Distribution of epibionts and their effects on the marine snail Littorina littorea in northern New England

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Distribution of epibionts and their effects on the marine snail Littorina littorea in northern New England

Abstract
Epibiosis, or the growth of one organism on another, is a common life history strategy in marine environments where space is at a premium. Many epibiotic organisms live on or in biotic hard substrates, such as shells. In the spatially competitive rocky intertidal of New England, hard substrate surface area is greatly increased by the presence of the non-native marine periwinkle snail Littorina littorea. The snail’s shell can be exploited by epibiotic organisms such as barnacles, bryozoans, and encrusting calcareous algae. However, an in-depth examination of the prevalence and impact of epibionts on Littorina littorea in New England has not been done to date.

In Chapter 1 of this thesis, I examine the distribution and prevalence of epibionts on Littorina littorea and other gastropod species in northern New England at four different tidal heights from Maine to Massachusetts. I then focus on local scale factors influencing patterns of distribution and abundance in the most common taxa of epibionts, encrusting calcareous red algae, in Chapter 2. In the final chapter, I examine the impact of algal fouling on Littorina littorea's physiological parameters, grazing rates, movement patterns, predation susceptibility, and survival.

Keywords
Biology, Ecology, Biology, Oceanography, Biology, Zoology

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DISTRIBUTION OF EPIBIONTS AND THEIR EFFECTS ON THE MARINE SNAIL *LITTORINA LITTOREA* IN NORTHERN NEW ENGLAND

BY

LAURA CHELYNNE PAGE
B.S., Wheaton College, IL, 2003

THESIS

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in
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This thesis has been examined and approved.

Thesis Director, Dr. James E. Byers, Associate Professor of Zoology

Dr. Larry Harris, Professor of Zoology

Dr. Art Mathieson, Professor of Plant Biology

12 August 2009

Date
DEDICATION

This thesis is dedicated to the One who made “the ocean, vast and wide, teeming with life of every kind, both large and small.” (Psalm 104). For creating the small curious creatures and indwelling me with a thirst for knowledge, thank You. I am grateful for the chance “To work in the service of life and living, in search of the answers of questions unknown, to be part of the movement and part of the growing, part of beginning to understand” the marvellous world You have created (John Denver, Calypso).
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Epibiosis, or the growth of one organism on another, is a common life history strategy in marine environments where space is at a premium. Many epibiotic organisms live on or in biotic hard substrates, such as shells. In the spatially competitive rocky intertidal of New England, hard substrate surface area is greatly increased by the presence of the non-native marine periwinkle snail *Littorina littorea*. The snail's shell can be exploited by epibiotic organisms such as barnacles, bryozoans, and encrusting calcareous algae. However, an in-depth examination of the prevalence and impact of epibionts on *Littorina littorea* in New England has not been done to date.

In Chapter 1 of this thesis, I examine the distribution and prevalence of epibionts on *Littorina littorea* and other gastropod species in northern New England at four different tidal heights from Maine to Massachusetts. I then focus on local scale factors influencing patterns of distribution and abundance in the
most common taxa of epibionts, encrusting calcareous red algae, in Chapter 2.

In the final chapter, I examine the impact of algal fouling on *Littorina littorea*'s physiological parameters, grazing rates, movement patterns, predation susceptibility, and survival.
GENERAL INTRODUCTION

Introduction to Epibiosis

In recent years ecologists have begun to examine increasingly complex categories of species interactions (e.g. multiple predator species as in Griffen 2006; multi species mutualisms reviewed in Stanton 2003; facilitation and positive interactions reviewed in Bruno et al. 2003). One well recognized but often cryptic species interaction is that of epibiosis, a facultative, non-trophic relationship in which one species (the epibiont) utilizes another (the host or basibiont) as living substrate (Wahl 1989). The nature of epibiont/host relationships spans the spectrum from truly symbiotic to parasitic. While the epibiont usually, though not always, benefits from the relationship, the impact of epibiosis on the host species may vary with identity and circumstance (Wahl 1989, Wahl 2008).

In the marine environment, epibionts can be either algal epiphytes or animal epizootes. The epibiont primarily benefits by having a place of attachment, but may also receive benefits such as increased nutrient availability, protection from predation, or expansion of environmental tolerances (Wahl 1989). The basibiont-epibiont relationship can act to facilitate the basibiont or host by increasing environmental tolerances, changing food resource use, or protecting from predation. Alternatively, it may hinder the basibiont in some way by
increasing the risk of predation, increasing metabolic cost, or competing for nutrients (Laudien & Wahl 2004, Wahl 1989, Wahl 1997, Wahl & Hay 1995, Vance 1978). Epibionts differ from external parasites in that the epibiont is not physiologically or metabolically dependent upon the host (Crofton 1971), and negative impacts are generally indirect. These impacts may manifest as changes in the growth, mortality, fecundity, movement, or behaviour of the basibiont. Epibiosis may also impact the population or community through indirect interactions such as habitat provision or modification or changes in predator/prey and feeding relationships (Bruno et al. 2003, Menge 1995, Wahl 2008).

There is a large body of literature on marine epibiosis, ranging from examples of mutualistic relationships such as the Hydractinia-hermit crab symbiosis to negative relationships where the epibiont causes some harm to the host, such as the 'shared doom' scenario where the basibiont (i.e. an urchin) is more susceptible to predation when its epibiont (algae) is equally or preferentially palatable to a mutual predator (Wahl & Hay 1995, Yund & Parker 1989). A few examples will elucidate the complicated nature of marine epibiosis. Anemones on the cockle Austrovenus stutchburyi Wood reduce host parasite load by intercepting trematode larvae, while the presence of Crepidula fornicata Linnaeus or algal epiphytes on Mytilus edulis Linnaeus shells increases drag and leads to costly byssal thread production and reduced growth (Mouritsen & Poulin 2003, Thielges 2005, Thielges & Buschbaum 2007a, Witman & Suchanek 1984).
Barnacle and oyster epibionts decrease reproductive fitness and the ability to move and increase metabolic oxygen demand in the tropical snail *Batillaria zonalis* Bruguiere (Chan 2005). Coral species are often protected from predation by the chemical properties of their algal epibionts (Stachowicz 1999).

Clearly, epibiosis is both widespread and complicated in marine ecosystems, and should be considered along with competition, predation, disease, and herbivory as a driving force in community structure. Epibionts that benefit their host in some way fall under the auspices of facilitation theory, while epibionts that negatively impact their host may be as ecologically important as internal parasites, which have been shown to have a substantial impact on the structure of intertidal communities (Bruno et al. 2003, Mouritsen & Poulin 2002, 2005).

**Epibiosis on *Littorina littorea***

In marine environments where hard substrate is a limiting resource, the shells of molluscs such as mussels and gastropods are often prime space for settling invertebrate and algal epibionts (e.g. Chan 2005, Saier 2002, Vasconcelas et al. 2007, and many others), and it has been suggested that through the provision of hard substrate via their shells molluscs act as ecosystem engineers by modifying the environmental characteristics and species composition in aquatic and marine habitats (Gutierrez et al. 2003). The snail *Littorina littorea* is one of the most common invertebrates (both in terms of
numbers and biomass) in the New England intertidal, and thus provides an excellent potential habitat for epibionts. Surprisingly, little information exists about epibiosis on *L. littorea* within this region or on the impact of local epibionts on their snail basibiont, in spite of the importance of the periwinkle in structuring intertidal communities (e.g. Bertness et al. 1983, Lubchencho 1983). The prevalence of the boring sponge *Cliona sp.* was examined on *L. littorea* on Appledore Island by Stefaniak et al. (2005). Several authors have examined hermit crab usage of *L. littorea* shells with reference to epibiont presence (Li & Pechenik 2004, McDermott 2001, Williams & McDermott 2004), but to date there has been no broad scale investigation of the incidence of epibiosis on *L. littorea* in New England, or on the impacts of the dominant local epibionts on their snail host. The present study seeks to fill this informational gap by examining the patterns and implications of epibiosis on *L. littorea*.

In chapter one, I examined patterns of epibiont distribution and abundance on *Littorina littorea* and other gastropods in the mid Gulf of Maine region based upon broad scale field surveys. In particular I looked for patterns in microhabitat use as well as correlations in the co-occurrence of multiple epibiotic species. In chapter two, I looked more closely at the primary epibiont taxa, encrusting calcareous red algae, on a local scale. I compared the algal communities on rocks and snails in different habitats at a single location, and I examined the interaction of habitat, shell substrate condition, and snail defenses in a field caging experiment. In the final chapter, I investigated the potential impacts
calcareous red algae may have upon the basibiont snail host and the community wide implications of this relationship. To examine whether snail investment in tissue differed depending on fouling status, I established the density (g/mL) of calcareous red algae, and determined length/weight regressions and tissue condition indices for algal fouled and unfouled snails. In a mark and release field experiment, I examined whether algal fouling impacts movement patterns and preferences of *L. littorea*. In a lab grazing experiment I investigated whether grazing rates of fouled snails differed from those of clean, unfouled snails. The community level impacts of changes in grazing rates on intertidal macroalgal composition was examined in a field caging experiment. A field tethering experiment determined rates of predation on algal fouled and unfouled snails, and a final laboratory experiment looked at snail survival under different submersion regimes.
CHAPTER 1: REGIONAL PATTERNS OF EPIBIOSIS ON LITTORINA LITTOREA IN NORTHERN NEW ENGLAND

Abstract

The periwinkle snail Littorina littorea serves as a basibiont for a variety of epibiont species worldwide. The snail has been shown to have little or no antifouling response, so a wide variety of epibionts are able to utilize the shell as a place of attachment. In its introduced North American range, the nature and magnitude of epibiosis on L. littorea is to date unknown. A large scale sampling scheme was initiated to elucidate the identity, prevalence, and patterns of epibiont presence on L. littorea throughout the northern New England rocky intertidal zone. Epibiosis by one or more species was common, with prevalence increasing with snail submersion time and size.

Introduction

The snail Littorina littorea Linnaeus is one of the most common invertebrates (both in terms of numbers and biomass) in the New England intertidal, and thus provides an excellent potential habitat for epibionts. It is an herbivore, grazing primarily on micro and macroalgae. Grazing action by L. littorea has profound impacts on the structure of the intertidal community
(Lubchencho & Cubit 1980, Bertness 1984). The snail is also a preferred prey item of several predators, including the invasive green crab Carcinus maenus Linnaeus (Hadlock 1980, Ojeda & Dearborn 1991). In North America, where L. littorea is an introduced species which has become a key structuring agent of the intertidal zone, it is critically important to understand how the presence of epibionts affects the snail at the individual and population level (Bertness 1984, Blakeslee et al. 2008, Lubchenco 1978, 1983). Despite its long history in New England, little information exists about epibiosis on L. littorea within the northwest Atlantic.

On the European side of the Atlantic, however, the periwinkle snail Littorina littorea is a known basibiont for a wide variety of epibiont species, including barnacles (Holmes 2005, Thielges & Buschbaum 2007b), polychaetes, (Thielges & Buschbaum 2007b, Wahl & Sonnichsen 1992, Warner 1997), filamentous algae (Wahl 1997), hydroids (Yund & Parker 1989) and bryozoans (Wahl & Sonnichsen 1992, Warner 1997). The snail has been shown to have few, if any, active or passive defences against epibionts, and so has the potential to be fouled by a wide range of epibiont species in both its native and introduced ranges (Wahl & Sonnichsen 1992).

The single previous study on non-hermit crab Littorina littorea shell utilization by epibionts within the geographical range of this study (mid Maine, south of Portland to mid Massachusetts, north of Cape Cod) examined the boring sponge Cliona sp. on snails from Appledore Island, part of the Isle of Shoals off
the coast of New Hampshire (Stefaniak et al. 2005). This was the first known record of boring sponges in *L. littorea*, and one of only a few studies on *Cliona* on gastropods (see also Smyth 1989). On Appledore, up to 80% of snails were infected with *Cliona*, and boring by sponges made the snails more susceptible to predation by *Cancer* crabs by decreasing the available size refuge for the snail and weakening its shell. The snail's shell repair response to sponge boring also resulted in decreased interior volume, thus reducing the space available for somatic and gonadal tissue. The high prevalence of infected snails indicated that, should patterns of *Cliona* infection on the mainland parallel those found by Stefaniak et al (2005) on Appledore Island, it could be a major selective force within the intertidal zone of the Gulf of Maine.

Preliminary field investigations (LCP) indicated that in addition to *Cliona*, encrusting calcareous red algae, barnacles, and spirorbid worms could also be found on many mainland snails. Preliminary investigation combined with the information presented in Stefaniak et al. (2005) suggested that there were marked differences in epibiont presence between habitats or tidal height, and I suspected that there might be latitudinal patterns of epibiosis as well in either overall epibiont presence or epibiont species. Therefore, in order to elucidate the geographic and environmental ranges and population dynamics of epibiont utilization of *Littorina littorea*, an extensive survey was conducted in the summer of 2006 of gastropods from four tidal heights at locations ranging from southern Maine to mid Massachusetts, including three locations on Appledore Island.
Methods

Distributional Survey

In order to determine the prevalence and patterns of epibiosis on *Littorina littorea* and other intertidal gastropods within the mid Gulf of Maine, an ambitious sampling scheme was undertaken during the summer of 2006. Nineteen locations were selected from southern Maine through Massachusetts, north of Cape Cod (Figure 1.1). Locations were selected for similarity in habitat (boulder or cobble field/bedrock tongues with cobble) and geographic spread. The northernmost and southernmost locations were 150 km apart, while most locations were 10-20 km apart (Table 1.1).

At each location, ten 0.25 m$^2$ quadrats were haphazardly selected from each of the following four habitat zones, determined by a combination of tidal height and dominant algal taxa: subtidal, generally characterized by encrusting algae and bedrock or gravel substrate (≈ -1.0 to -0.5 m); low intertidal, generally characterized by a mixed *Chondrus crispus/Mastocarpus stellatus* community (≈ -0.25 to 0.25 m); mid intertidal, generally characterized by a mixed *Fucus vesiculosus/Ascophyllum nodosum* community (≈ 0.5 to 1.0 m); and tidal pools located within the mid intertidal zones. These four zones (referred to hereafter as subtidal, *Chondrus, Ascophyllum*, and pools, respectively) were selected based on preliminary sampling that indicated a gradient might exist in epibiont presence with tidal height and submersion regime. Habitat type was chosen as being more ecologically relevant than actual measured tidal height, although the
canopy algal community closely matched tidal height. Sampling was conducted on low tides, to allow collection of samples from the lower tidal heights, between 6/11/2006 and 7/25/2006. Within each quadrat, all gastropods >10 mm were collected in separate labelled plastic bags and placed in laboratory cold storage (10°C) until processed within 10 days. Sampling was restricted to adult gastropods (>10 mm in length) as snails smaller than this lacked epibionts, were difficult to collect or were generally absent from the tidal heights sampled. Therefore, all mean snail lengths presented should be interpreted as mean length of the adult snails collected, >10mm, rather than true population means.

**Laboratory Analyses**

Each snail was identified to species, measured (total length, apex to bottom of aperture), and thoroughly examined under a dissecting microscope for the presence of *Cliona*, encrusting calcareous red algae, and other epibiont species. Snail counts and quadrat area were used to determine gastropod species density.

For each individual snail, a series of qualitative and quantitative variables were examined, including the identity and severity of any epibiont present. *Cliona* sp. infections were classified according to the total percent of the shell bored (to the nearest 5%) and ranked according to severity of infection (ranked from low=few holes, nacreous layer intact to high=shell extremely degraded or eroded,
nacreous layer bored, outer shell flaking away). Encrusting calcareous algal presence was classified according to the total percent of the shell surface encrusted (to the nearest 5%). Where calcareous red algae obscured the shell surface or the extent of *Cliona* boring was unclear, the algae was removed or the snail cracked open to ensure that no data was missed in examination. Other epibionts (barnacles, spionid and serpulid polychaetes, encrusting bryozoans, etc) were enumerated and identified to general taxonomic group. Taxa counts were used to calculate epibiont species richness and associations. The presence or absence of taxa was used for binomial analyses.

*Statistical Analyses*

All statistical analyses were performed using the statistical program JMP™ as described in results either on total numbers of snails within the relevant location/habitat (Tables 1.1, 1.2, 1.3, 1.4, 1.7, 1.8; Figures 1.8, 1.10, 1.13, 1.15, 1.17, 1.18, 1.19, 1.20), on quadrat mean data (Tables 1.5, 1.6; Figures 1.2, 1.3, 1.4, 1.5, 1.6, 1.7, 1.9, 1.11, 1.14, 1.16), or at the individual snail level (Figures 1.12, 1.21).
Results

Gastropod Species Totals

A total of 12,033 snails (10,324 live *Littorina littorea*, 405 dead *L. littorea* shells, 668 *Nucella lapillus*, 382 *L. obtusata*, 244 hermit crabs (inhabiting the shells of various gastropod species), and 10 snails of other or indeterminate gastropod species) were examined (Table 1.2). *L. littorea* was the most common gastropod collected at all locations (Table 1.2), followed by *N. lapillus*. Given the size restriction in the sampling protocol (only snails >10 mm were collected), *L. obtusata* is likely under-represented in the dataset, as 10 mm is approaching the upper size limit for this species. While present at most of the locations sampled, the native congener *L. saxatilis* occupied a higher tidal niche and so does not appear in the samples collected. No *L. saxatilis* were observed with either *Cliona* or calcareous algae during preliminary investigations. Hermit crabs, while rare, were collected at all locations, most commonly in *L. littorea* shells, reflecting the patterns of shell availability.

The two most common epibionts on *Littorina littorea*, calcareous encrusting algae and the boring sponge *Cliona sp.*, were also found on the other gastropods collected. While the sample sizes of non-*L. littorea* gastropods are too small to allow statistical analysis, the percent of each species that had either *Cliona sp.* or calcareous red algae (CA) present is noted in Table 1.2.
Densities of Littorina littorea

*Littorina littorea* reached very high densities (16 to 2400 snails/m²) with an overall density of 238 +/- 11 SE snails/m² (Figure 1.2). Density was variable between locations, with no discernible latitudinal gradient or site similarity patterns (Figure 1.3). Within each location, density varied between habitats, with pools and the *Chondrus* (low intertidal) zones generally having the highest densities (Figure 1.4). With all locations pooled, tidal pools had significantly higher densities than all other habitats (p<0.001, ANOVA) (Figure 1.4).

The mean length of (>10 mm) *Littorina littorea* also varied between locations (Figure 1.5), with a median length of 19.2 mm and a mean range of 15.5-23.4 mm. A size gradient was observed between habitats, with the subtidal having significantly larger snails than higher tidal elevations (Figure 1.6). Within each location, snail size followed a normal bell-curve distributional pattern, with few very large or small snails (excluding juvenile snails <10 mm, which were not collected). Table 1.3 shows the number of snails at each location (top) and all locations summed by habitat (bottom), with totals broken down into ten size class frequency categories.
Epibiont Species Prevalence and Patterns on Littorina littorea

Prevalence of Epibiosis

Epibiosis was extremely common on Littorina littorea, with 34% of all snails carrying at least one epibiont species, and 12.3% having an epibiont other than crustose coralline algae (Table 1.4). Of the 10,748 Littorina littorea snails examined (both living and empty shells), 9 taxa were encountered repeatedly: encrusting calcareous red algae (CA), spionid polychaete worms (likely Polydora sp.), serpulid polychaete worms, the boring sponge Cliona sp., encrusting bryozoans, the barnacle Semibalanus balanoides, the slipper limpet Crepidula fornicata, juvenile Mytilus edulis, and the tortoise shell limpet Acmaea testudinalis. As a mobile epibiont, the tortoise shell limpets tended to become dislodged or move off of shells before analysis took place; thus, they are not reported in the following analyses though their presence was relatively common. Encrusting coralline red algae were by far the most common epibiont encountered, followed by Cliona and polychaete worms.

Epibiosis prevalence varied by habitat. The subtidal habitat had significantly higher levels of epibiosis than the other three habitats when all taxa are included (Figure 1.7a). Most of this pattern, however, is driven by the habitat preferences of the most common epibiont taxa, encrusting coralline algae. If coralline algae is excluded from the analysis, epibiont prevalence varies with decreasing tidal height/increasing submergence time, such that the percent of snails with non-algal epibionts showed the following pattern of decreasing
infection: Subtidal>Chondrus> Pools> Ascophyllum (Figure 1.7b).

*Epibiosis and Snail Length*

Snails in the subtidal habitat were significantly larger than those in the three higher tidal heights (Figure 1.6). Epibiosis also varied with snail length, such that larger, older snails had increasing numbers of epibionts (Figure 1.19). Snails with one or more epibionts were larger than the average sized snail in each habitat (compare mean lengths in Figure 1.6 with Figure 1.19).

The general pattern of increasing epibiosis with snail length seen in Figure 1.19 was seen at each location for the two most common epibionts, the boring sponge and calcareous red algae. The percentage of snails in each size class with sponge or algae on their shell is also presented by location and habitat in Table 1.3.

*Calcareous Algal Epibiosis*

Various species of encrusting calcareous red algae (CA) were the most common epibiont, occurring on 30.3% of all *Littorina littorea*. The percentages of snails in each location and habitat with CA present are listed in Table 1.3 by size class within each location and by habitat pooled totals. The variability in CA prevalence by location can be seen in Figure 1.8. While CA prevalence varied (range 7.3 to 56.8% of *L. littorea* by location, maximum location/habitat prevalence was reached in the Wells subtidal with 97.7% of all snails), CA were
present on snail shells in all locations and habitats. Crustose corallines were most common in the two lowest tidal heights, with 54.7% subtidal and 33.95% low intertidal prevalence (Figure 1.9).

While crustose coralline algae were found on snails of all sizes, they were more common on the largest size classes in all habitats (Figure 1.10); algal-fouled snails were larger on average than those lacking calcareous algal presence (Table 1.5).

While the presence of calcareous red algae was common on snails, the level to which individual snails were impacted varied. The total area of shell covered by algal crusts was categorized as low (1-30% of shell covered), medium (31-69%), or high (70-100%). Medium or high levels of algal crust coverage were more common in the two lower tidal heights (Figure 1.11). The percent cover of algal crusts on each individual snail was also a function of length. Larger, older snails had higher algal coverage than smaller ones, and the relationship was strongest in the two lowest habitats (Figure 1.12). There was no evidence of snail density dependence for calcareous red algae presence (bivariate fit of percent snails with CA by quadrat snail density, $R^2=0.0005$, p=0.5484).

**Cliona sp. Epibiosis**

The boring sponge *Cliona sp.* was the second most common epibiont, found on 4.6% of all *Littorina littorea*. The percentage of snails in each location
and habitat with *Cliona* present is listed in Table 1.3 by size class and location or habitat total. The variability in *Cliona* prevalence by location can be seen in Figure 1.13. *Cliona* was found at all locations except Brant Rock, although overall prevalence was extremely low at most sites (max 13.45% at Beverley, with 33.3% in the subtidal). *Cliona* prevalence was significantly higher subtidally than in the other three intertidal habitats (Figure 1.14).

In contrast to calcareous red algae, *Cliona* was almost exclusively found on snails in large size classes in all habitats (Figure 1.15). Snails with epibiotic *Cliona* were larger on average than those lacking boring sponges (Table 1.5).

**Multiple Species Epibiosis**

Many snails had more than one epibiont present simultaneously on a shell, with a maximum of five taxa on a single individual. Incidence of multiple epibioses occurred almost exclusively on snails where calcareous red algae were present. Overall, more epibionts were present on snails that had CA than on those where CA was absent, both for mean species richness (mean # taxa present per individual snail) (Figure 1.16) and for percent of snails with non-CA epibionts present (Figure 1.17). Species (taxa) richness and percentage of snails with non-algal epibionts was significantly higher on algal covered snails in all habitats except for pools (Table 1.6). Multiple species epibioses was not limited merely to calcareous red algae plus one other epibiont, but in some cases
extended to 5 different taxa inhabiting a single snail (Figure 1.17). True species richness is higher, as calcareous red algae and polychaete worms were not identified to species level.

**Epibiont Species Associations**
Calcereous red algae were not only the most common epibiont present but were strongly associated with the presence of other specific epibionts. Spionids, serpulids, bryozoans, and *Cliona* were more common on snails when CA was present than absent (Figure 1.18). All species except *Mytilus* and barnacles were significantly associated with calcareous red algae (Two-way contingency tables, p<0.05, Table 5); these species were more common on snails where calcareous red algae were absent.

**Multiple Epibiosis and Snail Length**
As with calcareous red algae and *Cliona*, multiple epibioses were related to snail length (Figure 1.19). Mean snail length increased as total taxa richness increased. Hence snails with two or more epibiont species were larger than the mean snail length in each habitat (Figure 1.6).

**Multiple Epibiont Interactions**
It was noted during sample processing that burrowing spionid worms commonly inhabited *Cliona* sponge tunnels or created holes and tunnels within
layers of calcareous red algae and snail shells. Spionids were rare on snails lacking both *Cliona* and calcareous red algae, and when present were often large (>2 cm) and/or numerous (multiple worms per snail was not uncommon). Ten percent of *Littorina littorea* that had either *Cliona* or calcareous red algae present also had spionid worms, and when both sponge and algae occurred the percentage rose to 34% (Figure 1.20). A nominal logistic model for spionid presence with algae and sponge presence as nominal factors and length as a continuous variable showed that length, *Cliona* presence, and algal presence were all significant predictors of spionid presence (Table 1.8).

In addition to being positively associated with both calcareous red algae and *Cliona*, spionid worms exacerbate shell damage caused by these two organisms. On snails where the boring sponge *Cliona* was present, the integrity of the shell was ranked from low (little to no damage) to high (outer protein layer eroded, column bored, shell fragile or flaking). This shell damage index increased with the percentage of the shell surface bored (Figure 1.21), and snails with medium or high damage indices were often those where spionids were also present. The proportion of snails with high damage increased with the presence of calcareous red algae and spionid worms (Figure 1.21).
Discussion

Nine epibiotic taxa were found on *Littorina littorea* and other gastropods in the mid Gulf of Maine region. Overall, 34.01% of snails had at least one epibiont, and many snails had more than one. Given the high densities of *Littorina littorea* within the region, this represents a substantial potential for population and community level impacts by these epibiont species. In some locations, more than 80% of the snails experienced some degree of epibiosis. Although the extent of epibiosis was most common in the shallow subtidal habitat, it was curiously low in tidal pools that were also continually submerged, suggesting that some environmental variable other than submersion time might be driving the patterns of epibiont presence seen in this study. Epibiosis varied with location, but showed no discernible geographical or wave exposure gradient.

Of the taxa found during this survey, barnacles, bryozoans, juvenile mussels, and polychaetes were previously reported to utilize living *Littorina littorea* in the northeastern Atlantic (Buschbaum & Reise 1999, Buschbaum et al. 2007, Thielges & Buschbaum 2007b, Wahl & Sonnichsen 1992; Wahl 1996, Warner 1997). In the Gulf of Maine, the boring sponge *Cliona* has previously been reported on *L. littorea* from Appledore Island (Stefaniak et al. 2005), and the slippershell *Crepidula convexa* on *L. littorea* at Nahant, Massachusetts (Li & Pechenik 2004). While encrusting brown algae (*Ralfsia verrucosa* Aresch and unidentified species) and filamentous algae have been previously documented...
on *Littorina littorea* (Wahl & Sonnichsen 1992, Wahl 1996, Warner 1997), and coralline algae are well-known marine epiphytes (e.g. Adey & Adey 1973, Steneck 1986), the encrusting calcareous algal species seen in this study have not been well studied as epibionts on *L. littorea*.

Although hermit crab epibiosis was not specifically investigated in this study, some hermit crab inhabited *Littorina littorea* shells were collected during the survey (Table 1.2). The percentage of hermit crab inhabited *L. littorea* shells with either *Cliona* or calcareous algal epibionts was lower than those of snail inhabited shells, although this number was not significant due to low sample sizes. Hermit crabs are known to actively select shells that are structurally intact and to avoid shells of high weight (Conover 1976, 1978). Snail shells that have been bored by *Cliona* or covered by encrusting algae may not be suitable for hermit crab inhabitation. The high levels of epibiont fouling on *L. littorea* shells found in this survey may therefore have indirect effects on the hermit crab populations that are the secondary inhabitants of snail shells, although this hypothesis was not directly tested. In addition, while hermit crabs are known to have unique assemblages of epibionts on their shells, and indeed often actively select their shell companions (Stachowicz 1980, Williams & McDermott 2004), the few hermit crab inhabited shells examined in this study did not have any species present outside of those found on the live snail shells from the same location (data not shown). Further investigation into hermit crab preference for bored or algal covered shells or utilization of hermit crab inhabited shells by
these epibionts may prove informative.

While *Littorina littorea* is itself an introduced species (Blakeslee et al. 2008), most if not all of the epibiont species are native to this region of the Atlantic. This may represent an adaptation of native species to a new resource (space), or it may reflect the facultative tendency of fouling organisms to settle on any available substrate. In either case, it is clear that native epibiotic species are utilizing this introduced biotic substrate at high rates. *L. littorea*’s impacts on the New England intertidal extend beyond competitive and herbivore interactions (Lubchencho & Cubit 1980, Bertness 1984) to potentially changing the community composition of the intertidal by serving as habitat creating ecosystem engineers. While native littorinids and other snail species did (and do) exist in the New England intertidal prior to the arrival of *L. littorina littorea*, they were all much smaller and provided less surface area for epibiont settlement than the contemporary average *L. littorea* shell. The amount of ‘new’ habitat provided by *L. littorea* is substantial: If we assume that snails are roughly spherical, that the mean density of snails is 240/m$^2$, and that the mean diameter of a snail is 19.8 mm, then the mere presence of *L. littorea* increases the available substrate by approximately 0.30 m$^2$ per m$^2$. Within a rocky cobble bed this number may be small, but it does provide one third again the amount of available space (compared to a flat rock surface) for a significant number of propagule producing epibionts. As a mobile substrate, *L. littorea* shells may be a more advantageous location for organisms than cobble, as the snail can move to avoid environmental
extremes, predators, etc.

Both epibiosis and mean snail length increased with decreasing tidal height, which may be a function of epibiont environmental tolerances or snail age, which correlates with length (Figure 1.10, 1.15, 1.19). This pattern is likely driven by a combination of factors. *Littorina littorea* is known to move from the mid-intertidal to the deeper subtidal zone through time as it ages (Smith & Newell 1955, Warner 2001). An older, larger snail has been in the environment longer, and has thus had more exposure to epibiont propagules and a greater chance of epibiont accumulation. *Cliona* is a filter feeding sponge, while spirorbids are filter feeding, tube building worms that need regular submersion (as in pools or the shallow subtidal) to remain alive. Barnacles and *Mytilus* are also filter feeders, but can tolerate longer periods of desiccation. Spionids are somewhat protected from environmental fluctuations by burrowing into snail shell. Older, larger snails, with more worn shells and a longer time period for potential fouling exhibited the highest levels of fouling. What is not clear from this study is whether large, fouled snails move lower into the intertidal at a different rate than their unfouled conspecifics, or if the epibionts settle preferentially on large snails or those within a given habitat.

The most common epibiont taxa were the encrusting coralline algae, which were found on up to 97% of snails within a given location/habitat. While multiple calcareous algal species were observed, they were not differentiated to species during this study. Each species of algae has unique environmental
preferences (Adey 1970). More than half of all snails in the shallow subtidal were encrusted with calcareous algae, but curiously, that percentage was much lower in the tidal pools, the other continuously submerged habitat (Figure 1.9). Species level differences in habitat preferences may explain these patterns. As a group, the crustose coralline algae were not only the most common epibiont species but were correlated with the presence of all other epibionts, excluding Mytilus and barnacles, that were present exclusively on unfouled snails. Toxins in red algae and coralline crusts have been shown to inhibit barnacle and mussel settlement (Breitburg 1984, Nylund & Pavia 2003), so these two species may actively avoid snails with calcareous algal crusts. The spionid polychaetes were observed actively burrowing into both the algal crusts and the snail shell on heavily algal fouled snails. The patterns and impacts of calcareous algal fouling on Littorina littorea will be examined in greater detail in Chapters 2 and 3.

Cliona is a boring sponge that erodes calcium carbonate substrates such as shells, limestone, and coral reefs through a combination of mechanical and chemical processes (Cobb 1975, Hartman 1957, Hooper 2002, Old 1941, Rosell & Uriz 2002, Schonberg 2002, 2003). Members of the filter-feeding genus Cliona have a worldwide distribution, and are reported almost exclusively subtidally in coral or commercially important bivalve shells (Alagarswami & Chellam 1976, Evans 1969, Fromont et al. 2005, Thomas 1979). However, it is likely that Cliona is also ubiquitous in other molluscs (e.g. Barucca et al. 2007, Calcinai et al. 2000, Calcinai et al. 2005, Carballo et al. 2004, Hoeksema 1983,
Rosell & Uriz 1999, Rosell & Uriz 2002, Rützler 2002). Stefaniak et al. (2005) were the first to report *Cliona* on the gastropod *Littorina littorea* in New England, although it had previously been reported in other species within North America: oysters on the Atlantic seaboard (Schlesselman 1955, Wells 1959), a subtropical gastropod species in the Gulf of Mexico (Smyth 1989), oysters in New Hampshire's Great Bay (Ray Grizzle, personal communication), and in several other molluscan species throughout New England (personal observation).

The prevalence of *Cliona* on *Littorina littorea* in this study was much lower (4% across all locations) than that seen by Stefaniak et al. (2005) on Appledore Island (47% overall). While not a major epibiont species regionally, locally *Cliona* reached high prevalences (maximum prevalence 33%, Beverley subtidal), indicating that it might be an influential species in some locations. Despite its overall low abundance, the same pattern of increasing *Cliona* prevalence with increasing snail size and decreasing tidal height was observed. Older, larger snails, or those most likely to be reproductive, were the most impacted by the boring sponge. Snail shells were almost always initially bored around the aperture, where the shell touches the substrate. As *Cliona* infection increased, the sponge spread up through the interior column. The shell spire was often broken or eroded on heavily bored snails, which were weakened and subject to higher predation risk (Stefaniak et al. 2005). Thus, *Cliona* has the ability to impact regional, broadcast spawning *L. littorea* populations by increasing mortality at the local level.
Spionid polychaetes, the third most common epibiont in this survey, are one of the most commonly reported epibionts on *Littorina littorea* in Europe (Warner 1997; Buschbaum et al. 2007; Thieltges & Buschbaum 2007b), and are also common on other basibiont species worldwide (Bick 2001, Bick 2006, Blake 1969, Evans 1969, Haigler 1969, Khamdan 2001, Martin & Britayev 1998, Vasconcelos et al. 2007, Williams & McDermott 2004). Spionids are often destructive inhabitants of shells, creating holes and tunnels that may weaken the shell and increase susceptibility to predation or disease. Warner (1997) showed that polychaete presence on *L. littorea* in Great Britain was positively correlated with shell damage caused by barnacle epibionts, and as with *Cliona* and calcareous red algae, polychaete prevalence generally increases with increasing snail size (Buschbaum et al. 2007, Warner 1997).

Epibionts generally did not occur on snail shells in isolation. Many snails had three, four, or even five total epibiont species present on their shell, functioning as small mobile habitat 'islands.' Multiple species epibiosis was more common among larger, older snails, which may be a function of time, size, facilitation, or lowered defenses. Large snails have had more exposure to propagules of epibiont species simply as a function of time in the environment, and so an increase in epibiont species richness or percent cover may be merely a function of age and the increased probability of more than one settlement event through time. Older snails are also larger, and the increased surface area presents a larger patch of substrate for epibiotic species to inhabit, an application
of the island species/area relationship on a very small scale (Connor & McCoy 1979). Alternatively, the presence of one epibiont may facilitate the recruitment of others by altering the surface of the shell to create preferred microhabitats or by producing chemical cues that attract settling larvae of other species (cf. in Kingsford et al. 2002). The facilitation theory is supported by the locations in which epibiont species were found; barnacle recruits were often found nestled in the crevices left by Cliona borings, serpulids in valleys created by boring polychaetes, etc. Non-epiphytic algal crusts are also known to host a variety of macroinvertebrate species (e.g. Kelaher et al. 2001, Ojeda & Dearborn 1989, Steneck 1986).

It is possible that the presence of epibionts might be detrimental to the health of the host snail, by diverting energy away from growth to shell defenses or the consequences of increased drag and mass (Wahl 1996). A decrease in health may make the snail more vulnerable to subsequent epibiotic colonisation, though Wahl (1996) has shown that Littorina littorea has few active immune defences against shell inhabitants. It is likely that the causal mechanisms of multiple species epibiosis on L. littorea is some combination of these factors.

While many species combinations were noticed, multiple epibioses with calcareous red algae were most pronounced in the Cliona/spionid/calcareous red algal tripartite association (Figure 1.20). Spionids were rarely found in the absence of either Cliona or calcareous algae. Polychaete worms utilize the novel habitats created by the sponge (holes or burrows) and the algae (calcireous
layers) equally, but the frequency of snails with spionid worms is much higher when both *Cliona* and algae are present. As both *Cliona* and spionids are boring/burrowing organisms, this increases the damage caused to the *Littorina littorea* shell, as evidenced by the shell damage index (Figure 1.21). Polychaetes expand the caverns created by the boring sponge, creating warrens of sponge and worm filled tunnels held together by a thin layer of shell. On snails with encrusting calcareous algae, these caverns extended through both the biotic calcium carbonate layers of the algae and the snail shell, providing more living area for the worms and the sponge. Thus, multiple species epibiosis has a synergistic effect on shell integrity. A similar negative impact was seen with polychaetes and barnacles on *L. littorea* in the Wadden Sea (Thieltges & Buschbaum 2007b), where facilitation between barnacle and polychaete epibionts led to decreased fitness of snail hosts.

Snails carrying *Cliona* or spionid worms may also serve as travelling reservoirs of infection for commercially important bivalve species such as mussels and oysters. As both *Cliona* and spionid polychaetes are known pest species within the shellfish industry (cf. MacCallum & Blackbourn et al. 2001, MacCallum et al. 2001, Winstead et al. 2004, and references above), this previously unrecognized mobile reservoir within New England warrants further study and monitoring, particularly when mussels or oysters are cultured near rocky intertidal beds which might provide propagules or direct transfer of the boring sponge or polychaete.
The prevalence and patterns of calcareous algal fouling on *Littorina littorea* warrants further examination of the factors driving the distribution patterns and the impacts that algal fouling may have on its epibiont host.
## Table 1.1 List of sampling locations

The location and sampling date are given for each site sampled. 10 quadrats each of the *Ascophyllum, Chondrus*, Shallow Subtidal, and Tidal Pool habitats were examined at each site unless otherwise noted. Site number corresponds with the numbers given in the map, Figure 1.1. Odiorene 2, 3, 4, and 5 are four separate rocky outcroppings in NH, each approximately 500 m apart, numbered from the highway access turnouts south of Odiorene State Park.

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<th>Location</th>
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<th>Latitude</th>
<th>Longitude</th>
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<td>% CA</td>
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</table>

Table 1.2 Total number of gastropods collected from each location

The total number of gastropods and the percent of those snails with the two primary epibiont species (Cliona sp. and encrusting algae) is listed by location (all habitats pooled) and by habitat (all locations pooled). Hermit crab are listed by total number and by primary gastropod shell species.
### Table 1.3 Total number of snails, percent with *Cliona*, and percent of snail with calcareous algae

For each location, listed north to south, the total number of snails present (all habitats pooled) is broken down by size class (midpoint and range given in table). The percent of snails in each size class with the boring sponge *Cliona sp.* (CL) or encrusting calcareous algae (CA) follows. Totals by habitat (all locations pooled) and overall are presented at the bottom of the table. The final two sections present total number and percentages with CA or CL for snails <25 and >25 mm, and the percentage of those snails for which CA or CL are present that are represented by the respective size class (% all CL and % all CA, respectively). Table continues on the following page.
<table>
<thead>
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<th>Size Class Range</th>
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<th>33.75</th>
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<th>Snails &lt;25 mm</th>
<th>Snails &gt;25 mm</th>
</tr>
</thead>
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<td>0</td>
<td>517</td>
<td>30.06</td>
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<td>0</td>
<td>0</td>
<td>431</td>
<td>10.9</td>
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</table>

| Habitat          | 67    | 31.34 | 15    | 80     | 3             | 100           | 2173          | 30.33         | 26.2          | 77.36         | 65.65         | 22.64         |
| Chondrus         | 159   | 81.13 | 58    | 96.61  | 17            | 100           | 2204          | 86.44         | 10.42         |
| Poons            | 310   | 41.29 | 85    | 49.41  | 13            | 76.92         | 4015          | 44.55         | 10.29         |
| Subtidal         | 218   | 76.15 | 91    | 92.31  | 26            | 96.15         | 1872          | 78.71         | 100           |

**Table 1.3, continued**
A) Total number of *Littorina littorea* with epibiont taxa

<table>
<thead>
<tr>
<th></th>
<th>Ascophyllum</th>
<th>Chondrus</th>
<th>Pools</th>
<th>Subtidal</th>
<th>All Habitats</th>
</tr>
</thead>
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<td>22</td>
<td>29</td>
<td>31</td>
<td>103</td>
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<td>27</td>
<td>37</td>
<td>55</td>
<td>128</td>
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<tr>
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<td>127</td>
<td>169</td>
<td>186</td>
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<tr>
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<td>947</td>
<td>1048</td>
<td>3252</td>
</tr>
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<td>1</td>
<td>9</td>
<td>17</td>
</tr>
<tr>
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<td>1</td>
<td>2</td>
<td>6</td>
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<tr>
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<td>29</td>
<td>9</td>
<td>70</td>
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<tr>
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<td>102</td>
<td>193</td>
<td>431</td>
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<td>1162</td>
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B) Percent of *Littorina littorea* with epibiont taxa

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<tr>
<th></th>
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<th>Subtidal</th>
<th>All Habitats</th>
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<td>0.96</td>
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<td>0.86</td>
<td>2.81</td>
<td>1.19</td>
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<td>3.94</td>
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<td>4.88</td>
</tr>
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<td>0.02</td>
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<td>Limpet</td>
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<td>0.02</td>
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<td>Mytilus</td>
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<td>0.46</td>
<td>0.65</td>
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<tr>
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<td>2.71</td>
<td>3.71</td>
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<td>3.47</td>
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<tr>
<td>Total with Epibiont</td>
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<td>43.98</td>
<td>27.08</td>
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<td>34.81</td>
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<td>56.02</td>
<td>72.92</td>
<td>41.48</td>
<td>65.19</td>
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</table>

Table 1.4: Number and percent of *Littorina littorea* with each epibiont species

The total number of *Littorina littorea* (A) and percent of snails (B) with each of the nine epibiont taxa within each habitat type is listed. Note that percents will not sum to 100%, as some individual snails had multiple epibiont species present simultaneously.
<table>
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<th>Mean (SE)</th>
<th>Mean (SE)</th>
<th>p</th>
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</thead>
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<tr>
<td>Cliona absent</td>
<td>18.9 (0.22)</td>
<td>19.86 (0.48)</td>
<td>0.07</td>
</tr>
<tr>
<td>Cliona present</td>
<td>18.6 (0.25)</td>
<td>20.28 (0.43)</td>
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<tr>
<td>Pools</td>
<td>19.23 (0.24)</td>
<td>20.02 (0.33)</td>
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<tr>
<td>Subtidal</td>
<td>20.03 (0.30)</td>
<td>22.12 (0.42)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Algae absent</td>
<td>18.36 (0.28)</td>
<td>19.75 (0.27)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algae present</td>
<td>18.36 (0.49)</td>
<td>19.22 (0.25)</td>
<td>0.122</td>
</tr>
<tr>
<td>Pools</td>
<td>18.92 (0.41)</td>
<td>19.68 (0.22)</td>
<td>0.102</td>
</tr>
<tr>
<td>Subtidal</td>
<td>18.53 (0.75)</td>
<td>21.01 (0.26)</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

**Table 1.5: Mean lengths of *Littorina littorea* with boring sponge or encrusting algae**

The mean length (snails >10mm only) by habitat is given with one standard error for individual snail lengths of *Littorina littorea* with boring sponge *Cliona* or encrusting calcareous algae present or absent. P-values indicate significance in one-way Anovas for each epibiont/habitat combination. Snails with epibiont present were larger than snails without for both epibiont types across all habitats.
Table 1.6: ANOVA table for percent snails with epibionts and mean species richness by algal fouling level.

ANOVARs by habitat on the percent of all snails with a non-algal epibiont and mean species richness (any taxa, excluding calcareous algae), using each quadrat as a replicate and the presence or absence of calcareous algae on the snail as a fixed factor. In all habitats except the pools, both epibiont community species richness and percent of snails with non-algal epibionts was higher on snails which also had calcareous algal crusts.
Table 1.7: Contingency table of epibiont species association with calcareous algae

The p values for 2x2 contingency table analysis for Calcareous Algae (Present/Absent) and each epibiont species (Present/Absent) for all individual snails. Significant p values indicate positive association between calcareous algae and the species listed. Non-significant values (p>0.05) indicate a lack of positive association.
Figure 1.1: Map of sampling locations

The 19 numbered locations used for gastropod epibiont survey collections in Maine, New Hampshire, and Massachusetts correspond to the location descriptions in Table 1.1.
Figure 1.2 Density of *Littorina littorea* by location

Mean density (#/m² +/- 1SE) of all live *Littorina littorea* in the nineteen sampling locations, listed north to south. Sample sizes can be found in Tables 1.1 and 1.2.
Figure 1.3 Density of *Littorina littorea* by location and habitat

Mean density (#/m² +/- 1SE) of all live *Littorina littorea* in the nineteen sampling locations by habitat, listed north to south.
Figure 1.4: Mean density of *Littorina littorea* by habitat

Mean density (#/m² +/- standard error) of *Littorina littorea* across all locations, by habitat.
Figure 1.5 Mean length of *Littorina littorea* by location.

Mean length (median, n = 3) and standard error (±SE) of (>10 mm) *Littorina littorea* at each location.
Figure 1.6: Mean length of *Littorina littorea* by habitat

Mean length (mm) and standard error of (>10 mm) *Littorina littorea* across all locations, by habitat. Length of snails in the subtidal was significantly different from the other three habitats (ANOVA, MS 114.963, f 13.52, p <0.0001).
Figure 1.7: Percent of *Littorina littorea* with epibiont species present
a) all taxa including calcareous algae; b) excluding calcareous algae. Bars indicate means and SE from one-way ANOVA; letters indicate significance (Tukey-Kramer HSD, p<0.05).
Figure 1.8 Percent of Littorina littorea with encrusting calcareous algae present, by location and habitat.
Figure 1.9: Percent of *Littorina littorea* with calcareous algae by habitat

Bars indicate percent (+ 1SE) of live *Littorina littorea* in each habitat with encrusting calcareous algae present on the shell (n=number of quadrats in each habitat). Letters indicate significant difference between habitats (p<0.0001).
Figure 1.10: Length distribution of snails with and without calcareous algae present

Total number of snails from all habitats with encrusting calcareous algae (CA) (light bars) and without CA (dark bars) on their shell. Total number and percent of snails with CA and the size class range for each midpoint can be found in Table 1.3. Algae was more common on large snails than small, but was found in every length class in all habitats. Note different y-axis in C.
Figure 1.11: Percent of snails in each habitat by calcareous algae shell coverage

Bars indicate mean percent (+ 1SE) of *Littorina littorea* in each habitat by the percent coverage of calcareous algae on the shell. None=0% cover; Low=1-30% cover; Medium=31-69% cover; High=70-100% cover. The percent of each individual shell that was covered by encrusting calcareous algae generally increased with increasing submergence time/decreasing tidal height.
Figure 1.12: Bivariate fit of snail length by algal percent cover

The bivariate fit of length (mm) by algal percent cover for each individual snail is plotted by habitat. A) Ascophyllum, $r^2=0.151$; B) Chondrus $r^2=0.294$; C) Pools $r^2=0.166$; D) Subtidal $r^2=0.328$. P<0.001 for all habitats. Percent cover of algae increases with increasing snail length.
Figure 1.13: Percent of Littorina littorea with the boring sponge Cliona present, by location and habitat.
Figure 1.14: Percent of *Littorina littorea* with the boring sponge *Cliona* by habitat

Bars indicate percent (+ 1SE) of live *Littorina littorea* in each habitat with boring sponge present on the shell. Letters indicate significant difference between habitats (p<0.0001).
Figure 1.15: Length distribution of snails with and without *Cliona* present

Total number of snails from all habitats with *Cliona* (light bars) and without *Cliona* (dark bars) on their shell. Total number and percent of snails with *Cliona*, and the size class range for each midpoint, can be found in Table 1.3. *Cliona* was rare in snails less than 18 mm long.
Figure 1.16: Mean epibiont species richness by habitat

Mean species (taxa) richness of epibiont species, not including calcareous algae in count, on snails with and without calcareous algae present on shells. Asterisks indicate significant difference (p<0.05) between algal fouled and unfouled snails within each habitat type. ANOVA details in Table 1.4.
Figure 1.17: Percent of snails with non-algal epibiont species present

Total percent of snails with 0 (n=2424 with algae present, 7007 without), 1 (n=627 with algae present, 450 without), 2 (n=169 with algae present, 36 without), 3 (n=27 with algae present, 3 without), or 4 (n=5 with algae present) non-algal epibionts present on their shell. The mean percent of snails with non-algal epibionts present was significantly higher when algal epibionts were also present on the snail (Table 1.6). Multiple epibionts were more common on snails with calcareous algae.
Figure 1.18: Number of snails with each epibiont species

Total number of snails with each non-algal epibiont species, all habitats combined, split by presence of calcareous algae. Asterisk indicates a positive association between the presence/absence of calcareous algae and the presence/absence of the epibiont species two by two contingency table, Fisher's Exact Test, $p<0.05$, Table 1.7).
Figure 1.19: Mean lengths of *Littorina littorea* by number of epibiont species present.

The mean length (+/- 1SE) of (>10 mm) snails in each habitat, by total number of epibiont species (inclusive of calcareous algae). Letters indicate significant differences in length between epibiont number classes within each habitat (Tukey HSD, p<0.05). Results for length exclusive of calcareous algae were similar.
Figure 1.20: Three way epibiont interaction: spionid polychaete presence in the presence or absence of Cliona and calcareous algae

Each bar represents the percentage of snails with or without burrowing spionid polychaete worms, categorized by the presence (+) or absence (-) of the boring sponge Cliona sp. (CL) and/or calcareous algae (CA). Spionids were rarely found in the absence of the other two species, and 34% of snails with both Cliona and calcareous algae also had spionid worms.
Figure 1.21: Shell damage index with algal and clionid percent cover

For snails where the boring sponge *Cliona* was present, a relative damage index was assigned, ranked from low (no damage; light grey markers) to high (shell extremely fragile or broken, protein layer missing, column whorl broken; dark grey markers). The damage index was plotted by the percent cover of *Cliona sp.* (y axis) and calcareous algae (x axis). Shell damage increased with increasing sponge percent cover and in the presence of spionid polychaete worms (asterisks).
CHAPTER 2: LOCAL SCALE INVESTIGATION OF CALCAREOUS ALGAL FOULING ON *LITTORINA LITTOREA*

**Abstract**

The periwinkle snail *Littorina littorea* serves as a host for a variety of epibiont species in northern New England, the most common of which are the encrusting calcareous algae. There are several different algal species that utilize *Littorina littorea*, and the prevalence of each species varies widely between habitats at the local scale. The factors that drive algal presence on snail shells are a combination of algal environmental preferences, propagule settlement, shell substrate condition, and snail movement and grazing.

**Introduction**

Species distribution within the intertidal zone is driven by a combination of factors, including wave exposure, desiccation, temperature, propagule availability, individual movement, facilitation, predation, and substrate type (e.g. Benson 2002, Bruno et al. 2003, Davenport & Davenport 2005, Harley 2003, Lubchenco 1980, Scrosati & Heaven 2007, 2008, Somero 2002, Yamada & Boulding 1996). When patterns of epibiosis on basibionts are examined, the resulting distribution will be a combination of these factors on both the epibiont and basibiont species, complicated by any changes in behaviour or habitat
choices of the fouled basibiont. Epibiosis can also range from an obligatory symbiotic relationship, where the epibiont strongly prefers or requires the host to provide substrate, to a more facultative, incidental relationship, where the epibiont is likely to be found on living or abiotic substrates.

The gastropod *Littorina littorea* serves as a host for a variety of epibionts in the intertidal zones of the Gulf of Maine, with rates of epibiosis by the most common taxa, encrusting calcareous red algae, reaching nearly 100% of snails in some locations (Chapter 1). Larger, older snails are more likely to be algal fouled, but are also more likely to live subtidally or in the low intertidal, which are habitats in which algal epibiosis reached the highest prevalence (Gendron 1977, Saier 2000, Warner 2001, Vermeij 1972).

The epibiont species present on snail shells may be identical to or a subset of the species pool found on surrounding non-living hard substrate, or may include species that only utilize living shell and are not present elsewhere in the rocky intertidal. There is a large species pool of calcareous red algae in the New England intertidal (e.g. Adey 1962, Adey & Adey 1973, Mathieson et al. 1981, Sears 1998, Villalard-Bohnsack 1995), each with substrate and microhabitat preferences. Algal epibiosis on *Littorina littorea* is likely to be incidental, with algae settling on any hard substrate rather than actively selecting biotic or abiotic surfaces, but if an obligatory or preferential relationship exists between any algal species and substrate type, or the microhabitat of the snail shell differs from that of the rocks, then a difference in prevalence with substrate
type is to be expected. Settling on *L. littorea* may be beneficial to the algae, as
snails, unlike rocks, are mobile and can take shelter from ice scour, desiccation,
or other environmental disturbances. However, that very mobility makes snails a
risky substrate, as they may move beyond the environmental niche of the algal
epibiont (i.e., from a subtidal to an emerged location) or be consumed by
predators.

Both living and dead snails were fouled with crustose coralline algae.
Algal fouling was minimal in the upper intertidal zones, where snails are younger
and smaller, and their shells less damaged by erosion, predation, and exposure.
This pattern could be due to the longer time that older shells have been present
within the environment, thus providing more opportunity for algal settlement, or
could reflect behavioural (such as shell cleaning behaviours), shell structural
(intact organic matrix), or immunological responses of the snail to epibiosis. The
outer proteinaceous periostracum and calcium carbonate shell layers of *Littorina
littorea* becomes worn through time, and epibiosis has been shown to be related
to shell microstructure in other systems (Bell 2005, Smyth 1989, Taylor & Reid
*Littorina littorea* has no active immunological defense mechanism against
epibiosis, it is also possible that the aggregation behaviour of *Littorina littorea*,
with snails crawling and grazing on microalgae on each other's shells, could
impact the survival of algal recruits on snail shells, as some calcareous algal
species are more susceptible to disturbance than others (Abbott & Bergey 2007,
Anderson & Underwood 1997, Dethier & Steneck 2001). Algal species preferences (for both tidal height and substrate type/integrity) and snail grazing may impact the early settlement and recruitment of calcareous red algae to snail shells.

In this chapter, calcareous algal epibiosis on *Littorina littorea* is examined in detail at a Jaffrey Point, NH (Latitude 43.06, Longitude -70.71). The obligatory or facultative nature of algal epibiosis is examined in a field survey that compares established algal species presence and diversity on abiotic (rock) and snail shell substrate at different tidal heights. The role of algal recruitment across tidal heights and shell condition is also examined in a field experiment. The role of snail movement in maintaining observed epibiosis gradients will be addressed in Chapter 3.

**Methods**

*Field Site Description*

The two studies described in this chapter both took place at Fort Stark State Historical Park at Jaffrey Point, NH. Jaffrey Point is two miles southeast of Portsmouth, New Hampshire on New Castle island at the confluence of the Piscataqua River and the Atlantic Ocean. It is moderately protected from wave disturbance, but would not be considered sheltered (Mathieson et al. 1981).
Jaffrey Point is characterized by large granitic bedrock tongues interspersed with small boulders and cobble. Snail collections and experiments were conducted on the northern side of Jaffrey Point in a wide, flat, moderately exposed area with a broad shallow subtidal area; several large tidal pools were interspersed within the low and mid intertidal zones with a more protected cove on one side.

Comparison of Established Algal Communities on Shell vs Rocky Substrate

To determine if the mobile substrate of snail shells contains a unique species assemblage compared to its surroundings, or if algal use of snail shells appears to be facultative, both snail and rocky substrate were examined from four habitats: tidal pools, low *Ascophyllum*, and two shallow subtidal areas (a low wave exposure protected cove and higher wave exposure area). In each habitat, ten 0.25m$^2$ haphazardly selected quadrats were examined using a 30 point grid overlaid on each quadrat. At each point the presence of encrusting algal species, bare substrate (rock or sand/gravel), *Corallina* sp., and any other primary space holders was recorded. The point counts were converted to a percentage of suitable hard substrate (excluding sand/gravel) occupied by each algal species, in order to allow points to be compared to snails. After completing the rocky substrate point counts, all *Littorina littorea* within the quadrat were removed and examined for encrusting algal species presence. All snails were collected from each quadrat until ~100 snails had been examined in each habitat (snails counted from n=3 to 6 quadrats per habitat; see Table 2.4). Algal species
were identified according to standard keys (Villalard-Bohnsack 1995, Sears 1998), and identification confirmed by Art Mathieson (pers. comm.). The percentage of snails with each algal species present was calculated per quadrat. As many snails had >1 species of algae on their shell, total percentages may exceed 100%.

**Algal Settlement on Shell Substrates**

In order to determine if there are species specific differences in algal settlement by tidal height, if algal species preferentially settle on shells with different levels of integrity (peristracum intact or eroded), and if algal settlement is inhibited by live, moving snails, a nested block design caging experiment was conducted from 18 June to 25 October 2007 (19 weeks). Variables tested included tidal height, snail shell condition, and snail cleaning/movement behavior.

Snails were collected from and marked with Testor’s (TM) enamel to aid in treatment identification. Three snail condition and behavior treatments were designated: “Live” snails (snail live and capable of shell cleaning behavior, shell fully intact), “Intact” shells (snail dead, shell fully intact), and “Eroded” (snail dead, shell worn and eroded). “Intact” snails were collected live; the inhabitant was killed by freezing (the least destructive method to the shell) and the body removed. “Eroded” snails were collected from the field site, selecting for shells that were worn but not broken or otherwise fouled. Snails (n=30 snails per
treatment per cage) were placed into closed stainless steel cages (mesh size 4, 30.5 x 28 x 10 cm, for a surface area of 0.1 m²) which were bolted onto the rocks. Two cage types ("Live", containing all 3 snail treatments; "Dead", containing Intact (dead) and Eroded (dead) snails only) were blocked in 3 pairs within each of three habitats (mid intertidal/Ascophyllum zone; Tidal Pools; and Shallow Subtidal) for a total of 18 cages. The "Live" cage treatment was designed to investigate the potential impact of live, moving, grazing snails on algal settlement on cohorts, as snails are often seen moving and grazing over each other's shells.

Two weeks after cages were placed in the intertidal, it was noted that the "live" snails had experienced significant mortality across all tidal heights, likely due to a hot weather event. Additional live snails were added to each live treatment cage to bring the total number of live snails back to 30; final totals reflect the additions. While the addition of new snails may have biased the results slightly, as the added snails experienced a shorter algal recruitment period, all original snails were retained in the cages, and it was decided that maintaining the 'live grazing' treatment at constant strength was the more important variable.

After snails were retrieved on October 25, snails were re-classified as live, dead (intact) or dead (eroded) according to the state of the shell and the status of the inhabitant, such that a snail that was originally 'live', but had died during treatment was re-coded as dead (intact). In addition, due to loss of marking and continued erosion of shells, some shells that were originally considered "intact"
were re-classified as “eroded” based on the condition of the shell. The number of patches (individual settled algal colonies) of each species of algae was counted on each snail. The percentage of snails with each species present and the mean number of patches of each species was calculated for each cage. Substantial cage loss occurred in the final weeks of the experiment as a result of strong storms. The total number of snails present, and their final classification in each retrieved cage are summarized in Table 2.3. Loss of replication precluded full statistical analysis of the experiment, but trends and analysis on subsets of data are presented here.

**Results**

*Comparison of Established Algal Communities on Shell vs Rock Substrate*

Table 2.1 contains a summary of the sample size and results of the comparison of rocky substrate point count and snail algal species presence. The total number of quadrats examined for point counts and snail collections, with total number of *Littorina littorea* collected from quadrats, is listed. Individual points over suitable rocky substrate and individual snails were used as replicates; mean values represent means by quadrat.

Five species were encountered in sampling: *Phymatolithon lenormandii* (Areschoug in J. Agardh) Adey, *Hildenbrandia rubra* (Sommerfelt) Meneghini, *Clathromorphum circumspectum* (Strömfelt) Foslie, *Lithothamnion glacialie*
Kjellman, and *Corallina officinalis* L. *Corallina* is excluded from the following analyses as it was encountered rarely. The percent cover (# points/suitable points or # snails/total snails) of each species by habitat is presented in Table 2.1. Overall algal coverage was higher in the subtidal and lowest in the pools (Figure 2.1), a trend that matches that seen in Chapter 1 (Figure 1.18).

Significant differences were observed on rock vs snail substrate for *H. rubra*; *P. lenormandii* was marginally significant (p=0.08) and the remaining species were equally common on shell and rocky substrate (Table 2.2, two-way ANOVA with interaction of habitat and substrate type).

The mean species richness varied significantly with habitat and substrate type (Figure 2.2). In every habitat except pools, species richness was higher on rocks than snails. In pools, species richness was higher on snails, though pools had the lowest overall algal prevalence.

When each algal species is examined individually, a few other trends are evident. *Phymatolithon lenormandii* was the most common algal species present in all habitats (Figure 2.3), and likely drives much of the species richness pattern. *Phymatolithon* was more common on rocks than snails in the protected subtidal and the *Ascophyllum* zone, but equally prevalent on rocks and snails in the exposed subtidal and the pools. *Clathromorphum circumscrip tum* (Figure 2.4) was rare in tidal pools, and most prevalent in the mid intertidal/*Ascophyllum* zone. *Lithothamnion glaciale* (Figure 2.5) was quite rare, and was virtually absent on snails, although some snails with *Lithothamnion* were heavily fouled.
almost beyond recognition (personal observation). *Lithothamnion* was entirely absent in the *Ascophyllum* zone, and was found on only a few snails in the pools. *Hildenbrandia* (Figure 2.6) was entirely absent in the pools and on snails in the exposed subtidal. It was relatively common in the protected subtidal, where it was found equally on both shell and rocky substrate.

**Algal Settlement on Shell Substrates**

A summary of the cages successfully retrieved at the end of the experiment, and the final number of snails assigned to each treatment class is presented in Table 2.3. Unfortunately no "dead" cages were recovered from the shallow subtidal, the height at which algal prevalence was highest. The *Ascophyllum* and Pool habitats each had one complete pair present; cage pair 1 from each of those habitats was selected for further analysis.

Figure 2.7 presents the compiled values by habitat and cage type for the percent of snails and mean number of algal recruits per snail. Four species were present on snail shells: *Ralfsia verrucosa*, *Hildenbrandia rubra*, *Clathromorphum circumscriptum*, and *Phymatolithon lenormandii*. *Lithothamnion glaciale*, which was rare in the habitat sampling above, was absent from shells in this study.

The subtidal had the highest percent of snails with algal fouling, and also more species overall; *Clathromorphum circumscriptum* and *Hildenbrandia rubra*
were found exclusively in the subtidal. *Phymatolithon lenormandii* was found on more snails in the subtidal, but had fewer patches than *Clathromorphum circumscriptum* per snail. Algal presence on live snails in the subtidal was rare.

*Ralfsia verrucosa* was found only in pools, and was much more common on snails in the “live” cages than the dead ones. Up to 26 algal recruit patches were found on a single snail, and *R. verrucosa* recruits were more common on live (100%) > eroded (95%) > intact (80%). In the “dead” cages, where live snails with their attendant grazing were absent, *R. verrucosa* was only present on the eroded shells.

*Phymatolithon lenormandii* was the only species found in all 3 habitats. This species exhibited a strong preference for worn shells, as it was never found on live snails and was more common on eroded than intact dead shells. The prevalence of *P. lenormandii* was lower in “live” than “dead” cages, indicating that the grazing/moving pressure of live snails might impact algal settlement or recruitment for this species.

No relationship was observed between snail length and number of algal patches for any species (linear regression), indicating that the species/area relationship is negligible at this level of difference in snail size (data not shown).
Discussion

Epibiosis by calcareous red algae on Littorina littorea is driven by a combination of differential recruitment of algal species by habitat and survival of recruits to mature encrusting communities. The algal community found on snail shells is a subset of the algal species pool available in the surrounding habitat, and species richness is generally lower on snails than in quadrats in every habitat except pools (Figure 2.2). No algal species was found on snails that was not also found on rocky substrate, and vice-versa, indicating that there is no obligatory relationship between algal species and substrate type. Abiotic substrate, however, generally exhibited higher levels of algal fouling, both in terms of the percent of the substrate fouled and the algal community species richness. This may simply reflect the difference in community age between the abiotic and biotic substrate; rocks have had more time for algal communities to develop than the shorter lived, mobile snails. Snails, with their fragile proteinaceous layer, will also exhibit the effects of erosion due to tumbling and wave action more quickly than the resistant surfaces of granite bedrock.

Due to the loss of cage replicates in the algal recruitment experiment, it is difficult to draw firm conclusions, as variations in algal recruitment between cages may reflect variation in recruit supply or other environmental variability rather than a true treatment effect (Figure 2.7). It is also possible that the recruitment window of some species was missed in the duration of this experiment. However, if the results are indicative of the true relationship
between tidal height and algal recruitment, there are some interesting patterns. *Phymatolithon lenormandii*, the most common species on both snail and rocky substrate (Figure 2.3), almost never recruited to live snails in this study, and was more common on damaged (eroded) snails where no grazing activity occurred than on intact snails. It is possible that *P. lenormandii* recruitment to live snails may be rare but long term survival of *P. lenormandii* colonies may be greater than that of other algal species. Alternatively, the 'live' snails in this experiment may not have been the optimal substrate for *P. lenormandii*; older, larger snails, which exhibit the highest degrees of fouling, are often naturally worn and eroded. It may be that the degraded shell integrity rather than the dead status of the snail is what *P. lenormandii* prefers; as this experiment did not contain a “live but eroded” snail treatment, this hypothesis was not tested directly.

*Ralfsia verrucosa* was never found to settle on snails outside of tidal pools, and it was not discovered in the survey of rocky vs snail algal epibions. Again, this may be due to local variations in propagule abundance or environmental tolerances of *R. verrucosa*, or the discrepancy between settlement and adult algal colonies may result from differential movement of fouled snails into or out of tidal pools. *Ralfsia verrucosa* may also be inhibited by pre-existing crusts of *Hildenbrandia*, one of the common species on both rock and snail substrate in established communities (Bertness et al. 1983). Thus, the presence of *R. verrucosa* on the caged settlement experimental snails and not in the established rock/shell survey may be the result of capturing different
developmental snapshots of the algal community.

Algal recruitment patterns explain some, but not all, of the species prevalences seen on *Littorina littorea* and rocky substrate. Further investigation into the mechanisms driving algal epibiosis patterns on *L. littorea* is needed to fully understand the relationship of tidal height, substrate, and species preferences in this system.
### Table 2.1: Comparison of rock and snail shell substrate usage by calcareous algae

Within each habitat (shallow subtidal exposed, shallow subtidal protected cove, pools, Ascophyllum) the mean percent cover (abiotic substrate) and percentage of *Littorina littorea* with no calcareous algae and each of the five algal species are noted with standard error. The mean species richness for each habitat is also present.

<table>
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<tr>
<th>Substrate</th>
<th>Quadrat</th>
<th>Total # Snails</th>
<th>Snail Density Mean (S.E.)</th>
<th>No Algae Mean % (S.E.)</th>
<th>Corallina Mean % (S.E.)</th>
<th>Phymatolithon Mean % (S.E.)</th>
<th>Clathromorphum Mean % (S.E.)</th>
<th>Lithothamnion Mean % (S.E.)</th>
<th>Hildenbrandia Mean % (S.E.)</th>
<th>Species Richness Mean (S.E.)</th>
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</tr>
<tr>
<td>Snail</td>
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<td>131</td>
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<td>0 (0)</td>
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<td>24.4 (13.4)</td>
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<td>1.7 (1.1)</td>
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</table>

Within each habitat (shallow subtidal exposed, shallow subtidal protected cove, pools, Ascophyllum) the mean percent cover (abiotic substrate) and percentage of *Littorina littorea* with no calcareous algae and each of the five algal species are noted with standard error. The mean species richness for each habitat is also present.
### Table 2.2: ANOVA Tables for algal species percent cover by habitat and substrate type

ANOVA tables for percent of habitat usage by each algal species and overall algal species richness by habitat (shallow subtidal exposed, shallow subtidal protected cove, pools, Ascophyllum) and substrate type (abiotic substrate—percent cover on rock; biotic substrate—percentage of *Littorina littorea*).
### Number of Snails (Final)

<table>
<thead>
<tr>
<th>Cage Pair</th>
<th>Cage Type</th>
<th>Live</th>
<th>Dead-Intact</th>
<th>Dead-Eroded</th>
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### Summary

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</tr>
<tr>
<td>Ascophyllum</td>
<td>2</td>
</tr>
<tr>
<td>Pool</td>
<td>1</td>
</tr>
</tbody>
</table>

### Table 2.3: Summary of Algal Settlement Cage and Snail Recovery

Table presents the total number of cages and snails recovered from the algal settlement caging experiment. Cages with ("live") and without ("dead") live *Littorina littorea* and with (dead) eroded and intact shells were placed in pairs at each of the three habitats listed (n=30 snails per treatment initially). Cage loss and final snail counts are explained in the text.
Figure 2.1: Encrusting algal presence on rock and *Littorina littorea* shell substrate

The percent of A) individual points of suitable (rocky) substrate in quadrats and B) individual snails within quadrats (n quadrats in Table 2.1) with the four most common encrusting calcareous algal species, by tidal height/habitat (protected shallow subtidal cove, exposed shallow subtidal, tidal pools, Ascophyllum bed).
Figure 2.2: Encrusting algal species richness on rock and snail substrate by habitat

Mean encrusting algal species richness (+ 1 SE) on rock and snail shell substrate at different tidal heights (shallow subtidal protected cove, shallow subtidal exposed, Ascophyllum, and pools). Actual species richness can be found in Table 2.1. Species richness was higher on rocks than on snails in the shallow subtidal and mid intertidal (Ascophyllum) zones, but higher on snails than on rocks in tidal pools. Letters indicate significant differences between levels (Location*Substrate type, Tukey HSD LS Means differences, alpha=0.05)
Figure 2.3: *Phymatolithon lenormandii* prevalence on rock and snail substrate by habitat

Mean percent of quadrat points or individual snails (+ 1 SE) in the four habitat/tidal heights (shallow subtidal protected cove, shallow subtidal exposed, Ascophyllum, and pools) with *Phymatolithon lenormandii* present. Percents tabulated in Table 2.1. Letters indicate significant differences between levels (Location*Substrate type, Tukey HSD LS Means differences, alpha=0.05).
Figure 2.4: *Clathromorphum circumscriptum* prevalence on rock and snail substrate by habitat

Mean percent of quadrat points or individual snails (+ 1 SE) in the four habitat/tidal heights (shallow subtidal protected cove, shallow subtidal exposed, Ascophyllum, and pools) with *Clathromorphum circumscriptum* present. Percents tabulated in Table 2.1. Letters indicate significant differences between levels (Location*Substrate type, Tukey HSD LS Means differences, alpha=0.05).
Figure 2.5: *Lithothamnion glaciale* prevalence on rock and snail substrate by habitat

Mean percent of quadrat points or individual snails (+ 1 SE) in the four habitat/tidal heights (shallow subtidal protected cove, shallow subtidal exposed, Ascophyllum, and pools) with *Lithothamnion glaciale* present. Percents tabulated in Table 2.1. No significant differences were found between substrate/habitat (Location*Substrate type, Tukey HSD LS Means differences, alpha=0.05).
Figure 2.6: *Hildenbrandia rubra* prevalence on rock and snail substrate by habitat

Mean percent of quadrat points or individual snails (+ 1 SE) in the four habitat/tidal heights (shallow subtidal protected cove, shallow subtidal exposed, Ascophyllum, and pools) with *Hildenbrandia rubra* present. Percents tabulated in Table 2.1. Letters indicate significant differences between levels (Location*Substrate type, Tukey HSD LS Means differences, alpha=0.05).
Figure 2.7: Percent of *Littorina littorea* shells with algal recruits

Percent of snails in settlement caging experiment with algal recruits present by species per shell, on live snails, dead but intact shells, and dead eroded shells. "Live" cages contained all three snail types; "dead" cages contained intact and eroded shells only. Cages from some habitats missing (see Table 2.3 for summary); snails from remaining cages were pooled within each habitat for the percentages in this graph.
CHAPTER 3

IMPACTS OF CALCAREOUS ALGAL FOULING ON LITTORINA LITTOREA

Abstract

*Littorina littorea* is an introduced and highly common marine periwinkle snail in the Northwestern Atlantic intertidal zone. In northern New England, up to 80% of all snails are fouled with species of crustose coralline algae, increasing the weight and size of the snail and potentially impacting the snail host by changing grazing habits, limiting movement, causing physiological responses, or impacting predation rates. As *L. littorea* is an introduced species, it is critically important to understand how the presence of algal epibionts affects the snail at the individual and population level. These parameters were investigated in a series of laboratory and field studies. Algal fouled snails experienced differential movement, grazing, survival, and physiological condition.

Introduction

As an herbivore with high population sizes in its introduced range in the northwestern Atlantic, the snail *Littorina littorea* is a good candidate for intensive study on the impacts of epibiosis at an individual and population level. Chapter 1 demonstrated that crustose coralline algae often occurs abundantly as epibionts on *L. littorea* in northern New England. However, Chapter 2 suggested that the relationship of crustose coralline algae with snails was facultative and
that snails did not defend against algal fouling. Thus, *Littorina littorea*'s apparent lack of active defenses against epibiotic calcareous red algae suggests either that there has been insufficient selective pressure to develop such defenses, because calcareous red algae has negligible impact on the snail, or that *L. littorea* is not physiologically capable of a meaningful response, perhaps because it has not had enough time to respond to epibiosis as a new or changing phenomenon (Mouritsen & Bay 2000, Wahl & Sonnichsen 1992). In this chapter I sought to determine whether *L. littorea* was affected by calcareous algal epibiosis.

Depending on the magnitude and direction of impact on different life history parameters, epibiosis could be considered a form of parasitism (negative) or mutualism (positive) (Wahl & Mark 1999). A truly neutral or commensal interspecific relationship, benefiting only the epibiont and neutral to the host, is unlikely. To define a basibiont-epibiont relationship as positive or negative, both species must be examined for evidence of change in fitness (Bruno et al. 2003, Bertness & Leonard 1997). Epibionts can negatively impact basibiont fitness by decreasing survival through imposed costs or increased predation risk ("shared doom"), competing for or impeding nutrient availability, consuming basibiont young, increasing weight, or restricting growth or movement (Wahl 1989). On the other hand, epibionts could positively impact basibionts by providing protection from predation, providing nutrients in the form of excreted waste, or modifying the external environment experienced by the basibiont.
Previous studies on epibionts of *Littorina littorea* in other locations have shown primarily negative impacts of fouling for the snail. The barnacle *Balanus crenatus* Brugiere facilitates shell-destroying spionid polychaetes and trematode parasites in the northeastern Atlantic (Thieltges & Buschbaum 2007b, Warner 1997). Snails from the Wadden Sea fouled with the barnacle *Balanus improvisus* Darwin and filamentous algae experience increased drag and reduced growth rates (Wahl 1996, 1997). In the Gulf of Maine, clionid sponges decrease shell strength, increase predation risk, reduce predation size refuge, and divert energy to shell repair (Stefaniak et al. 2005).

While calcareous algal crusts are occasionally mentioned as an epibiont on *Littorina littorea* (Warner 1997), their impact on the snail has not previously been examined. Very few studies have looked at algal crusts on other species. Smyth (1989) found that gastropods in Guam were protected from boring by Clionid sponges and spionid polychaetes when their shells were covered with calcareous red algae. Crustose algal cover on *Tegula brunnea* Phillipi snails conferred associational resistance to predation by sea stars in the northeast Pacific (Thornber 2007). Several other studies mention calcareous red algae as an epibiont of various molluscan species or hermit crab shells (Bell 2005, McKinney 1996, Stachowicz 1980, Ward & Thorpe 1991) but do not examine the impact of that relationship.

Encrusting algal epibiosis on *Littorina littorea* may impact the snail in multiple ways. Algal crusts may restrict snail growth by preventing shell
expansion, or change snail weight, bouyancy, and drag, leading to reduced movement, grazing efficiency, or fecundity (Wahl 1997, Wahl & Mark 1999). The thickness of algal crusts may change predation refugia size (Raffaelli & Hughes 1978); increase or decrease predation success (Laudien & Wahl 2004, Wahl & Hay 1995); or change temperature and desiccation tolerances (Helmuth 2002; Somero 2002). This study will attempt to parse out the mechanisms by which calcareous red algae may affect Littorina littorea in the Gulf of Maine by examining potential influences on the snail’s physiology, movement, grazing rates, predation risk, and survival.

On snails that have > 75% coverage of calcareous red algae, the algae commonly forms concrete-like layers up to 1 cm thick (personal observation; thick crusts primarily Clathromorphum circumscriptum). Both calcareous red algae and the shell of Littorina littorea are primarily composed of calcium carbonate. Preliminary analysis shows that this algae is approximately the same density (mass/volume) as the snail shell, so fouling by crustose algae is relatively equivalent to having an extra thick shell (Palmer 1979). At first this might seem advantageous—a thicker shell may provide more protection from predation, and the snail does not have to exert energy to create the thick algal layer (Palmer 1981, 1992). However, the extreme thickness of the algal layer may in fact have a negative impact on snails (Day 2000, Trussell 2000, Vermeij 1993). The thick algal layers come with additional weight; fouled snails must carry around a proportionally greater weight relative to their body size at all times.
Increased weight burden on a snail that has equivalent body tissue and thus muscle and energy resources, is likely to increase stress and manifest itself in various ways. Changes in shell surface profiles by epibionts such as barnacles have been shown to increase drag and place a metabolic burden on the snail (Wahl 1997), and may change the hydrodynamic profile in such a way as to impact drag and lift forces (Denny 1999). Merely carrying the additional weight of an algal crust may stress the snail (Dixon et al 1981, Witman & Suchanek 1984). It is also likely that the long term energy demands of carrying the algal load may result in changes in individual physiological parameters such as total protein, lipid, and glycogen content, and tissue dry:wet weight ratio, which are indicators of condition and indicator reserve (Arakelova 2004, Lukambuzi 2005).

It is possible that fouling impairs the ability of snails to move and graze, particularly when emerged and water cannot supply a buoyant effect. Movement in *Littorina littorea* is known to be decreased under physiological stress (Buschbaum & Reise 1999). Presumably reduced movement translates to reduced or suboptimal grazing, if snails are unable to reach preferred, nutritionally favourable algae (Watson & Norton 1985). Alternatively, snails could increase grazing rates to meet the increased metabolic demands caused by epibiont presence. The oxygen demand of snails with algal fouling might be higher, because more oxygen is required to move the additional mass. This supposition is supported by field survey data (Chapter 1), which showed a
significantly smaller percentage of fouled snails and lesser algal percent cover on
snails found in tidal pools (Figure 1.7 and Figure 1.18), which are often lower or
more variable in dissolved oxygen than the nearby subtidal area (Hugget 1986,
Morris 1983). Even though snails in tidal pools were continually submerged
(which might provide buoyancy benefits to fouled snails), the percentage of algal
fouled snails was actually lower than expected within pools compared to the
lower intertidal and subtidal habitats. While this could be due to the
environmental tolerance of the algae, crustose algae were noted to be present on
the rocks and walls of the pools. Therefore, I suspect that fouled snails are
unable to meet their metabolic oxygen demand within tide pools, which often
experience lower dissolved oxygen, particularly when filled with detritus. Thus
epibiosis may be driving population distribution patterns. An active avoidance of
tide pools by algal encrusted L. littorea may help explain the discrepancies seen
between algal species composition on pool rocks and snails.

The presence of crustose coralline algae may also impact mortality and
predation rates of Littorina littorea. It is possible that algal fouling may actually
strengthen the shell with additional material (Smyth 1989, Taylor et al. 1999) or
that the algae may serve to camouflage the snail from predators such as crabs,
as well-covered snails visually resemble rocks (personal observation, Wahl and
Mark 1999). As algal crusts also increase the overall size of the snail (personal
observation), this may make the snail less desirable to predators with a preferred
prey size (Lawton & Hughes 1985, Yamada & Boulding 1988). Additionally, it may
also prevent the snail from utilizing refugia (Raffaelli & Hughes 1978), increasing its vulnerability. Many species of encrusting algae also contain chemical compounds that may be actively avoided by predators of L. littorea, particularly omnivorous crabs, conferring associational resistance upon the snail (Faulkner 1984, Lubchenco 1978, Nylund 1999, Paul 1997, Thornber 2007, Wahl & Hay 1995).

Optimal foraging theory states that predators should forage in the way that (MacArthur 1966, Pyke 1984) maximizes energetic returns. Snails covered with algae may be more difficult for predators such as crabs to break open, and thus fouled snails may experience lower predation risk (Currey 1982, Thornber 2007, Trussell 2000). This behaviour would be a form of associational resistance, where the predator is avoiding not a painful or noxious substance but the exertion of effort (Wahl & Hay 1995). In addition, the thick calcareous algal layer may allow snails to reach a size refuge at a smaller actual shell length, thus providing direct fitness benefits (Hadlock 1980). Increased size is likely more important for snails on the threshold of reaching refugia, but may protect even larger snails as some predators such as Cancer borealis Stimpson that are capable of eating snails up to 35 mm long (Lawton & Hughes 1985, Stefaniak et al. 2005).

In order to determine the extent to which calcareous algal fouling impacts Littorina littorea at the individual and population levels, several studies were conducted. The physiological impacts of carrying an algal crust was examined
by determining the density (g/mL) of snail shell and calcareous red algae, the magnitude of snail weight change when fouled, snail length/weight regressions, and basic snail condition indices for *L. littorea* with and without calcareous algal fouling. A mark/release experiment examined if algal fouling causes changes in snail movement and use of habitat. In a laboratory experiment, grazing rates of algal fouled and unfouled snails were compared, and the impact of grazing rate changes on community macroalgal composition was determined in a field caging experiment. Susceptibility to predation was determined in a field tethering experiment. Finally, evidence was collected on the long term cost of fouling on snail survival.

**Methods**

*Site Description*

All snail collections and field experiments in this chapter took place with snails from Jaffrey Point (Fort Stark), NH. The site is described in Chapter 2. Jaffrey Point was chosen due to the unusually high abundance of algal fouled snails as revealed by survey data from 2006 (Table 1.6). In the shallow subtidal, 42% or 69 snails per m$^2$ have heavy (70-100% coverage, often up to 1 cm thick) algal fouling, which both increases the potential for population and community level impacts of algal fouling and makes specimens for experiments easy to come by.
The following analyses were conducted with those snails for whom algal fouling is likely to have a significant impact: those in the 'high' percent cover category (>70% cover), that often had algal layers up to 1 cm thick. Observed impacts are expected to be less severe on snails with thinner algal crusts, but any potential positive or negative impacts should be maximized by examining the most heavily fouled snails.

**Density of Calcareous Algae and Shell**

In order to determine the relative weights of snail shell and crustose coralline algae, pieces of algae removed from snail shells, shells without algae and those with algae present (snail tissue removed for greater accuracy) were used to find the density (g/m$^3$) of each substance. As volumes of these irregular samples were difficult to determine, densities were calculated using the relationship:

\[
\text{Density of Object} = \frac{\text{Weight}}{\text{Density of Seawater} \times \text{Weight - Apparent Immersed Weight}}
\]

The apparent immersed weight was obtained using an immersed displacement technique where the immersed weight is obtained while the specimen is suspended below the balance while immersed in seawater (Palmer 1979).
**Length / Weight Regression and Condition Indices**

To investigate the change in weight and condition indices for heavily algal fouled snails compared to snails lacking calcareous algal crusts, 15 fouled and unfouled snails were collected from the shallow subtidal of Jaffrey Point. Each snail was measured and weighed (length, weight, immersed weight), and then the snail body was removed and wet and dry tissue weight (dried at 75°C for 3 days) were recorded. The difference between air and immersed weight was used to calculate the weight of the shell or the shell with calcareous red algae, using the immersed displacement technique described above. This immersion technique allows for both the calculation of density and an estimation of shell weight of live, intact snails, as tissue weight (which is mostly water) is negligible underwater. The difference between weight and immersed weight is shell weight; shell weights estimated by this method correlated strongly with directly measured dry weights for *Littorina littorea* shells from this location (regression of dry shell weight to estimated shell weight, $r^2 > 0.98$). The density and weight relationships thus determined allowed calculation of snail weight components. Calcareous algal crusts were not easily removed from the shell; thus calcareous algal weight was estimated as the difference between the air-immersed weight and the predicted weight from the length/weight regression of unfouled snails. The ratio of wet:dry tissue weights was calculated as an index of snail condition (Lukambuzi 2005). The resulting snail weight components (shell weight, wet tissue weight, calcareous red algae weight) for 12 size-matched pairs of snails
(lengths within 0.5mm) were compared.

**Movement**

In order to determine if algal fouling impacted snail movement patterns, 60 heavily fouled and 60 unfouled *Littorina littorea* were collected from the low intertidal/shallow subtidal at Jaffrey Point, within a 5m radius in early June, 2008. The collection area was limited to ensure that directional movements of snails would be due to preference and not to homing instinct (Petraitis 1982). In the laboratory, algal fouled and unfouled snails were painted with different colors of Testor's Enamel so as to be easily visible, and returned to the field at low tide the following day. All snails were released in a 0.75 m$^2$ area on a flat shelf of granite, within the original collection location. At intervals thereafter all visible marked snails were counted (and not removed) within a grid system of 9x14 0.75m$^2$ quadrats, yielding a time series of snails found per quadrat. Because of variability in tidal height and habitat within the grid system, each quadrat was coded according to tidal height/habitat type ("shelf", broad flat bedrock tongue with *Chondrus/Mastocarpus* cover, 0 m MLLW, 24 quadrats; "lower", sloping bedrock lower than the shelf area, <0 m MLLW, low algal coverage, 66 quadrats; "pool", a tidal pool continually submerged and protected from wave action by the surrounding bedrock, 24 quadrats; “higher”, granite boulders >0 m MLLW, characterized by *Ascophyllum*, 12 quadrats). The distance of each quadrat to the release origin was also calculated using the midpoint of each quadrat. For each
snail, mean midpoint distance traveled or distance classes (0 to 4 m, 4 to 8 m, and 8 to 12 m) from point of origin were used in analysis. Quadrat distance classes and habitat types are mapped (Figure 3.3).

**Grazing Rates**

To determine if fouling by calcareous red algae impacted grazing rates of *Littorina littorea*, a laboratory grazing experiment was conducted. Large, non-trematode infected unfouled (mean length 29.00 +/-0.25 mm) and heavily fouled (mean length 32.05 +/-0.25 mm) *Littorina littorea* were collected from the intertidal zone at Jaffrey Point and their length and weights measured. Blades of *Ulva lactuca* were collected at the same time. The weight of the fouled snails without calcareous algae was predicted using the regression line in Figure 3.1. The *Ulva* was torn into small (~0.3 g) pieces, patted dry, and weighed. Snails were randomly placed into individual compartments of tackleboxes, which were drilled with small holes to allow water exchange. One piece of pre-weighed algae was placed in each compartment, including empty control compartments. Tackleboxes were either entirely submerged in aerated, filtered seawater or placed in less than 1 mm of water (enough to dampen the algae but not submerge the snail, simulating low tide conditions) and kept in a temperature controlled (15C) chamber for 72 hours. The algae was removed and reweighed. The change in algal weight (corrected for growth by subtracting the control algal weight change), was considered to be the amount of *Ulva* consumed by the snail.
**Impact on Community Macroalgal Composition**

To determine if algal fouling of *Littorina littorea* impacts community composition, a field caging experiment was conducted at Jaffrey Point for 3 months during the summer of 2008.

Open bottom cages, 30x30x10 cm, were built out of 19 gauge ½ inch (1.3 cm) galvanized steel hardware cloth (n=12). On 9 May, 2009 the cages were placed in the shallow subtidal (~0.25 m tidal height) on flat boulders characterized by a mixed *Fucus/Chondrus/encrusting coralline algal community*. Each cage was bolted flush to the rock with 10cm flanges designed to prevent snail escape, and a lid was fastened on each cage. All non-experimental snails were removed from each cage, and cages were allowed to equilibrate for one month prior to the start of the experiment.

Large, non-trematode infected fouled and unfouled snails were collected and marked with Testor's enamel (to allow easy identification). Each cage (4 replicates per treatment) received either 30 fouled snails, 30 unfouled snails, or no snails (control). This sample size corresponds to a snail density of 333/m² and reflects both an intermediate value to the range of snail densities seen in the field throughout northern New England and the density of snails in the subtidal at Jaffrey Point (Figure 1.3). Cages were checked regularly for structural integrity and snail presence. No more than 15% of the original snail complement was gained or lost through emigration or immigration in any cage during the course of
At the beginning (3 June 2008) and end (2 August 2008) of the study, macroalgal abundance (percent cover) was quantified according to an 80-point grid survey. Algae were identified to species (Villalard-Bohnsack 1995, Sears 1998), and then categorized as ephemeral (primarily Ulva lactuca, Porphyra sp., and various species of green filamentous algae) or perennial (Fucus vesiculosus, Chondrus crispus, Mastocarpus stellatus, Corallina officinalis, and encrusting coralline) algae species. Point counts were converted to percent cover, and the change in percent cover of each category from the initial to final count was used for analysis.

*Predation*

To determine if the presence of an algal crust deters predators or increases predation risk, size matched pairs of heavily fouled and unfouled snails (mean length 21.32 + 2.13 SD mm, range 16.93 to 27.04 mm) were attached to tethers and placed at Jaffrey Point during June and July of 2007 (as in Rochette 2004, Stachowicz 1996, and others). Relatively small snails were chosen for this experiment as the primary predators (primarily decapods) in the intertidal do not eat snails greater than this range (Hadlock 1980, Lawton & Hughes 1985, Seed & Hughes 1995, Yamada & Boulding 1998). Tethers (15 cm lengths of monofilament) were attached to the snail shells using superglue, and tethers
were tied to rings attached to bricks. Size matched snail pairs were placed, five at a time, in each of four habitats (middle intertidal zone within in the Ascophyllum zone, n=23; tidal pools, n=17; and two shallow subtidal areas: a protected cove, n=26 and a wave exposed area, n=20). A caged pair to control for tether loss was also placed within each habitat. Tethers were checked daily. Pairs were replaced after three days or when one of the pair was missing, whichever came first. Several pairs were replaced early due to failures in the tether system; thus the total number of days each pair was deployed varies, but was never longer than 72 hours.

**Survival**

To investigate the long term impacts of algal fouling on the physiology and survival of *Littorina littorea*, a long term (4 month) study was conducted in flow-through sea tables at the University of New Hampshire Coastal Marine Lab from July through October 2008. Snails were collected from the shallow subtidal at Jaffrey Point. Three snail treatments were used: heavily algal fouled snails, unfouled snails, and unfouled snails that were coated with a layer of quick drying underwater concrete to serve as artificial fouling “mimics.” The mimic treatment was designed to measure acute, rather than chronic, effects of algal fouling. A non-toxic, quick drying, water resistant product (Activa Permastone © casting compound) with a density of 1.7 g/mL (equal to that of calcareous algae), was layered on snails to similar thickness as naturally occurring algal crusts, using
snails that were previously unfouled and therefore presumed 'healthy' prior to artificial fouling. In addition to fouling level, tidal regime was also examined. Snails were placed in two flow through tanks, one in which the snails were continually submerged to mimic subtidal conditions where weight gain from algae might be minimal due to buoyant properties, and another that had an artificial tidal cycle to mimic the effect of algal fouling on intertidal snails (tidal cycle 8:4:8:4 submerged:emerged). Both tanks flushed completely every day to keep water fresh and oxygenated. Snails were fed a mixture of algal species ad libitum, and air and water temperatures were similar to those in the natural environment.

Results

Density of Calcareous Algae and Shell

The density of calcareous red algae, snails without calcareous red algae, snails with calcareous red algae, and snails from which calcareous red algae had been removed did not differ significantly (oneway ANOVA, p>0.05), although algal density was slightly lower than that of shells ((1.77 g/m^3 vs 1.83 g/m^3; Table 3.1). Fouling by algae is equivalent to extra shell thickness. Shell density was constant with length (r^2<0.05) for unfouled snails; shell density does not change as shells become older and larger.
Length/Weight Regressions and Condition Indices

Figure 3.1 summarizes the length/weight regression between algal fouled (n=15, algal thickness 1-4 mm) and unfouled (n=14) Littorina littorea. Calcareous algal crusts are extremely thin or missing on the spires of algal fouled snails, and so accurate lengths are easily obtained even when algal crusts are extremely thick elsewhere on the snail. The difference between the regression line for unfouled and fouled snails is the change in weight of fouled snails, including both calcareous red algae and any change in wet tissue weight.

The calculated snail weight components (shell weight, crustose coralline algae weight, and tissue wet weight) for size matched algal fouled and unfouled snails is presented in Figure 3.2. Fouled snails on average weighed 34.14% (+/- 2.99SE) more than the size matched unfouled snail. The wet tissue weight of fouled and unfouled snails is not significantly different (one way ANOVA, p=0.18, Table 3.2); the shift in the regression line in Figure 3.1 is due almost entirely to the weight of the algal crust.

While the wet tissue weights are not significantly different, the dry tissue weights and wet:dry ratio are significantly different (one way ANOVAs, p<0.05, Table 3.2). A high wet:dry ratio indicates less organic material and more water in the wet snail tissue.
Movement

Recovery of marked fouled and unfouled snails was high throughout the duration of the experiment (Figure 3.4), with 72% of all snails found on day 1 and 13% of the original 120 snails recovered 43 days after the initial release. Algal fouled snails were consistently found more frequently than unfouled snails.

While a greater percentage of unfouled snails disappeared from the search area, the mean distance from the origin at which snails was found did not differ significantly with calcareous algal fouling (Figure 3.5). However, there was a trend for fouled snails to remain closer to the point of origin than unfouled snails (Figure 3.6). The percent of recovered snails is broken down by distance from origin at which they were found (0-4m, 4-8m, and 8-12m). Unfouled snails began appearing in the farthest distance class within 3 weeks; fouled snails remained within 8 m of the origin until 31 days after release. The observed patterns suggest that both fouled and unfouled snails exhibit relatively strong site fidelity but that unfouled snails move farther, faster.

In addition to overall distance moved, the directional selection of fouled and unfouled snails towards different tidal height or habitats was examined. Figure 3.7 shows the percent of snails found (# found by snail type/# found per day total) in the lower, pool, and shelf quadrat types. No graph is presented for the “higher” habitat as only one (unfouled) snail was ever found there. The percent of snails expected to be found within each habitat type if movement was random and equal in all directions was calculated by dividing the total number of
snails of each type by the proportion of total quadrats occupied by each habitat type; this expected value is presented on each graph as a horizontal line. Bars above the line indicate when a higher than expected percent of snails are found within the habitat. The pool area had lower than expected numbers of both fouled and unfouled snails, despite being a continually submerged, wave free area. In contrast, both the shelf and lower areas had higher than expected numbers of snails present. Most snails on the shelf were found hiding in cracks and crevices rather than on the flat surface.

**Grazing Rates**

Algal fouled snails consumed more *Ulva* in a 72 hour period than unfouled ones. Submerged snails of both types consumed more *Ulva* than emerged snails (Figure 3.8a), although these results were insignificant (nested ANOVA, snail type within submersion regime, p>0.05). Because fouled snails both weigh more than unfouled snails due to the calcareous algal coating, and were slightly but significantly larger than unfouled snails in this experiment (length unfouled 29.00 mm +/- 0.25 SE; fouled 32.03 mm +/- 0.25 SE), grazing rates were also compared to actual (unfouled snails) and predicted (fouled snails, using the length/weight regression in Figure 3.1) body tissue mass, as body tissue should be directly related to metabolic needs and snail size. When the amount of *Ulva* consumed was compared to the weight of the snail, fouled snails consumed less *Ulva* per gram of body weight than unfouled snails (Figure 3.8b), although these
results were also insignificant (nested ANOVA, snail type within submersion regime, p>0.05).

**Impact on Community Macroalgal Composition**

The initial percent cover of ephemeral and perennial macroalgae and bare rock was not significantly different between cages (Figure 3.9). At the conclusion of the experiment, the control cages had significantly higher levels of ephemeral algae and reduced coverage of perennial macroalgae and bare space. Final algal percent cover in cages with snails, both fouled and unfouled, was not significantly different from initial percent cover. Snail presence maintained algal community at initial conditions. Ephemeral algae, the preferred diet of *Littorina littorea*, was significantly higher in cages without snails (Figure 3.10). In cages with snails, final ephemeral algae abundance was significantly less than in the control cages and actually decreased below initial levels in cages with unfouled snails.

**Predation**

Of the 172 snails deployed, 26 disappeared during the 3 day deployment window of each pair and were classed as predation mortalities. In two instances, the snail shell remained on the tether but the body of the snail had been removed with no visible damage to the shell; the remainder of the snails had been forcibly
removed from the tethers, leaving no shell behind. Control cages experienced no snail mortality or tether loss; it is likely that snails that disappeared from tethers were pulled off by crabs or other predators, although it is impossible to know if they were actually consumed in the absence of shell remains.

The overall predation rate across all habitat types was 15% of all snails, and there was no difference between snail types, with 13 fouled and 13 unfouled snails consumed in all out of 172 total tethered snails (Figure 3.11). Numbers of missing snails were too low for chi square analysis, but presumed predation was slightly higher in the protected shallow subtidal and rare in the tidal pool. There was no evidence of predator preference for one type of snail within pairs, and in only one instance were both individuals of a pair eaten at the same time. Pairs were size matched, and missing snails were not significantly smaller than recovered snails (one way ANOVA, p>0.05). Algal fouling appeared to have no impact on the likelihood of predation on *Littorina littorea*.

**Survival**

Although originally designed to measure the long term physiological impacts of fouling and tidal exposure, high levels of mortality during the course of the experiment rendered the intended analysis of physiological parameters impossible. Both the continually submerged and artificially tidal tank experienced a severe mortality event in the last weeks of the experiment, perhaps due to a
die-off of mussels fouling the water intake lines. However, snail survival was significantly different by treatment in both tanks (Figure 3.12). Survival of all snails was much lower in the tidal vs the submerged tank, and survival of fouled (natural and artificial) snails was significantly different than that of unfouled snails ($p > \chi^2 < 0.0001$, nested nominal logistic analysis, snail type within submersion). Similar differences in fouled versus unfouled snail survival were seen in snails kept in the laboratory for other purposes. The differential survival suggests that algal fouling increases the risk of mortality in stressful situations such as hypoxic or toxic events, and that this risk increases with decreasing submergence time.

**Discussion**

Crustose coralline algae forms crusts on *Littorina littorea* shells that have the same density as the snail shell (Table 3.1). Fouled snails weighed significantly more than unfouled snails (Figure 3.1), due to the presence of concrete-like algal layers up to 1 cm thick that can increase the weight a snail must carry by one third or more (Figure 3.2). There may also be a physiological cost to carrying additional weight. In fact, the ratio of wet:dry tissue weight, which is an index of snail condition, is higher in fouled snails, indicating that algal fouled snails have greater water content in their bodies, even if dry tissue weights are similar (Table 3.2). The wet:dry ratio has been used as an index of stress in *L. littorea* for pollution and environmental stress gradients (Lukambuzi 2005, Van
den Broeck et al. 2007). Here the difference in wet:dry tissue weight for algal fouled vs unfouled snails indicates that fouled snails may be physiologically stressed or less capable of either obtaining or converting nutrients that lead to tissue growth. Energy assimilation into tissue, in terms of the wet:dry tissue index, is also often positively associated with other condition indices such as total energy reserves, cellular lipid, protein, and glycogen contents, which suggests that in addition to low tissue weight fouled snails may exhibit long-term physiological stress (Smolders et al. 2004).

Part of the differential in snail dry tissue weight might be due to reduced movement and, potentially, grazing rates, of algal fouled snails. Fouled snails did not differ in total mean distance moved during the duration of the mark/recapture study (Figure 3.5), but were more likely to be found near the point of origin for a longer period of time than unfouled snails (Figure 3.6). Snails lacking crustose algae disappeared from the search area more quickly, due perhaps to increased movement, increased predation, or search error. Fouled snails also avoided the tidal pool habitat (Figure 3.7), a fact that might explain the distribution patterns seen in Chapter 1, where tidal pools had significantly lower levels of calcareous algal prevalence than the shallow subtidal and Ascophyllum habitat types (Figure 1.4) despite having higher snail densities (Figure 1.9). Tidal pools might be expected to have similar algal fouling as the shallow subtidal (both continually submerged) or Ascophyllum habitat (pools were within the Ascophyllum tidal height), but the discrepancy may be explained if fouled snails actively avoided
pools due to low oxygen content, greater temperature fluctuations, or increased predation risk. Differential movement by fouled snails towards preferred habitats may help to maintain the tidal gradients in *Littorina littorea* size and the differential movement patterns exhibited by the snail in other studies (McCormack 1982; Petraitis 1982, Warner 2001).

The field and lab grazing experiments present an intriguing picture of the impact of algal fouling on *Littorina littorea*’s grazing rates and subsequent impact on macroalgal communities. While fouled snails consumed more *Ulva* overall than unfouled snails (Figure 3.8), they were also larger, both in terms of length and weight, than unfouled snails. Interestingly, when the amount of *Ulva* grazed was standardized by snail weight (exclusive of calcareous algae), fouled snails actually ate less per gram of body weight than did unfouled snails. This suggests that algal fouling of *L. littorea* depresses grazing rates. Both fouled and unfouled snails consumed more *Ulva* when continually submerged. Contrary to expectations, fouled snails did not appear to experience an increase in grazing when submerged, when buoyancy could be expected to counter some of the additional weight of the calcareous algae. The added weight of calcareous algae, while potentially increasing metabolic demand on the snail, appears to result in a decreased grazing rate, perhaps due to decreased ability to move. The reduced grazing rates of fouled snails seen in the laboratory may be even more pronounced in a natural setting, where conditions are less optimal and snails must move about more to forage. Impacts on movement and grazing that
are minimal or negligible in optimal conditions may become debilitating under stressful environmental conditions (Bruno et al. 2003). Chronic reduced grazing rates, even if slight, may decrease physiological fitness over the long term. Reduced fitness at the individual level may have population level impacts if reproductive rates or mortality are changed.

The reduced grazing rates of fouled snails suggested in the laboratory experiment resulted in community level changes in macroalgal abundance during the field caging experiment (Figure 3.9). The abundance of ephemeral macroalgae in cages containing *Littorina littorea* was significantly reduced compared to control cages, but in cages with algal fouled snails the reduction in ephemeral algae was less than that seen in cages with unfouled snails (Figure 3.10). Fouled snails with impaired movement may be unable to easily reach ephemeral species in the canopy layer. Thus, algal fouling may indirectly control community composition in the intertidal. A similar change in algal community composition was seen in *L.* *littorea* infected with trematode parasites, with infected snails consuming far less ephemeral algae than uninfected snails (Clausen et al. 2008, Wood et al 2007). As the likelihood of both trematode infection and algal fouling increase with age and size, snails that impacted by both species may experience even greater reductions in grazing rate and thus have a stronger impact on macroalgal community composition (Curtis 2002, Hughes & Answer 1982, Lauckner 1980, Mouritsen & Poulin 2005). Parasitic and epibiotic species may thus be significant and often overlooked indirect

While changes in movement and grazing rates may indirectly impact snail fitness, an increased or decreased risk of predation directly impacts the ability of the snail to produce offspring. In some instances, epibiosis has led to increased predation risk as predators key in on the epibiont as preferred prey ("shared doom", Wahl & Hay 1995) or reducing predation risk by acting as a deterrent or camouflage against predators (Laudien & Wahl 1999; Laudien & Wahl 2004). Crustose coralline algae are not eaten by many species (Faulkner 1984, Lubchenco 1978, Nylund 1999, Paul 1997), and thus many predators may actively avoid algal fouled snails (Thornber 2007). Fouled snails may also be camouflaged to blend in with the surrounding rocks. If so, one would expect that fouled snails would experience lower levels of predation than unfouled snails. However, the results of the snail tethering experiment did not show a significant difference in predation levels (Figure 3.11), although the sizes of snails used were well within the size range preferences of the green crab *Carcinus maenus* and the native crab *Cancer borealis*, the primary predators in the intertidal (Burch & Seed 2000, DeGraaf & Tyrrell 2004). Differences in handling time or prey selection might be seen using a different experimental setup, but the tethering experiment, which placed snails in their natural habitat with minimal restraint and full range of motion, failed to reveal either associational resistance or shared doom.

The extreme mortality experienced in artificial flow through tidal tanks by
naturally and artificially fouled *Littorina littorea* further corroborates the evidence from the physiological measurements (wet:dry index) and the movement experiment (avoidance of tidal pool habitat) that fouled *Littorina littorea* experiences greater stress, possibly in terms of metabolic oxygen demand, than unfouled snails in similar circumstances. The impacts of movement and (grazing) differences may be slight under most circumstances, but become costly under stressful environmental conditions such as hypoxic or extreme heat events. This finding has particular implications as the marine intertidal zone becomes increasingly affected by anthropogenically induced changes in temperature, salinity, and pollution (Crowe et al. 2000, Thompson et al. 2002).

It is likely that the increase in snail weight and size affects the snail in ways that were not tested. The change in snail shape caused by thick algal ridges may increase the drag forces experienced by the snail, although the effect is likely to be less than that seen by Wahl with filamentous algae and barnacles, as the calcareous red algae generally follows the shape of the snail for a lower profile (Wahl 1996, 1997). The increase in snail width, particularly on individuals with algal layers thicker than 0.5 cm, may cause the snail to become too large to fit in size refugia (Raffaelli & Hughes 1978). It is possible that the added weight may tax the snail’s ability to remain attached to substrate, if the change in buoyant forces overcomes the tenacity of the snail’s foot (Denny 1999, Trussell et al 1993).

Thick algal layers may also change effective shell strength by adding
additional thickness to deter shell cracking predators. However, the correlation seen between the boring clionid sponges and spionid worms with algal presence may negate this impact if they riddle the snail shell with holes (Figures 1.20 to 1.21).

Given the observed high levels of epibiosis, one would expect marine organisms to develop anti-fouling defences, if epibiosis has negative impacts on the basibiont. *Littorina littorea* surprisingly has no anti-fouling defences and also has high levels of fouling (Wahl & Sonnichsen 1992). Since so many *L. littorea* are both fouled and alive, epibiosis certainly does not cause immediate death; any impacts are likely to be chronic and long term. Additionally, as it is mostly older individuals who are fouled, an exoskeleton response may not be cost-effective. Shown here was a slight but significant influence of calcareous red algae on *L. littorea*’s tissue weight and condition index, movement, and mortality (albeit under extreme stress), and a slight but nonsignificant difference in grazing rates—all of which are minor, but might add up to larger consequences through time and across the large numbers of fouled *L. littorea* in the intertidal. Observed predation rates in the tethering experiment, which simply indicates presumed predation attempts, did not change. However, it is possible that undiscovered positive impacts of algal fouling may exist if fouling impacts predator handling time or handling success. Calcareous encrusting algae appears to be a facultative commensal on *Littorina littorea* which has negative impacts under certain high stress conditions.
### A) Percent of *Littorina littorea* with algal crust

<table>
<thead>
<tr>
<th>Algal Fouling</th>
<th>Ascophyllum</th>
<th>Chondrus</th>
<th>Pools</th>
<th>Subtidal</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>2.39 +/-1.25</td>
<td>10 +/-10</td>
<td>6.91 +/-6.64</td>
<td>42.42 +/-7.43</td>
</tr>
<tr>
<td>Medium</td>
<td>0.77 +/-0.77</td>
<td>0 +/-0</td>
<td>2.74 +/-2.48</td>
<td>16.49 +/-5.38</td>
</tr>
<tr>
<td>Low</td>
<td>6.23 +/-2.54</td>
<td>19.3 +/-5.98</td>
<td>8.43 +/-3.76</td>
<td>28.43 +/-5.97</td>
</tr>
<tr>
<td>None</td>
<td>90.61 +/-2.94</td>
<td>70.7 +/-9.64</td>
<td>81.91 +/-10.3</td>
<td>12.66 +/-4.57</td>
</tr>
</tbody>
</table>

### B) Snail density (#/m^2)

<table>
<thead>
<tr>
<th>Algal Fouling</th>
<th>Ascophyllum</th>
<th>Chondrus</th>
<th>Pools</th>
<th>Subtidal</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>4.8</td>
<td>1.6</td>
<td>8</td>
<td>68.8</td>
</tr>
<tr>
<td>Medium</td>
<td>1.6</td>
<td>0</td>
<td>6.4</td>
<td>24</td>
</tr>
<tr>
<td>Low</td>
<td>9.96</td>
<td>30.88</td>
<td>13.49</td>
<td>45.49</td>
</tr>
<tr>
<td>None</td>
<td>116.8</td>
<td>56</td>
<td>238.4</td>
<td>33.6</td>
</tr>
</tbody>
</table>

#### Table 3.1 Summary of *Littorina littorea* density and percent with algal fouling at Jaffrey Point, NH

Site characteristics of *Littorina littorea* in the four studied habitat zones at study location Jaffrey Point, NH. Data summarized from survey sampling reported in Chapter 1. A) Percent of *L. littorea* with high (>70), medium (31 to 69), low (1-30) or no percent cover of encrusting calcareous algae. B) Density (#/m^2) of *L. littorea*, by fouling level. Fouled snail abundance was exceptionally high at this site.
<table>
<thead>
<tr>
<th>Material</th>
<th>N</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcareous Algae</td>
<td>8</td>
<td>1.77000</td>
<td>0.02781</td>
</tr>
<tr>
<td>Shell, algae removed</td>
<td>13</td>
<td>1.83769</td>
<td>0.02181</td>
</tr>
<tr>
<td>Shell with algae</td>
<td>15</td>
<td>1.79733</td>
<td>0.02031</td>
</tr>
<tr>
<td>Shell, algae absent</td>
<td>14</td>
<td>1.82786</td>
<td>0.02102</td>
</tr>
</tbody>
</table>

**Table 3.3: Means table of shell and algal density**

The mean density (g/m³) of pieces of calcareous (crustose coralline) algae, *Littorina littorea* shells from which calcareous algae was absent, and shells with calcareous algae (with algae on and after algae was removed).
Figure 3.1: Length/weight regressions for algal fouled and unfouled snails

The length/weight regression for algal fouled (Weight = -16.9 + 0.92*Length, R² 0.73) and unfouled (Weight = -14.2 + 0.74*Length, R² 0.80). Weight is total snail weight (body tissue + shell + algae).
Figure 3.2 Weight components of fouled and unfouled *Littorina littorea*

Total weight of 12 size matched *Littorina littorea* with and without heavy (>90%) calcareous algal fouling. Weight components broken into tissue weight, shell weight, and calcareous algae weight.
Figure 3.3: Map of Mark/Recapture Survey Quadrats

Quadrat grid map for mark/recapture movement snail study. Each square represents a 0.75m² quadrat. Quadrats were characterized by habitat type (shelf, higher rock, pool, lower submerged; hashing marks) and midpoint distance from initial release point, marked with asterisks (0 to 4 m, 4 to 8 m, 8 to 12 m; square colors).
Figure 3.4: Percent of snails recovered in recapture study through time

Recovered algal fouled (black squares) and unfouled (white triangles) expressed as percent of original snails released is plotted against time (days since release, T0). Recapture success decreased with time, with fouled snails having higher recapture rates than unfouled snails throughout.
Figure 3.5: Mean distance of recovered snails from origin

The mean midpoint distance (+1SE) of algal fouled and unfouled snails from the point of origin is plotted by days since release. Unfouled snails were found on average slightly farther away than fouled snails, but this distance was not significant (oneway ANOVAs, distance by snail type, for each day; p>0.05).
Figure 3.6: Percent of original snails found by day and distance
The total number of A) algal fouled and B) unfouled snails is plotted as percent of original (n=60) snails released recovered by day. Each bar is broken into the percent of snails in each of 3 distance classes: 0 to 4 meters from the point of origin, 4 to 8 m, and 8 to 12 m. Fouled snails stayed closer to the origin longer than unfouled snails, which appeared in the farther distance classes sooner and more frequently. Snails that were not recovered may have moved out of the sample area.
Bars indicate the percent of snails recovered (number found divided by number in habitat), by day, for fouled (grey bars) and unfouled (white bars) *Littorina littorea*. Lines indicate expected recapture percent of total individuals if no habitat preference exists (proportionate to total habitat area as indicated in map, Figure 3.3; expected low and shelf 19%, pools 52%, not shown: higher rock habitat, explained in text). Bars above the expected line indicate a higher than expected number of snails within the habitat.
Figure 3.8: Grazing rates of fouled and unfouled *Littorina littorea* under different submersion regimes

The grazing rates of fouled and unfouled *Littorina littorea*, expressed as change in *Ulva* weight under continually submerged or emerged laboratory conditions over a 72 hour period. A) Change in *Ulva* weight and B) Change in *Ulva* weight per gram of total snail tissue weight. Error bars indicate SE, n=32 snails per treatment.
Figure 3.9: Initial and final macroalgal community composition in cage grazing experiment

Initial and final percent cover of ephemeral and perennial macroalgae and bare rock in control (no snail) cages, fouled snail cages, and unfouled snail cages. Initial conditions were not significantly different for each cage type. Final conditions were significantly different from initial where indicated by asterisk (p<0.05). Error bars indicate standard error, n=4 cages.
Figure 3.10: Change in percent cover of ephemeral algal species

The increase (positive change) or decrease (negative change) of percent cover of ephemeral macroalgal species in cages containing no snails (control), algal fouled snails, or unfouled snails over a 3 month period. Error bars indicates SE, asterisk indicates significant difference from control (ANOVA, p<0.05), n=4 cages.
Figure 3.11: Number of tethered snails eaten by habitat

The percent of algal fouled and unfouled snails presumed eaten (maximum t=3 days) in each habitat differed little with calcareous algal presence, and was slightly higher in the protected subtidal habitat. The number of snail pairs deployed per habitat is below each bar. The only snail eaten in the tidal pool, and one of the fouled subtidal protected snails had intact shells with bodies missing; the remainder were simply missing from their tethers.
Figure 3.12: Survival of snails under laboratory submersion regimes
Differential survival after mortality event of naturally and artificially fouled *Littorina littorea* after four months in continually submerged or artificially tidal flow-through sea water tanks.
GENERAL CONCLUSIONS

Epibiosis on *Littorina littorea* and other gastropods in the mid Gulf of Maine region, similar to snail populations in the Wadden and North Sea (Warner 1997; Buschbaum et al. 2007; Thieltges & Buschbaum 2007b), is extremely common. More than one third of all *Littorina littorea* have some level of fouling, and many snails are burdened by multiple epibionts. *Littorina littorea* has the potential to act as an ecosystem engineer, by providing hard substrate for invertebrate and algal species (Gutierrez et al. 2003). Whereas barnacles and spionid worms are the most commonly reported epibionts in the Eastern Atlantic, within the range of this study encrusting calcareous red algae were the most common species on snail shells. The prevalence of epibiosis was highly variable between locations, but a strong tidal gradient pattern existed across the surveyed area, with shallow subtidal areas exhibiting the highest levels of epibiosis.

Clionid sponges and spionid worms were each present in approximately 4% of snails, and snails that had both calcareous red algae and *Cliona* present were also more likely to have spionid worms. Multiple species epibiosis is detrimental to the integrity of the snail shell.

The high overall prevalence of epibiosis on *Littorina littorea*, the most common intertidal gastropod in the Gulf of Maine, also has application for the secondary users of snail shells, namely hermit crabs. Hermit crab behavior and shell choice has been shown to be impacted by the presence of epibionts and the condition of the shell (Bell 2005, Conover 1976, Li & Pechenik 2004, Yund &
Parker 1989). If epibiosis decreases empty shell desirability, the dynamics of hermit crab populations in locations with heavy epibiont prevalence may be affected.

Surprisingly, calcareous red algae had previously been little reported in the literature on any gastropod species, and even more rarely on Littorina littorea. At the local level, calcareous algal community composition on snails is similar to that on the surrounding rocky substrate, and distribution patterns are driven by a combination of snail grazing pressure, algal larval abundance and habitat preferences, and snail movement. Calcareous red algae, while positively associated with Littorina littorea, appears to utilize the snail shell in a facultative, rather than obligate, fashion.

Calcareous algal epibiosis has a negative impact on Littorina littorea, however all impacts seem to be either of low magnitude or existed only under extreme stress. Heavy algal fouling increases the overall weight of the snail, decreases the tissue weight, and increases the wet:dry tissue index. Under the relatively stress free conditions in the laboratory, grazing rates were impacted slightly; changes in grazing resulted in visible but nonsignificant changes in macroalgal community composition in field experiments. Field movement rates and habitat selection was different for fouled snails than unfouled snails. No predation refuge or associational resistance was seen in fouled snails. While the observed differences were slight, it is likely that when the chronic impact on the fitness of each individual snail is multiplied across the entire population,
particularly under stressful environmental conditions, calcareous algal epibiosis may have substantial community level impacts.

It is also likely that with further investigation, other individual and population level impacts of algal epibiosis might become evident. The oxygen demand of heavily fouled snails may be higher than those of unfouled snails, as the snail must carry more weight per unit of body mass. Fecundity may also decrease with chronic algal fouling, as snails have less energy to expend on reproduction. Further investigations into predator choice, handling time, and predation success may reveal other positive or negative impacts of algal fouling.

*Littorina littorea* is one of the most abundant and conspicuous intertidal organisms in northeastern North America. Its identity as a nonindigenous species has recently been confirmed (Blakeslee et al. 2008). Thus, it is imperative that we understand more about how this species is interacting within communities. Although many aspects of *Littorina littorea* have been well studied in the Northwestern Atlantic, heretofore, epibionts have been poorly studied. The present work contributes to the larger body of knowledge on epibiosis in the marine community.


macroalgae consumption by the common periwinkle *Littorina littorea.*


intertidal snail (Littorina sitkana)." Oecologia 54(2): 177-183.


Old, M. C. (1941). The taxonomy and distribution of the boring sponges (Clionidae) along the Atlantic Coast of North America. Chesapeake Biological Laboratory. 44.


