

# Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors

Meg M. Eastwood · Megan J. Donahue · Amy E. Fowler

Received: 11 February 2006 / Accepted: 12 July 2006 / Published online: 11 November 2006  
© Springer Science+Business Media B.V. 2006

**Abstract** Studying historic invasions can provide insight into the ongoing invasions that threaten global biodiversity. In this study, we reconsider the impacts of *Littorina littorea* and *Carcinus maenas* on the rocky intertidal community of the Gulf of Maine. Past research using invader-removal experiments demonstrated strong top-down effects of *L. littorea* on algal community structure; however, such removal experiments may overlook the long-term effects of niche shifts and local extinctions caused by invasive species. We considered how a niche-shift in the native littorine, *Littorina saxatilis*, may change the interpretation of *L. littorea* impacts. Using a factorial experiment crossing predator presence/absence with *L. littorea* presence/absence, we found

that *L. saxatilis* is able to exert top-down control on ephemeral algae similar to that exerted by *L. littorea* and that both competition by *L. littorea* and predation by *C. maenas* have strong, negative impacts on *L. saxatilis*. We also found higher predation rates on protected shores and at lower tidal heights and preferential predation on *L. saxatilis* compared to *L. littorea*. While movement experiments demonstrate that behavioral response to tidal height is the proximate cause of *L. saxatilis* exclusion from the lower intertidal, our study suggests that the ultimate causes are the additive effects of competition from and predation by invasive species.

**Keywords** *Carcinus maenas* · Competition · Gulf of Maine · Invasive species · *Littorina littorea* · *Littorina saxatilis* · Niche shift · Predation · Top-down effects · Trophic interactions

---

M. M. Eastwood  
Grinnell College, Grinnell, IA, USA

M. J. Donahue · A. E. Fowler · M. M. Eastwood  
Shoals Marine Laboratory, Isles of Shoals, ME, USA

M. J. Donahue  
Department of Biological Sciences, Humboldt State  
University, Arcata, CA, USA

A. E. Fowler  
University of New Hampshire, Durham, NH, USA

M. M. Eastwood (✉)  
2417 N. Fremont Blvd, Flagstaff, AZ 86001, USA  
e-mail: megeastwood@gmail.com

## Abbreviations

GOM Gulf of Maine

## Introduction

Invasive species are a growing threat to global biodiversity (Mack et al. 2000). Understanding the impacts of historical invasions can help us to predict the course of current invasions, because

the ecological effects of invasive species may change over time (Holway et al. 2002). Studies of past introductions demonstrate that the effects of invasive species are complex (Zavaleta et al. 2001) and can permanently alter the structure of communities (Carlton 2003) through niche shifts (Levin 2003), local extinctions (Dulvy et al. 2003), and changes in ecosystem processes (Simberloff and VonHolle 1999; Mack and D'Antonio 2003). The impacts of past invasions can be particularly challenging to interpret when multiple species have been introduced and native communities are changed through the additive or synergistic effects of interacting invaders (Simberloff and VonHolle 1999; Levin et al. 2002). Invader-removal experiments are a common approach (e.g., Bertness 1984; Mack and D'Antonio 2003) and a powerful tool for studying invader impacts; however, these experiments can neglect long-term changes, such as niche shifts and local extinctions, if the time scale of the experiment is short or the time since invasion is long.

In the Gulf of Maine (GOM), several introduced species have become numerically dominant, including the intertidal gastropod *Littorina littorea* and the European green crab *Carcinus maenas*. *L. littorea* arrived in New England in the mid-1800s, moving south from Nova Scotia, where it was either introduced from Europe (Bertness 1984; Carlton 1992; Ganong 1886) or emerged from glacial refugia in the North Atlantic (Wares et al. 2002). Today its population far surpasses that of any other herbivorous snail in the GOM (Lubchenco 1978) and several influential studies have demonstrated top-down control of the algal community by *L. littorea* on sheltered and wave-exposed shores (Bertness 1984; Lubchenco 1978; Lubchenco and Menge 1978). On rocky intertidal benches where predators control the abundance of the blue mussel *Mytilus edulis*, hardy perennial algae such as *Chondrus crispus* are the dominant space-holders. However, when *L. littorea* is removed, ephemeral algae overgrow the perennial algae (Lubchenco 1978; Lubchenco and Menge 1978) because *L. littorea* prefers to graze on the sporelings of ephemeral algae (Lubchenco 1978). Due to the dramatic changes in sedimentation and algal

cover with the removal of *L. littorea* (Lubchenco 1978; Lubchenco and Menge 1978; Bertness 1984), it is widely argued that the establishment of *L. littorea* caused profound top-down changes in the intertidal community (Bertness 1998; Carlton 1992; Vadas and Elner 1992). While this is certainly true, these conclusions are based on *L. littorea* removal experiments nearly 150 years after *L. littorea* introduction and may not account for long-term changes in the GOM community. Long-term changes, such as niche shifts and local extinctions in response to the arrival of *L. littorea* and the subsequent introduction of *C. maenas*, complicate the interpretation of removal experiments. In this paper, we reconsider the impacts of *L. littorea* in light of broader potential changes in the GOM community. We suggest that *L. littorea*'s current, dominant role in top-down control of the intertidal algal community might not be a new community process, but that the arrival of *L. littorea* and *C. maenas* may have displaced native grazers in that role. In particular, we consider the possibility of a niche shift in the native gastropod *Littorina saxatilis*.

Today in the GOM, *L. saxatilis* inhabits rock crevices in the high intertidal spray and barnacle zones and is found only rarely in the lower intertidal zone (Lubchenco and Menge 1978; Behrens Yamada and Mansour 1987; *personal observation*). However, several lines of evidence indicate that *L. saxatilis* had a more extensive tidal range before the arrival of *L. littorea* and *C. maenas*. First, transplant experiments in New England have shown that, in the absence of competition from *L. littorea*, *L. saxatilis* grows  $\sim 6 \times$  faster in the low intertidal than in the high intertidal where it is most abundant (Behrens Yamada and Mansour 1987), suggesting that *L. saxatilis* could have occupied a more extensive tidal range in the absence of *L. littorea*. Second, in the northern part of its range where *L. littorea* and *C. maenas* do not occur, higher densities of *L. saxatilis* extend to the middle intertidal (Johannesson and Johannesson 1990; Reid 1996, p. 326) and subtidal (Reid 1996, p. 326; Gilkinson and Methven 1991). Third, Ganong (1886) reports that native littorines declined dramatically with the expansion of *L. littorea*. Other native littorines, such as *Littorina obtusata* and *Lacuna*

*vincta*, may also have been more abundant in the low intertidal before *L. littorea* arrived. Currently, *Lacuna vincta* grazes on kelp and other brown algae, primarily in the subtidal (Johnson and Mann 1986; Thomas and Page 1983); at high abundance, it can have negative impacts on local populations of algae (Thomas and Page 1983; Fralick et al. 1974). Currently, *Littorina obtusata* occurs almost exclusively on *Ascophyllum nodosum* and other furoid algae in the mid-intertidal (Hadlock Seeley 1982, abstract only). In this study, we focused on the possibility of a niche shift in the native grazer *L. saxatilis* because it occurs across a wider variety of habitats than any other *Littorina* species (Reid 1996, p. 324) and it shows strong local adaptation to these habitats (Johannesson and Johannesson 1990). If native littorines, such as *L. saxatilis*, exerted top-down control on the algal community before the arrival of *L. littorea*, then the community impacts of *L. littorea* must be reinterpreted: instead of a dramatic shift in the algal community, *L. littorea* may have brought a dramatic shift in the distribution of the native grazers. While it is impossible to definitively determine whether *L. saxatilis* or other native littorines experienced niche shifts in the wake of *L. littorea* expansion (we have reviewed early accounts and know of no data on *L. saxatilis* distribution in the North American intertidal before the expansion of *L. littorea*), we can determine whether *L. saxatilis* is capable of top-down control on the algal community similar to that demonstrated by *L. littorea*.

A second invader may also exclude *L. saxatilis* from the lower intertidal: *Carcinus maenas*, the European green crab, was introduced to eastern North America in the early 1800s and expanded its range north of Cape Cod in the early 1900s (Grosholz and Ruiz 1996; Vermeij 1982). *C. maenas* has the highest per capita prey consumption rate of any intertidal predator on the New England coast (Menge 1983), and its introduction affected other native organisms, including the rapid decline in populations of *Mya arenaria* (Ropes 1968) and a change in the shell morphology of *Littorina obtusata* (Hadlock Seeley 1986; Trussell and Smith 2000). Notably, the arrival of *C. maenas* had little effect on *L. littorea*, resulting in an increase in the rate of shell repair,

but no change in shell thickness (Vermeij 1982). Vermeij (1982) suggests two hypotheses to explain this: (i) *L. littorea* and *C. maenas* share a long evolutionary history in Europe; if *L. littorea* was introduced from Europe, then it had little time to adapt to a low predation environment before the introduction of *C. maenas*. (ii) “Geographically haphazard” variation in predation pressure combined with widely dispersed pelagic larvae could prevent local adaptation to predation. The situation is different for North American populations of the native grazer, *L. saxatilis*, which is ovoviviparous, has a long history in North America without *C. maenas*, and exhibits strong local adaptation (Johannesson and Johannesson 1990; Johannesson 2003). These characteristics suggest the possibility of a niche shift in response to *C. maenas* introduction. In addition, in the northern part of *L. saxatilis*’ range where *C. maenas* is absent, *L. saxatilis* distribution extends into the mid- and lower intertidal (Reid 1996, p. 326). Predation by *C. maenas* could reinforce the exclusion of *L. saxatilis* from the lower intertidal additively, through direct predation, or synergistically, if *L. littorea* supports higher densities of *C. maenas* (i.e., apparent competition) and/or if *C. maenas* prefers *L. saxatilis* to *L. littorea*.

In this study, we investigated the impact of *L. littorea* and *C. maenas* on the GOM intertidal community, asking: (1) is *L. saxatilis* capable of top-down control of the algal community, similar to the effect exerted by *L. littorea*? and (2) how do competition by *L. littorea* and predation by *C. maenas* contribute to the exclusion of *L. saxatilis* from the lower intertidal?

## Materials and methods

### Field experiment

To investigate the relative effects of competition and predation on *L. saxatilis*, we added *L. saxatilis* to four caged treatments crossing competition (*L. littorea* included/excluded) with predation (predators excluded/not excluded) and measured *L. saxatilis* growth and mortality in each treatment. To compare the effect of *L. saxatilis* and

*L. littorea* grazing on the algal community, we measured the change in algal composition in each of these four treatments and in three additional controls: no cage with natural density of *L. littorea*, cage control with natural density of *L. littorea*, and full cage with *L. littorea* removed. There were seven treatments in total (Table 1). The experiment was conducted from July 10 to August 7, 2004, on the sheltered northeast shore of Appledore Island, a 38.44-ha island in the Isles of Shoals, Maine (42°58' N, 70°37' W). We used a randomized, complete-block design with each treatment replicated once in each of seven blocks; this design controls for between-block variability but precludes the analysis of block  $\times$  treatment interactions (Neter et al. 1996; Underwood 1997; Gotelli and Ellison 2004). We set up the seven experimental blocks on flat, rock benches in the *Chondrus/Mastocarpus* zone between 0.15 m and 0.6 m MLLW; each block contained one replicate each of seven treatments (Table 1). All treatments were circular plots (30 cm diameter) and cages were constructed of galvanized wire (13 cm tall, 1.27 cm  $\times$  1.27 cm mesh) with a flange that was bolted into the rocky bench. Cages were effective at including and excluding *L. littorea*, but *L. saxatilis* were small enough to fit through the mesh; therefore, all *L. saxatilis* were tethered to a lag screw secured in the middle of each cage (Rochette and Dill 2000). Predator-exclusion treatments were complete cages with galvanized wire lids while predator-access treatments were partial cages without lids and with windows cut in the sides. Every other day, cages were sampled to untangle the tethered snails, check for *L. saxatilis*

mortality, and add/remove *L. littorea* to maintain treatment densities.

#### Grazer impacts on algae

To measure the effect of grazers in different treatments, we performed initial and final algal surveys four weeks apart. A grid of 45 points was sampled in each treatment; if algae were layered or epiphytic, both species were recorded. For analysis, species were grouped into “edible algae” (*Ulva lactuca*, *Rhizoclonium tortuosum*, *Dumontia contorta*, *Polysiphonia* sp., *Ceramium* sp., *Porphyra* sp., *Spongomorpha*, *Acrosiphonia arcta*, and *Claudophora sericea*; ephemeral species ranked “high” preference in Lubchenco 1978) and “unpreferred algae” (*Chondrus crispus*, *Mastocarpus stellatus*, *Coralina officinalis*, *Codium fragile* subsp. *tomentosoides*, and *Fucus* sp; species ranked “medium” and “low” preference in Lubchenco 1978). Our response variable was the change in percent cover of edible algae. We analyzed this experiment as a two-way main-effects ANOVA with block as a random main-effect and treatment as a fixed-effect in JMP version 5.1; this is the appropriate analysis for a randomized complete-block design, which controls for between-block variance but precludes the analysis of a block  $\times$  treatment interaction (Neter et al. 1996; Gotelli and Ellison 2004). We used planned comparisons with Bonferonni correction to (i) test the effect of caging (Treatment 1 vs. Treatment 2), (ii) repeat past experiments on the effects of *L. littorea* removal on algal populations (Treatment 1 vs. Treatment 3), and (iii)

**Table 1** The seven treatments used in the field experiment

| Treatment                    | Predator manipulation              | <i>L. saxatilis</i> density | <i>L. littorea</i> density |
|------------------------------|------------------------------------|-----------------------------|----------------------------|
| 1 control                    | Allowed: no cage                   | 0                           | natural                    |
| 2 cage control               | Allowed: partial cage with lid     | 0                           | natural                    |
| 3 <i>L. littorea</i> removal | Allowed: complete cage without lid | 0                           | 0                          |
| 4 +competition, +predation   | Allowed: partial cage without lid  | 15                          | 15                         |
| 5 – competition, +predation  | Allowed: partial cage without lid  | 30                          | 0                          |
| 6 +competition, – predation  | Excluded: complete cage with lid   | 15                          | 15                         |
| 7 – competition, – predation | Excluded: complete cage with lid   | 30                          | 0                          |

Treatments were blocked at seven sites; each site contained one of each treatment ( $n = 7$ ). Predator exclusion cages had lids and complete sides; predator access cages had no lids and three windows cut into the sides. Even with windows, the cages were effective at retaining *L. littorea*; *L. littorea* densities were checked and adjusted every other day

test whether the top-down effect exerted by *L. saxatilis* is similar to that exerted by *L. littorea* (Treatment 7 vs. Treatment 3 and Treatment 7 vs. Treatment 2).

### *Snail growth and mortality*

To test the effects of competition and predation on *L. saxatilis* growth, we measured, tagged, and randomly assigned *L. saxatilis* to treatments in each block (Table 1). Snails were tagged at the edge of the aperture and growth was measured by growth beyond the tag (“lip increment”, see Behrens Yamada and Mansour 1987). We averaged lip increment per unit length across all snails in each cage and compared treatments using ANOVA with block as a random main effect and competition and predation as fixed, crossed factors. To test for the effects of competition and predation on *L. saxatilis* survivorship, we recorded mortality every other day. Mortality included obvious predation by crabs (crushed or peeled shell fragments) and missing individuals. Restricting the analysis to crushed and peeled snails did not change the patterns of significance and probably underestimates predation; therefore, we report total mortality. Using a multiplicative risk model for competition and predation (Sih et al. 1998), we compared  $\log(x+1)$ -transformed snail survival using ANOVA with block as a random main effect and competition and predation as fixed, crossed factors. We designed this experiment to compare the effects of interspecific competition and predation on the growth and mortality of *L. saxatilis* and not to compare intra- and inter-specific competition. (To compare intra- and inter-specific competition, a symmetric design would be preferred, though the strong competitive dominance of *L. littorea* over *L. saxatilis* makes this comparison possible even in the asymmetrical case (Underwood 1997)).

### *Tethering control*

To test for a tethering artifact, we performed tethering controls in the lab. Ten tethered and ten untethered *L. saxatilis* were placed in each of four

large containers with a male *C. maenas* (40–45 mm in carapace width) that had been starved for 48 h. Snail mortality was tracked for 18 h or until all snails had been consumed. Survival of tethered and untethered snails was compared using a Cox proportion hazards model (Hosmer and Lemeshow 1999); there was no effect of tethering on survival ( $P = 0.38$ ).

### *Predation by exposure, tidal height, size, and species*

To test for the effect of wave exposure and tidal height on predation pressure, fifty *L. saxatilis*, collected at 4 m MLLW from Broad Cove on Appledore Island were tethered in sheltered and wave-exposed areas at low and high tidal heights (low = 0.5 m, tidal height of the main experiment; high = 4 m, approximate height of peak *L. saxatilis* density on Appledore Island). Very few *L. saxatilis* are currently found near 0.5 m on Appledore Island (personal observation). Mortality on the tethers was monitored every day for six days and survival was compared across tidal height and exposure using a Cox proportional hazards survival analysis (Hosmer and Lemeshow 1999).

To compare the predation on *L. saxatilis* and *L. littorea* of different sizes along a depth gradient, individuals of both species were tethered to bricks placed at each of four depths (–4, –2, 0, and 0.5 m MLLW). At each depth, we tethered two *L. saxatilis* (one small, 7–9 mm, and one large, 11–14 mm) and three *L. littorea* (one small, 8–13 mm, one medium, 15–19 mm, and one large, 20–25 mm); for analysis, all *L. littorea* >15 mm were classified as “large”. Bricks were checked at dawn and dusk for seven days. We performed a Cox proportional hazard survival analysis to test the effect of size class, species, size class  $\times$  species, and depth on survival; preliminary analysis indicated no interactions with depth ( $P > 0.3$ ). Since size class and species are confounded, we also compared survival of small *L. littorea* (8–13 mm) and all *L. saxatilis* (7–9 mm and 11–14 mm) using a planned contrast (Hosmer and Lemeshow 1999).

## Snail movement

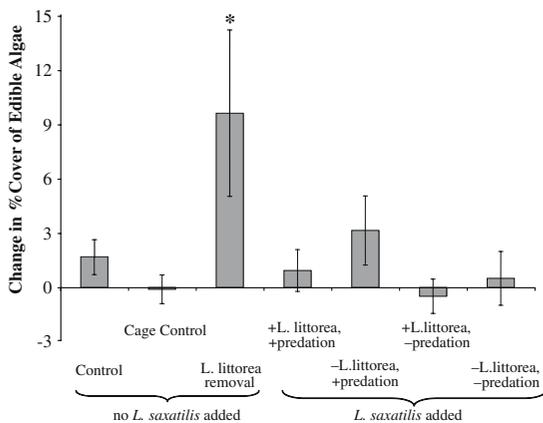
To assess the proximate cause of *L. saxatilis* distribution, fifty *L. saxatilis* were collected at 5 m, marked, and released at each of three tidal heights: 0.15, 5, and 7 m. Snails were transported to release sites in water and the release sites were moistened if dry. Twenty-four hours later, we searched within 3 m of the release point for marked snails and shell fragments (a pilot study indicated that no snail moved more than 2.2 m during a 24 h release period). For each recapture, we measured the total distance and the vertical distance moved from the release point and compared groups using a one-way ANOVA. Because no snails moved vertically in the 7 m treatment, there was heteroscedasticity among tidal heights despite  $\log(x+1)$  transformation. However, removing the 7 m group from the analysis did not affect the conclusions; therefore, we present the analysis on the entire dataset.

## Results

### Field experiment

#### Grazer impacts on algae

Edible algae responded to grazer density ( $F_{6,36} = 4.20$ ,  $P = 0.003$ , Fig. 1): the treatment

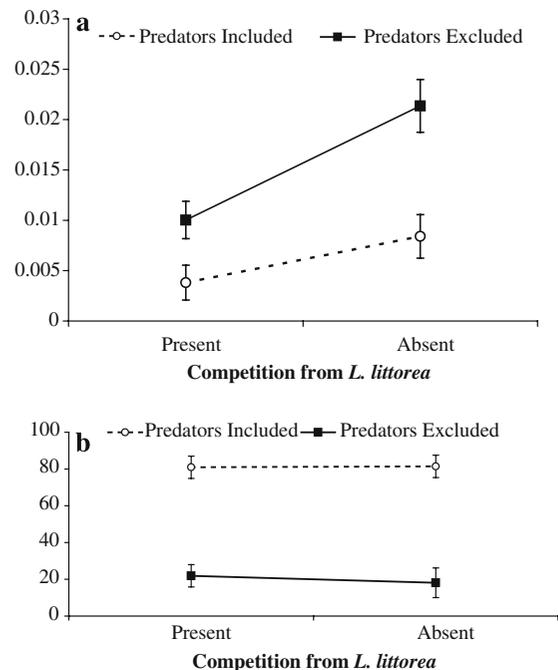


**Fig. 1** Change in percent cover of edible algae after four weeks. The *L. littorea* treatment was different from all other treatments. Treatments 4–7 include *L. saxatilis* (see Table 1). The error bars represent  $\pm$  standard error

with no snails had more edible algae than all other treatments (Treatment 3 vs. all other treatments,  $P < 0.001$ ). Edible algae increased in response to *L. littorea* removal compared to the control (Treatment 3 vs. Treatment 1,  $P = 0.001$ ) and the presence of *L. saxatilis* prevented this increase (Treatment 3 vs. Treatment 7,  $P < 0.002$ ). There was no difference in algal community response between cages with *L. littorea* and those with *L. saxatilis* (Treatment 2 vs. Treatment 7,  $P = 0.77$ ). Caging did not affect algal growth (Treatment 2 vs. Treatment 1,  $P = 0.45$ ) but algal growth varied from block to block ( $F_{6,36} = 4.52$ ,  $P = 0.0015$ ).

#### Snail growth and mortality

Competition with *L. littorea* reduced *L. saxatilis* growth rate in field cages by 44% ( $F_{1,18} = 29.3$ ,  $df = 1$ ,  $P < 0.0001$ ) and predation reduced *L. saxatilis* growth by 43% ( $F_{1,18} = 42.5$ ,  $P < 0.0001$ ) (Fig. 2a). However, there was an interaction between predation and competition moderating the effect of each in the presence



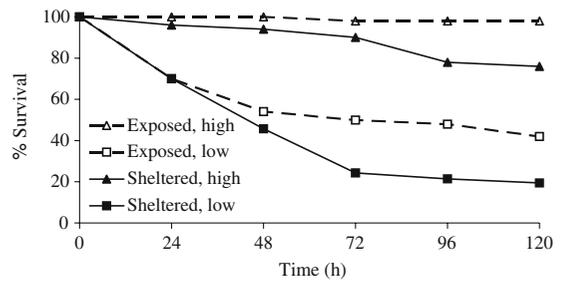
**Fig. 2** The effects of competition and predation on growth (a) and survivorship (b) of *L. saxatilis*. The error bars represent  $\pm$  standard error

of the other ( $F_{1,18} = 5.25$ ,  $P = 0.03$ , Fig. 2a). The combined effects of predation and competition produced an overall reduction in growth rate of 65%. Mortality rate was four-times higher in cages open to predation ( $F_{1,18}=127$ ,  $P < 0.0001$ ), while there was no effect of competition on mortality ( $F_{1,18}=0.027$ ,  $P = 0.87$ ) (Fig. 2b).

Predation by exposure, tidal height, size, and species

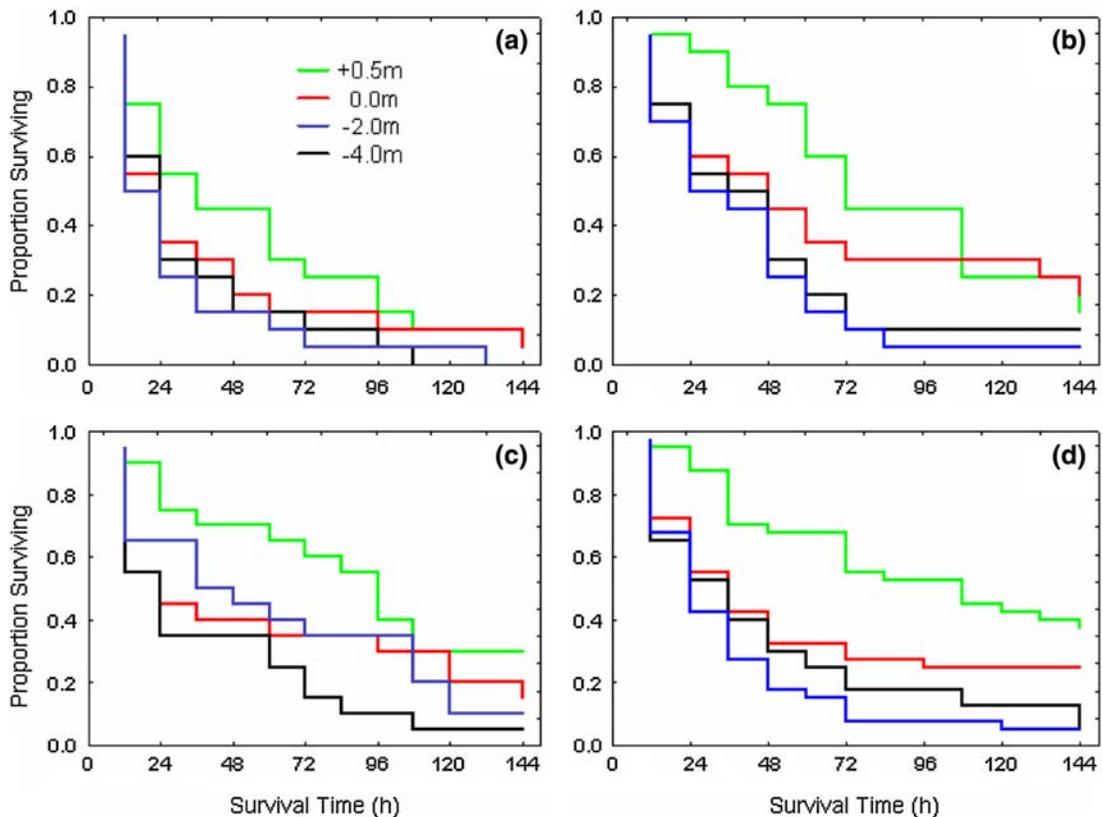
*L. saxatilis* in sheltered habitat were eaten at twice the rate of those in exposed habitat ( $P = 0.004$ ). Snails in the low intertidal were eaten at four times the rate of those in the high intertidal ( $P < 0.001$ ) (Fig. 3). The effect of tidal height was marginally stronger on sheltered shores ( $P = 0.054$ ).

The trend of increasing predation with decreasing tidal height continued into the subtidal (Fig. 4).



**Fig. 3** Survivorship of *L. saxatilis* tethered on the exposed (dashed lines) and sheltered (solid lines) sites at low (squares) and high (triangles) tidal heights

Snail survival rate decreased 14% every meter into the subtidal from 0.5 m MLLW to -4 m MLLW. Overall, *L. saxatilis* are 55% more likely to die than *L. littorea* ( $P = 0.008$ ) (Fig. 4, a and c vs. b and d) and large size class snails die at a rate 38% lower than small size class snails ( $P = 0.003$ ) (Fig. 4, a and b vs. c and d). However, there was no difference in hazard rate between small *L. littorea* and all



**Fig. 4** Survivorship of (a) small *L. saxatilis*, (b) small *L. littorea*, (c) large *L. saxatilis*, and (d) large *L. littorea* plotted for each depth. Overall survival decreased 14% for every meter into the subtidal

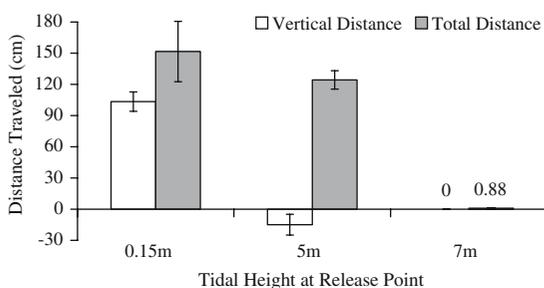
*L. saxatilis* (planned comparison,  $P = 0.93$ ), indicating that the interspecific difference in hazard rate is largely due to the interspecific size difference. Within species, smaller size was marginally more important in *L. saxatilis* (38% increase in mortality) than in *L. littorea* (5% increase in mortality) ( $P = 0.06$ , Fig. 4).

### Snail movement

In the mark-recapture study, 60%, 74%, and 100% of *L. saxatilis* released at the 0.15, 5, and 7 m were recovered, respectively. Concurrent tethering experiments indicated that the overnight mortality rate at the site was 30% and 8% at 0.5 and 5 m, respectively, accounting for most of the unrecovered snails. Snails released at 7 m moved very little (<1 cm), traveling a smaller total distance than those released at either 0.15 m (152 cm) or 5 m (124 cm) (Tukey HSD,  $P = 0.0001$ , Fig. 5). *L. saxatilis* released at 0.15 m traversed more vertical distance (103 cm) than those released at 5 m (–15 cm) and 7 m (0 cm) (Tukey HSD,  $P = 0.0001$ , Fig. 5). No snails released at 0.15 m moved down; snails released at 5 m moved both up and down but had a net downward movement.

### Discussion

Removing *L. littorea* increased the amount of edible algae, in accord with previous studies (Bertness 1984; Lubchenco 1978) (Fig. 1). The addition of *L. saxatilis* prevented this increase in edible algae (Fig. 1), indicating that *L. saxatilis*



**Fig. 5** The distance traveled by *L. saxatilis* at three different tidal heights (0.15, 5, and 7 m). The error bars represent  $\pm$  standard error

and *L. littorea* grazing have similar top-down effects on the algal community. Therefore, if *L. saxatilis* inhabited the lower intertidal region of the GOM before the arrival of *L. littorea*, *L. saxatilis* could have exerted top-down control on the algal community, precluding the dramatic shifts in the algal community of rocky benches suggested by *L. littorea* removal experiments alone.

Both competition and predation had strong negative effects on *L. saxatilis* (Fig. 2a, b). Competition decreased *L. saxatilis* growth rate by 44% (Fig. 2a) while predation decreased both growth rate (43%) (Fig. 2a) and survival (75%) (Fig. 2b). While Ganong (1886) links the decline of native littorines to increases in *L. littorea*, the subsequent northward expansion of *C. maenas* has reinforced this decline. Now that *L. littorea* and *C. maenas* are both abundant in the GOM, *C. maenas* may be more important than *L. littorea* in enforcing the lower boundary of *L. saxatilis*' distribution due to pronounced effects on both *L. saxatilis* growth and mortality (Fig. 2).

Our transplant experiment suggests that the proximate cause of current *L. saxatilis* distribution in the GOM is primarily behavioral. When moved to a lower tidal height, *L. saxatilis* moves vertically to regain its original tidal height (Fig. 5). Rochette and Dill (2000) found similar behavior in the intertidal littorines *L. sitkana* and *L. scutulata*, which moved shoreward when released subtidally. However, the ultimate factors excluding *L. saxatilis* from the lower intertidal include both competition and predation (Fig. 2). Previous research in New England (Behrens Yamada and Mansour 1987) demonstrated that in the absence of *L. littorea*, *L. saxatilis* grow 6  $\times$  faster at lower tidal heights than at the higher tidal heights where they are usually found. In our study, *L. saxatilis* growth rate was reduced dramatically due to competition with *L. littorea* (Fig. 2a), and this reduced growth rate leaves *L. saxatilis* more susceptible to predation by *C. maenas* as the crabs prefer to prey upon smaller snails (Fig. 4a and b vs. c and d). Similarly, Elner and Raffaelli (1980) compared predation by *C. maenas* on *L. saxatilis* (= *L. rudis*) and *L. compressa* (= *L. nigrolineata*) in the northeast Atlantic and found that *L. saxatilis*, the

smaller species, was more likely to be consumed; correspondingly, they found that *L. saxatilis* is higher on the shoreline than *L. compressa* in areas of high crab density. Predation is both a proximate and ultimate cause of *L. saxatilis* distribution: predators quickly consume any *L. saxatilis* that descend into the lower intertidal and predation negatively impacts both growth and survival of *L. saxatilis* (Fig. 2a, b). Rapid behavioral adaptation to higher competitor and predator pressure is possible in this species: *L. saxatilis* reproduces viviparously and studies of *L. saxatilis* have demonstrated strong local adaptation along tidal gradients (e.g., Johannesson 2003; Rolan-Alvarez et al. 1997).

Predators can decrease the growth rate of prey through behaviorally mediated indirect effects (reviewed in Werner and Peacor 2003). Our study demonstrates a 43% decrease in *L. saxatilis* growth rate in predator-access cages. Trussell et al. (2003) found that *L. littorea* and *Nucella lapillus* fed less and had reduced growth rates in the presence of *C. maenas* feeding on conspecific snails. Similarly, the presence of *Cancer productus* reduced the growth rate of *Littorina sitkana* only when *C. productus* was feeding on conspecifics (Behrens Yamada et al. 1998). All snails in our field experiment were exposed to ambient cues from local crab predators, but only those in predator-access cages were exposed to chemical signals from crushed conspecifics, likely leading to reduced growth rate.

Predation intensity varied by exposure and tidal height. Predation was higher at sheltered sites compared to exposed sites (Fig. 2b), which corresponds with previous observations that crab predators are at lower densities at more wave exposed sites (Grosholz and Ruiz 1996). Predation increased with decreasing tidal height, similar to *Littorina sitkana* and *Littorina scutulata* in the northeast Pacific, which experienced higher predation tethered in the lower intertidal than conspecifics tethered in their normal range, which is higher in the intertidal (Behrens Yamada and Boulding 1996; Rochette and Dill 2000). The upper intertidal provides a refuge from many marine predators, which are less tolerant to emersion (Behrens Yamada and Boulding 1996). Of the potential predators for *L. saxatilis* in the

GOM, only *C. maenas* may be found foraging above the waterline (*personal observation*). There are also native predators, including *Cancer borealis* (Jonah Crab), *Cancer irroratus*, *Homarus americanus* (American lobster), and *Tautoglabrus adspersus* (cunner), all of which were videotaped eating tethered snails at  $-2$  m MLLW (K. Perez, *personal communication*). However, the relative densities, feeding rates, and exposure tolerance of these predators make *C. maenas* the most important intertidal consumer of snails: *C. maenas* is  $9\times$  more abundant than either *C. borealis* or *C. irroratus* between 0 m and  $-3$  m MLLW around Appledore Island (M. Wood, J. Ellis, and M. Shulman unpublished data), and *C. maenas* is the most voracious of the three crab predators (Menge 1983).

This study indicates that the historical effects of invasions can be difficult to reconstruct. Niche shifts are a common and important effect of invaders on native communities (Levin 2003); however, they can be difficult to identify in old invasions because native species may adapt to new constraints and secondary invaders may reinforce these shifts. A straightforward invader-removal experiment apparently reveals the dramatic effects of *L. littorea* expansion on the rocky intertidal algal community (Bertness 1984; Fig. 1: Treatments 1 vs. 3). However, considering that native littorines were dramatically reduced in the wake of *L. littorea* expansion (Ganong 1886) and that *L. saxatilis* can regulate algal populations (Fig. 1), we should consider the possibility of niche shifts in *L. saxatilis* and other native species when interpreting the impacts of *L. littorea*. The evidence provided here suggests that such a niche shift was possible, but historical changes in *L. saxatilis* shell morphology would provide direct evidence. Evaluating historical changes in *L. saxatilis* morphology is the subject of our current work.

**Acknowledgements** This research was completed as part of an NSF-sponsored REU program at the Shoals Marine Lab (NSF-REU 0139556). We thank M. Shulman, April Blakeslee and two anonymous reviewers for comments on this manuscript. We thank all the REUs for help with tethering, K. Perez, T. Williamson, and M. Wood for help with subtidal experiments and K. Quinby, L. Shulman, and B. Shulman for help with fieldwork. We also thank M. Shulman and J. Morin for their invaluable advice and assistance.

## References

- Behrens Yamada SB, Boulding EG (1996) The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *J Exp Marine Biol Ecol* 204:59–83
- Behrens Yamada SB, Mansour RA (1987) Growth inhibition of native *L. saxatilis* (Olivi) by introduced *L. littorea* (L.). *J Exp Marine Biol Ecol* 185:187–196
- Behrens Yamada SB, Navarrete SA, Needham C (1998) Predation induced changes in behavior and growth rate of the intertidal snail *Littorina sitkana* (Philippi). *J Exp Marine Biol Ecol* 22:213–236
- Bertness MD (1984) Habitat and community modification by an introduced herbivorous snail. *Ecology* 65:370–381
- Bertness MD (1998) The ecology of Atlantic shorelines. Sinauer Sunderland, Massachusetts, 417 pp
- Carlton JT (1992) Introduced Marine and estuarine mollusks of North America: an end- of-the 20th-century perspective. *J Shellfish Res* 11:489–505
- Carlton JT (2003) Community assemblage and historical biogeography in the North Atlantic Ocean: the potential role of human-mediated dispersal vectors. *Hydrobiologia* 503:1–8
- Dulvy NK, Sadovy Y, Reynolds JD (2003) Extinction vulnerability in marine populations. *Fish Fisher* 4:25–64
- Elnor RW, Raffaelli DG (1980) Interactions between two marine snails, *Littorina rudis* (Maton) and *Littorina nigrolineata* (Gray), a predator, *Carcinus maenas* (L.), and a parasite, *Microphallus similis* (Jagerskiold). *J Exp Marine Biol Ecol* 43:151–160
- Fralick RA, Turgeon KW, Mathison AC (1974) Destruction of kelp populations by *Lacuna vineta* (Montagu). *Nautilus* 88:112–114
- Ganong WF (1886) Is *Littorina littorea* introduced or indigenous? *Am Nat* 20:931
- Gilkinson KD, Methven DA (1991) Observations on the sibtidal distributions of the intertidal rough periwinkle, *Littorina saxatilis*, and the common periwinkle, *L. littorea*, in a shallow embayment in eastern Newfoundland. *Can Field Nat* 105:522–525
- Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, 510 pp
- Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *C. maenas*. *Biol Conserv* 78:59–66
- Hadlock Seeley R (1982) Association of *Littorina obtusata* and fucoid algae: effects of competition with *Littorina littorea*. *Malacol Rev* 15:150
- Hadlock Seeley R (1986) Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc Natl Acad Sci USA* 83:6897–6901
- Holway DA, Lach L, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233
- Hosmer DW, Lemeshow S (1999) Applied survival analysis: regression modeling of time to event data. John Wiley & Sons, Inc, New York, 386 pp
- Johannesson B, Johannesson K (1990) *Littorina neglecta* Bean, a morphological form within the variable species *Littorina saxatilis* (Olivi)? *Hydrobiologia* 193:71–87
- Johannesson K (2003) Evolution in *Littorina*: ecology matters. *J Sea Res* 49:107–117
- Johnson CR, Mann KH (1986) The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicuris* de la Pylaie survives grazing by the snail *Lacuna vineta* (Montagu) at high population densities. *J Exp Marine Biol Ecol* 97:231–267
- Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology* 83:3182–3193
- Levin DA (2003) The ecological transition in speciation. *New Phytol* 161:91–96
- Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat* 112:23–39
- Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. *Ecol Monogr* 48:67–94
- Mack MC, D'Antonio CM (2003) Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecol Appl* 13:154–166
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Menge BA (1983) Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58:141–155
- Neter JM, Kutner H, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models. Fourth edition. Richard D. Irwin, Homewood, Illinois, USA
- Reid DG (1996) Systematics and evolution of *Littorina*. The Dorset Press, Dorchester, Dorset, 720 pp
- Rochette R, Dill LM (2000) Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *J Exp Marine Biol Ecol* 253:154–191
- Rolan-Alvarez E, Johannesson K, Erlandsson J (1997) The maintenance of a cline in the marine snail *Littorina saxatilis*: The role of home site advantage and hybrid fitness. *Evolution* 51:1838–1847
- Ropes JW (1968) The feeding habits of the green crab, *C. maenas* (L.). *Fish Bull* 67:183–203
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol Inv* 1:21–32
- Thomas MLH, Page FH (1983) Grazing by the gastropod, *Lacuna vineta*, in the lower intertidal area at Musquash Head, New Brunswick, Canada. *J Marine Biol Assoc UK* 63:737–739
- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains:

- predator risk cues alter prey feeding rates. *Ecology* 84:629–640
- Trussell GC, Smith LD (2000) Induced defenses in response to an invading crab predator: an explanation of historical and geographical phenotypic change. *Proc Natl Acad Sci USA* 97:2123–2127
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. University Press, Cambridge, 504 pp
- Vadas RL, Elner RW (1992) Plant-animal interactions in the north-west Atlantic. In: John DM, Hawkins SJ, Price JH (eds), *Plant-Animal Interactions in the Marine Benthos*. Oxford, Clarendon Press, pp. 33–60
- Vermeij GJ (1982) Environmental change and the evolutionary history of the periwinkle (*Littorina littorea*) in North America. *Evolution* 36:561–580
- Wares P, Goldwater DS, Koug BY, Cunningham CW (2002) Refuting a controversial case of human-mediated marine species introduction. *Ecol Lett* 5:577–584
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 94:1083–1100
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole ecosystem context. *Trends Ecol Evol* 16:454–459