



Multiple factors explain the covering behaviour in the green sea urchin, *Strongylocentrotus droebachiensis*

CLÉMENT P. DUMONT*†, DAVID DROLET*, ISABELLE DESCHÊNES* & JOHN H. HIMMELMAN*

*Département de Biologie, Québec-Océan, Université Laval

†CEAZA, Departamento de Biología Marina, Universidad Católica del Norte

(Received 26 March 2006; initial acceptance 29 August 2006;

final acceptance 13 November 2006; published online ■ ■ ■; MS. number: A10403)

Although numerous species of sea urchins often cover themselves with small rocks, shells and algal fragments, the function of this covering behaviour is poorly understood. Diving observations showed that the degree to which the sea urchin *Strongylocentrotus droebachiensis* covers itself in the field decreases with size. We performed laboratory experiments to examine how the sea urchin's covering behaviour is affected by the presence of predators, sea urchin size, wave surge, contact with moving algae blades and sunlight. The presence of two common sea urchin predators did not influence the degree to which sea urchins covered themselves. Covering responses of sea urchins that were exposed to a strong wave surge and sweeping algal blades were significantly greater than those of individuals that were maintained under still water conditions. The degree to which sea urchins covered themselves in the laboratory also tended to decrease with increasing size. Juveniles showed stronger covering responses than adults, possibly because they are more vulnerable to dislodgement and predation. We found that UV light stimulated a covering response, whereas UV-filtered sunlight and darkness did not, although the response to UV light was much weaker than that to waves and algal movement. Our observations suggest that the covering behaviour of *S. droebachiensis* has evolved as an adaptation to protect it from mechanical injuries associated with abrasion and dislodgement, and to a lesser extent as a defence against UV radiation. The covering behaviour may reduce the sea urchin's ability to move and this would limit its ability to forage and to flee from predators. In this case, the covering behaviour may have evolved as a trade-off between locomotion and limiting environmental stresses.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: age-related behaviour; behavioural plasticity; camouflage; covering behaviour; decoration; foraging; green sea urchin; physiological costs/benefits; protection; *Strongylocentrotus droebachiensis*

Animals have evolved a variety of strategies to protect themselves from biotic and abiotic stresses, and the vulnerability to such stresses often varies as animals increase in size. The covering behaviour (also referred to as camouflage), in which animals voluntarily cover themselves with materials from the surrounding environment, is often considered as an antipredator adaptation that makes an animal less visible to predators or creates a physical barrier

that reduces predator success. For example, many insect larvae attach materials to their bodies to protect themselves from visual predators (Brandt & Mahsberg 2002; Bacher & Luder 2005), and wolf spiders, *Lycosa tarantula*, cover their burrows with materials to decrease predation by scorpions (Williams et al. 2006). Similarly, decorator crabs commonly attach materials to their exoskeleton, and hermit crabs attach materials to the shells they occupy, as camouflage from visual predators, and they sometimes select materials that deter predators (Wicksten 1993; Stachowicz & Hay 2000; Williams & McDermott 2004). Polychaete worms can gain protection from predators by incorporating algal and shell fragments into their tubes (Brenchley 1976). All of these behaviours make the animal more cryptic, so they are generally interpreted as adaptations to avoid predators (Berke et al. 2006).

Correspondence and present address: C. P. Dumont, CEAZA, Departamento de Biología Marina, Universidad Católica del Norte, Larroñedo 1281, Casilla 117, Coquimbo, Chile (email: cdumont@ucn.cl). D. Drolet is now at the Department of Biology, University of New Brunswick, Fredericton, New Brunswick E3B 6E1, Canada. I. Deschênes and J. H. Himmelman are at the Département de Biologie, Université Laval, Québec G1K 7P4, Canada.

Covering behaviour is widespread among echinoids, but there is little consensus as to its function. Milligan (1915) and Douglas (1976) suggested that it functions as camouflage and physical protection from predators, but this has only been demonstrated recently for *Sterechinus neumayeri* (Amsler et al. 1999); covering increased the probability of surviving an encounter with predatory sea anemones, *Isotealia antarctica*. Sea urchins are sensitive to light (Millott 1975), and their sensitivity to sunlight, particularly UV radiation, may explain why sea urchins cover themselves (Millott 1956; Sharp & Gray 1962; Lees & Carter 1972; Adams 2001; Verling et al. 2002; Kehas et al. 2005). However, covered sea urchins can also be found in shaded or dark conditions (Dix 1970; Lees & Carter 1972; Douglas 1976), or at depths devoid of light (Levin et al. 2001). Several workers suggest that the covering behaviour in echinoids represents a food storage strategy (Ebert 1968; Dix 1970; Douglas 1976), because they often cover themselves with pieces of macroalgae. Finally, the behaviour could be a means to protect the animal from drifting materials and sediments (Richner & Milinski 2000), from dislodgement by wave surge (Lees & Carter 1972; James 2000), or from desiccation during low tides in the intertidal zone (Orton 1929; but see Millott 1956; Glynn 1968). Covering behaviour shows marked temporal variation within and between species. Some sea urchins cover themselves for days or weeks at a time (Douglas 1976; James 2000), whereas others pick up and drop materials within hours, and some sea urchins show a daily pattern in covering (Millott 1956; Sharp & Gray 1962; Lees & Carter 1972; Adams 2001; Barnes & Crook 2001). The covering behaviour of sea urchins can also vary between locations and even over short distances within a location (Douglas 1976; James 2000; Barnes & Crook 2001).

The wide array of biotic and abiotic factors known to affect the covering behaviour of sea urchins, as well as the spatial and temporal variations in the response, suggests that covering behaviour is determined by more than one factor. However, most studies on the covering behaviour in sea urchins report responses to a single factor, and limit consideration of other potential factors.

We performed experiments to examine the potential influence of a variety of factors on the covering response of the green sea urchin, *Strongylocentrotus droebachiensis*. In the western North Atlantic, *S. droebachiensis* is frequently observed holding materials from the surrounding environment on its aboral (upper) surface and sometimes on the sides as well (Fig. 1). The common covering materials include pieces of coralline algae, algal blades and sea urchin, and small stones and shells. We first report field observations showing that juveniles cover themselves more than adults. We then performed experiments considering a variety of factors that could induce the covering behaviour, taking into consideration the importance of sea urchin size. The high frequency of covering in juveniles indicates that this behaviour could represent a defence mechanism against predators, since juveniles are more vulnerable to predators (Scheibling & Hamm 1991). In this case, we would expect juveniles to react more strongly than adults to the presence of predators. We conducted laboratory experiments to test this prediction. We then



Figure 1. A sea urchin, *Strongylocentrotus droebachiensis*, heavily covered with pieces of coralline algae on sea urchin barren (the individual covered is delimited with a dashed line).

tested how wave surge affected sea urchins of different sizes. Finally, we conducted a series of laboratory experiments to examine the effect of moving algal blades, sunlight and depth from which sea urchins were collected on covering behaviour.

METHODS

Our study was conducted in the Mingan Islands in the northern Gulf of St Lawrence, eastern Canada (50°13.6'N, 63°41.12'W), during the summer in 2002, 2003 and 2004. Laboratory experiments were conducted in a wet laboratory located at Havre Saint-Pierre (within a few kilometres of our field sites) with running sea water pumped in from a depth of 10 m. Throughout our study, we quantified covering behaviour using a covering index of 0–3: 0 = no covering material; 1 = material covered less than 50% of the animal's surface; 2 = material covered more than 50% of the animal's surface when viewed from above; 3 = heavily covered (see Fig. 1), including materials on the sides, which could potentially impede movement.

Effect of Size of Sea Urchins in the Field

In August 2002 we quantified the covering behaviour of individuals on sea urchin barrens at two sites, Goéland East and Pointe Enragée, to determine whether the degree to which sea urchins cover themselves varies with sea urchin size. At each site, we noted the size and covering index of all sea urchins found in nine quadrats (25 × 25 cm) that were randomly placed at a depth of 5–7 m. For each quadrat, we later calculated the average covering index of the sea urchins in six size classes: <10, 10–15, 15–20, 20–25, 25–30 and >30 mm in diameter. Average covering indexes of sea urchins of different sizes were analysed using a mixed-model ANOVA with site and quadrat as random factors and size as the fixed factor. The form of the ANOVA table was determined with the

method proposed by Underwood (1997). Multiple comparisons were made using Tukey tests.

Effect of the Presence of Predators

We performed laboratory trials to examine whether the presence of predators affected the covering behaviour of juvenile (10–15 mm in diameter) and adult (30–50 mm) sea urchins. In each trial, we placed five sea urchins, either juvenile or adult, in a plastic tank (45 × 33 × 10 cm), the bottom of which was covered with pebbles and pieces of coralline algae, and introduced either a predator, the sea star *Crossaster papposus* or the crab *Cancer irroratus*, or a stone (no predator as control). *Crossaster papposus* and *Cancer irroratus* are common predators of sea urchins in the northern Gulf of St Lawrence (Himmelman 1991; Gaymer et al. 2004). After a 1-h period, we quantified the covering index of the five sea urchins (no predation occurred during these trials). The mean covering index of the five sea urchins for each trial was used as the dependant variable, and a fixed factorial ANOVA was applied to the data with the size of sea urchin (10–15 and 30–50 mm) and predator stimulus (absent, sea star or crab) as factors.

Effects of Sea Urchin Size and Wave Intensity

We conducted a factorial experiment in a wave tank (2.4 × 1.22 × 0.48 m; Gagnon et al. 2003) to evaluate the effect of sea urchin size and wave intensity on covering behaviour. Sea urchins of different sizes (10–15, 15–20, 20–25, 25–30 and 30–50 mm in diameter) were exposed to three wave intensities: (1) no waves, (2) weak waves (causing a horizontal flow of 10 cm/s) and (3) strong waves (25 cm/s). We first covered the bottom of the tank with concrete tiles, the surface of which mimicked a natural rocky substratum, then we spread potential covering material over the tiles (approximately 30 litres of pebbles and cobbles measuring 0.5–5 cm, 8 litres of pieces of coralline algae measuring 0.5–3 cm and 3 litres of whole and broken bivalve shells and calcareous sea urchin skeletons). To eliminate potential bias due to variation in light intensity, all trials were conducted in darkness. The water depth in the tank was maintained at 25 cm (when there were no waves) and temperature ranged from 3 to 10°C. Sea urchins were collected at depths of 5–7 m from a sea urchin barren at Île aux Goélands 2 days before the experiment and were periodically provided with food (blades of brown alga, *Alaria esculenta*). Before each trial, we placed 10 sea urchins of a specific size class in a 30 × 30-cm area in the centre of the wave tank and allowed them 2–3 min to attach and settle. In treatments without waves, each trial began immediately after the acclimation period, and in treatments with waves, each trial was started by turning on the motor that generated the waves. Each trial was run for 1 h, after which we noted the covering index of each sea urchin. In analysing these data, the average covering index for each of the five trials was treated as the dependant variable and these values were log-transformed (because variances tended to increase with an increase in the mean). We applied a two-way ANOVA with

size of sea urchin (10–15, 15–20, 20–25, 25–30 and 30–50 mm) and wave intensity (null, weak and strong) as fixed factors. When significant effects were detected, we followed with multiple comparisons using Tukey tests.

Effect of Moving Algal Blades

Our diving observations in the Mingan Islands indicated that the degree to which sea urchins covered themselves was greater for individuals close to macroalgae blades than for individuals further away from macroalgae (particularly when there were wavy conditions). Thus, we conducted a laboratory experiment to evaluate the effect of moving algae on the covering behaviour of large (30–50 mm) sea urchins (most sea urchins near the macroalgal zone are large). We used a factorial experimental design with presence and absence of algae in the presence of weak and strong waves. This experiment was run at the same time as the experiment investigating the effects of sea urchin size and wave intensity (see above), so we used the same trials for the treatments in absence of algae in both experiments. In treatments with algae, blades of the brown algae *Alaria esculenta* were wedged between a split in a plastic tube set across the bottom of the wave tank. Before each trial, we placed 10 sea urchins in a 30 × 30-cm area in the centre of the tank (and underneath the algae in the trials with algae) and allowed them 2–3 min to attach and settle. We then turned on the wave generator for 1 h. At the end of each trial (five trials for each sea urchin size, both with and without algal blades), we determined the covering index of the 10 sea urchins. We used the mean index for each trial as the dependant variable and analysed the data using a 2 × 2 factorial ANOVA with algae (presence, absence) and wave intensity (weak, strong) as fixed factors.

Effect of Sunlight Intensity and Depth of Origin

We performed an outdoor experiment to evaluate the effect of light intensity and UV radiation on the covering behaviour of sea urchins collected at different depths in the field. We ran trials between 1230 and 1500 hours on four sunny days. On the morning of each day, we collected sea urchins at two depths (2 and 15 m). We collected sea urchins from Petite Île au Marteau on two of the days and from Île aux Goélands on the other two days. In each trial, we placed five large sea urchins (30–50 mm in diameter) from a specific depth (2 or 15 m) in a plastic tank (45 × 33 × 10 cm), which had the bottom covered with pebbles and pieces of coralline algae. The tanks were either (1) exposed to direct sunlight, (2) exposed to sunlight with UV radiation filtered out (tank covered with a sheet of Plexiglas UF-5) or (3) in darkness (tank covered by opaque plastic sheet). Each day we ran 24 trials (sea urchins from the two depths tested under three light conditions, with four replicates of each treatment). In each trial, we exposed the five sea urchins to the experimental light condition for 1 h, then noted the covering index for each sea urchin. We used the mean index for each trial as the dependant

variable. A preliminary analysis showed no effect of the site of collection on either the covering index ($P = 0.96$), light treatment (interaction between site and light: $P = 0.39$) or depth of origin (interaction between site and depth of origin: $P = 0.91$), so we excluded site as a factor in the model. Thus, we analysed the data using a mixed-model ANOVA with day as a random factor (on which trials were performed) and depth of origin (2 and 15 m) and light condition (sunlight, UV radiation removed, darkness) as fixed factors. Data were Box–Cox transformed before analysis because the variances tended to increase as the mean values increased. Multiple comparisons on significant effects were made using Tukey tests.

RESULTS

Effect of the Size of Sea Urchins in the Field

The analyses applied to the size-specific covering index of sea urchins indicated no difference between sites (Table 1). Sea urchin size strongly affected the covering index, and the interaction between site and size was also significant (Table 1). We conducted multiple comparisons on the main effect of size despite the presence of a significant interaction between site and size, as suggested by Quinn & Keough (2002) for mixed-model ANOVAs. Tukey tests revealed that, for both sites combined, the smallest sea urchins (<10 mm) covered themselves more than all other size classes, and that the covering indexes of 10–15-mm sea urchins were intermediate between those of the smaller and larger size classes (Fig. 2).

Effect of the Presence of Predators

Covering indexes of sea urchins in the absence of a predator and in the presence of a predatory sea star or crab showed a strong effect of size of sea urchin (ANOVA: $F_{1,24} = 8.57$, $P = 0.007$), no effect of predator stimulus (ANOVA: $F_{2,24} = 0.03$, $P = 0.97$) and no interaction between the two factors (ANOVA: $F_{2,24} = 0.26$, $P = 0.78$). As observed in the field, juveniles covered themselves more than adults (Fig. 3).

Effects of Size of Sea Urchins and Wave Intensity

Covering indexes of sea urchins exposed to different wave intensities revealed an effect of both wave intensity

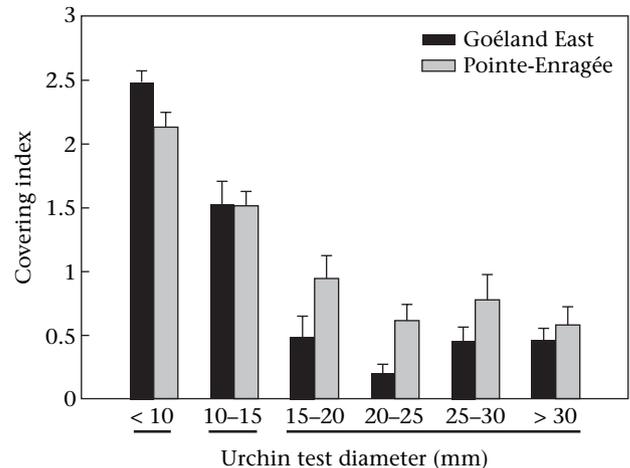


Figure 2. Mean + SE covering index of six size classes of sea urchins, *Strongylocentrotus droebachiensis*, at depths of 5–7 m on sea urchin barrens at two sites, Goéland East and Pointe-Enragée. Size classes not sharing a common line were significantly different ($P < 0.05$, Tukey multiple comparisons).

(ANOVA: $F_{2,45} = 45.82$, $P < 0.0001$) and size of sea urchin (ANOVA: $F_{4,45} = 5.18$, $P = 0.002$), but no interaction between the two factors (ANOVA: $F_{8,45} = 0.93$, $P = 0.51$). We therefore conducted multiple comparisons on the two factors separately. Tukey tests showed that covering indexes were similar in the treatments without waves and with weak waves, but were higher in the treatment with strong waves (Fig. 4). The covering index was highest for 10–15-mm sea urchins and significantly higher than that of all other size groups except for 15–20-mm sea urchins. The index did not differ between sea urchins measuring 15–20 and 30–50 mm in diameter (Fig. 4).

Effect of Moving Algal Blades

The covering index of large (30–50 mm) sea urchins showed an effect of both algal presence (ANOVA: $F_{1,12} = 47.83$, $P < 0.001$) and wave intensity (ANOVA: $F_{1,12} = 162.73$, $P < 0.001$) and an interaction between the two factors (ANOVA: $F_{1,12} = 10.42$, $P = 0.007$). In both the presence and the absence of algae, sea urchins covered themselves more under strong than weak wave intensity (Fig. 5). There was no difference in the covering index in the presence and the absence of algae under weak wave conditions, but the index was higher in the presence

Table 1. Results of the split-factorial ANOVA applied to the size-specific covering index of the green sea urchin, *Strongylocentrotus droebachiensis*, measured in the field at two sites

Source of variation	df	MS	Denominator	F	P
Site	1	0.59	Quadrat (size)	1.55	0.23
Quadrat (site)	16	0.38	No test		
Size	5	10.00	Site × size	19.25	0.003
Site × size	5	0.52	Quadrat (site) × size	4.45	0.001
Quadrat (site × size)	80	0.12	No test		

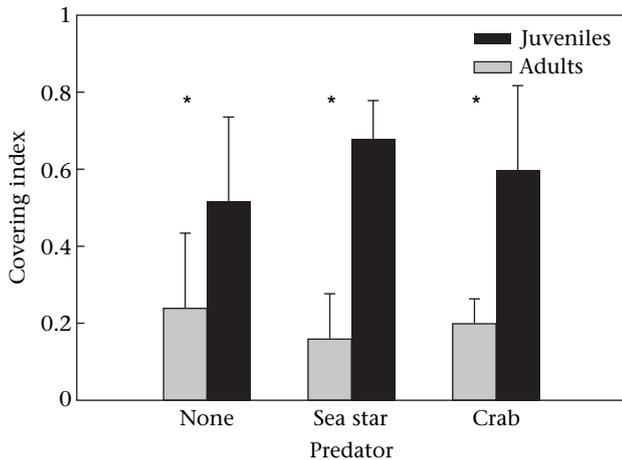


Figure 3. Mean + SE covering index of adult (30–50 mm in test diameter) and juvenile (10–15 mm) sea urchins, *Strongylocentrotus droebachiensis*, in the presence and absence of two common predators, the sea star *Crossaster papposus* and the crab *Cancer irroratus* (* $P < 0.05$, Tukey multiple comparisons).

than in the absence of algae under strong wave conditions (Fig. 5).

Effect of Light on Covering in the Laboratory

The covering behaviour of sea urchins collected at depths of 2 and 15 m showed a significant effect of light condition (Table 2). Sea urchins exposed to direct sunlight covered themselves significantly more than sea urchins in the other two treatments; however, when UV radiation was filtered from the sunlight, the sea urchins covered themselves to the same degree as in darkness (Fig. 6). Although we did not detect an effect of depth from which the sea urchins were collected (2 and 15 m), there was a significant interaction between the day of the trial and the depth from which the sea urchins were collected

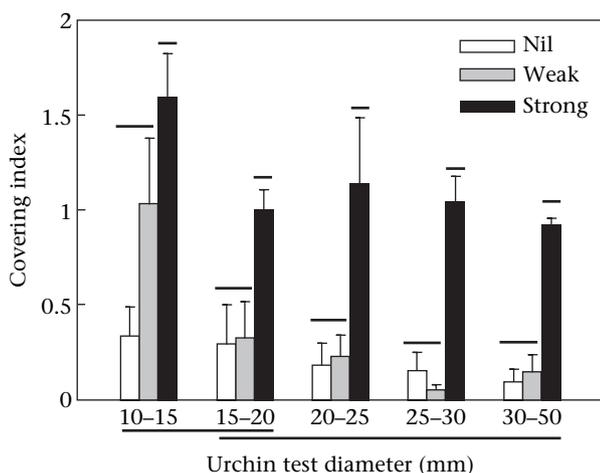


Figure 4. Mean + SE covering index of five size classes of sea urchins, *Strongylocentrotus droebachiensis*, when exposed for 1 h to three wave intensities (nil, weak, strong) in the laboratory. Urchin test diameters and wave intensities not sharing a common line were significantly different ($P < 0.05$, Tukey multiple comparisons for each factor).

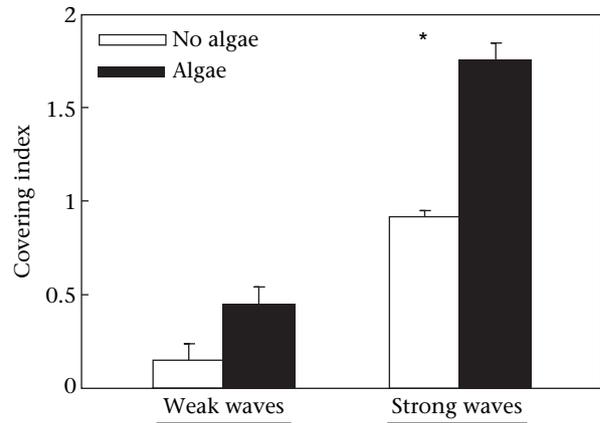


Figure 5. Mean + SE covering index of large adult sea urchins, *Strongylocentrotus droebachiensis* (30–50 mm in test diameter), maintained for 1 h in the presence or absence of algal blades in the presence of weak or strong wave conditions. Wave treatments not sharing a common line were significantly different ($P < 0.05$, Tukey multiple comparisons). An asterisk denotes a significant difference between treatments with and without algae ($P < 0.05$, Tukey multiple comparisons).

(Table 2). An analysis of the response of sea urchins for each of the four experimental days showed that sea urchins collected at a depth of 2 m covered themselves significantly more than those collected at a depth of 15 m on 2 of 4 days (1 of 2 days for each site). Overall, sea urchins collected at 2 m tended to cover themselves more than sea urchins collected at 15 m (Fig. 6).

DISCUSSION

We found that the covering behaviour of the green sea urchin, *Strongylocentrotus droebachiensis*, is influenced by a variety of proximal factors, suggesting that it serves as a protection against different environmental stresses. Our field survey showed that the degree to which sea urchins cover themselves decreases with increasing size until they reach about 15 mm in diameter. Interestingly, Dumont et al. (2004a, 2006) observed that the foraging behaviour of the sea urchin shifts at a similar size (15–20 mm). Sea urchins smaller than 20 mm move very little and usually remain cryptic, whereas larger individuals forage in open areas and actively move towards food sources. Although the cryptic behaviour of juveniles is reported to reduce predation risk (Scheibling & Hamm 1991; Agatsuma 2001), the covering behaviour of juveniles in our study was not affected by the presence of predators (the sea star *Crossaster papposus* or the crab *Cancer irroratus*). Furthermore, adult sea urchins did not cover themselves in response to the presence of predators, possibly because carrying materials is energetically costly (Berke et al. 2006) and/or reduces the efficiency of the fleeing response, which is triggered by chemical cues from predators (Mann et al. 1984; Hagen & Mann 1992; Hagen et al. 2002). Although the presence of predators (over the short term) did not provoke a covering response, covering behaviour may still offer protection against predation.

Table 2. Results of a mixed-model ANOVA applied to data from an experiment in which we evaluated the covering index of sea urchins, *Strongylocentrotus droebachiensis*, that were collected at depths of 2 and 15 m and exposed to different light conditions (direct sunlight, sunlight with UV radiation filtered out and darkness)

Source of variation	df	MS	Denominator	F	P
Day	3	0.03	Error	0.74	0.53
Light	2	1.20	Day×light	21.36	0.0023
Depth	1	0.78	Day×depth	4.27	0.13
Day×light	6	0.06	Error	1.48	0.20
Day×depth	3	0.18	Error	4.83	0.004
Light×depth	2	0.11	Day×light×depth	3.43	0.10
Day×light×depth	6	0.03	Error	0.84	0.54
Error	72	0.04			

Trials were run on 4 days, and day was treated as a random factor, whereas light and depth were treated as fixed factors. Analysis was conducted on the Box–Cox transformed data.

When exposed to wave surge, sea urchins of all sizes responded by holding more materials on their aboral surface. Although there was no significant interaction between wave intensity and sea urchin size, juveniles appeared to be more sensitive to wave action, because they increased covering even at a low wave surge, whereas adults increased covering only in response to strong waves (Fig. 4). Most of the adult sea urchins exposed to strong waves placed covering material along their sides rather than on the aboral surface. As a result, the sea urchin with its covering material formed a conical shape, which should be more resistant to wave surge (James 2000). Furthermore, when sea urchins were exposed to moving blades of the kelp *Alaria esculenta*, especially under strong wave conditions, they added significantly more covering material to their aboral surface than they did when algal blades were absent. Although algal blades smoothly pass over the surface of covered sea urchins, they could potentially get snagged on the spines of uncovered sea urchins, causing the sea urchin to be dislodged or suffer spine damage (C. Dumont & I. Deschênes, personal observation). Spine repair requires energy expenditure. Furthermore, spines that are damaged or abraded by moving macroalgae

appear to be more susceptible to infection (Dumont et al. 2004b). Thus, although spines protect echinoids from the impact of moving objects (Strathmann 1981) and increase their capacity to hold onto algal blades while capturing and feeding on drift algae (Ebert 1968; Duggins, 1981; Edwards & Ebert 1991), they clearly represent a disadvantage for sea urchins that are near moving algal blades.

Our observation that exposure to UV radiation increased the degree to which adult sea urchins covered themselves agrees with previous studies that have examined this factor (Adams 2001; Verling et al. 2002; Kehas et al. 2005). However, covering indexes were much lower in the trials with UV radiation than in the trials with moving algal blades, indicating a weaker response to UV light. Sea urchins taken from deeper water covered themselves less in response to UV light than sea urchins taken from shallow water, probably because sea urchins in deep water are rarely or never exposed to bright light. Kehas et al. (2005) observed a similar lack of the covering response with depth for the tropical sea urchin *Tripneustes ventricosus*. The reduced effect of UV radiation compared to other factors in stimulating the covering behaviour of *S. droebachiensis*, together with the report of Adams et al. (2001) that UV exposure does not stimulate production of UV protective substances (mycosporine-like amino acids) in the gonads of adults, suggest that UV radiation represents a minor stress to adult sea urchins.

Although the covering behaviour of sea urchins probably provides many advantages in terms of protection from environmental stresses, materials on the aboral surface probably increase the costs of locomotion and reduce the ability to manipulate food (Dumont et al. 2006), reflecting a trade-off between protection and foraging. Our results are consistent with previous studies reporting that sea urchins reduce their grazing activities under wavy conditions, in response to both the movement of the water itself (Gagnon et al. 2006) and the movement of algal blades (Velimirov & Griffiths 1979; Himmelman 1984; Kawamata 1998; Konar 2000). Sea urchins probably drop covering material when conditions become calm, so they can actively move onto algal blades to graze (C. Dumont, personal observation).

Our study shows that many factors, some of which have previously received little or no attention, can stimulate the covering response of the green sea urchin. Furthermore, our

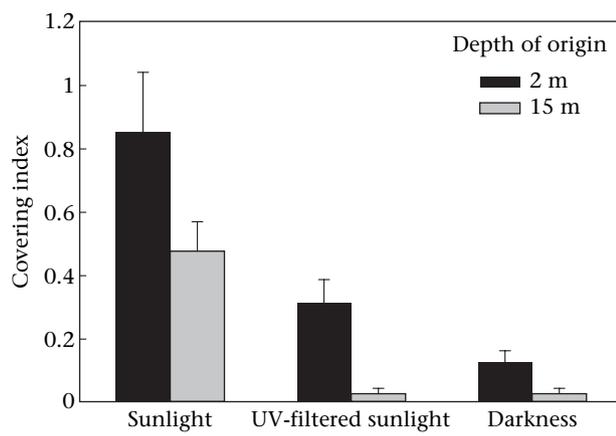


Figure 6. Mean + SE covering index of sea urchins, *Strongylocentrotus droebachiensis*, that were collected at depths of 2 and 15 m in the field and exposed for 1 h to three light conditions (sunlight, UV-filtered sunlight and darkness). Treatments not sharing a common line were significantly different ($P < 0.05$, Tukey multiple comparisons). See Table 2.

use of a standardized index across experiments allowed us to compare the relative importance of each factor. The factor that most strongly stimulated sea urchins to cover themselves was contact with macroalgal blades that were being moved about by waves (a factor not previously considered). Surprisingly, sunlight and presence of predators provoked only a weak covering response compared to wave surge and moving algae. Thus, while the covering behaviour may protect sea urchins from UV damage and visual predators, our results suggest that these stimuli do not act as selective forces in the development of the covering response. The importance of different environmental factors probably varies with the microhabitat and the species of sea urchin being considered. However, it is clear that only studies that consider multiple factors, using methods that permit comparison of responses to different factors, are likely to make significant advances in elucidating the function of the intriguing tendency of animals to cover themselves.

Acknowledgments

We are grateful to C. Vallières, P. Grondin, S.-P. Gingras, F. Praira, M. Thompson and M.-O. Nadon for their extensive help with the field and laboratory work. This study was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to J.H.H. Additional financial support to C.P.D. was provided by Québec-Océan and the Biology Department of Université Laval.

References

- Adams, N. L. 2001. UV radiation evokes negative phototaxis and covering behavior in the sea urchin *Strongylocentrotus droebachiensis*. *Marine Ecology Progress Series*, **213**, 87–95.
- Adams, N. L., Shick, J. M. & Dunlap, W. C. 2001. Selective accumulation of mycosporine-like amino acids in ovaries of the green sea urchin *Strongylocentrotus droebachiensis* is not affected by ultraviolet radiation. *Marine Biology*, **138**, 281–294.
- Agatsuma, Y. 2001. Effect of the covering behavior of the juvenile sea urchin *Strongylocentrotus intermedius* on predation by the spider crab *Pugettia quadridens*. *Fisheries Science*, **67**, 1181–1183.
- Amsler, C. D., McClintock, J. B. & Baker, B. J. 1999. An Antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones. *Marine Ecology Progress Series*, **183**, 105–114.
- Bacher, S. & Luder, S. 2005. Picky predators and the function of the faecal shield of a cassinid larva. *Functional Ecology*, **19**, 263–272.
- Barnes, D. & Crook, A. 2001. Quantifying behavioural determinants of the coastal European sea-urchin *Paracentrotus lividus*. *Marine Biology*, **138**, 1205–1212.
- Berke, S. K., Miller, M. & Woodin, S. A. 2006. Modeling the energy–mortality tradeoffs of invertebrate decorating behavior. *Evolutionary Ecology Research*, **8**, 1409–1425.
- Brandt, M. & Mahsberg, D. 2002. Bugs with a backpack: the function of nymphal camouflage in the West African assassin bugs *Paredocla* and *Acanthaspis* spp. *Animal Behaviour*, **63**, 277–284.
- Brenchley, G. A. 1976. Predator detection and avoidance: ornamentation of tube-caps of *Diopatra* spp. (Polychaeta: Onuphidae). *Marine Biology*, **38**, 179–188.
- Dix, T. G. 1970. Covering response of the echinoid *Evechinus chloroticus* (Val.). *Pacific Science*, **24**, 187–194.
- Douglas, C. A. 1976. Availability of drift materials and the covering response of the sea urchin *Strongylocentrotus purpuratus* (Stimpson). *Pacific Science*, **30**, 83–89.
- Duggins, D. O. 1981. Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia*, **48**, 157–163.
- Dumont, C., Himmelman, J. H. & Russell, M. P. 2004a. Size-specific movement of green sea urchins *Strongylocentrotus droebachiensis* on urchin barrens in eastern Canada. *Marine Ecology Progress Series*, **276**, 93–101.
- Dumont, C. P., Himmelman, J. H. & Russell, M. P. 2004b. Sea urchin mortality associated with algal debris from ice scour. In: *Echinoderms: München* (Ed. by T. Heinzeller & J. H. Nebelsick), pp. 177–182. Munich: Balkema.
- Dumont, C. P., Himmelman, J. H. & Russell, M. P. 2006. Daily movement of the sea urchin *Strongylocentrotus droebachiensis* in different subtidal habitats in eastern Canada. *Marine Ecology Progress Series*, **317**, 87–99.
- Ebert, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology*, **49**, 1075–1091.
- Edwards, P. B. & Ebert, T. A. 1991. Plastic responses to limited food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus* (Stimpson). *Journal of Experimental Marine Biology and Ecology*, **145**, 205–220.
- Gagnon, P., Wagner, G. & Himmelman, J. H. 2003. Use of a wave tank to study the effects of water motion and algal movement on the displacement of the sea star *Asterias vulgaris* towards its prey. *Marine Ecology Progress Series*, **125**, 125–132.
- Gagnon, P., St-Hilaire-Gravel, P., Himmelman, J. H. & Johnson, L. E. 2006. Organismal defenses versus environmentally-mediated protection from herbivores: unraveling the puzzling case of *Desmarestia viridis* (Phaeophyta). *Journal of Experimental Marine Biology and Ecology*, **334**, 10–19.
- Gaymer, C. F., Dutil, C. & Himmelman, J. H. 2004. Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community. *Journal of Experimental Marine Biology and Ecology*, **313**, 353–374.
- Glynn, P. W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. *Marine Biology*, **1**, 226–243.
- Hagen, N. T. & Mann, K. H. 1992. Functional response of the predators American lobster *Homarus americanus* (Milne-Edwards) and Atlantic wolffish *Anarhichas lupus* (L.) to increasing numbers of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *Journal of Experimental Marine Biology and Ecology*, **159**, 89–112.
- Hagen, N. T., Anderson, A. & Stabell, O. B. 2002. Alarm responses of the green sea urchin, *Strongylocentrotus droebachiensis*, induced by chemically labelled durophagous predators and simulated acts of predation. *Marine Biology*, **140**, 365–374.
- Himmelman, J. H. 1984. Urchin feeding and macroalgal distribution in Newfoundland, eastern Canada. *Le Naturaliste Canadien*, **111**, 337–348.
- Himmelman, J. 1991. Diving observations of subtidal communities in the northern Gulf of St Lawrence. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **113**, 319–332.
- James, D. W. 2000. Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, Mexico. *Marine Biology*, **137**, 913–923.
- Kawamata, S. 1998. Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin *Strongylocentrotus nudus* (A. Agassiz). *Journal of Experimental Marine Biology and Ecology*, **224**, 31–48.
- Kehas, A. J., Theoharides, K. A. & Gilbert, J. J. 2005. Effect of sunlight intensity and albinism on the covering response of the Caribbean sea urchin *Tripneustes ventricosus*. *Marine Biology*, **146**, 1111–1117.

- Konar, B. 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia*, **125**, 208–217.
- Lees, D. C. & Carter, G. A. 1972. The covering response to surge, sunlight, and ultraviolet light in *Lytechinus anamesus* (Echinoidea). *Ecology*, **53**, 1127–1133.
- Levin, L. A., Gooday, A. J. & James, D. W. 2001. Dressing up for the deep: agglutinated protists adorn an irregular urchin. *Journal of Marine Biological Association of the U.K.*, **81**, 881–882.
- Mann, K. H., Wright, J. L. C., Welsford, B. E. & Hatfield, E. 1984. Responses of the sea urchin *Strongylocentrotus droebachiensis* (O.F. Müller) to water-borne stimuli from potential predators and potential food algae. *Journal of Experimental Marine Biology and Ecology*, **79**, 233–244.
- Milligan, H. N. 1915. Observations on the scaling of the foreign objects carried by the purple-tipped sea urchin. *Zoologist*, **19**, 441–453.
- Millott, N. 1956. The covering reaction of sea urchins. I. A preliminary account of covering in the tropical echinoid *Lytechinus variegatus* (Lamarck) and its relation to light. *Journal of Experimental Biology*, **33**, 508–523.
- Millott, N. 1975. The photosensitivity of echinoids. *Advances in Marine Biology*, **13**, 1–52.
- Orton, J. H. 1929. On the occurrence of *Echinus esculentus* on the Foreshore in the British Isles. *Journal of Marine Biological Association of the U.K.*, **16**, 289–296.
- Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Richner, H. & Milinski, M. 2000. On the functional significance of masking behaviour in sea urchins: an experiment with *Paracentrotus lividus*. *Marine Ecology Progress Series*, **205**, 307–308.
- Scheibling, R. E. & Hamm, J. 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. *Marine Biology*, **110**, 105–116.
- Sharp, D. T. & Gray, I. E. 1962. Studies on factors affecting the local distribution of two sea urchins, *Arbacia punctulata* and *Lytechinus variegatus*. *Ecology*, **43**, 309–313.
- Stachowicz, J. J. & Hay, M. E. 2000. Geographic variation in camouflage specialization by a decorator crab. *American Naturalist*, **156**, 59–71.
- Strathmann, R. R. 1981. The role of spines in preventing structural damage to echinoid tests. *Paleobiology*, **7**, 400–406.
- Underwood, A. J. 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.
- Velimirov, B. & Griffiths, C. 1979. Wave-induced kelp movement and its importance for community structure. *Botanica Marina*, **22**, 169–172.
- Verling, E., Crook, A. C. & Barnes, D. K. A. 2002. Covering behaviour in *Paracentrotus lividus*: is light important?. *Marine Biology*, **140**, 391–396.
- Wicksten, M.-K. 1993. A review and a model of decorating behavior in spider crabs (Decapoda, Brachyura, Majidae). *Crustaceana*, **64**, 314–325.
- Williams, J. D. & McDermott, J. J. 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology*, **305**, 1–128.
- Williams, J. L., Moya-Larano, J. & Wise, D. H. 2006. Burrow decorations as antipredatory devices. *Behavioral Ecology*, **17**, 586–590.