

Outbreaks of the purple sea urchin are deforesting reefs in Southern Monterey Bay, California

Undergraduate Research Thesis

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Table of Contents

Abstract.....	2
Keywords	2
Introduction	2
Methods	4
Results.....	6
Discussion	7
Acknowledgements.....	10
Figures.....	11
Literature Cited	21

ABSTRACT

Since 2013, kelp abundance has rapidly declined around Southern Monterey Bay, California. One possible explanation for the sudden loss of kelp forests is the outbreak of voracious sea urchin grazers. When urchin populations are uncontrolled, they overgraze kelp forests, thereby shifting forested habitats to an alternative “barren” state. To evaluate whether the observed kelp declines around Monterey Bay might be attributed to increased sea urchin grazing, subtidal surveys were conducted to estimate the extent of barrens and forests around the region, and to evaluate sea urchin density, behavior (i.e., exposed, concealed) and biomass at depths of observed kelp loss. Also evaluated, was urchin condition (i.e., gonad index) among three habitat types (i.e., kelp forests, barrens and at urchin foraging fronts) as a measure of urchin health and grazing capacity. Purple sea urchins (*Strongylocentrotus purpuratus*) were found to have the greatest densities within barrens, suggesting that *S. purpuratus* exerts a stronger influence on observed kelp loss ($p=0.001$). *S. purpuratus* had a lower gonad index in barrens ($p=0.003$; $p<0.0001$), which likely reflects heightened hunger demands and starvation, leading to their increased foraging activity and exposure. Moreover, because urchin grazing fronts are comprised of only *S. purpuratus*, this suggests that they are fundamentally contributing to kelp deforestation.

Key words: Kelp forests, urchin barrens, ecosystem stability

INTRODUCTION

Species interactions are a fundamental process that shape the structure and function of ecological communities. A common goal in ecology is to understand the ways and magnitude to which one species impacts another, including how such interactions contribute both positively (i.e., feedback loops) and negatively (i.e., predation, competition) to shape the structure of communities. However, the outcome of species interactions at the community-level are non-intuitive. For example, a community can exist in multiple organizational states dependent on environmental conditions and assemblage structure. Alternate stable states describe this ability for a community to exist in multiple configurations (Beisner et al. 2003).

Ecosystem resistance (i.e., the ability for a system to maintain its organizational configuration) and resilience (i.e., the ability for a system to return to its former pre-perturbed state following a disturbance) limit shifts between alternating states (i.e., phase shifts). Both biotic (biological) and abiotic (physical) factors influence transitional thresholds between communities (*referred to as* environmental ‘tipping points’). The interplay of these ecological hurdles have the potential to weaken environmental ‘tipping points’ between stable states, thus compromising community stability and ecological function. However, studies examining the effects of drivers, such as anticipated climate scenarios (i.e., projections made by the International Panel on Climate Change (IPCC)), foresee amplified strength and frequency in disturbances (biotic, abiotic) that encourage phase shifts (Rasher et al., *in review*). Ocean ecosystems, such as habitat-defining temperate kelp forests are particularly susceptible to these changes (Finnegan et al. 2015, Ling et al. 2009, Holbrook et al. 1997).

Localized kelp deforestation is common during large winter storms, but more widespread loss is commonly due to overgrazing by sea urchins (**Fig. 1**). Kelp reduction or loss prompts behavioral changes in sea urchins from passive grazing on drift algae to active grazing on live, attached algae. When drift algae become limited, sea urchins emerge from microhabitats (i.e., cracks, crevices) and actively search for macroalgae. While few studies have recognized the

exact cues leading to overgrazing behavior, many have observed these plant-herbivore interactions (i.e., kelp-urchin interactions). Sea urchin barrens may persist for several years because of intrinsic feedback mechanisms that promote that community configuration (Baskett & Salomon 2014).

Ecosystem regulation, either naturally or guided, may reverse urchin barrens to a forested state. Guided regulation practices include population reduction (culling), translocation, or foraging behavior deterrent (Leinaas & Christie 1996). Natural ecosystem regulation may occur by bottom-up (environmental) or top-down (trophic interactions) control (Hairston et al. 1960). These practices may also be combined. For example, hysteresis by bottom-up control was observed in Southern California following a back-to-back strike of two large El Niño storms, the first removing kelp and the second removing urchins (Ebeling et al. 1985). Once urchins were cleared, kelps re-established. Similarly, overfishing in New Zealand kelp forests reduced large predatory fish (*Pagrus auratus*) and lobsters (*Jasus edwardsii*) to size classes incapable of consuming urchins and resulted in barrens (Babcock et al. 1999). Upon the implementation of Marine Protected Areas (MPA), barrens became limited to areas outside of MPAs by top-down control as predators regained size and numbers (Babcock et al. 1999). These studies highlight the importance of both natural ecosystem function and intervention practices that promote resiliency.

In kelp forest ecosystems, sea otters maintain kelp forests indirectly by top-down control of sea urchin populations (Estes & Palmisano 1974; Estes et al. 1978). Their important trophic role in regulating community structure was realized in the Aleutian Islands (and later Southeast Alaska) following their near-extinction and slow recolonization across the archipelago after the Russian Fur Trade (Estes & Steinberg 1988). The otter-urchin-kelp interaction is a classic example of a 'trophic cascade', or 'the effects of predators that propagate downward through food webs across multiple trophic levels' (Ripple et al. 2016). This interaction initiated a general paradigm to kelp forest communities and resulted in its interest, application, and enlistment of sea otters as an 'endangered' species, globally (Estes & Duggins 1995; Tinker et al. 2017; Doroff & Burdin 2015). Translocation of sea otters along the California coastline have reintroduced kelp forests into some areas, but whether the paradigm may be generalized to the central coast requires cross-examination (Tinker et al. 2017; Estes & Duggins 1995).

To date, the expansive studies surrounding alternate stable states in kelp forest communities have related the sea otter-sea urchin-kelp forest trophic cascade to almost any area in which kelp was lost. However, Monterey Bay, CA, consists of a unique habitat mosaic of barren-forest patches rather than broad spatial scales where nearly entire regions are either complete barren or forests. Otters are present in Monterey, but mesopredators, such as sunflower sea stars (*Pycnopodia helianthoides*), which are known to mediate abundant sea urchin populations alongside otters, are near local extinction (Burt et al. 2018; Rosenthal & Chess 1972; Duggins 1983; Rogers-Bennett 2007). Star populations recently experienced dramatic population reduction and ecological extinction on the eastern Pacific coast between Mexico and Alaska following Sea Star Wasting Disease (Hewson et al. 2014). While Sea Star Wasting Disease (SSWD) manifested differently depending on the affected species, *P. helianthoides* was particularly devastated and has since made little to no comeback compared to previous abundances in Monterey Bay (**Fig. 2**; Jim Watanabe & John Pearse, *pers. comm.*). Another growing concern is the diminishing nutritional quality of sea urchins in barren states. Urchins direct more energy into active grazing and survival (e.g., receiving nutritional input from sources other than kelp) and less into reproduction efforts by dissolving their gonadal mass (Pearse et al. 1970; Rogers-Bennet 2007). Urchins sustain themselves in a near 'dormant' condition having a virtually empty test and can do so for periods up to six months or longer (Rogers-Bennet 2007). Moreover, urchins in barrens receive very little outside predation from otters in Monterey. Because otters exhibit predator choice on urchins of a specific test diameter (>35-40 mm) and

of relative health (determined by their gonadal condition), barrens persist (Estes & Duggins 1995; Botham et al. 2015; Smith et al. *pers. comm.*).

The purpose of this study is to evaluate whether the observed decline in giant kelp (*Macrocystis pyrifera*) density (**Fig. 2**) and area (**Fig. 3**) might be attributable to increased grazing by the red sea urchin (*Mesocentrotus franciscanus*, *prev. Strongylocentrotus*) and the purple sea urchin (*Strongylocentrotus purpuratus*). Based on previous observations, if sea urchins are contributing to the decline of kelp in the Monterey peninsula (i) urchins should occur at depths where kelps are declining, (ii) the density and biomass of urchins should be greatest where kelp has been lost, (iii) these patterns of size distribution, density, and biomass should reflect changes in grazing behavior (i.e., concealed versus exposed), as well as (iv) hunger stress and condition (i.e., gonadal index). Therefore, this survey study was designed to test the following hypotheses: (i) either species of sea urchin that is contributing to kelp declines occurs across the depth range (5-20 m) that kelp has declined, (ii) density and biomass of sea urchins will be lowest in kelp forests, intermediate in barrens, and highest at fronts, (iii) urchins of small test diameters (i.e., >35 mm) will be abundant in the absence of *P. helianthoides*, and the proportion of exposed urchins will be greatest at fronts, intermediate in barrens, and lowest in the forests, and (iv) urchin condition (gonad index) will be highest in forests, intermediate at the fronts, and lowest in barrens.

METHODS

Study System. In Jun-Sept 2017, reefs along 5.23 km of coastline between Breakwater and Point Pinos (**Fig. 4A, 4B**) were sampled in Southern Monterey Bay, California (36° 36' 14.2344" N, 121° 53' 54.4560" W). Subtidal habitats vary between sand flats, rocky reefs, and pinnacles that extend to the outer continental slope and into the Monterey Canyon. Breakwater faces northeast and is predominantly protected, whereas, sites north of this area and at headlands (Pt. Pinos, Otter Point) are further exposed to open ocean influence. Unlike other systems where kelp forest-urchin barren dynamics have been studied, Monterey offers a unique patchwork mosaic of three fundamental habitat types (i.e., kelp forests, sea urchin barrens, and fronts) that exist adjacent to one another.

Field Sampling Design. Survey sites were selected using a randomization algorithm in ESRI ArcGIS (v. 2017) to identify points on hard substrate within a 5 to 25 m depth range (**Fig. 4B**). A total of 94 points were surveyed for this study. Each survey point was sampled using a random-stratified quadrat sampling design across eight 10-meter long transects. (**Fig. 5**). In a 1m² quadrat, habitat was classified as either kelp forest, barren, or urchin grazing front. SCUBA divers obtained visual density estimates and randomly collected up to 32 *S. purpuratus* and 16 *M. franciscanus* per site. Urchins at/near the two adjacent corners of both quadrats on each transect were collected to randomize the choice of sample. Urchins were stored on ice and transported to Long Marine Lab in Santa Cruz, CA. Upon arrival each urchin was weighed to record wet mass (g) and then injected with 2 to 10 mL (depending on size) of 10% neutral-buffered formalin to fix body tissue. Following fixation, urchins were measured (test diameter, test height) and dissected to remove gonads. All gonads were wet-weighed to the nearest 0.01g.

Distribution. Due to the patchy distribution of habitat types (forest, barren, front, neither) across the survey area, multiple habitat types may occur within a single site. Quadrats isolated variation in habitat type from within sites when comparing the number of observations of *S.*

purpuratus and *M. franciscanus*. In combining quadrats within a site, further site-specific qualities (i.e., quadrat similarities, community structure, depth) could be included and teased apart as potentially influencing factors on species distribution. This also allowed visualization of the habitat mosaic in Monterey Bay separate from urchin densities.

Size Structure. Mean test diameter (mm) from each site was compared between habitat type and across a depth gradient (m).

Density and Biomass. Sea urchin density and/or biomass were used to describe urchin habitat associations (i.e., ecosystem state, site depth), size structure, and behavior (i.e., exposed, concealed). Standalone density estimates may be misleading as a high density of urchins could vary in size and fail to capture full grazing potential. Biomass recognizes individual characteristics including wet weight, test diameter, and test height, but is limited to site subsamples. Combining both density and biomass may strengthen the power of statistical tests, but the potential of bias exists in both metrics. Biomass is summed across individuals collected and dissected at each survey site, while biomass estimates were constructed using species-specific equations. **Eq. 1** was fitted to a previous sample of over 400 purple sea urchins. The r^2 for this equation was 0.97 and the partitioned sum of squares gave $P < 0.0001$. For red sea urchins, **Eq. 2** was derived based upon data collected summer 2017 ($r^2 = 0.94$, $P < 0.001$). This approach included taking the overall mean of urchin test attributes (i.e., individual wet mass, test height, test diameter) and fitting an equation to match the generated slope. Urchin test attributes were measured with calipers to the nearest 0.1 mm, avoiding spines and nodes. In-lab estimates of preserved animals allow sharper accuracy than using calipers in a field setting as urchins clench the tool and create an overestimate (Ebert et al. 2018).

BIOMASS:

$$\text{Eq. 1) (Purple)} = -47.22 * \text{Test Height (mm)} + (\text{Test Height (mm)} - 20.27) * ((\text{Test Diameter (mm)} - 40.81) * 0.06) + 1.94 * \text{Test Diameter (mm)}$$

$$\text{Eq. 2) (Red)} = -84.58 + 0.15 * \text{Test Height (mm)} + (\text{Test Height (mm)} - 22.16) * ((\text{Test Diameter (mm)} - 48.75) * 0.10) + 2.79 * \text{Test Diameter (mm)}$$

(Above). The biomass equations generated for purple (**Eq. 1**) and red (**Eq. 2**) sea urchins.

Behavior. Still photographs from each quadrat were used to characterize urchin behavior. Urchins in the photo frame having at least 51 percent of their test visible were categorized as ‘exposed’. All other urchins counted by divers that were not visible in photos were considered ‘concealed’. Divers were very careful (e.g., turn over rocks, sort through algae) to identify and count all urchins within quadrats. Those hidden in algae from photos were also considered ‘concealed’ because the algae (e.g., coralline) provided cover. A ratio of exposed to concealed (total counted in quadrat) urchins (**Eq. 3**) allowed a behavior comparison between species within habitat types. This equation is bounded between 0 and 1, where 0 means that of all the urchins found were ‘concealed’ and 1 means that of all the urchins found were ‘exposed’.

$$\text{Eq. 3) [Exposed: Concealed Urchins]} = \left[\frac{\text{Total} - \text{Exposed}}{\text{Total}} \right]$$

Eq. 3 The proportion of exposed to concealed urchins. The number of exposed urchins was found by deducting the number of urchins at least 51% visible in video quadrats from the total number (i.e., exposed and concealed) found within that quadrat. This difference was then divided by the total number of urchins (i.e., Exposed + Concealed) found. The exposed: concealed urchin proportion ranges between 0-1.

Gonad Index. Gonad Index (GI) is the proportion of the animal's weight that is comprised by reproductive gonad (**Fig. 6**) and an accurate measure of animal health as the gonad is directly influenced by nutritional input from the environment (Rogers-Bennet 2013, Pearse et al. 1970). Gonad wet mass (to the nearest .01 g) was obtained from animal dissections and combined with urchin test attributes (i.e., test height, test diameter) to calculate GI, under the same methodology of *Conor* (1972). GI was calculated for both species (ranging 0-16.4% in the present data set) and compared across depth (site) and habitat types.

RESULTS

Distribution. The distribution of sea urchins is represented by a quadratic fit of the estimated mean population density/m² (**Fig. 7A**) and calculated biomass (g)/m² (**Fig. 7B**) for both purple sea urchins and red sea urchins across depth zones with 95% confidence intervals ($n_{\text{purple_density}} = 15304$; $n_{\text{purple_biomass}} = 1922$; $n_{\text{red_density}} = 2283$; $n_{\text{red_biomass}} = 169$). The highest densities and biomass of purple urchins occurred at depths that kelp had declined (i.e., at mid depths between 5-15 m) and tapered off at depths both shallower and greater, while red sea urchin biomass and density increased with depth (**Fig. 7A, 7B**).

Size structure. Results from an ANOVA showed purple urchins had a mean test diameter (TD) of 36.75 ± 0.2 mm, whereas red urchins had a mean TD equal to 46.05 ± 0.66 mm. (**Fig. 9**; $F = 181.2$, $DF = 1$, $n = 2091$) (**Fig. 9**). The linear regression with predictions (shaded area) shows a general increase of purple urchins with a smaller TD (5- 35 mm) occupying deeper depths, and larger individuals (>35 mm) in shallower zones (**Fig. 9**; $F < 0.0001$, $DF = 2$). The opposite is true for red urchins. Red urchins of small TD (5-45 mm) were observed in shallower depths than red urchins (**Fig. 9**). A likelihood ratio test (not shown) was used to explore the size-class interaction of urchin species with depth. At a mean site depth of 10.75 m (± 3.5 m), an urchin with an 85 mm TD is 88 percent more likely of being a red urchin ($\chi^2 < 0.0001$, $DF = 1$). An individual with 40 mm TD is 93 percent more likely of being a purple urchin, and of TD equal to 12 mm, 99.5 percent more likely of being a purple urchin. The greatest representation of depth was between 8-8.4 m (N: 181 spp.) and least, 17.4 m (N: 9 spp.; c.f., unsampled depths occurring within the sample range).

Density and Biomass. The distribution of sea urchins were divided into three habitat categories: sea urchin barrens, kelp forests, and fronts. The estimated biomass (calculated using the mean density of species at each site) of urchins per m² as a function of site location are shown in a bubble plot within the study area (**Fig. 10**), where a large bubble size indicates high biomass of a species at that location. Bar graphs of estimated urchin density/m² (**Fig. 11A**; ANOVA, $F = 17.70$, $p = 0.001$) and biomass/m² (**Fig. 11B**; ANOVA, $F = 567.2$, $p = 0.0001$) in barrens, fronts, and forests, show that purple urchins had a greater density and biomass than red urchins. Within their species' category, purple urchin populations (and biomass) were greatest at fronts, intermediate at barrens, and lowest in kelp forest; whereas red populations were greatest in barrens, intermediate at fronts, and lowest in kelp forests (**Fig. 11**). The

observed difference in red density and biomass between fronts and forests was not as distinct as the difference in purple urchins comprising those habitat types.

Behavior. (Eq. 3) showed the proportion (0-1) of exposed urchins (i.e., emergent, actively grazing) to be greatest in barrens. Higher proportions of red and purple urchins in front and forest sites were concealed in cracks and crevices (Fig. 12; ANOVA, $F=13.4996$, $p<0.0001$). Urchin behavior did not change significantly between fronts and forests but was different between species. Approximately 30 percent of purple urchins and 50 percent of red were exposed in fronts and forests. Almost 90 percent of red urchins and 75 percent of purple urchins were exposed in barren states.

Gonad Index. Gonad index (GI) of purple urchins declined with depth, while GI of red urchins increased (Fig. 13; ANCOVA, $p<0.0002$, $F=14.70$, $p=0.002$). Mean purple urchin GI (Fig. 15; ANOVA, $F=13.99$, $p=0.003$) was greatest in kelp forests. In contrast, red urchin GI was higher in barrens (Fig. 15).

The densities of purple (Fig. 16A) and red (Fig. 16B) sea urchins were superimposed onto heat maps of the study area using ArcGIS software (v.2017). Regions range in color between red (high), yellow (moderate), and blue (low) respective to urchin density observations. This metric was similarly applied to represent GI of both purple (Fig. 16C) and red (Fig. 16D) sea urchins. Regions of low gonad indices often lie in regions of high urchin densities for both species (Fig. 17).

DISCUSSION

This study examined distribution (along depth, within ecosystem states), size structure (test diameters, density, biomass), behavior (exposed, concealed), and condition (gonad indices) of purple and red sea urchins within Southern Monterey Bay, CA. Spatial and biological differences found between the species suggest that *S. purpuratus* may greatly influence habitat mosaic patterns (i.e., patches of kelp forests, barrens, fronts). *S. purpuratus* displayed higher densities and biomass than *M. franciscanus* (Fig. 7), as well as more frequently exposed behavior (indicating active foraging) in depth zones of observed kelp decline (Fig. 12). Additionally, in areas of high urchin density and biomass, the mean gonad index (GI) was found to be significantly low (Fig 15), which may indicate decreased nutritional intake within those areas (Pearse et al. 1970; Rogers-Bennet 2007; Druehl & Breen 1986). The observed differences in community structure vary not only between species and space, but through time.

The combination of over 20 years of long-term ecosystem monitoring (Fig. 2) and aerial kelp canopy biomass (Fig. 3) within the study region show a near constancy of kelp forest species abundances up until a sharp deviation in 2013. Kelp abundance fluctuates year-round, given seasonal quantities of light, nutrients, and storm presence. However, in 2013 the decline of kelp was also accompanied by a decline in *P. helianthoides* (Fig. 2). The present study evaluated traits of organismal behavior (i.e., the grazing mode of sea urchins, the foraging location of otters) and population structure that previous studies have deemed vital in considering these interactions (Rogers-Bennet 2007; Stevenson et al. 2016; Estes and Duggins 1995; Duggins 1983; Kenner 1992; Bernstein et al.1981). Consideration of past urchin outbreaks both within and outside the study region was taken, as predatory loss and water changes, both physical (e.g. temperature increase) and chemical (e.g., reduced water quality), additionally hinder these communities and constitute forest-to-barren transitions (Cowen 1986; Gerard 1976; Pearse and

Hines 1979; Tegner & Dayton 1991, Foster & Schiel 2010; Bodkin et al. 1987; Pearse & Hines 1987; Tegner & Dayton 1981; Watanabe 2018; Watanabe & Harrold 1991).

The higher density of large purple urchins at shallow depths (**Fig. 7A**) might occur for several reasons. For instance, distribution may be limited by physical attributes (e.g., the larger body of red urchins creates drag in high water velocity environments, like nearshore) as well as species-specific predation pressure (Rogers-Bennet 2013; Stevenson et al. 2016). The cumulative influence of multiple predators with common prey demonstrate their separate contributions on prey population dynamics such as size structure or composition (Owen-Smith & Mills 2008). In British Columbia, sunflower stars mediate small urchin size classes, while otters the upper size distribution (Burt et al. 2018). Moreover, *Foster et al. (2015)* found *P. helianthoides* prefer purple urchins to red urchins 98% of the time in lab trials. This may be due to the smaller test size and spines of *S. purpuratus* compared to *M. franciscanus*, which may ease handling. Additionally, *P. helianthoides* elicits a strong escape response in many *Strongylocentrotus* species, and its presence drastically suppresses the grazing pressure of green urchins (*Strongylocentrotus drobachiensis*) and small red urchins (Duggins 1983; Watson & Estes 2011; Freeman 2006). The loss of *P. helianthoides* may be reflected by a greater biomass of purple urchins compared to red urchins (**Fig. 7, 10, 11**) and upper and lower size class presence of red urchins (**Fig. 8**). However, this remains inconclusive and conditional upon population recovery.

Predatory influence by sea otters may further contribute to the larger density and biomass of purple sea urchins at shallow depths. Though capable of reaching depths up to 330 feet, otters typically make foraging dives lasting up to two minutes in less than 60 feet of water, conditionally dependent on region, gender, and prey availability (Bodkin et al. 2004). To compound this, otters are dietary specialists and exhibit predator choice (Botham et al. 2015; Estes et al. 1982). They not only selectively prey on sea urchins of test diameters >35-40 mm but select relatively 'healthy' urchins as determined by their gonadal condition (Estes & Duggins 1995; Smith et al. *unpublished data*). The mean test diameter of purple urchins was 36.75 ± 0.2 mm (**Fig. 8**) with a high density and biomass of gonad-rich individuals observed at average foraging depths within kelp forests (**Fig. 7, 13, 14**). Because fewer red urchins of optimum TD (i.e., >35-40 mm) and health occurred in shallow depths (**Fig. 9, 13, 14**) might suggest that otters consume red sea urchins more often than purple urchins. Urchin gonadal condition is dependent on algal (food) abundance; in barrens, decreased nutritional intake results in poor gonadal condition and was true for purple urchins, but not reds (**Fig. 14**) (Pearse et al. 1970). Therefore, the difference in TDs between habitat type may be explained by otter foraging tactics.

Otters often bring up, test and then discard prey items, including sea urchins that may be unprofitable (Smith et al. *unpublished data*; Tim Tinker, *pers. comm.*). This foraging tactic informs consecutive prey selection. Factors such as seasonality (e.g., in spring, urchins have spawned and are calorically empty) also affect prey profitability and influence trial-and-error behavior in sea otter foraging (Tim Tinker, *pers. comm.*). It is likely that this phenomenon also means that otters always need be "testing" different prey types (to monitor changes in abundance or profitability) and is one of the reasons that even dietary specialists still include small amounts of non-preferred prey (e.g., gonad-poor urchins) in their diets (Tinker et al. 2012; Smith et al. *pers. comm.*).

Higher proportions of sea urchins in front and forest sites were concealed (**Fig. 12**). This behavior was expected in forests but having found fewer exposed urchins in fronts than barrens may be a sampling area bias. As the transition zone, fronts are not as intuitive or frequent as

barrens or forests (Steneck 2002). They present a moving target and for this reason, offer a proxy of ecosystem collapse (Lauzon-Guay 2008; Konar & Estes 2003).

The determinants of community assemblage in Monterey may be the result of a species' biological ability to navigate changes in its environment. Differences existing in urchin distributions and health, suggest that urchins are contributing disproportionately to deforested states. Though both species are known to overgraze kelp and were similarly observed to increase in abundance following kelp loss (Circa 2014), the magnitudes of population increase differ by an order of 14:1 (**Fig. 2**). However, both populations subtly dropped in 2015, perhaps given the frequency of storms produced by the 2015-2016 El Niño. El Niño storms additionally facilitate recruitment in purple sea urchins, likewise, reduce kelp area and red sea urchin populations due to temperature sensitivity and physical disturbance (**Fig. 11, 12**; Ebert et al. 2018; Kenner 1992; Schiel et al. 2004; Tegner & Dayton 1991). This may be revealed through long term monitoring of urchin population dynamics between storm periods.

This study suggests a positive relationship between algal abundance and gonad index, particularly in purple sea urchins. Habitat type appeared to be most influential, but density, biomass, species, depth, and behavior also contribute to observed variation in the distribution and grazing capacity of red and purple sea urchins. Competition for space plays an important role in the distribution and abundance of purple urchins, and although the species overlap, purple urchins often dominate in both the intertidal and subtidal zones because they tolerate physical-chemical changes and swell action, while the reds are more abundant beyond five meters (here, 15 m) depth (Workman, 1999; Parnell et al. 2017). Several studies (including the present study) additionally aim to establish relationships between food availability (i.e., drift algae), urchin behavior, and physiology, as well the communities that they influence (Lees 1970; Pears et al., 1970; Mattinson et al. 1977; Dean et al. 1984; Ebeling et al. 1985; Harrold and Reed 1985). Fewer studies emphasize competition for space and niche differentiation (i.e., space partitioning, resource partitioning) between interacting echinoderm species (Pallerino-Nayar et al. 2008; Beas-Luna and Ladah 2014; Duggins 1981; Parnell et al. 2017).

This study highlights the dynamics of herbivores and their ability to structure ecosystems. The timing of biotic and abiotic factors may weaken stability, but ecosystems are self-sustaining. Those having alternative stable states such as kelp forests, exemplify a multi-faceted capability to persist through time. Whether they do so as a highly productive system remains dependent upon species interactions with one another and the changes they incur.

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FIGURES



KELP FOREST STATES

Fig. 1 Rocky reefs in Monterey Bay occur in a patchy distribution of three ecosystem states. **(A)** Kelp forests and **(B)** sea urchin barrens are alternating stable states. **(C)** Sea urchin fronts are a transitional margin between the two. Images obtained from Michael Langhans.



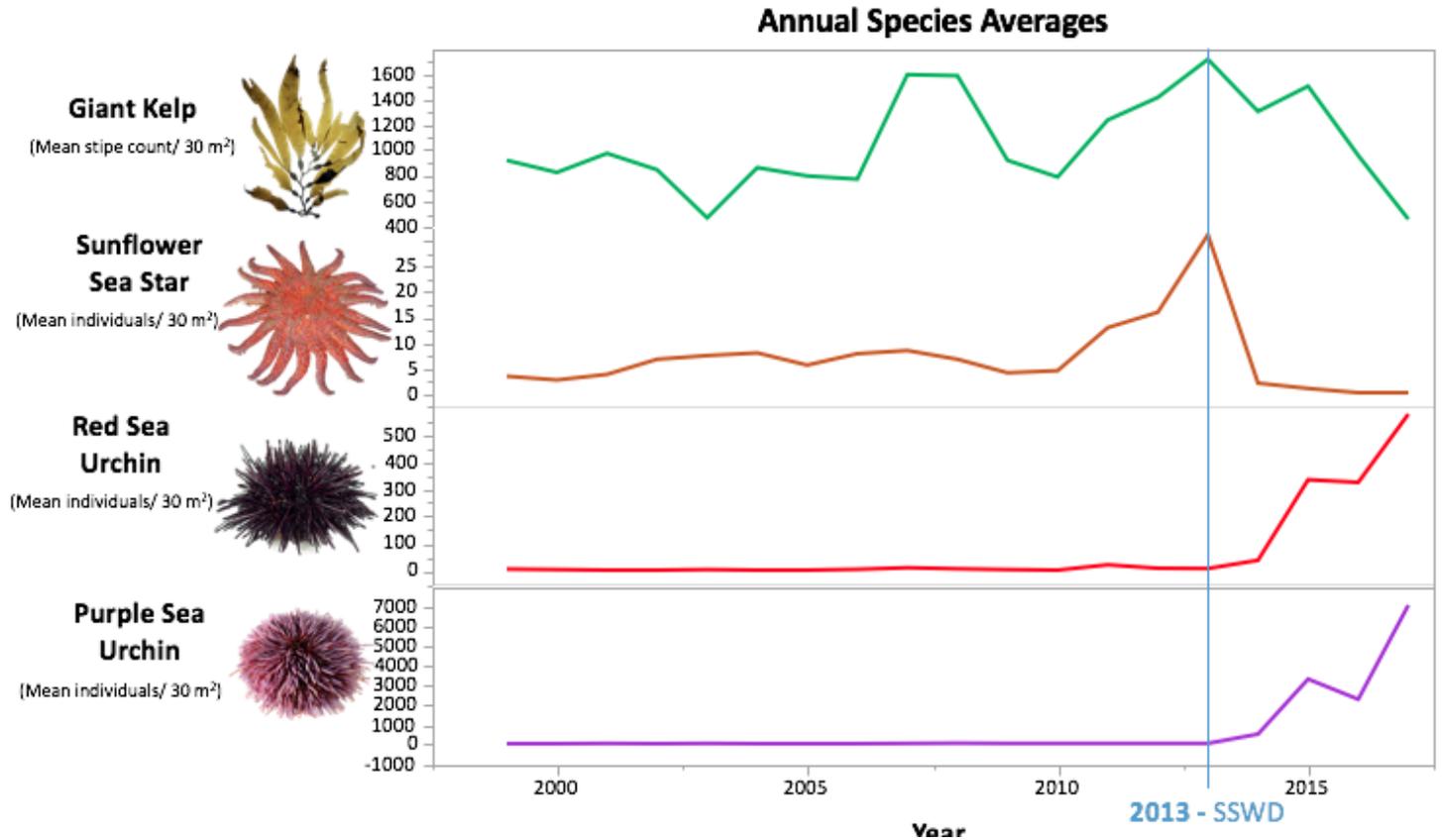


Fig. 2. Between 1999 and 2017, the annual species averages of kelp (mean stipe ct./ 30 m²), sunflower sea stars (mean no. indiv./ 30 m²), red sea urchins (mean no. indiv./ 30 m²), and purple sea urchins (mean no. indiv./ 30 m²), were collected and estimated by the Partnership of Interdisciplinary Science of Coastal Oceans (PISCO) from five sites overlapping with our study and depth (5-20 m) range of Monterey Bay, CA. Sea star wasting disease (SSWD) affected the Monterey peninsula in 2013.

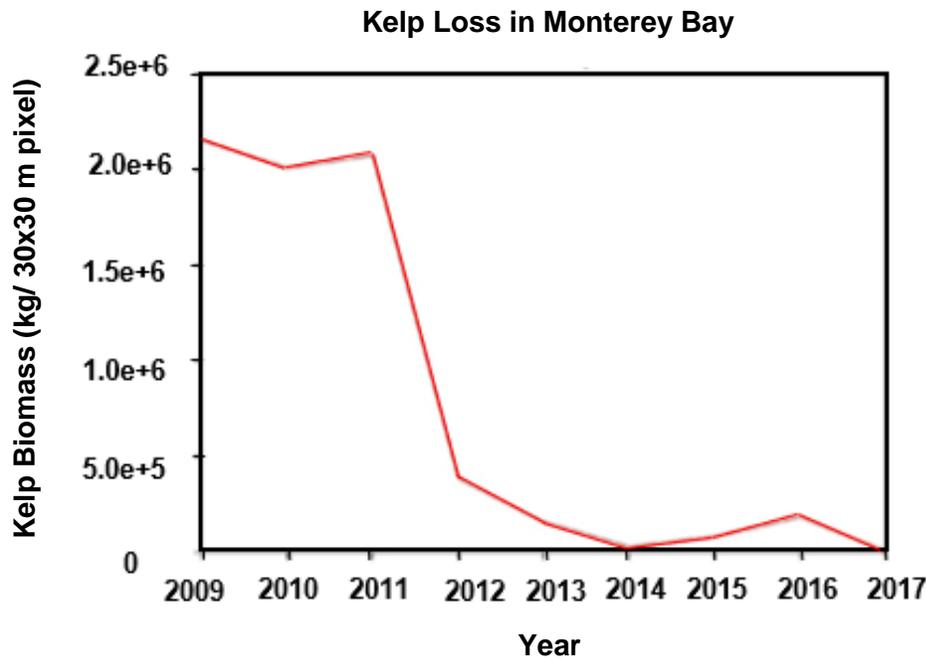


Fig. 3 (left). Kelp biomass (kg/30x30 m pixel) in Monterey Bay, CA, between 2009 and 2017. Graph produced via satellite imagery using ArcGIS software (v. 2017; obtained from Emily Saarman).

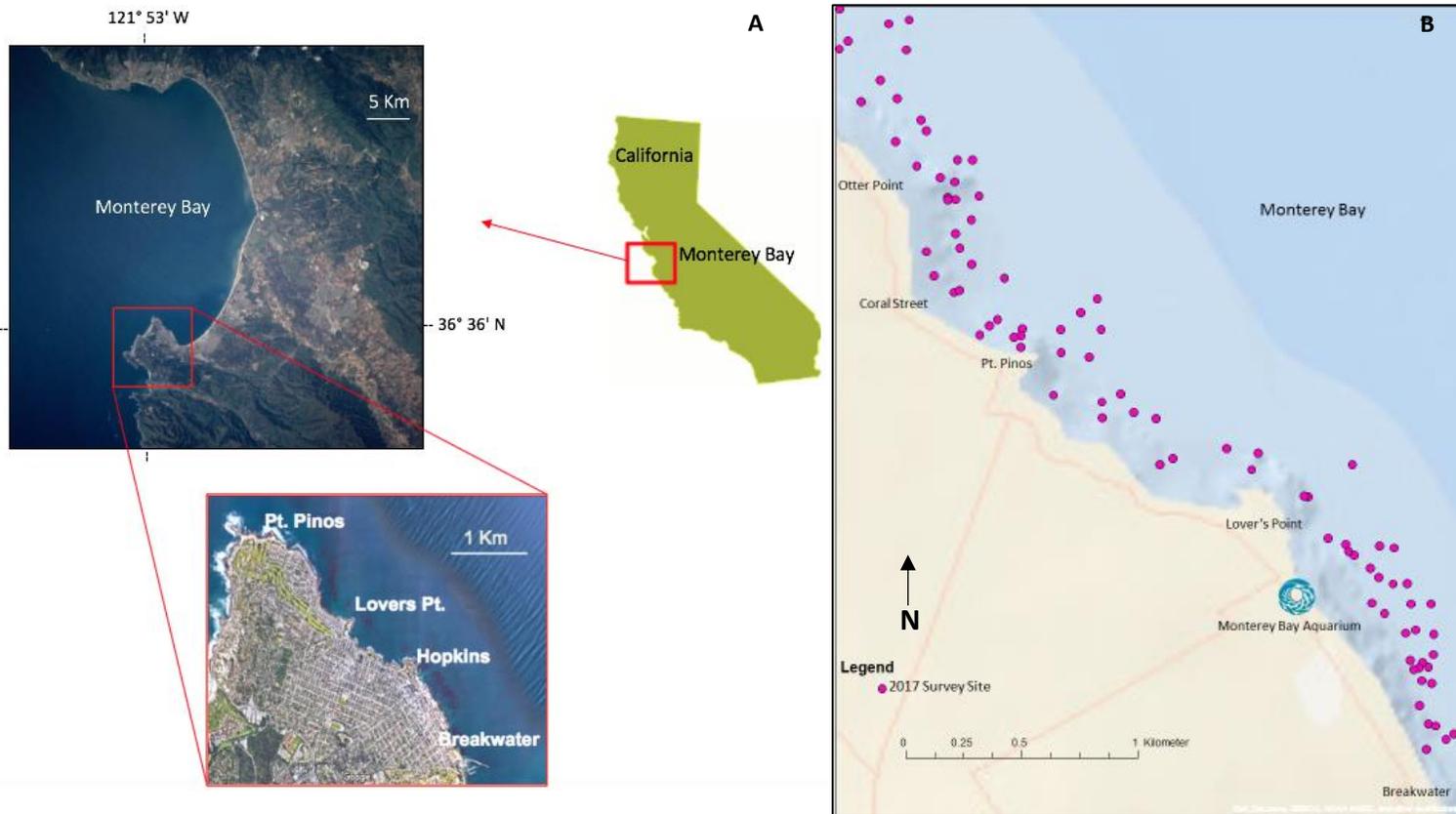


Fig. 4. Study area in Monterey Bay, CA (**A, left**). 2017 survey sites were randomly selected using ArcGIS programming (v. 2017); ArcGIS identified subtidal reefs located between Breakwater and Otter Point in a 5-25 m depth range (**B, right**).

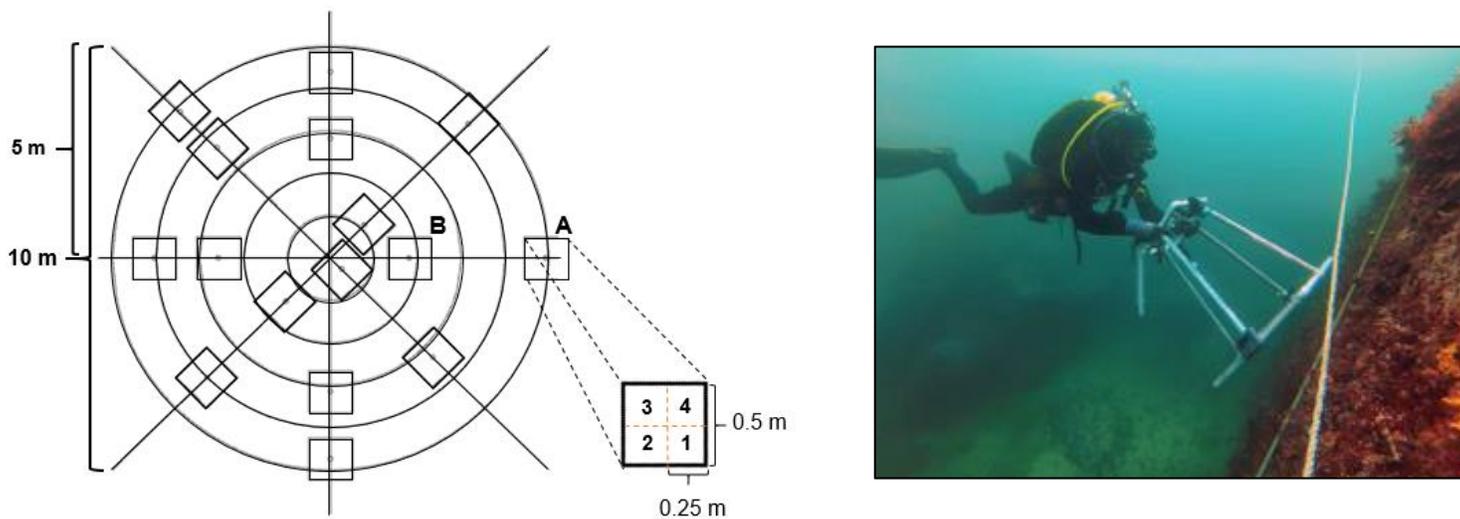


Fig. 5. (Left) Schematic of 10 m circular sample area. Eight 5-m radial transects diverged from a center (GPS) point. On each transect, a 0.5 m² quadrat was placed in four locations (1-4) to cover a 1 m² area (A, B). Urchins were collected from the outermost corners of quadrats (1A, 4A) on each transect. (Right) A diver holding the camera rig (nicknamed 'The Lantern', after the urchin jaw apparatus, Aristotle's Lantern) during a survey. 'The Lantern' was constructed from PVC pipes, weighted at the base, and equipped with a GoPro Hero 4. Later versions included mounted lights and a higher-resolution camera.

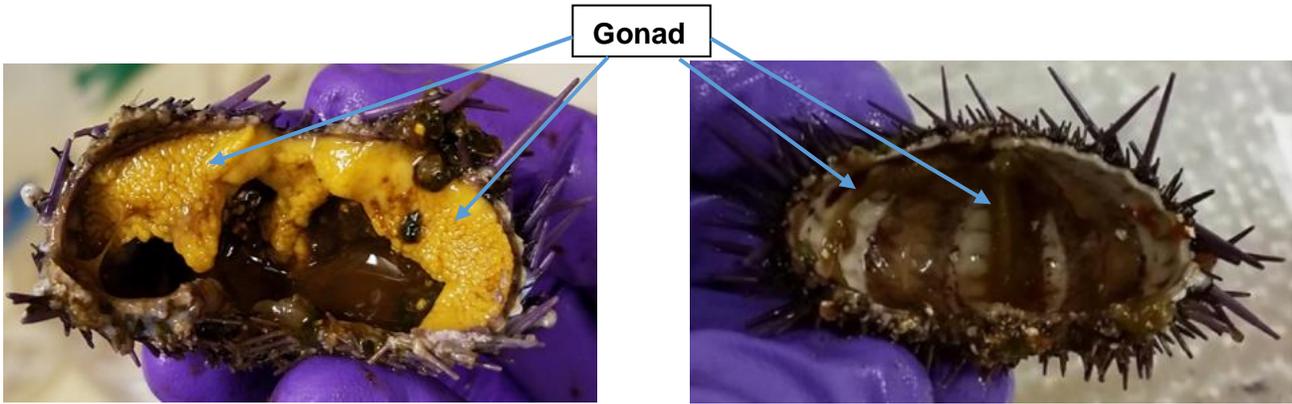


Fig. 6 (above). Purple urchin with visibly high gonad index from kelp forest or front site (**left**) and low gonad index from barren site (**right**).

Urchin Distribution Across Depth (m)

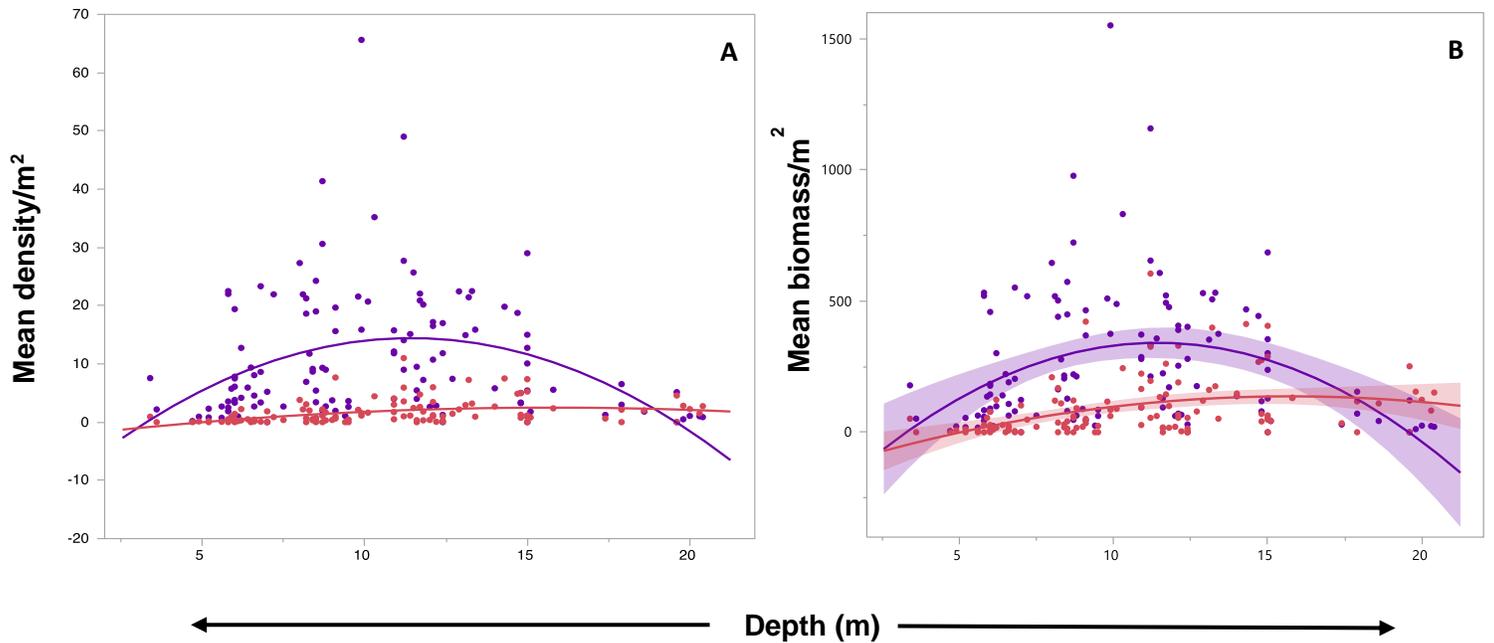


Fig. 7. The estimated (A) mean population density (individuals/m²) and (B) biomass (g/m²) of purple and red sea urchins across depth zones. Urchin species are represented by color in all graphs (e.g., red dots, red urchins; c.f., Fig. 8, 9).

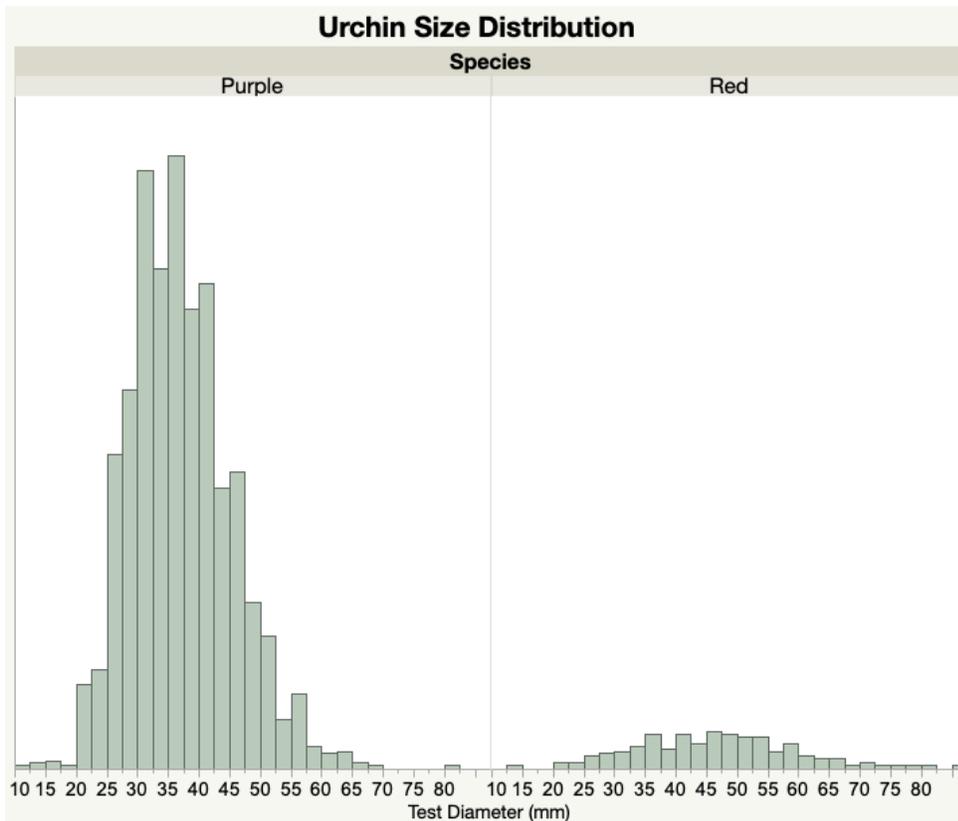


Fig. 8 (Left). Test diameter (mm) size distribution for subsampled (N: 2091) purple (n= 1922) and red (n= 169) sea urchins. Mean TD of purples: 36.75 ± 0.2 mm; mean TD of reds: 46.05 ± 0.66 mm.

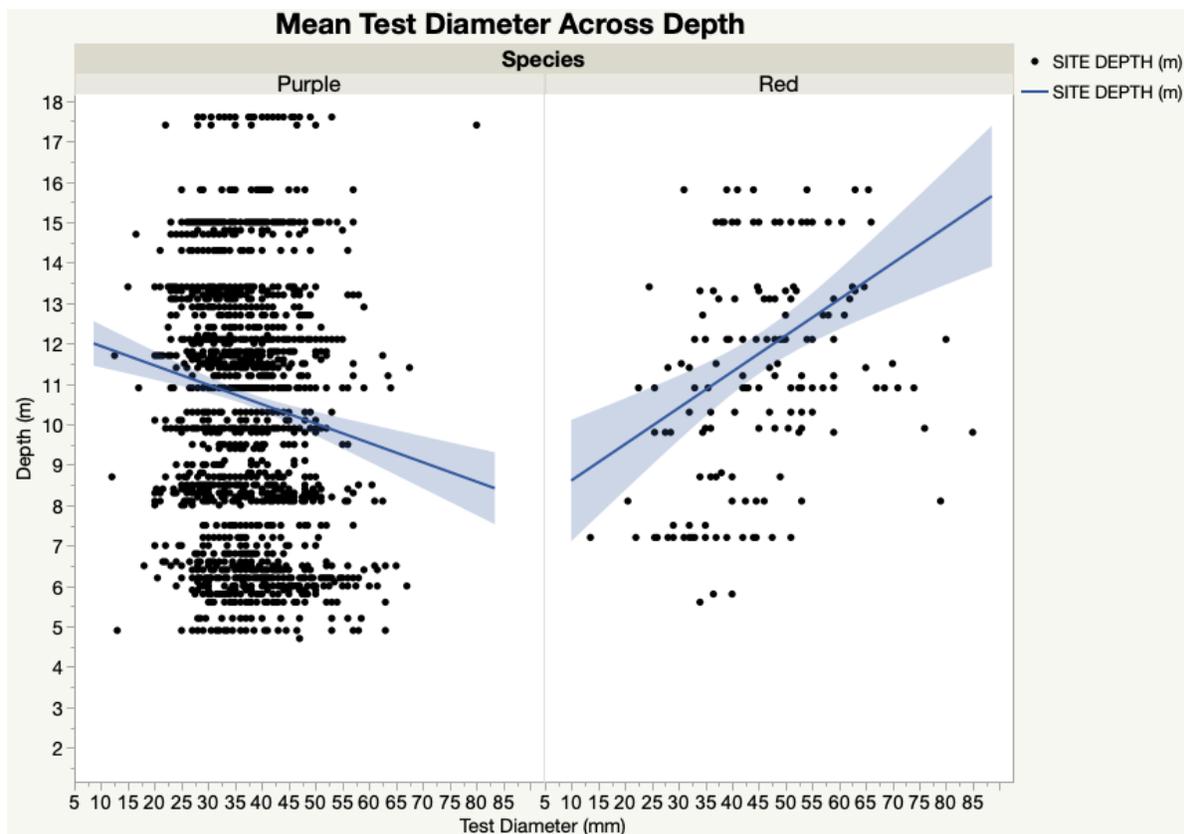


Fig. 9 (Below). Relationship of urchin test TD (mm) with depth (5-25 m).

Urchin Spatial Distribution Across Habitat Type

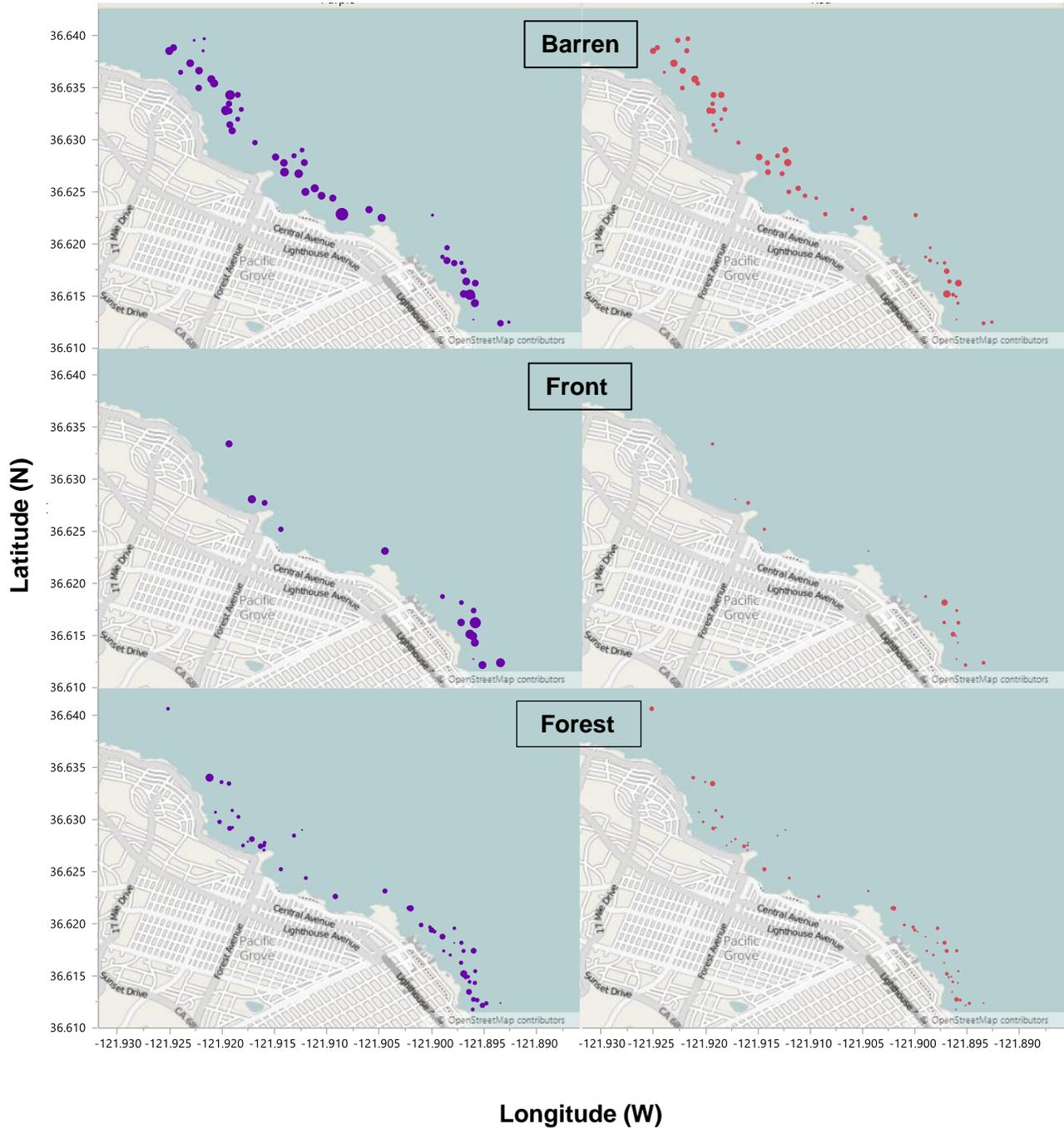


Fig. 10. A site-estimated spatial distribution of sea urchin biomass within sea urchin barrens, fronts, and forests of Southern Monterey Bay, CA.

Urchin Distribution Across Habitat Type

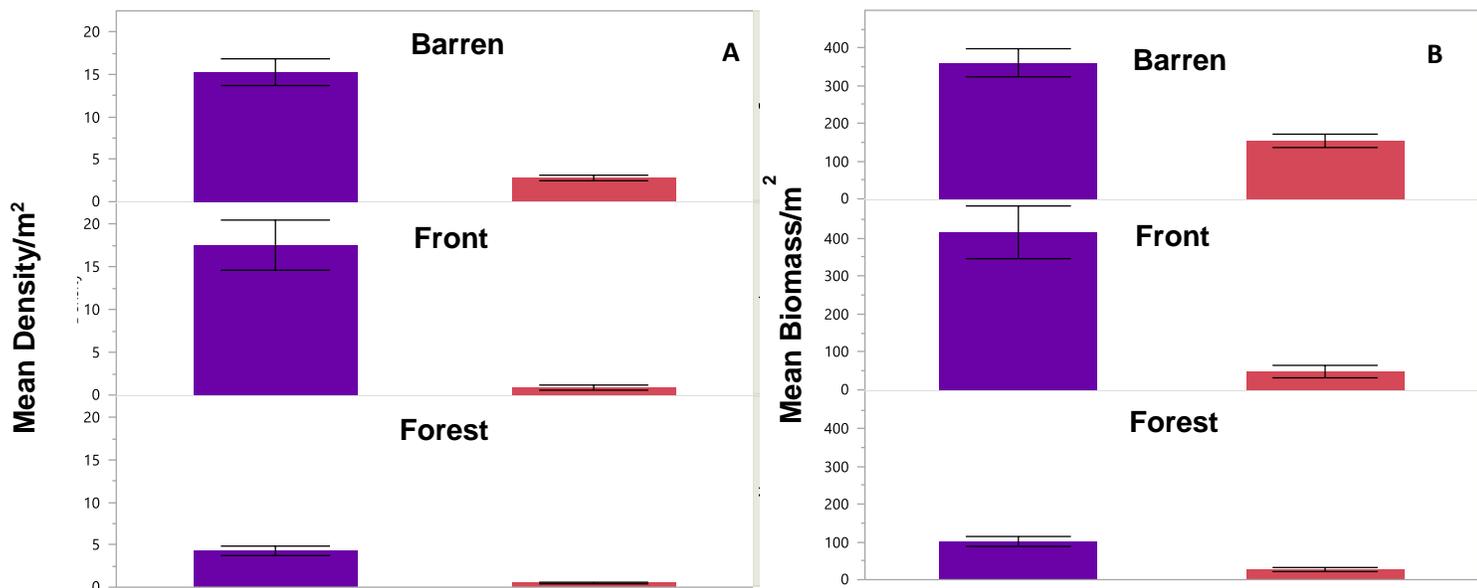


Fig. 11. The mean density (A) and biomass (B) of species within barrens, fronts, and kelp forests.

Urchin Behavior Across Habitat Type

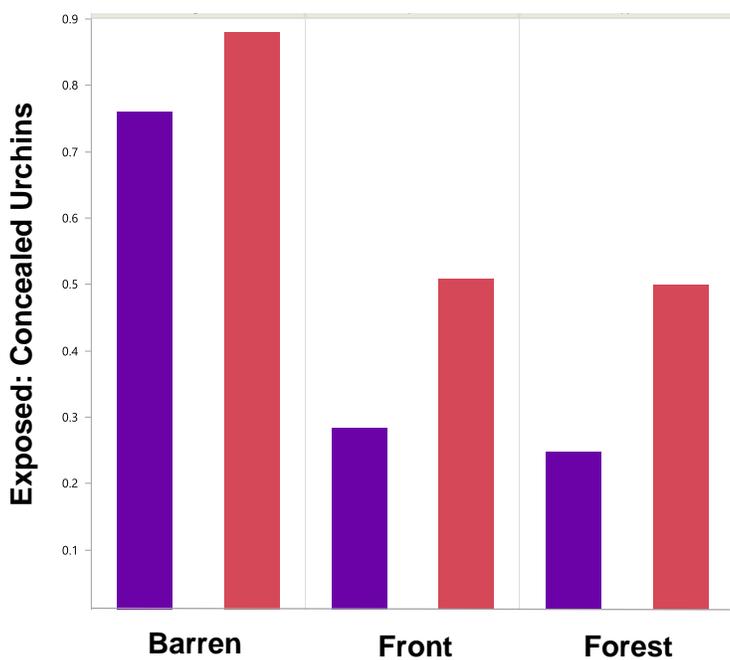


Fig. 12. The ratio of exposed sea urchins to the total found in quadrat areas of each state type (i.e., barrens, fronts, and kelp forests). Red urchins were more often exposed than purple, overall.

Urchin Condition Across Depth (m)

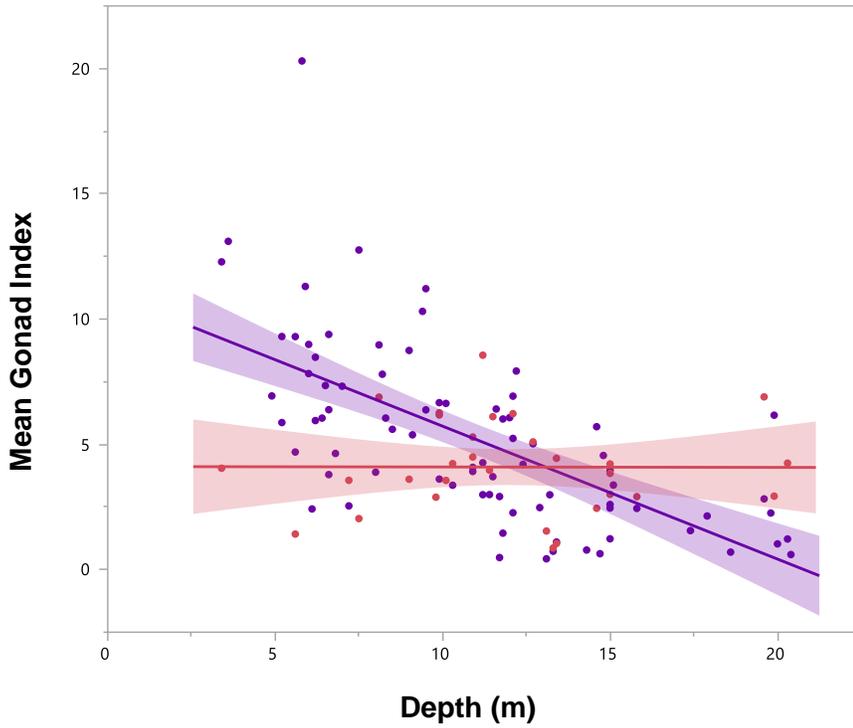


Fig. 13. The mean gonad index (GI) of purple urchins and red urchins as a function of depth (m). Prediction trends in the data are shaded.

Urchin Condition Across Habitat Type

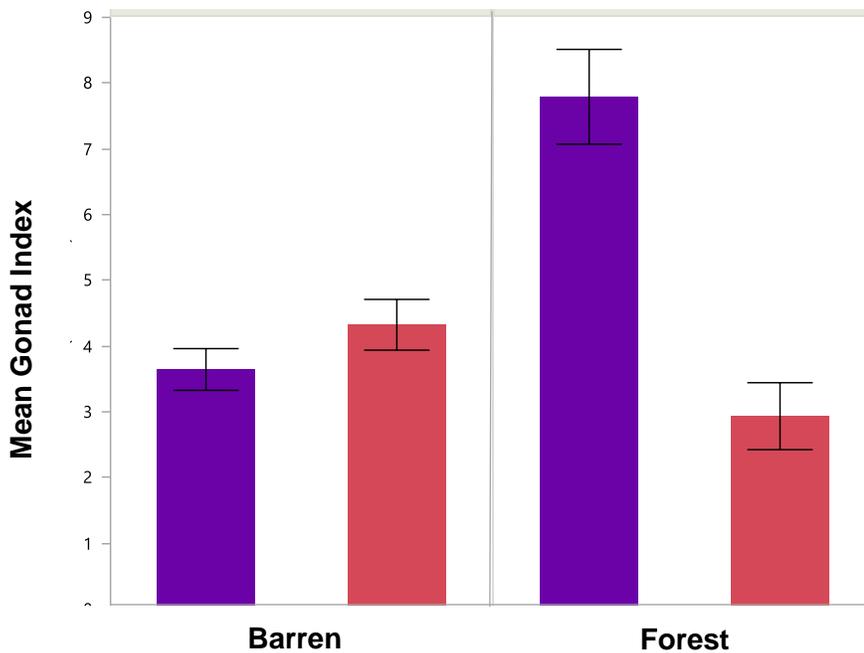


Fig. 14. The mean GI of purple and red urchins in forest and barren states. Fronts were excluded due the lack of significant data collected from those areas (i.e., too few fronts were sampled).

Urchin Condition & Density Distribution

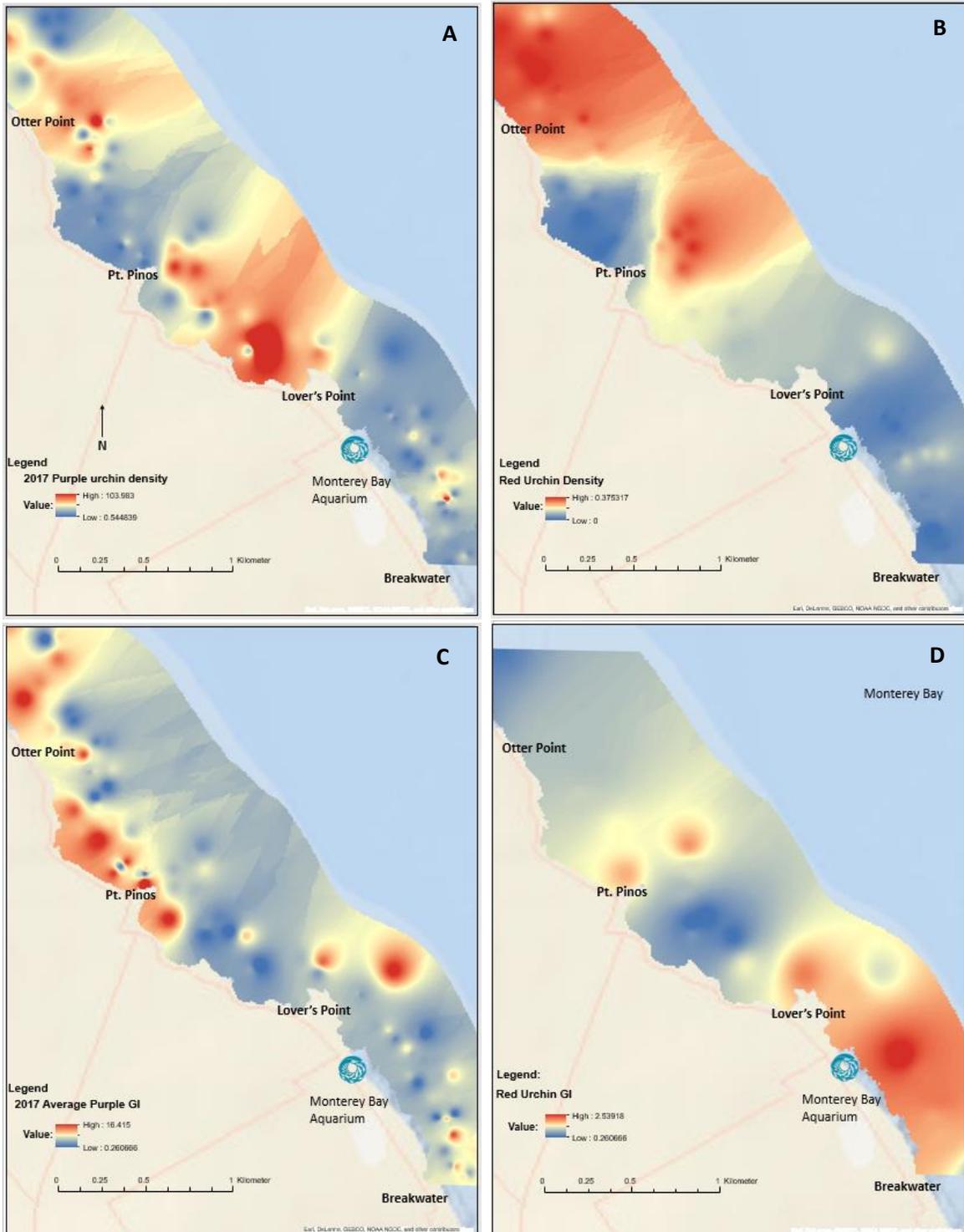


Fig. 15. Heat maps showing purple (A) and red (B) urchin densities, as well as purple (C) and red (D) urchin gonad indices within Monterey Bay, CA.

Urchin Condition & Density Distribution (cont.)

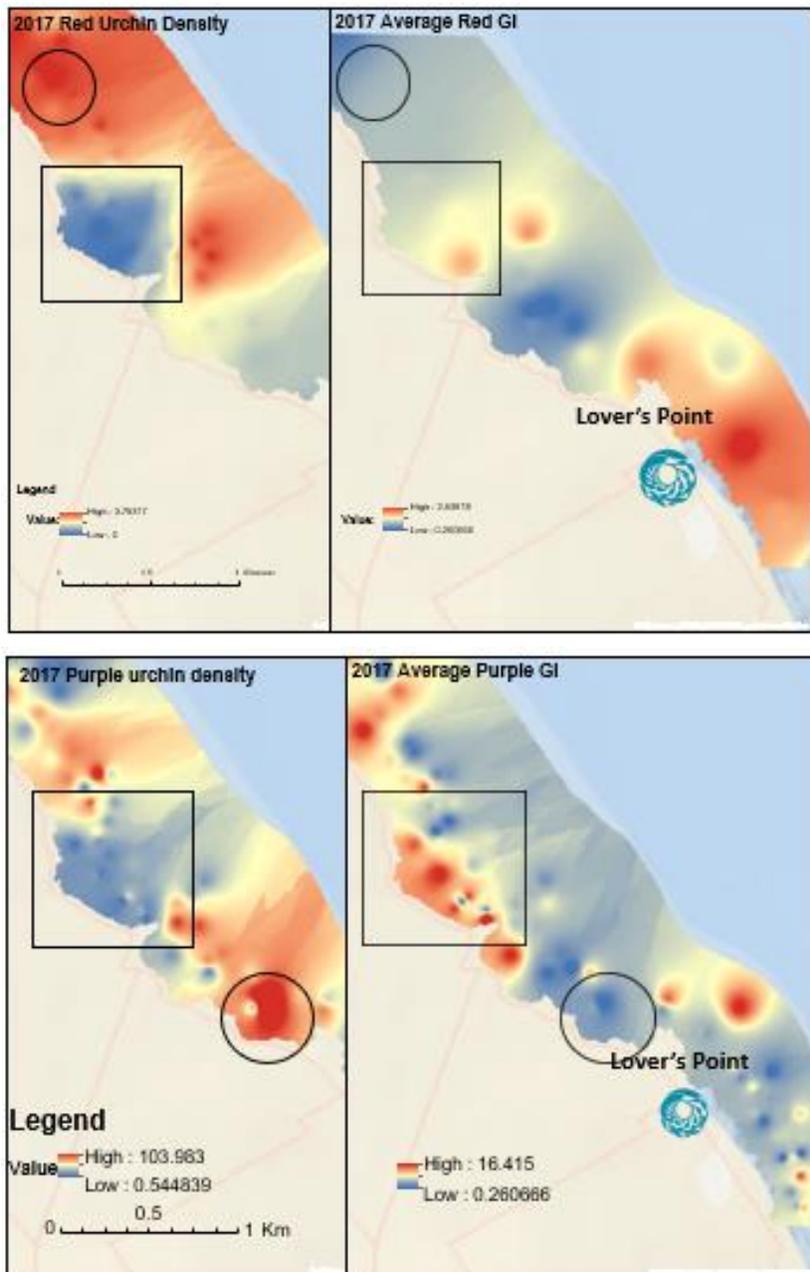


Fig. 16. Areas within the circles and squares reveal that high densities of sea urchins (Reds – Top; Purples – Bottom) often have lower gonad indices (GI) than those residing among lower densities for both species.

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