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Shifts in intertidal zonation and refuge use by prey after mass mortalities of two predators

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Abstract. Recent mass mortalities of two predatory sea star species provided an unprecedented opportunity to test the effect of predators on rocky intertidal prey. Mass mortalities provide insight that manipulative experiments cannot because they alter ecosystems on a larger scale, for longer time periods, and remove both organisms and their cues from the environment. We examined shifts in population size structure, vertical zonation, and use of emersed refuge habitats outside tidepools by the abundant herbivorous black turban snail *Tegula funebris*, both before and after the successive mortalities of two predatory sea stars. The small cryptic predator *Leptasterias* spp. suffered a localized but extreme mortality event in November 2010, followed by two mass mortalities of the keystone predator *Pisaster ochraceus* in August 2011 and autumn 2013. After the local extinction of *Leptasterias*, the population size of *Tegula* more than doubled. Also, since *Leptasterias* primarily inhabited only mid to low intertidal tidepools at this site, small and medium sized snails (which are preferred by *Leptasterias*) shifted lower in the intertidal and into tidepools after the mortality of *Leptasterias*. After the mortality of *Pisaster* in August 2011, large snails did not shift lower in the intertidal zone despite being preferred by *Pisaster*. Small and medium sized snails became denser in the higher zone and outside tidepools, which was not likely due to *Pisaster* mortality. Previous studies concluded that *Pisaster* maintained vertical size gradients of snails, but our data implicate the overlooked predator *Leptasterias* as the primary cause. This natural experiment indicated that (1) predators exert top-down control over prey population sizes and lower limits, (2) vertical zonation of prey are dynamic and controlled in part by prey behavior, and (3) predators exert the strongest effects on more vulnerable individuals, which typically inhabit stressful habitats higher on the shore or outside tidepools to avoid predation. Because the mass mortalities of two predators drastically reduced both the predation pressure and the chemical cues of predators in the environment, we were able to investigate both the effects of predators on prey populations and the effects on mobile prey behavior.

Key words: *intertidal zonation; Leptasterias spp.; mass mortality; natural experiment; nonconsumptive effects; Pisaster ochraceus; sea star wasting disease; size-dependent predation; Tegula funebris; tidepool; top-down control; vertical size gradient.*

INTRODUCTION

Natural experiments are some of the most powerful tools used by ecologists because they can reveal processes occurring in whole ecosystems over space or time. While local extinctions of species by disease, extirpation, or natural disasters are unfortunate events, they provide rare insights into community interactions that are usually impossible or unethical to obtain experimentally (Diamond 1983, Menge et al. 2016). Careful long-term monitoring is essential to capitalize on these rare opportunities. For example, monitoring coral reefs before and after hurricanes (Connell 1978) and the mass mortality of a sea urchin (Hughes 1994) transformed our understanding of

community stability and alternate stable states, respectively. Also, local extirpation or reintroduction of predators in lakes, tropical forests, and coniferous forests led to the reorganization of food webs, illustrating the complexity of trophic interactions and importance of top-down control (Zaret and Paine 1973, Terborgh et al. 2001, Ripple and Beschta 2012). More recently, climate change has served as a natural experiment demonstrating that species distributions, phenology, migration patterns, and species interactions are sensitive to warming temperatures (Parmesan 2006, Poloczanska et al. 2013).

Recent mortality events of predatory sea stars on the west coast of North America present a unique opportunity to investigate well-known concepts in ecology, including keystone predation, trophic cascades, and biotic control of intertidal zonation (Menge et al. 2016). The concept of intertidal zonation suggests that lower limits of species are controlled by biotic interactions while upper limits are controlled by abiotic stresses (Connell 1972, Robles et al. 2009, Mislan et al. 2014). It has also

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become increasingly apparent that vertical distributions in the intertidal zone are actually dynamic and not permanent spatial refuges from competition or predation (Robles and Desharnais 2002, Robles et al. 2009, Donahue et al. 2011). Vertical zonation may be especially dynamic for mobile species that may adjust distributions through behavior (Vermeij 1972, Rochette and Dill 2000). Predator control over dynamic lower limits would be supported if mobile prey species respond quickly to mass mortality of predators by moving lower on shore.

Unlike manual removals of predators in most field experiments, mass mortalities of predators may more thoroughly eradicate predators, last longer, and eliminate chemical cues that can strongly affect behavior of even far-away prey (Kats and Dill 1998, Laundré et al. 2010). When mortalities are extensive, the opportunity arises to assess the subtle, long-term effects of predators on prey species including (1) nonconsumptive effects on prey behavior and distribution and (2) survival and growth of prey released from predation. This thorough removal of predators and especially their chemical cues is much harder to obtain in a manipulative field experiment. On the other hand, mass mortalities of predators are natural experiments that typically lack experimental controls that capture influences of extraneous factors, and they lack replication that enables one to test for consistency in the responses (Diamond 1983). Thus, the experimenter is less able to attribute the responses by prey to release from predation. While this lack of control and replication is not ideal, extensive predator mortalities may enable unprecedented insight into predator–prey interactions (Menge et al. 2016).

One such interaction is the influence of predators on patterns of intertidal zonation; predators often drive variation in prey size among intertidal zones, which are referred to as “vertical size distributions” (Seed 1969, Vermeij 1972, McQuaid et al. 2000). For mobile prey

species, individuals must balance the conflicting demands of (1) avoiding stress near upper limits, (2) avoiding predation or competition near lower limits, and (3) seeking abundant food near lower limits (Paine 1969, Bertness 1977, Rochette and Dill 2000, Pincebourde et al. 2008). Importantly, the balance of these conflicting needs often depends on the size of the organism, resulting in vertical size gradients (Vermeij 1972). For example, large individuals may occur higher on the shore because they can better withstand physiological stress than juveniles (Vermeij 1972) or predators may preferentially consume large individuals low on the shore (Cushman 1989, Rochette and Dill 2000). Alternatively, the opposite pattern may arise when predators preferentially consume smaller individuals low on the shore or large individuals choose to risk predation for increased energetic gain low on the shore (Paine 1969, Vermeij 1972). Thus, mass mortalities of predators provide an opportunity to determine the effect of predators on vertical size distributions of prey.

In rocky intertidal communities on the west coast of North America, larger individuals of the abundant herbivorous gastropod, *Tegula* (formerly *Chlorostoma*) *funebralis* (Bouchet and Rosenberg 2015) generally occur lower on the shore than smaller ones (Fig. 1a; Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983, Fawcett 1984). This pattern has often been attributed to predation pressure by the original keystone species *Pisaster ochraceus*, which is most abundance lower on shore (Wara and Wright 1964, Paine 1969, Markowitz 1980). However, *Pisaster* preferentially consume large snails in the field and laboratory (Markowitz 1980). Thus, it is somewhat perplexing that large snails tend to be lower on shore where *Pisaster* is most abundant. Hence, it was proposed that *Pisaster* force all individuals upward but that large, reproductive snails (>12–14 mm diameter) risk venturing low on the shore to forage on

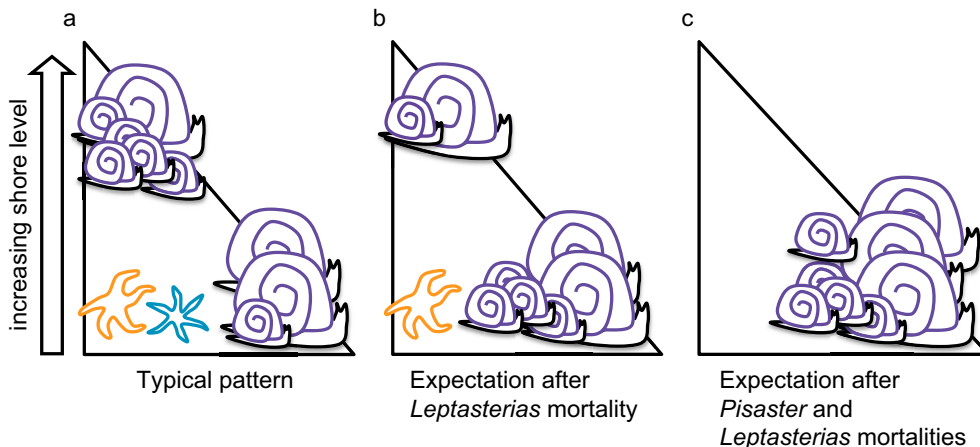


FIG. 1. (a) Diagram depicting the typical trend of decreasing *Tegula funebralis* size at higher shore levels. Since *Leptasterias* spp. (six arms) prefers smaller *Tegula*, we expected small *Tegula* to increase in the lower zone after (b) the *Leptasterias* mortality event. *Pisaster ochraceus* (five arms) prefers larger *Tegula*, which should increase in the lower zone after (c) the *Pisaster* mortality events. [Color figure can be viewed at wileyonlinelibrary.com]

abundant food and satisfy high energetic demands (Paine 1969, Markowitz 1980).

One piece of this long-standing puzzle may be missing. The small (1–5 cm diameter) predatory sea star, *Leptasterias* spp. (see Flowers and Foltz [2001] for species complex) co-occurs with *Tegula* in low to mid intertidal zones along the west coast of the United States (Morris et al. 1980). *Leptasterias* nearly exclusively prey on small and medium-sized *Tegula* (<18 mm) compared to large *Tegula* (>18 mm) in the field and laboratory (Bartl 1980, Gravem and Morgan 2016). Thus, it may be that *Leptasterias*, not *Pisaster*, are actually responsible for the decrease in *Tegula* size with shore level (Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983, Fawcett 1984).

We capitalized on natural mass mortality events of *Leptasterias* in November 2010 followed shortly thereafter by *Pisaster* in August 2011 and November 2013 in northern California (Fig. 2). Based on surveys over time at our study site in Horseshoe Cove, Bodega Head, California, USA (38°18'59.4" N, 123°4'16.3" W) and qualitative searches of *Leptasterias* in the surrounding area, the *Leptasterias* mortality event in November 2010 was, as far as we know, localized near Bodega Head but was severe with nearly 100% mortality and no recovery through the present because *Leptasterias* brood their larvae (Fig. 2; see Appendix S1 and Appendix S1: Fig. S1 for survey details, extent of mortality, and possible causes). The first *Pisaster* mortality event in August 2011 was caused by a harmful algal bloom that extended along 100 km of coastline, primarily in Sonoma County, California (Rogers-Bennett et al. 2012, Jurgens et al. 2015). The bloom killed nearly 100% of *Pisaster* at Schoolhouse Beach (Fig. 2, 38°22'28.4" N, 123°4'44.9" W), which is 6.4 km north of our study site at Horseshoe Cove.

The second *Pisaster* mortality was due to sea star wasting disease, which caused severe declines in *Pisaster* density from Mexico to Alaska (Hewson et al. 2014, Menge et al. 2016), including an 89% decline 6.4 km north of our site at Schoolhouse Beach (Fig. 2).

In addition to affecting vertical size distributions, predators commonly cause prey to increase use of refuges (Lima 1998), which in intertidal communities, may include emersed rock outside tidepools where predators cannot forage at low tide (Feder 1963, Menge and Lubchenco 1981). To first test this effect, we examined whether *Tegula* responded to *Leptasterias* presence in tidepools by increasing use of emersed refuges just outside tidepools in spring 2010, before any mortality events. After the *Leptasterias* mortality event in November 2010, we expected that survival of vulnerable smaller snails would increase and that smaller snails would move lower on shore (Fig. 1). We also expected smaller snails to move into tidepools since *Leptasterias* is primarily found only inside tidepools and not on emersed rock at this site. When the *Pisaster* mortalities occurred in August 2011 and November 2013, we expected that snails would descend on the shore and increasingly inhabit tidepools, and this would be most evident for the large snails that are preferred by *Pisaster* (Fig. 1; Markowitz 1980). Though *Pisaster* occurs in both tidepools and the emersed matrix, they are unable to forage at low tide when emersed (Menge and Lubchenco 1981). To test these hypotheses, we surveyed tidepools spanning the vertical range of *Tegula* and measured snail sizes and abundances in tidepools and emersed refuges. This natural experiment enabled us to investigate the potential top-down effects of two predators on prey population size, size distributions of prey, and prey refuge use at two spatial scales: among intertidal zones and in and out of tidepools.

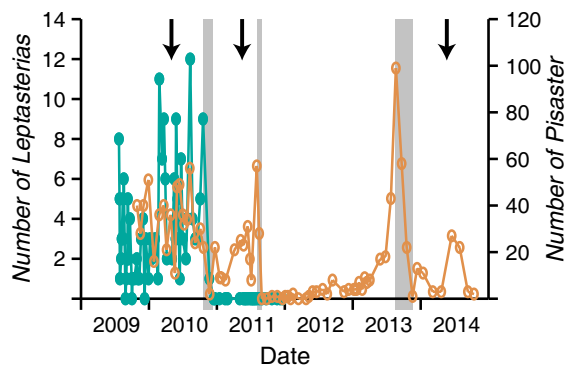


FIG. 2. Number of *Leptasterias* spp. (solid circles) removed weekly from eight tidepools in Horseshoe Cove, California, USA and number of *Pisaster ochraceus* (open circles) removed biweekly from 12 large intertidal boulders 6.4 km north at Schoolhouse Beach. Three mass mortality events occurred at our site (gray boxes): first of *Leptasterias* spp. in November 2010, second and third of *P. ochraceus* in late August 2011 and fall 2013, respectively. *Tegula funebris* were surveyed in 21, 44, and 30 tidepools in Horseshoe Cove in spring 2010, 2011, and 2014, respectively (black arrows). [Color figure can be viewed at wileyonlinelibrary.com]

METHODS

Shifts in prey population after predator mortalities

We determined whether *Tegula* populations or behavior changed in Horseshoe Cove after the mortalities of both sea star species by surveying the population size structure, vertical zonation, and refuge habitat use of *Tegula* in 21, 44, and 30 tidepools on 10 April 2010, 1–27 May 2011, and 10–19 April 2014, respectively (arrows in Fig. 2). Each survey was conducted in spring to control for seasonal differences in sea star and snail distributions and behaviors (Paine 1969, Menge 1972, Markowitz 1980).

To test size-dependent responses of snails to sea star mortalities, we counted and measured snails separately from inside tidepools and in refuge habitats just outside tidepools termed “halos.” Halos included a 15-cm band of emersed rock surrounding each tidepool where sea stars do not often forage at low tide (Menge and Menge 1974). The percentage of snails in the halo [(snails in the halo/snails in tidepool and halo) × 100] was used to estimate refuge use. Snails were considered to be in the

halo if they broke the water's surface. We restricted surveys to tidepools and halos because this was part of another study that focused on the effect of sea stars on microhabitat choice by snails (Gravem 2015). We divided snails by size into 3-mm increments at their widest shell diameter and defined small snails as <12 mm and not yet mature (Paine 1971), medium snails as 12–18 mm and newly mature, and large snails as >18 mm, mature, rarely eaten by *Leptasterias*, and preferred by *Pisaster* (Markowitz 1980, Gravem and Morgan 2016). In 2010, we surveyed tidepools with *Leptasterias* and tidepools where we had experimentally removed *Leptasterias* as part of another experiment (see Appendix S1 for removal methods) to determine size-dependent snail responses to *Leptasterias*. *Leptasterias* was absent from the site in 2011 and 2014. *Pisaster* was absent from all tidepools for all surveys though *Pisaster* occurred in the surrounding area, especially in 2010 and 2011.

We chose tidepools over a large vertical range that encompassed the *Tegula* zone, and used surveying equipment and United States Geological Survey benchmarks to measure the shore level of each tidepool surface (range 0.95–2.23 m above mean lower low water, MLLW). We categorized tidepools into lower, middle, and higher shore levels for statistical analysis (0.70–1.15, 1.15–1.50, and 1.50–2.30 m above MLLW). These categories do not match classic definitions of low, mid, and high zones, but rather characterize the distribution of *Tegula*. To estimate snail abundance among different sizes of tidepools, we estimated snail density per liter by quantifying water pumped from tidepools into buckets (range 1.2–85.0 L). This metric was used because tidepools were rugose and varied in depth, so using the surface area of tidepools would have overestimated densities. Further, this was part of a study focused on the effects of waterborne predator chemical cues on prey behavior (Gravem 2015).

Statistical analyses

All data were analyzed using mixed linear models fit using restricted maximum likelihood with Tukey-Kramer honestly significant difference post-hoc analyses using JMP 10 software (SAS Institute, Cary, North Carolina, USA). We analyzed whether the presence of *Leptasterias* and snail size influenced (1) use of halo refuges by snails in 2010 only and whether year, snail size and shore level influenced, (2) snail densities, and (3) use of halo refuges by snails in all years. Tidepool number was included in all models as a random factor (nested in other factors when appropriate) to account from non-independence of snails in separate size classes in the same tidepool (see Appendix S2 for statistical details). To test whether changes in snail densities among shore levels were due to behavioral shifts or simply to overall increases in population density, we used chi-square analyses on the expected vs. observed densities in each zone for each snail size in 2010 vs. 2011 and 2011 vs. 2014 (see Appendix S2 for details).

RESULTS

Predator avoidance

When *Leptasterias* was present in tidepools (2010 survey only), vulnerable small *Tegula* tended to be more common in halo refuges, whereas this was not the case for large snails (Fig. 3; Appendix S2: Table S1; *Leptasterias* presence \times Size $F_{6,54} = 2.77$, $P = 0.019$). However, pairwise tests within size classes were not significantly different. When *Leptasterias* was absent, the percentage of snails in halos was similar among size classes.

Population size structure before and after predator mortalities

The number of snails more than doubled (factor of 2.4) in 2011 after the *Leptasterias* mortality event (Fig. 4). After the *Pisaster* mortality events in 2014, the population again nearly doubled (factor of 1.7). The increase in 2011 was driven primarily by small snails in the 6–9 mm size class (401% average increase; Fig. 4; Appendix S2: Table S2a; Year \times Size $F_{12,554} = 7.82$, $P < 0.001$; Year $F_{2,554} = 8.90$, $P < 0.001$), and all other size classes also increased (66%, 112%, 104%, 144%, 95%, and 19% average increases for <6, 9–12, 12–15, 15–18, 18–21, and >21 mm sizes classes, respectively). Small and medium snails in the 9–12 and 12–15 mm size classes drove the population density increase from 2011 to 2014 (Fig. 4; Appendix S2: Table S2b; 108% and 108% average increases, respectively), with the 6–9 and 15–18 mm size classes also tending to increase (54% and 44% average increases, respectively). Snails that were 3–6 mm were

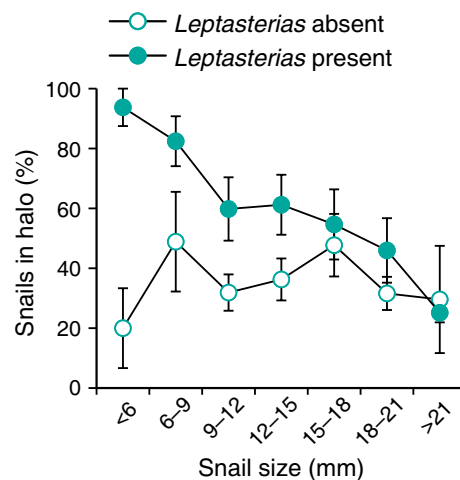


FIG. 3. Percentage (mean \pm SE) of total *Tegula funebralis* by size class (3 mm increments in shell diameter) inhabiting emersed halo refuges around tidepools vs. inside tidepools where *Leptasterias* spp. were present (solid circles, $n = 10$ tidepools) or where they had been experimentally removed (open circles, $n = 10$ tidepools). Data were taken on 10 April 2010 before sea star mortality events in Horseshoe Cove, California, USA. [Color figure can be viewed at wileyonlinelibrary.com]

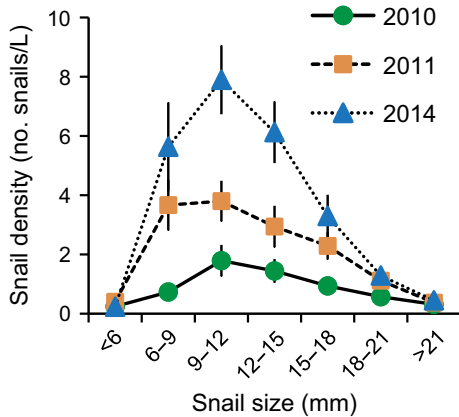


FIG. 4. Population size structure (3 mm increments in shell diameter) calculated as densities (mean \pm SE) of *Tegula funebralis* in tidepools and halo refuges combined in April 2010 before sea star mortality events (circles), May 2011 after a *Leptasterias* spp. mortality event (squares), and April 2014 after two *Pisaster ochraceus* mortality events (triangles). For 2010, 2011, and 2014, respectively, $n = 21$, 44, and 30 tidepools. [Color figure can be viewed at wileyonlinelibrary.com]

rare, likely because snails grow very quickly out of this stage and are not commonly found. We are confident we would have found any of these small snails present in tidepools.

Vertical distribution before and after predator mortalities

Snails shifted vertically after the sea star mortalities, but these responses depended on snail size (Fig. 5; Appendix S2: Table S2a; Year \times Shore level \times Size class: $F_{24,554} = 1.60$, $P = 0.037$). Small and medium snails tended to be denser in the highest zone in 2010, but shifted lower in 2011 after the *Leptasterias* mortality event: small snails became denser in the middle and lower than the

higher zone, and medium snails became more evenly distributed, though these differences were not significant in post-hoc analyses (Fig. 5; Appendix S2: Table S2c). To further investigate this pattern, we use chi-square analyses and found that more small and medium snails (<15 mm) occurred in the middle zone than expected based on population size changes, but fewer than expected small snails (6–12 mm) occurred in the higher zone ($\chi^2 = 1,110.3$, $df = 20$, $P < 0.0001$), indicating that snails most vulnerable to *Leptasterias* shifted to the middle zone when *Leptasterias* was absent. Fewer than expected snails of nearly all sizes (<18 mm) occurred in the lower zone in 2011, indicating more snails may have moved to the middle rather than lower zone. In 2014 after the *Pisaster* mortality events, small and medium snails remained dense in the lower and middle zones, but 9–15 mm snails became denser in the higher zone (Fig. 5; Appendix S2: Tables S2a and S2c; Year \times Shore level \times Size class $F_{24,554} = 1.60$, $P = 0.037$). Further, fewer than expected small snails occurred in the middle zone (6–9 mm) and more than expected small snails occurred in both the higher (9–12 mm) and lower zones (6–9 mm; $\chi^2 = 436.8$, $df = 20$, $P < 0.0001$). Again, fewer snails than expected of most sizes (9–18 mm) occurred in the lower zone during in 2014, indicating most snails still did not move to the lower zone despite the low densities of both sea stars. Surprisingly, large snails were never denser in the lower than middle and higher zones (Paine 1969, Markowitz 1980, Doering and Phillips 1983). Rather, large snails were evenly distributed among zones during all years and exhibited no clear responses to either *Leptasterias* or *Pisaster* mortalities (Fig. 5).

Microhabitat shifts before and after predator mortalities

Overall, halo refuge use was highest in 2010 before any sea star mortalities, lowest in 2011 after *Leptasterias*

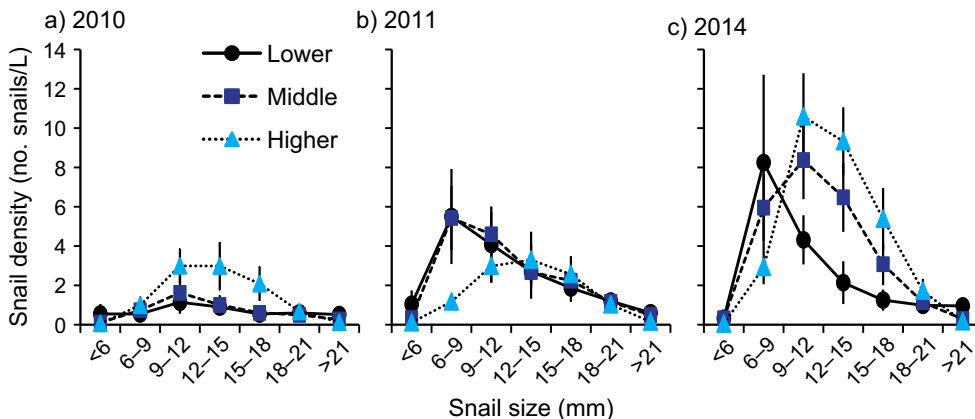


FIG. 5. Densities of *Tegula funebralis* (mean \pm SE) in tidepools and surrounding halo refuges by snail size class (3 mm increments in shell diameter) and shore level (a) in April 2010 before sea star mortality events, (b) in May 2011 after a *Leptasterias* spp. mortality event, and (c) in April 2014 after two *Pisaster ochraceus* mortality events. For lower, middle, and higher shore levels, respectively, $n = 7$, 9, and 5 tidepools in 2010 (panel a), $n = 10$, 16, and 18 tidepools in 2011 (panel b), and $n = 9$, 11, and 10 tidepools in 2014 (panel c). Shore levels in meters above mean lower low water are 0.70–1.15 m (lower; circles), 1.15–1.50 m (middle; squares), and 1.50–2.30 m (higher; triangles). [Color figure can be viewed at wileyonlinelibrary.com]

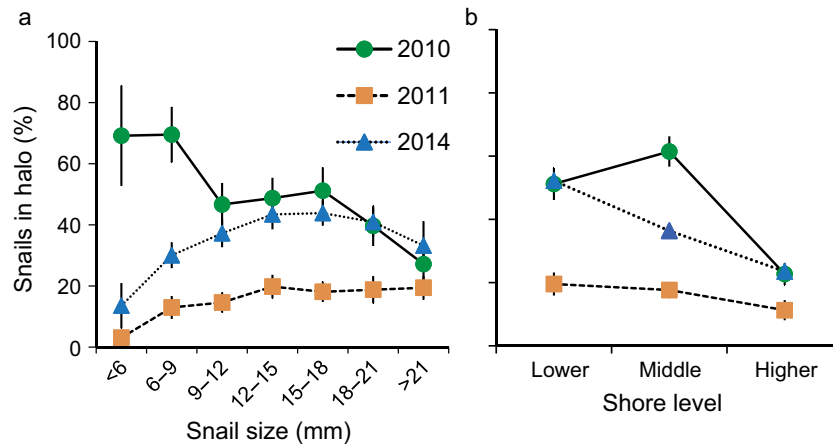


FIG. 6. Percentage (mean \pm SE) of *Tegula funebralis* inhabiting halo refuges surrounding tidepools in April 2010 before sea star mortality events (circles), May 2011 after a *Leptasterias* spp. mortality event (squares), and April 2014 after two *Pisaster ochraceus* mortality events (triangles) by (a) snail size classes (3 mm increments in shell diameter) and (b) shore levels. For 2010, 2011, and 2014, respectively, $n = 7, 10,$ and 9 tidepools in the lower zone, $n = 9, 16,$ and 11 tidepools in the middle zone, and $n = 5, 18,$ and 10 tidepools in the higher zone. Shore levels in meters above mean lower low water are $0.70\text{--}1.15$ m (lower), $1.15\text{--}1.50$ m (middle), and $1.50\text{--}2.30$ m (higher). [Color figure can be viewed at wileyonlinelibrary.com]

mortality, and intermediate in 2014 when both *Pisaster* and *Leptasterias* densities were low (Fig. 6a; Appendix S2: Table S3a; Year: $F_{2,345} = 27.13, P < 0.001$). Small and medium snails drove these changes over time; halo use decreased with snail size in 2010, but in 2011 snails <12 mm and $15\text{--}18$ mm were found in tidepools more often than in 2010, resulting in low halo use among all sizes of snails (Fig. 6a; Appendix S2: Tables S3a and S3b; Year \times Size class: $F_{12,345} = 6.86, P < 0.001$). In 2014 after the *Pisaster* mortality events, snails generally shifted from tidepools to halos, except for the smallest (<6 mm) and largest (>21 mm) snails, which remained in tidepools.

Snails generally used halos more often when lower on the shore in 2010 when *Leptasterias* was abundant, but tidepool use increased in the middle and low zones in 2011 after *Leptasterias* mortality (Fig. 6b; Appendix S2: Tables S3a and S3c; Year \times Shore level $F_{4,345} = 2.41, P = 0.057$). More snails occurred in the halos in the lower zone in 2014 than 2011, whereas snails in the higher zone tended to inhabit tidepools during all years. All sizes of snails showed these trends (Fig. 6b; Appendix S2: Table S3a; Year \times Shore level \times Size class $F_{24,345} = 0.82, P = 0.705$).

DISCUSSION

Similar to other natural experiments that have uncovered previously unrecognized ecological interactions (Zaret and Paine 1973, Hughes 1994, Terborgh et al. 2001, Ripple and Beschta 2012), this study suggests biotic control of *Tegula* populations and zonation by the less-studied sea star predator, *Leptasterias* spp., but not by the keystone predator, *P. ochraceus*. The vertical shift of smaller snails from higher to middle shore after *Leptasterias* died also supports Vermeij's (1972) generalization that predation pressure causes smaller individuals to flee from

lower to higher on shore. Further, it supports his hypothesis that this trend should be particularly strong when predators prefer smaller prey, as with *Leptasterias*, but less strong when predators prefer larger prey, as with *Pisaster*.

Top-down effects of predators on a prey population

Leptasterias apparently regulated *Tegula* populations prior to their mortality in 2010. After *Leptasterias* died, the population size of snails increased 2.4-fold, primarily due to a 401% increase in small snails (6–9 mm) less than 2 years old (Paine 1969). Small and medium *Tegula* are very vulnerable to *Leptasterias* predation and *Tegula* comprise between 14% and 24% of *Leptasterias* diets in their zone of overlap at this site (Bartl 1980, Gravem and Morgan 2016), suggesting that *Leptasterias* is capable of limiting juvenile survival. Though *Pisaster* were formerly implicated, *Leptasterias* predation may have also played a major role in the $\sim 60\%$ decrease in the abundance of *Tegula* during spring and summer in neighboring Marin County, California (Markowitz 1980).

Conversely, it is possible this surge in juvenile abundance was not due to decreased predation but simply to sporadically high *Tegula* recruitment. A lack of control for other factors, such as recruitment, is a common shortcoming of natural experiments. However, multiple lines of evidence suggest that recruitment may be consistently high at this site but juvenile survival may have been previously limited by *Leptasterias* predation. First, new recruits (6–9 mm) were abundant in both 2011 and 2014 (compared to 2010) with no obvious gaps in recruitment evident in the intervening years, suggesting at least two strong recruitment years occurred after the mortality of *Leptasterias*. Also, the population size structure both before and after mortalities was not multimodal, as is

common for species with sporadic recruitment (Menge et al. 2004). However, the long life span of *Tegula* (Paine 1969) could diminish the sharpness of recruitment peaks. In addition, the population size structure of *Tegula* between southern Oregon and Baja California, Mexico is consistently skewed toward juveniles, and reproduction and recruitment in these populations is high year-round (Frank 1975, Fawcett 1984, Cooper and Shanks 2011). Overall, this suggests that *Leptasterias* had consistently been reducing survival of juvenile *Tegula* for many years, just as other predators exert top-down control of prey populations by consuming juveniles (Hunt and Scheibling 1997). Since we rarely observed small snails in the emersed rock matrix between tidepools, it is also doubtful that the surge in juvenile abundance was due to juvenile snails shifting out of the matrix into tidepools and halos.

After *Pisaster* died, survival of juveniles and growth and survival of all snails continued to be high. Increases in abundance of the 9–12 and 12–15 mm snails in 2014 were consistent with the survival and growth of the abundant 6–9 mm cohort of snails from 2011 (Paine 1969). However, this was likely primarily due to continued low predation by *Leptasterias*, since *Pisaster* prefers large snails (Markowitz 1980). Snails grow to the size preferred by *Pisaster* (>17 mm, Markowitz 1980) at around 12 years old (Paine 1969), so it was unsurprising that the densities of large snails did not increase dramatically after *Pisaster* died. We expect the cohort of snails that appeared in 2010/2011 to grow large enough to substantially increase the densities of large snails within a decade (Paine 1969) unless *Pisaster* recover first. We also expect continued high survival and growth of small and medium snails because *Leptasterias* is still absent and, because it broods its larvae, is expected to return to the area slowly.

Effects of predators on prey behavior and distributions

Fairly rapid shifts (<5 months) by small and medium snails to the middle and lower zones and tidepools after the *Leptasterias* mortality event indicate that zonation is dynamic (Robles and Desharnais 2002, Robles et al. 2009, Donahue et al. 2011) and is partially maintained by antipredator behavior of prey, similar to other mobile intertidal species (Vermeij 1972, Cushman 1989, Rochette and Dill 2000). Further, *Leptasterias* rather than *Pisaster* likely relegated small and medium *Tegula* to the higher zone and outside tidepools. Small and medium snails likely balanced the risks of abiotic stress, predation by *Leptasterias*, and starvation (Paine 1969, Bertness 1977, Rochette and Dill 2000, Pincebourde et al. 2008). Snails descending lower on the shore and into tidepools in 2011 likely experienced reduced osmotic, desiccation and thermal stress, all of which may be especially harmful to smaller individuals (Marchetti and Geller 1987). Further, they likely benefitted from higher food availability and longer foraging bouts (Underwood 1984, Wright and Nybakken 2007). The fairly rapid behavioral shift after the *Leptasterias* mortality event is consistent with the

well-documented predation risk allocation hypothesis (Lima and Bednekoff 1999), which posits that at times or locations of lower risk, individuals should be more active and move into preferred habitat.

Since inhabiting lower shore levels or tidepools contributes to generally higher growth rates and fecundity (Paine 1971, Underwood and McFadyen 1983, Pardo and Johnson 2005, Perez et al. 2009), these behavioral shifts may have increased survival and growth of snails and contributed to the observed increases in population size over time. Though we cannot separate the nonconsumptive from consumptive effects of *Leptasterias*, both may have been important since *Leptasterias* apparently limited the abundance and altered the behavior of *Tegula*.

Unlike small snails, large snails remained evenly distributed among intertidal zones and did not shift into tidepools after the mortality of *Leptasterias*. Though large snails readily respond to contact and waterborne chemical cues of *Leptasterias* in the laboratory and in short-term field experiments, they are less vulnerable than small snails to *Leptasterias* predation (Gravem and Morgan 2016). It is likely that large snails are faster and easily outpace *Leptasterias* when contacted (Gravem and Morgan 2016), so it is unnecessary for large snails to react to sustained exposure to cues in the environment since *Leptasterias* pose little risk. On the other hand, small snails are likely less able to outpace *Leptasterias*, so they react to both temporary tactile and sustained waterborne cues with more apparent impacts on their long-term distributions. It is not known whether the lack of predator avoidance behavior by large snails to in response to sustained cues from *Leptasterias* is learned or innate.

We expected large snails to respond to *Pisaster* mortality by descending on the shore and perhaps into tidepools where *Pisaster* can continue to forage at low tide, but clear responses were not evident. Similarly, large snails in 2010 were not as abundant in the lower zone as expected (Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983). These outcomes were surprising since large snails grow faster and have larger gonads lower on the shore, suggesting that this is their preferred habitat (Paine 1969). Perhaps these two trends are linked, and snails at our study site are not as food limited as other sites, allowing larger snails to thrive in the upper intertidal zone. Most prior studies were conducted on exposed rock surfaces, but our site contains abundant tidepools. So large snails may be able to gain enough energy from tidepool algae even at higher shore levels, negating the need to descend lower on the shore. Future analyses of gonad size of large snails would demonstrate whether those inhabiting higher tidepools are food limited. Alternatively, the threat of predation may have been high for large snails in all years causing many to remain high on the shore. Indeed, some *Pisaster* remained after the mortality events. Further, other predators of large snails likely inhabited the low intertidal zone, including the crab *Cancer productus*, the octopi *Octopus rubescens* and *Octopus dofleini*, and fishes,

such as cabezon (*Scorpaenichthys marmoratus*). High combined densities of other octopi, crabs, and *Pisaster* in southern California were proposed to increase large *Tegula* abundance in the high zone (Fawcett 1984).

Since small and medium snails remain vulnerable to *Pisaster*, though not preferred over large snails, we expected them to occur even lower on the shore and more abundantly in tidepools after the *Pisaster* mortality event. Instead, their abundance remained fairly static in the lower zone and in tidepools, but increased in the higher zone and halo refuges. We do not believe this was a response to the mortality of *Pisaster*. Rather, snails may have been responding to an uncommonly large pulse in recruitment of *Pisaster* that occurred in summer and early fall 2013 (S. A. Gravem, *personal observation*). While none of the extremely small (<1 cm diameter in April 2014) *Pisaster* were observed during our surveys nor were capable of consuming the vast majority of the snails, their trace chemical cues may have been permeating the water column and causing snails to move upward or out of tidepools. Based on our observations, we have no evidence that snails are able to ascertain the size of their predator visually or through tactile means. Alternatively, some snails may have been forced into less preferred higher and emersed habitats as the population size grew and intraspecific competition intensified. This is consistent with our Chi-square analyses showing lower than expected small snails in the middle zone and higher than expected small snails in the lower and higher zones in 2014, suggesting that competition may have forced competitively inferior small snails to expand to all zones rather than concentrating in the apparently preferred middle zone.

Drivers of vertical size gradients

The next step is to determine the generality of the effect of *Leptasterias* on the vertical size gradient of *Tegula* by expanding investigations to include a larger geographic range. Since the range of *Leptasterias* (Morris et al. 1980, Foltz 1997, Carlton 2007), encompasses all sites previously studied (Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983, Fawcett 1984), *Leptasterias* could have contributed to the patterns that were attributed to *Pisaster* and other predators. When comparing patterns latitudinally, Fawcett (1984) found that the vertical size gradient (smaller snails higher on shore) was more consistent in Northern California and the Pacific Northwest than Southern California. This was attributed to higher combined densities of *Pisaster*, crabs, and especially octopi in southern California, which may have caused all snails to ascend, thereby precluding a vertical size gradient. However, this does not explain why the gradient existed in Northern California and the Pacific Northwest where sea stars and crabs also are extremely common (Morris et al. 1980, Fawcett 1984, Menge et al. 2004). On the other hand, *Leptasterias* are much more common in Northern California and the Pacific Northwest than in

Southern California (B. Menge, *personal communication*), and they may be responsible for driving smaller snails higher on the shore at more northern sites.

Though our study suggests *Leptasterias* influences vertical size distributions of *Tegula*, other factors are likely at play. For example, *Pisaster* recruitment is also more frequent in the Pacific Northwest than in California (Menge et al. 2004), so juvenile *Pisaster*, which presumably eat smaller snails, may contribute to the stronger vertical gradient at more northern sites (Fawcett 1984). Further, experiments showed that snails moved upward in the intertidal in response to *Pisaster* cues within days (Markowitz 1980). Doering and Phillips (1983) also suggested that the vertical distributions of *Tegula* are maintained proximally by ontogenetic shifts in responses to light and gravity. Further, some individuals may prefer certain shore levels or tidepool habitats (Frank 1975, Byers and Mitton 1981, Byers 1983), and wave exposure may affect population size structure among sites (Cooper and Shanks 2011); but how these factors drive vertical size distributions is unclear. Thus, *Leptasterias* as well as other factors may influence vertical size gradients of *Tegula* on rocky shores.

The oversight of *Leptasterias* as a strong interactor with *Tegula* is perhaps due to the notoriety of *Pisaster* as a keystone species and because it is large, colorful and iconic rather than small, cryptic, and nocturnal like *Leptasterias*. However, unlike humans, many invertebrates including *Tegula* primarily rely primarily on olfactory chemical rather than visual cues (Kosin 1964, Phillips 1978). The observed disparate behavioral responses by snails to these two predators are consistent with laboratory experiments, which suggested that *Tegula* is able to distinguish the chemical cues of the two sea star species rather than responding to a general chemical cue from sea stars (Bullock 1953, Yarnall 1964).

CONCLUSION

Our natural experiment on the consequences of successive mass mortality events of two predatory sea star species enabled us to test several key concepts in community ecology. We provided support for biotic control of species lower limits and top-down control of prey population size by predators. Combined consumptive and nonconsumptive effects of predators also likely resulted in dynamic zonation and vertical size gradients of mobile prey, because the most vulnerable individuals may typically be eaten or escape to stressful refuges higher on shore and outside tidepools. Strong responses after the *Leptasterias* mortality event, but not after the *Pisaster* mortality events, suggested that largely overlooked *Leptasterias* played a primary role in controlling juvenile survival, population size structure, vertical size gradient, and microhabitat choices of *Tegula*. Long-term and nonconsumptive effects of predators on prey are hard to test with the limited spatial and temporal scales of manipulative experiments where predators cannot be removed

completely. Conversely, mass mortalities of predators reduce the concentration of chemical cues from predators, (which can strongly influence prey behavior) and keep predator densities low for many years, allowing more extensive exploration of predator effects. This natural experiment adds new insights on the long-term and non-consumptive effects of predators on intertidal zonation.

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LITERATURE CITED

- Bartl, S. 1980. A comparison of the feeding behavior of the six-rayed seastar, *Leptasterias hexactis*, and from two intertidal habitats. Unpublished student report, Problems in Marine Biology course. Bodega Marine Laboratory Cadet Hand Library, Bodega Bay, California, USA.
- Bertness, M. D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* 58:86–97.
- Bouchet, P., and G. Rosenberg. 2015. *Tegula funebris*. In: MolluscaBase (2015). Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=534190> on 2015-09-15
- Bullock, T. H. 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. *Behaviour* 5:130–140.
- Byers, B. A. 1983. Enzyme polymorphism associated with habitat choice in the intertidal snail *Tegula funebris*. *Behavior Genetics* 13:65–75.
- Byers, B., and J. Mitton. 1981. Habitat choice in the intertidal snail *Tegula funebris*. *Marine Biology* 65:149–154.
- Carlton, J. T., editor. 2007. The Light and Smith manual: intertidal invertebrates from Central California to Oregon. Fourth edition. University of California Press, Berkeley, California, USA.
- Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3:169–192.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs—High diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199:1302–1310.
- Cooper, E. E., and A. L. Shanks. 2011. Latitude and coastline shape correlate with age-structure of *Chlorostoma (Tegula) funebris* populations. *Marine Ecology Progress Series* 424:133–143.
- Cushman, J. H. 1989. Vertical size gradients and migratory patterns of two *Nerita* species in the northern Gulf of California. *Veliger* 32:147–151.
- Diamond, J. M. 1983. Ecology—laboratory, field and natural experiments. *Nature* 304:586–587.
- Doering, P. H., and D. W. Phillips. 1983. Maintenance of the shore-level size gradient in the marine snail *Tegula funebris* (Adams, A.): importance of behavioral responses to light and sea star predators. *Journal of Experimental Marine Biology and Ecology* 67:159–173.
- Donahue, M. J., R. A. Desharnais, C. D. Robles, and P. Arriola. 2011. Mussel bed boundaries as dynamic equilibria: thresholds, phase shifts, and alternative states. *American Naturalist* 178:612–625.
- Fawcett, M. H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology* 65:1214–1230.
- Feder, H. M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology* 44:505–512.
- Flowers, J. M., and D. W. Foltz. 2001. Reconciling molecular systematics and traditional taxonomy in a species-rich clade of sea stars (*Leptasterias* subgenus *hexasterias*). *Marine Biology* 139:475–483.
- Foltz, D. W. 1997. Hybridization frequency is negatively correlated with divergence time of mitochondrial DNA haplotypes in a sea star (*Leptasterias* spp.) species complex. *Evolution* 51:283–288.
- Frank, P. 1975. Latitudinal variation in the life history features of the black turban snail *Tegula funebris* (Prosobranchia: Trochidae). *Marine Biology* 31:181–192.
- Gravem, S. A. 2015. Linking antipredator behavior of prey to intertidal zonation and community structure in rocky tidepools. Dissertation. University of California, Davis, California, USA.
- Gravem, S. A., and S. G. Morgan. 2016. Prey state alters trait-mediated indirect interactions in rocky tidepools. *Functional Ecology* 30:1574–1582.
- Hewson, I., et al. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences USA* 111:17278–17283.
- Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hunt, H. L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* 155:269–301.
- Jurgens, L. J., L. Rogers-Bennett, P. T. Raimondi, L. M. Schiebelhut, M. N. Dawson, R. K. Grosberg, and B. Gaylord. 2015. Patterns of mass mortality among rocky shore invertebrates across 100 km of Northeastern Pacific Coastline. *PLoS ONE* 10:e0126280.
- Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394.
- Kosin, D. 1964. The light responses of *Tegula funebris*. *Veliger* 6:46–50.
- Laundré, J. W., L. Hernandez, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–290.

- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Marchetti, K. E., and J. B. Geller. 1987. Effects of aggregation and habitat on desiccation and body temperature of the black turban snail, *Tegula funebris* (A. Adams, 1855). *Veliger* 30:127–133.
- Markowitz, D. V. 1980. Predator influence on shore-level size gradients in *Tegula funebris* (A. Adams). *Journal of Experimental Marine Biology and Ecology* 45:1–13.
- McQuaid, C., J. Lindsay, and T. Lindsay. 2000. Interactive effects of wave exposure and tidal height on population structure of the mussel *Perna perna*. *Marine Biology* 137:925–932.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecological Monographs* 42:25–50.
- Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Menge, B. A., E. B. Cerny-Chipman, A. Johnson, J. Sullivan, S. A. Gravem, and F. T. Chan. 2016. Ecology of the sea star wasting disease epidemic in the keystone predator *Pisaster ochraceus*: population impact, recovery potential, and predation rate. *PLoS ONE* 11:e0153994.
- Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* 51:429–450.
- Menge, J. L., and B. A. Menge. 1974. Role of resource allocation, aggression and spatial heterogeneity in coexistence of two competing intertidal starfish. *Ecological Monographs* 44:189–209.
- Mislan, K., B. Helmuth, and D. S. Wetthey. 2014. Geographical variation in climatic sensitivity of intertidal mussel zonation. *Global Ecology and Biogeography* 23:744–756.
- Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. *Intertidal invertebrates of California*. Stanford University Press, Stanford, California, USA.
- Paine, R. T. 1969. The *Pisaster-Tegula* interaction—prey patches, predator food preference and intertidal community structure. *Ecology* 50:950–961.
- Paine, R. T. 1971. Energy flow in a natural population of herbivorous gastropod *Tegula funebris*. *Limnology and Oceanography* 16:86–98.
- Pardo, L. M., and L. E. Johnson. 2005. Explaining variation in life-history traits: growth rate, size, and fecundity in a marine snail across an environmental gradient lacking predators. *Marine Ecology Progress Series* 296:229–239.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Perez, K. O., R. L. Carlson, M. J. Shulman, and J. C. Ellis. 2009. Why are intertidal snails rare in the subtidal? Predation, growth and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 369:79–86.
- Phillips, D. W. 1978. Chemical mediation of invertebrate defensive behaviors and ability to distinguish between foraging and inactive predators. *Marine Biology* 49:237–243.
- Pincebourde, S., E. Sanford, and B. Helmuth. 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnology and Oceanography* 53:1562–1573.
- Poloczanska, E. S., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919–925.
- Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145:205–213.
- Robles, C., and R. Desharnais. 2002. History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* 83:1521–1536.
- Robles, C. D., R. A. Desharnais, C. Garza, M. J. Donahue, and C. A. Martinez. 2009. Complex equilibria in the maintenance of boundaries: experiments with mussel beds. *Ecology* 90:985–995.
- Rochette, R., and L. M. Dill. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *Journal of Experimental Marine Biology and Ecology* 253:165–191.
- Rogers-Bennett, L., R. Kudela, K. Nielsen, A. Paquin, C. O'Kelly, G. Langlois, D. Crane, and J. Moore. 2012. Dinoflagellate bloom coincides with marine invertebrate mortalities in Northern California. *Harmful Algae News* 46:10–11.
- Seed, R. 1969. Ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. *Oecologia* 3:317–350.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, and T. D. Lambert. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.
- Underwood, A. J. 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* 64:211–222.
- Underwood, A. J., and K. E. McFadyen. 1983. Ecology of the intertidal snail *Littorina acutispira* (Smith). *Journal of Experimental Marine Biology and Ecology* 66:169–197.
- Vermeij, G. J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53:693–700.
- Wara, W. M., and B. B. Wright. 1964. The distribution and movement of *Tegula funebris* in the intertidal region of Monterey Bay, California. *Veliger* 6:30–37.
- Wright, W. G., and J. W. Nybakken. 2007. Effect of wave action on movement in the owl limpet, *Lottia gigantea*, in Santa Cruz, California. *Bulletin of Marine Science* 81:235–244.
- Yarnall, J. L. 1964. The responses of *Tegula funebris* to starfishes and predatory snails (Mollusca: Gastropoda). *Veliger* 6:56–58.
- Zaret, T. M., and R. Paine. 1973. Species introduction in a tropical lake. *Science* 182:449–455.

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