Contrasting behavioral responses to predatory risk cues reflect different foraging strategies in two Caribbean sea urchins

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ABSTRACT: Non-consumptive effects (NCEs) of predators on their prey can be an important influence on ecosystems because predators can suppress the ecological roles of far more prey than they can consume. However, responses to predatory risk cues can differ among species with similar ecological functions. We tested for NCEs on grazing and movement behaviors of 2 species of sea urchins that have the potential to affect coral–algal interactions on Caribbean coral reefs: the small-bodied reef urchin *Echinometra viridis* and the larger, longer-spined sea urchin *Diadema antillarum*. We found that cues from a generalist predator, the Caribbean spiny lobster *Panulirus argus*, strongly suppressed grazing by *D. antillarum* but not *E. viridis*. Conversely, cues from simulated predation, created by crushing conspecific urchins, caused reduced grazing by *E. viridis* but not *D. antillarum*. In field tests for NCEs on movement behavior, *E. viridis* consistently moved away from lobsters on coral colonies of a variety of structural complexity levels, but movement rates were reduced in response to lobster cues only when on highly rugose corals. *D. antillarum* movement was not affected by the presence of lobsters. The contrasting responses exhibited by these 2 urchins suggest that prey respond in unexpected ways to changes in predators and habitat complexity. Different foraging strategies and the degree to which each species recognizes this predator as a potential threat appear to be the primary influences observed here. Understanding the non-consumptive effects of predators on invertebrate reef herbivores is vital because of their important roles as bioeroders and grazers on Caribbean coral reefs.

KEY WORDS: Coral reef · Spiny lobster · Habitat complexity · Non-consumptive effect · Trait-mediated indirect interaction · Circular statistics

INTRODUCTION

The interactions between predators and prey are a ubiquitous influence on the structure of ecological communities (Borer et al. 2006, Estes et al. 2011). In addition to influencing prey through direct consumption, predators can also induce behavioral and morphological responses in prey by creating a 'landscape of fear' (Laundré et al. 2001). These non-consumptive effects (NCEs) of predators include

changes in the morphology, feeding rates, movement behavior, and reproductive success of prey (Lima & Dill 1990, Lima 1998, Tollrian & Harvell 1999). When prey in turn alter feeding rates or their spatial distributions, the effect on basal resources is known as a trait-mediated indirect interaction (TMII) (Werner & Peacor 2003). TMIIs are thus a mechanism underlying trophic cascades (Schmitz et al. 2004, Preisser et al. 2005), with implications for habitat structural complexity (Haggerty et al. 2018), primary production (Griffin et al. 2011), and even the stability of ecological communities at the landscape scale (Watson & Estes 2011).

Although TMIIs have received much of the attention of researchers testing for fear effects, defensive strategies adopted by prey can be important determinants of fitness for individual organisms. For instance, hiding to avoid predation can reduce foraging and thereby lower growth and fecundity of prey (Lima & Dill 1990, Orrock et al. 2013). Similarly, prey can lower their likelihood of mortality through induced morphological changes (Robinson et al. 2014), but these require allocating energy away from growth (Nakaoka 2000). Non-consumptive effects on prey demographic rates and foraging activity can be comparable to lethal predatory effects (Grabowski 2004), so an understanding of the likelihood of NCEs is vital to predict prey population dynamics and ecological function (Peckarsky et al. 2008).

Control of macroalgal cover by herbivores is an important structuring process on coral reefs (Ogden et al. 1973, Hughes 1994, Mumby et al. 2006). There is increasing evidence that within the Caribbean, large herbivorous fish are no longer able to control macroalgae and prevent or reverse the transition from coral to algal domination (Burkepile et al. 2013, Loh et al. 2015, Suchley et al. 2016). Therefore, other groups of herbivores, and urchins in particular, play the role of grazers on many reefs. For instance, the long-spined sea urchin *Diadema antillarum* can control macroalgae at sufficient scales to enhance recruitment of reef-building corals (Myhre & Acevedo Gutierrez 2007), but recovery from a disease-induced population collapse has been slow (Lessios 2016). Similarly, the reef urchin *Echinometra viridis*, which is found in the western Caribbean, can regulate algal cover (Sangil & Guzman 2016) and prevent shifts from coral to algal dominance (Aronson et al. 2004, Kuempel & Altieri 2017).

Several observations suggest that NCEs involving urchins could affect grazing rates on coral reefs. McClanahan (1999) observed that *E. viridis* on Be-lizean reefs are highly restricted to crevices and limit their movement and feeding activity in response to predation risk. *D. antillarum* also alter their foraging patterns, both spatially and temporally, to reduce predation risk (Carpenter 1984). On temperate rocky reefs, urchins do not reduce grazing when exposed to cues from a predatory crab, potentially due to rapid dissipation of cues in turbulent flow (Harding & Scheibling 2015). Conversely, a different species of temperate urchin responds strongly to risk cues from a predatory sea star (Manzur & Navarrete 2011). In both cases, cue detection by urchins is on the scale of tens of centimeters, which would limit the spatial extent of trait-mediated trophic cascades, particularly if predators are found at low densities. Coral structural complexity contributes to the densities of *E. viridis* (Dunn et al. 2017), but it is unclear whether habitat complexity also mediates the strength of NCEs for this or other tropical urchin species.

Given that Caribbean coral reefs have generally been overfished (Stallings 2009, Valdivia et al. 2017), NCEs induced by the remaining predators may play an increasingly important role (relative to density-mediated interactions) for herbivores. This could alter the ability of herbivores to mediate coral–algal dynamics on Caribbean reefs. To contribute to our understanding of NCEs on coral reefs, we conducted experiments to understand how prey feeding and movement are altered by exposure to predatory risk cues. These experiments also allowed us to resolve the spatial scale at which fear effects operate in nature and determine how habitat complexity affects prey responses to predator risk cues. Our focal species were sympatric Caribbean sea urchins that differ in the range of habitats that they are able to use and thus may be expected to differ in their anti-predator responses (Schmitz et al. 2004, Schmitz 2005). We used laboratory feeding assays to test the hypothesis that grazing by the sea urchins *E. viridis* and *D. antillarum* is reduced when they are exposed to predatory risk cues from the Caribbean spiny lobster *Panulirus argus* or from crushed conspecific urchins. Next, we conducted field experiments to explore whether the same sea urchin species alter their movement behavior in response to cues from a spiny lobster. For the reef-obligate species *E. viridis*, we conducted field experiments to compare urchin movement behavior on 3 coral species which differed in structural complexity, while for the more mobile *D. antillarum*, we tested the spatial extent at which predator cues could affect urchin movement.

MATERIALS AND METHODS

Study site and focal species

We conducted our study in the Bahia Almirante lagoon formed by the Bocas del Toro archipelago on the Caribbean coast of Panama, with field and lab work based at the Smithsonian Tropical Research Institute Bocas del Toro Research Station (STRI). The Bocas del Toro archipelago contains numerous islands surrounded by fringing coral reefs. The common coral species found in the shallow portions of these reefs include finger coral *Porites* spp., branching fire hydrocoral *Millepora alcicornis*, and thin leaf lettuce coral *Agaricia tenuifolia* (see Dunn et al. 2017 for a complete description of the study site). We examined how the reef urchin *Echinometra viridis*, and the long-spined sea urchin *Diadema antillarum* interact with a benthic predator also found in this system, the Caribbean spiny lobster *Panulirus argus*. *E. viridis* is commonly observed on reefs in the western Caribbean, is small-bodied (average body mass in Bahia Almirante ~8 g), and is hard substrate-dependent. *D. antillarum* is a more mobile and larger-bodied urchin (average body mass in Bahia Almirante ~200 g) with long protective spines. It was historically abundant on hard-bottom and adjacent seagrass beds throughout the Caribbean. Both urchins are typically nocturnally active, inhabiting crevices during the day and emerging at night to graze on macroalgae (e.g. species in the genera *Acanthophora*, *Lobophora*, and *Dictyota*, among others), algal turfs, and seagrasses (Ogden et al. 1973, Carpenter 1986, Sangil & Guzman 2016). *D. antillarum* typically consume specific algae and seagrasses in proportion to their abundance in the field (Ogden 1976). Within Bahia Almirante, where predators are rare, *E. viridis* and *D. antillarum* are active during both day and night. However, the scale of movement of *D. antillarum*, meters to tens of meters, is substantially greater than that of *E. viridis*, which typically move <1 m (Parker & Shulman 1986, Levitan & Genovese 1989, R. P. Dunn pers. obs.). We used *P. argus* as the experimental predator because of its generalist diet, including sea urchins (Randall et al. 1964, Cox et al. 1997, Segura-García et al. 2016) and because it is still observed on the reefs of Bocas del Toro. However, *P. argus* is heavily fished in this region, with lower lobster densities and smaller individuals observed here than in other parts of the Caribbean (Guzman & Tewfik 2004). Large predatory finfish, which are typically important predators of urchins on coral reefs (McClanahan 1999, Sheppard-

Brennand et al. 2017), are virtually absent from Bahia Almirante (Cramer 2013, Seemann et al. 2014). Overall, the Bocas del Toro lagoon can be characterized as a degraded but functioning coral reef system, with altered coral assemblages (though relatively high coral cover remains on many fringing reefs), herbivore biomass dominated by small-bodied individuals, and low predator biomass (Guzman & Tewfik 2004, Cramer 2013, Seemann et al. 2014, Kuempel & Altieri 2017).

Grazing assay

We used laboratory experiments to test whether *E. viridis* or *D. antillarum* altered their grazing in response to waterborne risk cues (lobster predator or crushed conspecific urchins) relative to a no-cue, seawater control. We used multiple risk cue treatments because different risk cues can elicit varying strengths and types of prey responses (Trussell & Nicklin 2002). We conducted experiments in 40 l glass aquaria (0.3 × 0.3 × 0.45 m) that held urchins and a single *Dictyota* spp. algal bundle. *Dictyota* was collected from reefs adjacent to the STRI Bocas Research Station. Each aquarium had an inflow pipe and drain for flow-through seawater and was furnished with a cobble-sized rock to serve as a refuge. Water entered aquaria through head tanks that administered either the seawater control or 1 of the 2 risk cue treatments. Thus, there were 6 treatment combinations in these assays: *D. antillarum* in seawater control, *D. antillarum* exposed to lobster cues, *D. antillarum* exposed to crushed conspecific cues, *E. viridis* in seawater control, *E. viridis* exposed to lobster cues, and *E. viridis* exposed to crushed conspecific cues. We ran 4 trials of this experiment with 4 replicates of each treatment combination per trial (n = 16 replicates per treatment).

We created waterborne predator cues using 12 locally collected *P. argus* (carapace length mean ± SE: 55.7 ± 1.3 mm) and held them in the head tanks which supplied water to experimental aquaria. A haphazardly selected lobster was starved for 1 d prior to each trial but was offered 2 live *E. viridis* (~20 mm test diameter, TD) or 1 live *D. antillarum* (~65 mm TD) each night during the trials (for *E. viridis* and *D. antillarum* trials, respectively). Lobsters were offered more *E. viridis* due to their smaller size, and urchins not consumed were removed the following morning. We created the crushed conspecific treatments by placing crushed urchins into a mesh container within the head tank. We removed all remains

of crushed conspecifics the following morning. To create the crushed *E. viridis* treatment, 2 urchins ~20 mm TD were crushed and placed in the head tank. To minimize the number of urchins sacrificed as part of the crushed *D. antillarum* treatment, and to make the biomass of crushed urchins more similar among the 2 crushed conspecific treatments, we cut 2 *D. antillarum* individuals into quarters, froze each quarter separately, and introduced a single urchin quarter each night into the head tank.

Because of differences in size between these 2 urchin species, we used 1 *D. antillarum* (TD mean ± SE: 67.9 ± 0.8 mm) and 4 *E. viridis* (TD: 19.9 ± 0.4 mm) within each experimental aquaria. Sea urchins were starved for 2 d prior to the start of each trial. *Dictyota* spp. algal bundles were held together with 1.5 kg test monofilament line (mean biomass ± SE: 4.38 ± 0.08 g). Algae were spun 25 revolutions in a salad spinner and then weighed, both prior to the experiment and after exposure to urchins, with the amount of algae consumed determined as the change in mass (urchins never consumed >~50% of algal biomass during a single trial). To account for any autogenic change in algal biomass during trials, we kept 3 non-grazing control bundles in a separate aquarium but otherwise treated them identically to bundles exposed to urchins. We used the mean change in mass of control bundles to correct for changes to algae in experimental aquaria. While *Dictyota* spp. can be chemically defended and therefore resistant to herbivory (Paul & Hay 1986, Fong & Paul 2011), there is ample evidence that sea urchins, including *D. antillarum* and *E. viridis*, consume *Dictyota* spp. (Littler et al. 1983, Morrison 1988, Kuempel & Altieri 2017). Also, the structural integrity of *Dictyota* persisted for the duration of grazing assays, thereby allowing us to quantify consumption. Other algal species we considered using often disintegrated or were too fragmented to re-weigh by the end of a multi-day experiment. Each trial lasted ~1.5 d, with urchins added to aquaria at 16:00 h and given 2 h to acclimate before algae and the cue treatments were introduced at 18:00 h. Trials ran until 08:00 h, 2 d later. This allowed for 2 nights of grazing, as urchins were more active at night, in line with previous observations (Nelson & Vance 1979, Carpenter 1984).

Given the differences in urchin mass and number of individuals used for each species, we analyzed data collected in this experiment separately for *E. viridis* and *D. antillarum.* We calculated the risk effect size for each urchin species by cue type combination to determine whether the 2 species responded differently to the 2 cue types. Replicate measures of risk effect size were calculated as $1 - (A_{(risk)}/A_{(control)})$, where $A_{(risk)}$ is the amount of algae consumed per day within each replicate risk cue treatment aquarium and $A_{(control)}$ is the experiment-wide mean amount of algae consumed per day by urchins of each species in the seawater controls (see Matassa 2010). We then compared mean risk effect sizes for each urchin by cue combination using Student's *t*-tests to determine if the effect size differed significantly from zero.

E. viridis movement in response to predator cues

To test whether the movement of *E. viridis* differed in the presence and absence of a spiny lobster, we used time-lapse photography to monitor urchin movement behavior on 3 different coral species (*Agaricia tenuifolia*, *Millepora alcicornis*, *Porites* spp.). These corals differ in their architecture, with increasing rugosity and crevice size moving from *Porites* to *A. tenuifolia* to *M. alcicornis* (Dunn et al. 2017). We deployed GoPro cameras at 1–3 m depth at 3 reefs (STRI Bay, San Cristobal North, San Cristobal South) with 3 replicate deployments spaced >100 m apart at each reef. At each deployment there was a camera focused on 1 coral colony of each species (n = 9 replicate sets of photos per coral species). We attached cameras to a rigid frame above a 0.25 m² quadrat such that the entire quadrat was visible in the camera's field of view. We placed these camera-quadrats over an individual coral colony of each species that had >5 *E. viridis* naturally present at the beginning of the trial. We then placed an empty plastic cage adjacent to the quadrat, and the camera took time lapse photographs every 5 s for 30 min. After this pre-exposure period, we placed a spiny lobster inside the cage, and the camera took another 30 min of time lapse photos. Lobsters did not actively feed during trials, but they had been fed *E. viridis* ad libitum in holding tanks prior to trials. Given the lagoonal nature of Bahia Almirante and that we only conducted these experiments on days with minimal wind, there was no directional water flow observed. We maximized the predatory chemical cues that urchins could experience by placing experimental cages as close as possible to the focal coral colony.

For each set of time lapse photos, we used the image analysis software ImageJ (Schneider et al. 2012) to measure the net distance and direction that each urchin moved in the quadrat. We measured both of these variables during the 30 min periods both before and during exposure to the lobster.

Direction of urchin movement was measured in 30° increments to facilitate image processing, with 0°/360° being directly towards the center of the cage and 180° directly away from the center of the cage. We excluded from the analysis urchins that did not remain in the field of view for the duration of the trial (<1% of all urchins tracked).

To determine if *E. viridis* responded to the presence of the lobster by altering their movement behavior, we conducted separate *t*-tests for each coral species (pooling across sites) to compare the mean difference in net distance moved during the pre- versus during-lobster exposure periods, calculated as pre-lobster distance − with-lobster distance. We compared movement direction in the presence versus absence of the lobster using circular statistics (Jammalamadaka & Sengupta 2001). Separate Watson's 2-sample tests for each coral type were used to compare distributions of movement angles during the pre- and during-lobster exposure periods. This analysis tests for goodness of fit of the circular uniform distribution, and in this case, the 2-sample version tests the hypothesis that movement directions prior to exposure were random and uniformly distributed while movement directions in the presence of the lobster were non-random. When we obtained a significant test statistic from the Watson's 2-sample test for a given coral type, we conducted a follow-up modified Rayleigh test on urchin movement data during the lobster exposure period. This test had an *a priori* alternative hypothesis that the mean direction of urchin movement was away from the lobster when it was present. We provide polar plots to show how movement direction interacted with the net distance moved in the presence and absence of the lobster.

D. antillarum movement in response to predator cues

To determine whether *D. antillarum* move in response to cues from predators under field conditions, we deployed caged lobsters in a before/after design similar to the experiments for *E. viridis* movement. At 3 locations on each of 3 different reefs (STRI Point, San Cristobal South, San Cristobal North), we located small groups of *D. antillarum* and placed an empty cage on the reef which was located directly adjacent to one focal urchin, ~1 m from a second focal urchin, and ~2 m from a third focal urchin. We measured the exact distance from the treatment cage for each focal urchin. For 20 min, we manually tracked the location of each of these 3 urchins using

small stakes (rather than cameras that could not contain the range of *D. antillarum* within the field of view), after which we measured the net distance and direction moved relative to the treatment cage. We then re-measured each urchin's starting distance, added a lobster to the cage, and for another 20 min we tracked the net distance and direction of movement in the presence of the predator.

Statistical procedures for the *D. antillarum* movement experiment were similar to those described for *E. viridis* above, but with the need to account for the 3 initial distance categories rather than different coral species. Briefly, we conducted separate *t*-tests for each distance category to test for an effect of the presence of the lobster on the difference in net movement distance before and during exposure to the caged lobster, pooling across reefs (n = 9 individuals for medium and far, n = 8 for near because we removed 1 outlier which moved ~40× farther than other urchins in this category). Movement direction in the presence and absence of the lobster was compared using circular statistics, as described above.

RESULTS

Grazing

The 2 urchin species demonstrated contrasting responses to lobster and conspecific cues. *Echinometra viridis* reduced grazing in response to crushed conspecifics but not in response to lobster cues (t_{15} = 2.90, p = 0.01, and t_{15} = 0.16, p = 0.87, respectively; Fig. 1). In contrast, *Diadema antillarum* did not respond to crushed conspecific cues but reduced grazing in the presence of lobster cues (t_{15} = −0.28, p = 0.782, and t_{15} = 3.20, p = 0.006, respectively; Fig. 1). Notably, experimental lobsters consumed both *E. viridis* offered within the head tanks, but they did not eat any *D. antillarum*, possibly due to their large size relative to the size of the lobsters. We examine the implications of this in the 'Discussion' section.

Movement: *E. viridis*

E. viridis located on *Millepora alcicornis* colonies exhibited reduced net movement in the presence of a lobster compared to the control period (t_{63} = 2.04, p = 0.045), but there was no effect of lobster presence on *E. viridis* net movement on *Agaricia tenuifolia* (t_{108} = 0.46, p = 0.644) or *Porites* colonies (t_{121} = 0.99, p = 0.324; Fig. 2A). However, lobster presence affected
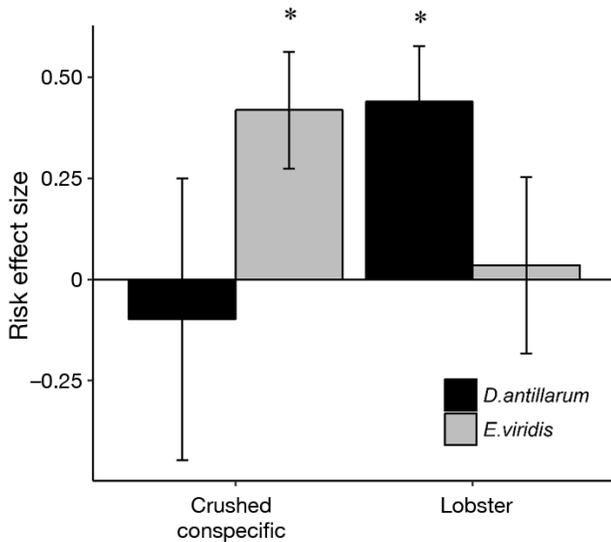
Fig. 1. Risk effect sizes for both urchin species (*Diadema antillarum* and *Echinometra viridis*) from the grazing assay. Risk cue treatments (crushed conspecifics and spiny lobster) were compared to the seawater controls. Asterisks indicate treatments that were significantly different from 0 (α = 0.05). Positive risk effect sizes signify reduced grazing in the presence of the cue versus the control. Error bars are ±1 SE

the directionality of *E. viridis* movement on all 3 coral species (all 2-sample Watson's tests p < 0.05). Urchins moved away from cages when the lobster was present but not when lobsters were absent (p < 0.03 for all post-hoc Rayleigh tests for all 3 coral species; Fig. 2B).

Movement: *D. antillarum*

Presence of a lobster did not affect net movement of *D. antillarum* for any of the 3 initial starting distances (*t*-tests, all p > 0.237; Fig. 3A). Nonetheless, interesting qualitative patterns did emerge when comparing the responses of urchins at different initial distances from the cages. *D. antillarum* starting at 1 m and 2 m distances generally moved more in the presence of the lobster than during the pre-exposure period (Fig. 3A), and there was a marginal effect of the presence of the lobster on movement distance for those urchins (*t*-test for pooled medium and far initial distances, $t_{17} = -1.80$, p = 0.088). Conversely, urchins starting adjacent to the cage moved very little overall and seemed to move more during the pre-exposure period than when the lobster was present (Fig. 3A). The direction of *D. antillarum* movement was not influenced by lobster presence for those urchins starting at the medium or far distances from the cage

(both 2-sample Watson's tests p > 0.05; Fig. 3B). An insufficient number of *D. antillarum* starting in the position nearest the cage moved to conduct statistical analyses on their movement directions.

DISCUSSION

Two sympatric Caribbean sea urchins exhibit contrasting grazing and movement responses to water-borne cues emanating from a generalist predator, the Caribbean spiny lobster. *Echinometra viridis* does not reduce its grazing in the presence of risk cues from predatory lobsters, while *Diadema antillarum* consumes less algae when lobster cues are added. However, *D. antillarum* movement is relatively unaffected by lobster risk cues, while *E. viridis* movement behavior is altered, particularly in structurally complex coral habitats. The contrasting responses, both between species and for different behaviors within species, are likely the result of different habitat associations, varying anti-predator strategies, and differential susceptibility to predation. Understanding behavioral responses to predatory cues for these 2 urchin species is important because of their functional roles as reef bioeroders (Ogden 1977, Griffin et al. 2003) and their ability to enhance coral recruitment by grazing macroalgae (Sammarco 1982, Myhre & Acevedo-Gutiérrez 2007).

Grazing

E. viridis do not appear to reduce their grazing rate in response to predatory cues from generalist Caribbean spiny lobsters, potentially due to this urchin's cryptic nature when predators are present (McClanahan 1999) or because they typically inhabit refuge-rich coral colonies (Dunn et al. 2017). In this study, small cobble refuges were available to urchins, so it is possible that the grazing response of *E. viridis* to spiny lobster cues was modified by the availability of this structure. This would be similar to the finding that *Strongylocentrotus purpuratus*, a temperate sea urchin, do not respond to cues from a predatory spiny lobster when refuge habitat is available (Green 2012). However, *E. viridis* in our experiments did significantly reduce grazing when exposed to cues from crushed conspecific urchins, suggesting that they do respond to some predation related cues and that the availability of habitat structure alone is not sufficient to pre-empt that response. Conversely, *D. antillarum* do not respond to crushed
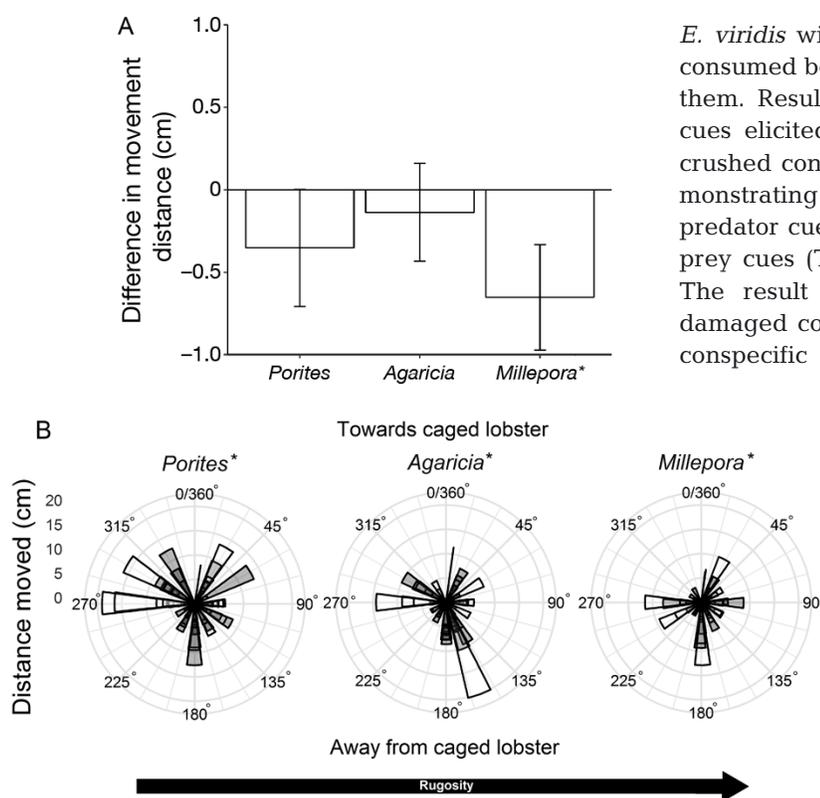
Fig. 2. Difference in (A) net distance moved and (B) net distance + direction moved by *Echinometra viridis* in the absence (white) and presence (grey) of a predatory spiny lobster on each of 3 coral species (*Porites* spp. *Agaricia tenuifolia*, *Millepora alcicornis*). Presence and absence periods were 30 min each. In (A), error bars are ±1 SE, and asterisk indicates the difference in urchin movement during pre- and post-exposure periods was statistically significant from 0 based on a *t*-test (α = 0.05). Negative values indicate reduced movement in the presence of the predatory cue. In (B), 0°/360° represents movement directly towards the empty cage or caged lobster predator while 180° represents movement directly away from the cage/lobster. Asterisks on coral genera indicate statistically significant results (α = 0.05) from post-hoc Rayleigh tests demonstrating directed movement away from the spiny lobster cue. Bars are jittered to reduce overplotting, and results are presented with coral colony rugosity increasing from left to right

E. viridis with lobster cue treatment nearly always consumed both of the *E. viridis* individuals offered to them. Results for *D. antillarum*, whereby predator cues elicited a stronger response than those from crushed conspecifics, agree with previous work demonstrating that these cue types are additive but predator cues are relatively stronger than damaged prey cues (Trussell & Nicklin 2002, Matassa 2010). The result of reduced grazing by *E. viridis* in damaged conspecific but not lobster with damaged conspecific treatments is surprising because both treatments had 2 damaged *E. viridis*. Lobsters likely consumed the *E. viridis* so quickly that damaged urchin cues did not persist in experimental tanks, while the crushed conspecific treatments had damaged urchin cues circulating for ~12 h.

E. viridis and *D. antillarum* may have also responded in contrasting ways to lobster cues because of their different predator avoidance strategies or because these 2 urchins do not recognize *Panulirus argus* as a predator to the same degree. Large *D. antillarum* are often observed grazing in seagrass beds adjacent to coral reefs (Ogden et al. 1973), and seagrass is also a productive foraging location for *P. argus* (Cox et al. 1997). Therefore, there is likely a high rate of encounter between these 2 species, and *D. antillarum* would need to be responsive to predators in such a habitat where it would be vulnerable. Conversely, in hundreds of hours underwater on fringing reefs in Bocas del Toro, we rarely observed *E. viridis* in seagrass habitat, while they were highly abundant on complex hard substrates. Given their size and habitat use patterns, echinometrid urchins may not need to reduce grazing to the same degree as *D. antillarum* because they are typically found within the refuge of either live or dead coral colonies where they are relatively invulnerable to predatory lobsters (Nelson et al. 2016, Dunn et al. 2017) and can continuously feed on drift algae (McClanahan 1999). The larger and substantially longer-spined *D. antillarum* often forages in seagrasses and on exposed patches of reef and does not rely on habitat refugia to the same degree. Instead, *D. antillarum* relies on either fleeing (Parker & Shulman 1986) or using its long spines for defense

conspecific cues but significantly reduce grazing in response to the presence of spiny lobster. This agrees with previous work showing that *D. antillarum* reduce grazing on both the calcareous alga *Halimeda* spp. and non-calcareous *Dictyota* spp. when exposed to cues from a different spiny lobster species, *Panulirus guttatus* (Kintzing & Butler 2014).

The risk cues provided to the 2 urchin species in this study may have differed slightly as a result of lobster behavior in the head tanks used to create the cue treatments. In the *D. antillarum* with lobster cue treatment, spiny lobsters were offered a live *D. antillarum* every night, but the lobsters did not consume these urchins during any trial. Lobsters in the
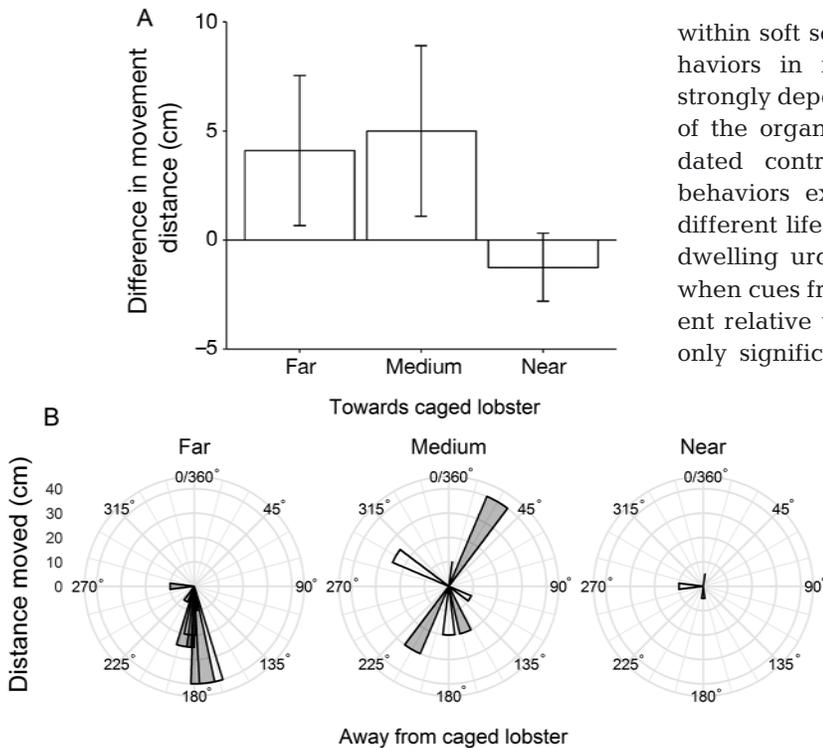
Fig. 3. Difference in (A) net distance moved and (B) net distance + direction moved by *Diadema antillarum* in the absence (white) and presence (grey) of a predatory spiny lobster. Urchins were initially located approximately 0.1 m (near), 1.0 m (medium), and 2 m (far) away from the empty cage. Presence and absence periods were 20 min each. In (A), error bars are ±1 SE. Negative values indicate reduced movement and positive values indicate increased movement in the presence of the predatory cue. In (B), 0°/360° represents movement directly towards the empty cage or caged lobster predator while 180° represents movement away from the cage/lobster. Bars are jittered to reduce overplotting, and note the scale in Panel B is double that in Fig. 2B

within soft sediments (Phillips 1977). Movement behaviors in response to predatory risk cues are strongly dependent on the life history and physiology of the organisms in question, and our study elucidated contrasting predator-associated movement behaviors exhibited by urchins with substantially different life histories. The smaller-bodied and reef-dwelling urchin *E. viridis* moved shorter distances when cues from a predatory spiny lobster were present relative to when risk cues were absent (though only significantly so on the rugose *Millepora alcicornis* colonies). *E. viridis* did, however, demonstrate directed movement away from the predator on all 3 coral types. *D. antillarum*, which are larger-bodied, have much longer spines, and forage on open reef flats or in seagrass beds, qualitatively appeared to increase their movement when predator cues were present. The latter finding agrees with a previous lab experiment in which *D. antillarum* moved further in response to waterborne cues from the spotted spiny lobster *P. guttatus* than to a seawater control (Kintzing & Butler 2014). Interestingly, *D. antillarum* responded more strongly to cues from *P. guttatus* than to cues from its congener *P. argus* (Kintzing & Butler 2014), the predator used in our experiments. This difference is likely due to different habitat usage patterns (Schmitz et al. 2004, Schmitz 2005) exhibited by these 2 palinurid lobsters, with the reef-obligate species *P. guttatus* eliciting a stronger response than *P. argus*, which utilizes a wide range of habitats.

The contrasting movement responses of the 2 urchin species tested are in line with expectations based on their distinct morphologic characteristics and different usage of protective habitats (as discussed above). For a species such as *E. viridis*, which is typically restricted to structurally complex coral colonies, a 'shelter in place' strategy requires only retreating a few centimeters into adjacent crevices. For *D. antillarum*, which uses a broader range of habitats, a more active 'fight or flight' strategy that takes advantage of their long spines and relatively rapid movement rate (Levitan & Genovese 1989) is well suited to their foraging range, where they may need to travel several meters to return to the shelter of a crevice.

when confronted with risk cues (Randall et al. 1964, Bodmer et al. 2017). *D. antillarum* confined within tanks may have reduced grazing as they minimized movement in response to a strong concentration of lobster cues. Given the potential for these sorts of laboratory artefacts, it will be important for future studies to test for TMIIs between urchin predators and coral reef macroalgae in a natural setting.

Movement

Mobile benthic organisms commonly use avoidance behaviors to minimize predation risk. These can include horizontal movement away from a waterborne risk cue (Snyder & Snyder 1970), vertical movement up and away from subtidal predators (Hovel et al. 2001) or down and into complex substrates (e.g. brittle stars; Drolet et al. 2004), and burial