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Emily R. Lyczkowski
Colby College

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Microhabitat Selection by the Tortoiseshell Limpet, *Tectura testudinalis* (Müller), in Tide Pools on the mid-Maine Coast

Emily R. Lyczkowski

Honors Thesis

Colby College Biology Department

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Microhabitat Selection by the Tortoiseshell Limpet, *Tectura testudinalis* (Müller), in Tide Pools on the mid-Maine Coast

by

E.R. Lyczkowski

A thesis submitted to the Biology Department in partial fulfillment of the requirement for graduation

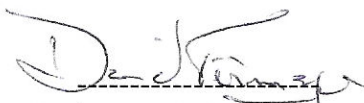
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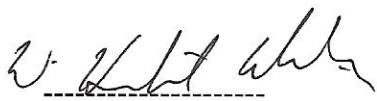
Approved:



Professor David Firmage



Professor Paul Greenwood



Professor W. Herbert Wilson

COLBY COLLEGE, Department of Biology
Waterville, Maine 04901

ABSTRACT

Microhabitat selection of the limpet *Tectura testudinalis*, an important grazer along the rocky Maine coast is examined using both mensurative and manipulative experiments. *T. testudinalis* substrate selection is essential to its survival in the unpredictable and harsh regime of the intertidal zone. At three sites studied in the Gulf of Maine, *T. testudinalis* selectively inhabits tidal pools and vertically oriented substrates. Both of these microhabitats reduce the degree of environmental stress (desiccation, extreme temperature, and hypersaline conditions) and predation experienced by individuals. Differences among sites are common, indicating the importance of varying environmental factors in regulating and influencing habitat selection in this species.

Microhabitat Selection by the Tortoiseshell Limpet, *Tectura testudinalis* (Müller), in Tide Pools on the mid-Maine Coast

Emily Lyczkowski
Colby College, Waterville, ME; erlyczko@colby.edu

ABSTRACT

Microhabitat selection of the limpet *Tectura testudinalis*, an important grazer along the rocky Maine coast is examined using both mensurative and manipulative experiments. *T. testudinalis* substrate selection is essential to its survival in the unpredictable and harsh regime of the intertidal zone. At three sites studied in the Gulf of Maine, *T. testudinalis* selectively inhabits tidal pools and vertically oriented substrates. Both of these microhabitats reduce the degree of environmental stress (desiccation, extreme temperature, and hypersaline conditions) and predation experienced by individuals. Differences among sites are common, indicating the importance of varying environmental factors in regulating and influencing habitat selection in this species.

INTRODUCTION

The Tortoiseshell Limpet, *Tectura testudinalis*, is a common inhabitant of the rocky intertidal zone of the Maine coast. In North America, its range extends from the Arctic to New York on the East Coast and to Alaska in the West. *T. testudinalis*, like other limpet species, is limited by desiccation (Wolcott 1973) to the lower and mid-intertidal zones (Wallace 1972, Branch 1981, Williams and Morritt 1995). These limpets are typically found in or near tide pools and are only rarely seen on fully exposed rock surfaces (Wallace 1972, pers. obs.).

Though little work has focused specifically on *T. testudinalis*, limpet ecology has been a popular research topic among benthic marine ecologists (Cook et. al. 1969, Wallace 1972, Branch 1975a,b, Denny et. al. 2006). Limpet abundance on many rocky coasts, their relative ease of access, their home-site specificity or limited home range, and their role as dominant grazers in marine communities make limpets ideal study organisms.

The well-known homing behavior of many limpet species has provided a source of interest for marine biologists for centuries (see Cook 1971). Limpets live where they will often

be exposed by emersion and since they lack an operculum, maintenance of a home-site is an important adaptation to the stresses of the intertidal habitat, most importantly desiccation (Hartnoll and Wright 1977). In some species, retention of water under the shell is enhanced in individuals whose shells precisely match a “home scar,” a small area of rock worn away by their continued presence, in size and orientation (Hewatt 1940, Cook et al. 1969). Cook et al. (1969) observed that some limpets (*Patella* spp.) did not settle into their “home” until their orientation specifically fit the scar.

Despite the obvious benefits of homing to a specific site, this behavior is not consistent across all limpet species. Branch (1975b) described variation in the degree of homing among species. While some species remain faithful to a scar for years, others switch home-sites randomly or do not home at all. *Tectura scutum*, for example, does not return to an exact site after each feeding excursion, but instead “homes” to a broader area that often contains its favored food resources (Kitting 1980). Willcox (1905) found no evidence of homing in *T. testudinalis*, specifying that the rocks in New England are not adequate for making a scar. More recently Steneck (1982) observed *T. testudinalis* returning to and remaining on home-sites during the day in the laboratory. His comments regarding this behavior were, however, vague and he did not provide concrete evidence for his laboratory observations nor did he observe homing in the field.

In addition to homing behavior, limpet movement has also been observed on a larger scale with some species exhibiting migrations up and down the intertidal zone over the course of a year. Tropical species for example are exposed during summer low tides to extremes of temperature and desiccation. Many species therefore migrate to the lower intertidal during the summer months and move back up in the winter (Branch 1975b). The tendency to migrate up from the lower intertidal during the winter is also seen in temperate species such as *Lottia*

digitalis. The migration of *L. digitalis* however is not driven by increased mortality in upper zones during the summer as it is in tropical species, but harsher conditions in the lower intertidal during the winter months (Frank 1965). Branch (1981) noted that seasonal migrations are not observed in all limpet species and also vary among conspecific populations. *T. testudinalis* is an example of a species whose migration pattern varies between populations. On the eastern coast of North America, this species retreats to the subtidal during the winter in the more southern parts of its range, but this movement does not occur as obviously in limpet populations along the Maine coast (Willcox 1905).

In addition to differences in homing and migration, different limpet species display a variety of activity patterns. While *T. testudinalis* is active while submerged at night (Branch 1981, Steneck 1982), other species move either while awash or only when they are exposed at low tide (Branch 1981). Discrete conspecific populations of limpets often differ in the periodicity of their activity. Individuals of *Patella vulgata* on horizontal surfaces, for example, are active while submerged during the day whereas those on vertical substrates are active during nighttime low tides (Hartnoll and Wright 1977, Little 1989).

The physical and biotic stresses of the intertidal zone, including predation from land and sea, desiccation, and osmotic stress are the driving forces behind habitat selection in intertidal gastropods (Frank 1965, Gendron 1977, Branch 1981, Garrity 1984, Denny et al. 2006). Studies of local habitat selection by limpets have focused on the avoidance of those pressures. These stresses, accompanied by the great environmental fluctuations that occur daily, necessitate the selection of microhabitats that alleviate potentially deadly conditions (Garrity 1984, Branch et al. 1988, Williams and Morritt 1995). Limpets, for example, maintain cooler body temperatures by remaining in rock crevices, near the pool/rock interface, or on vertical surfaces (Frank 1965,

Sutherland 1970, Wolcott 1973, Garrity 1984, Williams and Morritt 1995). Because rock surface temperatures have been shown to affect the operative temperature of individuals, behaviors that decrease exposure to sunlight, especially during emersion are particularly adaptive (Hayworth and Quinn 1990).

As with homing behavior and movement, the impact of specific environmental conditions on habitat selection varies between sites and individuals. Nakai et al. (2006) found that the limpet *Patelloida pygmaea* chooses a substrate that allows its shell to most effectively fit the substrate. Color also plays a role in this dynamic. In the thaidid gastropod, *Nucella lapillus* for example, dark morphs that heat up and desiccate faster than white morphs were more often found in cooler microhabitats (Etter 1988). Temperature is not the only factor related to color that affects habitat choice in the intertidal however. Giesel (1970) and Wootton (1992) demonstrated the importance of color in habitat selection of the limpet *Lottia digitalis*. Dark limpets chose darker substrates and light limpets chose lighter. In both studies, this selection was shown to be imperative to their avoidance of visual predators such as gulls and oystercatchers.

Because behavioral plasticity is common among limpets and other gastropods, Chelazzi (1982) warned of the danger of over-simplifying gastropod behavior. Environmental variations often result in changes in activity patterns or intertidal location. These variations may be explained by differences between sites or by seasonal changes. In order to most effectively understand limpet behavior and habitat selection, several test sites must be used. Assuming limpet behavior at one site (or during one season) is indicative of the behavior of another species or even of distinct conspecific populations can be misleading.

In this contribution I explore microhabitat selection of *T. testudinalis*. Specifically, I examine pool, substrate, and surface orientation preferences of this species and

compare the preferences at each of three sites. Use of three sites allows robust inferences on limpet habitat selection on the Maine coast as it relates to environmental variability and the prevailing stresses at each site. Finally, I offer suggestions for the observed preferences using studies of other species and information on the known pressures on the Maine coast.

MATERIALS AND METHODS

Study Area

General limpet density and substrate preference surveys were conducted at three sites along the mid-Maine coast. The sites, Pemaquid Point, Owls Head State Park, and Reid State Park, differ in topography and exposure (Fig. 1) but each supports a population of *T. testudinalis*.

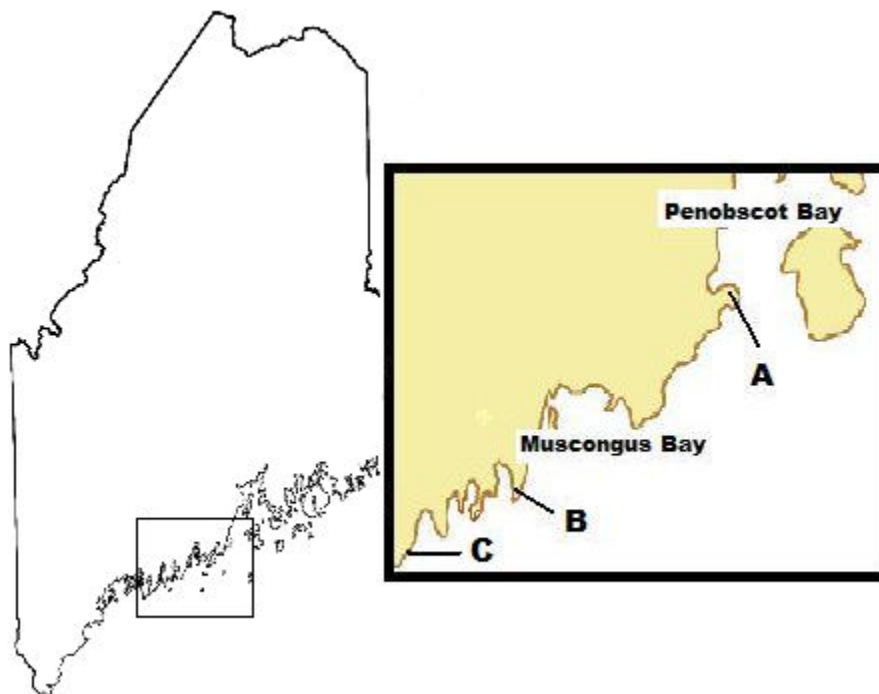


Figure 1. Locations of study sites on the mid-Maine coast. A: Owls Head, Rockland. B: Pemaquid Point. C: Reid State Park.

Pemaquid Point (44°30'N, 69°32'W), which has previously been described (Dudgeon et al. 1999), is an exposed rocky headland that can be divided into several areas that vary in degree

of wave action. The topography is characterized by large sloping rock shelves that support numerous pools. Pemaquid was divided into four regions in which both general surveys and manipulative experiments were carried out: Pemaquid Lighthouse, Pemaquid Loop Road, Pemaquid Point, and Johns Bay (Fig. 2). The term Pemaquid will be used to inclusively describe these four sub-sites.

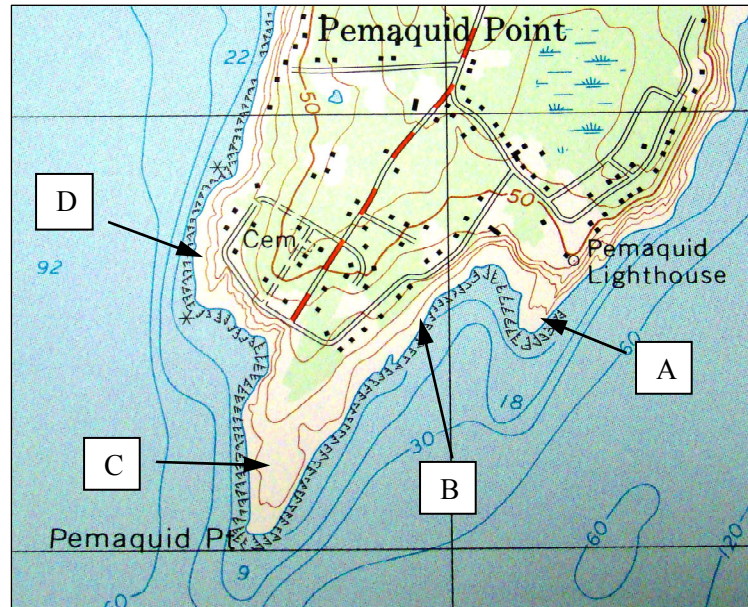


Figure 2. Four sites around Pemaquid Point, ME used for field surveys and field experiments. A: Pemaquid Lighthouse. B: Pemaquid Loop Road. C: Pemaquid Point. D: Johns Bay.

The shoreline at Owls Head near Rockland, Maine ($44^{\circ}5'N$, $69^{\circ}2'W$) is more sheltered from wave action than Pemaquid. Unlike the other sites, the rocky shore consists of loose boulders and cobblestones as well as the structuring bedrock.

The coastline at Reid State Park ($43^{\circ}47'N$, $69^{\circ}43'W$) consists of both rocky and sandy beaches. Offshore the sediment is largely sand, even where the coast is rocky. This sand is often moved into tidal pools with the waves. The limpet population here is mostly restricted to a rocky point in the southern part of the park.

Algal and Limpet Surveys

To determine general limpet density and substrate preference, surveys were conducted at all three sites in February-March 2008 during the daytime low tide. Limpet density and overall substrate percent cover at each site were measured using line transects. Transects extended from low water to the beginning of the barnacle/bare rock zone in the high intertidal, above the upper limit of *T. testudinalis*. Transect locations were randomly chosen across each site. To obtain substrate percent cover, the rock or algae underneath a measuring tape was noted every 25 cm. The presence or absence of a pool was also indicated every 25 cm. Limpet densities were found by counting the number of limpets, both in and out of pools, in a 30-cm wide band along the length of the transect. The zones in which limpets occurred were also recorded. Because of the difficulty of finding and accurately counting very small limpets, all surveys and experiments included only limpets greater than 8 mm in length.

General limpet substrate choice surveys were performed in areas of observed high limpet density. The substrate and surface orientation (vertical or horizontal) was recorded for each limpet within a 1/16 m² quadrat. The color class of each limpet within the quadrat was also recorded. Limpets at each sites were easily classified into one of three color categories based on the amount of white on their shell: light (70-100% white), mottled (30-70% white), and dark (0-30% white). Percent cover estimates of the major substrates in each quadrat were also obtained. Estimates of percent cover were used in preference to more time-consuming methods, such as a dot-quadrat, because exact percent cover was not needed (as in Dethier 1984). Relative percent cover provided the means for comparison necessary for this study.

Field Experiments

All field experiments were carried out during January 2008 at all four regions of Pemaquid close to the low tide between 0630h and 1700h. The purpose of each experiment was to determine the preferred microhabitat of limpets located in tide pools during the day at low tide. Throughout this paper, the day-time low tide location of a limpet will be referred to as its resting site rather than its “home,” a term often used to describe the location of limpets. Use of the term resting site allows for distinction of *T. testudinalis* whose homing behavior remains in question from those species that are known to have high “home site” fidelity.

To determine if individuals are specific to any given substrate in the selection of a resting site, limpets were collected from Pemaquid and separated by substrate and surface orientation. The snails were taken to the lab at the University of Maine’s Darling Marine Center in Walpole, Maine where they were labeled with small numbered tags attached with Superglue[®]. This labeling method has been shown to be effective in field conditions and in some cases the labels lasted for months or years (Frank 1965, Sutherland 1970, Haven 1973, Stimson 1973, Bretos 1980). In the laboratory, length and color (estimated percent white on the shell) were recorded for each.

Twelve pools, all less than 1 m² and representative of the substrate types typically available, were chosen and any limpets within the pools were removed. To each pool, four limpets per 1/16 m², of those collected on the previous day, were placed in the center on one substrate type. This density was chosen based on observed field densities. Limpets from each original substrate and orientation category were chosen for each pool.

Pools were examined every day for a week and the substrate and orientation of each limpet was recorded. Searching continued until all labeled limpets were located or until several

thorough searches revealed no additional limpets. Because the focus of this study was the specificity of an individual limpet for a given substrate, only the initial substrate and substrate on the final day were analyzed. One control group was established. In this pool, all limpets were removed from the pool, labeled in the lab, and put back into their original pool.

To be able to correct for the amount of substrate available to the limpets during analysis, percent cover estimates for both substrate and vertical vs. horizontal surfaces were gathered.

Laboratory Experiments

Substrate and microhabitat choice studies were conducted in the laboratory at Colby College, Waterville, ME. Limpets collected from Pemaquid were maintained in a cold room at 4.4° C in five-gallon aquaria with a 10/14 light/dark cycle for the duration of the study. Rocks partially covered with the pink encrusting algae *Clathromorphum circumscriptum* or a dark red encrusting algae, *Hildenbrandia rubra*, were collected from Pemaquid and Owls Head and maintained under the same conditions. Eight labeled limpets were placed in a shallow metal basin of seawater in the same cold room and light/dark cycle. They had the choice of three rocks each with *C. circumscriptum*, *H. rubra*, or no algae. Trials (three in all) ran for five days and a picture was taken of the basin once every five minutes. Following the five days, the photographs were analyzed and the amount of time spent on each substrate was determined for both the day and night. This procedure allowed for limpet resting site preference to be determined.

Data collected in a previous study indicate that light colored limpets choose a black background over a white background in substrate choice experiments (Lord and Lyczkowski 2007). The former work, however, relied on a very small sample size. Black vs. white color choice experiments were therefore conducted at the Darling Marine Center during January 2008.

Limpets, collected from Pemaquid, were maintained in flowing seawater tables at outside water temperature.

Testors enamel spray paint was used to paint cement blocks with two adjoining 12.5 cm x 12.5 cm squares of black and white. Limpets were previously observed to react negatively to direct contact with the paint, lifting off of the blocks and attempting to escape (Lord and Lyczkowski 2007). To avoid this response, a thin sheet of clear plastic was placed over the painted squares. A ¼ in mesh hardware cloth cage was attached around the colored area using Nashua Waterproofing Repair Tape®.

Six limpets were chosen randomly for each treatment and were placed on the mid-line between the two colors, facing either to the right or left, but not towards either color. Three light and three dark limpets were used for each trial. Each trial ran for two hours under ambient lighting. At the end of the trial the number of limpets on each color was recorded. In addition to the black/white choice trials, there were three controls for this experiment: unlabelled limpets on black vs. white, labeled limpets on a blank surface, and unlabelled on a blank surface. Black vs. white choice trails (with labeled limpets) were completed 39 times and each control was done 8 times. Fig. 3 shows the experimental set-up.



Figure 3. The experimental design for black/white color choice experiments.

RESULTS

General Algae and Limpet Surveys

Percent cover of the dominant and ecologically relevant substrata were determined by line transects at Owls Head (n=8), Pemaquid (n=10), and Reid State Park (n= 6). Ecologically relevant substrates were those upon which limpets were observed and included bare rock, the dark red encrusting alga *Hildenbrandia rubra*, and the pink calcareous encrusting alga *Clathromorphum circumscriptum*.

The dominant algae at these sites included *Ascophyllum nodosum*, *Chondrus crispus*, and *Fucus* spp. (usually *F. distichus* and less often *F. vesiculosus*) (Fig. 4). The percent cover of *A. nodosum* (ANOVA $F_{2,24} = 7.4$, $p < 0.01$), *Fucus* (ANOVA $F_{2,24} = 7.1$, $p < 0.01$), and *C. crispus* (ANOVA $F_{2,24} = 7.5$, $p < 0.01$) differed between the sites (Table 1). Bare rock was also common at all sites ranging from about 35% at Owls Head and Pemaquid to 22% at Reid though these percentages are not significantly different. Reid was the only site at which sand was commonly found in the intertidal, both in and out of pools. Sand accounted for 12% of the available area at this site, covering bare rock, *H. rubra* and *C. circumscriptum*. Both encrusting algae made up a small percentage of the overall cover at all three sites (Fig. 4).

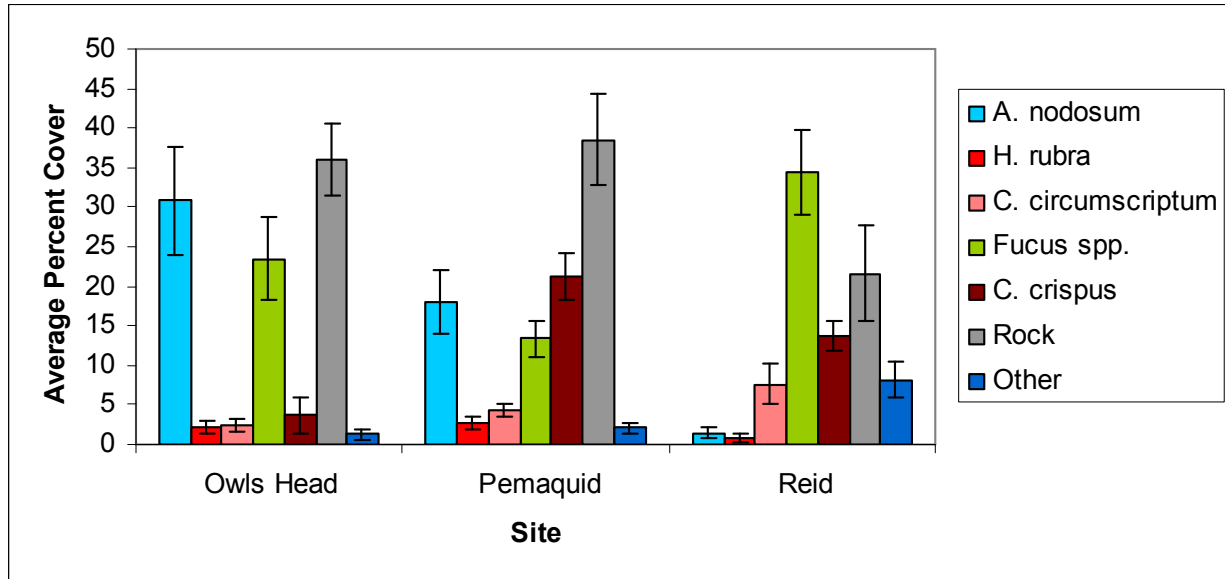


Figure 4. The average percent cover (\pm SE) of algae and rock at Owls Head, Pemaquid, and Reid State Park, ME. The composition of the “other” category differs slightly between sites and includes the algae *Corallina officianalis* and *Ulva lactuca*, the blue mussel, *Mytilus edulis*, and the acorn barnacle, *Semibalanus balanoides*.

Table 1. Average percent cover of each substrate based on line transect algal cover surveys at Owls Head, Pemaquid, and Reid State Park, ME. The significance of variation between the three sites was calculated using independent one-way ANOVA. The significance of differences between individual sites was found by Tukey HSD Tests ($p < 0.05$). ** indicates significance ($p < 0.01$). NS indicates non-significance.

Algae	Owls Head	Pemaquid	Reid	ANOVA p-value	Significant between (by Tukey HSD)
<i>A. nodosum</i>	30.8	18.0	1.4	**	O,R
<i>H. rubra</i>	2.1	2.6	0.8	NS	None
<i>C. circumscriptum</i>	2.4	4.2	7.7	NS	None
<i>Fucus</i> spp.	23.5	13.3	34.4	**	P,R
<i>C. crispus</i>	3.7	21.2	13.7	**	O,P and O,R
Rock	36.0	38.5	21.6	NS	None
Other	1.2	2.1	8.2	**	O,R and P,R

In addition to algal cover, pool cover was also obtained at the three sites. At low tide, pools covered 14% of the intertidal at Owls Head, 19% at Pemaquid, and 31% at Reid. ANOVA ($F_{2,22} = 4.9$, $p = 0.01$) showed variation between the sites though the difference was only significant between Owls Head and Reid (Tukey HSD Tests, $p < 0.05$).

The composition of algae and rock both in and out of pools was calculated for each site (Fig. 5). *Fucus* and *A. nodosum* were only rarely in the pools at each site. The amount of rock in versus out of the pool only differed significantly at Reid where rock made up a higher proportion

of the cover outside of the pools. *H. rubra* made up a higher percentage of cover within pools than on exposed surfaces at both Owls Head ($t = -3.1$, $df = 13$, $p < 0.01$) and Pemaquid ($t = -3.0$, $df = 18$, $p < 0.01$) (Figs. 5A,B). In the transects at both sites *H. rubra* was never found outside of the pools. *C. circumscriptum* was found only in the pools at all three sites.

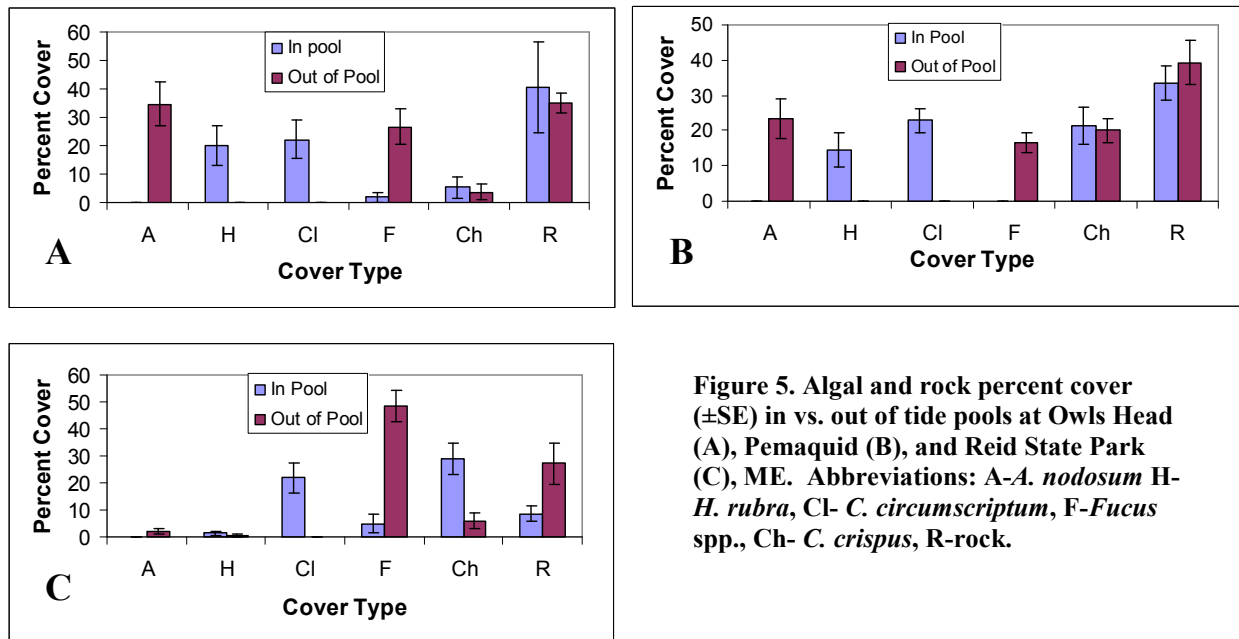


Figure 5. Algal and rock percent cover (\pm SE) in vs. out of tide pools at Owls Head (A), Pemaquid (B), and Reid State Park (C), ME. Abbreviations: A-*A. nodosum* H-*H. rubra*, Cl- *C. circumscriptum*, F-*Fucus* spp., Ch- *C. crispus*, R-rock.

In addition to algal cover, limpet densities were determined for each site. Because all surveys were conducted during the day-time low tide, data should be understood to specify limpet density only during that time. The overall density of *T. testudinalis* was 4.8 limpets/m² at Owls Head, 2.0/m² at Pemaquid, and 5.7/m² at Reid. Only the densities at Pemaquid and Reid differed significantly (Tukey HSD Test, $p < 0.05$). Limpet densities were highest within the tide pools at all sites (Fig. 6). At Owls Head there were 34.8 limpets/m² in pools and 3.1/m² on the exposed areas. At Pemaquid, there were 14.8 limpets/m² in pools and only 0.22/m² out of pools. At Reid, an average of 9.7 limpets/m² was found within the pools while 4.1/m² were found exposed. The difference between in pool and out of pool density was significant at Owls Head ($t = 2.0$, $df = 12$, $p < 0.05$), Pemaquid ($t = -2.2$, $df = 18$, $p < 0.05$) and Reid State Park ($t = 2.2$, $df =$

10, $p < 0.05$). The density within pools did not differ significantly between the three sites, but the density on exposed surfaces was significantly lower at Pemaquid than at both Owls Head and Reid (Tukey HSD Test, $p < 0.01$).

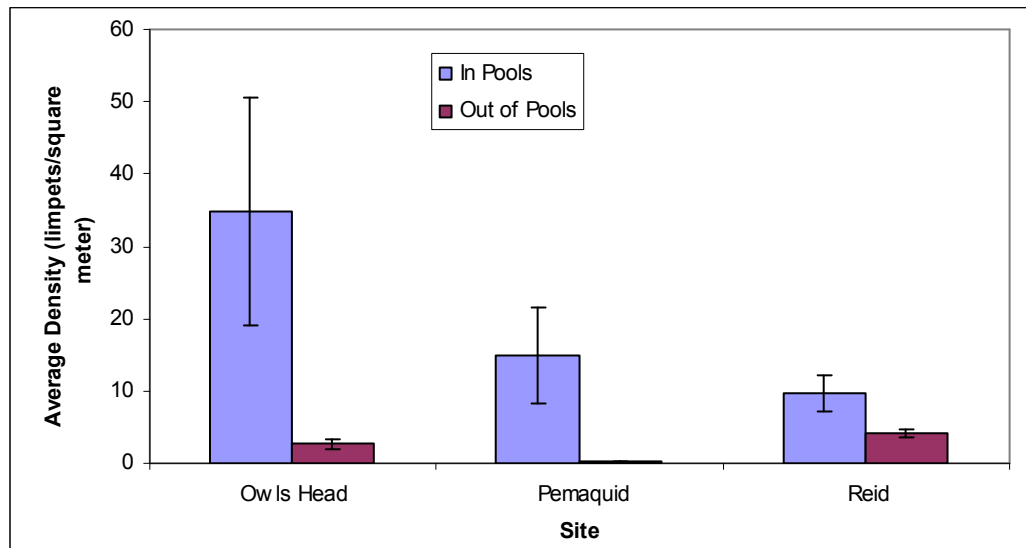


Figure 6. The average in pool vs. out of pool densities (\pm SE) (limpets/m²) in the intertidal zones of Owls Head, Pemaquid, and Reid State Park, ME. All differences within each site are significant (Student's t-test, $p < 0.05$).

The intertidal zones at Owls Head and Pemaquid could both be divided into distinct zones. The zones from lowest to highest intertidal height at Owls Head were *Fucus*, *Ascophyllum*, and Rock/Barnacle. At Pemaquid, the zones were *Chondrus*, *Fucus*, *Ascophyllum*, and Rock/Barnacle. The average density of limpets did not differ significantly between the zones at either Rockland (ANOVA $F_{2,6} = 0.27$, $p = 0.77$) or Pemaquid (ANOVA $F_{2,26} = 0.85$, $p = 0.44$). As was shown for overall limpet densities, the density of limpets in pools was significantly higher than the density out of pools in each zone.

Algal Composition and Limpet Substrate Preference in Regions of High Limpet Density

Quadrats placed in areas of high limpet density were used to determine *T. testudinalis* substrate and surface orientation preference. Rock, *H. rubra*, and *C. circumscriptum* were the

three substrates on which limpets were found and thus were the only substrates analyzed in this portion of the study. Limpets were rarely (one time each) seen on barnacles or mussels.

A total of 124 quadrats were studied: 33 at Owls Head, 60 at Pemaquid, and 31 at Reid. Rock accounted for the highest percent cover in areas of high limpet density at each of the sites: 47%, 54%, and 39% at Owls Head, Pemaquid, and Reid, respectively. The rock cover only differed significantly between Pemaquid and Reid (Tukey HSD Test, $p < 0.05$). The cover of *H. rubra* did not differ significantly among the sites, composing 19%, 13%, and 11% of the cover of high limpet density areas at Owls Head, Pemaquid, and Reid. *C. circumscriptum* cover had a trend opposite that of rock with a significantly higher percent cover in quadrats at Reid (34%) than at Pemaquid (21%) (Tukey HSD Test, $p < 0.01$).

At Owls Head rock was found at a significantly higher percentage than either of the two algae (ANOVA $F_{2,98} = 12.9$, $p < 0.001$) while *H. rubra* and *C. circumscriptum* did not differ from each other. This pattern was also true at Pemaquid where the dominance of rock over the two algae was highly significant (ANOVA $F_{2,179} = 68.5$, $p < 0.0001$). In the case of Reid State Park, the percent cover of rock and *C. circumscriptum* were similar though both covered a greater percentage of the site than *H. rubra* did (Tukey HSD Test, $p < 0.01$).

The average limpet density in the quadrats was 36.8 limpets/m², 54.7/m², and 83.6/m² in high density areas of Owls Head, Pemaquid and Reid respectively. Reid's density was significantly higher than the high limpet density at the other two sites (Tukey HSD Test, $p < 0.0001$).

At both Owls Head and Pemaquid, the density of limpets did not differ significantly between the three substrates. The density on *H. rubra* was however the lowest at both sites. At Owls Head the densities were 104/m², 62.5/m², and 95/m² on rock, *H. rubra* and *C.*

circumscriptum respectively while at Pemaquid the corresponding densities were 98/m², 65/m², and 97/m². At Reid State Park, the limpet density was significantly higher on *C. circumscriptum* (171 limpets/m²) than on rock (44 limpets/m²) (Tukey HSD Test, $p < 0.01$) but the density on *H. rubra* (121 limpets/m²) did not differ significantly from either of the other two substrates.

Limpet density on *H. rubra* did not differ among the sites. Density on rock, however, was significantly lower at Reid than at both Pemaquid and Owls Head (Tukey HSD Test, $p < 0.05$). *C. circumscriptum* showed the opposite pattern, supporting a significantly higher density at Reid than at either Pemaquid or Owls Head (Tukey HSD Test, $p < 0.05$) (Fig. 7).

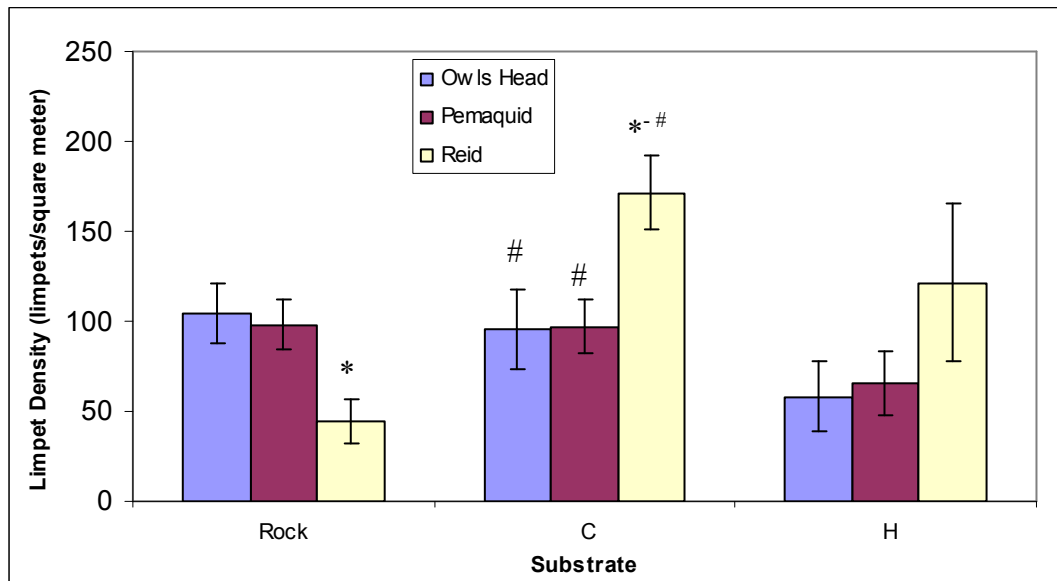


Figure 7. Limpet density (limpets/m²) (\pm SE) on rock, *C. circumscriptum* (C), and *H. rubra* (H) at Owls Head, Pemaquid, and Reid State Park, ME. *-indicates a significant difference (by Tukey HSD Test) among substrate types at Reid, #-indicates significant difference in *C. circumscriptum* cover between Reid the other two sites. All other differences are non-significant.

Limpets were found at significantly higher densities on vertically oriented substrates than on horizontal at Owls Head ($t = 4.3$, $df = 59$, $p < 0.0001$), Pemaquid ($t = 2.4$, $df = 89$, $p < 0.01$), and Reid State Park ($t = 6.1$, $df = 44$, $p < 0.0001$). At Owls Head, Pemaquid, and Reid, average densities were 236 limpets/m², 131/m², and 220/m² on vertical substrates (respectively), and 33/m² at Owls Head and 65/m² at both Pemaquid and Reid on horizontally oriented surfaces

(Fig. 8). No significant difference was found between densities on vertical surfaces between sites. On horizontal surfaces however, Owls Head had significantly lower density than both Reid and Pemaquid (Tukey HSD Test, $p < 0.01$).

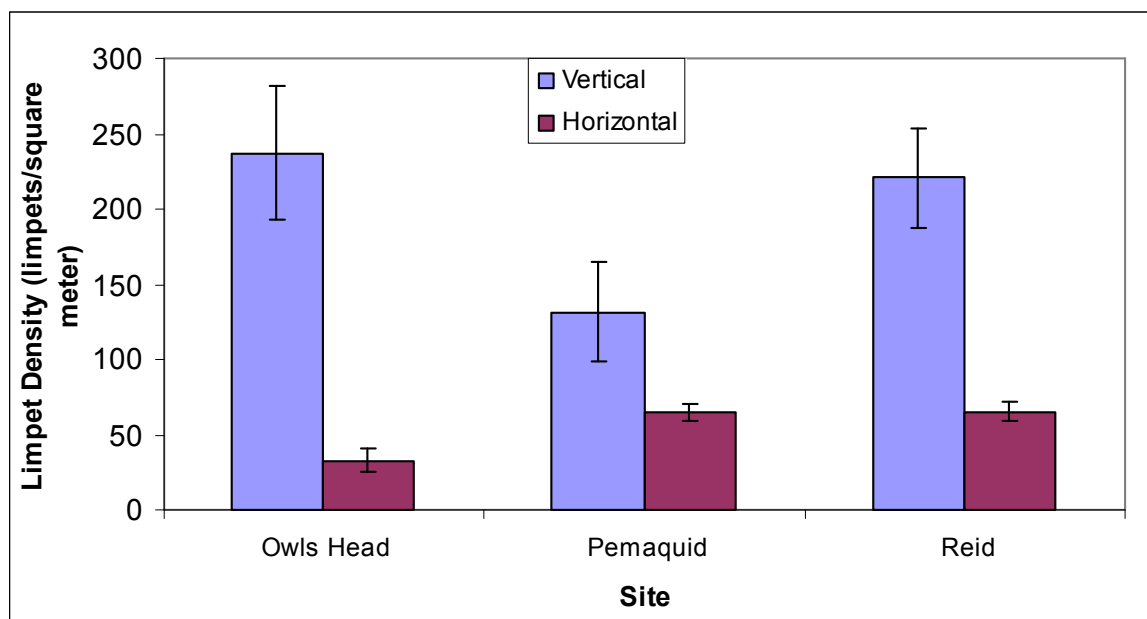


Figure 8. Average limpet density (\pm SE) on vertical vs. horizontal surfaces at Owls Head, Pemaquid, and Reid State Park, ME. All densities on vertical were significantly higher than horizontal.

Substrate cover did not differ between the vertical and horizontal surfaces at any of the three sites. Rock made up the greatest percent cover on both vertical and horizontal surfaces at each of the sites though it was only significantly higher than both *H. rubra* and *C. circumscriptum* at Owls Head and on the horizontal surface at Pemaquid (Tukey HSD Test, $p < 0.01$).

Limpet densities did not differ significantly among the three substrates on vertical or on horizontal surfaces at Owls Head and Pemaquid. The density on vertical rock however (257 limpets/m² at Owls Head and 181 limpets/m² at Pemaquid) was significantly higher than the density on horizontal rock at both sites (47 limpets/m² at Owls Head and 74 limpets/m² at Pemaquid) (Owls Head $t = 2.94$, $df = 54$, $p < 0.01$; Pemaquid $t = 3.23$, $df = 83$, $p < 0.001$). At Reid, there was no specific substrate preference on vertical surfaces. On horizontal surfaces

however, there was a higher density on *C. circumscriptum* (135 limpets/m²) than on rock (27 limpets/m²) ($t = -5.1$, $df = 57$, $p < 0.0001$).

Limpet Color and Substrate Preference

At both Owls Head and Reid State Park, limpets of all three color classes (light, dark, and mottled) were found at higher densities on vertical than horizontal surfaces. This pattern was not the case at Pemaquid where limpets of each color did not prefer either orientation though the trend toward vertical preference remains clear (Fig. 9).

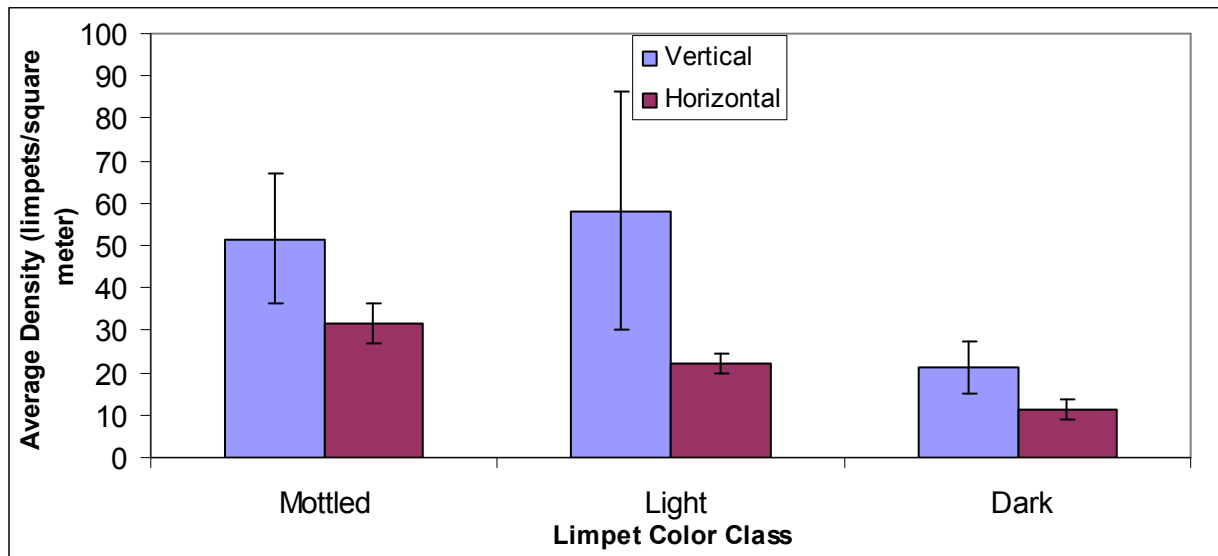


Figure 9. Average densities (\pm SE) of limpets in each color class on vertical vs. horizontal surfaces in regions of high limpet density at Pemaquid, ME. Differences within each color class are not significant (ANOVA $p < 0.05$).

At Owls Head, light limpets preferred *C. circumscriptum* to *H. rubra* ($t = -2.28$, $df = 53$, $p = 0.01$) though no preference was observed at the other sites. Mottled limpets at Reid State Park were found at higher densities on *C. circumscriptum* than on rock ($t = -3.27$, $df = 59$, $p = 0.0008$).

The density of limpets of each color differed on some substrates. At Owls Head, light limpets were found on *C. circumscriptum* at much higher densities (59 limpets/m²) than either mottled (21.8/m²) or dark limpets (13.7/m²) (ANOVA $F_{2,83} = 4.9$, $p < 0.01$). At Pemaquid,

mottled limpets were significantly denser on rock than dark limpets were (Tukey HSD Test, $p < 0.01$). There were no differences in density between the color classes on any substrate or orientation at Reid State Park. At Owls Head however, mottled limpets were found on vertical surfaces more often than dark limpets. The converse is true at Pemaquid where mottled limpets were found more often than dark limpets on horizontal surfaces.

Comparison of Areas of High Limpet Density to Overall and Pool Substrate Availability

Comparison of the cover of rock, *H. rubra*, and *C. circumscriptum* in regions of high limpet density (within $1/16 \text{ m}^2$ quadrats) to the overall cover (based on line transects) revealed that the percent cover of rock in high limpet density areas did not differ significantly from the overall rock cover at each site. At all three sites however, the cover of *C. circumscriptum* made up a greater percent cover of the quadrats than of the entire site (ANOVA Owls Head $F_{1,40} = 9.7$, $p < 0.01$; Pemaquid $F_{1,69} = 6.7$, $p < 0.02$; Reid $F_{1,36} = 11.4$, $p < 0.01$). The same was true for *H. rubra* at Owls Head ($F_{1,40} = 7.4$, $p < 0.01$) and Pemaquid ($F_{1,69} = 5.6$, $p < 0.03$) (Fig. 10).

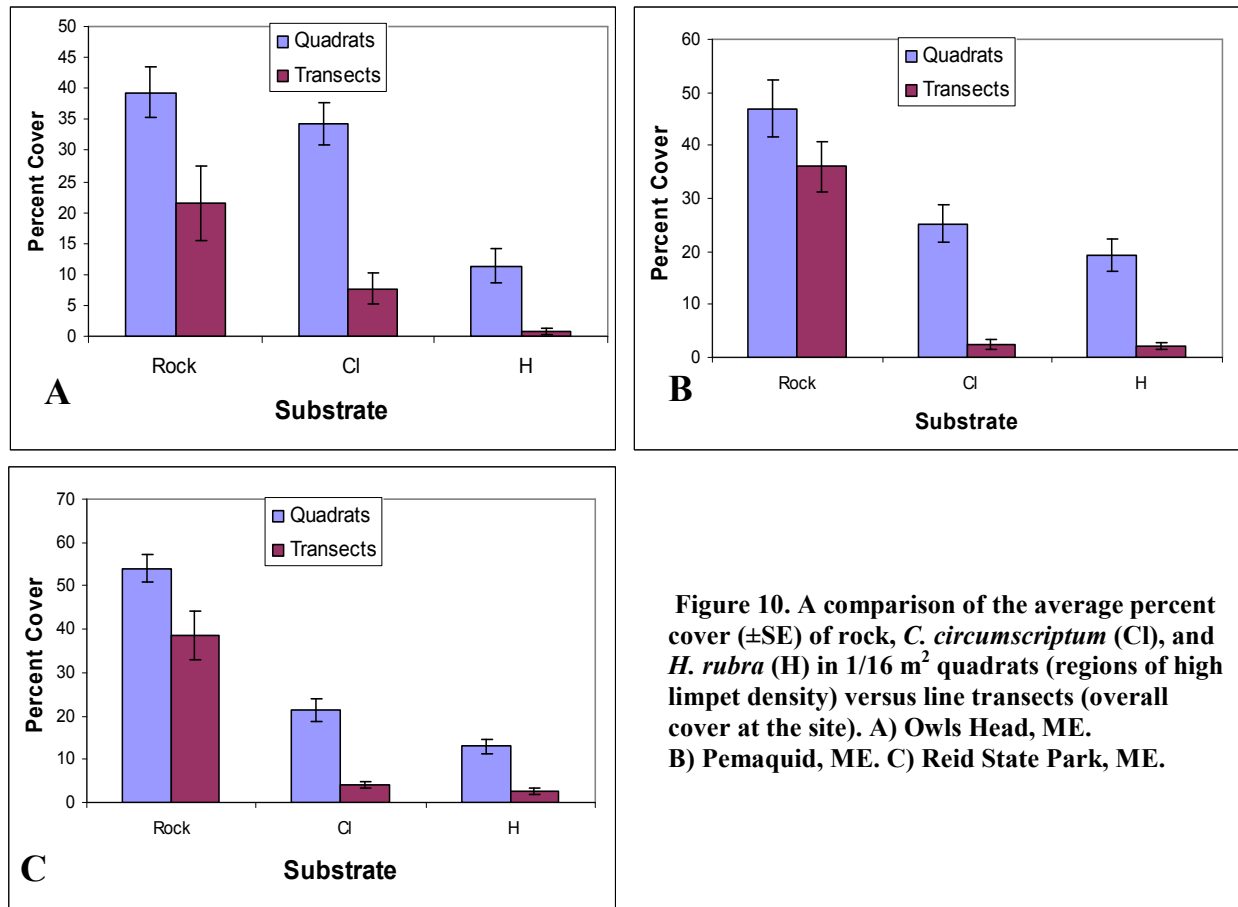


Figure 10. A comparison of the average percent cover (\pm SE) of rock, *C. circumscriptum* (Cl), and *H. rubra* (H) in 1/16 m² quadrats (regions of high limpet density) versus line transects (overall cover at the site). A) Owls Head, ME. B) Pemaquid, ME. C) Reid State Park, ME.

Field Experiments

Limpet Substrate Specificity

Limpets collected from a known substrate and surface orientation were placed into pools and their substrate choice was observed after seven days. A total of 103 limpets (69%) could be relocated at the end of the experimental period. No pool had a recovery rate of less than 50%. Of those limpets that could be located, 26% were on the same surface orientation (vertical or horizontal) and substrate (*H. rubra*, *C. circumscriptum*, rock) as that on which they were originally collected. A total of 58% were on the same orientation alone, and 46% were on only the same substrate. 22% were not on either the original orientation or substrate.

Correction for the amount of each substrate or surface orientation available in the pools reveals that the limpets were not actively selecting the substrate (Fisher Exact, $p = 1.0$) or surface orientation ($X^2=2.53$, $df = 1$, $p > 0.1$) on which they were originally found.

Laboratory Experiments

Lab Movement Studies

In lab movement studies, limpets in three individual trials lasting five days moved significantly less during the day than during the night ($t = -4.6$, $df = 46$, $p < 0.0001$). On average, the snails spent 3.1% of the day and 22.6% of the night moving (Fig. 11). Such movement patterns indicate a tendency to “rest” during the day and thus daytime locations were taken to be an individual’s chosen “resting site” and analyzed for preference.

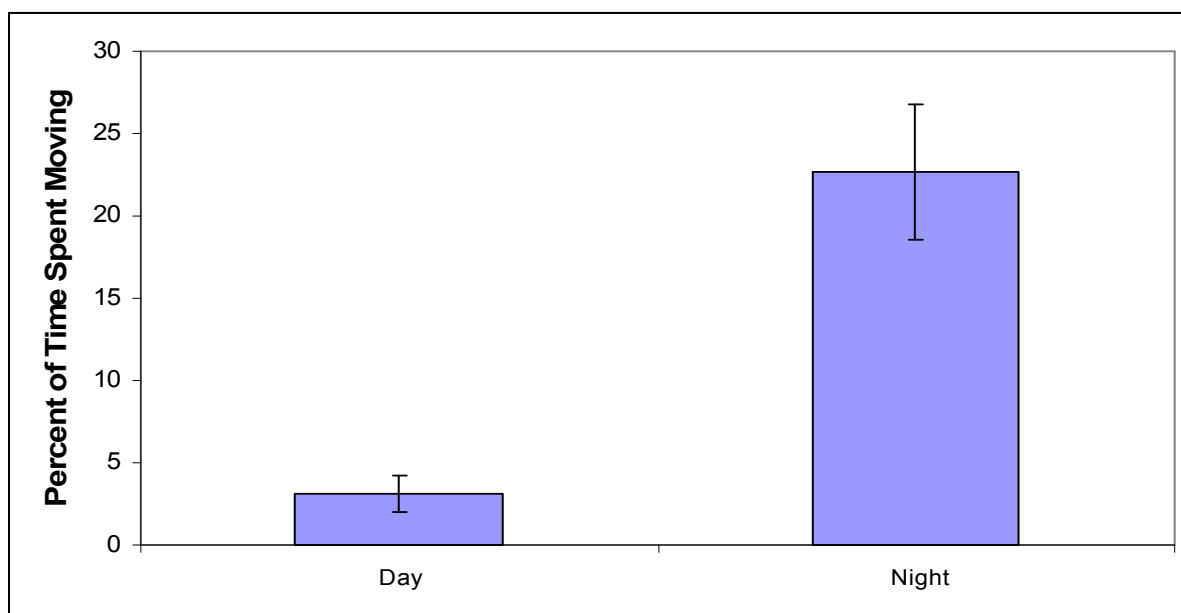


Figure 11. Time spent moving (\pm SE) as a percent of total daytime or nighttime in laboratory movement studies of *T. testudinalis*.

During the day, limpets were observed on rock 50% of the time, significantly more often than they were observed on either *H. rubra* (1.4%) or *C. circumscriptum* (13%) (Tukey HSD Test, $p < 0.05$). They were also found significantly more often on the pan (35%) than on *H. rubra* (Tukey HSD Test, $p < 0.05$) (Fig. 12). In addition, limpets spent 77% of their time on

vertical surfaces during the day. This value is significantly higher than the amount of time spent on horizontal surfaces (18%) (ANOVA $F_{1,41} = 44.8$, $p < 0.001$). Selective resting on vertical surfaces during the day is in contrast to their behavior patterns at nighttime during which there was no significant difference between the percentages of time spent on vertical versus horizontal surfaces ($F_{1,41} = 3.7$, $p = 0.06$) (Fig. 13). The amount of time spent on either surface orientation differed significantly between day and night. At night, limpets spent more time on horizontal surfaces (40%) than they did during the day (18%) (ANOVA $F_{1,41} = 4.7$, $p < 0.04$). They spent more time on vertical surfaces during the day (60%) than they did at night (ANOVA $F_{1,41} = 4.7$, $p < 0.04$).

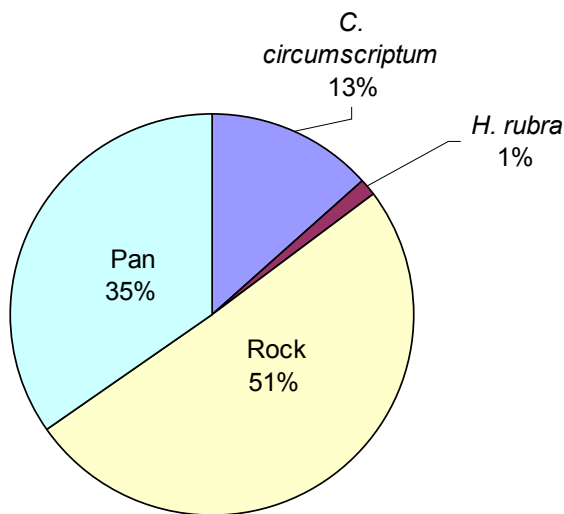


Figure 12. Amount of time spent by *T. testudinalis* on each substrate during the day in laboratory movement studies.

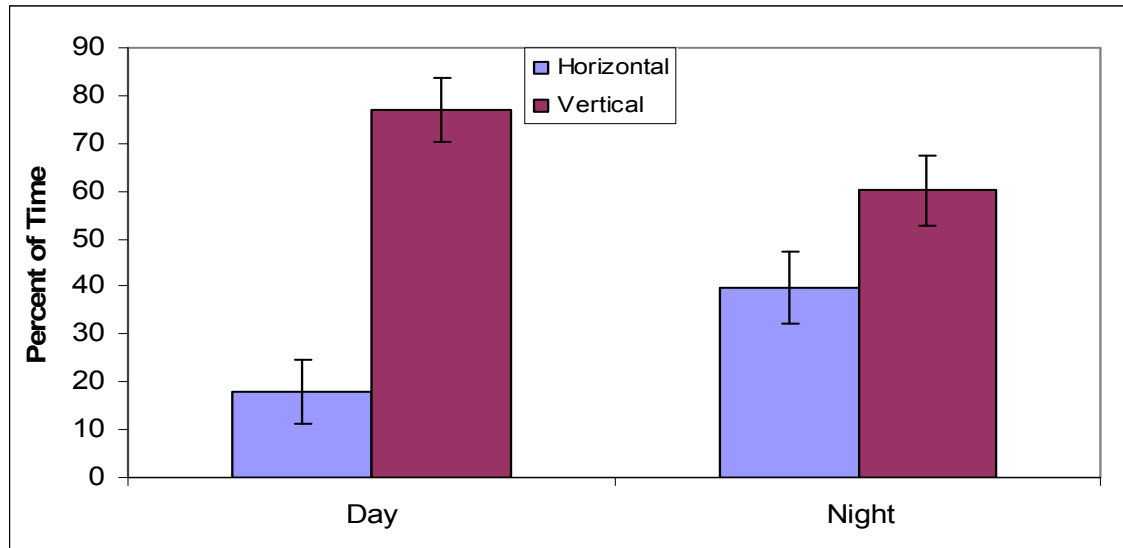


Figure 13. Average amount of time spent (\pm SE) by *T. testudinalis* on vertical and horizontal surfaces during the day and night of laboratory movement studies.

Laboratory Black vs. White Experiment

In substrate color choice experiments, limpets did not prefer a black surface to a white one (Mann-Whitney U-Test, $p > 0.05$). Furthermore, in each control (unlabelled in black-white chamber, labeled and unlabelled on blank), limpets did not show a significant preference for one color (or side of the chamber) over the other.

DISCUSSION

Microhabitat selection of *Tectura testudinalis* is a vital aspect of its survival and success in the highly unpredictable and stressful intertidal zone. Preference of tide pools to exposed surfaces, vertical to horizontal orientation, and of some algae to others are intriguing and unexplored aspects of this species' behavioral ecology. The factors that most directly influence an organism's habitat preferences include the alleviation of environmental stresses, predator avoidance (spatial, temporal, and through cryptic behavior), preferential proximity to food resources, and reproduction-related choices (such as preferred spawning sites or site selection by

immatures). The need for many of these preferences is magnified for limpets and other organisms with reduced mobility in the intertidal zone.

Organisms living in the intertidal are subject to extreme environmental fluctuations (Lewis 1954) and must cope with the stresses of those conditions. Desiccation and temperature stress are the most important of those stresses and tend to structure the populations of intertidal organisms by limiting their ranges, typically at their upper limits (Connell 1961a,b, Dayton 1971). Intertidal organisms need to maintain flexibility in their tolerance limits and behavior to survive seasonal extremes as well as the daily inundation and emersion patterns created by the tides.

During the daytime low-tide, when limpets were on their resting sites (Fig. 11), the densities of *T. testudinalis* were highest in the pools at each site (Fig. 6). This pattern, also observed by Wallace (1972), is in contrast to many other limpet species which tend to live on exposed rock surfaces (Giesel 1970, Branch 1975a,b, and Garrity 1984). Thermal tolerance, one of the primary determinants of habitat selection in marine organisms (Bates et al. 2005) contributes to the observed pattern. Because this study took place during the winter (January through March), the tendency of limpets to favor pools is probably due to their avoidance of the sub-zero air temperatures to which they would be exposed on open rock surfaces. Limpets exposed during early morning low-tides were sometimes frozen (pers. obs.). Limpets that had not been killed by complete freezing were unable to cling to the rock surface and would therefore have been more susceptible to injury and desiccation.

T. testudinalis would be expected to remain at higher densities within the tidepools during the summer months as well. Summer temperatures may prove to be important factors controlling limpet densities on exposed substrates because of the associated increase in

evaporation which leads to rapid desiccation and increasing tissue salinity. In addition to protection from extreme heat or cold, and perhaps more importantly, pools offer protection from desiccation, a stressful factor throughout the year. Wolcott (1973) suggested that *T. testudinalis* is extremely sensitive to desiccation, more so than other limpet species, a characteristic that would explain their clear preference for the pools.

While selectively choosing resting sites within pools is an important and straightforward way by which limpets can eliminate desiccation, other factors, especially at sites where pool cover is lower, may also be essential. On exposed surfaces of the three sites, *T. testudinalis* was found at the lowest density at Pemaquid (Fig. 6). Pemaquid is the most exposed of the three sites and may have consistently higher winds than both Reid State Park and Owls Head, increasing the rate of desiccation. Furthermore, because pools, and thus limpets, are found higher in the intertidal zone at Pemaquid (pers. obs.) those higher limpets may be exposed for close to six hours during spring tides. This is much longer than limpets at either of the other sites would ever be exposed. The length of exposure time and increased risk of desiccation is clearly important in driving habitat selection in this system.

In addition, both Owls Head and Reid State Park have higher percent covers of *Fucus* or *A. nodosum*, in their respective zones, than Pemaquid (Fig. 4, Table 1). These algae form dense mats that hold water and maintain moist conditions for neighboring organisms during low tide. Though *T. testudinalis* is not usually found underneath the algae (pers. obs.) as some species are (Menge 1995), the presence of dense algal mats may be enough to maintain humid conditions near the rock surface and prevent rapid desiccation of adjacent organisms. The percent of bare exposed rock is higher at Pemaquid than at the other sites (Fig. 5) and with the reduced

availability of *Fucus* and *A. nodosum*, these large areas of rock are likely to dry more quickly than the rock at the other sites.

An additional adaptation for limpets to reduce both radiant heating from the sun and desiccation is to rest on vertical surfaces during the day. At all three sites and in the laboratory, limpets were always found at higher densities on vertically oriented surfaces than on horizontal surfaces during the day (Fig. 8). It is important to note that this pattern was observed despite the fact that the percent cover of each substrate does not differ between the two surface orientations, indicating that the observed preference is indeed for vertical surfaces. Preference for vertical surfaces has been shown in several gastropods (Garrity 1984) and other limpet species such as *Cellana grata* (Williams and Morritt 1995). Limpets that are exposed in the field lose water more quickly on horizontal open surfaces than on vertical surfaces or in crevices (Williams and Morritt 1995). The tendency of limpets to rest on vertical surfaces is driven by the increase in temperature due to heating by the sun on completely horizontal substrata. Denny et al. (2006) found that the temperature of the limpet *Lottia gigantea* on vertical surfaces was always lower than the temperature of horizontal limpets. By their models, while limpets on horizontal surfaces suffer from heat and desiccation, no limpets on vertical surfaces would die from acute thermal stress within the five-year period of their study.

Avoidance of heating and desiccation by resting on vertical substrates during the day can also explain the night versus day pattern observed in the laboratory. Limpets in movement studies in the lab preferred vertical surfaces during the day but showed no preference at night. In fact, their density on horizontal substrates was higher at night than during the day (Fig. 13). At night, temperatures are cooler and limpets do not have to endure heating by the sun. Thus,

during nighttime low tides, horizontal substrates provide satisfactory surfaces on which to rest or graze.

Reduction of desiccation on vertical surfaces over horizontal is important only in limpets that are exposed at low tide. Most limpets, especially in areas of high limpet density, were found in pools (Fig. 6). Selection of vertically oriented substrates may remain adaptive even within pools because of the unpredictability of water levels and risk of emersion during low tide on particularly hot days. In addition, avoidance of direct sunlight may continue to be favorable even underwater. Vertical surfaces may also provide a refuge from predation as will be discussed below.

Shell coloration has been shown to influence the operative temperature of some gastropods (Etter 1988). Dark limpets may indeed be warmed by the sun more than both mottled and light-colored limpets. If limpets are strongly influenced by increases in their body temperature, dark limpets would be expected to be at higher densities than lighter limpets on vertical surfaces where they are less exposed to sunlight. This however, was not the case (Fig. 9), indicating that during the winter, limpet color does not affect choice of substrate orientation even though overall, vertical surfaces are preferred. Further work is needed, however, to determine if lack of preference is indeed seasonal or if shell coloration is unimportant in this aspect of limpet ecology.

In addition to selecting pools and vertical surfaces, *T. testudinalis* may select specific substrates under some conditions. Limpets were found only on rock or on either one of two encrusting algae: *Hildenbrandia rubra* or *Clathromorphum circumscriptum* (Fig. 7). This behavior is observed because, like most limpets which adhere to surfaces using both suction and adhesion, *T. testudinalis* needs a flat surface on which to cling. Adherence to smooth, flat

surfaces helps prevent their dislodgement by waves and enhances their ability to withstand removal attempts by predators (Steneck 1982). In addition, because limpets lack an operculum, the only way by which they can reduce desiccation if they are exposed is by tightly adhering to the substratum. All three substrates provide a planar surface which maximizes the efficiency of limpet adherence.

In general, no substrate preference could be established. Previous workers have suggested that *C. circumscriptum* is the preferred holding surface for *T. testudinalis* because of its consistently smooth, planar surface (Steneck 1982, Dethier and Steneck 2001). At Reid State Park, *C. circumscriptum* was indeed preferred over rock, but no preference for this alga was observed at the other sites (Fig. 7). This finding contradicts the work by Steneck (1982) which demonstrated that limpets were found at the highest density on *C. circumscriptum*. Steneck's (1982) work, unlike the present study, was carried out during the summer months and it is probable that *T. testudinalis* exhibits seasonal differences in behavior. Preference of *C. circumscriptum* during the summer may be due to the fact that the larvae of *T. testudinalis*, which recruit during those months (Wallace 1972), settle exclusively on the algae, an important and easily grazed food source (Steneck 1982). Although the smallest limpets were not considered in this study, they were not observed solely or in high densities on *C. circumscriptum* and thus their inclusion in the results would be unlikely to affect the determined preference.

Preference of *C. circumscriptum* during the summer may also be explained by differential heating of each substrate by the sun. Dark substrates such as most rock at the sites and the darker *H. rubra* which absorb sunlight, heat up more than light-colored substrates. Selection of *C. circumscriptum* during the summer, a light-colored substrate, may be an adaptation to alleviate temperature increases caused by the sun. The operative temperature of limpets is

known to be influenced by substrate temperature (Hayworth and Quinn 1990). The influence of substrate temperature on limpet temperature is most likely to be a factor on exposed surfaces, but slight warming may also occur in the pools. Such a warming, probably more exaggerated in the summer months and in small pools, may increase evaporation and thus the salinity of the pools, creating osmotic stress for the limpets. The actual impact of such temperature changes or salinity increases on this species is unknown.

Many limpet species exhibit strong vertical zonation patterns which can be predicted based on the seasonal stresses at that site. Tropical limpets for example are often found lower in the intertidal during the summer months when desiccation rates in upper zones are high. Even temperate species such as *Patella* spp. described by Lewis (1954) show decreased survival in the upper zones during the summer. Zonation patterns change with the seasons. Limpets that avoid the high intertidal during the summer may migrate up again for the winter months. *Lottia digitalis* also moves up for the winter months, but this movement is due to harsh winter conditions in the lower zones (Frank 1965).

T. testudinalis did not demonstrate an observable zonation pattern, but was found at constant density throughout the intertidal. Lack of an observable pattern may be explained in several ways. Though Willcox (1905) observed that *T. testudinalis* in Maine remained in the intertidal during the winter, migration patterns may still exist, but to a lesser degree than the migration exhibited by the same species to the south. If *T. testudinalis* migrates to lower zones during the summer months to avoid high temperatures and desiccation, zonation during the winter would be less obvious. This migration pattern may result because winter temperatures do not cause the heat stress seen in summer months. Furthermore, evaporation of the pools that can lead to hypersaline conditions during the summer is not a factor during the winter, creating less

need for the lower, more predictable pools. In addition, the angle of sun exposure is very low during the winter and the day-length is short, also reducing the heat and desiccation stress.

T. testudinalis may also move down in the intertidal during the winter months, as was seen in the southern parts of its range (Willcox 1905). Zonation of the limpets left behind would be less obvious. If limpets in Maine do exhibit this behavior, it is due to very cold temperatures that threaten to freeze the pools in which they live. Comparison of *T. testudinalis* behavior in the winter versus the summer has yet to be done. Without such a study, it is impossible to determine which migration pattern, if any, exists. In addition, it is important to look subtidally to determine if *T. testudinalis* populations change there throughout the year. Understanding the *T. testudinalis* zonation pattern, or apparent lack thereof during the winter, is not possible without detailed studies that trace their behavior and density throughout the year.

The substrate choices made by *T. testudinalis* may also be caused by the need to rest on substrates that reduce predation. As suggested earlier, preferential resting on vertical substrates may be such an adaptation. Most limpet species are preyed upon by birds such as gulls or oystercatchers (Frank 1965, Giesel 1970, Wootton 1992), seastars (Hewatt 1937, Feder 1963), crabs (Lowell 1986) and predatory fishes (Parry 1982). *T. testudinalis* is known to be eaten by the seastar *Asterias* spp. (Steneck 1990) and gulls (Steneck pers. comm.) and it is likely that both crabs and fishes will eat them as well. Residence on vertical substrates has been shown to greatly reduce the success of bird predators (Kitting 1980, Little 1989, Wootton 1992) as well as the frequency with which limpets are attacked by crabs (Thomson et al. 2000). This reduction in predation may be due to decreased visibility. In addition vertically oriented surfaces prevent birds and crabs from achieving an efficient angle of attack of their limpet prey, thus reducing the successful removal of limpets. The prevalence of limpets on vertical surfaces may be produced

by active selection by the limpets or selective elimination by predators of limpets on horizontal surfaces (Test 1945).

As was discussed previously, lack of preference for vertical substrates at night (Fig. 13) may indeed be due to the fact that nighttime temperatures and lack of sunlight allow limpets to be present on horizontal surfaces. A more likely explanation during the winter, when day and night temperatures remain similarly cold, is that limpets are freer to be on horizontal substrates at night because of decreased predation by visual predators such as gulls and crabs.

In some limpet species, coloration has been shown to play a role in habitat selection and in survival. Many limpets exhibit cryptic coloration and are found at high densities on substrates that match their color (Giesel 1970, Mercurio et al. 1985, Wootton 1992). At Owls Head, light-colored limpets were found at higher densities on *C. circumscriptum*, the lightest substrate available. Though this pattern may indeed be an example of cryptic coloration, this explanation is questionable because gulls were never observed at this site during this study.

Smooth substrates not only increase the ability of limpets to adhere to the surface, but also decrease the likelihood of seastar predation. Steneck (1990) demonstrated that *T. testudinalis* are more susceptible to predation by *Asterias* spp. while on branched coralline algae. This alga provides a rougher surface on which to rest and allows seastars to more easily remove limpets from the substratum. Preference for *C. circumscriptum* at Reid may be observed if the rock is rougher, making the encrusting alga a more favorable holding surface. Detailed analysis of the rock composition and texture at each site are necessary to examine this hypothesis.

In some intertidal gastropods, coloration has been suggested to be influenced by diet (see Etter 1988 for an example). While it is possible that the light coloration of some limpets may result from selective ingestion of *C. circumscriptum* (limpets eating this alga produce

characteristically white fecal pellets (Steneck 1982, pers. obs.)), this hypothesis is unlikely because of the mixed diet that these limpets appear to maintain. Like the limpets described by Kitting (1980), *T. testudinalis* eats a variety of food sources, including *C. circumscriptum*, *H. rubra*, diatoms, and sporelings of macroalgae. Coloration obtained due to one of those probably has little impact on overall shell color.

Habitat selection may also be driven by the patchy distribution of favored food resources. *T. testudinalis* has been shown to prefer *C. circumscriptum* to other food sources (Steneck 1982, Pueschel and Miller 1996). The two species are believed by some to have coevolved; the snails were able to specialize on the calcareous alga, while *C. circumscriptum* came to rely on limpet grazing to remove epiphytes from its surface (Steneck 1982). It is interesting that although *C. circumscriptum* was indeed an important food resource as shown by lab experiments (pers. obs.), limpets were not found on this substrate more often than would be expected by random selection. This pattern was observed both in the field and in the laboratory where they were observed to move to *C. circumscriptum* and *H. rubra* at night (pers. obs.), but move off of them during the day (Fig. 12).

The fact that *T. testudinalis* is not found on *C. circumscriptum* during the day more often than expected brings into question the theory of the alga's superiority as a holding surface (Steneck 1982). *T. testudinalis*, threatened to be dislodged by waves, should consistently be found on the surface that enables them to adhere most effectively. *C. circumscriptum* at Owls Head and Pemaquid may not provide an advantage over rock or *H. rubra*, explaining the lack of preference (Fig. 7). At Reid State Park however, *C. circumscriptum* supported a much higher density than rock. Differences in rock type and structure between the sites may explain the observed patterns.

Although limpets did not appear to selectively rest on *C. circumscriptum* during the day (at Owls Head and Pemaquid in the field, and also in the laboratory), the highest limpet densities were found in areas that had a much higher percent cover of *C. circumscriptum* and *H. rubra* than was seen overall at the site (Fig. 10). This indicates that limpets settle in areas near their favored food sources even though they do not remain on them during the day while they are resting.

Habitat selection in *T. testudinalis* may occur initially during the larval recruitment period. This species, which recruits during the summer (Wallace 1972), is seen during that time only on *C. circumscriptum* (Steneck 1982). Kay (2002) demonstrated that *L. digitalis* larvae recruit preferentially to areas that support adult populations. This behavior is adaptive because it puts the larvae near preferred foods and also in the proximity of others of their species with whom they will reproduce in the future. Recruiting *T. testudinalis* larvae appear to prefer *C. circumscriptum* (Steneck 1982) and this preference may be a result of either of the two explanations. At this point, I am unable to distinguish between the two.

Variation between the sites was common, as was individual variation. In experimental work in the field and the laboratory, individual limpets were not specific to a given substrate or surface orientation. The harshness and unpredictability of the intertidal habitat, as well as daily and seasonal changes that occur there, necessitate behavioral adaptations that protect intertidal organisms from environmental stress. Such conditions require behavioral plasticity as an important feature of success. Substrate or surface orientation choice is likely to be affected by food availability, predator prevalence, temperature, and degree of exposure at each site, on any given day or season.

In the future, study of limpet density in crevices as opposed to on open surfaces will be useful in understanding the importance of temperature and desiccation in their habitat selection as was suggested by Garrity (1984) for other species. Studies of limpet size as it relates to substrate selection, vertical location in the intertidal, and density are necessary. Small limpets of the species *Acmaea limatula* are more susceptible to death by physical conditions (Vermeij 1972) and Wallace (1972) suggests that this may also be the case in *T. testudinalis*. A study of substrate choice as it relates to size may prove fruitful in advancing our understanding of this species.

Determining the relative importance of physical and biotic stresses throughout the year at each site will be interesting. Predator exclusion, limpet transplant, and shading experiments are examples of studies that will help to reveal the dominant pressures driving limpet microhabitat selection. Most importantly, studies of *T. testudinalis* populations that follow the fluctuations in density and changes in substrate choice, degree of exposure, and predation throughout the year are essential. With such studies, our ability to characterize the behavior of this species as well as its role in the intertidal community will be greatly strengthened.

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