Linking Antipredator Behavior of Prey to Community Structure and Intertidal Zonation in Rocky Tidepools

By

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DISSERTATION ABSTRACT

While behavior occurs at the level of the individual organism, it can scale up to determine species distributions and community structure. My dissertation focused on the consequences of antipredator behavior of prey for larger-scale ecological processes and patterns that are often attributed to lethal effects of predators on prey. First, I suggest that predators caused changes in prey distribution and grazing, which resulted in cascading benefits to primary producers in a natural ecosystem where predator and prey movements were unrestricted. Second, I demonstrated that variation in individual prey traits (body size and hunger level) altered antipredator behavior and ultimately affected the strength of trophic cascades between predators and primary producers. Finally, I capitalized on mass mortalities of predators to provide evidence for multiple ecological paradigms, including top-down control by predators of the population size, intertidal zonation, and refuge use of prey. Further, these responses were likely due to a lesser-known small cryptic predator and not the keystone predator in the ecosystem.

In Chapter 1, "Trait-mediated indirect effects in a natural tidepool system," the small, cryptic, predatory seastar *Leptasterias* spp. evidently increased microalgae and macroalgae growth in tidepools by increasing refuge use and decreasing grazing by its herbivorous snail prey, *Chlorostoma* (formerly *Tegula*) *funebralis*. This trophic cascade is an example of a trait-mediated indirect interaction (TMII) because predators affected primary producers by altering behavioral traits of prey. This is in contrast with the typical mechanism for trophic cascades, termed density-mediated indirect interactions (DMIIs), whereby predators affect primary producers by consuming prey. Though well documented in laboratories and mesocosms, nearly all TMII studies in natural ecosystems restrict organism behavior by using cages, despite antipredator behavior being the primary mechanism through which many TMIIs manifest.

Caging also isolates the species from the rest of the community, often necessitates supplying non-natural prey resources, and may concentrate predator cues, all of which may lead to inaccurate estimates of TMIIs. Further, short experiments may detect strong prey reactions and TMIIs, but longer experiments may allow habituation to predators and detect weak TMIIs. Finally, the starting conditions of experiments, such as whether prey begin inside or outside refuges, can alter the information prey may possess regarding the risks and rewards of foraging, and change TMII strength.

Even without the use of cages, the seastar Leptasterias apparently exerted positive TMIIs on tidepool algae in natural communities over both short (~1 month) and long (~8 months) time scales by causing *Chlorostoma* snails to flee tidepools and reduce grazing. *Leptasterias* and Chlorostoma were also negatively associated with one another and each was associated with different algal communities, suggesting that this TMII has community-level impacts. Though it was not possible to fully separate TMIIs from DMIIs without caging, TMIIs are likely important in this system because 1) snails rapidly responded to seastars within hours to days, 2) seastars caused long-lasting effects (~10 months) on snail behavior, and 3) many more snails responded to seastars than could be eaten, particularly since large snails were not vulnerable to predation but still fled from seastars. In addition, the starting conditions of prey (inside and outside refuges, immigrating, or experimentally added) may have changed the information that snails possessed on risks and rewards of the foraging habitat, which may have affected their responses to seastars and ultimately TMII strength. Thus, subtle alterations in experimental setup of a behavioral experiment may strongly affect outcomes. Overall, I provide a rare example of TMIIs in a natural ecosystem without restricting predator and prey movement. I also emphasize the need to

incorporate nonconsumptive effects of predators when attempting to understand the cascading effects predators have on ecosystems.

In Chapter 2, "Prey state alters trait-mediated indirect interactions in rocky tidepools", I investigated the consequences of state-dependent individual prey behavior for community-level processes. Species interactions are typically approximated by lethal predation rates, and individuals are often assumed to be homogenous. However, foraging theory demonstrates that predators have sublethal effects on prey foraging decisions, and that this behavior is contingent on prey state, such as body size or hunger level. A surge in TMII studies over the past few decades connect these concepts and investigate the consequences of species interactions for a third species. For example, predators often have indirect cascading effects on primary producers by alter prey foraging behavior, rather than by consuming prey. However, much less is known about consequences of varying prey state for TMII strength. For example, TMIIs may be weakened when hungry prey forage despite risk of predation, or they may be strengthened when large prey reach a size refuge from predation but continue to flee from predators, thus mediating TMIIs but not DMIIs. Recent literature reviews have identified a need to connect state-dependent behavior to community processes, but few empirical studies have explored this concept.

I connect state-dependent behavior with trophic cascades by showing that TMII strength is contingent upon the hunger level and body size of prey. I again use the tritrophic interaction between *Leptasterias* spp., *Chlorostoma* and algae and test the strengths of short-term TMIIs in the laboratory and tidepools using snails of different hunger levels and sizes. Hungry snails mediated weaker TMIIs than fed snails in tidepools because they continued grazing despite predator presence, in accordance with foraging theory. Among snail sizes, medium snails mediated the strongest TMIIs in tidepools, but small snails did not mediate TMIIs because they

did not consume enough algae. Large snails fled from seastars despite reaching a refuge from predation, but their role in mediating TMIIs is unclear since they had variable effects on algae. In the laboratory, close proximity to seastars caused all snails to flee and all except small snails mediated TMIIs. Though my experiments were short, Chapter 1 demonstrates that TMIIs may occur over long time periods in this system. I also identify natural circumstances where the average size or hunger of *Chlorostoma* may predictably vary in space or time, potentially altering TMII strength in nature. Overall, these data illustrate that including only consumptive effects (predation rates) and assuming all individuals are the same may not always be sufficient to predict the effects of predators on communities. This study strengthens the connection between behavioral and community ecology paradigms by demonstrating that state-dependent foraging behavior by prey may alter TMII trophic cascades.

In Chapter 3, "Shifts in intertidal zonation of prey after mass mortalities of two predators", I utilized the sequential mass mortalities of two seastar predators to explore multiple facets of top-down control and the intertidal paradigm of vertical zonation. This type of natural experiment provided a rare opportunity to validate the concepts developed by classic manipulative experiments. Further, it allowed examination of the nonconsumptive and long-term effects of predators on prey, which are hard to test experimentally. In this case, the *Leptasterias* population declined first, followed by the keystone predator *Pisaster ochraceus*, and I examined population-level and behavioral responses by *Chlorostoma* before and after each mortality event. I also explore the possible causes of the *Leptasterias* mortality event.

After *Leptasterias* was eliminated from the study system, *Chlorostoma* population size doubled, most likely due to high juvenile survival. Small and medium sized *Chlorostoma*, which are most vulnerable to *Leptasterias*, also shifted lower in the intertidal zone and into tidepools.

These responses suggested that 1) predators exert top-down control over the population sizes and lower limits of their prey, 2) vertical zonation of prey are in dynamic equilibria controlled by both predation and nonconsumptive effects of predators on prey behavior, and 3) the nonconsumptive effects of predators are strongest for the most vulnerable individuals, which inhabit stressful habitats higher on the shore or outside tidepools to avoid predation. After the *Pisaster* mortality events, I expected preferred large snails to move lower on shore and into tidepools, but large snails showed no responses. Surprisingly, small and medium snails moved higher on the shore and out of tidepools, perhaps because intensifying intraspecific competition at high snail densities forced them to less preferred habitats.

Previous studies attributed the generally decreasing body size of *Chlorostoma* with shore level to high predation pressure by *Pisaster* in the lower intertidal zone, and secondarily to sizedependent energetic demands. However, *Pisaster* prefers large snails, which would predict that large snails should occur higher on the shore. In the aftermath of sequential mass mortalities, *Leptasterias*, which prefer smaller *Chlorostoma* in the laboratory and field, had a much stronger effect than *Pisaster* on the vertical size gradient and population size of *Chlorostoma*. Thus, it appears that *Leptasterias* may be primarily driving the vertical size distribution of *Chlorostoma* by preying upon and eliciting upward movement by small and medium snails in the lower zones. This small cryptic predator has received far less attention than the charismatic keystone predator *Pisaster*, highlighting the biases that we may acquire due to established paradigms.

Overall, the role of predators in ecological communities was more profound than predicted by their predation rates alone. By altering individual prey behavior, predators may alter emergent ecological patterns, including community structure and intertidal zonation. Predators can have long-term effects on communities by increasing refuge use and reducing foraging by

prey. Further, the effects of predators on ecosystems are not static; individual variation in prey traits, such as size or hunger level, may either exacerbate or ameliorate predator effects. Finally, natural experiments evinced several ecological paradigms by revealing apparent top-down effects of an overlooked predator on prey population size structure, distributions, and size-dependent refuge use.

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CHAPTER 1

Trait-mediated indirect effects in a natural tidepool system

ABSTRACT

I demonstrate trait-mediated indirect interactions (TMIIs) in a natural community over short and long time scales. These TMIIs occurred without using mesocosms or cages that can impede the movements or behaviors of organisms and cause inaccurate estimates of TMII strength. Small predatory seastars (Leptasterias spp.) caused herbivorous snails (Chlorostoma *funebralis*) added to rocky intertidal tidepools to quickly flee into refuge habitats outside tidepools. Removing seastars also resulted in snails entering tidepools from the surrounding area within days. When seastars were added to tidepools, snails from the surrounding area avoided tidepools for at least 10 months, snails present in the tidepools apparently grazed less, and growth of tidepool microalgae and macroalgae increased for at least 1 and 8 months, respectively. Densities of Leptasterias and Chlorostoma were also negatively associated in 63 unmanipulated tidepools, and the two species were associated with different algal communities, suggesting that this TMII has community-level impacts. In addition, the starting locations of prey may have changed the information that snails possessed on risks and rewards of foraging, which may have affected their responses to seastars and ultimately TMII strength. Overall, predators appeared to mediate long-term effects on algal growth and may alter algal community structure by changing prey herbivory even under unrestrained natural conditions. Although multiple lines of evidence indicate that TMIIs occurred over long periods in this natural community, complementary caging studies are necessary to definitively partition the relative contributions of TMIIs and density mediated indirect interactions (DMIIs).

INTRODUCTION

Trophic cascades are one of the central tenets of ecological theory (Hairston et al. 1960, Paine 1980) and their mechanism is typically described in terms of population size changes: predators reduce herbivore population sizes, thereby increasing the population sizes of primary producers. The cascading effects of predators on primary producers are termed density-mediated indirect interactions (DMII, Abrams 1995, Peacor and Werner 1997) or consumptive indirect effects (Abrams 2007), because herbivore densities are reduced by consumption. However, a second mechanism for trophic cascades has received much attention: predators do not only eat prey, they cause changes in prey traits (e.g. behavior, morphology, physiology), which can subsequently affect primary producers (Werner and Peacor 2003, Schmitz et al. 2004, Miner et al. 2005). This mechanism is termed a trait-mediated indirect interaction (TMII, Abrams 1995, Peacor and Werner 1997) or non-consumptive indirect effect (Abrams 2007). For example, predator presence can reduce prey foraging, which benefits the prey's resource (Huang and Sih 1991). These behavioral TMIIs can be much faster and stronger than DMIIs by immediately affecting many prey at once instead of prey being consumed slowly over a long time (Peacor and Werner 2001). Studies examining the relative strengths of TMIIs and DMIIs suggest that TMIIs are either partly or nearly entirely responsible for indirect effects within trophic cascades (Peacor and Werner 2001, Preisser et al. 2005, but see Weissburg et al. 2014).

Though TMIIs have been detected in many studies, it is imperative to assess the importance of TMIIs under natural field conditions over the long term. This is readily done when the initiating species rarely kills the mediating species, rendering DMIIs insignificant (e.g. many herbivores and parasites) or when the mediator's responses do not involve movement (e.g. physiological or morphological responses). However, it is much more difficult when DMII and

TMII effects occur simultaneously and mediators move, as in most trophic cascades. Most TMII studies in these systems are conducted in laboratories or mesocosms, which have the advantage of isolating TMII and DMII effects and manipulating species densities. However, many of these studies lack realism, are short, and may not accurately estimate TMII strength. First, constricting prey inherently limits their options for antipredator behavior, the key mechanism of many tritrophic TMIIs. Second, isolating the focal interactors from the rest of the community may overestimate TMIIs because indirect effects may be attenuated in more complex food webs (Strong 1992, but see Schmitz 1998). Third, resources must often be supplied to prey in mesocosms or are not allowed to grow naturally, making the quantification of the TMII unrealistic (Okuyama and Bolker 2007). Fourth, the length of the experiment can drastically affect the results; prey can temporarily abstain from feeding, causing initial overestimation of TMII strength, but over time they may become habituated to predation threats or hungry enough to risk foraging, causing underestimation of TMII strength (Luttbeg et al. 2003, Okuyama and Bolker 2007). Fifth, small areas and lack of normal air or water flow common in mesocosm experiments may cause predator cues to become unnaturally elevated, eliciting strong prey responses and causing overestimation of TMIIs (Long and Hay 2012, Weissburg et al. 2014). Finally, experimental designs dictate the starting location of prey in refuge or foraging habitat, and whether predators are removed or added. These starting conditions do not always mimic the predator-prey encounters occurring in nature, can affect information that prey posses regarding the presence of predators or resource availability, and can thus influence prey behavior and TMII strength (Sih 1992, Weissburg et al. 2014). For example, prey in refuges may possess less information on risks and rewards of foraging, while prey in foraging habitats are able to sample for information on both risks and rewards more easily (Sih 1997, Kats and Dill 1998). Similarly,

adding predators may provide more reliable information to prey on predator presence than does removing predators (Sih 1992, 1997, Kats and Dill 1998). Long-term field studies without caging generally remedy the above limitations of laboratory or mesocosm studies. Thus, TMIIs need to be demonstrated without restricting movement, within naturally complex communities, using natural prey resources, repeatedly over time, and under realistic conditions to evaluate their importance in nature.

Though some studies have overcome these limitations to demonstrate trophic cascade TMIIs in natural communities without restricting movement (Turner and Mittelbach 1990, Raimondi et al. 2000, Trussell et al. 2004, Ripple and Beschta 2006, Wada et al. 2013), examples remain sparse, and it important to explore the relevancy of TMIIs to natural systems. The problem with investigating TMIIs in natural communities is that TMIIs cannot be easily separated from DMIIs in most systems. When it is impossible to prevent predation while simultaneously allowing natural predator and prey behavior, it is necessary to marshal multiple lines of supporting evidence to make a compelling case for the importance of TMIIs. Peacor and Werner (2001) outlined three criteria for systems that should exhibit strong TMIIs versus DMIIs: rapid responses of prey to predators, many more prey responding to predators than can be eaten, and long-lasting effects. To establish these criteria, 1) field and laboratory surveys should show low predation rates, 2) predator removal or addition experiments should quickly alter behavior of many prey, followed by changes in prey resources, and 3) these behaviors and effects on prey resources should be consistent over time.

I examined a tri-trophic TMII by conducting field experiments in naturally occurring tidepool communities using unrestricted movement of predators and prey. I manipulated predator densities and monitored prey behavior and TMIIs on natural primary producers over multiple

time scales (days, weeks and months). Thus, I avoided the limitations faced by most laboratory and mesocosm studies, outlined above. I worked in the marine rocky intertidal environment where relatively few TMII studies have been performed (Long and Hay 2012). In this system, the small six-armed predatory seastar, *Leptasterias spp*. (see Flowers and Foltz 2001 for information on species complex) preys on the abundant herbivorous snail, *Chlorostoma* (formerly *Tegula*) funebralis. The snail grazes on microalgae and macroalgae and can affect macroalgal biomass and community structure in tidepools (Nielsen 2001).

Partitioning TMIIs from DMIIs in this system is challenging. To definitively parse the two mechanisms, I would have to cage seastars, but this would alter their hunting behavior and snails' antipredator behavior, which would lead to inaccurate TMII estimates. Conversely, uncaged predators provide realistic conditions for both predators and prey, but the effect of DMII cannot be entirely isolated. I elected to use uncaged predators to obtain the most realistic conditions possible at the expense of the most precise estimates of the relative magnitudes of the TMII and DMII in this system. However, other studies on *Leptasterias* partially satisfy Peacor and Werner's (2001) first and second criteria for strong TMIIs by showing that *Chlorostoma* 1) quickly flee from *Leptasterias* (Bullock 1953, Yarnall 1964), 2) is consumed less often than many other species (Bartl 1980, Chapter 2), and 3) at large sizes are not often consumed in the field and laboratory (Chapter 2). I further investigated the three criteria for strong TMIIs in this system by adding and removing predators and prey to monitor prey behavior and effects on algae over time, as outlined below. I found that TMIIs are likely to be much stronger than DMIIs in this system, diminishing the importance of precisely estimating DMIIs.

I began by determining whether seastar and snail densities were associated with algal community structure by characterizing algal communities, animal biota, and abiotic conditions in

63 tidepools. I expected seastars and snails to be negatively associated in tidepools, and algal community structure to depend on whether seastars or snails were common. I then experimentally tested whether seastars induce snails to shift to refuges outside tidepools at low tide and exert TMIIs on naturally growing microalgae and macroalgae over short and long periods (days to months); each of 37 tidepools began as either *Leptasterias*-dominated or *Chlorostoma*-dominated, and I either removed seastars/added snails or added seastars/removed snails, respectively, in a factorial design totaling 8 treatments (Fig. 1). I expected that snails would exert negative direct effects by consuming tidepool algae, while seastars would exert positive TMIIs on algae by reducing herbivory and increasing refuge habitat use by snails. I also expected that more palatable algal species would be more affected by snail and seastar treatments than less palatable algae.

By virtue of the 8 different experimental treatments, I was able to compare responses by snails under different starting conditions, providing insight into the decision-making process of snails. The 8 treatments were paired into 4 different starting conditions containing particular snail types, each with a predator present and absent treatment (Fig. 1). These starting conditions variously included four different 4 snail types: 1) snails marked and added to tidepools, 2) resident snails in emersed refuges surrounding tidepools, 3) resident snails in tidepool foraging habitat, and 4) immigrant snails from the surrounding area. I expected added snails to flee tidepools containing seastars, residents in halos to move into tidepools when seastars were removed, residents in tidepools to flee when seastars were added, and immigrants to choose tidepools when seastars were absent but halos when seastars were present. By comparing whether adding conspecific snails increased the use of tidepools by residents in halos and immigrant snails, I also tested if snails exhibited a "safety in numbers" or group size response,

which predicts increased risky behavior when conspecifics are present because risk of attack is diluted (Dehn 1990). Due to their varying starting conditions, each of the 4 snail types presumably varied in the amount of information they possessed regarding predation risk and food availability in tidepools. In general, I expected that seastars would induce the most refuge use and strongest positive TMIIs on algae when snails possessed more information on risk but less information on food abundance (Sih 1992).

METHODS

Predator and prey relation to community structure

Surveys. I surveyed spatial associations among Leptasterias, Chlorostoma, primary space holders (macroalgae and bare rock) and other tidepool macroinvertebrates in 63 small mid to high intertidal tidepools from July 6 to 14, 2009 in Horseshoe Cove, located within the Bodega Marine Reserve in northern California (38°19' N, 123°14' W). I calculated the macroinvertebrate densities as individuals per liter, which allowed comparisons among tidepools of different size and served as a proxy for chemical cue concentration. Chlorostoma refuge habitat was termed the "halo" and was defined as rock surfaces <15 cm above the waterline that encircled the perimeter of each tidepool. I estimated refuge use by snails by calculating the percentage of snails in the halo [(snails in the halo/ snails in tidepool and halo) x 100]. Leptasterias do not occur in halos during low tide, presumably due to physiological stress. To analyze the impacts of abiotic features on tidepool communities. I measured conditions in each tidepool as follows. Shore level (range of 0.60 - 2.25 meters above MLLW) was measured using surveying equipment and USGS benchmarks. Volume (range of 1.2 -107.1 L) was determined by measuring water manually pumped from tidepools. Average depth (range of 3.2 - 38.6 cm) was calculated from 5 random depth measurements. Perimeter and surface area (ranges of 1.04 - 4.75 m and 0.05 - 0.61 m², respectively) were quantified from digital photographs using ImageJ software.

Statistical analyses. Bivariate correlations between *Chlorostoma, Leptasterias,* bare space percent cover, macroalgal species percent cover and common macroinvertebrates were first transformed using log₁₀ (abundance data) and sine⁻¹ square root (proportional cover data) and analyzed using JMP software (SAS Institute Inc., Version 9, 2010). I classified tidepools into

algal community types using linear discriminant analysis and a canonical score plot in JMP. I then quantified community structure of primary space holders in each tidepool in PRIMER-e (Plymouth Routines in Multivariate Ecological Research, Version 6, 2006) with PERMANOVA+ add-on using a normalized and square-root transformed community matrix, Bray-Curtis similarities, and non-metric multidimensional scaling (NMDS) plots. To determine which abiotic (shore level, volume, area, perimeter, and mean depth) and biotic (mobile invertebrates) attributes of tidepools were most strongly associated with community structure, I ran a distance-based linear model (DistLM) using a R^2 selection criterion and 999 permutations and visualized the results using distance-based redundancy analysis (dbRDA) plots. I then used a permutational multivariate analysis of variance (PERMANOVA) model, where I first entered the significant abiotic and biotic factors from the DistLM model, followed by Chlorostoma and Leptasterias densities. This enabled me to test whether Chlorostoma or Leptasterias densities were associated with community structure after having already considered important abiotic and biotic factors. In the PERMANOVA I used 999 maximum permutations and excluded 3-way and higher order interactions due to limited degrees of freedom.

Predator-prey interactions

Experimental manipulations. To determine whether *Leptasterias* induced short and longterm habitat shifts by *Chlorostoma* and subsequently cause TMIIs on algae, I performed manipulative experiments in 37 of the surveyed tidepools. Tidepools ranged from 0.77 - 2.25 m above MLLW, 1.9 - 85.0 L in volume, and 0.05 - 0.51 m² in surface area. Before experiments began, each tidepool was designated as either originally "*Leptasterias*-dominated" (*Leptasterias* present and <1 snail L⁻¹) or originally "*Chlorostoma*-dominated" (*Leptasterias* absent and >1 snail L⁻¹) using the surveys above. For short-term experiments, I manipulated *Leptasterias* and Chlorostoma in 8 treatments by removing Leptasterias from and adding Chlorostoma to the originally Leptasterias-dominated tidepools, and removing Chlorostoma from and adding Leptasterias to the originally Chlorostoma-dominated tidepools in a factorial design with 4 or 5 tidepools per treatment (Fig. 1). This setup resulted in snails existing in 4 different experimental conditions, including 1) marked snails added to tidepools (treatments 1 & 2), 2) snails resident in halos (treatments 1 - 4), 3) snails resident in tidepools (treatments 5 & 6), and 4) snails immigrating to tidepools or halos (treatments 1 - 8). This enabled me to test the responses by snails that began under different experimental conditions ranging from manipulated (added snails) to unmanipulated (all other snails), and from beginning in foraging habitats (added snails and residents in tidepool) to beginning in refuge habitats (residents in halos and immigrants). Specific predictions for each snail type are included in Figure 1. To avoid tampering with snails and altering their natural behaviors, residents and immigrants were not marked, and were thus undistinguishable within treatments (Fig. 1). Thus, I examined their combined responses to seastars in some of the treatments. However, the overall response to seastars was predicted to be similar between residents and immigrants within a given treatment and I was able to assess the behaviors of immigrants in isolation in snail removal treatments (7 & 8). Safety in numbers responses were assessed by comparing behavior of unmarked snails (residents in halos and immigrant snails) with or without marked conspecifics added (treatments 1 vs. 3 and 2 vs. 4).

Snails and seastars were added to tidepools at the densities recorded during surveys of *Chlorostoma*-dominated and *Leptasterias*-dominated tidepools, respectively (12.8 snails L^{-1} and ~1.8 seastars L^{-1}), and the densities of *Leptasterias* were maintained throughout the study by replacing escaped seastars. All experimental treatments began between July 11 and 13, 2009. For short-term experiments only, snails were added twice, each at the beginning of consecutive 1-

month short-term experiments (July 13 to August 19, 2009 and October 1 to 28, 2009). Added snails were marked with fingernail enamel that remained on snail shells for many months. During short-term experiments snails in all 37 tidepools and halos were counted and the 8 treatments maintained almost daily during the first week then weekly for 3 weeks. The second short-term manipulation was concurrent with experiments testing TMII effects of seastars on microalgal growth.

To determine the long-term responses by snails to seastars, I maintained the above experimental treatments in the same 37 tidepools for 10 months. The only alteration was that no further snail additions were performed, so treatments 1 & 3 and treatments 2 & 4 were combined for analyses (Fig. 1). To maintain the remaining treatments, seastars were removed or added and immigrant snails were removed and counted approximately weekly, totaling 47 times. Long-term snail behavior was sampled in all 37 pools 5 times: during the first week of each short-term experiment (weeks of July 13 and October 1, 2009, behaviors over each time period were averaged) and on August 19, 2009, October 28, 2009 and April 10, 2010. This long-term manipulation was concurrent with experiments testing TMII effects of seastars on macroalgal cover, growth and recruitment and on microalgal growth.

Behavioral metrics. I assumed that the tidepool manipulations were operating independently from one another (i.e. snails and seastars were not fleeing from one tidepool to the next) for several reasons. First, ample snail and seastar habitat occurred in the matrix between my tidepools, including emersed rock, crevices and many large tidepools that were not part of the experiment. Second, many thousands of snails and seastars occurred in the area that were also not part of the experiment, so any immigrants to tidepools were not likely individuals that had recently emigrated from other experimental tidepools. Third, I observed only occasional

exchange of marked snails between tidepools and individual seastars often remained in the same tidepool for many weeks. Finally, many *Chlorostoma* and other prey species (Chapter 2) were available to seastars in tidepools, making it unnecessary for seastars to pursue fleeing snails.

I did not track individual snails, which could freely immigrate to and emigrate from tidepools; so all behaviors are the average for snails in the tidepool when measured. Similar to community surveys above, I used the percentage of snails in the halos to assess average use of refuges by snails. This metric did not include snails that emigrated away from tidepools or halos or immigrant snails that avoided the tidepool completely, so it likely underestimates refuge use in response to seastars. To estimate snail abundance, I used snail densities in tidepools (L⁻¹), because variation in tidepool size made using snail counts untenable. Increases in snail densities estimated immigration to a tidepool from the halo or surrounding area. Since I could not separate direct predation from emigration, decreases in snail densities estimated combined consumptive and non-consumptive effects (see the introduction and discussion for a commentary on the relative strengths of TMIIs versus DMIIs). I calculated the magnitude of responses by different snail types (percentage of snails in the halo and snail densities) as the difference between paired treatments (predator present versus absent) over the course of the short-term (excluding day 1) and the long-term experiments.

Statistical analyses. All statistical analyses on snail behavior and algae were analyzed in JMP using Restricted Maximum Likelihood (REML) mixed models with sequential sums of squares and Tukey's post-hoc analyses unless otherwise noted. Data were square-root or log₁₀ transformed to meet assumptions of normality and equal variances when necessary. Tidepools that were originally *Chlorostoma*-dominated and *Leptasterias*-dominated were analyzed separately because their treatments and starting conditions were different.

To test if *Leptasterias* affected the short-term behavior of a) snails added to tidepools (treatments 1 & 2), b) snails resident in halos or immigrating (treatments 1 - 4) and c) snails residents in or immigrating to tidepools (treatments 5 - 8), I tested the effects of time (days since snail addition began), seastar treatment and snail treatment on percentage of snails in the halo and snail density in tidepools. Tidepool number (nested within seastar and snail treatments) and experiment number were included as random factors to control for repeated sampling within tidepools and within the same experiment, respectively. Including snail treatment was unnecessary for models analyzing only the added snails (treatments 1 & 2). To analyze long-term snail behavior, I used REML models to test if snail refuge use and snail density in tidepools were affected by seastar and snail treatments. Tidepool number (nested within seastar and snail treatments) and treatments) and average sampling date were included as random factors to control for repeated sampling in the same tidepool and the same time period, respectively.

Impact on algae

Growth of microalgae. To determine the effects of snails and seastars on microalgae, I deployed 6 bare porcelain tiles (2.4 x 2.4 cm) using marine epoxy in each of the 37 experimental tidepools on September 3, 2009. After both 2 and 4 weeks (September 17 and October 1, 2009, respectively) I collected 3 tiles in each tidepool and measured chlorophyll-*a* concentration as a proxy for microalgal growth. I calculated the magnitude of the TMII as the difference in microalgal cover between paired treatments (predator present versus absent) at 2 and 4 weeks. Chlorophyll-*a* was extracted by placing each tile in acetone for 24 hours (as per Morelissen and Harley 2007) and analyzed using a fluorometer (TD-700, Turner Designs) with F4T4.5 B2 lamp with 436 nm excitation and 680 nm emission filters (as per Welschmeyer 1994). I analyzed the effects of week (2 or 4 weeks), seastar presence and snail treatment on chlorophyll-*a* using

REML. Tidepool number (nested within seastar and snail treatments) was included to account for repeated measures in tidepools. Unfortunately, too many tiles were lost in the originally *Leptasterias*-dominated tidepools to statistically analyze the 4-week tile collection, so only the 2-week tile collection was analyzed and week was dropped from the models.

Cover of macroalgae. Macroalgal surveys were conducted between July 6 and 8, 2009, just before the first snail addition experiment, and were repeated 1 month later on August 4 and 5, 2009 to determine the effects of *Leptasterias* and *Chlorostoma* manipulations on macroalgal cover in the 37 experimental tidepools. Additional macroalgal cover surveys were planned, but harbor seals (*Phoca vitulina*) killed the algae in many tidepools in fall 2009. I estimated cover of common macroalgal species by placing a large gridded quadrat (1 x 1.5 m with 2 x 2 cm cells) over each tidepool and tallying cells >50% occupied by a given species or bare space (double occupancy was allowed for overstory algae). I calculated percent cover for each species by dividing the surface area of occupied cells by the surface area of the tidepool (calculated from photos in Image J).

To test if snail and seastar treatments changed cover of individual macroalgal species in tidepools over 1 month, I ran multivariate analyses of variance (MANOVA) in JMP on change in percent cover of bare rock and the 19 common macroalgal species. I also analyzed the effects of survey date and overall treatment (included as a single factor with 4 levels) on algal community structure, with tidepool number (nested within overall treatment) included to control for repeated measures among tidepools (PERMANOVA using 999 maximum permutations).

Growth and recruitment of macroalgae. I also tested the effects of *Chlorostoma* and *Leptasterias* on macroalgal growth and recruitment in cleared plots since these tissues and stages of algae may be more vulnerable to *Chlorostoma* herbivory. In each of the 37 experimental

tidepools, I denuded 4 circular plots (5.08 cm diameter) with a small blowtorch between September 17 and September 22, 2009. Individual recruits were defined as individuals that settled within plots and were growing new thalli or crusts (typically *Mazzaella flaccida*, *Mastocarpus papillatus*, and encrusting coralline, red, or green algae). Growing algae was defined as existing nearby algae that had encroached into the plot (typically *Cladophora columbiana*, articulated coralline algae, and encrusting coralline or red algae). After ~8 months the number and percent cover of individual algal recruits and growing algae were surveyed (between April 26 and May 17, 2010), with percent cover calculated as the percent of cells that were >50% occupied in a gridded circular quadrat (5.08 cm diameter with 24 cells 0.84 x 0.84 cm each). I analyzed the effects of seastar and snail treatments on the number and cover of algal recruits and the cover of growing algae in each clearing plot using REML and included tidepool number nested within seastar and snail treatments as a random factor to control for nonindependence of plots within the same tidepool.

RESULTS

Predator and prey relation to community structure

Discriminant analyses identified 3 distinct tidepool community types (Fig. 2a; Wilk's λ : $F_{(2,60)} = 13.45$, p < 0.001) that were dominated by 1) articulated coralline algae, 2) *Cladophora columbiana*, and 3) bare rock and *Prionitis lanceolata*. *Chlorostoma* density was positively correlated with bare rock cover ($F_{(1,61)} = 32.84$, p < 0.001, $R^2 = 0.35$) and negatively correlated with articulated coralline algae cover ($F_{(1,61)} = 87.34$, p < 0.001, $R^2 = 0.59$). In contrast, *Leptasterias* density was positively correlated with articulated coralline algal cover ($F_{(1,60)} = 18.62$, p < 0.001, $R^2 = 0.23$) and was weakly negatively correlated with bare rock ($F_{(1,60)} = 4.64$, p = 0.035, $R^2 = 0.07$). Neither species was correlated with *Cladophora* cover.

Chlorostoma density, shore level, average depth, volume, *Leptasterias* density, periwinkle density (*Littorina* spp.), and hermit crab density (*Pagurus* spp.) were associated with algal community structure, in that order (Fig. 2b; DISTLM: $F_{(1,54)} = 16.22$, 15.54, 7.74, 6.33, 5.45, 4.98, and 2.50, respectively and p = 0.001 for all factors except *Pagurus* spp. where p = 0.033). Area and perimeter of tidepools were marginally nonsignificantly (DISTLM: $F_{(1,54)} =$ 2.34, p = 0.053) and not correlated (DISTLM: $F_{(1,54)} = 1.77$, p = 0.116) with algal community structure, respectively. *Chlorostoma* and *Leptasterias* densities continued to be significantly associated with algal community structure (PERMANOVA: $F_{(1,27)} = 4.62$, p = 0.001 and $F_{(1,27)} =$ 3.46, p = 0.007, respectively) even having already considered the effects of shore level, depth, volume and *Pagurus* spp. and *Littorina* spp. densities. Further, *Chlorostoma* at low densities were associated with different algal communities than *Chlorostoma* at medium and high densities (PERMANOVA post-hoc analyses: $t_{(27)} = 2.20$, p < 0.001 and $t_{(27)} = 2.24$, p < 0.001, respectively). Bare rock, *Prionitis lanceolata*, encrusting red algae and *Mastocarpus papillatus* were associated with the tidepools containing medium and high densities of snails. Articulated coralline algae, *Phyllospadix scouleri*, *Mazzaella* sp., crustose coralline algae and *Ulva* sp. were associated with the tidepools containing low densities of snails.

Predator-prey interactions

Surveys. Increased *Leptasterias* density in tidepools was correlated with both an increase of snails in halos and reduced densities of snails in tidepools (Fig. 3a and b; log-log correlations: $R^2 = 0.47$, $F_{(1,49)} = 23.51$, p < 0.001, and $R^2 = 0.24$, $F_{(1,61)} = 19.72$, p < 0.001, respectively).

Short-term experiments. Snails avoided seastars regardless of whether snails were 1) added, 2) initially resided outside or immigrated, 3) initially resided inside or immigrated, or 4) immigrated to tidepools. When added to tidepools containing seastars (Fig. 1, treatments 1 & 2), 28% more snails escaped to halos (Fig. 4a; seastar treatment: $F_{(1,89)} = 8.83$, p = 0.027) and snail densities tended to decrease (Fig. 4b; seastar treatment: $F_{(1,89)} = 5.28$, p = 0.062). Snails initially residing in halos or immigrating to tidepools (Fig. 1, treatments 1 - 4) responded to seastar removals by shifting habitats or immigrating into tidepools 25% more over time (Fig. 4c; time x seastar treatment: $F_{(1,127)} = 6.56$, p = 0.012) and by tending to be more dense in tidepools throughout the experiment (Fig. 4d; seastar treatment: $F_{(1,127)} = 3.98$, p = 0.070). These snails did not appear to exhibit a safety in numbers response; adding marked conspecifics did not decrease refuge use or increased density of unmarked snails in tidepools (Fig. 4c and d; time x snail treatment: $F_{(1,127)} = 0.003$, p = 0.957 and $F_{(1,127)} = 0.008$, p = 0.931, respectively).

Snails tended to use the refuges more often when *Leptasterias* were added (Fig. 4e; seastar treatment: $F_{(1,176)} = 3.32$, p = 0.088). Though not statistically different from one another (seastar x snail treatment: $F_{(1,176)} = 0.90$, p = 0.357), this was much more apparent when immigrants only were present (treatments 7 & 8, 24% greater refuge use) and less apparent when

residents and immigrants existed together (treatments 5 & 6, 5% greater refuge use). Extremely variable snail densities among tidepools resulted in seastars having no statistical effect on densities of snails whether immigrants only were present or immigrants and residents coexisted (Fig. 4f; seastar treatment: $F_{(1,176)} = 0.09$, p = 0.773). This variable density and the often rapid immigration between removals also resulted in snail removals only moderately reducing snail densities (snail treatment: $F_{(1,176)} = 3.46$, p = 0.081).

Long-term experiments. Over the 10-month experiment, snails consistently used halo refuges more when seastars were added to the originally Chlorostoma-dominated tidepools (Fig. 5; seastar treatment: $F_{(1,195)} = 6.89$, p = 0.020). Though no differences in refuge use were detected for resident plus immigrant versus immigrant only snails (Fig. 5; seastar x snail treatment: $F_{(1,195)} = 2.90$, p = 0.106), 30% more immigrant snails used the refuge when seastars were present, while only 5% of residents plus immigrants did (Fig. 5c). Conversely, densities in tidepools were not affected by seastar presence in any originally Chlorostoma-dominated tidepools (Fig. 5; seastar treatment: $F_{(1,273)} = 0.13$, p = 0.720; seastar x snail treatment: $F_{(1,273)} =$ 0.13, p = 0.723), which was again most likely an artifact of the high variability in snail densities among tidepools. On average, long-term snail removals decreased average snail densities in tidepools from 11.2 to 2.8 snails L^{-1} (75% decrease), though the effect was not significant due to high variability (Fig. 5; snail treatment: $F_{(1,273)} = 2.94$, p = 0.103). Contrary to short-term experiments, seastar removals from Leptasterias-dominated tidepools did not increase refuge use or decrease densities of snails in tidepools over the long term (seastar treatment: $F_{(1,57)} = 2.71$, p = 0.125 and $F_{(1,44)}$ = 2.50, p = 0.140, respectively). However, weekly *Leptasterias* removals may not have been frequent enough to keep Leptasterias densities near zero (seastars reinvaded between removals 35% of the time) and the generally very low densities of snails in these

tidepools may have made density changes hard to detect $(0.28 \pm 0.09 \text{ snails } \text{L}^{-1}, \text{ n} = 24 \text{ and } 1.27 \pm 0.54 \text{ snails } \text{L}^{-1}, \text{ n} = 18 \text{ with and without seastars, respectively}.$

Impacts on algae

Growth of microalgae. Seastars positively affected microalgae in tidepools. When seastars were added, microalgal growth (as chlorophyll *a* concentration) after 2 and 4 weeks was 70% and 83% higher, respectively, in tidepools containing resident plus immigrant snails, and 64% and 26% higher, respectively, in tidepools containing only immigrants (Fig. 6a and b; seastar treatment: $F_{(1.79)} = 12.66$, p = 0.001; seastar x snail treatment: $F_{(1.79)} < 0.01$, p = 0.975). The positive effect was consistent at both 2 and 4 weeks as algae grew (week x seastar treatment: $F_{(1,79)} = 0.29$, p = 0.589; week: $F_{(1,79)} = 49.74$, p < 0.001). As expected, snails were overall less effective at grazing algae when they were removed (snail treatment: $F_{(1,79)} = 10.72$, p = 0.002). When snails were added to the originally *Leptasterias*-dominated tidepools, seastars exerted a nonsignificant positive effect with a 58% increase in microalgal growth (seastar treatment: $F_{(1,79)}$ = 3.06, p = 0.091; seastar x snail treatment: $F_{(1.79)} = 21.69$, p < 0.001; Tukey: p = 0.137). Conversely, when snails were not added, seastars had an unexpected negative effect on microalgal growth (Tukey: p = 0.001). However, snail densities in these tidepools were extremely low (see specific densities above) so it is unlikely that *Chlorostoma* mediated this negative TMII.

Cover of macroalgae. No effects of seastar or snail treatment on established macroalgae were observed over the very short time period (~1 month) between macroalgal surveys. MANOVA results analyzing treatment effects on individual macroalgal species showed no significant changes for any species (Wilk's λ : F_(3,25) = 1.01, p = 0.491). Similarly, PERMANOVA analyses showed no significant effects of snail treatment or seastar treatment on community structure for either *Chlorostoma*-dominated or *Leptasterias*-dominated tidepools (overall treatment: $F_{(3,14)} = 0.45$, p = 0.928 and $F_{(3,11)} = 0.78$, p = 0.689, respectively).

Growth and recruitment of macroalgae. Seastars increased cover of macroalgae encroaching into clearing plots by 197% and 252% when added to tidepools containing resident plus immigrant snails or immigrant snails only, respectively (Fig. 6c; seastar treatment: $F_{(1,44)} =$ 5.26, p = 0.025; seastar x snail treatment: $F_{(1,44)} = 0.46$, p = 0.498). However, no effect of seastar removal on growing algae was found in the originally *Leptasterias*-dominated tidepools (seastar treatment: $F_{(1,37)} = 0.81$, p = 0.373), again likely because seastars often re-invaded tidepools between removals and snail densities were low. Because sample sizes were small when species were considered individually, no treatment effects were detected for any individual macroalgal species for either originally *Chlorostoma* or *Leptasterias*-dominated tidepools (MANOVA:

Wilks' λ : $F_{(3,64)} = 1.02$, p = 0.443 and $F_{(3,57)} = 1.42$, p = 0.106, respectively). However,

Cladophora columbiana was the most common algae recorded, and it grew most in tidepools where snails were removed and seastars were added. The number and cover of new algal recruits were not affected by seastars in the originally *Chlorostoma*-dominated (seastar treatment: $F_{(1,44)}$ = 0.33, p = 0.570 and $F_{(1,36)}$ = 0.13, p = 0.723, respectively) or *Leptasterias*-dominated tidepools (seastar treatment: $F_{(1,37)}$ = 0.19, p = 0.664 and $F_{(1,32)}$ = 0.51, p = 0.478, respectively), likely due to low recruitment (averaging less than one per plot) during the experiment.

DISCUSSION

Although I did not quantify DMIIs, TMIIs appeared to play a role in structuring rocky intertidal communities. *Leptasterias* caused *Chlorostoma* to use refuges outside of tidepools and graze less, which in turn likely had positive effects on both microalgae and macroalgae in tidepools. Though the observed effects on algae are a combination of TMII and DMII, attributing the results primarily to TMIIs is reasonable because the three criteria established by Peacor and Werner (2001) were satisfied; prey rapidly responded to predators, many more prey responded than could be eaten, and effects were long-lasting. Regarding the first criterion, snails added to tidepools containing seastars typically began climbing upward within minutes until they reached the waterline or emerged from the water, thereby evading seastars that always remained submerged. By the next day, the majority of snails had fled to halo refuges or had left the area when seastars were present. Further, effects of seastars on the other three snail types occurred within days. All snails likely responded to waterborne cues from seastars, which can elicit immediate escape responses in many snails simultaneously in the field and laboratory (Feder 1963, Chapter 2).

Regarding Peacor and Werner's (2001) second criterion for strong TMIIs versus DMIIs, adding seastars to tidepools often elicited escape responses by hundreds of snails. In contrast, of the 294 *Leptasterias* removed during the field experiment, fewer than 10 were consuming *Chlorostoma*. Further, *Leptasterias* ate at most only 2 *Chlorostoma* per day in the laboratory when confined with very small snails, and *Chlorostoma* are just one of many prey species consumed at this site (Bartl 1980, Chapter 2). In addition, large snails (>18 mm shell diameter) were rarely eaten by *Leptasterias* even under confined conditions, but surprisingly they still responded strongly to *Leptasterias* by fleeing and grazing less (Chapter 2). This size refuge for

large snails further increases the potential for TMIIs versus DMIIs in this system, because large snails are not eaten and thus cannot mediate DMIIs. In addition, large snails likely strongly mediate TMIIs because they comprise 29% of the population at this site and have higher grazing rates than small snails (Best 1964, Chapter 2). Certainly, some smaller snails are eaten by *Leptasterias*, somewhat inflating the experimental estimates of the strength of TMII relative to DMII. However, the above lines of evidence suggest the magnitude of DMII is likely much smaller than for TMIIs. To best determine the relative importance of DMIIs and TMIIs in this system, additional long-term caging studies are necessary to precisely estimate DMII for comparison to the present estimate of TMII using natural, unrestricted predators.

Regarding the third criterion (Peacor and Werner 2001), seastars added to tidepools also induced long-lasting refuge use, similar to other studies showing strong effects of predators on gastropod habitat use or grazing (Bernot and Turner 2001, Trussell et al. 2002, 2004, Matassa and Trussell 2011, Wada et al. 2013). Note that this sustained change in the average behavior of the snail population rather than a permanent habitat shift for particular individuals. *Chlorostoma* is quite mobile, and different individuals were likely sampled each time. On the other hand, individual *Leptasterias* were often observed in the same location for months even without caging, which maintained sustained behavioral responses by the snail population.

The duration and natural circumstances of the experiments further establish that TMIIs, which have been well established in laboratory and mesocosm experiments, may be also important in natural communities. First, seastar-induced refuge use by snails and subsequent effects on algae were consistent over short and long time scales (2 weeks to 10 months) for tidepools where seastars were added. The length of the experiments ensured that the apparent TMIIs in these tidepools were not an artifact of prey temporarily abstaining from grazing or only

exhibiting a short-term response to predators (Luttbeg et al. 2003, Werner and Peacor 2003, Okuyama and Bolker 2007). Also, the consistency in refuge use and apparent long-term TMII on macroalgae in seastar addition treatments showed that snails did not become accustomed to seastars and stop mediating TMIIs (Luttbeg et al. 2003, Werner and Peacor 2003, Okuyama and Bolker 2007). Second, apparent TMIIs occurred without caging or restricting the hunting behaviors of seastars or predator avoidance behaviors of snails. Thus, snails were not exposed to unnaturally strong predator cues that could have caused overestimation of TMII strength, and snails were not starved, which could have induced them to risk grazing in tidepools resulting in underestimation of TMII strength (Long and Hay 2012, Weissburg et al. 2014). Third, the apparent TMIIs detected were relevant for the ecosystem because the experiment used algae growing naturally, not algae introduced to the system or outplanted from the laboratory (Okuyama and Bolker 2007). Finally, the apparent TMII remained strong even while the focal interactors coexisted with other intertidal species, so it was not attenuated when embedded in a complex community (Strong 1992, Schmitz 1998).

Both the responsiveness of snails to seastars and the strength of the apparent TMII on algae depended on the type of snail examined. This suggests that the starting conditions of prey (e.g., starting habitat and vigilance level) and features of the environment (e.g., cue salience) may have altered the information available on risk and food availability and ultimately prey decision-making (Weissburg et al. 2014). It is well known that prey use informational cues on risks and rewards from the environment to make behavioral decisions, and that sampling increases information (Stephens and Krebs 1986, Bouskila and Blumstein 1992, Sih 1992). Recent studies suggest that the manner in which predator cues are delivered to prey (e.g. detectability, duration, intensity, timing) and the abiotic features of the environment or
experiment may strongly affect TMII strength (Luttbeg and Trussell 2013, Weissburg et al. 2014). Though I did not manipulate information specifically, below I discuss how possible differences in information on risk and food availability and vigilance levels of snails may have altered the outcomes among the treatments.

The strongest effects on both microalgae and macroalgae were observed in tidepools with seastars added, which mimicked natural invasions by predators into snail foraging habitat, This further suggests TMIIs may be prevalent and long lasting in this system. Though strong TMIIs were mediated by snails whether the snails were removed or not, immigrant snails strongly increased refuge use over the short and long term (24% and 30% increase, respectively) while residents in tidepools plus immigrants did not (5% and 5% increase, respectively). Immigrants (Fig. 1, treatments 7 & 8) were likely vigilant when encountering a new tidepools, actively sampling for information on predator presence, but perhaps had less information on food availability and opportunity cost, which may have induced increased refuge use when encountering predator cues (Sih 1992). Because residents plus immigrants in tidepools (Fig. 1, treatments 5 & 6) evidently mediated TMIIs without increased refuge use or decreased density when seastars were added, they likely reduced their grazing rates in response to predators, as found in many other tritrophic systems (Werner and Peacor 2003). Resident snails presumably had known opportunity costs of forsaking high quality habitat (Dill and Fraser 1997) so may have been less inclined to flee. Assuming immigration rate was the same regardless of snail removal treatment, at any given time the established tidepool residents outnumbered new immigrants to tidepools by 3:1, so even if the immigrants to tidepools containing residents (Fig. 1, treatments 5 & 6) were at first strongly responsive to seastars, their behaviors were likely undetectable. Further, it is possible that immigrants were more inclined to enter tidepools

containing high densities of resident snails even when seastars were present since the relative threat of predation is diluted by increasing group size (Dehn 1990). However, no "safety in numbers" behavior was observed for snails residing in halos or immigrating to tidepools when conspecifics were added (treatments 1 - 4), so the potential for this response by snails remains unknown. Overall, seastars appeared to exert TMIIs on algae in two different ways: causing immigrant snails to choose refuges and decreasing grazing by resident plus immigrant snails in tidepools. Thus, the starting condition of prey apparently influenced prey behavior and changed the mechanism of TMIIs (Kats and Dill 1998).

The strongest short-term snail responses occurred under the least realistic circumstances, where snails were added to tidepools containing seastars (Fig. 1, treatments 1 & 2). These snails were abruptly exposed to strong predator cues, perhaps before they had an opportunity to sample the habitat for food availability. Despite this strong response, TMIIs were not detected because the added snails had already emigrated from tidepools (and were not usually replaced by high densities of snails from halos or the surrounding area) by the time microalgae and macroalgae were sampled. In this case, strong avoidance behaviors over the short term could have resulted in a strong but perhaps unrealistic TMII had I artificially added algae to the system and sampled after a few days (Okuyama and Bolker 2007). However, algae were not affected because of the temporal disconnect between the behavior of the added snails and the growth of the algae. Hence, TMII experiments should use realistic prey manipulations to ensure behaviors are natural and test for the consistency of TMIIs over multiple time scales.

Snails initially residing in halos and immigrants (Fig. 1, treatments 1 - 4) invaded tidepools, but they did not mediate short or long-term TMIIs when seastars were present, probably because of their low densities. However, their strong short-term responses to seastars

show that these snails, and immigrant snails in all treatments, were able to overcome the seemingly challenging advective and turbulent environment at high tide, which is predicted to reduce cue detection (Large et al. 2011). Rather, they are apparently able to employ strategies to sample for risk and perhaps habitat quality when submerged, similar to other gastropods in turbulent environments (Ferner and Weissburg 2005).

Although the macroalgal community experiment was not as long as planned, I identify potential long-term effects of Leptasterias and Chlorostoma on algal communities based on the finding that Leptasterias may cause positive TMIIs on growing algae and on the multivariate analyses of community structure. The clearance experiment suggests that Leptasterias may indirectly enhance the seasonal growth or recovery after disturbance of macroalgae. The effects of Leptasterias and Chlorostoma presence was most apparent for fast-growing Cladophora *columbiana*, which is eaten by *Chlorostoma* (Aquilino et al. 2012). The surveys showed that bare rock is negatively associated with Leptasterias but positively associated with Chlorostoma, further suggesting that *Leptasterias* may cause positive TMIIs on macroalgal growth. On the other hand, the positive association of Leptasterias with coralline algae is probably caused by the seastars using coralline algae as habitat, not by a TMII, because coralline algae is not readily eaten by Chlorostoma. Overall, the multivariate analyses showed that Leptasterias and *Chlorostoma* densities were correlated with macroalgal community structure even having considered effects of many abiotic factors and other grazers, which agrees with previous experiments showing strong impacts of Chlorostoma herbivory on tidepool algal communities (Nielsen 2001). Others have also found that predators can cause alternate states by initiating TMIIs (Schmitz 2004). Though further experiments are necessary, Leptasterias may initiate transitions among the three surveyed tidepool community types through TMIIs.

In conclusion, TMII trophic cascades may be caused by mediating species changing their behavior, rather than by classic population size decreases, even under unrestrained natural conditions. Moreover, trophic cascades may occur even without predation risk, as is the case with nearly invulnerable large snails that continue to flee from their seastar predators. In addition, the starting conditions of prey and perhaps the information prey possess regarding the risks and rewards of foraging may fundamentally change the responses of individual prey and alter the indirect effects of predators. Overall, my study shows that predators may cause extended habitat shifts in many more prey than can be eaten, with both short- and long-term benefits for primary producers in natural ecosystems. Although the per-capita consumption rates typically are the primary mechanism of species interactions in population and food web models (Bolker et al. 2003, Persson and De Roos 2003), this study emphasizes the need to incorporate behavior to gain an inclusive, realistic estimation of the cascading effects of predators on communities. The next step is to further test these conclusions by conducting complementary caging studies to definitively partition the contributions of DMII and TMII in structuring communities in this study system.

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FIGURES

Originally Leptasterias-dominated tidepools



Figure 1. Eight experimental treatments for 37 tidepools in Horseshoe Cove, California used to test the effects of predatory *Leptasterias spp.* seastars on refuge use of *Chlorostoma funebralis* snails over the short (1 month) and long term (10 months) and subsequently on microalgae (2 and 4 weeks) and macroalgae (8 months) through TMIIs. Solid ovals indicate tidepools and dashed ovals indicate "halo" refuges (15 cm band of emersed rock surrounding the perimeter of each tidepool). Numbers indicate tidepool treatments, with treatments 1- 4 originally containing seastars and resident snails in the halo ("originally *Leptasterias*-dominated"), and treatments 5 - 8 originally containing resident snails in tidepools but no seastars ("originally *Chlorostoma*-dominated"). Manipulations included 1) snails added, 2) snails added, seastars removed, 3) control 4) seastars removed, 5) seastars added, 6) control, 7) snails removed, seastars added, and 8) snails removed. Four different snail types included snails 1) marked and added to tidepools

(treatments 1 & 2, black dots indicate markings), 2) residing in halo refuges surrounding tidepools (treatments 1 - 4), 3) residing in tidepool foraging habitat (treatments 5 & 6), and 4) immigrants from the surrounding area (treatments 1 - 8). Immigrants and unmarked halo or tidepool residents were indistinguishable from one another within treatments (*). Predicted outcomes are detailed below each treatment and graphically represented by arrows or large (positive TMII) and small algae (no TMII). When examining long-term snail behavior, treatments 1 & 3 and 2 & 4 were combined since snails were only added in the early part the experiment.



Figure 2. Canonical score plot (a) and distance-based redundancy analysis (dbRDA) plot (b) depicting coralline algae-dominated (open triangles), *Cladophora columbiana*-dominated (closed

circles) and bare rock and *Prionitis lanceolata*-dominated (open circles) tidepool communities. Discriminant analysis of the cover of algal species in 63 tidepools of Horseshoe Cove, California surveyed from July 6 to 14, 2009 was used to classify algal community types. Inner ellipses in the canonical plot (a) show the 95% confidence interval for group means (cross-hairs), and outer ellipses show the normal 50% contours. Vector overlays depict the algal species strongly driving separation among community types. Vector overlays in the dbRDA plot (b) depict the abiotic factors and animals that were most strongly associated with algal community structure.



Figure 3. Logarithmic correlations between seastar (*Leptasterias spp.*) density and a) snail (*Chlorostoma funebralis*) refuge habitat use or b) snail density in 63 unmanipulated tidepools surveyed in Horseshoe Cove, California between July 6 and 14, 2009.



Figure 4. Mean (\pm SE) refuge habitat use (left panels) and densities (right panels) of snails (*Chlorostoma funebralis*) during 2 replicate short-term experiments (1 month each from July 13 to August 20, 2009 and October 1 to 28, 2009) in 37 tidepools in Horseshoe Cove, California. Effects of experimental manipulation of seastar presence (closed circles with solid lines or gray bars) and absence (open circles with dotted lines or white bars) on habitat use was examined for snails added to tidepools (a and b, n = 4 tidepools, logistic fits shown), snails resident in refuge habitats or immigrating to tidepools (c and d, n = 8 tidepools) and snails resident in or immigrating to tidepools (e and f, n = 4, 6, 6 and 4 tidepools in order shown).



Figure 5. Mean (\pm SE) refuge habitat use (left panels) and densities (right panels) of snails (*Chlorostoma funebralis*) depending on *Leptasterias* spp. seastar presence over the long-term experiment (10 months from July 13 to May 17, 2010) in originally *Chlorostoma*-dominated tidepools in Horseshoe Cove, California. Seastars were either added (closed circles with solid lines) or not added (open circles with dotted lines) to tidepools. Treatments with unmanipulated snails were surveyed 5 times and contained both residents in tidepools and immigrants (a and b, n = 6 and 4 tidepools with seastars absent and added, respectively) while treatments with snails

removed were surveyed approximately weekly and contained only recent immigrants (c and d, n = 6 and 7 tidepools with seastars absent and added, respectively).



Figure 6. The effect of seastar (*Leptasterias spp.*) addition (gray bars) or absence (white bars) on algae (\pm SE) in originally *Chlorostoma funebralis*-dominated tidepools in Horseshoe Cove, California. Only recent immigrants were present in treatments where snails were removed weekly from tidepools. Microalgal growth was measured after a) 2 and b) 4 weeks on September 17 and October 1, 2009 in 18 tidepools (n = 4, 5, 5, and 4 tidepools for each treatment in order shown). Growth of macroalgae in cleared plots (c) was measured after 8 months (September 17, 2009 to May 17, 2010) in 18 tidepools (n = 5, 4, 4 and 5 tidepools for each treatment in order shown).

CHAPTER 2

Prey state alters trait-mediated indirect interactions in rocky tidepools

ABSTRACT

I investigated the link between individual behavior and community processes by testing whether prey state (body size and hunger level) altered antipredator behavior and thus changed the strength of trophic cascades between predators and primary producers. In rocky intertidal tidepools on the California Coast, waterborne cues from the seastar predator Leptasterias spp. initiated positive trait-mediated indirect interactions (TMIIs) on microalgae by causing mediumsized and fed individuals of *Chlorostoma funebralis* snails to reduce grazing and flee tidepools. In contrast, no TMIIs occurred when hungry and small snails were exposed to seastars in tidepools, because they continued grazing despite the risk of predation and ate little algae, respectfully. Large snails consistently fled from seastars and reduced grazing in the laboratory and field, which was surprising since they appear to reach a size refuge from predation. However, their role in mediating TMIIs was unclear since they had variable effects on algae. When confined with seastars in the laboratory, all snails fled and all except small snails mediated TMIIs, likely because tactile cues elicited stronger responses than waterborne cues. Overall, the strength of TMII trophic cascades in tidepools depended on individual prey state, supporting model predictions and contributing empirical evidence linking individual variation to community processes.

INTRODUCTION

Predator-prey interactions are often depicted as predation rates on prey, and for simplicity these metrics generally treat all individuals within a population as homogenous (Abrams 1995, Schmitz et al. 2003, Werner and Peacor 2003, Ohgushi et al. 2012). However, adaptive foraging theory unequivocally demonstrates that predators also exert nonconsumptive effects on prey by changing their foraging behavior (Mangel and Clark 1986, Gilliam and Fraser 1987, Houston et al. 1993, Werner and Anholt 1993, Lima and Bednekoff 1999), and these behaviors are contingent on individual variation in prev states, such as body size, energy reserves, reproductive status, or behavioral syndromes (Mangel and Clark 1986, Houston et al. 1993, Clark 1994, DeWitt et al. 1999, Lima and Bednekoff 1999, Sih et al. 2004). Trophic cascades connect predator-prey interactions to a third species, and the classic mechanism is a form of a densitymediated indirect interaction (DMIIs, Abrams 1995, Peacor and Werner 1997), whereby predators can benefit primary producers by reducing grazer population densities. Similar to foraging theory that focuses on the sublethal effects of predators on prey, trait-mediated indirect interactions (TMIIs, Abrams 1995, Peacor and Werner 1997) demonstrate that trophic cascades may also occur when predators exert sublethal effects on prey behavior, morphology, or physiology, which in turn indirectly affect primary producers (Werner and Peacor 2003, Schmitz et al. 2004, Miner et al. 2005). TMIIs weave a connection between behavioral, population, and community ecology by linking individuals to emergent community patterns and ecosystem processes (Schmitz 2000, Schmitz et al. 2003, Schmitz et al. 2008). Further, the proliferation of TMII studies in recent decades has demonstrated that TMIIs are common and often as strong as DMIIs (Schmitz 1998, Trussell et al. 2004, Preisser et al. 2005, Peckarsky et al. 2008).

Just as predator-prey interactions within foraging theory depend on the state of individuals, it is likely that TMII strength may also be contingent upon the individual state of the organisms involved. Multiple reviews and syntheses have identified this concept as understudied and called for studies connecting individual state variation to community-level patterns (Schmitz et al. 2003, Schmitz et al. 2004, Beckerman et al. 2010, Ohgushi et al. 2012, Railsback and Harvey 2013). In response, theoretical models have demonstrated that prey body size and hunger level may alter TMII strength (Schmitz 2000, Luttbeg et al. 2003, Persson and De Roos 2003). In addition, field and laboratory studies have demonstrated that TMIIs strengths may be contingent on prey body size, hunger level, and the combination of hunger and risk frequency (Kotler et al. 2004, Freeman 2006, Rudolf 2012, Matassa and Trussell 2014), though other experiments and models suggest that prey traits may be safely ignored in certain cases (Ovadia and Schmitz 2002, 2004, Ovadia et al. 2007). Overall, additional empirical studies are needed to more fully explore the consequences of prey state variation for TMIIs.

I investigated whether hunger level and body size of prey altered antipredator responses and the strength of TMIIs in a tritrophic food chain. The asset protection principle (Clark 1994) posits that prey with high energy reserves should be wary of predators, but prey with low energy reserves should continue foraging despite risk. Similarly, the risk allocation hypothesis (Lima and Bednekoff 1999) posits that prey in worse condition should more readily emerge from refuges to forage, even when predators are present. What are the consequences for a third trophic level, as in a TMII? Predators may exert positive TMIIs on primary producers when well-fed prey are wary, whereas the TMIIs may weaken when hungry prey forage despite risk (Heithaus et al. 2007, Matassa and Trussell 2014). In addition, the consumptive and nonconsumptive effects of predators on prey may change with prey body size, which may then alter effects on

prey resources (Rudolf 2012). For example, predators may select small size classes of prey due to ease of capture or shorter handling time (Macarthur and Pianka 1966). If all sizes of prey continue to exhibit antipredator responses, then small prey may mediate both TMIIs and DMIIs while large prey may mediate only TMIIs if they are much more difficult to capture. Alternatively, larger prey may stop responding to predators as they grow and risk abates, and thus cease to mediate TMIIs or DMIIs (Freeman 2006). Overall, failing to consider variation in prey traits may lead to erroneous estimates of the strength and importance of TMIIs (Rudolf 2012).

To determine whether body size or hunger level alters prey behavior and changes TMII strength, I examined a tritrophic food chain in tidepools where the small (1 - 5 cm diameter) seastar Leptasterias spp. (L. aequalis and L. hexactis, considered either sister species or subspecies, see Flowers and Foltz 2001 for species complex) consumes the common herbivorous intertidal snail Chlorostoma (formerly Tegula) funebralis, which grazes on algae. I first assessed the potential for size-dependent predation by Leptasterias on Chlorostoma by testing whether smaller snails were eaten more than larger snails in the laboratory and field. I then examined size-dependent antipredator behavior by comparing evasive behavior of different sized snails to both tactile (imminently threatening) and waterborne (prospectively threatening) predator cues. Finally, I tested if snail size (3 size classes) or hunger level (hungry versus fed) changed snail antipredator behavior, and consequently altered TMIIs on microalgae in the laboratory and field. While the TMII studies were very short and do not necessarily predict outcomes in nature, previous studies in this system demonstrated that Leptasterias consistently caused Chlorostoma to avoid tidepools and evidently reduced grazing for many months, increasing growth of microalgae and macroalgae in tidepools over the long term (Chapter 1). I also relate the results of

the short-term experiments to ecologically relevant scales in which the average hunger level and body size of natural population of snails differ predictably in space and time.

METHODS

Study site and species

Studies were conducted at the Bodega Marine Reserve in rocky tidepools of Horseshoe Cove in northern California, USA (38° 18' 59.37" N, 123° 4' 16.28" W) during the spring and summer from 2009 to 2013. Snails for laboratory experiments were collected from Horseshoe Cove either 1 day prior (size experiments) or 1 week prior (hunger experiments) to experiments and were maintained in outdoor, flow-through tanks where they either grazed on naturally growing microalgae (benthic diatoms) or were starved. Seastars were collected in Horseshoe Cove within days of experimental use until a local *Leptasterias* mass mortality event in Dec 2010. For later experiments, *Leptasterias* were collected 17 km north of Horseshoe Cove at Twin Coves (38° 27' 28.83" N, 123° 8' 42.85" W) or 104 km north at Point Arena (38° 54' 47.48" N, 123° 42' 37.83" W). *Leptasterias* were maintained in flow-through tanks and fed small *Chlorostoma* and *Littorina* spp. weekly. I measured maximum diameters of snails (sensu Paine 1969) as well as maximum diameter (between tips of 2 longest opposing arms).

Field experiments were conducted in small (1.2 - 9.3 L) mid-to-high (1.01 - 1.67 m above mean lower low water) tidepools. I measured tidepool shore levels using surveying equipment, tidepool volumes by emptying tidepools with a bilge pump, and tidepool surface areas and perimeters by analyzing photographs using ImageJ software (U.S. National Institutes of Health). *Consumptive and nonconsumptive effects on prey*

Predation and size refuge. I determined the frequency of predation on *Chlorostoma* and other invertebrate prey by examining the stomach contents of 102 *Leptasterias* throughout the intertidal zone. For each *Leptasterias*, I recorded the shore level (low, medium, high), seastar

oral disc diameter (which can influence potential prey size) and prey maximum diameter (gastropods) or length (mussels and chitons).

I tested for a size refuge of *Chlorostoma* from *Leptasterias* predation by confining 136 pairs of seastars and snails in very small (~125 cm³) flow-through seawater compartments that minimized the ability of snails to escape. Snails were grouped into six 3-mm size class increments with 22 - 24 snails each, and half of the snails in each size class were paired with either a large (3 - 5 cm diameter) or medium sized seastar (2 - 3 cm diameter). I recorded the outcome of predator-prey encounters daily for 16 days. I analyzed the main and interactive effects of seastar and snail size on the survival of snails using a nominal logistic regression and associated likelihood ratio tests using R statistical software.

Size-dependent responses of prey to predator cues. To determine if less vulnerable large snails responded less strongly to seastars than more vulnerable small snails, I determined the escape responses of snails to both tactile and waterborne chemical cues from *Leptasterias*. I placed small (6 - 12 mm), medium (12 - 18 mm), and large (18 - 25 mm, within the size refuge) snails in small shallow tanks (33 x 19 cm x 4 cm depth) with each individual located in the center of a "bulls eye" with five 1-cm concentric rings. On February 19, 2013, I exposed 12 - 20 snails of each size class to a tactile cue (direct contact with seastar in clean seawater), waterborne cue (seawater with dissolved chemical cues from seastars bathed for 2 hours at natural tidepool densities of ~0.41 seastars L⁻¹), or no cue (seawater alone). Once the snail emerged from its shell, I recorded the time elapsed at each 1-cm increment and noted if snails meandered between increments. I classified a meander as occurring when the snail turned 90° within a 1-cm increment, thereby proving a simple effective measurement of meandering during the

observation period. Snails were used only once and within a day of field collection. Seawater was changed after each trial, and tanks were washed to eliminate any residual cues.

The average speed (cm s⁻¹) between increments was recorded for each snail, excluding increments where snails meandered since the distance inherently increased. Because speed increases with size, I calculated "size-corrected relative speed" for each snail to determine whether the snail moved faster or slower than average for its size for each cue type (mean speed of an individual / mean speed of snails in the individual's size class for all cue types). Meandering frequency was calculated as the percent of 1-cm increments that meandering occurred. I analyzed the effects of seastar cue (no cue, waterborne or tactile) and snail size (small, medium or large) and their interactions on size-corrected relative speed and meandering frequency using General Linear Models (GLM) in JMP software (SAS Institute Inc., Version 9, 2010).

TMII experiments

TMII laboratory experiments. To test if the size or hunger level of snails changes their antipredator behaviors and alters TMII strength in the laboratory, I placed snails of different sizes and hunger levels in glass bowls (11 cm diameter x 5 cm deep) with and without medium to large seastars (2 - 5 cm diameter, with size randomized) and measured the time spent out of water, time grazing, and effect on microalgal cover. For size experiments, I factorially crossed seastar presence with small, medium, large or no snails totaling 8 treatments (n = 26 per treatment except the 2 "no snail" treatments where n = 9). I performed 3 replicate trials on July 5, August 3 and August 23 2012 with 54, 54 and 66 bowls per trial, respectively. For hunger experiments, I factorially crossed seastar presence with fed, hungry, or no snails totaling 6 treatments (n = 103 for *Leptasterias* absent treatments and n = 106 for *Leptasterias* present

treatments, except the 2 no snail treatments where n = 21). I performed 6 replicate trials on April 12, April 14, June 14, July 20, and August 24, 2012 and January 30, 2013 using 30, 30, 62, 36, 66 and 66 bowls per trial, respectively. Only medium snails (12 -18 mm) were used for hunger experiments. Snails were collected and starved overnight before size experiments. Snails for hunger experiments were collected 1 week before experiments and were either starved or fed microalgae. Outdoor flow-through tanks were used to grow a thin film of benthic diatoms on unglazed porcelain tiles (2.54 x 2.54 cm) for 1 - 2 weeks before experiments. Tiles were randomly assigned among replicates to account for any variation in algal biomass.

Each replicate bowl was filled halfway with seawater, and I sequentially added 2 algal tiles, 1 seastar, and 1 snail to each bowl, depending on the treatment. I added snails simultaneously to all bowls and recorded snail location and grazing activity every 5 minutes for 1 hour. I converted the categorical metrics of In vs. Out of water and Grazing vs. Not grazing into percent of time out of the water or percent of time grazing for analyses [((# of time points out of water or grazing) / (13 total time points)) x 100]. Grazing was identified as visible rasping on the algae-covered tiles, which invariably caused clearing of the thin layer of microalgae. Snails rarely dislodged algae without rasping. After 1 hour, remaining algal cover was measured using a gridded transparent quadrat (2.54 x 2.54 cm with 0.51 x 0.51 cm cells), and the data for the 2 tiles in each bowl were averaged. I analyzed the main and interactive effects of seastar and snail treatment on the percent time out of water, percent of time grazing, and percent algal cover using 2-way restricted maximum likelihood models (REML) in JMP. All response variables were arcsine square root transformed to meet statistical assumptions of normality and equal variances.

TMII field experiments. To test if snail size or hunger changes snail behavior and TMII strength in the field, I added snails of different size classes or hunger levels to 18 tidepools. Medium to large seastars (2 - 5 cm diameter, with size randomized) were added to half of the tidepools, which all contained microalgae-covered tiles (same preparation as the laboratory experiments), and I monitored snail habitat use, snail grazing activity, and changes in algal cover during low tide. Treatments without snails were included to control for any effects on algae due to handling, seastars or grazing by other herbivores. I performed 6 replicate size trials (May 24, May 25, June 22, June 26, July 20, and August 29, 2012) and 4 replicate hunger trials (July 18, August 2, August 30 and September 27, 2012). Treatments were randomly assigned to the 18 tidepools for each trial, resulting in a total of 9 - 15 replicates among all trials. Seastars were contained in small mesh pouches of plastic window screen affixed to eyebolts drilled into the substrate to prevent escape and predation on snails. To mimic natural predator cue accumulation during low tide, seastars were added to tidepools the day before the experiment at natural densities in tidepools of Horseshoe Cove prior to the Dec 2010 Leptasterias mortality event $(\sim 0.41 \text{ individuals } L^{-1})$. Snails were collected from experimental and nearby tidepools the day before experiments and kept in flow-through seawater overnight. Snails were added to tidepools at 50% natural field densities (13.6 individuals L⁻¹), because 100% density would have made treatments with large snails overcrowded. To ensure algal tiles were easily and equally accessible to snails among tidepools of different sizes, the tiles were densely distributed with the number of tiles scaled to the tidepool surface area $(0.010 \text{ tiles cm}^{-2})$, and they were randomly assigned among tidepools to control for variation in algal biomass. Steep sides in 1 tidepool limited the maximum density of tiles to 0.006 tiles cm⁻². Each tidepool and surrounding areas were cleared of *Chlorostoma*, other herbivorous gastropods, and hermit crabs both the day before and day of

each experiment. As a result of the mortality event, *Leptasterias* were naturally absent in the tidepools during the experiment.

On the day of experiments, I first deployed tiles in all tidepools, quickly followed by snails, taking care not to place snails on tiles. Snails typically avoid seastar cues by escaping tidepools to refuge habitats above the water line (Chapter 1), which I termed the "halo" and define as substrate 0 - 15 cm above the waterline in each tidepool. The number of snails in the water, in the halo, and grazing (defined above as snails rasping tiles) was sampled every 5 - 10 minutes in each pool for 1 hour (size trials) or 45 minutes (hunger trials). Any organisms other than *Chlorostoma* grazing on tiles were removed at each sampling, and tiles were removed at 1 hout for size trials and 45 minutes for hunger trials. Algal cover was determined as described above for laboratory experiments, and algal cover was averaged within each tidepool. To determine if hunger level or size cause individual snails to consume algae faster, individual snail feeding rate was estimated as the [(total algal surface area eaten) / (sum snails grazing * time)].

Since trends over time were not always linear, time was grouped into 15-minute increments and treated as a categorical variable. I tested the main and interactive effects of time frame, seastar treatment, and snail treatment on the arcsine square root transformed percent snails in the halos and grazing using REML models in JMP. The main and interactive effects of seastar and snail treatments on percent algal cover were also analyzed using REML. In each model, tidepool replicate was included as a random variable (nested within seastar and snail treatments) to account for repeated measures.

RESULTS

Predation and size refuge. Of the 102 *Leptasterias* observations in the field, only 5 seastars were consuming *Chlorostoma* (4.9 %), and 4 of these snails were small (<12 mm). The other snail was 18.5 mm in diameter, and was being eaten by an extremely large *Leptasterias* (12.6 mm oral disc diameter and at least 50 mm in arm span). Of the 21 seastars eating, at least 6 prey types were identified (Fig. 1a) including *Littorina* spp. (29%), *Lacuna marmorata* (24%), *Chlorostoma* (24%), limpets (10%), *Mytilus californianus* (10%) and chitons (5%). In the laboratory, vulnerability to predation decreased with snail size (Fig. 1b; logistic regression: $X^2 = 59.5$, p < 0.001), and increased with *Leptasterias* size ($X^2 = 6.46$, p = 0.011). Small and medium snails were eaten often (76.6% and 40.0% of snails, respectively) and only occasionally survived attacks (14.9% and 15.6%, respectively). Conversely, most large snails were not attacked (63.8% of snails) but when attacked they were rarely eaten and often survived (6.4% and 29.8 % of snails). Note that my goal was to establish the size refuge rather than to estimate size-dependent consumptive effects or predation rates in the field, and these estimates likely grossly overestimated predation risk in the field where snails can flee.

Size-dependent responses to predator cues. Despite low risk of predation, large snails reacted strongly to seastar cues, moving the fastest when exposed to imminently threatening tactile cues, less when exposed to prospectively threatening waterborne cues, and slowest when no cues were present (Fig. 2a; Seastar cue x Snail size: $F_{4,138} = 5.53$, p < 0.001). Medium snails also responded most strongly to tactile cues relative to controls (Fig. 2a; Tukey: p = 0.003). Surprisingly, neither tactile nor waterborne cues increased the speed of small snails relative to controls, despite their high vulnerability to predation (Fig. 2a; Tukey: p > 0.987 for all comparisons). However, small snails meandered more often than large snails regardless of the

cue (Fig. 2b; snail size: $F_{2,138} = 4.21$, p = 0.017). Overall, snails meandered most when exposed to nondirectional waterborne cues but went straightest when exposed to unidirectional tactile cues (Fig. 2b; seastar cue: $F_{2,138} = 3.16$, p = 0.046).

TMII laboratory experiments. Over the 1-hour trials, small, medium and large snails responded similarly to seastars by spending 59, 61, and 46 % more time out of the water, respectively (Fig. 3a; Seastar Treatment: $F_{(1,150)} = 154.3$, p < 0.001; Seastar treatment x Size: $F_{(2,150)} = 1.69$, p= 0.188). Seastars also reduced grazing by snails of all sizes (35, 37, and 20% for small, medium and large snails, respectively; Fig. 3b; Seastar treatment: $F_{(1,150)} = 112.9$, p < 0.001; Seastar treatment x Size: $F_{(2,150)} = 1.89$, p = 0.153). However, only medium and large snails mediated positive TMIIs on algae (47 and 51% increase in algal cover, respectively) when seastars were present (Fig. 3c; Seastar treatment: $F_{(1,165)} = 83.2$, p < 0.001; Seastar treatment x Size: $F_{(3,165)} = 8.24$, p < 0.001). Small snails, though responsive to seastars, did not mediate a detectable TMII because they grazed much less algae overall than medium and large snails (Fig. 3c; Size: $F_{(1,165)} = 24.4$, p < 0.001).

Though hungry snails spent more time in the water overall (Fig 3d; snail treatment: $F_{1,201}$ = 7.93, p = 0.005), fed and hungry snails had a similar response to seastars, spending 46% and 44% more time out of water, respectively (Fig 3d; seastar treatment: $F_{1,201}$ = 131.95, p < 0.001; seastar x snail treatment: $F_{1,201}$ = 0.23, p = 0.635). Because fed snails did not graze often regardless of treatment (Fig 3e; snail treatment: $F_{1,201}$ = 59.01, p < 0.001), they only decreased grazing time by 16% in response to seastars compared to 33% by hungry snails (seastar treatment: $F_{1,201}$ = 69.26, p < 0.001, seastar x snail treatment: $F_{1,201}$ = 3.43, p = 0.069). Both fed and hungry snails mediated positive TMIIs, with algal cover increased by 9% and 18%, respectively when seastars were present (Fig. 3f; seastar treatment: $F_{1,2}$ = 31.48, p < 0.001;

seastar x snail treatment: $F_{1,224} = 2.21$, p = 0.112). Overall, hungry snails ate more algae than fed snails, and algae were unaffected when snails were absent (Fig. 3f; snail treatment: $F_{1,224} = 84.13$, p < 0.001). No snails were captured or eaten during the laboratory study.

TMII field experiments. On average, medium and large snails escaped from seastars more quickly than small snails (Fig. 4a - c; Time x Seastar treatment x Snail size: $F_{8,899} = 2.32$, p = 0.018; Time x Seastar treatment: $F_{4,899} = 50.40$, p < 0.001). By the end of experiments, many snails of all sizes had fled tidepools in response to seastars (Fig. 4a - c; Mean % in halo at end \pm SE: 15.9 ± 2.4 , 23.4 ± 3.1 , and $21.4 \pm 1.7\%$ for small, medium and large, respectively). In contrast, few snails fled when seastars were absent (Mean % in halo at end \pm SE: 3.9 \pm 1.0, 4.1 \pm 0.8, and $4.9 \pm 0.7\%$ for small, medium and large, respectively). *Leptasterias* also caused fewer snails of all sizes to graze, especially between 30 and 60 minutes (Fig. 4d - e; Seastar treatment: $F_{1,856} = 14.37$, p = 0.003; Time x Seastar treatment: $F_{4,856} = 5.83$, p < 0.001; Time x Seastar treatment x Snail Size: $F_{8,856} = 0.79$, p = 0.611). More small snails grazed than medium or large snails after 30 minutes regardless of seastar presence (Snail size: $F_{1,856} = 19.36$, p < 0.001; Time x Snail Size: $F_{4,856} = 4.05$, p < 0.001). This was likely because medium and large snails quickly consumed the algae and stopped grazing, likely underestimating the potential grazing activity and TMII mediated by medium and large snails. Only medium snails mediated positive TMIIs on algae, and large snails surprisingly mediated negative TMIIs on algae (Fig. 5a; Seastar treatment: $F_{1,76} = 0.07$, p = 0.790; Seastar treatment x Snail size: $F_{3,76} = 2.86$, p = 0.042). This negative TMII may be linked to an increased grazing rate by individual large but not medium or small snails when Leptasterias were present, though this effect was not significant (seastar x snail treatment: $F_{2.55} = 1.30$, p = 0.290; Mean large snail grazing rate \pm SE: 0.41 \pm 0.07 and 0.29 \pm 0.05 with and without seastars, respectively, n = 14). Not surprisingly, grazing rates increased

with snail size (snail treatment: $F_{2,55} = 18.8$, p < 0.001; Mean grazing rate ± SE: 0.15 ± 0.04, 0.22 ± 0.03 and 0.35 ± 0.04 cm² grazing snail⁻¹ hour⁻¹ for small, medium and large, respectively, n = 28).

Fed snails mediated positive TMIIs on algae but hungry snails did not (Fig. 5b; Seastar x Snail treatment: $F_{3,44} = 3.65$, p = 0.033). On average, fed snails fled from tidepools more quickly than hungry snails when seastars were present (Fig. 6a & b; Time x Seastar treatment x Snail treatment: $F_{3,407} = 4.69$, p = 0.003). By the end of experiments, more fed than hungry snails left tidepools with seastars (Fig. 6a & b; Mean % in halo at end \pm SE: 31.7 ± 2.5 % and 10.2 ± 1.8 % of fed and hungry snails, respectively). Without seastars, very few fed or hungry snails left tidepools (Fig. 6a & b; Mean % in halo at end \pm SE: 3.0 ± 0.7 % and 0.8 ± 0.3 % of fed and hungry snails, respectively). Though on average throughout the experiment fewer fed snails grazed when *Leptasterias* were present (4.2% fewer), and hungry snails continued grazing (0.7% fewer), there were no statistical differences between the number of fed and hungry snails grazing with seastar presence (Fig. 6c & d; Time x Seastar treatment: $F_{3,407} = 5.25$, p = 0.001; Time x Seastar treatment x Snail treatment: $F_{3,407} = 1.76$, p = 0.153).

DISCUSSION

I link state-dependent behavior to community outcomes by showing that individual variation in prey hunger and size may alter the strength of TMII trophic cascades. Body size had complex implications for TMII strength in the field, because it potentially altered both the consumptive interactions (predation rates and foraging rates) and nonconsumptive effects of predators on prev. In field experiments when prev were well-fed, predators exerted stronger TMIIs on primary producers because prey grazed less; but when prey were hungry, predators had weaker effects on primary producers since prey foraged despite risk, consistent with predictions from foraging theory (Werner and Anholt 1993, Clark 1994, Lima and Bednekoff 1999). This study confirms model predictions (Schmitz 2000, de Roos et al. 2002, Luttbeg et al. 2003, Persson and De Roos 2003) that individual variation in prey state may change TMII strength, adding to the growing body of empirical evidence for this understudied concept (Ovadia and Schmitz 2002, Kotler et al. 2004, Freeman 2006, Heithaus et al. 2007, Matassa and Trussell 2014). While the very short-term TMIIs observed here do no necessarily predict TMII strengths at longer ecological time scales, I identify natural circumstances where average size or hunger level in snail populations may vary over time or space and discuss the potential ramifications for TMII strength. Further, my prior experiments suggest that *Leptasterias* exert positive long-term TMIIs on algal growth in this system by causing *Chlorostoma* to avoid tidepools and reduce grazing for many months (Chapter 1), indicating that the short-term results here may indeed manifest over the long-term.

Prey state and TMIIs

Medium snails escaped from seastars, reduced grazing and mediated positive TMIIs in both laboratory and the field experiments, suggesting that they may be important mediators of TMIIs in natural systems. Since small snails did not graze enough algae to mediate TMIIs in the laboratory or field despite strong behavioral responses, they may mediate weaker TMIIs than medium snails in nature. However at high densities or over longer periods, small snails probably would mediate stronger TMIIs on algae than were observed here. The slower escape response by small snails in the field experiments was likely due to both slower speed and increased meandering observed in the predator cue experiments in the laboratory. Like the predator cue experiments, large snails in both laboratory and field TMII experiments reacted to seastar presence by fleeing and grazing less. This resulted in positive TMIIs in the laboratory but not in the field, where large snails surprisingly mediated negative TMIIs. This counterintuitive result may have arisen because individual large snails increased their grazing rates in the presence of seastars. Thus, when seastars were present, fewer large snails grazed but individuals that did graze grazed faster, likely resulting in lower algal cover when seastars were present than absent. It is unclear how these results may translate to TMIIs mediated by large snails in nature, especially since large snails appear to be less responsive than medium and small snails over longer time scales; they co-occur with Leptasterias inside tidepools more often than small and medium snails in field surveys (Chapter 3) and generally reside lower in the intertidal zone where Leptasterias and other predatory seastars are abundant (Paine 1969, Doering and Phillips 1983).

In the field, hungry snails did not respond to seastar presence nor did they mediate TMIIs, suggesting they may not strongly mediate TMIIs in nature. These snails apparently risked predation to gain much-needed energy, similar to predictions of the risk allocation hypothesis

that suggests prey with lower energy reserves should forage despite risk (Lima and Bednekoff 1999). In contrast, fed snails presumably have higher energetic reserves, and in accordance with the asset protection principle, they did not risk foraging when seastars were present (Clark 1994). Thus, fed snails did mediate TMIIs, supporting models and prior experiments suggesting that TMIIs should be stronger when prey have high energy reserves, while TMIIs should weaken when low energy reserves force prey to continue foraging (Luttbeg et al. 2003, Heithaus et al. 2007, Matassa and Trussell 2014).

In TMII experiments in the laboratory, snails of all sizes and hunger levels reacted strongly to seastars, grazed less often, and all but small snails mediated positive TMIIs. The small confines of the laboratory experiments may be responsible for the magnified antipredator responses by all snails compared to those in the field; in laboratory TMII experiments, snails were frequently exposed to tactile cues that evoked strong responses in predator cue experiments. In TMII experiments in the field, snails were exposed only to waterborne cues that elicited weaker responses in predator cue experiments. Thus, TMII experiments in the laboratory may overestimate antipredator responses and TMIIs operating in nature, like TMII experiments conducted in mesocosms in other systems (Okuyama and Bolker 2007, Long and Hay 2012).

I did not explore the interaction between hunger and size, but it is possible they may not be independent of one another. Small snails in the field could have lower energetic reserves, and despite their strong short-term responses to *Leptasterias*, they may eventually re-enter tidepools to graze while large snails may be able to delay foraging for longer periods (Lima and Bednekoff 1999). In contrast, the energetic demands of reproduction apparently force medium and large *Chlorostoma* (>12 mm) to move lower on the shore despite higher predation risk by *Pisaster*
ochraceus (Paine 1969), so the interplay between size and energetic reserves in the presence of both predators remains to be determined.

Potential causes of large snail behavior

Interestingly, large snails responded to seastars in the laboratory and field even though they likely were at low risk of predation. Here, the prey's perceived risk of predation may be more important than actual risk for determining prey behavior (Lima and Dill 1990, Stankowich and Blumstein 2005). Since snails rely more on chemical than visual cues (Kosin 1964, Phillips 1978), large snails may not be able to detect that they are larger than their attacker, and so may behave suboptimally by fleeing. Though selection should favor large snails that cease responding to Leptasterias, strong selective pressure to flee from Leptasterias early in life could be carried over later in life with little cost (Yarnall 1964). Snails are probably not reacting to a general seastar cue, because they appear to distinguish *Leptasterias* cues from those of other predatory seastars, such as Pisaster ochraceus (Bullock 1953, Yarnall 1964, Chapter 3). Alternatively, evasive behavior by large snails may be advantageous because nonlethal attacks prevented snails from eating, mating and perhaps respiring and metabolizing normally from hours to 3.6 days in the laboratory (longest nonlethal attack duration). Regardless of the seemingly suboptimal responses by large snails, large snails seem to be less responsive to Leptasterias in natural conditions (Chapter 3), so some ontogenetic shifts in behavior are evident.

Evasive strategies by snails

The evasive responses by snails in the laboratory appeared to depend on the body size of snails and whether predator cues were tactile or waterborne. When touched by seastars, medium and large snails immediately fled in straight lines; but when exposed to waterborne cues they

meandered and fled more slowly. Waterborne cues may be diffuse, without clear directionality, and may have posed a less imminent threat than tactile cues that have a clear source posing an immediate threat. Meandering snails may have been casting across waterborne scent plumes to sense filaments of concentrated cues so they could avoid predatory seastars (Zimmer-Faust et al. 1995, DeBose and Nevitt 2008). Unlike medium and large snails, small snails meandered frequently when exposed to both tactile and waterborne cues, perhaps because they are less likely to "outrun" seastars. This switch from a straight, directed evasion to erratic zig-zagging or tacking is evident in diverse prey, especially when facing imminent attack, and it effectively increases the distance between the predator and prey (Humphrie and Driver 1967, Fitzgibbon 1990).

Scaling up to natural tidepool communities

I have shown that state-dependent prey behavior potentially alters TMII strength in short experiments, but further experiments are necessary to determine if individual variation in size and hunger level do indeed alter TMIIs in natural tidepools. Temporal mismatches are common challenges in experiments linking individuals to communities because decisions made by organisms occur nearly instantaneously while ecological outcomes may manifest on much longer time scales (Schmitz 2000). Further, some traits like hunger level are inherently fleeting so statedependent behaviors change on shorter time scales than ecological outcomes occur. To isolate the consequences of energetic state, experiments usually must statically manipulate energetic reserves or perform only short-term studies, whereas dynamic state variability is easier to incorporate in models (Clark 1994, Luttbeg et al. 2003, Abrams 2008). In this experiment, it was impossible to maintain uniformly sized or starved snails in the field for more than one low tide because snails easily left tidepools at high tide and grazed on naturally present algae. Further, the

brief experiments may overestimate TMII strength for two reasons. First, prey can temporarily abstain from feeding with little consequence. Second, by artificially supplying algae, I may inaccurately estimate TMIIs since algae in the field can regrow (Luttbeg et al. 2003, Okuyama and Bolker 2007). However, my prior research in this system suggested that *Leptasterias* caused *Chlorostoma* to reduce grazing and avoid tidepools for at least 10 months, thereby benefitting both microalgal and macroalgal growth over 1 and 8 months, respectively (Chapter 1). These longer-term TMIIs occurred without using cages, which may artificially concentrate chemical cues and induce unnatural behaviors, and algae grew naturally so the effects of snail grazing were much more realistic. Long-term TMIIs were also apparent in tidepools containing crabs, snails, and algae on the east coast of the USA (Trussell et al. 2004), further suggesting that the short-term observations here could result in long-term community effects.

Though prior studies demonstrated the potential for long-term TMIIs in this system, the uniformly sized or starved populations of snails used in the current experiment are unlikely to occur in natural tidepools. However, the average size or hunger level of snails can sometimes vary predictably in nature, which may then change TMII strengths as my experiments suggest. For example, average hunger level of snails may be higher and TMIIs may be weaker in the fall when algae senesce, during unproductive years with low upwelling, or at high shore levels where algae are sparse. Further, *Chlorostoma* size tends to decrease at higher shore levels (Paine 1969, Doering and Phillips 1983), and population size structure is skewed toward juveniles with decreasing latitude and wave exposure (Frank 1975, Fawcett 1984, Cooper and Shanks 2011). Where small snails are more common, TMII strength may decrease because they eat less algae; whereas DMII strength may increase because smaller snails are more vulnerable to predation. On the other hand, *Leptasterias* tends to occur lower in the intertidal zone than *Chlorostoma*, so both

TMIIs and DMIIs may be strongest at low shore levels. Regardless, the strength and relative importance of TMIIs and DMIIs should be a function of the density of *Leptasterias* and the density, size distribution and average energetic state of *Chlorostoma*, all of which may differ with shore level, sites, latitude, season, or year (Paine 1969, Frank 1975, Doering and Phillips 1983, Fawcett 1984, Cooper and Shanks 2011).

In conclusion, this study strengthens the connection between behavioral and community ecology paradigms by demonstrating that state-dependent foraging behavior by prey may alter TMII trophic cascades. The data support several theoretical models suggesting that prey body size and energetic reserves may alter the indirect cascading effects of predators on lower trophic levels (Schmitz 2000, Luttbeg et al. 2003, Persson and De Roos 2003, Ovadia and Schmitz 2004). I add to a small but growing body of experiments (Ovadia and Schmitz 2002, Kotler et al. 2004, Freeman 2006, Hawlena and Schmitz 2010, Rudolf 2012, Matassa and Trussell 2014) that aim to fulfill the well-recognized need to better link individual behavior to community processes (Schmitz et al. 2003, Schmitz et al. 2004, Beckerman et al. 2010, Ohgushi et al. 2012, Railsback and Harvey 2013). Further, I illustrate that including only consumptive effects (predation rates) and assuming all individuals are the same in trophic cascades may not always be sufficient to predict outcomes (Rudolf 2012). In my case, accurate estimates of trophic cascades require additional elements, including 1) the nonconsumptive effects of predators on prey foraging rates (as in all TMIIs), 2) variation in these nonconsumptive effects based on prey state (size and hunger), and 3) variation in the direct consumptive effects including size-dependent predation rate and size-dependent grazing rate. My insights resulted from conducting interdisciplinary experiments on the interplay between paradigms in two fields, foraging theory in behavioral ecology and TMIIs in community ecology, and this approach is likely to be a productive avenue

of further investigation.

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FIGURES



Figure 1. a) Diet of *Leptasterias* spp. surveyed throughout the intertidal zone in Horseshoe Cove, California (n = 21 seastars). b) Percentage of *Chlorostoma funebralis* in different size classes (3 mm increments) eaten by *Leptasterias* spp. when snails and seastars were paired in small tanks for 16 days in flowing seawater in the laboratory.



Figure 2. Mean (\pm SE) behavioral responses of small (<12 mm shell diameter), medium (12 - 18 mm), and large (>18 mm) *Chlorostoma funebralis* to no cues, waterborne cues, or tactile cues of the predatory seastar *Leptasterias* spp. in the laboratory. Responses include a) escape response of snails measured as size-corrected speed (mean speed of an individual / mean speed of snails in the individual's size class for all cue types) and b) meandering frequency (percentage of time points).



Figure 3. Mean (\pm SE) percentage of time that individual *Chlorostoma funebralis* spent out of water (left) or grazing (middle), and mean (\pm SE) algal cover remaining (right) after 60 minutes in laboratory tanks with and without individual *Leptasterias* spp. present. Top panels (a - c) compare snails of different sizes (small: <12 mm, medium: 12 - 18 mm, large: >18 mm shell diameter). Bottom panels (d - f) compare snails that were either fed or starved for 1 week in the laboratory before experiments.



Figure 4. Mean (\pm SE) percentage of *Chlorostoma funebralis* in refuge habitats (a - c) and grazing (d - e) with and without *Leptasterias* spp. present over 1 hour in rocky tidepools in Horseshoe Cove, California. Snails were grouped into size classes (small: <12 mm shell diameter, medium: 12 - 18 mm, large: > 18 mm). Densities of organisms were scaled to tidepool volume.



Figure 5. Mean (\pm SE) percent cover of microalgae remaining on tiles deployed in the presence or absence of *Leptasterias* spp. and *Chlorostoma funebralis* of different a) sizes after 1 hour or b) hunger levels after 45 minutes in rocky tidepools at Horseshoe Cove, California. Snails were grouped into size classes (small: <12 mm shell diameter, medium: 12 - 18 mm, large: > 18 mm). Densities of organisms and algae tiles were scaled to tidepool volume.



Figure 6. Mean (± SE) percentage of fed and hungry *Chlorostoma funebralis* in halos (a & b) and grazing (c & d) with and without *Leptasterias* spp. present over 45 minutes in rocky tidepools at Horseshoe Cove, California. Snails were either fed microalgae (a & c) or starved (b & d) for 1 week in the laboratory before experiments. Densities of organisms were scaled to tidepool

volume.

CHAPTER 3

Shifts in intertidal zonation of prey after mass mortalities of two predators

ABSTRACT

Recent mass mortalities of two predatory seastar species provided an unprecedented opportunity to test key concepts regarding the role of predation in structuring rocky shore communities, where many well-known concepts in ecology have been developed. I examined shifts in population size structure, vertical zonation, and use of emersed refuge habitats outside tidepools by the abundant herbivorous black turban snail Chlorostoma funebralis, both before and after the successive mortalities of two predatory seastars. The small cryptic predator Leptasterias spp. suffered a localized but extreme mortality event in November 2010, followed by mass mortalities of the keystone predator Pisaster ochraceus in August 2011 and fall 2013. After the local extinction of *Leptasterias*, the population size of *Chlorostoma* doubled and small and medium sized snails, which are preferred by Leptasterias, shifted from refuges in the upper intertidal zone and outside tidepools to the mid and lower intertidal zone and inside tidepools. After the mortality of *Pisaster* in August 2011, large snails did not shift lower in the intertidal zone despite being preferred by Pisaster. However, small and medium snails became denser in the high zone and outside tidepools, perhaps due to intensifying intraspecific competition. Previous studies concluded that vertical size gradients of snails were maintained by Pisaster predation, high energetic demands of large snails, and size-specific responses of snails to light and gravity, but the data implicate the overlooked predator *Leptasterias* as the primary cause. This natural experiment indicated that 1) predators exert top-down control over the population sizes and lower limits of their prey, 2) vertical zonation of prey are in dynamic equilibria controlled by both predation and nonconsumptive effects of predators on prey behavior, and 3) the nonconsumptive effects of predators are strongest for the most vulnerable individuals, which inhabit stressful habitats higher on the shore or outside tidepools to avoid predation. Long-term

monitoring is essential for capitalizing on rare mass mortality events, which provide powerful natural experiments to advance our understanding of community processes.

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 (Diamond 1983). 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). Careful long-term monitoring before and after mortality events is essential to capitalize on these rare opportunities. For example, monitoring coral reefs before and after hurricanes (Connell 1978) and mass mortality of an herbivorous sea urchin (Hughes 1994) transformed our understanding of community stability and of alternate stable states, respectively. Also, local extirpation of predators in lakes and tropical 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).

Recent natural mortality events of predatory seastars on the west coast of North America present a unique opportunity to investigate well-known concepts in ecology, including keystone predation, trophic cascades, competitive exclusion, and recruitment limitation (Connell 1961, Dayton 1971, Paine 1974, Menge and Sutherland 1987, Connolly et al. 2001). They also provide the opportunity to test the intertidal paradigm of vertical zonation positing that lower limits of species are controlled by biotic interactions while upper limits are controlled by abiotic stresses (Connell 1972, Robles and Desharnais 2002). It has become increasingly apparent that vertical distributions are actually in dynamic equilibrium determined by recruitment and mortality, rather than zones being permanent spatial refuges from competition and 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 the 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). 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 2) survival and growth of prey released from predation, and 3) development of intraspecific competition at high prey densities. Nonconsumptive effects of predators commonly increase refuge use (Lima 1998), which in intertidal communities may include physiologically stressful high zones and emersed rock outside tidepools at low tide or less physiologically stressful crevices (Feder 1963, Menge and Lubchenco 1981, Rochette and Dill 2000). Intraspecific competitive interactions may also intensify as densities of prey increase (Branch 1975, Bertness 1989), resulting in shifts to less-preferred habitats higher on the shore or outside tidepools by competitively inferior individuals (Houston and McNamara 1988, Alfaro and Carpenter 1999).

Mass mortalities of predators may also allow unprecedented insight into processes responsible for variation in prey size among intertidal zones, which I refer to as "vertical size distributions" (e.g. Seed 1969, Vermeij 1972, McQuaid et al. 2000). For mobile 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 high 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 risk higher predation for increased energetic gain low on shore (Paine 1969, Vermeij 1972). Thus, mass mortalities of predators provide an opportunity to determine the effect of predators in structuring vertical size distributions of prey.

In model rocky intertidal communities on the west coast of North America, larger individuals of the abundant herbivorous gastropod, *Chlorostoma* (formerly *Tegula*) *funebralis* generally occur lower on the shore than smaller ones (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* (Wara and Wright 1964, Paine 1969, Markowitz 1980). However, *Pisaster* is most abundant low on the shore and preferentially consume large snails in the field and laboratory (Markowitz 1980), which would result in the opposite pattern. Hence, it was also proposed that large reproductive snails venture low on the shore to forage on abundant food to 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 seastar, *Leptasterias* spp. (see Flowers and Foltz 2001 for species complex) co-occurs with *Chlorostoma* in low to mid intertidal zones along the West Coast (Morris et al. 1980). *Leptasterias* consumes *Chlorostoma* in the field and nearly exclusively preys on small and medium individuals (< 18 mm) in the field and laboratory (Bartl 1980, Chapter 2). *Leptasterias*

may eat small snails lower on shore or cause small snails to flee to the high intertidal zone (Bullock 1953, Yarnall 1964), resulting in the typical size distribution of *Chlorostoma* populations (Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983, Fawcett 1984).

I 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. 1). The two Pisaster mortality events were caused by a harmful algal bloom and seastar wasting disease, respectively (Rogers-Bennett et al. 2012, Hewson et al. 2014, Jurgens et al. in press), and I describe the extent and possible causes of the 2010 Leptasterias mortality below. In spring 2010, before any mortality events, I examined whether the presence of Leptasterias in 21 tidepools altered Chlorostoma's use of refuge habitats just outside tidepools. I expected that Leptasterias would increase refuge use by preferred small snails (Chapter 2), so I surveyed the abundance and size of snails in tidepools and refuges. After the Leptasterias mortality event in November 2010, I expected that all snails would descend in the intertidal zone and increase use of tidepools, since all sizes of snails responded to Leptasterias in short-term laboratory and field experiments (Chapter 2). I also expected that survival of smaller snails would increase since Leptasterias predation pressure had abated. To examine these hypotheses, I surveyed 44 tidepools (including the original 21) spanning the vertical range of *Chlorostoma* and measured snail sizes and abundances in tidepools and emersed refuges. When the *Pisaster* mortalities occurred in August 2011 and November 2013, I expected that snails would descend on the shore and increasingly inhabit tidepools, and preferred large snails would most strongly affected (Markowitz 1980). Thus, I resurveyed 30 tidepools in spring 2014. I also explored the possibility of intensifying intraspecific competition and habitat partitioning among different sizes of snails.

Thus, this natural experiment enabled us to investigate the potential top-down effects of two predators on prey population size, vertical size distributions of prey, and prey refuge use at two spatial scales: upper intertidal zone and refuges just outside tidepools.

METHODS

Seastar mortality events. Long-term experiments at two study sites enabled us to document mortality events of *Leptasterias* and *Pisaster*. I tracked trends in *Leptasterias* and *Chlorostoma* populations as part of a manipulative experiment on trait-mediated indirect effects of *Leptasterias* on tidepool algal communities (Chapter 1). I estimated *Leptasterias* population size (Fig. 1) by counting and removing them in 8 small mid to high intertidal tidepools (~1.3 m² total surface area) approximately weekly from July 24, 2009 to December 21, 2011 on the north side of Horseshoe Cove, Bodega Head, California (38°18'59.4"N, 123° 4'16.3"W). I tracked *Pisaster* population size (Fig. 1) as part of a separate study where I counted and removed *Pisaster* from 12 mid intertidal boulders approximately every two weeks from October 29, 2009 to October 15, 2014 at Schoolhouse Beach, which is 6.4 km north of Horseshoe Cove (38°22'28.4"N, 123° 4'44.9"W). The mortality events affected this *Pisaster* population similarly to the population in Horseshoe Cove. Though these removal experiments do not precisely quantify population density, I was able to track changes in population size (Fig 1).

Shortly after the mass mortality of *Leptasterias*, I searched nearby locations to establish its extent. I searched the south and north shores of Horseshoe Cove (~170 m apart) for remaining seastars in the low zone for 30 - 90 minutes each on December 29, 2010 and January 15, February 15, February 28, May 4, and June 2, 2011. I found only a single unhealthy seastar missing an arm on May 4, 2011, and a single healthy seastar on June 2, 2011. On June 7, 2011 I also searched the mid to low zone ~100 m alongshore to the south of the Bodega Harbor jetty (38°18'14.0"N, 123° 3'12.2"W), and on June 8, 2011 I searched ~200 m alongshore just north of Windmill Cove, Bodega Head (38°17'55.4"N, 123° 3'31.9"W) and found only 2 survivors. I am confident that many more *Leptasterias* would have been located if present, since I searched in

their preferred habitat (crevices, cobble and coralline algae) where I had easily located them in the past. I also noted a decrease in *Leptasterias* while searching for *Pisaster* at Schoolhouse Beach, indicating *Leptasterias* may have died there too. *Leptasterias* were abundant (~15 seastars per person per hour) 17 km north of Horseshoe Cove at Twin Coves near Jenner, California (38°27'28.8"N, 123° 8'42.9"W) on May 13, 2011 and June 15, 2011. Though I did not sample this location before the mortality event, the mortality event did not appear to extend there.

To investigate the cause of the *Leptasterias* mortality event, I queried the Bodega Ocean Observing Node (BOON) database (http://bml.ucdavis.edu/boon) for average hourly conditions from September 1, 2010 to Jan 31, 2011. Rainfall was measured ~100 m from the tidepools. Seawater temperature, salinity, and fluorescence were recorded ~60 m from the tidepools at ~4 m depth. pH was recorded hourly ~1 km offshore using a submersible autonomous moored instrument (SAMI, Sunburst Sensors) from November 19, 2010 to January 11, 2011. To investigate abundances of potentially harmful phytoplankton species, I obtained data from water samples taken monthly during 2010 at the US Coastguard Station just inside Bodega Harbor (38°18'46.0"N, 123° 3'5.7"W) by the California Department of Public Health Marine Biotoxin Monitoring Program.

Shifts in prey population after predator mortalities. I determined if the mortality of either seastar species may have affected *Chlorostoma* population size by surveying the population size structure, vertical zonation, and refuge habitat use of *Chlorostoma* in 21, 44 and 30 tidepools on April 10, 2010, May 18 to 27, 2011 and April 10 to 19, 2014, respectively. Refuge habitats were termed "halos" and included a 15 cm band of emersed rock surrounding each tidepool where seastars do not often forage at low tide (Menge and Menge 1974). Twenty-one of the tidepools

were surveyed each year to compare changes in population size. I restricted surveys to tidepools and halos because this was part of a broader study that focused on the effect of seastars on microhabitat choice by snails (Chapter 1). Each survey was conducted in spring to control for seasonal differences in seastar and snail distributions and behaviors (Paine 1969, Menge 1972, Markowitz 1980).

In 2010, I determined snail responses to the presence (n = 11) and absence (n = 10) of *Leptasterias* in tidepools; seastars were absent from tidepools during 2011 and 2014. To test for size-dependent responses by snails, I measured snails from tidepools and halos in 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, Chapter 2). The percentage of snails in the halo [(snails in the halo/snails in tidepool and halo) x 100] was used to estimate refuge use. Snails were considered to be in the halo if they broke the water's surface.

I chose tidepools over a large vertical area that encompassed the *Chlorostoma* zone, and used surveying equipment and USGS benchmarks to measure the shore level of each tidepool surface (range: 0.95 - 2.23m above mean lower low water, MLLW). I categorized tidepools into low, mid, and high shore levels for statistical analysis (0.7 - 1.15, 1.15 - 1.5, and 1.5 - 2.3m above MLLW and n = 10, 16 and 18, respectively). These categories do not match classic definitions of low, mid and high zones, but rather characterize the distribution of *Chlorostoma*. To compare snail abundance among different sizes of tidepools, I estimated snail density per liter by quantifying water pumped from tidepools into buckets (range: 1.2 - 85.0L).

To detect evidence of intensifying intraspecific competition and among intertidal zones, I tested whether snail size and snail density were negatively correlated. Since spatial partitioning

can alternately indicate strong competition or a lack of it (Schoener 1982), negative correlations do not necessarily indicate intraspecific competition. However, vertical spatial partitioning among size classes or species is suggestive of competition in other intertidal organisms (Connell 1961, Branch 1975, Branch 1981, Alfaro and Carpenter 1999), so my comparisons served as an exploration of possible habitat partitioning by snails of different sizes. Negative correlations may also indicate recent high recruitment, and comparing the slope of the correlations among shore levels over time may indicate where and when recruitment or intraspecific competition occurred.

Statistical analyses. All data were analyzed by analysis of variance (ANOVA) or restricted estimated maximum likelihood (REML) mixed models using JMP software. Data were either log₁₀ or arcsine square root transformed before analysis when necessary to meet model assumptions. For the percentage of snails in halos, size classes containing <3 snails in a tidepool were dropped from analyses to avoid allowing a small number of snails to obscure more meaningful results. Using only the 2010 survey, I tested the main and interactive effects of *Leptasterias* in tidepools and snail size on the percentage of snails in halos, with the identity of tidepools (nested within *Leptasterias* presence) included as a random effect to control for nonindependence of snails in separate size classes within the same tidepool.

For graphical presentation of changes in snail population size structure, I displayed the total number of snails (combined for halos and tidepools) in only the 21 tidepools that were consistently surveyed every year. To test for changes in snail population size structure and vertical zonation, I analyzed the main and interactive effects of survey (2010, 2011, 2014), snail size class (3-mm increments) and shore level (low, mid, and high) on the total density of snails in each size class in all tidepools. Again, tidepool identity (nested within shore level and survey) was included as a random factor to control for non-independence of snails in separate size

classes within the same tidepool. Because my goal was to assess the population-wide responses to seastar mortality events, I did not include the presence of *Leptasterias* in tidepools as a factor (2010 data only), and I combined counts of snails in the halo and the tidepool habitats.

I explored whether the changes in vertical distribution of *Chlorostoma* were due to differences in behavior or population growth using chi-squared analyses. I first conducted two chi-squared tests to determine whether the number of snails among size classes and shore levels changed more than expected in 2010 than 2011 and 2011 than 2014, having already considered observed population sizes increases in each size class. I then conducted individual chi-squared posthoc pairwise tests on changes among years within each size class and shore level to determine the size of snails exhibiting the strongest behavioral changes. I used a Bonferroni correction with a p-value threshold at p = 0.0011 to control for Type I error (0.05/40 pairwise comparisons). Since chi-squared tests can only be performed on count data, I only used the 21 tidepools that were surveyed all 3 years.

I compared shifts in refuge use by snails by analyzing the main and interactive effects of survey, shore level and size class on the percentage of snails in the halo for each size class. Tidepool identity (nested within shore level and survey) was included as a random factor to control for non-independence of snails in separate size classes within the same tidepool. Again, I did not I did not include the presence of *Leptasterias* in tidepools as a factor (2010 data only), because my goal was to assess the population-wide responses in habitat use after seastar mortality events.

RESULTS

Seastar mortality events. Leptasterias were nearly eradicated between November 8 and December 3, 2010 (Fig. 1) and did not recover over 4 years later. Large rain events occurred in late November 2010, but decreases in salinity were not apparent 4 m deep in Horseshoe Cove (Fig. 2a). Unusually low pH also was not evident from November 19, 2010 to January 11, 2011 (data not shown). An algal bloom occurred from November 20 to 24, 2010 (Fig. 2b), spanning the *Leptasterias* mortality event (Fig. 1). Fluorescence was not particularly high, peaking at 47.0 μ g L⁻¹ (peak not shown in hourly averages). Though overall densities of phytoplankton were not high, the harmful algal species, *Gonyaulux spinifera* was the most abundant species (36%) on November 18, 2010, 2 days before the bloom developed.

A sharp decrease in the population size of *Pisaster* occurred between August 17, 2011 and August 31, 2011 (Fig. 1), which coincided with a harmful algal bloom in the last days of August 2011 (Rogers-Bennett et al. 2012, Jurgens et al. in press). *Pisaster* briefly recovered at Schoolhouse Beach in the summer of 2013, but the population crashed again between August 21 and November 19, 2013 (Fig. 1). Many seastars looked shriveled on July 25, 2013, and by September 21, 2013, they were observed with white lesions, missing arms, and "melting", consistent with seastar wasting disease (Hewson et al. 2014). These symptoms continued into the summer of 2014, and *Pisaster* continues to be much less abundant than before the mortality events.

Predator avoidance. When *Leptasterias* was present in tidepools (2010 survey only), vulnerable small *Chlorostoma* were more common in halo refuges, whereas this was not the case

for large snails (Fig. 3; *Leptasterias* presence x Size: $F_{6,54} = 2.77$, p = 0.019). When *Leptasterias* was absent, the distribution of size classes was similar in tidepools and halos.

Population size structure before and after predator mortalities. The number of snails more than doubled (factor of 2.19) in 2011 after the *Leptasterias* mortality event (Fig. 4). After the *Pisaster* mortality events in 2014, the population again increased by a factor of 1.52. The increase in 2011 was driven primarily by small snails in the 6 - 9 mm size class (401% average increase; Fig. 4; Year: $F_{2,554} = 8.90$, p <0.001; Year x Size: $F_{12,554} = 7.82$, p <0.001), although all other size classes also increased (65, 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, 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).

Vertical distribution before and after predator mortalities. Snails shifted vertically after the seastar mortalities, but these responses depended on snail size (Fig. 5: Year x Shore level x Size class: $F_{24,554} = 1.60$, p = 0.037). Small and medium snails were denser in the highest zone in 2010, but shifted lower in 2011 after the *Leptasterias* mortality event: small snails became denser in the mid and low than the high zone, and medium snails became more evenly distributed (Fig. 5). More small and medium snails (<15 mm) occurred in the mid zone than expected based on population size changes, but fewer than expected small snails (6 - 12 mm) occurred in the high zone (X² = 1110.3, df = 20, p <0.001), indicating that snails most vulnerable to *Leptasterias* shifted to the mid zone when *Leptasterias* was absent. Fewer than expected snails of nearly all sizes (<18 mm) occurred in the low zone in 2011, indicating more snails may have moved to the mid rather than low zone. After the *Pisaster* mortality events, small and medium

snails in 2014 remained dense in the low and mid zones, but they increased in the high zone (Fig. 5). Further, fewer than expected snails mall occurred in the mid zone (6 - 9 mm) and more than expected small snails occurred in both the high (9 - 12 mm) and low zones (6 - 9 mm) (X^2 = 436.8, df = 20, p <0.0001). Again, fewer snails than expected of most sizes (9 - 18 mm) occurred in the low zone during in 2014, indicating most snails still did not move to the lowest limit despite the low densities of both seastars. Surprisingly, large snails were never denser in the low than mid and high 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 use was highest in 2010 before any seastar mortalities, lowest in 2011 after *Leptasterias* mortality, and intermediate in 2014 when both *Pisaster* and *Leptasterias* densities were low (Fig. 6a; Year: $F_{2,345} = 27.13$, p < 0.001). Small and medium snails drove these trends; halo use decreased with snail size in 2010, but snails <15 mm shifted into tidepools in 2011, resulting in low halo use among all sizes of snails (Fig. 6a; Year x 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 low on the shore in 2010 when *Leptasterias* was abundant, but halo use was low at all shore levels in 2011 after *Leptasterias* mortality (Fig. 6b; Year x Shore level: $F_{4,345} = 2.41$, p = 0.057). More snails occurred in the halos in the low and mid zones in 2014 than 2011, whereas snails in the high zone tended to inhabit tidepools during all years. All sizes of snails showed theses trends (Fig. 6b; Year x Shore level x Size class: $F_{24,345} = 0.82$, p = 0.705).

Intraspecific competition before and after predator mortalities. Negative relationships

between snail densities and sizes may indicate habitat partitioning by different sizes of snails under intensifying intraspecific competition. Snail size (avg. size in mm) and density (total snails L^{-1}) were not correlated in 2010 before seastars died (Fig. 7a). However in 2011, snail size and density were negatively correlated at the low and mid shore levels (Fig. 7b; low: $F_{1,58} = 8.69$, p =0.004, $R^2 = 0.13$, density = 7.51 - 0.32*size; mid: $F_{1,88} = 23.01$, p < 0.001, $R^2 = 0.21$, density = 7.83 - 0.34*size). In 2014, negative correlations occurred at all 3 shore levels, and the slopes for all 3 became steeper than in 2011 (Fig. 7c; low: $F_{1,52} = 8.50$, p = 0.005, $R^2 = 0.14$, density = 9.75 - 0.45* size; mid: $F_{1,64} = 21.43$, p < 0.001, $R^2 = 0.25$, density = 11.85 - 0.51* size; high: $F_{1,58} =$ 9.93, p = 0.003, $R^2 = 0.15$, density = 11.35 - 0.42* size).

DISCUSSION

Predation and the intertidal paradigm of vertical zonation

The combination of long-term monitoring and mass mortalities provided strong evidence of the biotic control of intertidal species distributions and serves as a natural demonstration of the intertidal paradigm of vertical zonation (Connell 1972, Robles and Desharnais 2002). Longterm 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 predator chemical cues (which can strongly affect prey behavior, Lima 1998) and keep predator densities low for many years, allowing more detailed exploration of predator effects. I provided evidence of long-term and nonconsumptive effects of predators on prey populations and resulting changes in population size structure, vertical distributions, and behavior of prey. Further, I suggest that intraspecific competition may intensify in the absence of predators and force competitively inferior smaller individuals into suboptimal habitats higher on shore and outside tidepools. These changes occurred fairly rapidly, demonstrating the dynamic nature of vertical zonation of mobile intertidal species (Robles and Desharnais 2002, Robles et al. 2009).

Similar to other natural experiments that have uncovered previously unrecognized ecological interactions (Zaret and Paine 1973, Connell 1978, Hughes 1994, Terborgh et al. 2001), this study suggests biotic control of *Chlorostoma* populations by an often-disregarded seastar predator, *Leptasterias* spp., but not by the keystone predator, *Pisaster ochraceus*. The vertical shift of smaller snails from high to mid shore after *Leptasterias* died also supports Vermeij's (1972) generalization that predation pressure causes small species to flee from low and mid intertidal zones to the high zone. 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 *Chlorostoma* populations over the long term. After *Leptasterias* died, the population size of snails doubled, primarily due to a 400% increase in small snails (6 - 9 mm) less than 2 years old (Paine 1969). Small and medium *Chlorostoma* are very vulnerable to *Leptasterias* predation (Chapter 2) and *Chlorostoma* comprise between 14 and 24% of *Leptasterias* diets in their zone of overlap at this site (Bartl 1980, Chapter 2), suggesting that *Leptasterias* is capable of limiting juvenile survival. Though *Pisaster* were formerly implicated, *Leptasterias* predation may also play a major role in the ~60% decrease in *Chlorostoma* during peak seastar activity from early spring to late 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 sporadic high *Chlorostoma* recruitment. A lack of control for other factors, such as recruitment, is a common shortcoming of natural experiments, but multiple lines of evidence suggest that high recruitment was not the sole cause of this increase in juvenile abundance. First, the population size structure shows consistently high abundance of new recruits for 3 years (2011-2014), indicating that recruitment may not be sporadic at this site. Further, the population size structure both before and after mortalities was not multimodal, as is common for species with sporadic recruitment (Menge et al. 2004), though the long life span of *Chlorostoma* (Paine 1969) could diminish the sharpness of recruitment peaks. In addition, the population size structure of *Chlorostoma* between southern Oregon and Baja California, Mexico is consistently

skewed toward juveniles (Frank 1975, Fawcett 1984, Cooper and Shanks 2011), and reproduction and recruitment in these populations is higher year-round than in northern Oregon and Washington (Frank 1975, Cooper 2010). The short pelagic duration (5-7 days) of Chlorostoma larvae (Moran 1997) likely also diminishes sporadic recruitment. Further, it is doubtful that this surge in juvenile abundance was due to juvenile snails shifting from emersed rock habitats to tidepools, since densities of snails less than 12 mm were very low in 2010 before any mortality events, and I rarely saw small snails outside tidepools or crevices unless Leptasterias was nearby. Overall, the surge in juvenile abundance for three years paired with the apparent lack of sporadic recruitment by Chlorostoma in other studies suggest that Leptasterias had consistently been reducing survival of juvenile *Chlorostoma* for many years, as do many other predators exerting top-down control of prey populations by consuming juveniles (Hunt and Scheibling 1997). Small increases in all the other size classes after *Leptasterias* mortality also suggest that *Leptasterias* may directly (through predation on snails <18 mm) or indirectly (through nonconsumptive effects on behavior of all snails) limit the abundance and growth of all sizes of snails.

After *Pisaster* died, survival of juveniles and growth and survival of all snails continued to be high. Growth curves of *Chlorostoma* (Paine 1969) indicated that the 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. However, this was likely primarily due to continued low predation by *Leptasterias*, which prefers small and medium snails (Chapter 2). Though *Pisaster* prefers larger snails, the lack of increase in density of large snails in 2014 was expected since *Chlorostoma* are very slow growing and may not reach the preferred size of *Pisaster* (> 17 mm, Markowitz 1980) until around 12 years old (Paine 1969). I expect continued

high survival and growth of small and medium snails, because brooding *Leptasterias* is still absent and expected to return to the area slowly. I also 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). However, if sizeable recruitment of planktonic *Pisaster* larvae occurs, then fewer snails in this cohort will reach 17 mm.

Effects of predators on prey behavior and distributions

Rapid shifts (<5 months) by small and medium snails to the mid and low zones and tidepools after the *Leptasterias* mortality events indicate that zonation is in a dynamic and complex equilibrium (Robles and Desharnais 2002, Robles et al. 2009, Donahue et al. 2011), which is partially maintained by antipredator behavior of prey. Further, *Leptasterias* rather than *Pisaster* likely relegated small and medium *Chlorostoma* to the high zone and outside tidepools. Small and medium snails had apparently been trading-off inhabiting their preferred habitats lower on shore or in tidepools for reduced risk of predation by *Leptasterias*. This behavioral shift 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.

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), which contribute to generally higher growth rates and fecundity at lower shore levels and inside tidepools (Paine 1971, Underwood and McFadyen 1983, Pardo and Johnson 2005, Perez et al.

2009). Hence, these behavioral shifts likely increased survival and growth of juvenile snails and contributed to the observed increases in population size. Thus, *Leptasterias* mortality may have directly and indirectly increased survival of juvenile snails. Though I cannot separate the nonconsumptive from consumptive effects of *Leptasterias*, both may have been important since *Leptasterias* apparently both limited the abundance and altered the behavior of *Chlorostoma*. Therefore, vertical zonation of *Chlorostoma* may be set by recruitment and mortality and reinforced by behavior, like other mobile intertidal species (Vermeij 1972, Cushman 1989, Rochette and Dill 2000).

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 (Chapter 2). Hence, large snails may adjust their responses to *Leptasterias* depending on whether it is a short-term encounter or a sustained exposure to cues in the environment, but small snails may react to both types of exposure more strongly affecting their distributions. It is not known whether this ameliorated response to sustained cues by large snails is a learned or innate trait.

I expected large snails to respond to *Pisaster* mortality by descending on the shore and into tidepools, but clear responses were not evident. Similarly, large snails in 2010 were not as abundant in the low 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 in the low than high zone, suggesting this is their preferred habitat (Paine 1969). Perhaps these two trends are linked, and snails at my 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 rather than tidepools; so large snails in upper tidepools may be able to gain enough energy from algae in tidepools, negating the need to descend lower on the shore. Further analyses of gonad size of large snails would demonstrate whether those inhabiting high intertidal tidepools are food limited, and further surveys of vertical size gradients for snails on surrounding emersed rock would demonstrate whether the trend was unique to tidepools. Alternatively, the threat of predation may have been high for large snails in all years causing many to remain high on the shore, because 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*). Indeed, high combined densities of other octopi (*Octopus bimaculoides* and *O. bimaculatus*), crabs (*Cancer* spp.) and *Pisaster* in southern California have been shown to increase the abundance of large *Chlorostoma* in the high zone (Fawcett 1984).

Since small and medium snails are vulnerable to *Pisaster*, I expected them to occur even lower on the shore and more abundantly in tidepools after the *Pisaster* mortality event. Instead, their abundance increased in the high zone and halo refuges. Rather than being a direct response to the mortality of *Pisaster*, I propose that they may have shifted to less preferred habitats as the population size grew and intraspecific competition intensified. High densities of snails and negative correlations between snail size and density occurred in the low and mid zones after the *Leptasterias* mortality event, and they again occurred in all zones after the *Pisaster* mortality events, indicating that competition may have intensified in the low and mid zones before spreading to the high zone. This is consistent with the chi-squared analyses showing lower than expected small snails in the mid zone and higher than expected small snails in the low and high

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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 mid zone. It is also consistent with ideal free distribution theory, which states that individuals should sort themselves among habitats according to resource availability, with competitively inferior individuals moving to less preferred habitats when competition is intense (Fretwell and Lucas 1970, Fretwell 1972, Houston and McNamara 1988). Further, intraspecific competition for food may also contribute to vertical partitioning by size in other intertidal species (Alfaro and Carpenter 1999, Boaventura et al. 2003). While the correlations between snail size and density do not demonstrate intraspecific competition, they may indicate some habitat partitioning among different sized snails, similar to vertical niche partitioning among closely related intertidal species (Connell 1961, Branch 1981). These correlations are intended to serve as a first step in exploring the possible contribution of competition to the observed shifts.

Snail densities in tidepools during 2014 were higher (1902 m⁻²) than observed on emersed rock at northern sites (<600 m⁻²), where energetic demands apparently caused large snails to descend to the low zone (Paine 1969). Competition may have been high even though food may have been more available in the tidepools than on emersed rock and the density estimate was inflated because it was standardized by the smaller surface area of water rather than rock in tidepools. On the other hand, negative correlations may also have been simple byproducts of high recruitment of the smallest snails after the seastar mortality events. Though *Chlorostoma* are thought to primarily recruit to the high zone (Paine 1969), they may have recruited or moved to low and mid zones in 2011 and all zones in 2014, resulting in the observed negative correlations. Further studies on vertical zonation of recruitment and density-dependent

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movement and growth rates among shore levels are necessary to determine if intraspecific competition or recruitment were indeed responsible for this pattern.

Comparative effects of two predators on vertical size gradients

Most prior studies have attributed increased numbers of small *Chlorostoma* higher on shore to predation by *Pisaster* (Wara and Wright 1964, Paine 1969, Markowitz 1980). But Pisaster primarily occurs lower on the shore and prefers large snails, and therefore large snails would be expected to be more abundant higher on the shore in opposition to the typical pattern (Markowitz 1980). Paine (1969) suggested that smaller snails recruit to and remain in the mid to high intertidal to avoid predation by *Pisaster* until they are 12 - 14 mm diameter, whereupon they migrate to the mid and low intertidal where food is more abundant due to the energetic demands of gamete production at maturity. Subsequent experiments indicated that short-term behavioral responses by small and medium snails to *Pisaster* maintained the gradient (Markowitz 1980). Doering and Phillips (1983) elaborated that the vertical distributions of *Chlorostoma* are maintained proximally by ontogenetic shifts in response to and light and gravity and ultimately by Pisaster. Wave exposure may also affect population size structure among sites (Cooper and Shanks 2011) and some individuals may genetically prefer certain shore levels or tidepools (Frank 1975, Byers and Mitton 1981, Byers 1983), although it is not clear that either factor affects vertical size gradients. Though the effect of *Leptasterias* has not been previously investigated, high densities of predatory seastars, crabs and especially octopi, which all likely prefer larger snails, were associated with more large snails at high shore levels in southern California (Fawcett (1984). However, this does not explain why smaller snails occur higher on the shore in Northern California and the Pacific Northwest where seastars and crabs also are extremely common (Morris et al. 1980, Fawcett 1984, Menge et al. 2004). Juvenile Pisaster (or

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juvenile crabs and octopi) may contribute to the vertical size gradient, because they eat similar sizes of prey as *Leptasterias* and occur low on the shore, though *Leptasterias* eat more mobile gastropods than juvenile *Pisaster* do (Menge and Menge 1974). *Pisaster* recruitment is more frequent in the Pacific Northwest than in California (Menge et al. 2004), so juvenile *Pisaster* may contribute to the more consistently observed decrease in size with shore level at northern than southern latitudes.

While all of the above factors are likely important and may even override the effects of Leptasterias on snail distributions, the prevalence of small snails high on the shore can readily be explained by the preference of *Leptasterias* for small snails. Unlike all other predators investigated, Leptasterias preys on small and medium but not large Chlorostoma (<18 mm, Chapter 2) and is the only predator whose preferences match the typical vertical size gradient of snails. The shift lower on shore and into tidepools by small and medium snails in 2011 suggests that Leptasterias are responsible for the typical vertical size gradient of Chlorostoma (Wara and Wright 1964, Paine 1969, Markowitz 1980, Byers and Mitton 1981, Doering and Phillips 1983). Because this shift occurred in the presence of *Pisaster* and it did not intensify after *Pisaster* died, Pisaster is apparently less important than Leptasterias for determining the vertical size gradient of *Chlorostoma* at this site. The ranges of *Chlorostoma* and *Leptasterias* spp. overlap between Catalina Island, California and Vancouver Island, Canada (Morris et al. 1980, Foltz 1997, Carlton 2007), encompassing the geographic extent of most of the study sites mentioned above. The next step is to determine the generality of the effect of *Leptasterias* on the vertical size gradient of *Chlorostoma* by expanding investigations to include a larger geographic range, especially previously studied sites.

The oversight of *Leptasterias* as a strong interactor with *Chlorostoma* 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, many invertebrates like *Chlorostoma* primarily rely on olfactory chemical rather than visual cues (Kosin 1964, Phillips 1978), rendering detection of visually cryptic predators easier. The disparate behavioral responses by snails to the two predators also are consistent with laboratory experiments, which suggested that *Chlorostoma* is able to distinguish the chemical cues of the two seastar species rather than responding to a general chemical cue from seastars (Bullock 1953, Yarnall 1964).

Extent and possible causes of Leptasterias mortality

Leptasterias suffered nearly 100% mortality between November 8 and December 3, 2010 on Bodega Head and has yet to recover. Mortality may have been localized near Bodega Head, because *Leptasterias* was less affected 6.4 km to the north and unaffected 17 km north, though the southern extent is unknown. A moderate algal bloom occurred from November 20 to 24, 2010 with relatively high concentrations of the dinoflagellate *Gonyaulux spinifera* occurring 2 days prior. Since poisonous yesotoxin released by *G. spinifera* is strongly suspected as the cause of the second mortality event in August 2011 that killed *Leptasterias, Pisaster* and many other species (Rogers-Bennett et al. 2012, Jurgens et al. in press), it is possible that the 2010 mortality of *Leptasterias* was also caused by a smaller, weaker bloom of *G. spinifera*. Though I did not observe mortality of any other species, *Leptasterias* may be particularly susceptible to yesotoxin due to their small size. However, the 2010 bloom occurred in the late fall, after rain events and under normal water temperatures (~12°C), whereas the 2011 bloom occurred in summer during abnormally warm (~14°C), calm conditions (Rogers-Bennett et al. 2012, Jurgens et al. in press). Disease also could have been responsible since the mortality event was abrupt, fairly localized, and specific to *Leptasterias*. Though symptoms of seastar wasting disease were not detected, the disease could have progressed swiftly in this small seastar with bodies being hard to see. However, other species were not affected and *Leptasterias* appeared to be more resistant to the disease than *Pisaster* on the open coasts of Oregon during the outbreak in fall 2013 (Jenna Sullivan, *pers. comm.*). I detected no other anomalous seawater or weather conditions that could have caused the mortality event. Strong rain events in November 2010 did not form a freshwater lens deep enough to kill subtidal *Leptasterias*, though some intertidal *Leptasterias* could have been killed. Low pH and anoxia also were unlikely culprits since animals held in the flow-though seawater system at BML did not die.

In conclusion, my natural experiment on the consequences of successive mass mortality events of two predatory seastar species enabled us to test several key concepts in community ecology. I 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 were apparently eaten or escaped to stressful refuges higher on shore and outside tidepools. Strong responses after the *Leptasterias* mortality events, but not after the *Pisaster* mortality event, suggested that largely overlooked *Leptasterias* played a primary role in controlling juvenile survival, population size structure, vertical size gradient and microhabitat choices of *Chlorostoma*. In addition, intraspecific competition may have influenced vertical size gradients in the absence of predators when crowding may have forced smaller inferior competitors to suboptimal habitats. Finally, I documented a localized extinction of *Leptasterias* spp. on Bodega Head in November 2010, which may have been caused by a

harmful algal bloom of *Gonyaulux spinifera* or seastar wasting disease. This natural experiment strongly supports the results of many manipulative field experiments, and adds new insights on the long-term and nonconsumptive effects of predators on intertidal zonation.

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FIGURES



Figure 1. Number of *Leptasterias* spp. (black lines and solid circles) in 8 tidepools in Horseshoe Cove, California and number of *Pisaster ochraceus* (dashed lines and open circles) on 12 large intertidal boulders 6.4 km north at Schoolhouse Beach removed approximately weekly and biweekly, respectively. Three mass mortality events occurred (gray boxes): first of *Leptasterias* spp. in Nov. 2010, second and third of *Pisaster ochraceus* in late August 2011 and fall 2013, respectively. *Chlorostoma funebralis* were surveyed in \geq 21 tidepools in Horseshoe Cove in spring 2010, 2011, and 2014 (black arrows).



Fig. 2. Time series of seawater conditions and precipitation (a & b) on Bodega Head, California from September 2010 through January 2011 and common phytoplankton in water samples (c) taken by the California Department of Public Health in Bodega Harbor during 2010 (note different time scales) relative to mass mortalities of *Leptasterias* spp. on Bodega Head (November 8 to December 3, 2010, gray boxes). Panel a shows hourly cumulative rainfall (gray lines) and salinity (black lines). Panel b shows hourly seawater temperature (black lines) and chlorophyll-*a* fluorescence (gray lines), which approximates phytoplankton concentration. Panel c shows the percent composition of common harmful algal species relative to total phytoplankton plus detritus. Note increase of *Gonyaulux spinifera* (dashed line) just before an algal bloom (dashed box). Salinity was recorded at 4 m depth in Horseshoe Cove and temperature and, fluorescence were recorded 60 m offshore. Rainfall was measured adjacent to Horseshoe Cove.



Figure 3. Percentage (mean \pm SE) of total *Chlorostoma funebralis* inhabiting halo refuges around tidepools by size class (3 mm increments in shell diameter) relative to the presence (closed circles, n = 10 tidepools) and absence (open circles, n = 11 tidepools) of *Leptasterias* spp. within tidepools on April 10, 2010 before seastar mortality events in Horseshoe Cove, California.



Figure 4. Population size structure (3 mm increments in shell diameter) of *Chlorostoma funebralis* in 21 tidepools and halo refuges in April 2010 before seastar mortality events (circles), May 2011 after a *Leptasterias* spp. mortality event (squares) and April 2014 after 2 *Pisaster ochraceus* mortality events (triangles).



Figure 5. Densities of *Chlorostoma funebralis* (mean \pm SE) in tidepools and surrounding halo refuges) by snail size class (3 mm increments in shell diameter) and shore level in April 2010 before seastar mortality events (circles), in May 2011 after a *Leptasterias* spp. mortality event (squares), and in April 2014 after 2 *Pisaster ochraceus* mortality events (triangles). For 2010, 2011 and 2014, respectively: n = 7, 10, and 9 tidepools (a, low), n = 9, 16, and 11 tidepools (b, mid) and n = 5, 18, and 10 tidepools (c, high). Shore levels are 0.7 - 1.15 (low), 1.15 - 1.5 (mid), and 1.5 - 2.3 (high) m above MLLW.



Figure 6. Percentage (mean \pm SE) of *Chlorostoma funebralis* inhabiting halo refuges surrounding tidepools in April 2010 before seastar mortality events (circles), May 2011 after a *Leptasterias* spp. mortality event (squares), and April 2014 after 2 *Pisaster ochraceus* mortality events (triangles) by a) snail size classes and b) shore levels. For 2010, 2011 and 2014 respectively: n = 7, 10 and 9 tidepools (low), n = 9, 16 and 11 tidepools (mid), and n = 5, 18 and 10 tidepools (high). Shore levels are 0.7 - 1.15 (low), 1.15 - 1.5 (mid), and 1.5 - 2.3 (high) m above MLLW.



Figure 7. Correlations between snail sizes and densities among shore levels in a) April 2010 before seastar mortality events, b) May 2011 after a *Leptasterias* spp. mortality event, and c) April 2014 after 2 *Pisaster ochraceus* mortality events. Shore levels are 0.7 - 1.15 (low: circles and solid lines), 1.15 - 1.5 (mid: squares and short dashed lines), and 1.5 - 2.3 (high: triangles and long dashed lines) m above MLLW.