Journal of Experimental Marine Biology and Ecology 361 (2008) 98–103

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Subtidal-intertidal trophic links: American lobsters [*Homarus americanus* (Milne-Edwards)] forage in the intertidal zone on nocturnal high tides

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ARTICLE INFO

Article history:
Received 11 November 2007
Received in revised form 8 May 2008
Accepted 12 May 2008

Keywords:
Cancer borealis
Cancer irroratus
Carcinus maenas
Chondrus crispus zone
Decapod
Food-web
Littorina littorea
Predation
Trophic level

ABSTRACT

Homarus americanus (Milne-Edwards), the American lobster, is a predator in New England subtidal communities, feeding on ecologically important grazers (sea urchins), mesopredators (crabs), and basal species (mussels). In this study, we provide the first report of adult American lobsters foraging in rocky intertidal habitats during nocturnal high tides. Censuses by SCUBA divers in the low intertidal (*Chondrus crispus* Stackhouse) zone showed mean densities of 2.2 lobsters/20 m^2 on nocturnal high tides, with contrasting low densities of 0.18/20 m^2 during diurnal high tides. Nocturnal high-tide intertidal densities were 62% of those reported in a previous study of lobsters in nearby subtidal rocky areas (Novak, 2004). The average carapace length of lobsters in the intertidal at night was >50 mm. These lobsters were actively foraging in the intertidal with collected individuals having a mean stomach fullness of 67%. Prey found in the stomach contents primarily consisted of crabs, mussels and snails. Field experiments showed that lobsters rarely fed on medium to large size individuals of the common intertidal snail, *Littorina littorea* (L.). In contrast, experiments with local crab species demonstrated that lobsters actively and readily prey on *Cancer irroratus* (Say) and *Carcinus maenas* (L.), but were significantly less likely to consume *Cancer borealis* (Stimpson). The abundance of *Carcinus maenas* and blue mussels (*Mytilus edulis* L.) in the intertidal zone may explain the upshore movement of lobsters. Since nocturnal migration of *Homarus americanus* into the intertidal zone has not been documented before, our understanding of the dynamics of New England intertidal communities needs to be expanded to include this predator.

1. Introduction

Intertidal communities are subject to two daily rhythms: tides and light cycles. The ebbing tide exposes intertidal organisms to predation by terrestrial predators, particularly birds (Wootton, 1992 and Ellis et al., 2007) and mammals (Smith and Partridge, 2004). In contrast, the rising tide allows exploitation of the littoral zone by mobile subtidal predators, most notably fishes and decapods (Edwards et al., 1982, Robles et al., 1989 and Boulding et al., 2001). Almost all of these animals have diel patterns of activity as well, with distinct suites of predators active during diurnal and nocturnal/crepuscular periods. Scientific investigations are similarly affected by diel tidal and light cycles. Being primarily diurnally-active, terrestrial animals, scientists have conducted most intertidal studies during daytime low tides. Many fewer studies have been done during high tide and very few during nocturnal high tides. Thus our knowledge of predator activity during these times is severely limited. The relatively few studies that have been done reveal that nocturnally active decapods, in particular, can migrate upwards into the intertidal on night-time high tides (Robles et al., 1989, 1990 and Holsman et al., 2006).

On New England rocky shores, much intertidal research has focused on resident predators, especially the native dogwhelk *Nucella lapillus* (L.) and the introduced green crab *Carcinus maenas* (see Bertness, 2006 and included references). However, recent studies have shown that the Jonah crab *Cancer borealis*, which is mainly found in the subtidal, migrates into intertidal zone where it impacts prey populations of mussels and snails (Ellis et al., 2007) *C. borealis*, in turn, is heavily preyed upon by gulls that forage in the intertidal and very shallow subtidal during diurnal low tides (Good, 1992 and Ellis et al., 2005).

Another subtidal decapod that has the potential to impact Northwest Atlantic intertidal communities is the American lobster *Homarus americanus*. In subtidal communities, lobsters are predators on foundational species (mussels), grazers (the green sea urchin *Strongylocentrotus droebachiensis*), other decapod predators (the crabs *Cancer borealis* and *Cancer irroratus*), and other invertebrates such as gastropods and polychaetes (Herrick, 1895, Breen and Mann, 1976, Cooper and Uzmann, 1980, Elner and Campbell, 1987, Hudon and Lamarche, 1989, Ojeda and Dearborn, 1991 and Gendron et al., 2001). Though found offshore in deeper waters during late fall and winter, larger American lobsters migrate into shallower inshore waters in the late spring and remain there into early fall (Herrick, 1895, Estrella and

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doi:10.1016/j.jembe.2008.05.004

Morrissey, 1997 and Childress and Jury, 2006) and juveniles are found under rocks at the subtidal-intertidal interface at low tide (MacKay, 1926, Cowan, 1999 and Ellis and Cowan, 2001). During colonial times (17th century), Native Americans were reported to harvest adult lobsters from shallow bays (Josselyn, 1865, Heath, 1963 and Piotrowski, 2002) and during the early years of the commercial fishery (late 1700s and early 1800s) lobsters were caught by dip nets and gaffs in very shallow water (Rathbun, 1887). In the modern fishery, lobsters are often caught in the summer in traps placed at 1–3 m depth (pers. obs.), and recent subtidal censuses in the Isles of Shoals (Maine and New Hampshire) found that lobsters were as abundant in these very shallow waters as they were at greater depth (Novak, 2004). Thus, adult American lobsters are occupying subtidal habitat immediately adjacent to the intertidal zone. Lobsters forage primarily during crepuscular and nocturnal periods (Herrick, 1909, Cooper and Uzmann, 1980, and Novak, 2004), can traverse large distances (up to 60 m) on a daily basis (Jury et al., 2005) and generally return to the same shelter sites (Karnofsky et al., 1989).

Despite the proximity of American lobsters to intertidal habitats in the late spring through early fall, we have been unable to find any studies examining their possible presence in the intertidal on nocturnal high tides. In this study we provide the first documentation of significant densities of foraging adult *Homarus americanus* in the intertidal zone. The stomach contents of these intertidally foraging individuals reveal they are feeding primarily on crabs, mussels and small snails. Laboratory studies indicate that the green crab (*Carcinus maenas*), which is highly abundant in the intertidal, is readily eaten by lobsters. In contrast, medium and large individuals of the abundant intertidal gastropod *Littorina littorea* are rarely consumed. Our results suggest that American lobsters are not just predators in subtidal communities but nearby intertidal habitats as well, where they consume crabs that are ecologically important mesopredators, and foundational sessile species.

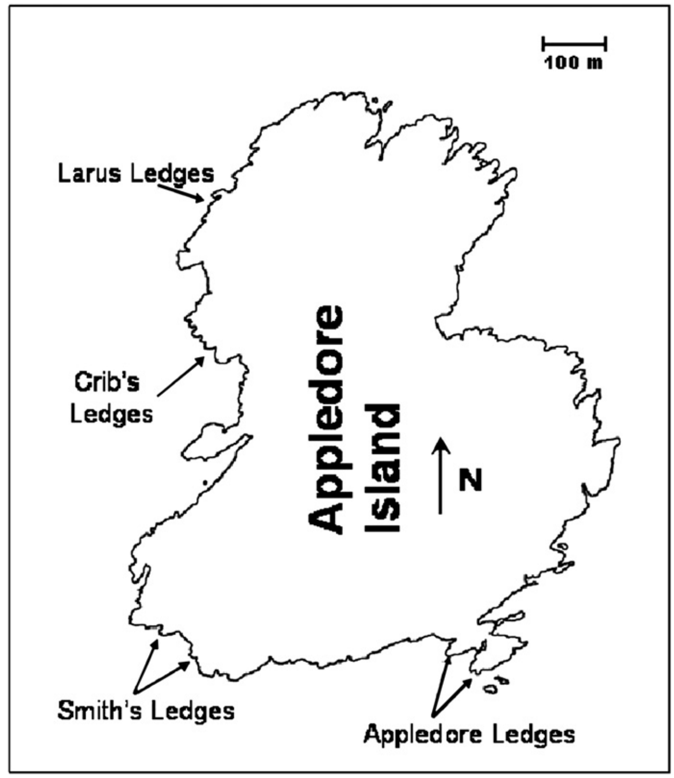

Fig. 1. Locations of the four study sites on Appledore Island, ME, U.S.A.

2. Materials and Methods

2.1. Lobster Censuses in the Intertidal Zone

Our study area, Appledore Island ME, USA (42°58′N; 70°37′W), is located in the Gulf of Maine, 10 km off the New Hampshire coast and is one of the 9-island Isles of Shoals archipelago. The shoreline consists of rocky ledge and cobble habitats and experiences semidiurnal tides of ~ 4 m amplitude. All of our surveys of lobster densities were done in rocky ledge habitat on the relatively protected western and southern shores of the island (Fig. 1).

We censused lobsters in the low *Chondrus crispus* zone (approximately 0.0 m relative to Mean Lower Low Water) during high tides. Two SCUBA divers counted lobsters within 10 m × 2 m band transects at four sites (Fig. 1): Appledore Ledges (n = 10 transects), Smith's Ledges (n = 10), Larus Ledges (n = 12), and Crib's Ledges (n = 5). Fewer transects were performed at Crib's Ledges due to the smaller area of that study site. At each site, lobsters were censused during a diurnal and a nocturnal high tide within a 24-hour period. We performed two sets of censuses at all sites, first during July 6–10 and again during July 19–23, 2006. During each census, we captured all lobsters that were out in the open and measured carapace length. For lobsters in crevices, we measured claw length *in situ* and then estimated carapace length based on a regression calculated from measurements of 65 individuals (see Results).

To determine the effects of site and time of day on the densities of lobsters present in the intertidal, we first performed a MANOVA on the data from each of the census dates (July 6–10 and 19–23) with day and night as repeated measures. We examined effects of census date by performing a MANOVA on the day and night data separately with census date as a repeated measure. All statistics were performed using JMP version 5.0.1a.

To test for differences in the sizes of lobsters (mean carapace length) across the four sites we used a one-way ANOVA to compare mean carapace lengths. There was a large difference in the number of lobsters observed between day and night censuses. Therefore, we used the non-parametric Median Test when contrasting the sizes of lobsters present during the day versus night.

2.2. Stomach Contents of Lobsters

To determine the prey of lobsters foraging in the rocky intertidal, we collected 43 lobsters for stomach content analysis. The lobsters were collected from the *Chondrus crispus* zone at each of the four sites (≥ 10 lobsters from each) 1–2 hrs after a nocturnal high tide. Each lobster was immediately injected through the mouthparts with formalin and put on ice until taken to the lab where they were frozen. To analyze the gut contents, the specimen was first thawed and measured (carapace length). We then removed the cardiac stomach, rinsed the contents into a gridded Petri dish, and examined them under a dissecting scope. We listed all the prey items present and identified those on each of 61 points of the grid. This information allowed us to determine both the percent of lobsters containing particular prey and the relative proportions of prey in the stomach contents.

2.3. Lobster Predation on Crabs: Laboratory Feeding Experiment

Crabs were common in the guts of lobsters foraging in the intertidal zone (see Results). To determine whether lobsters exhibit differential predation on different sizes and species of crabs available in the intertidal, we performed a laboratory feeding experiment in which lobsters were offered small and large individuals of each of three crab species (Table 1). We starved ten lobsters for 24 hours and then placed each individual into an opaque plastic tub (49 × 37 × 44 cm) supplied with flow-through seawater and a horizontally-

Table 1
Size classes of three crab species used in lobster predation experiment

Species	Carapace Width (mm)	
	Small	Large
Carcinus maenas	34.0–48.5	50.5–82.5
Cancer borealis	49.0–68.0	71.5–90.5
Cancer irroratus	35.0–56.5	60.0–79.5

placed section of PVC pipe (10 cm diameter, 20 cm length) for the lobster to use as shelter. A single, measured crab was placed into each of the containers and at the end of 24 hrs we recorded whether it had been eaten. Each lobster was then starved for another 24 hours before being given the next crab to consume. The order in which a given lobster received each of the 6 size/species of crabs was determined randomly.

We used a Generalized Estimating Equation (PROC GENMOD in SAS 9.1) with a binomial distribution to determine whether the probability of an individual crab being eaten was a function of its species or size. Data were blocked by individual lobster and the following effects included in the initial model: crab species, crab size, lobster size, and all 2-way interaction effects. We sequentially removed non-significant effects that had $p > 0.25$ and re-ran the analysis; the final model only included crab species.

2.4. Lobster Predation on Littorina littorea: Field Feeding Experiment

Though less common than crabs, snails were also frequently found in the stomach contents of lobsters (see Results). A very abundant snail in the low intertidal zone is *Littorina littorea* (Carlson et al., 2006). Preliminary experiments revealed that lobsters would not feed on *L. littorea* in the laboratory. Therefore, we performed feeding trials in field cages to determine whether lobsters would eat *L. littorea* under more natural conditions. We built fifteen 76 × 38 × 23 cm cages out of hardware cloth with 13 mm mesh and placed them at 3 m depth. A brick was placed in each cage to weight and stabilize it and provide some shelter for the lobster. We collected and measured fifteen lobsters from the shallow subtidal during nocturnal high tide, banded their claws, and starved them for 72 hours in the cages. We then added forty *L. littorea* to each cage, twenty each of two size classes: medium (shell height 18 – 21 mm) and large (shell height ≥ 25 mm). Claw bands were removed from 10 randomly chosen lobsters while the 5 remaining banded lobsters served as controls for possible snail escape from the cages. After 96 hours, we retrieved the cages and counted the remaining *L. littorea*. The number of each size class of snails removed after 96 hours in experimental and control treatments

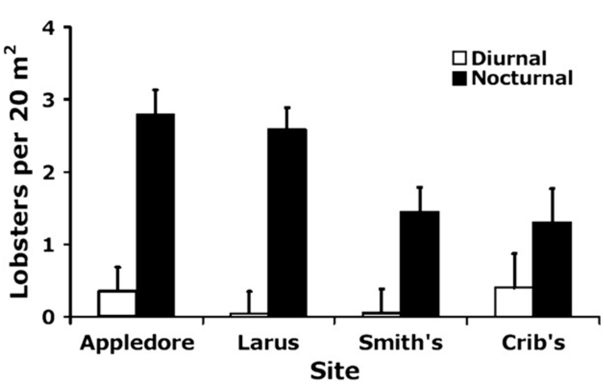

Fig. 2. Abundance (x̄ ± 1 SE) of American lobsters (*Homarus americanus*) along 20 m^2 transects in the intertidal zone during diurnal and nocturnal high tides. Lobster densities were significantly higher at night ($p < 0.0001$). There were no significant effects of site ($p = 0.22$), or of time of day × site ($p = 0.25$).

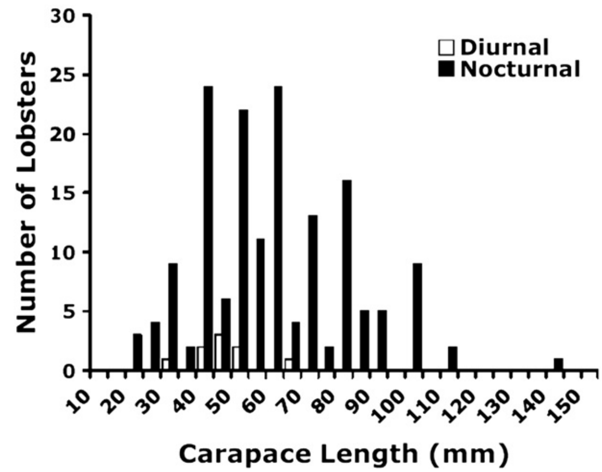

Fig. 3. Size distribution of American lobsters (*Homarus americanus*) observed in the intertidal zone during nocturnal and diurnal high tides.

was log (x + 1) transformed and compared in an ANCOVA with lobster size (carapace length) as a covariate.

3. Results

3.1. Lobster Censuses in the Intertidal Zone

The censuses revealed large numbers of lobsters (2.2/20 m^2 = 0.11/m^2) present in the low intertidal zone on nocturnal high tides. Significantly fewer lobsters were present in the daytime (0.18/20 m^2 = 0.0088/m^2) in both the early and late July censuses across all sites (MANOVA, $p < 0.0001$) (Fig. 2). The analysis revealed no significant effects of sites (both $p > 0.22$), and no significant interaction effects between site and time-of day (both $p > 0.25$). For the nocturnal data, we found no significant differences between the early and late census dates (repeated measures factor: $p = 0.65$), sites ($p = 0.23$), or their interaction ($p = 0.82$). For the diurnal data, however, we found a significant interaction effect between census dates and sites ($p = 0.034$). Separate repeated measure analyses

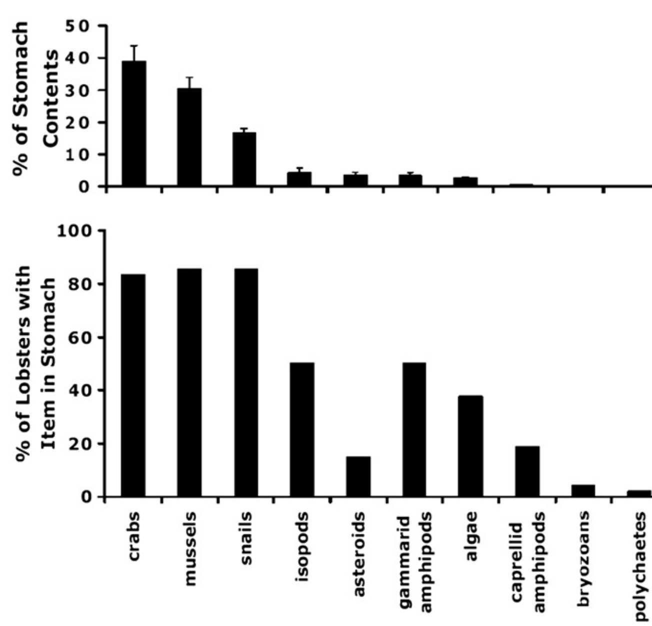

Fig. 4. Stomach content analyses of adult American Lobsters (*Homarus americanus*) collected from the intertidal zone at the end of a nocturnal high tide (N = 43). Top: Percent of lobsters with prey taxon in stomach. Bottom: Percent (x̄ ± 1 SE) of stomach contents for each prey taxon.

for each site revealed that only Appledore Ledges had a significant difference in diurnal abundance between census dates (p = 0.015), with higher densities in late July.

To determine the sizes of lobsters found in the intertidal zone, we first converted claw length to carapace length for the seven lobsters that were found in crevices. Measurements from 65 lobsters produced the following regressions between claw (crusher or ripper) lengths and carapace length (CL):

$$\mathrm{CL\,(mm)} = 6.8 + 0.8\,[\mathrm{Crusher\ length\ (mm)}] \quad \left[R^2 = 0.90\right]$$
$$\mathrm{CL\,(mm)} = 8.9 + 0.7\,[\mathrm{Ripper\ length\ (mm)}] \quad \left[R^2 = 0.80\right]$$

Lobsters present in the intertidal zone during nocturnal high tides averaged 59 mm CL (n = 164; range = 30–140 cm), significantly larger than the average of 42 mm CL (n = 9; range = 30–64 cm) of lobsters present in the intertidal during daytime high tides (Median test: p = 0.023; Fig. 3). The size of lobsters in the intertidal at night varied significantly across sites; lobsters at Appledore Ledges were significantly smaller than those at Larus and Smith's Ledges (ANOVA, $p < 0.0001$; Tukey's, $p < 0.05$).

3.2. Stomach Contents of Lobsters

Lobsters collected at night in the low intertidal zone appeared to have been actively feeding; mean cardiac stomach fullness was 67%. The stomach contents (Fig. 4) included 10 different major categories of prey: mussels, snails, crabs, isopods, gammarid amphipods, caprellid amphipods, asteroids (*Asterias*), polychaetes, bryozoans, and algae. However, crabs, mussels, and snails predominated; the three taxa together accounted for 85% of the stomach contents and were consumed by more than 80% of individual lobsters.

3.3. Lobster Predation on Crabs: Laboratory Feeding Experiment

Predation rates on crabs in the laboratory were very high, with 35–75% of crabs being eaten during the 24 hr trials (Fig. 5). Crab size did not influence the probability of being eaten, but there was a significant effect of crab species (Generalized Estimating Equation Analysis: χ^2=6.7, df=2, p=0.036). *Cancer irroratus* and Carcinus maenus were consumed significantly more often than *Cancer borealis* (post-hoc tests: p=0.0003; p=0.011). While predation on *C. irroratus* was higher than on *Carcinus maenas*, differences were not significant (p=0.073).

3.4. Lobster Predation on Littorina littorea: Field Feeding Experiment

Approximately 90% of *L. littorea* remained alive in the lobster feeding experiment after 96 hrs. Data analyzes revealed no effects

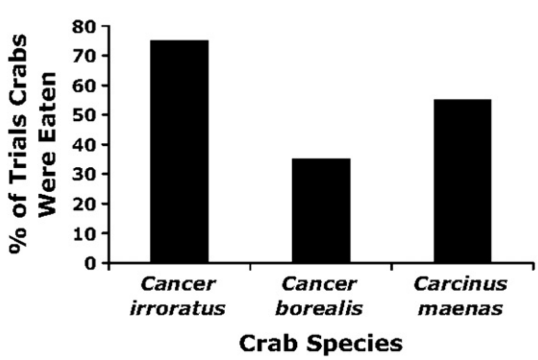

Fig. 5. Lobster predation on crabs: percent of feeding trials in which the lobster consumed the crab. *Cancer borealis* was consumed significantly less frequently than *C. irroratus* (p=0.0003) or *Carcinus maenas* (p=0.011).

(all p>0.33) of treatment (banded vs non-banded lobsters), lobster size, or their interaction for either medium or large *L. littorea*.

4. Discussion:

American lobsters (*Homarus americanus*) are well known to be predators on a range of invertebrate taxa and guilds in subtidal communities of New England. In this study, we provide the first documentation that American lobsters are also abundant and actively foraging in the intertidal zone during nocturnal high tides. The lobsters present in the intertidal ranged from juvenile to adult, with 68% of the lobsters≥50 mm CL. Nocturnal, high-tide densities of lobsters in the intertidal (=0.11/m) were about two-thirds of those found in shallow subtidal habitats (2–10 m depth) in a previous study at Appledore Island (Novak, 2004). Lobsters found in the intertidal at night did not remain there during daytime; densities during diurnal high tides were extremely low. Instead, lobsters appear to be migrating up into the intertidal from the subtidal zone as the tide rises and falls at night. Lobsters have been recorded to travel an average 4 m/hr at night (Jury et al., 2005) and generally return to "home" shelter sites before dawn (Childress and Jury, 2006).

The intertidal and shallow subtidal areas we studied were rocky ledges covered in the algae *Chondrus crispus* and *Mastocarpus stellatus*. Unlike cobble shores, this habitat does not provide the shelter required for high densities of juvenile lobsters (Cowan et al., 2001 and Cobb and Castro, 2006). However, rocky habitat colonized by macroalgae hosts the highest densities of larger (31 to 92 mm CL) lobsters (Hudon and Lamarche, 1989), which generally prefer habitats that are more structurally complex (Cobb and Castro, 2006). The structurally complex, algal-covered rocky habitat in the shallow subtidal around the Isles of Shoals almost certainly provides a large source of lobsters for foraging incursions into the intertidal zone.

American lobsters collected from the intertidal at night were feeding primarily on crabs, mussels and gastropods. This suite of taxa is similar to that found in lobsters collected in the subtidal (Elner and Campbell, 1987, Hudon and Lamarche, 1989 and Ojeda and Dearborn, 1991). However, within these taxonomic groups, there are large differences in the intertidal/subtidal distribution of prey species and size classes in the Isles of Shoals. *Carcinus maenas*, particularly smaller sized individuals, are far more abundant in the intertidal, as is the gastropod *Littorina littorea* (Carlson et al., 2006, Perez et al., in review). Mussels, though very patchy in distribution, are more abundant in the shallow subtidal than in the intertidal zone (P. League-Pike, unpub. data). The higher density of *Carcinus* is the most likely factor driving the nocturnal movement of lobsters from the subtidal into the intertidal. The availability of Carcinus may be particularly important for larger lobsters; the proportion of crabs in lobster diets increases as they age (Sainte-Marie and Chabot, 2002) and feeding experiments (using *Cancer irroratus*) showed that crab consumption was required for growth and ovary development (Gendron et al., 2001).

American lobsters do not appear to prey on the intertidally-abundant medium to large *Littorina littorea*. *L. littorea* of these sizes were not consumed in field caging experiments and almost all the gastropods found in the stomach contents were small individuals with intact shells. One possibility is that these small snails were consumed along with mussel spat, with which they are often closely associated (personal observation). It is most likely therefore, that lobster foraging is having more of an impact on mussels and crabs than on older size classes of *L. littorea*.

Our lab experiment results indicate that *Cancer irroratus* and *Carcinus maenas* are preferred over *Cancer borealis* as prey for lobsters. The high predation on Carcinus, a species primarily restricted to the intertidal, suggests that Carcinus availability may be an important driver of the upshore migration of foraging lobsters. The size distributions of crabs change from the intertidal to the subtidal. *Carcinus maenas* and *Cancer borealis* present in the intertidal zone are significantly smaller than those found in the subtidal (P. League-Pike, unpubl. data). It is also possible, therefore, that lobsters are moving into the intertidal because they prefer to forage on smaller crabs which presumably pose less risk of inflicting defensive injuries.

Interactions between lobsters and crabs are not solely limited to lobster predation on crabs. Depending on the relative size of the lobster and crab, these taxa are competitors for food and either may prey on the other. A variety of behavioral interactions have been reported among these decapods. *Carcinus maenas* will defend mussel prey from larger sub-adult lobsters (Williams et al., 2006). In the presence of adult lobsters, however, Carcinus actively climb up onto available structures or bury themselves completely beneath gravel or rocks (P. League-Pike, unpub. data). Lobsters also affect *Cancer borealis* behavior, having a positive indirect effect on mussel abundance by decreasing *C. borealis* predation (Siddon and Witman, 2004). Lobsters are also capable of displacing *C. borealis* from shelters, thereby increasing *C. borealis* mortality by fish predators (Richards and Cobb, 1986 and Richards, 1992). *Cancer irroratus* and *C. borealis* are more active during the day than at night, which may also allow them to avoid predation by, and competition with, *Homarus americanus* (Novak, 2004). These studies suggest that in addition to direct predation and competition, behavioral modification of crab species could be important effects of the nocturnal foraging of lobsters in the intertidal.

Another seeming advantage to lobsters of foraging in the intertidal might be a refuge from predation (Cowan et al., 2001). Juvenile lobsters are preyed upon by several small fishes and fishes (Barshaw and Lavalli, 1988, Hudon and Lamarche, 1989 and Wahle and Steneck, 1992). In contrast, Atlantic cod (*Gadus morhua*) has historically been the main vertebrate predator on adult lobsters, but is presently unimportant due to severe overfishing (Bigelow and Schroeder, 1953, Scott and Scott, 1988, and Butler et al., 2006).

Lobsters are known to be predators on the green sea urchin *Strongylocentrotus droebachiensis* in subtidal kelp habitats (Breen and Mann, 1976, Wharton and Mann, 1981, Miller, 1985 and Elner and Vadas, 1990). Although we found some echinoderm remains in the stomachs of lobsters collected in the intertidal, they consisted entirely of ossicles of the sea stars *Asterias* spp. Sea urchins were scarce at Appledore Island in 2006 (League-Pike, unpubl. data), presumably due to intense human fishing pressure throughout the Gulf of Maine during the previous decade (Steneck et al., 2002, 2004). Lobster predation on sea urchins may have been important in intertidal habitats, but investigation of this possibility will depend on future recovery of sea urchin populations.

This study is the first report of adult American lobsters, in relatively high densities, foraging in the intertidal zone. The presence of lobsters in the intertidal zone in other geographic areas and habitats, and their ecological effects require much further investigation. Both modeling and experimental data indicate that the subtidal seascape is very important in determining the strength of subtidal-intertidal trophic connections (Rilov and Schiel, 2006). The densities of lobsters in shallow subtidal communities, surely influenced by habitat structure and ecological interactions, in turn should be expected to affect the role of lobsters in intertidal communities. Understanding the ecological dynamics of New England intertidal communities requires that we include the role of American lobsters and other subtidal predators, such as crabs and fishes, that migrate into the intertidal to feed (Edwards et al., 1982, Ellis et al., 2007).

Acknowledgements

We thank P. League-Pike for assistance with lobster censuses and field experiments and J.C. Ellis, J.G. Morin, and R.H. Seeley for insightful comments on the manuscript. Funding was provided by the National Science Foundation's Research Experience for Undergraduates Program at the Shoals Marine Laboratory. This is contribution number 150 from the Shoals Marine Laboratory. **[ST]**

References

Barshaw, D.E., Lavalli, K.L., 1988. Predation upon postlarval lobsters *Homarus americanus* by cunners Tautogolabrus adspersus and mud crabs Neopanope sayi on 3 different substrates - eelgrass, mud and rocks. Mar. Ecol. Prog. Ser. 48, 119–123.

Bertness, M.D., 2006. Atlantic shorelines: natural history and ecology. Princeton University Press, Princeton, NJ, p. 446 pp.

Bigelow, H.B., Schroeder, W.C., 1953. Fishes of the Gulf of Maine. Fish. Bull. 53, 1–577.

Boulding, E.G., Pakes, D., Kamel, S., 2001. Predation by the pile perch, Rhacochilus vacca, on aggregations of the gastropod Littorina sitkana. J. Shellfish Res. 20, 403–409.

Breen, P.A., Mann, K.H., 1976. Changing lobster abundance and destruction of kelp beds by sea-urchins. Mar. Biol. 34, 137–142.

Butler, M.J., Steneck, R.S., Herrnkind, W.F., 2006. Juvenile and adult ecology. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, Oxford, UK.

Carlson, R.L., Shulman, M.J., Ellis, J.C., 2006. Factors contributing to spatial heterogeneity in the abundance of the common periwinkle *Littorina littorea* (L.). J. Molluscan Stud. 72, 149–156.

Childress, M.J., Jury, S.H., 2006. Behaviour. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, Oxford, UK.

Cobb, J.S., Castro, K.M., 2006. Homarus species. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, p. Oxford, UK.

Cooper, R.A., Uzmann, J.R., 1980. Ecology of juvenile and adult lobsters, Homarus. In: Cobb, J.S., Phillips, B.F. (Eds.), The Biology and Management of Lobsters. Academic Press, NY.

Cowan, D.F., 1999. Method for assessing relative abundance, size distribution, and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal, zone. J. Crustac. Biol. 19, 738–751.

Cowan, D.F., Solow, A.R., Beet, A., 2001. Patterns in abundance and growth of juvenile lobster, *Homarus americanus*. Mar. Freshwater Res. 52, 1095–1102.

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

Ellis, S.L., Cowan, D.F., 2001. Volunteer-based monitoring of juvenile American lobster, *Homarus americanus*. Mar. Freshwater Res. 52, 1103–1112.

Ellis, J.C., Chen, W., O'Keefe, B., Shulman, M.J., Witman, J.D., 2005. Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 324, 31–43.

Ellis, J.C., Shulman, M.J., Wood, M., Witman, J.D., Lozyniak, S., 2007. Regulation of intertidal food webs by avian predators on New England rocky shores. Ecology 88, 853–863.

Elner, R.W., Campbell, A., 1987. Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 37, 131–140.

Elner, R.W., Vadas, R.L., 1990. Inference in ecology - the sea-urchin phenomenon in the northwestern Atlantic. Amer. Nat. 136, 108–125.

Estrella, B.T., Morrissey, T.D., 1997. Seasonal movement of offshore American lobster, *Homarus americanus* tagged along the eastern shore of Cape Cod, Massachusetts. Fish. Bull. 95, 466–476.

Gendron, L., Fradette, P., Godbout, G., 2001. The importance of rock crab (*Cancer irroratus*) for growth, condition and ovary development of adult American lobster (*Homarus americanus*). J. Exp. Mar. Biol. Ecol. 262, 221–241.

Good, T.P., 1992. Experimental assessment of gull predation on the Jonah crab *Cancer borealis* (Stimpson) in New-England rocky intertidal and shallow subtidal zones. J. Exp. Mar. Biol. Ecol. 157, 275–284.

Heath, D.B., 1963. A Journal of the Pilgrims at Plymouth; Mourt's Relation: A Relation or Journal of the English Plantation settled at Plymouth in New England, by certain English adventurers both merchants and others. Corinth Books, New York, NY.

Herrick, F.H., 1895. The American lobster: a study of its habits and development. Bulletin of the US Fish Commission for 1895.

Herrick, F.H., 1909. Natural history of the American lobster, vol. XXIX, pp. 149–408.

Holsman, K.K., McDonald, P.S., Armstrong, D.A., 2006. Intertidal migration and habitat use by subadult Dungeness crab Cancer magister in a NE Pacific estuary. Mar. Ecol. Prog. Ser. 183–195.

Hudon, C., Lamarche, G., 1989. Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. Mar. Ecol. Prog. Ser. 52, 155–168.

Josselyn, J., 1865. An Account of Two Voyages to New-England: Made during the Years 1638, 1663. William Veazie, Boston.

Jury, S.H., Chabot, C.C., Watson, W.H., 2005. Daily and circadian rhythms of locomotor activity in the American lobster, *Homarus americanus*. J. Exp. Mar. Biol. Ecol. 318, 61–70.

Karnofsky, E.B., Atema, J., Elgin, R.H., 1989. Natural dynamics of population-structure and habitat use of the lobster, *Homarus americanus*, in a shallow cove. Biological Bulletin 176, 247–256.

MacKay, D.A., 1926. Post-larval lobsters. Science 64, 530.

Miller, R.J., 1985. Seaweeds, sea-urchins, and lobsters - a reappraisal. Can. J. Fish. Aquat. Sci. 42, 2061–2072.

Novak, M., 2004. Diurnal activity in a group of Gulf of Maine decapods. Crustaceana 77, 603–620.

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

Piotrowski, T., 2002. The Indian heritage of New Hampshire and northern New England. McFarland, Jefferson, NC, p. 221.

Rathbun, R., 1887. The lobster fishery. In: Goode, G.B. (Ed.), The Fisheries and Fishery Industries of the United States. Section V. History and Methods of the Fisheries. USA Government Printing Office, Washington, D.C., pp. 658–794.

Richards, R.A., 1992. Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). J. Exp. Mar. Biol. Ecol. 156, 187–197.
Richards, R.A., Cobb, J.S., 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. Can. J. Fish. Aquat. Sci. 43, 2250–2255.
Rilov, G., Schiel, D.R., 2006. Seascape-dependent subtidal-intertidal trophic linkages. Ecology 87, 731–744.
Robles, C., Sweetnam, D.A., Dittman, D., 1989. Diel variation of intertidal foraging by Cancer productus L. in British-Columbia. Journal of Natural History 23, 1041–1049.
Robles, C., Sweetnam, D., Eminike, J., 1990. Lobster predation on mussels - shore-level differences in prey vulnerability and predator preference. Ecology 71, 1564–1577.
Sainte-Marie, B., Chabot, D., 2002. Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*) off the Magdalen Islands. Fishery Bulletin 100, 106–116.
Scott, W.B., Scott, M.G., 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 1–731.
Siddon, C.E., Witman, J.D., 2004. Behavioral indirect interactions: Multiple predator effects and prey switching in the rocky subtidal. Ecology 85, 2938–2945.
Smith, T.S., Partridge, S.T., 2004. Dynamics of intertidal foraging by coastal brown bears in southwestern Alaska. J. Wildl. Manage. 68, 233–240.
Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29, 436–459.
Steneck, R.S., Vavrinec, J., Leland, A.V., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems 7, 323–332.
Wahle, R.A., Steneck, R.S., 1992. Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157, 91–114.
Wharton, W.G., Mann, K.H., 1981. Relationship between destructive grazing by the sea-urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova-Scotia. Can. J. Fish. Aquat. Sci. 38, 1339–1349.
Williams, P.J., Floyd, T.A., Rossong, M.A., 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). J. Exp. Mar. Biol. Ecol. 329, 66–74.
Wootton, J.T., 1992. Indirect effects, prey susceptibility, and habitat selection - Impacts of birds on limpets and algae. Ecology 73, 981–991.