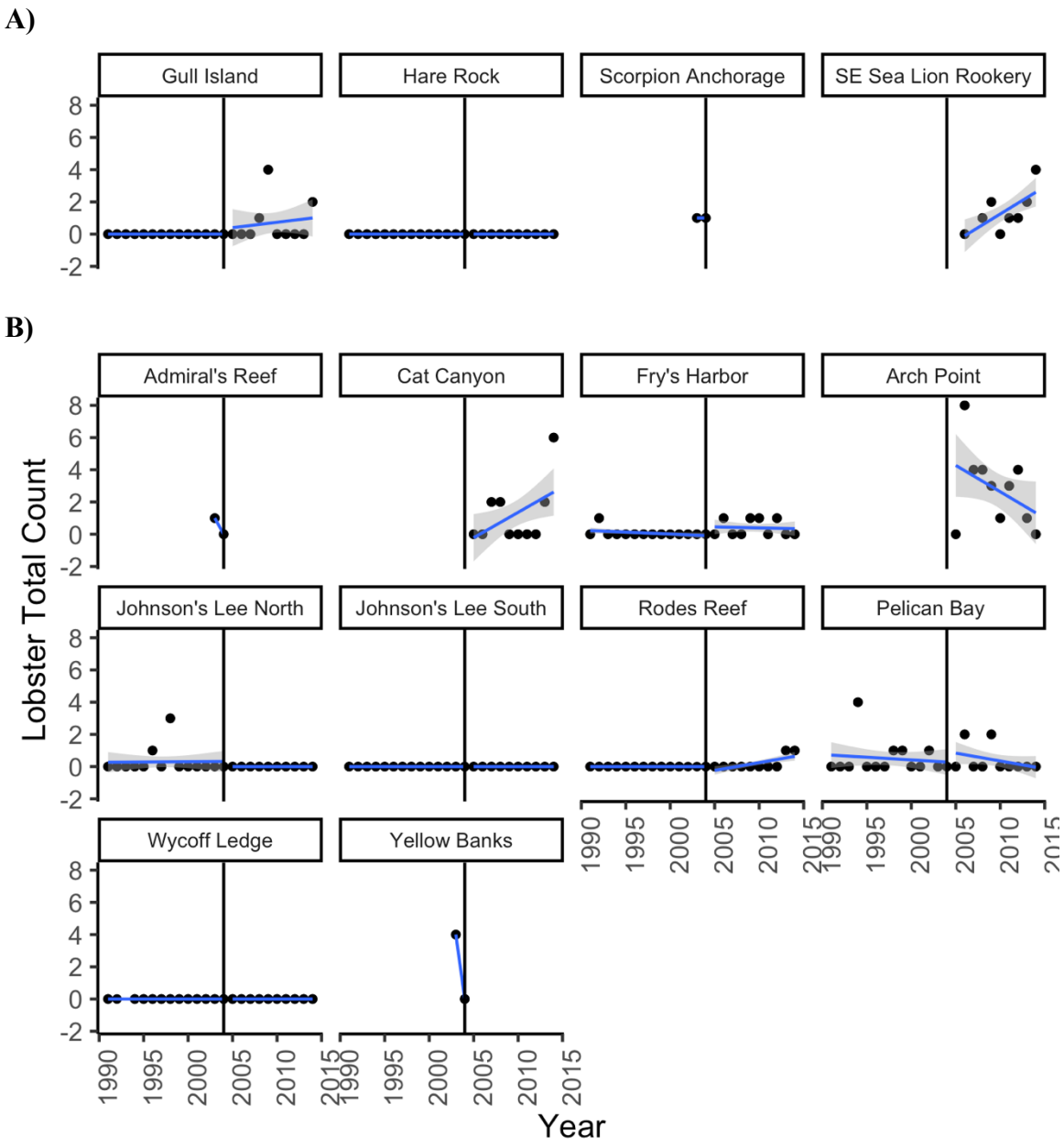

Figure A1.5. Changes in lobster counts over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical lines) at reserve (**A**) and control (**B**) sites.

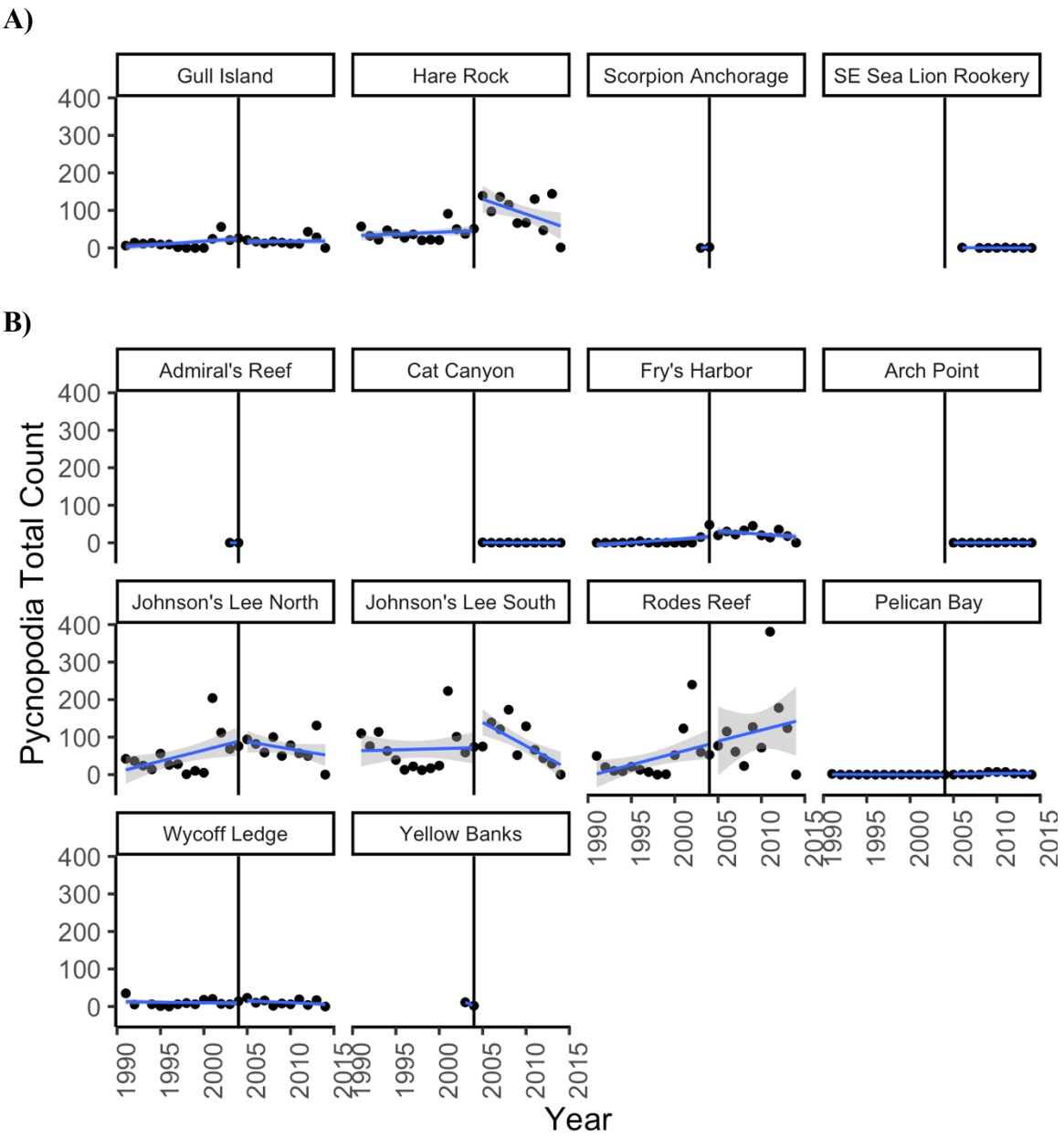

Figure A1.6. Changes in sunflower star counts over time with regression lines fit before and after the establishment of marine reserves in 2004 (vertical lines) at reserve (**A**) and control (**B**) sites.

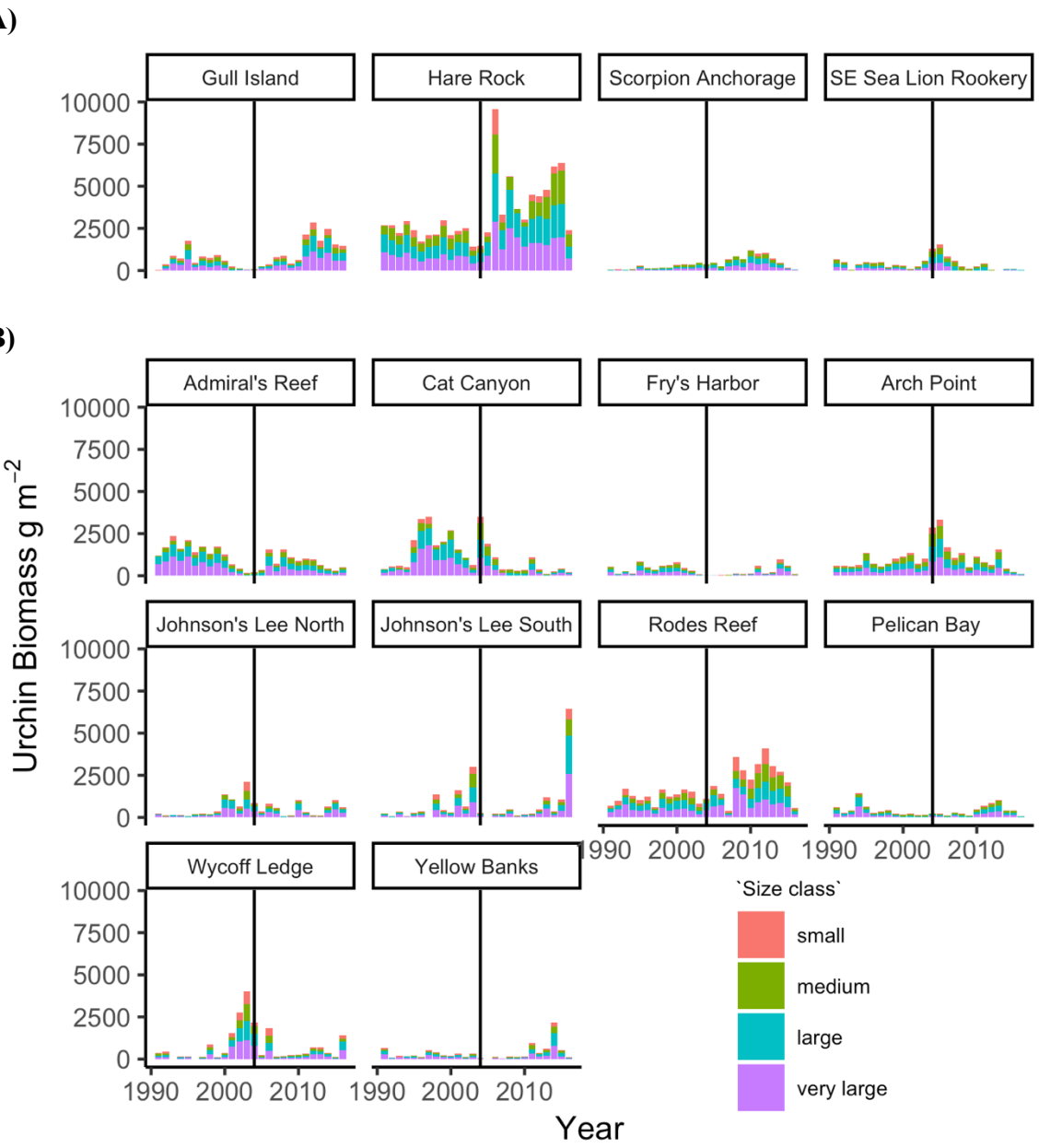

Figure A1.7. Biomass occupied by four size classes of **red** urchins over time, grouped by test diameter: small (<35 mm), medium (35-50 mm), large (50-70 mm), and very large (>70 mm) before and after the establishment of marine reserves in 2004 (vertical line) at reserve (top row, circled) and control sites.

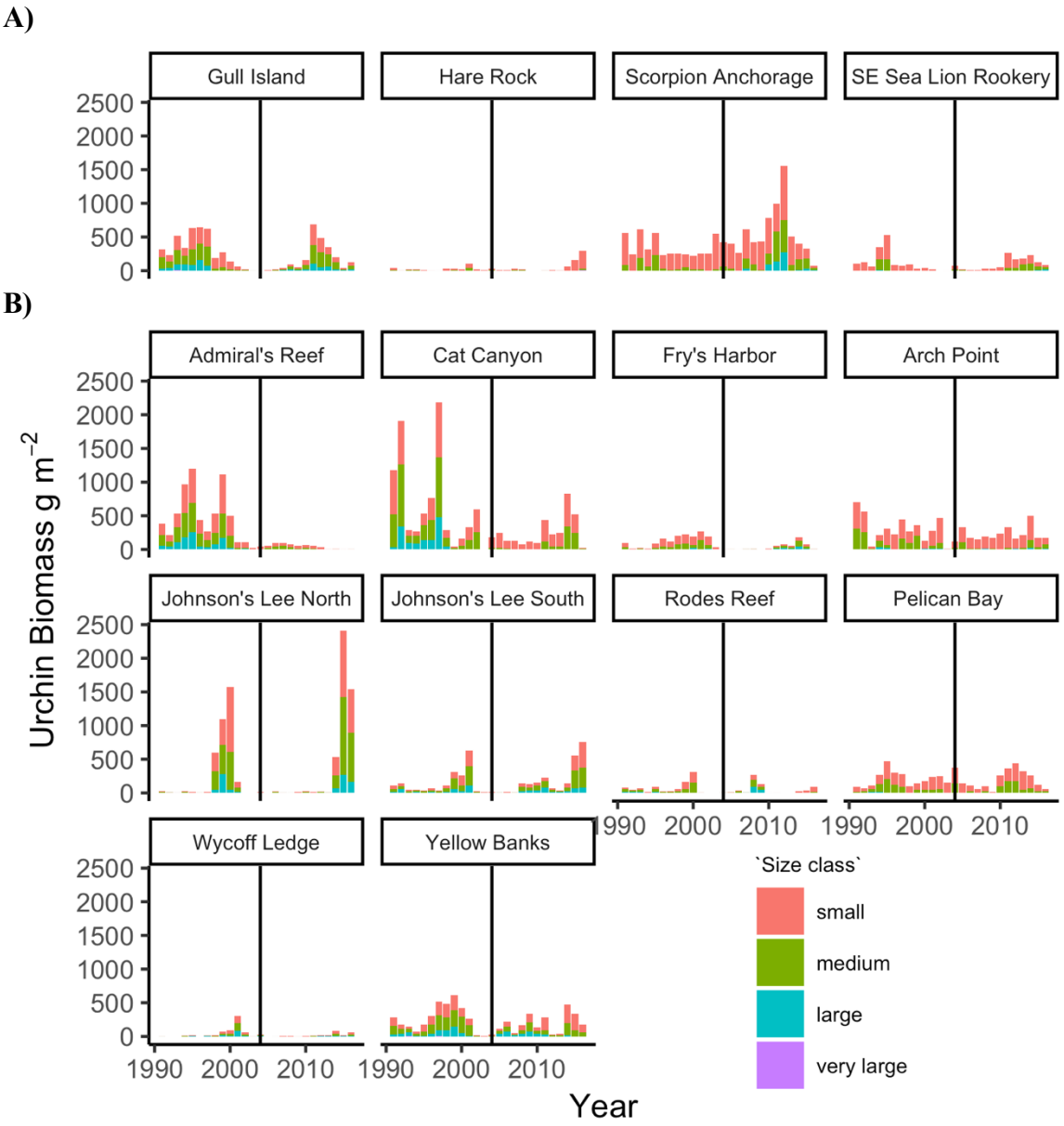

Figure A1.8. Biomass occupied by four size classes of **purple** urchins over time, grouped by test diameter: small(<35 mm), medium (35-50 mm), large (50-70 mm), and very large (>70 mm) before and after the establishment of marine reserves in 2004 (vertical line) at reserve (**A**) and control (**B**) sites.

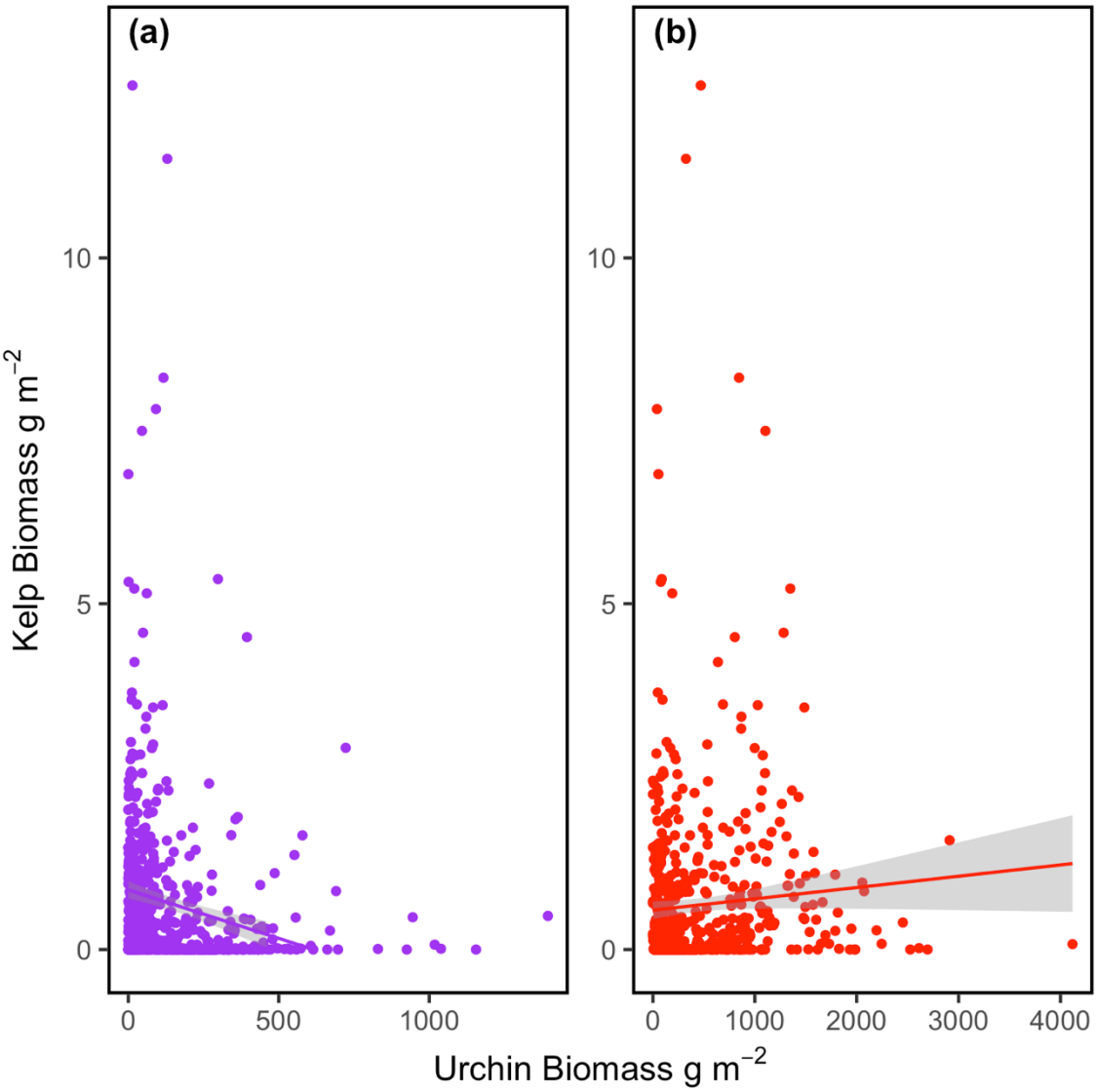

Figure A1.9. Kelp biomass by urchin biomass across all sites and years for **a)** purple urchins and **b)** red urchins.

II. Variability in urchin populations in response to environmental change and fishing pressure

Abstract

In Chapter 1, I found that *Mesocentrotus franciscanus* (red sea urchin) and *Strongylocentrotus purpuratus* (purple sea urchin) populations were responding to marine reserve protection in different ways, with purple urchin populations relatively unaffected by reserves, and red urchin biomass significantly increasing in response to protection from fishing. This chapter extends that analysis with statistical modeling of urchin populations in response to both fishing pressure and environmental change. I investigated how red and purple urchin populations fluctuate with variation in sea surface temperature, marine heatwave days, wave height, surface chlorophyll-a concentrations, kelp density, site depth, marine reserve age, and red urchin catch. Using a combination of parametric and nonparametric approaches, I determined that purple urchin biomass was positively associated with increases in the annual number of heatwave days and negatively associated with kelp density, while red urchin biomass was positively associated with the age of a marine reserve and with catch in the surrounding fishing block. Red and purple urchin populations were positively correlated, providing no clear evidence of competition between them. This modeling approach demonstrated that the relative importance of top-down and bottom-up effects on key herbivores is species-specific.

Introduction

Sustainable fisheries management relies on our ability to estimate the demographics of harvested stocks and predict how these populations might change in the future. It is often

challenging to separate out the effects of environmental forcing (such as changes in temperature, wave exposure, or primary production) from the effects of harvest. Further complications arise when fishing occurs on multiple trophic levels, as is the case in Southern California, where both carnivores (California spiny lobster, California sheephead) and their herbivore prey (red sea urchins) are harvested. In an ideal scenario, to quantify the effects of fishing in a complex system, we would need to be able to examine fluctuations in identical populations under different levels of fishing pressure and under shared environmental conditions. Although conducting a manipulative experiment on such a broad scale is not currently feasible, the Santa Barbara Channel provides the conditions for a natural experiment along these lines. In the Santa Barbara Channel, two species of sea urchins are abundant: the red urchin *Mesocentrotus franciscanus*, which is targeted by an economically valuable fishery, and the purple urchin *Strongylocentrotus purpuratus*, which is virtually unfished. These two species overlap in habitat, dietary niche, and functional role in the kelp forest community, allowing me to contrast the effects of the sea urchin fishery and environmental change on two similar (although not identical) populations. The Santa Barbara Channel Islands are also home to a network of no-take marine reserves, allowing me to examine populations across a wide gradient in fishing pressure. Thus, the conditions of this area are ripe for examining anthropogenic forcing in the context of a multi-trophic level fishery. I investigated the population dynamics of red and purple sea urchins in response to environmental change and fluctuations in fishing pressure in order to determine how urchin populations might change in the future and to assess ecologically relevant differences between these two important herbivore species.

The widespread fishing efforts on red sea urchins over purple urchins has vast potential consequences for urchin populations. The California sea urchin fishery has targeted red sea urchins for statewide harvest since 1971. In Southern California, red urchin harvest reached its peak in 1990 at over 27 million pounds, but landings have steadily declined thereafter (CDFW 2019). In 2021, the red sea urchin fishery was California's fifth largest fishery by ex-vessel value and the eighth largest fishery by weight (CDFW 2021). Fishing for purple urchins, in contrast, has been negligible due to their low economic value. The intense harvesting of adult red urchins has resulted in decreases in their body size distribution at many sites (Babcock et al., 1999) with potential implications for the resilience of red urchin populations. Despite the increase in urchin predators such as the California spiny lobster (*Panulirus interruptus*) and California sheephead (*Semicossyphus pulcher*) inside marine reserves (Teck et al., 2017; Hamilton & Caselle, 2015), red urchins may actually respond positively to protection from fishing pressure (Teck et al., 2017; Malakhoff & Miller, 2021). On the other hand, purple urchin populations are expected to decrease in biomass inside marine reserves, where they are subject to increased predation and potentially increased competition with their red counterparts for space (Schroeter, S.C., 1978; Selden et al., 2017).

We are often precluded from detecting the indirect effects of protection from fishing by lack of replication, confounding environmental gradients, and insufficient time series. In many regions, there may only be a single marine reserve site, which naturally leads to a small number of study sites and therefore limits spatial comparisons (Sale et al., 2005). Fortunately, the Channel Islands National Marine Sanctuary includes a total of 11 marine reserves of varying sizes, monitored at a total of 37 sites by the National Parks Service Kelp

Forest Monitoring Program. Sixteen of these sites have been continuously monitored since 1981, offering a wealth of data to investigate direct and indirect effects. The network of marine reserves was established in 2003 and enforcement began in 2004, yielding 20 years of data with which to monitor reserve effects. Environmental data for the Channel Islands is available through satellite imagery, buoys, and coastal cruises. The strength of this long-term dataset has enabled me to perform statistically rigorous analyses investigating the relative impact and importance of different environmental parameters.

In the previous chapter, I used the extensive subtidal surveys conducted as part of the Kelp Forest Monitoring Program (KFM) to evaluate how sea urchin densities have changed with the introduction of marine reserves. Here, I extend that analysis to investigate whether there is evidence for interspecific differences in the response of sea urchin populations to environmental change, and the role of the urchin fishery in mediating that response. This will allow us to make more accurate predictions of fluctuations in urchin populations and better parameterize models of kelp forest dynamics in the face of climate change.

Methods

Diver surveys

The National Parks Service's Kelp Forest Monitoring Program (KFM) has been annually collecting data at 37 sites throughout the Channel Islands, with 16 original sites established between 1981 and 1986 (see map, Fig 1.1). Divers collected data annually on the density and sizes of sea urchins – along with metrics on many other species – on a 100-meter permanent transect line at each site. Beginning with an initial random sampling point between 0-7 m, a pair of 1 m^2 quadrats were laid out on either side of the transect line at

8.33 meter intervals. A total of 12 quadrat pairs were sampled for counts of 25 target species, including *M. franciscanus* and *S. purpuratus*. The first 200 urchins of each species, or all individuals if less than 200, were sampled along the transect line and test diameter measured to the nearest millimeter using calipers. In this analysis, we also used data collected by KFM on giant kelp (*Macrocystis pyrifera*). Kelp was surveyed along the 100 m permanent transect lines by counting the number of kelp stipes at 1m above the bottom in 40 5m^2 quadrats that covered the entire span of the transect line on each side.

Environmental Covariates

Coastal SST (°C) and chlorophyll-a concentration (mg m−3) were estimated from composite satellite measurements. Daily SST values at 1 km spatial resolution were taken from the Multi-scale Ultra-high Resolution Sea Surface Temperature dataset (JPL MUR SST). Using the R package akima, we interpolated a two-dimensional surface and extracted daily temperature values for each of our sites. Annual averages, minimum and maximum values, and the average daily temperature in the coldest month were calculated for each site from all daily values from 1991-2016. Chlorophyll-a concentration was based on Aqua MODIS, which provides monthly chlorophyll-a concentration at a 1.25 km spatial resolution. Annual values for each site were calculated as an average of monthly concentrations or as the average monthly concentration during sea urchin spawning season (March-June). Maximum significant wave height at each site was estimated using significant wave height and surface wave period data from the Coastal Data Information Program (CDIP) following methods from Lamy et al. (2018) and Bell et al. (2015). Maximum daily values were used in lieu of mean daily values because extreme wave events are most influential in structuring kelp

forest communities (Reed et al., 2008). Daily values for each site were averaged to establish an annual metric, as well as the minimum and maximum values for the year. Annual harvest (in pounds) of red urchins in the previous year was calculated for each site based on their associated fishing block (10 minute by 10 minute squares, data via CDFW). Marine heatwave (MHW) events were identified at each site following the methodology of Hobday et al. (2016). A discrete MHW event was defined as periods when sea surface temperature (SST) exceeded the threshold for at least five consecutive days. The threshold was set as the 90th percentile of all daily SST observations from 2002-2024. Events separated by less than two days were merged into a single event. The "duration" of an event represents the number of days from its start to end for a given event, while the "intensity" refers to the average temperature anomaly relative to the daily mean during the event. All heatwave metrics were calculated using the heatwaveR package in R (Schlegel & Smit, 2018). A variable for "time since reserve established" was created with 0 indicating no reserve status, and for reserve sites, the value indicated the age of the reserve in years.

Statistical Analysis

Average urchin biomass values for each transect/site/year combination were calculated using test diameter (size) information converted to mass using allometric equations (Reed et al., 2016) and then multiplied by average density (individuals per m^2). To select the environmental variables to use as covariates in the urchin biomass model, I first used a random forest approach to identify variables with the highest predictive power. A random forest classifier uses a large number of individual decision trees to make predictions. Then, using the variables identified via this approach, I checked for multicollinearity using VIF

(variance inflation factor method). This function is an iterative process for stepwise removal of environmental predictor variables that are collinear. For paired variables with VIF exceeding the threshold (indicating multicollinearity), I selected one, fit the model, then selected the other, and compared models using AIC (Akaike information criterion). To account for spatial heterogeneity, I used a mixed effects modeling approach, with site as a random effect. To account for temporal autocorrelation, I generated time series models on yearly biomass averages for both species. Using autocorrelation function (ACF) and partial autocorrelation (pACF) plots to determine lags, I identified autoregressive and moving average terms for autoregressive integrated moving average (ARIMA) models that could be used to forecast future trends in urchin biomass. The majority of these models revealed significant lags of 1, indicating that urchin biomass is temporally autocorrelated with urchin biomass one year previous, and this correlation tapers off with increasing time separation between datapoints. Because biomass is the product of counts (a poisson or negative binomial distribution) and size (a slightly right-skewed normal distribution), I tried model fits using the negative binomial family, Gaussian, and lognormal. All models were fit and analyzed using GLMMtmb (generalized linear mixed effect model template model builder) in R. Data was scaled using the Z-norm (mean=0, standard deviation=1).

Results

I considered the effect of the following explanatory variables on urchin biomass: average, minimum, and maximum annual sea surface chlorophyll-a concentration (chlA); average, minimum, and maximum annual sea surface temperature (SST); average and maximum significant wave height (SWH); number of heatwave days in a year; average kelp stipes m^{-2};

site depth; annual red urchin catch (pounds per fishing block); and age of marine reserve (years).

In a fully parameterized linear model, the following variables were significant predictors of purple urchin biomass: average SST, number of heatwave days, minimum SST, maximum SST, average kelp density, and annual catch of red urchins. For red urchin biomass, the following variables were significant predictors: minimum SST, annual catch of red urchins, and age of reserve. However, several of these covariates were correlated or represented the same environmental parameter, so many of these variables were dropped from the final model.

I also tested these potential covariates using a random forest approach to calculate importance as measured by the percent increase in mean squared error as a result of permuting the variable of interest. The random forest approach identified kelp stipe density, average chlA, and biomass of red urchins as the most important variables in predicting changes in purple urchin biomass, and identified annual catch, average chlA, maximum chlA, and minimum SST as the most important variables in predicting changes in red urchin biomass (see table 2.2).

Considering these two approaches in conjunction, along with multicollinearity testing, model diagnostics, and sensitivity analysis, the final models for red and purple biomass were as follows (linear mixed effects using normally distributed scaled data, with site as random effect and an autoregressive correlation coefficient of 1):

$$R_i \sim N\left(\beta_0 + \beta_1 purple + \ \beta_2 catch + \beta_3 reserveage + \ \alpha_{s[i]}, \sigma^2\right)$$

$$\alpha_s \sim N(0, \sigma_\alpha^2)$$

Where *R* is red urchin biomass (g m^{-2}), *purple* is purple urchin biomass, *catch* is annual catch of red urchins in the associated fishing block (lbs), *reserveage* is the time since marine reserve establishment in years (all non-reserve sites = 0), s[i] denotes the site *s* that urchin biomass measurement *i* belongs to, and α_s is the random intercept term.

$$P_i \sim N\left(\beta_0 + \beta_1 red + \beta_2 heatwave + \beta_3 kelp + \alpha_{s[i]}, \sigma^2\right)$$

$$\alpha_s \sim N(0, \sigma_\alpha^2)$$

Where *P* is purple urchin biomass (g m^{-2}), *red* is red urchin biomass, *heatwave* is the number of heatwave days in that year, and *kelp* is average kelp stipe density (stipes m^{-2}). For model parameter estimates, see table 2.1.

I performed a series of correlation tests to determine if a change in red urchin biomass was associated with a change in purple urchin biomass or vice versa. Using the generalized linear mixed effects model on scaled data described above, I found that purple urchins had a significant and positive effect on red urchins (p=0.00527). Similarly, the model for purple urchin biomass including the selected covariates revealed that red urchins had a significant and positive effect on purple urchins (p=0.00359).

Kelp stipe density was a significant negative predictor of purple urchin biomass (p=.00255) but not red urchin biomass (p=0.88352). The directionality of this relationship is likely reversed (more purple urchin biomass leads to less kelp), but as a predictor of purple urchin biomass, kelp density is a useful metric.

Using annual catch data from the red sea urchin fishery, I modeled the relationship between each species biomass and the annual catch in the previous year in the associated fishing block. There was a weak positive relationship between total urchin biomass and

annual catch, indicating there are higher urchin densities in fishing blocks where more urchins are caught. This positive relationship between catch and urchin biomass was highly significant for red urchins (p=0.00121).

RESPONSE	SCALED PARAMETER	ESTIMATE	STANDARD ERROR	P-VALUE
RED URCHIN BIOMASS	purple biomass	0.17	0.06	0.007
	annual catch	0.31	0.09	0.001
	reserve Age	0.02	0.01	0.035
	intercept	-0.15	0.13	0.251
PURPLE URCHIN BIOMASS	red biomass	0.15	0.05	0.004
	number of heatwave days	0.12	0.04	0.002
	kelp density	-0.16	0.05	0.003
	intercept	0.02	0.13	0.898

Table 2.1: Parameter estimates, standard error, and p-values for generalized linear mixed effects models of urchin biomass. All models include a random effect of site (i.e. intercepts vary by site) and an AR(1) autocorrelation structure (the correlation between biomass values decreases with increased time lag). Predictor variables are all scaled in these analyses.

VARIABLE	PURPLE URCHIN BIOMASS %INCREASE MSE	RED URCHIN BIOMASS %INCREASE MSE
KELP STIPE DENSITY (STIPES M^{-2})	19.31	8.83
AVERAGE CHLA	18.04	15.79
BIOMASS OF OTHER URCHIN SPECIES	15.81	9.66
MAXIMUM CHLA	12.83	15.59
NUMBER OF HEATWAVE DAYS	11.49	6.01
AVERAGE SST	11.33	13.72
ANNUAL CATCH OF RED URCHINS	9.42	17.20
MAXIMUM SIGNIFICANT WAVE HEIGHT	6.94	13.18
MINIMUM SST	6.74	16.04
AVERAGE WAVE HEIGHT	6.05	14.95

Table 2.2: All tested variables ranked by importance in predicting variation in urchin biomass, based off the percent increase in mean squared error as measured via random forest procedure.

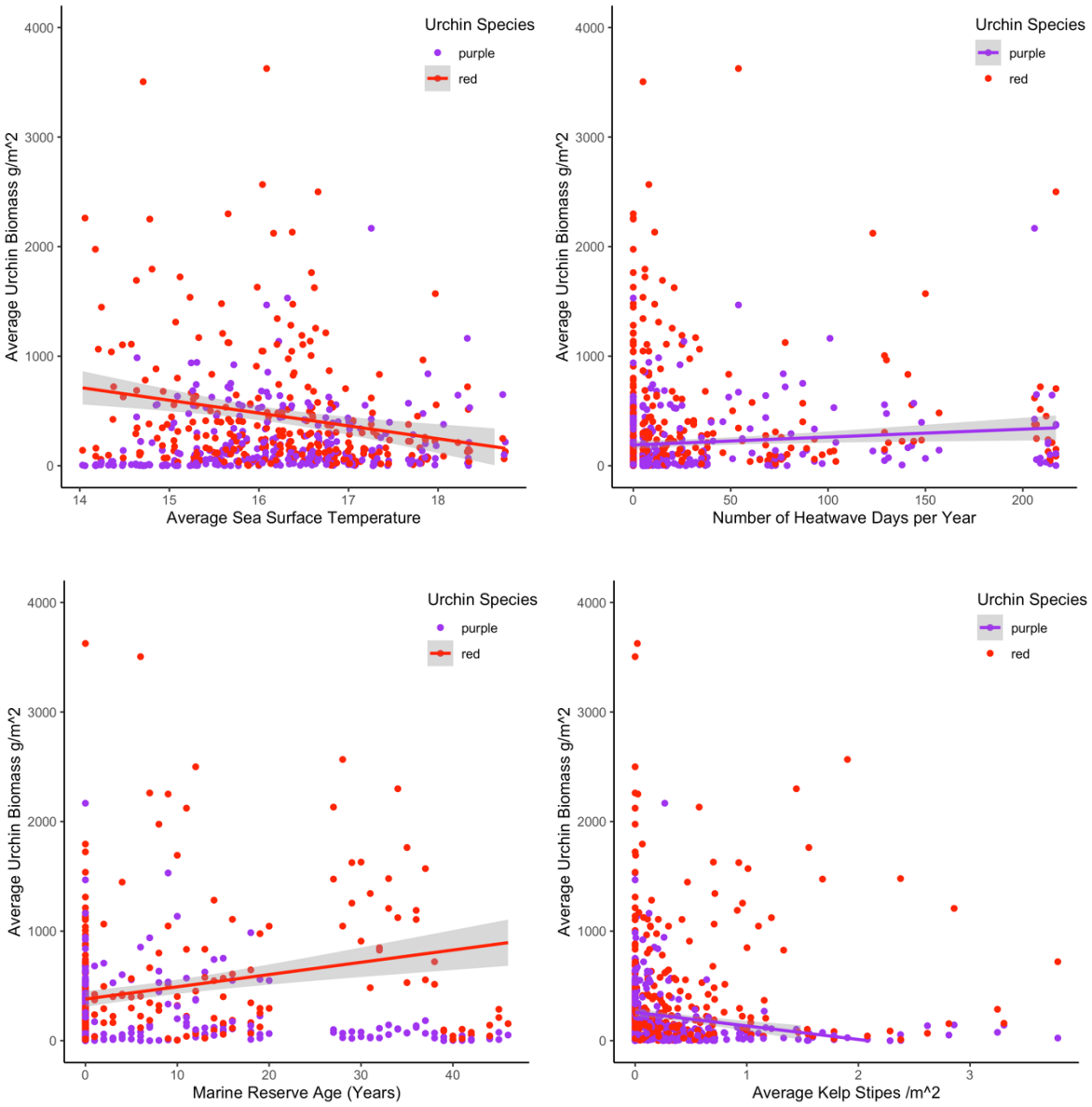

Figure 2.1: Overview plots of urchin biomass of red and purple urchins by significant explanatory variables. Regression lines with 95% confidence intervals shown for significant relationships.

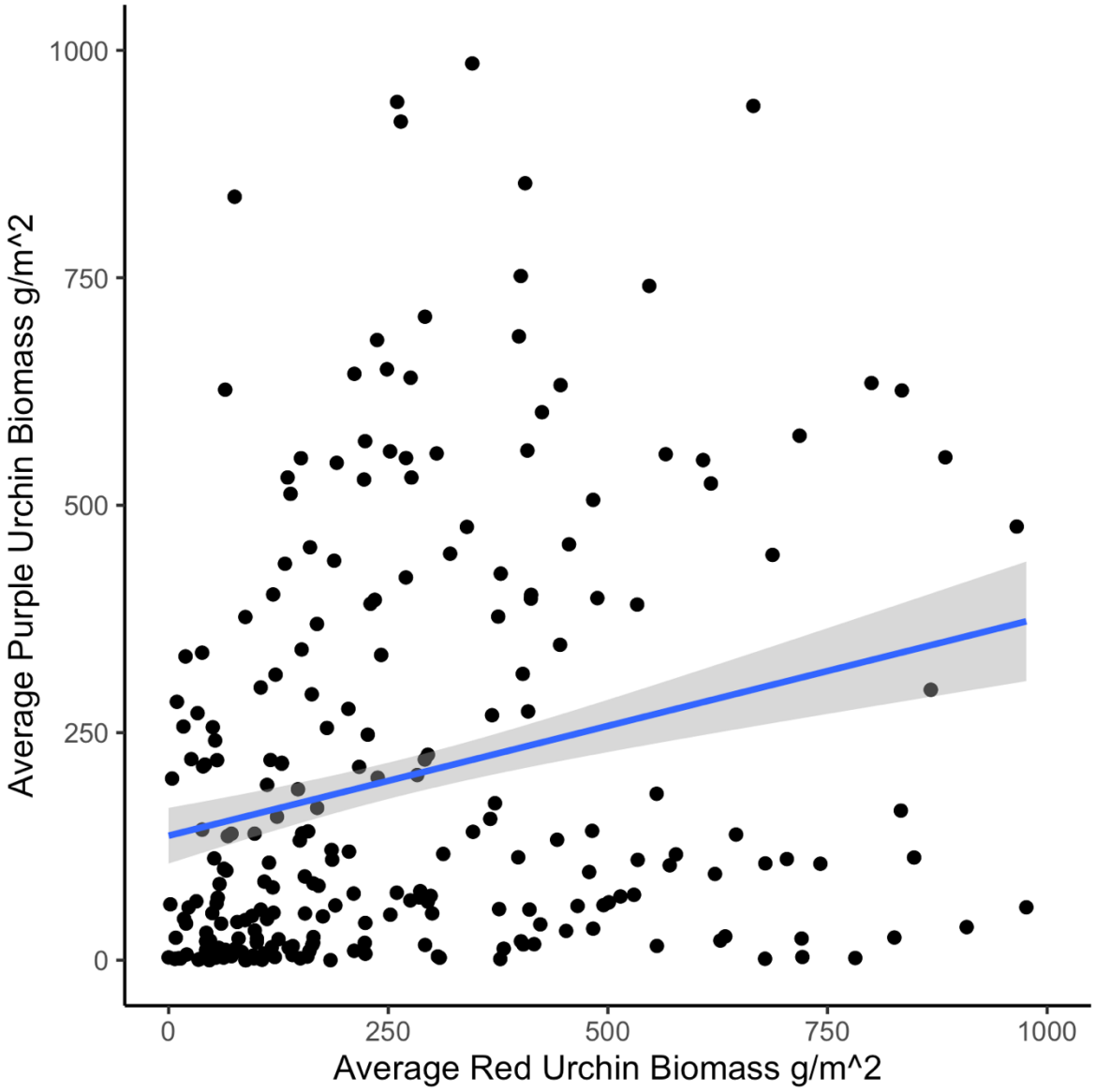

Figure 2.2: Average purple urchin biomass (g m^{-2}) by red urchin biomass (g m^{-2}) with regression line and 95% confidence interval.

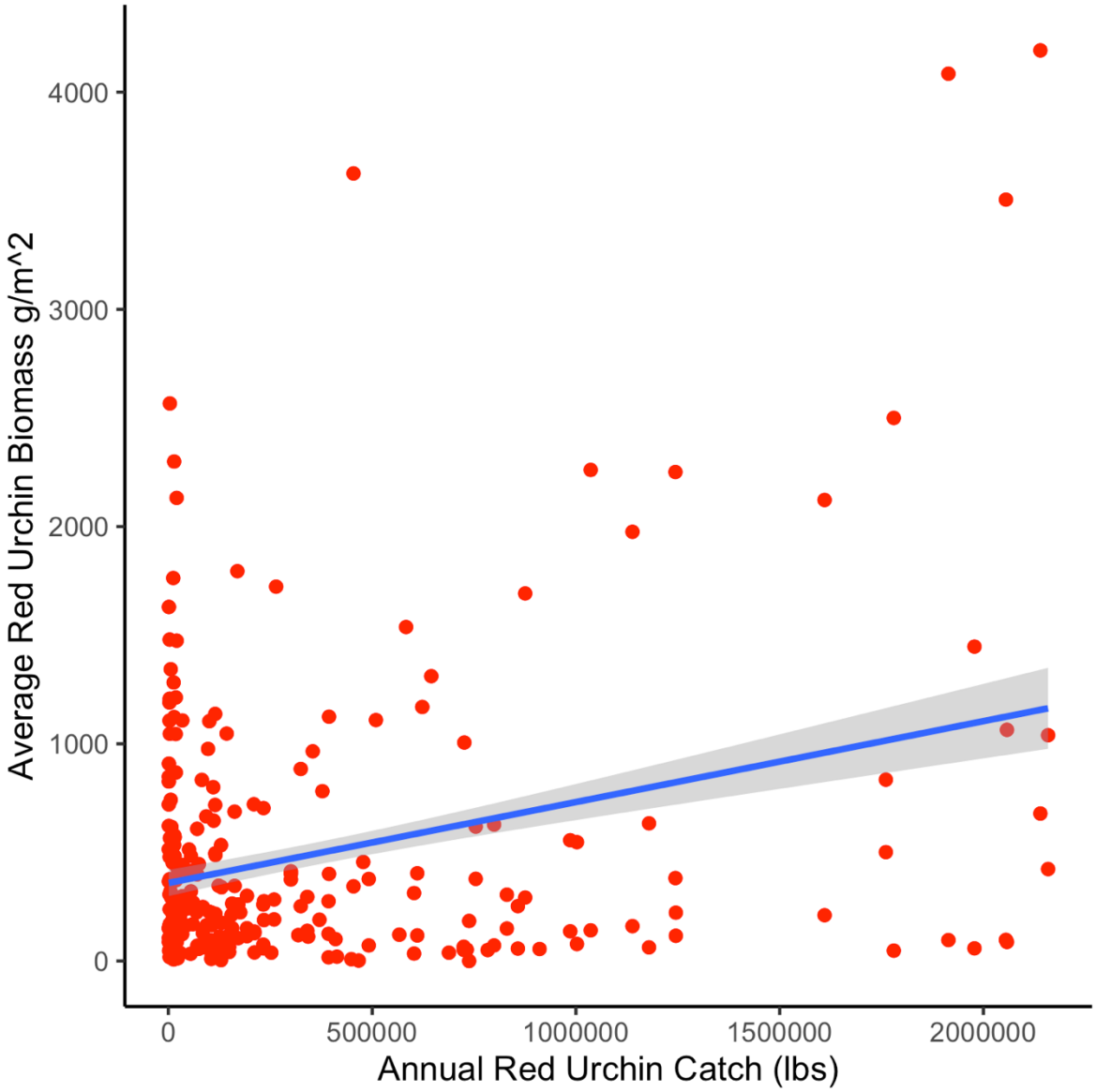

Figure 2.3: Average red urchin biomass (g m^{-2}) by annual catch of red urchins (lbs) in the associated fishing block.

Discussion

These results suggest the influence of temperature on urchins is an important driver of urchin populations. My results align with a previous study of temperature preferences for these urchin species: purple sea urchins preferred warmer temperatures (18.8 ± 0.2 °C during the day, 17.4 ± 0.3 °C at night) while red urchins preferred cooler temperatures (17.5

± 0.3 °C during the day, 16.8 ± 0.4 °C at night) (Salas et al., 2012). Purple urchins are also found more commonly in the intertidal, where temperature fluctuations are more severe and average temperatures are higher, while red urchins are generally restricted to the cooler and less variable subtidal (Basch & Tegner, 2007; Rogers-Bennett et al., 1995; Schroeter, S.C., 1978). The positive association of purple urchins with heatwaves may be a result of their higher thermal tolerance.

Controlling for other environmental parameters, areas with higher harvest of red urchins are associated with higher populations of red urchins, which may be something of a circular causality paradox since urchin harvesters are likely to target areas with high densities of red urchins, and thus there is a positive correlation between catch and red urchins.

Both the random forest and the linear modeling approach highlight the importance of kelp biomass on purple urchin populations but not on red urchin populations. This may be linked to differences in behavioral responses to the availability of drift kelp. In general, increases in urchin grazing intensity on understory algae are associated with lower availability of drift kelp (Ebeling et al., 1985; Harrold & Reed, 1985). However, red urchins may be more dependent on drift kelp than purple urchins. Red sea urchins demonstrate behavioral changes in grazing patterns based on the availability of drift algae, with red urchins in drift-sparse environments more likely to occupy open, unprotected microhabitats, while red urchins in areas with abundant drift algae are more likely to shelter in cracks and crevices (Harrold & Reed, 1985). Red urchins are larger and more vulnerable to the effects of surge, exhibiting a tendency to rapidly retreat to more sheltered habitats when swell increases, in contrast with purple urchins which tend to cluster together at lower surge

before moving to topographic shelters at higher surge (Parnell et al., 2017). Purple urchins also move more throughout the day in comparison to red urchins (Parnell et al. 2017). In a study of intertidal purple urchins, they did not increase grazing intensity when deprived of drift algae (Alifano, 2008). The tendency of red urchins to spend more time sheltering in cracks and crevices may indicate a greater reliance on drift algae than their smaller, more active, purple counterparts, and therefore red urchins may be less directly impacted by the local vagaries of kelp growth.

For both populations, chlorophyll-a was found to be an important covariate, but subsequent testing revealed a higher variance inflation factor (VIF) than the established threshold (an indicator of multicollinearity), and therefore chlA was dropped from subsequent models. There is no known biological reason for chlA to directly influence adult urchin abundance – adult urchins do not feed on surface chlorophyll, but rather rely on understory algae and drift detrital algae.

Of interest are the covariates that are not significant predictors – wave height and depth were not significant for either species. Transects are located at within a narrow depth range of 6-16 meters. At these depths, urchins are not exposed to the buffeting forces of the intertidal, and the strength of wave exposure attenuates at depth. This could explain why these covariates were not significant drivers of variation in urchin populations at these sites.

These results do not provide clear evidence of competition between red and purple urchins. In fact, increases in the population of one urchin species is positively associated with increases in the population of the other. This is potentially the result of urchins preferentially inhabiting areas with favorable environmental conditions or substrate type, with those conditions favorably affecting both species. Competition may play a larger role

in the liminal zones where the fight for survival against environmental extremes takes on greater prominence.

The red sea urchin industry does not appear to be having a suppressive effect on the red urchin population, when controlling for other environmental parameters. Both red and purple urchins were positively correlated with the annual catch of red urchins in the associated fishing block. Urchin harvesters likely target their catch to areas with naturally high urchin abundances. Despite the opportunity for a natural experiment presented by two urchin species occupying the same habitats and functional roles within the kelp forest, these two species differ in their responses to some environmental changes, with purple urchin populations significantly correlated with marine heatwaves and kelp abundance, while red urchin populations were significantly correlated with urchin harvest and the age of the marine reserves they occupied.

The increases in red urchins with marine reserve age suggest that increased predator abundances inside marine reserves has not stymied red urchin population growth. The vulnerability of an urchin to predation is driven by a combination of morphological characteristics (size, spine thickness and length, test thickness), behavior (sheltering, concealment, and spine orientation), and availability (especially in comparison to other prey types). Red urchins display many characteristics consistent with increased predator avoidance in comparison to purple urchins: on average, they are larger, have longer spines, and retreat to shelter more rapidly. As demonstrated in chapter 1, humans are likely the most effective predator of red urchins, with release from fishing pressure inside reserves outweighing any increased predation from lobster or sheephead. Therefore, higher

abundances of red urchins, but not purple urchins, in older reserves are consistent with my expectations based on predation vulnerability.

Ultimately, these results showcase several important interspecific differences between red and purple urchins with respect to environmental drivers. Lumping urchins together as a functionally homogeneous group can obscure population trends and ignores the differential top-down pressure of the urchin fishing industry. Urchin species identity has been shown to influence predation rates and drive changes in trophic cascades in speciose food webs (Wiltman, Smith, & Novak 2017), which is highly relevant to the kelp forest ecosystem. Further interrogation is needed into the niche differentiation of these two species, which will allow us to make better predictions about how these populations will respond in the future to environmental change, reserve protection, and fishing pressure.

Acknowledgements

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environmental covariates, and Tom Bell of Woods Hole Oceanographic Institution, who ran CDIP models to calculate wave height parameters.

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Appendix

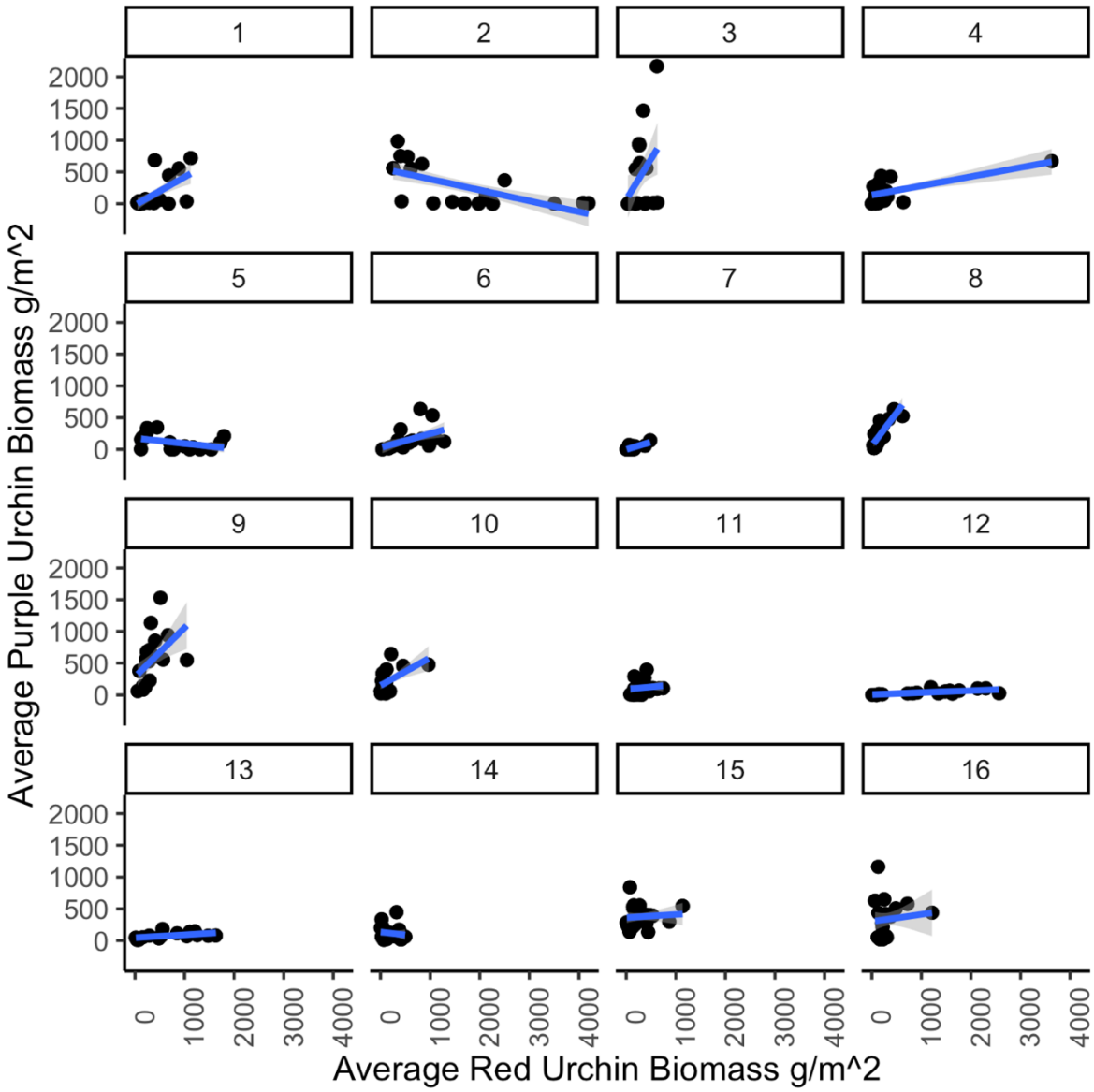

Figure A2.1: Average purple urchin biomass (g m^{-2}) by red urchin biomass (g m^{-2}) for each of 16 original kelp forest monitoring sites.

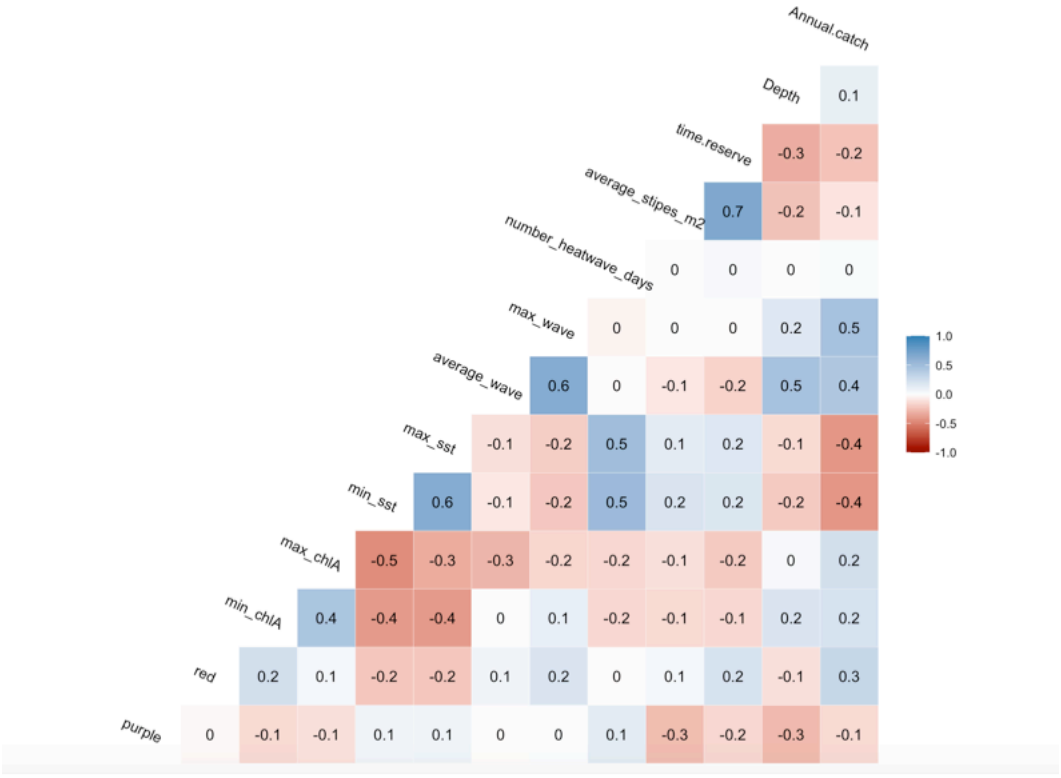

Figure A2.2: Correlation plot used in conjunction with variance inflation test (VIF) to check for multicollinearity of explanatory variables.

III. Interspecific differences in urchin foraging rate and ecological impact on common understory algae

Abstract

Chapters 1 and 2 have established that populations of the sea urchins *Mesocentrotus franciscanus* (red urchins) and *Strongylocentrotus purpuratus* (purple urchins) are responding in different ways to top-down (fishing, predation) and bottom-up (temperature, kelp density) forcing. In this chapter, I analyze the ecological impact of these population differences. Although most ecological research in Southern Californian kelp forests has focused on a single urchin species or grouped red and purple urchins together, we know that their autecology differs and this could obviate the assumption that they are functionally homogenous grazers. Therefore, I used laboratory feeding assays to measure differences in red and purple urchin consumption rates of four common understory algal species in order to assess potential differences in dietary niche. I found significant interspecific differences in mass-specific feeding rates, with purple urchins consuming significantly more algae on average than red urchins. Purple urchins consumed significantly more *Chondracanthus*, *Pterygophora*, and *Macrocystis* than *Stephanocystis*, while red urchins ate similar low levels of every algae species tested. Using these foraging rates, I conducted an ecological modeling study to estimate the potential removal of kelp forest algal biomass by urchins at long-term research sites. The predicted impact of urchin feeding on understory algal biomass was strongly dependent on urchin species identity and season. Overall, total removal potential of macroalgae by urchins was a significant negative predictor of mean net primary productivity (NPP) across the four algae species considered, but on the species level, purple urchin

consumption had a significant negative effect on future understory algal growth but red urchins did not, and red urchin consumption actually had a significant *positive* effect on future growth of *Chondracanthus*. Despite their theoretical potential to do so, urchins never eliminated even their most consumed species, *Chondracanthus*, providing evidence for the mixed diet hypothesis. My results highlight the importance of urchin species identity in kelp forest community ecology and demonstrate that these two species have key functional differences.

Introduction

As voracious omnivorous grazers, sea urchins play a major role in coastal marine ecosystems worldwide. From controlling turf algae overgrowing coral reefs (Glynn and Enochs 2011) to overgrazing seagrass beds (Eklöf et al. 2008) and mowing down macroalgal forests (Steneck et al. 2002), sea urchins have the ability to drastically alter many of the ecosystems in which they are found. In kelp forests, changes in urchin grazing patterns due to their abundance (Rogers-Bennett & Catton 2019), behavior (Smith & Tinker 2022), or food availability (Harrold & Reed 1985, Rennick et al. 2022) can catalyze transitions from lush, biodiverse kelp forests to urchin barrens that are relatively devoid of macroalgae. Across the globe, different sea urchin species are transforming community structure with their feasting: *Evechinus chloroticus* overgraze the brown alga *Eklonia radiata* in New Zealand (Andrew 1988); *Strongylocentrotus droebachiensis* destroy *Laminaria* and *Agarum* kelp beds along the east coast of North America (Mann 1982); and *Strongylocentrotus polyacanthus* sweep through *Alaria fistulosa* forests in the Aleutian Islands (Estes and Duggins 1995).

The ecological role of sea urchins varies based on environmental context and species identity. Across the approximately 950 sea urchin species globally, there is a wide variety of morphologies, diets, predator-prey dynamics, habitat preferences, and behavior patterns. In the Santa Barbara Channel, there are two dominant sea urchin species: the red urchin *Mesocentrotus franciscanus*, which is fished extensively, and the purple urchin *Strongylocentrotus purpuratus*, which is virtually unfished. Kelp forests are dominated by the giant kelp, *Macrocystis pyrifera*. While to date, most research on sea urchin ecology in this region has focused on one species (typically purple urchins, which are smaller and easier to collect for laboratory study) or aggregated both species as a homogenous group, we know that these two common species differ in many ways that can alter their ecological impact, including in their distribution, competitive ability, vulnerability to predation, and harvest rates.

While the spatial distribution of red and purple urchins does overlap extensively, the two species are not evenly distributed across the benthos. Red urchins tend to be restricted to the subtidal, whereas purple urchins can be abundant in the intertidal zone (Basch & Tegner, 2007; Rogers-Bennett et al., 1995; Schroeter, S.C., 1978). Purple urchins can dominate areas with small boulders and cobble, while red urchins are more abundant in habitats with larger boulders (Schroeter 1978). This uneven distribution suggests that purple and red urchins are not interchangeable, and that red urchins may be occupying more stable and less exposed habitats, while purple urchins opportunistically occupy more unstable habitats and may be better adapted to the thermal stress and wave exposure of the intertidal zone. This prevalence of purple urchins in the intertidal zone in comparison to red urchins may also result in differential disease risk and sensitivity to disturbance. Both red and

purple urchins are vulnerable to disease outbreaks such as “black-ring” and “red-spot” diseases, although the mechanisms behind these diseases are poorly understood (Lester et al., 2007). Disease prevalence has been positively correlated with sea surface temperatures at some sites, suggesting that thermal stress may increase urchin susceptibility to disease (Lester et al., 2007). Because purple urchins are more commonly found in warmer intertidal waters, and often at higher densities, they may be more susceptible to these epidemics than red urchins (Rogers-Bennett & Okamoto, 2020). Intertidal purple urchins are also more exposed to the mechanical stress of wave action than their subtidal counterparts, and while there has been no direct comparison of attachment strength between purple and red urchins, purple urchins had significantly higher adhesive properties (tube foot disc tenacity, attachment area, and whole animal adhesive force) than *Strongylocentrotus droebachiensis* which occupied areas more protected from wave action (Oceguera & Narvaez, 2022).

Previous work by S.C. Schroeter (1978) demonstrated that red and purple urchins can compete for space, with larger and longer-spined red urchins capable of “spine-fencing” away smaller purple urchins from favored habitats (sheltered ledges and crevices with sufficient flow to carry drift algae). Experimental removals of red urchins from the sheltered bases of boulders led to rapid recolonization by purple urchins, and abundances of red and purple urchins were negatively correlated, supporting the spatial competition hypothesis. In contrast, Tegner & Dayton (1981) found that differential vulnerability to predation outweighed competitive interactions in regulating the distribution of red and purple urchins. They found that red and purple urchins coexist at high densities in the same subtidal boulder piles, and they identified variation in predation pressure as the primary driver behind differences in small-scale distribution patterns. With their shorter spines,

purple urchins were susceptible to attack by spiny lobsters (*Panulirus interruptus*) from all sides, while the longer-spined red urchins presented more of a challenge to their predators. When presented with a mixture of purple and red urchins, lobsters generally ate the purple urchins first. In field trials with sheephead (*Semicossyphus pulcher*), large purple urchins were always consumed before large red urchins, despite large red urchins having gonads up to 10 times larger than purple urchins (with the gonads being the most nutritionally valuable organ of an urchin). These experiments demonstrated that beyond interspecific differences in average size, spine length is a key determinant in predation risk for red and purple urchins.

In addition to these dynamics, red and purple urchins experience vastly different levels of fishing pressure. For the past three decades, large-scale removal of red sea urchins has been underway in California via a booming fishing industry. The southern California red urchin harvest reached its peak in 1990 at over 27 million pounds, but landings have steadily declined thereafter (CDFW 2019). Fishing for purple urchins, in contrast, has been negligible due to their low economic value. The intense harvesting of adult red urchins has resulted in decreases in their body size distribution at many sites (Babcock et al. 1999), with potential implications for the resilience of red urchin populations. Despite the increase in urchin predators such as the California spiny lobster (*Panulirus interruptus*) and California sheephead (*Semicossyphus pulcher*) inside a network of marine reserves (Hamilton and Caselle 2015, Kay et al., 2012), red urchins in some cases respond positively to protection from fishing pressure, whereas purple urchins, even at small sizes, do not appear to be unaffected by reserve status (Malakhoff & Miller, 2021; Teck et al., 2017). Red urchins have increased in size and density most notably inside Harris Point Marine Reserve, the

northernmost surveyed marine reserve, which is surrounded by an urchin fishing hotspot. Thus, fishing pressure appears to play a significant role in regulating red urchin populations.

Differences between red and purple urchin competitive ability, susceptibility to predation, disturbance tolerance, and fishing pressure may contribute to variation in their abundance and distribution across spatial and temporal scales. The ecological impact of these urchin species is dependent not only on where they are found but also on what they are eating.

Strongylocentrotus purpuratus and *Mesocentrotus franciscanus* are some of the most researched echinoids in the world due to their outsized influence on kelp forest communities, but relatively little attention has been given to potential dietary differences between them. Although much study has been devoted to urchin grazing rates and the formation of urchin grazing fronts in response to low food supply and/or low availability of drift algae (Harrold & Reed, 1985; Mattison et al., 1977; Rennick et al. 2022), these studies primarily focus on a single species. It is commonly assumed that both species prefer giant kelp, *Macrocystis pyrifera* (Rogers-Bennett, 2007) but to date there has been little in the way of preference studies or comparison across species. Gut content analyses have been performed in a number of different studies, again often focusing on a single species. Kenner (1992) sampled the gut contents of *S. purpuratus* and broadly categorized algae type as coralline, fleshy red, and fleshy brown algae. Coralline algae were dominant food items during all times of the year, while fleshy brown algae was second most abundant, and fleshy red algae made up most of the remainder of the diet (Kenner, 1992). Harrold and Reed (1985) performed gut content analysis of *M. franciscanus* following similar methods, examining diets of urchins from both kelp forests and urchin barrens across five different

time points. Contrary to Kenner's results from purple urchins, Harrold and Reed found diets of red urchins from both kelp forest and barrens to be primarily brown algae, although fleshy red algae initially constituted a higher proportion of the diet in urchins from their barrens site. Coralline alga was found in the lowest amounts, and during later time points the diets of the barrens and kelp forest urchins were indistinguishable. The fact that these two studies, conducted in similar areas with almost identical methods, found different results for purple urchin versus red urchin diets, indicates that perhaps the feeding patterns of these two species are not the same as is commonly assumed. To address this knowledge gap, I quantifed interspecific differences in *M. franciscanus* and *S. purpuratus* foraging rates across four common understory algae species that make up a large proportion of the macroalgal community. I also analyzed traits of these algal species that could influence palatability by urchins. As a result of interspecific differences in urchin distribution, any differences in dietary patterns between red and purple urchins could be amplified on the ecological scale. Therefore, after quantifying feeding rates in the laboratory, I used these measurements to provide a more robust estimate of the potential removal of kelp forest algal biomass by urchins in the Santa Barbara Channel. Through laboratory feeding assays and population modeling, I have sought to broaden our understanding of the diets of these two important herbivores and predict how that might impact the understory algae community.

Methods

Feeding Trials

Mesocentrotus franciscanus and *Strongylocentrotus purpuratus* individuals across a broad range of sizes were collected from Mohawk reef and Arroyo Quemado reef, non-reserve

kelp forest sites off the coast of Santa Barbara that have been monitored by the Santa Barbara Coastal Long-Term Ecological Research group (SBC LTER) since April 2000. Care was taken to transport urchins with minimal damage to flow-through seawater tanks with ambient temperature (average: 14 °C). Urchins were fasted for one week to control for previous feeding, as the gut residency time for urchins is approximately four days (Ebert et al., 1999). Urchins were weighed and their test diameters measured before placing in individual plastic containers. Urchins were randomly assigned to one of four algal treatments: *Macrocystis pyrifera*, *Chondracanthus corymbiferus*, *Stephanocystis osmundacea*, *Pterygophora californica* (see Fig. 3.1). Algae was blotted dry and weighed into 40 (±.01) gram samples. This amount was determined to be sufficient for four days of urchin feeding by a previous study by Foster et al (2015). I conducted a pilot study to assess the methodology for taking wet weight measurements (blotting dry, using a salad spinner, or a combination), and the blot-dry method was determined to yield the most precision upon replication. Each container was supplied with one type of algae, and urchins were left to feed *ad libitum* for four days. No urchin consumed the entire quantity of algae. After four days, all algae were removed, patted dry, and weighed, and urchins were weighed and measured. Algae were collected from the following Santa Barbara Coastal LTER sites: Mohawk, Bullito, and Arroyo Quemado. Subsamples were saved and frozen from each site for future analysis. The experiment consisted of ten trials of 24 urchins each (12 red, 12 purple, allocating 3 in each treatment). 40 grams of each algal species were placed in separate containers with no urchins as controls for growth or degradation, and were also weighed after each trial. Feeding trial statistics were analyzed in R (R Core Team, 2023).

Pterygophora californica | *Macrocystis pyrifera* | *Stephanocystis osmundacea* | *Chondracanthus corymbiferus*

Figure 3.1: Algae species selected for this study. Photos courtesy of Santa Barbara Coastal Marine Biodiversity Observation Network.

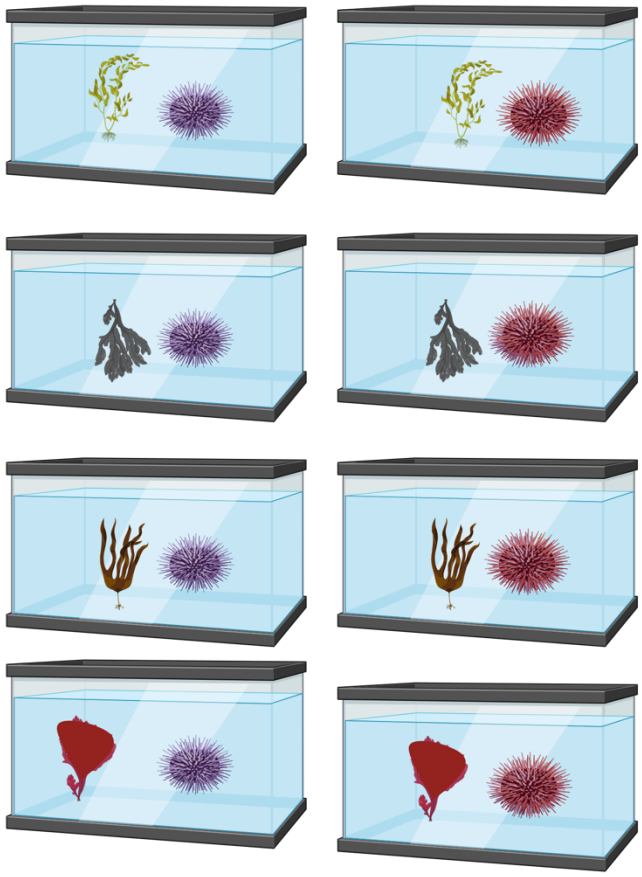

Figure 3.2: Experimental setup: With three replicates of each treatment per round, and ten rounds of feeding trials, for a total of 30 replicates per treatment.

Algal Traits

Elasticity

Urchins use their Aristotle's lantern – five calcified plates that form a beak-like structure – to scrape rocks and consume algae (Yorke et al., 2019). They are capable of catching drifting algae using their tube feet and transferring the food to their oral side. Because of the mechanics of scraping through algae, one important algal trait that could influence palatability is the elasticity and hardness of the material. I hypothesized that algae that is easier to puncture would be easier to consume. Therefore, I tested the elastic properties of the four algal species used in the feeding trials using a tensile tester to generate stress-displacement curves. Materials were cut into a "dog bone" shape to reduce the chance of failure (material fracturing) at the clamps on the machine. Stress-displacement curves were generated and used to calculate the stiffness of the material. The elasticity was measured as the proportionality constant *k* given Hooke's Law:

$$F = k\Delta L$$

where ΔL is the amount of deformation (change in length of the algae) produced by force F (N/mm^2). Hooke's Law only holds for the linear portion of the stress-displacement curve.

C:N ratios

A simple proxy for nutritional quality in algae is the relative carbon to nitrogen content. Algae with more nitrogen have higher protein content, which is often considered more nutritious. I examined carbon: nitrogen ratios of the four algae species tested to find which had the highest protein content. During the course of the feeding experiment, a total of 23-33 samples of each algae species were weighed, dried, and ground to a fine powder for CHN

(carbon, hydrogen, nitrogen) elemental analysis in the Analytical Lab using the CHN elemental analyzer (Carlo-Erba Flash EA 1112 series, Thermo-Finnigan Italia, precision +/- 0.3%) in the Marine Science Institute's Analytical Laboratory at the University of California Santa Barbara.

Caloric density

For each algae type, six ground and weighed samples (~0.2 g) were placed in a fuel capsule, pelletized, and combusted in a bomb calorimeter (Parr 6725 semimicro calorimeter) to determine the average kCal/g of a blade (Hasshaw, in prep).

Physical properties of blades

Samples of *Chondracanthus*, *Macrocystis, Stephanocystis*, and *Pterygophora* were collected on SCUBA at three reefs off the Santa Barbara coast – Arroyo Burro, Naples, and Mohawk reefs. Blades were separated out from each alga and then measured for blade thickness using digital calipers (Mitutoyo). Blades were weighed (wetmass in grams) and area was calculated in ImageJ by tracing images with scale rulers, to calculate the blade area per unit mass ($cm^2\ g^{-1}$).

Modeling Urchin Consumption at LTER Sites

After obtaining laboratory measurements of urchin feeding rates, I used urchin and macroalgal biomass measurements from seasonally monitored LTER sites to model urchin consumption in the field.

For the dataset measuring NPP of understory algae species, macroalgal biomass and irradiance data were collected at five reefs as part of a long-term experiment designed to evaluate the effects of disturbance to giant kelp on the structure and productivity of the benthic community (Miller et al 2015, Castorani et al. 2018). The five reefs (Arroyo Quemado, Carpinteria, Isla Vista, Mohawk, and Naples) ranged in depth from 5.8 m to 8.9 m (MLLW) and were chosen to represent a range of physical and biological characteristics known to influence subtidal macroalgal assemblages in the region. This dataset includes measurements taken at plots where *Macrocystis pyrifera* was removed (continuously or annually) as part of the long-term experiment. The NPP values for each algae species of interest were calculated as follows: All macroalgae were surveyed along permanent 40 m x 2 m transects located in the center of each plot twice per season (approximately every six weeks) from January 2008 through December 2012 and once per season (approximately every twelve weeks) beginning in the winter of 2013. Time series data of the abundance of all understory species including small M. pyrifera (< 1 m in height) were converted to dry mass using species-specific relationships generated from field measurements of abundance and laboratory measurements of mass (Reed et al. 2016). These relationships were combined with taxon-specific measurements of abundance and size to estimate standing biomass for each taxa. Daily NPP (g C m^{-2} d^{-1}) was calculated for each taxon using a bioptic model incorporating species-specific photosynthesis irradiance curves, measurements of standing biomass, and the information from photosynthetically active radiation (PAR) sensors placed at each site (Miller et al. 2012). Taxon-specific estimates of daily NPP in each plot were averaged over all days in a season (defined by the solar solstices and equinoxes) to produce

mean daily values of NPP (kg C m^{-2} d^{-1}) by season for each taxon in each year of the time series (Harrer et al. 2013).

On the same fixed transect surveys described above, red and purple urchins (along with other key species) were counted and classified by test diameter. This information was used along with the allometric calculations by Reed et al. (2016) to convert field measurements to urchin biomass in grams wetmass per m^2.

Combining these field measurements with laboratory measurements of urchin feeding rates, I calculated the NPP removal potential by urchins for each algae by urchin species combination in grams algae m^{-2} day^{-2} using the formula:

$$NPP\ removal\ potential_{uat} = b_{ut} \times r_{ua}$$

Where b_{ut} is the biomass of urchin species *u* at time *t* and r_{ua} is the species-specific feeding rate of urchin species *u* on algal species *a.*

I also calculated the theoretical NPP that would remain after urchin consumption and the proportion of the generated NPP the urchins could consume per day using the formulas:

$$NPP\ remaining_{uat} = NPP_{at} - NPP\ removal\ potential_{uat}$$

$$Proportion\ NPP\ consumed_{uat} = \frac{NPP\ removal\ potential_{uat}}{NPP_{at}}$$

Where NPP_{at} is the generated NPP by algal species *a* at time *t* and $NPP\ removal\ potential_{uat}$ is the removal potential of algal species *a* by urchin species *u* at time *t*.

Additionally, I calculated the total standing stock algal biomass on a monthly basis as the sum of the total algal biomass measured along the transect plus the theoretical amount of NPP generated over the course of the month.

These calculations were performed with the intention of assessing whether urchin consumption potential could be used to predict understory algal biomass and growth. Therefore, I constructed a series of generalized linear mixed effects models (using GLMMTMB, Brooks et al. 2017) using mean daily grams NPP or total standing stock algal biomass as the response variable and removal potential by urchins as the explanatory variable, with site as a random effect, splitting up the models by urchin species and algae species, as well as examining the effect of the removal by urchins from one to four seasons prior to the NPP measurement.

Results

Feeding Trials

There was no significant difference in algal wet mass in the controls from before and after each trial ($p=0.114$). The data distribution was right-skewed and pairwise parametric tests assume normality, so using a boxcox transformation I determined the optimal lambda (transformation parameter). Since the optimal lambda for red urchin measurements was .15-.2, and the data were zero-inflated, no simple transformation was possible, so data were fit to the Poisson family. For purple urchin measurements, a lambda of ~0.5 indicated that a square root transformation was appropriate. Models used algae consumed per urchin starting weight per day as the response variable and urchin starting weight and algae treatment as covariates. To isolate the variability driven by differences in the timing of

experiment rounds, date was added as a random effect. Sensitivity analyses were performed to calculate the effect of removing outliers. Results of the final model for red urchins with the non-significant interaction term removed indicate no significant differences in consumption rates across the algae types. For the most part red urchins consumed similar low quantities of algae regardless of size or algae type (see figures 3.3 and 3.4). Results of the final model for purple urchins (linear model with square root transformation of response variable and interaction term between algae type and urchin starting weight) indicate that both algal treatment and the purple urchin starting weight influenced the amount of algae consumed. A further test of pairwise relationships (Tukey method) revealed a significant difference between the following treatments: *Stephanocystis & Chondracanthus* ($t(92.9)=3.822$, $p=0.001$), *Stephanocystis* & *Macrocystis* ($t(92.9)=3.925$, $p=0.002$), and *Stephanocystis* & *Pterygophora* ($t(92.3)=4.460$, $p<0.001$). *Stephanocystis* was the least consumed of all the algae tested and was significantly different from the consumption rates of all the other treatments. Initial urchin weight also influenced the amount consumed (p chisq<0.001) with larger purple urchins consuming more (see fig. 3.3). A two-sample t-test reveals that purple urchins ate significantly more algae/day proportional to their body weight than red urchins ($p<0.001$) (mean purple: 0.037 g algae/g body mass/day, mean red: 0.01 g algae/g body mass/day).

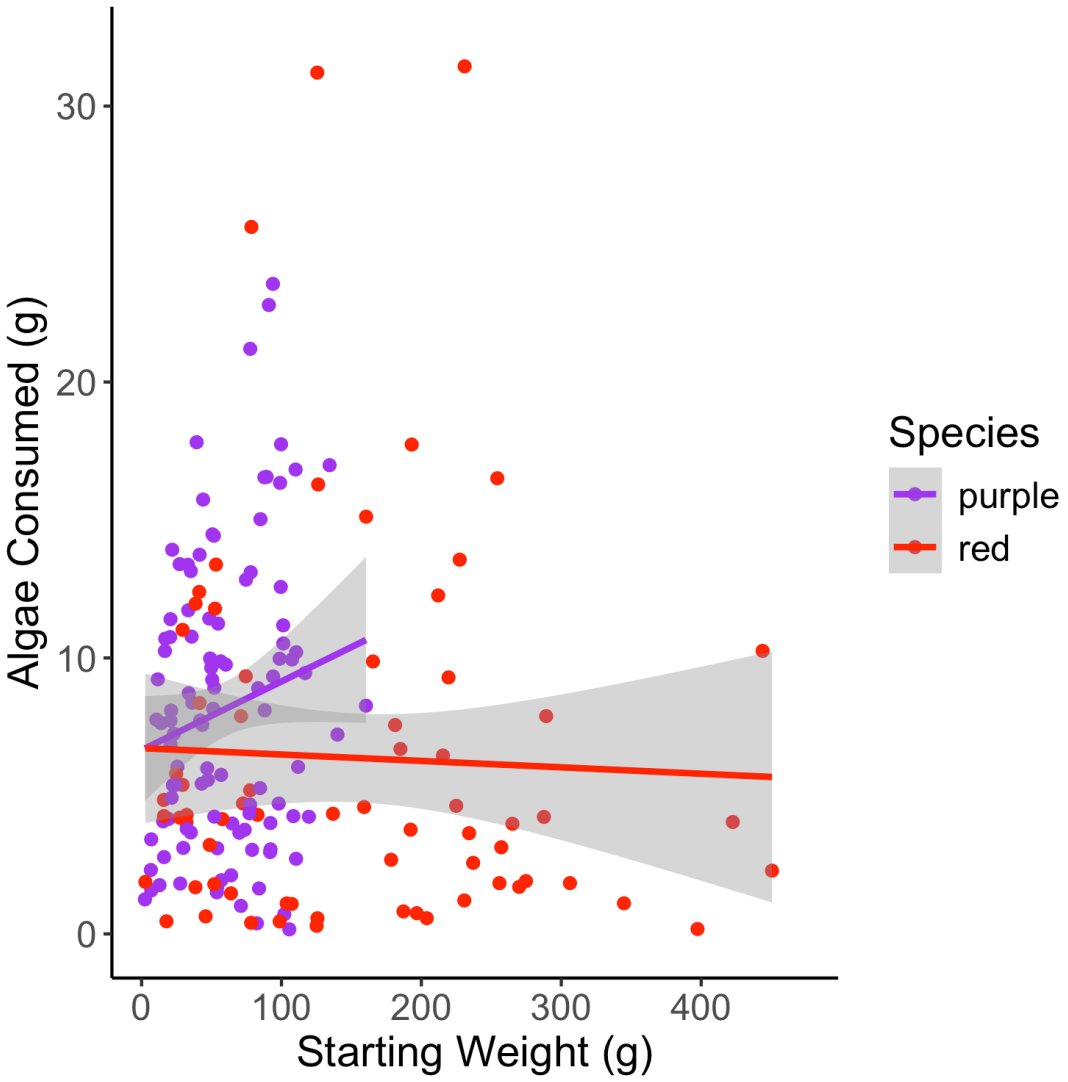

Figure 3.3: Algae consumed (g) by urchin starting weight (g) with regression lines fit for each species.

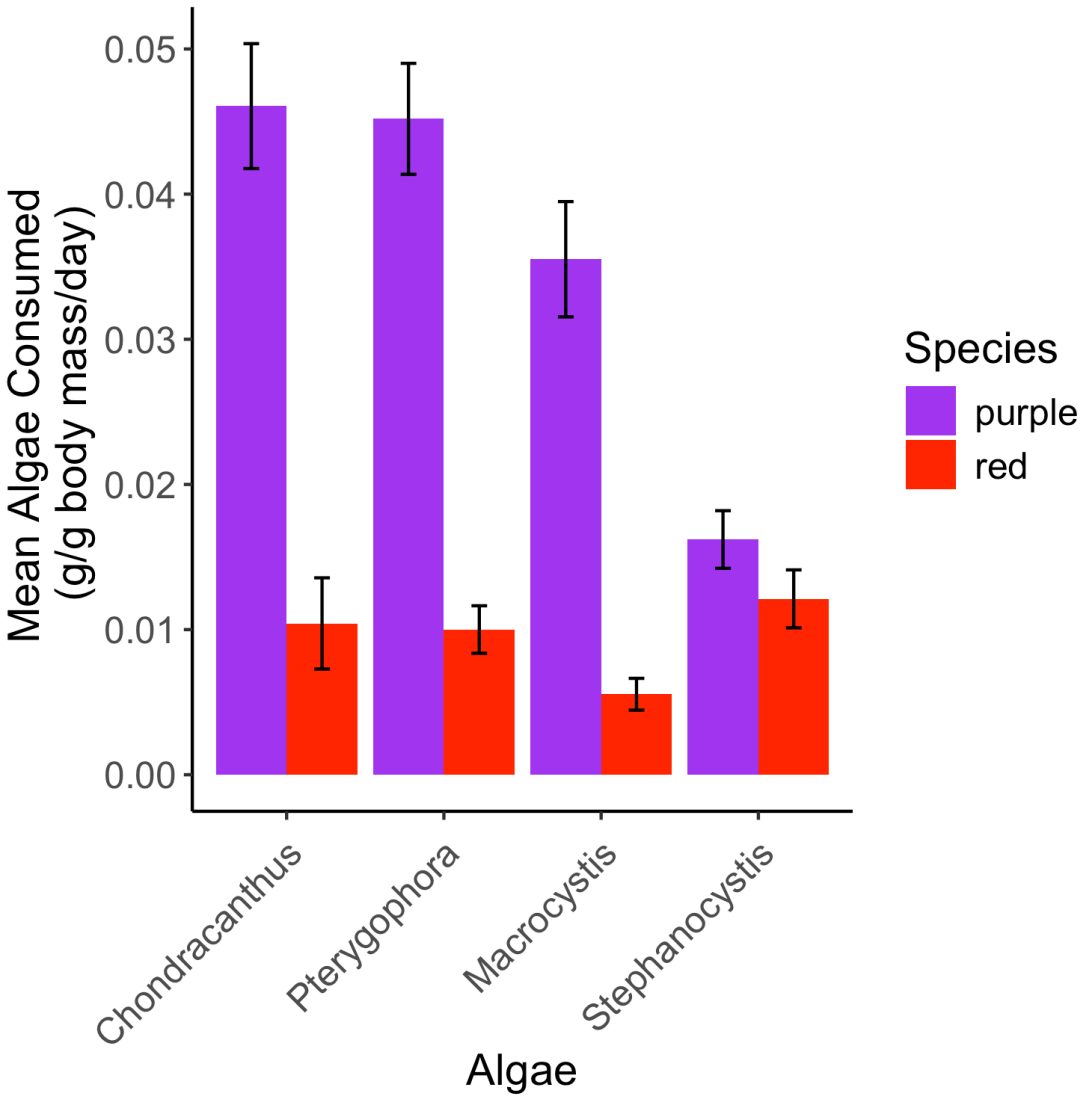

Figure 3.4: Mean algae consumed (g) with error bars +/- SE for each urchin species and algal treatment.

Algal Traits

A one-way ANOVA indicated significant differences in the C:N ratio between different algal species. A Tukey HSD test with correction for multiple comparison revealed significant pairwise differences in all comparisons at $\alpha<.05$ except *Pterygophora* with *Chondracanthus* or *Stephanocystis*. *Macrocystis* had the highest C:N ratio (24.8 ± 5.41) while *Chondracanthus* had the lowest (14.3 ± 3.67).

Of the four species tested, *Chondracanthus* had lowest Young's Modulus, indicating it was the most elastic material (see table 3.1). *Chondracanthus* also had the second highest blade area per unit mass and the lowest C:N ratio. Overall, urchins consumed more of the high protein, high surface area species. For red urchins, *Macrocystis* was consumed the least, and consumption patterns follow C:N ratio (low to high). High surface area to mass ratio algae were more consumed than low ratio types. For purple urchins, *Stephanocystis* was consumed the least, significantly less than the other algae species tested. *Stephanocystis* was the least elastic algae and had the lowest surface area to mass ratio, both traits that may influence an urchin's capacity to shred the blades.

ALGAE SPECIES	YOUNG'S MODULUS (N/CM)	KCAL/G	BLADE AREA PER MASS (CM^2/G)	C:N RATIO
CHONDRACANTHUS	0.104 ±0.013	2.719 ±0.357	12.463 ±2.877	14.281 ±0.981
PTERYGOPHORA	0.131 ±0.016	2.723 ±0.285	8.964 ±4.196	17.117 ±0.869
MACROCYSTIS	0.183 ±0.007	2.076 ±0.285	24.684 ±6.395	24.764 ±0.928
STEPHANOCYSTIS	1.574 ±0.265	3.186 ±0.186	6.037 ±2.543	20.376 ±0.827

Table 3.1. Algal trait metrics for four species of interest. Reported values are means ± standard deviation.

Modeling Urchin Consumption at LTER Sites

The results of the feeding trials provided an estimation of the amount of algae an urchin of each species could consume per day for the 4 different algae types tested. I took these values as upper bounds to the consumption rate by urchins in situ (since urchins were

provided with one food source only, and were fasted prior to the beginning of the experiment). Urchin density and NPP of understory algae is measured 4 times annually during seasonal surveys at LTE sites. Looking at the urchin biomass across these sites, red and purple urchins show similar patterns in biomass fluctuations over time. Naples Reef, a deeper site, is dominated by red urchins, and Carpinteria Reef, a shallower site, is dominated by purple urchins (see fig. 3.5). I found no clear evidence of competition, with a Pearson's correlation test indicating that there was not a significant correlation between the biomass of red and purple urchins ($p=0.526$).

In many cases the potential consumption by urchins exceeded the total available primary production (see fig. 3.6). To assess whether urchin consumption could affect future growth, I performed a mixed effects gamma model (with log link and random effect of site and algae species), which indicated that the removal potential by urchins was a highly significant predictor of mean NPP ($p<0.001$). *Macrocystis* biomass was an order of magnitude higher than the other three algal species, which swamped trends in the NPP of these species when looking at the four algae types collectively, so for the purposes of further analysis I analyzed each species individually. I considered the removal potential by urchins for one to four seasons (one year) prior to the NPP estimate. I found that removal potential by urchins of both species one season previous is a significant predictor of NPP for *Macrocystis* ($p<0.001$), *Pterygophora* ($p=0.043$), and *Stephanocystis* ($p<0.001$) but surprisingly, not for their most consumed food source, *Chondracanthus* ($p=0.237$). When considering each urchin species individually, removal potential by purple urchins in the previous time step was a significant predictor of total (four species) NPP in each subsequent time step across 1 through 4 seasons. However, removal potential by red urchins was only

significant at one previous time step, and the effect was *positive* (indicating higher consumption potential was associated with increased NPP in the next season). When looking at each urchin AND algae species individually, removal potential by red urchins was a significant predictor of *Macrocystis* NPP in the subsequent time step ($p=0.002$) but removal potential by purple urchins was not ($p=0.105$). The results of this analysis are summarized in table 3.2 and figure 3.7.

I then examined the impact of urchin consumption on the total available algal biomass, a value that includes both the algal biomass measured at transect level during seasonal surveys and the amount of accumulated NPP over the course of a set time frame. I calculated the seasonally available algal biomass, the theoretical amount of time it would take urchin populations to consume that biomass, and the effect of urchin consumption on future biomass. The median number of days it would take for urchins (both species) to consume all the available algae was 199.6 days for *Macrocystis*, 24.7 days for *Stephanocystis*, 10.9 days for *Pterygophora*, and 1.2 days for *Chondracanthus*.

I tested the effect of removing a highly abundant prey item on the other available prey items by examining sites where the most abundant algae, *Macrocystis,* was removed annually, and compared the impact of urchin consumption on the understory algal biomass in the next season at *Macrocystis* removal sites versus control sites. If urchin consumption of *Macrocystis* has a satiating effect that reduces their need to consume other understory algae, I would expect urchin consumption to have a greater impact on other understory algae species in areas where *Macrocystis* is absent. The results of this analysis were mixed (see Table 3.3). Purple urchins had a significant negative impact on *Chondracanthus* in removal sites, while red urchins had a significant *positive* impact on *Chondracanthus* in control sites.

Purple urchins had a significant negative impact on *Stephanocystis* in both removal and control sites, although the effect size was larger in removal sites, and red urchins had a significant negative impact on *Stephanocystis* in removal sites (Table 3.3). I also considered the presence of *Macrocystis* as a continuous variable, rather than a binary of presence/absence. Seasonal *Macrocystis* biomass interacted significantly with red urchin consumption on influencing the biomass of *Stephanocystis* (p=0.002) and *Chondracanthus* (p=0.020) but not *Pterygophora* (p=0.074). For purple urchins, the opposite occurred: seasonal *Macrocystis* biomass interacted significantly with consumption of *Pterygophora* (p<0.001) but not with *Stephanocystis* (0.477) or *Chondracanthus* (p=0.470).

ALGAE SPECIES	URCHIN SPECIES	URCHIN EFFECT	P-VALUE
CHONDRACANTHUS	*S. purpuratus*	**-0.021**	**<0.001**
	M. franciscanus	**0.084**	**9.61×10^{-4}**
PTERYGOPHORA	*S. purpuratus*	**-0.026**	**<0.001**
	M. franciscanus	-0.042	0.0781
STEPHANOCYSTIS	*S. purpuratus*	**-0.184**	**<0.001**
	M. franciscanus	**-0.069**	**0.0011**
MACROCYSTIS	*S. purpuratus*	-0.090	0.356
	M. franciscanus	**-1.869**	**0.0012**

Table 3.2: Model fitting results: Impact of urchin removal potential one season previous on NPP of 4 understory algae species. Significant relationships are in bold.

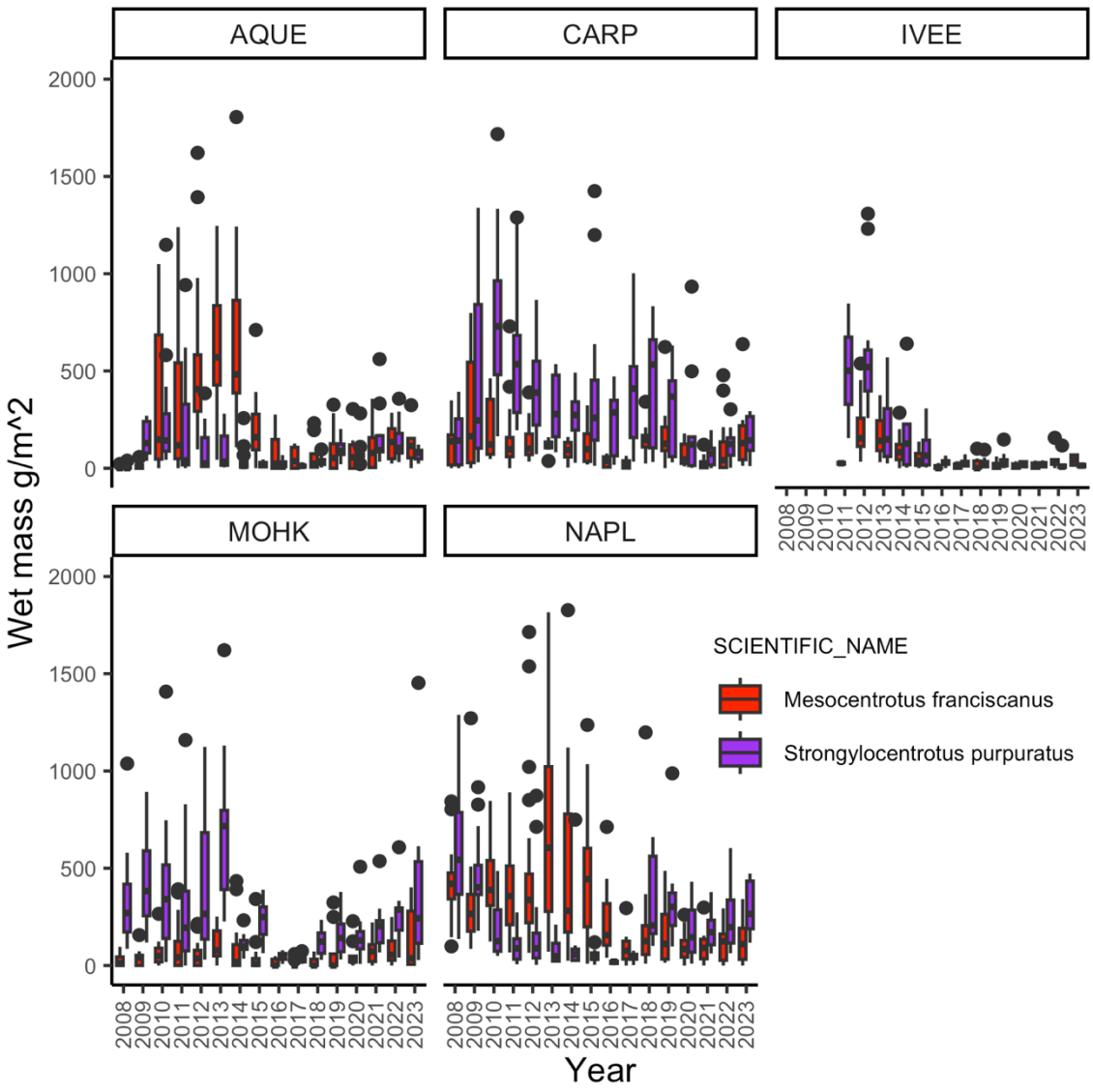

Figure 3.5: Boxplots of biomass of red vs purple urchins (wet mass g/m^2) over time, grouped by site

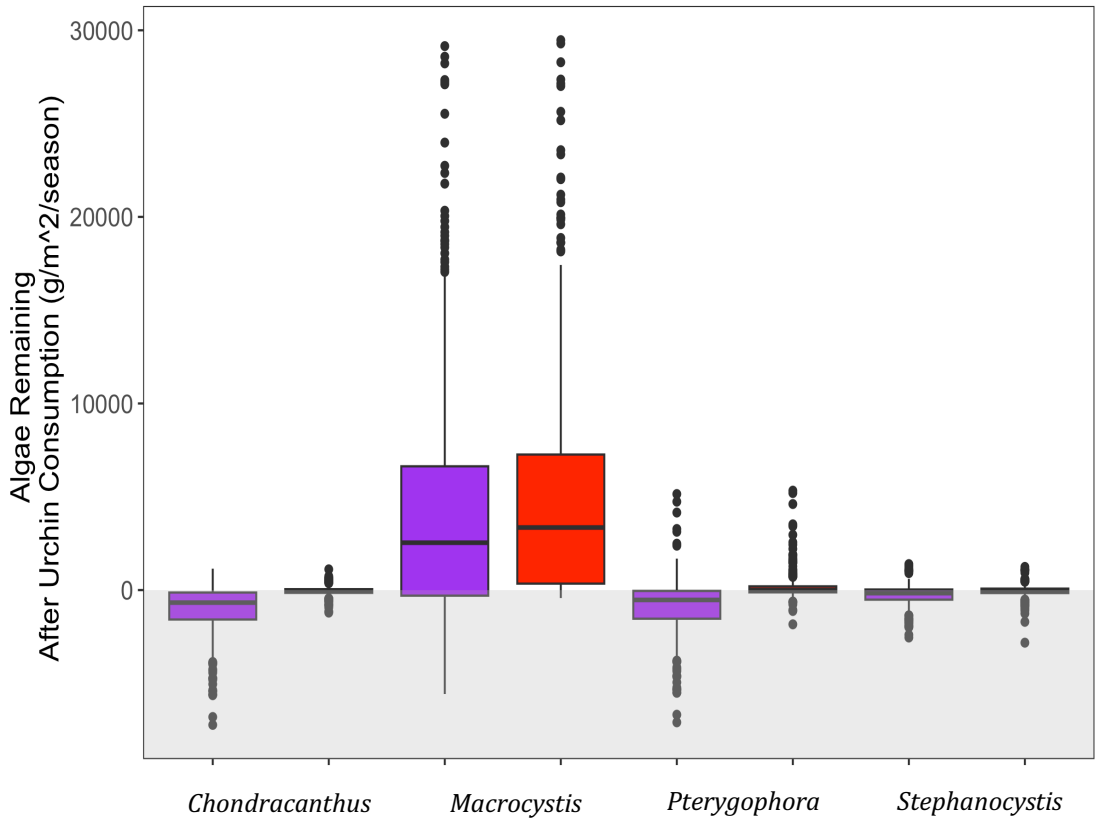

Figure 3.6: Boxplots of the remaining grams algae m^{-2} after consumption by urchins across the surveyed years at LTE sites

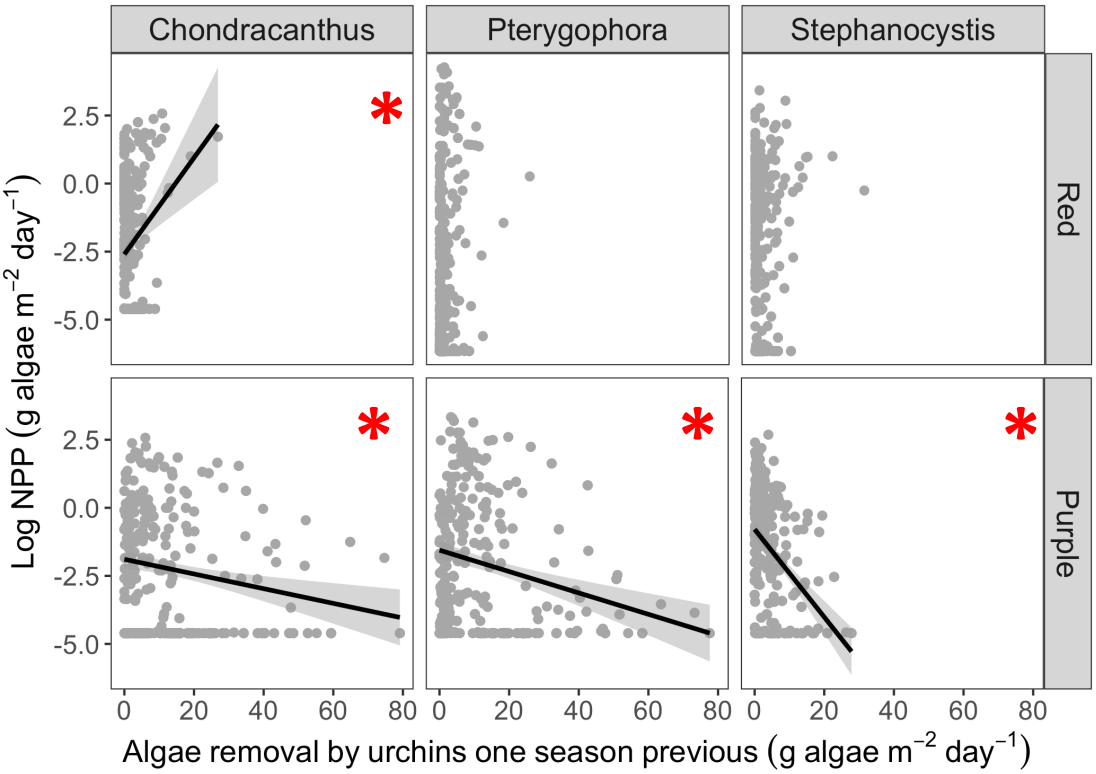

Figure 3.7: Relationship between log generated NPP (g algae/m^2/day) and the NPP removal potential by urchins one season previous (g algae/m^2/day). Linear regression lines with error displayed for each algae species. Macrocystis was not included here because its biomass was so high it swamped the trends for the other three species. Starred plots indicate significant relationships.

ALGAE SPECIES	URCHIN SPECIES	ANNUAL KELP REMOVAL URCHIN EFFECT	P-VALUE	CONTROL URCHIN EFFECT	P-VALUE
CHONDRACANTHUS	*S.purpuratus*	**-0.035**	**0.012**	-0.007	0.662
	M.franciscanus	0.094	0.928	**0.243**	**0.016**
PTERYGOPHORA	*S.purpuratus*	0.015	0.281	-0.033	0.761
	M.franciscanus	-0.153	0.448	-0.258	0.419
STEPHANOCYSTIS	*S.purpuratus*	**-0.277**	**<0.001**	**-0.076**	**<0.001**
	M.franciscanus	**-0.247**	**<0.001**	0.020	0.570

Table 3.3: Model fitting results: Impact of urchin removal potential one season previous on total biomass (g m^{-2}) of 3 understory algae species, at annual *Macrocystis* removal sites and control sites. Significant relationships are in bold.

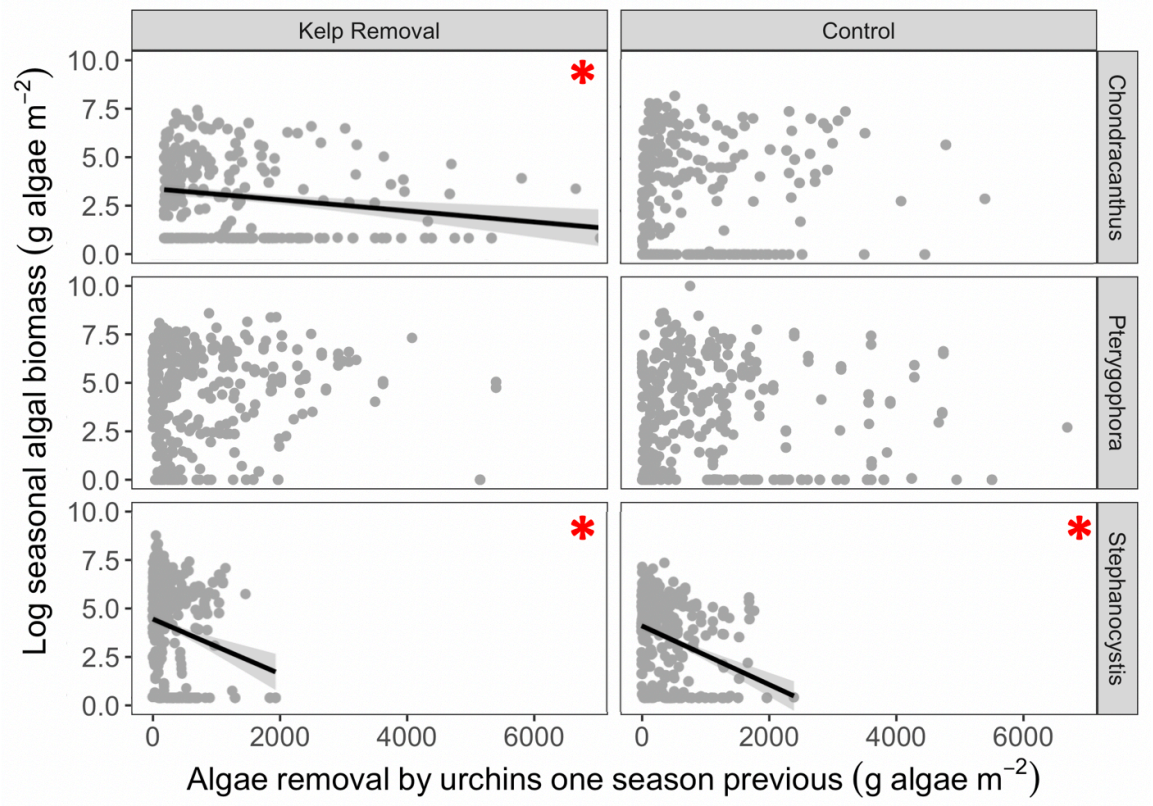

Figure 3.8: Log of NPP in grams algae/m^2/day by **purple** urchin removal potential one season previously, split up by algae type and by experimental treatment – annual *Macrocystis* removal plots and control plots (no *Macrocystis* removed). Starred plots indicate statistically significant linear relationships.

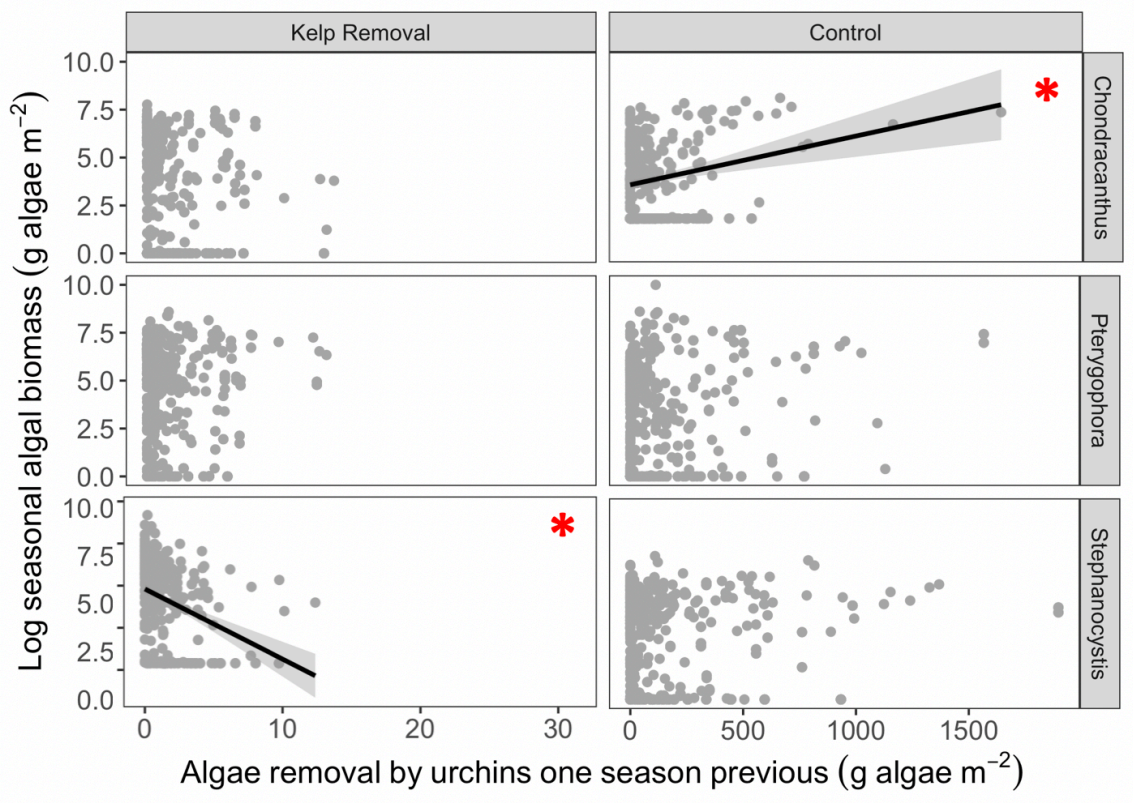

Figure 3.9: Log of NPP in grams algae/m^2/day by **red** urchin removal potential one season previously, split up by algae type and by experimental treatment – annual *Macrocystis* removal plots and control plots (no *Macrocystis* removed). Starred plots indicate statistically significant linear relationships

Discussion

Urchin Diets

The species identity of algal prey influences urchin foraging rates, particularly for purple urchins. While it is often assumed that *Macrocystis* is the primary food source for red and purple urchins, this assumption has not been directly tested as of yet. This study demonstrates that urchins in isolation will consume *Chondracanthus*, a red alga, at equal or higher rates than *Macrocystis*. This aligns with previous work by Foster et al. (2015), who examined the growth rates, gonad indices, and consumption rates of purple urchins fed five different algal diets. Urchins were fed either *Macrocystis pyrifera*, *Pterygophora*

californica, *Chondracanthus corymbiferus*, *Rhodymenia californica*, or a mixed diet with all four algae species. Purple urchins had the highest growth rates on *Chondracanthus*, *Macrocystis*, and the mixed diet. Purple urchins consumed *Macrocystis* at highest rate when offered a mixture, but consumed *Chondracanthus* and *Macrocystis* at similar rates when the two algae were offered alone (Foster et al., 2015). I measured consumption rates of purple urchins on *Pterygophora* which were much higher than those in the Foster study, where it was the least consumed species. Unlike purple urchins, red urchins showed no demonstrable changes in feeding rate based on the algal meal proffered.

Several algal traits were qualitatively linked with increases in urchin consumption. The two most consumed algae species (*Chondracanthus* and *Pterygophora*) also had the lowest C:N ratios, indicating higher protein content. *Macrocystis* had the lowest protein content of the species measured – a contrast with Foster (2015), perhaps due to the seasonality of measurements (summer/fall sampling vs winter) or a greater sample size in this study (n=33). It is possible that urchins consumed more proteinaceous species because these species were harder to digest, and they needed to eat more to meet their caloric needs. This possibility is tested in chapter 4.

It is also possible that urchins prefer to feed on high-protein red algae, but since giant kelp is in such great supply, their encounter rate is higher and they are more frequently documented feeding on it. Future research is needed to assess whether the consumption rates by these two urchin species represent true feeding preferences.

The increased consumption of *Chondracanthus* by purple urchins may be related to nutritional quality. Many properties other than protein are linked with nutritional value including lipid content and composition, fiber content, and the presence of phytochemical

defense compounds such as phenolics, terpenoids, and alkaloids (Konno, 2011). Nutritional value to urchins is often assessed by measuring the response in urchin gonad quality as an indicator of health. Gonad quality is central to the urchin fishery, so a number of studies have been performed on the effect of different diets (Azad et al., 2011; Foster et al., 2015; McBride et al., 1997). Initial tests with commercially prepared diets showed that red urchins consumed significantly more bull kelp (*Nereocystis luetkeana*) than commercially prepared diets, and that red urchins tended to eat more in spring than in fall (McBride et al., 1997). However, later tests with prepared feed and three fleshy brown algal species (*Macrocystis integrifolia*, *Nereocystis luetkeana*, *Saccharina latissima*) found that the commercially prepared diet produced better gonads (in terms of color, texture, and firmness) than any of the kelp diets (McBride, 2004). Gonad quality showed little difference among kelp treatments at different temperatures. A closely related species, the green sea urchin *Strongylocentrotus droebachiensis*, exhibited fastest and highest roe enhancement from a red algae-based diet, with lowest yields from brown algae based diets (*Alaria esculenta* and *Laminaria saccharina*) (Vadas et al. 2000). Gonad quality was associated with protein levels in the algae. These gonad quality studies, importantly, demonstrate that urchin consumption patterns are not linearly correlated with gonad quality – in essence, eating more of a single-species diet is not necessarily "healthier." Mixed diets often lend more nutritional value. This is intuitive from a nutrition standpoint but often overlooked when considering urchin dietary patterns. A red algae-based diet produced larger, higher quality gonads than urchins fed on brown algae for both Vadas (2000) and Foster (2015), potentially explaining the increased feeding rates by purple urchins on *Chondracanthus* over *Macrocystis.*

Although this feeding study did not identify dietary niche separation between red and purple urchins, the significant disparity in mass-adjusted feeding rates has potential ecological ramifications. Since purple urchins on average consumed more algae than reds per unit body mass, purple urchins likely have a greater potential to consume the four species of algae tested than red urchins. The mechanisms behind this disparity are not well understood. Possible reasons include: 1) red urchins have adapted more sedentary behaviors and therefore have lower caloric requirements, 2) red urchins were more stressed by the laboratory conditions than purple urchins and fed less, 3) red urchins preferentially feed on food sources other than those offered. Options 1 and 2 have some basis of support, while we have no information to indicate the veracity of option 3. In terms of sedentary behavior, the (anecdotally) observed urchin behavior in this feeding experiment reflect conditions observed in the field (Parnell et al., 2017): larger red urchins tended to limit movement and active grazing, while smaller purple urchins grazed actively and in larger quantities. Red urchins, due to their longer spines, can preclude purple urchins from occupying more favorable habitats (Schroeter, 1978; Tegner & Dayton, 1981). These ideal habitats include cracks and crevices which provide protection from predators while receiving enough drift algae to sustain the urchins living inside (Schroeter, 1978). Red urchins (and purple urchins as well) are able to carve out homes for themselves, often literally by bioeroding the rock substrate into a bowl-like depression (Rogers-Bennett & Okamoto, 2020; Russell et al., 2018). Once situated in these "safe zones," urchins have less incentive to actively forage, and therefore it would follow that larger, protected red urchins have lower caloric requirements. Metabolic requirements are explored further in chapter 4. In terms of interspecific differences in stress response, I noted that red urchins were more sensitive to

handling, and were more likely to lose their spines and die following transportation from the field to the lab (something also noted by C. Nelson and D. Reed, pers. comm). Further research is needed to determine whether this handling sensitivity is real or a sampling artifact.

Regardless of the mechanistic reason behind interspecific differences in overall foraging rates, quantifying these rates can help us predict how urchin foraging might shape the understory algae community within the kelp forest. Although red urchin biomass is increasing inside some marine reserves (Malakhoff & Miller, 2021), that increase in biomass might not translate to an increase in overall algae consumption when compared to an equivalent increase in purple urchin biomass. Larger red urchins in reserves, freed from fishing pressure, might only consume quantities of ecologically important *Macrocystis* on par with much smaller purple urchins. Therefore, the distribution of these two urchin species across a kelp forest could play a far greater role in structuring the primary producer community than previously thought.

Modeling Urchin Consumption

Results from modeling urchin consumption rates in the field tell a complex story not always in support of my original hypotheses. Although urchins have the theoretical capacity to consume all the available understory algae of their favored species (*Chondracanthus*) in a little over a day, the relationship between actual urchin and algal biomass is mixed. Given that *Chondracanthus* is the most rapidly consumed algae species by purple urchins but also much less abundant than *Macrocystis*, it is unsurprising that urchins have the potential to remove all the *Chondracanthus* in a given area if they are consuming at their theoretical

maximum. However, since *Chondracanthus* is not completely disappearing from these sites, it is apparent that urchins are not solely targeting this species to meet their nutritional needs – likely their consumption increases proportionate to the relative abundance of each algae type, which maintains the coexistence of producer species (Brose, 2008).

Overall, removal potential by urchins as a whole is a significant negative predictor of total (four species) primary productivity. This fits with the classification of sea urchins as ecosystem engineers, because their grazing directly and indirectly controls the availability of primary consumers for other species within the community assemblage (Jones et al., 1994; Rogers-Bennett & Pearse, 2001). However, when examining these relationships on the urchin and algae species level, many of these relationships were not significant. Purple urchin consumption had a significant negative association with the next season's growth of *Chondracanthus, Pterygophora*, and *Stephanocystis,* but higher consumption potential by red urchins was actually associated with *higher* NPP of *Chondracanthus* in the next season, and this trend held for *Chondracanthus* production in control sites where no kelp removal was taking place. Why might red urchins have this positive association with *Chondracanthus*? Perhaps it is due to differences in the distribution of red and purple urchins: in areas with higher densities of red urchins, they may prevent more voracious purple urchins from occupying that space, and therefore allow for more growth of understory algae. However, I found no direct evidence of competition between red and purple urchins (there was no negative correlation between their abundances). Perhaps, then, the structure of the habitat is more important – urchins and understory algae both prefer more rocky substrate that allows for protection/concealment (for urchins) and attachment

(for algae) (Lamy et al., 2020; Miller et al., 2018). Therefore, areas that can support higher red urchin densities are also conducive to higher algae densities.

Many studies have demonstrated that the relationship between urchin densities (or biomass) and grazing rates is not linear (Byrnes et al., 2013; Harrold & Reed, 1985). Areas with high densities of urchins can also support high densities of macroalgae if there is sufficient supply of drift algae or other factors that mitigate the formation of urchin feeding fronts. This study demonstrates that variations in the abundance of red and purple urchins across reefs can affect the composition of the understory algae community via their foraging rates. The lack of a clear negative relationship between urchin densities and species-specific algal biomass is indicative of a more complex community ecology, involving the interplay of algal availability, predator densities, urchin behavior, and environmental variation, among many other factors. Ultimately, this study demonstrates that urchin species identity is important in models predicting algal biomass and growth. A community dominated by red urchins may see a lower impact on understory algal biomass than a system dominated by more voracious purple urchins. Projects that seek to facilitate kelp growth and recovery via urchin control may find that targeting areas with higher purple-to-red-urchin ratios yields greater results.

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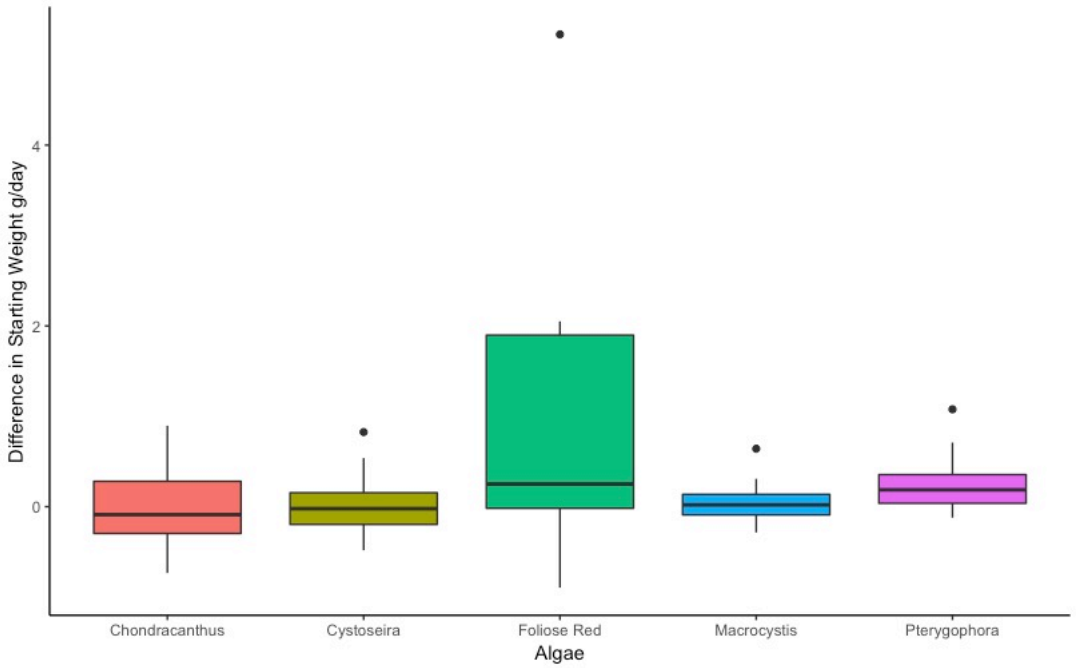
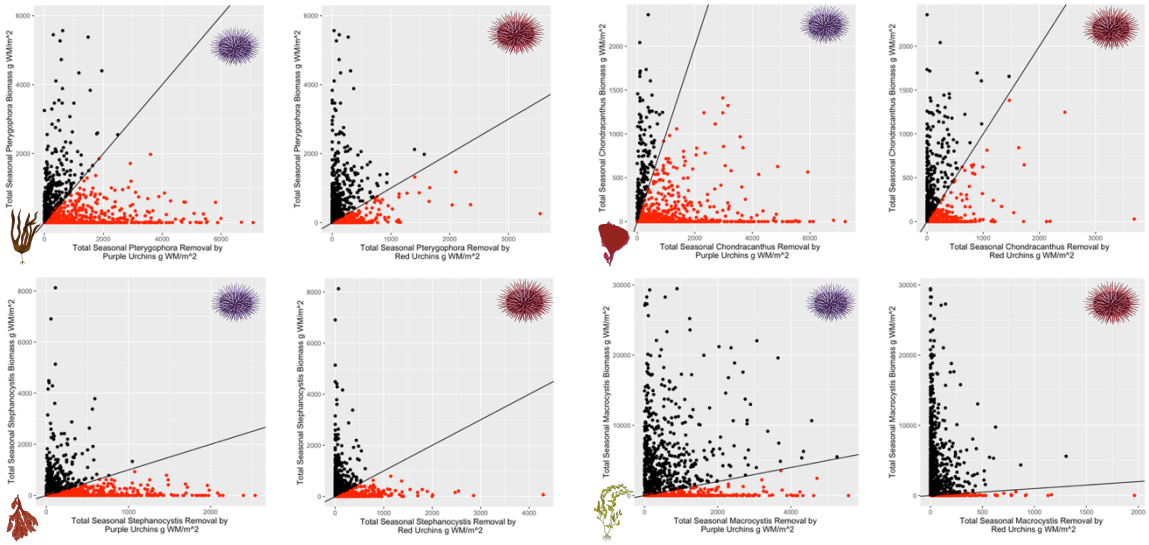
Appendix



A3.1: Difference in final versus starting weight of algal controls



A3.2: Total accumulated seasonal biomass of *Pterygophora, Chondracanthus, Stephanocystis,* and *Macrocystis* versus the total consumption by purple and red urchins, respectively. Line represents 1:1 production versus consumption. Points colored in red fall below the 1:1 line.

IV. Digestive physiology of *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*

Abstract

In the kelp forests of Southern California, the red sea urchin *Mesoentrotus franciscanus* and the purple sea urchin *Strongylocentrotus purpuratus* are dominant herbivores which often coexist synchronously with biodiverse macroalgal assemblages, but, under certain conditions, these urchins can overgraze areas to such an extent that they transform kelp forests into barren, species-poor urchin-riddled wastelands. The mechanisms that lead to urchin overgrazing are extensively studied but still not fully understood. An area that has received little attention thus far is the digestive physiology of these species. Quantifying resting metabolism and the energy resources urchins devote to digesting their meals can help us budget how much energy urchins have available to devote to other processes such as growth and reproduction. In turn, we can use this information to better parameterize models of urchin foraging and make predictions about where overgrazing may occur. I measured the standard metabolic rate (SMR) and metabolic cost of digestion, also known as specific dynamic action (SDA) for red and purple urchins fed two different algal diets – the red alga *Chondracanthus corymbiferus* and the brown alga *Macrocystis pyrifera* – using custom built intermittent-flow respirometers. I found no interspecific differences in mass-adjusted SMR or SDA. However, the SDA coefficient of *Macrocystis* was significantly higher than *Chondracanthus*, indicating the red alga was easier for urchins to digest, which lends credence to my previous feeding study results. The cost of digestion was quite low for all urchins tested, representing less than 1% of their energy budget on average, but there were

no energetic cost-savings associated with consuming a larger meal. These metabolic characteristics can help explain these urchins' particular voraciousness – they have a high capacity for eating large meals because they take very little energy to digest – while also giving us more insight into why overgrazing is not occurring everywhere – if there are not energetic cost-savings to eating a larger meal, eating a smaller, nutritionally adequate meal would be advantageous. This study lays the foundation for further investigation of urchin digestive physiology, particularly across a broader spectrum of algal meals.

Introduction

Sea urchins are critically important herbivores worldwide, capable of transforming biodiverse, algal-dominated ecosystems into species-poor barrens overrun with urchins (Filbee-Dexter & Scheibling, 2014; Karatayev & Baskett, 2020; Rustici et al., 2017). Sea urchin grazing has been the subject of extensive scientific study, because the causative mechanisms behind urchin-led transitions from forests to barrens remains poorly understood and difficult to predict (Rogers-Bennett & Okamoto, 2020). While stable assemblages of urchins and macroalgae coexist in many areas, shifts in urchin foraging behavior to more destructive grazing have been associated with reductions in the supply of detrital kelp. Urchins that were passively relying on drift kelp for food emerge from their sheltered ledges and crevices to form active feeding fronts that rapidly consume standing algal biomass (Harrold & Reed, 1985; Kriegisch et al., 2019).

In the Santa Barbara Channel, the dominant urchin species *Mesocentrotus franciscanus* (red urchins) and *Strongylocentrotus purpuratus* (purple urchins) can catalyze the transition between lush, structured *Macrocystis pyrifera* (giant kelp) forests and bare

substrate nearly devoid of macroalgae. The feeding behavior of *M. franciscanus* and *S. purpuratus* has been extensively studied due to their role as a key herbivore, but little is known about how they metabolize the meals they ingest. Studies of urchin metabolism have typically focused on the effects of climatic changes (increasing seawater temperature, ocean acidification) on their standard metabolic rate (SMR) in adults (Carey et al., 2016; Uthicke et al., 2014; Watson et al., 2014) or during embryonic development (Wong & Hofmann, 2020). A deeper understanding of urchin metabolism with respect to their diets could help parameterize energy budget models and enhance our ability to predict changes in foraging rates based on available algal biomass.

In energy budget models for sea urchins, most energy is allocated to respiration, growth, and gonad production (Greenwood, 1980; Hill & Lawrence, 2006; Yeruham et al., 2019). Energy expenditure on digestion may account for only a small portion of their overall energy budget, but any expenditure reduces an urchin's scope for growth and reproductive output. This has significant implications for urchins grazing on a wide array of primary producers. To date, there have been no studies comparing specific dynamic action (SDA), also known as the metabolic cost of feeding or the thermic effect of food, on red and purple urchins. As an urchin digests a meal, its metabolic rate rapidly rises to a short-lived peak (SDA_{peak}) and then slowly declines back down to a baseline standard metabolic rate (SMR). Understanding the properties associated with this increase in metabolism can help illuminate dietary patterns by identifying meals that are harder or easier to digest. It is commonly assumed that sea urchins will preferentially consume the keystone species *Macrocystis pyrifera* over other types of understory macroalgae, but feeding preference studies have shown that in the presence of a mixed algal resources urchins will often feed

preferentially on other algae species such as *Chondracanthus, Gracillaria,* and *Rhodymenia* (Foster et al., 2015; Hasshaw, in prep). In feeding trials that I conducted with four common understory algae species, *Chondracanthus,* a blady red alga, was consumed at the highest rate by purple urchins. These results were intriguing, and led me to two questions: 1) Is *Chondracanthus* more nutritionally suitable for urchins and therefore preferred over *Macrocystis*? 2) Is this a case of compensatory feeding, where urchins need to consume more *Chondracanthus* than *Macrocystis* to obtain an equivalent amount of calories or nutrients? I opted to investigate urchin metabolic responses to meals of *Chondracanthus* or *Macrocystis* because these species represent a significant proportion of the understory algal biomass in the Santa Barbara Channel, occupy two different algal clades (Rhodophyta and Phaeophyta, respectively), and were consumed at similar high rates by *M. franciscanus* and *S. purpuratus* in feeding trials.

In addition to testing different diets, I tested interspecific metabolic differences in *M. franciscanus* and *S. purpuratus*. While red and purple urchins are often considered interchangeably, since they are sympatric with overlapping niche spaces, my feeding study showed that there are significant differences in consumption rates between red and purple urchins after controlling for body mass. Purple urchins have been documented as more active grazers, emerging more frequently from sheltered habitats to feed on understory algae, while red urchins may rely to a greater extent on the passive accumulation of detrital drift kelp (Britton-Simmons et al., 2009; Parnell et al., 2017). If purple urchins have higher metabolic requirements, that might explain this dichotomy in urchin feeding behavior. Therefore, I sought to investigate potential drivers behind interspecific differences in urchin

foraging rates by analyzing the standard metabolic rate and SDA for *M. franciscanus* and *S. purpuratus* given the same diet.

Methods

I quantified the standard metabolic rate (SMR) and specific dynamic action (SDA) of *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus* for two algal treatments (*Chondracanthus corymbiferus* and *Macrocystis pyrifera*), with 8 respirometers running simultaneously per trial and a total of 11 trials. Small adult urchins (average 44.7±23.9 g wetmass) were collected via SCUBA at Naples Reef off the coast of Santa Barbara, and held in flow-through seawater tanks maintained at 20°C, which was on the upper end of the typical ambient bottom temperature of the kelp forest during summer months (10-20°C, see Hirsh et al.) but well within the tolerated thermal range for both urchin species. Urchins were fasted for 8 days prior to the start of each respirometry test, as this was the starvation period I determined (via preliminary trials) that would result in algal consumption that was at least 2-4% body mass within a five hour feeding window, and which resulted in evidence of digestion (fecal pellets) within 24 hours. Following this fasting period, urchins were placed in custom-made intermittent flow respirometers to measure oxygen consumption rates (M_{O2}=mg O_2 kg^{-1} min^{-1}). A water table held at a constant 20°C contained 8 submerged respirometers, which were custom-made from polyvinyl Tupperware (Lock & Lock), plumbed with PVC tubing to recirculation pumps (Eheim Universal 300 pump, average flow rate 2 L min^{-1}) and flush pumps (Eheim compactON 300 pump, flow rate to each respirometer averaged 1.4 L min^{-1}) (total respirometer volume = 1.437 L). Because the volume of water in the respirometers was so small, flush pumps were split between 2 respirometers. FireSting Robust Oxygen probes (PyroScience, Aachen, Germany) were

fitted into the recirculation loop to continuously measure oxygen levels. Recirculation pumps continuously pumped water through the closed loop, and flush pumps were set on a timer to automatically turn on intermittently (7 minutes on, 30 minutes off) to flush fresh seawater throughout the respirometers and ensure the dissolved oxygen levels did not drop below 70%. The laboratory room was kept on a 12 hour light/dark cycle.

To account for bacterial respiration, background respiration was measured before and after each trial on shortened intermittent flush cycles (5 minutes on, 15 minutes off), and all respirometry experiments were conducted in tanks with filtered seawater (UV and mesh filters – Pentair 0.34, 1, 5, and 20 micron filters) to reduce bacterial respiration as much as possible. The entire setup was drained, rinsed with freshwater, and cleaned with bleach between each trial to minimize bacterial growth.

Urchins were left in the respirometers overnight (12 hours) during which time I measured standard metabolic rate. They were then given a pre-weighed quantity of algae to feed *ad lib* for 5 hours. Algae was removed and weighed using the blot-dry method – the same procedure developed during previous feeding trials as the most accurate wet mass measurement – to determine the mass of algae consumed as a percentage of urchin body weight. Oxygen readings were recorded for six days. These experiments were performed across multiple time points (fall through spring) to determine if there was any seasonal signal in SMR or SDA.

MO_2 Analysis

MO_2 data were analyzed in R (version 4.2.3) using the *AnalyzeResp* package (Kraskura 2024). Mass-specific MO_2 (mg O_2 kg^{-1} min^{-1}) was calculated from the change in

oxygen concentration over time (ΔO_2) in the respirometer using the formula $MO_2 = (\Delta O_2 \times (v_R - v_F))/m$, where v_R is the respirometer volume, v_F is the volume of the urchin (L, assuming 1 kg=1 L), and m is the urchin mass (kg). All measurement period dissolved oxygen regressions were checked for linear and negative oxygen slopes (R^2 threshold = 0.9). All MO_2 values were corrected for bacterial background respiration. Background respiration was calculated based off a linear regression calculated between the average initial and ending background measurements for each respirometer, and then subtracted from the slope of each associated MO_2 measurement. Background respiration was measured with shortened flush cycles (5/15) for at least 6 cycles before and after each trial.

SMR was calculated as the mean of the lowest ten values of all MO_2 measurements (n=24) taken during the overnight period with $R^2>0.9$. To account for any handling effect on oxygen consumption, I incorporated a delay of 1 hour for the MO_2 measurements included in the SDA analyses, and integrated the difference between the starting MO_2 measurement and SMR for that 1 hour period to add to the total SDA. After approximately 30 hours, all urchins had returned to their baseline standard metabolic rate, and MO_2 values rose thereafter, likely as a result of increased bacterial respiration, so all SDA analyses were cut off at the 30 hour mark. I calculated the following SDA associated variables:

SDA_{peak}	*maximum postprandial MO_2*
SDA_{peak_time}	*time from feeding to reach peak SDA*
$SDA_{duration}$	*time from feeding until MO_2 crossed the SMR threshold*
SMR_{SDA}	*SMR threshold, the mean of the 10 lowest values of all postprandial MO_2 measurements*

SDA	*integrated area under the curve between first postprandial MO_2 measurement and SMR_{SDA}*
SDA_{cost}	*the cost of digestion, representing the percentage of energy consumed, calculated as $SDA_{cost} = E_{SDA}/E_{meal\_cal}$ x 100, where E_{SDA} is the energy spent on SDA (assuming 1 g O_2 = 10 kJ of energy, see supplementary info), and E_{meal_cal} is the energy of the algae meal, calculated as the mass of algae fed multiplied by the average calories per gram (as measured in a bomb calorimeter) and a corrective factor of 0.7 (Leighton, D.L., 1968) to account for absorption inefficiency.*

Algal Traits

In order to estimate the energy absorbed per gram of algae consumed, I quantified traits that had potential biological relevance to urchin digestion (See *Algal Traits* methods, Chapter 3).

Statistical Analysis

All statistical analysis was performed in R (R Core Team, 2024). Values are presented as mean ± standard deviation, with statistical significance set at $p<0.05$. Normality assumptions were checked using Shapiro-Wilk tests and quantile-quantile plots, and homogeneity of variance assumptions were checked with Levene's test. To meet normality assumptions, the response variables SMR, SDA, and SDA_{cost} were log transformed. To examine how SMR varied by urchin species, I used a one-way ANOVA. To determine how SMR and SDA varied by urchin species and algal meal, I used two-way ANOVAs. Experimental date was included as an interaction term, but it had no significant effect and

was dropped from the final model. Any nonsignificant interactions between urchin and algae species were also dropped. To determine if relative meal size affected cost of digestion, I used a linear model with SDA_{cost} as the response variable and relative meal size as the explanatory variable, with separate models for red and purple urchins.

Results

SMR

There was no significant difference in standard metabolic rates between *M. franciscanus* and *S. purpuratus* ($p=0.348$) and no effect of algae treatment ($p=0.111$) or interaction between the two (see fig. 4.1). SMR increased significantly with body size by a factor of 0.83 on the log-log scale ($p<0.001$) (see fig. 4.2). However, there was no evidence that standard metabolism was different between these red and purple urchins ($p=0.265$) (see fig. 4.2).

SDA

Urchins consumed algae between 0.12-11.58% of their body weight. This represents a broad range in consumption, with urchins on average consuming around 3.4% of their body mass within a 5-hour feeding window (Table 4.1). Although red urchins on average ate more, there was no significant difference in mass-adjusted meal size between red and purple urchins ($p=0.157$) (see Fig. 4.3). Across this range in consumption, I found no significant difference in SDA between urchin species fed on the same diet ($p=0.882$)(Fig. 4.4). I did, however, find a significant difference in SDA between algae treatments, with urchins exhibiting significantly higher SDA when digesting *Macrocystis* than when digesting *Chondracanthus* ($p=0.001$)(Fig. 4.4). SDA increased with meal size for both urchin species

feeding on *Macrocystis,* but this increase was slightly above the threshold of significance (red: p=0.060, purple: p=0.059). I found no significant increases in SDA with meal size for urchins feeding on *Chondracanthus* (see Fig. 4.5). Trial date was not significant (p=0.226), indicating a lack of a seasonal signal in SDA measurements. The calculated thermic effect of food (SDA_{cost}) ranged from 0.02-3.76%, with an average of 0.43% of the urchin's energy budget, although this did not correlate with the percentage of urchin body mass consumed (p=0.336)(Fig. 4.6).

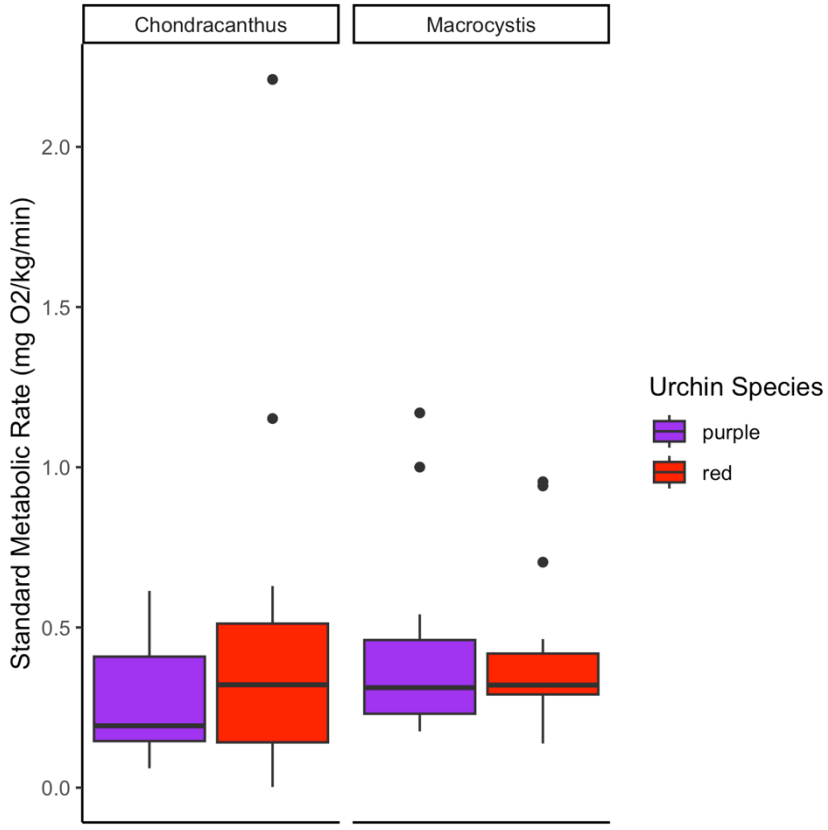


Figure 4.1: Standard metabolic rate (SMR) by algae treatment and urchin species.

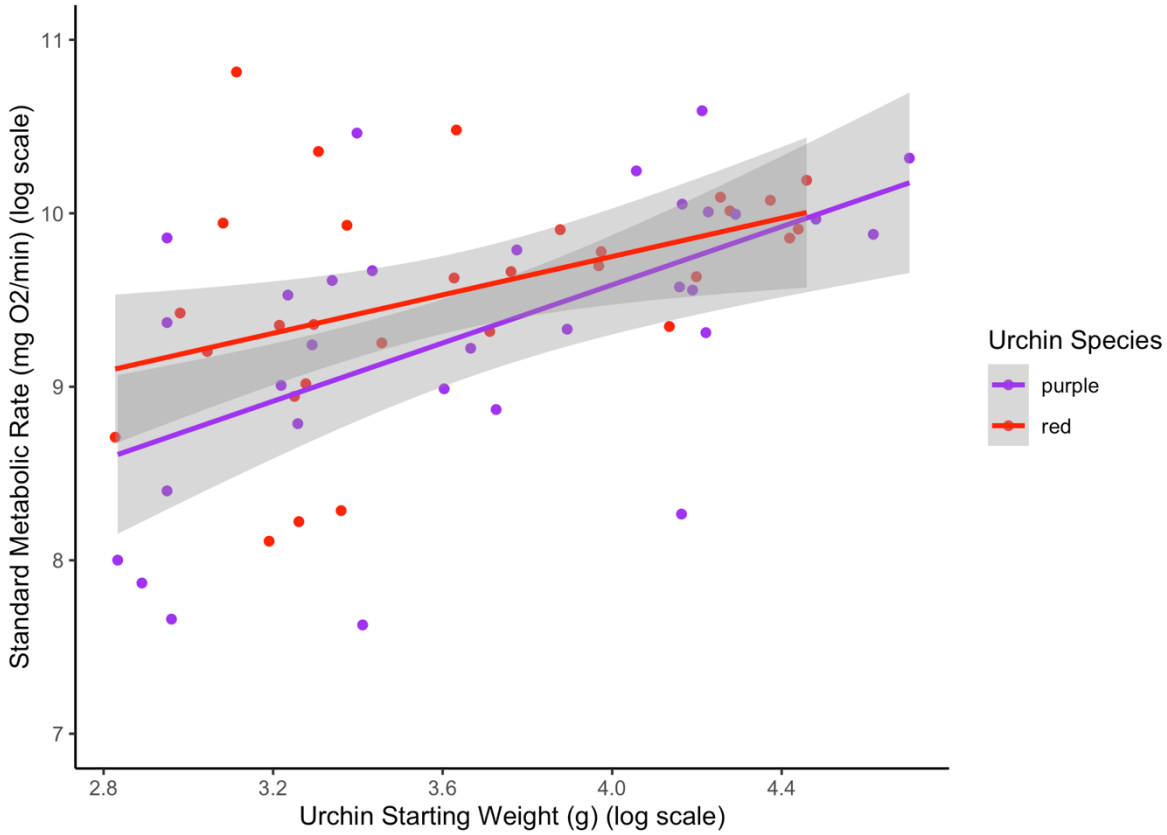


Figure 4.2: Standard metabolic rate (mg O_2 kg^{-1} min^{-1}) by urchin weight (g) on the log-log scale, with regression lines fit for purple and red urchins, respectively. 95% confidence intervals shown in gray.

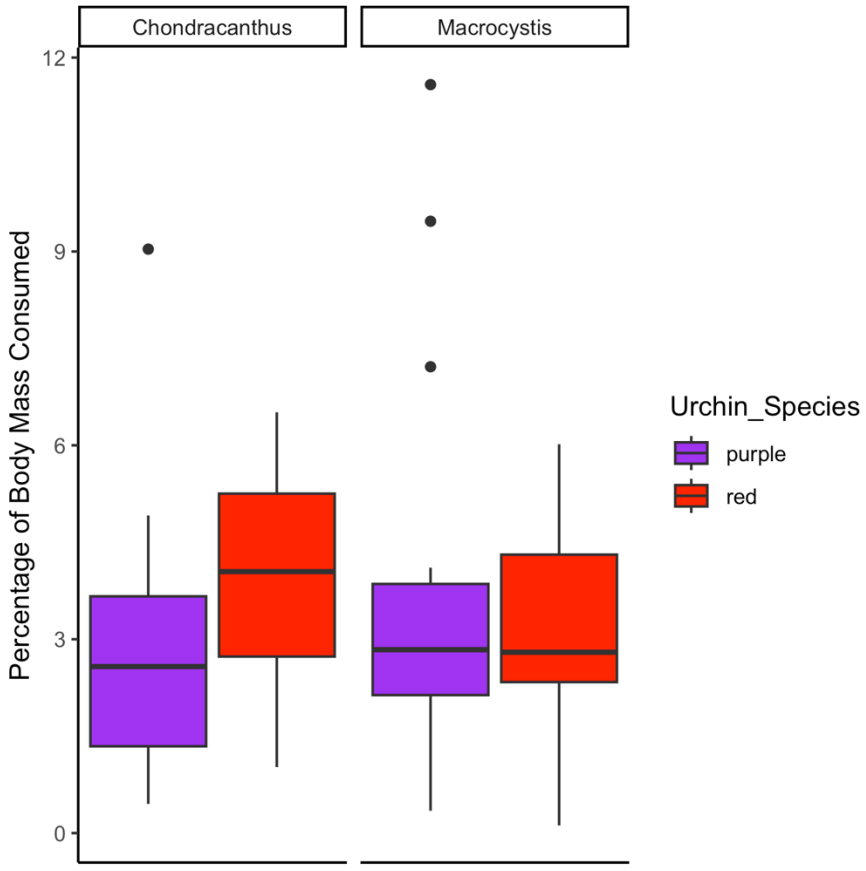


Figure 4.3: Percentage of body mass consumed by algae treatment and urchin species.

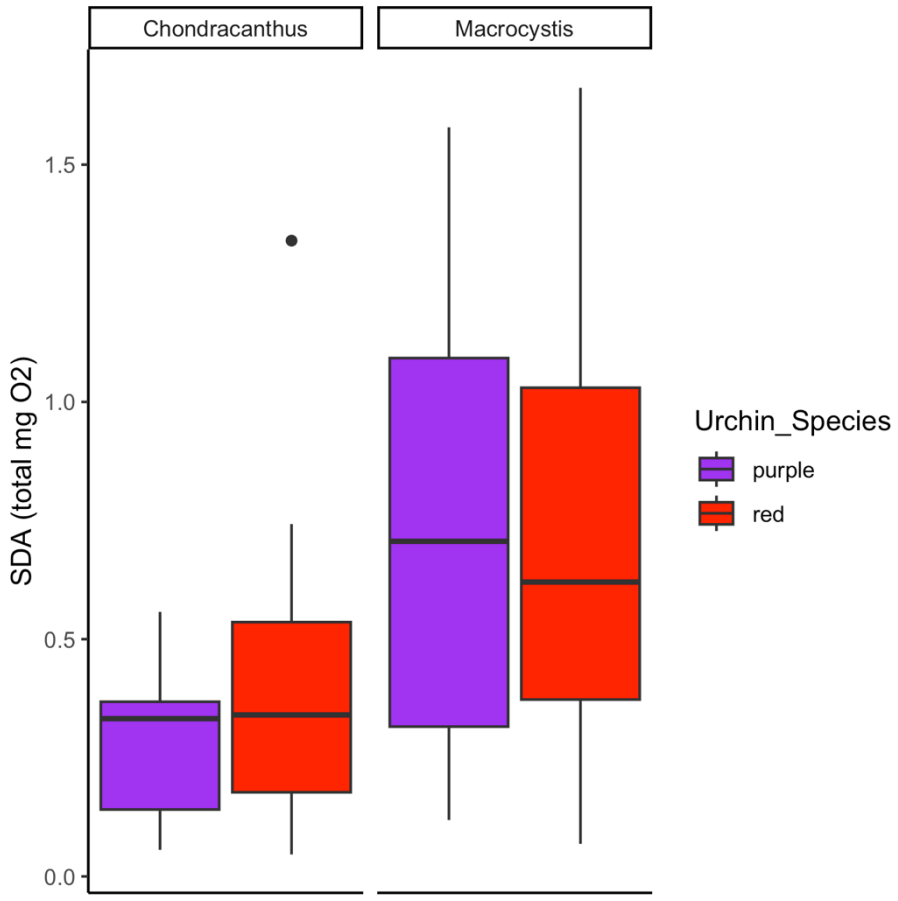


Figure 4.4: Boxplots of SDA values split up by algae treatment and urchin species.

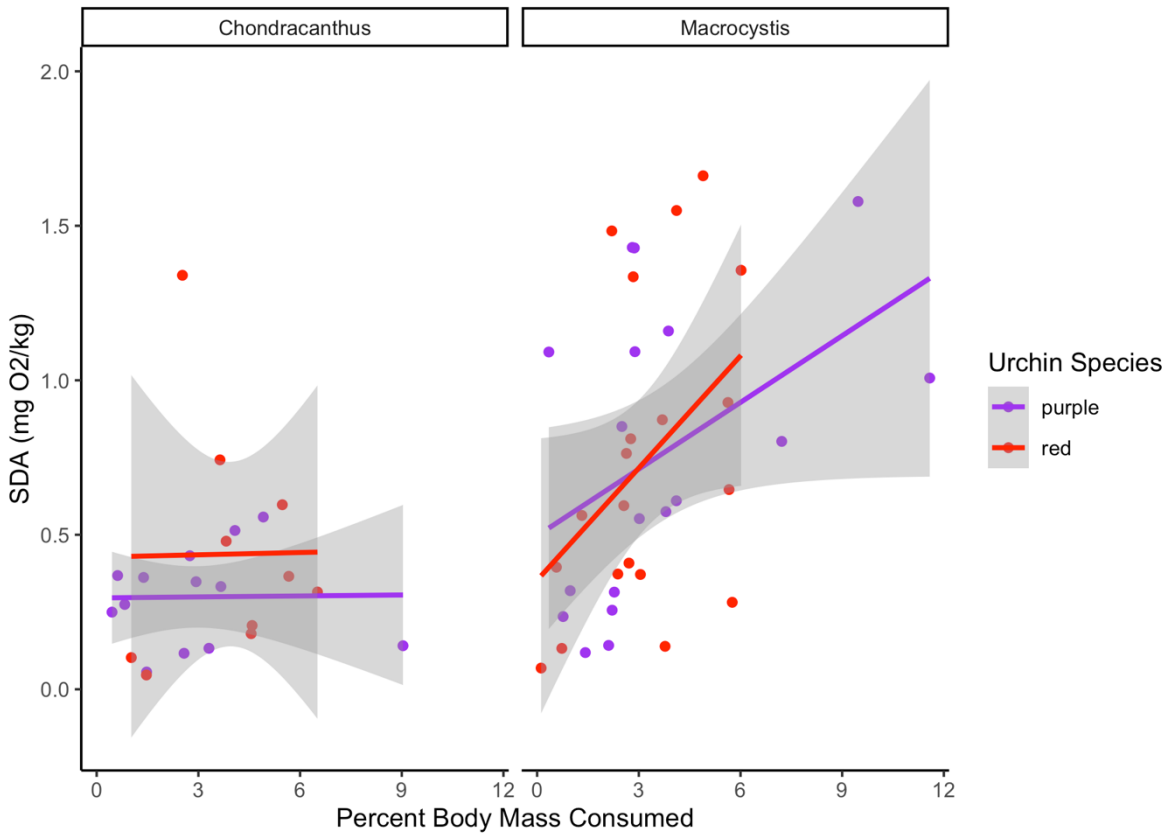


Figure 4.5: SDA by percent body mass consumed, with linear regressions for each algae treatment and urchin species. 95% confidence intervals shown in gray. The slopes for these regressions are as follows: red urchins feeding on *Chondracanthus*: m=0.002, purple urchins feeding on *Chondracanthus*: m=0.001, red urchins feeding on *Macrocystis*: m=0.121, purple urchins feeding on *Macrocystis*: m=0.072.

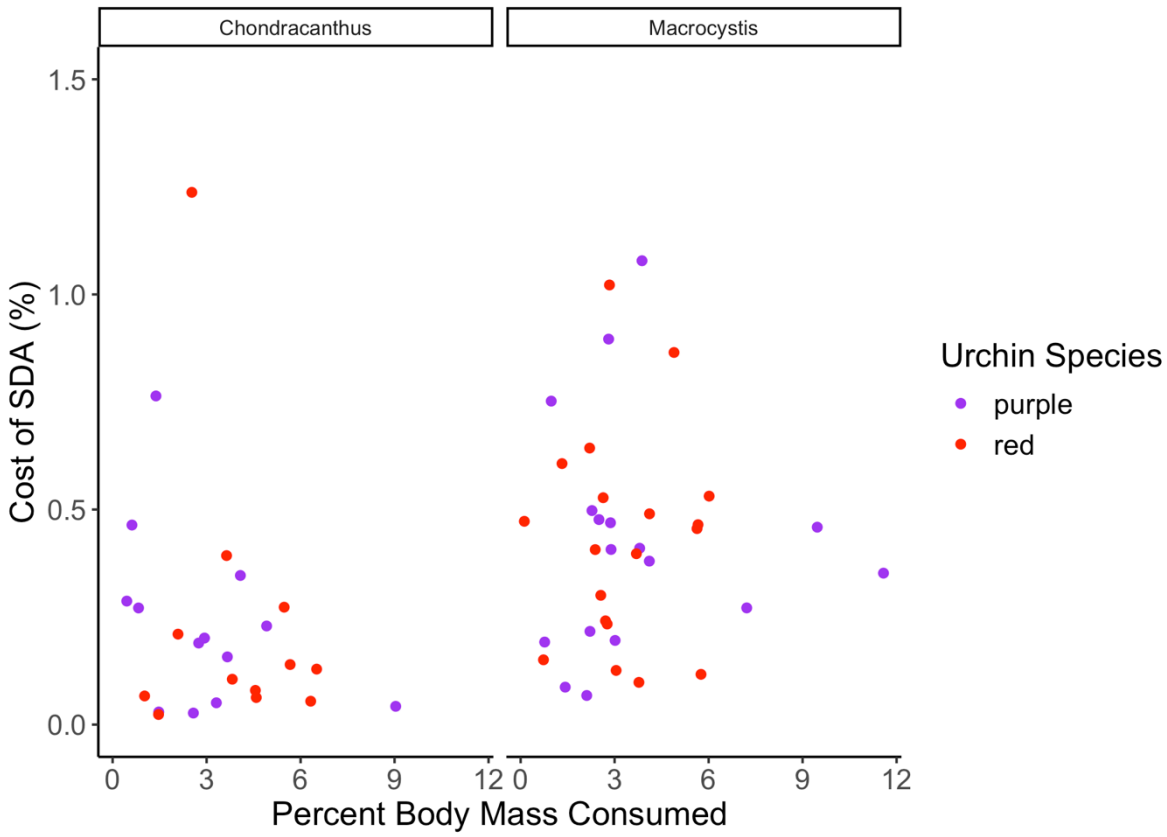


Figure 4.6: SDA_{cost} by percent body mass consumed for purple and red urchins.

Urchin Species	Algae Species	n	BM fed (%)	SMR (mg O_2 kg^{-1})	$SDA_{duration}$ (h)	SDA (mg O_2 kg^{-1})	SDA_{cost} (%)
M.franciscanus	*M. pyrifera*	20	3.17 ± 1.77	0.40 ± 0.22	14.05 ± 6.89	0.74 ± 0.50	0.52 ± 0.46
S. purpuratus	*M. pyrifera*	18	3.57 ± 2.98	0.40 ± 0.27	14.33 ± 5.42	0.75 ± 0.47	0.61 ± 0.23
M.franciscanus	*C. corymbiferus*	12	3.97 ± 1.87	0.50 ± 0.62	11.00 ± 4.32	0.42 ± 0.36	0.23 ± 0.33
S. purpuratus	*C. corymbiferus*	13	2.82 ± 2.35	0.27 ± 0.19	9.50 ± 5.51	0.30 ± 0.16	0.24 ± 0.21

Table 4.1: Summary statistics for SDA metabolism. SDA metrics (sample size (n), percentage of body mass consumed (BM fed %), SMR, $SDA_{duration}$, SDA, and SDA_{cost}) across 2 urchin species and 2 algae treatments.

Discussion

M. francsicanus and *S. purpuratus* showed no significant differences in their baseline metabolism (SMR). Values for SMR were 12-50% higher than, but still within the measured range, of a previous study conducted at the same temperature with the same urchin species (Ulbricht & Pritchard, 1972). There was no support for my hypothesis that red urchins have lower baseline caloric needs than purple urchins. However, the urchins used in this study were all small adult individuals (less than 115 g wet weight). Smaller urchins devote a higher proportion of their energy budget to growth (Greenwood, 1980) than larger urchins, which devote a significant proportion of their energy budget to gonad development. Red urchins have been found with gonads up to 10 times the size (over 200 g vs 20 g) of those found in the largest purple urchins (M. Tegner & Dayton, 1981). It is possible that, amongst larger urchins, the metabolic requirements to support gonad growth are lower than those to support growth of an urchin's test (the calcified outer shell). Future work is needed to assess SMR in urchins across their entire size range.

The lack of seasonality in urchin metabolism is consistent with preliminary evidence which suggests that urchin gonad weight (and therefore the resources allocated to creating them) is not directly associated with seasonality or egg production, but is rather linked with the nutritional quality and availability of consumed algae (Teck et al., 2018). The urchins selected for this study were small but still sexually mature (red urchins reach maturity at around 2 years of age and 40-50 mm in test diameter, purple urchins reach maturity around the same age and at 25 mm in test diameter). Since urchins were maintained in tanks at constant temperature with the same access to algae (prior to their fasting period) regardless of the time of year, the fact that trial date was insignificant is a reassuring indicator of proper replication.

The extremely high foraging rates seen by urchins in the field are supported by the low energetic cost of digestion. At maximum, digesting an algal meal required 3.8% of an urchin's energy budget. On average, the cost of SDA was less than 1% for all treatments. When the SDA coefficient is low, more resources can be allocated to growth and reproduction, and there is no evolutionary advantage to consuming smaller meals. Similarly to Lilly (1975), I found that the metabolic cost of digesting a meal per gram of absorbed food did not change with the size of the meal consumed. There are no apparent metabolic cost savings to urchins associated with larger meal size.

Calculating the SDA coefficient required a number of assumptions (see appendix). First, the absorption efficiency for these species is not fully established, so I synthesized values from multiple studies of the same or similar species (Dethier et al., 2019; Leighton, D.L., 1968; Lilly, G.R., 1975) to determine a best estimate (i.e. 70% of total energy determined from bomb calorimetry). Second, there is a paucity of research on the

bioenergetics of these urchin species, thus I converted MO_2 to calories using literature values from comparable species. Quantifying this conversion will be important for future studies of urchin metabolism. Despite these assumptions, though the exact SDA coefficient values may be different based on conversion estimates, the patterns described here, with the SDA coefficient not varying with meal size, are robust.

The measured C:N ratios of *Chondracanthus* are indicative of higher protein content than *Macrocystis*, with protein being harder to digest than simple carbohydrates (Lawrence et al., 2020). Thus, I would expect *Chondracanthus* meals to elicit a higher SDA response. Contrary to expectations, *Macrocystis* had a significantly higher cost of digestion than *Chondracanthus*. Many properties other than protein are associated with cost of digestion, including lipid content and composition, fiber content, and the presence of phytochemical defense compounds such as phenolics, terpenoids, and alkaloids (Konno, 2011). The significant difference in the cost of digestion between these two common algae types favors the consumption of *Chondracanthus* over *Macrocystis* if urchins were to eat for caloric value alone. However, beyond just caloric value, urchins eat for nutrients (both macro and micro) to fulfill their dietary needs.

This study demonstrates that red and purple urchins are capable of consuming large meals that require very little energy expenditure to digest. The formation of overgrazed urchin barrens is no surprise, then, given the urchin's extraordinary capacity for gluttony. However, urchins at rest have quite low metabolic requirements, and there are no cost-savings associated with consuming larger meals, so the formation of voracious feeding fronts are not the default. There are many habitats where high densities of urchins and macroalgae coexist. Quantifying the metabolic cost of digesting other algae types will be

important to our overall understanding of urchin diets and could help us predict areas where feeding fronts may occur.

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Appendix

Calculating E_{SDA} and E_{meal_cal}

There are currently limited data on these two species of urchins in terms of the caloric release associated with changes in oxygen consumption. Lilly (1975) estimated a Q_{ox} coefficient of 1g O_2 = 3.54 kJ energy released for the urchin *Strongylocentrotus droebachiensis* (green sea urchin) feeding on *Nereocystis* (bull kelp, a brown macroalga). Estimates for salmonids put the coefficient at 1g O_2 = 13.6 kJ (Cho et al., 1982). The conversion coefficient for *M. franciscanus* and *S. purpuratus* likely falls somewhere between these two values, so I tested how varying the conversion coefficient between these values would effect E_{SDA}. Changing the scaling factor from 3.54 to 13.6 resulted in a 74% change to E_{SDA}. 3.54 kJ/g O_2 is the same as the coefficient for combustion of pure carbohydrate in Lilly (1975), and this value should be higher for a complex organism like an urchin, so I therefore selected a scaling factor of 1 g O_2 = 10 kJ as a rough approximation. The conversion factor for E_{meal_cal} is determined by the urchin's assimilation efficiency. The previously referenced study calculating SDA with *T. ventricosus* quantified an assimilation efficiency of 49% feeding on *Dictyota* (a branching brown alga) (Lilly 1975). A study of *M. franciscanus* feeding on *Nereocystis* (bull kelp, a brown macroalga) calculated an average assimilation efficiency of 87% (Dethier et al., 2019). *S. purpuratus* tested at temperatures between 8-16 °C fed on *Nereocystis* with assimilation efficiencies between 80-90% and on *Macrocystis integrifolia* with high assimilation efficiencies between 80-93%. Leighton (1968) calculated the absorption efficiency of *S. purpuratus* feeding on *M. pyrifera* as 70%. The Leighton study used one of the same urchin-algae species pairs under similar

conditions, and this value fell between the assumed upper and lower bounds for assimilation efficiency, so I chose to use an adjustment of 0.7 for E_{meal_cal}.