ELSEVIER

In Collaboration with
the Netherlands Institute for Sea Research

JOURNAL OF SEA RESEARCH

Journal of Sea Research 49 (2003) 119–132

www.elsevier.com/locate/seares

# The effect of life-history variation on the population size structure of a rocky intertidal snail (*Littorina sitkana*)

Rémy Rochette[a,b,*], Karen Dunmall[c], Lawrence M. Dill[d]

[a] *Simon Fraser University, Burnaby, BC, Canada V5A 1S6*
[b] *Bamfield Marine Sciences Centre, Bamfield, BC, Canada V0R 1B0*
[c] *Department of Biology, University of Waterloo, Waterloo, ON, Canada N2L 3G1*
[d] *Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6*

Received 15 May 2002; accepted 1 October 2002

**Abstract**

On wave-sheltered shores of the northeastern Pacific, the population size structure of *Littorina sitkana* varies with intertidal height, as larger snails are mostly found only in the upper intertidal. This pattern has been attributed to high predation rates by crabs (and perhaps fish) on large snails inhabiting low-intertidal areas; i.e., large snails are presumed to be rare there simply because predators kill them. In this study we investigate the hypothesis that predation contributes to the shore-level size gradient displayed by *L. sitkana* by selecting for (or inducing) earlier sexual maturation and reduced somatic growth in low-shore snails relative to high-shore individuals.

In the first part of our study, we carried out laboratory dissections, field experiments (mark-release-recapture and caging), and field surveys on a wave-protected shore in Bamfield Inlet, Barkley Sound (British Columbia, Canada). The principal results were: (1) adult survivorship was greater at higher, than at lower, intertidal level, (2) snails displayed a preference for their shore level of origin, (3) immature adults from the high intertidal displayed greater rates of somatic growth relative to immature adults from the low intertidal, and (4) low-shore snails matured at a smaller size than high-shore individuals. In the second part of the study, a large-scale survey showed intra-specific variation in size at sexual maturity (point 4 above) to be relatively consistent over time (winter of 1999 and 2001 for snails from our main study site) and space (13 different sites in winter 2001), although the magnitude of these differences varied greatly from shore to shore.

Our results indicate that *L. sitkana* individuals inhabiting upper and lower parts of their intertidal range allocate resources differently to somatic and gonadal growth, an intra-specific difference that is best interpreted as a response to spatial and size-dependent variation in predation pressure. Taken together, results of this and other recent studies indicate that phenotypic responses to contrasting selection pressures operating in upper- and lower-intertidal areas contribute to the intertidal size gradient of *L. sitkana*. We believe that greater consideration of evolutionary processes in ecological studies will lead to a more complete understanding of the mechanisms responsible for structuring marine coastal communities.


*Keywords:* Intertidal ecology; Life-history theory; Predation pressure; Population demography; *Littorina sitkana*; Bamfield, British Columbia; Northeastern Pacific

* Corresponding author. Current address: Department of Biology, University of New Brunswick, P.O. Box 5050, Saint John, NB, Canada E2L 4L5.

*E-mail address:* rochette@unbsj.ca (R. Rochette).

1385-1101/02/$ - see front matter © 2002 Elsevier Science B.V. All rights reserved.
doi:10.1016/S1385-1101(02)00217-4

## 1. Introduction

Many species of intertidal gastropods display vertical size gradients, whereby mean shell length or body mass varies with height in the intertidal zone (see review by Vermeij, 1972). This is true of the littorinid snail *Littorina sitkana*. On wave-sheltered shores of the northeastern Pacific, larger *L. sitkana* snails are found in upper, than in lower, parts of the species' intertidal range (McCormack, 1982). Three independent studies that have quantified predation patterns on these shores (McCormack, 1982; Behrens Yamada and Boulding, 1996; Rochette and Dill, 2000) suggest that this vertical size gradient is largely due to predators, because predation rates are much greater in lower- than higher-intertidal areas, and on large than on small individuals. McCormack (1982) proposed that the pile perch *Rhacochilus vacca* was responsible for most of this mortality, but more recent studies indicate that the red rock crab *Cancer productus* is probably the most important predator of adult snails on these shores (Behrens Yamada and Boulding, 1996; Boulding et al., 1999; Rochette and Dill, 2000). Because *C. productus* only forages when submerged, making shoreward foraging excursions when the tide is high (Robles et al., 1989), it kills many more snails in lower than in upper parts of the intertidal (Behrens Yamada and Boulding, 1996; Rochette and Dill, 2000). Furthermore, laboratory experiments (Behrens Yamada et al., 1998) have shown that adult *C. productus* preys more heavily on larger *L. sitkana*.

Whoever the culprit, spatial and size-dependent patterns of predation are at least partly responsible for the scarcity of large adult snails in low-intertidal areas. The hypothesised mechanism of demographic control involves differential survival of same-phenotype *L. sitkana* snails inhabiting different shore levels. In other words, large snails are presumed to be rare at low-shore levels simply because predatory crabs kill them when they are in these areas. However, predation may also 'indirectly' contribute to this shore-level size gradient, by selecting for (or inducing) earlier sexual maturation and reduced somatic growth in low-shore snails (i.e., those in high-risk areas) relative to high-shore snails. Such a phenotypic response is predicted by life-history theory, which holds that under conditions of reduced adult survival, phenotypes will be favored that are capable of reproducing earlier, at a smaller size and with a greater reproductive effort (Stearns, 1976). Such patterns of phenotypic variation, which have been documented for a variety of aquatic organisms (see Discussion), may result from genetic adaptation to contrasting selective pressures (e.g., Reznick and Bryga, 1996), or the capacity of a single genotype to produce different phenotypes when exposed to different environments (e.g., Crowl and Covich, 1990). *L. sitkana* undergoes 'direct' benthic larval development, and hence experiences relatively limited larval dispersal, which is expected to be conducive to genetic differentiation over small spatial scales (e.g. see McQuaid, 1996; De Wolf et al., 1998).

In the first part of this study, we investigated the hypothesis that life-history variation between high-shore and low-shore snails contributes to the shore-level size gradient observed in *L. sitkana*. We carried out a number of field experiments and surveys to assess mortality, movement, growth and sexual maturation of high-shore and low-shore snails on a wave-protected shore in British Columbia, Canada. The main predictions we aimed to test were that: (1) adult mortality is greater at lower, than at higher, intertidal level, (2) immature adults from the high intertidal display increased rates of somatic growth relative to immature adults from the low intertidal, and (3) low-shore snails mature at a smaller size than high-shore individuals. We also quantified the movement patterns of snails to assess their 'fidelity' to different shore levels. In the second part of the study, we assessed the consistency of intra-specific variation in life history by re-surveying the same shore in a different year, and surveying for the first time an additional 12 sites.

## 2. Study area and methods

We conducted our study between October 1998 and January 2001 in Bamfield Inlet (48°50′, 125°08′), Barkley Sound (British Columbia, Canada), northeastern Pacific (see map in Boulding et al., 1999). On these wave-sheltered shores, *L. sitkana* generally thrives between approximately 1 and 3 m above 0 datum (Canadian Hydrographic Service), occurring on barnacle-covered cobbles and oyster shells in the lower intertidal (ca. 1–2 m), and on

boulders and bedrock colonised by the brown algae *Fucus distichus* in the upper intertidal (ca. 2.5–3 m) (Rochette and Dill, 2000).

Our main study site was 6 m wide (parallel to water) by 13 m long (perpendicular to water, between ≈ 1 and 3 m in intertidal height). The majority of snails used in the study were randomly collected from this site, either from the 'barnacle zone', between 1.2–1.6 m (henceforth 'low-shore' snails or habitat), or from the '*Fucus* zone', between 2.5–3.0 m (henceforth 'high-shore' snails or habitat). In the last part of the study, however, we assessed the relationship between size and sexual maturation for low-shore and high-shore snails from an additional 12 similar shores within Bamfield Inlet. All snails used in this study were randomly collected from a 6 m (parallel to water) × 2 m (perpendicular to water) sampling area of a particular high-shore or low-shore site; we collected snails inside 10 × 10 cm quadrats, which were randomly positioned in the sampling areas using a random number generator (x and y coordinates ± 1 cm).

### 2.1. Field snails: mark-release-recapture experiment

We conducted a mark-release-recapture experiment spanning 32 days to compare the behaviour and mortality of high-shore and low-shore snails released at both intertidal levels. On 30 October 1998, we haphazardly collected 100 *L. sitkana* snails measuring 4.5–5.5 mm in shell length from each of the high- and low-shore levels of our principal study site; we measured the maximum shell length of each snail to the nearest 0.01 mm using Fowler Ultracal II digital calipers. In order to facilitate snail recovery and identification, we then individually marked each snail's shell with enamel-based spray paint and Blue-strip™ numbers. We painted high-origin snails fluorescent green and low-origin snails fluorescent orange. The snails were then held in flowing seawater until they were returned to the field 6 d later.

To facilitate quantification of snail movement, we used monofilament (800 μm diam.) line to divide the study area into 13 quadrats, each 1 x 6 m with the longest side parallel to the water. On 6 November 1998, we returned 100 high-origin and 100 low-origin snails to both intertidal heights. Snails released in the high- and low-intertidal areas were placed in the middle of the recapture area at the 2.8 and 1.5 m levels, respectively. We released high- and low-shore snails such that both had approximately 3 h before being submerged by the incoming tide.

After releasing the snails, we conducted three recapture sessions each separated by 9–10 d. Tidal anomalies due to low-pressure systems and high winds forced each recapture session to span two days. In addition, in order to finish the second recapture, we had to use snorkeling gear to search the three lowest quadrats. We recorded the identity of each recaptured snail by noting its colour and tag number. For the first two recaptures, snails found within a quadrat were collected in a small plastic vial until the entire quadrat was searched, and they were then replaced in the middle of the quadrat. This ensured that the snails were not crushed as the quadrat was being searched, and it reduced the horizontal migration of snails out of the search area. During the final recapture, we used an ultraviolet light to find as many snails as possible. We increased sampling effort for the last recovery because preliminary analyses had revealed variable (high confidence intervals) estimates of mortality due to relatively low recovery rates.

#### 2.1.1. Statistical analyses

We used MARK, a statistical package designed to analyse data from mark-release-recapture experiments, to compare survivorship of snails at high- and low-intertidal levels within our study site. The difficulty inherent in a mark-release-recapture experiment is that animals not found could be either dead, alive and in the search area (i.e., missed by the observer), or alive and outside the search area. By considering the entire recovery history, MARK estimates the probability (and associated confidence intervals) that animals of a given treatment survive and remain within the search area between recovery sessions.

We used a Mann-Whitney U-test (with $\chi^2$ approximation) to compare the movement (i.e., position at last recovery) of high-origin and low-origin snails released at a given tidal level. We used a non-parametric test for these comparisons because variances were heterogeneous; all snails moved relatively little when released at their original shore-level, but several made long migrations when released at a foreign shore level.

### 2.2. Field snails: growth experiment

Between 6 and 8 November 1998, we randomly collected 120 high-shore and 120 low-shore snails measuring 3.7–4.7 mm in shell length. *L. sitkana* is reported to attain sexual maturity at about 4.7 mm in shell length (Reid, 1996), so we expected most of these snails to be sexually immature. We measured the maximum shell length of each snail to the nearest 0.01 mm, and marked each individual using Bluestrip™ numbers epoxy-glued to the shell.

On 9 November 1998, 12 cages (20 × 14 × 14 cm) with 1-mm mesh screen on their sides were placed in the field, 6 in the high (ca. 2.8 m) and 6 in the low (ca. 1.4 m) intertidal regions. Three cages at both intertidal heights each received 20 low-origin snails, and the other three received 20 high-origin snails. The 12 cages were half-filled with substrate mimicking the natural microhabitat of snails at each tidal level (i.e., we put small barnacle-covered rocks in the low-intertidal cages, and *Fucus*-covered pieces of [chiselled] bedrock in the high-intertidal cages).

We recovered the cages on 2 January 1999, after slightly less than 2 mo. in the field, because strong winds and unusually low temperatures had displaced some of the cages and killed many snails (particularly in the high intertidal). Upon recovery from the field, all live snails were stored in a deep-freezer to interrupt growth. They were later measured (shell length) and dissected for gender determination.

#### 2.2.1. Statistical analyses

We analysed snail growth (final minus initial shell length) with a randomised block partial hierarchical (i.e., nested) design (Kirk, 1982), using initial shell length as a covariate. We used general principles of ANOVA to build the model and determine the appropriate error terms for computation of F-ratios (see Underwood, 1997). The linear model describing snail growth is:

$$Y = \mu + O + D + G + L + C[OD] + OD + OG + DG + GC[OD] + ODG + \varepsilon$$

where $Y$ represents the predicted growth response of a particular snail; $\mu$ represents the mean growth response of all snails; $O$, $D$, and $G$, are fixed-effect factors representing snail origin, destination, and gender; $L$ represents initial shell length, which is a covariate in our model; and $\varepsilon$ represents the model residual (variability among individual snails within the same treatment). $O$, $D$, and $G$, are fully orthogonal, and therefore generate four higher-order effects (i.e., interaction terms $OD$, $OG$, $DG$ and $ODG$). $C[OD]$ represents our random-effect caging factor, which is nested within snail origin and destination. Because both genders are found in all cages (i.e., gender and cage are orthogonal), they generate a fifth interaction term, $GC[OD]$. We used the statistical software JMP® version 4.0.1 (SAS Institute, Inc.) for MS estimates, and computed F ratios from first principles (Underwood, 1997); error terms used for significance testing ($\alpha = 0.05$) of the various effects are indicated in Table 1.

We conducted several tests to determine whether our data violated model assumptions. First, the assumption that the effect of initial length (the covariate) was homogeneous among treatments (parallel slopes) was satisfactorily upheld, as the SS associated with the error term of the full model (i.e., including interaction terms involving length) did not differ significantly ($F_{7,155} = 0.93$, $p = 0.48$) from that of the reduced model (without interaction terms) (Hendrix et al., 1982). Second, we conducted a Shapiro-Wilk W test on the model's residuals, which indicated that the data did not violate the normality assumption ($N = 187$, $W = 0.98$, $p = 0.67$). Finally, we used the Box-Scheffé test, also applied to the model residuals, to examine the homoscedasticity assumption (see Kirk, 1982, p. 78–81 for computation details); variances were similar across treatment combinations ($F_{7,31} = 1.10$, $p = 0.39$).

### 2.3. Field snails: size at sexual maturation

In December 1999, we randomly collected ca. 300 snails (using 10 × 10 cm quadrats) from both the high- and low-intertidal areas. We then brought these snails to the laboratory, and dissected 110 individuals originating from each shore level; we chose these snails haphazardly to provide a wide size range.

The snails measured between 3 and 10 mm in shell length, and dissections were done under a dissecting microscope. In order to facilitate pulling snails out of their shell, they were put in boiling seawater for 5–10

Table 1
Field snails: growth experiment

| Source of variation | df | SS | Denominator of F ratio | F | p |
|---|---|---|---|---|---|
| *Between cages* | | | | | |
| Snail origin (O) | 1 | 4.422 | Cage [O, D] | 10.055 | 0.013 |
| Destination (D) | 1 | 3.377 | Cage [O, D] | 7.679 | 0.024 |
| O × D | 1 | 0.528 | Cage [O, D] | 1.201 | 0.305 |
| Cage [O, D] | 8 | 3.518 | Residual | 6.384 | <0.001 |
| *Within cages* | | | | | |
| Gender (G) | 1 | 0.338 | G × Cage [O, D] | 6.665 | 0.033 |
| O × G | 1 | 0.030 | G × Cage [O, D] | 0.594 | 0.463 |
| D × G | 1 | 0.005 | G × Cage [O, D] | 0.099 | 0.761 |
| O × D × G | 1 | 0.030 | G × Cage [O, D] | 0.594 | 0.463 |
| G × Cage [O, D] | 8 | 0.406 | Residual | 0.736 | 0.659 |
| Initial length (L) | 1 | 6.567 | Residual | 95.314 | <0.001 |
| Residual | 162 | 11.161 | | | |

Results of a randomized block partial hierarchical ANCOVA testing the effects of snail origin (high- versus low-intertidal), destination (high- versus low-intertidal), gender, and initial length on the growth of *L. sitkana* snails. In addition to standard ANOVA parameters (i.e., df, SS, F, and p), the table shows the MS error term used as the denominator to compute the various F ratios (see Underwood, 1997).

sec (depending on size) prior to being dissected (snails died almost instantly), which softened the columella muscle and weakened its attachment to the shell. We then measured the length of the snail's shell to the nearest 0.01 mm using digital calipers, pulled the snail out of its shell using a fine entomological needle (that we had curved and mounted on a stick), and assessed its gender and reproductive status.

*L. sitkana* is dioecious. Adult males possess a large penis and seminal vesicle, whereas females possess a pallial oviduct, an elaborate system of tubules and glands used for sperm reception, transport and storage, and also to encapsulate the eggs and protect the embryos (Reid, 1996). Upon dissection, each snail was classified in one of five categories: (1) juvenile, (2) immature adult male, (3) immature adult female, (4) mature adult male, or (5) mature adult female. Juveniles were snails that could not be classified as males or females, because they had not yet developed gender-specific reproductive structures. The distinction between immature and mature adults was based on the development (i.e., size and swelling) of the penis and seminal vesicle for males and pallial oviduct (particularly the jelly gland) for females. Because this assessment was somewhat subjective, we did the dissections 'blind' (i.e., R.R. did not know the origin of the snails he was dissecting).

Species of littorinids with highly seasonal reproductive activity often show a regression of reproductive structures outside the breeding season (Reid, 1996). In the northeast Pacific, *L. sitkana* reproduces year round, with peaks in egg laying activity in spring and fall (Buckland-Nicks et al., 1973; Sacchi and Voltolina, 1987; Behrens Yamada, 1989). There was no evidence of regression of sexual organs in our snails (e.g., we found a strong relationship between size and maturity status in all snail groups), and we did observe egg masses in both high- and low-intertidal parts of our study site, indicating that both snail groups were 'sexually active' when we conducted this study. Another factor that can affect maturation of reproductive organs is parasitic infection by trematodes (e.g., Huxham et al., 1993), but we found no evidence of this during this study (incidence of parasitism is very low in Bamfield Inlet; R.R. pers. obs.).

### 2.3.1. Statistical analyses

We used a multiple logistic regression model (Hosmer and Lemeshow, 2000) to investigate the effect of snail origin (high-shore or low-shore) on size at sexual maturation. We did three separate analyses, each involving shell length and snail origin as independent variables, and one of three indicators of maturity status (see below) as the dichotomous (i.e., yes or no) dependent variable. The first analysis investigated the 'size at onset of sexual maturation', and was based on all snails dissected; each individual was classified as a juvenile or an adult based on the absence/presence of sexual structures. The second and third analyses investigated the 'size at maturity' for males and females, respectively, and involved categorisation of each snail as an immature or mature adult (see above). For graphical purposes, we used the inverse prediction function to estimate the size (with 95% confidence intervals) at which 50% of snails had attained a particular maturity

status (e.g., size at which 50% of the females were judged to be sexually mature).

We analysed the maturity data with the statistical software JMP® version 4.0.1 (SAS Institute, Inc.). To assess the impact of snail size and origin on a given dependent variable, we used the Likelihood-ratio (L-R) test, which is generally considered to be more reliable than the Wald test (Agresti, 1996, p. 89). We fitted the size × origin interaction term in the initial logistic regression models, but dropped it from the three final models because it was not significant at the 0.05 level (Hosmer and Lemeshow, 2000).

### 2.4. January 2001 large-scale survey: size at sexual maturity

To investigate the consistency of phenotypic differences in size at sexual maturation between high-shore and low-shore snails, in January 2001 we re-assessed maturity status of snails from our main study site, and dissected snails from an additional 12 shores within Bamfield Inlet. The 13 'sites' were all 6 m wide, extended from ≈ 1–3 m in intertidal height, had hard substrates at both high-shore and low-shore levels (e.g., cobbles, oyster shells, boulders and bedrock), and were separated by a minimum of 15 m. Otherwise, the sites differed in a number of aspects, including slope, orientation (and therefore exposure to direct sunlight), abundance of bedrock or boulders, and extent of algal cover. We made no attempt to quantify differences in habitat characteristics among sites.

#### 2.4.1. Statistical analyses

We assessed the maturity status of high-shore and low-shore snails from these 13 sites as outlined earlier for our main study site. In a first series of analyses, we conducted multiple logistic regressions (Hosmer and Lemeshow, 2000) to determine whether the size at sexual maturation of snails from our main study site differed between our December 1999 and January 2001 samples. We did six separate analyses, one for each combination of our three maturity indicators and two shore levels. In all cases, the length × year interaction term was non-significant (all $p>0.05$), and was not included in the models (Hosmer and Lemeshow, 2000).

Then, for each of the 13 sites sampled in January 2001, we conducted three separate multiple logistic regressions to investigate the effect of snail origin (high- or low-shore) on size at sexual maturation. These analyses were the same as those conducted for snails collected from our main study site in December 1999. In all cases, the length × origin interaction term was non-significant (all $p>0.05$), and was not included in the models (Hosmer and Lemeshow, 2000).

Finally, in addition to the within-site comparisons, we also compared predicted size at sexual maturation of high-shore and low-shore snails across the 13 study sites. These analyses involved first estimating, for each snail group separately: (i) size at onset of sexual maturation, (ii) size at maturity for females, and (iii) size at maturity for males; we used the inverse prediction function to determine the size at which 50% of snails had reached a particular maturity status. We then used a paired t-test to test the hypothesis that the mean (of the 13 study sites) difference in predicted size at sexual maturation between high- and low-shore snails was '0'. In all three analyses, the distribution of these size differences did not deviate significantly from normality ($p>0.05$ in all cases).

## 3. Results

### 3.1. Field snails: mark-release-recapture experiment

The mark-release-recapture analysis indicated that high-origin snails released in the high intertidal experienced the greatest survival rate within the study area of all snail groups, whereas low-origin snails released in the low intertidal experienced the lowest survival (Fig. 1). Snail survival was affected by both snail origin and release height. Thus, both high- and low-origin snails experienced significantly greater survival rates in the upper part of the intertidal (Fig. 1). And, when released at the same shore level, high-origin snails experienced greater survival rates than low-origin individuals (although confidence intervals and mean values overlapped slightly for the high-intertidal release), probably because of behavioral differences between these two groups of snails (see below).

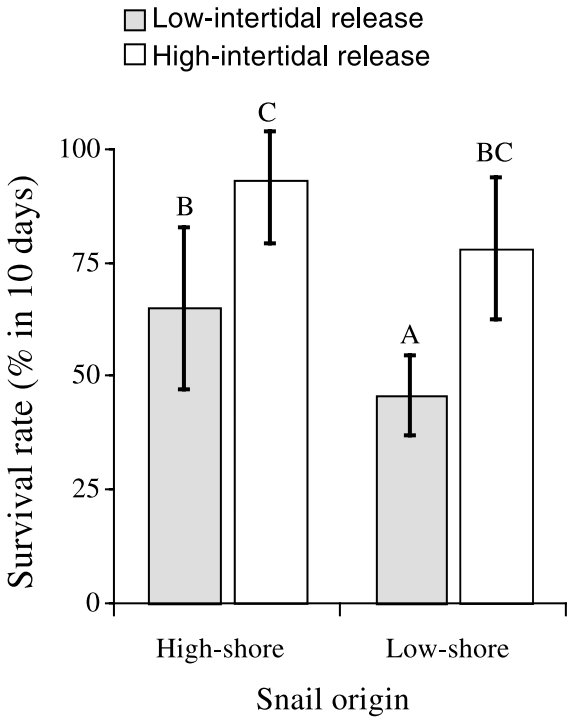


Fig. 1. Mark-release-recapture experiment. Survival rate (% snails surviving over 10 d ± 95% confidence intervals) of high-origin and low-origin *L. sitkana* snails released at both intertidal heights (N = 100 for each treatment combination) of our main study site. Based on the 95% confidence intervals estimated by MARK, snail groups labelled with different letters experienced significantly different survival rates.

At the termination of the experiment, the vertical distribution of high-origin and low-origin snails was markedly different (Fig. 2); these differences were statistically significant for both the high- ($\chi^2 = 25.32$, df = 1, $p < 0.001$) and low-intertidal releases ($\chi^2 = 10.69$, df = 1, $p = 0.001$). When released at their native shore level, virtually all snails of both intertidal origins remained there (Fig. 2). In contrast, snails transplanted to a foreign level showed broader vertical distributions at the end of the experiment, with many individuals having undergone 6 to 9 m of net movement perpendicular to the shore in 32 days to regain their shore level of origin (Fig. 2).

### 3.2. Field snails: growth experiment

Mean growth (shell length increment) of snails during our caging experiment was 0.34 mm, and it varied greatly among treatments (Fig. 3, Table 1). After accounting for the fact that smaller snails grew significantly more than larger individuals (i.e., initial shell length was used as a covariate), we found that all main effects in our model significantly affected growth (Fig. 3, Table 1). First, and most importantly, snails originating from the low intertidal grew significantly less ($p = 0.01$) than individuals originating from the high intertidal, which is consistent with our hypothesis that low-origin snails start investing in reproductive organs and structures at a smaller size than high-origin individuals. Second, snails grew significantly more rapidly in the low intertidal than

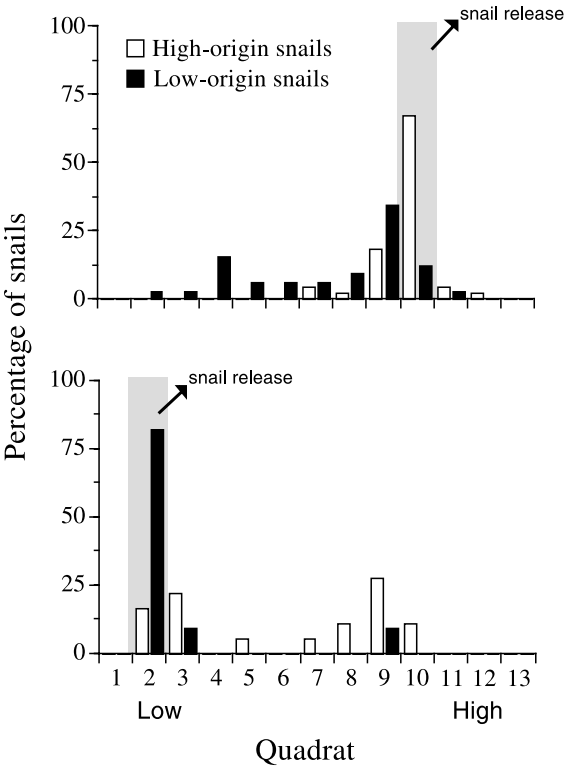


Fig. 2. Mark-release-recapture experiment. Vertical distribution of live snails recovered at the end of the mark-release-recapture experiments (32 d) conducted in both the high- (upper graph) and low-intertidal (lower graph) regions of our main study site. The graphs show the frequency distribution of high-origin (high release: N = 43; low release: N = 18) and low-origin (high release: N = 32; low release: N = 11) snails among the 13 (1 × 6 m) vertical quadrats spanning 1.2 to 3 m in intertidal height.

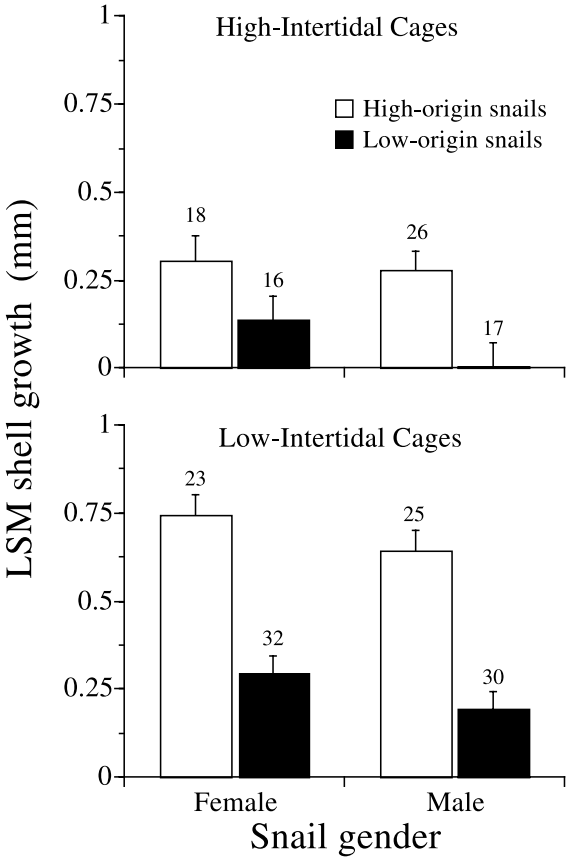


Fig. 3. Field caging experiment. Least-squared mean (i.e., standardised for size) shell length increment (+SE) of small (3.7–4.7 mm) male and female snails originating from the high- and low-intertidal regions of our main study site. Snails were grown for 54 days inside cages placed in the high-intertidal (upper graph) and low-intertidal (lower graph). Numbers above each column indicate sample size.

in the high intertidal ($p = 0.02$), which is likely related to variation in grazing potential at different intertidal heights (see also McCormack, 1982). Third, and somewhat unexpectedly, females grew more than males in all treatments ($p = 0.03$). The interaction terms involving the three fixed-effect factors (snail origin, destination and gender) were all non-significant ($p > 0.30$).

### 3.3. Field snails: size at sexual maturation

We obtained maturity information for a total of 104 high-shore and 94 low-shore snails; when they were pulled out of their shell, 6 high-origin and 16 low-origin snails (mainly smaller individuals) were damaged and could not be examined for maturity status. High-origin snails ranged from 2.64 to 9.78 mm in shell length, whereas low-origin snails ranged form 2.71 to 6.47 mm (larger snails were not present at low shore level).

Snail size (i.e., shell length) was a strong predictor of maturity status ($p \ll 0.001$ in all three analyses), with reproductive structures more likely present and well developed in larger individuals. After accounting for the effect of size, all three analyses indicated that maturity status was also significantly affected by the origin (high- or low-shore) of the snails. First, reproductive structures (i.e., penis and pallial oviduct) became apparent at a smaller size in snails collected from the low- than the high-intertidal area (L-R $\chi^2 = 13.98$, $df = 1$, $p < 0.001$). For example, in December 1999, the inverse prediction function indicated that 50% of low-origin snails had started investing in reproductive structures at 3.02 mm in shell length, compared with 3.81 mm for high-origin individuals (Fig. 4). Second, male and female snails from the low intertidal became sexually mature at a smaller size than individuals from the high intertidal (males: L-R $\chi^2 = 10.27$, $df = 1$, $p = 0.001$; females: L-R $\chi^2 = 12.08$, $df = 1$, $p < 0.001$). For example, in December 1999, the size at which 50% of males were predicted to be sexually mature was 3.55 mm for low-origin snails, compared with 4.34 mm for high-origin snails (Fig. 4). Similarly, the size at which 50% of females were predicted to be sexually mature was 4.48 mm for low-origin snails, compared to 5.43 mm for high-origin snails (Fig. 4).

### 3.4. January 2001 large-scale survey: size at sexual maturity

At our main study site, the effect of shore level on size at sexual maturity was consistent across years. Thus, as was observed in December 1999, our January 2001 samples indicated that low-shore snails from our main study site started investing in reproductive structures, and reached sexual maturity (males and females), at a significantly smaller size than high-shore individuals (Fig. 4). Furthermore, the relationship between snail size and maturity status, for both high-shore and low-shore snails, did not differ between our December 1999 and

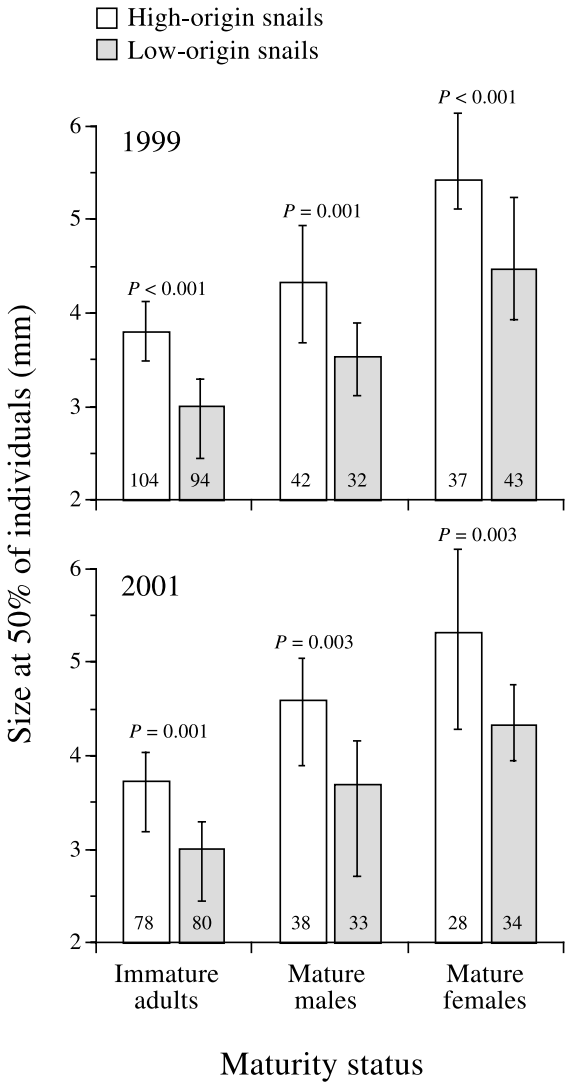


Fig. 4. Sexual maturation of snails from our main study site. Shell length ( ± 95% confidence interval) at which 50% of juvenile snails were predicted to become immature adults (i.e., when reproductive organs became visible), and 50% of immature adults (males and females) were predicted to become sexually mature (see Methods). We made these estimates in December 1999 and January 2001. We indicate in each bar the number of snails upon which the estimate is based, and show the probability that the relation between shell length and maturity status is the same for high-origin and low-origin snails.

January 2001 samples (Fig. 4; p>0.25 in all six comparisons).

However, the relationship between shore level and size at sexual maturation varied among sites. In gen-

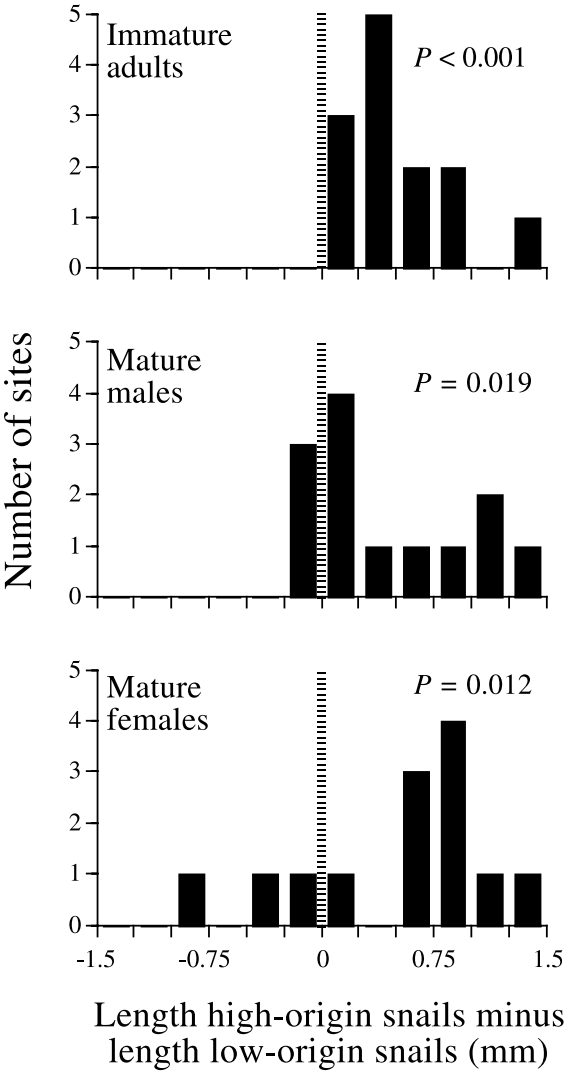


Fig. 5. Large-scale field survey. Difference between the size (shell length in mm) at which high-origin and low-origin snails (high minus low) from a given site are predicted to attain a particular descriptor of maturity status (see Methods); each graph summarises this information for the 13 different study sites. The upper graph is based on the size at which 50% of snails were predicted to become immature adults (i.e., when reproductive organs became visible), whereas the middle and lower graphs are based on the size at which 50% of male and female snails, respectively, were predicted to become sexually mature adults. Under the hypothesis that high- and low-origin snails mature at a similar size, differences for the 13 sites are expected to distribute uniformly on both sides of the dashed line. The p-value is the result of a paired t-test addressing this hypothesis.

eral, low-shore snails matured at a smaller size than high-shore individuals, as at our main study site, but these differences were not significant at all sites. For example, size at maturation onset differed significantly at 7 of our 13 sites, and in all cases low-shores snails were found to invest in reproductive structures at a significantly smaller size than high-shore individuals ($p < 0.05$). Similarly, at 8 sites, low-shore female snails reached sexual maturity at a significantly smaller size than high-shore individuals ($p < 0.05$), although the reverse pattern was observed at one site ($p < 0.05$). Finally, at 4 sites, low-shore males became sexually mature at a smaller size than high-shore males ($p < 0.05$), and the reverse pattern was not seen at a single site.

The paired t-tests conducted across our 13 study sites support the hypothesis that low-shore snails invest in reproductive tissues and structures at a smaller size than high-shore individuals (Fig. 5). Thus, the sizes at which 50% of same-origin (i.e., site and shore height) snails were predicted to have (i) started allocating resources to reproductive structures, and (ii) attained sexual maturity (males and females) were significantly smaller in low-shore snails than in high-shore individuals from the same site (Fig. 5; onset of sexual maturation: $df = 12$, $t = 4.92$, $p < 0.001$; female sexual maturity: $df = 12$, $t = 2.95$, $p = 0.012$; male sexual maturity: $df = 12$, $t = 2.71$, $p = 0.019$).

## 4. Discussion

In constructing mechanistic models of population/community structure, ecologists typically ask how biotic and abiotic factors affect the biological 'performance' (i.e., survivorship, growth, reproduction) of individual organisms and species, but they rarely consider how genotypic and/or phenotypic responses to these same factors affect the demography of populations. The results of the present study indicate that phenotypic (resource allocation) differences between *L. sitkana* snails inhabiting upper and lower intertidal areas contribute to the species' vertical size gradient, a pattern that has hitherto been attributed to size-dependent and spatial variation in predation mortality (McCormack, 1982; Behrens Yamada and Boulding, 1996; Rochette and Dill, 2000).

### 4.1. Life-history variation: the role of predation

Several field studies have now shown that crabs (and perhaps fish) exert strong predation pressure on large adult littorinids inhabiting low-intertidal levels of wave-sheltered shores of the northeastern Pacific (McCormack, 1982; Behrens Yamada and Boulding, 1996; Rochette and Dill, 2000). We believe these same predation patterns are responsible for the earlier sexual maturation of low-shore vs. high-shore *L. sitkana* snails. Under such conditions of reduced adult survival, life-history theory predicts that phenotypes will be favored that are capable of reproducing earlier, at a smaller size and with greater reproductive effort (Stearns, 1976). Our large-scale survey indicates that this intra-specific variation in life history is fairly consistent within Bamfield Inlet, although its magnitude varies from shore to shore. Interestingly, we have since found evidence that variation in size at sexual maturity among snails inhabiting low-intertidal levels of our 13 different sites is related to differences in predation pressure across these sites (ms. in prep.), supporting our conclusion that predation pressure is at least partially responsible for life-history variation among *L. sitkana* snails. Similar phenotypic and/or genotypic responses to size-selective sources of mortality (e.g., predation, parasitism) have been documented for a variety of aquatic organisms, including cladocerans (e.g., Riessen, 1999, reviews cases of induced responses), isopods (e.g., Sparkes, 1996), amphipods (e.g., Wellborn, 1994; Glazier, 1999), gastropods (e.g., Crowl and Covich, 1990; Lafferty, 1993), and fish (e.g., Reznick and Endler, 1982; Reznick et al., 1996; but see Reznick et al., 2001).

Another agent of mortality (aside from predation) that might favour larger body sizes in high-shore snails is desiccation. Because a snail's surface area increases less rapidly with body size than does its volume, small snails may be more susceptible to desiccation than larger individuals. And, the argument goes, because aerial exposure is greater in upper than in lower parts of the intertidal zone, snails living in the high intertidal might be selected to more rapidly attain large, less desiccation-susceptible body sizes than low-shore snails. We believe that this hypothesis can be rejected, however, because the advantage of a large body size in terms of reduced desiccation rate is probably outweighed

by a concomitant (and similarly mediated) decrease in capacity to dissipate heat. Because large snails have a relatively small surface area, they are more dependent on evaporative cooling (and therefore increased water loss) to reduce their body temperature when exposed to sunlight. Indeed, gastropods inhabiting the littoral fringe, that portion of the intertidal zone that is only wetted during the highest tides, actually tend to have relatively small, not large, adult body sizes (McMahon, 1990).

### 4.2. Life-history variation: the adaptive value

At our main study site, the size at which 50% of females (males) were predicted to have reached sexual maturity was 5.43 mm (4.34 mm) for high-shore snails, and 4.48 mm (3.55 mm) for low-shore individuals. Based on these maturity differences and the growth rates recorded during our field caging experiment, we estimate that the high-shore female (male) phenotype would require approximately 67 d (65 d) more than the low-shore phenotype to reach sexual maturity if it lived in the low-intertidal zone. The high rate at which snails 'disappeared' from the low-intertidal area of our study site suggests that such delayed reproduction would carry important survivorship costs. For example, assuming that predators killed all low-origin snails that disappeared from the low intertidal during our mark-release-recapture experiment, we estimate they would consume 99% of high-shore phenotypes during this additional 65-d period of growth in the low-intertidal zone. Furthermore, even if predators only killed half of these snails (the others having moved outside the search area), they would still consume as many as 87% of high-shore snails over this period. Tethering experiments, in which snail losses can be more directly attributed to predation, have reported similarly high predation rates on *L. sitkana* snails inhabiting low-intertidal areas of northeastern Pacific wave-sheltered shores (Behrens Yamada and Boulding, 1996; Rochette and Dill, 2000).

The greater growth rate of female versus male snails observed during the caging experiment suggests that the evolutionary costs and benefits of a large body size may differ between the sexes. One advantage of delayed maturity for females in the high-intertidal zone is an increased reproductive output per reproductive event, because larger littorinids produce more embryos than smaller individuals (e.g., Hughes and Answer, 1982). Based on egg counts from females inhabiting a similar site in Bamfield Inlet (unpub. data), we estimate that a female measuring 5.43 mm in shell length (i.e., size at 50% maturity for high-shore females) would produce approximately three times as many eggs per spawning event as a 4.48 mm female (i.e., size at 50% maturity for low-shore females). A larger body size may also be advantageous for males, because positive size assortative mating, whereby larger males mate with larger (more fecund) females, has been documented in a number of littorinid populations (e.g., Erlandsson and Rolan-Alvárez, 1998; Hull, 1998). Another potential advantage of delayed reproductive allocation in high-shore snails, which would presumably apply to both females and males, is retarded senescence (i.e., increased longevity) and an increased number of lifetime reproductive events. *L. sitkana* has a life span of at least 2 years (Buckland-Nicks et al., 1973; Sacchi and Voltolina, 1987), but no study has yet directly assessed longevity in any single population, or tested whether longevity varies among shores or across shore levels.

Low-shore *L. sitkana* snails clearly fall more on the r-side, and high-shore snails on the K side, of the metaphorical r-K continuum (Pianka, 1970), and the reported patterns of intra-specific variation in resource allocation are consistent with life history theory (Stearns, 1976). Nevertheless, a more rigorous test of this adaptationist hypothesis will require integrating information pertaining to size-dependent variation in growth, mortality and reproduction to quantify and compare the expected lifetime reproductive success of competing strategies in different environments.

### 4.3. Life-history variation: the role of genes

At our main study site, high-shore and low-shore *L. sitkana* snails displayed consistent differences in growth rates when caged at the same shore level, and the sizes at which each type reached sexual maturity were similar in December 1999 and January 2001. These results suggest that life-history variation between high-shore and low-shore areas may have at least a partial genetic basis. The reproductive strategy of *L. sitkana* (i.e., internal fertilisation and benthic larval

development) is expected to be conducive to genetic differentiation over relatively small spatial scales (e.g. see McQuaid, 1996; De Wolf et al., 1998), and the high fidelity displayed by adult snails to their native shore level (see also McCormack, 1982; Rochette and Dill, 2000) would also tend to reduce gene flow between high-shore and low-shore populations. Future studies should investigate the population genetic structure of *L. sitkana* snails on these wave-sheltered shores, particularly in relation to the vertical gradient in selection pressures.

### *4.4. Life-history variation and population demography*

Earlier studies have shown that the positive relation between *L. sitkana* body size and intertidal height (McCormack, 1982) is partly due to predation mortality (McCormack, 1982; Behrens Yamada and Boulding, 1996, Rochette and Dill, 2000), and partly to behavior (Rochette and Dill, 2000); larger snails are more likely than smaller individuals to move shoreward if translocated to lower-shore levels. The present study suggests another mechanism by which predators contribute to the snails' population size-structure, namely selection on life histories; predators have apparently selected for (or they induce) earlier sexual maturation and reduced somatic growth in snails inhabiting lower-shore levels.

On wave-exposed shores of Spain, another littorinid with 'direct' development, *L. saxatilis*, displays a similar vertical size gradient (e.g., Johannesson et al., 1993). There, crab predation is believed to be greater in the upper intertidal (because heavy wave action prevents crabs from foraging at lower-shore levels), and because these crabs prefer smaller snails, it has been hypothesised that predation has selected for the faster growth rates of high-shore snails (Johannesson et al., 1997). Results of reciprocal transplant experiments suggest that these differences in growth rates are at least partly due to genetic differences between high-shore and low-shore snails (Janson, 1982; Johannesson et al., 1997). Indeed, *L. saxatilis* shows remarkable phenotypic variation across its range, and much of this variation appears to be under genetic control (Johannesson et al., 1993; Johannesson et al., 1995; Rolán-Alvarez et al., 1996). Local adaptation to spatial variation in predation pressure may thus be responsible for the vertical size gradient observed in this species as well.

Other studies have shown similar dual effects of predators (i.e., mortality and life history shifts) on the demography (e.g., size structure, sex ratio) of freshwater fish, crustacean, and insect populations (e.g., Vonder Brink and Vanni, 1993; Rodd and Reznick, 1997; McPeek and Peckarsky, 1998), and a few of these have quantified (using demographic and individual-based modelling approaches) the relative importance of lethal and life history effects (Rodd and Reznick, 1997; McPeek and Peckarsky, 1998). Few such studies have exploited the variation to be found among the selective environments of marine coastal invertebrates. We believe that greater consideration of evolutionary processes will lead to a more complete understanding of the mechanisms responsible for structuring marine coastal communities (e.g., McPeek and Miller, 1996).

## Acknowledgements

We are extremely grateful to Dr. B. Anholt for analysing the mark-release-recapture data, and to Kristina Holm for assistance in the recovery of snails during the same experiment. An anonymous reviewer provided insightful comments on an earlier version of the manuscript. R. Rochette was supported by a NSERC postdoctoral fellowship and a WCUMBS Research Associate Award (Bamfield Marine Science Centre, British Columbia). K. Dunmall was supported by a Science Incentive Scholarship from the University of Waterloo. The research was funded by NSERC operating grant A6869 to L.M. Dill and a WCUMBS Research Associate Award to R. Rochette.

## References

Agresti, A., 1996. An Introduction to Categorical Data Analysis. John Wiley and Sons Inc., New York.

Behrens Yamada, S., 1989. Are direct developers more locally adapted than planktonic developers? Mar. Biol. 103, 403–411.

Behrens Yamada, S., Boulding, E.G., 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. J. Exp. Mar. Biol. Ecol. 204, 59–83.

Behrens Yamada, S., Navarrete, S.A., Needham, C., 1998. Preda-

tion induced changes in behaviour and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi). J. Exp. Mar. Biol. Ecol. 220, 213–226.

Boulding, E.G., Holst, M., Pilon, V., 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on Northeastern Pacific shores. J. Exp. Mar. Biol. Ecol. 232, 217–239.

Buckland-Nicks, J., Chia, F.-S., Behrens, S., 1973. Oviposition and development of two intertidal snails, *Littorina sitkana* and *Littorina scutulata*. Can. J. Zool. 51, 359–365.

Crowl, T.A., Covich, A.P., 1990. Predator-induced life-history shifts in a freshwater snail. Science 247, 949–951.

De Wolf, H., Backeljau, T., Verhagen, R., 1998. Spatio-temporal genetic structure and gene flow between two distinct shell morphs of the planktonic developing periwinkle *Littorina striata* (Mollusca: Prosobranchia). Mar Ecol. Prog. Ser. 163, 155–163.

Erlandsson, J., Rolan-Alvárez, E., 1998. Sexual selection and assortative mating by size and their roles in the maintenance of a polymorphism in Swedish *Littorina saxatilis* populations. Hydrobiologia 378, 59–69.

Glazier, D.S., 1999. Variation in offspring investment within and among populations of *Gammarus minus* Say (Crustacea: Amphipoda) in ten mid-Appalachian springs (U.S.A.). Arch. Hydrobiol. 146, 257–283.

Hendrix, L.J., Carter, M.W., Scott, D.T., 1982. Covariance analyses with heterogeneity of slopes in fixed models. Biometrics 38, 641–650.

Hosmer, D.W., Lemeshow, S., 2000. Applied logistic regression, 2nd edition. John Wiley and Sons Inc., New York.

Hughes, R.N., Answer, P., 1982. Growth, spawning and trematode infection of *Littorina littorea* (L.) from an exposed shore on north Wales. J. Moll. Stud. 48, 321–330.

Hull, S.L., 1998. Assortative mating between two distinct micro-allopatric populations of *Littorina saxatilis* (Olivi) on the north-east coast of England. Hydrobiologia 378, 79–88.

Huxham, M., Raffaelli, D., Pike, A., 1993. The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. J. Exp. Mar. Biol. Ecol. 168, 223–238.

Janson, K., 1982. Genetic and environmental effects on the growth rate of *Littorina saxatilis*. Mar. Biol. 69, 73–78.

Johannesson, K., Johannesson, B., Rolán-Alvarez, E., 1993. Morphological differentiation and genetic cohesiveness over a microenvironmental gradient in the marine snail *Littorina saxatilis*. Evolution 47, 1770–1787.

Johannesson, K., Rolán-Alvarez, E., Ekendahl, A., 1995. Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. Evolution 49, 1180–1190.

Johannesson, K., Rolán-Alvarez, E., Erlandsson, J., 1997. Growth rate differences between upper and lower shore ecotypes of the marine snail *Littorina saxatilis* (Olivi) (Gastropoda). Biol. J. Linn. Soc. 61, 267–279.

Kirk, R.E., 1982. Experimental design: procedures for the behavioral sciences, 2nd edition. Brooks/Cole, Monterey, USA.

Lafferty, K.D., 1993. The marine snail, *Cerithidea californica*, matures at smaller sizes where parasitism is high. Oikos 68, 3–11.

McCormack, S.M.D., 1982. The maintenance of shore-level size gradients in an intertidal snail (*Littorina sitkana*). Oecologia 54, 117–183.

McMahon, R.F., 1990. Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. Hydrobiologia 193, 241–260.

McPeek, M.A., Miller, T.E. (Eds.), 1996. Evolutionary biology and community ecology. Ecology (Special Feature), vol. 77, pp. 1319–1378.

McPeek, M.A., Peckarsky, B.L., 1998. Life histories and the strengths of species interactions: combining mortality, growth and fecundity effects. Ecology 79, 867–879.

McQuaid, C.D., 1996. Biology of the gastropod family Littorinidae. I. Evolutionary aspects. Oceanography and Marine Biology: an Annual Review 34, 233–262.

Pianka, E.R., 1970. On *r*- and *K*- selection. Am. Nat. 104, 592–597.

Reid, D.G., 1996. Systematics and evolution of Littorina. Ray Society, London, No. 164.

Reznick, D.N., Bryga, H.A., 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. Am. Nat. 147, 339–359.

Reznick, D.N., Endler, J.A., 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36, 160–177.

Reznick, D.N., Rodd, F.H., Cardenas, M., 1996. Life-history evolution in guppies (*Poecilia reticulate*: Poeciliidae). IV. Parallelism in life-history phenotypes. Am. Nat. 147, 319–338.

Reznick, D., Butler, M.J., Rodd, H., 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. Am. Nat. 157, 126–140.

Riessen, H.P., 1999. Predator-induced life history shifts in *Daphnia*: a synthesis of studies using meta-analysis. Can. J. Fish. Aquat. Sci. 56, 2487–2494.

Robles, C., Sweetnam, D.A., Dittman, D., 1989. Diel variation of intertidal foraging by *Cancer productus* L. in British Columbia. J. Nat. Hist. 23, 1041–1049.

Rochette, R., Dill, L.M., 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. J. Exp. Mar. Biol. Ecol. 253, 165–191.

Rodd, F.H., Reznick, D.N., 1997. Variation in the demography of guppy populations: the importance of predation and life histories. Ecology 78, 405–418.

Rolán-Alvarez, E., Rolán, E., Johannesson, K., 1996. Differentiation in radular and embryonic characters, and further comments on gene flow, between two sympatric morphs of *Littorina saxatilis* (Olivi). Ophelia 45, 1–15.

Sacchi, C.F., Voltolina, D., 1987. Recherches sur l'écologie comparée des littorines (Gastropoda, Prosobranchia) dans l'île de Vancouver (British Columbia, Canada). Atti. Soc. ital. Sci. nat. Museo. civ. Stor. nat. Milano 128, 209–234.

Sparkes, T.C., 1996. Effects of predation risk on population variation in adult size in a stream-dwelling isopod. Oecologia 106, 85–92.

Stearns, S.C., 1976. Life history tactics: a review of the ideas. Q. Rev. Biol. 51, 3–47.

Underwood, A.J., 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Vermeij, G.J., 1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology 53, 693–700.

Vonder Brink, R.H., Vanni, M.J., 1993. Demographic and life history response of the cladoceran *Bosmina longirostris* to variation in predator abundance. Oecologia 95, 70–80.

Wellborn, G.A., 1994. Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. Ecology 75, 2104–2117.