Prey state alters trait-mediated indirect interactions in rocky tide pools

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Summary

1. Several studies on trait-mediated indirect interactions (TMIIs) have shown that predators can initiate trophic cascades by altering prey behaviour. Although it is well recognized that individual prey state alters antipredator and foraging behaviour, few studies explore whether this state-dependent prey behaviour can alter the strength of the ensuing tritrophic cascade. Here, we link state-dependent individual behaviour to community processes by experimentally testing whether hunger level and body size of prey altered antipredator behaviour and thus changed the strength of trophic cascades between predators and primary producers.

2. In rocky intertidal tide pools on the California Coast, waterborne cues from the predatory seastar *Leptasterias* spp. (Stimpson) can cause the herbivorous snail *Tegula (Chlorostoma) funebralis* (A. Adams) to reduce grazing and flee tide pools, resulting in positive indirect effects on tide pool microalgae.

3. However, we show that the strength of this behaviourally-mediated cascade may be contingent on prey hunger level and body size. During short field experiments at low tide, medium-sized snails that were either newly collected from the field or fed for 1 week in the laboratory mediated strong TMIIs because they grazed less when seastars were present. In contrast, no TMIIs occurred when medium-sized snails had been starved for 1 week because they continued grazing regardless of seastar presence. Newly collected small snails fled from seastars but did not mediate cascades because they ate little algae. Despite reaching an apparent size refuge from predation, many newly collected large snails fled from seastars, but those individuals that remained tended to graze the algae more quickly, resulting in unexpected negative indirect effects of seastars on algae cover. The implication of this pattern for the natural system is unclear.

4. Because average hunger level and size of snails vary over time and space in nature, a mosaic of TMII strength may exist.

5. Overall, the strength of tritrophic TMIIs in tide pools depended on individual prey state, supporting model predictions and adding to sparse empirical evidence. This outcome suggests that patterns occurring system-wide over the long term may be influenced by the state-dependent decisions made by the individuals present.

Key-words: adaptive foraging theory, antipredator behaviour, *Leptasterias*, nonconsumptive effect, predator–prey interaction, *Tegula funebralis*, trait-mediated indirect interaction, trophic cascade

Introduction

Predator–prey interactions are often expressed as predation rates on prey, and for simplicity these metrics generally treat all individuals within a population as homogenous (Schmitz, Adler & Agrawal 2003; Ohgushi, Schmitz & Holt 2012). However, adaptive foraging theory unequivocally demonstrates that predators also exert non-consumptive effects on prey by changing their foraging behaviour, and that these behaviours are contingent on individual variation in prey states, such as body size, energy reserves, reproductive status or behavioural syndromes (Mangel & Clark 1986; Houston, McNamara & Hutchinson 1993; Werner & Anholt 1993; Clark 1994;

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Lima 1998; Sih, Bell & Johnson 2004). Trophic cascades connect predator–prey interactions to a third species, and the classic mechanism is a form of a density-mediated indirect interaction (DMIIs, Abrams 1995; Peacor & 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, studies on trait-mediated indirect interactions (TMIIs, Abrams 1995; Peacor & Werner 1997) demonstrate that predators often exert sublethal effects on prey behaviour, morphology or physiology that cause indirect cascading effects on primary producers (Werner & Peacor 2003; Schmitz, Krivan & Ovadia 2004; Miner *et al.* 2005). TMII studies weave a connection between behavioural, population and community ecology by linking individuals to emergent community patterns and ecosystem processes (Schmitz, Adler & Agrawal 2003; Schmitz *et al.* 2008).

Just as predator–prey interactions within foraging theory depend on the state of individuals, it is likely that TMII strength may be contingent upon the individual state of the organisms involved. Multiple reviews and syntheses have identified this concept as underexplored and called for studies connecting individual state variation to community-level patterns (Schmitz, Adler & Agrawal 2003; Schmitz, Krivan & Ovadia 2004; Agrawal *et al.* 2007; Beckerman, Petchey & Morin 2010; Ohgushi, Schmitz & Holt 2012; Rudolf 2012; Railsback & Harvey 2013). For example, Beckerman, Petchey & Morin (2010) point out that there are '…precious few advances towards truly synthesizing the connections between individuals, populations and large interconnected food webs'. In response, theoretical models have demonstrated that prey body size and hunger level may alter TMII strength (Schmitz 2000; Luttbeg, Rowe & Mangel 2003; Persson & De Roos 2003). In addition, field and laboratory studies have demonstrated that TMII strengths may be contingent on prey body size, hunger level and the combination of hunger and risk frequency (Ovadia & Schmitz 2002; Kotler, Brown & Bouskila 2004; Freeman 2006; Hawlena & Schmitz 2010; Rudolf 2012; Matassa & Trussell 2014) though other studies suggest that prey traits may be safely ignored in certain cases (Ovadia & 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.

We investigated whether hunger level and body size of prey altered antipredator behaviour and the strength of TMIIs in a tritrophic food chain. Adaptive foraging theory and the threat-sensitivity hypothesis (Helfman 1989; Werner & Anholt 1993; Clark 1994; Lima 1998) posit that prey with high-energy reserves or at higher risk should be wary of predators and increase refuge use, but prey with low-energy reserves or at lower risk should forage despite predator presence. 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 they may initiate weak or no TMIIs when hungry prey forage despite risk (Heithaus *et al.* 2007; Matassa & Trussell 2014). In addition, both the consumptive and the 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 the ease of capture or shorter handling time (MacArthur & 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 rarely captured. 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 behaviour and changes TMII strength, we examined a tritrophic food chain in tide pools where the small (1–5 cm diameter) seastar *Leptasterias* spp. (*L. aequalis* and *L. hexactis*, considered either sister species or subspecies, Flowers & Foltz 2001) consumes the common herbivorous intertidal snail *Tegula* (formerly *Chlorostoma*) *funebralis* (Bouchet & Rosenberg 2015), which grazes on algae (Fig. 1). To provide context for the study, we first assessed the potential for size-dependent predation by *Leptasterias* on *Tegula* by testing whether smaller snails were eaten more than larger snails in the laboratory and field. We also examined size-dependent antipredator responses by comparing evasive behaviour of different sized snails to both tactile (imminently threatening) and waterborne (prospectively threatening) predator cues. These experiments provide important supplemental information on these predator–prey interactions for interpreting the results of our focal experiments on the effect of prey state on TMIIs. With this information in hand, we then tested if snail hunger level (hungry vs. fed) or body size (3 size classes) changed snail antipredator behaviour, and consequently altered TMIIs on microalgae in the field during
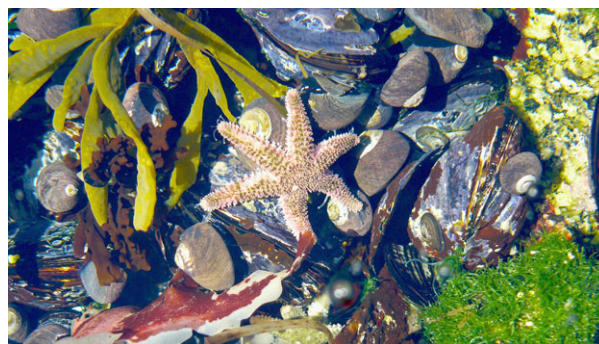

Fig. 1. *Leptasterias* sp. hunting *Tegula funebralis* in a rocky intertidal pool. Various macroalgae species shown. Photograph by Sarah A. Gravem.

low tide. We also discuss the ecological relevance of our short-term experiments to natural populations of snails.

Materials and methods

EXPERIMENTS ON CONSUMPTIVE AND NONCONSUMPTIVE EFFECTS ON PREY

To determine the frequency of predation by *Leptasterias* on *Tegula* relative to other prey species, we first surveyed the diets of *Leptasterias* in the intertidal zone in July 2009 (see Appendix S1, Supporting information for details) at the Bodega Marine Reserve at Horseshoe Cove in northern California, USA (38° 18′ 59·37″ N, 123° 4′ 16·28″ W). To test our expectation that predation risk decreases with *Tegula* size, we paired single *Leptasterias* with single *Tegula* in varying size combinations in very small seawater tanks to test whether *Tegula* reach a size refuge from *Leptasterias* predation (see Appendix S1). Finally, we tested the escape responses (fleeing and meandering) of varying sizes of *Tegula* to tactile, waterborne or no *Leptasterias* cues to test whether all sizes of snails respond to seastars (see Appendix S1).

TMII FIELD EXPERIMENTS

We tested if *Tegula* size or hunger level changed their antipredator behaviours and thus changed the strength of the TMII between *Leptasterias* spp. and microalgae in tide pools of Horseshoe Cove. We added snails of different hunger levels or size classes to 18 small mid-to-high tide pools (1·2–9·3 L, 1·01–1·67 m above mean lower low water). In hunger experiments, we factorially crossed seastar presence with fed, hungry or no snails totalling six treatments. In size experiments, we used eight total treatments by factorially crossing seastar presence with small, medium, large or no snails. Small, medium and large size classes were defined as 6–12, 12–18 and 18–25 mm at the widest shell width, respectively (*sensu* Paine 1969). Only medium-sized snails were used in hunger experiments. We performed four separate hunger trials (18 July, 2 August, 30 August and 27 September, 2012) and six separate size trials (24 May, 25 May, 22 June, 26 June, 20 July and 29 August, 2012). Though tide pool water temperatures were likely warmer, average daily seawater temperatures (mean ± SD) recorded by the Bodega Marine Laboratory seawater system were 12·3 ± 0·3 and 12·1 ± 0·8 °C for hunger and size trials, respectively. Treatments without snails were included to control for any effects on algae due to handling, seastars, or grazing by other herbivores. During each trial, treatments were randomly assigned to the 18 tide pools, resulting in a cumulative total of 9–15 replicate tide pools per treatment. One week prior to hunger experiments, snails were collected from Horseshoe Cove and held in outdoor, flow-through tanks where they either were starved or allowed to graze *ad libitum* on a thick layer of microalgae (benthic diatoms) that had been growing naturally in tanks for the ~2 preceding weeks. One day prior to size experiments, snails were collected from Horseshoe Cove, measured, and held in indoor flow-through aquaria overnight.

Medium to large seastars (2–5 cm diameter across two longest opposing arms) were added to half of the tide pools and were contained in small mesh pouches of plastic window screen that were affixed to eyebolts drilled into the substrate to prevent escape. Because of local *Leptasterias* mass mortality events in November 2010 and August 2011 (Gravem 2015; Jurgens *et al.* 2015), *Leptasterias* were collected 104 km north of Horseshoe Cove at Point Arena (38° 54′ 47·48″ N, 123° 42′ 37·83″ W). *Leptasterias* were maintained in flow-through tanks and fed small *Tegula* and *Littorina* spp. weekly. We mimicked natural predator cue accumulation during low tide by adding seastars to tide pools the day before the experiment. To keep waterborne seastar cue concentration similar and ecologically relevant among tide pools, we scaled the number of predators to tide pool volume using natural *Leptasterias* densities (~0·41 individuals L^{-1}) that we recorded in tide pools at Horseshoe Cove in July 2009, prior to the November 2010 *Leptasterias* mortality event. We haphazardly assigned individual seastars to tide pools, taking care to keep average seastar size similar among tide pools. As a result of the 2010 and 2011 mortality events, *Leptasterias* were naturally absent in the tide pools during the experiment unless experimentally added. We also scaled snail densities to tide pool volume and they were added to tide pools at 50% natural field densities recorded in tide pools in July 2009 (13·6 individuals L^{-1}), because 100% density would have made treatments with large snails overcrowded. We chose to use constant densities of snails rather than constant biomass because more conspecifics can decrease individual responsiveness to predators since the chance of being eaten decreases with group size (Dehn 1990).

To assess grazing in TMII experiments, we used unglazed porcelain tiles (2·54 × 2·54 cm) placed in outdoor flow-through tanks 1–2 weeks before experiments to grow a thin film of benthic diatoms. Since it was not possible to manipulate algal biomass, algae tiles were haphazardly assigned among tide pools and care was taken to maintain similar average algal biomass among tide pools. To ensure algal tiles were easily and equally accessible to snails among tide pools of different sizes, the tiles were densely distributed with the number of tiles scaled to the tide pool surface area (0·010 tiles cm^{-2}). Steep sides in one tide pool limited the maximum density of tiles to 0·006 tiles cm^{-2}. Each tide pool and surrounding areas were cleared of *Tegula*, other herbivorous gastropods and hermit crabs both the day before and day of each experiment. Algal cover on tiles was measured at the end of each experiment using a gridded transparent quadrat (2·54 × 2·54 cm with 25 cells measuring 0·51 × 0·51 cm); tiles always began with 100% algae cover.

On the day of experiments, we first deployed tiles in all tide pools, quickly followed by snails, taking care not to place snails on tiles (seastars had been deployed the day before). Snails typically avoid seastar cues by escaping tide pools to refuge habitats above the water line (Gravem 2015), which we termed the 'halo' and defined as substrate 0–15 cm above the waterline in each tide pool. The numbers of snails in the water, in the halo, and grazing were sampled every 5–10 min in each tide pool for 1 h (size trials) or 45 min (hunger trials). 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. To determine whether seastars, hunger level or size caused those individuals grazing to consume algae faster, snail grazing 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-min increments and treated as a categorical variable during statistical analyses. We calculated the percentage of total snails out of water or grazing at each time frame ([snails out of water or grazing/total snails] * 100) and the percentage algae cover at the end of the experiments. We tested the main and interactive effects of time frame, seastar treatment and snail treatment on the per cent snails in the halos and grazing using restricted maximum likelihood (REML) mixed models in JMP software (SAS Institute, Cary, NC, USA). The main and interactive effects of seastar and snail treatments on per cent algal cover and grazing rate were also analysed using REML. In each model, tide pool replicate was included as a random variable (nested within seastar and snail treatments) to account for non-independence of measures in the same tide pool over time. All response variables were arcsine square root transformed to meet statistical assumptions of normality and equal variances.

Results

EXPERIMENTS ON CONSUMPTIVE AND NONCONSUMPTIVE EFFECTS ON PREY

In the field, *Tegula* comprised 24% of *Leptasterias* diets, and small snails (<12 mm) constituted 80% of *Tegula* eaten (Fig. 2a, Appendix S1). In the laboratory, predation decreased with snail size with small and medium snails eaten often and large snails eaten rarely (Fig. 2b, Appendix S1, 76·6%, 40·0% and 6·4% of small, medium and large snails, respectively). Overall, snails exhibited the strongest fleeing responses from tactile, followed by waterborne, then no cue and meandered more when exposed to waterborne than tactile cues (Fig. S1, Appendix S1). However, these differences were strongest for large snails, followed by medium snails. Small snails did not change speed and meandered frequently regardless of cue type (Fig. S1, Appendix S1).

TMII FIELD EXPERIMENTS

On average, newly collected medium and large snails escaped from seastars more quickly than newly collected small snails (Fig. 3a–c; Time × Seastar treatment × Snail size: $F_{8,899} = 2·32$, $P = 0·018$; Time × Seastar treatment: $F_{4,899} = 50·40$, $P < 0·001$). By the end of experiments, many snails of all sizes had fled tide pools in response to seastars (Fig. 3a–c; Mean % in halo at end ± SE: 15·9 ± 2·4, 23·4 ± 3·1, and 21·4 ± 1·7% for small, medium and large, respectively). In contrast, few snails fled when seastars were absent (Mean % in halo at end ± SE: 3·9 ± 1·0, 4·1 ± 0·8, and 4·9 ± 0·7% for small, medium and large, respectively). *Leptasterias* also caused fewer snails of all sizes to graze, especially between 30 and 60 min (Fig. 3d–e; Seastar treatment: $F_{1,856} = 14·37$, $P = 0·003$; Time × Seastar treatment: $F_{4,856} = 5·83$, $P < 0·001$; Time × Seastar treatment × Snail Size: $F_{8,856} = 0·79$, $P = 0·611$). More small snails grazed than medium or large snails after 30 min regardless of seastar presence

(Snail size: $F_{1,856} = 19·36$, $P < 0·001$; Time × 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, which may underestimate the potential effects of seastars on the grazing activity by medium and large snails and on TMII strength. Only medium snails mediated positive TMIIs on algae, and large snails surprisingly mediated negative TMIIs on algae (Fig. 4a; Seastar treatment: $F_{1,76} = 0·07$, $P = 0·790$; Seastar treatment × 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 × snail treatment: $F_{2,55} = 1·3$, $P = 0·29$; Mean large snail grazing rate ± SE: 0·41 ± 0·07 and 0·29 ± 0·05 cm^2 grazing snail^{-1} h^{-1} 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 cm^2 grazing snail^{-1} h^{-1} for small, medium and large, respectively, $n = 28$).

Fed snails of medium size mediated positive TMIIs on algae but medium-sized hungry snails did not (Fig. 4b; Seastar × Snail treatment: $F_{3,44} = 3·65$, $P = 0·033$). On average, fed snails fled from tide pools more quickly than hungry snails when seastars were present (Fig. 5a,b; Time × Seastar treatment × Snail treatment: $F_{3,407} = 4·69$, $P = 0·003$). By the end of experiments, more fed than hungry snails left tide pools with seastars (Fig. 5a,b; Mean % in halo at end ± 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 tide pools (Fig. 5a,b; Mean % in halo at end ± SE: 3·0 ± 0·7% and 0·8 ± 0·3% of fed and hungry snails, respectively). Though on average throughout the experiment the presence of *Leptasterias* caused fed snails to graze less, hungry snails only reduced grazing somewhat (59% and 10% decrease in snails grazing, respectively), there were no statistical differences between the number of fed and hungry snails grazing with seastar presence (Fig. 5c,d;
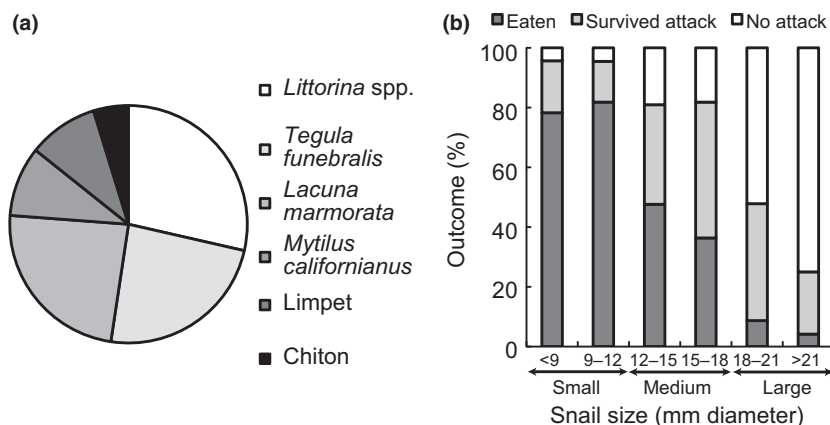

(a)

□ *Littorina* spp.

□ *Tegula funebralis*

□ *Lacuna marmorata*

□ *Mytilus californianus*

▨ Limpet

■ Chiton

(b) ■ Eaten □ Survived attack □ No attack

Outcome (%)

Snail size (mm diameter)

Fig 2. (a) Diet of *Leptasterias* spp. surveyed throughout the intertidal zone in Horseshoe Cove, California ($n = 21$ seastars). (b) Percentage of *Tegula funebralis* in different size classes (3 mm increments) that were eaten, survived an attack or not attacked by *Leptasterias* spp. when snails and seastars were paired in small tanks for 16 days in flowing seawater in the laboratory.
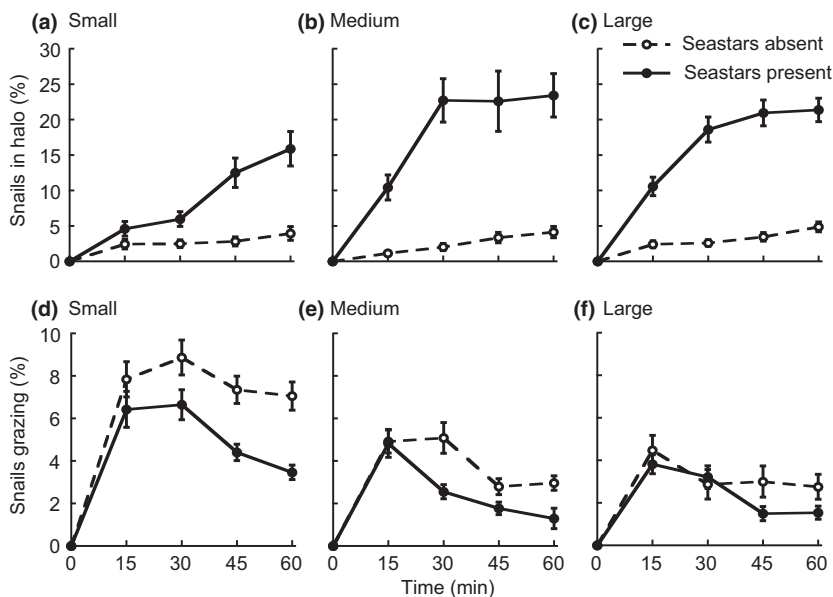
Fig 3. Mean (±SE) percentage of *Tegula funebralis* in refuge habitats (a–c) and grazing (d–f) with and without *Leptasterias* spp. present over 1 h in rocky tide pools in Horseshoe Cove, California. Snails were grouped into size classes (small: <12 mm shell diameter, medium: 12–18 mm, large: >18 mm). Organism densities were scaled to tide pool volume.
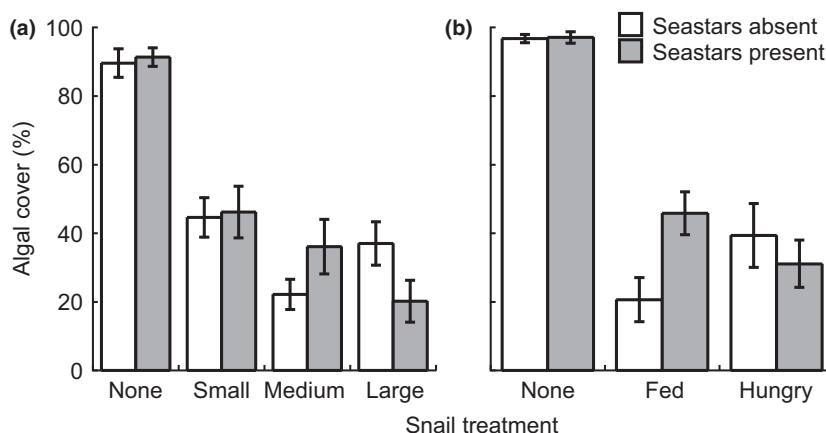

Fig 4. Mean (±SE) percent cover of microalgae remaining on tiles deployed in the presence or absence of *Leptasterias* spp. and *Tegula funebralis* of different (a) sizes after 1 h or (b) hunger levels after 45 min in rocky tide pools at Horseshoe Cove, California. Snails were grouped into size classes (small: <12 mm shell diameter, medium: 12–18 mm, large: >18 mm). Densities of organisms and algae tiles were scaled to tide pool volume.

Time × Seastar treatment: $F_{3,407} = 5.25$, $P = 0.001$; Time × Seastar treatment × Snail treatment: $F_{3,407} = 1.76$, $P = 0.153$).

Discussion

We link state-dependent behaviour to community outcomes by showing that individual variation in prey hunger and size may alter the strength of TMII trophic cascades. Our study confirms model predictions (Schmitz 2000; Luttbeg, Rowe & Mangel 2003; Persson & 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 (e.g. Ovadia & Schmitz 2002; Rudolf 2012; Matassa & Trussell 2014). While the very short-term TMIIs observed here do not necessarily predict TMII strengths at longer ecological time-scales, we 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, our prior experiments suggest that *Leptasterias* exert positive long-term TMIIs on algal growth in this system by causing *Tegula* to avoid tide pools and reduce grazing for many months (Gravem 2015), indicating that our short-term results here may indeed manifest over the long term.

PREY STATE AND TMIIS

Newly collected medium snails escaped from seastars, reduced grazing and mediated positive TMIIs, suggesting that they may be important mediators of TMIIs in natural systems. Newly collected small snails did not graze enough algae to mediate TMIIs despite strong behavioural responses. Thus, they may mediate weaker TMIIs than medium snails in nature, similar to model predictions where smaller individuals exhibit slower consumption rates and likely mediate weaker cascading effects (Schmitz 2000; Persson & De Roos 2003). However at high densities or over longer periods, small snails probably would have stronger effects on algae than were observed here. In addition, over time their energetic demands for growth may cause them to become less wary and graze more
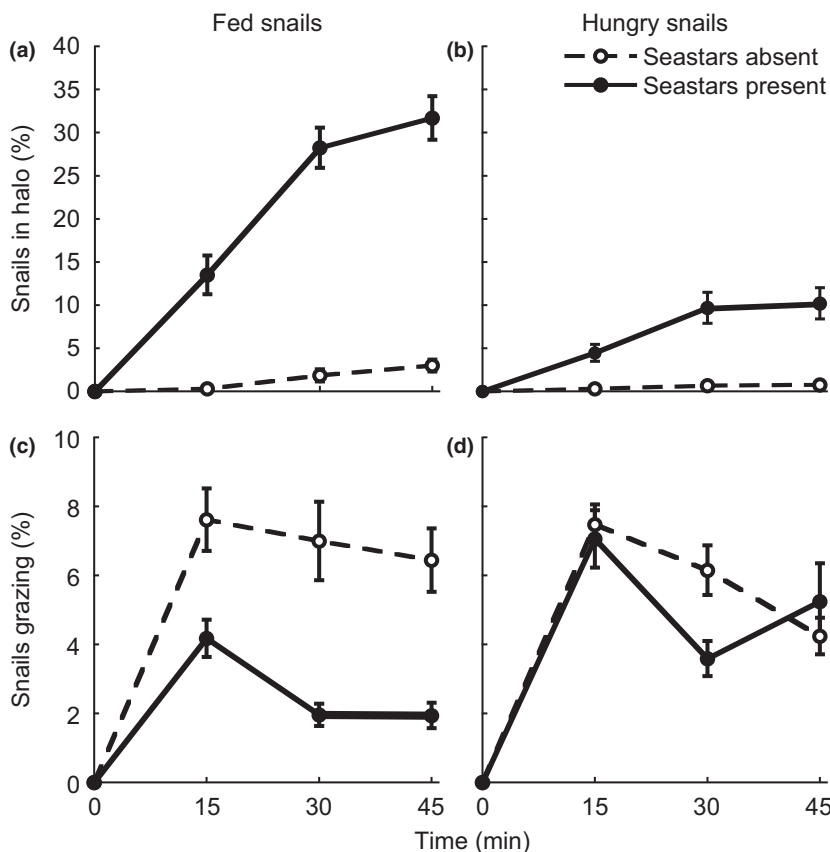
Fig 5. Mean (±SE) percentage of fed and hungry *Tegula funebralis* in halos (a, b) and grazing (c, d) with and without *Leptasterias* spp. present over 45 min in rocky tide pools at Horseshoe Cove, California. Snails were either fed microalgae (a, c) or starved (b, d) for 1 week in the laboratory before experiments. Organism densities were scaled to tide pool volume.

frequently regardless of predator presence, similar to small grasshoppers in other tritrophic TMIIs (Ovadia & Schmitz 2002, 2004). The slower escape response by small snails was likely due to both slower speed and increased meandering observed in the predator cue experiments in the laboratory (Fig. S1 and Appendix S1).

As in the predator cue experiments, newly collected large snails in field experiments reacted to seastar presence by fleeing and grazing less. However, this surprisingly resulted in negative TMII effects of seastar presence of algae. This counterintuitive result may have arisen because individual large snails tended to increase their grazing rates in the presence of seastars. Thus, when seastars were present, fewer large snails grazed but those individuals grazed faster, likely resulting in lower algal cover when seastars were present than absent. This may have occurred because large snails had known low risk of predation and high opportunity costs of forsaking the available algae, so some chose to devour the algae quickly before fleeing. However, we found no other TMII studies indicating that larger or less vulnerable individuals mediate negative TMIIs because they increase feeding when predators are present. It is unclear how our 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 tide pools more often than small and medium snails in field surveys (Gravem 2015) and generally reside

lower in the intertidal zone where *Leptasterias* and other predatory seastars are abundant (Paine 1969). Large individuals in other systems may mediate strong positive TMIIs because they have strong effects on their resources but possess the energy reserves to easily stop feeding for extended periods of time when predators are present (Luttbeg, Rowe & Mangel 2003). Alternatively, they may not mediate TMIIs because they have reached a size refuge and continue feeding regardless of predator presence, as do larger individual sea urchins in the presence of predatory seastars that prefer smaller sea urchin prey (Freeman 2006). Studies on large snail behaviour over varying time-scales in this system are necessary to determine their role in the tritrophic cascade.

Hungry snails of medium size responded weakly to seastar presence and did not 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 adaptive foraging theory that suggests prey with lower energy reserves should forage despite risk (Werner & Anholt 1993; Clark 1994; Lima 1998). In contrast, fed snails of medium size presumably had higher energetic reserves and they did not risk foraging when seastars were present. Thus, fed snails did mediate TMIIs, supporting models predictions 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, Rowe & Mangel

2003). Similar results are found in other tritrophic systems; when tiger sharks were present, sea turtles in better body condition foraged less often in high-quality seagrass beds than turtles in worse body condition (Heithaus *et al.* 2007), and predatory crabs more strongly reduced consumption of mussels by well-fed than hungry intertidal snails (Matassa & Trussell 2014).

We did not explore the interaction between hunger and size, but it is possible they are not independent of one another. Small snails in the field could have lower energetic reserves, and despite fleeing from *Leptasterias*, they may eventually re-enter tide pools to graze while large snails may be able to delay foraging for longer periods (Peters 1986; Luttbeg, Rowe & Mangel 2003). In contrast, the energetic demands of reproduction apparently force medium and large *Tegula* (>12 mm) to move lower on the shore despite higher predation risk by *Pisaster ochraceus* Brandt (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 BEHAVIOUR

Interestingly, many newly collected large snails responded to seastars by fleeing and grazing less, even though they likely were at low risk of predation (Appendix S1). Here, the prey's perceived risk of predation may be more important than actual risk for determining prey behaviour (Stankowich & Blumstein 2005). Since snails rely more on chemical than visual cues (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 favour 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* (Yarnall 1964; Gravem 2015). Alternatively, evasive behaviour by large snails may be advantageous because nonlethal attacks prevented snails from eating, mating and perhaps respiring and metabolizing normally from hours to as many as 3·6 days in the laboratory (Appendix S1). Regardless of their seemingly suboptimal short-term responses, large snails seem to be less responsive to *Leptasterias* than small and medium snails over longer periods of time (Gravem 2015), so some ontogenetic shifts in behaviour 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 (Appendix S1). When touched by seastars, newly collected medium and large snails immediately fled in predominantly straight lines, but when exposed to waterborne cues they meandered more 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 also 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 & Nevitt 2008). Unlike medium and large snails, newly collected small snails meandered frequently when exposed all cue types, perhaps because they are less likely to 'outrun' seastars. A switch from a straight, directed evasion to erratic zig-zagging or tacking when facing imminent attack is evident in diverse prey and it effectively increases the distance between the predator and the prey (Humphries & Driver 1967; Fitzgibbon 1990).

TMII STRENGTH IN NATURE

We have shown that state-dependent prey behaviour potentially alters TMII strength in short experiments, but further experiments are necessary to determine whether individual variation in size and hunger level do indeed alter TMIIs in natural tide pools. 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 such as hunger level are inherently fleeting so state-dependent behaviours change on shorter time-scales than ecological outcomes occur. To isolate the consequences of energetic state, experiments must be short or must keep energetic reserves static, whereas dynamic state variability is easier to incorporate in models (Luttbeg, Rowe & Mangel 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 tide pools at high tide and grazed on naturally present algae. Our brief experiments may overestimate TMII strength for two reasons. First, it is common for short-term TMII experiments to overestimate the true strength of TMIIs because prey can temporarily abstain from feeding with little consequence. Over time, behavioural responses and TMIIs may weaken because energetic demands can cause prey to resume feeding even when predators are present or prey may become acclimated to predator cues (Luttbeg, Rowe & Mangel 2003; Okuyama & Bolker 2007). Secondly, by artificially supplying algae, we may inaccurately estimate TMIIs since algae in the field can regrow (Okuyama & Bolker 2007). However, our prior research in this system suggested that *Leptasterias* caused *Tegula* to reduce grazing and avoid tide pools for at least 10 months, thereby benefitting both microalgal and macroalgal growth over 1 and 8 months, respectively (Gravem 2015). These longer-term TMIIs occurred in the absence of cages, which may artificially concentrate chemical cues and induce unnatural behaviours, and algae grew naturally so the effects of snail grazing were much more

realistic. Long-term TMIIs were also apparent in tide pools containing crabs, snails and algae on the east coast of the USA (Trussell *et al.* 2004), further suggesting that our short-term observations here could result in long-term community effects.

Though our 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 tide pools. However, the average size or hunger level of snails can sometimes vary predictably in nature, which may then change TMII strengths as suggested by our experiments. For example, average hunger level of snails may be higher and TMIIs may be weaker in the fall and winter when algae senesce, during unproductive years with low upwelling, or at high shore levels where algae are sparse. Alternatively, when resources are abundant, TMII strength should increase and DMII strength decrease because prey become more wary (Wojdak & Luttbeg 2005). 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. *Tegula* tend to be smaller at higher shore levels (Paine 1969; Doering & Phillips 1983), and population size structure is skewed towards juveniles with decreasing latitude and wave exposure (Frank 1975; Fawcett 1984; Cooper & Shanks 2011). On the other hand, *Leptasterias* tends to occur lower in the intertidal zone than *Tegula*, so both TMIIs and DMIIs may be strongest at low shore levels. Overall, a mosaic of varying TMII strength may exist as the density of *Leptasterias* and the density, population size distribution, and average energetic state of *Tegula* vary over space and time.

Conclusion

This study strengthens the connection between behavioural and community ecology paradigms by demonstrating that state-dependent foraging behaviour by prey may alter TMII trophic cascades. Our 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. We add to a small but growing body of experiments that aim to fulfil the well-recognized need to better link individual behaviour to community processes. Further, we 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 this case, accurate estimates of trophic cascades require additional elements, including (i) the nonconsumptive effects of predators on prey foraging rates (as in all TMIIs), (ii) variation in these nonconsumptive effects based on prey state (e.g. size and hunger) and (iii) variation in the direct consumptive effects including size-dependent predation rate and size-dependent grazing rate. Our insights resulted from conducting interdisciplinary

experiments on the interplay between foraging theory in behavioural ecology and TMIIs in community ecology, and this approach is likely to be a productive avenue of further investigation.

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.89qp4.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Experiments testing the consumptive and non-consumptive effects of *Leptasterias* on varying sizes of *Tegula*.

Figure S1. Responses of different sized *Tegula* to tactile and waterborne cues of *Leptasterias* in the laboratory.