Does vulnerability influence trade-offs made by whelks between predation risk and feeding opportunities?

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Abstract. In the northern Gulf of St Lawrence, eastern Canada, the whelk *Buccinum undatum* occasionally aggregates near the feeding asteroid *Leptasterias polaris* to obtain food. This is surprising considering that whelks are frequently preyed upon by *L. polaris* and have developed a violent escape response to this predator. Almost all whelks in aggregations near feeding asteroids are large. This study suggests that small whelks do not approach feeding *L. polaris* because they are more vulnerable to this predator. Predation experiments demonstrated that the vulnerability of whelks to *L. polaris* decreases with increasing whelk size. Sampling in the field showed that 97% of whelks measuring more than 5 cm in shell length are found in the sediment zone, where *L. polaris* extracts large endobenthic bivalves, but whelks less than 5 cm are equally abundant in the rocky (49.5%) and sediment (50.5%) zones. Field experiments showed that whelks within 50 cm of large bivalves being ingested by *L. polaris* were larger than those within 50 cm of bivalves placed by themselves on the bottom. Finally, laboratory measurements showed that the influence of predator threat on the time whelks spent feeding decreased with whelk size, but the influence of feeding motivation on the time whelks spent feeding increased with whelk size. In the situation where motivation to feed was high and size-related differences in vulnerability were large, the impact of the predator decreased significantly with increasing whelk size. Whelks show threat-sensitive decision making adjusted to potential feeding benefits and vulnerability to predation.

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Anti-predator mechanisms are frequently flexible and can be adjusted during the lifetime of prey in response to the current risk of predation (Lima & Dill 1990). For instance, manipulation of the environment in which prey are raised (presence and activity of predators) modifies the development of protective exoskeletons in rotifers (Gilbert 1966), small pelagic crustaceans (Krueger & Dodson 1981; Hebert & Grewe 1985) and gastropods (Appleton & Palmer 1988; Palmer 1990). Also, early experience with predators affects the schooling behaviour of minnows (Magurran 1990) and avoidance behaviours in two species of tadpoles (Semlitsch & Reyer 1992). Prey animals may further display threat-sensitive predator avoidance (Helfman 1989), adjusting behavioural responses to the threat associated with each encounter with a predator. Threat-sensitive avoidance has been documented in gastropods (reviewed by Dix & Hamilton 1993), echinoids (Dayton et al. 1977; Phillips 1978), fish (Helfman 1989; Licht 1989; Bishop & Brown 1992) and mammals (Walther 1969; Hennessy & Owings 1978).

Many prey animals make adaptive trade-offs in situations where the need to avoid predation conflicts with essential activities such as feeding and reproduction (reviewed by Sih 1987; Lima & Dill 1990). Cost–benefit analyses have frequently been used in laboratory studies in which predator avoidance is placed in conflict with food acquisition to predict the relative responses of different types of individuals to similar conditions and those of similar types of individuals to different conditions. The effect of predator threat on feeding activity usually increases with an increase in prey vulnerability (e.g. Stein & Magnuson 1976; Sih 1982; Ramcharan et al. 1992), and decreases with an increase in prey energetic requirements

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(e.g. Giles 1983, 1987; Dill & Fraser 1984; Godin & Sproul 1988; Abrahams & Dill 1989; McKillup & McKillup 1994).

The common whelk *Buccinum undatum* and the asteroid *Leptasterias polaris* are the most conspicuous subtidal carnivores in the Mingan Islands, northern Gulf of St Lawrence, eastern Canada (Jalbert et al. 1989). *Leptasterias polaris* is a major predator of macro-invertebrates in these communities (Himmelman & Dutil 1991), and Dutil (1988) estimated that they consumed 4.4% of the total whelk biomass in 100 days. Whelks show strong escape responses to both odours of, and contact with, *L. polaris* (Harvey et al. 1987). Although whelks generally avoid *L. polaris*, they occasionally inhibit their escape response and aggregate around feeding individuals to obtain food (Rochette et al. 1995). On a few occasions we have observed a feeding asteroid take advantage of a whelk's temerity to make an easy second catch. Whelks are capable of detecting and localizing decaying matter from considerable distances (Himmelman 1988; McQuinn et al. 1988; Lapointe & Sainte-Marie 1992), and are probably attracted to the feeding *L. polaris* by the chemical cues emanating from their prey. In the northern Gulf, *L. polaris* occurs in high densities (Dutil 1988), however, its importance in supplying food for whelks varies with the type of prey on which it is feeding. For example, few feeding opportunities are provided by small *L. polaris* (<20 cm in diameter) foraging on small bivalves in the shallow rocky zone (Himmelman & Dutil 1991), because the asteroids completely cover their prey while feeding and do not leave prey remains. In contrast, frequent feeding opportunities are probably provided by large *L. polaris* foraging on large endobenthic bivalves in the deeper sediment zone (Himmelman & Dutil 1991), because (1) the prey are often only partially covered (thus leaving space for the insertion of the whelk's proboscis), (2) the asteroid may leave its prey before it is completely ingested (S. Morissette, personal communication), and (3) the digging activities of *L. polaris* may expose other infaunal organisms (e.g. polychaetes) that can be eaten by whelks (personal observations).

A striking aspect of the *Buccinum/Leptasterias* interaction is that almost all whelks approaching feeding *L. polaris* are large and mature (>7 cm in shell length). We proposed that smaller whelks are less abundant in the vicinity of feeding asteroids because they are more vulnerable to *L. polaris* (Rochette et al. 1995). The object of the present study was to evaluate the hypothesis that the vulnerability of whelks influences their decisions when confronted with situations where feeding opportunities conflict with predator avoidance. We tested the following correlates of this hypothesis: (1) that the vulnerability of whelks to asteroids decreases with size of the whelk, (2) that large whelks show a greater tendency to inhabit the sediment zone where asteroids extract large bivalves, (3) that the size of whelks in the vicinity of feeding asteroids is larger than in the vicinity of food sources devoid of asteroids, and (4) that the presence of the predatory asteroid *L. polaris* has a greater impact on the feeding activity of smaller whelks.

MATERIALS AND METHODS

Our study was conducted using SCUBA during the summer months (May to late August) in 1992, 1993 and 1994 in the Mingan Islands, northern Gulf of St Lawrence (50°14′N, 63°35′W). The field work was conducted at Cap du Corbeau on Île du Havre (Himmelman & Dutil 1991), and all asteroids and whelks used in the laboratory were collected on sediment bottom from 7 to 15 m depth at the same site.

Relationship Between Whelk Size and Vulnerability

The vulnerability of different sized whelks in encounters with *L. polaris* was determined by exposing them to different sized asteroids. Six whelks of each of three size classes, 2–4, 5–7 and 8–10 cm in shell length, were placed in each of nine cages ($1.3 × 1.3 × 0.3$ m, with plastic bottoms) maintained on the bottom at 10 m depth. The whelks in three cages were exposed to nine *L. polaris* measuring 10–15 cm in diameter, those in three others were exposed to six 20–25 cm asteroids, and those in the remaining three cages were exposed to three 35–40 cm asteroids. The number of asteroids was varied to obtain a high whelk mortality rate without exceeding the carrying capacity of the cages. The cages were visited at 3-day intervals over a 3-month period to record mortalities, replace dead whelks (by whelks of the same size class), and replace asteroids that were found feeding on a whelk.

Each kill was considered a statistically independent event. It was unlikely that the same asteroid ate several whelks during the experiment, given the short interval between our visits and the feeding habits of *L. polaris* (slow ingestion of prey and long interval between successive meals). In all three predator treatments, the observed numbers of whelks killed in the different size classes were compared with the numbers expected to be killed if whelks in all three size classes were equally vulnerable using a goodness-of-fit test (Zar 1984). Numbers expected were one third of the total number of whelks killed in a given predator treatment.

Relationship Between Whelk Size and Habitat Use

In August 1994, to test the prediction that large whelks have a greater tendency to inhabit sediment areas than small whelks, we carefully examined 382 1-m² quadrats placed regularly along alternative sides of three transects (measuring 62, 63 and 85 m in length, respectively) spaced ≈ 50 m from one another across the zone where whelks and asteroids were most abundant (from 0 to ≈ 20 m in depth). We recorded the shell length of each whelk and noted whether it was in the rocky zone, where endobenthic bivalves were absent, or in the sediment zone, where endobenthic bivalves were present. We did not count whelks <1 cm because of the difficulty of thoroughly sampling such small individuals (Jalbert et al. 1989). We also examined 3-m corridors on both sides of each transect to determine the abundance and size structure of asteroids in the rocky and sediment zones. The rocky zone extended from the intertidal to ≈ 5–7 m in depth where boulders gradually gave place to cobbles and gravel and then sand and mud. Overall, 40% of the quadrats sampled were in the rocky zone and 60% in the sediment zone.

To investigate changes in habitat use with size, we grouped whelks in 1-cm size classes and asteroids in 5-cm size classes. For each size class, we used a goodness-of-fit test (Zar 1984) to compare the number of individuals encountered in the rocky and sediment zones with the numbers expected if their distribution was uniform (40% rocky and 60% sediment zone).

Relationship Between Decision Making and Whelk Size: Field Study

To determine whether whelks more readily approach predators to obtain feeding benefits as they increase in size, we compared the shell length of whelks that approached surf clams *Spisula polynyma* being consumed by *L. polaris* with the size of whelks that approached unattended surf clams (in the absence of *L. polaris*). To do this, we randomly placed asteroids with surf clams and surf clams alone at ≈ 20 m intervals along two 160-m long transects on sediment substratum at 9 and 15 m depth. The adductor mussel of all surf clams was cut at the onset of the experiment. Furthermore, the unattended clams (without a *L. polaris*) were placed in vexor sacs (5 mm mesh) to prevent feeding by whelks and other carnivores. The asteroids had previously been starved for ≈ 7 days to increase the probability they would feed on the surf clams. Each day, at approximately the same time (1000 hours), we collected all whelks within 50 cm of each surf clam. In the treatment with predators, sampling continued until the asteroid left its prey (this usually took 2–6 days). In the treatment without predators, sampling was stopped after 5–6 days (when all asteroids had left their prey in the other treatment). We made two experimental runs, one from 10–15 May 1994 (eight asteroids with clams and four unattended clams), prior to copulation and egg laying by the whelks, and the second from 17–21 August 1994 (10 asteroids with clams and six unattended clams), when reproduction was finished (Martel et al. 1986). We set out more feeding asteroids with clams than unattended clams to decrease the difference between the two treatments in the numbers of whelks sampled. We tested for the influence of the asteroid's presence in May and in August using a non-parametric Mann–Whitney test (Zar 1984; data in some groups were not normally distributed).

We further sampled the above study area between 22 and 24 August 1994 to determine the size distribution of whelks. At regular intervals along both transects, divers closed their eyes and swam either shoreward or seaward for a random number of kicks (1–10), sank to the bottom, drove a stake into the substratum, and then measured the size of whelks within a 1.5-m radius.

Relationship Between Decision Making and Whelk Size: Laboratory Experiment

To determine whether the effect of the predatory asteroid *L. polaris* on the feeding activity of whelks decreases with whelk size, we examined
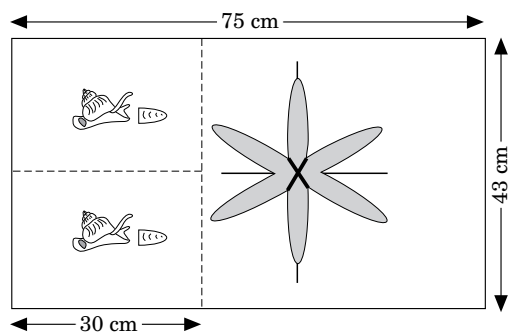
Figure 1. Experimental set-up to test the effect of the presence of tethered predatory asteroids *L. polaris* on the feeding activity of different-sized short-term or long-term starved whelks. Dashed lines indicate where 5-mm mesh plastic screening divided the aquarium into compartments.

the tendency of small (2–4 cm), medium-sized (5–7 cm) and large (8–10 cm) whelks to feed under different levels of risk of predation. Following their collection, whelks were initially kept for 10 days in 70-litre tanks with a 2–3-cm sand bottom under a 12:12 h light:dark cycle. To obtain two groups differing in feeding motivation, half the whelks of each size class were supplied ad libitum with bivalve flesh (*Spisula polynyma* and *Mya truncata*) for the first 2 days, and the other half received food for the first 7 days. The experiments were conducted from the 11th to the 13th day. Thus, the whelks had been starved for either a short (4–6 days) or a long (9–11 days) period prior to testing.

The feeding trials were conducted in still water in plastic aquaria (75 × 43 × 29 cm) which had 2–3 cm deep sand bottoms (Fig. 1) in a wet laboratory at Havre-Saint-Pierre that was supplied with running sea water (at 7–10°C) pumped from a depth of 15 m. The first 30 cm of each tank was divided by 5-mm mesh plastic screening into two adjacent compartments. Each trial began by placing one short-term and one long-term starved whelk from a given size group into these compartments. The side of the aquarium on which the short-term and long-term starved whelks were tested was chosen at random. At the same time a piece of a macerated siphon of the clam *M. truncata* was placed about 1 cm from each whelk (Fig. 1). The behaviour patterns and feeding activity of whelks was observed for 30 min. Experiments were simultaneously conducted under

three levels of predator threat (by three observers): (1) absence of *L. polaris*, (2) presence of a small *L. polaris* (10–15 cm in diameter) and (3) presence of a large *L. polaris* (25–40 cm). Each whelk was tested only once and for each combination of whelk size, feeding motivation and predator threat, 13–15 whelks were tested. Five minutes before each trial with *L. polaris*, the asteroid was tethered in the larger compartment to standardize its position relative to the whelks (Fig. 1). All asteroids and whelks were returned to their natural habitat after the experiments.

To examine the impact of predator threat (no asteroid, small asteroid and large asteroid) and motivation to feed (short and long starvation period) on the time whelks spent feeding, we first applied a two-way non-parametric ANOVA (data in some groups were not normally distributed) with equal replication and a correction factor (*C*) for tied values (Zar 1984) for each of the three size classes of whelks. Based on this analysis and definitions proposed by Fraser & Huntingford (1986), we categorized the trade-off made by whelks of each size class. Potential response categories were: (1) avoiding the hazard and minimizing eating (risk avoiding); (2) reducing feeding irrespective of feeding motivation but making greater reductions as hazard increases (risk adjusting); (3) reducing feeding at low levels of food, while accepting a greater hazard when feeding motivation is high (risk balancing); and (4) ignoring the hazard and eating maximally at all levels of feeding motivation (risk reckless). These categories reflect a decreasing influence of predator threat relative to feeding benefits. We predicted that the influence of predator threat relative to feeding motivation in whelks' trade-offs would decrease with increasing whelk size. Small whelks should be more risk-avoiding and large whelks more risk-reckless.

We also analysed changes in predator impact with increasing whelk size in each of four situations: whelks with low and high motivation to feed tested in the presence of low or high predation threat (small and large asteroid, respectively). In all situations, the impact of asteroids on whelks of each size class was calculated as the average time whelks spent feeding in the absence of an asteroid minus the average time spent feeding in the presence of the asteroid. For each situation, we determined whether predator impact differed between the three whelk size classes by

calculating the sum of the differences in the impact for (1) small versus large whelks, (2) small versus medium-sized whelks and (3) medium-sized versus large whelks. This sum was compared to a frequency distribution of the sums obtained using a randomization procedure (see Manly 1991 for a comprehensive presentation of 'computer-intensive' randomization and Monte Carlo methods) in which values obtained for time spent feeding for small, medium-sized and large whelks, in either the absence or presence of a predator, were randomly assigned to the three size classes. This iteration was repeated 5000 times, and on each occasion the sum of differences was calculated to provide the randomization distribution of sums for a population having no differences in predator impact with whelk size. This procedure enabled us to determine the probability of obtaining a sum of differences equivalent to or greater than that observed.

RESULTS

Relationship Between Whelk Size and Vulnerability

The size of whelks killed by small ($\chi^2=252.8$, $df=2$, $N=194$, $P<0.0001$), medium-sized ($\chi^2=115.2$, $df=2$, $N=211$, $P<0.0001$), and large ($\chi^2=12.8$, $df=2$, $N=80$, $P<0.005$) *L. polaris* during the predation experiment indicated that whelk vulnerability decreases with increasing size (Fig. 2). The relationship between whelk size and vulnerability weakened with increasing asteroid size; the relative number of small whelks killed decreased ($\chi^2=46.3$, $df=2$, $P<0.001$), and the relative numbers of medium-sized ($\chi^2=22.8$, $df=2$, $P<0.001$) and large whelks ($\chi^2=34.6$, $df=2$, $P<0.001$) increased.

Relationship Between Whelk Size and Habitat Use

We collected 915 asteroids, 98% of which were smaller than 15 cm in diameter (see also Himmelman & Dutil 1991). Asteroids smaller than 15 cm were more frequently encountered in the rocky zone than expected considering the surfaces sampled in each zone ($P<0.001$ for all three size classes of <15 cm asteroids), and asteroids larger than 25 cm were more frequently
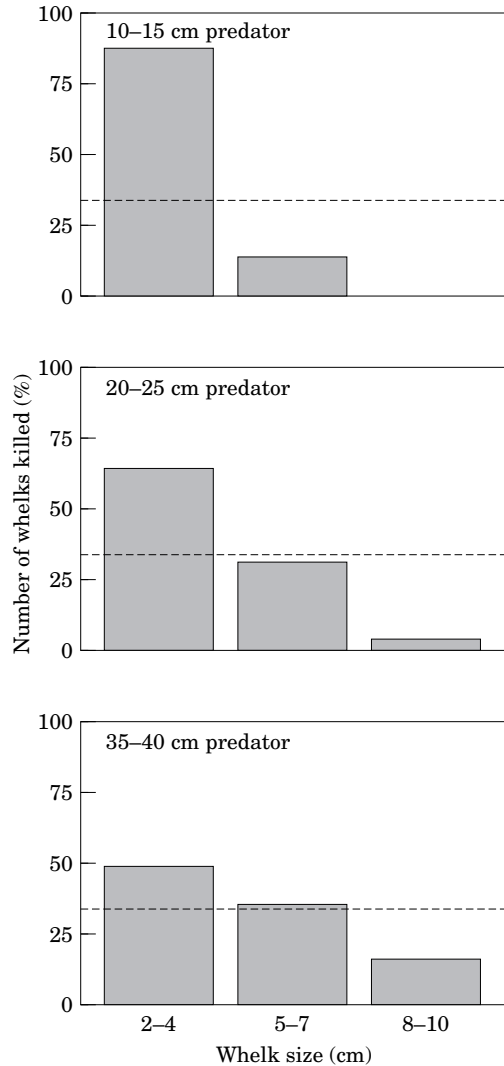

Figure 2. Size frequency distribution of whelks killed in experiments where whelks were exposed to small (10–15 cm in diameter), medium-sized (20–25 cm in diameter) and large (35–40 cm in diameter) predatory asteroids *L. polaris*. Dashed lines indicate the frequencies expected if whelks in all three size classes were equally vulnerable.

encountered in the sediment zone ($P<0.05$; Fig. 3).

We collected 366 whelks, and the size structure was similar to that reported from more extensive sampling in the Mingan Islands (Jalbert et al. 1989). There was an abundance of 1–3 cm whelks, followed by a sharp drop to low numbers of
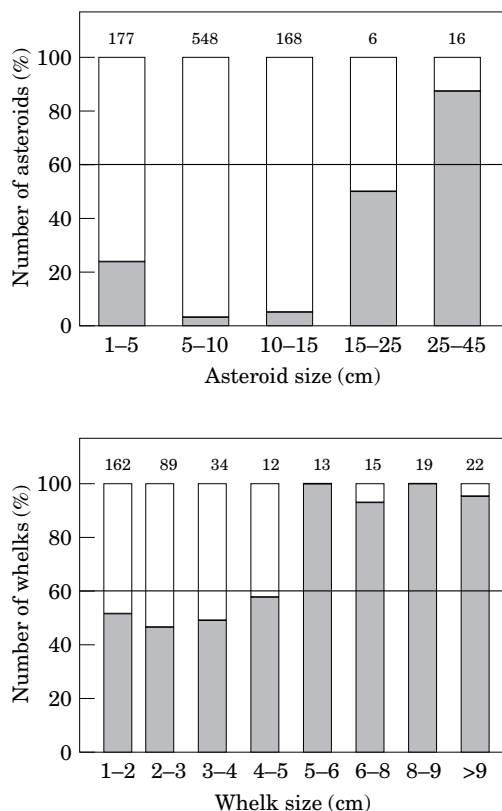
Figure 3. Proportion of predatory asteroids *L. polaris* (top) and whelks (bottom) of different sizes encountered in the sediment (shaded portion of the bars) and rocky (open portion of the bars) zones. Asteroids measuring 15–25 cm in diameter, and whelks measuring 6–8 cm in shell length, were each grouped into one class because of low frequencies. Total number of whelks and *L. polaris* in each size class is indicated above the bars. The horizontal lines show the frequencies expected in the rocky and sediment zones if asteroids and whelks were uniformly distributed between both habitats.

Figure 4. Relative numbers of <5 cm whelks (black bars) and <15 cm predatory asteroids *L. polaris* (open bars) encountered at 2-m intervals along three transects running from the low tide level to the end of rocky substrata.

individuals measuring 5 cm and larger. For the three transects, the average ($\pm$ SE) density of whelks in the rocky (0.89 ± 0.19 individuals per m^2) and sediment (0.94 ± 0.19 individuals per m^2) zones was similar, but the distribution within these habitats varied with whelk size (Fig. 3). Whelks smaller than 3 cm were more frequently encountered in the rocky zone than expected considering the number of quadrats taken in each zone ($P<0.05$ for both size classes of <3 cm whelks), and whelks larger than 5 cm were more frequently encountered in the sediment zone
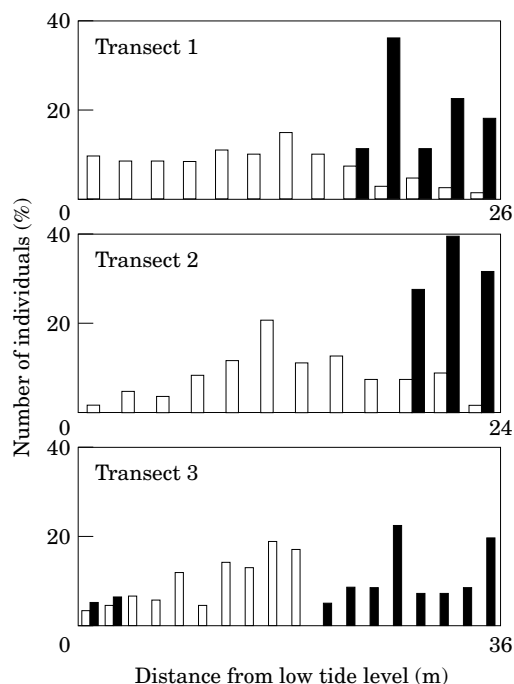
($P<0.001$ for all four size classes of >5 cm whelks). The proportion of 1–5 cm whelks on sediment substratum (50.5%) was approximately half that for larger whelks (97.0%), and a 2×2 contingency table indicated that these differences were significant ($\chi^2 = 50.37$, $df=1$, $P<0.001$). It may seem a contradiction to find small whelks in the rocky zone because small asteroids are abundant there (Himmelman & Dutil 1991; this study); however, they were concentrated in the lower part of the rocky zone where asteroids were least abundant (Fig. 4).

Relationship Between Decision Making and Whelk Size: Field Study

We collected 61 whelks (42 in May and 19 in August) in the vicinity of surf clams being eaten by *L. polaris*, and 96 (56 in May and 40 in August) in the vicinity of unattended surf clams. The low number of whelks sampled near feeding asteroids in August was partly because four *L. polaris*
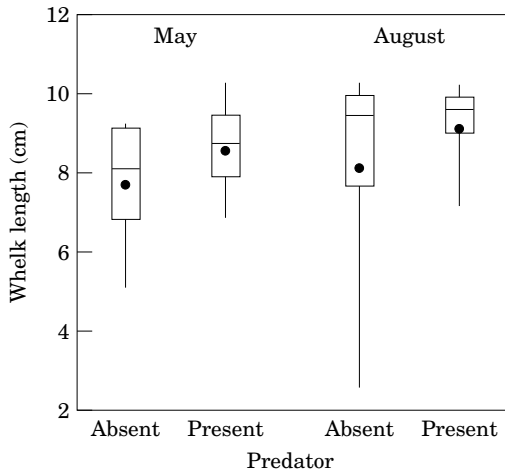
Figure 5. Box plot chart showing the size of whelks within 50 cm of unattended surf clams *S. polynyma* and surf clams being ingested by the asteroid predator *L. polaris* for experiments conducted in May and August 1994. The top, middle and bottom horizontal lines show the 75th, 50th and 25th percentiles, respectively. The black circle indicates the mean, and the vertical lines extend from the 10th to the 90th percentile.

Figure 6. Size structure of whelks in the vicinity of unattended *S. polynyma* (black bars, 96 whelks); *S. polynyma* being consumed by *L. polaris* (open bars, 61 whelks); and at random points in the same study area (solid line, 118 whelks). Data from sampling in May and August 1994 were pooled.

abandoned surf clams within the first 2 days (in response to the presence of the competing asteroid, *A. vulgaris*). In May, (but not in August), the presence of *L. polaris* had a significant effect on the size of whelks approaching the food source (Fig. 5): whelks that approached *S. polynyma* in the presence of the asteroid were larger ($Z=2.51$, $P<0.02$). When the data from May and August were pooled (Fig. 6), the influence of the predator's presence on the size of whelks sampled was significant ($Z=2.45$, $P<0.02$): the relative abundance of <5 cm whelks was greater in the absence of *L. polaris* ($\chi^2=6.51$, $df=1$, $P<0.025$). Surprisingly, whether a predator was present or not, small whelks were strongly under-represented near the bivalves compared with the general population (Fig. 6).

Relationship Between Decision Making and Whelk Size: Laboratory Experiment

Whelks tested in the presence of a predator frequently showed defensive responses such as swinging of the shell and violent foot contortions, behaviour patterns never observed in the absence of a predator. That many whelks fed in the
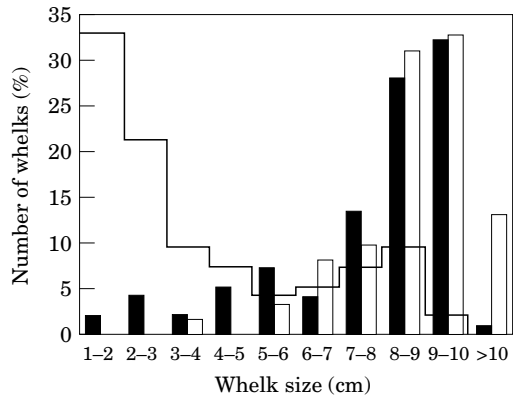
presence of the predator, even though they displayed agitated behaviour patterns, indicated that flight was not simply coupled to the detection of a predator (Ydenberg & Dill 1986). Nevertheless, the presence of *L. polaris* affected the number of whelks that fed and the duration of feeding. Whelks tested in the presence of a predator often took longer to approach the food item, and in a number of cases they alternatively abandoned and returned to the food item several times within the 30-min experimental period.

Predator threat and feeding motivation had different effects on the feeding activity of small, medium-sized and large whelks (Fig. 7, Table I). The influence of predator threat relative to feeding motivation decreased with increasing whelk size (with increasing whelk size, the *H*-statistic for the influence of predator threat decreased and that for the influence of feeding motivation increased, Table I). Small whelks (2–4 cm) were only affected by predator threat, medium-sized whelks (5–7 cm) were affected by both predator threat and feeding motivation, and large whelks (8–10 cm) were only affected by feeding motivation. According to the definitions of Fraser & Huntingford (1986), the response of small whelks was either risk avoiding or risk adjusting, medium-size whelks clearly displayed a risk adjusting strategy, and large whelks showed a risk reckless behaviour. Thus, as we predicted, responses of whelks tended to change from risk-avoiding to risk-reckless with increasing whelk size.
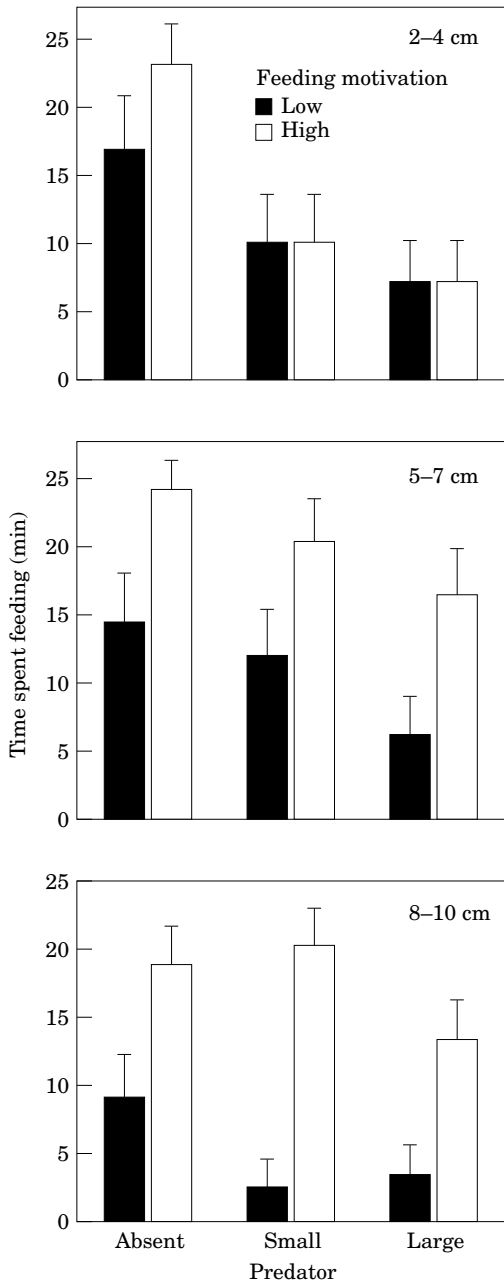
Figure 7. Mean ± SE time spent feeding for three size classes of whelks (2–4, 5–7 and 8–10 cm in shell length) with low and high motivation to feed exposed to three levels of predator threat: absence of a predator; presence of a small *L. polaris*; and presence of a large *L. polaris*.

Predator impact (the reduction in time whelks spent feeding owing to the predator's presence) was independent of size for whelks which had low feeding motivation (Fig. 8). In contrast, predator impact declined with increasing size when whelks that had a high feeding motivation were tested in the presence of small asteroid predators (Fig. 8). The decrease in predator impact between small and medium-sized whelks was approximately twice that observed between medium-sized and large whelks. The same results were obtained when the randomization procedure was applied to the percentage decrease in time spent feeding (relative to the time spent feeding in the absence of a predator) instead of the absolute decrease in time spent feeding.

DISCUSSION

This study investigated the response of a marine gastropod, the common whelk *B. undatum,* in situations in which the need to avoid the predatory asteroid *L. polaris* conflicted with the acquisition of food resources. Many prey species trade off these two essential activities during their lifetime. The *Buccinum–Leptasterias* interaction is unique in that whelks have aversive responses to *L. polaris* that must be inhibited when they approach feeding *L. polaris* to obtain food. Our laboratory and field studies indicate that the degree to which whelks associate with *L. polaris* to gain food varies inversely with their vulnerability.

The vulnerability of whelks to *L. polaris* markedly decreases with increasing size. Because we simultaneously offered different-sized whelks to the asteroids during the predation experiments, their relative vulnerability may reflect differences in their capacity to deter predators as well as in predator preferences. Although we cannot state the mechanisms involved, our experiment showed that larger whelks have a greater probability of surviving encounters with *L. polaris*.

Although the general size–structure pattern of whelks is similar throughout the subtidal zone (Jalbert et al. 1989; this study), larger, less vulnerable whelks have a greater tendency to inhabit sediment areas where feeding opportunities are made available by the foraging activities of *L. polaris*. The habitat shift is abrupt (Fig. 3). Only 51% of small whelks (<5 cm) are encountered on sediment bottoms, compared with 97% of large

Table I. The response of different sized whelks to a conflict situation

| Size of whelks (cm) | Source of variation | | | Classification of whelk response[a] |
	Motivation to feed (1 *df*)	Predator threat (2 *df*)	Interaction (2 *df*)	
2–4	1.06 (0.303)	10.72 (0.004)	1.27 (0.530)	Risk avoiding/adjusting
5–7	10.88 (0.001)	6.81 (0.027)	0.28 (0.869)	Risk adjusting
8–10	21.98 (0.000)	4.08 (0.099)	3.08 (0.214)	Risk reckless

[a]After Fraser & Huntingford (1986).
Results of two-way non-parametric ANOVAs, applied to whelks of three size groups, testing for the impact of motivation to feed and predator threat on the time whelks spent feeding. Values of the *H*-statistic are followed by their associated probabilities (in parentheses).

whelks (>5 cm). The hypothesis that this habitat shift is related to changes in food resources exploited is supported by the greater tendency of

Figure 8. Impact of the predatory asteroid *L. polaris* on the time spent feeding for three size classes of whelks (2–4, 5–7 and 8–10 cm in shell length) tested in four situations: whelks with low or high feeding motivation in the presence of a small or a large *L. polaris*. Impact is the difference between the average time spent feeding in the absence and presence of *L. polaris*. In each situation, we used a randomization procedure to determine the indicated probability of obtaining differences in predator impact with whelk size equivalent to or greater than those observed during the experiment.

large whelks to approach bivalves placed on the substratum, either unattended or being consumed by *L. polaris*. Stealing prey from large *L. polaris* or feeding on remains may provide an important part of the diet of large whelks (Jalbert et al. 1989; Himmelman & Dutil 1991; Himmelman & Hamel 1993). This hypothesis is supported by the fact that the stomach contents of whelks leaving a site where *L. polaris* has been feeding on bivalves may weigh 15 times more than those of whelks approaching a feeding asteroid (Rochette et al. 1995). Predator threat appears to account at least partially for the absence of small whelks near feeding asteroids, because the whelks approaching unattended *S. polynyma* were smaller. Although differences between small and large whelks in sensory or locomotory capacities could influence their attraction to bait, such differences are unlikely to account for the differences in sizes of whelks approaching an unattended bivalve compared to the sizes approaching a similar bivalve being ingested by an asteroid.

The laboratory data also support the hypothesis that vulnerability influences how whelks trade off predation risk and feeding opportunities. With increasing size, and thus decreasing vulnerability, the effect of predator threat on time whelks spent feeding decreases, but the effect of feeding motivation increases (Table I). The latter trend is not because starvation had a greater impact on the motivation of larger whelks to feed, because when we applied a randomization procedure to estimate the impact of the starvation period (long-term versus short-term) on time spent feeding in the absence of *L. polaris*, there were no differences between the three size groups of whelks ($P=0.85$;
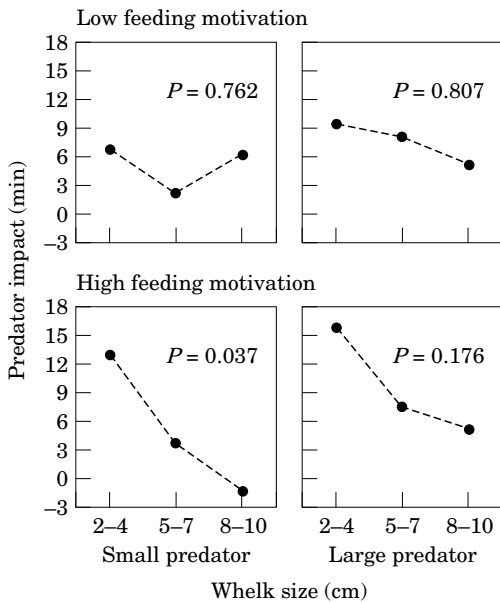
we used the same randomization procedure as used to estimate the impact of predators). The decreasing impact of small asteroids with increasing size of long-term starved whelks (Fig. 8) suggests the integration of vulnerability in decision making. In these analysis, we controlled for possible differences in feeding motivation with whelk size, because predator impact was the difference in time spent feeding in the absence and presence of *L. polaris*.

Many studies indicate that habitat shifts can be related to energetic needs and vulnerability. For example, Werner et al. (1983) showed that when predatory bass, *Micropterus salmoides*, are present, smaller, more vulnerable bluegill sunfish, *Lepomis macrochirus*, show a greater reduction in their use of food-rich habitats than larger less vulnerable sunfish. Also, Wahle (1992) reported that young lobsters, *Homarus americanus*, leave protective habitats as their energetic demands increase and their vulnerability decreases. L'Abée-Lund et al. (1993) indicated a size partitioning of Arctic charr, *Salvelinus alpinus*, that appears to be related to changes in trade-offs between feeding possibilities and predation risk. Sih (1982) reported a situation similar to ours in which younger more vulnerable instars of the aquatic insect *Notonecta hoffmanni* accepted lower feeding levels to reduce predation risk.

Additional experiments are required to address several questions raised by this study. First, in nature, small whelks show a weak tendency to approach large bivalves, even in the absence of a predator. We do not believe that this is due to reduced sensory or locomotory capacities of smaller whelks, because on several occasions we have observed large numbers of small whelks near dead crabs (or crab moults). Approaching a decaying bivalve may involve risks so that vulnerability is involved. For example, predatory asteroids and crabs are virtually always present when decaying bivalves are at the surface, but not when crab carcasses are at the surface. Alternatively, small whelks might be so strongly disadvantaged in competing with larger whelks for prey items that the gains in approaching decaying clams may be negligible compared with associated costs (locomotion and exposure to predators). Finally, feeding preferences of whelks may change with size. Determining the food resources of whelks is difficult because they are rarely observed feeding, they usually have empty stomachs, and the rare materials found in their stomach are in most cases difficult to identify (Himmelman & Hamel 1993).

That a significant relationship between whelk size and predator impact was observed in only one of the four experimental situations also warrants further investigation. We believe that this situation reflects the complexity of the interaction between predator threat, feeding motivation and vulnerability in determining the whelk's decision making. In the experiments on whelks with a high feeding motivation, a significant relationship between predator impact and whelk size was obtained for whelks tested with small but not large asteroids, which might reflect the more pronounced decline in vulnerability with whelk size as the size of the asteroid predator decreases (Fig. 2). Similarly, in the experiments on whelks with a high feeding motivation tested in the presence of a small asteroid, the decrease of predator impact was greater between small and medium-sized whelks than between medium-sized and large whelks, which parallels the decrease in relative vulnerability for these size groups of whelks to small asteroids (Fig. 2). Our laboratory studies indicate the importance of simulating varying conditions of feeding benefits and predation hazard when comparing the response of different individuals in conflict situations. The operational definitions proposed by Fraser & Huntingford (1986) are useful in illustrating how both factors can interact; however, estimating predator impact provides a more direct means of comparing responses between individuals.

Many studies have shown that animal decision making and anti-predator mechanisms can be adjusted to current risk of predation. The elegant study by Crowl & Covich (1990) on the freshwater gastropod *Physella virgata virgata* even shows that age at first reproduction and longevity can be modified by detection of foraging crayfish. Studies are needed to assess the importance of phenotypic plasticity in the expression of life-history characteristics, morphological features and behavioural responses in prey animals.

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