

Scales of detection and escape of the sea urchin *Tetrapygus niger* in interactions with the predatory sun star *Heliaster helianthus*

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ABSTRACT

Predators can simultaneously have lethal (consumption) and non-lethal (modification of traits) effects on their prey. Prey escape or fleeing from potential predators is a common form of a non-lethal predator effect. The efficiency of this response depends on the prey's ability to detect and correctly identify its predator far enough to increase the probability of successful escape, yet short enough to allow it to allocate time to other activities (e.g. foraging). In this study, we characterized the non-lethal effect of the sun star *Heliaster helianthus* on the black sea urchin *Tetrapygus niger* by assessing the nature of predator detection and the spatial scale involved both in predator detection and in the escape response. Through field and laboratory experiments we demonstrate that *T. niger* detects chemical cues released by *H. helianthus*. In the laboratory, these chemical signals can be detected at distances of up to about 50 cm. In the field, the distance traveled by urchins when escaping, after recognition of the predation risk, was also restricted to about 40 cm. Thus, considering the sizes of the predator and prey, the spatial scale of both detection and escape is comparatively small suggesting that non-lethal effects of *H. helianthus* (e.g. how it modifies the behavior of *T. niger*) should be important at local spatial scales and highly variable at the landscape scale.

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1. Introduction

In natural systems predators can simultaneously have lethal (consumption) and non-lethal (modification of traits) effects on their prey, which in many cases can indirectly affect the community (e.g. trait-mediated trophic cascades; Turner and Mittelbach, 1990; Abrams et al., 1996; Schmitz et al., 1997). Experimental studies have shown that in some situations, the non-lethal effects of predators on natural communities can be as strong or even stronger than the lethal effects on the prey species (Trussell et al., 2004; Trussell et al., 2006a; Trussell et al., 2006b; Matassa, 2010). Non-lethal effects are important because they frequently lead to immediate and fast responses, they can simultaneously affect a large number of individuals and can have an effect throughout the lifespan of the prey (Lima, 1998a; Turner and Montgomery, 2003; Werner and Peacor, 2006). Therefore, there is a need to elucidate the nature, magnitude and variability of non-lethal predator effects on prey, as well as lethal effects.

The mechanisms that reduce predation risk are usually costly for prey in that they can reduce survival, foraging or reproduction (Lima,

1998b; Lima and Dill, 1990). Therefore, the prey responses should be rapid, flexible (reversible) and specific (low recognition error) to minimize these costs (Hagen et al., 2002). Among these flexible responses, reduction in activity, use of refugia, avoidance and escape have been documented (Kats and Dill, 1998; Wisenden, 2000). Active escape, in which prey flee to get out of reach of potential predators or to seek a refuge is widespread among many marine taxa (Dayton et al., 1977; Escobar and Navarrete, 2011; Espoz and Castilla, 2000; Jacobsen and Stabell, 2004; Mann and Wright 1984; Phillips, 1978; Schmitt, 1981). Successful escape requires prey to accurately assess predation risk using visual, mechanical or chemical “cues” released by either predators or injured conspecifics (Kats and Dill, 1998), in a way that allows the prey to anticipate and increase the chances of surviving an attack. The sensory mode and physical environment affects information transfer between predator and prey and strongly affects detection distance (Sih, 1997; Smee et al., 2010). Therefore, understanding of non-lethal predator effects requires that the types of detection cues be identified.

The distance over which preys react to predators (perception distance) and the spatial extension and duration of the escape responses will largely determine the spatio-temporal scale of non-lethal predator effects in the system (Turner and Montgomery, 2003; Smee et al., 2008). These two components, predator detection and escape distances, along with predator–prey encounter rates, will affect the ecological importance of the non-lethal effects of predators at larger spatial scales. Yet,

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most studies have only characterized prey escape responses in the laboratory, usually maximizing the predator signal and physically restricting the spatial scale of animals' movement, and only a few have estimated the scale of predator perception by the prey and the escape distances under field conditions (see Turner and Montgomery, 2003; Smee et al., 2008; Urriago et al., 2011). Here, we show that a sea urchin prey can detect predatory sunstars at a distance by using chemical cues. We determined how specific is the response, measured the distance required for predator detection by the sea urchin and the distance of the escape response once the predator is detected.

Along the coast of central Chile, the black sea urchin, *Tetrapygus niger* [Molina, 1782] (hereafter *Tetrapygus*) is the most abundant echinoid in shallow subtidal environments down to about 40 m deep, but aggregations of this species are also common and abundant in intertidal pools, channels and the low intertidal zone of wave exposed and semi-exposed shores (Santelices, 1980; 1990; Stotz and Pérez, 1990; Vásquez and Buschmann, 1997). *Tetrapygus* feed on most benthic algal species and small invertebrates (e.g. barnacles, limpets), thereby freeing primary space on rocky substrata (Contreras and Castilla, 1987; Camus, 2008; Stotz et al., 1992). In subtidal habitats, *Tetrapygus* is consumed mostly by the asteroid species *Meyenaster gelatinosus* [Meyen, 1834] and *Heliaster helianthus* [Lamarck, 1816] (Dayton et al., 1977; Gaymer and Himmelman, 2008), and occasionally by fish (Rodríguez and Ojeda, 1998). In the wave exposed intertidal zone, from where *M. gelatinosus* is absent, the sun star *H. helianthus* (hereafter *Heliaster*) is by far the most important predator of *Tetrapygus* (Castilla, 1981; Castilla and Paine, 1987), although birds can also occasionally consume individuals found in shallow tidepools and channels (S. A. Navarrete pers. obs.). In a recent publication, Urriago et al. (2011), demonstrated through field manipulations in shallow subtidal areas (ca. 3 m deep) that adult individuals of *Tetrapygus* respond rapidly to direct contact (simulated attacks) with *Heliaster* and *Meyenaster*. They further showed that a large fraction of urchin individuals (>80%) can detect the presence of these asteroid predators at close distances (< 20 cm), before physical contact, and that the escape response to *Heliaster* decays more rapidly with distance than to *Meyenaster*.

Our own observations and field manipulations of *Heliaster* in rocky intertidal shores in central Chile have shown that the experimental removal or natural absence of this sun star leads to a rapid increase in the abundance of black sea urchins on the low shore, at the interface of the subtidal–intertidal zones (S.A. Navarrete unpublished data). These changes could be produced by decreased urchin mortality due to *Heliaster* (density effects), but the rapid response suggests that a non-lethal predator effect restricts the vertical incursion of urchins to the low intertidal shore during high tides. It is therefore of interest to further assess the nature of this apparent non-lethal interaction.

The main goals of our study were to characterize the non-lethal effects of *Heliaster* on *Tetrapygus*, using laboratory and field experiments to specifically assess whether *Tetrapygus* detects *Heliaster* using chemical cues released by the sun star and which are the spatial scales of detection and escape.

2. Methods

Laboratory experiments were carried out at the Estación Costera de Investigaciones Marinas located in Las Cruces (33°30'S, 71°30'W), central Chile, between 2009 and 2010. The *Tetrapygus* and *Heliaster* individuals were collected from the low intertidal and shallow subtidal shore near the laboratory. Urchins and sun stars were maintained in separate 100 l running seawater tanks (for no longer than 4 days), and were food deprived for 24 to 48 h prior to trials. Fieldwork to assess the duration and distance of escape responses was conducted by free-diving in large channels that were relatively protected from direct wave action (to the south of the laboratory), but still subjected to high surf swash and currents.

2.1. Escape response in the field

We ran field experiments at the interface intertidal–subtidal zone to determine the responses of an undisturbed *Tetrapygus* (individuals that were not moving and that were not near a sea star) exposed to three manipulations, (1) direct contact with *Heliaster* (17.4 to 24.0 cm in diameter), by placing 2–3 of the sun star arms on top on the side of an urchin for up to 180 s, (2) direct contact (same procedure than with *Heliaster* but with one arm) with the sea star *Stichaster striatus* (13.0 to 18.7 cm), which does not prey on black sea urchins, and (3) direct contact with a plastic tube, a control for the effect of mechanical contact (see Escobar and Navarrete, 2011). Our preliminary observations suggested that aggregated urchins might respond different than isolated individuals to predatory risks and, therefore, we repeated the above assays including single and aggregated urchins into our experimental design. Under the turbulent conditions typically encountered at the transition between the intertidal and the shallow subtidal zones, it was not possible to unequivocally identify a sea urchin response when a sun star were placed a distance away and therefore all field assays were conducted only considering direct contact with the asteroids and mechanical control. To ensure independence of observations, each assay was performed with 15 different prey individuals (ranging between 3.0 and 8.0 cm in diameter) found in aggregations and 15 more individuals in isolation, all located tens of meters from each other. Predator individuals were used once. Once a sea urchin was chosen for the experiment, it was randomly assigned to one of the three treatments. In each assay, we quantified whether and when the urchin reacted (lifting and movement of spines and/or elongation and movement of podia) within 6 min of contact, the total distance traveled and the total time until the urchin stopped moving. After this, we measured the size of the sea urchin and expressed the distance traveled in units of body length (distance traveled/individual body length), to reduce possible variation due to size.

2.2. Predator detection by prey

To determine whether the urchin could detect water-borne chemical cues of the predator, we performed laboratory assays in which individual urchins were exposed to *Heliaster* exudates in a rectangular plastic tank (0.20×1.40×0.10 m) supplied with running sea water. The urchin was placed at the outlet (downstream) of the tank and the treatment solutions were added 1 m upstream from urchins. Three solutions were tested: 1) 7 ml of *Heliaster* exudates mixed with 3 ml of the dye methylene blue (*Heliaster* treatment). The dye allowed us to observe the displacement of the exudates in the tank. 2) 7 ml of raw seawater mixed with 3 ml of methylene blue ('Methylene' treatment). This treatment allowed us to determine whether the dye had an effect on the behavior of the urchin and 3) 10 ml of raw seawater ('Control' treatment), to allow us to determine whether the addition of a solution alone affected the urchin. Since this experiment was design only to determined whether chemical cues were in some way involved in the process of predator detection, we arbitrarily decided to use these concentrations. *Heliaster* exudates were prepared by immersing a single individual (24.0 to 29.0 cm in diameter) for 3 h in an 8 l tank with filtered (45 µm) seawater.

Each assay was performed with a different sea urchin and the urchin's behavior was observed for 5 min after the addition of the treatment solution. Prior to each assay, the urchin was allowed to acclimate in the experimental tank for 5 to 10 min, but it was discarded if it continued moving after this time. The occurrence and type of urchin behavioral response indicating predator detection (elongation and movement of podia, lifting and movement of spines, and displacement) and the time to respond were registered continuously following the addition of the treatment solution. A total of 10 adult individuals (7.4±0.1 cm in diameter) was tested for each treatment. Between trials, the experimental tank was washed

with ethanol (70%), thoroughly scrubbed and rinsed with fresh water and then with filtered sea water.

2.3. Detection distance

To estimate at which distance the urchin can detect the sun star, we ran laboratory trials in which urchins (6.2 to 8.6 cm in diameter) were placed at different distances, 0–10, 10–40 and 40–70 cm, from sun stars (19.0 to 26.0 cm), both under still (no flow) and flowing water conditions ('flow' of 1 l/min). One urchin was tested at a time and in each trial the sun star was placed upstream of the urchin. We further ran a control treatment in which we recorded the behavior of the urchin in the absence of a sun star. Ten trials were run for each treatment (distance and flow conditions). Replicate trials of each distance and flow condition treatments were performed with different, randomly chosen urchin and sun star. Urchins were placed in the experimental 40 l ($0.20 \times 1.50 \times 0.13$ m) tanks for a 5–10 min acclimation period before placing the sun star in the tank, and the urchin's responses were observed for a period of 5 min. Sun stars were tethered with a string to the tank wall to prevent them from attacking the urchin. The number of reacting urchins (displaying the behaviors described above), the time to respond (detection time) and the exact distance of the urchin from the sun star at the time of first response were measured.

2.4. Data analysis

To evaluate if black sea urchins were capable of detecting water-borne chemical cues from the predator, we compared the frequency (%) of response between "Control," "Methylene" and *Heliaster* treatments using the Log likelihood Chi-square test (χ^2) in a contingency table (Sokal and Rohlf, 1981).

To evaluate how detection changes with distance to predator, we compared the frequencies of responding urchins among distance ranges and between flowing and still water using log-linear modeling, a generalized linear model extension of contingency tables (Agresti, 1996). In addition, to determine the critical predator–prey distance at which the probability of detection of the predator decreased to near zero, we used logistic regression between the binary response variable (whether urchins responded or not) and the measured distance between predator and prey. Since there were no differences in detection frequency between flowing and still sea water (see Results), the logistic regression was performed on pooled data for this treatment to increase degrees of freedom.

Differences in detection times among different distance ranges and sea water flows were assessed first with a two-way factorial analysis of variance (ANOVA), with distance ranges and still/flow water as fixed factors. Again, no main effect of flow or its interaction with distance were significant at $\alpha=0.05$ (Flow: $F_{1,3}=0.37$, $P=0.5441$; Flow \times Distance, $F_{3,71}=0.63$, $P=0.5978$), or using the more conservative significance level of $\alpha=0.25$ suggested by Winer et al. (1991). Therefore, we pooled data from the two flow conditions and conducted a one-way ANOVA to compare distances.

The frequencies at which urchins responded and escaped to the stimulus in the field were compared among the different treatments and between levels of aggregation using log-linear modeling. The reaction time and the standardized displacement distances were analyzed separately with a two-way factorial ANOVA, with treatment and aggregation as fixed factors. Data were square root transformed to improve homoscedasticity and normality.

3. Results

3.1. Escape response in the field

In field trials, all (100%) urchins that were touched with *Heliaster* initiated an escape response within 8 s of contact, regardless of

whether they were alone or in aggregations (Fig. 1A, B). The reaction time was significantly faster in the *Heliaster* than in the other two treatments and there was no interaction with aggregation level (Table 1a). In contrast, when urchins were stimulated with a plastic tube (control) or with *Stichaster* fewer than 50% of the individuals responded (Fig. 1A). Although there appeared to be a difference in the proportion of individuals responding when they were alone compared to being in aggregations (Fig. 1A), the log-linear analysis showed only a significant effect of treatment and no interaction between treatment and aggregation level (Table 2a). Since lack of interaction between these factors might have been driven by the absence of variation in responses in the *Heliaster* treatment (central bars in Fig. 1A), we further contrasted the prey responses between control and *Stichaster* (eliminating the *Heliaster* treatment), correcting probabilities for multiple testing with the Bonferroni adjustment. In this case, the log linear analysis showed no significant differences between the control and *Stichaster* treatments, but a higher proportion of urchins responding when single than when in aggregations (Table 2b).

The maximum distance moved by an urchin escaping from the predator stimulus did not exceed 45 cm. Sea urchins traveled longer distances when stimulated by *Heliaster* than with *Stichaster* or the plastic tube (Control; Fig. 1C), and the distance traveled varied significantly depending on whether the individuals were single or aggregated (Table 1b). In general and across treatments, single individuals traveled longer distances than individuals in aggregations (Table 1). In addition, urchins spent more time escaping when stimulated by *Heliaster* ($128.9 \text{ s} \pm 11.7$) than in other two treatments (Control: $37.6 \text{ s} \pm 11.1$; *Stichaster*: $35.5 \text{ s} \pm 12.5$), and, across treatments, this time was greater when individuals were single ($42.9 \text{ s} \pm 8.6$) than when they were in aggregations ($91.7 \text{ s} \pm 13.0$).

3.2. Predator detection by prey

In laboratory experiments to evaluate the nature of predator detection, a higher frequency of individuals modified their behavior in the *Heliaster* treatment than in the other treatments (Fig. 2, Log likelihood Chi-square Test; $\chi^2=17.369$, $df=2$, $P=0.0002$), indicating that the black sea urchin was capable of detecting chemical signals that *Heliaster* released into the sea water. Frequency of response was similar between the water only and the water with methylene treatments.

3.3. Detection distance

In experimental trials, to determine responses at different distances from the predator, we observed that when no predators were added, only a small percentage (< 20%) of urchins displayed a response akin to predator detection (elongating and moving podia and/or lifting and moving spines and/or displacement) within the 5 min observation window (Fig. 3). The average detection time of this treatment group was nearly 5 min (Fig. 3B). In contrast, when a predator was added at distances between 0 and 10 cm, all (100%) sea urchins responded within 30 s and when the predator was placed between 10 and 40 cm away, over 90% of urchins reacted, although the reaction time increased to more than 120 s (Fig. 3). Placing the predator at distances between 40 and 70 cm from the prey elicited a response in less than 35% of the prey and the time to react was similar to that in the control treatment (Fig. 3). Thus, predator–prey distance had significant effects on the number of urchins responding (Table 3) and on detection time (one way ANOVA pooling flow and still water, $F_{3,75}=46.145$, $P=0.0001$).

Finally, the logistic regression applied to the data on detection distances showed that the probability of detection decreased rapidly after a distance of 54 cm, reaching near zero probability of detection at about 70 cm (Fig. 4, $R^2=0.6131$, $P=0.0001$).

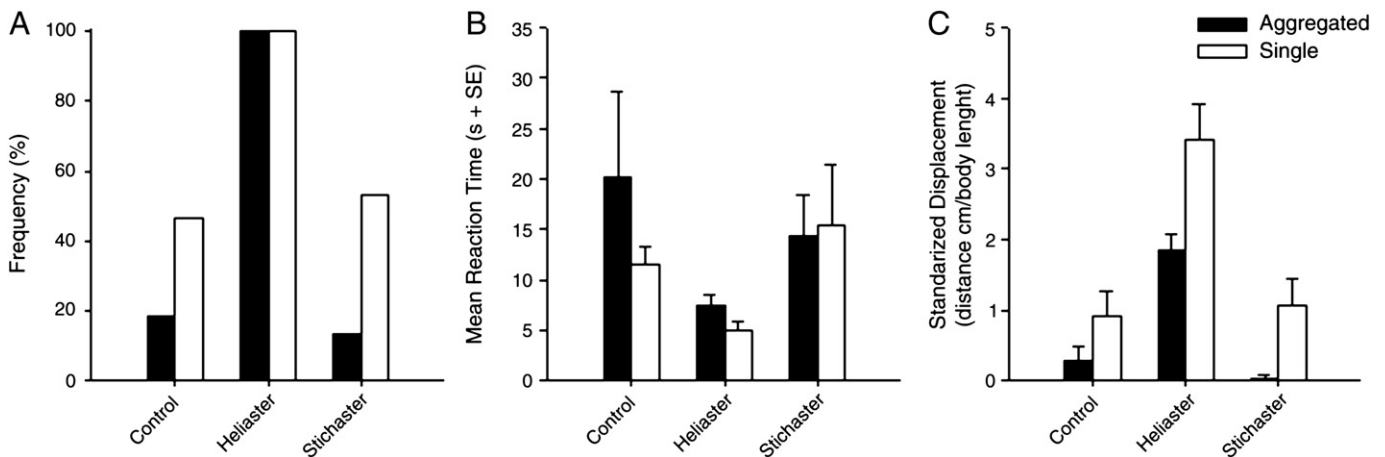


Fig. 1. A) Frequency of escape, B) Mean reaction time and C) Mean standardized displacement distance (distance in cm/ body length + SE) by *T. niger* under field conditions for grouped and single individuals for different treatments. Control: plastic tube; *Heliaster*: predator; *Stichaster*: non-predatory sea star.

5. Discussion

In this study we demonstrated that under field conditions encountered at the interface between intertidal and subtidal zones, the sea urchin *T. niger* can recognize and quickly escape from simulated attacks by the sun star *H. helianthus*. The linear distance (displacement) of the escape response varied depending on whether urchins were in isolation or in aggregations, but it did not surpass 50 cm. Through laboratory manipulations, we demonstrate that urchins can detect water-born predator cues and that the detection distance takes place in a few tens of centimeters.

As previously shown for a number of other sea urchin species (Hagen et al., 2002; Mann and Wright, 1984; Scheibling and Hamm, 1991; Tegner and Levin, 1983), *Tetrapygus* uses water-borne chemical cues to detect its predator prior to physical contact, and actively responds with an escape response initially involving extending and opening its globiferous pedicellariae and raising spines. The same mechanism of chemical predator recognition has been attributed to the sea urchin *Strongylocentrotus purpuratus* when it detects the sea star *Pycnopodia helianthoides* at a distance (Phillips, 1978). In the case of *T. niger*, Rodríguez and Ojeda (1998) in the laboratory and Urriago et al. (2011) in the field demonstrated that urchins can respond to predation threats imposed by seastars (*Meyenaster gelatinosus* and *H. helianthus*) before physical contact takes place, suggesting again the capacity to detect water-born cues.

Several studies have reported stronger responses of urchins when there is detection of a predator that has been feeding on conspecifics (Hagen et al., 2002; Parker and Shulman, 1986). Since intertidal *Heliaster* feed mostly on mussels, limpets and only occasionally on urchins (Navarrete and Manzur, 2008), and our focus was on characterizing the

scale of the predator-induced response by urchins found in the subtidal–intertidal interface to the mostly intertidal *Heliaster*, we did not include a treatment of starfish feeding on conspecifics in this study. Results show that *Tetrapygus* recognize and display a clear response to the presence of waterborne cues of *Heliaster*, even though the sun stars had been starved for at least 24 h prior to assays. Moreover, additional laboratory experiments (Manzur, unpublished data) showed that feeding and non-feeding (on urchins) *Heliaster* have the same effect on urchin behavior and feeding rates. Recognition of waterborne cues from starved predators have also been observed for *S. droebrachiensis*, which reduces its foraging rate in the presence of starved *P. helianthoides* (Freeman, 2006) and from starved echinivorous *Cancer borealis* (McKay and Heck, 2008). Thus, while further experiments are needed to evaluate whether the magnitude of the urchin response varies with predator's diet and general foraging activity, it seems that *Tetrapygus* and other urchin species can react to the mere presence of a predator.

We conducted laboratory trials under still and flowing water conditions to evaluate potential effects on urchin behavior. These two conditions are not meant to reproduce the complex turbulent environment and high flows that can be encountered in wave exposed intertidal shores (Denny, 1988). The physical environment is expected to largely influence both prey and predator perception, and therefore, the environmental context must be considered when attempting to predict the spatio-temporal scale of non-lethal responses and the extent of the indirect effects of predators in natural systems (Powers and Kittinger, 2002; Smee et al., 2008; Smee et al., 2010). As expected, in this laboratory study detection was less likely (fewer prey individuals respond) with increasing distance from the predator (Fig. 2a) and it occurred faster at shorter distances

Table 1

Two-way ANOVA for a) reaction time and b) standardized displacement for sea urchin individuals under different stimulus treatment and aggregation level. Bold face indicates significance at $\alpha = 0.05$.

Source	df	MS	F Ratio	P
<i>a) Reaction time</i>				
Treatment	2	10,400	3,535	0.0335
Aggregation	1	3,512	1,194	0.2776
Treatment \times Aggregation	2	0,442	0,150	0.8608
Error	85	2,942		
<i>b) Standardized displacement</i>				
Treatment	2	13,090	43,071	<0.0001
Aggregation	1	5,834	19,198	<0.0001
Treatment \times Aggregation	2	0,068	0,224	0,7999
Error	85	0,304		

Table 2

Log linear analysis of the two-way contingency table for a) frequency of escape under the three considered treatments (*Heliaster*, Control y *Stichaster*) and for the two levels of aggregation (Aggregated, Single) and b) the same analysis but just considering Control and *Stichaster* treatments (see results for a detailed explanation). Bold face indicates significance at the Bonferroni corrected probability of $\alpha' = 0.0167$.

Source	χ^2	df	P
<i>a)</i>			
Treatment	48.850	2	0.0001
Aggregation	0.0001	1	0.9933
Treatment \times Aggregation	0.300	2	0.8606
<i>b)</i>			
Treatment	0.013	1	0.9106
Aggregation	8.289	1	0.004
Treatment \times Aggregation	0.300	1	0.5837

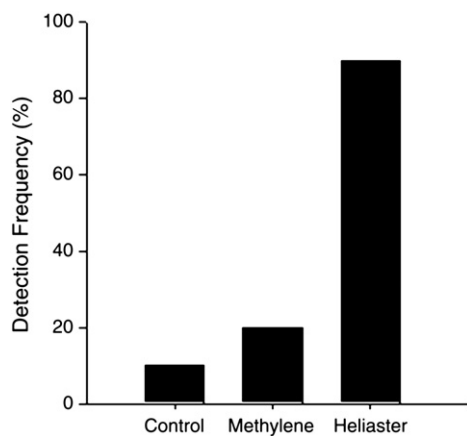


Fig. 2. Frequency of chemical predator detection by *T. niger* under laboratory conditions for Control, Methylene and *Heliaster* (predator chemical cues) treatments.

(10–20 cm, Fig. 3B). Similar results were obtained by Urriago et al. (2011) in the field at about 2–10 m deep in the shallow subtidal zone of Bahía Cisnes, northern Chile. In those field trials, Urriago et al. (2011) determined that *Tetrapygyus* can detect *Heliaster* up to 30 cm away, a shorter distance than the about 50 cm estimated from our laboratory studies under controlled conditions. We believe that these differences are probably related to the local turbulence and currents encountered the days of the field trials, which were undoubtedly more complex than those recreated in our laboratory trials. Evidence from other predator–prey systems suggest that turbulence and increased water velocity diminishes the probability of predator detection by prey (Smee and Weissburg, 2006), or prey detection by predators (Weissburg and Zimmer-Faust, 1993), coincident with the observed difference between ours and the Urriago et al. (2011) study. But there is also evidence that suggest that hydrodynamic effects on prey detection distance vary with the strength or quality of the predator chemical cue under different physical conditions (Smee and Weissburg, 2006), and/or on the risk that prey assign to a particular predator under particular environmental conditions. Further advances in this predator–prey system can be possible only through the combination of laboratory experiments and field observations under a wide range of environmental conditions because, on the one hand, although further experiments under controlled flow can shed light on predator and prey perception, we cannot reproduce in the laboratory realistic levels of turbulence and wave forces typical of the intertidal–subtidal interface. On the other hand, these same conditions

Table 3

Log linear analysis of the two-way contingency table for the four predator–prey distance ranges and for the two levels of sea water flow (Flow and Still Water (No Flow)) that behaviorally responds to predator presence. Bold face indicates significance at $\alpha = 0.05$.

Source	df	χ^2	P
Distance range	3	56.143	0.0001
Flow	1	0.000	0.9932
Distance range \times Flow	3	5.272	0.1529

restrict field observations to comparatively calm-water environments such as bays and subtidal areas (e.g. Urriago et al. 2011).

The behavior of urchins to the predator at distances beyond 40–50 cm (see Detection distance; Fig. 3A) was similar to that observed in the control treatment without a predator. This suggests that there is some error in attributing behavioral responses to predator detection in these assays. But even with a determination error of about 20% (proportion of urchins displaying ‘detection behavior’ in the controls), the detection frequency at shorter distances was significantly higher. Thus, urchins do not appear to be able to detect *Heliaster* at distances greater than about 50 cm. Urriago et al. (2011) found an even shorter detecting distance of 30 cm to *Heliaster*, but a detection distance of 50 cm to the presence of *Meyenaster gelatinosus*. It is unclear whether 50 cm distance reflects an absolute limitation in the urchin’s sensory abilities to detect any predator or in the strength or quality of the chemical signal of asteroid predators. Perhaps these short distances are sufficient to allow the urchin to successfully escape from these relatively slow moving predators. This hypothesis should be evaluated by making field observations of successful and unsuccessful predator attacks.

In our study, whether *Tetrapygyus* was isolated or in aggregation did not change the proportion of individuals responding or their reaction time, but it did reduce the distance traveled while escaping (Fig. 1). This suggests that the time needed by urchins to recognize a threat depends on the type (identity) of stimulus and the physical environment, and that once a predation threat has been recognized, the aggregation changes sea urchin perception of risk (i.e. aggregated individuals might perceive lower risk levels when within an aggregation than when alone). This explanation is in line with the increased “erroneous” responses of individuals to either the mechanical control or the non-predatory sun star observed when they were alone than when they were within an aggregation.

After an escape response was initiated, the distance traveled was within the scale of few centimeters, and the longest distance traveled did not exceeded 45 cm. Thus the spatial scale of escape response is

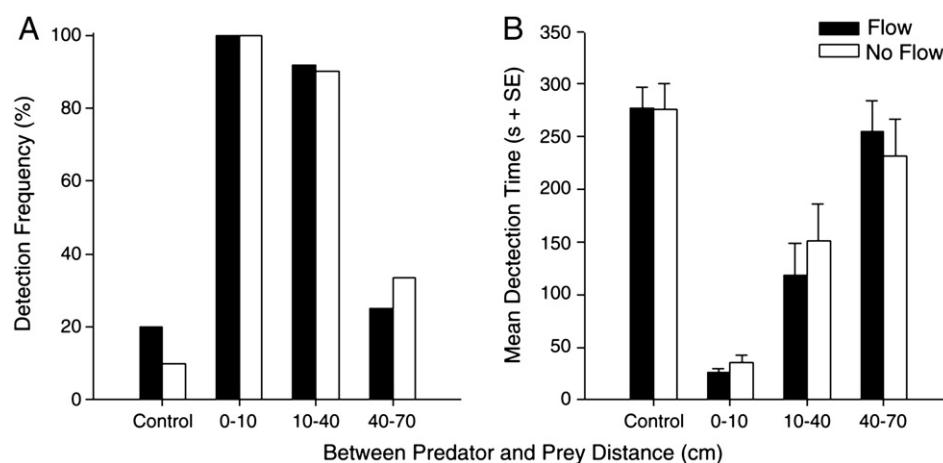


Fig. 3. A) Frequency of predator detection and B) Mean detection time (s + SE) of predator presence by *T. niger* under laboratory conditions, for different between predator and prey distance ranges and under flow and no flow water conditions.

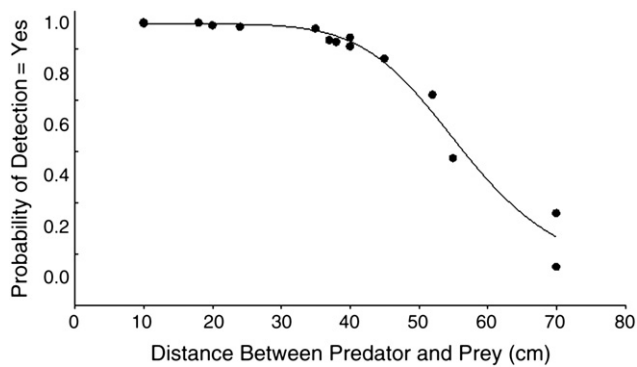


Fig. 4. Logistic regression for the probability of detection at different distances between predator and prey in *T. niger*.

comparatively small and generally corresponds to the critical detection distance. Thus the black sea urchin detects *Heliaster* and moves away to a distance at which predator signal is no longer perceived, meaning that for *Tetrapygius* a predator–prey distance of about 50 cm seems to be perceived as sufficient to prevent predation by *Heliaster*. Whether such distance is indeed effective in limiting predation must be evaluated in the field since it is difficult to reproduce the physical characteristics of the natural environment in the laboratory. In any case, these distances seem rather small considering the sizes of the predator and prey (as compared to other systems) and suggest that either the risk of predation is low (e.g. urchin moves fast enough that there is no great risk), which seems at odds with our field observations, or the costs of the response is high for the urchins.

How intermediate consumers evaluate and respond to predation risk is important not only for the evolution of the system, but also because these foraging decisions contribute to the strength and prevalence of indirect predator effects (Large and Smee, 2010). Sea urchins are important herbivores, capable of structuring low intertidal and shallow subtidal habitats (Santelices, 1990; Stotz et al., 1992 and, therefore, the non-consumptive effects of its predators can have large impact on the low shore community. Our results show that *Tetrapygius* displays fast escape responses to *Heliaster* and that it is capable of detecting chemical cues released by the predator at distances up to about 50 cm under laboratory conditions. We also show that both detection and escape responses are restricted to comparatively small spatial scales (40–50 cm). Thus, possible indirect effects on the community, transmitted through behavioral modification, could be important at small spatial scales and must be highly variable at larger spatial scales, especially considering that *Heliaster* is a relatively sedentary species (Barahona and Navarrete, 2010). Therefore, consideration of spatial scale of non-lethal predator effects, ideally under field conditions, must be considered when addressing the importance of behaviorally mediated indirect interactions in the community context.

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