

# Influence of water motion and reproductive attributes on movement and shelter use in the marine snail *Littorina saxatilis*

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**ABSTRACT:** Extrinsic factors such as the physical environment can control the activities of animals, but their effect on behaviour can vary substantially among individuals within a given population depending on more intrinsic factors such as differences in the need to search for food or mates. We examined the activity of the brooding intertidal gastropod *Littorina saxatilis* under a range of different physical stressors experienced during high tide to test 2 hypotheses: (1) activity is affected by hydrodynamic conditions and (2) different reproductive groups respond in different ways to these conditions, specifically that gravid females exhibit more risk-avoidance behaviour in relation to other individuals. Two components of activity (magnitude of movement and shelter use) were measured for 3 reproductive groups (males, non-gravid females and gravid females) under temporally varying conditions of different environmental factors, including water flow, maximum wave force and water temperature. Movement (specifically, net distance displaced) of snails decreased with increases in water flow and maximum wave force. Reproductive groups did not differ in the form of their response function to water flow, but instead differed in the magnitude of their response, with gravid females moving the shortest distances. Gravid females were also the only group to increase their use of shelters in response to increases in maximum wave force, and this response was positively related to their fecundity. We interpret these behaviours as responses to increased risk of dislodgment and conclude that the behaviour of gravid females (i.e. use of shelters and reduced movements) should increase their survival as well as that of the offspring they carry.

**KEY WORDS:** Brooding · Foraging · Gastropod · Intertidal ecology · Movement · Risk avoidance · Shelter use

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## INTRODUCTION

The modern view of optimal foraging behaviour relies on the trade-off between energy intake and the risk of mortality from predation (Sih 1980, Lima & Dill 1990) or stresses associated with environmental conditions, i.e. stressors (Moran 1985). In areas where predation pressure is not a strong source of selection, physical conditions should be the principal factors controlling animal activity. Behaviours, such as the timing or level of activity, can be adjusted to avoid or reduce potential physiological stress, injury, or death (e.g.

extreme temperatures, wind, currents). Examples include the pollinating activity of bees that cease foraging in moderate winds or light rain (Vicens & Bosh 2000), reduced activity of lizards with increased rainfall and humidity (Sound & Veith 2000), or shifts in habitat selection by fish in lotic environments that depend on water velocity (Heggenes 2002).

Individuals are expected to change their behaviour to maximise their fitness with respect to the risks associated with a given level of environmental stressors. However, not all individuals can be expected to respond similarly, and individual attributes must also

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be taken into account to assess accurately the relationship between activity and environmental conditions. Consistent differences may thus be observed among different groups according to their age, size, gender, or ecotype (Erlandsson et al. 1998, Dewitt et al. 1999, Jones & Boulding 1999, Rochette et al. 2001, Brokordt et al. 2003). Such differences are especially likely in comparisons between sexes, as reproductive investments are not always similar, either before mating (e.g. energetic allocation towards gamete production) or after mating (e.g. brooding). Individuals of different genders and reproductive conditions should, therefore, respond differentially to a given risk, and the interplay between these individual attributes and the intensity of an environmental stressor could produce substantial variation in behaviour at the population level. Species that provide parental care might be particularly variable in this regard, as parents often decrease their level of foraging activity (Crawford & Balon 1996, Crump 1996, Anderson 1997, Jormalainen et al. 2001), which should maximise offspring survival.

Environmental stress (*sensu* Menge & Sutherland 1987) could be particularly severe in rocky intertidal habitats, where marine organisms must live in a world of alternating conditions of low and high tide. During low tide, they can be exposed to terrestrial conditions of desiccation, high light levels and extreme temperatures, whereas during high tide they can experience considerable hydrodynamic forces from waves and currents. Environmental stress in this habitat has been shown to affect behaviour directly, but most studies have focused on the effects of the physical environment experienced during low tide (reviewed by Little 1989, Norton et al. 1990). Studies on the influence of physical factors on behaviour during high tide (e.g. Judge 1988) are much less common in spite of the fact that the activity of intertidal animals is often restricted to high tides when desiccation does not occur (Little 1989). In addition, the physical environment is rarely well characterised, especially hydrodynamic stressors (Bell & Denny 1994).

Snails, especially those in the family Littorinidae, have been often used as models to test the influence of the environment on behaviour (Norton et al. 1990). A striking behaviour is the use of irregularities in the rock surfaces (e.g. crevices or holes) as shelters from unfavourable conditions, including wave action (Addy & Johnson 2001), desiccation and extreme temperatures (Minton & Gochfeld 2001). The availability of such refuges has been experimentally shown to control the local abundance of littorinid snails (Emson & Faller-Fritsch 1976, Raffaelli & Hughes 1978, Menge et al. 1983). The use of shelters is, however, incompatible with foraging for food, since these snails graze on the microscopic flora that lives on exposed rock surfaces

(i.e. epilithic microalgae). The high densities of snails in crevices probably lower the food availability in the area immediately adjacent to shelters, and, thus, because littorinid snails graze as they crawl (Norton et al. 1990), our working assumption is that snails that move greater distances are better able to acquire food, both by grazing a greater area of the rock surface and by increasing the probability of encountering ungrazed areas. In addition, movement could also be related to reproductive behaviour such as searching for mates. Assortative mating for size or phenotype has been described for littorinids, and males may actively search for females with specific characteristics (Saur 1990, Takada & Rolan-Alvarez 2000). Thus, a trade-off between maximising access to food resources or mates and minimising exposure to abiotic stressors should exist.

Here, we assess the behavioural activity of the littorinid snail *Littorina saxatilis* (Olivi), a common marine intertidal grazer, across a range of the physical conditions experienced during high tide, the most important period of activity for this species at our study site (Pardo & Johnson 2004). In particular, we quantified the relationship between activity and various measures of key environmental factors to test the hypothesis that activity decreases with increasing severity of environmental stressors. We further predicted that there would be high intra-population variability in activity because this species is ovoviviparous, i.e. internal fertilisation results in embryos that are retained by the female in an internal brood pouch until juveniles are released as a crawling stage (Reid 1989). In particular, we wanted to test the hypothesis that gravid females would exhibit more 'risk-avoidance' behaviours (i.e. reduced displacements and increased shelter use) relative to non-gravid females and males. Specifically, we asked the following questions: (1) Is the activity of snails correlated to environmental conditions? (2) Is the response of males different from that of females? (3) Among females, do gravid females differ relative to non-gravid females? (4) Among gravid females, are responses related to fecundity? To evaluate these questions, we determined the distance of excursions and the degree of shelter use of different reproductive groups (males, non-gravid females and gravid females) over a range of environmental conditions.

## MATERIALS AND METHODS

The study was conducted in the intertidal zone at Pointe-Mitis (48° 41' N, 67° 02' W), located in the St. Lawrence maritime estuary, Québec, Canada. This site is an extensive rocky shore with a series of prominent rock ridges running parallel to the shoreline. The surface of these ridges is smooth except for occasional

shallow crevices (<3 cm deep). The herbivorous snail *Littorina saxatilis* is the most commonly observed invertebrate grazer and is distributed across the entire intertidal zone, with highest abundance in the mid-intertidal zone (Pardo & Johnson 2005). Snails in this zone are most active during the period of high tide and can move over a metre per day (Pardo & Johnson 2004). They often use surface irregularities as shelters from wave forces (Addy & Johnson 2001), but there is no evidence for any homing behaviour (Pardo & Johnson 2004). Due to the intense ice scouring at this site, the rock surface outside of crevices is generally devoid of organisms, except for foraging snails and epilithic microalgae (Lamontagne et al. 1989), the snail's principal food in the mid-intertidal zone (Konan et al. 1992). Ephemeral algal mats (primarily filamentous green algae) can form seasonally in areas of greater wave exposure where foraging by snails is reduced (Addy & Johnson 2001), but organisms common on more temperate shores (e.g. barnacles, mussels and perennial seaweeds) only occur in areas protected from ice scour, such as the base of rock ridges and between boulders.

Two north-facing rock walls, 2 m in height and of similar topography, were selected in the mid-intertidal zone. Snails were marked individually using bee tags and a fast-setting epoxy glue. To minimise disturbance, marking was done *in situ* without dislodging the snails. Two behavioural responses were then recorded during the subsequent period of immersion (henceforth referred to as 'high tide'): movement and the use of shelters. To estimate the movement of each individual during high tide, its Cartesian location was determined just before the site was submerged by the incoming tide and immediately after it was exposed by the receding tide by measuring the linear distance between the snail and 2 fixed reference points (screws set into the rock) separated by 40 cm. The distance between the 2 locations (i.e. the net distance displaced, NDD) was determined by triangulation (Underwood 1977). Whereas NDD is the measure of the minimum distance potentially moved by the snail (i.e. straight-line distance) and thus undoubtedly underestimates the actual distance displaced, it is likely to be positively correlated with the actual distance displaced (Pardo & Johnson 2004). The location of snails vis-à-vis shelter use (i.e. inside or outside of crevices) was also recorded before and after high tide. We interpret the use of crevices as a refuge-seeking behaviour and the use of exposed rock surfaces as a foraging or searching behaviour. This site was positioned in the middle of the cross-shore gradient of wave forces, where snails are regularly found both inside and outside of shelters during low tides. At lower, more wave-exposed levels, most snails are found in shelters, whereas, at higher levels on the shore, most snails are found outside of

shelters (Addy & Johnson 2001). Wave forces (see below) on the 2 walls were generally below the threshold value above which snails are mostly found within shelters (Addy & Johnson 2001). Tethering experiments at this site suggest that wave forces are a considerable risk to littorines (Pardo & Johnson 2005).

Six environmental variables that might potentially be related to the activity of snails were also measured or estimated during each behavioural trial: (1) water flow, (2) maximum wave force, (3) wind speed, (4) water temperature, (5) tidal height and (6) snail density. An index of water flow (the integrated measure of the average hydrodynamic conditions) was calculated from the dissolution of 4 plaster cylinders positioned at the corners of the rock wall using the normalised change in mass ( $[\text{initial dry weight} - \text{final dry weight}] / \text{initial dry weight}$  standardised for a 6 h period; Thompson & Glenn 1994). Mean index values ranged from 0.08 to 0.26 for the various trials, well within the range in which water flow and dissolution are linearly related (Thompson & Glenn 1994). Maximum wave force, the extreme hydrodynamic condition with respect to dislodgment, was estimated using simple force transducer devices (Bell & Denny 1994) placed at the top and bottom of walls as well as in the middle of an adjacent rock wall (we did not measure wave force in the middle of the experimental rock wall because the mechanism of the transducer might have disturbed the snails). Data from all positions were averaged to obtain a mean maximum wave force per rock wall per trial. This measure provides only a relative estimate of the hydrodynamic environment and not the actual drag force experienced by the snails. Average wind speed during the high-tide period, a proxy for general wave action at this location (because there is no oceanic swell, waves are formed principally by wind surface shear), was obtained from a meteorological station located 50 m from the study site. Tidal amplitude, a measure of lunar rhythmicity that is known to affect snail feeding behaviour (Hawkins & Hartnoll 1983, Konan et al. 1992), was estimated from tidal tables. Water temperature was measured every 15 min by an Onset data logger located 0.5 km away. Although summer water temperature at this site (9 to 13°C) is unlikely to be stressful in itself (especially considering the more extreme air temperatures experienced during low tide), temperature can affect a number of physiological processes that might influence behaviour. Finally, in addition to these physical variables, the local density of snails was measured in 5 permanent  $10 \times 10 \text{ cm}^2$  quadrats positioned systematically on the wall rock (centre and 4 corners).

These dependent and independent variables were recorded for a total of 30 high tides between June and August 2001, with trials alternating between the 2 rock

walls. Because the duration of the high tide varied from 5 to 7 h, NDD was standardised to a 6 h period, the average length of the high tide at this tidal height. For each trial, 50 snails were marked during the low tide. The choice of snails was haphazard except that we only selected snails >4 mm in shell length (the approximate size of sexual maturity for this population; Pardo 2004), and we attempted to choose snails equally from crevice and exposed rock surfaces. Individuals recovered at the end of the trial were collected and dissected to determine shell length (the maximum dimension along the axis of the shell), sex and reproductive condition (i.e. gravid females, non-gravid females and males). In the case of gravid females, the embryos in the internal brood sac were counted. Snails showing signs of parasitism (i.e. castration, reduced penis size; generally <6% of all individuals) were not used in the analyses, as this condition can drastically modify behaviour (Levri & Lively 1996, Levri 1998). Removal of snails had no apparent effect on the population, since density did not decline during the experiment (data not shown).

To examine which physical and biological variables affected the movement of snails in each reproductive group, a forward stepwise multiple regression analysis was performed (Hair et al. 1998) for each reproductive group. The significant factors affecting NDD were then used as covariates for an ANCOVA (analysis of covariance), in which walls were treated as a random factor and reproductive group as a fixed factor. Size was not, however, used as a covariate, since there is no effect of size on NDD above a shell length of 4 mm (Pardo & Johnson 2004). In the initial analysis, a saturated model was run, and interactions between independent variables and covariates were not significant ( $\alpha > 0.25$ ). They were thus eliminated from the final analysis. Natural-log transformation of NDD was required to meet the assumption of homogeneous variances and of linearity between covariates and NDD. Because the individuals were selected randomly from the same population, the ANCOVA could be interpreted despite the fact that covariates were random and measured with error (Huitema 1980).

As for the analyses of NDD, the relationship between snail location at the end of high tide (i.e. shelter use) and the independent environmental variables was analysed with a forward stepwise multiple regression analysis for each reproductive group. In spite of the fact that the variable response was binomial (inside or outside of shelters), we used a multiple linear regression rather than a logistic regression given that a binomial distribution approaches a normal distribution when the number of samples used to calculate proportions is high (Hair et al. 1998). In this case, we used 39 to 50 individuals for each trial (sample sizes varied

depending on the success of recovering marked snails) to calculate the proportion of individuals using shelters, which approximated a normal distribution. We also compared the reproductive condition of snails located in shelters at the start of high tide with those in shelters at the end of high tide using a 2-way ANOVA (analysis of variance). Given that measurements of a single individual at the start and the end of high tide cannot be considered independent, snails were randomly separated into 2 groups: one for the start and the other for the end of high tide. In addition, data were arcsine transformed to insure homogeneous variances for the ANOVA (Underwood 1997).

The relationship between brood size and movement of gravid females was evaluated with Spearman correlations between fecundity (number of embryos per female) and NDD for each trial. To avoid any effect of body size, a well-recognised covariate of fecundity in marine invertebrates (Ramirez Llodra 2002), we restricted our analysis to data from gravid females between 5.5 and 6.5 mm in shell length (44% of total gravid females recovered). Only trials in which there were at least 8 gravid females (21 out of 30) were used. We also examined reproductive output (i.e. mass-specific fecundity) to control for any effect of size, but results were similar to those using the restricted size class and are thus not shown. Dry weight of individuals was estimated from a regression between shell length (SL, in cm) and the tissue dry weight (DW, in mg):  $DW = 0.48 SL^{2.6}$ ,  $r^2 = 0.95$ ,  $n = 65$ .

To further evaluate the relationship between shelter use, individual size and brood size, gravid females were separated into 4 subgroups according to their location at the start and end of high tide: individuals sheltered in crevices at both the start and end of high tide ('always sheltered'); individuals in crevices at the start of high tide, but foraging at the end of high tide ('sheltered then foraging'); individuals foraging at the start of high tide, but in crevices at the end of high tide ('foraging then sheltered'); and individuals foraging at both the start and end of high tide ('always foraging'). A multiple discriminant analysis was used to determine if individuals belonging to a specific behavioural group differed in either size or fecundity. Differences were tested with the square of the Mahalanobis distance ( $D^2$ ) between groups (centroids). The discrimination power of size and fecundity was assessed using the Wilk's lambda criterion (Hair et al. 1998). This analysis was selected over a more classic ANOVA approach due to the categorical nature of the dependent variable and the continuous or quasi-continuous nature of the independent variables. In other words, we examined if fecundity and size influenced the shelter-use behaviour of gravid females rather than if different behavioural groups had different fecundity or size.

Table 1. Mean values (SD) for 5 physical factors, *Littorina saxatilis* density and net distance displaced (NDD) by snails during high tide for trials conducted at 2 intertidal rock walls (n = 15 dates for each wall). Statistical comparisons (p) performed with Student's *t*-test

	Water flow (index)	Max. wave force (N)	Wind speed (m s <sup>-1</sup> )	Temp. (°C)	Tidal height (m)	Density (ind. m <sup>-2</sup> )	NDD (cm)
Wall 1	0.17 (0.05)	3.4 (1.6)	3.0 (1.9)	11.4 (1.4)	3.6 (0.3)	29 (14)	33 (8.8)
Wall 2	0.16 (0.03)	3.7 (1.7)	3.3 (1.1)	11.2 (1.0)	3.5 (0.3)	58 (15)	30 (18.8)
p	0.65	0.66	0.59	0.94	0.89	<0.01	0.48

## RESULTS

For the 30 trials, a mean of 89.9% (SD = 7.9) of the snails was recovered at the end of high tide. Of the recovered individuals, 44% (SD = 7) were gravid females, 14% (SD = 5) were non-gravid females and 42% (SD = 9) were males. The physical factors identified as significant in preliminary analyses (water flow and maximum wave force) were similar for the 2 rock walls studied (Table 1), and neither exhibited any temporal tendencies (Pardo 2004).

Most snails changed locations during the high-tide period, with an average NDD > 30 cm (Table 1) for those that moved (i.e. NDD > 1 cm, the precision of the triangulation method). Overall, NDD was much greater (40% on average) for males than for females, especially gravid females. Adjusted means of NDD varied significantly among reproductive groups (Table 2, Fig. 1). A Tukey HSD post hoc test indicated that the differences between males and gravid females were significant and between non-gravid and gravid females nearly significant at the alpha = 0.05 level (Table 2). Significant relationships between one or more physical variables and NDD were seen in the multiple regression analyses for the different reproductive groups (gravid females:  $F_{3,26} = 7.33$ ,  $p < 0.001$ , adjusted  $r^2 = 0.47$ ; non-gravid females:  $F_{1,18} = 5.58$ ,  $p < 0.05$ , adjusted  $r^2 = 0.19$ ; and males:  $F_{2,27} = 12.07$ ,  $p < 0.001$ ; adjusted  $r^2 = 0.43$ ; Table 3). Water flow was clearly the most important physical factor influencing the NDD of snails for all reproductive groups, whereas wave force was of secondary importance for males and gravid females. NDD de-

Table 2. *Littorina saxatilis*. Results of analysis of covariance and post hoc Tukey tests of honestly significantly differences (HSD) for unequal sample number testing of the net distance displaced for 3 different reproductive groups (RG). Covariates are water flow and maximum wave force. Data were ln-transformed before analysis (GF: gravid females; NGF: non-gravid females)

Source of variability	df	MS	Error	F	p
Water flow	1	2.05	0.18	11.7	<0.001
Maximum wave force	1	0.53	0.18	3.03	0.08
Wall	1	0.02	0.05	0.4	0.59
Reproductive group	2	2.05	0.05	39.2	0.025
Wall × RG	2	0.05	0.18	0.3	0.74
Error	71	0.18			
Tukey HSD test					
	NGF	vs.	Males		0.26
	GF	vs.	Males		<0.001
	GF	vs.	NGF		0.07

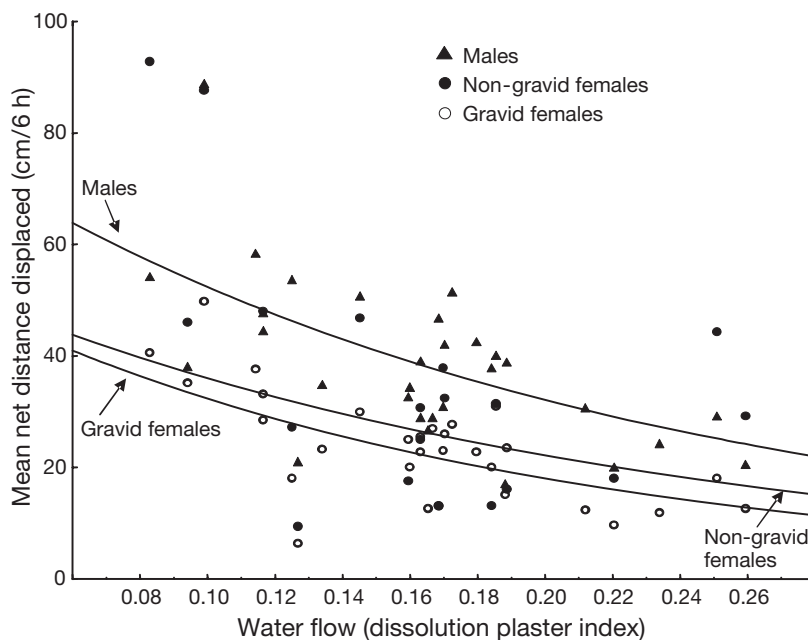


Fig. 1. *Littorina saxatilis*. Relationship between water flow and net distance displaced (NDD) for different reproductive groups. Each point represents the mean NDD and the mean water flow index (n = 4) for 1 of 30 trials. When a reproductive group included <5 individuals for a given trial, it was not included in the analysis



Table 3. *Littorina saxatilis*. Multiple regression of the net distance displaced (NDD) by snails and physical and biological variables. Variables not included in equations for forward stepwise method: wind, temperature, tide height and density. Critical tolerance = 0.1

Reproductive condition	Independent variables	Partial correlation	Beta	SE	p
Non-gravid females	Water flow	-0.49	-0.49	0.21	0.03
Gravid females	Water flow	-0.54	-0.53	0.17	<0.01
	Maximum wave force	-0.32	-0.25	0.15	0.10
Males	Water flow	0.32	-0.46	0.12	0.01
	Maximum wave force	0.15	-0.32	0.15	0.04

creased exponentially with water flow for all reproductive groups (Fig. 1). The absence of any significant interaction (i.e. parallel slopes of the regression lines of transformed data, not shown) between reproductive condition and covariates in the ANCOVA indicates that the NDD of all reproductive groups was affected in a similar way by water flow and maximum wave force.

Shelter use by different reproductive groups was different at the start of high tide, with a higher proportion of females than males in shelters (Fig. 2). In contrast, at the end of high tide, there were no differences among the 3 groups, as the proportion of females inside the shelters decreased to the level seen for males (Fig. 2, significant statistical interaction between tidal period and reproductive condition,  $F_{2,74} = 4.44$ ,  $p < 0.015$ ). The multiple regression between the proportion of individuals in shelters at the end of the high tide and environmental variables was only significant for gravid females (gravid females:  $F_{5,24} = 3.81$ ,  $p < 0.011$ , adjusted  $r^2 = 0.33$ ; non-gravid females:  $F_{5,15} = 1.33$ ,  $p > 0.25$ , adjusted  $r^2 = 0.07$ ; males:  $F_{5,24} = 0.63$ ,  $p > 0.25$ ; adjusted  $r^2 < 0.01$ ). Maximum wave force was the only in-

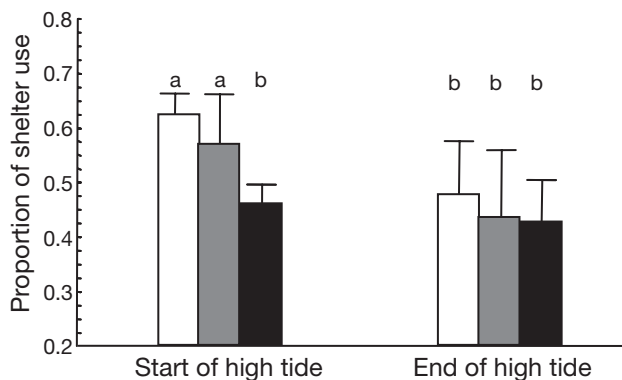


Fig. 2. *Littorina saxatilis*. Mean (+SE) of the proportion of shelter use at the start and the end of high tide (ANOVA interaction between reproductive group and time,  $p = 0.015$ ) (open: gravid females; grey: non-gravid females; black: males)

dependent factor retained in the model, with a clear positive relationship between the proportion of gravid females in shelters and the maximum wave force (Fig. 3).

The mean brood size was 35 (SD = 18;  $n = 502$ ) embryos, and the mean reproductive output was 2.1 (SD = 0.9) embryos  $\text{mg}^{-1}$ . Spearman correlations between fecundity and NDD were only significant in 2 trials out of 21, 1 negative and 1 positive correlation, which most likely represent spurious correlations. Discriminant analysis of shelter

use by gravid females showed that different shelter-use groups were of a similar size and fecundity, except for the extreme comparison between snails that always took shelter and those always foraging (Fig. 4,  $D^2 = 1.22$ ,  $p < 0.01$ ). This difference was due to fecundity (Wilk's lambda = 0.94;  $p = 0.02$ ) and not to size (Wilk's lambda = 0.89,  $p = 0.27$ ) with the fecundity of the always sheltered group being 16 to 28% greater than that of the other 3 foraging groups.

## DISCUSSION

The hydrodynamic environment is clearly an important factor constraining the activity of these snails. These results are consistent with previous studies of behaviour in this species (Addy & Johnson 2001) and other aquatic organisms (Hawkins & Hartnoll 1983, Judge 1988, Heggenes 2002), where activity generally decreases with increasing water flow. Surprisingly, the density of conspecifics had little or no effect on activity, unlike observations in other systems, especially vertebrates (Metcalf & Gochfeld 2001). Thus, direct or indirect interactions (e.g. trail-following; Erlandsson & Kostylev 1995) do not appear to influence the behaviour we observed. Although the presence of predators can affect the behaviour of snails, known predators of littorinid snails, such as crabs, fish and birds (Rochette & Dill 2000, Boulding et al. 2001), were rarely observed at our site, and we have seen no evidence of crab or fish predation (Pardo & Johnson 2005).

The hydrodynamic environment is often invoked to explain patterns in the structure and organisation of marine nearshore communities (Menge et al. 1994), but our understanding of the quantitative relationship between the biological and the physical environment is often limited by a reliance on the investigator's impression of 'wave exposure', a subjective term that provides at best only ordinal data (Bell & Denny 1994). In our case, we were able to determine more precisely the nature of the relationship between the physical

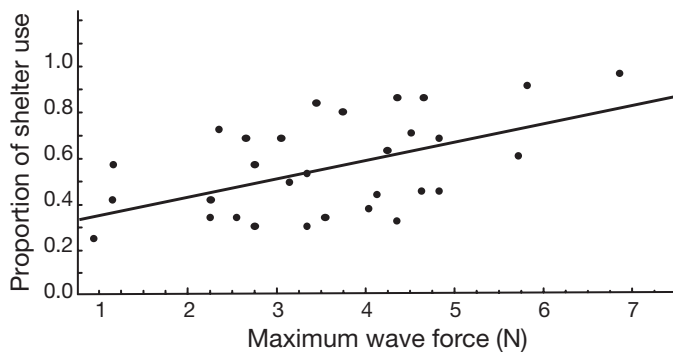


Fig. 3. *Littorina saxatilis*. Relationship between the proportion of shelter use at the end of high tide for gravid females and relative maximum wave force during high tide

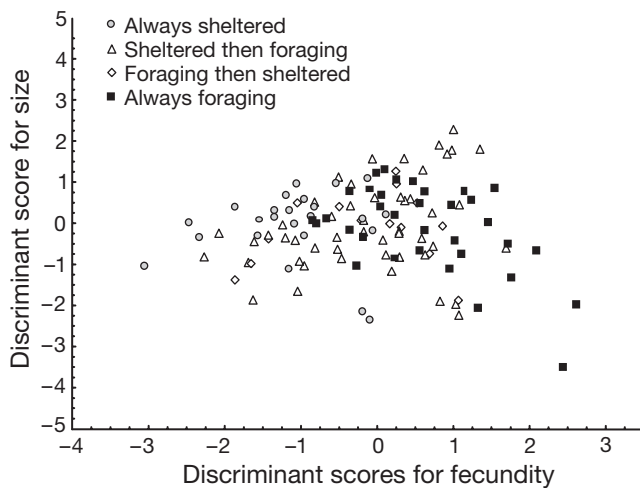


Fig. 4. *Littorina saxatilis*. Discriminant analysis function of gravid females grouped according to 4 shelter-use behaviours. A significant difference was observed between 'always sheltered' and 'always foraging' groups of snails,  $D^2 = 1.22$ ,  $p < 0.01$

environment and the behaviour of the snails by quantifying different elements of the hydrodynamic environment (i.e. water flow and maximum wave force). Still, an exact interpretation of the cause and effect nature of this relationship is difficult, because water flow is an integrative measure of the hydrodynamic environment that includes water velocity, oscillatory motions and turbulence, which can all be influenced by wave action. Indeed, water flow and maximum wave force were positively correlated (data not shown). Regardless, we have interpreted shelter use as an avoidance of the risk of dislodgment as it was better explained by maximum wave force. In contrast, the decreased NDD at higher water flow may represent a reduction in crawling speed in response to increases in drag forces, which can dislodge the snail or increase the energetic cost of displacement. Differentiating between these 2 possibilities will eventually be important as the consequences are quite different: dislodg-

ment may result in death, whereas increased energetic costs may only have a marginal effect on performance (e.g. growth).

Variation of behaviour with physical conditions is not, in itself, surprising. The more interesting question concerns the plasticity of the behavioural response. Most previous studies have relied on site-to-site comparisons along a gradient of the physical factor of interest (e.g. 'exposed' vs. 'protected' sites), which are often located far from each other. Whereas such comparisons can reveal striking differences in behaviour (e.g. Boulding & Van Alstyne 1993, Chapman 1998) and morphology (Boulding et al. 1999), the results can be difficult to interpret due to the confounding factor of local acclimation or adaptation (Trussell 2000). The limited dispersal in this species should permit local adaptation, and such divergence has already been observed elsewhere in this species (Johannesson 2003). In our study, we examined temporal variations in both the physical environment and the behaviour of snails exposed to varying conditions during their lifetime at a single site and demonstrated that at least a part of the variation in behaviour was due to phenotypic plasticity. However, given the restricted spatial and temporal domain of our study, care should be taken in extrapolating our results to other systems.

The above discussion addresses extrinsic factors, but intrinsic sources of variation were also evident as the effect of physical conditions on foraging activity depended on the reproductive condition of individuals. Although water flow had a general overall negative relationship with NDD for all groups, gravid females showed a consistent reduction in displacement relative to males. Because of the intimate link between the fate of gravid females and their offspring (Trivers 1974), we would expect them to exhibit risk avoidance, because any lethal or sublethal effect of the physical environment could lead directly to the death or damage of offspring. This difference is consistent with the asset-protection principle (Clark 1994) and with studies of other taxonomic groups, in which a negative relationship between foraging time and offspring survival has been observed (Smith 1976, Smith & Wootton 1995, Crump 1996). However, most these other studies involved nesting species in which individuals are spatially constrained to a single location, whereas this study concerns an ovoviviparous species.

Alternatively, greater NDD by males could represent additional movement associated with seeking mates, since mating and foraging are generally mutually exclusive activities (Blanckenhorn & Viele 1999), although contact with mates might not be limiting given

the high local density of snails. The intermediate level of NDD by non-gravid females suggests, however, that the difference between males and females is not strictly due to mating efforts, and their high individual variability (i.e. greatest value of residuals in regression analysis) may reflect both females replenishing their energy reserve after brooding (i.e. high energetic needs) and females just before egg maturation (i.e. low energetic needs). Indeed, the lower NDD by gravid females could simply reflect lower energetic needs, but the effects of water movement on NDD and shelter use (see below) clearly demonstrate that snails would increase their activity if conditions permitted. Nevertheless, additional information on their reproductive physiology (e.g. when energetic needs are greatest during the reproductive cycle) would help in our interpretation of female behaviour.

Differences in shelter use among the reproductive groups were consistent with the idea of risk avoidance by females as they use crevices more often than males, at least at the start of high tide. In this case, however, females exhibited this behaviour regardless of their reproductive condition. Thus, it appears that there is a differential movement of females toward crevices during low tide (due perhaps to a negative effect of air temperature or desiccation; gravid females were the only group in which NDD was negatively correlated with air temperature during low tide; Pardo & Johnson 2004). The equal proportion of males and females in shelters at the end of high tide suggests that, overall, females are more likely to leave shelters while immersed, but because shelter use increased with increasing wave force for gravid females, they apparently left shelters mostly when hydrodynamic conditions were calmer. Finally, among gravid females, individuals with a higher number of embryos appear to remain in shelters, suggesting that those snails with more to lose are those more likely to avoid risk (i.e. risk aversion). Thus, several lines of evidence support the idea that females, especially when gravid, alter their behaviour to reduce exposure to stress or danger. Alternatively, lower activity in gravid females could be explained by anatomical or physiological constraints of brooding embryos internally (e.g. higher energetic cost of movement). However, if this were the case, distance moved would be expected to be negatively related to the number of embryos carried by females (i.e. fecundity). This was not the case, because only 2 of out 21 correlations were significant, a number expected by chance alone.

Given that time and energy are limited, individuals are forced to make trade-offs to achieve a balance among survival, reproduction and growth (Roff 1992, Werner & Anholt 1993). Different components of a population may, however, have different fitness-maximising strategies and thus exhibit alternative

choices for these trade-offs (Trivers 1974). In the present study, gravid females appear to consistently avoid risk more than males and non-gravid females, both in having shorter excursions under all conditions of water flow and in being the only group in which shelter use depended on the maximum wave forces. These data support the idea that females should change their behaviour during gestation of their young as the balance shifts from maximising the benefits of foraging to minimising the risk of dislodgment. Thus, variability in activity patterns of individual *Littorina saxatilis* may be due to alternative fitness strategies for different groups of the population in response to a given set of abiotic conditions. Similar behavioural variability has been seen in several other aquatic animals. For example, when compared to males, brooding females of the isopod *Idotea baltica* decreased movements and selected a microhabitat with a lower risk of predation (Jormalainen et al. 2001). Brooding males of the water bug *Abedus herberti* did not forage when they were carrying embryos (Smith 1976), and brooding females of the hermit crab *Pagurus bernhardus* minimised exposure to predation by reducing the frequency of shell-changing behaviour relative to both males and non-gravid females (Neil & Elwood 1985). However, given the inherent variability of the physical environment, organisms should maintain a certain level of behavioural plasticity in response to this variation. Thus, an interplay exists between the effects of the physical environment and the intrinsic attributes of the individual; this is ultimately manifested in the individual's precise behavioural response.

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