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A field test of threat sensitivity in a marine gastropod

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Abstract. In the Mingan Islands, the whelk *Buccinum undatum* displays defensive manoeuvres to both contact and water-borne chemical cues from the predatory asteroid *Leptasterias polaris*. In spite of this, whelks occasionally aggregate in great numbers near *L. polaris* while it is ingesting a prey; they then attempt to steal food from their predator and also wait for leftovers. In this study, the response of whelks in different types of encounters with *L. polaris* was examined to test the hypothesis that whelks are sensitive to the magnitude of the threat their predator represents. In a field experiment, whelks consistently fled both non-feeding and feeding *L. polaris* (asteroids used were consuming small prey items that were unlikely to provide food for whelks). When current flow was stable, whelks fled more directly down current and more frequently displayed violent defensive behaviours, in response to non-feeding *L. polaris*, which presented a higher risk, than in response to feeding asteroids (lower risk; 47% versus 2%). Consequently, whelks tested with non-feeding asteroids more rapidly distanced themselves from the predators than did whelks tested with feeding asteroids. In a field survey, there were more active whelks in the vicinity of cruising (higher risk) than stationary (lower risk) *L. polaris* (53% versus 14%). Among those whelks that were active, defensive behaviour patterns such as shell rocking and leaping escape movements were frequently shown by whelks near cruising predators (69%), but never by whelks near stationary predators (0%). The discriminative capabilities apparent in these results are likely to be adaptive, because they enable whelks to limit the cost of escape responses while still keeping predation risk low, and also because they facilitate a close association with *L. polaris* from which the whelks receive feeding benefits.

Anti-predator characteristics of prey animals are frequently flexible and well adjusted to spatial and temporal variations in predation risk (e.g. Sih 1987; Lima & Dill 1990). Animals as diverse as protozoans (Kusch 1993), rotifers (Gilbert 1966), gastropods (Appleton & Palmer 1988), crustaceans (Krueger & Dodson 1981; Hebert & Grewe 1985), insects (Craig 1994), fishes (Magurran 1990; Chivers & Smith 1994), amphibians (Semlitsch & Reyer 1992) and mammals (Caro 1994) develop protective morphological structures or behavioural patterns when they experience predation risk. Life-history characteristics, such as age at first reproduction and longevity, can also be adjusted on an ecological time scale to prevailing levels of predation risk (Crowl & Covich 1990). Furthermore, animals do not always flee as soon as they detect predators, because flight responses incur direct energetic costs and indirect costs of lost feeding and reproductive opportunities, which may outweigh the benefits of flight in some circumstances (Ydenberg & Dill 1986). Considerable evidence suggests that prey trade off predator avoidance and other activities by adjusting their response to the magnitude of the predatory threat. For example, more vulnerable individuals of a population usually compromise feeding activities to avoid predators more than less vulnerable individuals (e.g. Sih 1982; Werner et al. 1983; Wahle 1992; Rochette & Himmelman 1996). Furthermore, when they encounter predators, many animals adjust the

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nature and intensity of their responses to the predator's species (e.g. Hennessy & Owings 1978; Curio et al. 1983; Moore & Williams 1990), its attack characteristics (e.g. Dill 1974; Bishop & Brown 1992), or its feeding status (Licht 1989). Helfman (1989) referred to this response selectivity as 'threat sensitivity'.

In the Mingan Islands in the northern Gulf of St Lawrence (eastern Canada), a fascinating predator–prey relationship exists between the common northern whelk, *Buccinum undatum* (gastropod) and the asteroid (starfish) *Leptasterias polaris* (Himmelman & Dutil 1991; Rochette et al. 1995). Contact and chemical cues from *L. polaris* induce escape responses in whelks (Harvey et al. 1987; Rochette et al. 1996), which include increased crawling activity, mucus secretion, shell-rocking behaviour and leaping escape movements (henceforth called 'foot contortions'). This response of whelks to *L. polaris* is not unusual; many marine molluscs (reviewed in Ansell 1969), and invertebrates in general (reviewed in Feder 1972), have evolved similar defensive behaviours to counter asteroid predation. The uniqueness of this particular interaction stems from the somewhat peculiar feeding habits of whelks. Although *B. undatum* is the most abundant macrobenthic carnivore in the Mingan Islands (Jalbert et al. 1989), how it acquires its food resources is still largely unknown. Whelks are rarely observed feeding. When collected, they usually have empty stomachs and the rare stomach contents sampled are difficult to identify (Himmelman & Hamel 1993). Whelks occasionally aggregate in large numbers near asteroids (*L. polaris*) that are in the process of ingesting a prey, and they might gain a substantial part of their diet by kleptoparasitic activities (Jalbert et al. 1989; Himmelman & Dutil 1991; Himmelman & Hamel 1993). Rochette et al. (1995) demonstrated that stomach content mass was 15 times greater for whelks leaving *L. polaris* feeding on large surf clams, *Spisula polynyma*, than for whelks arriving near a feeding *L. polaris*. The whelk occasionally uses its long proboscis to steal some of the asteroid's prey while it is feeding, and to capture infaunal organisms (such as polychaetes and bivalves) that have been exposed by the asteroid's digging activity (R. Rochette, personal observations). They apparently make most of their gains, however, by exploiting the remains of the asteroid's kill once the satiated starfish moves away, or when it is forced to abandon the prey by *Asterias vulgaris*, a competing asteroid (Morissette 1996). *Asterias vulgaris* is less of a threat to whelks than *L. polaris* and induces weaker escape responses (Legault & Himmelman 1993). Because *A. vulgaris* has more difficulty covering large bivalve prey than *L. polaris*, whelks also have a better chance of gaining access to prey being ingested by *A. vulgaris*.

Whelks rely on chemical cues to detect and locate food (Himmelman 1988; Lapointe & Sainte-Marie 1992), predators (Harvey et al. 1987) and feeding *L. polaris* (Morissette 1996). Since *L. polaris* is abundant ($0.44/m^2$) in the Mingan Islands (Jalbert et al. 1989), and the whelks' chemosensory capacities are acute (they can localize food items from 30–50 m; Himmelman 1988), whelks probably frequently pick up water-borne chemical cues that their predator exudes. Not all encounters with *L. polaris* are equally threatening to whelks, however. Dutil (1988) estimated that in the Mingan Islands, *L. polaris* spends about 25% of its time stationary and apparently resting. *Leptasterias polaris* does not represent an immediate threat to whelks when stationary, and it may remain in a 'resting' state for up to several days. In contrast, asteroids that are cruising represent an immediate danger, because they are probably looking for a meal (Dutil 1988). Once *L. polaris* starts feeding on a prey captured from the sediment zone, it typically will not search for another one for 6–16 days (Dutil 1988). Feeding asteroids represent little danger; during our numerous hours of video recordings and diving observations, we never saw *L. polaris* abandon a prey to chase a nearby whelk. Nevertheless, there is some risk to whelks, because several times we observed a feeding *L. polaris* make an easy second catch of a whelk that was attempting to steal food from it.

When whelks approach feeding asteroids, they often exhibit agitated behaviours, suggesting detection of negative (predators) as well as positive (food) chemical stimuli (Rochette et al. 1995). To exploit the feeding opportunities provided by *L. polaris*, whelks must inhibit their defensive responses and approach their predator. Potential nutritional gains would be more likely to override the defensive response to predators if whelks were sensitive to the lower immediate threat represented by feeding asteroids. The objective of our study was to test the hypothesis that whelks are sensitive to the threat associated with the activity of predatory *L. polaris*. We conducted one field experiment and one field survey to test the following predictions: (1) whelks display stronger defensive responses to non-feeding than to feeding *L. polaris,* and (2) whelks display stronger defensive responses to cruising than to stationary *L. polaris*.

MATERIALS AND METHODS

This study was conducted using SCUBA during May to late August of 1990 and 1991 at Cap du Corbeau off Île du Havre (50°14′N; 63°35′W), in the northern Gulf of St Lawrence, Canada. Experiments and observations were made along 170 m of the coast on a sediment bottom (gravel to mud), 8–18 m in depth, through which we placed a permanent transect (12 m deep) marked at 5-m intervals to aid orientation during dives.

To determine whether *B. undatum* perceives the lower immediate threat associated with feeding *L. polaris,* we compared the behaviour of whelks that were placed 30 cm down current from feeding and non-feeding *L. polaris* during the summer of 1990. Experiments were conducted on a relatively uniform sediment bottom ($\approx$400 m^2 in area) at 10–13 m in depth. Two divers first searched the area for a *L. polaris* that was feeding on a small prey item (e.g. *Mya truncata*, *Clinocardium ciliatum*) because such prey were less likely to provide whelks with feeding opportunities (Morissette 1996). We hoped to have whelks flee both feeding and non-feeding *L. polaris* so we could compare the intensity of their flight response to these two types of predators. Once we found an asteroid feeding on a small prey item, we noted its position relative to the permanent transect and then searched for a similarly sized asteroid that was not feeding (all asteroids measured $\approx$25–35 cm in diameter). The non-feeding asteroid was brought within $\approx$8–10 m of the feeding one, and each was covered with a circular cage (30 cm diameter, 4 cm mesh). Ten whelks over 7 cm in shell length were then collected for each treatment and brought to the test area (the whelks were kept at least 5 m across current from the asteroids, so they could not detect predator or food odours before the experiment).

We began the experiment approximately 15–30 min after the non-feeding asteroid was brought to the test area. Each trial consisted of placing one whelk 30 cm down current from an asteroid and recording its behaviours and movements for 4 min, starting as soon as the whelk was placed on the bottom. The position of each whelk after 4 min was plotted on a Plexiglas sheet by referring to a grid (nine 20 × 20-cm squares) in front on the cage. Using trigonometry, we then determined the direction in which whelks fled feeding and non-feeding *L. polaris,* and the distance that separated whelks from *L. polaris* (a measure of escape speed). We performed two control experiments: whelks were placed 30 cm down current from either an empty cage or a cage containing food items (two cut-open bivalves, *C. ciliatum*). The number of replicates conducted per treatment were as follows: 11 for feeding *L. polaris*, 11 for non-feeding *L. polaris*, 13 for prey only and five for empty cages. For all treatments, seven whelks were tested per replicate. Because currents should influence the whelks' ability to determine the origin of chemicals eliciting particular responses, in each trial two observers categorized the stability of current orientation as either 'regular' (particles moved in a straight line across the grid used to monitor the movements of whelks) or 'irregular' (particles moved back and forth over the grid to some extent). In the analyses, we separated the experiments into two groups, stable current flow (where both observers noted regular movement of particles) and unstable current flow (where one or both observers noted irregular movement of particles). This grouping allowed us to investigate the importance of the stability of current direction on the responses of whelks.

To determine whether *B. undatum* perceives the greater immediate threat associated with asteroids that are cruising over the benthos, we compared, during the summer of 1991, the occurrence and behaviour of whelks in the vicinity of stationary and cruising asteroids (asteroids ingesting prey or digging for one were not surveyed) measuring 25–40 cm in diameter. We recorded the behaviour of each whelk within 1 m of the asteroid and measured its distance from the predator. Whelks were categorized as less than or greater than 5 cm in shell length because of known differences in the responsiveness of different sizes of whelks to chemical cues of *L. polaris* (Harvey et al. 1987; Rochette et al. 1996). After the area had been carefully examined for whelks that might have been buried (siphons are visible at the surface), we measured the asteroid's diameter. We surveyed the vicinities of 73 *L. polaris* that were stationary and 33 that were cruising.

Statistical Analysis

For the field experiment, we first tested for directionality (H_1) in the movement of whelks using Rayleigh's tests (Batschelet 1981), and then compared the flight orientation of whelks tested with feeding and non-feeding *L. polaris* with a Watson–Williams test (Batschelet 1981). Whelks that moved less than 5 cm were not included in these analysis. We used *G*-tests (Zar 1984) to compare the number of whelks that exhibited foot contortions in the presence of feeding and non-feeding asteroids. Finally, we used a nested ANOVA (Zar 1984) to compare the distance separating whelks from feeding and non-feeding asteroids at the end of the 4-min experimental period, each asteroid (used to test 7 whelks) being nested within predator treatment.

For the field survey, we first used a *G*-test to compare frequency distributions of the number of whelks encountered within 1 m of stationary and cruising asteroids. We then used a Mann–Whitney *U*-test (Zar 1984) to compare the distance separating whelks from stationary and cruising *L. polaris*, and another *G*-test to compare the number of whelks that were active near stationary and cruising *L. polaris*. Finally, to isolate the influence of predator activity on the behaviour of whelks, from that of predator distance, we used *G*-tests (Fisher's exact probability test was used when expected frequencies were low) to compare the number of whelks that were active in three 25-cm wide concentric bands near stationary and cruising asteroids. The 25-cm band closest to the asteroid was not analysed, because only one whelk was encountered within 25 cm of either stationary or cruising asteroids.

RESULTS

Feeding versus Non-feeding *L. polaris*

In all treatments, when replicate experiments were pooled, the movement of whelks was significantly oriented (Fig. 1). The direction in which they moved differed markedly among treatments, however; whelks moved up current when tested with prey items, somewhat up and cross current when tested with empty cages, and down current when tested with predators. Whelks consistently fled both feeding and non-feeding *L. polaris*, re-orienting themselves by nearly 180° with respect to their orientation at the start of the trial (up current) to move down current and away from the predators.

Several observations made when current flow was stable suggested that whelks perceived non-feeding predators to be a greater threat. First, whelks were significantly oriented in 71% of the replicates conducted with non-feeding *L. polaris*, but only in 14% of those conducted with feeding asteroids (Table I); the indices of concentration for the orientation of whelks (*r*) were significantly higher in experiments conducted with non-feeding predators (Mann–Whitney *U*-test: $Z=2.17$, $P=0.03$). When current flow was unstable, whelks were significantly oriented in 25% of the replicates conducted with both feeding and non-feeding *L. polaris*, and the indices of concentration *r* did not differ between the two predator treatments ($Z=-0.43$, $P=0.67$).

Some whelks fled the predator by moving to their right, and others by moving to their left (Fig. 1). The mean vectors were somewhat misleading, because the distributions of the angular orientation of the whelks were not unimodal (Batschelet 1981). We therefore transformed the data and represented the orientation of each whelk relative to the down-current direction (180°) on a single side of the 0–180° axis (Fig. 2). Whelks tested with non-feeding *L. polaris* moved more directly down current and away from the predator than did whelks that were tested with feeding *L. polaris* (Watson–Williams test: $F_{1,92}=10.3$, $P<0.005$).

Although directional movement was demonstrated in each of the treatments, movement was never directly upstream or downstream; rather, the mean vector was always to some degree towards the left. We suspect that this reflected the asymmetry in the whelk's morphology because the siphon (which brings water to the chemosensory apparatus) is on the left side. We also observed in the laboratory that whelks move towards the side of the siphon.

The third and most compelling line of evidence that whelks responded more strongly to non-feeding *L. polaris* comes from the number of individuals that displayed violent defensive

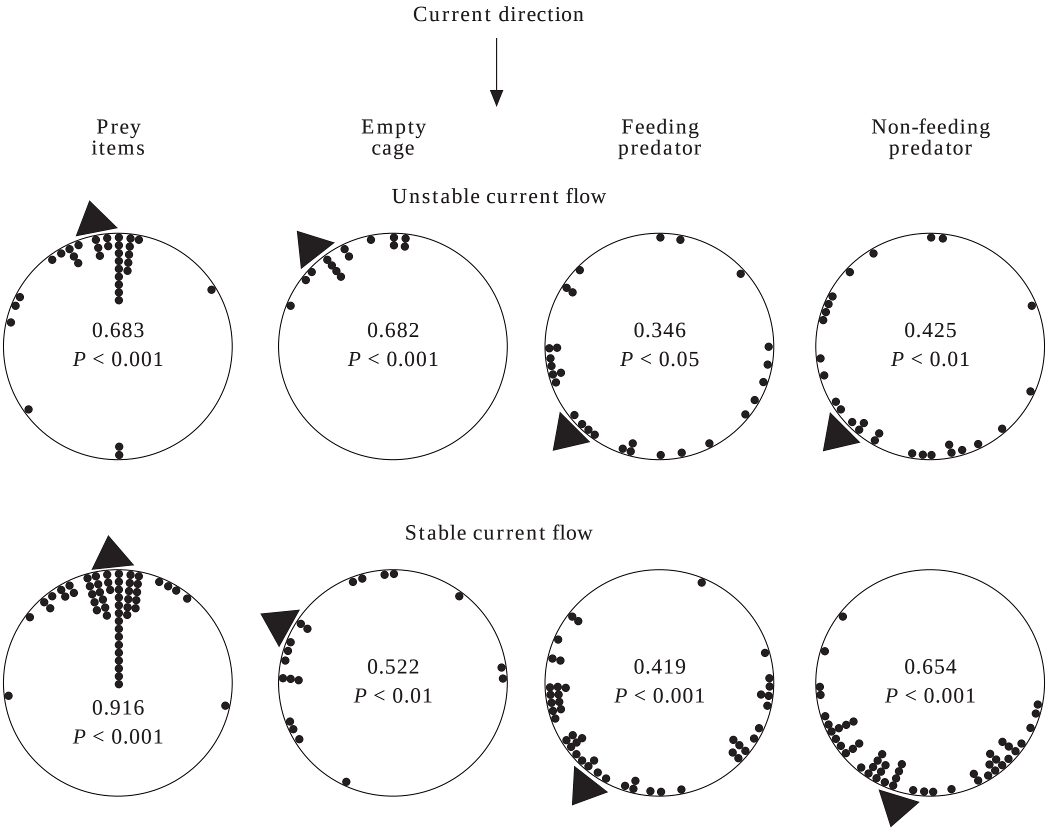

Figure 1. Orientation of the movement of whelks placed 30 cm down current from: (1) prey items; (2) an empty cage; (3) a feeding *L. polaris*; and (4) a non-feeding *L. polaris*, in conditions of unstable and stable current flow. Each point represents the direction in which one whelk fled, determined from its position 4 min after the beginning of the experiment (points are stacked when two or more whelks moved in the same direction). For whelks tested under the same conditions, the value of the *r*-statistic, the *P*-value of the Rayleigh's test, and the mean direction of movement (arrowheads) are indicated.

behaviours. When current flow was stable, 47% of the whelks tested with non-feeding *L. polaris* displayed foot contortions, but only 2% of whelks that were tested with feeding *L. polaris* did so ($G_1 = 31.6$, $P < 0.0001$). When current flow was unstable, 14% of the whelks tested with non-feeding *L. polaris* displayed foot contortions, compared with 7% of whelks tested with feeding asteroids ($G_1 = 0.76$, $P = 0.38$). None of the 35 whelks tested with an empty cage, and only two of the 91 whelks tested with food items, displayed this behaviour.

At the end of the 4-min experimental period in stable current conditions, whelks tested with non-feeding *L. polaris* were further from their predator than whelks tested with feeding *L. polaris* ($F_{1,12} = 9.36$, $P = 0.01$; Fig. 3). The mean distances separating whelks from feeding and non-feeding predators were similar when current flow was unstable ($F_{1,6} = 0.04$, $P = 0.85$; Fig. 3)

Stationary versus Cruising *L. polaris*

The number of whelks encountered within 1 m of stationary and cruising *L. polaris* was usually quite low and independent of predator activity ($G_2 = 1.01$, $P = 0.60$; Fig. 4 samples with more than one whelk were grouped for statistical analysis because of low expected frequencies). Whelks were encountered closer to predators that were cruising compared to stationary predators ($Z = -2.46$, $P = 0.014$; Fig. 5). Whelks

Table I. Number of *B. undatum* that moved at least 5 cm and index of concentration of orientation (*r*), and its associated probability, for whelks placed 30 cm down current from feeding and non-feeding *L. polaris* in conditions of unstable and stable current flow (seven whelks in each replicate, but in five trials one whelk did not move 5 cm)

Feeding *L. polaris*			Non-feeding *L. polaris*		
N	*r*	*P*	*N*	*r*	*P*
Unstable current flow					
7	0.35	NS	7	0.77	<0.05
7	0.62	NS	7	0.15	NS
7	0.69	<0.05	7	0.41	NS
7	0.59	NS	6	0.51	NS
	$\bar{X}=0.56$			$\bar{X}=0.46$	
Stable current flow					
6	0.31	NS	6	0.67	NS
7	0.25	NS	7	0.84	<0.005
7	0.50	NS	7	0.63	NS
7	0.48	NS	7	0.81	<0.005
7	0.43	NS	7	0.83	<0.005
6	0.86	<0.05	7	0.71	<0.05
6	0.47	NS	7	0.76	<0.05
	$\bar{X}=0.47$			$\bar{X}=0.75$	

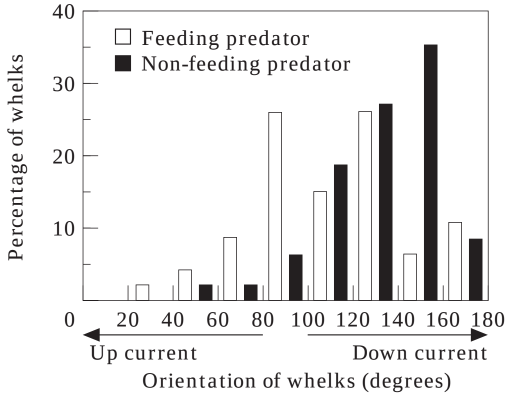

Figure 2. Frequency distribution of the orientation of the movement of whelks placed 30 cm down current from feeding and non-feeding *L. polaris* when current flow was stable.

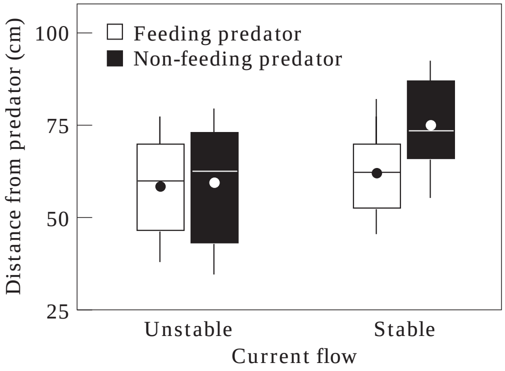

Figure 3. Box-plot charts showing the distance separating whelks from feeding and non-feeding *L. polaris* 4 min after the beginning of experiments conducted in conditions of unstable and stable current flow. The top, middle and lower horizontal lines show the 75th, 50th and 25th percentiles, respectively. The circle indicates the mean, and the vertical lines extend from the 10th to the 90th percentile.

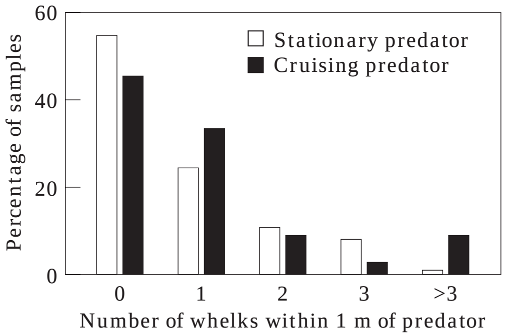

Figure 4. Frequency of samples, taken within 1 m of stationary and cruising *L. polaris*, containing different numbers of whelks.

encountered within 1 m of cruising *L. polaris*, however, were more frequently active and exhibiting defensive behaviour patterns than whelks encountered within the same distance of stationary *L. polaris* ($G_1=16.2$, $P<0.0001$). Near cruising asteroids, 53% of whelks were active (17% crawling, 28% shell-rocking and 8% showing foot contortions); near stationary asteroids only 14% were active (all crawling). The greater activity level of whelks in response to cruising than to stationary asteroids was not simply due to their overall closer proximity to predators (Fig. 5), because differences in activity levels persisted when the data were analysed for individual 25-cm wide concentric bands around the asteroids (within each band whelks were at similar distances from stationary and cruising asteroids, $P>0.25$ in all cases; Fig. 6). Thus, the behaviour of whelks was influenced by predator distance and activity (Fig. 6).

We found no evidence that whelk size had an effect on the relations just described. Small (<5 cm)

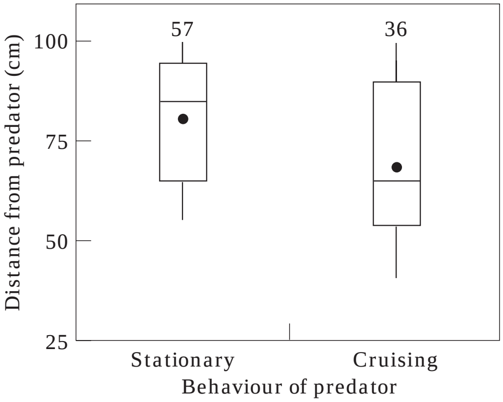

Figure 5. Box-plot charts showing the distance separating whelks from stationary and cruising *L. polaris*; the numbers of whelks sampled are indicated above the plots. Other conventions are as in Fig. 3.

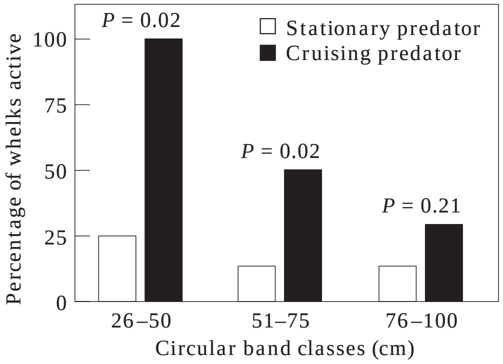

Figure 6. The percentage of whelks that were active in three concentric bands around stationary and cruising *L. polaris*. The influence of predator behaviour on the proportion of whelks that were active was determined with Fisher's exact probability test for whelks within 26–50 cm of the asteroids, and with *G*-tests for whelks within 51–75 cm and 76–100 cm of the asteroids.

and large (>5 cm) whelks were found at similar distances from both stationary ($Z = 0.68$, $P = 0.497$) and cruising ($Z = 0.15$, $P = 0.879$) *L. polaris*, and a similar proportion of small and large whelks were active near stationary ($G_1 = 0.46$, $P = 0.50$) and cruising ($G_1 = 0.03$, $P = 0.75$) asteroids.

DISCUSSION

The results suggest that whelks are sensitive to the threat associated with the activity of the predatory asteroid *L. polaris*. In the field experiment, whelks tested with non-feeding *L. polaris* were more strongly oriented, moved more directly down current, and more frequently displayed foot contortions than whelks tested with feeding *L. polaris*. A potential problem with our experimental design was that non-feeding asteroids, but not feeding asteroids, were moved just before the experiment; this could have created a bias if this manipulation caused changes in the release of chemical cues which induce escape behaviours in whelks. Although we cannot rule out this possibility, it was nevertheless notable that so few whelks placed 30 cm from feeding asteroids (4%) displayed strong responses (foot contortions).

In the field survey, whelks were more frequently active near cruising *L. polaris* than near stationary ones, and among those whelks that were active, defensive behavioural patterns such as shell-rocking and leaping escape movements were frequently displayed by whelks near cruising predators, but never by whelks near stationary predators. Twice during these surveys, we arrived near a *L. polaris* just before it started moving, and both times three whelks that were sitting motionless within 30–70 cm of the asteroid fled as the latter started moving (three were rocking their shell as they fled and one displayed foot contortions).

Such discriminative capacities are probably adaptive for whelks because (1) their escape responses are costly, (2) encounters with *L. polaris*, while frequent, are not all equally dangerous, and (3) some encounters with *L. polaris* may entail benefits. Muscular activity and mucus production by whelks during locomotion and flight require large amounts of energy (Denny 1980; Koormann & Grieshaber 1980; Kideys & Hartnoll 1991). The significance of these costs is emphasized by the fact that whelks at Cap du Corbeau are usually stationary on the substratum, buried in the sediments or sheltered in crevices between rocks (Himmelman & Hamel 1993; R. Rochette, unpublished data). Not only does threat sensitivity enable whelks to expend energy only in dangerous situations, but it probably also facilitates the exploitation of feeding opportunities provided by *L. polaris* by increasing the likelihood that 'positive' food stimuli will override 'negative' predator stimuli in encounters with feeding *L. polaris*.

Our study is only the second to provide experimental evidence of sensitivity to predator foraging state in marine invertebrates, and the only one based on data collected in the field. In a laboratory study, Phillips (1978) observed that the sea urchin *Strongylocentrotus purpuratus* displayed stronger pedicellaria responses to odours of active than inactive asteroids, *Pycnopodia helianthoides*. There are also a few pertinent anecdotal reports. For instance, Mauzey et al. (1968) stated from laboratory observations that when *P. helianthoides* was feeding on clams, ‘urchins [*S. purpuratus*] no longer showed a tendency to remain on the opposite side of the tank’ (pp. 614–615). Also, while studying the feeding biology of asteroids in Chile, Dayton et al. (1977) mentioned being ‘occasionally made aware of a foraging *Meyenaster gelatinosus* by being showered with escaping prey . . .’ (page 364), whereas ‘. . . almost all non-foraging *M. gelatinosus* were accompanied by prey species which showed no indication of stress whatever’ (page 366).

Chemicals (steroid glycosides) that naturally diffuse through the tube feet of the hydrovascular system of asteroids induce defensive responses in many marine invertebrates (e.g. Feder 1963; Feder & Lasker 1964; Mackie et al. 1968), including *B. undatum* (Harvey et al. 1987). The diffusion of chemicals into the water is probably increased when asteroids move because (1) the boundary layer around the tube feet is likely to be disrupted more often, (2) there is greater contact between the tube feet and the water, and (3) the operation of the tube feet causes an increase in hydraulic pressure within the hydrovascular system. Whelks might discriminate stationary, cruising and feeding *L. polaris* by qualitative or quantitative differences in the chemicals the asteroids exude during different activities. Whelks might also use the presence of digestive enzymes and chemical cues from prey to discriminate between feeding and non-feeding *L. polaris*.

When the directional stability of the current was low, the chemoreceptors of whelks were probably stimulated less regularly by predator cues such that they were provided with imperfect information about the predator’s status or its relative position. This might explain why whelks responded similarly, and weakly, to non-feeding and feeding *L. polaris* when current flow was unstable. Similarly, whelks are less efficient at locating baited traps when the directional stability of the current is low (Lapointe & Sainte-Marie 1992). These observations suggest that, if an evolutionary arms race (sensu Dawkins & Krebs 1979) is occurring between *L. polaris* and *B. undatum* (or other mobile prey), asteroids would evolve current-related search tactics that reduce their conspicuousness to prey species. In spite of the greater responsiveness of whelks to cruising *L. polaris*, which we observed in the field surveys, whelks were equally abundant near stationary and cruising asteroids and were frequently closer to the latter, supporting the hypothesis that the foraging tactics of *L. polaris* permit close approaches to prey.

The efficiency of a prey’s defensive mechanisms, and the frequency of encounters with its predators, are probably important factors in the evolution of threat-sensitive predator avoidance. Animals with efficient escape mechanisms can afford to delay their response until predation risk is high, and animals that frequently encounter predators will benefit more from such discriminative abilities. There is now evidence of threat sensitivity for animals as diverse as gastropods (e.g. Legault & Himmelman 1993; this study), echinoids (e.g. Mauzey et al. 1968; Dayton et al. 1977; Phillips 1978), insects (e.g. Sih 1982; Moore & Williams 1990), larval (e.g. Bishop & Brown 1992) and adult fish (e.g. Helfman 1989; Licht 1989), birds (e.g. Curio et al. 1983), and mammals (e.g. Walther 1969; Hennessy & Owings 1978). The widespread occurrence of threat sensitivity within the animal kingdom points to the evolutionary significance of such discriminative capabilities.

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