Journal of Experimental Marine Biology and Ecology 327 (2005) 103–114

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

The costs of being bored: Effects of a clionid sponge on the gastropod *Littorina littorea* (L)

Lauren M. Stefaniak, Jesse McAtee, Myra J. Shulman *

Shoals Marine Laboratory, Cornell University, G14 Stimson Hall, Ithaca, NY 14853, USA

Received 9 March 2005; received in revised form 7 June 2005; accepted 9 June 2005

Abstract

Mollusc shells provide a major defense against predators, but changes in shell properties may alter the effectiveness of this defense. An endolithic boring sponge, *Cliona* sp., infests many shells of the gastropod *Littorina littorea* in the southern Gulf of Maine. *Cliona* excavates ramifying chambers within the shell but does not affect tissue directly. Field surveys showed that 22–83% of snails were infected with *Cliona* at the Isles of Shoals; the prevalence of infection declined with increasing tidal height and increased with increasing snail size. We also investigated potential costs to *L. littorea* of infection by *Cliona*. *L. littorea* appeared to respond to sponge boring by laying down additional material on the interior of the shell, which reduced interior shell volume and was associated with smaller dry body mass for a given shell length. Biomechanical studies showed that sponge boring weakened shells: the mean compressive force required to break severely bored *L. littorea* was 29% lower than that required to break unbored snails. *Cliona* infection increased vulnerability of snails to predation by the crab, *Cancer borealis* Stimpson, which attacks molluscs by crushing or peeling shells. Unlike uninfected snails, predation risk did not decline with increasing size in bored *L. littorea*. In addition, bored snails were generally crushed by the crab, regardless of snail size, whereas large unbored snails could only be attacked by peeling. Thus, costs to *L. littorea* of *Cliona* boring included the following: (1) increased vulnerability to predation due to structural changes in the shell; (2) reduction or elimination of the size-refuge advantage; and (3) a potential decrease in growth and fecundity due to diversion of energy to supplemental interior layers to the shell and the consequent reduction in interior shell living space and body mass.

Keywords: Clionid sponge; Gastropod *Littorina littorea* (L); Sponge boring; Crab predation; Biomechanics; Shell strength; Induced defenses

---

1. Introduction

Sponges of the family Clionidae commonly live in a fine network of tunnels and cavities that they excavate in calcium carbonate substrates, including the shells and skeletons of living molluscs and corals (Hartman, 1957, 1958; Guida,

---

* Corresponding author. Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY, 14853, USA. Tel.: +1 607 254 4225; fax: +1 607 255 8088.

E-mail address: mjs59@cornell.edu (M.J. Shulman).

0022-0981/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2005.06.007

1976; Pomponi, 1980). Although the sponge does not directly feed on host tissue, boring may impose a variety of costs in hosts, including increased likelihood of skeletal breakage and/or direct and indirect costs of shell repair. In molluscs, shells provide protection from predation, and shell thickness and strength directly affect an individual's vulnerability to shell-breaking predators such as lobsters, crabs, and durophagous fishes (Kitching and Lockwood, 1974; Palmer, 1985). Boring by clionid sponges may weaken shells, thus increasing susceptibility to predation. Molluscs can respond to boring by laying down additional shell material, as shown in slipper shells (*Crepidula fornicata*) (Hoeksema, 1983) and oysters (*Ostrea edulis*) (Rosell et al., 1999). The energetic costs of shell production are considerable, however, and reduce energy available for somatic growth and reproduction (Palmer, 1981, 1992). Furthermore, accreting material on the shell interior reduces snail living space with a consequent potential reduction in body size and fecundity (Hughes and Roberts, 1980).

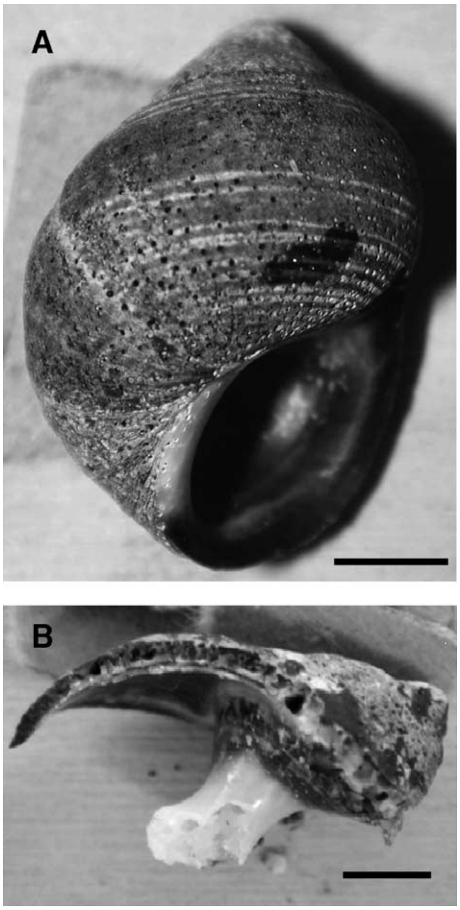

Fig. 1. (A) External view of *Littorina littorea* bored by the sponge *Cliona* sp. A reticulate pattern of boreholes is visible on the shell surface. (B) Cross-sectional view of the sponge-excavated cavities in the shell body whorl and columella. Scale bars = 5 mm.

We observed *Cliona* sp. living in the shells of the common intertidal snail *Littorina littorea* (Fig. 1) in the Gulf of Maine. *Cliona* infection in *L. littorea* has not previously been reported, so we document here the demographic and tidal distribution of *Cliona* in this species. The main goal of our study, however, was to examine the impact of sponge boring on the gastropod host: (1) Does *Cliona* boring weaken the shell? (2) Are bored snails more vulnerable to a crushing predator? (3) Do snails bored by *Cliona* have thicker shells with less internal volume, and if so, do they have smaller body sizes?

2. Materials and methods

2.1. Study sites

This study took place in June–September 2002 and June–August 2003 in the southern Gulf of Maine at the Isles of Shoals in the vicinity of the Shoals Marine Laboratory. This small archipelago consists of 9 main granitic islands located 10 km off the coast of New Hampshire, USA. *Cliona* infection in *L. littorea* was studied at three field sites with high *L. littorea* densities: (1) Broad Cove [42.989°N, 70.613°W]—a 30-m-wide semi-exposed inlet on the northeast side of Appledore Island; (2) Smith's Cove [42.985°N, 70.618°W]—a 20-m protected bay on the west side of Appledore Island; and (3) a 10-m-wide cove formed by the isthmus connecting White and Seavey Islands [42.968°N, 70.625°W]. At all three sites, the substratum was cobble and boulders mixed with sand and shell rubble. The mid-intertidal regions were dominated by the brown algae *Ascophyllum nodosum* Scorpiodes and *Fucus vesiculosus* L, while the red alga *Chondrus crispus* Stackhouse and crustose coralline algae dominated the low shore. In the shallow subtidal zone, the red algae *Polysiphonia* spp. and the kelp *Laminaria saccharina* (L) predominated.

2.2. Study organisms

L. littorea is a common intertidal gastropod found throughout the North Atlantic (Reid, 1996). It grazes on a wide range of diatoms and algae, preferring small ephemeral species often found in the low intertidal and shallow subtidal (Lubchenco, 1978, 1983; McQuaid, 1996). Predators on *L. littorea* include crushing decapod predators such as the Jonah crab (*Cancer borealis* Stimpson), the rock crab (*C. irroratus* Say), the green crab [*Carcinus maenas* (L)] and the American lobster (*Homarus americanus* Milne-Edwards) (Hadlock, 1980; Ojeda and Dearborn, 1991; Trussell et al., 2002; Perez and Shulman, unpublished data). The calcium carbonate shell of *L. littorea* has three layers: a thick outer layer of calcite, a thin layer of aragonite, and an interior, infill layer of aragonite found solely in the spire (Taylor and Reid, 1990).

Two described species of *Cliona* (*C. celata* Grant and *C. vastifica* Hancock) and possibly additional undescribed species occur in the Gulf of Maine (Hartman, 1957). The unidentified *Cliona* sp. found in *L. littorea* is bright yellow and grows entirely beneath the surface of the shell with periodic perforations to the exterior, a growth form referred to as the alpha-stage in boring sponges (Vosmaer, 1933). We have not observed this sponge overgrowing the surface of shells (beta-stage) or free-living (gamma-stage). The sponge excavates interconnected galleries within the shell, with a reticulate pattern of boreholes on the external surface of the shell.

2.3. *Cliona* infection in individual *L. littorea*

The externally visible signs of *Cliona* infection are boreholes on the shell exterior (Fig. 1). To determine whether the spatial distribution of boreholes accurately reflected the spatial extent of infection within the shell, we broke open 20 infected *L. littorea* and examined the relationship between external boreholes and the distribution of sponge-inhabited excavations within the shell.

2.4. Demographic and spatial distribution of *Cliona* infection in *L. littorea*

L. littorea were collected from 0.25 m × 0.25 m quadrats at +1.0 m, +0.5 m, 0.0 m, and −0.5 m relative to Mean Lower Low Water (MLLW) at three sites: Broad Cove, Smith's Cove and White Island. At each tidal height, a 10-m line was run parallel to shore along the depth contour and 10 quadrats sampled at randomly determined points along the transect.

We sorted the *L. littorea* into bored and unbored, and then counted and measured shell height (maximum dimension parallel to the axis of coiling; Reid, 1996) of all individuals in most quadrats. Due to high densities in some sampling areas, we measured only a random subset of 75–140 unbored snails from each tidal height at Broad Cove and 237 bored snails from 0.0 m at White Island.

We calculated prevalence (percent of the population infected) in each quadrat that had ≥ 5 individuals, and determined the mean and standard error for prevalence for each site/tidal-height combination. We analyzed the prevalence of *Cliona* infection across sites at 0.0 m using a one-way ANOVA after examination of residual plots revealed similar variances with no outliers; Tukey's HSD post-hoc test was used for pairwise comparison between sites.

To determine which factors affect the probability of an individual snail being bored, we performed a logistic regression that included shell height, tidal height and site as main effects, as well as all possible interaction effects. This initial analysis revealed a significant three-way interaction effect, suggesting that shell size and tidal height interacted in different ways at different sites. Therefore, we performed separate logistic regressions for each site, and adjusted the critical value to $p = 0.017$ by applying the highly conservative Bonferroni correction.

2.5. Morphometrics and shell strength of unbored and severely bored *L. littorea*

To investigate the effects of sponge boring on shell strength in *L. littorea*, we measured the peak compression load that shells could sustain before failure. Live *L. littorea* were used to avoid possible changes in shell strength due to preservation methods. Fifty unbored and fifty severely bored *L. littorea* were collected from Broad Cove at 0.0 m tidal height, and shell height, breadth, and aperture lip thickness measured. Shell breadth was measured as the widest dimension perpendicular to shell height (Reid, 1996);

aperture lip thickness was measured at the point between the aperture connection with the body whorl and the columella. Shell strength was measured in an Instron Corporation Series IX Automated Materials Testing System. Each snail was oriented between two flat plates with the shell aperture placed against the bottom plate and subjected to compression at a rate of 2 mm/min with a maximum load of 5 kN. Shell failure was designated as a precipitous drop in the force readout and was usually accompanied by a loud crack as the shell broke. Peak load before shell failure was used as the measure of shell strength. Shells and bodies were separated after crushing and dried at 80 °C to a constant weight.

Bored and unbored snails differed in size distribution (see Results). To separate effects due to boring from those associated with size, we restricted our data analyses to the 66 snails that fell within the range of size overlap of bored and unbored snails (22.0–28.0 mm shell height; 13.2–16.4 mm shell breadth). The effect of boring on shell strength was examined using ANCOVAs with shell size as a covariate. We used the same analytical approach to examine the effects of boring on the thickness of the aperture lip, dry body mass, and dry shell mass. Because shell spires can be eroded or broken over time, two sets of ANCOVAs were performed, one set using shell height and the second using shell breadth as the measure of shell size. The same analyses were also performed on log-transformed data.

2.6. Relationship between internal shell volume and body mass

Preliminary observations suggested that bored snails might have thicker shells with less living space (internal volume) than unbored snails. To determine whether snails with smaller shell volume also had less body tissue, we measured shell volume, shell height, and dry body mass in 78 individuals collected from White Island and Smith's Cove. To facilitate removal of the snail body from an intact shell, the specimen was frozen and thawed before the animal was extracted. Body tissue was dried at 83 °C to constant weight. Shell volume was determined by filling the shell with water via a calibrated syringe. Each shell was first balanced on its spire in clay; once the spire was filled with water, the shell was tilted and turned to ensure all air bubbles were released, and more water added until it was level with the aperture opening. To determine the error in volume measurements, we made 10 measurements on each of 13 randomly selected shells. The range of estimates on a single shell was a maximum of 5.7% of the mean for shells with volumes ≥ 0.25 ml. Very small shells (<0.25 ml) had measurements that differed by up to 26% of the mean. The relationship between dry body mass and shell volume was analyzed with a simple linear regression; examination of the residuals indicated that they were normally distributed.

2.7. C. borealis predation on bored vs. unbored L. littorea

2.7.1. Effect of sponge boring on prey size refuge

To determine whether *L. littorea* has a size refuge from predation by *C. borealis*, and, if so, whether this size refuge was reduced by *Cliona* boring, we collected *L. littorea* of four size classes [shell height (± 1 mm): 20, 24, 28, and 30 mm] in each of two boring categories (unbored or severely bored) from the intertidal zone of Smith's Cove. Severely bored snails had bore holes on both the spire and the body whorl. Medium-size *C. borealis* (carapace width 85 ± 5 mm) were collected by snorkelers and kept without food for 60 h in sea tables at the Shoals Marine Laboratory. Each crab was used in only a single experimental trial. In each trial, a single crab was introduced into a feeding container [7.6 L plastic wash pan with mesh cover] provided with flow-through seawater and offered a single *L. littorea*. After 23 h we noted whether the snail was consumed and the consumption method (crushing or peeling) was identified. Crushing was recorded when the columella was broken, while peeling was defined by an intact columella and a chipped aperture. If the snail was not consumed, the crab was fed the same snail crushed to test for willingness to feed in the laboratory setting. The few cases in which crabs would not feed were excluded and replaced with additional trials. Except for the largest *L. littorea*, we performed 30–36 trials on each size/boring category. Due to the rarity of large, unbored snails, only 5–6 trials were run for each of the 30-mm categories.

We performed a contingency table analysis on unbored snails to determine whether probability of being eaten was affected by size category and repeated the same analysis on bored snails to determine whether any possible size refuge was reduced or eliminated. For snails that were eaten, we used a logistic regression to determine whether the probability of being crushed vs. peeled was affected by *Cliona* boring and/or by snail size. We excluded the >30-mm size class from this analysis because only two were consumed.

2.7.2. Prey-choice experiment 1: single predator, two prey

Two prey-choice experiments tested whether *C. borealis* preferentially preyed upon bored vs. unbored snails. In the first, a single, starved crab (carapace width = 85 ± 5 mm) was placed in a feeding tank with one bored and one unbored snail of equal size (shell height = 24 ± 2 mm). Feeding tanks consisted of 7.6 L wash tubs covered with plastic mesh as before. A rock for shelter was placed in each tub and flow-through seawater provided. Crabs were collected from the shallow subtidal and starved for 48–72 h before being placed in the feeding tank. For the first 2 h of observation, crabs were monitored approximately every 15 min, and then periodically over the following 22 h. For each trial, we recorded the order in which snails were eaten. If neither snail was eaten, the crab was offered a crushed snail to assess whether failure to feed was due to a lack of hunger; any trials in which the crab would not feed were excluded from the analyses. We used a contingency table analysis to determine whether bored or unbored snails were eaten first more often than expected under a null hypothesis of no prey preference.

2.7.3. Prey-choice experiment 2: multiple predators, multiple prey

Whether prey choice occurs may be influenced by predator hunger, prey availability, and number of predators. In a second prey-choice experiment, we measured survivorship of multiple prey exposed to multiple, non-starved predators. We collected snails belonging to five categories of shell height [22, 24, 26, 28 (all ± 0.9 mm); ≥ 30 mm], and three categories of *Cliona* boring (unbored, moderately bored, severely bored): moderately bored snails had bore holes present only on the spire, whereas severely bored snails had bore holes on both the spire and body whorl. A code for size/boring category was written in permanent marker on the upper surface of the shell so that counts could be made during the experiment without disturbing the animals. Ten snails of each size/boring category combination (except for the ≥ 30 mm category, which had no moderately bored snails) were placed in a flow-through seawater table (1.5 m × 0.76 m × 11 cm). Ten large (115 ± 5 mm) *C. borealis* collected from the shallow subtidal were added to the sea table. The experiment was monitored every 12 h for 4 days and the number of surviving periwinkles of each size/boring category recorded. Kaplan–Meier survival estimates were computed and log-rank tests used to compare survivorship across sizes and boring categories (Lee, 1992).

3. Results

3.1. Extent of Cliona infection within shells

The location of bore holes on the shell exterior matched well with the location of *Cliona* excavations and tissue in the shell spire and body whorl. What was not visible externally, however, was infection in the columella, which often occurred in snails that were extensively bored elsewhere in the shell.

3.2. Prevalence and distribution of Cliona infection in L. littorea

Cliona was quite prevalent in *L. littorea* shells, with 47% of all snails sampled showing evidence of infection. However, densities of snails and prevalence of *Cliona* boring varied widely among sites and tidal heights (Fig. 2). At 0.0 m, the tidal height at which *L. littorea* generally had the greatest density, *Cliona* infection differed significantly across sites, from a low of 16% at Broad Cove to a high of 80% at White Island (ANOVA, $p < 0.0001$; Tukey's HSD, all $p < 0.05$).

At all three sites (Fig. 3), the probability of a snail being bored increased with increasing shell size and decreasing tidal heights (logistic regression, likelihood ratio test: $p = 0.01$ for shell height at Broad Cove; $p \leq 0.0001$ for all other sites and main effects). A significant interaction effect occurred between shell size and tidal height at Broad Cove ($p = 0.0001$); the effect of shell size was reduced at lower tidal heights.

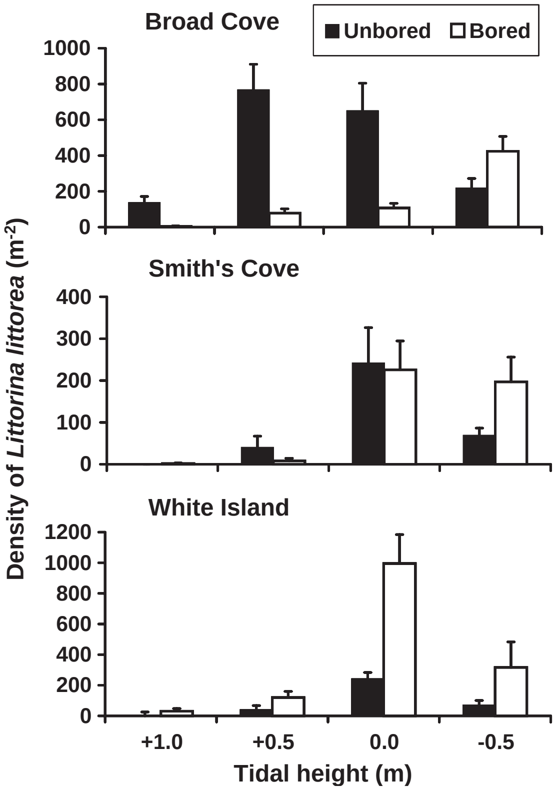

Fig. 2. Mean (+1SE) densities of *Cliona*-bored and unbored *Littorina littorea* at four tidal heights at each of the three study sites.

3.3. Morphometrics and shell strength of severely bored vs. unbored L. littorea

ANCOVAs examining the effects of boring on three snail morphological measures (lip thickness, dry shell mass, dry body mass) using shell height as the covariate produced nearly identical results to those performed with shell breadth as the covariate controlling for snail size. Additionally, log-transformations of the data had virtually no effect on residuals or model fit. Therefore, we report here only the results from the analyses performed with shell height on non-transformed data.

All three morphological measures differed significantly between bored and unbored snails (ANCOVA: lip thickness, $p = 0.0285$, dry shell mass, $p < 0.0001$, dry body mass, $p = 0.0006$; Fig. 4). Bored snails had 14.1% thicker aperture lips, but 7.1% less shell mass and 8.3% less dry body mass than unbored snails of the same shell height. As expected, shell height also had a significant effect on these three morphological variables: lip thickness, dry shell mass and dry body mass all increased significantly with shell height (lip thickness, $p < 0.0001$, dry shell mass, $p < 0.0001$, dry body mass, $p = 0.0002$). No significant interactions occurred between shell height and boring for any of the three morphological traits.

Bored and unbored snails subjected to compression force showed quite different relationships between load and displacement. Unbored shells were stiff, with a steep, smooth rise in load over a short displacement distance until the shell failed and load dropped sharply. In contrast, most bored shells sustained several microfractures, indicated as short drops in load (probably due to sponge cavities collapsing) before final shell failure.

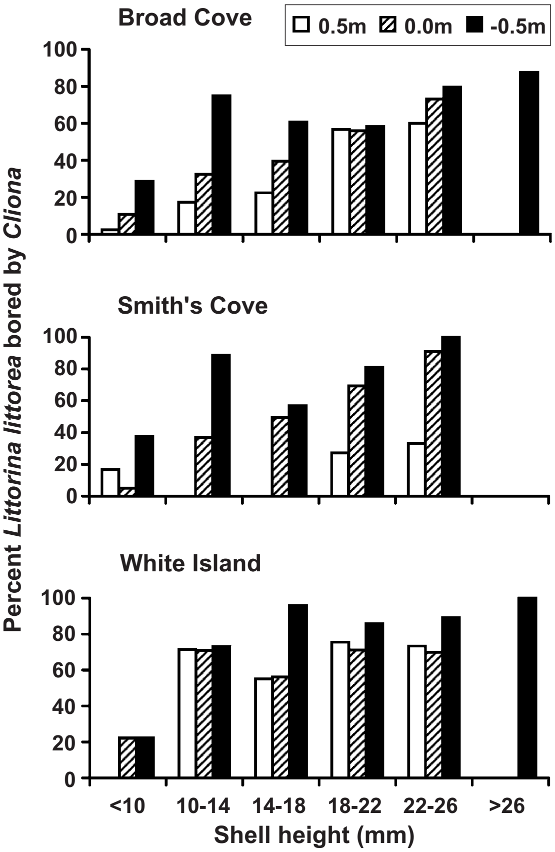

Fig. 3. Prevalence of *Cliona* boring across size classes of *Littorina littorea* at three tidal heights at each of the three study sites. The +1.0-m tidal height was excluded due to low densities of *L. littorea*.

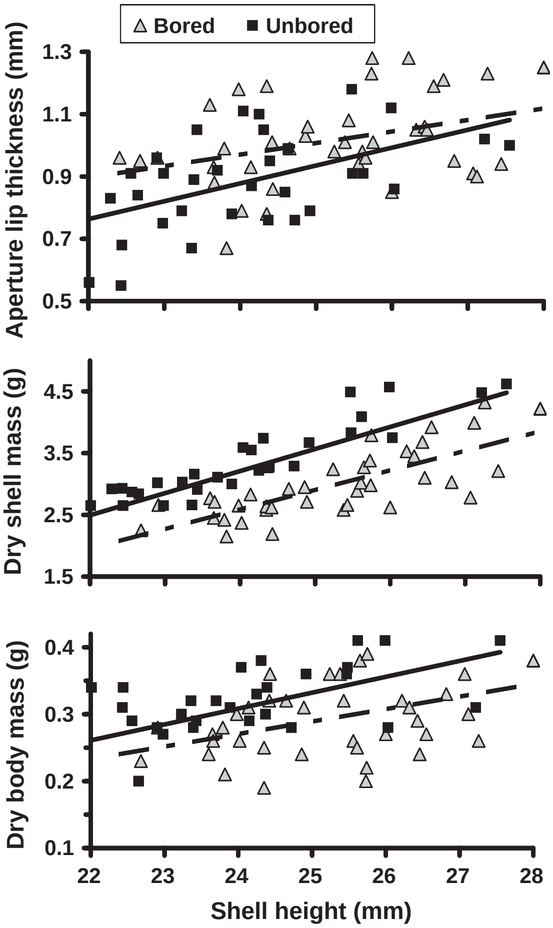

Fig. 4. Three morphological measurements of *Cliona*-bored and unbored *Littorina littorea* as a function of shell height. Solid lines = linear regressions for unbored snails; broken lines = linear regressions for bored snails.

Boring had a significant effect on the peak load before failure but shell height did not (ANCOVA: boring, $p < 0.0001$; shell height, $p = 0.29$; Fig. 5), with no significant interaction effect. On average, unbored shells could resist 40% greater crushing force than bored ones.

3.4. Relationship between shell volume and dry body mass in L. littorea

Dry body mass exhibited a highly significant ($p < 0.0001$) linear relationship with shell volume of *L. littorea*, with variation in shell volume explaining 92% of the variation in dry body mass. The linear regression equation was as follows: Dry body mass (g) = 0.1648 × Shell volume (ml) + 0.0002; Slope SE = 0.0056.

3.5. Effect of Cliona boring on vulnerability of L. littorea to predation by C. borealis

3.5.1. Size refuge experiment

For unbored *L. littorea*, shell size significantly affected the probability of being eaten (χ^2 test: $p = 0.01$; Fig. 6A). Over two-thirds of the smallest size class (20 mm) of unbored snails were eaten, while only slightly more than one-third of the medium-size classes (24 and 28 mm) and one-sixth of the largest (30 mm) were eaten. In contrast, for bored snails, shell size did not significantly affect the probability of being eaten (χ^2 test: $p = 0.58$).

The method of successful crab attack was strongly affected by both boring and shell size (logistic regression, likelihood ratio tests: size effect, $p = 0.0005$; boring effect, $p = 0.0002$). For unbored snails, shell crushing decreased dramatically with increasing shell size, from a high of 83% for 20 mm snails to a low of 23% for 28 mm snails (Fig. 6B). In contrast, for bored snails the frequency of crushing was high (80–94%), and decreased very little with increasing shell size. However, there was no significant interaction effect of boring and size on the crab attack method ($p = 0.23$).

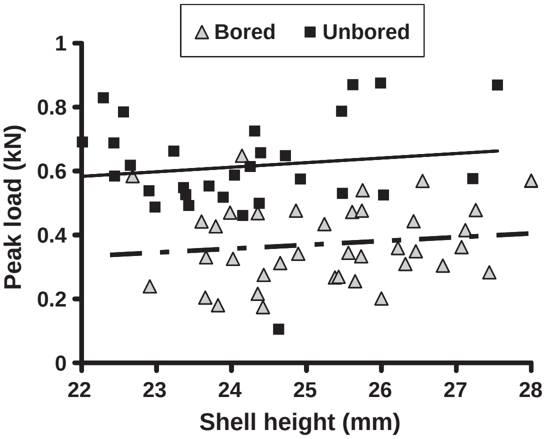

Fig. 5. Peak compressive load prior to shell fracture, plotted against shell height for *Cliona*-bored and unbored *Littorina littorea*. Solid line = linear regression for unbored snails; broken line = linear regression for bored snails.

3.5.2. Prey-choice experiment 1: single predator, two prey

When offered equal sized bored and unbored *L. littorea, C. borealis* ate the bored snail first in 7 of 17 total trials. These results do not differ statistically from the null hypothesis of no preference (χ^2 test, $p > 0.5$).

3.5.3. Prey-choice experiment 2: multiple predators, multiple prey

Approximately 50% of the snails were consumed by 36 h and all but one were eaten by 96 h. The mortality rate was fairly constant during the first 60 h and then rose as prey number dropped below 10%. Due to this effect of increasing predator/prey ratio, we restricted our survival analysis to the first 60 h of the experiment.

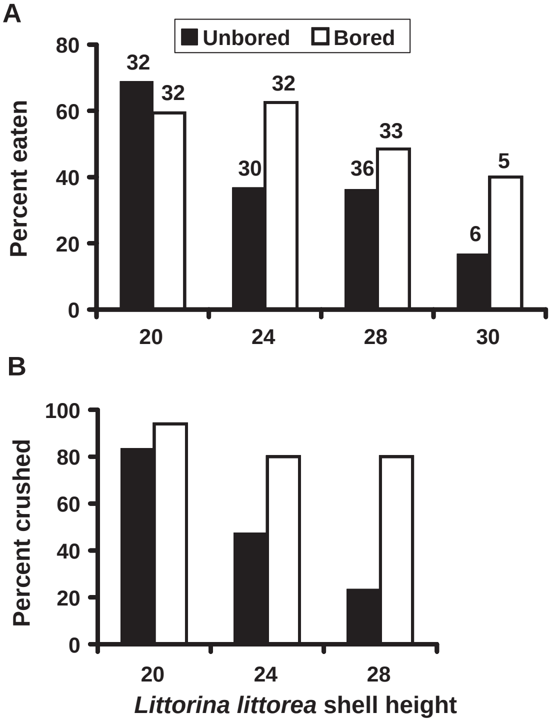

Fig. 6. Results from Prey-choice experiment 1: single predator, multiple prey. (A) Percent of bored and unbored *Littorina littorea* in different size-classes that were eaten by *Cancer borealis* (carapace widths = 85 ± 5 mm). Number of trials is shown above each bar. (B) For *L. littorea* that were eaten, the percent of each size class of that was crushed (as opposed to peeled) by *C. borealis*. See text for description of methods of attack used by the crabs.

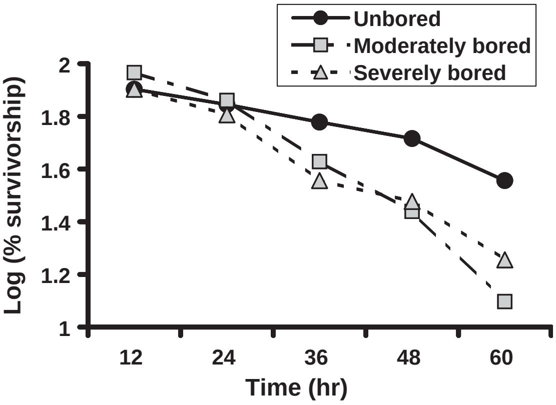

Fig. 7. Results from Prey-choice experiment 2: multiple predators, multiple prey. Survivorship of *Littorina littorea* as a function of time for three categories of *Cliona* boring: unbored, moderately bored (bored on spire only); severely bored (bored on both spire and body whorl).

Kaplan–Meier survival estimates revealed no overall effect of snail size (Log-Rank test; $p = 0.30$). However, survival plots were similar among the smallest four size categories (22, 24, 26, 28 mm); thus we grouped these categories and compared their survivorship to snails in the largest size category (≥30 mm). The largest snails had significantly higher survivorship than smaller ones (Log-Rank test; $p = 0.05$): at 36 h, 50% more of the largest snails were surviving relative to the smaller size classes.

Boring also had a significant effect on survivorship (Fig. 7; Log-Rank test, $p = 0.037$) with unbored snails having the lowest mortality rate. Survivorship curves for moderately and severely bored *L. littorea* were similar (Log-Rank test; $p = 0.85$). A comparison of unbored vs. bored (severely and moderately bored combined) showed significantly higher survivorship of unbored snails (Log-Rank test; $p = 0.01$). At 36 h, unbored snails had 54% higher survivorship than bored snails.

4. Discussion

Cliona infection in *L. littorea* was quite prevalent, with nearly half the sampled Isles of Shoals population infected. *Cliona* boring was found in *L. littorea* of all sizes but prevalence increased with increasing shell size. This pattern probably results from increasing cumulative probability of exposure to *Cliona* larvae with increasing age (and size) of snails. The frequency of *Cliona* infection also varied across tidal heights, with boring much more common in low intertidal and shallow subtidal periwinkles. Snails that consistently remain lower on the shore may be exposed to more *Cliona* larvae, or bored snails may be more likely to migrate to lower tidal heights.

Increased lip thickness of infected *L. littorea* indicates that snails respond to boring by adding more material on the inside of the shell, as seen in slipper shells and oysters (Hoeksema, 1983; Rosell et al., 1999). Unlike sponge growth on shell debris (Hartman, 1957), *Cliona* excavations do not penetrate the interior surface of the shells of live snails. Apparently, secretion of additional interior shell material allows the snail host to prevent or repair such penetrations. However, investment of energy and material in thickening the shell interior presumably decreases the amount available for reproduction and both body and shell growth (Rosell et al., 1999). Such an effect on reproduction has been reported in two species of *Nucella* in which thick-shelled snails produced fewer eggs than thin-shelled individuals of similar body mass (Etter, 1989; Geller, 1990). Boring will also indirectly reduce fecundity due to the decrease in shell living space (volume) that results from shell thickening. As reported elsewhere (Hughes, 1986), we found that dry body mass was tightly correlated with shell volume, and thus bored snails of a given shell height had less shell volume and smaller body sizes than unbored snails. Fecundity in another littorinid, *L. neritoides*, varies in proportion to body mass (Hughes and Roberts, 1980; Hughes, 1986); thus, shell thickening in response to boring likely results indirectly in lowered fecundity.

The added shell material does not compensate completely for shell lost to sponge cavities: bored snails have less shell mass than equal size unbored snails. More importantly, thickening of the shell does not completely restore shell strength. Reduced shell mass, and the change from a solid to a lattice-like shell structure in severely bored snails, reduced by 29% the force required to crush the shell. This contrasts with shell repair following apertural chipping, where shell strength is completely restored (Blundon and Vermeij, 1983). *L. littorea* bored by *Cliona* are weaker and thus more vulnerable to shell breakage under conditions, such as crushing predators or rolling boulders, where shells may be subjected to high compression loads.

L. littorea co-occur in the New England intertidal and shallow subtidal zones with a variety of predators that crush or peel mollusc shells. These include fishes [pollock: *Pollachius virens* (L); cunner: *Tautogolabrus adspersus* (Walbaum)] and decapods [American lobster (*H. americanus*), green crab (*Carcinus maenas*), Jonah crab (*C. borealis*), and rock crab (*C. irroratus*)]. During high tide, both fishes (Edwards et al., 1982; Ojeda and Dearborn, 1991) and crabs (*C. borealis*, large *Car. maenas*; Lozyniak, 2003) migrate up into the intertidal, feeding on a variety of invertebrate prey including *L. littorea.*

The ability of these predators to crush molluscs depends on the force and gape size of the jaws or chelae, which vary among species and increase with increasing predator size (Wainwright, 1987; Preston et al., 1996). Many studies, including this one, have shown that molluscan prey have a size refuge from crushing predators, but that the size refuge decreases with increasing predator size (Bertness and Cunningham, 1981; Creswell and McLay, 1990; Sousa, 1993). For unbored *L. littorea*, vulnerability to medium-sized (carapace width 85 mm) *C. borealis* decreased significantly as shell height reached 24 mm. In contrast, for large *C. borealis* (115 mm), predation declined only for snails ≥30 mm. The method the crabs used to attack unbored *L. littorea* also varied with snail size; smaller snails were crushed while larger snails were usually peeled. Crushing generally takes much less time, and requires fewer chelae compressions, than peeling (Hughes, 1993; Behrens Yamada and Boulding, 1998). Thus, the reduction in mortality risk with increasing prey size may be due to increased time, energy, or risk of chelae wear or breakage when feeding on larger snails, rather than a mechanical limitation on the ability of *C. borealis* to break open their shells (Juanes and Hartwick, 1990; Juanes, 1992; Palmer et al., 1999).

The prey size refuge in unbored *L. littorea* was eliminated or severely reduced by sponge boring; *Cliona* infected snails showed no significant reduction in mortality with increased shell size. Additionally, when feeding on bored snails, *C. borealis* did not switch from crushing to peeling with increasing prey size. Increased vulnerability to a crushing predator translated into increased mortality for bored snails when crabs were offered large numbers of both bored and unbored prey. The higher predation rate on bored snails does not appear to be due to active selection of *Cliona* infected *L. littorea*: when offered a pair of bored and unbored snails, the crab did not attack the bored individual first. This result is consistent with prior studies. Hughes and Seed (1995) found that crabs attack each sequentially encountered prey, regardless of prey size, and only abandon a prey after unsuccessful attempts to break the shell. In addition, crabs may be more persistent when attacking bored snails because initial chelae compressions are likely to produce microfractures in the shell. Crab-inflicted damage to a mollusc shell may also result in longer predator persistence times (Abby-Kalio, 1989).

Boring may also indirectly affect size refuges from *C. borealis* via reduced growth rates. Our data show bored snails devoted energy to thickening their shells and thicker shells are associated with slower growth rates in gastropods (Palmer, 1981). If the bored snails grow more slowly than unbored ones, they may experience more predation not only because they must grow to a larger size to escape crab predation, but also because they take longer to get there. Boring by *Cliona* is not the only cause of shell-thickening. Chemical cues indicating the presence of shell-breaking predators also stimulates the growth of thicker shells in snails (Palmer, 1990; Trussell, 1996). This induced defense decreases vulnerability of unbored snails to crab predation, but involves the same trade-offs in growth, body size, and potential decreases in fecundity associated with thicker shells (Palmer, 1985; Hughes, 1986).

In addition to the direct and indirect effects resulting from structural changes in their shells, *Cliona* boring may have other effects on *L. littorea*. For example, in our study bored periwinkles hosted more fouling organisms such as bryozoans, encrusting and erect algae, spirorbid polychaetes, and nematodes. To understand fully the costs to *L. littorea* of being bored, these additional indirect costs (and possible benefits) of sponge infection need to be quantified.

In other systems, the effects of boring sponges on hosts are not all negative. Boring sponges have been shown to increase erosion on coral reefs, particularly on reefs dominated by branching and plating corals where a relatively small area of infection can undermine the support of a colony (Rützler, 1975; Sammarco et al., 1987; Risk et al., 1995; Lopez-Victoria and Zea, 2004). However, many branching corals reproduce asexually via fragmentation; sponge bioerosion accelerates this process and thus may increase fitness, especially for species such as *Acropora cervicornis* that rarely reproduce sexually (Risk et al., 1995).

Overall, for *L. littorea*, infection by *Cliona* has both direct and indirect negative impacts on components of fitness. Infected snails produce interior shell layers with a concomitant decrease in potential body size and fecundity. In addition, by diverting energy to shell, bored *L. littorea* have less energy for reproduction and growth. Boring directly increases vulnerability to predation by weakening the shell, and structural changes increase the frequency of low-force microfractures that may increase predator persistence times. Finally, reduced growth rates increase predation risk because the snail remains in vulnerable size classes longer.

Shell boring may have additional downstream effects. Hermit crabs occupy empty gastropod shells and are preyed upon by the same suite of durophagous predators that feed on snails. However, postmortem changes result in a considerable reduction in the strength of shells borne by hermit crabs and reduce the size-dependence of vulnerability to predators (LaBarbera and Merz, 1992). In our study, boring by endobionts modified shell robustness even in living snails, thus weakening further the predictive value of shell size as a measure of shell strength. As a result, selection for size-discrimination by shell-breaking predators is diminished and unbored snails too large to be subjugated suffer sublethal attacks that weaken their shells and necessitate investment in repair (LaBarbera and Merz, 1992).

Boring by endobionts, therefore, has ecological and evolutionary ramifications for mollusc prey and their durophagous predators. Vermeij (1977, 1987) attributed the middle Mesozoic appearance of gastropod shell-strengthening features to the concurrent evolution of a number of durophagous molluscivores, including brachyuran crabs, lobsters, and bony and cartilaginous fishes. The evolutionary interplay between gastropods and their shell-breaking enemies continued through the late Mesozic and Cenozoic. The role of boring endobionts, which weaken shells of both live snails and those carried by hermit crabs, has been to decrease the effectiveness of shell defenses as well as the benefits to increased shell size, and to reduce selection for predators to avoid attacking seemingly well-defended prey.

Acknowledgements

We thank J. Bartsch, Cornell University, for providing training and time on the Instron machine, and research interns and staff at the Shoals Marine Laboratory for assistance in the field. Comments on an earlier draft provided by J. Morin, R. Palmer, R. Seeley, and N. Tisch were greatly appreciated. Funding for this research was provided by the NSF Research Experiences for Undergraduates at the Shoals Marine Laboratory and the Cornell Hughes Scholars Program. This is contribution number 121 from the Shoals Marine Laboratory. **[AU]**

References

Abby-Kalio, N.J., 1989. Learning and the role of cue reinforcement in the shell cracking behaviour of the shore crab: *Carcinus maenas* (L.). Behav. Processes 18, 141–153.

Behrens Yamada, S., Boulding, E.G., 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. J. Exp. Mar. Biol. Ecol. 220, 191–211.

Bertness, M.D., Cunningham, C., 1981. Crab shell-crushing predation and gastropod architectural defense. J. Exp. Mar. Biol. Ecol. 50, 213–230.

Blundon, J.A., Vermeij, G.J., 1983. Effect of shell repair on shell strength in the gastropod *Littorina irrorata*. Mar. Biol. 76, 41–45.

Creswell, P.D., McLay, C.L., 1990. Handling times, prey size and species selection by *Cancer novaezelandiae* (Jacquinot, 1853) feeding on molluscan prey. J. Exp. Mar. Biol. Ecol. 140, 13–28.

Edwards, D.C., Conover, D.O., Sutter III, F., 1982. Mobile predators and the structure of marine intertidal communities. Ecology 63, 1175–1180.

Etter, R.J., 1989. Life history variation in the intertidal snail *Nucella lapillus* across a wave-exposure gradient. Ecology 70, 1857–1876.

Geller, J.B., 1990. Consequences of a morphological defense: growth, repair and reproduction by thin- and thick-shelled morphs of *Nucella emarginata* (Deshayes) (Gastropoda: Prosobranchia). J. Exp. Mar. Biol. Ecol. 144, 173–184.

Guida, V.G., 1976. Sponge predation in the oyster reef community as demonstrated with *Cliona-celata*. J. Exp. Mar. Biol. Ecol. 25, 109–122.

Hadlock, R.P., 1980. Alarm response of the inter-tidal snail *Littorina littorea* (L) to predation by the crab *Carcinus maenas* (L). Biol. Bull. 159, 269–279.

Hartman, W.D., 1957. Ecological niche differentiation in the boring sponges (*Clionidae*). Evolution 11, 294–297.

Hartman, W.D., 1958. Natural history of the marine sponges of southern New England. Bull.-Peabody Mus. Nat. Hist. 12, 1–144.

Hoeksema, B.W., 1983. Excavation patterns and spiculae dimensions of the boring sponge *Cliona celata* from the Southwestern Netherlands. Senckenberg. Marit. 15, 55–85.

Hughes, R.N., 1986. A Functional Biology of Marine Gastropods. Johns Hopkins University Press, Baltimore, MD.

Hughes, R.N., 1993. Consumption of gastropods by the reef crab, *Ozius truncates* H. Milne-Edwards: the role of opportunistic foraging behaviour. In: Wells, F.E., Walker, D.I., Kirkman, H., Lethbridge, R. (Eds.), The Marine Flora and Fauna of Rottnest Island, Western Australia. Perth, W.A. (Australia), Western Australia Museum, pp. 443–454.

Hughes, R.N., Roberts, D.J., 1980. Growth and reproductive rates of *Littorina neritoides* (L.) in North Wales. J. Mar. Biol. Assoc. UK 60 (3), 591–600.

Hughes, R.N., Seed, R., 1995. Behavioural mechanisms of prey selection in crabs. J. Exp. Mar. Biol. Ecol. 193, 225–238.

Juanes, F., 1992. Why do decapod crustaceans prefer small-sized molluscan prey? Mar. Ecol. Prog. Ser. 87, 239–249.

Juanes, F., Hartwick, E.B., 1990. Prey size selection in Dungeness crabs: the effect of claw damage. Ecology 71, 744–758.

Kitching, J.A., Lockwood, J., 1974. Observations on shell form and its ecological significance in thaid gastropods of the genus *Lepsiella* in New Zealand. Mar. Biol. 28, 131–141.

LaBarbera, M., Merz, R.A., 1992. Postmortem changes in strength of gastropod shells: evolutionary implications for hermit crabs, snails, and their mutual predators. Paleobiology 18, 367–377.

Lee, E.T., 1992. Statistical Methods for Survival Data Analysis, 2nd ed. John Wiley & Sons, New York.

Lopez-Victoria, M., Zea, S., 2004. Storm-mediated coral colonization by an excavating Caribbean sponge. Clim. Res. 26, 251–256.

Lozyniak, S., 2003. Making connections across ecosystems: tidal and seasonal movements of the marine crab *Cancer borealis*. Biology Honors Thesis, Cornell University, Ithaca, New York.

Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112, 23–29.

Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64, 1116–1123.

McQuaid, C.D., 1996. Biology of the gastropod family Littorinideae: II. Role in the ecology of intertidal and shallow marine ecosystems. Oceanogr. Mar. Biol. 34, 263–302.

Ojeda, F.P., Dearborn, J.H., 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities in the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 149, 13–44.

Palmer, A.R., 1981. Do carbonate skeletons limit the rate of body growth? Nature 292, 150–152.

Palmer, A.R., 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. Veliger 27, 349–356.

Palmer, A.R., 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). Hydrobiologia 193, 155–182.

Palmer, A.R., 1992. Calcification in marine molluscs: how costly is it? Proc. Natl. Acad. Sci. U. S. A. 89, 1379–1382.

Palmer, A.R., Taylor, G.M., Barton, A., 1999. Cuticle strength and the size-dependence of safety factors in *Cancer* crab claws. Biol. Bull. 196, 281–294.

Pomponi, S.A., 1980. Cytological mechanisms of calcium carbonate excavation by boring sponges. Int. Rev. Cyt. 65, 301–319.

Preston, S.J., Revie, I.C., Orr, J.F., Roberts, D., 1996. A comparison of the strengths of gastropod shells with forces generated by potential crab predators. J. Zool. 238, 181–193.

Reid, D.G., 1996. Systematics and Evolution of *Littorina*. The Ray Society, London.

Risk, M.J., Sammarco, P.W., Edinger, E.N., 1995. Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. Coral Reefs 14, 79–86.

Rosell, D., Uriz, M.J., Martin, D., 1999. Infestation by excavating sponges on the oyster (*Ostrea edulis*) populations of the Blanes littoral zone (north-western Mediterranean Sea). J. Exp. Mar. Biol. Ecol. 79, 409–413.

Rützler, K., 1975. The role of burrowing sponges in bioerosion. Oecologia 19, 203–216.

Sammarco, P.W., Risk, M.J., Rose, C., 1987. Effects of grazing and damselfish territory on internal bioerosion of dead corals: indirect effects. J. Exp. Mar. Biol. Ecol. 112, 185–199.

Sousa, W.P., 1993. Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman. J. Exp. Mar. Biol. Ecol. 166, 19–37.

Taylor, J.D., Reid, D.G., 1990. Shell microstructure and mineralogy of the Littorinidae: ecological and evolutionary significance. Hydrobiologia 193, 199–215.

Trussell, G.C., 1996. Phenotypic plasticity in an intertidal snail: the role of a common crab predator. Evolution 50, 448–454.

Trussell, G.C., Ewanchuk, P.J., Bertness, M.D., 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecol. Lett. 5, 241–245.

Vermeij, G.J., 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3, 245–258.

Vermeij, G.J., 1987. Evolution and Escalation. Princeton University Press, Princeton, NJ.

Vosmaer, G.C.J., 1933. The Sponges of the Bay of Naples: *Porifera incalcaria*, vol. 1. Martinus Nijhoff, The Hague, pp. 1–456.

Wainwright, P.C., 1987. Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish *Lachnolaimus maximus*. J. Zool. 213, 283–297.