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Title: Experiments reveal limited top-down control of key herbivores in southern California kelp forests

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Abstract

Predator responses to gradients in prey density have important implications for population regulation and are a potential structuring force for subtidal marine communities, particularly on rocky reefs where herbivorous sea urchins can drive community state shifts. On rocky reefs in southern California where predatory sea otters have been extirpated, top-down control of sea urchins by alternative predators has been hypothesized but rarely tested experimentally. In laboratory feeding assays, predatory spiny lobsters (*Panulirus interruptus*) demonstrated a saturating functional response to urchin prey, whereby urchin proportional mortality was inversely density-dependent. In field experiments on rocky reefs near San Diego, CA, predators (primarily the labrid fish California sheephead, *Semicossyphus pulcher*) inflicted highly variable mortality on purple urchin (*Strongylocentrotus purpuratus*) prey across all density levels. However, at low to moderate densities commonly observed within kelp forests, purple urchin mortality increased to a peak at a density of ~11 m^{-2}. Above that level, at densities typical of urchin barrens, purple urchin mortality was density-independent. When larger red urchins (*Mesocentrotus franciscanus*) were offered to predators simultaneously with purple urchins, mortality was density-independent. Underwater videography revealed a positive relationship between purple urchin density and both the number and richness of fish predators, but these correlations were not observed when red urchins were present. Our results demonstrate highly variable mortality rates across prey densities in this system and suggest that top-down control of urchins can occur only under limited circumstances. Our findings provide insight into the dynamics of alternate community states observed on rocky reefs.

Key words: functional response, density dependence, rocky reef, *Macrocystis pyrifera, Panulirus interruptus, Strongylocentrotus purpuratus, Mesocentrotus franciscanus, Semicossyphus pulcher*

Introduction

In ecology, longstanding debates center on the frequency, strength, and causes of population regulation (Nicholson 1933, Hairston et al. 1960, Turchin 1995). Predatory, or top-down, regulation of prey requires direct density-dependent mortality, which bounds prey above extinction and below limitless growth (Murdoch 1994). Direct density dependence in at least one demographic rate is a necessary but not sufficient condition, by itself, for temporal population regulation (Hixon and Webster 2002). Alternatively, inverse density dependence and density independence occur when a demographic rate scales negatively or independently of density, respectively. Top-down regulation of prey often is inferred from correlative evidence, including time series meta-analysis (Worm and Myers 2003) and variance partitioning of community data (Halpern et al. 2006). A more rigorous test requires experimental manipulation of prey density followed by analysis of demographic rates or population size to explicitly test for a density-dependent change (Harrison and Cappuccino 1995, Hixon and Webster 2002). Such experiments have been used to document spatial (Hixon and Carr 1997) and temporal (Webster 2003, Johnson 2006) density-dependent predation mortality. This manipulative approach, which we adopt here, is particularly useful because it can provide insight on the mechanisms driving observed mortality rates. Top-down control of prey has implications for community structure and biodiversity (Paine 1974), ecosystem function (DeAngelis 1992), and population stability

(Murdoch and Oaten 1975), so a mechanistic understanding of predator-prey interactions is vital, particularly for ecosystems subject to anthropogenic stressors and those of conservation concern.

Predatory functional responses to gradients in prey density represent this mechanistic understanding, can be characterized experimentally, and are often incorporated into population dynamics models. The type II functional response is a saturating curve with high proportional mortality at low prey densities and rapidly decaying mortality rate as prey density increases (Holling 1959). Type II responses are considered de-stabilizing for predator-prey interactions and are common for specialist predators feeding on a single prey species which can be driven to extinction. Generalist predators that can switch to alternate prey at low prey densities are typically characterized by type III responses (Gascoigne and Lipcius 2004) which involve increasing proportional mortality as prey density increases from low to moderate levels. Intraspecific differences in body size and/or morphology can affect functional response shapes and parameter values (Eggleston 1990, Toscano and Griffen 2013), and the implications of observing a type II versus type III functional response for community structure and stability are substantial. A type II response can cause local extinction of prey when they fall below a low density threshold (Oaten and Murdoch 1975), while a type III response allows for top-down regulation (but persistence) of prey due to low mortality rates at low prey densities.

At the population level, mechanisms leading to density-dependent predation over short time-scales include refuge limitation for prey (Forrester and Steele 2004), predator aggregation (Anderson 2001), and stabilizing, type III functional responses of predators to prey density (Holling 1965). However, the spatial distribution of habitat can affect mortality patterns, with prey located on isolated patches more likely to suffer density-dependent predation than those in closely-spaced patches (Overholtzer-McLeod 2006) or within continuous habitats (Sandin and Pacala 2005). This is because transient predators are more likely to consume resources from closely spaced patches due to higher visitation rates (Overholtzer-McLeod 2006) or due to reduced predator selectivity among foraging patches (Sandin and Pacala 2005). On longer time-scales, or across a heterogenous landscape with multiple habitat types, regulation of prey can occur through a numerical response of predators (Solomon 1949), or via habitat-specific regulation (Seitz et al. 2001, Boada et al. 2018). Inferences about the density-mortality relationship are highly dependent upon the configuration and scale at which experiments are conducted (White et al. 2010). For instance, if habitat quality is spatially heterogeneous, prey in high and low quality habitats, respectively, could be consumed at different rates, independent of their density (Johnson 2006), producing a temporally stable prey population (at a large scale) even though observed patterns of mortality could be density-independent within some smaller patches.

We investigated the importance of top-down control for regulation of herbivorous invertebrates that can drive community state shifts in a widespread marine habitat. On nearshore rocky reefs, top-down control of herbivorous sea urchins by dominant predators like sea otters (*Enhydra lutris*) has strong effects on macroalgal persistence and faunal community structure (Estes et al. 1998). In southern California (SC), where sea otters have been extirpated, predatory fish, such as the California sheephead, *Semicossyphus pulcher*, and spiny lobsters, *Panulirus interruptus*, consume the dominant herbivores in this system, the sea urchins *Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus* (Cowen 1983, Tegner and Levin 1983, Dayton et al. 1998). Correlative and theoretical evidence suggest that when rocky reef-associated predators are removed, kelp forests are susceptible to a shift into urchin barrens (Scheibling 1996, Lafferty 2004, Hamilton and Caselle 2015, Dunn et al. 2017). However, physical forces also affect the distribution and persistence of habitat-providing macroalgae in this region (reviewed in Schiel and Foster 2015), and the relative importance of top-down control remains contentious (Halpern et al. 2006, Foster et al. 2006, Foster and Schiel 2010). Trophic control of rocky reefs has been experimentally confirmed in New Zealand (Shears and Babcock 2002), but clear experimental support for direct density-dependent mortality of urchins on SC rocky reefs remains lacking.

We quantified urchin mortality patterns in the lab and field across a gradient of prey density in two alternate urchin species combinations: purple urchins (*S. purpuratus*) alone and purple urchins with larger red urchins (*M. franciscanus*). Large red urchins can provide refuge to smaller urchins through a spine canopy refuge (Tegner and Dayton 1977) but are also an alternative prey item for both sheephead and spiny lobsters. Red urchins are also targeted in a fishery and are most abundant in marine reserves (Nichols et al. 2015, Teck et al. 2017), so their ability to mediate interactions between purple urchins and rocky reef predators may be spatially variable. We discriminated between potential mechanisms underlying the observed mortality patterns by characterizing the functional responses of spiny lobsters and quantifying the aggregative response of fishes foraging on urchins in the field.

Methods

Spiny lobster functional response to urchin density

We conducted experiments to determine the functional responses (Holling 1959) of spiny lobster predators to two alternate urchin species combinations: purple urchins alone and purple plus red urchins. We conducted feeding experiments within mesocosms at the San Diego State Coastal and Marine Institute Laboratory (CMIL) using lobsters (69-81 mm carapace length, CL) and urchins (15-86 mm test diameter, TD, for purple and 67-105 mm TD for red) collected from the Point Loma kelp forest or from rock jetties within Mission Bay, San Diego. Urchins were haphazardly selected for experimental trials to include a range of sizes within each of six density treatments in each trial: 2, 3, 5, 10, 16, or 26 urchins, which represent urchin densities commonly found on macroalgal-dominated rocky reefs (1 – 14 m^{-2}). We measured the TD of each urchin to facilitate identification of mortalities following trials. We used the same prey densities in both urchin species combination experiments by substituting one to three red urchins for purple urchins in each assay. We starved lobsters for 48 h prior to beginning the trials and used new lobsters in each trial. Following a 2 h urchin acclimation period, we added a haphazardly selected lobster to each experimental arena and allowed them to feed for 48 h, at which point remaining live urchins were counted and measured. When empty urchin test(s) were left over, we could directly identify which urchin(s) had been eaten. If no remains were left and no live urchins fit the TD of an urchin initially introduced, the missing urchin was assumed to have been eaten whole. We conducted trials between March-May 2014 for purple urchins (n = 11 replicate trials) and December 2016-March 2017 for purple plus red urchins (n = 9).

We compared the fits of two versions of the generalized functional response model (Real 1977) using AIC, one in which the scaling exponent was allowed to vary (providing a density-dependent, type III sigmoidal shape) and one in which we held the scaling exponent constant (for a type II saturating shape). Finding little evidence for the sigmoidal shape (see Appendix S1), we used the saturating Rogers random predator equation (Rogers 1972) for parameter estimation for both sets of feeding assays because this function describes an asymptotic response when prey are not replaced upon consumption. We fit the Rogers equation $Ne = N_0\left[1 - e^{a(N_e h - T)}\right]$ using maximum likelihood (Bolker 2008), where N_e and N_0 are the number of prey eaten and offered, respectively, a is the instantaneous attack/capture rate of the predator, T is experimental duration, and h is handling and ingesting time (units = day). All functional response fitting and tests were conducted in the R statistical environment with the *FRAIR* package (Pritchard et al. 2017).

To determine if predation by lobsters is size-structured, we estimated size-dependent survival probabilities for urchins in both sets of feeding experiments using logistic regression [generalized linear models (GLMs) with a binomial response and logit link]. Due to strong evidence in the overall model that the effect of urchin size on mortality probability varied between species combination treatments ($p = 0.053$), we fit separate GLMs for purple urchin-only data versus purple plus red urchin data. See Appendix S1 for additional experimental and analytical details.

Field experiment

To test for density-dependent mortality of sea urchins on rocky reefs in the field, in the summers of 2014 and 2017 we conducted manipulative experiments in two kelp forests near San Diego, California, USA (see Appendix S1 for description of study sites and experimental methods). Urchin densities on experimental plots ranged from 3.5-35.5 m^{-2} corresponding to 2, 3, 6, 9, 13, or 20 urchins per plot, and we recorded the TD of all urchins prior to deployment. Divers placed urchins on plots between 0900-1100 by removing the top layer of rocks, introducing the urchins, and then replacing the rocks. Divers remained on site for 1 min. to ensure urchins were firmly sheltered and then returned after 1 h and 24 h to count remaining urchins. We conducted trials with only purple urchins (16-73 mm TD) in both 2014 and 2017, while trials with purple urchins (22-75 mm TD) plus red urchins (58-111 mm TD) were conducted only in 2017 and used the same substitutive design as the feeding assays described above. Each trial included one replicate per urchin density (n = 11 trials for purple urchins, n = 6 with red urchins).

We used an information theoretic model selection approach to test for effects of urchin density, urchin species combination (purple only versus purple plus red urchins), site, experimental year, and sampling period on urchin mortality. We fit a set of generalized linear mixed models (GLMMs) using a binomial distribution, with candidate models based on *a priori* hypotheses of interest. We included a random effect of experimental reef nested within trial to account for the multiple urchin counts made on each reef for a given trial (the experimental unit in our case), at 1 h and 24 h after initial urchin deployment. For a given reef during each trial, we modeled the number of urchins eaten and number of urchins not eaten as the ‘successes’ and ‘failures’, respectively, for a series of binomial trials (Bolker 2008). We used the change in Akaike’s information criterion (ΔAIC) and AIC weights to gauge support for candidate models.

We initially included interaction terms of interest (e.g., urchin density*year and urchin density*site), but these were never included in the final model based on our model selection procedure. We fit GLMMs using Laplace approximation with the glmer() function from the *lme4* package in R (Bates et al. 2015).

To investigate feeding behavior in response to gradients in urchin density, we opportunistically deployed underwater video cameras at plots of each treatment density (N = 26 in purple only trials and N = 14 in purple + red trials). Video cameras recorded a single plot for the first 1 h after urchins were deployed. All individual fish that were actively foraging around the plot during the video were enumerated. California sheephead would initiate attacks on experimental urchins in most cases (see Appendix S1 for a list of predator and scavenger fish species). To test for an aggregative response, we measured the highest number of individual fish foraging simultaneously, MaxN (Ellis and DeMartini 1995). We also calculated the species richness of the foraging community observed in each video, to test whether higher density patches attract a more speciose suite of foragers. Data for both response variables were fit with linear models using prey density as the predictor, and including site, experimental year, and interactions as appropriate (model selection based on AIC, as above). Both sets of video data met assumptions of linear regression based on visual inspection of residuals and Levene's test for homoscedasticity.

Results

We found no compelling evidence for direct density-dependent mortality of urchins via the functional response of spiny lobsters, as lobsters in both feeding experiments exhibited saturating responses causing inversely density-dependent urchin mortality (Fig. 1, Appendix S1). Bootstrapped estimates of attack rate and handling time were similar for both experiments and had largely overlapping 95% confidence intervals [purple urchins: $a = 0.194$, 95% CI = (0.107, 0.373), and $h = 0.741$ (0.346, 1.237); purple plus red: $a = 0.127$ (0.074, 0.26), and $h = 0.594$ (0.203, 1.271)]. Survival probability increased with urchin size in both sets of experiments (both $p < 0.0001$; Appendix S1: Fig. S1). However, survival probability of purple urchins < 35 mm TD was higher when red urchins were offered as additional prey (Appendix S1: Fig. S1), and the regression coefficient for the binomial GLM testing for an effect of urchin size on mortality was 33% steeper for purple urchin-only trials (coefficient ± SE = 0.095 ± 0.011) compared to trials with red urchins (0.063 ± 0.011), demonstrating the mitigating effect of red urchins on predation of small purple urchins.

In the field, there was substantial variation in urchin proportional mortality across purple urchin-only and purple with red urchin experiments (Fig. 2). For the full dataset, the model with the most support (55% of AIC weight) included significant effects of urchin species combination, experimental site, and sampling period, and a non-significant effect of urchin density (Table 1). Because of the significant effect of urchin species combination ($p = 0.011$), we next conducted separate analyses for each species combination treatment, following the same model selection procedure described above. For purple urchin-only trials, the dominant model (90% of AIC weight) did not include urchin density as a predictor variable, and density was non-significant in all of the models in which it was included, suggesting that urchin mortality was density-independent across the full range of experimental densities. Experimental site, year, and sampling period were all significant predictors of urchin mortality (Table 1), and post-hoc comparisons demonstrated that urchin mortality was higher in South La Jolla and during trials conducted in 2014 ($p = 0.015$ and < 0.001, respectively). For trials including red and purple urchins together, the selected model (70% of AIC weight) included experimental site and sampling period as significant fixed factors and a non-significant fixed effect of initial urchin density (Table 1), also suggesting density-independent predation mortality. Trials conducted in South La Jolla again had higher proportional mortality than those in Point Loma based on a post-hoc means comparison ($p < 0.001$).

Overall, we found no evidence that urchin mortality was directly or inversely density-dependent across the complete range of densities we included in these experiments. However, our experimental urchin densities span the range observed under natural conditions across two rocky reef communities which may be alternative stable states exhibiting hysteresis (Filbee-Dexter and Scheibling 2014, Ling et al. 2015). Thus, the ability of predators to provide top-down control could depend on which stable state the system currently occupies. For purple urchin-only trials we observed a positive trend in proportional mortality across the three density levels which would typically characterize a macroalgal-dominated rocky reef (based on a LOESS visualization; Appendix S1: Fig S2A, B), so we conducted a subsequent analysis that separated data from reefs with urchin densities typically observed in the macroalgal-dominated state (3.5, 5.3 and 10.7 m^{-2}) from those typical of urchin barrens (16, 23.1, 35.5 m^{-2}). We then used a similar information theoretic model selection procedure with a binomial GLMM (as described above) to test for an effect of urchin density on proportional mortality. We found that at low densities typically observed in kelp forests, purple urchins alone suffer direct density-dependent predation mortality, as the coefficient for the fixed effect of initial urchin density was significantly positive (0.15, $p = 0.02$; Table 2), leading to mortality increasing from low (3.5 m^{-2}) to medium densities (10.7 m^{-2}; Fig. 2A, B). At high purple urchin densities observed in barrens, mortality was density-independent (Fig. 2A, B) and urchin density was not selected as a predictor in the final model (Table 2). As expected from our initial analysis, when red urchins were combined with purple urchins, mortality was density-independent for both low- and high-density datasets as urchin density was not selected as a predictor in the final model in either case (Fig. 2C, D; Table 2). This finding of a shift in top-down control at ~11 purple urchins m^{-2} aligns closely with the global estimate of the kelp forest to urchin barren threshold density (see Discussion and Appendix S1).

Due to strong evidence that site influenced the relationship between urchin density and MaxN ($p = 0.07$, Fig. 3), we fit separate linear models for each site. Site-specific models indicated that fish exhibited an aggregative response to increasing purple urchin density in South La Jolla ($F_{1,10} = 29.93$, $p < 0.001$), but not in Point Loma ($F_{1,12} = 1.37$, $p = 0.264$; Fig. 3A). When red urchins were also available, fish did not demonstrate an aggregative response ($p = 0.801$; Fig. 3B). For species richness of the fish assemblage during purple urchin-only trials, there was a significant interaction between urchin density and experimental year ($p = 0.013$). When analyzed separately for each year, fish species richness was positively correlated with purple urchin density for trials conducted in 2014 ($F_{1,10} = 23.75$, $p < 0.001$), but not in 2017 ($F_{1,12} = 2.33$, $p = 0.15$; Appendix S1: Fig. S3A). Urchin density was not a significant predictor of fish species richness when red urchins were also present ($p = 0.645$), though richness was significantly higher in South La Jolla than Point Loma ($p = 0.04$; Appendix S1: Fig. S3B).

Discussion

Correlative evidence has suggested a strong link between rocky reef predators and their urchin prey, and that top-down regulation of urchins helps maintain kelp forests and their associated high levels of biodiversity (Sala et al. 1998, Lafferty 2004, Hamilton and Caselle 2015). We found that the relationship between sea urchin density and proportional mortality on rocky reefs is dependent on predator and prey assemblages and varies between areas of low versus high prey density, resulting in top-down control only under limited circumstances. Purple urchin density-dependent mortality occurred where sheephead were large and abundant, which is common within southern California marine protected areas (MPAs) (Hamilton and Caselle 2015, Selden et al. 2017). However, sheephead and other predators only regulated purple urchins when large red urchins were absent, a condition consistent with fished areas but not typically observed within MPAs (Nichols et al. 2015, Teck et al. 2017). While individual spiny lobsters ate relatively few urchins and did not cause direct density-dependent mortality via their functional response, fish predators did induce a region of increasing proportional mortality at low prey densities by aggregating to higher density prey patches. However, this result is dependent on initial urchin densities being consistent with those found in kelp forests rather than in urchin barrens, and an urchin recruitment pulse (Hart and Scheibling 1988, Cardona et al. 2013) could overwhelm the narrow region of directly density-dependent mortality that we detected. We also observed substantial variability in predation mortality across all six experimental density levels (Fig. 2), which represent natural urchin densities across two alternate community states. For example, at the highest urchin density level, predators consumed between 0 and 17 purple urchins within the first hour of the experiment (Fig. 2B). This level of variability is similar to that previously documented in this system (Nichols et al. 2015), and is likely due to rapid, localized responses of fish predators to urchin prey in some cases. Overall, our results suggest a need to re-evaluate the paradigm of top-down control on SC rocky reefs in the absence of sea otters.

Trophic cascades are a common occurrence on rocky reefs globally (Shears and Babcock 2002, Lafferty 2004, Guidetti 2006), and our results suggest that under certain circumstances, predatory fish, more so than lobsters, contribute to persistence of kelp forests in SC by consuming urchins. This is similar to other temperate and tropical regions in which predatory fish generally exert a stronger influence on urchins than do lobsters (Sheppard-Brennand et al. 2017). Others have also suggested that fishing for spiny lobsters does not inevitably induce a trophic cascade (Guenther et al. 2012), yet the paradigm of top-down control by lobsters in SC has remained prevalent despite a lack of experimental evidence for such an effect. It is possible that spiny lobster populations have been size-truncated by fishing such that they are no longer able to provide top-down control in this region (McArdle 2008). Though some large lobsters (> 100 mm CL) remain on rocky reefs in SC, particularly around the Channel Islands or within MPAs (Kay et al. 2012, Yaeger et al. 2017), the size range we used here (< 81 mm CL) are the most abundant size class caught along the mainland (Hovel et al. 2015, Yaeger et al. 2017). Results from our functional response experiments suggest that lobsters in this size range are unable to exert top-down control on sea urchins inhabiting SC rocky reefs. While we do document density-dependent mortality under certain field conditions, our estimate regarding the strength of this effect is likely conservative given our inability to account for the "ghosts of missing animals" within kelp forests which have been highly altered by humans (Dayton et al. 1998). The ongoing recovery of sea otters in southern California (Lafferty and Tinker 2014) should strengthen the top-down control exerted by predators in this ecosystem (Watson and Estes 2011). This could drastically alter our findings of context-specific density-dependent mortality of sea urchins, particularly because otters preferentially consume large red urchins (Stevenson et al. 2016) and can interact with mesopredators to partition size-structured sea urchin prey (Burt et al. 2018), both of which strengthen the trophic cascade leading to kelp forest dominance.

Our results differ from the findings of a previous experimental test of top-down control on SC rocky reefs, which found that purple urchins suffered inversely density-dependent or density-independent mortality depending on the time of day and surrounding substrate cover (Nichols et al. 2015). Our experiments incorporated a wider size range of prey than this previous study, including urchins < 35 mm TD. Large sheephead are required to consume the largest urchins (Selden et al. 2017), and lobsters in our study more readily consumed small urchins than larger urchins. However, the introduction of refuge-providing red urchins modulated some of the threat of predation for small urchins (Appendix S1: Fig. S1) and eliminated the potential for density-dependent mortality (Fig. 2C, D). Two potential mechanisms may have caused this result: direct sheltering underneath the spine canopy by small urchins or reduced predatory dependence on purple urchins because of increased available biomass of an alternative, larger-bodied prey item. We believe the latter to be the likely mechanism operating here, because when red urchins were included as a potential prey item, the difference in urchin biomass across density levels was small (~3x) relative to differences in density (~10x). Body size plays a key role in trophic interactions and can determine the strength of trophic cascades (Shurin and Seabloom 2005), so we strongly advocate for including the full size range of prey items in studies of predator-prey interactions. This is particularly important in the case of mixed prey assemblages of different body sizes, where the presence of a high biomass prey item could strongly affect mortality rates at low levels of prey density but have less effect at high prey densities, as we observed on experimental reefs with red and purple urchins offered together.

The discrete plots of granite cobble that we used in these experiments could overestimate urchin mortality rates relative to other urchin habitats (bedrock, urchin cups/bowls) if predators are more likely to consume urchins from experimental reefs than natural habitats. However, experimental plots are an established method used to test for density-dependent mortality of subtidal prey (Schmitt 1987, Hixon and Carr 1997, Webster 2003), and the critical time at which population regulation must occur to prevent a shift from a kelp forest to an urchin barren is when urchins exhibit reduced crypsis when inadequate drift kelp forces them to emerge from shelter to forage. Our reefs approximate this level of protection. Moreover, a recent meta-analysis showed that predatory impacts on urchins increase with longer experimental duration and do not vary with the size of the experimental plot (Sheppard-Brennand et al. 2017), so our short-term, small-scale field experiment may actually be a conservative estimate of urchin mortality.

While urchin barrens and kelp forests are proposed to be alternative stable states (Filbee-Dexter and Scheibling 2014, Ling et al. 2015), direct empirical evidence of their stability remains lacking due to the difficulty of manipulating ecosystems at the spatial and temporal scales required, and some authors have questioned whether rocky reefs truly support stable alternative communities (Petraitis and Dudgeon 2004). The narrow region of direct density-dependent mortality we observed is not sufficient on its own to confirm the idea of alternative stable states on rocky reefs but does provide evidence that predators may be able to prevent a forward shift from a kelp forest into an urchin barren if large red urchins are absent (due to fishing, disease, etc.). This region of direct density dependence requires beginning in the kelp forest state, and an urchin recruitment pulse (Hart and Scheibling 1988, Cardona et al. 2013) could push the system beyond the threshold of where top-down control can act. At low prey densities, predators exert top-down control on purple urchins via aggregation and size-selective predation on small individuals, while at higher prey densities, similar to those in urchin barrens, mortality is density-independent and top-down control no longer acts. This conceptual model is supported by the overlap between our region of increasing proportional mortality and the estimate of urchin biomass at which a forward shift from kelp forest dominance into urchin barrens occurs on rocky reefs globally (Ling et al. 2015). Using test diameter-to-biomass conversions (Shears et al. 2012), we estimated the density of urchins in our experiments (back-calculated from mean biomass, see Appendix S1) at which the forward transition would occur based on Ling et al.'s (2015) global mean estimate of this threshold. This estimate of 12.3 m^{-2} is notably close to the point at which we document mortality shifting from density-dependent to density-independent (~ 11 m^{-2}; Fig. 2, Appendix S1: Fig. S2). Our threshold density is also similar to the urchin density threshold between macroalgal and barren states on rocky reefs in the northeast Atlantic (10 m^{-2}, Leinaas and Christie 1996). Across the northern Channel Islands, kelp density and percent cover are negatively correlated with urchin density, which itself is negatively related to sheephead biomass, though no threshold relationships are apparent (Hamilton and Caselle 2015). Importantly, only in areas where large sheephead are present (mainly MPAs) can they strongly affect urchin grazing potential via top-down control (Hamilton and Caselle 2015). Spiny lobster and sheephead density, size, and diet are all spatially variable across the SC Bight (Hamilton et al. 2011, Caselle et al. 2011, Yaeger et al. 2017), and there is variation in the strength of trophic cascades induced by fishing for urchin predators across environmental gradients (Shears et al. 2008, Guenther et al. 2012). Thus, further tests are needed to identify the contexts in which top-down control structures SC rocky reefs, particularly in the face of growing anthropogenic threats to these systems.

Experimental manipulation of prey density can reveal mechanisms driving mortality patterns, and knowledge of these mechanisms allows for predictions about whether density-dependent mortality scales from small experimental plots up to larger areas (Steele and Forrester 2005). However, simply detecting a region of direct density dependence should not be interpreted as a finding that predators are regulating their prey at the population level because spatial density dependence does not necessarily lead to temporal density dependence (Forrester et al. 2008), which is required to stabilize populations (Murdoch 1994). Using experimental tests, we found that predators can cause spatial density dependence in mortality for urchins in some cases, but that pattern is far from ubiquitous. We recommend that manipulative experiments should accompany correlative surveys when attempting to determine the strength of top-down population regulation.

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Table 1: Results of generalized linear mixed models (GLMMs) testing for density-dependent urchin mortality in field experiments.

Models and effects	*Estimate/Variance*	*Std. Error/Std. Deviation*	*z*	*p*
Full model				
Fixed effects				
Intercept	-3.504	0.531	-6.602	<0.001
Initial density	-0.001	0.010	-0.139	0.889
Urchin treatment	1.257	0.496	2.534	0.011
Experimental site	1.054	0.470	2.243	0.025
Sampling period	1.995	0.139	14.293	<0.001
Random effects				
Reef:Trial	0.763	0.873		
Trial	0.695	0.834		
Purple urchin- only model				
Fixed effects				
Intercept	-1.256	0.226	-5.551	<0.001
Experimental site	0.727	0.299	2.433	0.015
Experimental year	-1.800	0.304	-5.918	<0.001
Sampling period	1.906	0.161	11.842	<0.001
Random effects				
Reef:Trial	0.774	0.879		
Trial	0.000	0.000		

Purple + red model				
Fixed effects				
Intercept	-4.319	0.517	-8.35	<0.001
Initial density	-0.006	0.015	-0.428	0.669
Experimental site	2.558	0.410	6.231	<0.001
Sampling period	2.223	0.278	7.986	<0.00
Random effects				
Reef:Trial	0.319	0.565		
Trial	0.047	0.217		

Notes: For each analysis we show only the output for the final selected model. Estimate and standard error values are for coefficients of fixed factors, with Point Loma, 2014, and 1 h sampling periods as references, respectively. Variance and standard deviation apply to random effects. Model AICs are as follows: full model = 635.2; purple urchin-only model = 427.6; purple + red model = 181.4.

Table 2: Results of generalized linear mixed models (GLMMs) testing for density-dependent urchin mortality in low vs. high urchin density plots, which are representative of kelp forest and urchin barrens, respectively.

Density and effects	*Estimate/Variance*	*Std. Error/Std. Deviation*	*z*	*p*
Purple-only low density				
Fixed effects				
Intercept	-2.251	0.639	-3.522	<0.001
Initial density	0.150	0.065	2.325	0.020
Experimental year	-1.636	0.476	-3.435	<0.001
Sampling period	2.257	0.376	6.00	<0.001
Random effects				
Reef:Trial	0.309	0.556		

Trial	0.153	0.391		
Purple-only high density				
Fixed effects				
Intercept	-1.382	0.283	-4.874	<0.001
Experimental site	1.144	0.376	3.038	0.002
Experimental year	-1.928	0.383	-5.036	<0.001
Sampling period	1.818	0.178	10.22	<0.001
Random effects				
Reef:Trial	0.775	0.88		
Trial	0.000	0.000		
Purple + red low density				
Fixed effects				
Intercept	-4.08	0.880	-4.634	<0.001
Experimental site	2.939	0.847	3.469	<0.001
Sampling period	1.638	0.546	3.001	0.003
Random effects				
Reef: Trial	0.530	0.728		
Trial	<0.001	<0.001		
Purple + red high density				
Fixed effects				
Intercept	-4.644	0.476	-9.748	<0.001
Experimental site	2.403	0.459	5.235	<0.001
Sampling period	2.452	0.333	7.358	<0.001
Random effects				
Reef:Trial	0.277	0.527		
Trial	0.057	0.239		

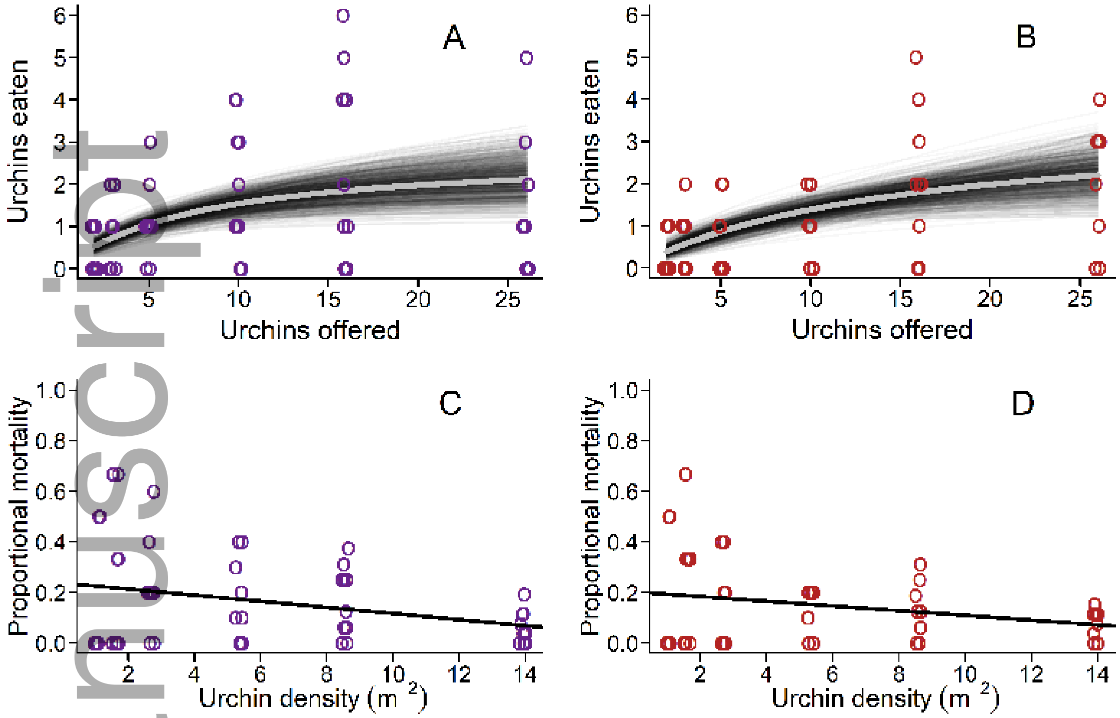
Notes: For each analysis we show only the output for the final selected model. Estimate and standard error values are for coefficients of fixed factors, with the same references as Table 1. Variance and standard deviation apply to random effects. Density AICs are as follows: purple-only low density = 146.5; purple-only high density = 282.9; purple + red low density = 68.3; purple + red high density = 117.5.

Figure legends

Fig. 1: Functional responses of individual spiny lobster predators to purple urchin prey (A) and purple plus red urchin prey offered simultaneously (B). In each, the thick gray line is the best-fit functional response, and thin, dark lines are bootstrapped estimates. Points are raw data jittered horizontally. Panels C and D show proportional mortality of urchin prey fit with linear regression (Panel C, purple urchins only: $F_{1,64} = 5.398$, $p = 0.0233$; Panel D, purple plus red urchins: $F_{1,52} = 3.625$, $p = 0.0624$). Both show a decline in mortality with increasing prey density, characteristic of a saturating functional response.

Fig. 2: Proportional mortality of urchins in field trials for purple urchins alone, (Panels A, B; n = 11 trials) and for purple plus red urchins offered together (Panels C, D; n = 6 trials) after 1 h (A, C) and 24 h (B, D). Points are jittered horizontally. Mortality prediction curves are from the models with the lowest AIC for low and high density reefs analyzed separately for each urchin species combination. Data are pooled across experimental sites and years (for purple urchin-only trials); see Table 2 for statistical output for all factors.

Fig. 3: Fish aggregative response to sea urchin density in the field. The response variable, MaxN, is the highest number of fish simultaneously foraging. Panel A shows results for purple urchin only trials (2014 and 2017), with trials conducted in Point Loma as diamonds and those in South La Jolla as open circles. Site and urchin density interacted in our full model, so while we plot prediction lines for both sites, urchin density was a significant predictor for South La Jolla ($p < 0.001$, $R^2 = 0.75$, solid purple line) but not Point Loma ($p = 0.264$, $R^2=0.10$, dashed grey). Panel B shows data from trials with purple plus red urchins. Urchin density was not a significant predictor of MaxN when red and purple urchins were offered together ($p = 0.801$).



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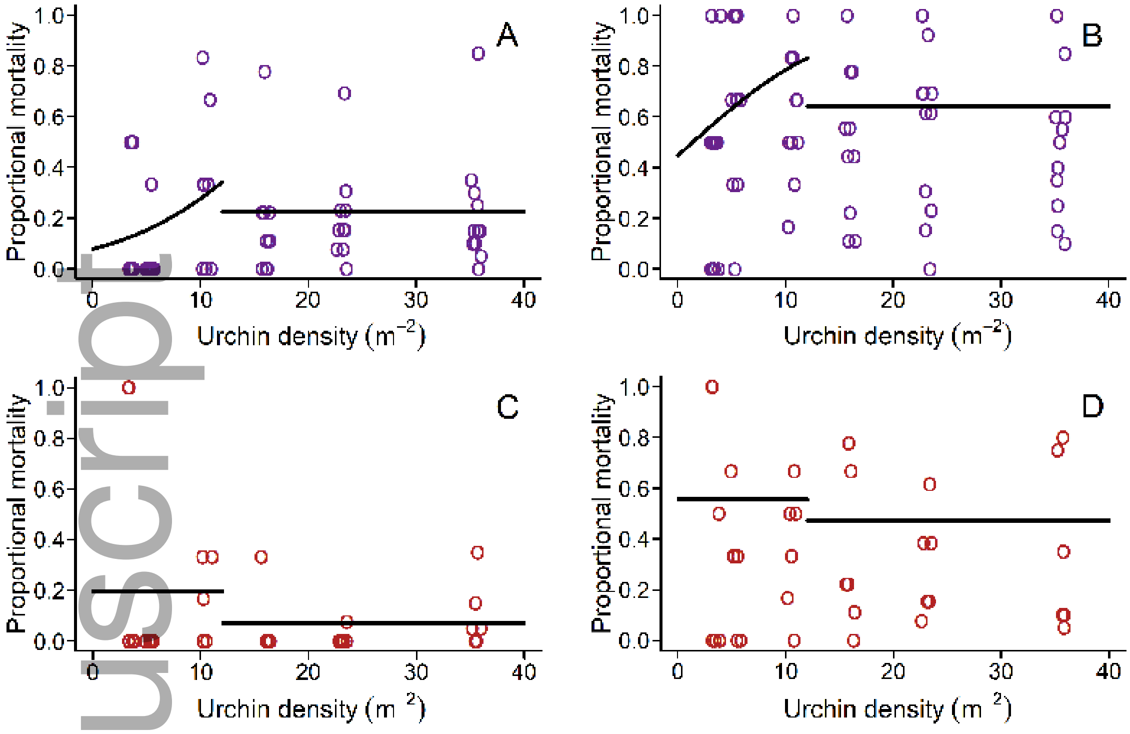

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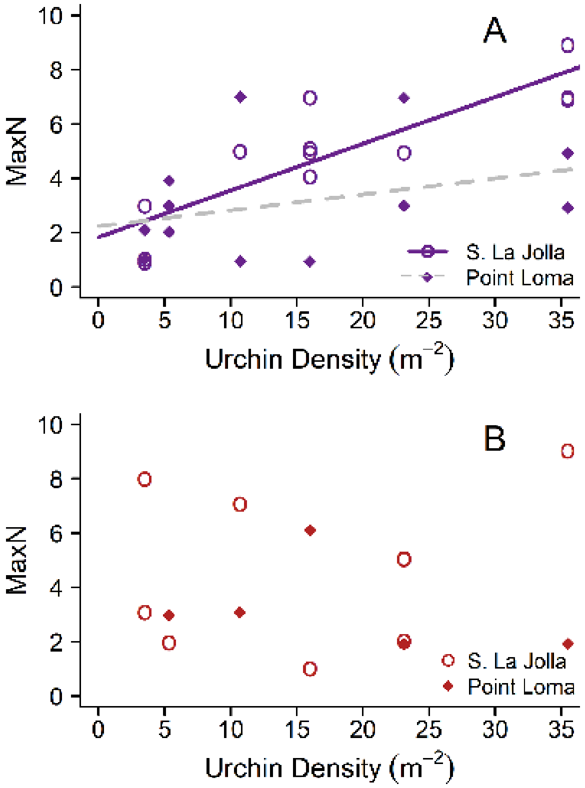

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