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A flexible response to a major predator provides the whelk *Buccinum undatum* L. with nutritional gains

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Abstract

We examined the association of the common whelk *Buccinum undatum* with the predatory asteroid *Leptasterias polaris* in the Mingan Islands, northern Gulf of St. Lawrence. Quantitative sampling, using SCUBA diving, of surfaces of the sea floor in the vicinity (within 150 cm) of feeding and non feeding *L. polaris* and surfaces devoid of asteroids showed that both immature and mature whelks generally avoid *L. polaris*. Surprisingly, densities of mature whelks up to 12 times the average were occasionally encountered near asteroids when they were consuming a large prey, usually the surf clam *Spisula polynyma*. Comparisons of the stomach-content mass of whelks approaching *L. polaris* feeding on *S. polynyma* with that of whelks which were departing from the same type of feeding bout demonstrated that whelks obtained significant food gains by approaching *L. polaris*. Previous studies failed to identify the food resources that could account for the high biomass of whelks in the Mingan Islands. The association with *L. polaris* potentially explains a substantial part of the whelk's diet. Whelks of the Mingan Islands have evolved a flexible behavioural response to *L. polaris* which permits them to make adaptive and risk-sensitive decisions when choosing between avoiding a major predator and taking advantage of food resources it makes available.

Keywords: *Buccinum undatum*; Escape response; Feeding behaviour; Predation risk; Whelk

1. Introduction

Predators not only have a negative impact on prey populations through their harvesting activities (Sih et al., 1985), but may also hamper feeding and possibly other

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essential activities of their prey. This has been documented in controlled laboratory experiments for a variety of animals such as gastropods (Richardson & Brown, 1992), crabs (Scarratt & Godin, 1992), insects (Sih, 1982), larval (Williams & Brown, 1991) and adult fish (Milinski & Heller, 1978; Cerri & Fraser, 1983; Dill & Fraser, 1984; Fraser & Huntingford, 1986; Dill, 1987; Giles, 1987; Bishop & Brown, 1992; Utne et al., 1993) and rodents (Phelan & Baker, 1992). The strong selective pressure of predation has profoundly influenced the life-style of prey animals (Sih, 1987). This is evidenced by the numerous and diverse behavioural, morphological and chemical defensive adaptations of prey to their predators and by the distribution and activity patterns which prey have evolved to reduce encounters with predators (reviewed by Sih, 1987). Finally, many prey species have evolved the ability to evaluate the threat of a given encounter with a predator and to use this information to make adaptive behavioural decisions (Lima & Dill, 1990).

The common whelk *Buccinum undatum* L. and the six-rayed asteroid *Leptasterias polaris* (Müller and Troshel) are the most abundant carnivores in the northern Gulf of St. Lawrence (Jalbert et al., 1989), and both are abundant throughout the subtidal zone. There is a size partitioning of *L. polaris* with depth and large-sized asteroids are concentrated on sediment bottoms where they forage on large endobenthic bivalves and epibenthic gastropods including *B. undatum* (Himmelman & Dutil, 1991). *L. polaris* appears to be the predator that has the greatest impact on whelks, for example Dutil (1988) calculates that it consumes $\approx 4.4\%$ of their biomass in 100 days in one benthic community in the Mingan Islands. This is also suggested by the violent defensive response of whelks to *L. polaris* which is much stronger than to other asteroids in the region (Legault & Himmelman, 1993). Surprisingly, whelks occasionally aggregate near *L. polaris* when it is ingesting prey (Fig. 1, Jalbert et al., 1989; Himmelman & Dutil, 1991; Himmelman & Hamel, 1993). This suggests whelks may at times approach their predator to obtain feeding opportunities. In nature, whelks are rarely observed attacking other organisms and although they readily feed on carrion, it is dubious whether such food resources are sufficient to support the biomass of whelks found in the northern Gulf (Himmelman & Hamel, 1993).

Our observations while diving in the Mingan Islands suggest that adaptive trade-offs are involved in the whelk's decision to approach or avoid a feeding *L. polaris*. Aggregations near asteroids seem mainly to involve large sexually mature whelks (Himmelman & Dutil, 1991; Himmelman & Hamel, 1993), possibly because defensive responses are better developed in mature than in immature whelks (Harvey et al., 1987). Also, Himmelman & Hamel (1993) suggest that whelks are more likely to approach a feeding asteroid when it is consuming a large prey, which indicates that the whelk's willingness to expose itself to predation risk may be adjusted to potential benefits.

In the present study, we first determine whether the distribution of immature and mature whelks is influenced by the presence and activity of *L. polaris*. To achieve this we examined (1) whether the density of whelks near *L. polaris* differs from that in areas devoid of asteroids, and (2) whether the density of whelks near non-feeding *L. polaris* differs from that near feeding *L. polaris*. Secondly, we determine whether whelks that approach a feeding asteroid obtain food and if so, through what mechanisms?

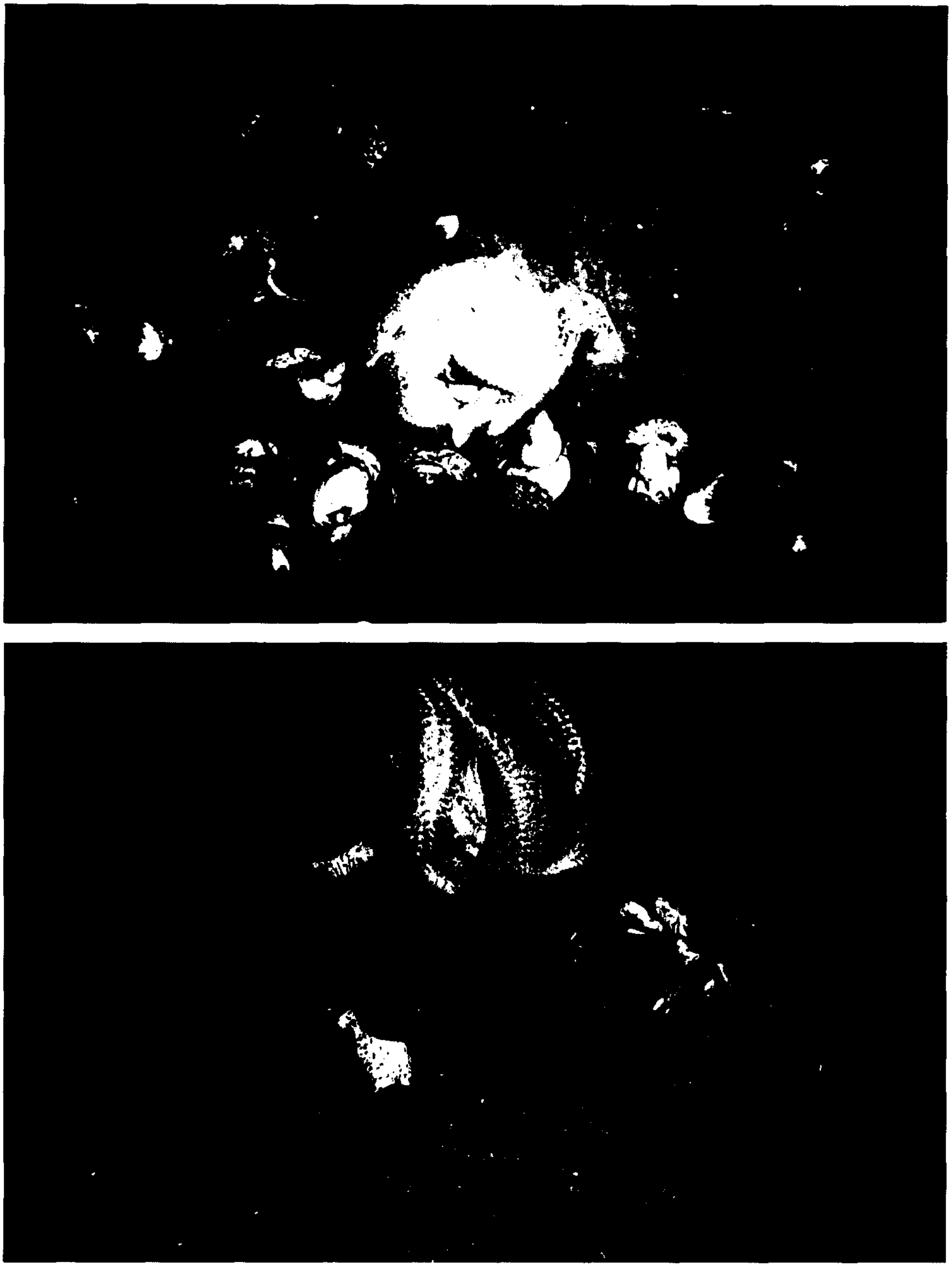

Fig. 1. Photos of whelks *B. undatum* aggregated near a feeding asteroid *L. polaris*. In the upper photo, a large aggregation of whelks is surrounding an asteroid feeding on a large clam *S. polynyma*. In the bottom photo, one whelks is in contact with its asteroid predator and a nearby crab *Cancer irroratus* is awaiting an opportunity to feed.

2. Materials and methods

Our study was conducted, using SCUBA diving, during June through August in 1991 and 1992 at Cap du Corbeau, Ile du Havre, near Havre-Saint-Pierre in the Mingan Islands (50° 14′ N; 63° 35′ W). We examined the same whelk population that was previously examined by Himmelman & Hamel (1993) in their investigation of the food resources of the whelk. Our observations were made on a sediment bottom (gravel to mud) where *L. polaris* frequently feeds on infaunal bivalves (Himmelman & Dutil, 1991). To facilitate the periodic observations and sampling, we defined a specific work area, a 15-m wide zone between 8 and 18 m in depth along 170 m of the coast. To aid orientation during dives, a permanent transect marked at 5-m intervals was placed at about 12 m in depth through this zone.

2.1. Are whelks influenced by their major predator?

To determine if the distribution of whelks is influenced by *L. polaris*, we used chi-square calculations on contingency tables (Zar, 1984) to compare density-frequency distributions of whelks collected within 150 cm radius of asteroids to those samples collected in circular surfaces of similar size where asteroids were absent. To further examine the influence of *L. polaris*, we used Mann-Whitney U tests (Siegel, 1956) to compare the density of whelks within each of six concentric surfaces around non-feeding and feeding asteroids. The positions of the above samples were determined as follows. Divers swam a random number of kicks (0 to 10) with their eyes closed, either shoreward or seaward, from randomly chosen positions along the permanent transect and then sank to the bottom. Once on the bottom, they drove a stake into the substratum. If no asteroid was present within ≈ 300 cm radius, they determined the number and size of whelks within 150 cm of the stake. When an asteroid was present, they recorded the number and size of whelks in each of six concentric zones around the asteroid, 0–25, 25–50, 50–75, 75–100, 100–125 and 125–150 cm from the asteroid. They then measured the diameter of the asteroid and noted whether it was feeding (ingesting a prey) and the identity and size of its prey. When more than one asteroid (*L. polaris* or other species) was present within 300 cm of the stake, the area was not sampled. During this survey, a total of 60 circular surfaces devoid of *L. polaris* and 111 surfaces near *L. polaris* (60 were not feeding and 51 were feeding) were sampled. All surfaces were carefully examined for whelks which might have been buried (the siphon was visible at the surface). Whelks encountered were classified as immature (measuring < 7 cm in shell length) or mature (measuring > 7 cm in shell length), based on the size at sexual maturity of *B. undatum* in the Mingan Islands as reported by Martel et al. (1986).

2.2. Do whelks gain food by approaching their predator?

To determine whether whelks gain food by approaching feeding asteroids, we used the Kolmogorov-Smirnov test for continuous data (Zar, 1984) to compare the mass of stomach contents of whelks collected as they arrived at and as they left a site where

L. polaris was feeding. To increase the potential number of whelks involved in these interactions, we examined feeding bouts in which *L. polaris* was feeding on the large bivalve *Spisula polynyma*. These feeding bouts were provoked by placing *S. polynyma* underneath an asteroid that was digging for a prey. A total of 20 whelks were collected as they first came within 20 cm of feeding asteroids (three individuals) and 58 whelks as they left the 20 cm zone around feeding asteroids (five individuals).

In the first samplings we followed the interactions between whelks and feeding asteroids by diving at frequent intervals. For the collection of whelks approaching two feeding asteroids we dived at 15- to 45-min intervals throughout the daylight period (0500 to 2100), depending on the abundance and activity of whelks in the area. This high diving frequency provided a reasonable assurance that whelks did not feed prior to being collected. We then dived at 8-h intervals (0600, 1400, 2200) to collect whelks as they left three feeding asteroids. In these cases, all whelks were tagged by placing a rubber band around the apex of the shell when they were first observed within 20 cm of an asteroid and collected on subsequent dives if they had moved out of the 20 cm radius around the asteroid.

In spite of the frequent dives made to observe whelks, activities were missed. For example, about 40% of the tagged whelks were not observed in subsequent dives. Losses were more frequent when the observations were made at night. To provide a better record of events, we continuously observed (day and night) the following three feeding bouts using an underwater camera which was connected to a video system and monitor on the shore. The camera's height was adjusted so it recorded events over a surface which extended ≈20 cm from the asteroids. The camera was mounted on a rack which was supported by four slender (1 cm in diameter) posts. The slender supports should have minimized turbulence which could interfere with the propagation of odours. During one of these three events, whelks were sampled as they approached within 20 cm of a feeding asteroid and in the other two, they were sampled as they left the same area. This sampling technique provided detailed information about the activity of whelks and on other events occurring during the interactions.

Whelks brought to the surface were placed in a 4% formaldehyde solution in individual plastic sacs to interrupt digestion of food and ensure that regurgitated materials were not lost. Between 4 and 6 days after collection, the shell length and wet mass (after draining for 5 min on paper toweling) of the whelks was determined and the content of the esophagus and stomach dissected out and weighed together with regurgitated materials to the nearest 0.01 g. Henceforth, the term "stomach-content mass" will refer to materials in the stomach and esophagus as well as regurgitated items.

3. Results

3.1. *Are whelks influenced by their major predator?*

Surfaces without *L. polaris* had a mean density of 0.35 immature whelks $\cdot$ m^{-2} (SE = 0.03) and 0.50 mature whelks $\cdot$ m^{-2} (SE = 0.05). The density-frequency distributions were strongly skewed towards the lower density classes when asteroids were present compared to when they were absent ($p < 0.005$, Fig. 2) indicating that whelks avoid *L. polaris*. A striking exception to this pattern was that the highest densities recorded (> 1.4 ind.$\cdot$m^{-2}) were for mature whelks (> 7 cm shell length) near asteroids which were feeding (Fig. 2). In 5 of the 51 samples taken near feeding asteroids, the density of mature whelks ranged from 1.5 to 6.0 ind.$\cdot$m^{-2}, 3 to 12 times the average density of mature whelks in the absence of asteroids. The whelks in these five samples accounted for 51% (107/208) of all the mature individuals encountered near feeding asteroids.

For each of the six concentric surfaces around *L. polaris*, the density of immature whelks did not differ between samples taken near non-feeding and feeding asteroids ($p > 0.4$, Fig. 3). In contrast, densities of mature whelks within the two first concentric surfaces (0 to 25 cm and 25 to 50 cm) were greater near feeding *L. polaris* ($p < 0.05$, Fig. 3). A similar but non-significant ($p = 0.10$) trend was also indicated for the third surface, 50 to 75 cm from the asteroid.

These results indicate that mature whelks occasionally aggregate within ≈ 75 cm of feeding *L. polaris*. These aggregations were most frequently observed when the asteroid was consuming a large prey (Fig. 4). In 8 of the 20 (40%) predatory events observed where the asteroid's prey weighed > 25 g, the density of mature whelks was > 1.4 ind.$\cdot$m^{-2} (Fig. 4). In seven of these, *L. polaris* was consuming the large surf clam *S. polynyma*.

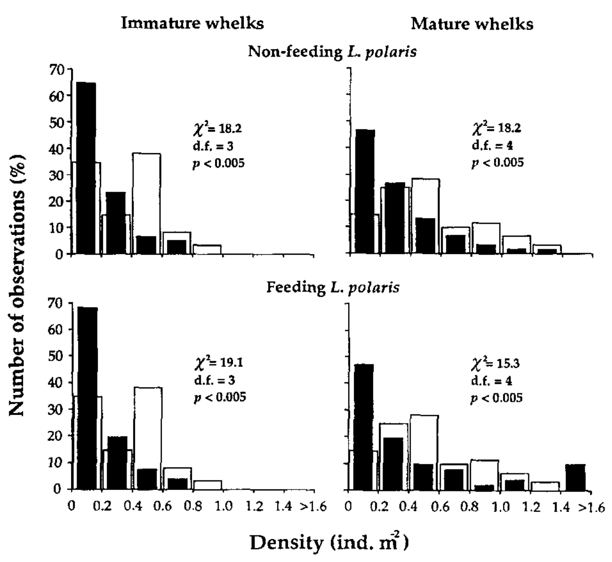

Fig. 2. Density-frequency distribution for immature and mature whelks *B. undatum* within 150 cm of non-feeding and feeding asteroids *L. polaris* (black bars) compared to their density-frequency distribution in areas devoid of asteroids (white bars). Chi-square tests applied to contingency tables were used to compare density distributions near asteroids and in areas devoid of asteroids. Densities of > 0.6 for immature whelks and > 0.8 for mature whelks were combined so that no cell had an expected frequency of less than 1 and not more than 20% of the cells had an expected frequency of less than 5 (Zar, 1984).

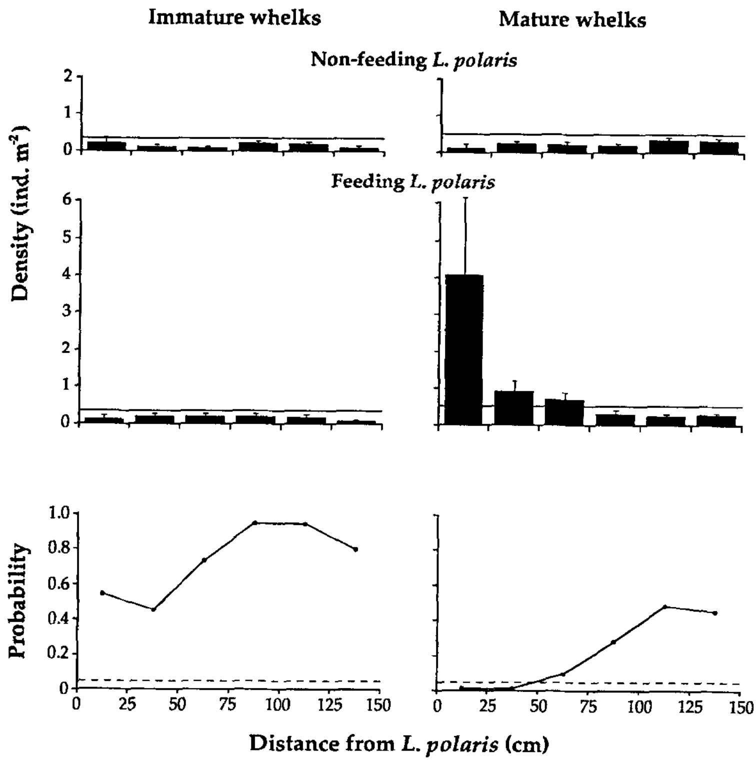

Fig. 3. Mean density of immature and mature whelks *B. undatum* in six concentric zones around non-feeding and feeding asteroids *L. polaris*. Vertical bars represent the standard error and the full horizontal lines indicate the density of whelks in areas devoid of asteroids. The bottom figures show, for each concentric zone, the probability that the density of whelks near non-feeding and feeding asteroids is the same (Mann-Whitney *U* test) and the dashed horizontal line indicates the 0.05 significance level.

3.2. Do whelks gain food by approaching their predator?

Most whelks (91%) captured while approaching or leaving feeding *L. polaris* were sexually mature (> 7 cm shell length). Those approaching generally had little food in their stomachs ($\bar{x} = 0.15$ g, SE = 0.04 g) and the stomach-mass distribution was similar to that observed by Hamel (1989) for whelks randomly sampled during the summer from the same area ($p = 0.55$, Fig. 5). In contrast, whelks leaving feeding asteroids had more food ($\bar{x} = 2.44$ g: se = 0.32 g) in their stomachs ($p < 0.05$, Fig. 5). A stomach-content mass of < 0.10 g was observed for 55% of the approaching whelks, compared to only 12% of those leaving a feeding asteroid. Most of the stomach contents were difficult to identify, although gill fragments and pieces of the foot of *S. polynyma* which is purple in colour were sometimes recognizable. One whelk stomach contained an entire polychaete measuring about 5 cm.

The three filmed feeding bouts of *L. polaris* on *S. polynyma* provided information on food acquisition by whelks. Whelks first appeared 2.5 to 5 h after the bivalve was placed

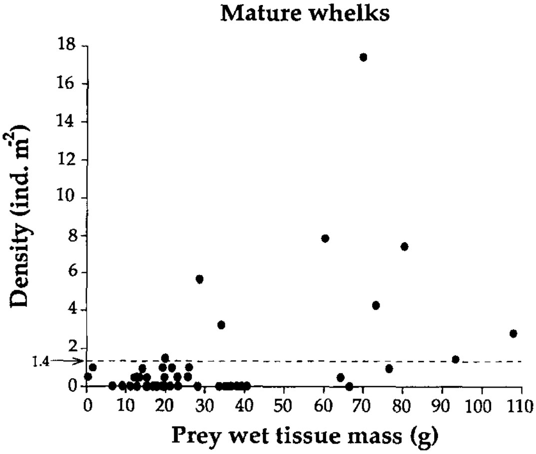

Fig. 4. Density of mature whelks *B. undatum* within 75 cm of feeding asteroids *L. polaris* in relation to the wet tissue mass of the asteroid's prey. Prey mass was estimated using regressions with shell length (Dutil, 1988). Densities of mature whelks > 1.4 ind.$\cdot$m^{-2} (dashed line) were only observed in the vicinity of feeding asteroids.

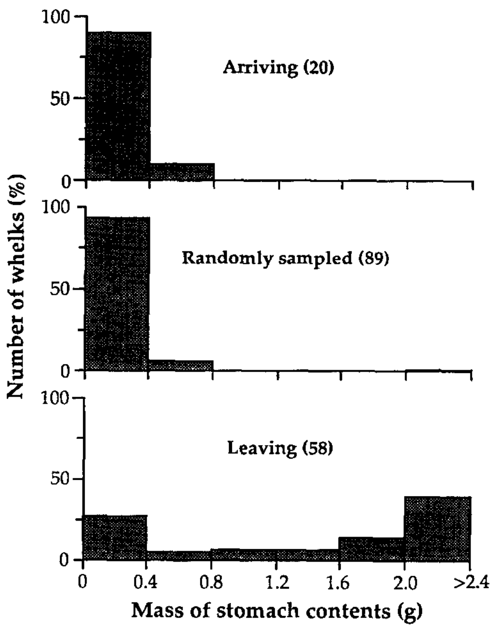

Fig. 5. Frequency distributions of stomach-content mass for whelks *B. undatum* arriving in the vicinity of a feeding bout of *L. polaris*, randomly sampled in the subtidal zone, and leaving a feeding bout of *L. polaris*. Numbers in parenthesis indicate the number of whelks sampled for each distribution.

under the asteroid. They generally remained several centimeters from the asteroid but occasionally touched and in some cases forced their way underneath it. These whelks were attempting to get access to the asteroid's prey. Furthermore, whelks often explored sediments that had been disturbed by the asteroid in extracting its prey. During two bouts, the surf clam (about 12 h after the beginning of the attack) vigorously extended its foot to escape from the asteroid. Whereas this activity was unsuccessful, it was important for the whelks as it caused the asteroid (with its prey) to move from the hole it had dug. Following this, the hole was explored by several whelks. Other events also influenced the quantity of food available to whelks. The crabs, *Hyas araneus* (L.) and *Cancer irroratus* Say, and the asteroid *Asterias vulgaris* Verrill, were also attracted to feeding *L. polaris*. In two of the three filmed events, *L. polaris* abandoned its prey upon the arrival of *A. vulgaris* at 16 and 30 h, respectively, after the beginning of the feeding bout. This caused a sudden aggregation of nearby whelks on the prey. The shorter arms of *A. vulgaris* permitted increased access to the prey and the whelks were less cautious in approaching *A. vulgaris* than *L. polaris*. They readily crawled over and under *A. vulgaris* in an attempt to feed.

4. Discussion

4.1. Importance of *L. polaris* to the feeding biology of whelks

Whelks that approach a feeding *L. polaris* may acquire food through three mechanisms: (1) stealing food from the asteroid using their long proboscis (about as long as the whelk's shell), (2) feeding on remains after the asteroid has left its prey, and (3) exploiting prey, such as polychaetes and bivalves, exposed by the digging activity of the asteroid. The quantity of food *B. undatum* may acquire from the feeding activity of *L. polaris* is likely influenced by their ability to perceive and localize a feeding asteroid. Current conditions are critical in this regard since current direction, velocity and stability strongly affect the rate at which whelks come to baited traps (Himmelman, 1988; McQuinn et al., 1988; Lapointe & Sainte-Marie, 1992). It seems that whelks are more likely to obtain food if the asteroid is consuming a large bivalve such as *S. polynyma* because (1) larger prey likely emit greater quantities of chemical cues which facilitate food detection and localization by whelks, (2) *L. polaris* has more difficulty covering large prey, thus the prey is more accessible to the whelks, and (3) the asteroid more likely becomes satiated when feeding on a large prey so that it leaves more prey remains. Finally, our observations indicate that the gains for whelks are strongly affected by interactions with other opportunistic carnivores. Even though *Asterias vulgaris* competes with whelks for the same food resource, its interaction with *L. polaris* may result in increased feeding opportunities for whelks. *A. vulgaris* does not represent as great a risk of predation and elicits a less intense escape response from whelks than does *L. polaris* (Legault & Himmelman, 1993).

In spite of variations in the gains which whelks can obtain from the foraging activities of *L. polaris*, our data indicate that these gains can be substantial. The mean mass of stomach contents for whelks leaving a feeding asteroid was 15 times greater than that of whelks just arriving near a feeding asteroid. We calculated the percentage of whelks leaving a feeding asteroid with a stomach-content mass that exceeded the highest mass recorded for whelks just arriving at a feeding bout (0.71 g). This indicated that 70% of the whelks gained food. Individual gains may be striking. One departing whelk contained 10.3 g of food in its stomach, which represented 22% of its body weight (without the shell). Although our study was not designed to estimate the proportion of whelks' food resources that is obtained through the association with *L. polaris*, several observations suggest it to be important. (1) In nature, large whelks are usually inactive and virtually never observed feeding (Martel et al., 1986; Himmelman & Hamel, 1993, the present study). Himmelman & Hamel (1993) observed the behaviour of 750 large whelks, none was clearly attacking or ingesting prey. Ten had their proboscis extended into the sediments so they were probably searching for prey. Thus, whelks with ample food in their stomach, such as we observed for individuals leaving feeding *L. polaris*, are among the few clear instances of feeding. (2) Himmelman & Hamel (1993) report that 86% of the stomach contents of large whelks are unidentifiable, because of the lack of rigid structure. This would be expected if most of the whelks' food resources were portions of the prey of large *L. polaris*. (3) The sympatry between the two species, and in particular that mature whelks and large asteroids are most abundant in the same habitat (sediment bottoms below the shallower rocky zone) suggests that large whelks voluntarily associate with large *L. polaris*.

The harvesting activities of predators are usually considered to have negative effects on prey populations (Sih et al., 1985). Abrams (1992) suggests that this might not always be so and proposes mechanisms by which predators may be beneficial to their prey. Our study shows that large whelks benefit from *L. polaris* because it makes prey resources available to the whelk. The extent to which this interaction accounts for the abundance of whelks in the Mingan Islands needs to be further investigated. Whereas in nature large whelks are only occasionally caught by *L. polaris*, we have observed that juvenile and immature whelks are more vulnerable (unpubl. data). We know nothing about the feeding biology of smaller immature whelks except that like mature whelks, they are rarely observed moving, attacking prey or ingesting carrion. The impact of *L. polaris* on the biological success of whelks should be determined by comparing the growth and reproductive output of whelks in habitats where the asteroid is present and absent (using large enclosures or areas where *L. polaris* has been removed).

4.2. *Evaluation of risk and ability to make adaptive trade-offs*

Fine-tuning of the behaviour of whelks to predation risk is indicated by their response to various benthic asteroid predators of the Mingan Islands. Legault & Himmelman (1993) show that the intensity of escape responses by whelks when subjected to different predatory asteroids increased in the same way as predation risk. Furthermore, the response of mature whelks towards *L. polaris* varies according to the risks and benefits associated with each particular encounter. We demonstrate that mature whelks distinguish between feeding asteroids which likely represent decreased risk and possible immediate feeding opportunities, and non-feeding asteroids, which represent greater risk and no potential gains. Our numerous diving observations and the video recordings indicate that whelks integrate information about potential food gains and risk of predation when approaching feeding asteroids. They do not appear to be responding only to food odours because they are cautious and frequently agitated. Most whelks remain several centimeters from asteroids and make few attempts to steal food. Our results agree with a growing body of evidences indicating that prey species are capable of estimating the risk associated with the species (Walther, 1969; Hennessy & Owings, 1978; Thomas & Himmelman, 1988; Legault & Himmelman, 1993), size (Helfman, 1989; Bishop & Brown, 1992), activity (Mauzey et al., 1968; Walther, 1969; Dayton et al., 1977; Phillips, 1978; Bishop & Brown, 1992), posture (Helfman, 1989) and even the feeding status (Licht, 1989) of their predator.

That practically all whelks approaching feeding *L. polaris* are sexually mature might be related to differences between matures and immatures in respect to their vulnerability to predation by *L. polaris*. Sih (1980, 1982) reports a similar situation. Older instars of the back swimmer *Notonecta hoffmanni* more readily feed in areas where predators are present than the younger instars which are more vulnerable to predators. However, that baited traps are similarly selective and catch mostly large whelks seems to mitigate the vulnerability hypothesis. Alternatively, mature whelks might approach feeding asteroids more readily than immatures because they have greater energetic requirements. Numerous factors affecting the energetic requirements of animals have been shown to influence their decision to feed when there is a risk of predation. These include nutritional status (scavenging gastropods, McKillup & McKillup, 1994), sex (guppies, Abrahams & Dill, 1989) and presence and load of parasites (sticklebacks, Milinski, 1985; Giles, 1987; Godin & Sproul, 1988). We are currently investigating whether the above factors as well as the vulnerability to predation intervene in the whelk's decision to feed under the risk of predation.

Another aspect of the behaviour of whelks that seems adaptive is that mature individuals more readily accept the risk of closely associating with *L. polaris* when the asteroid is consuming a large prey. However, we cannot exclude the hypothesis that greater aggregation of whelks are due to increased amounts of chemical cues emitted by larger prey.

4.3. Evolutionary considerations

Whereas our observations are for whelks in the Mingan Islands, the interaction may be similar over areas of the northern Gulf of St. Lawrence, Newfoundland and Labrador where *B. undatum* and *L. polaris* are both common in the subtidal zone. A similar interaction has been reported from the northeast Pacific, near San Diego. The asteroid *Pisaster giganteus* and one of its prey, the gastropod *Kelletia kelletii*, frequently feed on the same items (Rosenthal, 1971). However, the interaction differs in that *K. kelletii* displays no escape responses to *P. giganteus*. Rosenthal suggests that the lack of defensive response is an adaptation permitting close association with *P. giganteus*. *B. undatum* displays violent escape responses to *L. polaris*. Further, it appears capable of assessing risks and benefits and adjusting its response accordingly. We suggest that this sensitivity to predation risk and ability to make adaptive trade-offs enables whelks to benefit from the foraging activities of their predator.

For such flexible behavioural responses towards a predator to evolve, prey have to pass through a risky sampling process to gather information relative to the costs and benefits of approaching the predator (Sih, 1987). During their evolution, whelks which suppressed escape responses to approach a feeding asteroid probably acquired additional food resources which increased fitness compared to individuals that avoided the asteroids. We hypothesize that the risk of approaching an asteroid is greatly reduced for whelks because of their efficient escape mechanisms, the violent contortions of the foot and twisting of the shell. The evolution of such elaborate defensive responses and sensitivity to predation risk by *B. undatum* has possibly been favoured because its larval development is benthic. Recruits are born into an environment where former generations, through natural selection, have adapted responses to local predation risks. Such fine-tuned responses might not be possible if the larval stage was pelagic since there would be genetic exchange with individuals of geographic areas with different predator fields. The evidence we present about the capacity of whelks to adjust behaviours to predation risk and variable feeding opportunities suggests that its neural system permits greater integration of information than is usually assumed to exist for invertebrates (see also Bellman & Krasne, 1983).

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