

Size-dependent trait-mediated indirect interactions among sea urchin herbivores

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Despite their importance in community interactions, nonlethal indirect effects of predators are not well understood in many marine food webs. In this study, I found that within a guild of herbivorous sea urchins, small urchins (*Strongylocentrotus droebachiensis* and small *Strongylocentrotus franciscanus*) altered grazing rates in the presence of the predatory sea star (*Pycnopodia helianthoides*) and were highly preferred by the predator. In contrast, large urchins (adult *S. franciscanus*) did not significantly alter grazing in the presence of cues from the sea star and, when immobile, were less frequently attacked by the predator. However, the sea star's preference (active predator choice) was obscured by sea urchin mobility, that is, small *S. franciscanus* was only most preferred when unable to escape. These results suggest that by identifying the relative threat of predation facing guild members and the degree to which individuals transmit trait-mediated indirect interactions, these indirect effects may be predictably incorporated in community interactions. **Key words:** predator avoidance behavior, prey size selection, *Pycnopodia helianthoides*, *S. franciscanus*, *Strongylocentrotus droebachiensis*. [*Behav Ecol* 17:182–187 (2006)]

Optimality theory suggests that behavioral responses of prey are often influenced by the relative threat of predation (Lima and Dill, 1989). Because ontogenetic changes in prey affect both susceptibility to predation and size-specific behavioral responses, even members of an otherwise similar guild may respond very differently to predation threat (Dixon and Baker, 1988; Eklov and Werner, 2000; Luttbegg et al., 2003; Peacor and Werner, 2001; Werner and Hall, 1988). Many intermediate trophic-level species participate in trophic cascades due to the trade-off between adaptive predator avoidance and acquiring food (Lima, 1998). A growing body of research has recognized that in addition to numerical responses of intermediate trophic levels (i.e., density-mediated indirect interactions or DMIs), the alteration of interaction coefficients between existing community members (i.e., trait-mediated indirect interactions or TMIs) can propagate trophic cascades (Peacor and Werner, 2001; Schmitz et al., 2004; Werner and Peacor, 2003). These TMIs can have strong community effects (Schmitz et al., 2004; Trussell et al., 2002, 2003) and immediately affect an entire local community (Grabowski, 2004; Peacor and Werner, 2001; Trussell et al., 2004).

Trophic cascades can derive from various combinations of TMIs and DMIs (Werner and Peacor, 2003). A guild of otherwise similar herbivores can transmit strong TMIs with a wide range of DMIs if the adaptive behavioral responses of some herbivores effectively reduce predation and others do not. Conversely, herbivores can transmit consistent DMIs but a wide variety of TMIs if some guild members respond to predator cues and others do not. Thus, a mechanistic understanding of these factors requires unmasking behavioral responses by simulating predation threat without actual predation, comparisons of predation intensity on various herbivores, and comparisons of how herbivores reduce vulnerability to predators (Schmitz et al., 2004). In this paper, I have examined the

alteration of grazing rates among several sizes and species of an important marine herbivore, sea urchins, in response to waterborne cues from a sea star predator and related these patterns to the sea star's active predator choice for the various urchins.

Nonlethal impacts of predators are known to affect sea urchin behaviors, such as aggregation (Dayton, 1973; Scheibling and Hamm, 1991; Vadas et al., 1986), movement patterns (Duggins, 1983; Hagen et al., 1998, 2002; Mann et al., 1984), homing behavior (Carpenter, 1984), and use of refuges (Nelson and Vance, 1979). Several studies have also noted size-related behavioral changes in sea urchins, including foraging (Hart and Chia, 1990), use of refuges/spine canopies (Bernstein et al., 1981; Tegner and Levin, 1983; Williamson et al., 2004), aggregation (Bernstein et al., 1981; Hagen and Mann, 1994; Tegner and Levin, 1983), and flight response (Duggins, 1983). These ontogenetic changes in behavior may correspond to size (and species)-related differences in vulnerability to predators (Duggins, 1983; Moitoza and Phillips, 1979; Tegner and Levin, 1983). Additionally, actively feeding sea urchins are more likely to be dislodged from substrates by predators (Dayton, 1973; Tegner and Levin, 1983), suggesting there is a trade-off between foraging and predator avoidance behaviors, a trade-off often seen when prey face conflicting demands (Lima, 1998). While aspects of sea urchin ecology (protection under conspecific spine canopies and their similar role as herbivores) justify grouping them as a single guild (Bernstein et al., 1981; Duggins, 1981; Tegner and Dayton, 1977; Tegner and Levin, 1983), guilds often overlook biologically relevant interactions such as TMIs (Schmitz and Suttle, 2001). The degree to which adaptive behavioral responses reduce the grazing rates of urchins and the foraging efficiency of urchin predators will directly influence the relative importance of TMIs and DMIs in this system.

Pycnopodia helianthoides is the dominant invertebrate predator on sea urchins on the Pacific coast of North America, north of Oregon, USA. (Duggins, 1981; Mauzey et al., 1968; Pearse and Hines, 1987) and is often incorporated in interaction webs (Paine, 1980; Wootton, 1997). Physical contact with *P. helianthoides* elicits an escape response in the sea urchin *Strongylocentrotus franciscanus* (Duggins, 1983; Moitoza and

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Phillips, 1979) and the sea star's waterborne cues elicit defensive movements of spines in these sea urchins (Phillips, 1978). Although *P. helianthoides* has cascading impacts on the algal community by reducing local densities of sea urchins through direct predation and physical contact (Duggins, 1983), the impact of waterborne cues from the predator on grazing has not been investigated. This distinction is important given that waterborne cues potentially affect far more individuals than predation or physical contact. Given the importance of sea urchin grazing in many marine food webs (Paine, 1992; Sala and Graham, 2002), the influence of waterborne cues may be quite large relative to direct contact and predation.

To determine the relationship between the degree that urchins alter grazing rates and the relative threat of predation, I quantified the grazing rates of two species and sizes of sea urchins (adult *Strongylocentrotus droebachiensis* and adult and juvenile *S. franciscanus*) in the presence and absence of waterborne cues from *P. helianthoides*. I then measured the preference of *P. helianthoides* when feeding on three classes of urchins and examined the efficacy of antipredator responses by manipulating urchin mobility. Ultimately, my results suggest that the general predictability of TMIs may benefit from incorporating general adaptive behavioral responses even within this guild of herbivores.

MATERIALS AND METHODS

Predation experiments

Between December 2000 and December 2002, I conducted several predation experiments at Friday Harbor Laboratories (FHL), Washington, USA. These were designed to determine the predation threat of *P. helianthoides* on *S. droebachiensis* and large and small *S. franciscanus*. Prior to each trial, I collected *S. droebachiensis* (6–8 cm test diam) and large (i.e., adult) and small *S. franciscanus* (13–17 cm test diam and 5–8 cm test diam, respectively) from the shallow subtidal zone within 7 km of FHL. All predation and grazing experiments used similar size classes of sea urchins. In one series of predation experiments, I examined the preference of *P. helianthoides* for large and small *S. franciscanus* and the influence of sea urchin escape behaviors. For this experiment, I placed one large *S. franciscanus* and one small *S. franciscanus* in seawater tanks with a single *P. helianthoides* (45–65 cm diam). Each tank (120 × 60 × 60 cm, 1 × w × h) contained paired sea urchins both randomly assigned to one of two treatments: “tethered” or “free”. In the tethered treatment ($n = 11$), both large and small *S. franciscanus* were restrained by a monofilament line around the test that was attached to a dive weight, making it impossible for the urchins to escape the predator. In the free treatment ($n = 18$), both large and small *S. franciscanus* were unrestrained in their movement. After the sea star consumed one of the sea urchins, both sea urchins were replaced with a pair of similar urchins randomly assigned as tethered or free. The number of large and small *S. franciscanus* consumed was then compared using the chi-square goodness-of-fit tests (Zar, 1996). For this, and subsequent predation experiments, I used the null hypothesis that urchins were consumed at similar rates ($\alpha = 0.05$).

Sea urchins often occur at high densities, providing refuge for smaller urchins under the spine canopy of large individuals (Duggins, 1981; Tegner and Dayton, 1977). For this reason I ran a second predation experiment to determine the influence of density and large individuals on predation on small size classes. I placed three large *S. franciscanus*, three small *S. franciscanus* and three *S. droebachiensis* in seawater tanks (dimensions as above) with two *P. helianthoides* (30–40 cm diam) and recorded the first sea urchin consumed. I repeated

this predation experiment 11 times, always with new sea urchins, and then compared the total number of each sea urchin species consumed by *P. helianthoides* using chi-square goodness-of-fit tests (Zar, 1996).

Grazing experiments

Between October 2000 and February 2001, I conducted three separate sea urchin grazing experiments designed to test the impact of waterborne cues from *P. helianthoides* on the grazing behavior of three species/size classes of urchins (i.e., *S. droebachiensis* and large and small *S. franciscanus*). All sea urchin grazing experiments were conducted using 14 tanks (120 × 60 × 24 cm; 1 × w × h) with a shared seawater source and drain. Each tank had water inflow at one end, a standpipe drain at the other end, and was divided into compartments by fiber-glass window screening such that seawater flowed through each compartment sequentially. I conducted all grazing experiments in a similar fashion: sea urchins, kelp (*Laminaria saccharina*), and *P. helianthoides* were collected from the shallow subtidal within 7 km of FHL, and animals were starved for 5 days prior to each grazing trial. Kelp blades were cut into 10 × 5 cm pieces and allowed to sit in running seawater for 4–12 h. Six randomly selected kelp pieces were blotted dry, weighed together, and placed in tanks at the beginning of the grazing experiments (six kelp pieces/tank). After each grazing experiment (described below), kelp pieces were again blotted dry and weighed to assess sea urchin grazing rates. Individual sea urchins and *P. helianthoides* were only used in one grazing trial, and tanks were cleaned between trials.

In the first grazing experiment, I placed a single *S. droebachiensis* in the downstream compartment of each of the previously described seawater tanks. Seven of these 14 tanks contained individual *P. helianthoides* in the upstream compartment, randomly assigned to tanks, and separated from the grazing sea urchin by screening. I then added the preweighed *L. saccharina* to compartments with urchins and monitored the sea urchin's grazing daily. To mitigate the effect of food limitation on urchin grazing, when sea urchins in any of the replicates had consumed more than half the algae supplied, I terminated the grazing experiment (all 14 replicates) and reweighed the kelp. Using the same design, I repeated this experiment with small *S. franciscanus*, then large *S. franciscanus*, each grazing on *L. saccharina*. Thus, the grazing trials lasted 6 days (small *S. franciscanus* and *S. droebachiensis*) and 10 days (large *S. franciscanus*). I compared the daily weight change of algae grazed by each sea urchin species, with and without waterborne cues from *P. helianthoides* using *t*-tests ($\alpha = 0.05$). I log (+1) transformed the daily grazing rates of small *S. franciscanus* to meet the assumptions of homogeneity of variances. Similar quantities of *L. saccharina* held in a third downstream compartment of each tank without an urchin served as predator controls. These controls showed limited growth during the experiment (1.4–3.2% wet weight increase) and no effect of predator cue treatment on growth (p always > .33).

Because the above single species/size class grazing experiments may have been independently influenced by a variety of factors, I ran a second series of grazing experiments in November and December of 2002 to directly compare the impact of waterborne cues from *P. helianthoides* on the grazing behavior of large and small *S. franciscanus*. I collected sea urchins from near Turn Island, Washington, USA, and starved them for 5–10 days prior to each grazing trial. This experiment had an orthogonal design, crossing *S. franciscanus* size (large or small) with waterborne cues from *P. helianthoides* (present or absent). I prepared and weighed *L. saccharina* in a fashion similar to the previously described grazing experiments.

Table 1
Results of predation experiments involving *Pycnopodia helianthoides* feeding on sea urchins

| Treatment | Rank of predator choice | <i>n</i> | Chi ² <i>p</i> value |
|--|---|-----------|---------------------------------|
| <i>Strongylocentrotus franciscanus</i> (paired/tethered) | Small <i>S. f.</i> > large <i>S. f.</i> | 9 > 2 | .035 |
| <i>S. franciscanus</i> (paired/free) | Large <i>S. f.</i> = small <i>S. f.</i> | 10 = 8 | >.5 |
| High density (three sizes/classes) | <i>S. d.</i> > large <i>S. f.</i> = small <i>S. f.</i> ^a | 9 > 2 = 0 | .002 |

Paired *S. franciscanus* treatments had one large and one small sea urchin/tank. The high-density treatment had nine sea urchins/tank. "n" indicates the number of predation events observed; "Small *S. f.*" = small *S. franciscanus* (5–8 cm test diam); "Large *S. f.*" = large *S. franciscanus* (13–17 cm test diam); "S. d." = *Strongylocentrotus droebachiensis* (6–8 cm test diam).

^a Subdivided chi-square test: *S. d.* > large *S. f.* ($p = .035$); large *S. f.* = small *S. f.* ($p = .157$).

Three large or three small *S. franciscanus* grazed on kelp in each replicate tank (described earlier). I conducted a total of nine, 6-day grazing trials. In the first of these trials, I ran three simultaneous replicates of each treatment and used the means of each treatment in the final analysis. All other trials (eight) consisted of one replicate tank for each of the four treatments. Each animal was used in only one trial, and tanks were cleaned between trials. Results were analyzed using an ANOVA with urchin size and *P. helianthoides* presence as fixed factors and time block as a random factor using JMP statistical software (SAS Institute Inc., Cary, NC). In several of the replicates, the kelp was not consumed and grew up to 2 g, I therefore log (+3) transformed the weight change of *L. saccharina* to remove heteroscedasticity of variances. Interactions were removed only when $p > .20$. *A priori* linear contrasts of least-square means were then used to determine if exposure to *P. helianthoides* cues affected the grazing rates of large or small *S. franciscanus*.

RESULTS

Predation experiments

Pycnopodia helianthoides preferred small *S. franciscanus* over large *S. franciscanus* when both were paired, tethered to weights, and therefore unable to escape; the sea star showed no preference for large or small *S. franciscanus* when both were free to move ($\chi^2 = 4.455$, $df = 1$, $p = .0348$, and $\chi^2 = 0.222$, $df = 1$, $p = .637$, respectively; Table 1). Thus, *P. helianthoides* showed active predator choice for small urchins (sensu Sih and Christensen, 2001); however, this preference was obscured when sea urchin escape behaviors were permitted. In predation experiments on high densities of the three species/size class aggregations of sea urchins, *P. helianthoides* preferred *S. droebachiensis* over large *S. franciscanus*, but did not show preference for large *S. franciscanus* over small *S. franciscanus*

(Table 2; subdivided chi-square test, $\chi^2 = 4.455$, $df = 1$, $p = .0348$ and $\chi^2 = 2$, $df = 1$, $p = .157$, respectively). These results indicate that *S. droebachiensis* is a highly preferred prey, relative to large and small *S. franciscanus*.

Grazing experiments

In the single species/size class grazing trials, *S. droebachiensis* (6–8 cm test diam) and small *S. franciscanus* (5–8 cm test diam) in the presence of waterborne cues from *P. helianthoides* consumed significantly less *L. saccharina* than in the absence of cues from the predator (*t*-test: $df = 12$, $t = 4.39$, $p = .0009$, and $df = 12$, $t = 3.08$, $p = .0096$, respectively; Figure 1). However, adult *S. franciscanus* (13–17 cm test diam) did not alter its algal consumption significantly in the presence of waterborne cues from *P. helianthoides* (*t*-test: $df = 12$, $t = 0.49$, $p = .6335$; Figure 1). The grazing trials directly comparing large and small *S. franciscanus* grazing in the presence and absence of cues from *P. helianthoides* revealed an interaction between urchin size and predator presence/absence ($F_{1,8} = 5.141$, $p = .0376$; Table 2; Figure 2). *A priori* linear contrasts indicated that small *S. franciscanus* grazed significantly less in the presence of waterborne cues from the sea star while large *S. franciscanus* did not ($p = .0109$ and $p = .5816$, respectively). These results are further evidence that there is an ontogenetic shift in the response of *S. franciscanus* to predator cues: large individuals do not significantly alter grazing in the presence of cues from *P. helianthoides*, while smaller conspecifics reduce grazing in the presence of cues from the predator.

DISCUSSION

Results from this study demonstrate a TMII in sea urchins; exposure to waterborne cues from a sea star predator affected the grazing rates of small urchins from two species. Furthermore,

Table 2
ANOVA of weight change in *Laminaria saccharina* when grazed on by small or large *Strongylocentrotus franciscanus* (sizes as above) in the presence or absence of cues from *Pycnopodia helianthoides*

| Source | SS | MS | df | <i>F</i> ratio | Probability > <i>F</i> |
|---------------------------|---------|---------|----|----------------|------------------------|
| Urchin size | 0.56305 | 0.56305 | 1 | 2.7239 | .1183 |
| Pycnopodia | 1.84617 | 1.84617 | 1 | 5.1020 | .0538 |
| Urchin size × Pycnopodia | 1.06275 | 1.06275 | 1 | 5.1413 | .0376 |
| Block&Random | 2.96538 | 0.37067 | 8 | 1.0244 | .4868 |
| Block × Pycnopodia&Random | 2.89484 | 0.36186 | 8 | 1.7506 | .1620 |
| Error | 3.3073 | 0.2067 | 16 | | |

All trials are blocked by time, which is considered a random variable as are all interactions involving block; [response variable = log (*L. saccharina* weight change + 3)].

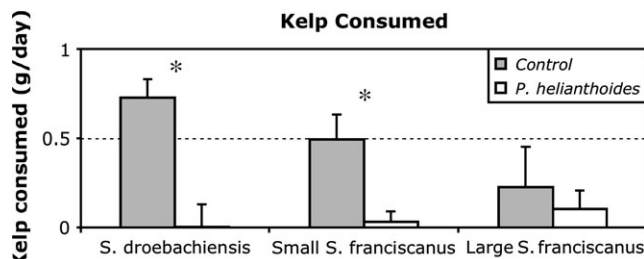


Figure 1

Amounts of kelp (*L. saccharina*) consumed (± 1 se) by sea urchins with and without waterborne cues from *P. helianthoides*. Significant *t*-test comparisons are indicated by an asterisk. Kelp consumed is the untransformed, daily weight change (initial weight – final weight) from grazing experiments lasting 6 days (*S. droebachiensis* and small *S. franciscanus*) and 10 days (large *S. franciscanus*).

the extent that urchins altered grazing rates was related to the preference of the sea star for the various urchins tested (i.e., active predator choice; sensu Sih and Christensen, 2001). The sea star showed active predator choice for small urchins but not for large urchins; accordingly, both small urchins significantly reduced grazing in the presence of cues from the sea star but large urchins did not. However, the relationship between the degree that sea urchins alter grazing rates and active predator choice is only apparent in the absence of sea urchin escape behaviors. Thus, the adaptive behavioral responses of both small urchins influence grazing rates but only in small *S. franciscanus* does it influence predation rates.

Several factors likely influence the apparent predator choice of *P. helianthoides*. Clearly, *P. helianthoides* shows a strong preference for *S. droebachiensis*; *S. droebachiensis* was consumed more often than both sizes of *S. franciscanus* (Table 1). Adult *S. droebachiensis* are small urchins (6–8 cm test diam) with short spines that are a less effective defense against the sea star. *Strongylocentrotus franciscanus* possess more formidable spines, and although small *S. franciscanus* are usually digested internally by *P. helianthoides*, large *S. franciscanus* have attained a partial size refuge and are digested extraorally (Duggins, 1983; A. Freeman, personal observation), the latter being less efficient for the sea star. When both large and small *S. franciscanus* were unable to move, *P. helianthoides* showed a clear tendency to attack small *S. franciscanus* more frequently. In contrast, manipulations of urchin mobility and density suggest that the sea star's active predator choice for small *S. franciscanus* (over large *S. franciscanus*) can be obscured by (1) the stronger escape behavior of small *S. franciscanus* (Duggins, 1983), (2) the presence of a more preferred prey (i.e.,

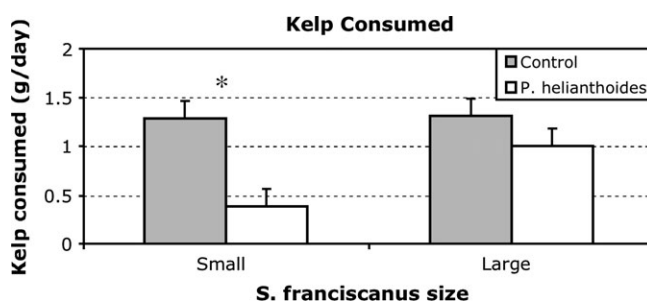


Figure 2

Amount of kelp (*L. saccharina*) consumed (± 1 se) by large and small *S. franciscanus* in the presence or absence of waterborne cues from *P. helianthoides*. An asterisk indicates a significant post-hoc comparison. Kelp consumed is the untransformed, weight change (initial weight – final weight).

S. droebachiensis), and/or (3) the ability of small *S. franciscanus* to use the spine canopy of large conspecifics (Bernstein et al., 1981; Duggins, 1981; Tegner and Dayton, 1977; Tegner and Levin, 1983). Any of these factors may obfuscate active predator choice by interfering with the predator/prey encounter rate, capture success, or consumption probability (Sih and Christenson, 2001). By making prey less vulnerable to predators, these adaptive behavioral responses can make predator preference difficult to judge (Feder, 1963; Lima and Dill, 1989; Sih, 1986) due to altered consumption rates, a trait-mediated effect.

Results from this study are the first to indicate that sea urchin grazing rates are directly influenced by waterborne cues from a predator and that this influence varies with sea urchin size. Similar ontogenetic responses to predators have been well established in freshwater systems (Eklov and Werner, 2000; Van Buskirk, 2001; Werner and Gilliam, 1984). The significance of this indirect effect on primary producers should not be overlooked in community-wide estimates of interaction strength; small *S. franciscanus* suppressed grazing by 93% and 70% (Figures 1 and 2, respectively) and *S. droebachiensis* suppressed grazing by 99% in response to cues from *P. helianthoides*. In a survey of diverse systems, Peacor and Werner (2004) found that nonlethal predator effects measured in laboratory settings often reduced consumer-resource interaction coefficients by 20–80%. In this context, the nonlethal effect of *P. helianthoides* on urchin grazing appears to be quite strong; however, several factors must be taken into consideration before making inferences to the field, including state dependence and mechanisms underlying this indirect effect, such as cue intensity.

In addition to size-selective predation by *P. helianthoides*, individual-level state-dependent decisions may influence size-specific responses to the predator. For instance, higher metabolic needs of large *S. franciscanus* or the effect of long-term starvation on small urchins may promote the risk-prone behavior of feeding in the presence of predator cues. However, sea urchins can mitigate the effects of food limitation on fecundity and survival by reducing body size and gonad volume to track rapidly changing resources (Levitan, 1989). In addition, sea urchins can live more than 100 years (Ebert and Southon, 2003) and likely do not face the short-term constraints promoting risk-prone behaviors in other systems (Ovadia and Schmitz, 2004). These characteristics of sea urchins likely reduce the relative importance of state-dependent decisions and the attenuation of nonlethal effects with time.

In aquatic systems, TMIs may more rapidly affect primary producers by influencing more herbivores simultaneously than direct predation or physical contact because they are often mediated by waterborne cues (Peacor and Werner, 2001; Trussell et al., 2004). However, in contrast to these laboratory conditions, predator cues (and nonlethal effects) in the field may be influenced by diffusion in three dimensions, advection, intermittent tidal flow, etc. Mechanistically, sea urchins grazing may be precluded during predator-induced movement (i.e., “stampeding”; Duggins, 1983) or when urchins manipulate macroalgae in a defensive manner to interfere with predator foraging (Amsler et al., 1999). However, I observed no predator cue-related differences in shielding behavior or tank areas occupied by urchins during the grazing experiments, suggesting neither behavior fully explains the reduced grazing I observed. A fundamental trade-off likely occurs because actively grazing urchins are more easily dislodged by predators (Dayton, 1973; Tegner and Levin, 1983) due to the fact that sea urchins use tube feet for feeding, locomotion, and remaining attached to substrates.

Although the indirect effects on algae in this simplified system are quite clear, the direct effects of predation (i.e.,

predator choice) are obscured by the adaptive behavioral responses of some preferred prey. Specifically, both small sea urchins alter grazing in response to waterborne cues from the sea star (a TMII), but the direct effects of the sea star are very different: *S. droebachiensis* is highly preyed on and small *S. franciscanus* successfully reduces encounters with the sea star due to its escape response. Thus, because both density and trait-mediated indirect effects are apparent, trophic cascades involving *S. droebachiensis* are likely stronger than those with *S. franciscanus*. In addition, the active predator choice underlying these historically strong interactions is still present, but through the adaptive evolution of the response of *S. franciscanus* these appear as weak direct interactions in present day experiments. This has been referred to as the “ghosts of interaction past” (Bender et al., 1984) and underscores the importance of distinguishing the strengths of both direct and indirect interactions (Abrams, 1995).

Partly due to the difficulty of manipulating all relevant species combinations (Laska and Wootton, 1998; Relyea and Yurewicz, 2002) patterns of TMIs have not been incorporated into models estimating community-wide interaction strength. My results suggest that as *S. franciscanus* grows it passes through different ontogenetic niches (sensu Werner and Gilliam, 1984) in which risk-sensitive behaviors are largely expressed by small, highly preferred, sea urchins. Existing models of community-wide interaction strengths based on guild member biomass (Sala and Graham, 2002) may incorporate these size-specific patterns in TMIs. Thus, generalizations about direct and indirect effects in this multitrophic system (kelp-sea urchins-predators) may be tractably incorporated in estimates of community-wide interaction strengths.

Sea urchins are important herbivores, structuring subtidal habitats in near-coastal systems worldwide. Although DMIs are certainly important in urchin-algae interactions, results of this study suggest that TMIs can have a large impact and urchins species/size class composition greatly influences the relative importance of these two indirect effects. Incorporating observed patterns in TMIs with estimates of interaction strength based on organism size may retain relevant biological interactions but allow some generalizations of an otherwise intractable system. Finally, these size-specific responses may be particularly important as humans continue to alter size classes of several harvested marine organisms, including sea urchins (Dayton et al., 1998; McNaughton et al., 1995; Pfister and Bradbury, 1996). Clearly, given the importance of ontogenetic changes in behavioral responses, such size class alterations may have significant impacts on community interactions.

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