



A field test of threat sensitivity in a marine gastropod

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(Received 23 April 1996; initial acceptance 24 July 1996;
final acceptance 16 January 1997; MS. number: A7592R)

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.

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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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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 ($\approx 400 \text{ m}^2$ 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 ≈ 25 –35 cm in diameter). The non-feeding asteroid was brought within ≈ 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

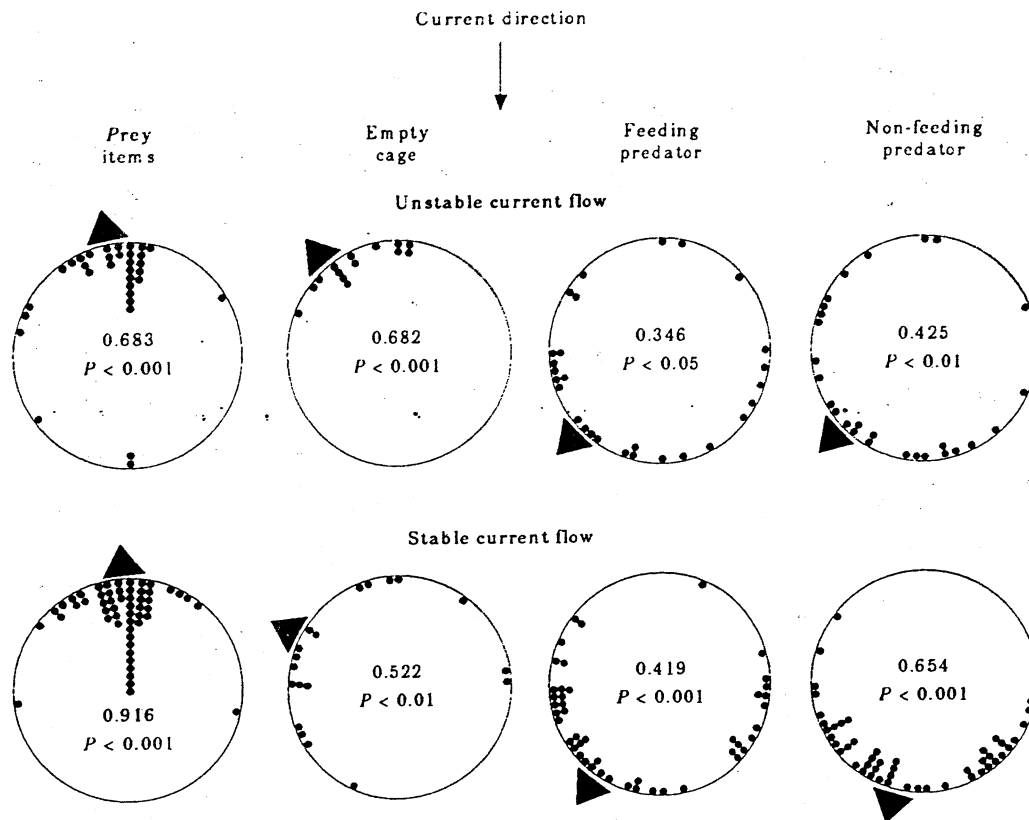


Figure 1. Orientation of the movement of whelks placed 30 cm down current from: (1) prey items; (2) an empty cage; (3) a feeding *L. polaris*; and (4) a non-feeding *L. polaris*, in conditions of unstable and stable current flow. Each point represents the direction in which one whelk fled, determined 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 *L. polaris* ($G_1=0.76$, $P=0.38$). 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

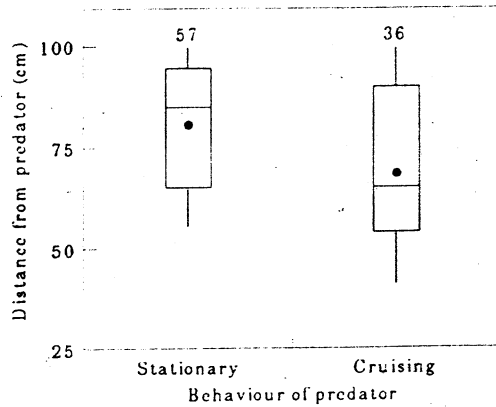


Figure 5. Box-plot charts showing the distance separating whelks from stationary and cruising *L. polaris*; the numbers of whelks sampled are indicated above the plots. Other conventions are as in Fig. 3.

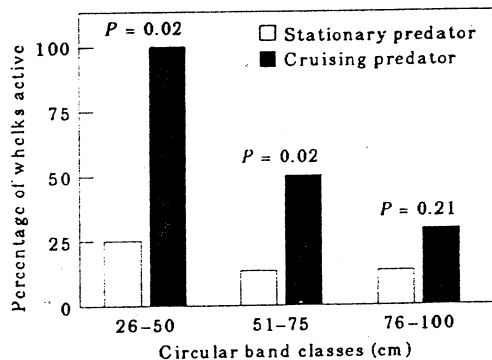


Figure 6. The percentage of whelks that were active in three concentric bands around stationary and cruising *L. polaris*. The influence of predator behaviour on the proportion of whelks that were active was determined with Fisher's exact probability test for whelks within 26–50 cm of the asteroids,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

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