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Drivers Of Intertidal Purple Sea Urchin (Strongylocentrotus purpuratus) Reproductive Capacity Along The Central Coast Of California and Implications For Kelp Forest Recovery

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DRIVERS OF INTERTIDAL PURPLE SEA URCHIN (*STRONGYLOCENTROTUS PURPURATUS*) REPRODUCTIVE CAPACITY ALONG THE CENTRAL COAST OF CALIFORNIA AND IMPLICATIONS FOR KELP FOREST RECOVERY.

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Master of Science
in
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by
Isaak Haberman
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CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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DEDICATION

My thesis is dedicated to my family (Mom, Dad, Cory, Harmony, Riley), who love me unconditionally and always encourage me to do what is necessary to reach my goals, my friends (Jack, Emma, Rachel, Grace, Nina, José, Mer, Mike + many more) who kept me laughing and enjoying life in Monterey, my Haupt Lab friends (Paige, Cristian, Liz, MJ, Zach, etc.), and my academic support system and wonderful teachers (Alison, Amanda, Tom, Patrick, Bridgette) who encourage me to keep asking questions, finding answers, and having fun!

ABSTRACT

Drivers Of Intertidal Purple Sea Urchin (*Strongylocentrotus purpuratus*) Reproductive Capacity Along The Central Coast Of California And Implications For Kelp Forest Recovery.

by
Isaak Haberman
Master of Science in Marine Science
California State University Monterey Bay, 2024

Kelp forests are integrally important ecosystems along eastern Pacific coastlines, sequestering carbon, reducing wave erosion, and increasing biodiversity in coastal marine communities. However, kelp forest coverage in central California has experienced major decline in the past decade, being replaced with unproductive urchin barren habitats. The factors affecting the establishment and persistence of urchin barrens have been extensively researched in the subtidal, but the influence of intertidal sea urchin populations is unknown. Moreover, intertidal populations are likely connected to subtidal communities via larval dispersal, so an understanding of intertidal urchin reproductive dynamics is important. I collected urchins and biological and environmental data from nine sites along the Monterey Peninsula in central California with varying algal communities, urchin densities, and wave exposures. I weighed and extracted the gonads from urchins at each site to measure gonadal somatic index (GSI%), a representation of reproductive capacity proportional to urchin size. I found that intertidal urchin reproductive capacity is unrelated to coralline algae cover or urchin density; contrary to what is seen in the subtidal. There is a weak positive relationship in the intertidal between fleshy algae coverage and reproductive capacity. Moreover, urchins collected from sites that had higher drift algae presence exhibited higher reproductive capacities. This indicates that urchins in the intertidal can be resilient to poor fleshy algae coverage where they are living because drift algae is continually deposited into intertidal environments for them to consume. Therefore, the intertidal can support higher densities of healthy sea urchins that may represent an important contribution of urchin larval supply to subtidal urchin barrens. Kelp restoration efforts must be amended to include intertidal areas – especially those of high urchin densities – in order to maximize their efficacy.

Introduction

Foundation species can enhance biodiversity in ecosystems by creating locations that offer three dimensional areas for habitation and thus have a disproportionate effect on the ecosystem they occur in. These species are important across diverse habitats and include shrubs in deserts (Lortie et al. 2016), cordgrass in salt marshes (Silliman et al. 2005), Douglas firs in old growth forests (Ellison et al. 2005), and mangrove plants in tropical estuaries (Ellison et al. 2005), among others. Understanding factors that affect foundation species is necessary for effective management, conservation, and restoration efforts to prevent global biodiversity decline. When foundation species are primary producers, they are often negatively impacted by herbivores that can consume large amounts of foundation species biomass. This can negatively impact ecosystem stability, as the destruction (in the form of grazing) of foundation species removes important habitat for the other organisms in an ecosystem (e.g. Silliman et al. 2005, Duffy et al. 2015, Qian et al. 2021).

Kelps (order Laminariales) are an important foundation species in nearshore marine environments that modify water flow around shorelines (Gaylord et al. 2007), create habitat, support high levels of biodiversity ranging from invertebrates to fish to marine mammals (Graham 2004, Carr & Syms 2006), and provide food for marine herbivores (Duggins et al. 1989, Krumhansl & Scheibling 2012). However, kelp biomass is declining globally (Steneck et al. 2002, Rogers-Bennett & Catton 2019, McPherson et al. 2021). Top-down control on kelps by marine herbivores and environmental changes along the eastern Pacific coast are integral drivers of kelp forest loss (McPherson et al. 2021). Globally, kelp has experienced varying levels of decline over the past half century (Krumhansl et al. 2016). In the eastern Pacific, warm ocean temperatures, low nutrient availability, and increased urchin herbivory initiated a large kelp die-off along the California coast in 2014 (Rogers-Bennett & Catton 2019).

Environmental factors such as marine heat waves (Thomsen et al. 2019, Rogers-Bennett & Catton 2019), El Niño (Tegner & Dayton 1991), and trophic disturbances including keystone predator removal can threaten the productivity of kelp forest ecosystems and cause transitions to urchin barrens (McPherson et al. 2021). These barrens, characterized by high urchin density and low food (i.e. kelp) availability, lack the kelp flora that provide important habitat and protection from predators (Levin 1994, Konar & Estes 2003). Urchin barrens are a stable ecosystem state that does not support the same level of biodiversity as the kelp forests they replace (Graham 2004, Filbee-Dexter & Scheibling 2014). The recent fragility in kelp forest ecosystems as well as the low productivity of barrens compared to kelp forests has led kelp to being an important target for restoration and management efforts. To design effective management for kelps, we must understand both the top-down and bottom-up pressures facing kelp populations. This includes understanding how herbivores responsible for kelp deforestation interact with their environment and with other organisms. Kelp forest restoration is an ongoing effort globally, and has experienced varying levels of success. It has been shown that barrens can switch back to kelp forests following years of dedicated restoration efforts, often through the restoration of predator-prey interactions that aid kelp recovery (i.e. the protection or reintroduction of urchin predators) (e.g. Babcock et al. 1999, Shears & Babcock 2003).

When compared to an urchin barren, urchin populations in healthy kelp forests are less dense (e.g. Harrold & Reed 1985), mainly feed on drift algae (Mattison et al. 1977, Harrold & Reed 1985), and are often controlled by predators (Tegner & Dayton 1981, Steneck et al. 2002). A wide array of urchin predators stabilizes the community via preferential consumption of different sizes of urchins (Hamilton & Caselle 2015, Burt et al. 2018), making the diversity and population size of urchin predators that exist in an ecosystem an important factor for kelp forest stability (Nichols et al. 2015, Eisaguirre et al. 2020). The removal of predation pressure allows urchin populations to actively graze on living, attached algae (e.g. Mann & Breen 1972). This behavior soon becomes a necessity since active grazing reduces drift algae presence, and urchins must feed on encrusting coralline algae (e.g. Ling & Johnson 2009). The resulting barren is devoid of floral and faunal diversity, with urchins and coralline algae dominating (Pearse et al. 1970). The transition from kelp forest to urchin barren can be permanent due to the lack of top-down control that keeps herbivore populations low (Steneck 2013) as well as similar levels of urchin recruitment in kelp forests and urchin barrens (Rowley 1989).

Importantly, urchins in barrens exhibit a reduction in their gonads, the part of the urchin that is consumed by predators (Lawrence 2001, Stewart & Konar 2012). Therefore, it has been shown that urchins in barrens are less likely to be eaten than healthy urchins from kelp forests (e.g. Eurich et al. 2014). When roaming and feeding, urchins sever kelp stipes, permanently preventing kelp from regaining its habitat (Filbee-Dexter & Scheibling 2014). A lack of standing stock of kelp brings with it a lack of detrital algae that could otherwise act to satiate herbivores (Rennick et al. 2022). Additionally, kelp spores are short-lived and must settle near parent thalli (Norton 1992, Gaylord et al. 2012), so it is uncommon for kelp spores to germinate in kelp-free barrens, making it more likely that barrens will not shift back to a kelp forest habitat. Moreover, urchins living in barrens destroy potential kelp recruits when they consume the crustose coralline algae that covers the substrate of urchin barrens (Jones & Kain 1967, Chapman 1981).

Purple sea urchins live in both intertidal (Haberman pers. obs.) and subtidal rocky intertidal areas (Morris et al. 1980, Harrold & Pearse 1987). Urchins in subtidal barrens have dramatically reduced gonadosomatic index (GSI – a metric indicating the relative amount of reproductive output for an organism) compared to urchins living in kelp forests (Lawrence 2001, Stewart &

Konar 2012), but the reproductive capacity of intertidal urchin populations is largely unknown. The fleshy algae cover in intertidal areas with high urchin densities (similar to urchin barrens) is often dense (Haberman pers. obs.), so it is unlikely that the GSI trends seen in urchin barrens persist into similar intertidal areas.

Importantly, there is a potential connection between intertidal urchin populations and subtidal urchin barrens. Sea urchins have a planktonic larval phase that lasts 1-3 months (Strathmann 1987) and larvae produced in the intertidal could settle in nearby urchin barrens and act as a reproductive refuge for subtidal urchin barrens where urchin reproduction is far lower. Moreover, urchin barrens are characterized by high coralline algal coverage, which is known to induce urchin larval settlement via chemical cues (Pearce & Scheibling 1990), making it possible that the offspring of intertidal urchins are more likely to settle in areas of high coralline algae such as urchin barrens. The settling and abundance of larval sea urchins likely plays a major role in the ability of urchin populations to establish, thrive, and potentially destroy kelp forests (Watanabe & Harrold 1991). In addition to potentially affecting the longevity of urchin barrens, a continuous supply of urchins to subtidal areas from intertidal populations may have implications for areas where kelp restoration efforts are focused. Increases in urchins living intertidally adjacent to urchin barrens has been observed corresponding to increases in subtidal urchins living within barrens, and intertidal urchin populations have increased in density (Haupt et al., unpub. data; Fig. 1). The theory that intertidal urchins may settle in subtidal barrens contributing to their persistence makes an analysis into their reproductive capacity important.

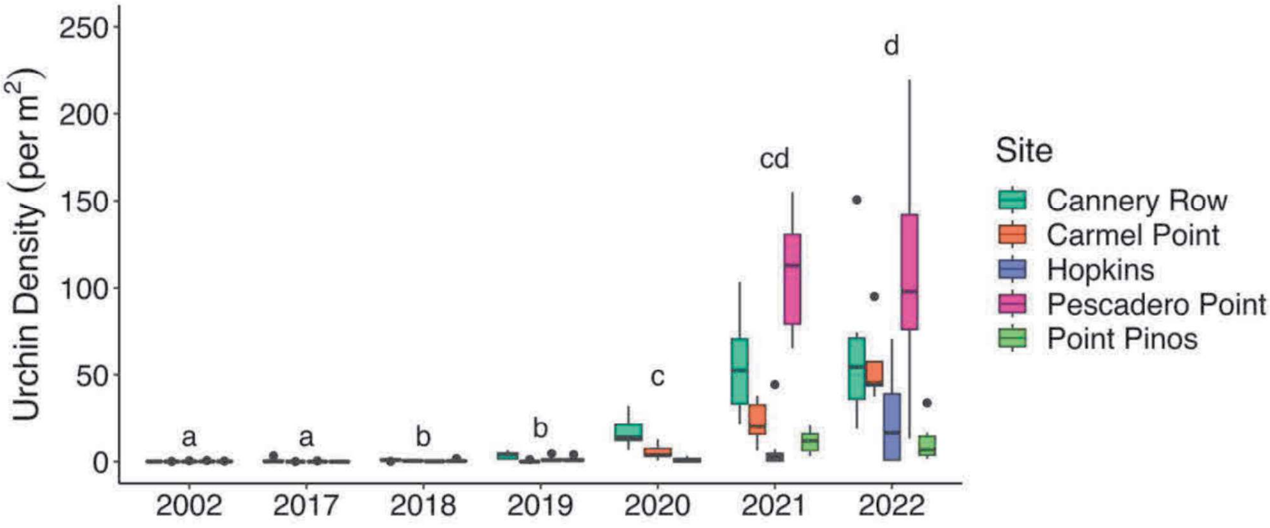

Figure 1. Increases in Purple urchin densities at 5 sites along the Monterey Peninsula between 2002-2022. Different letters represent significant ($p < 0.05$) differences in Kruskal-Wallis Dunn post-hoc test ($\chi^2_6 = 139.4$, $p < 0.001$).

The relationship between urchin reproductive capacity and environmental and biological factors is well documented in the subtidal. There is a strong positive relationship between fleshy algae coverage and urchin reproductive capacity (Smith & Garcia 2021). Additionally, in areas of high coralline algae coverage, indicative of an urchin barren, urchins exhibit low reproductive capacity (Smith & Garcia 2021). Finally, There is a negative relationship between urchin density and reproductive capacity (Andrew 1986, Smith et al. 2021). However, an understanding of how these factors influence reproductive capacity of intertidal sea urchins is equally important since these populations are likely not reproductively isolated from one another.

This thesis focused on the reproductive capacity of intertidal urchins at multiple sites along the central coast of California. I expected to find that intertidal urchins would have higher reproductive capacity (GSI) compared to the urchins in nearby subtidal barrens. Previous studies exhibit mixed results regarding the temporal variation in *S. purpuratus* spawning. Some studies show an increase in the proportion of gonadal cells compared to somatic cells in the late winter and early spring followed by a releasing of gametes into the water column in the spring and early summer (Bennett & Giese 1955), while others indicate that gonads are at their largest in the late fall and spawning occurs between December and March followed by low gonadal mass in spring and summer (Giese et al. 1959, Gonor 1973). Differences in temporal and spatial variation of intertidal urchin reproductive capacities are important for urchin removal efforts as it is important to focus restoration efforts where and when urchins are most reproductive and are more likely to contribute to kelp deforestation.

In this thesis, I asked how intertidal purple sea urchin (*Strongylocentrotus purpuratus*) reproductive capacity varies over season and urchin size at each of nine sites around the Monterey Peninsula. I also asked how different environmental and biological factors affect intertidal urchin gonad size on in the same area and how the drivers identified in the intertidal as affecting reproductive capacity compares to the known drivers of subtidal urchin reproductive capacity. Understanding the spatial and temporal variation of intertidal urchin reproductive capacity as well as environmental and biological factors that drive intertidal urchin reproductive capacity will help inform areas of importance for kelp restoration strategies aiming to include intertidal urchin population management.

Methods

Study species - Strongylocentrotus purpuratus

Like all members of the phylum Echinodermata, urchins are invertebrates characterized by exhibiting pentaradial symmetry. As a result, urchins form with five distinct sets of gonads separated by the ambulacra (Walker et al. 2007). Urchins are dioecious broadcast spawners who release their gametes into the open ocean and have a planktonic larval duration of 1-3 months, during which larvae can potentially travel hundreds of kilometers before settling (Strathmann 1987). *Strongylocentrotus purpuratus* are important contributors to urchin barrens (via overgrazing of kelp) along the west coast of California (Duggins 1980, Dayton et al. 1984) and comprise the overwhelming majority of sea urchins found in the intertidal as well as in urchin barrens. These urchins measure up to 7 cm in test diameter (Haberman pers. obs.) and are ubiquitous in the intertidal and nearshore subtidal areas along the Monterey Peninsula.

Site selection

Sampling sites (Fig. 2) were selected based on their proximity to previous intertidal urchin field surveys (Micheli, unpublished data - 2002) where varying densities of urchins and algal communities have been located. Sites varied in their proximity to kelp forests and urchin barrens as well as their location inside and outside Monterey Bay (Table 1).

Table 1. Sites selected for reproductive analysis, their nearest subtidal ecosystem, and their location inside or outside Monterey Bay.

Site	Closer to Kelp Forest / Urchin Barren	Inside / Outside Monterey Bay
Cannery Row	Urchin barren	Inside bay
Hopkins Marine Station	Kelp forest	Inside bay
Otter Cove	Kelp forest	Inside bay
Pt. Pinos	Urchin barren	Inside bay
China Rock	Urchin barren	Outside bay
Pescadero Pt.	Urchin barren	Outside bay
Carmel Pt.	Urchin barren	Outside bay
Pt. Lobos	Kelp forest	Outside bay
Soberanes Pt.	Kelp forest	Outside bay

Figure 2. Intertidal sites along the Monterey Peninsula selected for reproductive capacity analysis.

Field data collection

Urchins exhibit a seasonal reproductive cycle (Meidel & Scheibling 1998), so urchin collections occurred once per season between July 11, 2022, and April 23, 2023 to encompass one full reproductive cycle. The summer collection occurred between July 11, 2022, and August 14, 2022, the fall collection occurred between October 26, 2022, and November 26, 2022, the winter collection occurred between January 18, 2023, and February 4, 2023, and the spring collection occurred between April 13, 2023, and April 23, 2023.

During collections, five 1 m^2 quadrats were randomly placed within suitable urchin habitat where at least 5 urchins were present. Within each quadrat, algae cover was quantified using percent cover of functional groups adapted from Steneck and Watling (1982). These groups included crustose non-corallines, crustose corallines, articulated corallines, corticated macrophytes, filamentous, foliose, leathery, kelps, seagrass, bare rock, mussels, barnacles, anemones, and other (Table 2). For each quadrat, the percent cover of corticated macrophytes, filamentous, foliose, leathery, kelps, and seagrass was added to make a fleshy algae group. Crustose and articulated corallines were added to form a calcified group, and bare rock, mussels, barnacles, anemones, and other were added to form a non-algae group. The number of urchins with test diameter larger than 2 cm in test diameter was also counted within each quadrat.

Additionally, surveys of drift algae were completed from February 17-20, 2023 at each site except Pt. Lobos and Pt. Pinos and at every site during May 10-23, 2023 to quantify the amount of drift algae present at each site. At each site, tape measures were laid to form two boxes, varying in area between 91 m^2 and 400 m^2 depending on space accessibility and urchin habitat suitability (i.e. we were not sampling for drift algae in sand where urchins were unlikely to be living). Within each box, all fleshy (non-calcified) algae not attached to the substrate was collected, sorted, and weighed to determine the amount of drift algae present at each site. Drift algae amounts were then normalized by area of collection. Due to small sample sizes, sites were sorted into high, medium, and low drift algae presence based on the density of drift algae found at each site. Sites with 0 - 1.2 g/m^2 of drift algae were categorized as low drift availability sites. Sites with 1.21- 3.0 g/m^2 of drift algae were categorized as having medium drift availability, and sites with more than 3.0 g/m^2 of drift algae were categorized as having high drift availability.

Table 2. Functional groups and example algae taxa for urchin habitat analysis.

Functional group	Example taxa
Crustose non-coralline	*Hildenbrandia sp., Mastocarpus sp.* (Petrocelis phase)
Crustose coralline	*Chamberlainium tumidum*
Articulated coralline	*Bossiella sp., Calliarthron tuberculosum, Corallina sp.*
Corticated macrophyte	*Endocladia muricata, Microcladia sp.*
Filamentous	*Cladophora columbiana, Acrosiphonia coalita*
Foliose	*Mazzaella sp., Ulva sp.*
Leathery	*Chondracanthus sp., Mastocarpus sp., Fucus sp.*
Kelps	*Egregia menziesii, Laminaria setchellii*
Seagrass	*Phyllospadix scouleri*
Non-algae	*Balanus glandula, Anthopleura elegantissima, Mytilus californianus*

Estimates of reproductive capacity

Five urchins larger than 2.5 cm in test diameter were randomly collected from each quadrat, totaling 25 urchins per site per collection period. Collected urchins were brought to the lab where test diameter, test height, and wet weight was measured. Urchins were then dissected, and their gonads were extracted and weighed after drying for ~10 minutes to remove excess moisture. Prior to and during dissection, urchins often started spawning. Since I was interested in reproductive capacity, it was important to document spawning. The level of spawning that occurred at time of weighing was approximated on a 0-5 scale and the presence of coralline algae within the stomach of each urchin was noted. Urchins that did not spawn were assigned a 0 spawning level, and urchins that spawned the most relative to gonad size were assigned a 5.

To estimate reproductive capacity, the gonadosomatic index (GSI) of each urchin was calculated. GSI is calculated as (gonad wet weight / urchin wet weight) * 100. GSI is a well-established method to determine reproductive capacity in animals where gonads can be accurately weighed (Pearse et al. 1986). To ensure that all urchins collected were reproductively mature, only urchins larger than 2.5 cm in test diameter were collected. I determined 2.5 cm to be a conservative estimate for minimum reproductive test diameter following the dissection and analysis of 212 urchins collected from Hopkins, Pt. Pinos, and Pescadero Pt. from June 1, 2022 to July 1, 2022.

To determine the exact size at which purple sea urchins are no longer reproductively mature, an additional 25 urchins smaller than 3 cm in test diameter were collected using the methods above from each of the 9 sites except Pt. Lobos between February 17, 2023, and February 21, 2023. This ensured that I would collect urchins during the winter collection period that were both reproductively mature and immature, making it possible to determine the size and weight at which intertidal purple urchins became reproductively mature. These urchins are not the same as those that were initially used to preliminarily determine the size of adult urchins to be collected for the rest of my analyses.

Wave Exposure Data

To assess potential differences in urchin reproductive capacity based on wave exposure, the average daily maximum wave height in the month prior to collection was calculated for each collection site using daily maximum wave height data from the Coastal Data Information Program Monitoring and Prediction System model (CDIP – MOP) (O'Reilly et al. 2016).

Gonad-weight Calculations

In order to determine overall gonad production at each site, I used data from the 2021-2023 Haupt Lab summer urchin surveys as well as size-specific gonad weight data from this project at all sites except Otter Cove. In Haupt Lab surveys, quadrats were randomly placed throughout a site and all urchins within a quadrat were counted and measured into 1 cm bins by test diameter. Using these metrics, I was able to calculate approximate gonad-weight per unit area for the intertidal sites and for the subtidal using data from Smith & Garcia (2021). To make this calculation for intertidal sites, I multiplied the average urchin density at each site by the frequency of urchins of each 1 cm size bin to obtain the approximate number of urchins of each size at each site. I then multiplied these data by the average gonad-weight for an urchin of each size bin. Within each site, I added the gonad-weight for all size bins to obtain the average gonad weight per m^2 at each site. Size-frequency data were unavailable for the subtidal, so I executed the same calculations but assumed that urchins collected from each quadrat were representative of the average size of urchins within that site.

Assessing size and seasonal-based variation in reproductive capacity

To assess the seasonal variation in urchin reproductive capacity, I used a Kruskal-Wallis ANOVA since data exhibited non-normality in residuals (Shapiro $W = 0.97$, $p < 0.001$) and did not have equal variances among seasons (Levene's Test $F_{3,935} = 100.24$, $p < 0.001$).

To assess the relationship between urchin size and reproductive capacity, it was appropriate to analyze the linear relationship between gonad wet weight and test diameter cubed, since mass is a cubed function of length. Additionally, I analyzed the linear relationship between gonad wet weight and urchin wet weight. Winter collections of adult urchins took place less than a month prior, so the small urchin data were combined with the winter adult urchin data to establish a dataset with urchins ranging in test diameter from 1.3 cm to 6.2 cm. To locate the minimum test diameter for a reproductively mature urchin, I found the maximum test diameter below which there was no longer a significant relationship ($p > 0.05$) between gonad wet weight and test diameter[3]. The same was done for gonad wet weight and urchin wet weight to determine the minimum weight at which purple urchins are not reproductively mature.

Assessing drivers of intertidal urchin reproductive capacity

To identify the drivers of intertidal urchin reproductive capacity, I used a linear mixed-effects model approach. These data exhibited a three-level structure (Fig. 3), with explanatory variables at the urchin level (spawning intensity, coralline algae presence in stomach), the quadrat level (fleshy algae, calcified algae, non-food), and the site level (wave height and drift algae). To do this, a mixed-effects model was used using site or quadrat as random effects for each continuous predictor variable and GSI as the response variable. Wave height (site-specific), drift algae (site-specific), fleshy algae percent cover (quadrat-specific), calcified algae percent cover (quadrat-specific), non-food percent cover (quadrat-specific), urchin spawning level (urchin-specific), and coralline algae presence in stomach (urchin-specific) were the potential predictor variables used for analysis. Fall data exhibited normality for spawning intensity (Shapiro-Wilk $W = 0.99$, $p = 0.079$), drift algae level ($W = 1.0$, $p = 0.983$), and coralline algae presence ($W = 0.99$, $p = 0.632$) and equal variance for spawning intensity (Levene's $F_{5,220} = 1.84$, $p = 0.105$) and coralline algae presence ($F_{1,224} = 1.99$, $p = 0.159$). Therefore, I used ANOVAs followed by Tukey post-hoc tests in the fall to assess the effect of spawning intensity on GSI. Fall data exhibited unequal variance for drift algae level ($F_{2,223} = 3.36$, $p = 0.036$), so I used a Welch's ANOVA followed by a Games-Howell post-hoc test to assess the effect of drift algae on GSI. I used a t-test to assess the effect of coralline algae in the stomach of urchins on GSI in the fall. Spring, winter, and summer data exhibited non-normality for spawning intensity (Shapiro-Wilk $W = 0.89$, $p < 0.001$ for spring; $W = 0.92$, $p < 0.001$ for winter; $W = 0.95$, $p < 0.001$ for summer), drift algae level ($W = 0.87$, $p < 0.001$ for spring; $W = 0.95$, $p < 0.001$ for winter; $W = 0.97$, $p < 0.001$ for summer), and coralline algae presence ($W = 0.90$, $p < 0.001$ for spring; $W = 0.95$, $p < 0.001$ for winter; $W = 0.98$, $p < 0.001$ for summer), so I used a non-parametric Kruskal-Wallis ANOVAs followed by Dunn post-hoc tests for the winter, spring, and summer seasons to assess the effect of spawning intensity and drift algae level on reproductive capacity and a non-parametric Wilcoxon signed-rank test assess the effect of coralline algae in the stomach of urchins on GSI in the winter, spring, and summer. All models were run separately for each season to account for seasonality in urchin reproduction. Due to large variability across different levels of different variables, as well as unequal sampling across potential drivers, interactions between variables were not tested for.

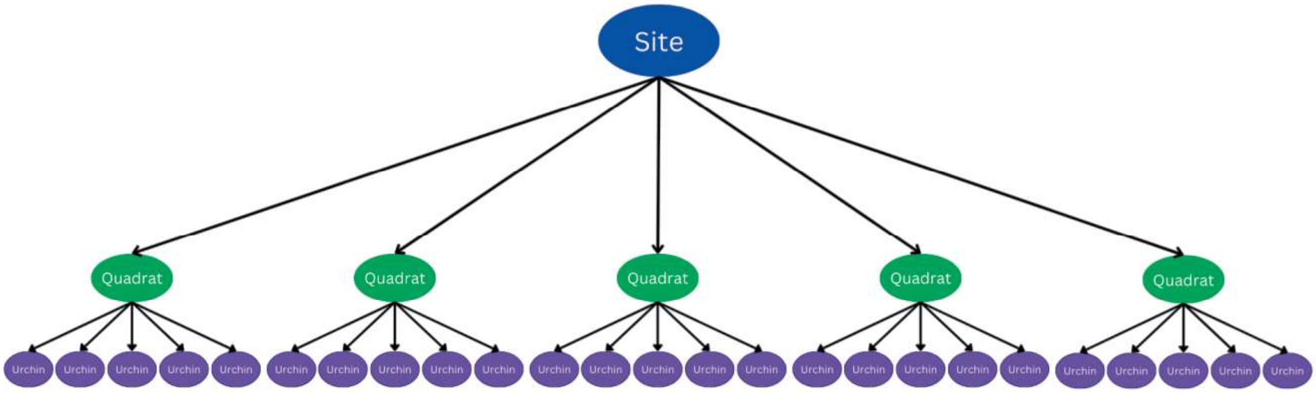

Figure 3. Schematic depicting the multilevel data structure for one site of urchin collections. In total, this data structure was collected at 9 sites with one collection at each site per season.

Assessing how known drivers of urchin reproductive capacity in the subtidal affect intertidal urchin reproductive capacity

To assess how fleshy algae coverage, coralline algae coverage, and urchin density (known drivers of subtidal urchin reproductive capacity) affect reproductive health in the intertidal, I ran a mixed-effects model using each of these three variables as the predictor variables and GSI as the response variable. Quadrat ID was used as the random effect. Effect size for each variable was estimated across all combinations of predictor variables to understand how each variable affects gonad size independently and in the presence of other variables. All variables were scaled and collinearity was tested for prior to model running. Models were compared and coefficients were averaged using Akaike Information Criterion (AIC) values to examine model coefficients for each predictor variable across all model combinations.

To directly compare known drivers of subtidal urchin GSI to the same variables in the intertidal, I used data collected on urchin GSI and fleshy algae coverage, encrusting algae coverage, and urchin density in the subtidal around the Monterey Peninsula during summer 2017 from Smith & Garcia (2021). For this part of my analysis, I only used data from the summer collection period, which is when subtidal data were collected, and averaged urchin GSI within each quadrat to mirror the methods from the subtidal datasets. I used linear regression to compare relationships between environmental predictor variables and urchin GSI in the intertidal and subtidal.

Results

Question 1A - How does intertidal sea urchin reproductive capacity vary between seasons across the Monterey Peninsula?

Average urchin GSI (± SE) across all sites was highest in the fall, followed by a sharp decrease into winter and a further decrease into spring (Fig. 4, Table 3). GSI then increases into summer (Fig. 4, Table 3). The highest average GSI was observed at Pt. Pinos in the spring, Otter Cove in the winter and summer, and Pt. Pinos in the fall (Fig. 4, Table 3).

Table 3. Gonadosomatic indices (GSI) of urchins collected at each site during the 2022-2023 collection period.

Site	Spring GSI (%) (± SE)	Winter GSI (%) (± SE)	Summer GSI (%) (± SE)	Fall GSI (%) (± SE)
All Sites	1.53 (± 0.09)	3.03 (± 0.11)	5.35 (± 0.18)	10.60 (± 0.28)
Cannery Row	1.49 (± 0.27)	3.71 (± 0.34)	3.57 (± 0.42)	9.43 (± 0.56)
Hopkins	1.04 (± 0.22)	2.11 (± 0.25)	3.02 (± 0.33)	7.13 (± 0.74)
Otter Cove	2.09 (± 0.24)	3.77 (± 0.41)	7.01 (± 0.52)	11.78 (± 0.72)
Pt. Pinos	2.47 (± 0.30)	3.37 (± 0.39)	5.37 (± 0.42)	15.52 (± 0.67)
China Rock	1.22 (± 0.14)	3.32 (± 0.31)	6.89 (± 0.46)	11.40 (± 0.60)
Pescadero Pt.	2.07 (± 0.38)	3.18 (± 0.31)	6.71 (± 0.81)	10.66 (± 0.65)
Carmel Pt.	1.48 (± 0.24)	3.22 (± 0.27)	6.42 (± 0.48)	8.94 (± 0.86)
Pt. Lobos	1.45 (± 0.25)	2.40 (± 0.29)	4.84 (± 0.53)	11.18 (± 0.55)
Soberanes Pt.	0.87 (± 0.14)	2.27 (± 0.29)	4.17 (± 0.40)	9.31 (± 0.99)

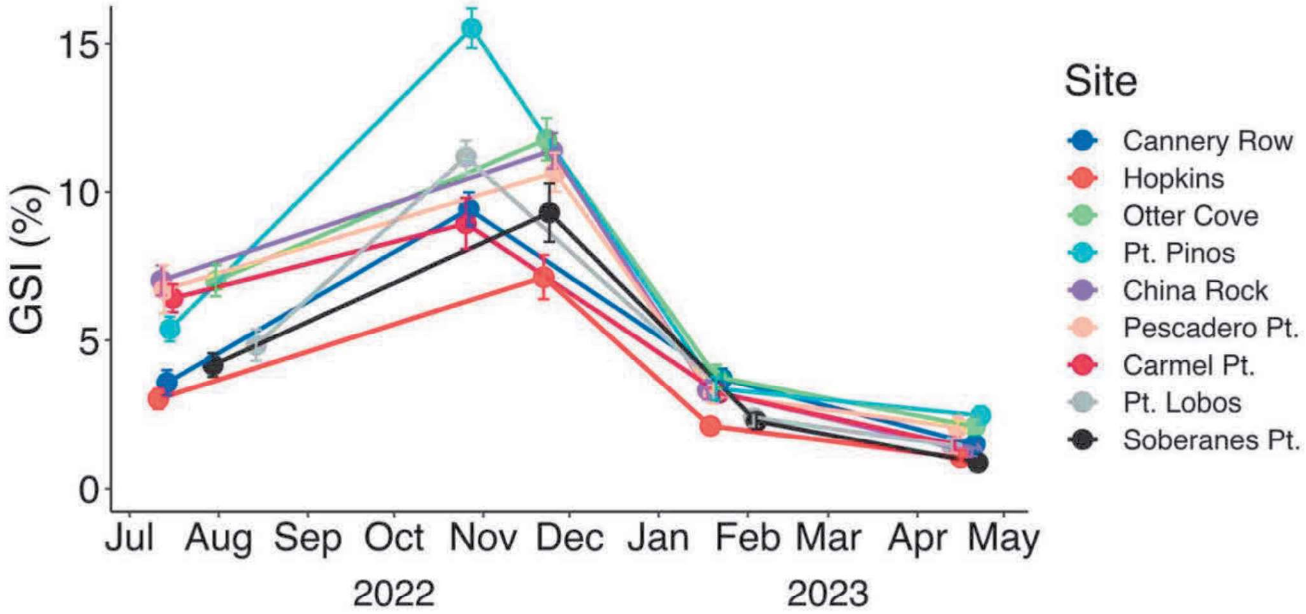

Figure 4. Average (± SE) gonadosomatic index (GSI) of urchins collected at each site during the 2022-2023 collection period.

A Kruskal-Wallis ANOVA revealed that GSI significantly differed over each season (Kruskal-Wallis ANOVA, $\chi^2_3 = 554.7$, $p < 0.001$), and a subsequent Dunn's post-hoc test further revealed that each season's GSI was significantly different than the GSI of all other seasons (Dunn's post hoc test, $p < 0.001$ for all; Table 4).

Table 4. Comparison between GSI (%) for each collection season using Dunn's post-hoc test.

Comparison	Dunn's post-hoc Z	P-value
Spring – Winter	-6.63	< 0.001
Spring – Summer	-13.46	< 0.001
Spring – Fall	-22.41	< 0.001
Winter – Summer	-6.97	< 0.001
Winter – Fall	-16.04	< 0.001
Summer – Fall	-9.00	< 0.001

Question 1B - How does intertidal sea urchin reproductive capacity vary with urchin size across the Monterey Peninsula?

In order to determine how urchin reproductive capacity is affected by urchin size, I combined the data from the winter 2023 collection period with the data from the small (less than 3 cm test diameter) urchins I collected and dissected during winter 2023. I found a strong linear relationship between gonad wet weight and urchin test diameter^3 ($F_{1,428} = 718.3$, $R^2 = 0.63$, $p < 0.001$) with an equation of gonad wet weight = $(1.32*10^{-5})$ * (test diameter)^3 – 0.053 (Fig. 5A). When urchins larger than 1.831 cm were excluded from analysis, there was no longer a significant relationship between gonad wet weight and urchin test diameter^3 ($F_{1,17} = 4.18$, $R^2 = 0.15$, $p = 0.057$). The significant relationship between gonad wet weight and test diameter^3 remained when only urchins larger than 1.831 cm were included ($F_{1,408} = 652$, $R^2 = 0.61$, $p < 0.001$). Therefore, I determined the cutoff point of 1.831 cm to be the test diameter at which urchins are reproductively mature.

Using the same process for urchin wet weight and urchin gonad weight, I identified a strong linear relationship between urchin wet weight and gonad weight ($F_{1,428} = 849.4$, $R^2 = 0.66$, $p < 0.001$) with an equation of gonad wet weight = 0.034 * urchin weight – 0.11 (Fig. 5B). When including only urchins lighter than 3.13g, this relationship diminished ($F_{1,19} = 3.36$, $R^2 = 0.11$, $p = 0.082$). However, there was still a linear relationship when including only urchins heavier than 3.13g ($F_{1,407} = 770$, $R^2 = 0.65$, $p < 0.001$) with an equation of gonad wet weight = 0.034 * urchin weight – 0.11.

Using data for all urchins collected, there was a strong relationship between test diameter^3 and urchin wet weight ($R^2 = 0.97$, $p < 0.001$). Using this relationship, the test diameter cut off of 1.831 cm translated to a wet weight of 5.11g. The wet weight cut off of 3.13g translated to a test diameter of 1.51 cm. Therefore, the cutoff for adult purple sea urchins was found to be 1.51-1.83 cm in test diameter and 3.13-5.11g in weight.

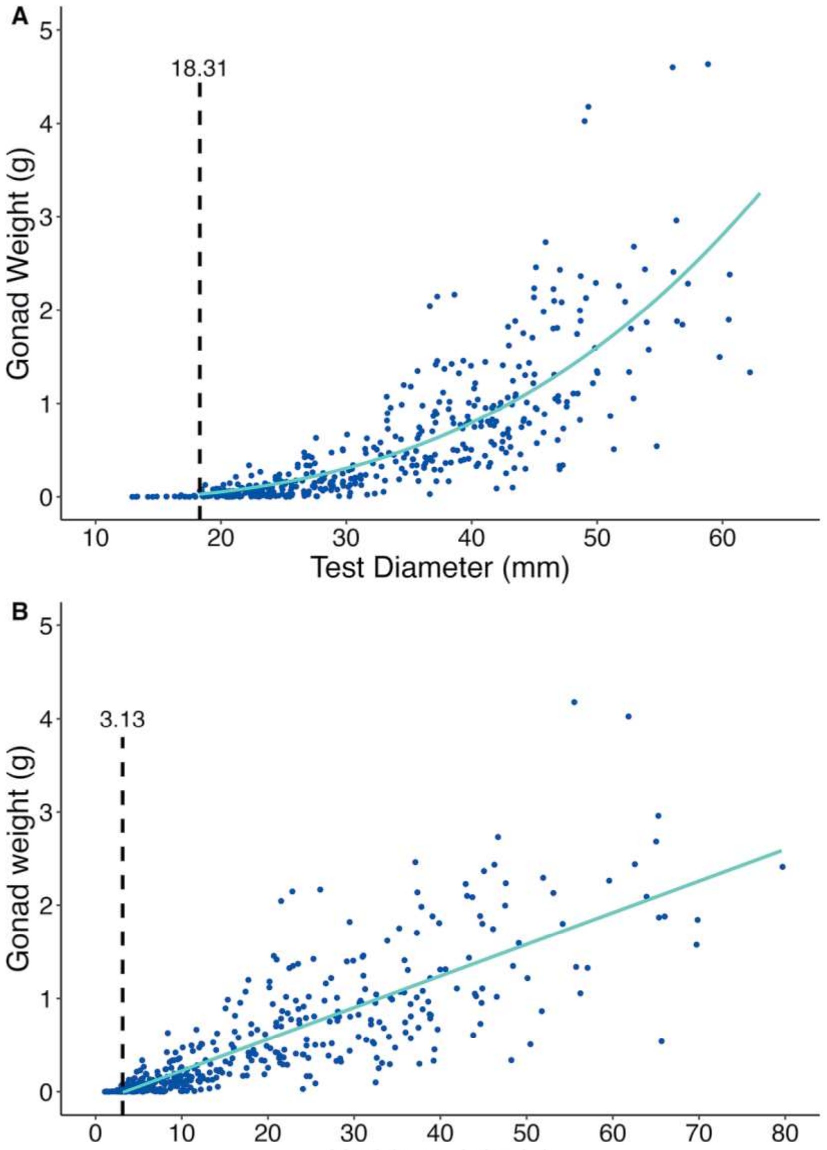

Figure 5. Winter 2023 adult and small urchin collections A) Relationship between gonad wet weight and test diameter and B) Relationship between gonad wet weight and urchin wet weight. Light blue lines represent linear relationships between variables. Dashed lines represent the cutoff point below which a linear relationship was no longer statistically significant ($p > 0.05$).

Question 2 - What are the drivers of intertidal urchin gonad health on and around the Monterey Peninsula?

Urchin-specific variables included the percent of urchins dissected that had coralline algae in their stomachs and the relative spawning level (0-5) of urchins at time of gonad weighing. At all sites except for Soberanes Pt., I found that the highest percent of urchins with coralline algae in their stomach occurred during the winter collection period (Fig. 7). This was in conjunction overall low rates of fleshy algae coverage in quadrats during the winter (Fig. 8A). There was a low percent of urchins with coralline algae in their stomach in summer and fall, followed by a sharp increase into the winter and continued high levels of coralline algae found in urchin stomachs in spring (Fig. 7). This pattern was not reflected at Pt. Lobos and Soberanes Pt., where more than 50% of urchins had coralline algae in their stomach when dissected during all collection seasons (Fig. 7). Pt. Lobos and Soberanes Pt. also had the highest coralline algae coverage in the quadrats across all four seasons (Fig. 8B).

Relative urchins spawning level at the time of dissection was higher in the fall and winter compared to the spring and summer (Fig. 6). Sites did not generally exhibit consistently higher or lower spawning levels relative to other sites.

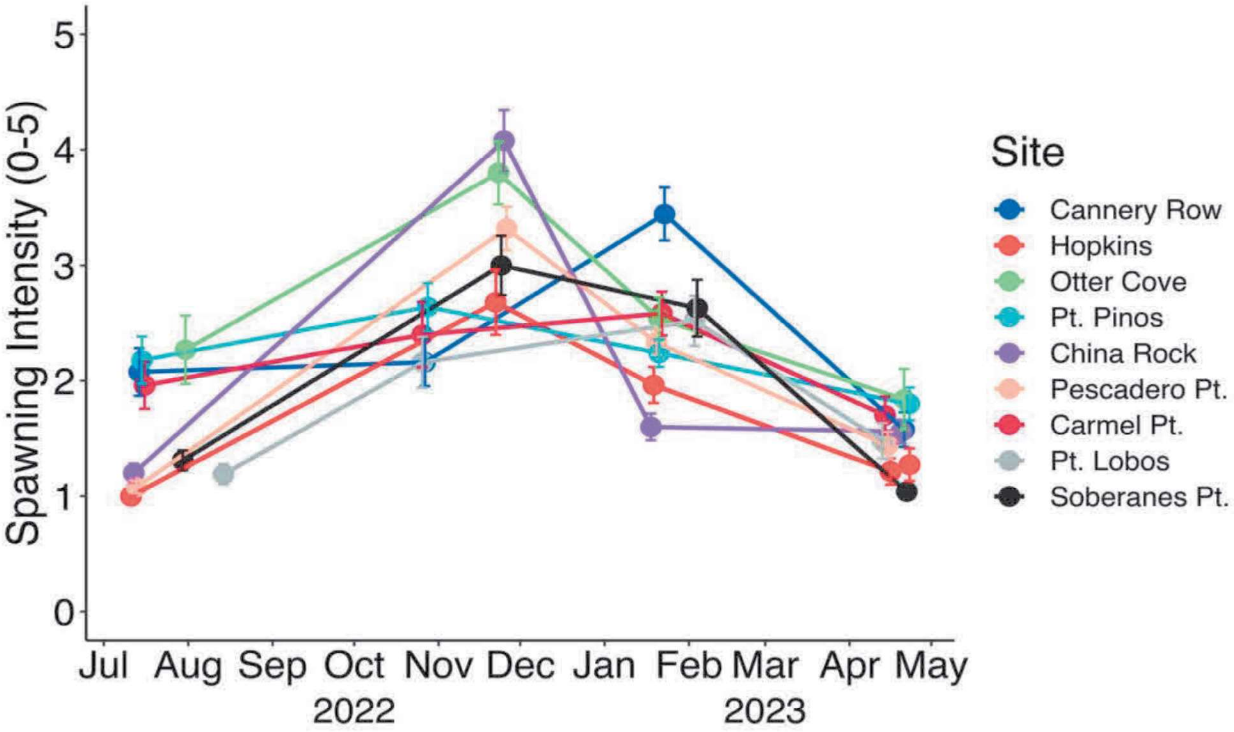

Figure 6. Average (± SE) spawning intensity of urchins collected at each site during the 2022-2023 collection period.

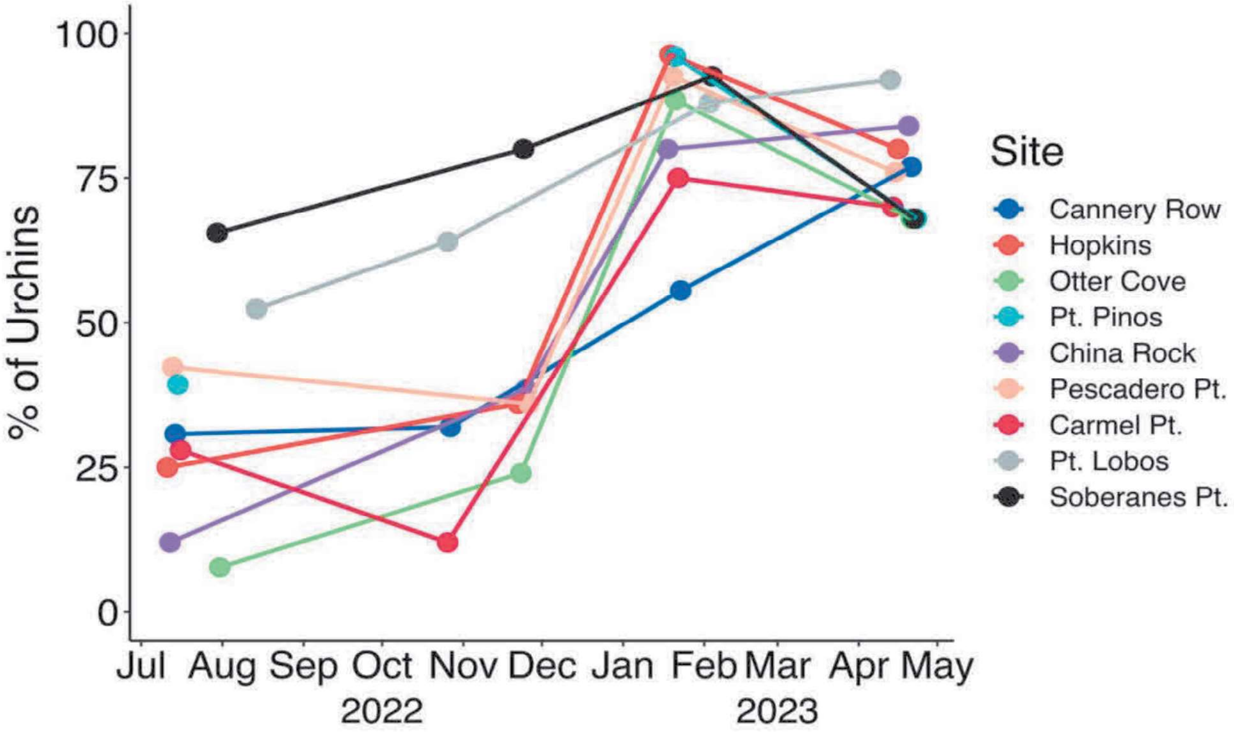

Figure 7. Average (± SE) Percent of urchins with coralline algae found in their stomach collected at each site during the 2022-2023 collection period.

Fleshy algae percent coverage was similarly high in the summer and fall, and similarly low in the winter and spring (Fig. 8A, 9). Unlike fleshy algae, coralline, crustose non-coralline, and non-algae percent coverages did not exhibit a seasonal cycle (Fig 8B-D). Pt. Lobos and Soberanes Pt., the two southernmost collection sites, exhibited highest coralline algae coverage year-round (Fig. 8B). Hopkins and Cannery Row, both sites with high mussel coverage, exhibited high non-algae coverage (Fig. 8D). There were no notable trends in crustose non-coralline coverage (Fig. 8C).

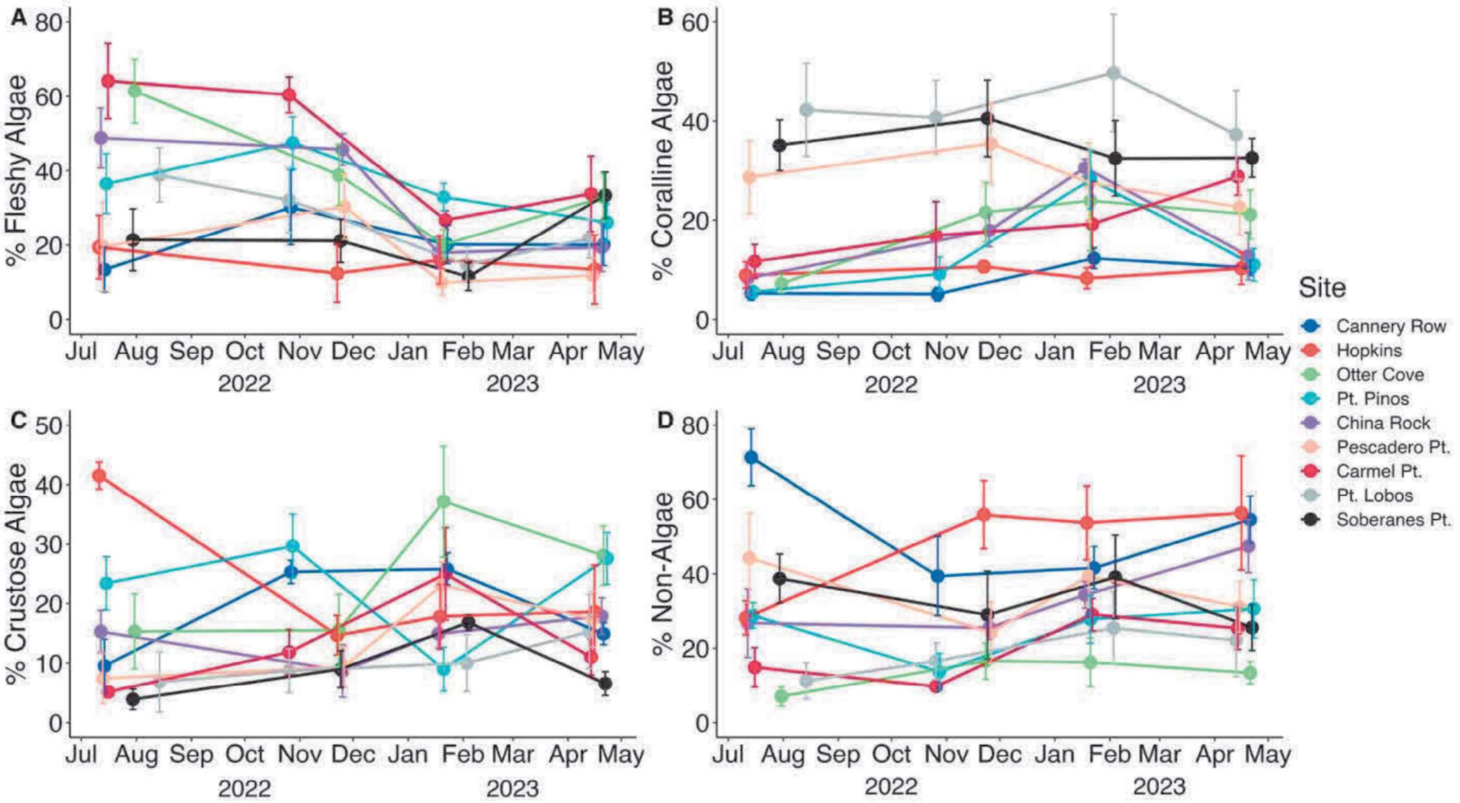

Figure 8. Average (± SE) A) Fleshy algae, B) coralline algae, C) crustose non-coralline algae, and D) non-algae percent cover at each site during the 2022-2023 collection period.

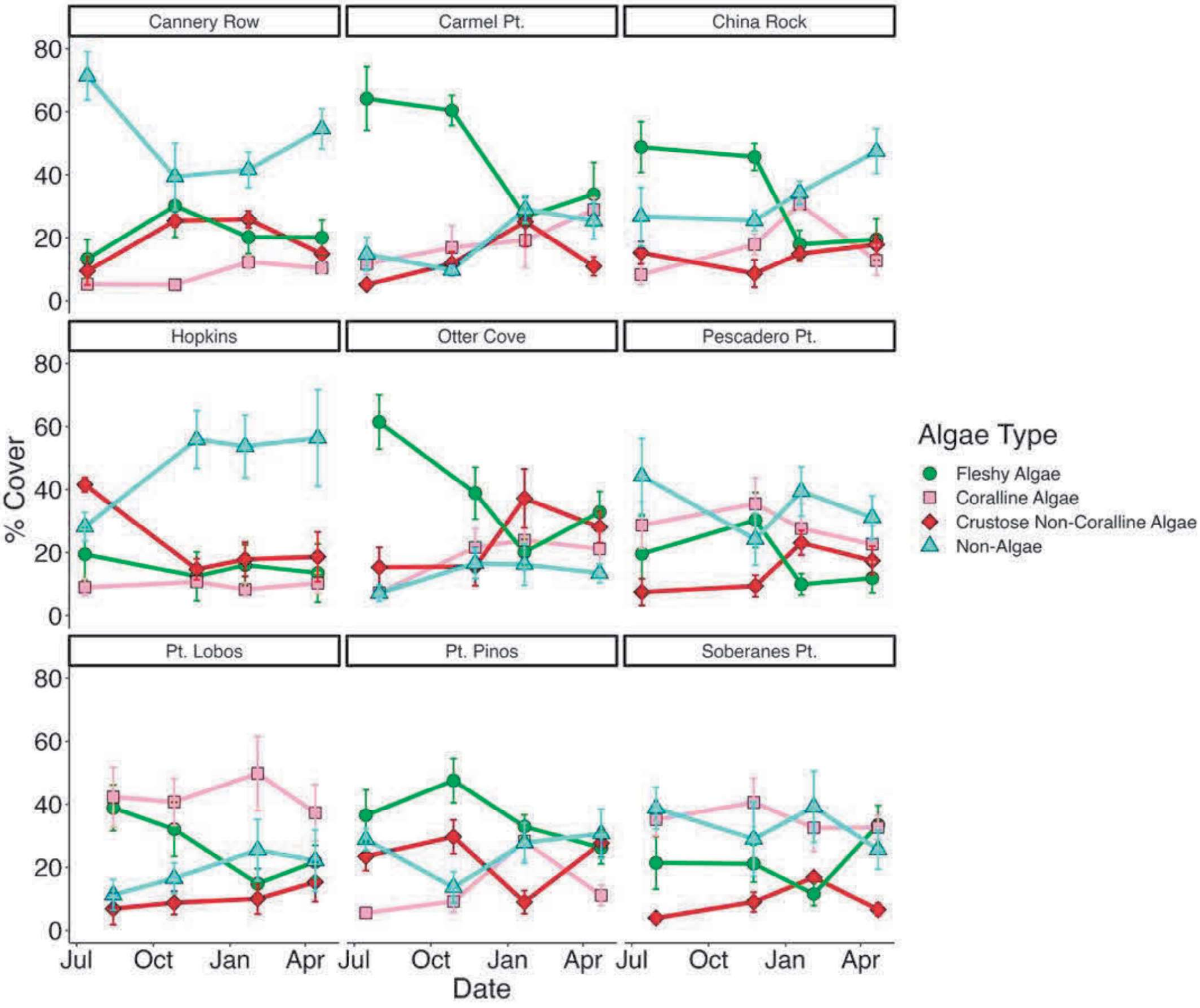

Figure 9. Average quadrat makeup at each site during the 2022-2023 collection period.

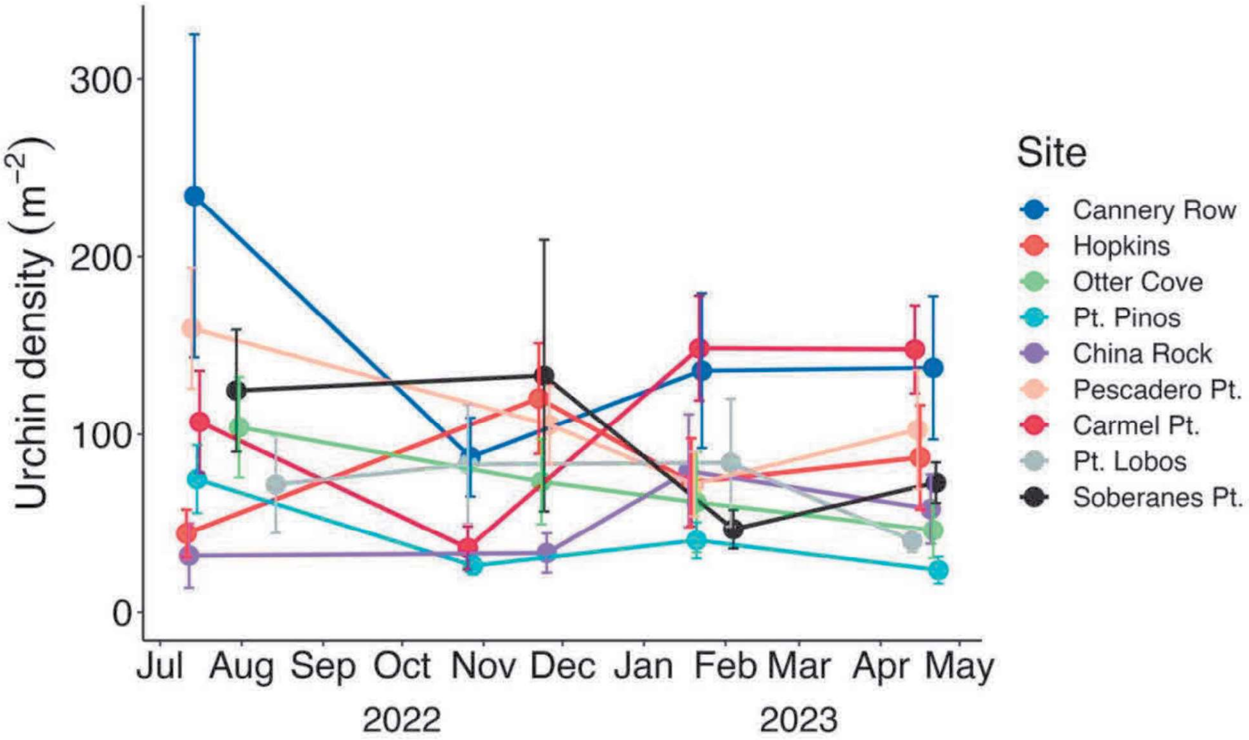

Figure 10. Average (± SE) urchin density within each quadrat at each site during the 2022-2023 collection period.

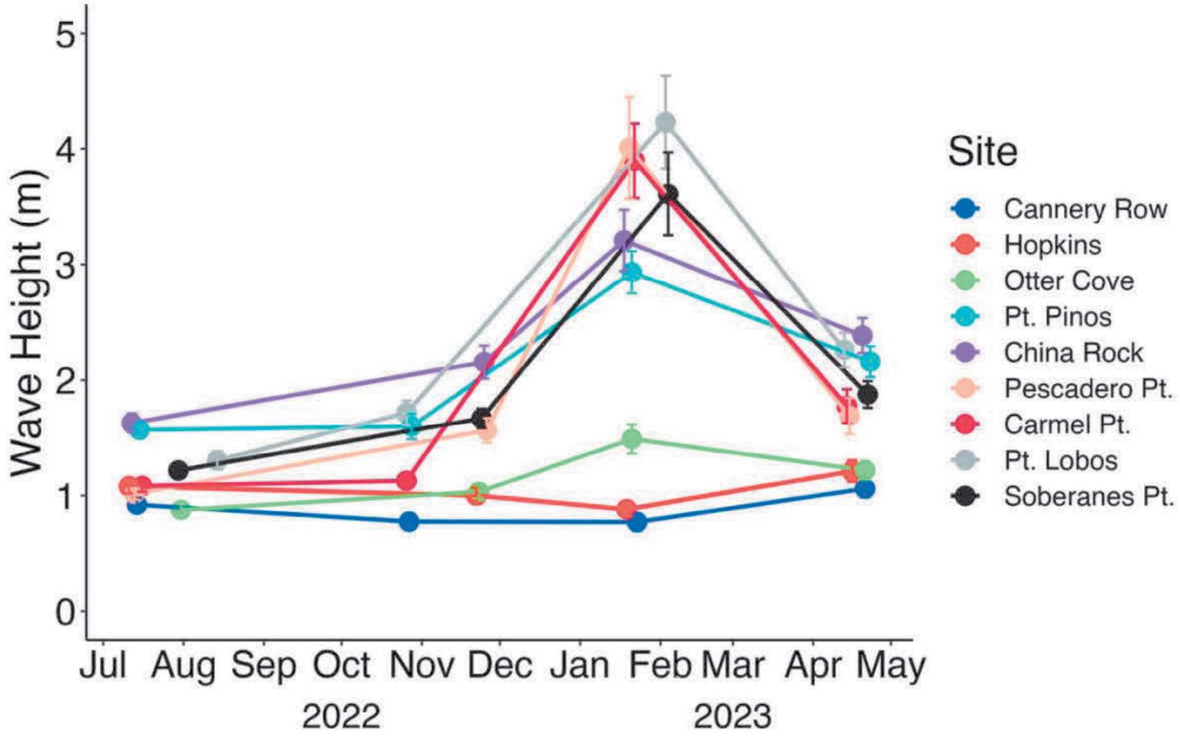

Figure 11. Average daily maximum wave height 30 days prior to urchin collection at each site during the 2022-2023 collection period. Wave data comes from Coastal Data Information Program Monitoring and Prediction System (CDIP – MOP).

Average wave height 30 days prior to urchin collection was 1.68m (± 0.15m) in the spring, 2.78m (± 0.46m) in the winter, 1.19m (± 0.089m) in the summer, and 1.40m (± 0.15m) in the fall (Fig. 11). There was a large peak in wave height at all sites except Hopkins, Cannery Row, and Otter Cove during winter when large storms passed through the Monterey area, as these three sites are located within Monterey Bay which protected them from the large swell experienced by the more west-facing, unprotected sites.

Drift algae presence was variable between site and season, and did not experience any major trend in abundance between winter and spring (Fig. 12, Table 5). Drift algae was consistently high at Otter Cove and Carmel Pt. and consistently low at Hopkins and Pescadero Pt. Drift algae presence was 2.99 g/m^2 (± 0.67 g/m^2) in the spring and 2.45 g/m^2 (± 0.93 g/m^2) in the winter. Drift algae presence ranged from 0.054 g/m^2 (Hopkins) to 5.48 g/m^2 (Carmel Pt.) in the spring and from 0.011 g/m^2 (Hopkins) to 8.10 g/m^2 (Carmel Pt.) in the winter (Fig. 12, Table 5).

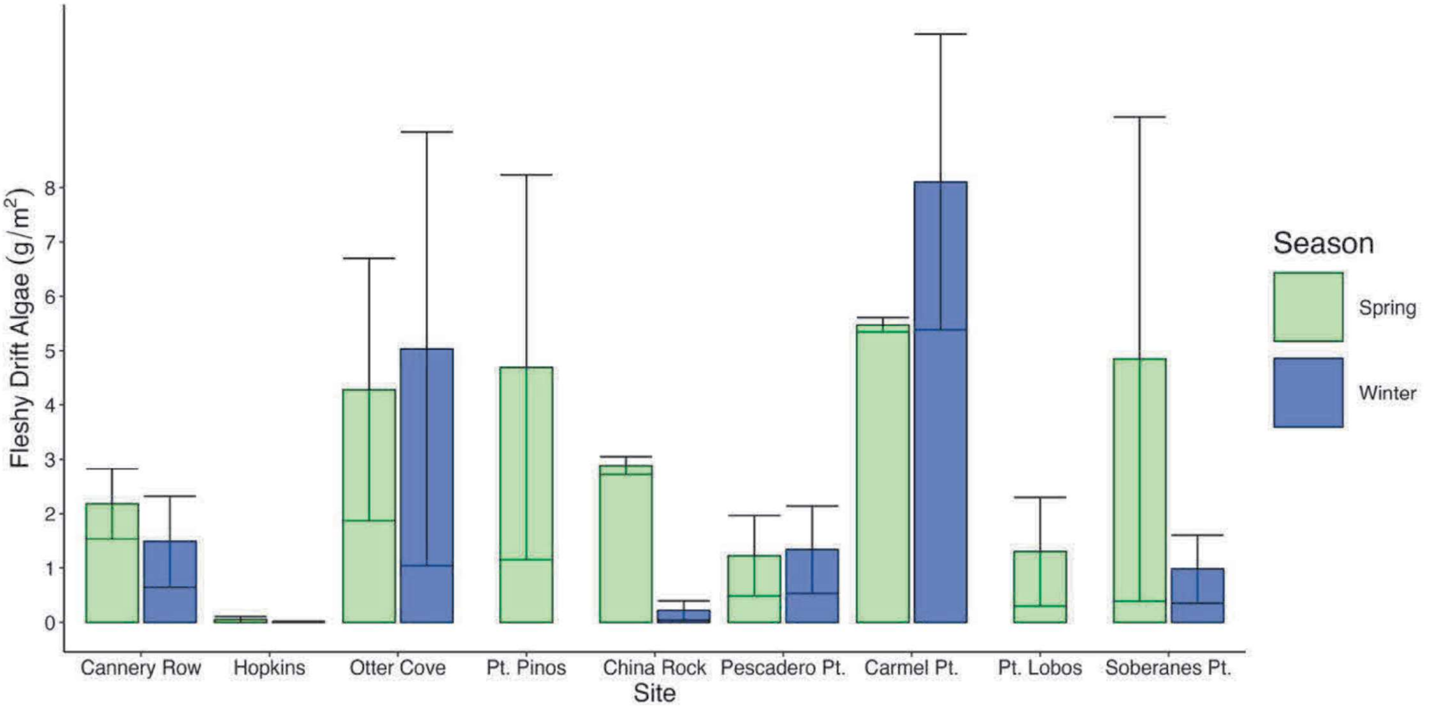

Figure 12. Drift algae density (g/m^2) at each of the 9 sites during winter (February 17-20, 2023) and spring (May 10-22, 2023) drift algae surveys.

Table 5. Site specific predictor variables and their average (± SE) values during each collection period.

		Spring		Winter		Summer	Fall
	Drift Algae Level	Wave Height (m)	Drift Algae (g/m^2)	Wave Height (m)	Drift Algae (g/m^2)	Wave Height (m)	Wave Height (m)
All Sites (± SE)		1.68 (± 0.15)	2.99 (± 0.67)	2.78 (± 0.46)	2.45 (± 0.93)	1.19 (± 0.089)	1.40 (± 0.15)
Cannery Row	Medium	1.06	2.18	0.77	1.48	0.92	0.77
Hopkins	Low	1.22	0.054	0.88	0.011	1.08	1.00
Otter Cove	High	1.22	4.28	1.49	5.03	0.88	1.03
Pt. Pinos	High	2.16	4.69	2.93	N/A	1.57	1.60
China Rock	Medium	2.39	2.89	3.21	0.22	1.63	2.16
Pescadero Pt.	Medium	1.69	1.22	4.01	1.33	1.02	1.57
Carmel Pt.	High	1.78	5.48	3.90	8.10	1.08	1.13
Pt. Lobos	Medium	2.26	1.30	4.23	N/A	1.31	1.72
Soberanes Pt.	Medium	1.88	4.84	3.61	0.98	1.22	1.67

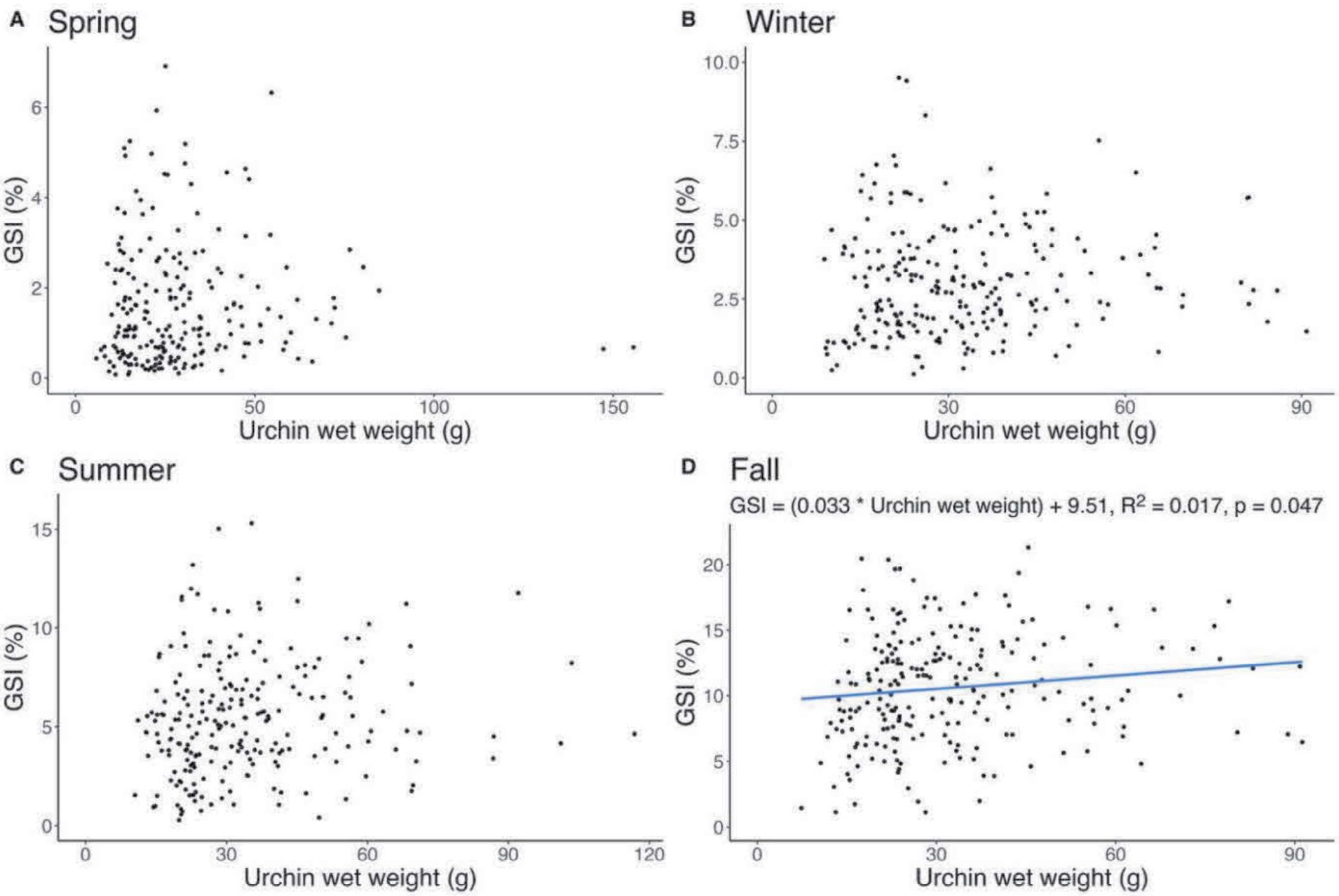

Figure 13. Urchin GSI vs. wet weight for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Blue lines indicate a significant relationship between GSI and wet weight.

Urchin weight was only significantly related to GSI in the fall ($F_{1,224} = 3.98$, p = 0.047; Fig. 13D), and the linear relationship between urchin weight and GSI was very weak in the fall, despite its statistical significance ($R^2 = 0.017$). Spawning intensity was positively correlated with urchin GSI in the spring (Kruskal-Wallis ($\chi_4 = 66.44$, $p < 0.001$; Fig. 14A), winter ($\chi_5 = 33.12$, $p < 0.001$; Fig. 14B), summer ($\chi_5 = 27.37$, $p < 0.001$; Fig 14C), and fall (ANOVA $F_{5,220} = 7.33$, $p < 0.001$; Fig. 14D). The presence of coralline algae was negatively correlated with GSI in the spring (Wilcoxon rank sum W = 5322, p = 0.032; Fig. 15A), winter (W = 4420, p = 0.009; Fig. 15B), summer (W = 7517, $p < 0.001$; Fig. 15C), and fall (T-test $t_{183.7} = 2.89$, p = 0.004; Fig. 15D).

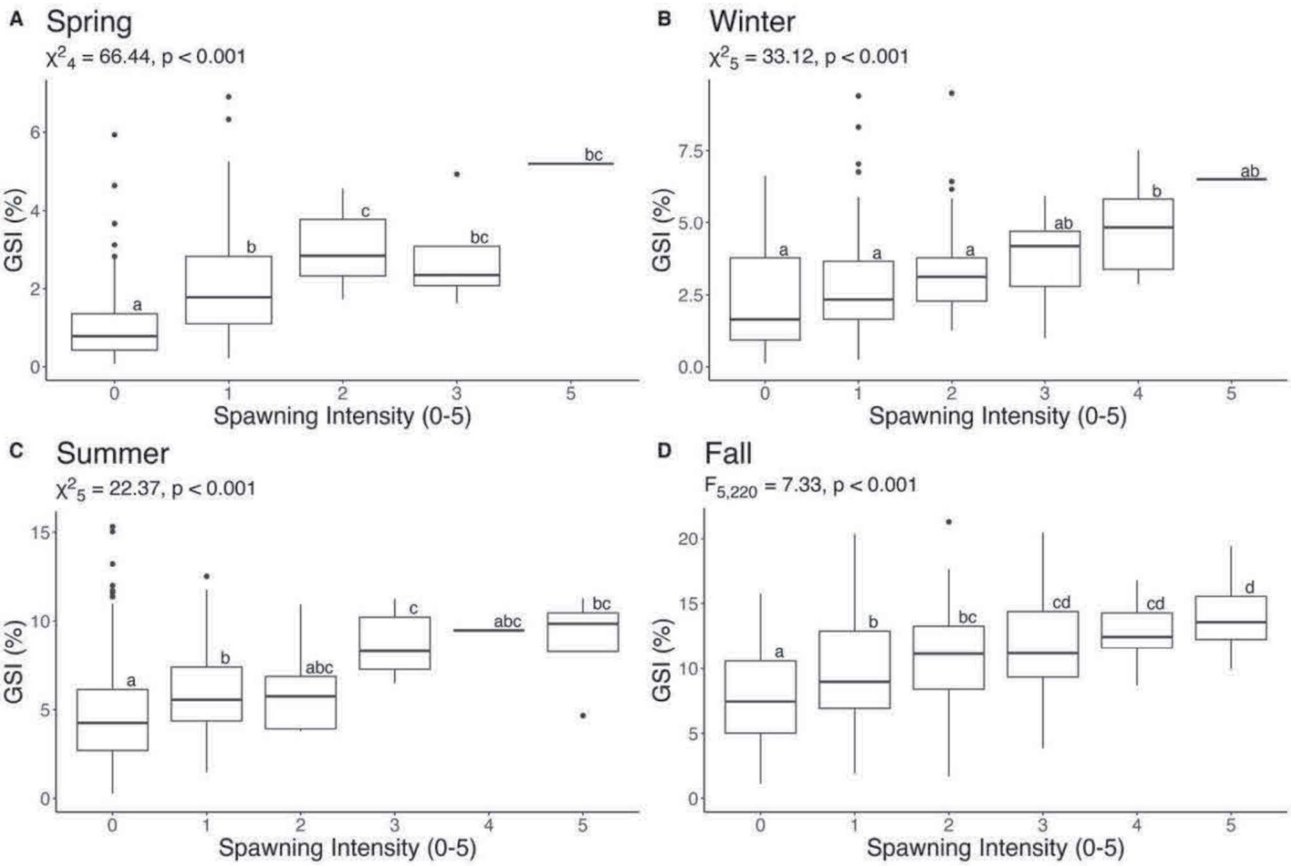

Figure 14. Urchin GSI in relation to spawning intensity for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Different letters represent significant differences ($p < 0.05$) for Dunn post-hoc (A-C) or Tukey post-hoc (D) tests between GSIs.

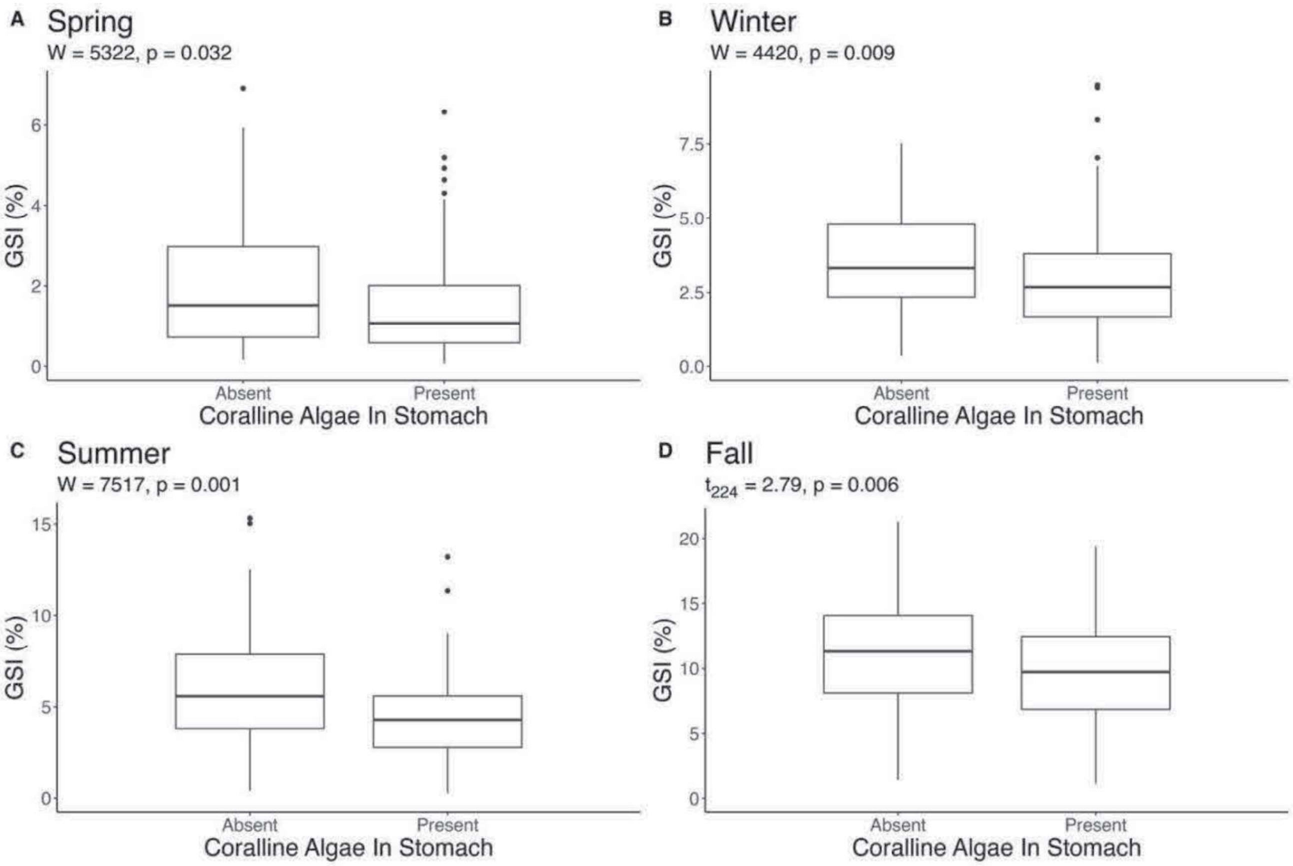

Figure 15. GSI for urchins found with and without coralline algae in their stomachs for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. All seasons exhibited a significant ($p < 0.05$) difference in GSI.

At the quadrat level, correlations between GSI and algal cover (fleshy algae percent cover, coralline algae percent cover, crustose non-coralline algae percent cover), non-algae percent cover, and urchin density were assessed for a relationship with GSI using linear regression. Fleshy algae percent cover was positively correlated to urchin GSI in the summer ($t_{39.9} = 2.88$, $R^2 = 0.085$, $p = 0.006$; Fig. 16C) and fall ($t_{43.0} = 2.14$, $R^2 = 0.046$, $p = 0.038$; Fig. 16D), but not in the spring ($t_{42.1} = 1.68$, $R^2 = 0.030$, $p = 0.10$; Fig. 16A) or winter ($t_{43.1} = 1.39$, $R^2 = 0.016$, $p = 0.17$; Fig. 16B). Additionally, the relationship between fleshy algae coverage and GSI in the summer and fall was affected by whether sites were located inside or outside Monterey Bay, as the interaction between fleshy algae coverage and site location was also significant in the summer (Interaction $t_{3,222} = -2.31$, $p = 0.022$; Fig. 24A) and fall ($t_{3,222} = -5.15$, $p < 0.001$; Fig. 24B) . Coralline algae and non-coralline crustose algae percent cover was not significantly associated with GSI in any season (Fig. 17, Fig. 18). Non-algae percent cover was negatively correlated with urchin GSI in the spring ($t_{41.5} = -2.87$, $R^2 = 0.079$, $p = 0.007$; Fig. 19A), summer ($t_{40.1} = -2.23$, $R^2 = 0.054$, $p = 0.031$; Fig. 19C), and fall ($t_{43.0} = -3.31$, $R^2 = 0.096$, $p = 0.002$; Fig. 19D), but not in the winter ($t_{43.8} = -1.07$, $R^2 < 0.01$, $p = 0.29$; Fig. 19B). Urchin density was negatively correlated with urchin GSI in the spring ($t_{41.2} = -2.05$, $R^2 = 0.045$, $p = 0.047$; Fig. 20A), but not in the winter ($t_{44.2} = 0.55$, $R^2 < 0.01$, $p = 0.59$; Fig. 20B), summer ($t_{39.6} = -0.35$, $R^2 < 0.01$, $p = 0.73$; Fig. 20C), or fall ($t_{43.0} = -0.63$, $R^2 < 0.01$, $p = 0.53$; Fig. 20D).

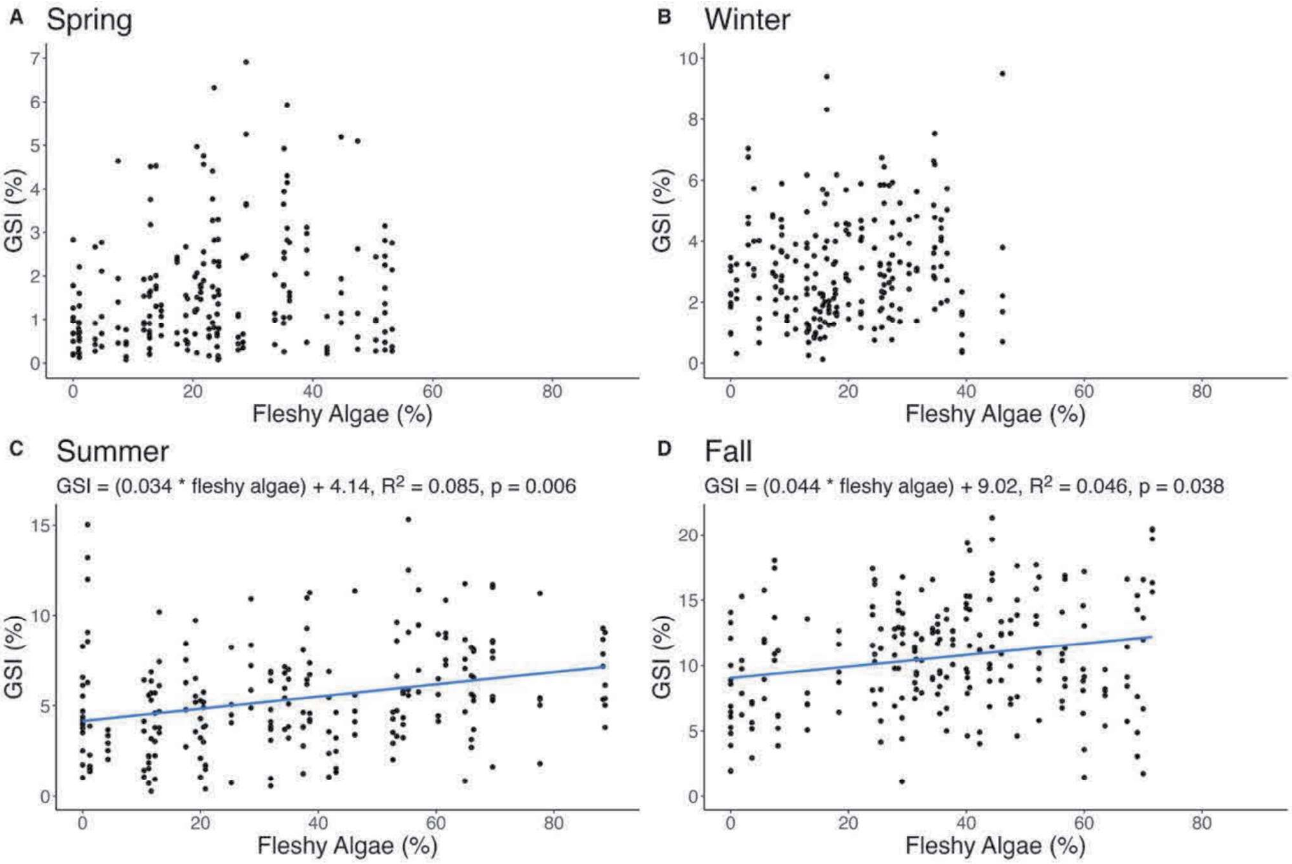

Figure 16. Relationship between urchin GSI and fleshy algae percent cover for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Blue lines indicate a significant relationship between GSI and fleshy algae percent cover.

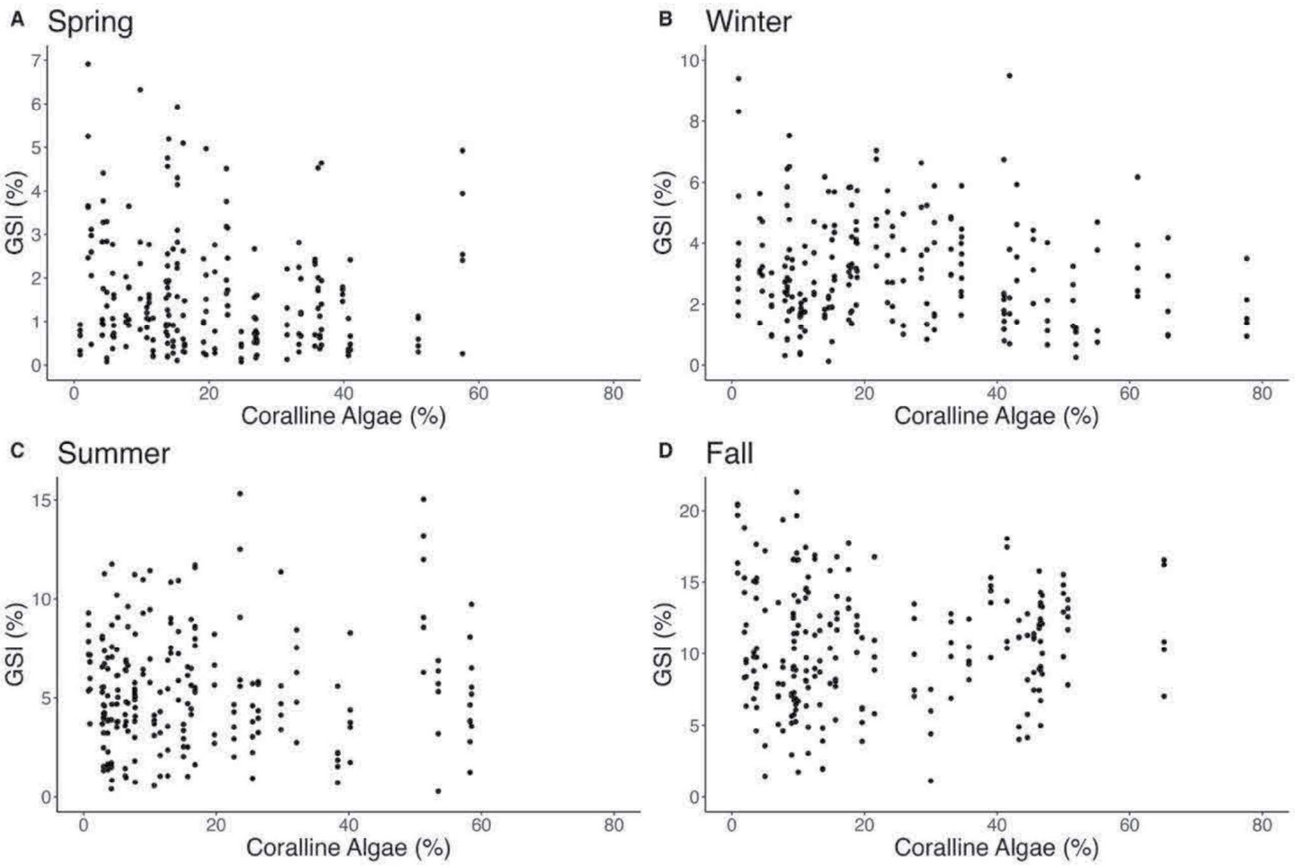

Figure 17. Relationship between urchin GSI and coralline algae percent cover for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons.

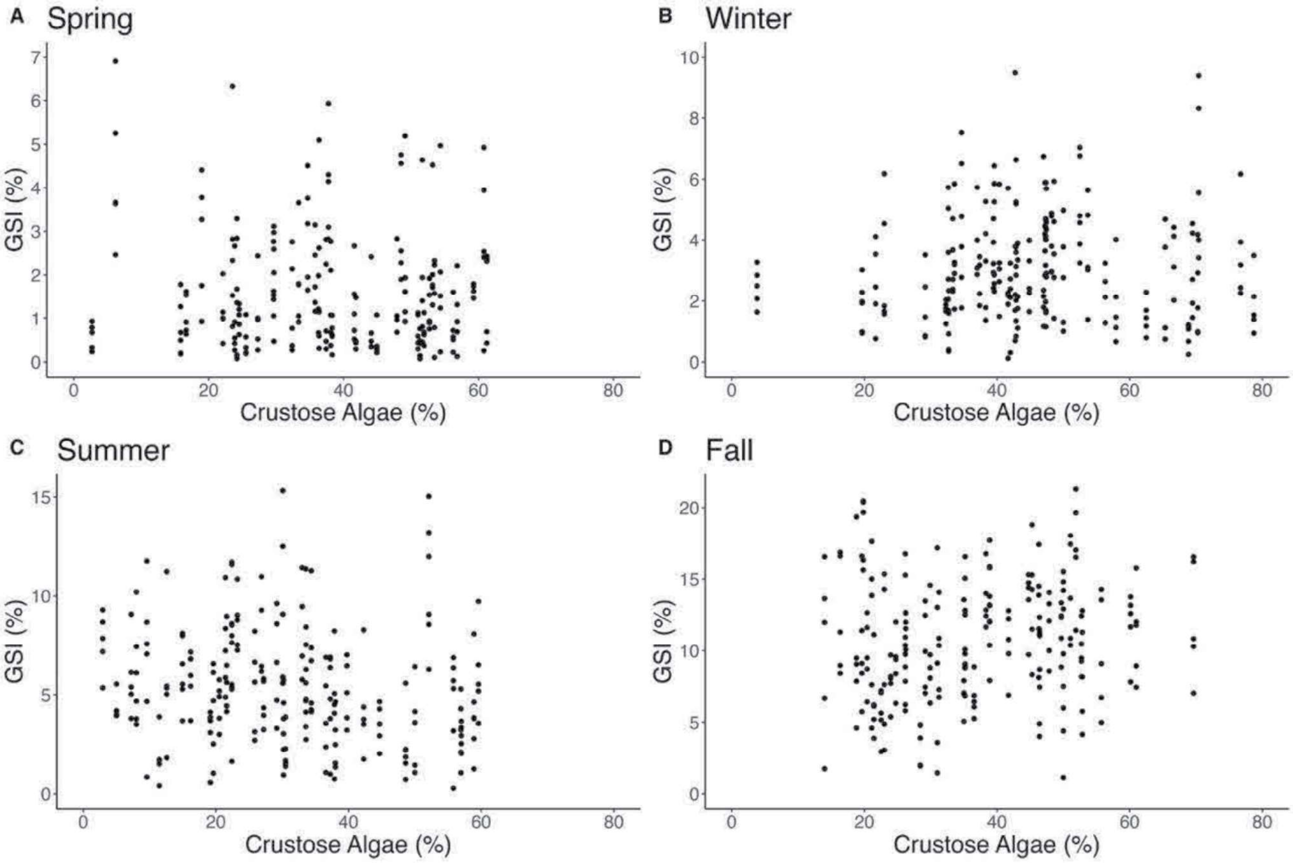

Figure 18. Relationship between urchin GSI and crustose non-coralline algae percent cover for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons.

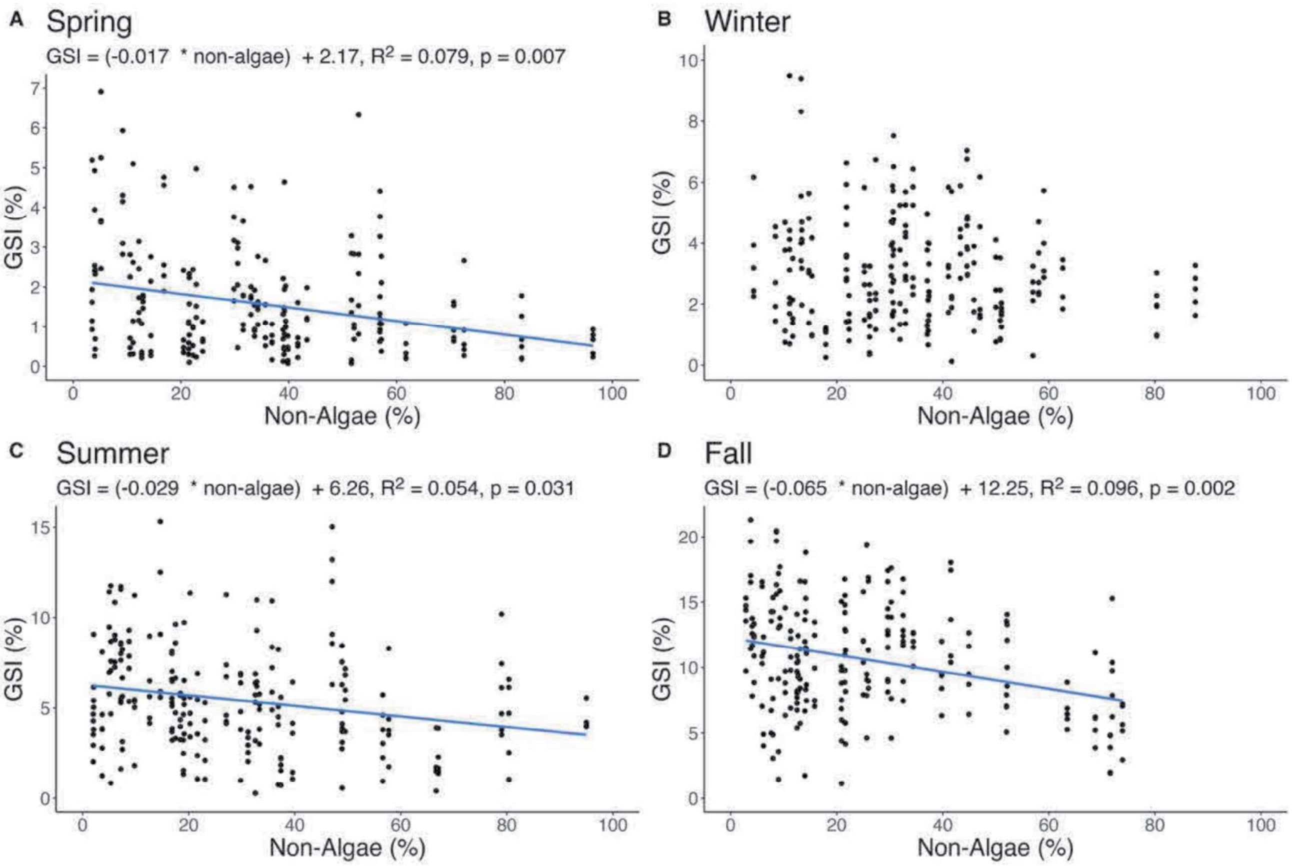

Figure 19. Relationship between urchin GSI and non-algae percent cover for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Blue lines indicate a significant relationship between GSI and non-algae percent cover.

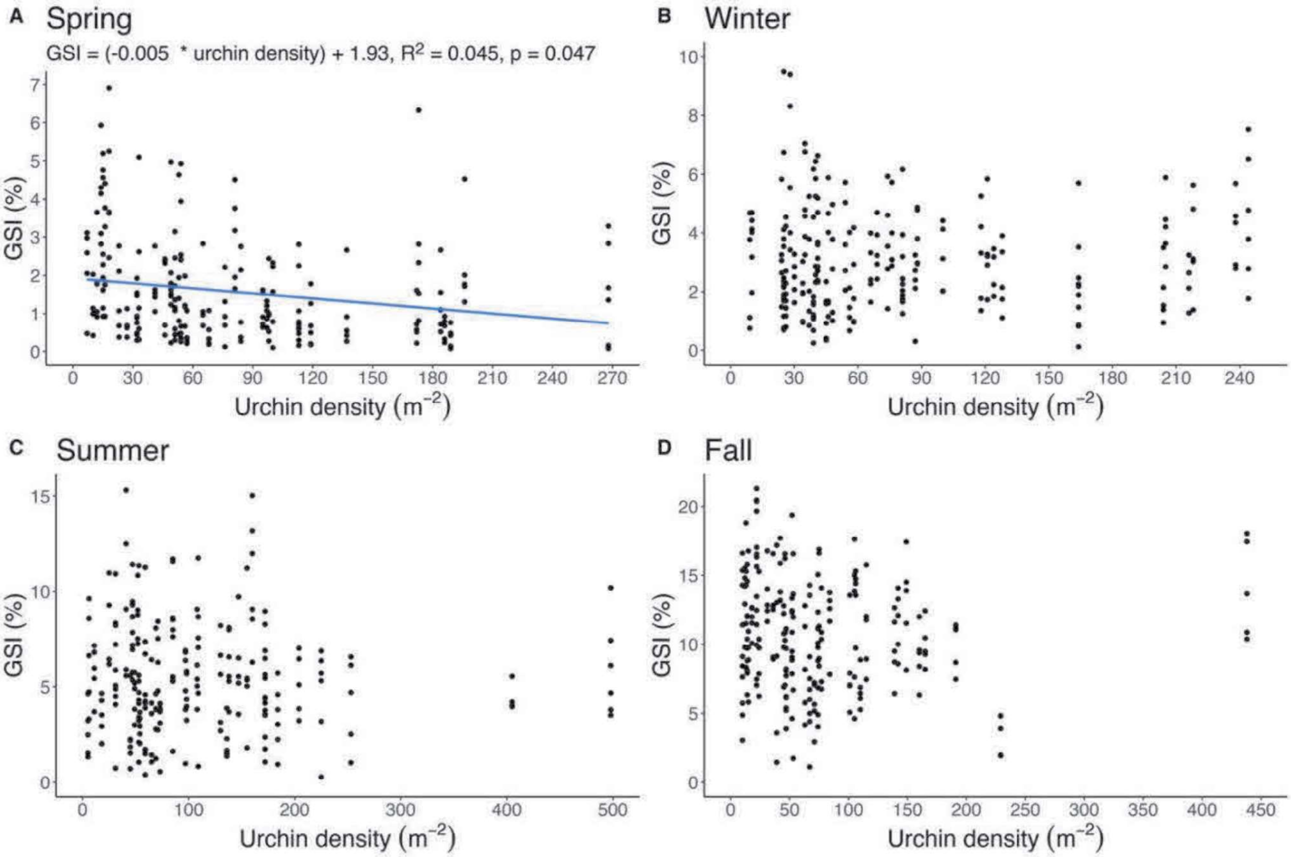

Figure 20. Relationship between urchin GSI and urchin density for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Blue lines indicate a significant relationship between GSI and urchin density.

Drift algae presence at a site was positively correlated with urchin GSI in the spring ($\chi^2_2 = 22.03$, $p < 0.001$; Fig. 22A), winter ($\chi^2_2 = 13.87$, $p < 0.001$; Fig. 22B), summer ($\chi^2_2 = 28.16$, $p < 0.001$; Fig. 22C), and fall (Welch's ANOVA $F_{2,64.2} = 14.51$, $p < 0.001$; Fig 22D). Wave height was not related to GSI in any season (Fig. 21).

Table 6. Individual model results for each predictor variable for urchins collected during spring 2023.

Variable	Analysis	Df	Slope	Intercept	R^2	Test statistic	p-value
Urchin Weight	Linear regression	219	0.0010	1.55	< 0.01	0.23	0.82
Spawning intensity	**KW ANOVA**	**4**				**66.44**	**< 0.001**
Coralline algae in stomach	**Wilcoxon Signed Rank**	**-**				**5322**	**0.032**
Fleshy Algae	Linear regression	42.05	0.015	1.22	0.030	1.68	0.10
Coralline Algae	Linear regression	42.09	-0.012	1.84	0.016	-1.22	0.23
Non-coralline crust Algae	Linear regression	41.84	-0.0053	1.78	0.0034	-0.55	0.59
Non-algae	**Linear regression**	**41.48**	**-0.017**	**2.17**	**0.079**	**-2.87**	**0.0065**
Urchin density	**Linear regression**	**41.18**	**-0.0045**	**1.93**	**0.045**	**-2.05**	**0.047**
Wave Height	Linear regression	7.06	0.047	1.50	< 0.01	0.11	0.91
Drift Algae	**KW ANOVA**	**2**				**22.03**	**< 0.001**

Table 7. Individual model results for each predictor variable for urchins collected during winter 2023.

Variable	Analysis	Df	Slope	Intercept	R^2	Test statistic	p-value
Urchin Weight	Linear regression	231	0.0063	2.83	< 0.01	0.93	0.35
Spawning intensity	**KW ANOVA**	**5, 227**				**33.12**	**< 0.001**
Coralline algae in stomach	**Wilcoxon Signed Rank**	**-**				**4420**	**0.009**
Fleshy Algae	Linear regression	43.14	0.019	2.67	0.016	1.39	0.17
Coralline Algae	Linear regression	45.19	-0.014	3.38	0.022	-1.67	0.10
Non-coralline crust Algae	Linear regression	44.34	0.0031	2.89	< 0.01	0.31	0.76
Non-algae	Linear regression	43.76	-0.0090	3.34	< 0.01	-1.07	0.29
Urchin density	Linear regression	44.24	0.0013	2.92	< 0.01	0.55	0.59
Wave Height	Linear regression	7.02	-0.10	3.32	< 0.01	-0.61	0.56
Drift Algae	**KW ANOVA**	**2**				**13.87**	**0.001**

Table 8. Individual model results for each predictor variable for urchins collected during summer 2022.

Variable	Analysis	Df	Slope	Intercept	R^2	Test statistic	p-value
Urchin Weight	Linear regression	224	0.020	4.71	0.015	1.84	0.067
Spawning intensity	**KW ANOVA**	**5, 220**				**27.37**	**< 0.001**
Coralline algae in stomach	**Wilcoxon Signed Rank**	**-**				**7517**	**< 0.001**
Fleshy Algae	**Linear regression**	**59.59**	**0.028**	**4.23**	**0.064**	**2.74**	**0.0082**
Coralline Algae	Linear regression	53.50	0.0047	5.18	< 0.01	0.25	0.80
Non-coralline crust Algae	Linear regression	49.39	-0.027	6.07	0.021	-1.43	0.16
Non-algae	**Linear regression**	**49.16**	**-0.025**	**6.04**	**0.043**	**-2.10**	**0.041**
Urchin density	Linear regression	46.72	-0.00049	5.31	< 0.01	-0.16	0.87
Wave Height	Linear regression	6.90	0.87	4.32	< 0.01	0.41	0.69
Drift Algae	**KW ANOVA**	**2**				**28.16**	**< 0.001**

Table 9. Individual model results for each predictor variable for urchins collected during fall 2022.

Variable	Analysis	Df	Slope	Intercept	R^2	Test statistic	p-value
Urchin Weight	**Linear regression**	**224**	**0.033**	**9.51**	**0.017**	**2.00**	**0.047**
Spawning intensity	**ANOVA**	**5, 220**				**7.33**	**< 0.001**
Coralline algae in stomach	**T test**	**224**				**2.79**	**0.006**
Fleshy Algae	**Linear regression**	**43.03**	**0.044**	**9.024**	**0.046**	**2.14**	**0.038**
Coralline Algae	Linear regression	42.98	0.0083	10.41	< 0.01	0.33	0.75
Non-coralline crust Algae	Linear regression	43.03	0.043	9.01	0.020	1.37	0.18
Non-algae	**Linear regression**	**43.05**	**-0.065**	**12.25**	**0.096**	**-3.31**	**0.0019**
Urchin density	Linear regression	42.99	-0.0037	10.88	< 0.01	-0.63	0.53
Wave Height	Linear regression	6.98	2.27	7.40	0.049	1.25	0.25
Drift Algae	**Welch's ANOVA**	**2, 64.19**				**14.51**	**< 0.001**

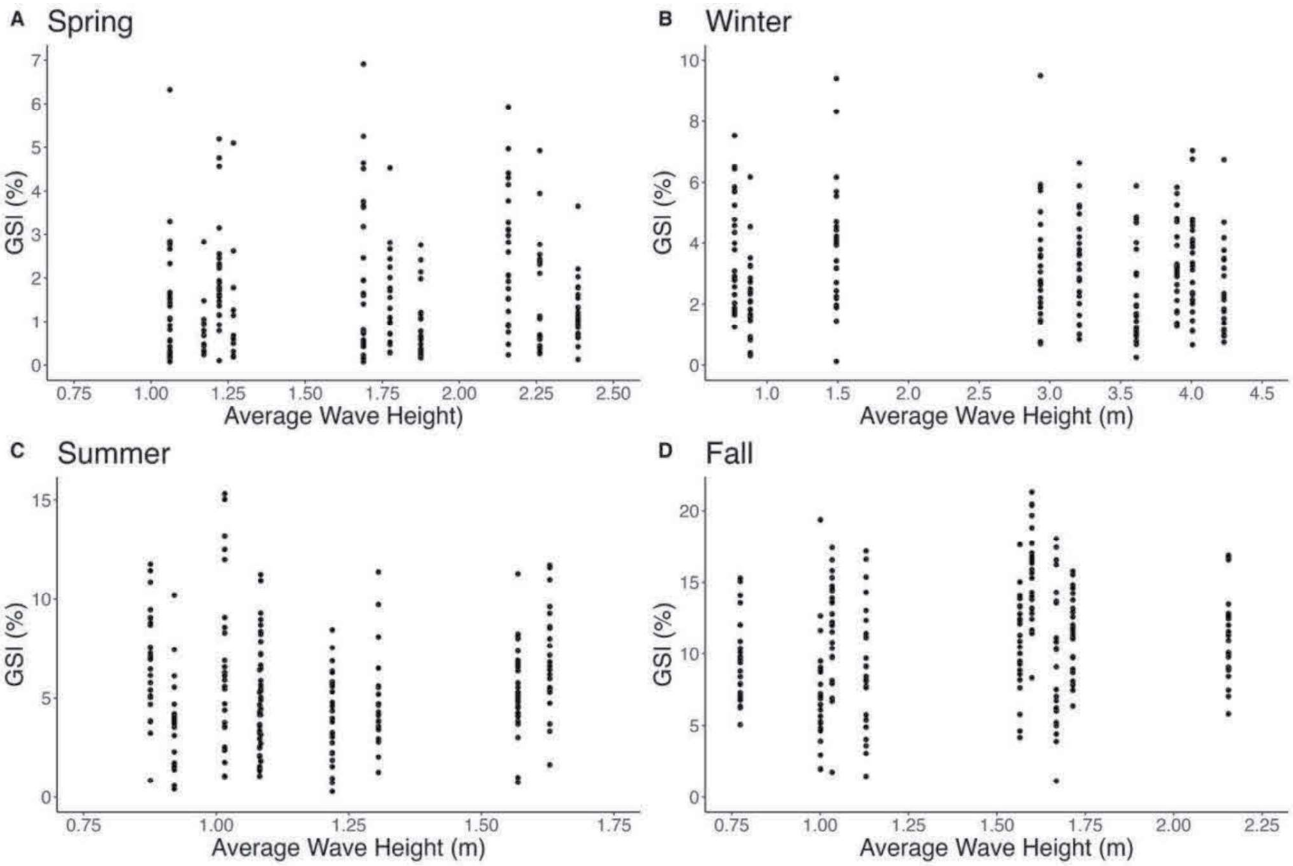

Figure 21. Relationship between urchin GSI and wave height for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Wave data comes from Coastal Data Information Program Monitoring and Prediction System (CDIP – MOP).

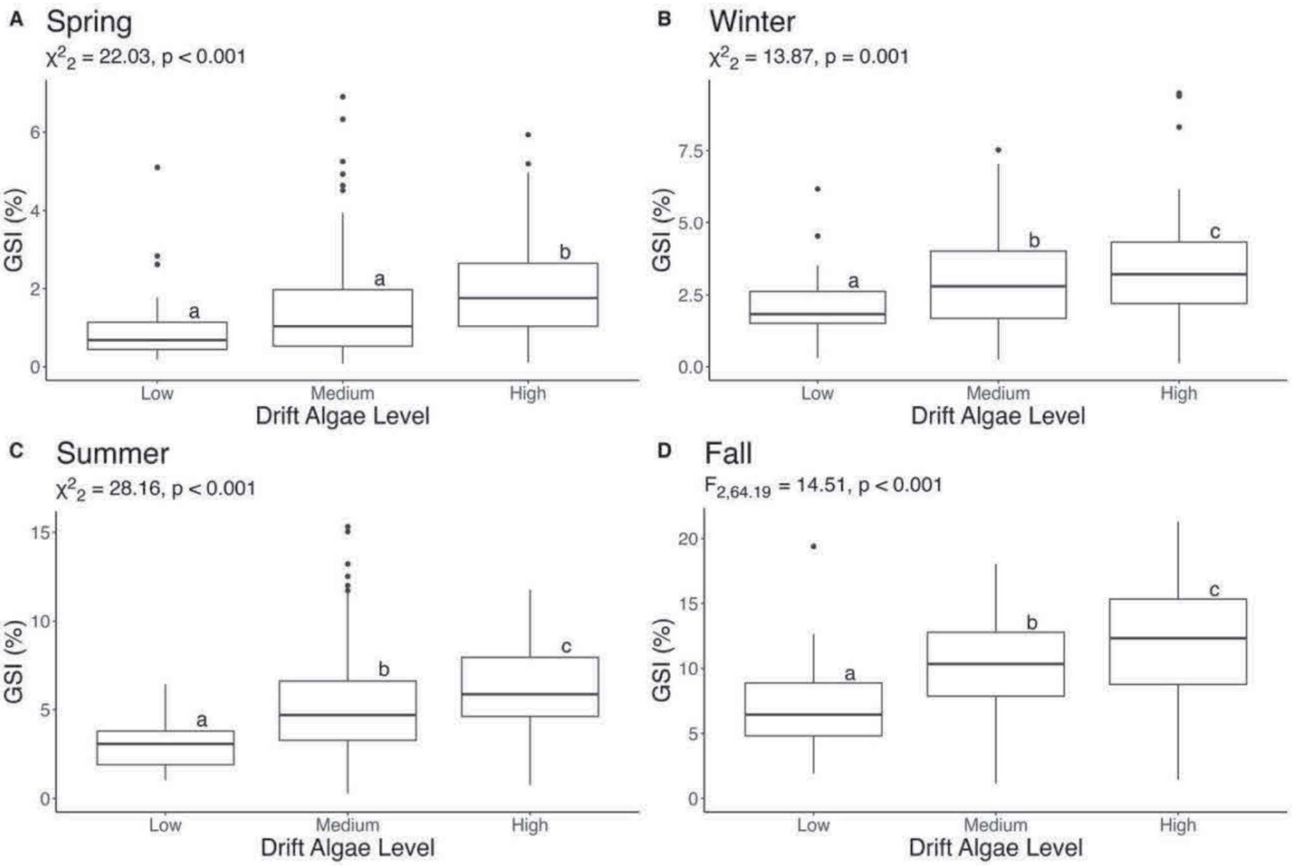

Figure 22. Relationship between urchin GSI and drift algae levels for A) Spring, B) Winter, C) Summer, and D) Fall collection seasons. Drift algae level is based on spring and winter drift algae surveys. Different letters represent significant differences ($p < 0.05$) from Dunn (A-C) or Games-Howell (D) post-hoc tests between GSIs.

There was a positive relationship between winter and spring average drift algae density and average fleshy algae coverage for all seasons across all sites ($F_{1,34} = 17.92$, $p < 0.001$; Fig. 23).

Results indicated that in the intertidal, gonadal production outweighed that in the subtidal at all sites except China Rock (Fig. 25). Intertidal gonad production ranged from 8.58 g/m^2 (± 3.48 SE) at China Rock to 136.28 (± 25.81) g/m^2 at Pescadero Pt. In the subtidal, gonad production averaged 11.29 (±1.35) g/m^2.

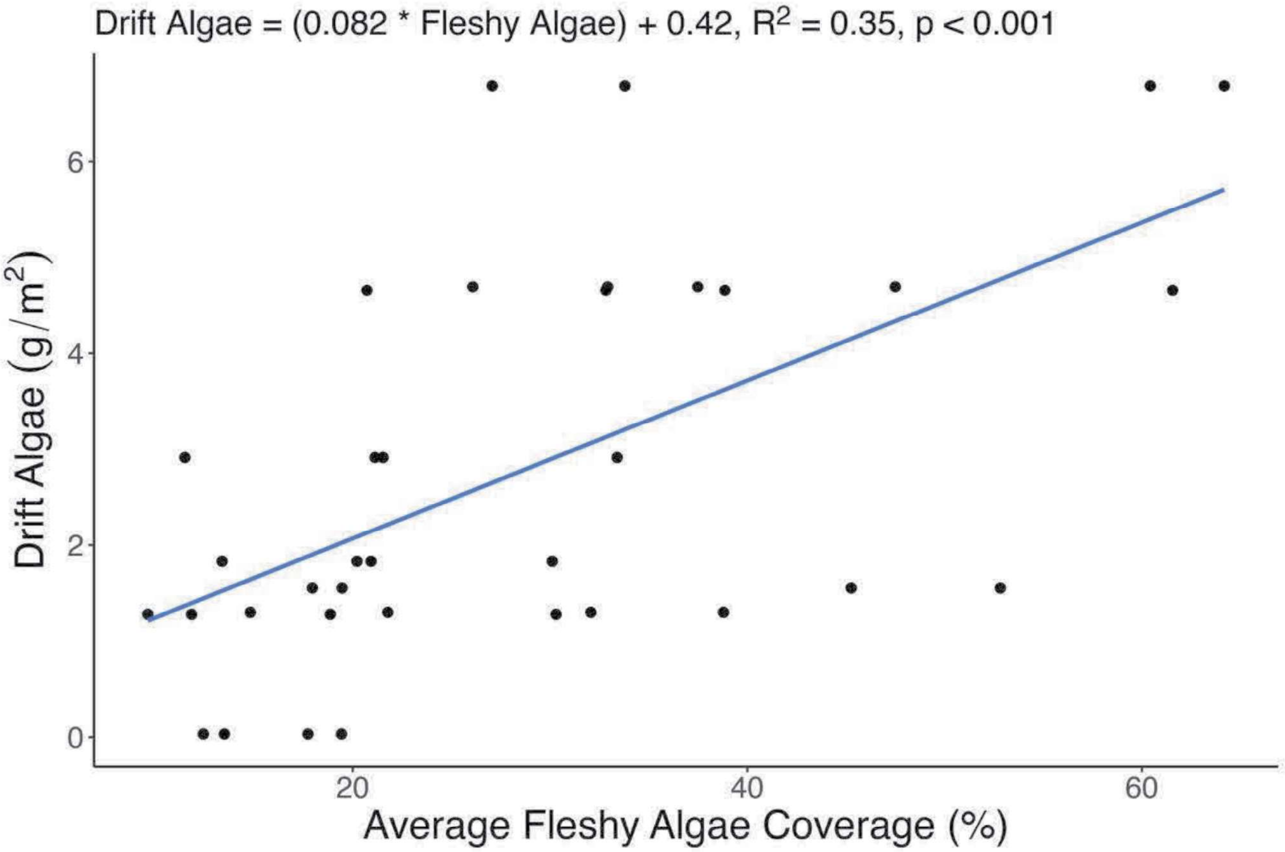

Figure 23. Relationship between average winter and spring drift algae density and average fleshy algae coverage across all seasons at each site. Blue line indicates a significant relationship between the two variables.

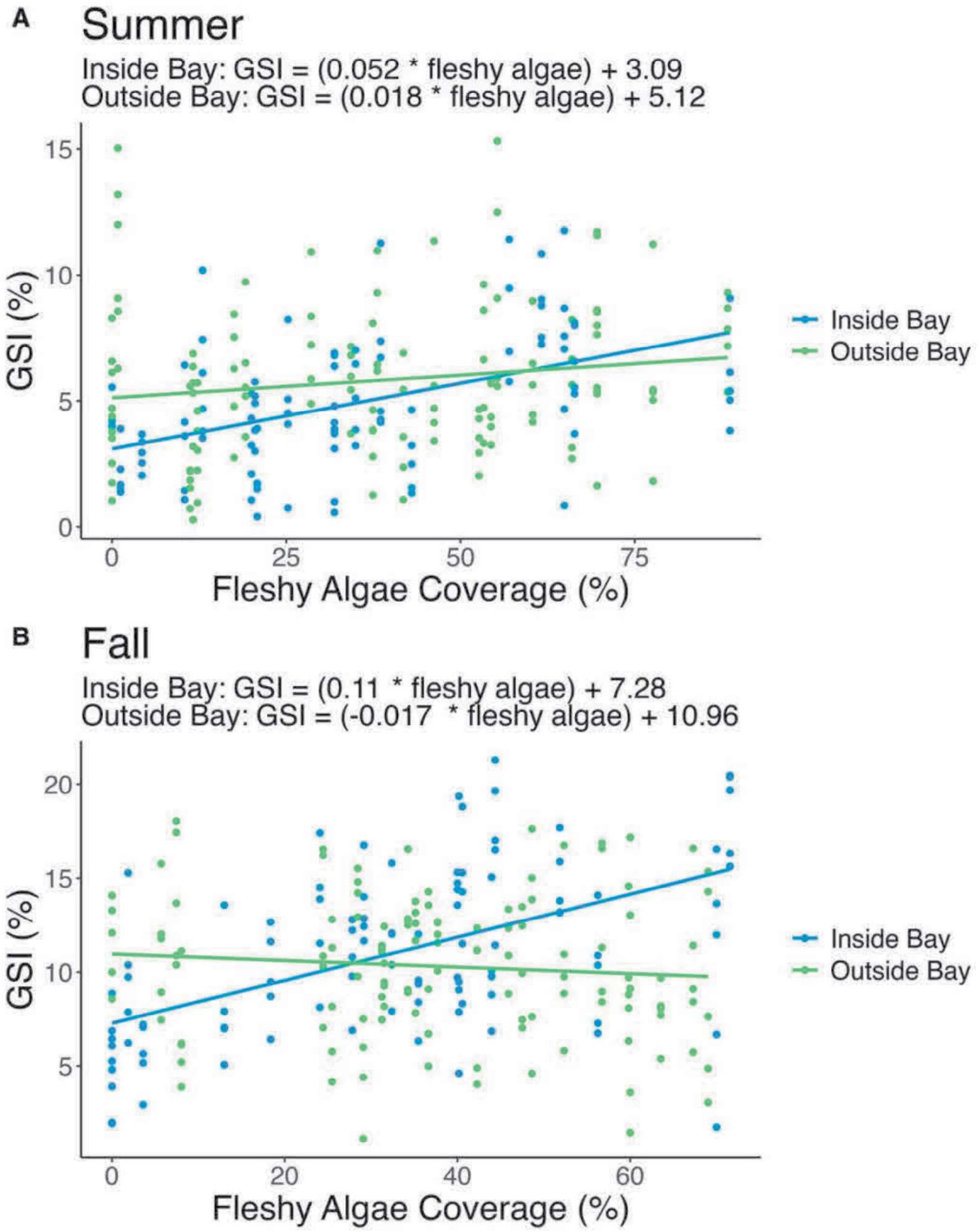

Figure 24. Relationship between urchin GSI and fleshy algae coverage for sites within (Cannery Row, Hopkins, Otter Cove, Pt. Pinos) and outside (China Rock, Pescadero Pt., Carmel Pt., Pt. Lobos, Soberanes Pt.) Monterey Bay during the A) Summer and B) Fall collection seasons. All linear and interaction terms were significant ($p < 0.06$).

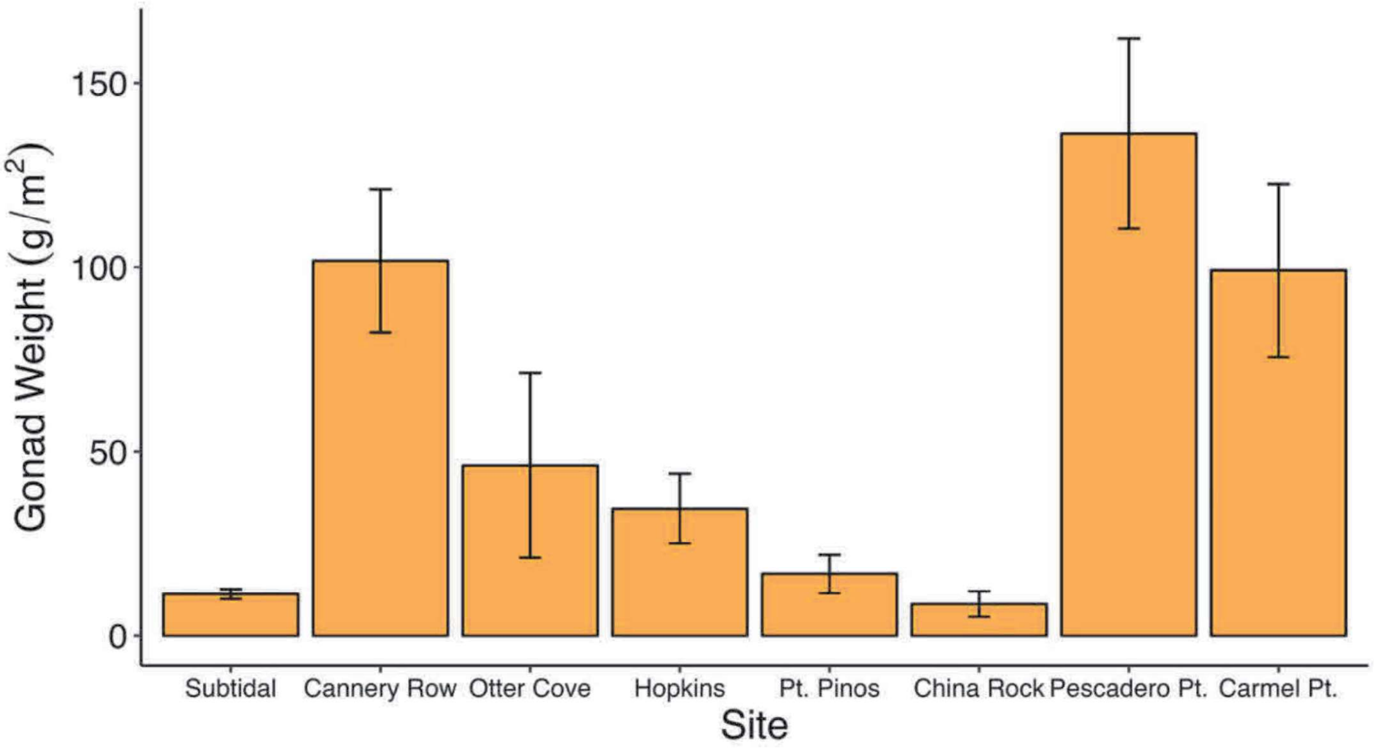

Figure 25. Gonad weight per m^2 (± SE) at each intertidal site and the subtidal. Size frequency distributions were not available for Pt. Lobos or Soberanes Pt., so data for these sites was not included.

Question 3 - How does the relationship of known drivers of urchin reproductive capacity in the intertidal and subtidal urchin populations (fleshy and coralline algae coverage and urchin density) compare to what is seen in the intertidal?

Factors known to affect subtidal urchin reproductive capacity varied in average coefficient (± SE) in the spring from -0.26 ± 0.14 (fleshy algae) to 0.20 ± 0.14 (urchin density) (Fig. 26A). In the winter, coefficients ranged from -0.25 ± 0.15 (fleshy algae) to 0.21 ± 0.15 (coralline algae) (Fig. 26B). In the summer, coefficients ranged from 0.19 ± 0.31 (urchin density) to 0.93 ± 0.31 (fleshy algae) (Fig. 26C). Finally, in the fall, coefficients ranged from 0.02 ± 0.27 (urchin density) to 0.76 ± 0.55 (fleshy algae) (Fig. 26D).

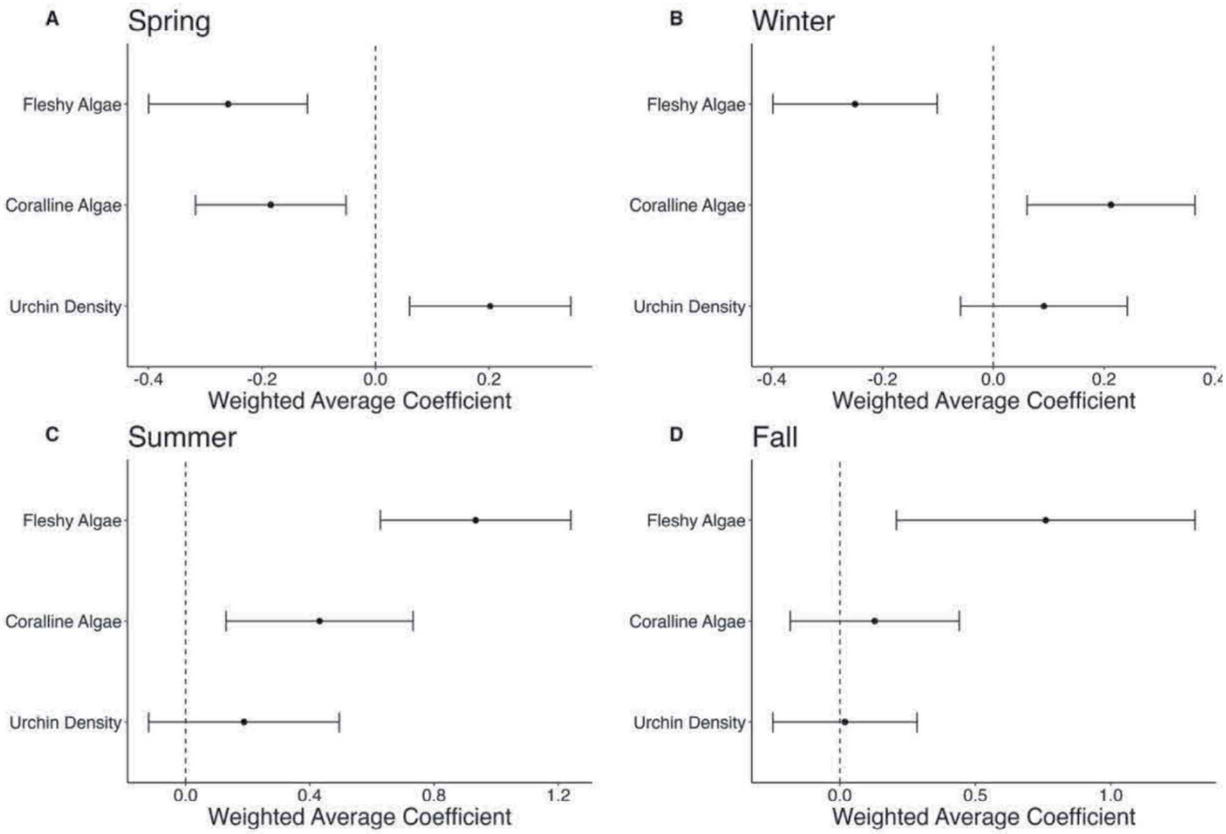

Figure 26. Average (± standard error) model coefficients using GSI as a predictor and fleshy algae, coralline algae, and urchin density as explanatory variables. Coefficients were weighted using AIC values for each combination of factors.

In the intertidal, there was a positive relationship between fleshy algae percent cover and GSI ($F_{1,40} = 8.36$, $p = 0.006$, Fig. 27B). In the subtidal, this relationship was present as well ($F_{1,81} = 44.75$, $p < 0.001$, Fig. 27A), but was almost twice as strong as in the intertidal (0.058 vs. 0.034 model coefficients), and accounts for more than twice the variance as in the intertidal ($R^2 = 0.36$ and $R^2 = 0.17$, respectively). However, in the subtidal, there was a relationship between GSI and both coralline algae coverage ($F_{1,81} = 54.5$, $p < 0.001$, Fig. 28A) and urchin density ($F_{1,81} = 4.59$, $p = 0.035$, Fig. 29A) where in the intertidal these relationships were not present ($F_{1,40} = 0.189$, $p = 0.67$, Fig. 28B and $F_{1,38} = 0.254$, $p = 0.62$, Fig. 29B, respectively).

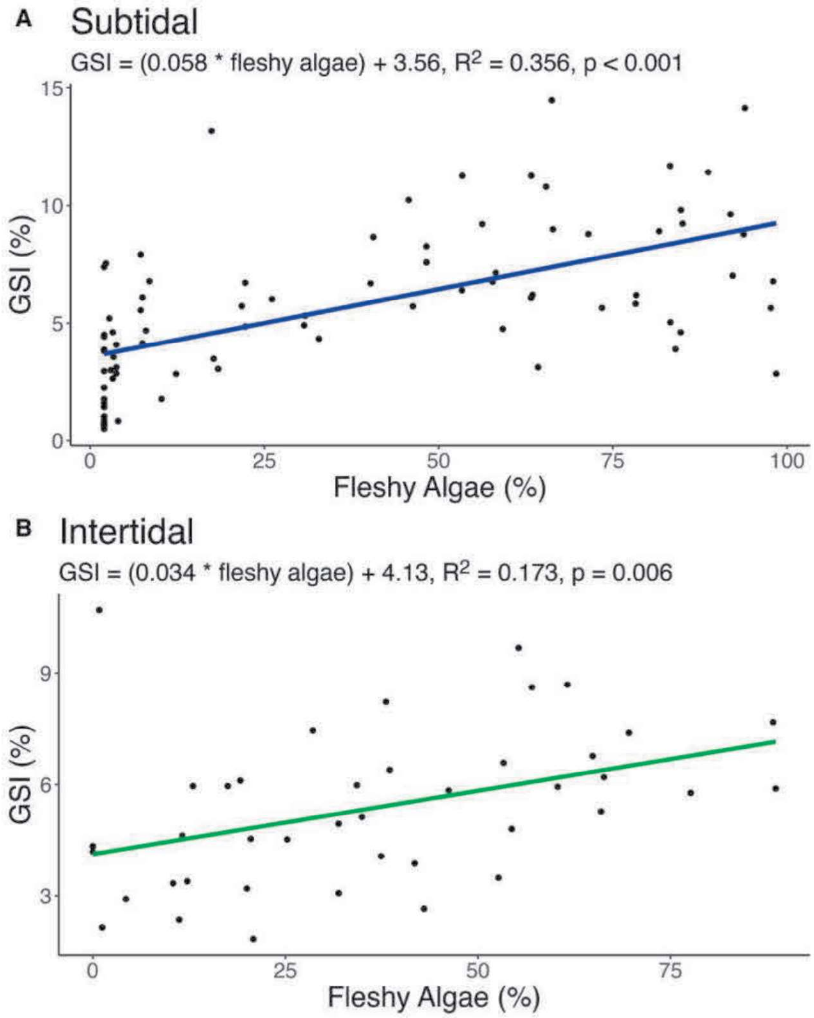

Figure 27. Relationship between urchin GSI and fleshy algae coverage in the A) Subtidal from summer 2017 and B) Intertidal from summer 2022 around the Monterey Peninsula. Subtidal data are from Smith & Garcia (2021). Lines represent significant relationships between GSI and fleshy algae coverage ($p < 0.05$). Note the maximum fleshy algae coverage in the intertidal is ~80%.

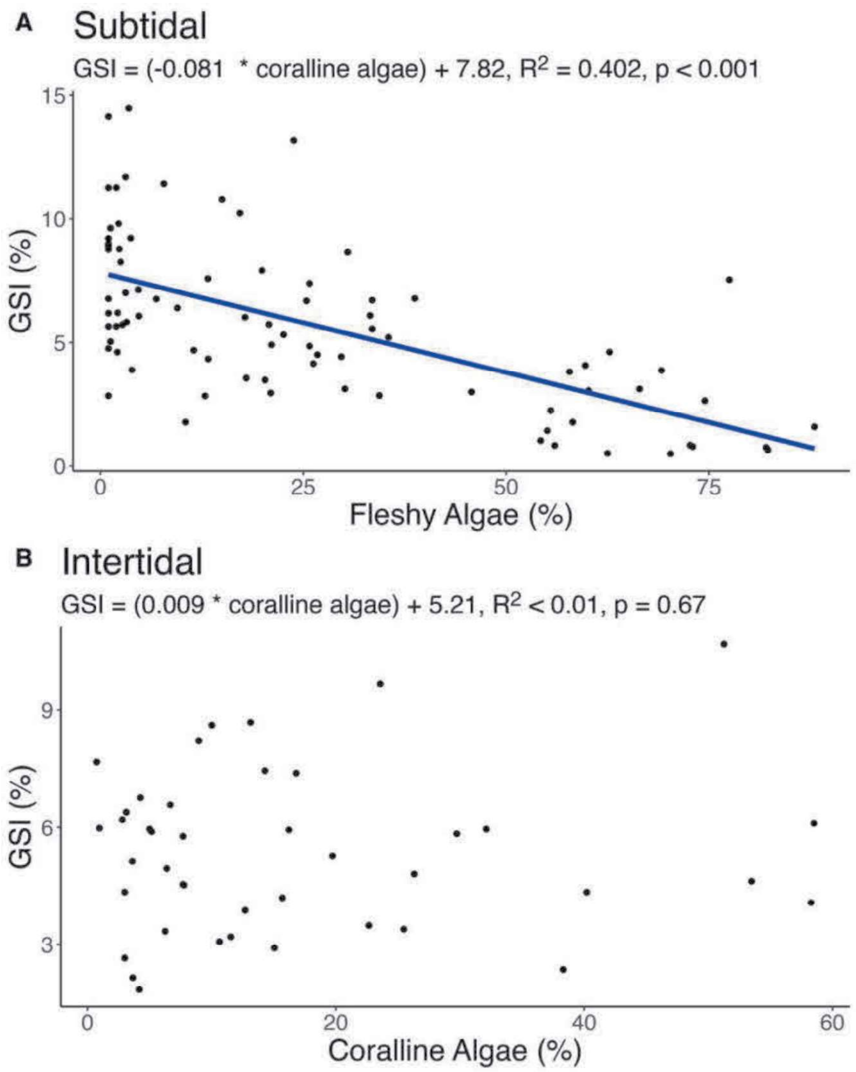

Figure 28. Relationship between urchin GSI and coralline algae coverage in the A) Subtidal from summer 2017 and B) Intertidal from summer 2022 around the Monterey Peninsula. Subtidal data are from Smith & Garcia (2021). Lines represent significant relationships between GSI and coralline algae coverage ($p < 0.05$). Note the maximum coralline algae coverage in the intertidal is ~60% and ~80% in the subtidal.

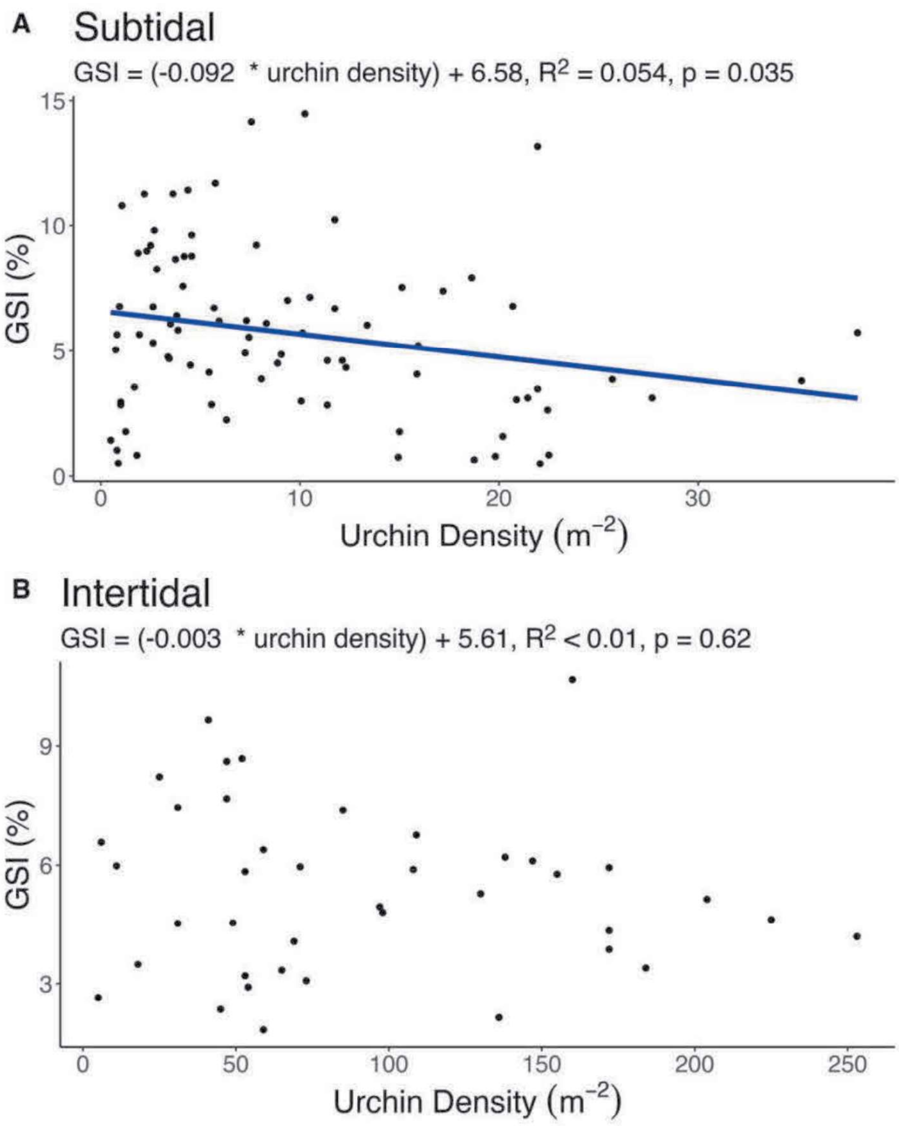

Figure 29. Relationship between urchin GSI and urchin density in the A) Subtidal from summer 2017 and B) Intertidal from summer 2022 around the Monterey Peninsula. Subtidal data are from Smith & Garcia (2021). Lines represent significant relationships between GSI and urchin density ($p < 0.05$). Note the maximum urchin density in the subtidal is ~40 m^{-2} and ~250 m^{-2} in the intertidal.

Discussion

Important management implications can be made using the urchin reproductive capacity data collected in this study. Seasonal trends in relative urchin reproductive capacity are important to consider for the timing of urchin removal efforts. Size-based reproductive capacities indicate that larger urchins should be prioritized for removal and that urchins smaller than 1.8 cm should not be considered reproductive when assessing population-wide effects of urchin reproduction. Intertidal algae community composition and drift algae availability data suggest that urchins in the intertidal depend on both algae growing where they are living as well as drift algae which continually supplements their food availability, even in areas of low intertidal fleshy algae availability. These findings together with the findings that urchins in the intertidal are far denser than those in the subtidal (even compared to subtidal urchin barrens) suggest that the intertidal may represent a large portion of urchin population reproduction and should be a focus of management efforts.

Understanding temporal and size-based trends in purple urchin reproduction

There is a clear temporal trend in urchin gonadosomatic index (GSI) reflected by the large difference in GSI during each collection period. The spike of GSI in the fall followed by a steady decline through winter and spring followed by an increase in the summer generally reflects the trends seen in Giese et al. (1959), Lawrence et al. (1965), and Gonor (1973). However, other sources suggest that *S. purpuratus* may exhibit high GSIs through winter, spring, and into summer, with the sharp decline that occurred between the fall and winter collections in this study not occurring until early June (Bennett & Giese 1955). Due to temporal trends persisting over two locations but differing on an annual basis, Bennett & Giese (1955) posit that climactic factors such as ocean temperature may affect purple urchin reproductive cycles.

In this study, the highest GSI's were seen during the fall, which is also when spawning intensity was at its highest, indicating that there is a mass spawning event that took place between the fall and winter collection periods resulting in a dramatic decrease in GSI. The summertime increase in urchin GSI is conducive to a time when fleshy algae makes up a large portion of intertidal habitat. Within-year variation in algal assemblages is affected by a wide variety of factors including both anticipatory and stochastic forces. Anticipatory forces affecting algal assemblages include seasonal peaks in recruitment and blade production (in the summer and early fall) followed by blade senescence (Foster et al. 1988). Stochastic forces, including winter storms also often contribute to the decline of algal coverage in the winter and spring (Foster et al. 1988). This study indicated a steep decline in fleshy algae coverage between fall and winter, likely due to annual blade senescence as well as an increase in mortality following the severe storms seen in central California during January 2023. Food availability is known to be tightly correlated with urchin gonad health (Smith & Garcia 2021, Dolinar & Edwards 2021), indicating that seasonal fluctuations in resource availability may contribute towards the timing of the seasonal reproductive cycle seen in *S. purpuratus*. Understanding the timing of urchin reproduction is important for management efforts aiming to remove urchins from their habitat to mitigate their effect on kelp forests. Urchins should be removed prior to annual spawning events to minimize their potential impact on the urchin population supply.

Few previous projects have assessed the test diameter (or urchin weight) of purple sea urchins in relation to reproduction, but it has been suggested that urchin size at reproductive maturity is tied to predator abundance (Estes et al. 1978) and diet (Dix 1970, Thompson 1983, Pearse et al.

1986). Kenner and Lares (1991) found that purple urchins collected in the subtidal around the Monterey Peninsula became reproductively mature at a minimum of 1.6 cm test diameter and that all urchins were reproductively mature at 2.2 cm. These findings are within the minimum test diameter of 1.8 cm found in this study. Gonor (1972), however, found that purple urchins collected from Oregon did not show reproductive maturity until reaching a test diameter of 2.5 - 3.5 cm. Differences in GSI between sites in this study indicate that urchins may reach reproductive maturity at different sizes depending on habitat (and therefore food availability), but I did not collect enough small urchins at each site to adequately assess this hypothesis.

The identification of an approximate adult size cut off is particularly important regarding the study of conspicuous, dense populations of *S. purpuratus*. Long term population studies have indicated that *S. purpuratus* have dramatically increased in density in the last 6 years in the intertidal in central California (Haupt et al. unpubl. data, Fig. 1), having potentially large ecological consequences as discussed previously. It is necessary to separate juvenile from adult urchin populations because both the resource usage and reproductive output are unequal for juveniles and adults (Suskiewicz & Johnson 2017, this study). Therefore, including juveniles in overall population estimates will overestimate the impacts of urchin populations on their habitats as well as overall reproductive output. Long term urchin population monitoring projects should consider these differences in their data, and the size cut-off established in this project provides for a way to account for important differences between juvenile and adult urchins depending on the context and purpose of the project. Difficulties in the ability to locate and count juvenile urchins will also affect population estimates in studies that choose to count juveniles. Additionally, the establishment of a reliable estimate for minimum adult urchin size is important to consider for future work on urchin reproductive capacities. Collecting urchins across their full adult size range ensures that findings related to urchin reproductive capacity are relevant to entire adult populations.

The sources and effects of food availability on purple urchin reproductive capacity

There were five main drivers of intertidal *S. purpuratus* reproductive capacity that can fit into three categories: internal effects (spawning intensity), resource availability and usage (algae consumed and algae found at collection sites), and population effects (urchin density). Predictors of reproductive capacity are more important to analyze in the summer and fall when urchin GSIs were highest and exhibited greatest variability. The main positive drivers of urchin reproductive capacity were fleshy algae coverage, spawning intensity, and drift algae availability. Negative drivers of urchin reproductive capacity were coralline algae presence in an urchin's stomach and non-algae coverage. Spawning intensity is the only significant predictor that is not directly related to urchin food availability.

Previous studies have shown that when urchins consume coralline algae, their reproductive capacities are reduced (Meidel & Scheibling 1999), and this study indicated that when urchins were found with coralline in their stomach, they exhibited reduced GSIs. Therefore, the fact that I saw no relationship between GSI and coralline algae coverage suggests that urchins in these areas are not consuming enough coralline algae to negatively impact their reproductive capacity. Therefore, urchins in areas of high coralline algae coverage must have access to an adequate food supply from elsewhere.

One source of sustenance for urchins living in the intertidal is the consumption of fleshy algae growing in the areas where I collected them in the intertidal. Fleshy algae coverage was found to be a positive predictor of GSI in the summer and fall. The lack of a relationship between GSI and fleshy algae cover in the winter and spring can likely be attributed to the low overall coverage of fleshy algae and the low GSI variance in the winter and spring. Fleshy algae often exhibits an annual cycle of blade senescence in the winter, and this, coupled with the January 2023 wave of atmospheric rivers to central California removed a large portion of fleshy algae at collection sites (Haberman pers. obs.). Food availability is tightly correlated with urchin reproductive capacity (Lau et al. 2009, Dodge & Edwards 2012), and urchins consuming fleshy algae are known to exhibit higher reproductive capacities (Meidel & Scheibling 1999). Therefore, the positive relationship between fleshy algae coverage and urchin GSI in this study indicates that a portion of intertidal urchin diet includes fleshy algae that is attached to the substrate. Moreover, sites located inside Monterey Bay exhibited a much stronger relationship between fleshy algae coverage and GSI that sites located outside Monterey Bay. This indicates that the diet for urchins located outside Monterey Bay may differ from the diet of urchins located within Monterey Bay, where intertidal areas are protected from wave exposure by the Monterey Peninsula. Bustamante & Branch (1996) showed that intertidal areas along protected shorelines experienced less drifting algae from the subtidal compared to intertidal areas along exposed shorelines. Urchins living at protected sites within Monterey Bay may then rely more on algae originating from the intertidal rather than drifting algae, thus explaining why the relationship between intertidal fleshy algae and GSI was stronger at sites protected within Monterey Bay (Fig. 24). Conversely, data from Rodríguez (2003) indicated that the highest levels of drift algae occurred at intertidal areas where wave action was not strong. Further discussion of drift algae can be found below.

Since fleshy algae growing in the quadrats where urchins were collected did not explain a large portion of GSI variance, it is likely that urchins were consuming food not captured in quadrat algae data. Another potential source of food for urchins in addition to algae growing where they were collected from include algae growing in nearby intertidal areas that were not quantified in the 1 m^2 quadrats. Movement data on *Strongylocentrotus purpuratus* is not widely available, but *S. droebachensis* has been show to move between 0.4 m – 1.7 m per day (Dumont et al. 2006) and *Mesocentrotus franciscanus* has been shown to move between 0.1 m – 0.5 m per day (Mattison et al. 1977). Due to this relatively low rate of movement, it is not likely that urchins consumed algae far from where I found them in time for food consumption to be reflected in reproductive capacity results. To confirm this, future studies should assess movement rates of *S. purpuratus* and analyze correlations between reproductive capacity of urchins and algae growing from successively further away locations from where urchins were collected.

A final hypothesis for where intertidal urchins are obtaining their food suggests that intertidal urchins consume drift algae to supplement their diet. This mechanism for food procurement has much more support and was reflected by the results of this study. Subtidal urchins are widely known to consume drift algae (Vadas 1977, Ogden et al. 1989, Vanderklift & Kendrick 2005, Vanderklift et al. 2009, Britton-Simmons et al. 2009, Kelly et al. 2012), but the influence of drift algae on intertidal urchins has only been documented to be important in *Tetrapygus niger*, a species present in the southern hemisphere (Rodríguez 2003). Similarly, while Basch and Tegner (2007) indicated that intertidal populations of *S. purpuratus* likely feed on drift algae, drift algae abundances in the intertidal in this study were not high enough to support the dense populations of intertidal urchins that were often less reproductive than those living in the subtidal.

The results from this study indicate that drift algae is an important part of intertidal urchin diets, with urchins from higher drift availability sites exhibiting higher GSIs (Fig. 22). Factors such as wave exposure (Bustamante & Branch 1996, Rodríguez 2003), bottom topography, water movement, substrate (Gerard 1976), and proximity to subtidal kelp forests (Rodríguez 2003) can affect drift algae availability at a site. Understanding these factors in areas where intertidal urchin populations are dense is therefore important to predicting the reproductive capacity of these populations. Wave exposure alone was not sufficient to explain drift algae abundance in this study, as sites protected from wave exposure within Monterey Bay experienced high (Otter Cove), medium (Cannery Row), and low (Hopkins) drift algae abundances. Similarly, sites exposed to high wave action were seen to have both high (Pt. Pinos, Carmel Pt.) and medium (China Rock, Pescadero Pt., Pt. Lobos, Soberanes Pt) drift algae abundances. Rodríguez (2003) asserts that lower wave exposure is conducive to high intertidal drift accumulation. The results from this study that showed that urchins at lower wave exposure sites rely more heavily on non-drift intertidal algae defy these findings and suggest that more factors are at play. A potential mechanism for the difference in the reliance on fleshy algae between urchins at protected (inside Monterey Bay) and exposed (outside Monterey Bay) sites may be differences in the foraging behavior of urchins located at protected and exposed sites. Urchins have been shown to exhibit reduced movement (and therefore less time spent foraging) when exposed to greater wave heights (Lissner 1980, Lauzon-Guay & Scheibling 2007). Therefore, urchins at more exposed sites may be more reliant on drift algae landing where they are compared to urchins at protected sites that can spend time foraging on exposed rock.

Future studies should explore the impact of a multitude of factors on drift algae abundance. When collecting urchins, I did not note whether or not an urchin was collected from a tidepool or not, and drift algae surveys encompassed large areas within the rocky intertidal. However, it is possible that differences in topography (i.e. tidepools) at small spatial scales within a site cause large differences in drift algae accumulation, even in areas that are close to one another. Similarly, proximity to kelp forests and/or offshore kelp density should be noted in future analyses. Studies aiming to test for interactions and combinations of effects between many different environmental variables should limit sampling to specific areas in few (or one) sites over short time periods. Site-wide differences in temporal trends in both algae growth and urchin reproductive cycles can add complexity to the responses of urchin reproductive capacity to different environmental variables.

Beyond the need for more variables collected in future studies, there were methodological limitations in the way I collected my drift algae data. First, drift algae surveys were only done during the spring and winter, when urchin GSIs exhibited low variance and low values. Future research explicitly examining the role of drift algae in intertidal urchin diet should complete more temporally exhaustive drift algae surveys. Additionally, the positive relationship seen between drift algae abundance and fleshy algae coverage at a site (Fig. 23) indicate that much of the drift algae seen in surveys was likely growing in the intertidal, not the subtidal. This makes it difficult to isolate the origin of drift algae in surveys. My data showed that some of the species existing as drift algae in surveys are strictly subtidal species (e.g. *Macrocystis pyrifera*). This finding indicates that while it is likely much of the drift algae seen in surveys originated from the intertidal, a portion of intertidal drift algae must have originated from the subtidal. Since it is likely that urchins rely on drift algae for a large portion of their diet, it is important to know the origin of this drift algae in order to make predictions for where intertidal communities are more likely to be able to support highly reproductive urchins (intertidal areas with high amounts of fleshy algae or intertidal areas near subtidal kelp forests).

Comparing subtidal and intertidal urchin drivers of reproductive capacity

It is clear that algae, in the form of drift and growing in the intertidal, is important for urchin reproductive health. However, in order to fully understand the importance of this finding, it is necessary to compare what I found in the intertidal to what we know about subtidal urchin reproductive capacity in relation to food availability.

Most of the research regarding purple urchin reproductive dynamics has been done on subtidal urchins; it is important to directly compare what is known to affect urchin GSI in the subtidal to what I have found affects GSI in the intertidal. In the subtidal, there is a clear and strong positive relationship between GSI and fleshy algae coverage and a negative relationships between GSI and coralline algae coverage and GSI and urchin density (Smith & Garcia 2021). These correlations suggest that urchins in the subtidal are largely consuming algae that is growing near where they live. However, in the intertidal, there was a positive relationship between fleshy algae and GSI (only at protected sites) and no relationship between GSI and coralline algae coverage and GSI and urchin density. Thus, we cannot apply the same response to intertidal urchin populations as we have to subtidal urchin populations. In subtidal urchin barrens, urchins are largely consuming coralline algae, and live in higher densities, and therefore exhibit low GSIs (Pearse et al. 1970, Smith & Garcia 2021). In kelp forests, where urchins can more readily eat kelp and other fleshy algae and live at lower densities, they exhibit higher GSIs. This simple dichotomy does not exist in the intertidal where the mechanism for reproductive capacity is complicated by the ability of intertidal urchins to avoid consuming coralline algae even in areas where coralline algae is the dominant algae growing in the intertidal. My thesis research suggests that urchins in the intertidal are likely consuming drift algae, allowing them to maintain a strong reproductive output despite living in high densities of predominantly coralline-covered habitat.

It is important to note that urchins in the intertidal were seen at densities ten times higher than those seen in the subtidal surveys and therefore likely represent a higher reproductive source compared to subtidal populations. However, intertidal urchins are often smaller than subtidal urchins (Basch & Tegner 2007), and therefore have smaller gonads and a smaller per capita reproductive output. Despite intertidal urchins' smaller size and individual reproductive capacity, due to their densities their overall gonad production (and therefore reproductive capacity) per m^2 is far higher in the intertidal compared to the subtidal, especially at very urchin dense sites such as Pescadero Pt., Carmel Pt., and Cannery Row (Fig. 25). Therefore, established subtidal dynamics do not apply to intertidal habitats. Intertidal urchins live in denser populations, in areas that look like subtidal urchin barrens (with high coralline algae coverage), but still exhibit relatively high reproductive capacities. Therefore, intertidal urchins represent an important potential source population for subtidal urchin barrens and must be considered for inclusion in kelp restoration efforts that involve the removal of urchins.

Management efforts aimed to restore kelp forest ecosystems are almost exclusively focused on subtidal urchin and kelp populations and include the transplanting (Watanuki et al. 2010), killing (Leighton et al. 1966, Wilson & North 2009, House et al. 2018), and harvesting (Piazzi & Ceccherelli 2019) of urchin populations. However, if intertidal populations are acting as reproductive refuges, contributing to urchin barren populations with a continual supply of new urchins, they must be considered for restoration efforts to reach full efficacy. Urchin removals and culls are a widespread subtidal management technique that should be employed in the intertidal as well. Using data from this project, we can identify priority areas for urchin removal where urchin densities and drift algae availability is high. Other next steps for this project include examining the recruitment rate of urchin larvae from intertidal urchins into subtidal urchin barrens.

Limitations and Future Work

The intensity with which urchins spawned correlated strongly with urchin GSI (Fig. 14). Spawning intensity was heavily dependent on temporal reproductive cycles, with urchins reaching peak spawning intensity in the fall when GSI was highest. Despite a drop in GSI during the winter collections, spawning intensity was still relatively high. This, coupled with the fact that urchins had depleted much of their gonad mass by spring, with GSIs that were even lower than in winter, indicated that although urchins had depleted much of their gonad mass, they were still actively spawning. Measuring spawning intensity has not been done with regularity in urchin reproductive capacity analyses, so the continuation of spawning after gonad mass depletion is a novel finding and deserves further research. Within a season, there was individual variation as well. Urchins that were spawned more heavily also exhibited higher GSIs (Fig. 14). These individuals were likely more fecund and therefore quicker to spawn upon disturbance (i.e. collection and dissection). The fact that there was individual variation in spawning intensity and that this was correlated positively with GSI introduced a methodological covariate that reduced my ability to assess variation in GSI based solely on food availability and other environmental factors.

Although it is possible that urchins that had higher GSIs were likely more fecund and therefore more likely to spawn upon dissection, it is also possible that as spawning intensity increased, the material properties of the gonad changed (from solid gonad to liquid spawn) and affected GSI. This would indicate that spawning intensity itself increased GSI rather than the two variables depending on reproductive fecundity in parallel (see previous paragraph). It is difficult to determine whether GSI affected spawning intensity (e.g. high GSI urchins were more likely to be spawning) or whether spawning intensity affected GSI (e.g. urchins who exhibited high spawning intensities were likely to exhibit high GSIs). Despite the interesting implications regarding spawning urchins, it would be best to mitigate spawning entirely when dissecting and removing gonads, as spawning intensity was not the focus of my research questions and changes in gonad mass from gonad to spawn introduce new sources of variation in GSI. Physical stress is suspected to induce spawning in *S. purpuratus* (Leahy et al. 1978) and other invertebrates (Heasman et al. 1995, Grubert & Ritar 2005) and although urchins were transported in water cooled with ice packets, physical stress during dissection is inevitable, so freezing or preserving urchins prior to dissection may better reduce spawning during dissection.

Future work should also consider how interactions between what urchins are consuming and what kind of algae is growing where urchins are living may affect reproductive capacity, but the way my data was collected made this difficult. Differences in both temporal and spatial scales at which urchins consume food introduce complexities that were not controlled for in this study. For example, the presence of coralline algae inside an urchin's stomach indicates recent consumption of coralline algae, but this is simply a snapshot of food consumption and does not necessarily represent an entire summary of an urchin's diet. The tropical urchin *Diadema antillarum* was shown to pass algal material 8-12 hours after ingestion, indicating that what is found in an urchin's stomach at the time of dissection likely represents a very short time period (Lewis 1964). Along the same lines, fleshy algae coverage in the quadrat where urchins are collected does not necessarily represent the food available to urchins, as they are mobile and may not consume food only in the area that they were collected from. As I mentioned previously, urchins likely move less than 0.5 m – 1.7 m per day, depending on species (Dumont et al. 2006, Mattison et al. 1977). However, urchin movement can vary vastly based on size (Dumont et al. 2004), time of day (Parnell et al. 2017, Dance 1987), wave exposure (Lauzon-Guay and Scheibling 2007), water movement (Dance 1987), local habitat (Parnell et al. 2017, Mattison et al. 1977, Andrew and Stocker 1986), and food availability (Dumont et al. 2004, Andrew and Stocker 1986), so it is still important to consider in analyses. These complexities in these data make it difficult to quantify a large amount of variance seen in urchin reproductive capacity and make the interpretation of models including all potential predictors difficult. In the future, it would be interesting to see how the relationship between algae percent cover and GSI changes depending on quadrat size, or how the relationship between coralline algae presence in an urchin's stomach and GSI changes depending on how recently the urchin was exposed to coralline algae that it consumed. In summary, the interpretation of complex models that combine effects of multiple different environmental and biological variables that vary both spatially and temporally and explore interactions between these variables is not necessarily relevant given the amount of variance seen in these data both among individual variables and among subsets of interaction variables. Because of the complexities mentioned above, my analysis is limited to one predictor variable at a time combined with a random effect representing the scale at which the variable was collected at (quadrat or site).

Conclusion

Purple urchins are major contributors of kelp deforestation across the west coast of California. As broadcast spawners, urchins from intertidal areas may be acting as sources for urchins consuming kelp in the subtidal. My study has shown that not only are intertidal urchin populations far denser than subtidal populations, but that they are an important contributor to their reproduction at the level of a metapopulation (through the seeding of subtidal populations with intertidal offspring). In addition, reproductive capacity for intertidal urchins may be linked to the amount of drift algae present where they are living. Therefore, intertidal urchins living near kelp forests are likely to be provided with an abundance of food, increasing the likelihood that they will be able to successfully reproduce and populate subtidal kelp forests with a consistent supply of sea urchins. Therefore, management efforts aimed to restore kelp forests must consider intertidal urchin populations in order for restoration to maximize its efficacy.

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Supplementary Material

Table 1A. Percent of urchins with coralline algae in their stomach and spawning level for each season of urchin collections.

	Spring		Winter		Summer		Fall	
Site	% with coralline in stomach	Spawning Level (± SE)	% with coralline in stomach	Spawning Level (± SE)	% with coralline in stomach	Spawning Level (± SE)	% with coralline in stomach	Spawning Level (± SE)
All Sites	76.0	1.52 (± 0.05)	85.0	2.43 (± 0.07)	33.6	1.61 (± 0.06)	35.8	2.92 (± 0.09)
Cannery Row	76.9	1.58 (± 0.15)	55.6	3.44 (± 0.23)	30.8	2.08 (± 0.21)	32.0	2.16 (± 0.21)
Hopkins	80.0	1.24 (± 0.09)	96.3	1.96 (± 0.16)	25.0	1.00 (± 0.00)	36.0	2.68 (± 0.28)
Otter Cove	68.0	1.84 (± 0.26)	88.5	2.54 (± 0.19)	7.69	2.27 (± 0.30)	24.0	3.80 (± 0.27)
Pt. Pinos	68.0	1.80 (± 0.14)	96.0	2.24 (± 0.12)	39.3	2.18 (± 0.21)	0.0	2.64 (± 0.21)
China Rock	84.0	1.56 (± 0.10)	80.0	1.60 (± 0.12)	10.7	1.21 (± 0.08)	38.5	4.08 (± 0.27)
Pescadero Pt.	76.0	1.44 (± 0.12)	92.6	2.33 (± 0.11)	42.3	1.08 (± 0.05)	36.0	3.32 (± 0.19)
Carmel Pt.	70.0	1.70 (± 0.16)	75.0	2.58 (± 0.19)	28.0	1.96 (± 0.20)	12.0	2.40 (± 0.28)
Pt. Lobos	92.0	1.48 (± 0.15)	88.0	2.52 (± 0.22)	52.4	1.19 (± 0.09)	64.0	2.16 (± 0.22)
Soberanes Pt.	68.0	1.04 (± 0.04)	92.6	2.63 (± 0.25)	65.5	1.31 (± 0.09)	80.0	3.00 (± 0.26)

Table 2A. Quadrat percent coverage for each site during each season during the 2022-2023 collection seasons.

	Site	All Sites	Soberanes Pt.	Pt. Lobos	Carmel Pt.	Pescadero Pt.	China Rock	Pt. Pinos	Otter Cove	Hopkins	Cannery Row
Spring	% Fleshy Algae (± SE)	23.41 (± 2.32)	33.40 (± 6.26)	21.78 (± 5.14)	33.79 (± 10.14)	11.83 (± 4.67)	19.46 (± 6.53)	26.09 (± 5.00)	32.83 (± 6.47)	13.49 (± 9.24)	20.05 (± 5.52)
	% Coralline Algae (± SE)	20.61 (± 2.10)	32.61 (± 3.91)	37.30 (± 8.95)	28.86 (± 3.78)	22.63 (± 5.68)	12.81 (± 4.76)	11.07 (± 3.28)	21.15 (± 4.95)	10.29 (± 3.24)	10.43 (± 1.61)
	% Crustose Non-coralline (± SE)	17.64 (± 1.73)	6.58 (± 2.00)	15.32 (± 6.23)	11.00 (± 3.00)	17.39 (± 4.65)	17.88 (± 3.07)	27.62 (± 4.35)	28.08 (± 4.98)	18.64 (± 7.88)	14.92 (± 1.85
	% Non-Algae (± SE)	34.27 (± 3.33)	25.56 (± 6.17)	22.14 (± 9.71)	25.35 (± 5.72)	31.13 (± 6.81)	47.47 (± 7.12)	30.61 (± 7.81)	13.41 (± 2.98)	56.37 (± 15.31)	54.60 (± 6.31)
Winter	% Fleshy Algae (± SE)	18.90 (± 1.68)	11.53 (± 3.74)	14.81 (± 4.78)	26.69 (± 2.53)	9.92 (± 3.38)	17.95 (± 4.40)	32.92 (± 3.79)	20.12 (± 4.06)	16.01 (± 6.49)	20.18 (± 5.10)
	% Coralline Algae (± SE)	25.84 (± 2.81)	32.50 (± 7.60)	49.73 (± 11.82)	19.25 (± 8.61)	27.64 (± 7.93)	30.61 (± 1.73)	28.21 (± 5.96)	23.95 (± 10.07)	8.31 (± 2.13)	12.35 (± 2.07)
	% Crustose Non-coralline (± SE)	19.96 (± 2.01)	16.82 (± 1.30)	10.01 (± 4.80)	25.01 (± 7.78)	23.06 (± 3.94)	14.95 (± 2.39)	8.99 (± 3.68)	37.16 (± 9.35)	17.82 (± 5.45)	25.84 (± 2.67)
	% Non-Algae (± SE)	34.07 (± 2.79)	39.15 (± 11.26)	25.45 (± 9.77)	29.05 (± 4.32)	39.37 (± 7.82)	34.31 (± 3.60)	27.75 (± 6.41)	16.21 (± 6.58)	53.72(± 9.93)	41.63 (± 5.65)
Summer	% Fleshy Algae (± SE)	35.97 (± 3.89)	21.40 (± 8.32)	38.86 (± 7.28)	64.17 (± 10.12)	19.58 (± 12.01)	48.82 (± 8.06)	36.51 (± 8.06)	61.42 (± 8.59)	19.43 (± 8.50)	13.39 (± 6.03)
	% Coralline Algae (± SE)	16.82 (± 2.49)	35.14 (± 5.13)	43.30 (± 9.40)	11.73 (± 3.38)	28.68 (± 7.39)	8.34 (± 3.28)	5.55 (± 1.09)	7.23 (± 1.85)	8.96 (± 2.69)	5.29 (± 1.38)
	% Crustose Non-coralline (± SE)	13.78 (± 2.08)	3.93 (± 1.72)	6.87 (± 5.09)	5.15 (± 0.83)	7.44 (± 4.22)	15.31 (± 3.57)	23.43 (± 4.47)	15.33 (± 6.31)	41.52 (± 2.28)	9.53 (± 4.50)
	% Non-Algae (± SE)	30.73 (± 3.62)	38.77 (± 6.62)	11.27 (± 4.88)	14.87 (± 5.28)	44.29 (± 12.01)	26.76 (± 9.24)	28.78 (± 3.42)	7.06 (± 2.54)	28.21 (± 4.55)	71.34 (± 7.62)
Fall	% Fleshy Algae (± SE)	35.39 (± 3.05)	21.13 (± 5.80)	32.07 (± 8.63)	60.43 (± 4.80)	30.31 (± 8.72)	45.71 (± 4.26)	47.50 (± 7.04)	38.86 (± 8.22)	12.43 (± 7.72)	30.11 (± 9.99)
	% Coralline Algae (± SE)	22.03 (± 2.59)	40.58 (± 7.72)	40.75 (± 7.45)	16.95 (± 6.81)	35.47 (± 8.20)	17.92 (± 3.24)	9.19 (± 3.45)	21.60 (± 6.02)	10.65 (± 1.19)	5.11 (± 1.34)
	% Crustose Non-coralline (± SE)	14.76 (± 1.65)	8.99 (± 3.12)	8.74 (± 3.69)	11.84 (± 3.82)	9.38 (± 3.40)	8.70 (± 4.40)	29.65 (± 5.38)	15.53 (± 6.06)	14.69 (± 3.32)	25.35 (± 1.97)
	% Non-Algae (± SE)	25.61 (± 3.03)	28.94 (± 11.81)	16.54 (± 4.90)	9.75 (± 1.33)	24.24 (± 8.21)	25.47 (± 3.21)	13.66 (± 4.99)	16.56 (± 4.82)	55.89 (± 9.12)	39.43 (± 10.69)

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