The zombification and reanimation of purple urchins (Strongylocentrotus purpuratus) in response to food availability

Dillon Dolinar (dillonpdolinar@gmail.com)
San Diego State University https://orcid.org/0000-0003-3392-7446
Mathew Edwards
San Diego State University

Research Article

Keywords: Kelp Forests, Metabolism, Physiology, Purple Sea Urchin, Respiration, Starvation, Urchin Barren

Posted Date: April 29th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-452705/v1

Abstract

To survive periods of starvation, organisms can reduce their metabolism and/or decrease energy allocation to reproduction. This is especially important for coastal rocky reefs where widespread kelp deforestation has become increasingly common in recent decades. This deforestation often results in the formation of urchin barrens that have high densities of herbivorous sea urchins and little macroalgae for them to consume. While it is clear that these barrens can persist for years to decades, it is unclear how the urchins within them survive such prolonged periods without regular access to macroalgae. Here, we show that urchin metabolism and gonad mass both decrease significantly when the urchins are starved, and that these urchins regain normal metabolic activity and gonad masses when access to food is restored. However, if urchins occur in barren areas that receive drift algae from nearby kelp forests, it appears they can maintain normal metabolic activity and gonad mass. Together, our results provide experimental evidence that reducing metabolism may be a primary strategy for avoiding starvation in urchins occurring within barrens. Our results can be especially important to researchers looking to restore kelp forests and to urchin fishers who seek to harvest these urchins for their gonads but currently cannot because their gonads are of poor quality. Additionally, this has important implications for consumers in other ecosystems where access to energetic resources is spatially or temporally variable and can point to new avenues of research to explain how organisms adjust their energetic needs to survive extended periods of starvation.

Introduction

The ability to survive extended periods of food limitation is essential to survival in habitats where access to energetic resources is temporally or spatially variable. To do this, organisms can reduce their metabolism (Pinter et al 1984; Guidetti et al 2011; Geiser 2004; Careau et al 2014; Crowe 1971) or rely on dormant alternate life stages (Tauber and Tauber 1978; Hochachka and Guppy 1987; Carney and Edwards 2006; Edwards 2000) during periods of resource limitation, and then resume normal metabolic activity or emerge from dormancy once access to resources is restored. The suppression of metabolism can also allow for survival in habitats where environmental conditions, such as temperature and/or rainfall, vary temporally and therefore create periods when conditions are hostile for survival. Indeed, the reliance on dormant alternate life stages has been observed across a wide range of taxa, including terrestrial plants (Venable and Lawlor 1980; Keeley 1987; Leck et al 1989), marine macroalgae (Edwards 2000; Carney and Edwards 2010; Carney et al 2013), microalgae (Hollibaugh et al 1981), terrestrial insects (Tauber and Tauber 1978) and marine crustaceans (Grice and Marcus 1981; Maier 1990). Alternatively, many birds and mammals exhibit seasonal hibernation or daily torpor to survive unfavorable conditions or periods of food limitation (Pinter et al 1984, Heldmaier et al 2004; Tøien et al 2011). However, some species such as the common shrew (*Sorex araneus*) can starve to death if deprived of food for just a few hours (Crowcraft 1954; Hawkins and Jewell 1962), while others such as the northern sea otter (*Enhydus lutris*) need to consume large proportions (e.g. 20–50%) of their body mass in prey items per day to survive (Kenyon 1969; Costa and Kooyman 1982; Yeates et al 2007). This

can be especially important for herbivores given that climate change is expected to result in changes to the abundance and distribution of many plants (Bakkenes et al 2002; Jump and Peñuelas 2005) and macroalgae (Kroeker et al 2013; Kim et al 2016; Beas-Luna et al 2020). Thus, understanding how organisms cope with food limitation can be crucial to predicting how their populations will respond to a changing world.

Herbivores play key roles in structuring natural ecosystems (Hairston 1960; Terborgh and Estes 2010). In extreme cases, they can reduce the abundance and/or alter the distribution of ecosystem engineers such as forest-forming trees (Ripple and Beschta 2004; Beschta and Ripple 2010) and thereby affect biogenic structure, energy flow, and nutrient cycling within their ecosystem (Ellison et al 2005). In coastal marine ecosystems, herbivores can overgraze forest-forming kelps (Ebeling et al 1985; Estes et al 1998; Steneck et al 2013), which similarly create biogenic structure that reduces current flow (Jackson and Winant 1983; Hondolero and Edwards 2017), alter nutrient (Pfister et al 2019) and light (Edwards 1998; Clark et al 2004) conditions, and enhance biodiversity (Graham 2004; Metzger et al 2019), primary production (Miller and Page 2012; Edwards et al 2020; Spector and Edwards 2020), and carbon sequestration (Wilmers et al 2012; Filbee-Dexter and Wernberg 2020). These kelps and the understory macroalgae their forests support also provide food to their respective communities (Teagle et al 2017; Gabara et al 2021), and their losses can result in food deprivation for many of the herbivores that feed on them. This is especially important given that kelp forests have suffered drastic declines in many areas of the world over the past few decades due to both biological and physical stressors (Smale 2020; Connell et al 2008; Ling et al 2015; Krumhansl et al 2016; Burt et al 2018; Wernberg et al 2018). While some of these forests recover soon after these stressors disappear (Ebeling et al 1985, Pearse and Hines 1979; Scheibling et al 1999; Bolton et al 2012; Fagerli et al 2013; Edwards and Estes 2006), others have failed to recover or required decades to do so (Ebeling et al 1985; Metzger et al 2019; Pearse and Hines 1979; Scheibling et al 1999; Bolton et al 2012; Fagerli et al 2013; Edwards and Estes 2006; Konar et al 2014; Konar et al 2015). In the Aleutian Archipelago, for example, widespread losses of the *Eualaria fistulosa* kelp forests that began in the 1980s due to changes in trophic interactions (Estes et al 1998) have been maintained by continued overgrazing by herbivorous green sea urchins (*Strongylocentrotus droebachiensis*) (Konar et al 2014). This has resulted in the formation of barren grounds with extremely high densities of urchins and little-to-no macroalgae (Estes et al 1998; Metzger et al 2019). In northern California, USA, the loss of nearly 90% of the *Nereocystis leutkeana* kelp forests that began in 2014 following a marine heatwave and a strong El Niño Southern Oscillation, both of which resulted in a period of elevated seawater temperatures in the region (Bond et al 2015; Fewings et al 2019), has also been maintained by overgrazing by purple sea urchins (*S. purpuratus*) (Rogers-Bennett and Catton 2019). Similar patterns of urchin barren formation have been observed in Western Australia (Vanderklift and Wernberg 2008), South Korea (Jeon et al 2015), Maine, USA (Steneck et al 2013). Nova Scotia (Scheibling et al 1999), Norway (Fagerli et al 2013) British Columbia (Spindel et al. 2020), central and southern California, USA (Ebeling et al 1985;Pearse and Hines 1971; Parnell 2015). One commonality among these studies is that the formation of urchin barrens generally results in the near complete loss of all macroalgae, which can lead to reduced urchin feeding

(Harrold and Reed 1985), decreased gonad development (Thompson 1983; Dodge and Edwards 2012), and reduced metabolic rates (Spindel et al. 2020) relative to urchins in kelp forests.

Urchins residing within persistent barren grounds can survive by consuming drift macroalgae that originates from nearby kelp forests (Vanderklift and Wernberg 2008; Harrold and Reed 1985; Konar and Estes 2003; Rodríguez 2003;Britton-Simmons et al 2009; Renaud et al 2015; Quintanilla-Ahumada et al 2018). In doing so, they can exhibit normal feeding and gonad development (Harrold and Reed 1985; Rodríguez 2003; Britton-Simmons 2009; Kelly et al 2012), which we hypothesize will also result in normal metabolic rates. This is especially important for barren grounds that are in close proximity to healthy kelp forests and that receive large amounts of drift algae (Vanderklift and Werngerg 2008; Rodríguez 2003; Kelly et al 2012; Figurski 2010; Filbee-Dexter and Scheilbling 2016). However, it remains unclear how these urchins survive for extended periods without regular access to these resources. Over shorter time periods, they can resorb their gonads and other organs to meet their metabolic demands (Russell 1998; Secor and Carey 2016; Carey et al 2016). Over longer time periods, they might lower their metabolic rates, becoming “zombies” (Spindel et al. 2021), and then regain normal metabolic activity, becoming “reanimated”, once food access is restored. To examine this, we conducted a laboratory experiment where we measured the metabolic rates and gonad masses of urchins that were starved for 14 weeks, and then regained access to food for an additional seven weeks. We compared these metabolic rates and gonad masses to those in urchins that received regular access to food during the 21-week period. We hypothesized that 1) urchins deprived of food will reduce their metabolic rates, 2) these urchins will return normal metabolic activity when access to food is restored, and 3) urchin gonad mass relative to body size (GSI) will also decrease during starvation and then recover once feeding resumes. Additionally, we examined whether urchins residing in a barren ground that occurs in close proximity to healthy kelp forests and therefore should receive abundant drift macroalgae, exhibit similar metabolic activity and gonad masses to urchins in the nearby kelp forest. We hypothesized that the urchins in these two habitats would not exhibit substantial differences in either metabolic rates or gonad masses.

Materials And Methods

Feeding Experiment

To examine the effects of starvation on urchin metabolism and gonad mass, we collected approximately 180 purple urchins (*Strongylocentrous purpuratus*) while on scuba from a 14.5 m deep area within the Point Loma Kelp Forest, USA during late-January and early-February 2020. The Point Loma kelp forest, which is located near San Diego, California, is approximately 11 km long by 1 km wide and occurs over a low-relief sandstone reef at a depth of 7–24 m. This forest is known for supporting high densities of the canopy-forming kelp *Macrocystis pyrifera* (Fagerli et al 2013; Neushul 1959; Edwards et al 2004), abundant populations of the understory kelps *Laminaria farlowii, Pterygophora californica, Egregia menzeseii*, and *Ecklonia arborea*, and numerous species of understory red and brown macroalgae (Dayton 1984; 1992; 1999), all of which contribute to seasonally variable patterns of primary production (Spector and Edwards 2020). The forest also provides habitat and food for numerous invertebrates and

fishes, especially large populations of purple urchins, *S. purpuratus* (Parnell 2015; Dayton et al 1999). Like many other kelp forests along the California coast (Ebeling et al 1985; Pearse and Hines 1979; Watanabe and Harrold 1991), parts of the Point Loma kelp forest have historically become devoid of fleshy macroalgae due to overgrazing by urchins (Parnell 2015). However, there were no such barren areas at the time of this study in Point Loma and the urchins were collected from an area within the kelp forest that had a high density of *M. pyrifera* and other foliose algae. All urchins were immediately transported to San Diego State University's Coastal and Marine Institute Laboratory (CMIL) where they were haphazardly allocated to one of twelve 3 L aquaria that received flowing seawater from a 1500 gal recirculating seawater system, with seawater kept at a constant 14.45 ± 0.44 ℃ (mean ± SE, n = 59). To prevent spawning during transit, which could have affected their gonad mass, the urchins were placed upside-down on top of damp towels on top of frozen water bottles within a cooler, then covered by separate damp towel before shutting the cooler (Robert Dunn, personal communication). In all, ten haphazardly selected urchins were placed in each aquarium and fed *M. pyrifera* blades *ad libitum* over a seven-day conditioning period.

After the urchins had acclimated to the aquaria for seven days, six of the twelve aquaria were randomly selected and designated as "Fed" tanks, and the remaining six aquaria were designated as "Starved" tanks. The aquaria were then arranged in an alternating pattern with every other tank being either "Fed" or "Starved". The urchins in the "Fed" tanks continued to receive food at near *ad libitum* levels over the following seven weeks while the urchins in the "Starved" tanks were deprived of food. After nearly four weeks, daily access to the CMIL became limited due to COVID-19 restrictions, and the urchins in the "Fed" tanks were therefore fed once per week over the following seven weeks with enough *M. py*rifera to last several days, while the urchins in the "Starved" tanks continued to be deprived of food. However, access to the CMIL was restricted during a two-week period (weeks 13 and 14) due to COVID-19, and it is therefore likely the fed urchins spent one to two weeks without access to food. Then, after 14 weeks, access to the CMIL was improved and the urchins in all the tanks were fed approximately twice weekly over the following seven weeks with a sufficient amount of *M. pyrifera* to allow feeding near *ad libitum* levels.

To examine how the different feeding regimes affected urchin metabolism, their respiration rates (i.e. oxygen consumption) were measured on five occasions following the different feeding schedules. Specifically, respiration measurements were made 1) at the start of the experiment (week 0) when all urchins had been fed at near *ad libitum* levels for seven days, 2) after seven weeks (week 7) during which the "Fed" urchins were fed at near *ad libitum* levels but the "Staved" urchins were deprived of food), 3) after another seven weeks (week 14) during which the "Fed" urchins were fed weekly but the "Staved" urchins remained deprived of food, 4) after another five weeks (week 19) during which all urchins were fed weekly at near *ad libitum* levels, and 5) after another two weeks (week 21) when all urchins continued to receive food weekly at near *ad libitum* levels. To measure urchin respiration, a haphazardly selected urchin was removed from each tank and placed individually into a 1 L water-jacketed respiration chamber that was connected to the recirculating sea water system. This kept the respiration chamber at the same temperature (14.45 ± 0.44 ℃, n = 59) that the urchins experienced during the feeding schedules. The

chamber was then connected to a YSI OBOD probe (self-stirring Optical BOD probe) that recorded the seawater temperature and dissolved oxygen (DO) within the chamber every five seconds using a ProODO optical DO meter (YSI Inc., Yellow Springs, OH, USA). The urchins were allowed to respire for 15 minutes, and their respiration rates were measured by calculating the rate of change in DO (Δ mg O_2 ind^{-1} 5 sec^{-1}) within the chamber using linear regressions. The volume of seawater in the chamber was adjusted to account for each urchin's presence by subtracting the urchin's volume (measured according to Ebert 1988) from the 1 L chamber volume. A "blank" (i.e. the chamber was filled with seawater but did not contain an urchin) was also measured to estimate respiration by microbes and microalgae within the seawater. We then scaled the "blank" respiration value by the volume of seawater in the chamber during each trial and this value was subtracted from the measurements for each urchin. Estimates of each individual urchin's respiration (mg O_2 ind^{-1} hr^{-1}) were then scaled by its test diameter (mm), and the resulting size dependent respiration (SDR) values were expanded to reflect hourly rates (mg O_2 mm^{-1} hr^{-1}). Following each respiration measurement, the urchin was removed from the chamber and its mass determined using a digital scale (to the nearest 0.01g). Also, the urchin's test diameter and height were measured with calipers (to the nearest 0.1mm). Following this, the urchin was sacrificed and its gonads were removed and weighed using the same digital scale. Additionally, we opportunistically repeated these measurements on an unreplicated set of five purple urchins that were collected from the Palos Verdes peninsula (ca 160 km away) and held in a single tank without food for 16 months. While these urchins were collected for an unrelated study and not included in our formal analyses, we present data on the metabolism and gonad mass for a single individual on each sample date to gain insight into the effects of long-term (> 1 year) starvation.

Comparing urchins from barrens and kelp forests

To compare the metabolisms and gonad masses between urchins living in an urchin barren and a nearby kelp forest, we collected 40 purple urchins from Stillwater Cove, located near Pacific Grove, California, USA in February 2020. Stillwater Cove is characterized by moderate-relief granite, sandstone and conglomerate terraces that are separated by cobble and sand channels at depths from 6–14 m. The kelp forest has historically supported a dense surface canopy of *M. pyrifera*, an abundant subsurface canopy of *P. californica*, and a diverse assemblage of understory red and brown algae (Edwards 1998; Clark et al 2004), all of which contribute to seasonally variable patterns of primary production (Spector and Edwards 2020). The cove has recently (ca within last 5 years) experienced substantial losses of kelps and understory algae due to large increases in urchin abundances, as large swaths of the cove have been deforested and become urchin barrens. Stillwater Cove was opportunistically selected as our sample site because it has a barren with high urchin density that is near areas of high kelp density. Additionally, its proximity to Moss Landing Marine Lab (MLML) greatly reduced transport time and chances of urchin mortality among the individuals that we collected. Twenty of the urchins were collected from a 7.5 m deep area of Stillwater Cove that had abundant *M. pyrifera* and understory algae, and the other twenty urchins were collected from a large nearby (ca 200 m away) 12 m deep urchin barren that was surrounded by abundant macroalgae. The urchins from each habitat were placed in separate mesh bags

upside down over a damp towel in dark cooler and immediately transported to the aquaculture facility at MLML. At MLML, the urchins from each habitat were divided into two groups and placed into separate floating baskets (n = 10 urchins per basket). All four baskets were placed in a flow-through seawater tank and the urchins allowed to acclimate to the seawater conditions for 16 hrs. After this acclimation period, urchin respiration was measured using the same methods described above for the laboratory measurements, with the respiration chamber's water jacket connected to a water chiller that maintained the seawater at ambient temperatures (13.28 ± 0.59 °C, n = 20).

Statistical Analysis

All statistical analyses were done using the statistical software R-Studio Version 1.2.5001, R Version 3.5.2., and Primer-E Ver. 6. Before analyses, all data were checked for normality using Shapiro's test, and for equal variances using Bartlett's and/or Levene's tests. We used Box-Cox transformation to satisfy assumptions of parametric statistics when necessary. However, data for size dependent respiration (SDR) within the starved treatment were both non-normal (Shapiro test: $p = 0.043$) and heteroscedastic among measurement weeks (Levene's Test: $p = 0.02$), and these problems could not be corrected by transformation. Therefore, we used a two-way fixed factor permutation analysis of variance (PERMANOVA) on a Euclidean distance-based resemblance matrix to evaluate differences in SDR between the fed and starved urchins (i.e. treatment), and among the five sample dates (i.e. weeks) (Anderson et al 2006). Data were square-root transformed prior to analysis. We then used individual parametric t-tests as post hoc tests to evaluate *a priori* hypotheses regarding differences in SDR among feeding treatments during each sample week separately. Here, all data met the assumptions of parametric statistics. We used Benjamin-Hochberg adjusted p-values to control for Type I error inflation due to the multiple tests (Benjamin and Hochberg 1995). We similarly used a two-way fixed-factor ANOVA to evaluate differences in GSI between the fed and starved urchins, and among the five sample dates, and followed this with individual parametric t-tests to evaluate *a priori* hypotheses regarding differences in GSI among treatments during each sample week separately. We again adjusted the resulting p-values to control for Type I error inflation due to the multiple tests (Benjamin and Hochberg 1995). Here, data for GSI were heteroscedastic between the treatments during week 7, and we therefore used a Welch's t-test for unequal variances for this comparison. We used separate 3-factor ANCOVAs to evaluate differences in the relationship between individual urchin metabolic rate and urchin test diameter, and between GSI and urchin test diameter, among feeding treatments and weeks. We followed each of these with separate 2-factor ANCOVAs as post hoc tests to evaluate *a priori* hypotheses regarding differences in the relationship between individual urchin metabolic rate and urchin test diameter, and between GSI and test diameter, between the two feeding treatments within each week separately. We then used ANCOVA to evaluate differences in the relationship between SDR and GSI between the two feeding treatments. Lastly, we used separate t-tests to evaluate differences in SDR and GSI between urchins collected from the kelp forest and urchins barren areas within Stillwater Cove. Data for SDR were heteroscedastic and therefore square-root transformed prior to analysis.

Results

Urchin respiration

Urchin size-dependent respiration rates (SDR) varied significantly between the fed and starved urchins (PERMANOVA: pseudo-$F_{1,49}$ =7.970, p(perm) = 0.008) and among sample weeks (pseudo-$F_{4,49}$ = 8.628, p(perm) = 0.001), but these factors did not interact with each other (Treatment*Week interaction: pseudo-$F_{4,49}$ = 1.117, p(perm) = 0.361) (Figure 1, Table 1A). However, when a prior hypothesis regarding differences between feeding treatments were examined within each week separately, these patterns varied among sample weeks (Table 1B). Specifically, at the start of the experiment, before the feeding manipulations began, SDR did not differ between the urchins that would later be starved (0.027 ± 0.002 mg O_2 mm^{-1} hr^{-1}, n = 6) and the urchins that would remain fed (0.026 ± 0.003 mg O_2 mm^{-1} hr^{-1}, n = 6) (week 0: t-test: t = -0.468, df = 10, p-adjust = 0.811). In contrast, after seven weeks without access to food, SDR had decreased by approximately 60% in the starved urchins and was consequently significantly lower (0.011 ± 0.001 mg O_2 mm^{-1} hr^{-1}, n =6) than in the fed urchins (0.027 ± 0.003 mg O_2 mm^{-1} hr^{-1}, n =6) (week 7: t-test: t = 3.810, df = 10, p-adjust = 0.017). SDR then remained significantly lower in the starved urchins (0.012 ± 0.002 mg O_2 $mm^{-1}hr^{-1}$, n = 6) than in the fed urchins (0.018 ± 0.001 mg O_2 $mm^{-1}hr^{-1}$, n=6) after an additional seven weeks of starvation (week 14: t-test: t = 3.080, df = 10, p-adjust = 0.028). Interestingly, we observed a 33% decrease in SDR in the fed urchins between week seven and fourteen, which we believe resulted from these urchins not receiving food during the previous one to two weeks because of difficulties accessing our marine lab (CMIL) during COVID-19 restrictions (see Methods). Then, after all urchins began receiving regular access to food over the following five weeks, SDR increased in both the previously starved urchins (0.032 ± 0.001 mg O_2 mm^{-1} hr^{-1}, n = 6) and the continuously fed urchins (0.033 ± 0.001 mg O_2 mm^{-1} hr^{-1}, n = 6) urchins, which resulted in SDR not being different between the two groups (week 19: t-test: t = 0.672, df = 10, p-adjust = 0.860). Similarly, after an additional two weeks of feeding, SDR remained similar between the urchins that had previously been starved (0.035 ± 0.003 mg O_2 $mm^{-1}hr^{-1}$, n = 5) and the urchins that had been fed regularly over the entire 21 week experiment (0.036 ± 003 mg O_2 mm^{-1} hr^{-1}, n = 6) (week 21: t-test: t = 0.173, df = 9, p-adjust = 0.867). Additionally, the opportunistic examination of the five urchins that were collected from Palos Verdes, CA as part of an unrelated study and then held in our tanks without food for sixteen months showed that these urchins exhibited respiration that was far lower (0.00425 ± 0.00283, mg O_2 mm^{-1} hr^{-1}, mean ± SD, n = 5) than those in any of our feeding treatments across the five measurement dates.

Urchin GSI

Gonad Somatic Indices (GSIs) varied significantly between the starved and fed urchins (ANOVA: $F_{1,48}$ = 11.436, p = 0.001) and among measurement weeks ($F_{4,48}$ = 12.535, p < 0.001), but these factors did not interact with each other (treatment*week interaction: $F_{4,48}$ = 0.505, p=0.732) (Figure 2, Table 2A). However, as with SDR, when *a prior* hypotheses regarding differences between feeding treatments were examined within each week separately, these patterns varied among sample weeks (Table 2B). Specifically, and similar to SDR, GSI did not differ between the urchins that would later be starved (2.15 ±

0.22 %, mean ± SE, n = 6) and those that would be fed regularly (2.87 ± 0.37 %, n = 6) at the start of the experiment (week 0: t-test: t = 1.682, df = 10, p-adjust = 0.163). However, GSI had decreased in the starved urchins after seven weeks without food (0.38 ± 0.11 %, n = 6) but not in the fed urchins (2.53 ± 0.78 %, n = 6), although these differences were only marginally statistically significant (week 7: Welch's t-test: t = 3.180, df = 5.21, p-adjust = 0.090). After an additional seven weeks of starvation, GSIs remained lower in the starved urchins (1.42 ± 0.66 %, n = 6) than in the fed urchins (3.99 ± .69%, n = 6), (week 14: t-test: t = 3.080, df = 10, p-adjust = 0.057). Following this, the starved urchins began receiving regular access to food over the following five weeks and their GSIs increased (4.53 ± 0.62 %, n = 6), but they remained lower than in the urchins that had received regular access to food (6.49 ± 0.56 %, n = 6) (week 19: t-test: t = 672, df = 10, p-adjust = 0.070). Then, after an additional two weeks of feeding, GSIs in the starved urchins continued to increase (5.57 ± 0.84 %, n = 5) such that they were no longer different than those in the fed urchins that had received regular access to food during the 21-week experiment (6.55 ± 1.70 %, n = 6) (week 21: t-test: t = 0.484, df = 9, p-adjust = 0.620). Together, this indicated that GSI followed similar, albeit less pronounced and perhaps slightly delayed, responses to starvation and feeding as SDR. Additionally, examination of the five urchins that were collected from Palos Verdes, CA revealed that these urchins had no identifiable gonads (GSI = 0%) on any of the five measurement dates.

We observed an overall positive relationship between individual urchin respiration (mg O_2 ind^{-1} hr^{-1}) and urchin test diameter (mm) when examined across both feeding treatments and all sample weeks (ANCOVA: $F_{1,39}$ = 9.264, p = 0.004) (Table 3A, Figure S1). However, when *a prior* hypotheses regarding differences in the relationship between individual respiration and test diameter were examined between the two feeding treatments within each week separately, these patterns varied among sample weeks (Table 3B). Specifically, similar to patterns observed for SDR, individual respiration rates did not differ between the feeding treatments at the start of the experiment (ANCOVA, week 0: $F_{1,8}$ = 0.011, p = 0.918), but they were significantly lower in the starved urchins than the fed urchins after both seven (week 7: $F_{1,8}$ = 22.829, p = 0.001) and fourteen (week 14: $F_{1,8}$ = 4.919, p = 0.057) weeks of starvation across the range of observed urchin sizes. Then, after the starved urchins began receiving regular access food, individual respiration increased such that it was only marginally lower in the starved urchins than the fed urchins (week 19: $F_{1,8}$ = 4.432, p = 0.068) after five weeks of feeding, and it was not different between the two feeding treatments after an additional two weeks of feeding (week 21: $F_{1,8}$ = 0.054, p = 0.824) (Table 3B, Figure S1). Interestingly, the relationship (slope) between individual respiration and test diameter did not differ between the feeding treatments in any of the sample weeks (treatment*diameter interaction: p > 0.1 for all five weeks, Table S3B).

Unlike respiration rates for individual urchins, we did not observe an overall significant relationship between urchin GSI (%) and urchin test diameter (mm) when examined across both feeding treatments and all sample weeks (ANCOVA: $F_{1,38}$ 0.112, p = 0.734) (Table 4A, Figure S2). However, when *a prior* hypothesis regarding differences in the relationship between GSI and test diameter were examined between the two feeding treatments within each week separately, these patterns did vary among sample weeks (Table 4B). Specifically, GSI did not differ between the feeding treatments at the start of the

experiment (ANCOVA, week 0: $F_{1,8}$ = 2.332, p = 0.165) or after seven weeks of starvation (week 7: $F_{1,8}$ = 0.655, p = 0.442). Then, after an additional seven weeks of starvation, GSIs were significantly lower in the starved urchins than in the fed urchins (week 14: $F_{1,8}$ = 6.120, p = 0.038). GSIs remained lower in these urchins even after they began receiving food over the following five weeks (week 19: $F_{1,8}$ = 11.023, p = 0.011), but were not different between the two feeding treatments two weeks later (week 21: $F_{1,8}$ = 0.367, p = 0.564) (Table 4B, Figure S2). However, the relationship between GSI and test diameter did not differ between the feeding treatments during any of the sample dates during the first fourteen weeks of the experiment (treatment*diameter interaction: p > 0.5 for all three sample weeks), but it did differ between the feeding treatments on both sample dates during the last seven weeks (treatment*diameter interaction: p < 0.05 for the last two sample weeks) (Table 4B). Lastly, SDR was positively related to GSI when examined across all urchins used in this study (ANCOVA: $F_{1,41}$=51.711, p < 0.001), but the relationship between SDR and GSI did not vary among the urchins that were fed consistently throughout the study, those that were starved for the first fourteen weeks of the study, or those that regained access to food during the last seven weeks of the study (GSI*treatment interaction: F2,41 = 1.180, p = 0.328) (Table 5, Figure 3).

Comparing urchins from a barrens and nearby kelp forest

Urchins collected from within a barren area of Stillwater Cove did not show the same effects of starvation as those observed in the feeding experiment, even though no macroalgae were observed within the barren at the time of collection. Specifically, SDR did not differ between the urchins that were collected from within the Stillwater Cove urchin barren (0.018 ± 0.006 mg O_2 mm^{-1} hr^{-1}, n = 10) and those that were collected from the nearby kelp forest (0.020 ± 0.006 mg O_2 mm^{-1} hr^{-1}, n = 10) (t-test: t=0.981, df=18, p=0.340) (Table 6, Figure 4A). Likewise, GSI also did not differ between the urchins collected from within the kelp forest (4.03 ± 2.69 %, n =10) and those collected from within the nearby urchin barren (2.66 ± 1.56 %, n = 10) (t-test: t = -1.386, df = 18, p= 0.183) (Table 6, Figure 4B).

Discussion

The primary result of our study is that purple urchins decrease their metabolism when access to food is eliminated and then restore normal metabolism once access to food is regained, and that this occurs over a time frame of a few weeks (Fig 1). This may allow urchins occurring within barren grounds that are devoid of macroalgae algae and that do not receive adequate drift algae to survive prolonged periods of starvation, which has led to some urchin species being characterized as “zombie urchins” (Spindel et al. 2021). Further, our data show that these urchins regain normal metabolic activity (i.e. they become “reanimated”) if they regain access to food, such as would be expected when the kelp forests recover or if the urchins receive drift algae from nearby kelp forests. Thus, patterns of kelp deforestation and recovery, and of proximity to nearby forests are likely important drivers of urchin metabolism. Specifically, although the urchins used in this study exhibited similar metabolic activity at the start of the experiment prior to any manipulation, the urchins that were subsequently starved for seven to fourteen weeks exhibited

substantially lower metabolic rates than urchins of similar size that were fed consistently during this period. Then, when these starved urchins regained regular access to food during the subsequent five to seven weeks, their metabolisms returned to levels that were similar to those at the start of the experiment, and to the urchins that were fed regularly during the 21-week experiment. In contrast, the urchins that were fed regularly throughout the experiment did not alter their metabolisms, except for a smaller decrease that occurred in week 14 following a period when all urchins were presumably deprived of food for one to two weeks because of limited access to them due to COVID-19 restrictions. Additionally, we opportunistically examined the effects of long-term starvation on a group of five purple urchins that were collected from Palos Verdes peninsula as part of an unrelated study. All five urchins survived 16 months without access to food and exhibited substantially reduced metabolic activity. Thus, it is likely that metabolic activity in our starved urchins from Point Loma would have continued to decrease if the experiment had run longer. We also observed that urchin metabolism was, in general, positively related to urchin size, but this was not significant in all feeding treatments and weeks (Fig S1). We believe this lack of significance was likely due to low sample sizes (n = 6 for each treatment*week commination), as other studies have found urchin metabolism to be significantly linked with size (Spindel et al. 2021, M. Edwards, unpublished data).

Our findings have important implications not only for urchins within barrens but also for those occurring in areas where kelp forests recover following extended periods of deforestation, such as has been observed in numerous areas of the world (Ebeling et al 1985; Estes et al 1998; Pearse and Hines 1979; Scheibling et al 1999; Bolton et al 2012; Fagerli et al 2013). Indeed, our study suggests that these urchins can restore normal metabolic activity within a few weeks once the kelp forests recover and access to food is restored. Our study further suggests that urchins residing in barren grounds that receive adequate drift algae from nearby kelp forests (Vanderklift and Wermberg 2008; Harrold and Reed 1985; Konar and Estes 2003; Rodríguez 2003; Britton Simmons et al 2009; Renaud et al 2015) can maintain normal metabolic activity. Indeed, the urchins from within the barren in ground Stillwater Cove did not exhibit significantly different metabolic rates than the urchins from within the nearby kelp forest, both of which were similar to the rates observed within the urchins that had been fed regularly throughout the 21-week feeding experiment (Figs. 1, 4A). We believe that this was because the urchin barren ground in Stillwater Cove was surrounded by healthy kelp forests that provided large amounts of drift algae (Figurski 2010; Edwards unpublished data). Additionally, the primary substrates in Stillwater Cove are dominated by crustose coralline algae (Edwards 1998), which can serve as an alternative food source for the urchins (Harold and Reed 1985), but it is unclear if this is sufficient to meet their energetic needs. Thus, future research should focus on the importance of allochthons transport of drift algae to the barren grounds and on the energetic value of crustose coralline algae.

Much like with urchin metabolism, we observed a significant decrease in urchin GSIs within the urchins that were starved but not in the urchins that received food on a regular basis (Fig. 2). GSIs were similar among the urchins at the start of the experiment but decreased in the starved urchins over the next seven to fourteen weeks. In contrast, GSI did not change in the urchins that received regular access to food over this period. This is not surprising given that previous studies that have found GSIs to be influenced by

food availability (Thompson 1983; Dodge and Edwards 2012). However, while significant decreases in metabolism in the starved urchins occurred within the first seven weeks of the experiment (i.e. by week 7), we did not observe significant decreases in GSIs in these urchins until the second seven weeks of the experiment (i.e. by week 14) (Figs. 2, S2). This again is not surprising given previous studies that have shown urchins can resorb their gonad tissue and thereby reduce their GSIs when starved (Russell 1998; Secor and Carey 2016). We interpret this to mean that when deprived of food, the urchins first decrease their metabolic demands, and then resorb their gonad tissues if starvation continues. Indeed, no identifiable gonads were found in the urchins from Palos Verdes after they were starved for sixteen months. However, once the urchins from Point Loma began feeding, we observed a complete return of normal metabolic activity within five weeks, but we did not see a return to normal GSI until two weeks later, which we interpret to mean that gonad recovery began after metabolism was restored. This was further supported by the observation that GSIs were positively related to metabolism regardless of whether they had access to food or not, though the strength of this relationship varied depending on the urchin's feeding history (Fig. 3). Additionally, GSIs in the urchins within the Stillwater Cove barren ground were not different from those in the kelp forests (Fig. 4B), which also supports our hypothesis that access to drift algae can maintain both normal metabolism and reproductive condition.

Together, our study shows that purple urchins are indeed capable of becoming "zombies" by reducing their metabolic activity, resorbing their gonad tissue, and surviving long periods without food. These urchins can then become "reanimated" by restoring normal metabolic activity and increasing their gonad masses once access to food is regained, or if they have access to drift algae. This may explain how urchins living in persistent urchin barrens are able to survive for years without apparent access to food, such as those within the long-standing barren grounds of the Aleutian Islands (Estes et al 1998; Konar et al 2014; Konar and Estes 2003), and it may help predict their survival in the newly established barren grounds in northern California (Rogers-Bennett and Catton 2019). Unfortunately, COVID-19 related restrictions reduced access to the CMIL for activities other than feeding the urchins on all but a few dates when metabolisms were measured, and therefore prevented us from examining finer scale time-dependent changes in metabolism and GSI. Future studies should examine variation in metabolic activity in shorter time intervals, which will also provide a clearer understanding of how quickly increasing respiration can drive gonad tissue recovery. In addition, future studies should examine the viability of the gonad of reanimated urchins. Furthermore, it is important to understand how starvation affects other species of urchins that form barrens. In particular, red urchins (*Mesocentrotus franciscanus*) are an important barren forming species in central and northern California (*58, 68*), and in British Columbia (Spindel et al. 2021) that similarly exhibits reduced metabolism relative to when they live in kelp forests (Spindel et al. 2021). Crowned urchins (*Centrostephanus coronatus*) are expanding their range expansion northward along the southern California coast and are becoming more influential in the ecology of California's kelp forests (Freiwald et al 2016). Green urchins (*Strongylocentrotus drobeacheinsis*) form extensive urchin barren grounds in Alaska's Aleutian Islands (Estes et al 1998), the east coast of Maine (Steneck et al 2013), Nova Scotia (Scheibling et al 1999), and northern Europe (Fagerli et al 2013). Likewise, *S. nudus* and *S. interemedius* form barren grounds along the east coast of South Korea (Jeon et

al 2015). Indeed, urchin barren formation has become more common worldwide in recent years due to both physical and biological drivers (Estes et al 1998; Ling et al 2015; Jeon et al 2015; Sheppard-Brennand 2017), and they have been observed to persist for years until disease or environmental perturbation removes them and allows the kelp forests to recover (Ebeling et al 1985; Steneck et al 2002; Feehan and Scheibling 2014; Hereu et al 2012; Filbee-Dexter and Scheibling 2014). Thus, unless they receive sufficient amounts of drift algae, these urchins must survive extended periods without access to food, and reducing metabolic activity appears to be an important strategy for doing this.

Declarations

Ethical Standards

Funding: Funding was provided by two grants from California State University COAST to DD.

Conflicts of Interest : The authors declare that they have no conficts of interest.

Availability of data and material: The data sets and code used during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' Contributions: DD contributed to funding,conceptual development, research, analysis and interpretation, writing and editing. ME contributed to research, analysis and interpretation, writing and editing

Ethics approval: Permission to collect *S purpuratus* and *M. pyrifera* was provided by CA Fish & Wildlife Entity Permit to M. Edwards (#SC-751).

Consent to participate: All people involved in this study did so voluntarily and with consent.

Consent for publication: All authors of this study consent to it's publication.

Acknowledgments

We are grateful for the funding provided by two grants from California State University COAST to DD.We would like to thank Renee Angwin, Mike Anghera and the staff at CMIL for fostering a scientific culture that encourages undergraduate research. We are especially grateful to Darrin Ambat, Billie Beckley, Leslie Booher, Ehrick Costello, Natalie Goetz, Max Liebergesell, Ilham Naili-Ridout, John O'Connor, Torre Polizzi and Sara Rosenblatt for their efforts to help us collect both *S. purpuratus* and *M. pyrifera*. We would also like to thank Bennett Bugbee, Dan Gossard, Mike Graham, Scott Hamilton and Diana Steller from MLML for housing, providing lab space for and overseeing diving operations for DD and N Goetz for the duration of that portion of the study in Stillwater Cove. We would also like to thank Robert Dunn, Christopher Knight and Scott Gabara for providing insights contributing to a variety of aspects of this study. Lastly, we would like to thank all SDSU BEER PIGs for their support and helpful critiques during all phases of this study.

References

Anderson MJ, Gorley RN, Clarke KR (2006) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth.

Bakkenes M, Alkemade JRM, Ihle F, Leemans FR, Latour RJB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob. Chang. Biol. 8:390-407. doi:10.1046/j.1354-1013.2001.00467.x.

Beas-Luna R, et al (2020) Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes. Glob. Chang. Biol. 26:6457-6473. doi:10.1111/gcb.15273.

Benjamin Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological). 57, 289-300.

Beschta RL, Ripple WJ (2010) Recovering riparian plant communities with wolves in northern Yellowstone, U.S.A. Restor. Ecol. 18:380-389. doi:10.1111/j.1526-100X.2008.00450.x.

Bolton JJ, Anderson RJ, Smit AJ, Rothman MD (2012) South African Kelp Moving Eastwards: The Discovery of Ecklonia Maxima (Osbeck) Papenfuss at De Hoop Nature Reserve on the South Coast of South Africa. African J. Mar. Sci. 34:147-151. doi:10.2989/1814232X.2012.675125.

Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42:4102-4109. doi:10.1002/2015GL063306.

Britton-Simmons KH, Foley G, Okamoto D (2009) Spatial subsidy in the subtidal zone: Utilization of drift algae by a deep subtidal sea urchin. Aquat. Biol. 5:233–243.

Burt J M, et al. (2018) Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. Proc. R. Soc. B Biol. Sci. 285:20180553. doi:10.1098/rspb.2018.0553.

Careau V,Gifford ME, Biro PA (2014) Individual (co)variation in thermal reaction norms of standard and maximal metabolic rates in wild-caught slimy salamanders. Funct. Ecol. 28:1175-118. doi:10.1111/1365-2435.12259.

Carey N, Harianto J, Byrne M (2016) Sea urchins in a high-CO2 world: Partitioned effects of body size, ocean warming and acidification on metabolic rate. J. Exp. Biol. 219:1178-1186. doi:10.1242/jeb.136101.

Carney LT, Bohonak AJ, Edwards MS, Alberto F (2013) Genetic and experimental evidence for a mixed-age, mixed-origin bank of kelp microscopic stages in southern California. Ecology 94:1955-1965. doi:10.1890/13-0250.1

Carney LT, Edwards MS (2006) Cryptic processes in the sea: a review of delayed development in the microscopic life stages of marine macroalgae. Algae 21:161-168. doi:10.4490/algae.2006.21.2.161

Carney LT, Edwards MS (2010) Role of nutrient fluctuations and delayed development in gametophyte reproduction by Macrocystis pyrifera (phaeophyceae) in Southern California. J. Phycol. 46:987-996. doi:10.1111/j.1529-8817.2010.00882.x.

Clark RP, Edwards MS, Foster MS (2004) Effects of shade from multiple kelp canopies on an understory algal assemblage. Mar. Ecol. Prog. Ser. 267:107-119. doi:10.3354/meps267107.

Connell SD et al (2008) Recovering a lost baseline: Missing kelp forests from a metropolitan coast. Mar. Ecol. Prog. Ser. 75:267-274 doi:10.3354/meps07526.

Costa DP, Kooyman GL (1982) Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, Enhydra lutris. Can. J. Zool. 60:2761-2767. doi:10.1139/z82-354.

Crowcroft P (1954) The daily cycle of activity in British shrews. Proc. Zool. Soc. London 123:715-730. doi:10.1111/j.1096-3642.1954.tb00197.x.

Crowe JH (1971) Anhydrobiosis: an unsolved problem. The American Naturalist 105:563-573.

Dayton PK et al (1984) Patch Dynamics and Stability of Some California Kelp Communities. Ecol. Monogr. 54:253-289. doi:10.2307/1942498.

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: The role of oceanographic climate. Ecol. Monogr. 69:219-250. doi:10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2.

Dayton PK, Tegner MJ, Parnell, P. E. & Edwards, P. B. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol. Monogr. 62, 421-445 (1992) doi:10.2307/2937118.

Dodge CA, Edwards MS (2012) Seasonal variation in the effects of food availability on gametogenesis in the purple urchin (Strongylocentrotus purpuratus). Mar. Biol. 15:427-433. doi:10.1007/s00227-011-1820-6.

Ebeling AW, Laur DR, Rowley RJ (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar. Biol. 84:287-294. doi:10.1007/BF00392498.

Ebert TA (1988) Allometry, design and constraint of body components and of shape in sea urchins. Journal of Natural History 22:1407-1425.

Edwards MS (1998) Effects of long-term kelp canopy exclusion on the abundance of the annual alga Desmarestia ligulata (Light F). J. Exp. Mar. Bio. Ecol. 200:309-326. doi:10.1016/S0022-0981(98)00046-X.

Edwards MS (2000) The role of alternate life-history stages of a marine macroalga: A seed bank analogue? Ecology 8:2402-2415. doi:10.1890/00129658(2000)081[2404:TROALH]2.0.CO;2.

Edwards MS (2004) Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. Oecologia. 138:436-447. doi:10.1007/s00442-003-1452-8.

Edwards MS, Estes JA (2006) Catastrophe, recovery and range limitation in NE Pacific kelp forests: A large-scale perspective. Marine Ecology Progress Series. 320:79-87. doi:10.3354/meps320079.

Edwards MS, Konar B, Kim JH, Gabara S, Sullaway G, McHugh T, Spector M, Small S (2020) Marine deforestation leads to widespread loss of ecosystem function. PLoS One. 15 doi:10.1371/journal.pone.0226173.

Ellison, AM et al (2005) Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3:479-486.

Estes JA, Tinker MT, Williams TM, Doak, DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science. 282:473-476. doi:10.1126/science.282.5388.473.

Fagerli CW, Norderhaug KM, Christie HC (2013) Lack of sea urchin settlement may explain kelp forest recovery in overgrazed areas in Norway. Mar. Ecol. Prog. Ser. 488:119-132. doi:10.3354/meps10413.

Feehan CJ & Scheibling RE (2014) Effects of sea urchin disease on coastal marine ecosystems. Marine Biology. 161:1467-1485. doi:10.1007/s00227-014-2452-4.

Fewings MR, Brown KS (2019) Regional Structure in the Marine Heat Wave of Summer 2015 Off the Western United States. Front. Mar. Sci. 6:1-14 doi:10.3389/fmars.2019.00564.

Figurski J (2010) Patterns and sources of variation in drift algae and the ecological consequences for kelp forests. UMI Dissertation Publishing.

Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Marine Ecology Progress Series. 495:1-25 doi:10.3354/meps10573.

Filbee-Dexter K, Scheibling RE (2016) Spatial Patterns and Predictors of Drift Algal Subsidy in Deep Subtidal Environments. Estuaries and Coasts. 39:1724-1734. doi:10.1007/s12237-016-0101-5.

Filbee-Dexter K, Wernberg T, (2020) Substantial blue carbon in overlooked Australian kelp forests. Sci. Rep. 10:1-6. doi:10.1038/s41598-020-69258-7.

Freiwald J, Wisniewski CJ, & Abbott D (2016) Northward range extension of the crowned sea urchin (Centrostephanus coronatus) to Monterey Bay, California. Calif. Fish Game. 102:37-40.

Gabara S, Konar B, Edwards M (2021). Biodiversity loss leads to reductions in community-wide trophic complexity. Ecosphere 12, e03361.

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Ann. Rev. Physiol. 66:239-274. doi:10.1146/annurev.physiol.66.032102.115105.

Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems. 7:341-357. doi:10.1007/s10021-003-0245-6.

Grice GD, Marcus NH (1981) Dormant eggs of marine copepods. Oceanog. Mar. Biol.: Ann. Rev. 19, 125-140.

Guidetti R, Altiero T,Rebecch L (2011) On dormancy strategies in tartigrades. J. Insect Physiol. 57:567-576. https://doi.org/10.1016/j.jinsphys.2011.03.003

Hairston NG, Smith FE, Slobodkin LB (1960) Community Structure, Population Control, and Competition. Am. Nat. 94:421-425. doi:10.1086/282146.

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology. 66:1160-1169. doi:10.2307/1939168.

Hawkins AE, Jewell PA (1962) Food consumption and energy requirements of captive British Shrews and the mole. Proc. Zool. Soc. London 4:715-730. doi:10.1111/j.1469-7998.1962.tb05692.x.

Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and daily torpor in mammals. Respir. Physiol. Neurobiol. 141:317-329. doi:10.1016/j.resp.2004.03.014.

Hereu B et al (2012) Multiple processes regulate long-term population dynamics of sea urchins on Mediterranean rocky reefs. PLoS One. 7, e36901. doi:10.1371/journal.pone.0036901.

Hochachka PW, Guppy M (1987) Metabolic arrest and the control of biological time. Harvard University Press.

Hollibaugh JT, Seibert DLR, Thomas WH (1981) Observations on the survival and germination of resting spores of three Chaetoceros (Bacillariophyceae) species. J. Phycol. 171–9.

Hondolero D, Edwards MS (2017) Physical and biological characteristics of kelp forests in Kachemak Bay, Alaska. Mar Biol. 164:81-93.

Jackson GA, & Winant CD (1983) Effect of a kelp forest on coastal currents. Cont. Shelf Res. 2:75-80. doi:10.1016/0278-4343(83)90023-7.

Jeon BH, Yang KM, Kim JH (2015) Changes in macroalgal assemblage with sea urchin density on the east coast of South Korea. Algae. 30:139-146. doi:10.4490/algae.2015.30.2.139

Jump AS, Peñuelas J (2005) Running to stand still: Adaptation and the response of plants to rapid climate change. Ecol. Lett. 8:1010-1020. doi:10.1111/j.1461-0248.2005.00796.x.

Kelly JR, Krumhansl KA, Scheibling RE (2012) Drift algal subsidies to sea urchins in low-productivity habitats. Mar. Ecol. Prog. Ser. 452:145-157. doi:10.3354/meps09628.

Keeley JE (1987) Role of fire in seed germination of woody taxa in California Chaparral. Ecology 68:434–443

Kenyon KW (1969) The sea otter in the eastern Pacific Ocean. North Am. Fauna 68:1-352. doi:10.3996/nafa.68.0001.

Kim JH, Edwards MS, Kitack L, Jeong HJ, Kim KY, Species-specific responses of temperate macroalgae with different photosynthetic strategies to ocean acidification: A mesocosm study. Algae 31:243-256. doi:10.4490/algae.2016.31.8.20.

Konar B, Edwards M, Efird T (2015) Local habitat and regional oceanographic influence on fish distribution patterns in the diminishing kelp forests across the Aleutian Archipelago. Environ. Biol. Fishes. 98:1935-1951. doi:10.1007/s10641-015-0412-6.

Konar B, Edwards MS, Estes JA (2014) Biological interactions maintain the boundaries between kelp forests and urchin barrens in the Aleutian Archipelago. Hydrobiologia. 724:91-107. doi:10.1007/s10750-013-1727-y.

Konar B, Estes JA (2003) The stability of boundary regions between kelp beds and deforested areas. Ecology. 84:174-185. doi:10.1890/0012-9658(2003)084[0174:TSOBRB]2.0.CO;2.

Kroeker KJ et al (2013) Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. Glob. Chang. Biol. 19:1884-1896. doi:10.1111/gcb.12179.

Krumhansl KA et al. (2016) Global patterns of kelp forest change over the past half-century. Proc. Natl. Acad. Sci. U. S. A. 3:165-170. doi:10.1073/pnas.1606102113.

Leck MA, Parker VT, Simpson RL (1989) Ecology of soil seed banks. Academic Press, San Diego, California, USA.

Ling SD et al (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. Philos. Trans. R. Soc. B Biol. Sci. 370:20130269. doi:10.1098/rstb.2013.0269.

Maier G (1990) Spatial distribution of resting stages, rate of emergence from diapause, and times to adulthood and to the appearance of the first clutch in three species of cyclopoid copepods. Hydrobiologia 206:11–18.

Metzger JR, Konar B, Edwards MS (2019) Assessing a macroalgal foundation species: community variation with shifting algal assemblages. Mar. Biol. 166:1-17. doi:10.1007/s00227-019-3606-1.

Miller RJ, Page HM (2012) Kelp as a trophic resource for marine suspension feeders: A review of isotope-based evidence. Marine Biology. 159:1391-1402. doi:10.1007/s00227-012-1929-2.

Neushul M (1959) Studies on the growth and reproduction of the giant kelp, Macrocystis. University of California, Los Angeles.

Parnell PE (2015) The effects of seascape pattern on algal patch structure, sea urchin barrens, and ecological processes. J. Exp. Mar. Bio. Ecol. 465:64-76. doi:10.1016/j.jembe.2015.01.010.

Pearse JS, Hines AH (1979) Expansion of a central California kelp forest following the mass mortality of sea urchins. Mar. Biol. 51:83-91. doi:10.1007/BF00389034.

Pfister CA, Altabet MA,Weigel BL (2019) Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. Ecology 100. doi:10.1002/ecy.2798.

Pinter AJ, Lyman CP, Willis JS, Malan A, Wang LCH (1984) Hibernation and Torpor in Mammals and Birds. J. Mammal. 65:172-175. doi:10.2307/1381227.

Quintanilla-Ahumada D, Quijón PA, Navarro JM, Pulgar J, Duarte C (2018) Living on a trophic subsidy: Algal quality drives an upper-shore herbivore's consumption, preference and absorption but not growth rates. PLoS One. 13. doi:10.1371/journal.pone.0196121.

Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front. Mar. Sci. 2:1-15. doi:10.3389/fmars.2015.00031.

Ripple WJ, Beschta RL (2004) Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. For. Ecol. Manage. 200:161-181. doi:10.1016/j.foreco.2004.06.017.

Rodríguez SR (2003) Consumption of drift kelp by intertidal populations of the sea urchin Tetrapygus niger on the central Chilean coast: Possible consequences at different ecological levels. Mar. Ecol. Prog. Ser. 251:141-151. doi:10.3354/meps251141.

Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci. Rep. 9:1-9. doi:10.1038/s41598-019-51114-y.

Russell MP (1998) Resource allocation plasticity in sea urchins: Rapid, diet induced, phenotypic changes in the green sea urchin, Strongylocentrotus droebachiensis. J. Exp. Mar. Bio. Ecol. 220:1-14. doi:10.1016/S0022-0981(97)00079-8.

Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: The dynamics of sea urchin - kelp interactions in Nova Scotia. Can. J. Fish. Aquatf. Sci. 56:2300-2314. doi:10.1139/f99-163.

Secor SM, Carey HV (2016) Integrative physiology of fasting. Compr. Physiol. 6:773-825. doi:10.1002/cphy.c150013.

Sheppard-Brennand H, Dworjanyn SA, Poore AGB (2017) Global patterns in the effects of predator declines on sea urchins. Ecography (Cop.). 40:1029-1039. doi:10.1111/ecog.02380.

Smale DA, (2020) Impacts of ocean warming on kelp forest ecosystems. New Phytologist. 225:1447-1454. doi:10.1111/nph.16107.

Spector M, Edwards MS (2020) Species-specific biomass drives macroalgal benthic primary production on temperate rocky reefs. Algae. 35:1-16. doi:10.4490/algae.2020.35.8.19.

Spindel NB, Lee LC, Okmoto DK (2020) Zombies of the nearshore: Metabolic depression in sea urchin barrens associated with food deprivation. bioRixivb https://doi.org/10.1101/2020.11.28.402156;

Steneck RS et al (2002) Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation. 436-459. doi:10.1017/S0376892902000322.

Steneck RS, Leland A, McNaught DC, Vavrinec J (2013) Ecosystem flips, locks, and feedbacks: The lasting effects of fisheries on Maine's kelp forest ecosystem. Bull. Mar. Sci. 89:31-55. doi:10.5343/bms.2011.1148.

Tauber MJ, Tauber CA (1978) Evolution of Phenological Strategies in Insects: a Comparative Approach with Eco-Physiological and Genetic Considerations. In: Dingle H. (eds) Evolution of Insect Migration and Diapause. Proc Biol Sci. Springer, New York, NY. https://doi.org/10.1007/978-1-4615-6941-1_3

Teagle H, Hawkins SJ, Moore PJ, Smale DA (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J. Exp. Mar. Bio. Ecol. 492:81-98 doi:10.1016/j.jembe.2017.01.017.

Terborgh J, Estes JA (2010) Trophic Cascades: Predators, prey and the Changing Dynamics of Nature. Island Press.

Thompson RJ (1983) The relationship between food ration and reproductive effort in the green sea urchin, Strongylocentrotus droebachiensis. Oecologia. 56:50-57. doi:10.1007/BF00378216.

Tøien Ø, Blake J, Edgar DM, Grahn DA, Hdller HC, Barnes BM (2011) Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 331:906-909. doi:10.1126/science.1199435.

Vanderklift MA, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia. 157:327-335. doi:10.1007/s00442-008-1061-7.

Venable DL, Lawlor L (1980) Delayed germination and dispersal in desert annuals: Escape in space and time. Oecologia 46:272-281. doi:10.1007/BF00540137.

Watanabe JM, Harrold C (1991) Destructive grazing by sea urchins Strongylocentrotus spp. in a central California kelp forest: potential roles of recruitment, depth, and predation. Mar. Ecol. Prog. Ser. 72:125-

141. doi:10.3354/meps071125.

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2018) Status and trends for the world's kelp forests. in World Seas: An Environmental Evaluation Volume III: Ecological Issues and Environmental Impacts. doi:10.1016/B978-0-12-805052-1.00003-6.

Wilmers CC, Estes JA, Edwards M, Laidre KL, Konar B (2012) Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. Front. Ecol. Environ.10:409-415. doi:10.1890/110176.

Yeates LC, Williams TM, Fink TL (2007) Diving and foraging energetics of the smallest marine mammal, the sea otter (Enhydra lutris). J. Exp. Biol. 210:196-1970. doi:10.1242/jeb.02767.

Tables

Table 1. A) Results of a two-way fixed-factor PERMANOVA testing differences in size-dependent respiration (SDR) in purple sea urchins between feeding treatments (fed, starved) and among the five sample weeks (weeks 0, 7, 14, 19, 21). B) Results of separate t-tests examining *a prior* hypotheses regarding differences in SDR between feeding treatments during each sample week separately. Both uncorrected (p-value) and Benjamin-Hochberg corrected (p-adj) p-values are given, the later of which were adjusted according to avoid alpha error inflation due to the multiple tests (*102*) (n = 6 for each feeding treatment and each sample week).

A PERMANOVA

Source	SS	df	MS	Pseudo-F	P(perm)
Treatment	2.950	1	2.950	7.970	0.008
Week	12.776	4	3.194	8.628	0.001
Treatment x Week	1.654	4	0.413	1.117	0.362
Residual	18.138	49	0.37		

B Separate t-tests

Week	t	df	p-value	p-adj
0	-0.468	10	0.649	0.811
7	3.81	10	0.003	0.017
14	3.08	10	0.012	0.028
19	0.672	10	0.517	0.86
21	0.173	9	0.867	0.867

Table 2. A) Results of a two-way fixed-factor PERMANOVA testing differences gonad somatic indices (GSI) in purple sea urchins between feeding treatments (fed, starved) and among the five sample weeks (weeks 0, 7, 14, 19, 21). B) Results of separate t-tests examining *a prior* hypotheses regarding differences in GSI between feeding treatments during each sample week separately. Both uncorrected (p-value) and Benjamin-Hochberg corrected (p-adj) p-values are given, the later of which were adjusted according to avoid alpha error inflation due to the multiple tests (*102*). A Welch's t-test for unequal variances was used in week 7 (n = 6 for each feeding treatment and each sample week).

A PERMANOVA

Source	SS	df	MS	F	p-value
Treatment	41.430	1	41.43	11.436	0.001
Week	181.650	4	45.41	12.535	<0.001
Treatment x Week	7.310	4	1.83	0.505	0.732
Residual	173.890	48	3.62		

B Separate t-tests

Week	t	df	p-value	p-adj
0	1.682	10	0.130	0.163
7	3.810	5.21	0.018	0.090
14	3.080	10	0.023	0.057
19	0.672	10	0.042	0.070
21	0.173	9	0.620	0.620

Table 3. A) Results of a three-way ANCOVA testing differences in the relationship between urchin test diameter (mm) and respiration (mg O_2 individual^{-1}) in purple sea urchins between feeding treatments (fed, starved) and among the five sample weeks (weeks 0, 7, 14, 19, 21). B) Results of separate two-way ANCOVAs examining *a prior* hypotheses regarding differences in the relationship between urchin test diameter and respiration in purple sea urchins between feeding treatments during each of the five sample weeks. (n = 6 for each feeding treatment and each sample week).

A) 3-Way ANCOVA

Source	Df	Sum Sq	Mean Sq	F value	p-value
Week	4	6.488	1.622	17.442	<0.001
Treatment	1	1.043	1.043	11.215	0.002
Diameter	1	0.861	0.861	9.263	0.004
Week:Treatment	4	1.503	0.376	4.040	0.008
Treatment:Diameter	1	0.001	0.001	0.014	0.907
Week:Diameter	4	0.739	0.185	1.986	0.116
Week:Diameter:Treatment	4	0.250	0.063	0.672	0.615
Residuals	39	3.627	0.093		

B) Separate 2-way ANCOVAs

Week 0

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	0.003	0.003	0.011	0.918
Diameter	1	0.437	0.437	1.929	0.202
Treatment:Diameter	1	0.052	0.052	0.229	0.645
Residuals	8	1.813	0.227		

Week 7

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	1.782	1.782	22.829	0.001
Diameter	1	1.082	1.082	13.867	0.006
Treatment:Diameter	1	0.235	0.235	3.018	0.121
Residuals	8	0.624	0.078		

Week 14

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	0.362	0.362	4.919	0.057
Diameter	1	0.014	0.014	0.192	0.673
Treatment:Diameter	1	0.000	0.000	0.001	0.982
Residuals	8	0.589	0.074		

Week 19

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	0.043	0.043	4.432	0.068
Diameter	1	0.462	0.462	47.529	<0.001
Treatment:Diameter	1	0.001	0.001	0.093	0.769
Residuals	8	0.078	0.010		

Week 21

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	0.006	0.006	0.054	0.824
Diameter	1	0.006	0.006	0.050	0.829
Treatment:Diameter	1	0.014	0.014	0.130	0.729
Residuals	7	0.776	0.111		

Table 4. A) Results of a three-way ANCOVA testing differences in the relationship between urchin test diameter (mm) and gonad somatic indices (GSI) in purple sea urchins between feeding treatments (fed, starved) and among the five sample weeks (weeks 0, 7, 14, 19, 21). B) Results of separate two-way ANCOVAs examining *a prior* hypotheses regarding differences in the relationship between urchin test diameter and GSI in purple sea urchins between feeding treatments during each of the five sample weeks. (n = 6 for each feeding treatment and each sample week).

A Three-way ANCOVA

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Week	4	182.095	45.524	16.856	<0.001
Treatment	1	40.982	40.982	15.174	<0.001
Diameter	1	0.316	0.316	0.117	0.734
Week:Treatment	4	6.997	1.749	0.648	0.632
Treatment:Diameter	1	6.339	6.339	2.347	0.134
Week:Diameter	4	9.123	2.281	0.844	0.506
Week:Treatment:Diameter	4	55.795	13.949	5.165	0.002
Residuals	38	102631.000	2.701		

B Separate two-way ANCOVAs

Week 0

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	1.582	1.582	2.332	0.165
Diameter	1	0.167	0.167	0.246	0.633
Treatment:Diameter	1	0.000	0.000	0.000	0.985
Residuals	8	5.425	0.678		

Week 7

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	3.654	3.654	0.655	0.442
Diameter	1	6.142	6.142	1.101	0.325
Treatment:Diameter	1	1.018	1.019	0.183	0.680
Residuals	8	44.618	5.577		

Week 14

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	19.880	19.880	6.120	0.038
Diameter	1	0.192	0.192	0.059	0.814
Treatment: Diameter	1	1.423	1.423	0.438	0.527
Residuals	8	25.986	3.248		

Week 19

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	11.553	11.553	11.023	0.011
Diameter	1	0.829	0.829	0.791	0.400
Treatment:Diameter	1	11.978	11.978	11.429	0.010
Residuals	8	8.384	1.048		

Week 21

Source	Df	Sum Sq	Mean Sq	F-value	p-value
Treatment	1	2.625	2.625	0.367	0.564
Diameter	1	2.252	2.252	0.315	0.592
Treatment:Diameter	1	48.464	48.464	6.770	0.035
Residuals	7	50.113	7.159		

Table 5. Results of two-way ANCOVA testing differences in the relationship between gonad somatic indices (GSI) and respiration (mg O_2 individual^{-1}) in purple urchins from three different feeding treatments (fed regularly through throughout the entire experiment, starved during the first 14 weeks of the experiment, and fed during the last seven weeks of the experiment following a period of starvation) (n = 24, 12, and 11, respectively).

Source	Sum Sq	Df	Mean Sq	F-value	p-value
GSI	0.002	1	0.00214	51.711	<0.001
Treatment	0.001	2	0.00072	17.328	<0.001
GSI:Treatment	0.000	2	0.00005	1.180	0.318
Residuals	0.002	41	0.00004		

Table 6. Results of separate t-tests examining differences in A) size-dependent respiration (SDR) and B) gonad somatic indices (GSI) in purple sea urchins collected from a kelp forest and a nearby urchin barren in Stillwater Cove.

Variable	t	df	p-value
SDR	0.981	18	0.340
GSI	-1.386	18	0.183

Figures

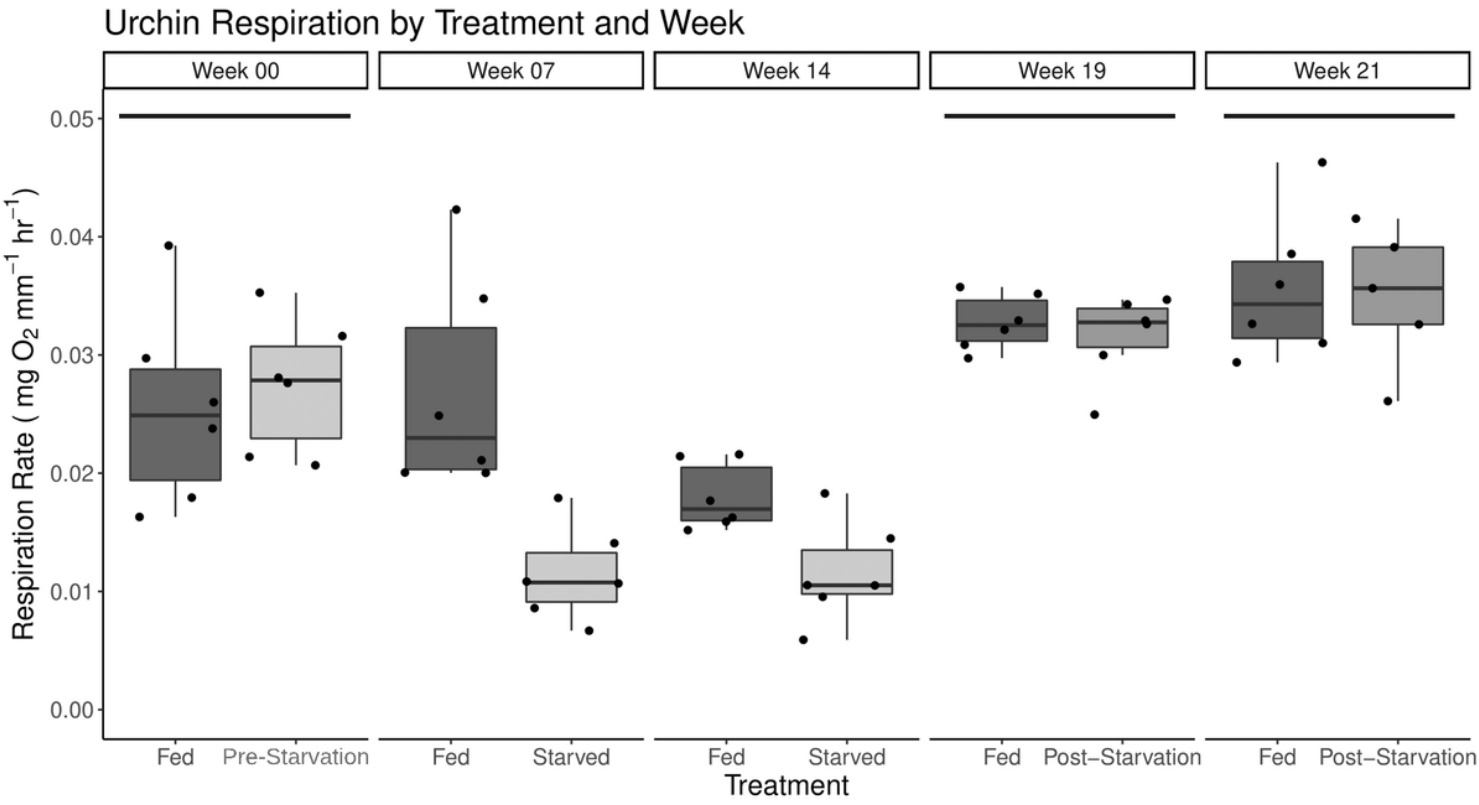

Figure 1

Boxplots showing differences in size dependent respiration (SDR [mg O2mm-1hr-1]) in purple urchins among both the fed and the starved treatments throughout time. Black horizontal lines above pairs of boxes within weeks 0, 19, and 21 denote non-significant difference in respiration rates between the feeding treatments. “Week 0” measurements were taken before feeding manipulations began. “Week 7” and “Week14” measurements occurred while the “Starved” urchins had no access to food while “Week 19” and “Week 21” measurements occurred while both “Starved” and “Fed” urchins were receiving equal amounts of food.

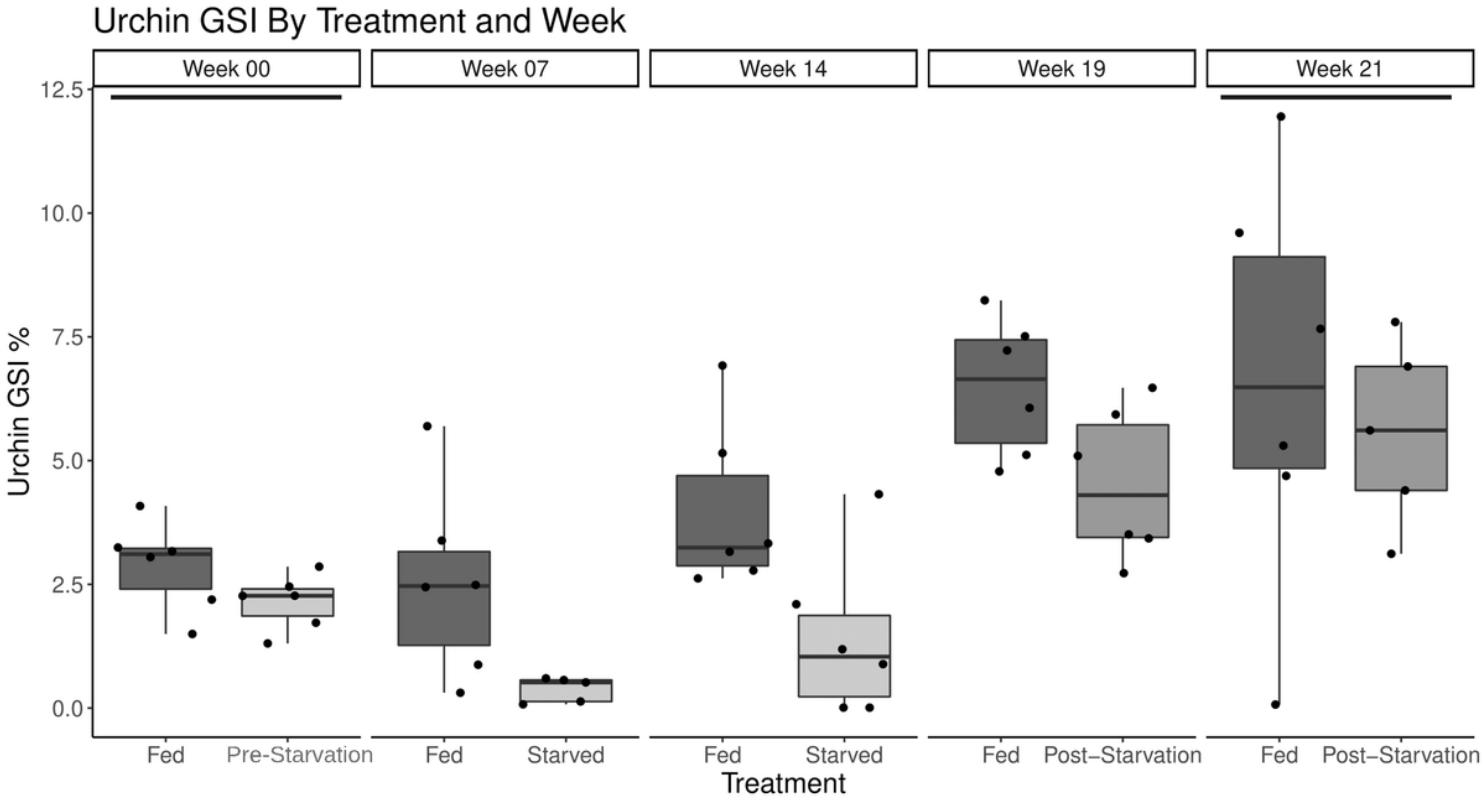

Figure 2

Boxplots showing differences in Gonad Somatic Index (GSI [%]) in purple urchins among both the fed and the starved treatments throughout time. . Black horizontal lines above pairs of boxes within weeks 0 and 21 denote non-significant difference in GSI among the feeding treatments. “Week 0” measurements were taken before any manipulation occurred to the “Starve” treatment’s feeding regiment. Week 0” measurements were taken before feeding manipulations began. “Week 7” and “Week14” measurements occurred while the “Starved” urchins had no access to food while “Week 19” and “Week 21” measurements occurred while both “Starved” and “Fed” urchins were receiving equal amounts of food.

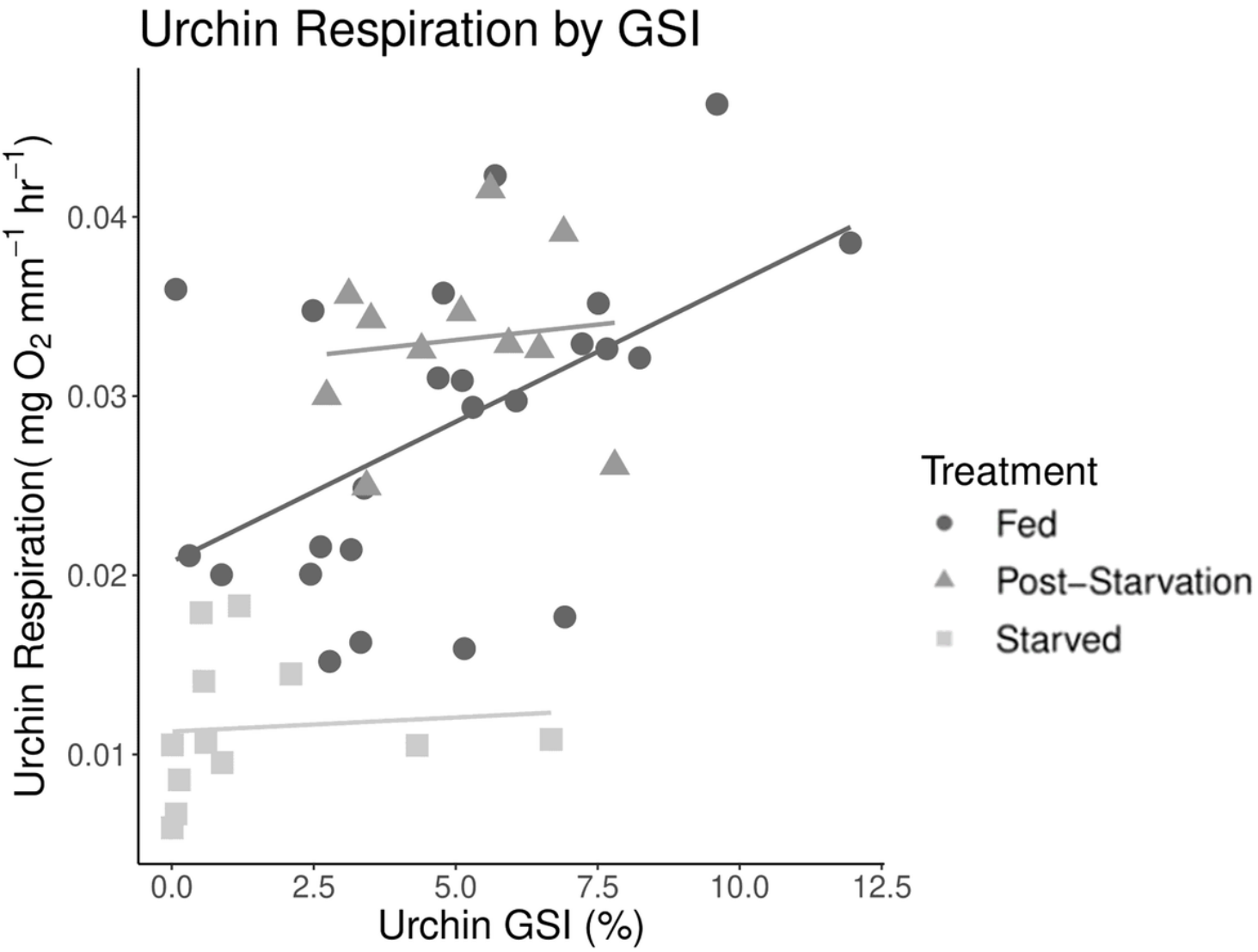

Figure 3

Regressions showing the relationships between size dependent respiration (SDR) and gonad somatic indices (GSI) in purple urchins within each of the feeding treatments. Urchins in the “Fed” group were measured on each of the sample dates (weeks 7, 14, 19 and 21) during which time they received regular access to food over the 21 week experiment (n = 24). Urchins in the “Post-Starvation” group were urchins that were measured during the last seven weeks of the experiment (weeks 19 and 21) after they began receiving regular access to food following being starved for the first 14 weeks of the experiment (n = 11). Urchins in the “Starved” group were urchins that were measured during the first 14 weeks of the experiments (weeks 7 and 14) during which time they were deprived of food (n = 12).

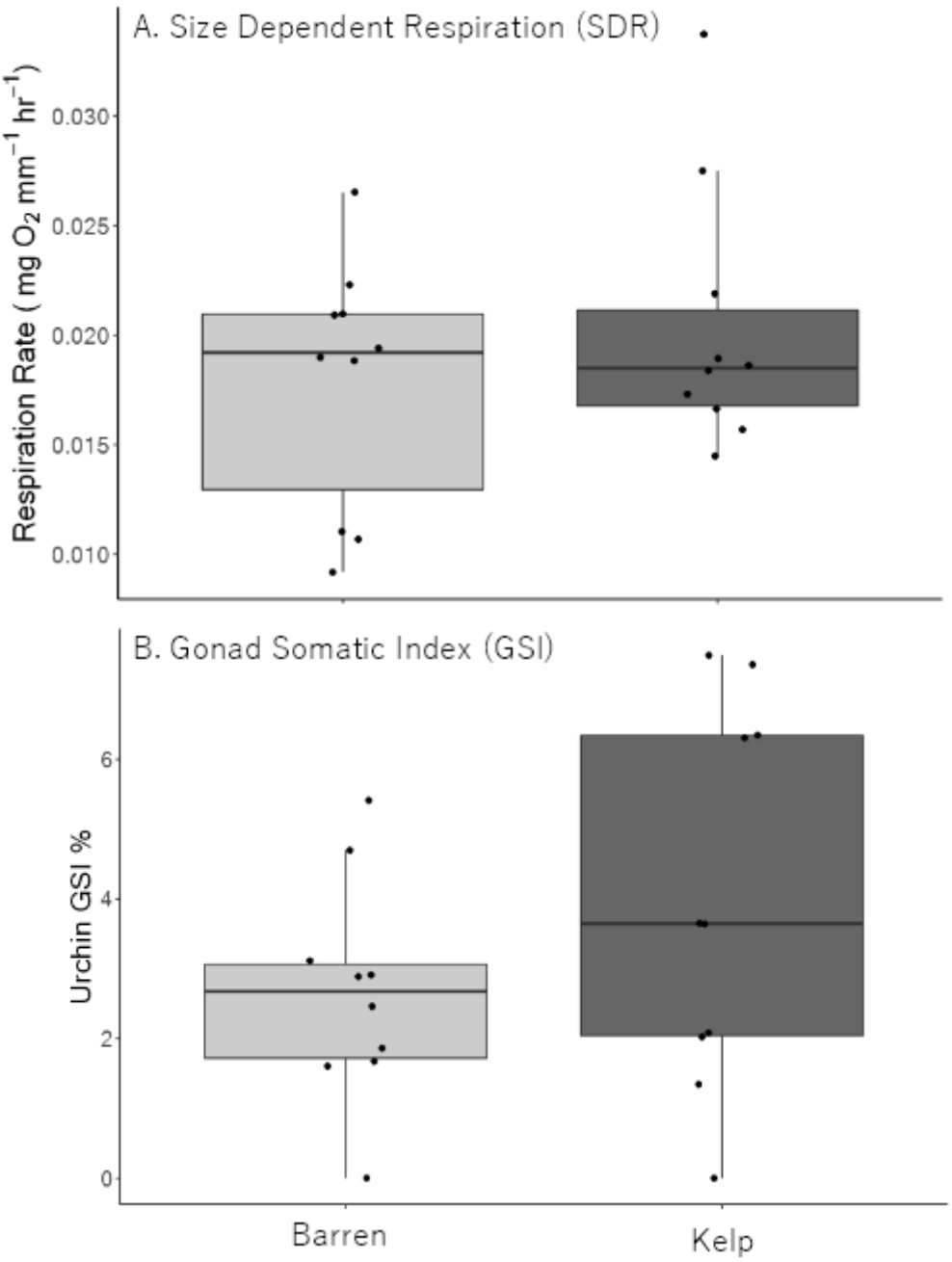

Figure 4

A) Boxplots showing size dependent respiration (SDR; mg O2 mm-1 hr-1) and B) gonad somatic indices (GSI; %) for purple urchins occurring in an urchin barren and a nearby kelp forest in Stillwater Cove, CA (n = 10).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- MBSupMat.docx