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Aggregation of whelks, *Buccinum undatum*, near feeding predators: the role of reproductive requirements

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In the Mingan Islands, northern Gulf of St Lawrence (eastern Canada), the whelk *Buccinum undatum* displays a strong escape response to its predator, the asteroid *Leptasterias polaris*, nevertheless large sexually mature individuals occasionally approach feeding *L. polaris* to obtain food. In this study, we investigated the hypothesis that reproductive requirements increase the tendency of sexually mature whelks to approach feeding asteroids. Prior to egg laying, females (which invest more energy than males into the production of reproductive structures) represented 72% of the adult whelks that approached feeding *L. polaris*, but only 36% of the adults randomly collected from the study area. Furthermore, females that were attracted to feeding asteroids had smaller reproductive organs (after accounting for body size) than females randomly collected from the study area. Similarly, prior to egg laying, females fed longer and ingested more food than males when tested in the presence of *L. polaris* in the laboratory. After egg laying, however, females and males displayed a similar tendency to feed in the presence of a predator, both in the field and in the laboratory. Predator-impact indices, computed by contrasting the feeding activity of whelks in the absence and presence of a predator, indicated that females (but not males) responded more boldly to predators prior to than after egg laying, despite a general decrease in feeding activity at that period. Taken together, our observations indicate that the tendency of adult whelks to approach feeding predators is influenced by potential reproductive gains. Because such gains are presumably more directly linked to a given feeding opportunity in sexually active individuals, whelks may be selected to display increased levels of boldness towards predators with the onset of sexual maturity. Thus, potential reproductive benefits may partly explain the size-dependent tendency of whelks to approach feeding asteroids.

Animals routinely prioritize their activities in relation to costs and benefits of alternative behavioural options. For instance, when deciding where, what and when to eat, they usually 'consider' the risk of being preyed upon by other animals (see reviews by Sih 1987; Lima & Dill 1990; Lima 1998). The ecological significance of animal decision making (McFarland 1977) is indicated in a growing number of studies showing how behaviour varies in relation to individual characteristics and environmental factors. For example, an animal's tendency to compromise feeding to lower predation risk generally increases with its vulnerability (e.g. Stein & Magnuson 1976; Sih 1982; Ramcharan et al. 1992; Rochette & Himmelman 1996), and decreases as its energetic requirements increase (e.g. Dill & Fraser 1984; Giles 1987; Godin & Sproul 1988; Abrahams & Dill 1989; McKillup & McKillup 1994). Furthermore, a given individual is more likely to reject a feeding opportunity when predation risk is high (e.g. Dill & Fraser 1984; Bishop & Brown 1992; Gotceitas & Godin 1993), or food reward low (e.g. Gilliam & Fraser 1987; Abrahams & Dill 1989).

Decision making in situations involving predation risk and feeding opportunities is an important aspect of the ecology of the common whelk *Buccinum undatum*. When attacked by the predatory asteroid *Leptasterias polaris*, the whelk displays vigorous escape responses, including rapid flight, shell rocking and foot contortions (Harvey et al. 1987; Rochette et al. 1996). The whelk may also display these behaviours following distance chemodetection of

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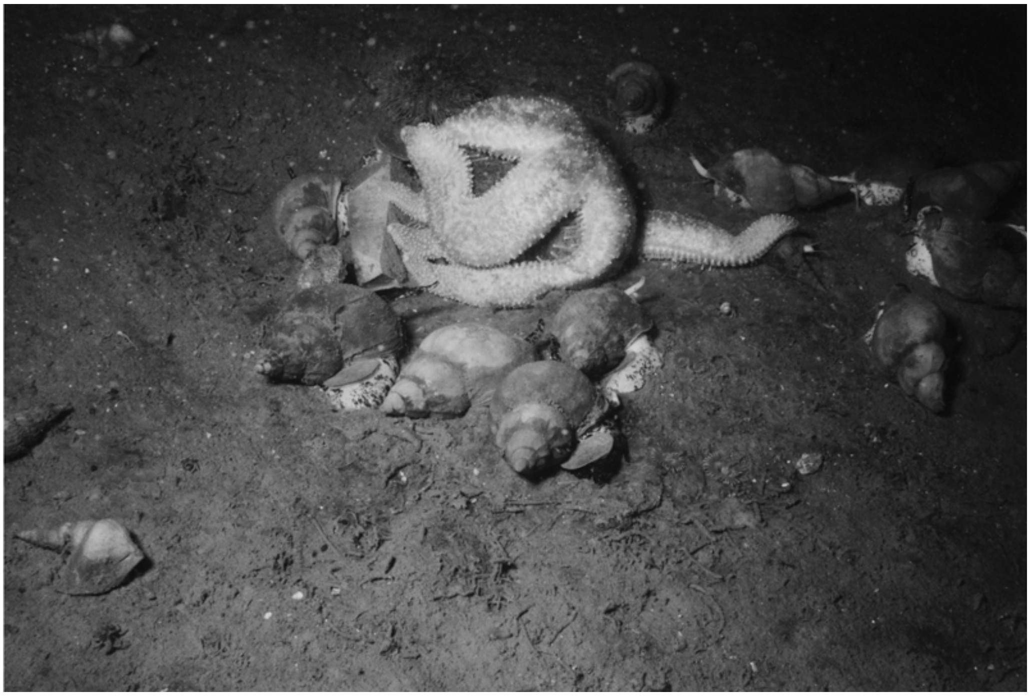

Figure 1. Photo of whelks, *Buccinum undatum*, aggregating near a feeding asteroid, *Leptasterias polaris*.

L. polaris, especially if the asteroid is actively searching for a prey (Rochette et al. 1997). However, when *L. polaris* is feeding on a large bivalve, whelks often aggregate in the vicinity of their predator and wait for leftovers, and at times even crawl alongside the asteroid in search of openings to insert their proboscis to steal fragments of the prey (Fig. 1). Whelks in such aggregations generally remain outside the asteroid's reach and occasionally display defensive behaviours, indicating that they have detected both predator and prey (Rochette et al. 1995). Interestingly, not all whelks participate in feeding aggregations; small whelks, measuring 50–70 mm or less in shell length, although abundant in the population, are virtually never found in the vicinity of feeding asteroids (Rochette et al. 1995; Rochette & Himmelman 1996). Rochette & Himmelman (1996) provide evidence that large whelks are more likely to approach feeding *L. polaris* because they are less vulnerable to this predator.

An additional hypothesis for the greater tendency of larger whelks to approach feeding asteroids is that they derive greater fitness benefits from the potential food gains associated with this behaviour. In the Mingan Islands, approximately 95% of the whelks that approach feeding asteroids measure more than 70 mm in shell length (Rochette & Himmelman 1996), which is about the size at sexual maturity (70–80 mm for females and 70 mm for males; Martel et al. 1986). The close match between the size at which whelks start approaching feeding asteroids and the size at maturity suggests that adults may take greater risks to obtain food because of increased energy requirements for reproduction. These costs are likely to be particularly important for females, which produce lipid-rich oocytes and a large gland to encapsulate the embryos. Based on the decrease in mass of reproductive organs during reproduction, Martel et al. (1986) estimate that the 'reproductive effort' is more than six times greater for females than for males, and they indicate that this figure is probably an underestimate because the lipid content of the female's ovary is far greater than that of the male's testis. Furthermore, whereas all adult males develop a large testis annually, 20–40% of females do not reproduce in any given year (prior to the onset of reproductive activities, the ovaries are underdeveloped and lack large mature oocytes; Martel et al. 1986). The above observations suggest that adult females are more energy limited than adult males.

The main objective of this study was to investigate the hypothesis that reproductive requirements influence the tendency of *B. undatum* to approach feeding asteroids. Using field and laboratory experiments, we quantified the feeding activity of sexually mature whelks in the presence and absence of a predatory asteroid, both prior to and after the period of egg laying, and tested the following predictions: (1) females take greater risks to obtain food than males, (2) females with poorly developed reproductive organs take greater risks than females with well-developed reproductive organs, and (3) the feeding response of whelks is less affected by the presence of a predator (i.e. whelks respond more boldly) prior to egg laying, when the reproductive benefits of feeding are more immediate.

METHODS

During the summer of 1994, we investigated the behaviour of sexually mature whelks from Cap du Corbeau (50°14′N, 63°35′W) on Île du Havre in the Mingan Islands, northern Gulf of St Lawrence, eastern Canada.

We conducted field and laboratory experiments both prior to (May), and after (August), the period of egg laying at this site (Martel et al. 1986). In both periods, we first used SCUBA diving to take a large random sample of sexually mature whelks by collecting all individuals (both buried and nonburied) measuring more than 80 mm in shell length (Martel et al. 1986) within 1 m on either side of two 160-m-long transects parallel to the shoreline, one at 9 m and the other at 15 m in depth. A total of 228 whelks were sampled in May and 249 in August. These whelks were first used in a laboratory experiment (see below), and then dissected to determine the sex ratio within our study site and the reproductive status of the females. During the dissections, we measured shell length with calipers (± 0.1 mm), and then broke the shell with a hammer to remove the soft tissues. The gonad, pallial oviduct (mainly the capsule gland, but also the seminal receptacle, albumin gland and bursa), digestive gland and the remaining body components of females were then drained on paper towelling for 10 min and weighed (± 0.01 g).

Buccinum undatum is often parasitized by the trematode *Neophasis* sp., which causes extensive damage to the reproductive organs and digestive gland (Køie 1969; Tétreault et al. 2000). The gonad of whelks infected by *Neophasis* sp. is greyish in colour, in contrast to the usual yellow-orange. Tissue damage caused by *Neophasis* sp. is so extensive that the production of viable gametes is certainly impaired, and perhaps null. Similar infections have been shown to decrease survivorship and reproductive output in other gastropods (e.g. Huxham et al. 1993; Lafferty 1993). During our study, 20% of females and 15% of males were parasitized by *Neophasis* sp. in May and 25% of females and 16% of males in August. Parasitized whelks were excluded from the main analyses, although we briefly compare behavioural differences between parasitized and nonparasitized individuals when sample size permits. An additional 14 whelks in May and four in August were excluded from the analysis because of procedural errors.

Field Experiments

To determine whether gender affects the tendency of whelks to approach feeding *L. polaris*, we studied whelks that approached feeding bouts of the asteroid that we initiated in the field. To do this, we provided asteroids (25–35 cm in diameter) with a large bivalve, the surf clam *Spisula polynyma*, which had its adductor muscles cut. The asteroids had been starved in the laboratory for ca. 7 days prior to the experiment to increase their incentive to feed. We then returned to the site at approximately the same time every day (1000 hours), until *L. polaris* stopped feeding, and collected all whelks found within a 50-cm radius of the asteroid. In parallel, we sampled whelks within a 50-cm radius of unattended (i.e. predator absent) *S. polynyma* (again with the adductor muscles cut) attached to the bottom in plastic 5-mm mesh sacs (to prevent feeding by whelks and other carnivores).

To facilitate underwater sampling, we placed the bivalves at ca. 20-m intervals along the two transects, determining treatment order at random. In the treatment with predators, sampling continued until the asteroid left its prey (usually in 2–6 days). In the treatment without predators, sampling was stopped after 6 days when all the asteroids in the predator treatments had left their prey. The experiments were conducted between 10 and 15 May (8 feeding asteroids and 4 unattended bivalves), and between 17 and 21 August (10 feeding asteroids and 6 unattended bivalves). We collected sexually mature whelks (i.e. >80 mm in shell length) near feeding asteroids and unattended bivalves and dissected them to evaluate the sex ratio and the reproductive status of females. (The tendency of different-size whelks to approach these food sources is described by Rochette & Himmelman 1996.)

Statistical analysis

To test the prediction that females take greater risks to obtain food than males, we used *G* tests to compare the sex ratio of whelks collected in the vicinity of feeding predators (or unattended bivalves) with that of whelks randomly sampled in the study area (Zar 1984). To test the prediction that females with poorly developed reproductive organs take greater risks to obtain food than females with well-developed organs, we used regression and residual analyses. First, we determined the relationship between the mass of reproductive organs (ovaries plus pallial oviduct) and body mass (total mass minus mass of the shell, digestive gland and reproductive organs) for females collected at random in the study area, and then evaluated the extent to which the mass of reproductive organs of females collected near feeding asteroids (and unattended bivalves) deviated from this relationship (i.e. we estimated residuals). Finally, we used the Wilcoxon signed-ranks test to evaluate the hypothesis that the median value of the residuals was 0 (Zar 1984); a significant deviation from 0 (i.e. more and larger negative than positive residuals, or vice versa) implies that the reproductive organ mass of females collected near feeding asteroids (or unattended bivalves) differed from that of similar-sized females collected at random in the study area. Because of potential biases associated with asymptotic testing with small sample sizes (Mundry & Fischer 1998), we used critical values of the Wilcoxon *T* distribution (Zar 1984, Table B. 11) to evaluate the significance of our results.

Laboratory Experiments

We conducted laboratory studies on the feeding behaviour of whelks both prior to (10–22 May) and after egg laying (4–19 August). We performed the experiments in plastic containers (75 × 43 × 29 cm) filled with sand to a depth of 2–3 cm. On one side of the container we placed a whelk and a piece of food (a siphon of the bivalve *Mya truncata*) separated by a few centimeters. The whelk was allowed 15 min to commence feeding. Whelks that did not feed were not studied further. After 2 min of feeding, we placed an asteroid (25–35 cm in diameter) in a 5-mm mesh Vexar sac on the other side of the container. In randomly chosen trials, we introduced an empty Vexar sac instead of a sac containing the predator. In both cases, we recorded the duration of feeding by whelks for a maximum of 90 min, and determined the mass (± 0.01 g) of food ingested from measurements of the mass of the blotted siphon tissue taken just before and after the trials. Between trials, we changed the water and top ca. 5 mm of sand in the experimental containers. The temperature increased by less than 1°C during any given trial, and was about 4°C in May and 7°C in August. To limit the influence of recent feeding history on behaviour, the whelks were fed for 5 h one week before the experiment and then starved until the experiment.

Statistical analysis

To test the prediction that females take greater risks to obtain food than males, we used *G* tests to compare the proportion of males and females that fed for the entire 90-min experimental period following the introduction of a predator (we did not use time spent feeding as a continuous variable because most whelks that accepted food fed for 90 min), and *t* tests to compare the mass of food ingested (variances were homogeneous, Bartlett's test: NS in both May and August).

To test the prediction that females with 'poorly developed' reproductive organs take greater risks to obtain food than 'well-developed' (ripe) individuals, we proceeded with tests similar to those applied to the field data. We first estimated the reproductive organ mass residuals for females used in the laboratory experiment (see above). Then, we used *t* tests to compare residuals for females that did and did not feed (variances were homogeneous, Bartlett's test: NS in both May and August), and Mann–Whitney *U* tests to compare residuals for females that fed for 90 min and for less than 90 min (some variances were heterogeneous, Bartlett's test: $P<0.05$). We used critical values of the Mann–Whitney *U* distribution to evaluate the significance of our results (Mundry & Fischer 1998) except when sample sizes exceeded those presented in Zar (1984, Table B. 10), where asymptotic testing (normal approximation) was used.

To test the prediction that the feeding activity of whelks is less affected by the presence of a predator prior to egg laying, we used a randomization procedure (Manly 1991) to compare the impact of predators in May and in August (males and females separately). First, we calculated predator impact indices by contrasting the proportions of whelks that fed for 90 min (amongst those that accepted the food items) in the absence and presence of a predator:

$$PI_{\mathrm{M}}=\pi_{\mathrm{M,pa}}-\pi_{\mathrm{M,pp}}$$

$$PI_{\mathrm{A}}=\pi_{\mathrm{A,pa}}-\pi_{\mathrm{A,pp}}$$

where PI=predator impact index, M=May, A=August, π=proportion of whelks that fed for 90 min, pa=predator absent trials, and pp=predator present trials. Then we estimated seasonal variation in whelk boldness towards predators (ΔPI) by calculating the difference in the (predator impact) indices between May and August. Finally, we compared this value to the randomization frequency distribution of ΔPI to evaluate the probability of obtaining, by chance alone, an absolute ΔPI as great or greater than that observed. The randomization distribution of ΔPIs was established by recalculating ΔPI after the score of each individual whelk (a score of 0 for whelks that fed for less than 90 min and of 1 for whelks that fed for 90 min) was randomly assigned to one of the four treatment categories (May predator absent; May predator present; August predator absent; August predator present), and repeating this randomization procedure a total of 10 000 times. The only constraint to the randomization procedure was that it respected the sample size of each treatment category.

We used a similar procedure to compare the impact that predators had on the amount of food whelks ingested, except that the variable being randomized was the quantity of food each individual ingested (rather than a score of 0 or 1), and the statistic was based on the average quantity of food ingested (rather than the proportion of whelks that fed for 90 min).

RESULTS

Field Study

Do females take greater risks than males?

In May, prior to egg laying, females represented 72% of the whelks collected in the vicinity of feeding asteroids, but only 36% of those randomly sampled in the study area (Fig. 2; G_1=9.4, P=0.002), suggesting they had a greater tendency than males to approach feeding asteroids to obtain food. In contrast, in August, the proportion of females in the vicinity of feeding asteroids and in the random sampling of the study area were similar (64 and 53%, respectively; G_1=0.64, P=0.42), suggesting that both sexes were equally likely to approach, or remain near, feeding asteroids after egg laying (Fig. 2). The size (shell length) of sexually mature whelks that approached feeding asteroids (males in May: $\bar{X}$=89.1 ± 1.8 mm; females in May: 88.5 ± 1.3 mm; males in August: 88.2 ± 1.0 mm; females in August: 91.7 ± 1.8 mm) was similar to that of mature individuals randomly collected from the study area (males in May: 90.1 ± 0.4 mm; females in May: 90.9 ± 0.7 mm; males in August: 89.0 ± 0.5 mm; females in August: 90.4 ± 0.5 mm) (Mann–Whitney *U* tests, NS for all comparisons).

The proportion of females near unattended bivalves (Fig. 2) was similar to that in the random sampling in both May (G_1=1.58, P=0.21) and August (G_1=0.81, P=0.37), indicating that the tendency of females and males to approach food sources was similar when no predator was present. The size (shell length) of sexually mature whelks that approached unattended bivalves (males in May: 87.7 ± 1.3 mm; females in May: 87.6 ± 1.5 mm; males in August: 89.0 ± 1.3 mm; females in August: 90.4 ± 1.4 mm) was similar to that of mature individuals randomly collected from the study area (see above) (Mann–Whitney *U* tests, NS for all comparisons).

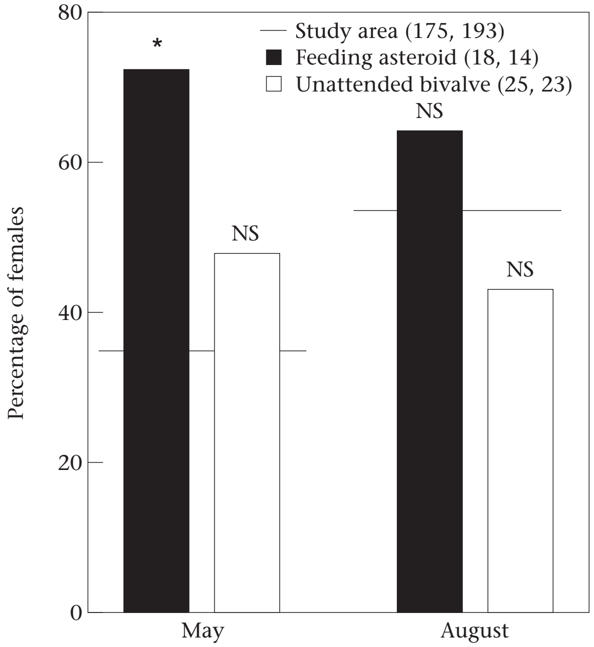

Figure 2. Percentage of female whelks, *Buccinum undatum*, in samples collected in the vicinity of bivalves, *Spisula polynyma*, being consumed by the asteroid *Leptasterias polaris*, and in the vicinity of unattended *S. polynyma*, compared to the sex ratio in the study area (horizontal line). Numbers in parentheses are total numbers of whelks collected in May and August 1994, respectively. We used *G* tests to compare the sex ratio of whelks randomly collected from the study area to that near food sources. $^*P<0.005$.

Is risk taking by females related to their reproductive status?

For females, the mass of reproductive organs was positively related to body mass (Fig. 3), in both May ($r^2=0.16$, $P=0.002$) and August ($r^2=0.38$, $P<0.0001$). An analysis of covariance, using body mass as the covariate, showed that females had smaller reproductive organs in August than in May ($F_{1,161}=24.6$, $P<0.0001$; slopes were parallel: $F_{1,160}=0.09$, $P=0.77$), indicating that many of them had laid their eggs by the second sampling period (Fig. 3).

The dissections further indicated that reproductive status affected the tendency of females to approach food sources prior to egg laying. In May, the mass of the reproductive organs of females sampled in the vicinity of food sources (i.e. feeding asteroids and unattended bivalves pooled) generally fell below the regression line for randomly sampled females (Fig. 3), and the residuals (i.e. observed minus expected mass of reproductive organs) were biased towards negative values ($\bar{X}=-1.83$, $T^{+}=53$, $N=25$, $P<0.005$). This negative bias in the mass of the reproductive organs was still significant when only females collected near feeding asteroids were analysed ($\bar{X}=-2.17$, $T^{+}=8$, $N=13$, $P<0.01$), but not when only females collected near unattended bivalves were analysed ($\bar{X}=-1.47$, $T^{+}=19$, $N=12$, NS). In August, the mass of reproductive organs of females sampled near food sources was comparable to that of similar-sized females randomly sampled from the study area (residuals for feeding asteroids and unattended bivalves pooled: $\bar{X}=0.50$, $T^{-}=93$, $N=19$, NS; feeding asteroids alone: $\bar{X}=-0.17$, $T^{+}=22$, $N=9$, NS; unattended bivalves alone: $\bar{X}=1.11$, $T^{-}=20$, $N=10$, NS), suggesting that after egg laying the tendency of females to approach food sources was not influenced by reproductive condition (Fig. 3).

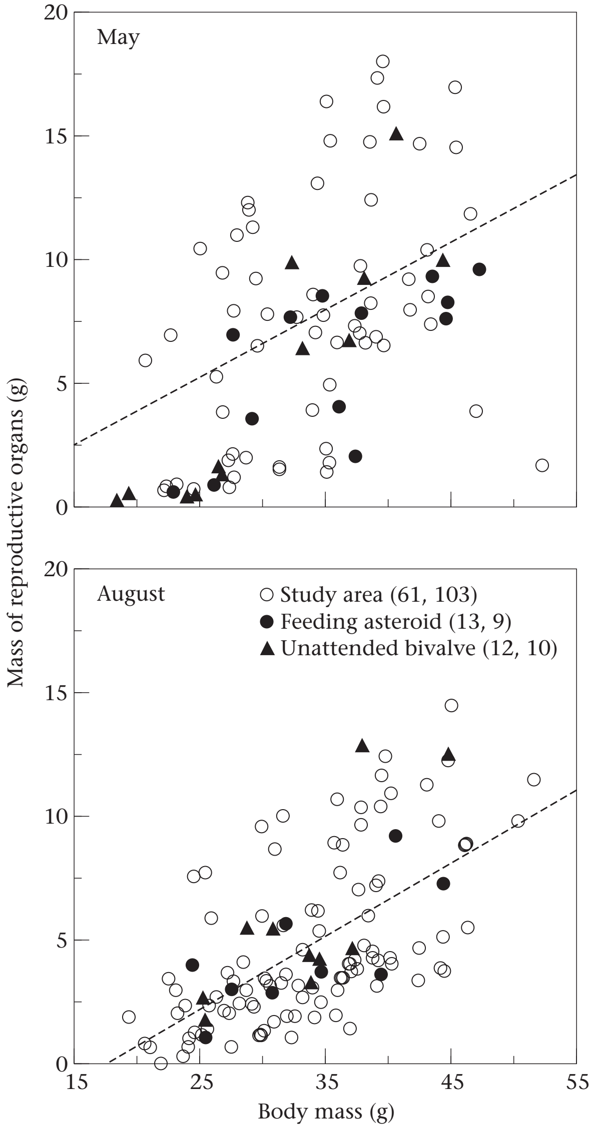

Figure 3. Relationship of reproductive organ mass (gonads and accessory reproductive structures) to body mass for female whelks, *Buccinum undatum*, collected in May and August 1994 at random in the study area, in the vicinity of feeding asteroids, and in the vicinity of unattended bivalves. Numbers in parentheses are total numbers of female whelks collected in May and August 1994, respectively. The regression lines are for the whelks randomly collected from the study area.

Laboratory Experiments

Do females take greater risks than males?

We documented marked seasonal changes in the propensity of whelks to feed in the laboratory as the proportion increased two-fold from May to August (females: $G_1=32.4$, $N=164$, $P<0.001$; males: $G_1=55.0$, $N=204$,

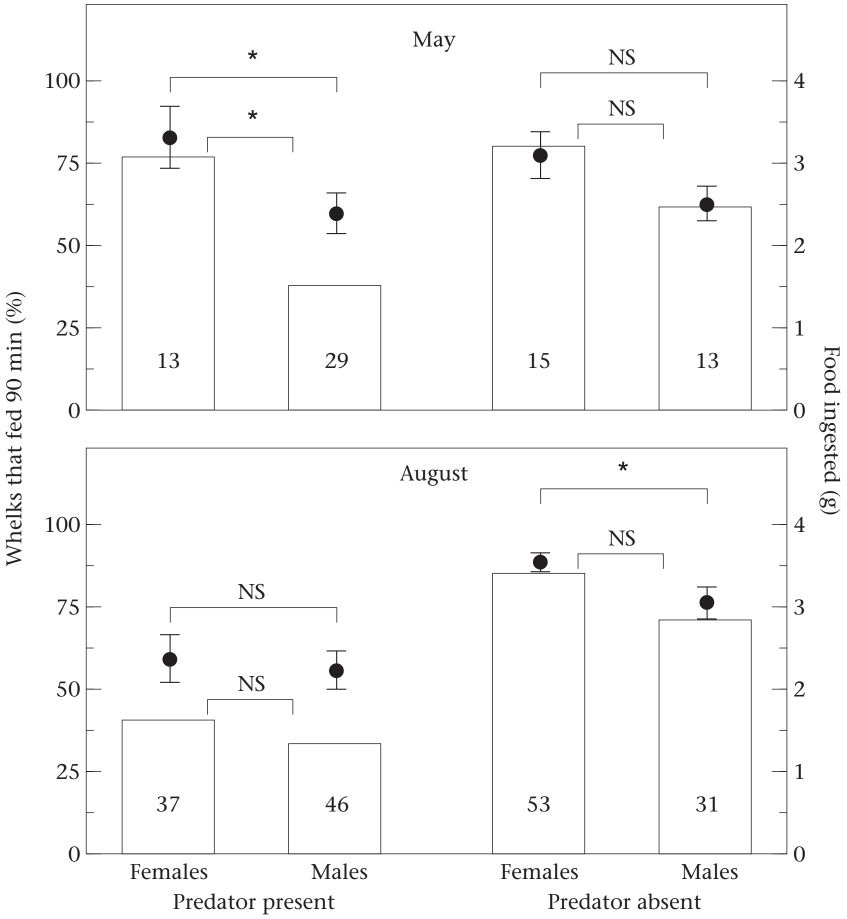

Figure 4. Percentage of whelks, *Buccinum undatum*, that fed for the entire 90-min experimental period (bars) and mean±SE quantity of food ingested (●; including whelks that fed for <90 min) during laboratory experiments conducted in the presence and absence of the predator *Leptasterias polaris* in May and August 1994. We used *G* tests to compare the proportion of females and males that fed for 90 min, and *t* tests to compare the mass of food ingested. Numbers in bars indicate sample sizes. $*P<0.05$.

$P<0.001$). In both months the proportion of females and males that fed were similar (May: $G_1=1.35$, $N=175$, $P=0.25$; August: $G_1=0.14$, $N=193$, $P=0.71$). However, in the trials with a predator present, differences between the sexes were observed in May, prior to egg laying (Fig. 4), when females more frequently fed until the end of the experiment ($G_1=5.68$, $P=0.017$) and ingested more food than males ($t_{40}=2.03$, $P=0.049$). In August, a similar proportion of females and males fed throughout the experimental period in the presence of a predator ($G_1=0.59$, $P=0.29$), and the two sexes ingested a similar quantity of food ($t_{81}=0.37$, $P=0.71$; Fig. 4).

The effect of gender on the feeding behaviour of whelks in the absence of a predator differed somewhat from the trials with a predator (Fig. 4). In May, the feeding behaviour of males and females in the absence of a predator did not differ significantly, either in terms of the number of individuals that fed for 90 min ($G_1=1.17$, $P=0.28$), or the quantity of food ingested ($t_{26}=1.63$, $P=0.12$). In August, there was also no difference between the number of females and males that fed throughout the entire experimental period ($G_1=2.29$, $P=0.13$), but females ingested more food than males ($t_{82}=2.14$, $P=0.035$).

Is risk taking by females related to their reproductive status?

In the laboratory, as was observed in the field, reproductive status influenced the feeding response of females before, but not after, egg laying. Thus, in May, females that accepted the food item had smaller reproductive organs than similarly sized females that rejected it ($t_{59}=3.02$, $P=0.004$; Fig. 5). Furthermore, amongst the females that accepted the food item, those that fed for the entire 90-min experimental period (predator and control trials pooled) had smaller reproductive organs than those that stopped feeding prior to 90 min (Mann–Whitney *U* test: $U=108$, $N_1=22$, $N_2=6$, $P<0.05$). The small number of whelks that fed for less than 90 min in May prevented this analysis from being conducted for predator and control trials separately ($N=3$ in both trials). In contrast, in August, females that accepted the food item did not have smaller reproductive organs than similarly sized females that rejected it ($t_{101}=0.13$, $P=0.90$; Fig. 5), and female reproductive condition did not influence feeding duration, either when the results for control and predator trials were pooled ($Z=0.56$, $N_1=60$, $N_2=30$, $P=0.58$) or

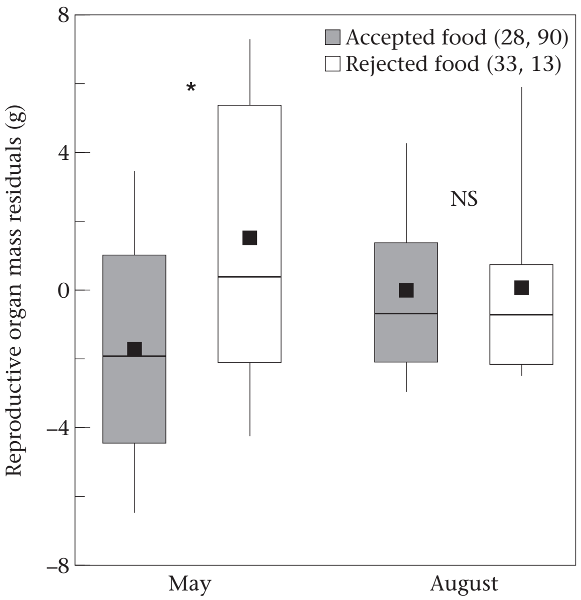

Figure 5. Box-plot charts showing the residuals for the mass of the reproductive organs (see Methods) for females that accepted and rejected food during the laboratory experiments in May and August 1994. The top, middle and lower horizontal lines show the 75th, 50th and 25th percentiles, respectively. The black squares indicate the means, and the vertical lines extend from the 10th to the 90th percentile. Numbers in parentheses indicate sample size in May and August, respectively. We used *t* tests to compare residuals estimated for females that accepted and rejected food items. *$P<0.005$.

analysed separately (control: $Z=-0.41$, $N_1=45$, $N_2=8$, $P=0.68$; predator: $U=210$, $N_1=15$, $N_2=22$, NS).

Do whelks respond more boldly to predators before egg laying?

Predator impact indices (see Methods) provided evidence that the negative influence of the predator on feeding activity of females was less before than after egg laying. The presence of a predator caused only a 3% decrease in the number of females that fed for 90 min in May, compared with a 44% decrease in August ($\Delta PI=41\%$; randomization $P=0.037$). Similarly, the decrease in the average quantity of food females ingested due to the presence of a predator was less in May (-0.2 g) than in August (1.2 g) ($\Delta PI=1.4$ g; randomization $P=0.017$). In contrast, we found no seasonal variation in the impact of predators on the percentage of males that fed for 90 min (*PI* May 24% versus *PI* August 37%, $P=0.51$), nor on the quantity of food they ingested (*PI* May 0.1 g versus *PI* August 0.8 g, $P=0.20$). These observations indicate that females, but not males, responded more boldly to predators prior to, rather than after, egg laying.

The effect of castrating parasites on whelk behaviour

Small sample sizes prevented a rigorous analysis of the effect of the castrating trematode *Neophasis* sp. on the behaviour of *B. undatum*. Nevertheless, a few interesting patterns emerged. Males collected in the vicinity of feeding asteroids in May (but not in August) were more frequently parasitized than males randomly collected in the study area (7/12 versus 21/133, $G_1=10.0$, $P=0.002$). Also, parasitized males tended to be more likely than nonparasitized individuals to feed during the entire 90-min experimental period in the presence of *L. polaris*, both in May (3/3 parasitized versus 11/29 nonparasitized) and in August (8/12 parasitized versus 16/46 nonparasitized), although these differences were not significant (Fisher's exact probability tests: May: $P=0.073$; August: $P=0.057$). Finally, the tendency of parasitized males to approach feeding asteroids appeared related to the severity of their infection, as in May, 57% (4/7) of the parasitized males that approached feeding asteroids had more than 50% of the digestive gland occupied by the parasite, compared with only 5% (1/21) for parasitized males randomly collected in the study area (Fisher exact probability test: $P=0.008$). We found no evidence that parasitic infection influenced the feeding behaviour of females, either in May or in August, even though sample sizes were comparable to those for males.

DISCUSSION

Variation in Whelk Decision Making: the Ultimate Cause

In most species, males and females make different contributions to the production, development and protection of offspring. Female neogastropods invest large amounts of energy in the production of jelly masses or egg capsules, which serve to nourish and protect their embryos. Martel et al. (1986) estimated that a standardized adult female *B. undatum* from our study site, measuring 88 mm in shell length, loses ca. 10.5% of its body mass during reproduction, compared with only ca. 1.6% for the same-sized male. As the estimated value for females includes individuals with small reproductive organs (gonads and accessory reproductive structures) that were probably incapable of reproducing that season (Martel et al. 1986), the decrease in body mass for reproducing females is probably even greater. Finally, the caloric content of the female ovary is higher than that of the male testis, because of its greater lipid content (see references in Martel et al. 1986), further increasing the difference between female and male reproductive effort.

These gender differences in reproductive effort may explain why females often took greater risks than males to obtain food during our study; females may have fed more readily in the presence of a predator in the field and laboratory because feeding opportunities were more likely to increase their reproductive success than was the case for males. One might argue that the field results were caused by males displaying decreased responsiveness to food during the breeding season, perhaps because they are too busy looking for mates. However, the sex ratio observed among whelks collected near unattended bivalves did not differ from that of the study population, and the proportion of males and females that accepted food items during the laboratory trials was similar. Therefore, both genders seemed equally responsive to food stimuli, but females appeared more willing to feed despite

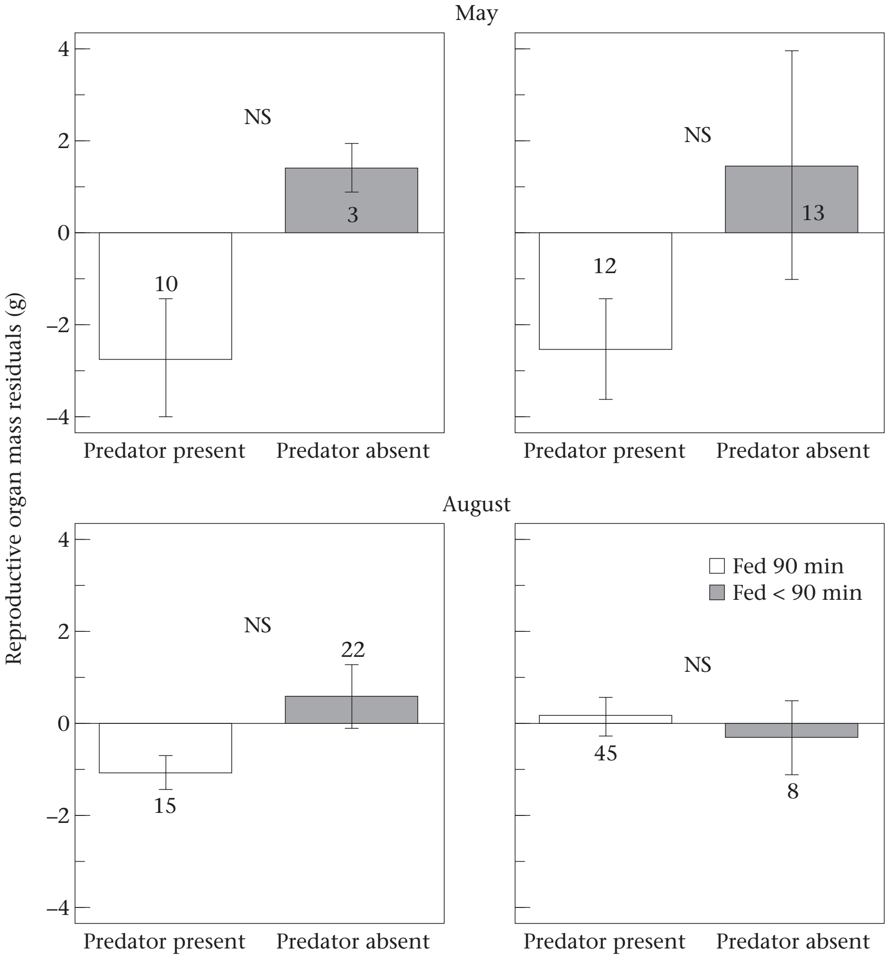

Figure 6. Mean (±SE) residuals for the mass of reproductive organs (see Methods) of females that accepted food during the laboratory experiments in May and August 1994. Numbers associated with columns indicate sample size. We used Mann–Whitney *U* tests to compare residuals estimated for females that fed during the entire 90-min experimental period to the residuals of females that fed for less than 90 min.

predation threat than males, both in the field and in the laboratory.

The hypothesis that gender-based differences in whelk behaviour are related to reproductive requirements/ benefits is supported by variation in whelk behaviour based on female reproductive condition and season. First, females with the greatest potential for reproductive gain were most likely to feed in the face of predation threat. For example, in the field, females that had small reproductive organs were more likely to approach food sources than well-developed individuals, a pattern that was especially apparent when feeding asteroids were present. Similarly, in the laboratory, females with poorly developed reproductive structures were also more likely to accept food items and feed throughout the entire experimental period (control and predator trials pooled). Second, our predator impact indices indicated that the feeding response of females (but not that of males) was less affected by the presence of a predator in May (prior to reproduction) than in August (when most females had laid their eggs). The temporal variation in decision making may enable females to take advantage of risky feeding opportunities when feeding is most likely to enhance fitness, that is just prior to reproduction. (The low incidence of females in the random sampling of the study site in May was probably because many of them had moved to shallower water in search of rocky sites for egg laying.)

The seasonal variation in predator impact on female feeding behaviour is particularly significant considering that our two sampling periods only imperfectly represented pre- and postreproductive conditions (numerous females collected in August still had large gonads). Furthermore, increased female boldness was observed prior to reproduction, when most adults in the populations were displaying a low tendency to feed (46% of females accepted food in May compared with 87% in August). The low feeding activity of whelks prior to reproduction is consistent with stomach content analyses of field-collected animals (Himmelman & Hamel 1993), and is probably because most adults are preoccupied by reproductive activities (i.e. searching for mates, copulating and laying eggs) at this time of the year (Martel et al. 1986). Nevertheless, whelks are considered to be highly opportunistic scavengers (Himmelman 1988), which might partly explain why significant differences in feeding behaviour related to gender and female reproductive status were only evident prior to reproduction (i.e. when interindividual differences in gains to be made by feeding, in terms of increased reproductive potential, were probably most pronounced). The whelks' opportunistic feeding behaviour might also explain why interindividual differences in feeding behaviour were less pronounced in the absence than in the presence of a predator (although similar patterns were apparent).

Reproductive activities often increase susceptibility to predators (Magnhagen 1991), and recent studies have shown that predation risk can affect mate choice (e.g. Forsgren 1992; Hedrick & Dill 1993; Gong & Gibson 1996), mating strategy (e.g. Godin 1995; Fuller & Berglund 1996), parental behaviour (e.g. Rangeley & Godin 1992; Harfenist & Ydenberg 1995) and spawning intensity (e.g. Rawlings 1994) in a variety of organisms. To our knowledge, however, only two previous studies have examined whether gender and reproductive status affect how animals trade off predation risk and foraging. Abrahams & Dill (1989) found that female guppies, *Poecilia reticulata*, take greater risks to obtain food than males. Similarly, Levri & Lively (1996) found that in the freshwater snail *Potamopyrgus antipodarum*, nonbrooding females spend more time foraging on the upper surfaces of rocks than males and brooding females. Because the upper surfaces of rocks are richer in the snail's food (diatoms and algae), but also more exposed to predatory fish and waterfowl, nonbrooding females apparently take greater risks to assure their next brood. These results parallel those of the present study. Because the fitness of females is often limited by energy intake whereas that of males is more limited by access to mates, females may be selected for greater boldness towards predators in the context of food acquisition. However, the fitness of males may be more strongly limited by food acquisition in species where there is intense intrasexual competition based on honest displays or nuptial gifts (e.g. Thornhill & Alcock 1983, page 372). Furthermore, the evolution of gender-mediated differences in boldness towards predators will probably depend on the relationship between current and (potential) lifetime reproductive output (see below).

Influence of Parasitism on Whelk Behaviour

Although small sample sizes prevented a rigorous analysis of the effects of the castrating trematode *Neophasis* sp. on the behaviour of adult *B. undatum*, we nevertheless found evidence that parasitic infection increased the feeding activity of male whelks (but not of females). This increased feeding activity could have evolved to moderate the damage inflicted by *Neophasis* to the whelks' gonadic tissues, thus enabling infected individuals to have some reproductive success. For example, in the intertidal periwinkle *Littorina littorea*, parasitic 'castration' causes a gradual reduction in egg production, and even highly parasitized females produce some eggs (Huxham et al. 1993). Alternatively, whelks parasitized by *Neophasis* sp. may be manipulated to increase their foraging activity, even if they are no longer able to reproduce (which seems likely considering the highly degenerative appearance of their gonads; see Tétreault et al. 2000). An increase in whelk foraging activity may be adaptive to the parasite; whelks that are searching for food are probably more conspicuous to predators, and are therefore more likely to transmit the parasite to its final host (see also Giles 1987; Levri & Lively 1996). The most likely final host of *Neophasis* sp. in the Mingan Islands is the migratory Atlantic wolfish *Anarhichas lupus*, a known predator of the whelk. The infective stage of *Neophasis* sp. is present in whelks between June and August, when *A. lupus* is present in the Mingan Islands. This period also coincides with a decline of severely infected whelks from the population (F. Tétreault, unpublished data), perhaps because of predation. These two hypotheses are not mutually exclusive, as the increased feeding activity of infected whelks could be advantageous to both the whelk and the parasite.

Why Do Juveniles Not Approach Feeding Asteroid Predators?

In the Mingan Islands, large adult whelks occasionally aggregate near feeding *L. polaris* to steal fragments of prey or await leftovers (Rochette et al. 1995). Smaller immature whelks rarely participate in such aggregations, probably because of their greater vulnerability to the predatory asteroids (Rochette & Himmelman 1996). Although this study examined the behaviour of adult whelks only, it provides a complimentary explanation for the weak tendency of small whelks to approach feeding asteroids, namely that this behaviour imparts no immediate reproductive benefits to immature individuals. *Buccinum undatum* is a long-lived and slow-growing species that potentially reproduces over many years. Based on the examination of operculum annuli, Gendron (1992) estimated that whelks in the Mingan Islands attain sexual maturity at 5–7 years of age, and can live up to 12 years. Therefore, food rewards provided from approaching a feeding asteroid may not sufficiently increase the lifetime reproductive success of immature whelks to justify employing this risky behaviour. According to life-history theory, investment in reproductive activities should reflect a trade-off between current and future reproductive opportunities (Williams 1966); animals with a high potential for future reproduction are therefore expected to take fewer risks when trading off the risk of predation with other activities. An interesting avenue for future investigation would consist of deciphering the relative importance of vulnerability and reproductive benefits in influencing the tendency of different-size whelks to approach feeding asteroids. This line of research would provide insight into the evolutionary mechanisms of animal decision making.

Concluding Remarks

The results of our study support the hypothesis that reproductive requirements influence the tendency of *B. undatum* to feed in the presence of a predation threat. This conclusion appears to be robust, considering the agreement between field and laboratory findings, and the congruity among results based on gender, female reproductive condition and season. As a further test of this hypothesis, one could manipulate female reproductive condition and evaluate how this affects their feeding behaviour in the presence of a predation threat. This could be done by submitting females to different feeding regimes over a long period of time (e.g. several months) and then controlling for stomach fullness immediately prior to the trials.

Our study was concerned with the adaptive value of interindividual differences in whelk decision making. At the proximate level, there are two mechanisms that could account for our results; either females are more responsive to food stimuli than males prior to reproduction, especially if they have poorly developed reproductive organs, or they are less responsive to predator stimuli. Although our study did not address this question, some of our results provide suggestions. Interindividual differences in feeding behaviour prior to reproduction were never observed in the absence of a predator, neither in the field nor in the laboratory, suggesting that males were as responsive as females to food stimuli. An attempt at comparing the impact of predation threat on the feeding behaviour of males and females (not reported) revealed few differences, suggesting that responsiveness to predators is also similar between genders. Perhaps both mechanisms are involved, and our tests were not sensitive enough to detect either. Answering this question may require monitoring the feeding response of whelks using several combinations of predation threat and feeding benefits (e.g. Fraser & Huntingford 1986; Rochette & Himmelman 1996).

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