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Interpopulation and context-related differences in responses of a marine gastropod to predation risk

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We conducted laboratory experiments to investigate interpopulation differences in the behavioural responses of the whelk *Buccinum undatum* to the predatory lobster *Homarus americanus* and the asteroid *Leptasterias polaris*, both in the absence and presence of feeding opportunities. Whelks from three populations in the eastern North Atlantic (1) responded to lobsters by displaying avoidance behaviours (burrowing in the sediments or retreating inside their shell), (2) responded to asteroids by displaying escape responses (rapid crawling, shell rocking behaviour or foot contortions), and (3) more often refrained from feeding in the presence of a lobster than in the presence of an asteroid. Although whelks from the three populations responded similarly to lobsters and asteroids, interpopulation differences were evident. Thus, whelks from populations sympatric with a given predator more frequently displayed 'appropriate' antipredator behaviours (i.e. avoidance in the presence of a lobster, and escape in the presence of an asteroid) than did whelks allopatric with that predator. Also, whelks from a population sympatric with both predators fed less readily in the presence of a given predator than did whelks allopatric with that predator. However, the presence of a lobster or an asteroid had the same impact on the feeding response of whelks from two populations with contrasting predator fields, one sympatric with lobsters, but allopatric with asteroids, and one sympatric with asteroids, but allopatric with lobsters. The results of our study indicate that coexistence (over evolutionary or ecological time) with lobsters and asteroids increases the propensity of the whelk to display avoidance and escape behaviours in the presence of lobsters and asteroids, respectively, but has a less predictable effect on how whelks trade off predation risk and food acquisition. Studies are needed to investigate the roles of inheritance and experience on the development of antipredator behaviours and decision making by prey animals when predation risk conflicts with other fitness-related activities such as the acquisition of food or reproductive opportunities.

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Antipredator behaviours have been divided into two categories based on whether they act before or after prey have been detected by predators (Sih 1987). Avoidance behaviours such as low activity levels and crypsis reduce the probability of detection by predators. In contrast, escape responses such as rapid flight and jerky movements render prey more difficult to catch and manipulate once they have been detected. The adaptive value of these behaviours is a function of, amongst other things, the sensory and locomotory capacities of the predator and environmental characteristics (e.g. structural complexity). Furthermore, minimizing predation risk is not always the objective because energetic costs of antipredator behaviours, and their indirect costs in terms of lost foraging (reviewed by Sih 1987; Lima & Dill 1990) and reproductive opportunities (reviewed by Magnhagen 1991), may in some circumstances outweigh the value of the increased protection they offer. Accordingly, prey often appear to trade off predation risk and other activities in relation to the costs and benefits of alternative behavioural options (reviewed by Sih 1987; Lima & Dill 1990).

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Many studies report interpopulation differences in antipredator behaviours that reflect variations in predation pressure to which a species is exposed over its geographical range; individuals from populations sympatric with a given predator typically display stronger and more effective antipredator behaviours than those from populations that are allopatric with the same predator (many examples can be found in Huntingford & Wright 1993; Mathis et al. 1993). However, few studies have investigated whether interpopulation differences in predation pressure affect how animals trade off predation risk and other fitness-related activities, such as feeding. One might expect strongly responsive animals from sympatric populations to compromise feeding more readily in response to predation hazard than predator-naive conspecifics. In accord with this prediction, Magurran (1986) observed that European minnows, *Phoxinus phoxinus*, from a population sympatric with the pike *Esox lucius*, resume foraging less rapidly after being presented a stalking predator model than do minnows from a population allopatric with the pike (Magurran 1986). However, Fraser & Gilliam (1987) observed the opposite trend. They found that the guppy *Poecilia reticulata* and the Hart rivulus, *Rivulus harti*, from populations sympatric with piscivorous fish feed more readily in the presence of predation risk than naive conspecifics. Fraser & Gilliam (1987) proposed that the sympatric guppies and rivulus may be exposed to such chronically high predation risk that waiting for safe conditions to feed would be a costly strategy; thus there has been selection for a certain level of 'boldness' towards predators to increase feeding opportunities.

The whelk *Buccinum undatum* is a common carnivorous gastropod of coastal areas of the North Atlantic Ocean (Caddy et al. 1974; Nielsen 1975) and possesses acute chemosensory abilities allowing detection and localization of food (Himmelman 1988; Lapointe & Sainte-Marie 1992) and predators (Harvey et al. 1987; Rochette et al. 1996). Over its geographical range, the whelk coexists with different types of predators, including asteroids and decapods (i.e. crabs and lobsters). In response to contact by, or odours of, the asteroid *Leptasterias polaris*, whelks display escape responses that include increased crawling activity, mucus secretion, shell rocking and foot contortions, which generate somersault-like escape movements (Harvey et al. 1987; Rochette et al. 1996). Furthermore, whelks display threat sensitivity, adjusting responses to the magnitude of danger and potential benefits of different encounters with *L. polaris* (Rochette et al. 1995; Rochette & Himmelman 1996; Rochette et al. 1997). Recently, whelks from a population sympatric with *L. polaris* (in the Gulf of St Lawrence, eastern Canada) were found to display stronger and more consistent responses to both contact with and odours of this predator than whelks from an allopatric population (in the Bay of Fundy) (Rochette et al. 1996). In particular, whelks sympatric with *L. polaris* displayed foot contortions (the whelk's most violent escape response) more readily to elude predatory attacks than did predator-naive whelks.

Behavioural responses of whelks to predatory decapods have not previously been investigated. The lobster *Homarus americanus* uses vision and chemodetection to locate prey (Hirtle & Mann 1978). The vigorous escape responses whelks display towards *L. polaris* would probably offer no protection against *H. americanus*, because the lobster is much faster than any whelk. However, whelks could presumably reduce their vulnerability to lobsters by displaying avoidance behaviours that would render them less conspicuous. For instance, by reducing activity levels, burrowing in the sediments and retreating inside the shell, whelks may reduce the likelihood of being detected by lobsters. Such behaviours should be particularly effective against lobsters, as they can only detect moving prey (Hirtle & Mann 1978).

In this study, we investigate antipredator behaviours and feeding responses of whelks from three populations with contrasting predator fields (i.e. that coexist with different predators) during encounters with the lobster *H. americanus* and the asteroid *L. polaris*. One population is sympatric with lobsters, but allopatric with asteroids, the second is sympatric with asteroids, but allopatric with lobsters, and the third is sympatric with both predators. We first examine the hypothesis that whelks are sensitive to the risk of predation represented by both predators. In particular, we test the predictions that whelks should display avoidance behaviours in the presence of a lobster and escape responses in the presence of an asteroid. We then examine the hypotheses that coexistence with a particular predator influences the whelk's propensity to display antipredator behaviours, and its decision making when exposed to a feeding opportunity with a risk of predation. In particular, we test the predictions that whelks from sympatric populations will display avoidance behaviours more readily in the presence of lobsters, and display escape responses more readily in the presence of asteroids than whelks allopatric with these predators, and that whelks with different predator fields will differ in their willingness to feed when a predator is present (henceforth referred to as 'boldness').

METHODS

Study Sites and Animals

In August 1994, 60 sexually mature adult whelks, *B. undatum*, were collected by scuba divers from each of three localities in eastern Canada (Fig. 1): (1) Havre-Saint-Pierre (HSP; 8–11 cm shell length), in the northern Gulf of St Lawrence, (2) Percé (P; 4–7 cm shell length), at the extremity of the Gaspé Peninsula in the Gulf of St Lawrence, and (3) St Andrews (SA; 5–7 cm shell length), in the Bay of Fundy. The differences in size range between populations reflect the fact that size at sexual maturity is highly variable in *B. undatum*. In general, whelks from the northern Gulf of St Lawrence mature at a greater size and age than whelks from more southerly regions (Gendron 1992). The reason for these differences is not known.

Whelks from these three localities have contrasting predator fields (Fig. 1). Thus, lobsters, *H. americanus*, are found in great numbers off the coasts of Maine, southern New Brunswick, southwestern Nova Scotia and in the southern Gulf of St Lawrence (Rutherford et al. 1967). They are, however, less abundant along the northern

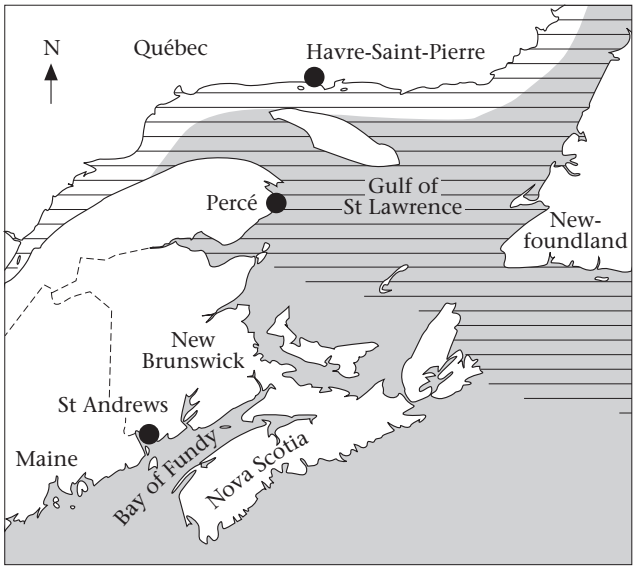

Figure 1. Map of eastern Canada showing the three localities where the whelk *Buccinum undatum* was collected (●). The whelk is found throughout the area depicted on the map, whereas the predatory asteroid *Leptasterias polaris*, is restricted to northern regions (hatched area), and is most abundant in the St Lawrence Estuary and along the north shore of the Gulf (white hatched area), and the predatory lobster *Homarus americanus*, is common in most regions (grey area), but uncommon along the north shore of the Gulf (white hatched area) and absent in the St Lawrence Estuary and in the vicinity of Havre-Saint-Pierre.

shore of the Gulf of St Lawrence, and are absent from Havre-Saint-Pierre (we have seen lobsters ca. 35 km east of our study site). The relative scarcity of lobsters on the northern shore of the Gulf of St Lawrence is possibly due to low summer temperatures, caused by the Labrador current, which hinder larval development. In contrast, the subarctic asteroid *L. polaris* is most abundant in northern parts of the Gulf and is not found in the Bay of Fundy. Table 1 summarizes the differences in predator fields between the three whelks populations, and introduces abbreviations based on whelk origin and predator field used hereafter to identify the three populations. We will hereafter use the general terms 'whelk', 'lobster' (or L) and 'asteroid' (or A) to refer to *B. undatum*, *H. americanus* and *L. polaris*, respectively.

In the recent study by Rochette et al. (1996), escape responses towards predatory asteroids were compared between whelks from Havre-Saint-Pierre (the same site as in the present study) and St Andrews (ca. 4 km from the St Andrews site used in this study). The behaviour of whelks from the Gaspé region has not previously been investigated.

Eight lobsters and eight asteroids were used throughout our study. The lobsters (25–30 cm rostrum to telson length, caught in Newfoundland) were bought from a fish market, whereas the asteroids (20–30 cm in diameter) were collected by scuba divers from Havre-Saint-Pierre.

Holding Conditions

After collection, the whelks were taken to a wet laboratory at Havre-Saint-Pierre, tagged with a numbered rubber band wound around the shell, and left to acclimate for approximately 3 weeks in running sea water in 90-litre tanks with a sand bottom, under a 12:12 h light:dark cycle. A total of eight tanks were used, four for HSP(A) whelks and two each for SA(L) and P(A+L) whelks. During this period, the whelks were fed dead herring, *Clupea harengus*, ad libitum. Water temperature throughout our study varied between 5 and 9°C, temperatures normally encountered by whelks from all three populations.

The lobsters and asteroids were held in running water in a 1200-litre holding tank, on a 12:12 h light:dark cycle. The tank contained large rocks to provide shelters. The predators were fed bivalves (*Mya truncata* and *Spisula polynyma*) every 5 days but were deprived of food 5 days prior to the experiments.

Experimental Protocol

To examine the effects of predator type and whelk origin on the response of whelks to predation risk, we conducted experiments in still water (ca. 70 litres) in plastic aquaria (75 × 43 × 29 cm) with 2–3 cm of sand covering the bottom. Five minutes before the start of an experiment, we introduced a 1-cm mesh cage containing either a lobster, an asteroid, or nothing at one end of the experimental aquarium. We then placed four whelks from a given population in the aquarium 5–10 cm from one another, approximately 20 cm from the cage and facing

Table 1. Summary of abbreviations used to identify three populations of whelks, *Buccinum undatum*, based on their origin (i.e. sampling location) and predator field (i.e. predators with which they coexist)

			Predicted response to	
Abbreviations	Whelk origin	Predator field	Asteroid	Lobster
HSP(A)	Havre-Saint-Pierre	Asteroid	Escape+	Avoidance
P(A+L)	Percé	Asteroid and Lobster	Escape+	Avoidance+
SA(L)	St Andrews	Lobster	Escape	Avoidance+

Also indicated are the predicted responses of whelks to the presence of a predatory asteroid or a lobster; +: indicates that whelks sympatric with a given predator are predicted to display antipredator behaviours more frequently than whelks allopatric with that predator. The description of escape and avoidance behaviours is presented in Table 2.

Table 2. Behavioural categories used to categorize the response of the whelk *Buccinum undatum* to different predator treatments before food was introduced into the experimental aquarium

Category	Behaviour
Escape	Foot contortions
	Shell rocking
	Rapid crawling with foot extended beyond shell apex
Avoidance	Retreating inside shell
	Burrowing into the sand
Nondefensive	Resuming an on-foot position and remaining still
	Crawling without showing signs of agitation (i.e. foot not extended beyond the shell's apex and no shell rocking behaviour).

During any given trial, individual whelks frequently displayed more than one behaviour of a given category, but they did not display both avoidance and escape responses.

it. We then categorized the response of each individual as (1) an escape, (2) an avoidance, or (3) a nondefensive response based on the behavioural patterns they displayed during the following 5 min (see Table 2). We then returned the whelks to their initial positions and introduced a herring filet (15–20 cm long, ca. 100 g) approximately half way between them and the cage. In the following 10-min period, we recorded how many whelks approached the herring to feed. We did not allow whelks to feed, however, and removed them from the aquarium as soon as they extended their proboscis to do so.

On a given day, we tested whelks from a single population successively in the three predator treatments, with a 4–5-h interval between trials for any given individual. We first tested whelks in the absence of a predator, then in the presence of a lobster, and finally in the presence of an asteroid. Between trials on different groups of four whelks, we brushed the side walls of the aquaria to remove mucus trails made by the whelks, changed the water and the top 5 mm of sand, refilled the aquaria and changed the predator. Between each predator treatment, the aquaria were emptied, thoroughly washed, refilled with new sand and kept in running sea water until the water was cleared of finer sand particles. Because of temporal and logistic limitations, we could not randomize the order of the predator treatments in which each replicate group of whelks was tested. However, this limitation is unlikely to have influenced the major conclusions of our study (see Discussion).

Because feeding status influences how whelks trade off predation risk and feeding opportunities (Rochette & Himmelman 1996), we tested the whelks after 5- and 15-day starvation periods; whelks were first tested after a starvation period of 5 days, then deprived of food for an additional 10 days and tested again. For each population, and after both starvation periods, we conducted a total of 15 replicate tests (four whelks per replicate) in each predator treatment. Because our laboratory water supply prevented us from keeping more than eight lobsters and asteroids, we used most predators twice in a given experiment. There were, however, no obvious differences in the responses of whelks to different asteroids or lobsters (asteroids were differentiated by colour patterns, and lobsters by size and colour of elastics bands around their chelipeds).

Statistical Analysis

The effect of predator type

We used the nonparametric Wilcoxon signed-ranks test (Zar 1984) to test the predictions that whelks would display avoidance behaviours more readily in the presence of a lobster than in either the presence of an asteroid or the absence of a predator, and that they would display escape responses more readily in the presence of an asteroid than in either the presence of a lobster or the absence of a predator. We conducted separate analyses for each combination of whelk population and starvation period. Because our planned comparisons were not orthogonal (mutually independent), we adjusted the significance level of these tests to $\alpha'=0.0253$ using Bonferroni's inequality so that the experimentwise error rate would remain below $\alpha=0.05$ (Sokal & Rohlf 1981). Finally, because our predictions were directional, we used one-tailed probability distributions.

We also used the Wilcoxon signed-ranks test to compare the number of whelks that attempted to feed in the presence of lobsters and asteroids. We conducted separate analyses for each combination of whelk population and starvation period, using two-tailed probability distributions.

The effect of whelk origin

To investigate interpopulation differences in the behaviour of whelks, we calculated two indices of whelk responsiveness, the first in the absence of food and the second in the presence of food. In the absence of food, we calculated the defensive-response index, which was a measure of the degree to which whelks from each population displayed avoidance behaviours and escape responses in response to predatory lobsters and asteroids, respectively. For the lobster (or asteroid) trials, each whelk was given a score of +1 if it displayed avoidance (escape) in the presence of a lobster (asteroid) but not in the absence of a predator, 0 if it displayed avoidance (escape) neither in the presence of a lobster (asteroid) nor in the absence of a predator, and -1 if it did not display avoidance (escape) in the presence of a lobster (asteroid) but did so in the absence of a predator. Whelks that displayed avoidance (or escape) behaviours in the presence and absence of a lobster (asteroid) were excluded from the analyses because their behaviours could not be unambiguously attributed to the predator's presence. For each replicate (four whelks that were tested together), we calculated the defensive-response index by averaging the scores of the four whelks. We compared indices between the population allopatric with a given predator and each of the two sympatric populations using the nonparametric Mann–Whitney *U* test (Zar 1984). These comparisons

were not orthogonal so we used a significance level of $\alpha'=0.0253$, and because our predictions were directional (higher indices for sympatric whelks), we used one-tailed probability distributions.

In the presence of food, we calculated the predator-impact index to measure the degree to which whelks refrained from feeding owing to the presence of a predator. For the lobster (or asteroid) trials, each whelk was given a score of +1 if it attempted to feed in the absence of a predator but not in the presence of a lobster (asteroid), 0 if it attempted to feed in the presence of a lobster (asteroid) and in the absence of a predator, and −1 if it attempted to feed in the presence of a lobster (asteroid) but not in the absence of a predator. Whelks that did not attempt to feed in either the presence of a lobster (asteroid) or the absence of a predator were excluded from the analyses because their failure to feed could not be attributed to the predator's presence. For each replicate (four whelks tested together), we calculated the predator-impact index by averaging the scores of the four whelks. We compared indices between the population allopatric with a given predator and the two sympatric populations using Mann–Whitney *U* tests (Zar 1984). Again we used a significance level of $\alpha'=0.0253$ because the comparisons were not orthogonal. However, our predictions regarding the boldness of whelks from different populations were not directional, so we used two-tailed probability distributions.

RESULTS

Responses of Whelks to Lobsters and Asteroids

The responses of whelks to predatory lobsters and asteroids were generally consistent with our predictions. Before food was introduced to the experimental aquarium, whelks displayed avoidance behaviours more frequently in the presence of the lobster than in either the presence of the asteroid, or the absence of a predator (Fig. 2), and they displayed escape responses more frequently in the presence of the asteroid than in either the presence of the lobster or the absence of a predator (Fig. 3). These patterns were relatively consistent across populations and starvation periods, although SA(L) whelks displayed no noticeable behavioural changes in response to either predator when tested after the 15-day starvation period (Figs 2, 3), and HSP(A) whelks displayed avoidance behaviours as frequently during the control and lobster trials after the 5-day starvation period (Fig. 2). That whelks frequently displayed avoidance behaviours in the absence of a predator probably made it more difficult to detect significant responses to lobsters, and thus more detailed behavioural categories might have been necessary to gain further insight into the whelk's responses to this predator. For instance, after the 5-day starvation period, HSP(A) whelks more frequently burrowed deeply in the sediments (i.e. with only a small portion of the shell remaining visible at the surface) during the lobster trials than during the control trials (Wilcoxon signed-ranks test: one-tailed $P<0.01$). Note, however, that SA(L) whelks tested after the 15-day starvation period (i.e. the other case in which no significant response to lobsters was detected) did not burrow deeply in the sediments more frequently during the lobster trials than during the control trials ($P>0.4$).

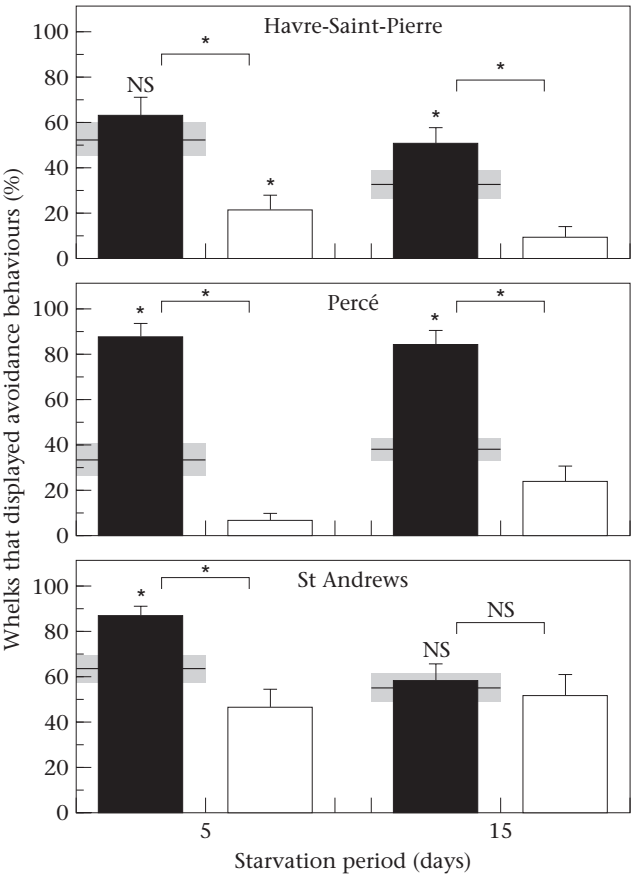

Figure 2. Mean (+SE) percentage of whelks from three populations that displayed avoidance behaviours (burrowing in the sediments or retreating inside the shell), after starvation periods of 5 and 15 days, when tested in the presence of a predatory lobster, *Homarus americanus* (■), or of a predatory asteroid, *Leptasterias polaris* (□), and in the absence of a predator (horizontal lines, shaded areas show the SE). NS: Nonsignificant; *$P<0.0253$.

We also found evidence that predatory lobsters and asteroids had a different impact on the feeding response of whelks. Thus, whelks from the three populations more often refrained from feeding in the presence of a lobster than in the presence of an asteroid (Fig. 4). The effect of predator type on the feeding activity of whelks was relatively consistent across populations and starvation periods, although it was only significant for one of the two starvation periods for P(A+L) whelks (15-day) and SA(L) whelks (5-day).

Starvation period had a marked effect on the feeding response of whelks in the presence, but not in the absence, of a predator (Fig. 4). For the three populations combined, only 24% of the whelks that attempted to feed in the absence of a predator after the 15-day starvation period had not attempted to feed in the absence of a predator after the 5-day starvation period. These figures increase to 85 and 67% for the lobster and asteroid trials, respectively.

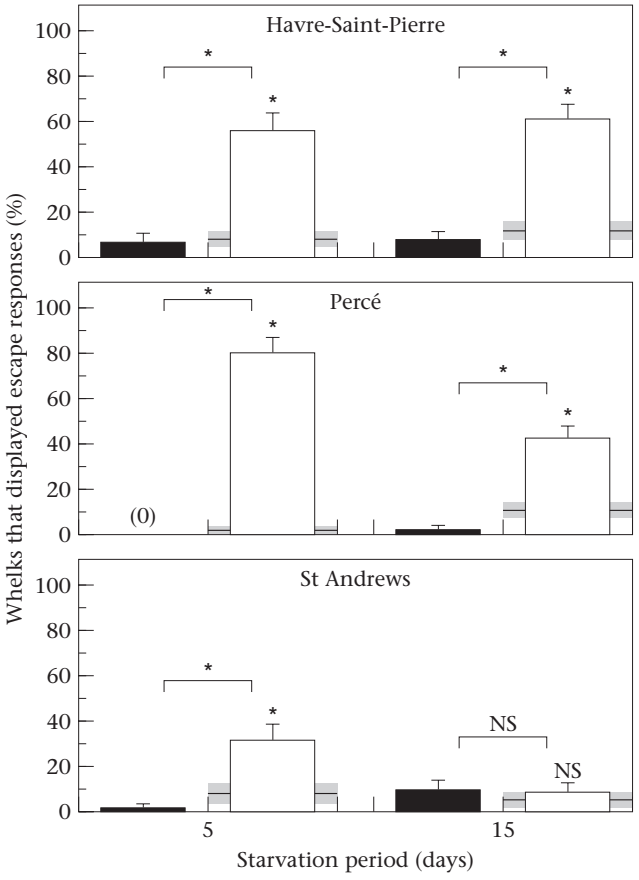

Figure 3. Mean (+SE) percentage of whelks from three populations that displayed escape responses (rapid flight, shell rocking or foot contortions), after starvation periods of 5 and 15 days, when tested in the presence of a predatory lobster, *Homarus americanus* (■), or of a predatory asteroid, *Leptasterias polaris* (□), and in the absence of a predator (horizontal lines, shaded areas show the SE). NS: Nonsignificant; **P*<0.0253.

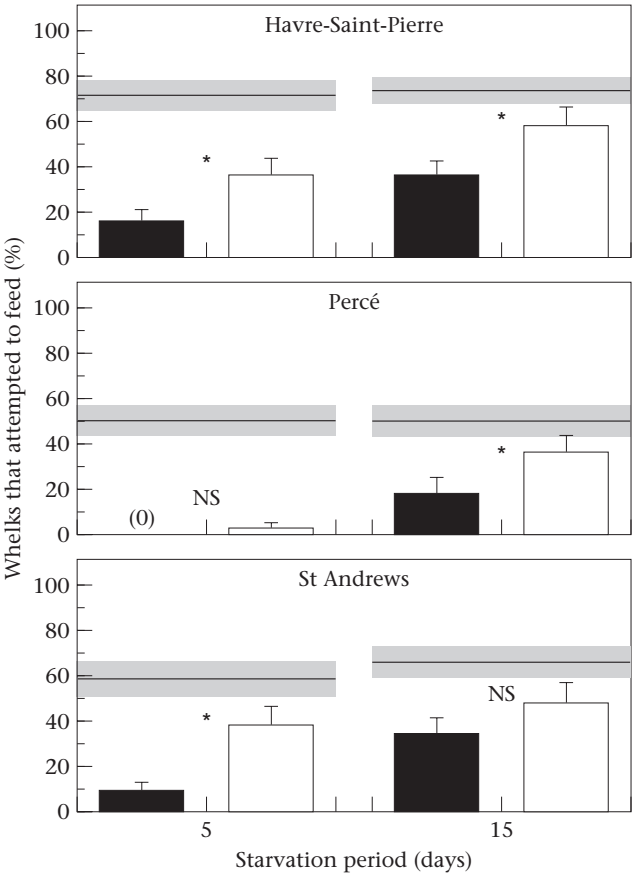

Figure 4. Mean (+SE) percentage of whelks from three population that attempted to feed in the presence of a predatory lobster, *Homarus americanus* (■), or of a predatory asteroid, *Leptasterias polaris* (□), and in the absence of a predator (horizontal lines, shaded areas show the SE), after starvation periods of 5 and 15 days. The percentages of whelks attempting to feed in the presence of lobsters and asteroids were compared using two-tailed Wilcoxon signed-ranks tests. NS: Nonsignificant; **P*<0.05.

Interpopulation Differences in Whelk Behaviour

Although whelks from the three populations displayed similar responses to lobsters and asteroids, the indices we calculated in the absence (defensive response) and presence (predator impact) of food revealed interpopulation differences in the consistency with which these responses were displayed. The defensive-response index was generally greater for whelks sympatric with a given predator than for those allopatric with that predator, but predator impact did not vary consistently between sympatric and allopatric populations.

Thus, for the lobster trials, the defensive-response indices calculated after the 5-day starvation period indicated that P(A+L) and SA(L) whelks, both sympatric with lobsters, more readily displayed avoidance behaviours in response to the lobster than did HSP(A) whelks (Fig. 5a). The difference between P(A+L) and HSP(A) whelks in terms of responsiveness to lobsters was also significant after the 15-day starvation period, but that between SA(L) and HSP(A) whelks was not (recall that SA(L) whelks displayed similar behaviours in all three predator treatments after the 15-day starvation period). In contrast, only P(A+L) whelks compromised feeding to a greater extent than HSP(A) whelks in the presence of a lobster (Fig. 5b). Thus, after both starvation periods, predator impact was similar for HSP(A) and SA(L) whelks. Note that after the 15-day starvation period, the presence of a lobster had a significant (Wilcoxon signed-ranks test: one-tailed $P=0.002$) effect on the feeding response of SA(L) whelks, even though the latter did not display obvious responses to the lobster before food was introduced to the experimental aquarium.

During the asteroid trials, the defensive-response index was significantly greater, after both starvation periods, for HSP(A) and P(A+L) whelks, both sympatric with asteroids, than for SA(L) whelks (Fig. 6a). In contrast, only after the 5-day starvation period did P(A+L) whelks compromise feeding to a greater extent than SA(L) whelks, and predator impact did not differ between HSP(A) and SA(L) whelks after either of the two starvation periods (Fig. 6b).

Overall, we found significant differences in seven of the eight comparisons involving defensive-response indices (88%), but in only three of the eight comparisons

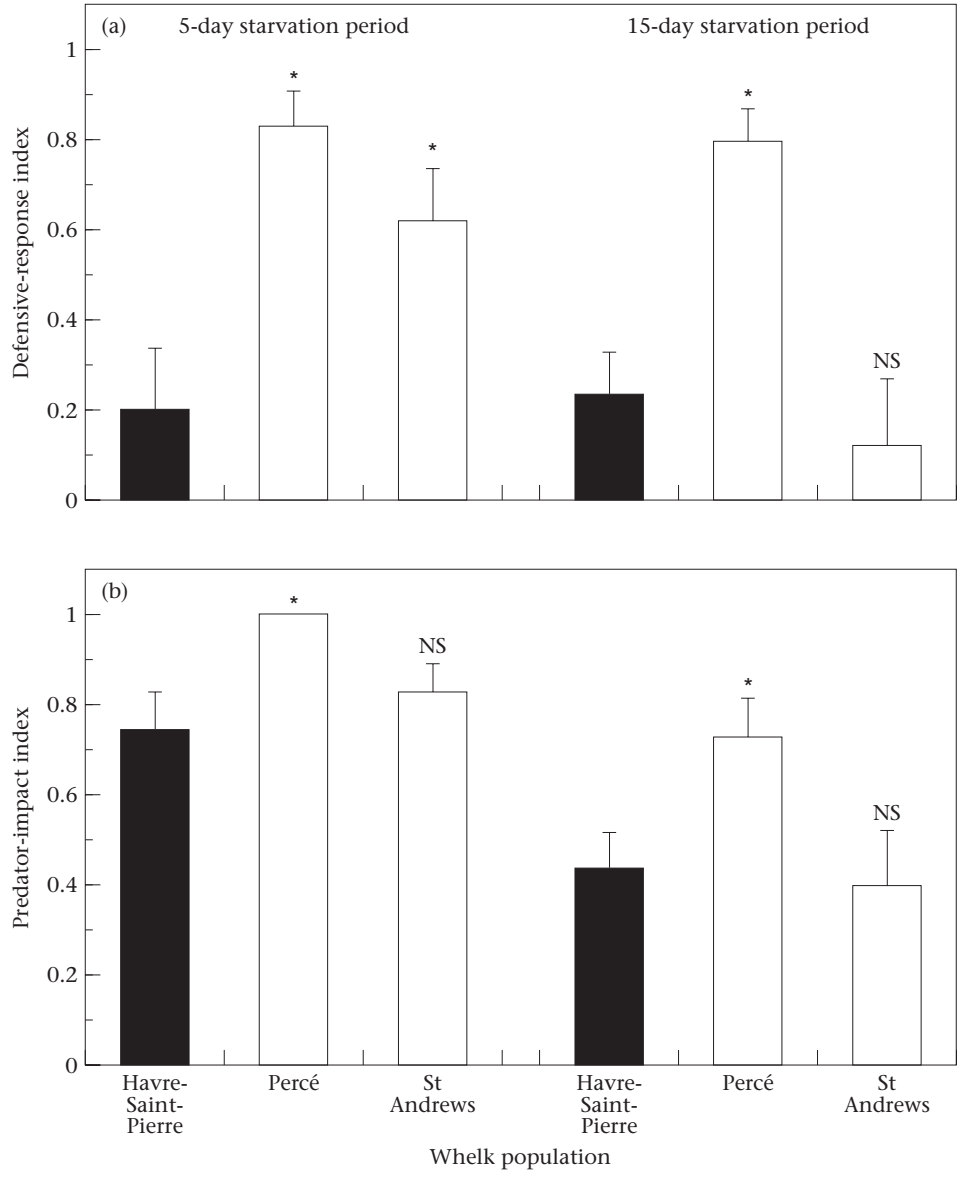

Figure 5. Defensive-response (a) and predator-impact (b) indices illustrating the responsiveness of whelks to the predatory lobster *Homarus americanus* in the absence and presence of food, respectively (see Methods for details). The indices were evaluated for whelks from three populations tested after starvation periods of 5 and 15 days. Indicated above the columns for populations sympatric with *H. americanus* (□) are the statistical results of comparisons with the allopatric population (■). Sample sizes varied between 13 and 15 for these comparisons, because in a few replicates all four whelk populations were excluded from the analysis (see Methods). NS: Nonsignificant; **P*<0.0253.

involving predator-impact indices (38%). Of particular interest, HSP(A) and SA(L) whelks, the populations with the most contrasting predator fields, displayed no noticeable difference in boldness towards either predator, even though HSP(A) whelks displayed avoidance behaviours less readily in response to lobsters, and displayed escape responses more frequently in response to asteroids, than did SA(L) whelks.

DISCUSSION

Threat Sensitivity

Animals from a variety of taxa adjust their behaviours to the threat different types of predators represent (e.g. molluscs: Barbeau & Scheibling 1994; aquatic insects: Moore & Williams 1990; fish: Magnhagen & Forsgren 1991; rodents: Hennessy & Owings 1978; ungulates: Walther 1969; primates: Seyfarth et al. 1980). Our study provides evidence that the marine gastropod *B. undatum* is sensitive to the predatory threat associated with the lobster *H. americanus* and the asteroid *L. polaris*.

Presumably because asteroids are relatively slow-moving animals, many molluscs and echinoderms have evolved flight responses to deter this predator (reviewed by Ansell 1969; Feder 1972). Whelks use rapid crawling, shell rocking and foot contortions to distance themselves from potentially dangerous asteroids (Rochette et al. 1997) and to elude attacks (Rochette et al. 1996). These

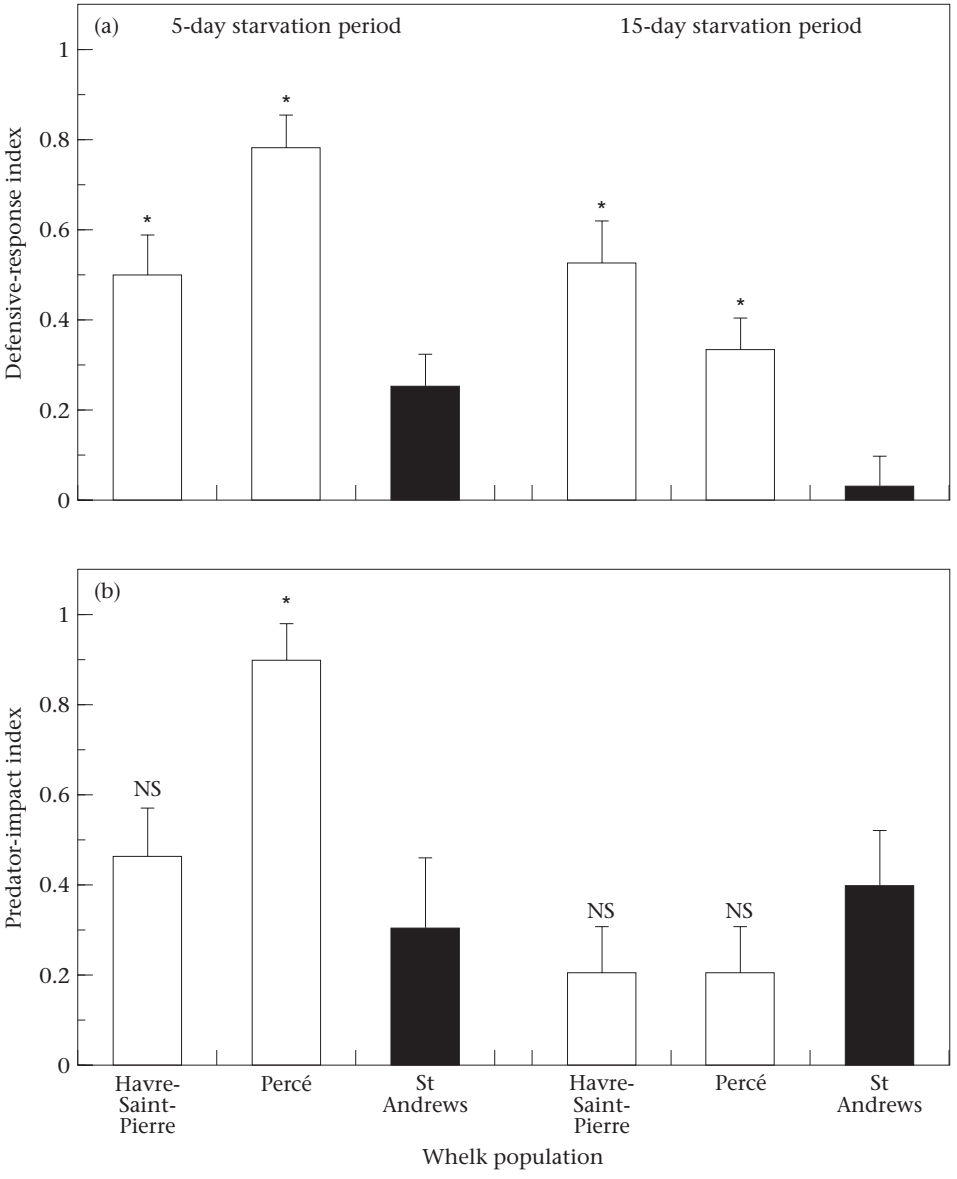

Figure 6. Defensive-response (a) and predator-impact (b) indices illustrating the responsiveness of whelks to the predatory asteroid *Leptasterias polaris* in the absence and presence of food, respectively (see Methods for details). The indices were evaluated for whelks from three populations tested after starvation periods of 5 and 15 days. Indicated above the columns for populations sympatric with *L. polaris* (□) are the statistical results of comparisons with the allopatric population (■). Sample sizes varied between 13 and 15 for these comparisons, because in a few replicates all four whelk populations were excluded from the analysis (see Methods). NS: Nonsignificant; *P<0.0253.

escape responses, however, would probably be ineffective against lobsters, which move more rapidly than whelks. The protection of whelks (Thomas & Himmelman 1988) and other gastropods (e.g. Zipser & Vermeij 1978; Bertness & Cunningham 1981) against fast-moving predators such as decapods and fish is generally attributed to characteristics of the shell (e.g. thickness, aperture width, presence of spines or ridges) that render it more difficult to break open. However, as the production of a thick or heavy armour involves various types of costs (Palmer 1981, 1992) and typically offers only partial protection, gastropods should benefit from using anti-predator behaviours in conjunction with morphological defenses to decrease their vulnerability to shell-breaking predators. Accordingly, the intertidal gastropod *Tegula funebralis* crawls out of aquaria when exposed to chemical cues from the crab *Cancer antennarius* (Geller 1982), and the periwinkle *Littorina irrorata* avoids predation by the crab *Callinectes sapidus* by migrating up cordgrass stems during tidal inundation (Vaughn & Fisher 1988). Such vertical migrations above the water line cannot be used by subtidal species such as the whelk *B. undatum*, however. Displaying reduced activity levels, burrowing in the sediments and retreating into the shell are probably the most effective behaviours whelks can use to decrease their vulnerability to lobsters (and other fast-moving predators such as the Atlantic wolfish *Anarhichas lupus*). These behaviours should be particularly effective considering

that lobsters can only visually detect moving prey (Hirtle & Mann 1978), and they probably also reduce the whelk's chemical conspicuousness to predators by reducing the degree of exposure of their soft tissues to the environment.

Whereas avoidance behaviours render prey less conspicuous to predators, escape responses such as flight and jerky movements render them more difficult to capture and manipulate (Sih 1987). However, we believe it may be misleading to dichotomize avoidance and escape behaviours based on whether they act before or after predators detect and recognize prey, as suggested by Sih (1987, page 204). Prey animals presumably often do not know whether or not they have been detected by a predator (see Sih 1992 for theoretical considerations of the effects of uncertainty on prey decision making), yet they must continuously choose among alternative behavioural options. The survival value of different antipredator behaviours (e.g. avoidance versus escape) will depend on the probability that the prey has been detected and the extent to which these behaviours increase survival, both prior to and after detection by a predator.

During our experiment, whelks were more likely to have been detected by the lobster than by the asteroid, because asteroids cannot visually detect prey and have relatively limited olfactory capacities (Feder & Christensen 1966). Although whelks probably had been detected by the lobster, there is the possibility that they may have remained hidden because of the possibility (however slight) that they had not been detected, and because of the very low efficacy of escape responses against this predator (whelks cannot outrun lobsters). In contrast, fleeing may have been the best response to the asteroid, even if the whelks had not yet been detected, because they had a very high probability of outrunning the asteroid if they fled before being grasped. Furthermore, it may be maladaptive for gastropods to remain in the vicinity of asteroids, because the chemicals these predators naturally exude may be toxic (Lucas et al. 1979; Iorizzi et al. 1995) and cause habituation (Margolin 1964; Justome et al. 1998). Finally, the asteroids usually moved about in the cages during our experiments and whelks have been shown to respond more strongly to moving than to stationary asteroids (Rochette et al. 1997).

The whelk's feeding response was also affected by predator type; whelks from the three populations fed less readily in the presence of a lobster than in the presence of an asteroid. Whelks may have perceived a greater immediate danger from lobsters than from asteroids. Even when an asteroid has successively attached some of its tube feet to a whelk's shell, violent foot contortions and shell rocking by the whelk can free it from this predator's grasp (R. Rochette, personal observation). In contrast, even the most resistant of whelk shells can be cracked open or gradually chipped away by a lobster of the size used in our experiment (Thomas & Himmelman 1988). Few studies have investigated whether the prey's decision to feed in the presence of predation risk is a function of the magnitude of predatory threat, and those that have, report variable results (e.g. Gotceitas & Godin 1993; Scrimgeour & Culp 1994).

Starvation period also had a marked effect on the feeding response of whelks. The effect of increased starvation was mainly to increase the boldness of whelks that were 'motivated' to feed, rather than to increase the number of 'motivated' whelks.

Interpopulation Differences in Behaviour

Our study corroborates a recent study showing that whelks sympatric with the asteroid *L. polaris* display escape responses more readily in the presence of this predator than do whelks allopatric with *L. polaris* (Rochette et al. 1996). Furthermore, we provide evidence that whelks sympatric with the lobster *H. americanus* hide in the sediments and retreat inside their shell when they detect the presence of a lobster more readily than do whelks allopatric with this predator. The only inconsistency in these patterns was after the 15-day starvation period, when SA(L) whelks did not show a stronger tendency to display avoidance behaviours in the presence of a lobster than did HSP(A) whelks. The weak tendency of SA(L) whelks to display avoidance behaviours in the presence of a lobster after 15 days of starvation is particularly intriguing considering that they did respond to this predator by decreasing their feeding activity.

The few studies that have investigated how animals from different populations trade off predation risk and food acquisition suggest that boldness towards predators cannot be predicted on the basis of differences in predation pressure alone (see Introduction). Similarly, we found evidence that P(A+L) whelks feed less readily in the presence of lobsters and asteroids than whelks allopatric with these predators, but we found no difference in boldness towards either predator between HSP(A) and SA(L) whelks, even though the former are allopatric with lobsters (but sympatric with asteroids), and the latter allopatric with asteroids (but sympatric with lobsters).

We believe that the similar level of boldness of HSP(A) and SA(L) whelks reflects two important aspects of whelk decision making. First, even whelks that do not naturally coexist with lobsters or asteroids seem to perceive a risk when they detect these predators. Although lobsters and asteroids presumably represented novel stimuli (which in itself may warrant caution) to HSP(A) and SA(L) whelks, respectively, it is possible these predators emit stimuli (e.g. chemical cues) that resemble those emitted by similar predators with which these whelks coexist. For instance, small whelks in Havre-Saint-Pierre are preyed upon by the crabs *Hyas araneus* and *Cancer irroratus*, and St Andrews whelks are sympatric with the predatory asteroids *Asterias vulgaris* and *Crossaster papposus* (it is doubtful, however, that these asteroids are important predators of whelks). Second, even whelks that naturally coexist with lobsters and asteroids don't completely abstain from feeding when they detect these predators. Boldness towards predators may be selected for if it enables increased opportunities (e.g. feeding and reproduction) whose value outweighs the costs of increased predation risk. For example, despite their strong responsiveness to the asteroid *L. polaris*, whelks from Havre-Saint-Pierre in the Mingan Islands occasionally aggregate

near an asteroid that is feeding on a large endobenthic bivalve, to steal some of its prey or to feed on left-overs (Rochette et al. 1995; Rochette & Himmelman 1996). These nutritional gains seem to represent a significant portion of their diet, so HSP(A) whelks may have been selected for a relatively high level of boldness towards asteroids, which may partly explain why they were as likely to feed in the presence of asteroids as were SA(L) whelks.

Several studies report that seemingly independent behavioural patterns can be correlated, both at the population and individual levels. For instance, in the spider *Agelenopsis aperta* (Riechert & Hedrick 1993) and in the three-spined stickleback *Gasterosteus aculeatus* (Huntingford 1976), responsiveness to predators and aggressiveness towards conspecifics are correlated. Such behavioural correlations may arise through gene linkage or pleiotropy, in which case the different behaviours cannot evolve independently of one another. In contrast, the relation between how strongly prey from different populations respond to predators in the absence and presence of food is seemingly quite variable (Magurran 1986; Fraser & Gilliam 1987; this study), suggesting that responses to predators in different contexts can evolve, or develop (i.e. via learning), independently. This is also supported by size- and context-dependent behaviours of whelks in the Mingan Islands; whelks that approach feeding asteroids, *L. polaris*, to acquire feeding opportunities (adults; Rochette et al. 1995) also display the strongest and most consistent escape responses to both contact with and odours of this predator (Rochette et al. 1996).

In summary, our principal conclusions are that (1) whelks, *B. undatum*, adjust their defensive responses to the threat predatory lobsters and asteroids represent, and (2) whelks that naturally co-occur with lobsters or asteroids respond to these predators by displaying stronger defensive responses, but not necessarily by feeding less, than whelks from allopatric populations. We believe our results reflect true differences in responses of whelks from different populations to different predation threats, and that our conclusions are not affected by the fact that we could not randomize the order of the predator treatments during our experiment. Thus, although they had previously been tested in the presence of a lobster, whelks responded to asteroids as predicted from previous studies, by displaying increased crawling activity, shell rocking behaviour and foot contortions (Harvey et al. 1987; Rochette et al. 1996; Rochette et al. 1997), and rarely by displaying avoidance behaviours. In any case, if prior exposure to a lobster had an effect on the response of whelks to asteroids, it should have been to increase their tendency to display avoidance behaviours and to reject food items, in which case the differences we calculated between responses to lobsters and asteroids (both in the absence and presence of food) were conservative. Also, carry-over effects were not responsible for the fact that population-related differences in behaviour were consistent in the absence of food, but not in the presence of food, because we observed this pattern the very first time whelks were tested (lobster trial, 5-days of starvation).

Most antipredator behaviours probably have both a genetic and an environmental basis (e.g. Magurran 1990). In contrast to most marine invertebrates, whelks do not have a pelagic larval stage and their recruits emerge from egg capsules deposited on rocks and algal stipes. Because benthic development can favour adaptation to local conditions (Behrens Yamada 1989), it may have contributed to the evolution of differences in antipredator responses of whelks from different localities. However, a recent study demonstrated that the escape responses of whelks, *B. undatum*, develop as young individuals are exposed to predation-related stimuli, including chemical cues from the asteroid *L. polaris*, and from damaged or 'alarmed' conspecifics (Rochette et al. 1998). We are currently comparing the behaviour of congeneric marine snails with different dispersal capacities to gain insight into the roles of inheritance and experience in determining how prey animals trade off predation risk and other activities.

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