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Shifts in seawater chemistry disrupt trophic links within a simple shoreline food web

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Abstract

Marine intertidal systems have long served as focal environments for ecological research, yet these environments are changing due to the entry of human-produced carbon dioxide into seawater, which causes 'ocean acidification' (OA). One component of OA is a decline in seawater pH, an alteration known to disrupt organism behaviors underlying predator–prey interactions. To date, however, studies examining OA's effects on feeding relationships consider predominantly simple direct interactions between consumers and their food sources. Here, we extended these established approaches to test how decreased seawater pH might alter cascading effects that span tiered linkages in trophic networks. We employed a model shoreline food web incorporating a sea star predator (*Leptasterias hexactis*), an herbivorous snail prey (*Tegula funebralis*), and a common macroalgal resource for the prey (*Mazzaella flaccida*). Results demonstrate direct negative effects of low pH on anti-predator behavior of snails, but also weakened indirect interactions, driven by increased snail consumption of macroalgae even as sea stars ate more snails. This latter outcome arose because low pH induced 'foolhardy' behaviors in snails, whereby their flight responses were supplanted by other activities that allowed for foraging. These findings highlight the potential for human-induced changes in seawater chemistry to perturb prey behaviors and trophic dynamics with accompanying community-level consequences.

Keywords Carbon dioxide · Tidepool · Predator–prey interaction · Invertebrates · Behavior · Non-consumptive effects

Introduction

Predation operates as a key organizing process governing community structure. It influences the behavior and abundance of prey taxa and modulates species diversity and energy flow within food webs (Paine 1969; Lubchenco 1978; Ripple and Beschta 2004; Ritchie and Johnson 2009). In a subset of cases, predation and its effects are strong enough to propagate through prey species to affect trophic levels below. Indeed, many studies now document such top-down 'indirect effects' and how they manifest (e.g., Lima and Dill 1990; Schmitz et al. 2004; Haggerty et al. 2018). One class of indirect effect arises when predators remove intermediate consumers, which decreases feeding pressure on basal taxa (density-mediated indirect interactions, DMIIs). Another class derives from the tendency, when predators are present, for intermediate consumers to change their behavior, physiology, or morphology in ways that alter their foraging activities (trait-mediated indirect interactions, TMIIs). A classic example is a prey species that becomes sufficiently fearful of a predator that it feeds less on a basal resource. Both these density- and trait-mediated pathways are now believed to contribute with comparable strength to indirect effects of predation (Werner and Peacor 2003).

It is also well recognized that direct and indirect consequences of predation can vary strongly through time (Kimbro 2012; Wada et al. 2017), across space (Matassa and Trussell 2015), and as a function of various community attributes. For instance, the availability and identity of resources (Luttbeg et al. 2003; Werner and Peacor 2006),

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habitat complexity (Trussell et al. 2006; Grabowski et al. 2008), the physiological state and life-history stage of prey (Gravem and Morgan 2016), and the abundance, energetic condition, and foraging mode of predators (Bernot and Turner 2001; Preisser et al. 2007) can all affect outcomes. Physical factors play an additional, crucial role. In environments subjected to mechanical or thermal stress, rates of predation can decline due to differential vulnerabilities of predators to such stresses (Menge and Sutherland 1987; Voigt et al. 2003; O'Connor 2009). Ecologists are, moreover, increasingly aware of the capacity for abiotic factors (e.g., light levels, turbidity, intensities of fluid mixing, elevated background noise, freshwater pH, and pollutants) to modulate how predators and prey detect one another (Leduc et al. 2013; Weissburg et al. 2014; Saaristo et al. 2018). For example, chemical cues from predatory crabs are disrupted in high flow environments, which can reduce TMIIs as well as make crabs more vulnerable to predation. At the same time, rapid velocities may impede a prey's ability to forage; together these effects may shift the relative importance of TMIIs versus DMIIs (Pruett and Weissburg 2018). Understanding the consequences of abiotic factors for trophic interactions is, therefore, a vital component to discerning how contemporary properties of the environment and those expected for the future can and will influence communities.

In marine systems, animal sensing and species interactions—including cascading top-down indirect effects—have the potential to be affected by global-scale anthropogenic modifications to seawater chemistry (Leduc et al. 2013). Human-produced carbon dioxide that absorbs into the sea decreases its pH ('ocean acidification,' or OA; Caldeira and Wickett 2003; note that other alterations to the carbonate system of seawater accrue at the same time). Emerging data indicate that these changes can alter cue detection and information processing by a variety of marine species (Munday et al. 2010; Clements and Hunt 2015), much as it does in freshwater taxa (Turner and Chislock 2010; Leduc et al. 2013; Ou et al. 2015; Weiss et al. 2018). Reef sharks, for example, exhibit a reduced ability to track the chemical signatures of their prey under low-pH conditions (Pistevos et al. 2015). Similarly, shoreline snails display confused behavior under decreased seawater pH and fail to enter refuge in the presence of predators (Jellison et al. 2016). Although it remains unclear how common such effects might be across ocean taxa, there is obvious capacity for perturbed pH to influence a range of species interactions underlying the structure and function of marine communities (e.g., Fabricius et al. 2013; Gaylord et al. 2015; Connell et al. 2017; Goldenberg et al. 2017).

Importantly, although ongoing work is chronicling the detrimental effects of reduced ocean pH on predator–prey interactions (Ferrari et al. 2011), studies to date have focused primarily on simple direct interactions between consumers and their food sources (but see Alsterberg et al. 2013; Nagelkerken and Connell 2015; Goldenberg et al. 2017; Lord et al. 2017; Vizzini et al. 2017). In contrast, much less is known about the capacity for decreased pH to alter density- and trait-mediated indirect effects in biological communities, in particular, those that cascade vertically through more than two trophic levels.

In light of this information gap, we provide here a beginning examination of the effects of altered pH on a simple three-level, marine food web. The model system that we employ operates as one trophic module within a broader array of interactions characterizing rocky intertidal communities along northeastern Pacific shores. It focuses on a widespread sea star predator (the six-armed star, *Leptasterias hexactis)*, an herbivorous intermediate consumer (the black turban snail, *Tegula funebralis*), and a common shoreline macroalga (*Mazzaella flaccida*). These three species are abundant on hard-substrate sites within the California Current Eastern Boundary system, where they routinely experience seasonal upwelling that brings deeper waters to the surface that are naturally high in CO_2 and, thus, have lower pH than the open ocean (CO_2 and pH negatively co-vary in seawater at chemical equilibrium; Zeebe and Wolf-Gladrow 2001). As a consequence of such upwelling dynamics, pH in surface waters can decline to as low as 7.4 even today (Feely et al. 2016; Chan et al. 2017). By contrast, such low values of pH are not expected in most surface waters globally for decades. Low-pH conditions associated with upwelling can also be exacerbated within intertidal rock pools commonly inhabited by *Leptasterias*, *Tegula*, and *Mazzaella* during low tides that occur at night when respiratory CO_2 released by resident organisms accumulates, while the pools are isolated from the adjacent ocean. Records demonstrate that pH in such pools can drop to 7.1 and below (Jellison et al. 2016; Kwiatkowski et al. 2016; Silbiger and Sorte 2018). Moreover, during high-amplitude spring tides, the low-pH excursions may occur every night for 5 days or more. These patterns in carbonate chemistry suggest that predator–prey interactions occurring in rock pools within eastern boundary systems might already be operating under environmental conditions expected more broadly in future decades, and, thus, may provide useful insights into community-level consequences of ocean acidification.

Our selection of this model system is motivated further by the fact that, as with many tri-trophic food webs, the combined sea star, snail, and macroalgal interaction presages an innately unpredictable set of outcomes from altered seawater pH. It is nearly impossible to project a priori whether a shift in pH will result in a more positive or more negative indirect effect of predation. Although we have previously documented impairment under low pH of anti-predator responses in *Tegula* that could affect the survival and/or foraging behaviors of this snail (Jellison et al. 2016), these changes could actuate either of two scenarios of cascading impact. First, they could make prey more vulnerable to predation, decreasing the number of grazing snails. This result would strengthen density-mediated indirect effects of sea star predators on a macroalgal basal resource relative to TMIIs, as has been seen in other systems where environmental conditions affect indirect interactions (e.g., Wojdak and Luttbeg 2005; Pruett and Weissburg 2018). On the other hand, if snails become less responsive to predators under low pH, but do not experience an accompanying elevation in mortality (perhaps, the snails do not respond to the risk of predation by sea stars, are not killed by them, and continue to forage under risky conditions), macroalgal consumption might increase (attenuated TMII but unaltered DMII; see, e.g., Pangle et al. 2012). This second scenario embodies a weakening of the total positive indirect effect of predation. Our study explores the ambiguity of these opposing scenarios by employing a fully factorial mesocosm experiment involving different combinations of sea star predator, grazing snail prey, and macroalgal basal resource exposed to either ambient or reduced seawater pH.

Materials and methods

Study species

The six-armed sea star, *Leptasterias hexactis*, is a common predator in mid and low intertidal zones of rocky shores, often in tide pools, along the west coast of North America (but see Jurgens et al. 2015 for recent regional declines). It is a generalist carnivore and consumes several types of gastropods including the black turban snail, *Tegula funebralis* (Gravem and Morgan 2019). The latter is one of the most abundant and visible herbivores in the system and can be a prominent resident of tide pools (Nielsen 2001). *Mazzaella flaccida* is a red alga common to the mid and low intertidal zones of moderately exposed rocky shores and is a common food source for *Tegula* (Aquilino et al. 2012). During collection, *Tegula* and *Leptasterias* were acquired from mid-intertidal pools at Arena Cove in Point Arena, California, in June of 2015, and *Mazzaella* was acquired from mid-intertidal pools at Horseshoe Cove in Bodega Bay, California, in July of 2015. The sizes (mean ± se) of sea stars and snails were standardized (sea star arm length and central disk diameter = 9.3 ± 0.4 and 6.8 ± 0.2 mm; snail height and diameter = 4.4 ± 0.1 and 7.1 ± 0.1 mm, respectively). After collection, sea stars, snails, and macroalgae were placed in flow-through aquaria at Bodega Marine Laboratory (BML) for 3 weeks prior to experimentation, during which the sea stars were fed *Tegula* and snails *Mazzaella*, both ad libitum.

Experiment overview

Effects of seawater pH on indirect interactions among the sea stars, snails, and macroalgae were examined in two phases. First, *Leptasterias* and *Tegula* were acclimated to either control (i.e., ambient seawater) or reduced-pH seawater conditions. This initial phase was implemented because prior work has demonstrated that behavioral changes induced by OA manifest most strongly following several days of advance exposure to altered seawater chemistry (e.g., Watson et al. 2013). The *Mazzaella* were not pH acclimated at the start, because, although some macroalgae can increase growth under OA (e.g., Koch et al. 2013), our study targeted top-down rather than bottom-up processes. It will be important for future work to address the bottom-up effects of OA in the system. Once the acclimation phase was completed, then the study's second phase began, involving factorial mesocosm trials characterized by multiple combinations of predator, prey, and macroalgae under low pH or not. Further details regarding the protocol used for pH manipulation, the acclimation phase, and the mesocosms appear below.

pH manipulation

A simplified OA exposure regime was employed to hone in on the signature property of tidepools (their markedly low pH values) in dissecting consequences for top-down direct and indirect effects. Two static pH levels characterized the exposure regime: an ambient level consistent with contemporary conditions at BML (pH ~ 8.0 on the total scale; Table 1), and a low one corresponding to minima expected in future decades within tidepools (pH ~ 6.9, 0.1 units below what we have recorded in tidepools at our field site currently but likely to be encountered in coming decades; Jellison et al. 2016). We acknowledge that a more idealized experiment for a tidepool system might also incorporate diurnal fluctuations in pH, given that nighttime pH minima can be accompanied by pH increases during the day when photosynthesizers take up aqueous carbon. Such an experiment (i.e., one focused on features of environmental variation—but perhaps less on trophic dynamics) might also modulate pH excursions according to lunar periodicities of the tides and would do this for many weeks or months to allow for phenotypic changes that can be initiated by organisms over extended durations (e.g., Russell et al. 2011). However, an elaborate experimental design like the above is beyond the capability of most research facilities, including ours, and may not always be necessary. In prior work, we have shown that pH-induced behavioral changes in our prey species (*Tegula funebralis*) manifest almost identically in either static or diurnally varying pH conditions (Jellison et al. 2016). Nevertheless, it is clear that future research should

Table 1 Seawater parameters for each treatment level averaged over 5 days during the pH-acclimation phase of the experiment and for the 7-day mesocosm trials for both pre- and post-water change

Experimental phase	pH level	Treatment	Pre/post-water change	Salinity (ppt)	SE	DO (mg/L)	SE	Temp (ºC)	SE	pH (total)	SE	Alk (μmol/kgSW)	SE
pH acclimation	Ambient	Sea star	Pre	33.3	0.03	7.7	0.1	16.3	0.3	8.01	0.00	2225	3
			Post	33.1	0.03	7.8	0.1	16.3	0.3	7.96	0.02		
		Snail	Pre	33.2	0.02	6.5	0.2	15.3	0.2	7.89	0.02	2222	3
			Post	33.1	0.02	7.7	0.1	16.2	0.2	7.96	0.01		
	Low	Sea star	Pre	33.2	0.03	7.8	0.1	16.2	0.4	6.95	0.02	2227	11
			Post	33.0	0.02	7.8	0.2	16.4	0.3	6.92	0.01		
		Snail	Pre	33.2	0.02	6.7	0.2	15.3	0.2	6.91	0.01	2218	7
			Post	33.1	0.01	7.5	0.1	16.2	0.2	6.92	0.01		
Mesocosm	Ambient	Complete interaction	Pre	33.2	0.03	6.7	0.1	15.7	0.2	7.79	0.03	2252	4
			Post	33.2	0.02	6.9	0.2	15.5	0.3	7.85	0.03		
		Cue only	Pre	33.2	0.03	6.6	0.1	15.8	0.2	7.80	0.03	2249	5
			Post	33.2	0.02	6.9	0.2	15.5	0.3	7.85	0.03		
		No predator	Pre	33.3	0.05	6.6	0.1	15.9	0.2	7.79	0.02	2245	3
			Post	33.2	0.02	7.0	0.2	15.5	0.3	7.83	0.03		
		No grazing	Pre	33.2	0.03	6.7	0.1	15.8	0.2	7.78	0.03	2245	5
			Post	33.2	0.02	6.9	0.2	15.5	0.3	7.85	0.03		
	Low	Complete interaction	Pre	33.3	0.04	6.6	0.1	15.8	0.2	6.94	0.01	2249	4
			Post	33.1	0.01	7.1	0.2	15.6	0.2	6.94	0.01		
		Cue only	Pre	33.3	0.03	6.7	0.1	15.8	0.2	6.94	0.01	2253	5
			Post	33.1	0.02	7.1	0.2	15.6	0.2	6.94	0.01		
		No predator	Pre	33.3	0.05	6.7	0.1	15.8	0.2	6.93	0.01	2245	3
			Post	33.1	0.02	7.1	0.2	15.6	0.2	6.93	0.01		
		No grazing	Pre	33.3	0.04	6.6	0.1	15.8	0.2	6.93	0.01	2247	6
			Post	33.1	0.02	7.0	0.2	15.6	0.2	6.93	0.01		

SE standard error

more fully examine the implications of substantial fluctuations in carbonate system parameters that arise in tidepools.

Methods for manipulating seawater chemistry for the two pH exposure levels duplicated those of Jellison et al. (2016). The pH was modified using equimolar additions of sodium bicarbonate ($NaHCO_3$) and hydrochloric acid (HCl). This direct chemical modification of seawater increases dissolved inorganic carbon (DIC) without altering total alkalinity (TA), reproducing the same chemical changes that occur when bubbling CO_2 gas through seawater (Schulz et al. 2009; Riebesell et al. 2010). Before and after daily water changes of treatment containers, a YSI ProPlus sensor was used to measure in situ pH, temperature, salinity, and dissolved oxygen (calibrated in low-ionic-strength certified buffers), and pH values from this instrument were recalibrated daily to the total scale (Zeebe and Wolf-Gladrow 2001) by means of water samples from four treatment containers analyzed via a Sunburst SAMI spectrophotometer. This approach validated the pH manipulations and verified acceptably stable seawater chemistry between water changes (Table 1), as facilitated by the large container volumes (13 L) and their lids that minimized air–water gas exchange. Bottle samples were also collected from each container after water changes for analysis of total alkalinity via Gran titration (Riebesell et al. 2010) standardized using certified reference material (A. Dickson, Scripps Institution of Oceanography).

Pre-trial pH acclimation

The two pH exposure levels were implemented first to acclimate sea stars and snails to ambient or reduced-pH seawater for 5 days. The most extreme pH minima in rock pools occur during the highest amplitude spring tides, and such tides span 5–7 days locally. Each species was separated from the others, and individuals were partitioned among multiple 13-L containers (2 species × 15 replicates × 2 pH = 60 containers) held within a seawater table that maintained temperatures at ambient conditions (Table 1). Containers either held four snails or one sea star (60 total snails and 15 total sea stars). During this time, water changes were conducted daily, and animals were not fed to ensure that they were hungry for subsequent trials of trophic interactions.

Mesocosm trials

To investigate the central question of how pH influences trophic links, the sea stars, snails, and macroalgae were next placed for 7 days in mesocosms containing seawater adjusted to the same pH levels as during acclimation. The water in each container was changed daily as before. The mesocosm array consisted of 40, 13-L circular plastic containers with a mesh barrier down the center to separate predator, prey, and/or basal resource but allowing for passage of waterborne cue. Mesocosms were filled halfway with seawater, allowing 10 cm of refuge space for snails above the waterline. Mesocosms were held within a seawater table under constant flow to maintain consistent temperatures (Table 1).

Trophic treatments

Each mesocosm was assigned to one of four trophic treatments and one of two pH levels, resulting in five replicates per treatment and pH (4 trophic × 2 pH × 5 replicates = 40 mesocosms). The first trophic treatment was a "no-predator" configuration, composed of four snails and four 3-cm-diameter circular pieces of *Mazzaella* macroalgae cut out of blades (four pieces = 0.33 g ± 0.03 in total, with each piece standardized to have similar initial mass), both placed on one side of the central barrier of the mesocosm (Fig. 1a). This treatment was used to quantify the net loss of macroalgal mass in the presence of grazing. The second trophic treatment was a "cue only" treatment in which one sea star was housed on one side of the barrier with four snails and macroalgae on the other side (Fig. 1b). This treatment was used to assay changes in snail foraging in the presence of predator cue, and, thus, provided a mechanism for quantifying trait-mediated indirect interactions. The third was a "complete interaction" treatment in which one sea star, four snails, and macroalgae were all located on the same side of the barrier (Fig. 1c). This third treatment allowed for the operation of the full suite of interactions, and the manifestation of both density-mediated and trait-mediated indirect effects. The final trophic treatment was a "no prey/no grazing" configuration, for which one sea star was placed on one side of the barrier with the macroalgae on the other (Fig. 1d). It was used primarily as a control for predator behavior in the absence of prey, and also provided a control for any changes in macroalgal mass that might occur without grazing, due, for example, to growth or senescence.

Behavioral assays

During the 7-day mesocosm trials, sea star and snail behavior were quantified using image analysis of photographs of animal position recorded every 2 min for 16 min daily (see, e.g., Jellison et al. 2016), starting immediately after the organisms were placed into the mesocosms. Pilot experiments indicated that 16-min recording sessions were adequate to characterize the positional behaviors. The behaviors were also stable through time and were, therefore, quantified only over the first 4 days of the experiment, following each water change (in contrast, measurements of macroalgal consumption—a slower process—were made after 7 days). For the purposes of this experiment, slightly different behaviors were evaluated for the snails and sea stars. Black turban snails normally flee the water upon detection of cue from

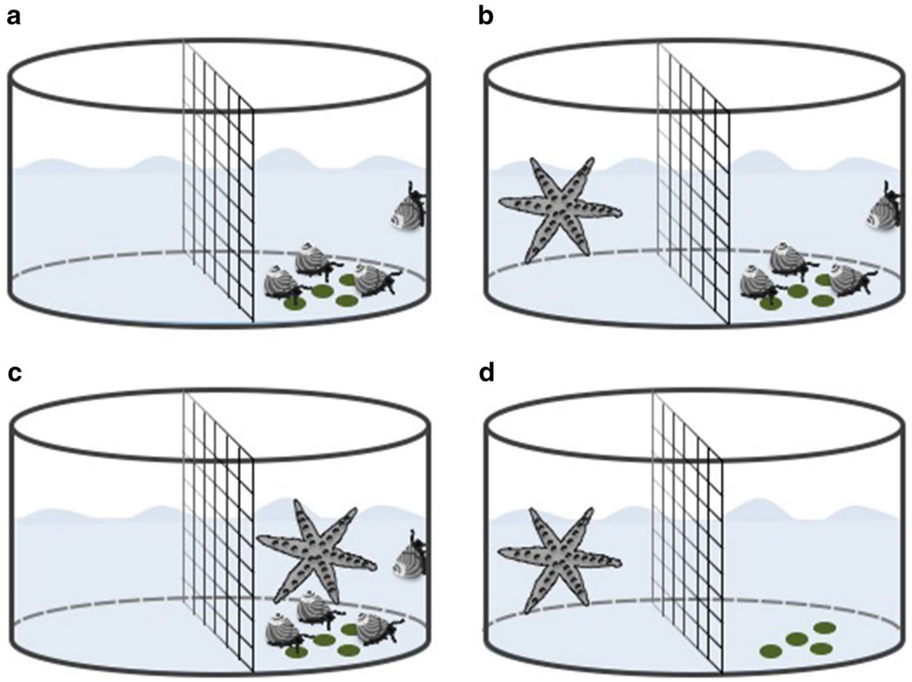

Fig. 1 Conceptual representation of mesocosm species combinations. **a** "No predator", **b** "cue only", **c** "complete interaction," and **d** "no prey/no grazing," each implemented with either low or ambient pH seawater ($n = 5$ mesocosm containers per species combination and pH)

sea stars, so a key metric of snail refuge-seeking behavior is the proportion of time out of the water (Jellison et al. 2016). This quantity was calculated as the fraction of images for which a given snail was above the waterline. In the case of sea stars, their capacity and/or propensity to forage was evaluated through their tendency to move and the distance that they traveled during the assessment period.

Evaluation of prey survival

The effect of pH on the strength of direct trophic effects was estimated from measurements of sea star consumption of snails in the complete interaction treatment across pH levels. The number of snails eaten was determined by visually assessing containers to determine if sea stars were actively eating a snail and then removing and counting the number of consumed snails (empty shells) in the complete interaction containers at the end of each day. Consumed snails were not replaced, as was necessary for determining DMII strength, and snail numbers never dropped below two snails per container (Online Resource 1: Fig. S5).

Indirect effects

Consequences of pH for the strength of net top-down indirect effects were estimated from relative reductions in mass of macroalgae in the no-predator treatment, the cue-only treatment, and the complete interaction treatment across pH levels. Wet weight of disks excised from *Mazzaella* blades was measured before and after the 7 days to assess macroalgal mass loss. First-order estimates of macroalgal consumption were calculated as the difference in macroalgal mass loss between each container of a trophic treatment and the group mean from the no-grazing treatment for each pH level.

The effect sizes for the indirect effects of predators on the amount of macroalgae eaten (M) were also estimated, using ratio methods (Wojdak and Luttbeg 2005; Okuyama and Bolker 2007), by comparing the amount of macroalgae eaten when predators were present and able to kill prey, versus when predators were behind the mesh barrier and could only alter the anti-predator behavior of prey. The effect sizes of TMII, DMII, and total indirect interaction (TII) were calculated as follows:

$$\mathrm{TMII} = 1 - \frac{M_{\text{cue only}}}{M_{\text{no predator}}}, \quad \mathrm{DMII} = 1 - \frac{M_{\text{complete interaction}}}{M_{\text{cue only}}}, \quad \mathrm{TII} = 1 - \frac{M_{\text{complete interaction}}}{M_{\text{no predator}}}, \tag{1}$$

where the numerator is calculated on a per-replicate basis as the estimate of macroalgae grazed at the end of the experiment for a particular treatment, and the denominator is computed as the average across replicates. Each effect size calculation thus estimated the proportional decrease in basal resource consumed due to changes in prey traits (TMIIs), changes in the density of prey (DMIIs), or both (TII). This method assumes that TMIIs and DMIIs operate additively, neglecting any interactions between the two (Wojdak and Luttbeg 2005).

Statistical analysis

The influence of predator cue, pH, and day on the proportion of time that snails were out of the water was assessed using a generalized linear mixed-effects model (binomial GLMM, logit-link). Snails that were actively being eaten or had been eaten by sea stars were not included in this analysis. Container and snail identity were included as random effects, the latter to account for repeated behavioral measurements on individual snails and to obtain robust estimates given the unbalanced data due to the exclusion of consumed snails in the complete interaction treatments. To determine the influence of prey presence and pH on the behavior of sea stars, a two-part hurdle model was used, which incorporated two generalized linear models, since the response variable, distance traveled (cm), was positive, continuous, and zero inflated. The first generalized linear model assessed the influence of pH and the presence of prey cue on the probability of a sea star moving during a given observation period (binomial GLMM, logit-link), and then, the second model assessed the influence of each treatment on the distance traveled by a sea star if it moved (linear mixed effect model). As for the snail data, both sea star models included a random effect for container. The possibility that snail consumption was influenced by pH was tested using a generalized linear model, with consumption coded as the fraction of snails eaten per container (binomial GLM, logit-link). The possibility that macroalgal consumption (g) was influenced by pH and trophic treatment was tested using a general linear model, including pH and trophic treatment as independent variables. The interaction term was then used to assess whether the strength of indirect effects (difference in macroalgae consumed in the presence or absence of predator or cue from sea stars) was different between the two pH treatments. Two mesocosms were excluded from the macroalgal analysis, because the macroalgae fragmented during extraction, preventing assessment of the quantity consumed by the snails. Scaled residuals were assessed to verify assumptions for generalized linear mixed-effects models using the DHARMa package in R. For linear mixed-effects models and general linear models, assumptions of normality were assessed by inspecting plots of expected versus actual quantiles and with the Shapiro–Wilk's test, and homoscedasticity by inspecting plots of predicted versus residual values. All mixed-effects models were run using the lme4 package in the statistical software, R.

Results

Snail anti-predator behavior

Reduced pH disrupted the response of snails to predation risk, consistent with prior findings (Jellison et al. 2016). In particular, under low pH, snails exposed to a predator or predator cue decreased the proportion of time spent out of the water by almost half, such that the time in refuge was similar regardless of the presence or absence of a predator (Fig. 2a; low pH × cue interaction coefficient estimate $= -3.72$, Wald $z = -3.07$, $P = < 0.001$; Online Resource 1: Table S2).

Sea star behavior

Reduced pH also affected sea star behavior (Fig. 2b, c). Among *Leptasterias* individuals that exhibited locomotory activity, those exposed to low pH moved less than half the distance traveled by sea stars in ambient seawater (Fig. 2b,

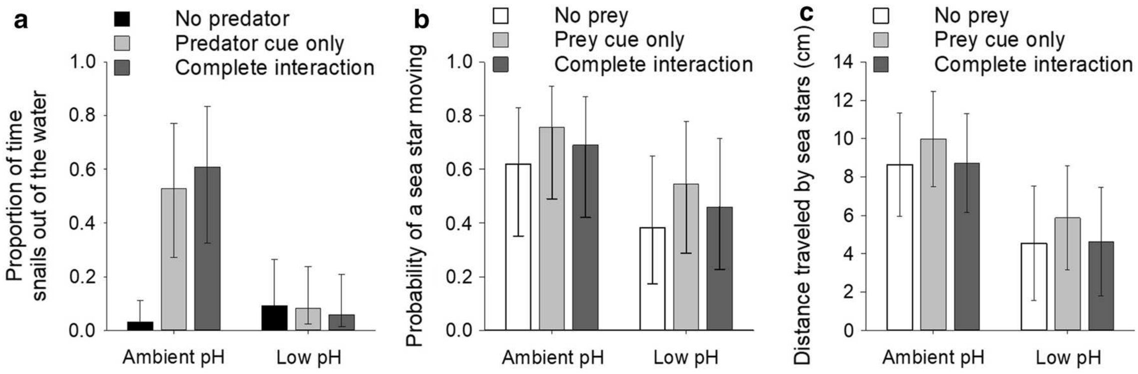

Fig. 2 Effect of reduced seawater pH on snail and sea star behavior ($n = 5$ per treatment). **a** Low pH attenuates the refuge-seeking behaviors of black turban snails (*Tegula funebralis*), as exemplified by a decreased tendency for snails to exit the water in the presence of sea stars (dark gray) or cue from them (light gray). **b** Low pH does not affect the tendency of the sea star, *Leptasterias hexactis*, to move in the absence (white) or presence (dark gray) of its prey, or in the presence of cue from snails (light gray), but **c** does decrease the distance sea stars travel if they do move. Bars represent means predicted from a generalized linear mixed effect models (**a** and **b**) and a linear mixed-effects model (**c**). Error bars represent predicted 95% confidence intervals

c; low-pH coefficient = − 4.11, $t = -3.01$, $P = 0.004$; Online Resource 1: Table S1). The presence of snails, however, did not affect whether or how far a sea star moved (Fig. 2b, c; Online Resource 1: Table S1).

Sea star predation on snails

The net effect of reduced refuge seeking by snails and decreased locomotory movements of sea stars was an elevation in sea star consumption of snails under low pH. In particular, sea stars ate three times more snails per container in the low-pH treatments (Fig. 3; low pH coefficient = 2.33, Wald z = − 2.06, $P = 0.039$; Online Resource 1: Table S1). Most snails were consumed within the first 3 days, but never were all individuals in a mesocosm eaten (Online Resource 1: Figure S5).

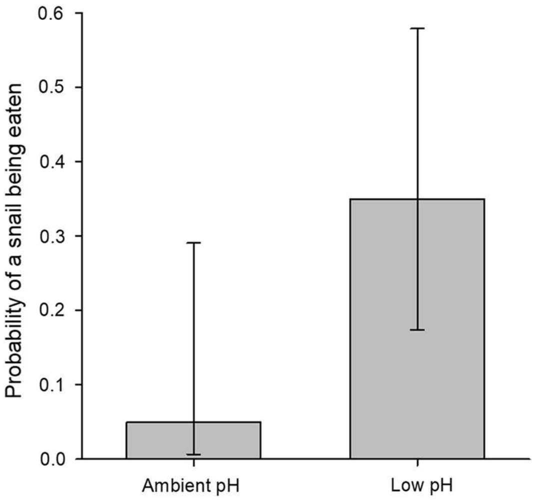

Fig. 3 More snails are consumed by sea stars under low pH. Bars represent the predicted proportion of snails eaten by sea stars per container in the predation treatments based on a binomial generalized linear model ($n = 5$ per treatment). Error bars represent 95% confidence intervals

Strength of indirect effects

The first three trophic treatments (Fig. 1a–c) account for indirect effects of predation but also include bottom-up processes (e.g., macroalgal growth or effects of senescence). We first address these overall effects (combined top-down plus bottom-up) and then turn to predator effects per se by incorporating results from the no-grazing treatment (Fig. 1d).

Net consequences for the basal resource

Macroalgal biomass was statistically indistinguishable across treatments at the outset of the mesocosm trials, but differed significantly among them at the experiment's conclusion (Fig. 4). In ambient seawater, net declines in macroalgal mass were greatest when snails were present without predators or predator cue (Fig. 4c). Less mass was lost in the no-predator and no-grazing treatments under reduced pH, but more mass was lost in treatments with predators or predator cue (low pH × cue interaction coefficient estimate = 0.06, $t = 3.17$, $P = < 0.01$; low pH × complete interaction coefficient estimate = 0.05, $t = 2.65$, $P = 0.01$; reference = no-predator cue and ambient pH). Macroalgal mass declined even without grazing, suggesting senescence dominated over growth.

Indirect effects of predation

Macroalgal consumption by snails was estimated to first order as the macroalgal mass lost above that without grazing (Fig. 5). Here, caution is warranted given that bottom-up effects were also likely active. Estimated macroalgae eaten by snails in the presence of predator or predator cue under low pH resembled that under ambient pH without a predator (Fig. 5; low pH × cue interaction coefficient estimate = 0.06, $t = 3.17$, $P = < 0.01$; low pH × complete interaction coefficient estimate = 0.05, $t = 2.65$, $P = 0.01$; reference = no-predator cue and ambient pH). Thus, although lower pH increased snail mortality through greater consumption by

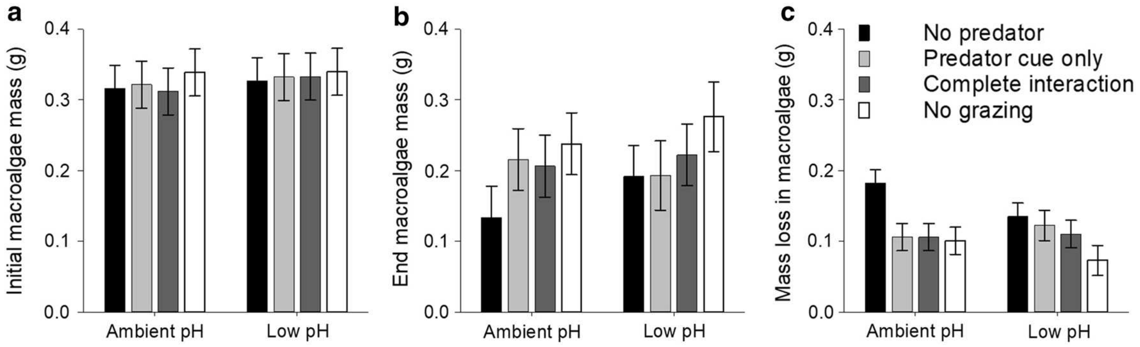

Fig. 4 The average amount of macroalgae (g) per container at the **a** start and **b** end of the mesocosm experiment, as well as **c** the difference in macroalgal mass between the start and end of the mesocosm trial. Bars depict predicted means based on a general linear model ($n = 5$ per treatment). Error bars represent predicted 95% confidence intervals

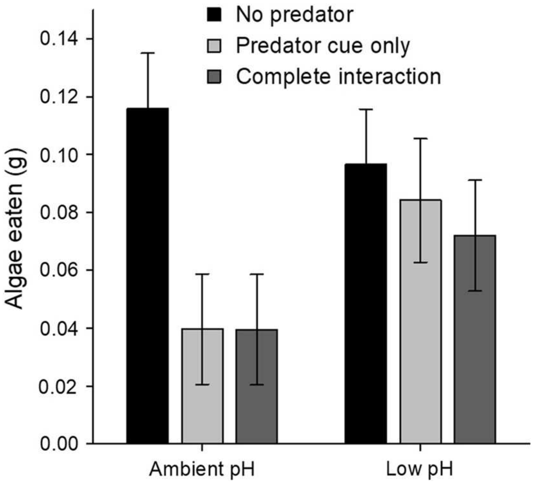

Fig. 5 The amount of macroalgae snails consume in the presence of a predator (dark gray) or predator cue (light gray) under low pH resembles the quantities that snails graze under ambient pH in the absence of a sea star (black). Bars depict estimated macroalgal consumption by *Tegula funebralis* [macroalgae mass loss per trophic treatment container (g)—mean macroalgae mass loss for no-grazing trophic treatment (g)] for each pH level ($n=4$ for with predator cue × low pH, $n=5$ for all other treatment combinations). Predicted means and 95% confidence intervals are based on a general linear model

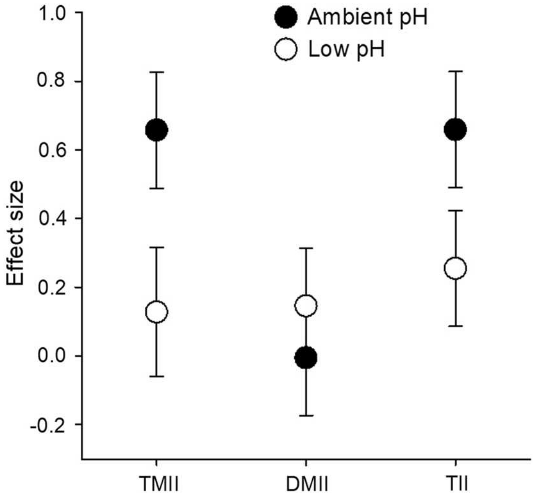

Fig. 6 Decreases in seawater pH alter the relative strength of estimated TMIIs and DMIIs, as well as the strength of total indirect effects (TII). TMIIs dominate in this system under ambient pH, and there are substantial total indirect effects (TIIs) of predators on macroalgae. In contrast, under low pH, the strength of TMIIs declines without a concomitant increase in DMIIs, such that the strength of total indirect effects declines. Bars depict the estimated effect size of TMIIs, DMIIs, and TIIs under either ambient pH (black) or low pH (white) based on a general linear model. Error bars represent predicted 95% confidence intervals

sea stars (Fig. 3, thereby elevating density-mediated indirect effects of predation on macroalgae), it simultaneously weakened the trait-mediated indirect effects of predation. This latter effect likely arose through the reduced tendency of snails to seek refuge under low pH (Fig. 2), which concomitantly increased the fraction of time that each individual spent in the water where foraging was possible (Online Resource 1: Table S1).

The overall result of these trends was that the relative strength of estimated TMIIs and DMIIs as calculated by Eq. 1 shifted with reductions in pH (Fig. 6; low pH × DMII interaction coefficient estimate = 0.68, $t=3.84$, $P=0.001$, reference = ambient pH and TMII; Online Resource 1: Table S1). Under ambient conditions, cascading effects of sea star predators on the macroalgal resource were driven primarily by behaviorally mediated reductions in snail foraging (TMIIs), rather than by effects on snail survival (DMIIs). In other words, trait-mediated indirect effects were much stronger under ambient conditions than density-mediated indirect effects (Fig. 6). However, under low-pH conditions, the estimated effect sizes of TMIIs and DMIIs converged and the total strength of indirect effects was reduced (Fig. 6).

Discussion

Reduced seawater pH alters direct predator–prey interactions between six-armed sea stars and black turban snails, with effects that cascade through the system to induce greater estimated consumption of macroalgae. As with many tri-trophic systems where both density-mediated and trait-mediated indirect interactions manifest, this outcome was not obvious in advance given that simultaneous operation of the two pathways creates ambiguity as to their net consequences. Since impairments to anti-predator behaviors should increase prey mortality, abiotic disruption (here through decreased pH) of such anti-predator responses could either (1) decrease the density of prey that feed on a basal resource, fostering the latter's success (increased DMIIs; also seen in state-dependent models of hungry or resource-limited prey; Luttbeg et al. 2003), or (2) induce less cautious behaviors on the part of prey that spur greater consumption of the basal resource (decreased TMIIs; Pangle et al. 2012). In the case of our model system under low pH, the second process dominated. These findings highlight the potential for ocean acidification to weaken the strength of behaviorally mediated trophic cascades through degradation of anti-predator traits of intermediate consumers.

Although not designed to isolate bottom-up effects, our study also suggests some role for pH (or CO_2) in influencing the macroalgal basal resource itself. Because a pH effect on macroalgae would apply across all trophic treatments associated with the TMII, DMII, or TII estimates at a given pH, the relative magnitudes of these quantities are unlikely to be influenced. Nevertheless, the no-grazer treatments in low pH exhibited less mass loss than the ambient treatments (Fig. 4).

Whether this pattern derived from pH-driven changes to the relative importance of growth and senescence, or only from a pH effect on the latter remains unclear. We do know that the excision protocol used to isolate macroalgal disks from the originating *Mazzaella* blades unavoidably caused tissue damage and probably stimulated senescence. That said, it is also possible that the macroalgal disks maintained some residual carbon fixation. Although ambient light levels in the mesocosm trials were not supplemented with photosynthetically active radiation (PAR), the lids to the containers were transparent. Thus, it is conceivable that elevated seawater CO_2 associated with the low-pH treatments could have bolstered carbon uptake. Alternatively, any microbes degrading the macroalgae may have been less active under reduced seawater pH. Such questions regarding bottom-up effects, as well as the potential for nutrient loading from sea star and snail excretion to influence carbon fixation by the macroalgae (see, e.g., Aquilino et al. 2009; Poore et al. 2016; Bracken et al. 2018), warrant additional attention (also consult Online Resource 2 for further details on this topic).

To our knowledge, this study is one of the first to experimentally examine whether the relative strength of estimated TMIIs and DMIIs might depend on seawater pH (see also Lord et al. 2017). Although models predict that environmental conditions that increase the willingness of prey to forage under risky conditions should simultaneously reduce TMIIs, while also making prey more vulnerable to consumption (and thus increasing DMIIs; Luttbeg et al. 2003), we observed a subtly different outcome. In particular, we found that the strength of the estimated DMII remained relatively constant even as decreases in pH attenuated the TMII. These changes led, in turn, to a reduction in the overall strength of the estimated total indirect effects (TII) in this system (Fig. 6). Although additional experiments (e.g., those involving culling; Peacor and Werner 2001; Okuyama and Bolker 2007) are required to conclusively characterize the strength of the DMIIs (since our approach relied upon a ratio-based index), and although the applicability of this finding to other species and food webs remains yet unknown, it points to an important avenue by which low seawater pH could influence marine communities.

In evaluating the capacity for abiotic factors to affect indirect interactions more broadly, we can anticipate that the ultimate consequences of altered TMIIs and DMIIs may depend on the relative importance of these two types of cascading effects. In our system, TMIIs dominate under contemporary seawater conditions, and this feature could apply even more strongly in the field. *Leptasterias* is a generalist consumer and preferentially targets prey other than *Tegula* (Gravem and Morgan 2019); this point suggests that DMIIs involving black turban snails could be weaker in nature compared to our laboratory experiment. TMIIs, by contrast, are more likely to be heightened in the field given the potential for sea star cue to influence relatively more significant numbers of snails (although the ratio of snail to sea star density used in our experiment was consistent with common field patterns, snails also reach higher densities in some pools; Gravem and Morgan 2019). In this regard, our data may provide conservative estimates of the potential for pH-induced alterations to prey behavior to weaken TMIIs and total indirect interactions (TIIs) relative to DMIIs. In contrast, in systems where DMIIs dominate (see, e.g., Trussell et al. 2006), there may be little potential for OA-induced shifts in prey behavior to depress total indirect effects. Given growing interest in how OA might influence links in food webs (e.g., Gaylord et al. 2015), additional studies should be prioritized in this area, along with complementary experiments that alter the initial densities of herbivores and the duration of predator exposures (Luttbeg et al. 2003; Wada et al. 2013).

In our model system, the behavior of the prey species was affected more negatively by decreased pH than that of the predator, as evidenced by higher rates of consumption of snails under altered seawater conditions (Fig. 3). However, under other circumstances or in other trophic networks, shifts in seawater pH could differentially influence the predator instead of the prey, or affect both comparably. In previous work involving fish, for instance, researchers found that although elevated seawater CO_2 negatively impacted the behavior of both predator and prey, neither gained an advantage when held together (Allan et al. 2013). In many cases, therefore, net outcomes of species interactions under environmental change will not be simple to predict and must be determined empirically. The trend of unpredictability is common to a number of recent studies (e.g., Alsterberg et al. 2013; Nagelkerken and Connell 2015; Connell et al. 2017).

In addition to acting as a sensory stressor, low pH (and its accompaniments of higher CO_2 and reduced carbonate ion concentration) can also act as a physiological challenge (Pörtner 2008; Kroeker et al. 2010). In this case, OA might weaken DMIIs if foraging abilities of predators are degraded more than that of prey, in analogy to predictions of consumer stress models where difficult environmental conditions have a similar effect (Menge and Sutherland 1987). Alternatively, other workers have suggested that OA might make feeding in sea stars more efficient (Gooding et al. 2009). In our system, although sea stars did decrease their locomotory activity under low pH, consumption of snails rose rather than fell. Further work is required to determine the drivers of altered movements of *Leptasterias* under OA, possible shifts in efficiencies of feeding or handling times, and the mechanistic basis of riskier behaviors of snails. Likewise, there is still much to learn regarding longer term physiological responses, including the capacity for plasticity in growth, metabolism, motility, and feeding.

The relative strength of TMIIs and DMIIs under environmental change may, furthermore, connect to the sensory modalities of interacting species. In our model system, snails predominantly use olfactory and tactile cues when responding to sea star predators (Feder 1963). In contrast, *Leptasterias* sea stars do not appear to employ olfaction when searching for food (Online Resource 1: Fig. S1). Instead, they seem to find prey through foraging trajectories that mimic a random walk. The net result is that although movement in sea stars declines with decreasing pH, their use of a randomly oriented search process coupled with impaired anti-predator behaviors of snails (which keeps the latter underwater where *Leptasterias* can find them) likely ensures a reasonable chance of contact between the two species. In other trophic networks where species may rely on more distinct sensory modalities (e.g., one species depends on hearing, another on olfaction), strongly divergent responses to OA may arise. Such possibilities point to the value of understanding the bidirectional transfer of information in any given predator–prey interaction (Weissburg et al. 2014).

The capacity of low pH to modulate cascading effects of predators, as documented here, could, moreover, be operating as a largely unrecognized contributor to landscape-level patterns in marine systems. Especially, in coastal regions, pH can vary strongly in space and time (Chan et al. 2017). Even at a single site, we have measured differences in seawater chemistry of up to 1.0 pH unit between tidepools separated by only a few meters. This existing variability in tidepool pH is driven by differences in aerial exposure time, surface area-to-volume ratios of pools, and the abundance and identity of organisms within pools (Jellison et al. 2016; Silbiger and Sorte 2018). Although the implications of such spatial heterogeneity in pH conditions have not been fully examined, they have the potential to foster differences in community composition within and across these ecosystems. As just one observation, (Gravem and Morgan 2019) found that *Leptasterias* in tidepools indirectly influenced algal biodiversity, but also that the magnitude of the responses to this sea star varied across tidepools. One could easily envision a role for seawater pH in driving portions of this variability. As a consequence, even as we work to improve our characterization of pH conditions across marine habitats and the potential for these conditions to be exacerbated by ocean acidification, we must also strive to evaluate the effects of seawater chemistry on species interactions and trophic links. Doing so will be a crucial component of attempts to understand how predator effects cascade through natural communities currently and into the future.

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Author contribution statement BMJ and BG conceived and designed the experiments. BMJ performed the experiment and analyzed the data with input from BG. BMJ and BG wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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