

Injured conspecifics as an alarm cue for the sea urchin *Evechinus chloroticus*

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ABSTRACT: Predator mediation of sea urchin grazing pressure may occur via lethal removal of individual sea urchins or non-lethal modification of sea urchin behaviour. Several studies have shown that predation-related cues can affect sea urchin movement and grazing rates, but generalisations about the types of cues that prompt responses and the magnitude of those responses will require further research on a wider variety of species. We examined the effects of potential alarm cues on behaviour of the habitat-forming sea urchin *Evechinus chloroticus* (Echinometridae) on fished rocky reefs in northeastern New Zealand, where predators are uncommon and the sea urchins form barrens. Exposed *E. chloroticus* (i.e. those not in crevices) rapidly fled from injured conspecifics within a 1 m radius of the cue, but showed no apparent reaction to injured sea urchins belonging to another family (*Centrostephanus rodgersii*, Diadematidae), diced pilchards or the disturbance caused by fish attracted to the cues. Densities of exposed sea urchins in an area containing injured conspecifics did not return to control values for at least 20 h, while cryptic individuals remained crevice-bound when injured conspecifics were nearby. Injured conspecifics thus provide a strong, albeit localised, cue for *E. chloroticus*. By restricting sea urchins to crevices where they have a reduced impact on living kelp, this non-consumptive effect may complement the lethal effects of predation in marine reserves where populations of predators such as rock lobsters and large fish are allowed to recover from overharvesting by humans, thereby reinforcing the trophic cascade initiated by those predators.

KEY WORDS: Alarm cues · Non-consumptive effects · Sub-lethal effects · Active space · Trophic cascade · Rocky reef

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1. INTRODUCTION

Many prey species respond to the presence of predators by modifying their behaviour to reduce the chances of being attacked (Kats & Dill 1998). Prey rely on visual, mechanical or chemical cues to provide information about predators (Dicke & Grostal 2001). Chemical cues are widely used in the sea (Hay 2009). They have the advantage of being able to be detected from a distance, even in low visibility or areas of high habitat complexity (Weissburg 2012). Anti-predator behavioural responses reflect a trade-off between safety and the benefits gained from

other activities (Lima & Dill 1990). Predation cues often prompt prey to spend less time in risky, food-rich habitats and more time in safer, food-poor habitats (Beckerman et al. 1997, Cowlshaw 1997). Non-consumptive effects (NCEs) of predators on prey foraging behaviour may therefore indirectly influence the abundance and biomass of lower trophic levels, potentially strengthening trophic cascades (Werner & Peacor 2003, Schmitz et al. 2004). The strength of NCEs will depend on the spatial and temporal scales over which predation cues act (Turner & Montgomery 2003, Van Buskirk et al. 2014), the level of risk inferred from the cues (Turner

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2008, Schoeppner & Relyea 2009) and the individual prey response. Knowledge of these factors is therefore necessary for understanding the ecological importance of NCEs.

On many temperate rocky reefs, the overharvesting of predatory fishes, lobsters and sea otters by humans has allowed sea urchins to transform large areas of kelp forest into unproductive barrens (Tegner & Dayton 2000, Ling et al. 2015). Predators can suppress sea urchin grazing on kelp either lethally by removing individuals (Estes & Duggins 1995, Shears & Babcock 2002, Blamey & Branch 2012) or sublethally by reducing their feeding rates (Duggins 1983, Hagen et al. 2002, Byrnes et al. 2006). Sea urchins alter their behaviour in response to kairomones released directly from predators (Manzur & Navarrete 2011, Urriago et al. 2011) and/or cues from injured or killed conspecifics and other prey (Hagen et al. 2002, Morishita & Barreto 2011, Watson & Estes 2011, Spyksma et al. 2017). Injured conspecifics provoke a behavioural response in all sea urchins tested to date (Snyder & Snyder 1970, Mann et al. 1984, Parker & Shulman 1986, Vadas et al. 1986, Campbell et al. 2001, Hagen et al. 2002, Vadas & Elner 2003, Morishita & Barreto 2011, Watson & Estes 2011, Spyksma et al. 2017), but it is less certain how predation on other species affects sea urchins, as responses to injured heterospecifics are variable and difficult to account for in terms of phylogeny or other factors (Snyder & Snyder 1970, Parker & Shulman 1986). The most common behavioural responses to predation-related cues are fleeing from the immediate area (Mann et al. 1984, Parker & Shulman 1986, Rodriguez & Ojeda 1998, Hagen et al. 2002, Vadas & Elner 2003, Manzur & Navarrete 2011, Urriago et al. 2011, Watson & Estes 2011) and sheltering in crevices or aggregations (Bernstein et al. 1981, Scheibling & Hamm 1991, Spyksma et al. 2017). The response could be expected to differ by microhabitat, with individuals that are exposed to predators in the open being more likely to benefit from fleeing than those already in refugia. The maximum distances over which sea urchins respond to predation cues ('active spaces') are variable, ranging from <1 m (Vadas et al. 1986, Manzur & Navarrete 2011, Urriago et al. 2011) up to several metres (Snyder & Snyder 1970, Watson & Estes 2011). The time taken for sea urchins to recolonise a patch vacated in response to a predation cue has only been investigated once to our knowledge, with *Strongylocentrotus franciscanus* densities in 5 m × 5 m plots still depressed 17 d after the addition of eviscerated conspecifics (Watson & Estes 2011). Understanding the effect of NCEs on the behaviour

of any sea urchin species, and the subsequent impacts on seaweeds, clearly requires information on cue specificity, active space, the influence of microhabitat and response duration, but these have rarely been addressed in an integrated manner.

On wave-exposed rocky reefs in northeastern New Zealand, the endemic sea urchin *Evechinus chloroticus* (Family Echinometridae) plays a central role in a trophic cascade comprising predators (snapper *Chrysophrys auratus* and southern rock lobster *Jasus edwardsii*), sea urchins and kelp *Ecklonia radiata*. On reefs where predators have been overfished, *E. chloroticus* typically form a barrens zone in which abundant individuals graze in the open, whereas in well-established marine reserves with higher densities of large predators, sea urchins are less abundant and more cryptic, and do not maintain extensive barrens (Babcock et al. 1999, Shears & Babcock 2002, 2003, Shears et al. 2008, Spyksma et al. 2017). These patterns suggest that both consumptive effects and NCEs of predators on *E. chloroticus* may influence the intensity of grazing by sea urchins on kelp. A recent mesocosm study found that the presence of injured conspecifics increased crevice occupancy by *E. chloroticus*, showing that this species recognises and responds to predation cues (Spyksma et al. 2017), but the importance of those cues in the field has not been explored.

In this study, we examined the response of *E. chloroticus* to injured conspecifics in the field. We asked: (1) Is the cue specific to injured conspecifics? (2) What is the spatial extent of the response? (3) Does the response differ between exposed and cryptic sea urchins? (4) How long does the effect last?

2. MATERIALS AND METHODS

2.1. Field sites

All experiments were carried out on a large area of shallow rocky reef on fished coastline near Daniels Reef, Leigh, in northeastern New Zealand (36° 18' 9.52" S, 174° 48' 1.65" E). This site consisted of large expanses of urchin barrens, with areas of low topographical complexity interspersed with deep vertical crevices. *Evechinus chloroticus* were abundant on the reef and also within some of the crevices. Sizes of *E. chloroticus* within the barrens were typical of the area (Cole & Keuskamp 1998), with most exposed individuals having test diameters of 50–80 mm. The open nature of the crevices interspersed through the site was not suitable for small sea urchins (<40 mm

test diameter); consequently, sea urchins using these areas for refuge were of similar size to those observed on the barrens proper.

2.2. Camera and experimental set up

Field experiments were conducted using time-lapse photography. Cameras, with an image aspect ratio of 4:3, were set up, facing directly down onto the reef substrate, on custom-built quadpods (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m641p135_supp/). Quadpods consisted of a metal frame with 4 adjustable legs, allowing the camera to be positioned 1.12–2.04 m above the reef, giving an in-frame seafloor area of 6.6–10.9 m². Daytime experiments used GoPro cameras, recording a single photo every minute, while night-time experiments used Panasonic Lumix TS4 cameras, with in-built flash. The limited time-lapse capability of the Lumix cameras (60 photos maximum) allowed for 1 photo every 15–20 min.

Sea urchin behaviour was observed in response to chemical cues. Cues were placed within a 1.5 l container ('bait pot') on the reef below the camera. Empty bait pots were used for controls. All bait pots had 30 evenly spaced 5 mm holes drilled through the walls so that chemical cues could permeate into the water column. To avoid any undue disturbance to sea urchins prior to or during the experiments, reference measurements were made at the end of each observation period so that accurate movement distances could be calculated using ImageJ.

2.3. Cue specificity

We ran 3 experiments to determine whether the previously reported behavioural response of *E. chloroticus* to injured conspecifics (Spyksma et al. 2017) is specific to that cue or more generalised. In the first experiment, done in December 2014, we measured the responses of *E. chloroticus* to an injured conspecific (1 *E. chloroticus* of ~70–80 mm test diameter collected from nearby and cracked open immediately before deployment) and a crushed pilchard *Sardinops neopilchardus* ~120–150 mm length. Pilchards are pelagic fish that do not share the same habitat or guild of predators as *E. chloroticus* (Paul et al. 2001). Two controls were also used: an empty bait pot to replicate disturbance caused by placing a cue, and no-bait pot to assess if the pot itself affected urchin movement. Quadpods were set up during day-

time over groups of sea urchins (>5 ind. m⁻²) on 'barren' reefs and filmed for 60 min. Two quadpods were used so the 4 treatments were randomly applied in 2 consecutive 60 min trials. Quadpods were set up at least 5 m apart and moved at least 10 m between trials. Cues were introduced at the 20 min mark, with the time period prior to this used to evaluate natural movement patterns, and ensure the quadpods did not create undue amounts of disturbance. The 40 min period post-cue was used to investigate the behavioural response to the cues. Movement distances of each sea urchin within a 0.5 m radius of the bait pot were tracked every minute over the 60 min period, using the ImageJ plugin 'Manual Track'. This allowed the average per minute movement rate, for each individual, to be calculated for the pre- and post-cue periods. Five replicates were run. Differences in movement rate per minute between treatments, based on the average movement rate for each replicate, were analysed post-cue using a non-parametric Kruskal-Wallis tests, as the log-transformed data failed to meet the assumptions of ANOVA. Where significant differences were found, post hoc testing using the Dunn test was performed.

As *E. chloroticus* showed a minimal response to the pilchard cues, a second experiment was run in February 2015 to determine whether cues from a more closely related prey species induced a behavioural response. The sea urchin *Centrostephanus rodgersii* (Family Diadematidae) was chosen as the most functionally similar common sea urchin to *E. chloroticus* found on shallow rocky reefs in northern New Zealand (Pecorino et al. 2012). It is widespread on mainland reefs, but occurs at much lower densities than *E. chloroticus* (Andrew 1988).

A quadpod experiment, set up as described above, compared the behavioural response of live *E. chloroticus* to cues emanating from an injured *C. rodgersii* (~100–120 mm test diameter) versus an injured *E. chloroticus* (70–80 mm test diameter). Five replicates were run over the course of 3 d. Quadpods were set up at least 5 m apart and moved at least 10 m between trials. As with the previous experiment, movement rates per minute (average rate per replicate) were analysed as the response variable. Due to similarities in the pre- and post-cue movement rates of *E. chloroticus* in both controls from the previous experiment, a specific control was not used for this experiment. Instead, inspection of movement pre-cue (compared to rates observed in the previous experiment) was used to validate that changes in post-cue movement were not being influenced by factors prior to cue placement. Differences in move-

ment rates between the 2 treatments post-cue were assessed using a 2-tailed *t*-test.

Fish were attracted to all bait pots containing chemical cues, and may have therefore affected sea urchin movement behaviour by creating a disturbance or releasing cues. A third quadpod experiment was run in March 2015 to test for this possibility. Quadpods were set up using the above method, with an injured *E. chloroticus* in a bait pot as a cue. Fish were allowed access to the bait pot in one treatment and excluded in another by enclosing the quadpod within a 10 mm mesh net that was weighted at the bottom and held up with floats at the top. The area of seafloor within the mesh net was between 0.79 and 2.13 m². All fish were gently coaxed (with no physical contact occurring) from the area within the net prior to recording, and no re-entry was observed over the duration of the experiment. Four replicates were run over the course of 2 d. Quadpods were set up at least 5 m apart and moved at least 10 m between trials. The net physically constrained the outward movement of at least some individual sea urchins. This would have biased estimates of distance moved relative to the unconstrained controls, so we instead used the proportion of sea urchins moving as the response variable. Straight-line distances were measured between the initial position at the time of the cue placement (20 min) and the position at the end of the recording (60 min) for each individual sea urchin within 0.5 m of the bait pot. Individuals were deemed to have moved if their position changed by >100 mm (roughly 1 body length) during the post-cue period. Differences in the proportion of sea urchins moving in both treatments were analysed using a chi-squared test.

2.4. Spatial extent of the behavioural response

The spatial extent over which *E. chloroticus* responded to injured conspecifics was determined using footage from the December 2014 quadpod experiment, using an empty bait pot as a control. Using Image J, we drew 0.5, 1.0 and 1.5 m diameter rings around the bait pots. All exposed sea urchins within each ring were identified and their post-cue straight-line distance was measured. The proportion of sea urchins within each ring that had moved post-cue was analysed. Movement was deemed to be a straight-line distance measuring greater than 100 mm (movement of roughly 1 body length) over the 40 min post-cue period. A generalised linear model (family = binomial) with 2 fixed factors, treatment (control and conspecific) and starting ring (0.5, 1, 1.5 m) was used

to analyse whether the proportions of sea urchins moving (moving = yes or no) differed between treatments and/or distance from the cue.

2.5. Responses of exposed versus cryptic sea urchins

Sea urchins, including *E. chloroticus*, are often more active at night (Tuya et al. 2004, Dumont et al. 2006, Young & Bellwood 2011), with feeding rates being highest around dusk and dawn (Radford et al. 2008). It was therefore necessary to include night-time observations in our study to fully assess how predation cues affected sea urchin behaviour. Overnight experiments were run using the quadpods between July and September 2015.

Exposed sea urchins (i.e. those not in crevices) on 'barren' reefs were filmed at night to see how they behaved, and whether the addition of a predation cue altered normal behavioural patterns. The behaviour in response to an injured conspecific was compared against that of an empty bait pot as the control. Quadpods were set up over patches of sea urchins (<5 ind. m⁻²) at roughly 11:00 h New Zealand standard time. Sea urchins were initially filmed using GoPro cameras, before these were replaced by Panasonic Lumix cameras at 12:00 h. The Lumix cameras continued to film for 20 h, with a photo taken every 20 min. On swapping over the cameras (i.e. after 1 h) the contents from the injured conspecific bait pots were emptied onto the reef beneath the bait pot, allowing cues to then dissipate naturally as predators consumed the then dead conspecific *in situ*. Four spatially and temporally independent trials were run. The response variable analysed was sea urchin density within a 0.5 m radius of the initial bait pot position. Differences in density between the cue and control treatments were analysed using a generalised mixed effects model (family = Poisson) using penalised quasi-likelihood ('glmmPQL' from the MASS package, R v3.6.1). The model included an autoregressive process (AR1) to account for any autocorrelation with time. The model had 2 fixed factors, treatment (cue and control) and time (each observational time period post cue, n = 14). Replicate was treated as a random factor.

Sea urchins that were cryptic (i.e. occupying crevices) during daylight hours were observed through the night to see if crevice occupancy continued after dark and additionally if predation cues altered crevice occupancy by sea urchins at night. Quadpods were set up over open, vertical crevices

containing sea urchins. Open crevices were crevices with an opening width of >100 mm (mean ± SE opening width of crevices used = 200 ± 12 mm). Using the Lumix cameras, 1 photo was taken every 15 min between 16:00 and 07:00 h the following morning. Two treatments, i.e. an injured conspecific and an empty bait pot as the control, were used, with 5 spatial and temporally independent replicates.

The variable analysed was the proportion of sea urchins exposed at any one time. This metric was used instead of density because it gave a better representation of cryptic versus exposed sea urchins. Urchins were considered cryptic if they remained below the lip of the crevice. Sea urchins that left the field of view continued to be recorded with their last observed position (cryptic or exposed) being used for the remainder of the observation. The proportion of exposed sea urchins was analysed using a generalised mixed effects model (family = binomial) using penalised quasi-likelihood ('glmmPQL' from the MASS package, R v3.6.1). The model included an autoregressive process (AR1) to account for auto-correlation. The model had 2 fixed factors, i.e. treatment (cue and control) and time (each observational time period post cue, n = 14). Replicate was treated as a random factor. The optimal model was selected through backwards elimination of non-significant interaction terms. This resulted in the final model having no interaction terms.

3. RESULTS

3.1. Cue specificity

Sea urchin movement rates increased 8.4-fold in response to an injured conspecific (Fig. 1A), with most individuals (60 ± 14 [SE]%) fleeing from the cue (Video S1 in the Supplement). Flight was considered to occur if a sea urchin's end position was at least 10 cm further from the cue source than its start position (when the cue was placed). Movement rates were significantly elevated in response to an injured conspecific, compared to the

corresponding movement rates of sea urchins in the control groups (Table 1). No significant variation in movement rates post cue was observed between the crushed pilchard treatment or either control. In response to the empty bait pot, 97 ± 3% of sea urchins showed no discernible change in movement behaviour (end position was within 10 cm of start position) (Video S2).

Evechinus chloroticus did not respond to cues from an injured *Centrostephanus rodgersii*, a hetero-specific sea urchin, but greatly increased their

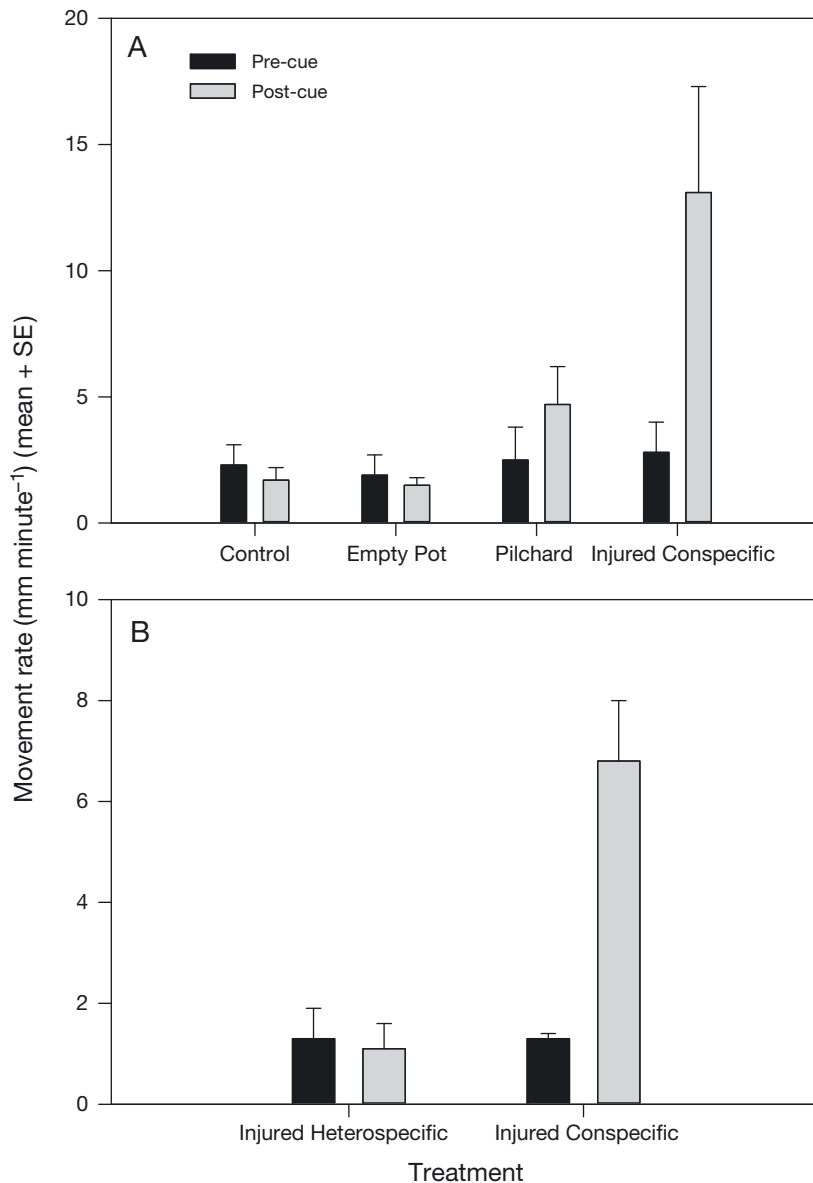


Fig. 1. Movement rates pre- and post-cue for the sea urchin *Evechinus chloroticus* in response to (A) an empty bait pot or cues from an extraneous source (crushed pilchard) or alarm cues from an injured conspecific and (B) alarm cues from an injured heterospecific or from an injured conspecific. Values are averages + 1 SE

Table 1. Results from Kruskal-Wallis test and post hoc Dunn test comparing post-cue urchin movement rates between treatments

Comparison of post-cue movement rates between treatments			
	χ^2	df	p
Post-cue	10.943	3	0.012
Differences between treatments (p-values)			
	Empty pot	Control bait	Injured conspecific
Control	0.457		
Injured conspecific	0.002	0.003	
Crushed pilchard	0.082	0.099	0.067

movement rates in response to injured conspecifics as seen in the previous experiment ($t = 3.875$, $p = 0.01$, Fig. 1B).

Fish activity around the bait pot did not influence sea urchin behaviour ($\chi^2 = 0.488$, $p = 0.485$). Approximately 60% of all sea urchins within 0.5 m of the cue moved (fled) in response to the injured conspecific cue, regardless of whether or not fish were excluded from the bait pot ($67 \pm 7\%$ when fish had access, $57 \pm 7\%$ when fish were excluded).

3.2. Spatial extent of behavioural response

Exposed sea urchins responded to injured conspecifics over a relatively small spatial scale (Table 2, Fig. 2). As distance from the cue increased, the proportion of sea urchins moving fell from 65% at 0–0.5 m to 40% at 0.5–1 m, with the value of 18% at 1.0–1.5 m being similar to the control. Sea urchins exposed to

an injured conspecific were 4.2 times more likely to be moving if they were within 0.5 m of the cue than if they were beyond 1 m.

3.3. Responses of exposed versus cryptic sea urchins

Exposed sea urchins avoided the area immediately around injured conspecifics throughout the night (Fig. 3, Table S1). After the initial drop in density from 7.8 ± 0.6 to 2.5 ± 1.2 ind. m^{-2} within a 0.5 m radius of

the cue, densities fell further during the early evening (17:00–22:00 h) to 0.3 ± 0.3 ind. m^{-2} . Densities remained low through the night and into the following morning. In contrast, densities in the control plots remained high in the immediate area throughout the night. They dropped slightly between 17:00 and 22:00 h, then remained stable at 5–6 ind. m^{-2} .

Nocturnal emergence of cryptic sea urchins from their crevice was suppressed by the presence of an injured conspecific (Fig. 4, Table S2). Sea urchins generally moved out of their crevices onto the reef from 17:00 h onwards, with a significantly higher likelihood of urchins being exposed from 20:00 h onwards (Table S2). The overall likelihood of exposure was lower in the presence of predation cues throughout the night. In controls, emigration peaked at 22:00 h, with $57 \pm 9\%$ of sea urchins being observed outside of their crevice. From this point on there was a slow progression of crevice re-entry. In contrast, only $20 \pm 9\%$ of individuals

Table 2. Generalised linear regression (family = binomial) results investigating the effects of treatment (empty bait pot [control] and injured conspecific) and distance from cue (0.0–0.5, 0.5–1.0, 1.0–1.5 m) on the response level of sea urchins. Baseline values are empty bait pot and 0.0–0.5 m from the cue except for comparisons made between 0.5–1.0 and 1.0–1.5 m, where baseline values are empty bait pot and 0.5–1.0 m

Variables	Coefficient	SE	Z	p	Odds ratio
Intercept	-2.128	0.473	-4.499	<0.001	NA
Distance from source (0.5–1.0 m)	0.182	0.644	0.283	0.777	1.200
Distance from source (1.0–1.5 m)	0.379	0.719	0.527	0.598	1.461
One crushed sea urchin	2.591	0.564	4.583	<0.001	13.342
0.5–1.0 m × 1 crushed sea urchin	-1.063	0.756	-1.406	0.116	0.415
1.0–1.5 m × 1 crushed sea urchin	-2.318	0.876	-2.647	0.008	0.240
Comparison between 0.5–1.0 and 1.0–1.5 m					
1.0–1.5 m × 1 crushed sea urchin	-1.2549	0.836	-1.5091	0.333	0.347

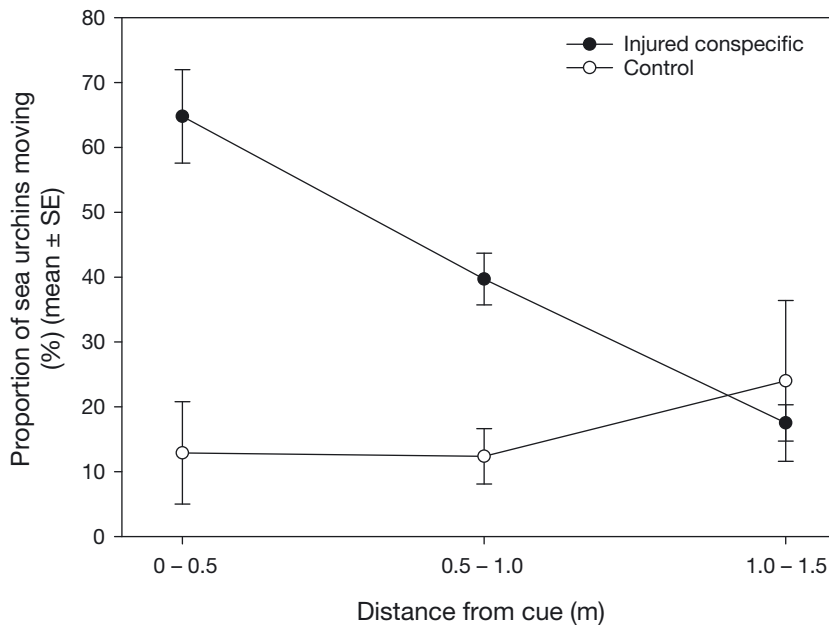


Fig. 2. Spatial extent of the behavioural (movement) response of *Evechinus chloroticus* to alarm cues from an injured conspecific. Values are averages ± 1 SE

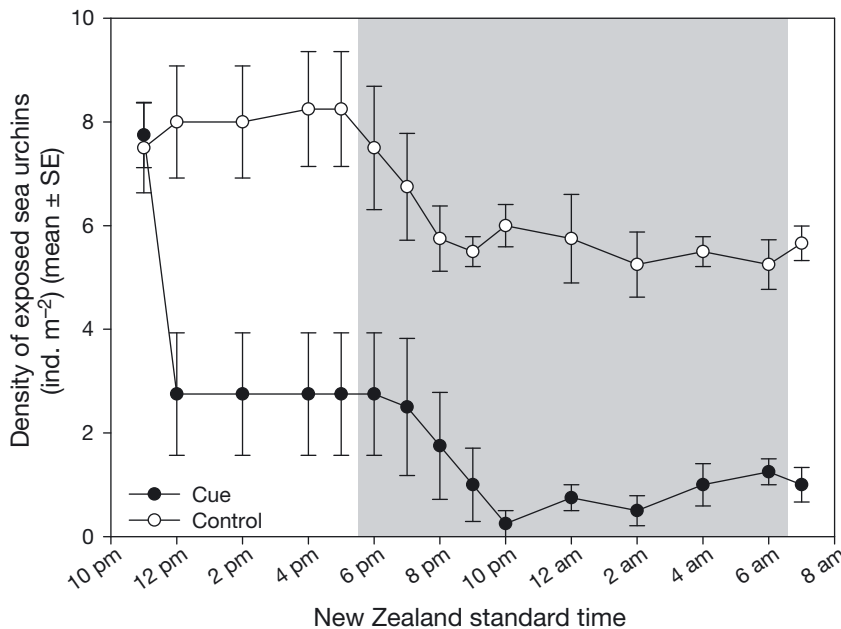


Fig. 3. Density of exposed *Evechinus chloroticus* through the night within a 0.5 m radius of a patch of reef containing cues from an injured conspecific. Cues were added 20 min after filming commenced. Grey shaded area represents night time hours. Values are averages ± 1 SE

were exposed at 22:00 h when an injured conspecific was present on the reef above. The proportion of exposed individuals peaked at $25 \pm 9\%$ in the treatment trials.

4. DISCUSSION

Injured conspecifics caused exposed individuals of the sea urchin *Evechinus chloroticus* to flee the immediate area (within 1 m), and suppressed the nocturnal emergence of cryptic individuals from their crevices. There was no apparent response to other cues tested, including injured sea urchins of another species.

4.1. Cue specificity

The strong tendency for *E. chloroticus* to move away from injured conspecifics is typical of most of the taxonomically and geographically diverse sea urchin species that have been examined (Snyder & Snyder 1970, Mann et al. 1984, Parker & Shulman 1986, Vadas et al. 1986, Campbell et al. 2001, Hagen et al. 2002, Vadas & Elnor 2003, Morishita & Barreto 2011, Watson & Estes 2011, Spyksma et al. 2017). In our study, *E. chloroticus* did not respond to other potential predation cues tested, which included injured individuals of another sea urchin species from a different family (*Centrostephanus rodgersii*), crushed pilchards (an oily fish) and the disturbance created by fish feeding on crushed urchins and pilchards. The cue for *E. chloroticus* therefore appears to be specific to injured conspecifics. There is a widespread tendency for animals to respond most strongly to cues from closely related species (Hume & Wagner 2018) that is seen in other sea urchin species subjected to injured conspecifics and heterospecifics (Snyder & Snyder 1970, Parker & Shulman 1986, Hagen et al. 2002, Vadas & Elnor 2003, Morishita & Barreto 2011). The nature of the alarm cue emanating from injured conspecifics is unknown

for sea urchins, though it is specific to internal rather than external tissues in *Psammechinus miliaris* and *Echinus esculentus* (Campbell et al. 2001).

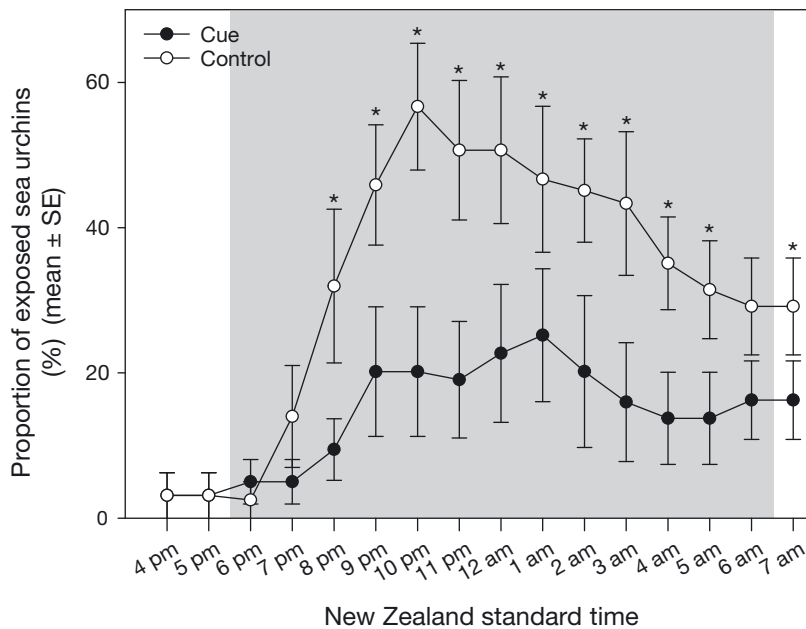


Fig. 4. Proportion of exposed sea urchins through the night when cues from an injured conspecific are situated above the crevice lip. Cues were added 20 min after filming commenced. Grey shaded area represents night time hours. Values are averages \pm 1 SE. Asterisk denotes time periods where there is a significant difference in the proportion of exposed sea urchins between control and cue treatments. Refer to Table S2 for further details

4.2. Spatial extent of behavioural response to an injured conspecific

E. chloroticus reacted to injured conspecifics up to a distance of about 1 m. This is broadly consistent with most results of field experiments done on other sea urchins. *Tetrapygus niger* fled from predatory starfish that were closer than 0.5 m (Manzur & Navarrete 2011, Urriago et al. 2011), while *Strongylocentrotus droebachiensis* moved away from crushed conspecifics from up to 0.5 m (Vadas et al. 1986). Other relatively sedentary aquatic invertebrates also respond to predation cues up to about 1 m away, e.g. the keyhole limpet *Fissurella limbata* recognising the sea star *Heliaster helianthus* (Manzur et al. 2018), and freshwater snails *Physa acuta* reacting to the sunfish *Lepomis gibbosus* (Turner & Montgomery 2003). Greater distances were reported for *S. franciscanus*, which responded to eviscerated conspecifics from at least 2.5 m away (although the reaction of distant individuals may have been influenced by movement of closer individuals rather than direct sensing of the cue) (Watson & Estes 2011), and *Diadema antillarum* responded to crushed conspecifics placed 8 m up current (Snyder & Snyder 1970). In aquatic habitats, the spatial scale is likely to

4.3. Microhabitat-specific response

While not quantified, it was obvious from the recorded images that both exposed and cryptic sea urchins were more active at night, which is consistent with other studies of *E. chloroticus* (Andrew & MacDiarmid 1991, Spyksma et al. 2017), and other species such as *Paracentrotus lividus* (Hereu 2005). In controls, exposed sea urchins grazed close to where they had been during the day, while cryptic sea urchins left their shelter around dusk to feed on the reef before returning to the same crevice by dawn. This homing behaviour is also consistent with other species of sea urchins occupying daytime crevices (Nelson & Vance 1979, Andrew 1993, Tuya et al. 2004). Injured conspecifics caused exposed sea urchins to flee and they did not fully recolonise the area containing the cue for the duration of the recording (20 h), while most cryptic individuals remained within their crevices throughout the night when the alarm cue was placed above the crevice opening (although the tendency of the controls to return to crevices as dawn approached makes it difficult to distinguish the effect of the cue during the latter part of the night from the underlying movement pattern). This is significant because it shows that

be determined by how quickly chemical cues are diluted by water motion (Weissburg & Zimmer-Faust 1993, Webster & Weissburg 2009, Large et al. 2011, Pruett & Weissburg 2018). As our study site was shallow and relatively exposed to open ocean swell, it was constantly affected by wave action. This is likely to quickly disperse chemical cues from injured conspecifics, reducing the spatial scale over which the alarm cues act. However, the perforated pots used to contain the cues likely slowed the natural rate at which the cues were diluted by water motion, elevating the cue concentration near the pots. This may have offset the effect of dilution due to water movement. On a local scale, sedentary predators, or in our case a stationary cue, are more likely than mobile predators to provoke behavioural responses because the cues are relatively persistent (Preisser et al. 2007, Miller et al. 2014).

alarm cues alone can restrict the spatial and temporal distribution of sea urchins and create areas where very little sea urchin grazing activity occurs, even during dusk, a peak feeding period (Radford et al. 2008). Sea urchins restricted to crevices tend to feed on drift algae rather than living kelp (Harrold & Pearse 1987).

4.4. Conclusion

Our study builds upon previous research by quantifying multiple components of the response to predation cues for a single species of sea urchin, with our model organism being *E. chloroticus*, an important habitat-forming sea urchin in northern New Zealand. We found a strong but localised effect of injured conspecifics on the behaviour of *E. chloroticus*, suggesting the cue would have a limited effect in habitats where populations are dominated by exposed sea urchins, i.e. in fished areas where predators are generally rare. In these areas, NCEs that change prey behaviour are unlikely to be important initially in facilitating the recovery of kelp. However, the finding that sea urchins were less likely to emerge from crevices in the presence of conspecific alarm cues could have important ecological implications. Sea urchins increase shelter use when predators, and predation cues such as conspecific alarm cues, are abundant (Spyksma et al. 2017), and theory predicts that prey should remain within refuge habitats long after predators have left the area (Sih 1992). As conspecific alarm cues are important for maintaining sheltering behaviour, this may represent an important feedback that helps to maintain or enhance kelp forests by restricting the amount of time individuals spend actively foraging.

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