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## Movement patterns and feeding behavior of the limpet *tectura testudinalis* (Müller) along the mid-Maine Coast

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**Movement Patterns and Feeding Behavior of the Limpet  
*Tectura testudinalis* (Müller) along the mid-Maine Coast**

**Joshua Lord**

Honors Thesis

Colby College Biology Department

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Movement Patterns and Feeding Behavior in the Limpet  
*Tectura testudinalis* (Müller) along the mid-Maine Coast

by

Joshua Lord '08

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

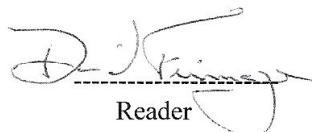
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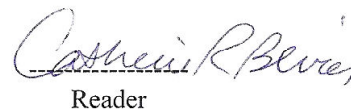
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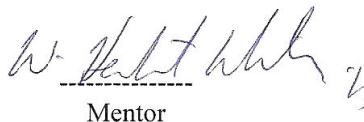
in

Biology

Approved:

  
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Mentor

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## **Movement Patterns and Feeding Behavior in the Limpet *Tectura testudinalis* (Müller) along the mid-Maine Coast**

**Joshua Lord**

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### **ABSTRACT**

*Tectura testudinalis* is a limpet that lives in the mid-intertidal zone along the coast of Maine and grazes on a variety of encrusting algae. A previous study asserted that *T. testudinalis* preferred to feed and rest on the encrusting alga *Clathromorphum circumscriptum* and that this species of limpet displayed homing behavior. However, I show that *T. testudinalis* does not home or return to any specific substrate while resting. Conclusive evidence was found for nocturnal movement. I show that *C. circumscriptum* was the preferred food source for this limpet, closely followed by *Hildenbrandia rubra*, another encrusting alga. Field and lab experiments showed that *T. testudinalis* individuals feed and search for food at night and then move to vertical surfaces and become stationary during the day.

## INTRODUCTION

*Tectura testudinalis*, the tortoise-shell limpet, is a species of prosobranch limpet that lives in the rocky intertidal and subtidal zones along the northeastern coast of North America (Steneck 1982). This species lives on bare rock and a variety of algal substrates, primarily in tide pools and subtidal environments. They have an average life span of three years and reach a maximum length of 30 mm (Pizzola 2003). *Tectura testudinalis* is a grazer that feeds on both diatoms and several species of encrusting algae, though it has been shown to feed preferentially on the encrusting coralline alga, *Clathromorphum circumscriptum* (Steneck 1982). A mutualistic relationship between *T. testudinalis* and *C. circumscriptum* has been suggested by Steneck (1982), but this assertion has since been disputed (Pueschel and Miller 1996). *Tectura testudinalis* is a free spawner with larvae that settle in tide pools and then move downward in the intertidal zone over the course their lives (Kessel 1964, Wallace 1972). This study documents the movement and feeding patterns of *T. testudinalis* and the homing behavior of this species.

Limpets play a strong role in intertidal communities, as they help to maintain the mosaic of algae that occurs in tide pools (Connell 1972, Dungan 1986, Fletcher 1987, Johnson et al., 1997). Limpets are grazers, feeding on diatoms or macroalgae, depending on the species of limpet. Species such as *T. testudinalis* affect algae in multiple ways, as they both feed on algae sporelings and push other sporelings out of the way as they scrape along the surface of the substratum. Therefore, limpets can have a significant effect on the algal species composition of the tide pools in which they live. This ecological importance, combined with their small size and relative lack of movement, makes them ideal study organisms.

Several species of limpets display homing behavior, the consistent return of individuals to a specific location on the substratum while not feeding or searching for food (Villee and

Groody 1940, Steneck 1982, Santina 1993, Jakob et al. 2001, Shanks 2002). This behavior is an adaptation to avoid predation, to prevent limpets from getting knocked off by waves, and to reduce desiccation stress in limpets that are exposed at low tide (Wallace 1972). Species that home, such as *Patella rustica*, spend most of their time on a home scar, with short feeding excursions (Evans and Willams 1991). Movement is quick while moving away from the home and searching for food, slow while feeding, and then quick again as they follow their mucous trail back to the home scar (Santina 1993). This homing instinct is extremely strong in many species of limpets, but is markedly less so in others. Species such as *Cellana toreuma* only display strong site fidelity when there is a high amount of food or predation, which generally occurs in the high and low extremes of the intertidal zone (Iwasaki 1992).

*Tectura testudinalis* has been shown to display homing behavior both in subtidal environments and in laboratory experiments (Steneck 1982). Unlike other strictly homing species, individuals do not have a sunken home scar that they fit into. Both *T. testudinalis* and the congeneric *T. scutum* have been found to return to a certain site while not feeding (Kitting 1980, Steneck 1982). However, Kitting (1980) refrained from terming this behavior as homing because individuals were not found to consistently return to the exact same location. It is also notable that *T. scutum* preferred to rest in areas with little or no encrusting algae, despite feeding primarily on encrusting algae. Differences between the interpretations of Kitting (1980) and Steneck (1982) indicate the uncertainty that still surrounds the movement patterns of *T. testudinalis*.

Closely related to homing behavior is territorial behavior, which is displayed by *Lottia gigantea*. Individuals of this limpet species defend an area around their home site from both conspecific and heterospecific limpets. The areas that are defended are thick algal fields that

serve as a rich food source and are maintained via sustainable grazing by the territorial limpet (Shanks 2002). This defense of a specific territory has not been shown to occur in individuals of *T. testudinalis*. However, territorial behavior is closely linked to intraspecific competition and population density in general, which have been shown to be factors in determining the distribution of this species (Steneck 1982).

Intraspecific competition is one of several factors that cause variation in the vertical distribution of limpets in the intertidal zone (Wallace 1972). Populations of *T. testudinalis* display a density gradient, with limpet density increasing lower in the intertidal zone and into subtidal habitats (Ojeda and Dearborn 1989). Shell size also increases in the down-shore direction, largely because *T. testudinalis* larvae settle in tide pools in the mid-intertidal zone. (Wallace 1972). These gradients in limpet density and size are thought to be a result of downward migration throughout their lives, though reasons for this movement are unclear (Vermeij 1972).

As with many aspects of limpet behavior, there is great interspecific variation with regard to the factors that influence movement patterns. There are several different diurnal, seasonal, interspecific, and intraspecific cues that influence movement. One such movement cue is the tides, with most limpet species preferring to feed and search for food at high tide, when they are covered with water (Branch 1975, 1981; Black 1979). Since desiccation stress is one of the main factors driving limpet distribution, it is likely that many species move during high tide because it is the only time during which they are submerged. *Tectura testudinalis* is different from most limpet species in that the majority of individuals live in areas where they are constantly submerged (Wallace 1972, Steneck 1982). As a result, tides matter less to this species than to others.

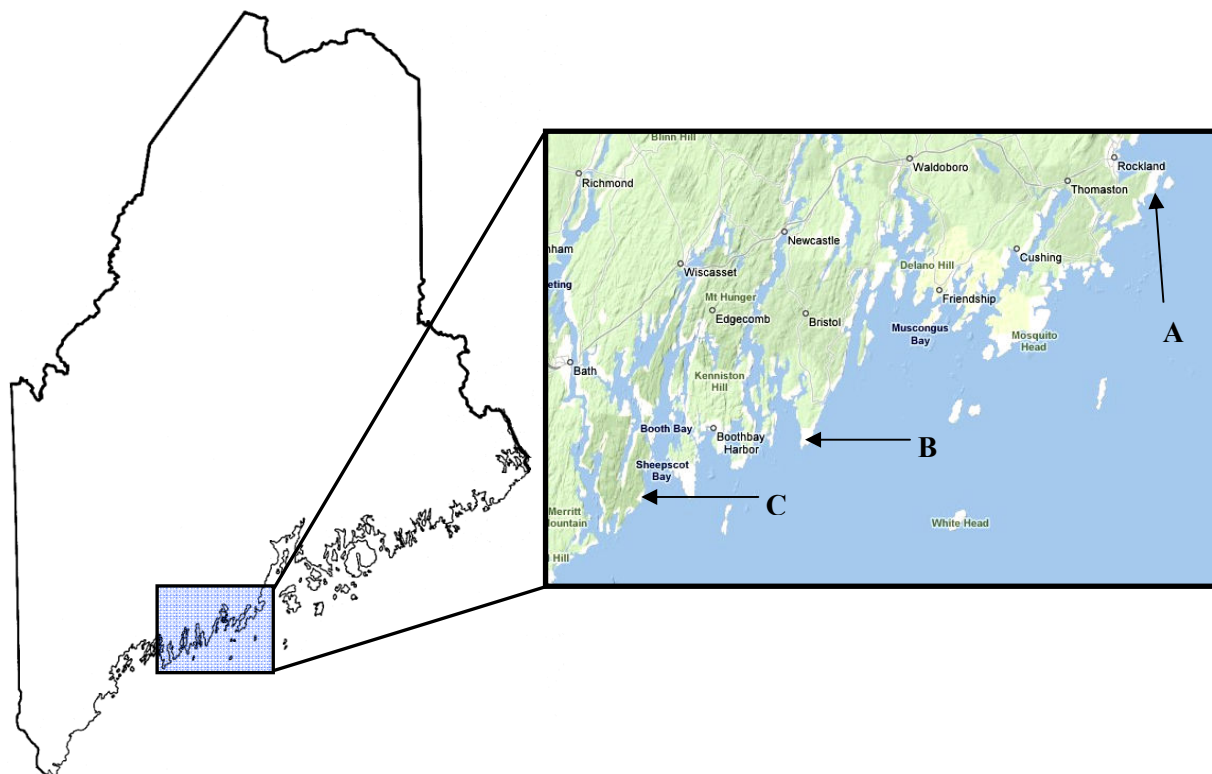
Light cycles also influence limpet movement, though this effect again varies by species. Individuals of *T. testudinalis* feed and search for food at night, while species such as *Cellana toreuma* and *Patella flexuosa* move at any low tide or just during the day, respectively (Branch 1981, Steneck 1982, Iwasaki 1992, 1999). While there is no clear reason why *T. testudinalis* is nocturnal, it could potentially help this species avoid threats posed by visual predators such as birds. It is preyed upon by a variety of predators, including gulls, crabs, and sea stars (Margolin 1964, Steneck 1982, Lowell 1986). Individuals of *T. testudinalis* actively respond to attempted predation by sea stars, as they exhibit a running response when touched by a sea star (Margolin 1964, personal obs.).

Limpet species vary greatly in natural history characteristics, so the behavior of any one species cannot necessarily be extrapolated to others. Varying diets and substrate preferences likely influence and alter movement and overall behavior. Therefore, even though much work has been done on limpets, relatively little of it can be applied specifically to *T. testudinalis*. This study focused on movement patterns of *T. testudinalis* and the various factors that influence its behavior. Specifically, I predicted that individuals would display a greater movement rate during the night, based on previous suggestions that *T. testudinalis* feeds more at night (Steneck 1982; Branch 1981). I also expected that feeding and searching for food would occur primarily at night. As a result of the abundance of encrusting algae in tide pools and in lab experiments, I also predicted that individual limpets would spend the most time on the substrate that they prefer to feed on to conserve energy. Since food is a vital resource and *T. testudinalis* is exposed to few stresses, I believe diet and substrate preference are the most important factors in determining the movement patterns and distribution of individuals of this species.



## MATERIALS AND METHODS

The movement and behavior of *T. testudinalis* were studied in both the field and the laboratory. Field surveys were conducted during February and early March 2008 at three sites in the rocky intertidal zone along the mid-Maine coast. One site was near the Owl's Head Lighthouse, Owl's Head, Maine (44°5'N, 69°2'W) (Fig. 1A). A second site included four locations around Pemaquid Point, Maine (44°30'N, 69°32'W) (Fig. 1B). The third site included Outer Head and Little River Ledges at Reid State Park, Maine (43°47'N, 69°43'W) (Fig. 1C).



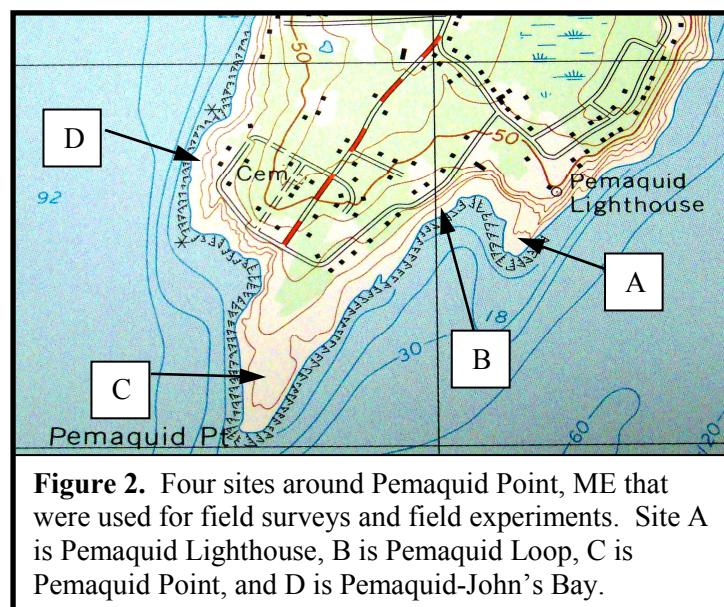
**Figure 1.** Survey sites along the Maine coast at Owl's Head Lighthouse (A), Pemaquid Point (B), and Reid State Park (C)

In the first part of the field survey, line transects were run from the low-tide level in the *Chondrus crispus* zone up to the barnacle zone and bare rock. The *C. crispus* zone is the lowest zone exposed during low tide, so the transects reached from the lowest accessible zone to the highest one, encompassing the area in which limpets could be found. The total distance for each

of these transects was 10-20 meters, based on the distance from the water to the barnacle zone, above the macro-algae cover. Transects were placed randomly along the coast at each site, perpendicular to the shore. Substrate was noted every  $\frac{1}{4}$  meter along the length of the transect. To determine overall limpet density, limpets within a swath 30-cm wide along the transect were counted and recorded. At least eight line transects were done at each of the three sites.

The second part of the field survey focused on the substrates occupied by the individual limpets at each site. At low tide,  $\frac{1}{16}$  m<sup>2</sup> quadrats were placed in areas of high limpet density. Percent cover of the quadrat and of each tide pool was estimated visually for each main substrate type, as done by Dethier (1984). The limpets within each quadrat were counted, and their shell color and the type of substrate on which they rested were recorded. Sixty quadrats were surveyed in the Pemaquid region, 33 at Owl's Head, and 31 at Reid State Park, with a total of over 600 limpets surveyed.

Several field experiments were performed in January 2008 during the daytime low tide at four sites in the Pemaquid Point region (Fig. 2). Sites A and C were on exposed points, while sites B and D were more protected from wave action.



Removal experiments were conducted at all of these sites, in a total of eight small ( $<1 \text{ m}^2$ ) tide pools that were chosen at random. All limpets in these pools were removed, labeled, and placed in the part of the ocean closest to each tide pool. The labels were permanently marked numbers cut from a vinyl sheet and super glued to the back of the shell of each limpet. Removal pools were checked for the presence of marked limpets once daily for five days and then periodically for two weeks.

Addition experiments were also conducted at the four sites in the Pemaquid region. Individual *T. testudinalis* were collected from a variety of pools and substrates in the Pemaquid area and were tagged in the lab. They were kept in flowing seawater tanks at the Darling Marine Center, where their length was measured and their color was estimated in terms of percent white. Twelve small ( $<1 \text{ m}^2$ ) tide pools in the Pemaquid region observed to contain several substrate choices were selected for the additions. Pools were measured roughly with  $1/16 \text{ m}^2$  quadrats and four limpets per quadrat (based on observed natural density) were placed in the center of each pool. Collected limpets from each substrate and from both vertical and horizontal surfaces were placed in each pool. Control pools were also set up, in which limpets were taken out, labeled, and put back in the same location. All pools were examined every day at daytime low tide for seven days, with substrate and vertical/horizontal orientation noted each day for all numbered limpets. Visual percent cover estimates were made of these pools to accurately assess the limpets' substrate choices.

Intra-tide pool movement experiments were done at the Pemaquid sites as well. Large pools ( $>1 \text{ m}^2$ ) were used for this experiment, with between one and four  $1/16 \text{ m}^2$  quadrats in each pool, based on pool size and limpet density. Areas with relatively high limpet density were

chosen for each of these quadrats. Limpets in each quadrat were taken out, measured, labeled, and had their original substrate noted. They were assigned one of four treatments (control, 0 m, 0.5 m, 1 m) and were placed back in the pool accordingly. Control treatment limpets were placed back in their original locations, the 0 m limpets were placed just outside the quadrat, and the 0.5 m and 1 m treatment limpets were placed 0.5 and 1 meter outside the quadrat, respectively. A total of 24 of these experiments were done, six for each treatment. Quadrats were checked every day for six days and then periodically for two weeks. Each time it was noted which limpet numbers were in the quadrat and what substrates they were on. Unlabeled limpets that moved into these quadrats were also categorized in order to gain a further understanding of intra-tide pool movement.

Laboratory experiments to further explore *T. testudinalis* movement and behavior were conducted in February and March 2008 in a refrigerated room at Colby College in Waterville, Maine. Limpets and sea water were collected from the Pemaquid Point region and were kept in the refrigerated room at approximately 4.4°C. The limpets were stored in multiple aquaria with flowing water, rocks, and lamps set with a timer to replicate the actual day-night cycle. Five-day substrate choice experiments were conducted in this room, with pictures taken automatically every five minutes with a digital camera and The Time Machine™ photo timer. For this experiment, randomly selected limpets were placed in a shallow pan filled with fresh sea water. The pan contained bare rocks, as well as rocks covered with *C. circumscriptum* and *H. rubra*. Eight limpets were used in each trial, with two initially placed on each available substrate. Three trials were run for five days each on a timed day-night light cycle. After the trials, the photos were analyzed using accurate digital marking and measuring tools in Adobe Photoshop. The movements of each limpet were marked on the photos and then digitized, producing a track that

showed the detailed movements of each individual. The amount and rate of movement for each individual was calculated and recorded.

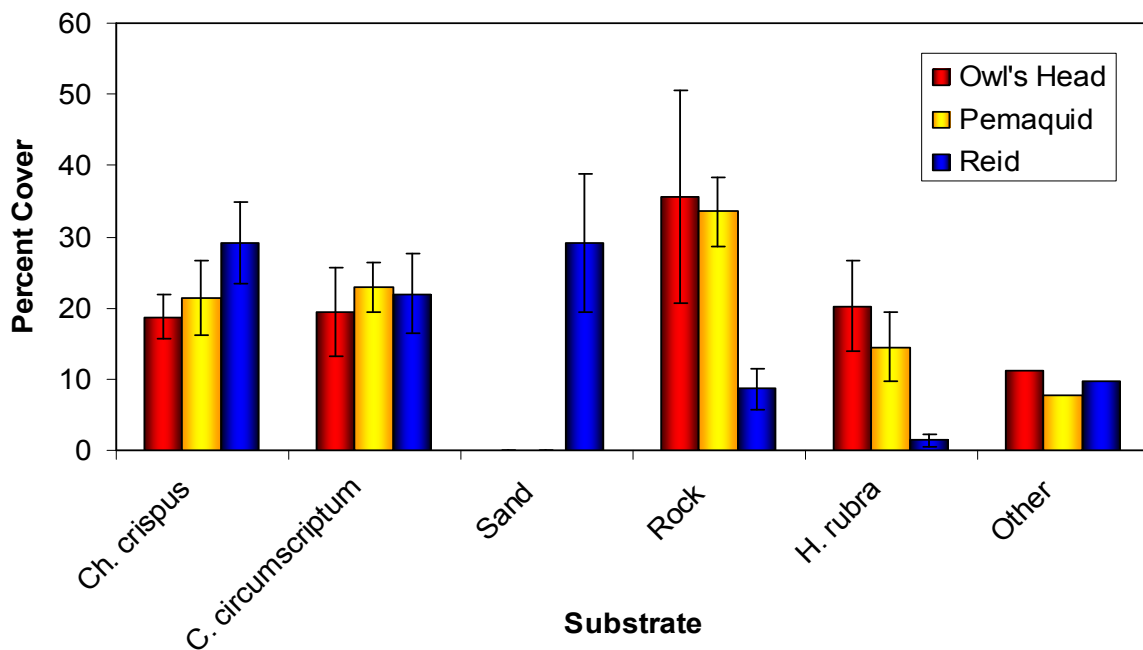
Digital tracking allowed me to make several general observations about the behavior of this species and to quantify many of the movement patterns that were observed. The following aspects of limpet movement patterns were computed for every limpet:

- (1) Total distance travelled each day and night
- (2) Amount of time on each substrate
- (3) Percent of time searching versus feeding on each substrate
- (4) Rates of movement on each substrate day and night
- (5) Movement rates before and after discovering food source
- (6) Number of times that each limpet changed substrates day and night

This protocol not only enabled an in-depth analysis of limpet movement, but also served as a more controlled and closely observed version of the addition experiments that were conducted in the field.

## RESULTS

The overall density of *T. testudinalis* in the intertidal zone at Owl's Head Lighthouse was  $4.8/\text{m}^2$ , with a density of  $34.8/\text{m}^2$  in tide pools based on the line transects that were done. In the Pemaquid area there were  $2.0$  limpets/ $\text{m}^2$  overall and  $14.8/\text{m}^2$  in the tide pools. Reid State Park had an overall limpet density of  $5.7/\text{m}^2$  and a tide pool density of  $9.7/\text{m}^2$ . Based on the line transect data, the predominant algae were *Fucus* spp. (*distichlis*+*vesiculosus*), *Ascophyllum nodosum*, and *Chondrus crispus*. In the tide pools, the most common substrates were rock, sand, *Ch. crispus*, and the two encrusting algae, *H. rubra* and *C. circumscriptum* (Fig. 3). The prevalence of some of these substrates varied significantly by site, as is shown in Figure 3.

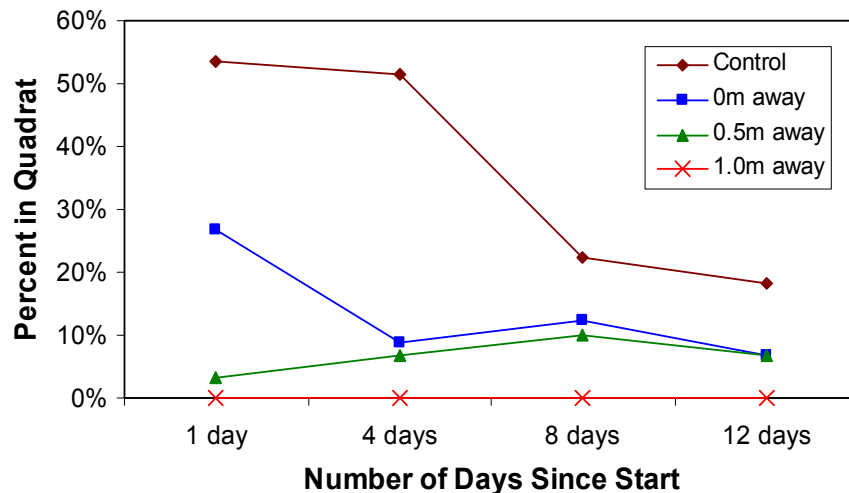


**Figure 3.** Average percent cover ( $\pm$ SE) of different substrates in tide pools at Owl's Head, the Pemaquid region, and Reid State Park. There was significantly more rock and *H. rubra* at Owl's Head and Pemaquid than at Reid State Park (ANOVA,  $F_{14,225} = 7.38$ ,  $p < 0.05$ ). Reid was the only site at which sand was found as a common substrate in the pools. Amounts of *Ch. crispus* and *C. circumscriptum* did not vary significantly by site.

In the removal experiments that were conducted in the Pemaquid region, none of the 78 limpets that were removed from their tide pools and placed in the ocean returned to the original tide pool. Only one of the 78 was found in any other tide pool in the surrounding area. Since some unlabeled limpets moved into the removal pools, the durability of the tags was tested in the laboratory and in the field. The tags were found to stay on even after high pressure water spraying in the lab and after at least two months in the field.

Intra-tide pool movement experiments ( $\frac{1}{16} \text{ m}^2$  removals) showed a high level of day-to-day *T. testudinalis* movement within the pools. In 24  $\frac{1}{16} \text{ m}^2$  quadrats, 121 different unlabeled limpets moved into the quadrat for at least one day, an average of 5.3 per quadrat. Of the 121 limpets moved into the quadrat for at least one day, an average of 5.3 per quadrat. Of the 121 limpets, 63 remained in the quadrat for more than one day. Since only limpets inside each quadrat were labeled at the beginning of the experiment, these unlabeled limpets moved into the quadrat from somewhere else in the pool.

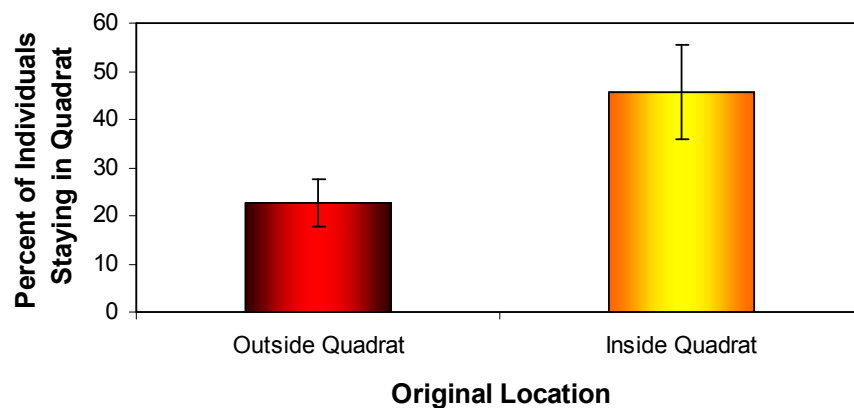
Very few of the limpets that were moved 0.5 m or 1 m away from the original quadrat found their way back. In addition, individuals that were initially in or next to the quadrat generally moved out of the quadrat over the duration of the experiment (Fig. 4).



**Figure 4.** Percent of original labeled limpets in each quadrat over the course of the intra-tide pool movement experiment. The four treatments were different removal distances, including a control, 0 m, 0.5 m, and 1 m distances away from the quadrat. Individuals in the control and 0 m treatments moved out over the course of the experiment, while those moved 0.5 m and 1 m away rarely came back to the original quadrat.

No limpets that were placed one meter away from the quadrat returned over the two-week monitoring period. At the end of this experiment the overall (labeled+unlabeled) density in the quadrats was 2.5 limpets per quadrat. The average density before the experimental removals was 5.3 limpets per quadrat. The pre-experimental limpet densities in the different quadrats did not differ significantly.

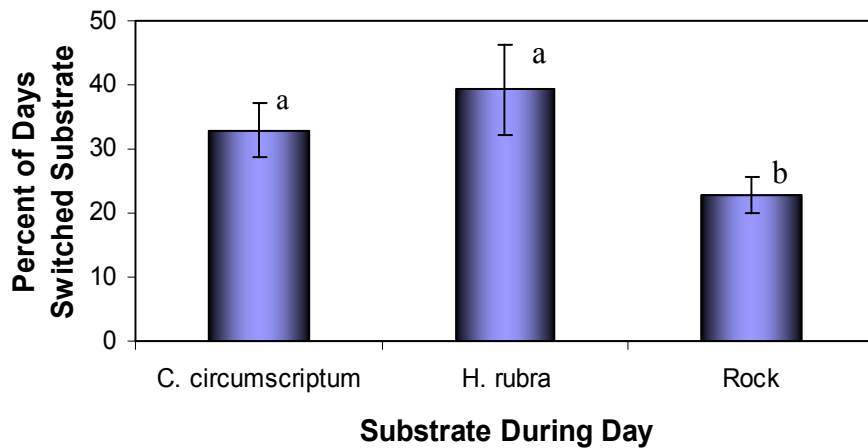
The labeled and unlabeled limpets combined to switch substrates from one day to the next 30.6% of the time. Limpets that were found in the quadrat and labeled when the experiment started switched substrates less, but not significantly less than did limpets that moved into the quadrat later. The number of substrate switches from day-to-day did not vary significantly based on the original substrate of each individual. Limpets that were originally in the quadrat were significantly more likely to remain in the quadrat than individuals that were not originally in the quadrat but moved in during the experiment (T-test,  $t_{15} = -2.08$ ,  $p < 0.05$ ) (Fig. 5).



**Figure 5.** Percent of individuals that remained in the quadrat after moving in. Significantly more limpets that were originally in the quadrat stayed there (T-test,  $t_{15} = -2.08$ ,  $p < 0.05$ ).

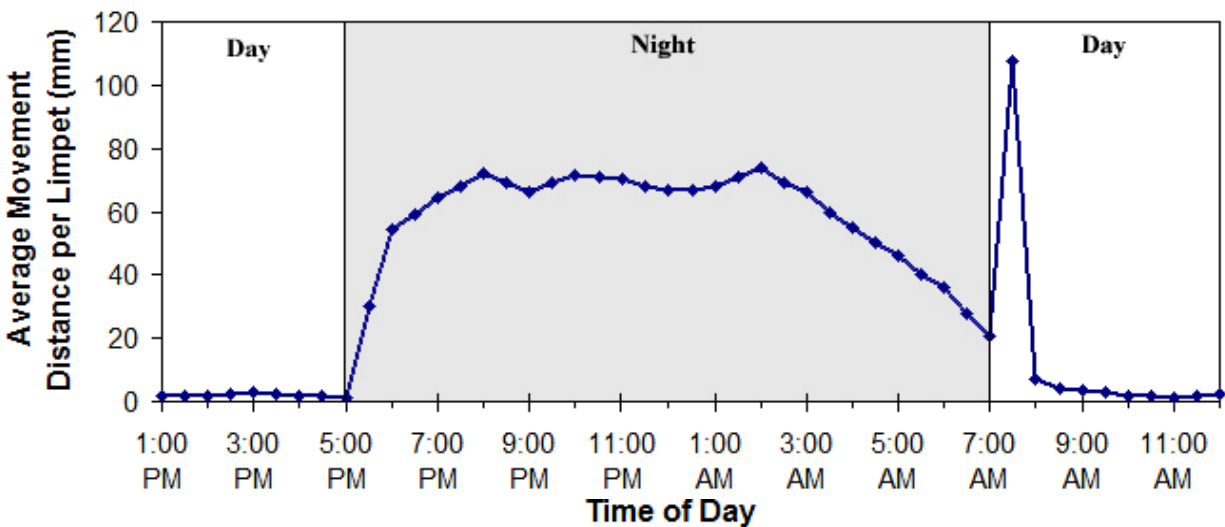
In the addition experiments, *T. testudinalis* limpets switched substrates from one day to the next 29.0% of the time. There was no relationship found between the amount of substrate switching by individual limpets and shell color (Pearson correlation coefficient,  $r = 0.084$ ,  $p = 0.31$ ) or shell length (Pearson correlation coefficient,  $r = 0.129$ ,  $p = 0.12$ ). Limpets that were on *H. rubra* switched substrates significantly more than those found on rock during the day (T-test,  $t_{89} = -2.39$ ,  $p < 0.01$ ) (Fig. 6).





**Figure 6.** Average percent of days that individual limpets switched substrates from the previous day ( $\pm$ SE). Limpets on *H. rubra* switched a significantly higher percent of the time than did limpets on the rock (T-test  $t_{89} = -2.39$ ,  $p < 0.01$ ).

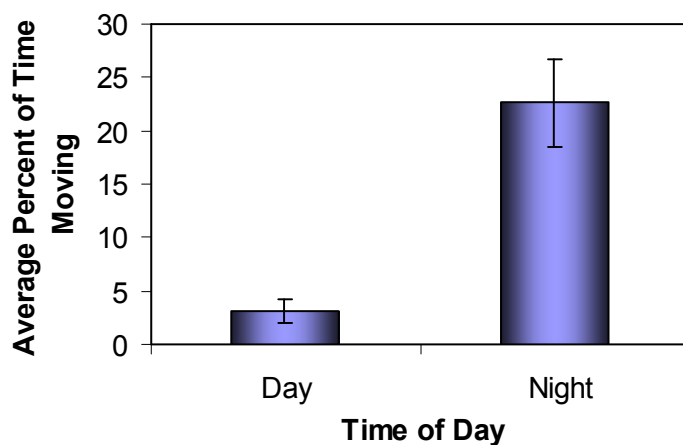
Five-day substrate choice experiments conducted in the lab showed a drastic difference between *T. testudinalis* movement and feeding behavior during the day and the night. Rapid increases in activity occurred when the lights turned off at the beginning of the night and when the lights turned back on in the morning. The half-hour in which the most movement occurred was from 7:00 to 7:30 AM, immediately following the turning on of the lights at 7 AM (Fig. 7).



**Figure 7.** Average amount of movement (total mm each half hour) of individual limpets over a 24-hour cycle. Each point is the average distance travelled of 24 limpets over five-day experiment periods ( $N = 120$ ). Movement distances are consistently low during the day with the exception of a spike immediately after the lights came on at 7 AM.

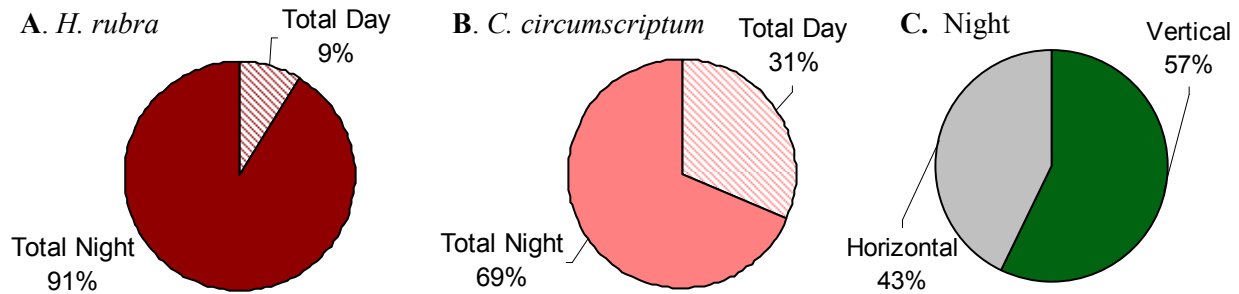
This spike in movement at the beginning of the day accounted for 59.9% of the total movement for the entire day. During this time, individuals were observed to move quickly to a vertical surface (not the same spot from day-to-day). After this initial spike, movement rates were consistently low during daylight hours, with night movement distances approximately 30 times higher than those during the day.

Individual *T. testudinalis* individuals moved a significantly greater percent of the time at night than during the day (Wilcoxon signed rank test,  $W = -280$ ,  $z = -3.99$ ,  $p < 0.0001$ ) (Fig. 8). They moved an average of 3.1% of the time during the day and 22.6% of the time during the night, an increase of over 300% (Fig. 8).



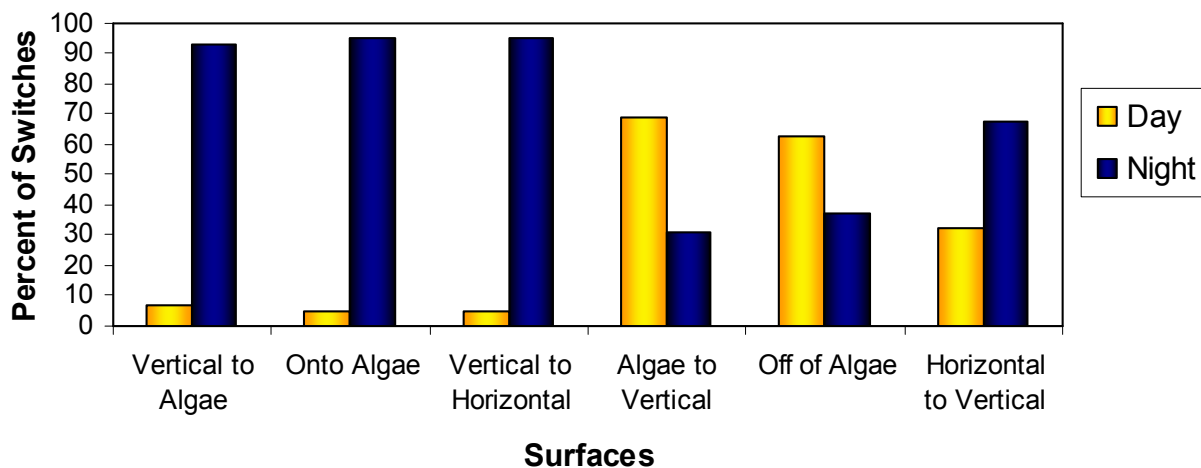
**Figure 8.** Average percent of time individuals were moving during the day and the night ( $\pm$ SE). Limpets moved a significantly higher percent of the time during the night than the day (Wilcoxon test,  $W = -280$ ,  $z = -3.99$ ,  $p < 0.05$ ).

In addition to moving more at night, individuals spent much more time on the two types of encrusting algae during the day than at night (Fig. 9A, B). During the day, limpets spent 80.9% of the time on vertical surfaces, compared to 57.4% of the time at night, shown in Figure 9C.



**Figure 9.** Amount of time spent on different substrates during the day and at night. (A) Percent of time that individuals spent on *H. rubra*. The vast majority of the time spent on this substrate was at night. (B) Percent of time that individuals spent on *C. circumscriptum*. Most of the time spent on this alga was at night. (C) Percent of time spent on vertical and horizontal surfaces during the night.

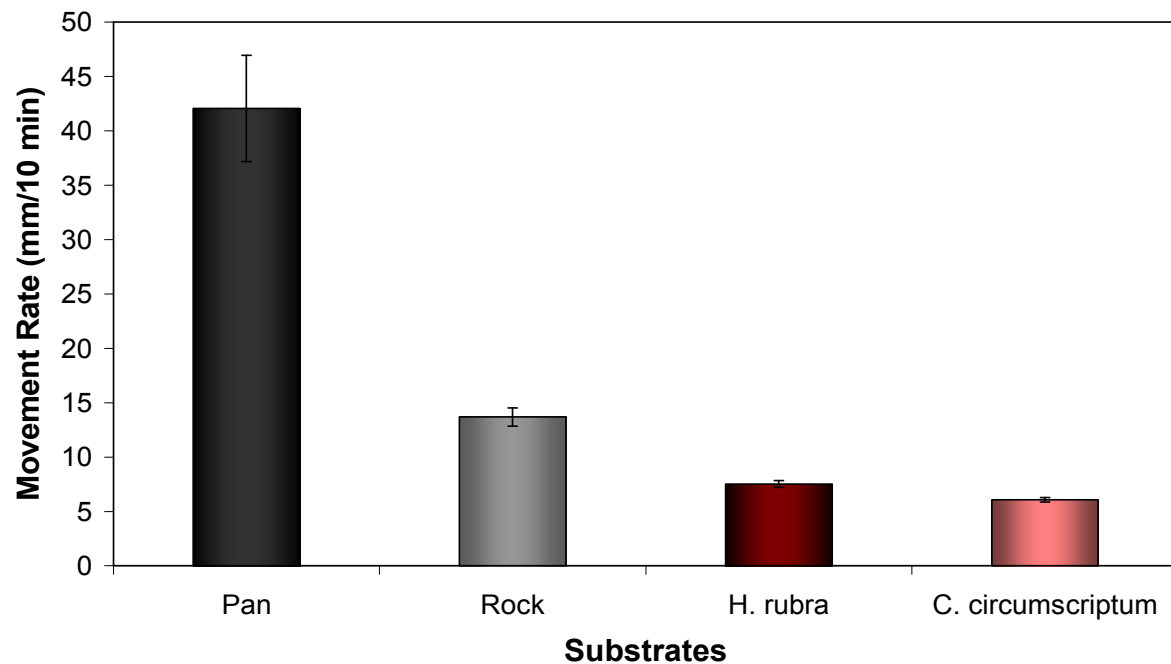
There were also considerable differences in the time of day when individual limpets switched substrates or vertical/horizontal orientation. During daylight hours, individuals switched from a horizontal surface to a vertical one 700% more than from vertical to horizontal. This pattern of movement to vertical surfaces during the day did not apply to the night, as 58% of all orientation switches at night were individuals moving onto horizontal surfaces. Over 90% of all switches from vertical surfaces to encrusting algae, from vertical to horizontal, and from any surface onto encrusting algae occurred during the night. In contrast, nearly 70% of movement from algae to vertical surfaces occurred during daylight hours (Fig. 10).



**Figure 10.** Percentages of substrate or vertical/horizontal surface switches occurring during day and night.

Overall, *T. testudinalis* individuals switched substrates significantly more during the night than during the day (Wilcoxon signed rank test,  $W = -175$ ,  $z = -3.51$ ,  $p < 0.001$ ). Of 229 substrate switches by 24 limpets over 15 days, only 30 switches occurred during the day, approximately 13% of the number that occurred during nighttime hours.

From the measurements of the distance moved every ten minutes, movement rates on each substrate were calculated, with the greatest rate occurring on the pan. The rates were successively lower on the rock, *H. rubra*, and *C. circumscriptum*, respectively. All differences in rates between substrates were statistically significant (significance values in Table 1) (Fig. 11).



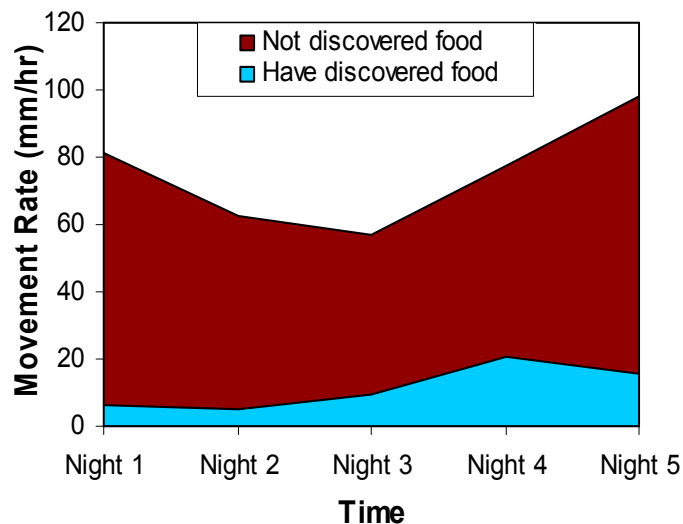
**Figure 11.** Average movement rate ( $\pm$ SE) on different substrates in the five-day experiments. The rate of movement on each substrate was significantly different than the rates on all of the other substrates (see table 1 for significance values).

Substrates	$U_A$	z-value	p-value
Pan v. Rock	40292	12.51	< 0.0001
Pan v. <i>H. rubra</i>	17251	13.60	< 0.0001
Pan v. <i>C. circumscriptum</i>	8981	18.51	< 0.0001
Rock v. <i>H. rubra</i>	16586	5.40	< 0.0001
Rock v. <i>C. circumscriptum</i>	13788	9.75	< 0.0001
<i>H. rubra</i> v. <i>C. circumscriptum</i>	13201	4.48	< 0.0001

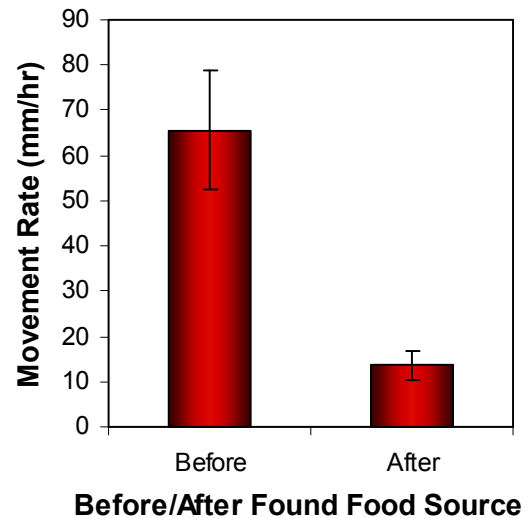
**Table 1.** Results of pair-wise Mann-Whitney U-tests for the movement rates in Figure 10. The differences in movement rate between all of the substrates were highly significant.

In these multiple-substrate pool experiments in the lab, limpets that had discovered both *C. circumscriptum* and *H. rubra* kept coming back to *C. circumscriptum* 100% of the time. While several limpets did feed on *H. rubra*, no limpet that subsequently discovered *C. circumscriptum* then went back to feed on the other species of encrusting algae.

As in the field experiments, there was no relationship between the distance that each limpet travelled and shell size (Pearson correlation coefficient,  $r = 0.084$ ,  $p = 0.70$ ) or shell color (Pearson correlation coefficient,  $r = 0.237$ ,  $p = 0.28$ ). However, several factors were found to influence the movement of this species of limpet. The rate of movement for individual limpets dropped significantly and drastically after the individual discovered *C. circumscriptum* or *H. rubra*, their observed food sources (pair-wise Mann-Whitney U-test,  $U_A = 11$ ,  $z = 3.2$ ,  $p < 0.001$ ). The average movement rate of individual limpets before finding *C. circumscriptum* or *H. rubra* was over four times higher than the movement rate after discovering a food source (Figs. 12, 13).

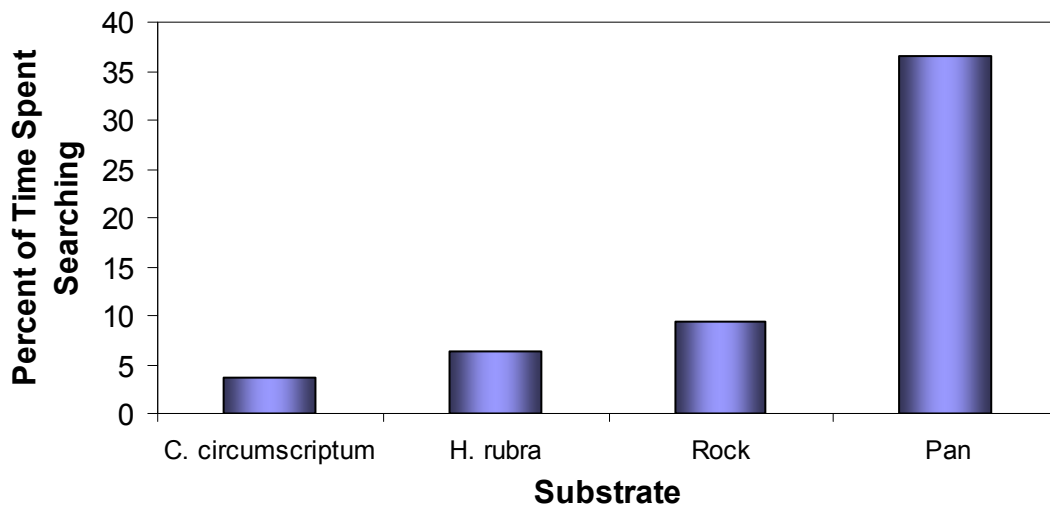


**Figure 12.** Average rate of movement, by days of the experiment, for limpets that had and had not discovered *H. rubra* or *C. circumscriptum*. Once an individual found either encrusting alga for the first time, it was counted as “have discovered food” for the remainder of the experiment



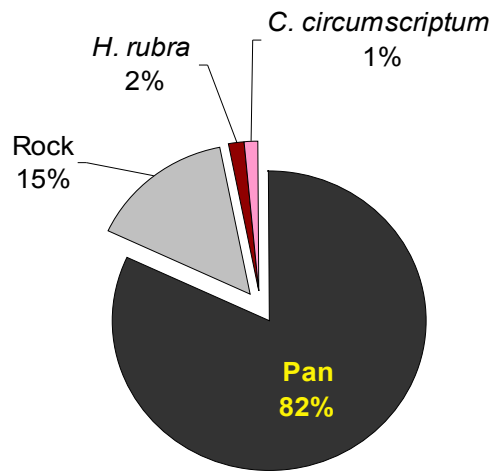
**Figure 13.** Average rate of movement of individual limpets before and after finding *H. rubra* or *C. circumscriptum* ( $\pm$ SE). Movement rate is significantly higher before discovery (pair-wise Mann-Whitney U-test,  $U_A = 11$ ,  $z = 3.2$ ,  $p < 0.001$ ).

When limpets were not feeding, they were usually either resting or searching for food. While searching, limpets moved at a faster rate and over greater distances. For this experiment, searching was classified as movement of at or over 15 mm per 10 minutes. This rate of movement was quick for these individuals, so was fast enough to exclude feeding movement but slow enough to account for individual variation in movement rate. In the three five-day lab experiments, individuals were searching for food 36.7% of the time spent on the pan, 9.4% of the time on rock, 6.2% on *H. rubra*, and 3.7% of the time on *C. circumscriptum* (Fig. 14). The ratios between the amounts of searching movement on these substrates only changed minimally if searching movement was defined as 10 mm or 20 mm per 10 minutes.



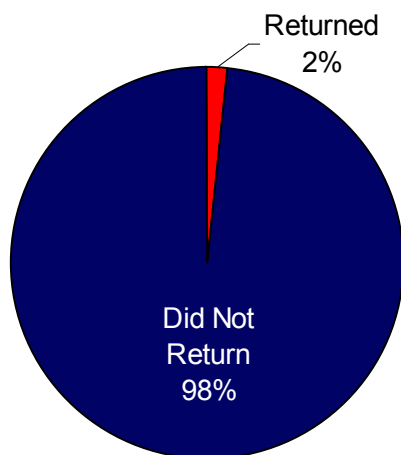
**Figure 14.** Percent of time searching on each of four substrates available. The pan was the only non-natural surface.

Of all the food-searching that the 24 total limpets did over the course of three five-day experiments, only 1% of the searching occurred on *C. circumscriptum* and 2% on *H. rubra* (Fig. 15). Most of the searching (82%) occurred on the pan, where no algae or other forms of food were present.



**Figure 15.** Percent of total searching movement (greater than 15 mm /10 min) on each substrate. Of over 211 hours spent on the two species of encrusting algae by individuals during the 15 days of trials, only two hours and twenty minutes was spent searching for food. The percentages remained relatively constant even if the definition of searching was altered to 10 mm or 20 mm per 10 minutes.

Over the course of the five-day substrate choice experiments, no pushing by limpets or other density-dependent interactions were observed. In addition, none of the 24 individuals followed the same route back to their original location when they finished feeding or searching for food. Only two limpets returned to the exact same location where they had been the previous night (out of 120 chances) (Fig. 16), and these two individuals only returned once each.



**Figure 16.** Percent of individuals that returned to the exact same resting location from one day to the next. Includes all three five-day substrate choice experiments and a total of 24 limpets. A limpet was considered to return if it came back and rested in the exact location as it had previously.

## DISCUSSION

In the five-day substrate choice experiments conducted in the lab, *T. testudinalis* was nocturnal. They moved significantly greater distances and amounts of time during the night, supporting the conclusions by Branch (1981) and Steneck (1982) that this species of limpet feeds and searches for food during the night (Figs. 7, 8, 9, 10). As a result, the predictions that individuals of *T. testudinalis* would have a greater movement rate at night and that they would search and feed more at night were supported. The vast majority of the time that individuals spent on *C. circumscriptum* and *H. rubra* was during the night (Fig. 9), indicating that feeding was a nocturnal activity. Over 90% of the movements onto the two species of encrusting algae occurred at night (Fig. 10), showing again that this was the only time that individuals preferred to feed. Searching for food, which involves much faster movement than feeding (Santina 1993), was also shown to occur at night. This was illustrated by the dramatically increased rates of movement and distances travelled by *T. testudinalis* individuals during the night (Figs. 7, 11). No conclusive reason for this pattern was found, though nocturnal movement by this species could have evolved to avoid either visual predators or the higher temperatures resulting from direct exposure to sunlight.

Detailed analysis of night-time feeding and searching movements provided for a better understanding of feeding preferences in *T. testudinalis* than did previous studies (Steneck 1982). The five-day substrate choice experiments supported earlier findings by Steneck (1982) that *T. testudinalis* prefers to feed on *C. circumscriptum*. This preference for *C. circumscriptum* was evidenced by an unusually low movement rate of individuals on this substrate, the lowest of any substrate present (Fig. 11). Since feeding is characterized by slow movement (Steneck 1982, Santina 1993, Shanks 2002), the low movement rates indicate elevated amounts of feeding.



These rates were only based on the times when individuals were moving around, so were not skewed by movement rates of zero when individuals were resting. The lowest amount of searching movement was found on *C. circumscriptum* as well (Fig. 14), indicating that limpets stopped searching for a food source upon discovery of this substrate. The preference of *T. testudinalis* for *C. circumscriptum* was also affirmed by the fact that even though some individuals fed on *H. rubra*, no individual that subsequently discovered *C. circumscriptum* returned to *H. rubra*. This behavior clearly confirms the status of *C. circumscriptum* as the preferred food source of *T. testudinalis*.

Analysis of the nocturnal feeding behavior of this species also revealed a previously undocumented rank preference of different food sources. As shown by the line transects, the most common substrates in the tide pools (excluding macroalgae, which this species does not feed on) were rock, *C. circumscriptum*, and *H. rubra* (Fig. 3). All three of these prominent substrata were present in the substrate choice experiments in the lab. Figures 11, 14 and 15 clearly illustrate the rank preference of *T. testudinalis*, with *C. circumscriptum* as the preferred food source, followed by *H. rubra*, rock, and lastly the pan which served as a pool in this experiment.

Rates of movement on the two species of encrusting algae, while significantly different, did not differ drastically (Fig. 11). This similarity in movement indicates that individuals prefer the encrusting algae to other forms of food available in tide pools. The higher movement rate on rock was expected but was not nearly as high as the rate of movement on the pan. This difference between rock and pan is likely a result of the presence of food sources such as diatoms or algae sporelings on the rock, causing individuals to occasionally graze on these potential but not preferred food sources (Steneck 1982). The rank preference based on movement rate is

backed up by the amount of searching for food that occurred on each substrate. The extremely high percentage of searching movement on the pan indicates a lack of food there, while lower percentages on other substrates illustrate the discovery of some type of food (Figs. 14, 15). The relative percentages of searching movement on rock and the two encrusting algae species demonstrate the amount that individuals were still searching for alternate food options. The low percentage on *H. rubra* and lowest percentage on *C. circumscriptum* indicates increasing satisfaction with each substrate as a food source.

The rank preference of *T. testudinalis* for *C. circumscriptum* then *H. rubra*, rock, and the pan demonstrates not only a preference for *C. circumscriptum*, but also a conclusive preference for the two types of encrusting algae over other substrates. This preference for encrusting algae could be a byproduct of the grazing mechanics of *T. testudinalis*, which uses its radula to scrape off algal epithelial cells, diatoms, or algae sporelings. Design of the radula and radular teeth has been shown to effect dietary preferences in this and closely related species (Kitting 1980, Steneck 1982, Pueschel and Miller 1996). Studies on *T. testudinalis* and *T. scutum* have shown that they both prefer specific types of encrusting algae because of the structure of their radulae, though both species are able to graze on other substrates as well (Kitting 1980, Steneck 1982). Kitting (1980) reported *T. scutum* to feed occasionally on a species of *Hildenbrandia*, though it fed on another encrusting alga more because *Hildenbrandia* was too tough and caused excessive tooth wear. It is possible that *T. testudinalis* preferred *H. rubra* less because of its toughness, though this explanation is unlikely since *C. circumscriptum* is calcareous and *H. rubra* is not. Therefore, it is more likely that either *T. testudinalis* is morphologically adapted to feed on *C. circumscriptum* or that *C. circumscriptum* provides some type of dietary benefit.

The results of the five-day substrate choice experiments in the lab and several field experiments indicated that *T. testudinalis* limpets in the mid-intertidal zone do not display homing behavior (Figs. 4, 5, 16). Removal experiments showed that individuals do not return to their original location or even their original tide pool when placed in the ocean. Given the slow movement rate of this species, it was unlikely that individuals would be able to make their way back from great distances even if they did home. These removal experiments provided a baseline, showing that limpets did not return when removed from their original tide pool.

The intra-tide pool movement experiment showed conclusively that *T. testudinalis* does not display strict homing behavior, despite a previous finding to the contrary (Steneck 1982). Homing behavior has been defined by several sources as the return of an individual to a precise location on the substratum while not feeding (Steneck 1982, Santina 1993, Jakob, et al. 2001, Shanks 2002). Since the current study and others have shown that this species searches for food and feeds at night, individuals are stationary during the day. Therefore, if *T. testudinalis* did display homing behavior, individuals would be found in the exact same location during every day. In addition, if Steneck (1982) was correct in his assertion that *C. circumscriptum* was a superior holding surface for *T. testudinalis* and holding surface quality was the most important factor driving distribution, then individuals should have been found primarily on *C. circumscriptum* during the day. However, *T. testudinalis* was found to be on different substrates from one day to the next over 30% of the time, showing that individuals do not return consistently to the same substrate. Though exact location was not noted, individual limpets could not have consistently returned to a precise location each day, since they often did not even return to the same substrate.

In addition, *T. testudinalis* individuals did not return to and remain in the same  $\frac{1}{16} \text{ m}^2$  quadrat in which they were originally found (Fig. 4). There was a very low rate of return for those limpets that were moved more than 0.5 meters from the original quadrat, indicating that they did not find their way back to their previous location. This low return rate is not remarkable in itself, since homing limpets often follow a mucous trail back to their original position (Santina 1993) and these experimental individuals were manually placed in a different spot. However, even individuals that were put back in their original location moved out of the quadrat over the course of the experiment. This indicates a low level of site fidelity and does not support any form of homing behavior.

Furthermore, over 120 limpets that were not originally in the 24 experimental quadrats moved in over the course of the intra-tide pool movement experiment. This movement within the pools demonstrates that these individuals were not returning to a home site. While this movement into quadrats cleared of limpets could appear to be a density-dependent response, the movement in did not occur significantly less in controls, when no limpets were removed. In addition, many individuals that moved into the quadrats moved out again (Fig. 5), indicating that they had more likely moved in by chance than because of low limpet densities in the quadrats. These limpets from outside the quadrat switched substrates more, but not significantly more than those from inside the quadrat. This trend was possibly a result of the individuals from inside the quadrat knowing the area better and preferring to return to certain types of locations while not feeding. This form of behavior is consistent with that of *T. scutum*, which prefers to rest on rock when not feeding on encrusting algae (Kitting 1980).

Though Steneck (1982) proposed that *T. testudinalis* did not stay exclusively on *C. circumscriptum* during the day subtidally because of the rarity of this substrate and the high

density of limpets, that explanation is unlikely for the mid-intertidal zone. There was not significantly less *C. circumscriptum* in the tide pools than any other substrate, yet individual limpets commonly switched substrates from day-to-day. Furthermore, addition experiments showed that individuals found on the two species of encrusting algae switched substrates more than those on the rock. While this disparity in switching rates could be an artifact of the varying amounts of each substrate from pool to pool, it clearly demonstrates that individuals showed no consistent preference for *C. circumscriptum* during the day. Since lab experiments showed that *T. testudinalis* preferred to feed on this substrate (Figs. 11, 14), it is evident that individuals leave *C. circumscriptum* or *H. rubra* when they are not feeding. There was no consistent return to any of the different substrates during the day in the field (Figs. 4, 6), illustrating that unlike at night, there was no substrate fidelity, let alone return to a precise location on the substratum. These field experiments provided a solid base of evidence against any semblance of homing behavior by *T. testudinalis*.

The results of the field experiments with regard to homing behavior were corroborated and extended by the results of the five-day substrate choice experiments in the lab. Individuals only returned to the exact same location two times out of a possible 120 and never followed the same route back, even when they returned to a similar location (Fig. 16). This lack of fidelity is antithetical to the pattern of homing behavior, which generally involves individuals moving away from their home, feeding, and then following their mucous trail back to the original location (Steneck 1982, Santana 1993). The laboratory experiments demonstrated a significant preference by *T. testudinalis* for vertical surfaces during the day (Fig. 9), as well as for surfaces other than the two species of encrusting algae (Figs. 9, 10). Over the course of three five-day experiments with eight limpets in each, no individuals consistently returned to either of the

species of encrusting algae other than for nighttime grazing. The clear preference of every individual was to feed on *C. circumscriptum* and *H. rubra* and then return to another substrate after feeding. Though individuals did move to similar types of surfaces while not feeding, such as vertical rock or the pan, they did not return to precise locations. This type of movement pattern closely mimics that observed by Kitting (1980) in *T. scutum*, in which individuals consistently return to a substrate other than that which they feed upon, although not to the same location.

The aversion to *C. circumscriptum*, *H. rubra*, and horizontal surfaces in general during the day indicates that holding surface is not the primary factor influencing the resting site selection of *T. testudinalis* individuals. They moved to vertical surfaces significantly more than they did to horizontal surfaces during the day, with the opposite occurring at night, irrespective of substrate. Therefore, surface orientation is a more important factor than substrate in determining the type of location that individuals are likely to return to when not feeding. Though the suitability of the different substrates as holding surfaces was not investigated, this factor was clearly not an important influence on limpet distribution.

It is also unlikely that density was an important factor in determining *T. testudinalis* movement because no density-dependent interactions were observed in the five-day substrate choice experiments. No individuals stayed on *C. circumscriptum* consistently during the day, so there was no lack of availability of this substrate during the day. Since density did not appear to be a factor, it is even more unlikely that individuals avoid resting on this substrate because of the density-dependent interactions. Overall, *T. testudinalis* did return consistently to vertical surfaces during the day (Fig. 9), though not to a specific location and clearly not because of density or substrate. Non-homing behavior was shown conclusively in two different types of

field experiments (Figs. 4, 5, 6) and in many different ways in the lab (Fig. 16), making a very compelling case against *T. testudinalis* homing behavior in the mid-intertidal zone.

This study also showed that *T. testudinalis* does not display territorial behavior. The high amounts of substrate switching in the field and laboratory experiments indicated that individuals did not stay on, maintain, or defend specific areas, as has been described in some other species such as *Lottia gigantea* (Shanks 2002). The high densities on *C. circumscriptum* and *H. rubra* while limpets were feeding also illustrate a lack of territorial behavior. Individuals were often seen in proximity to one another in the field and no pushing or other territorial behavior was noted in the field or the lab.

In addition to providing conclusive evidence for substrate preference and against homing behavior in this species of limpet, the five-day substrate choice experiments also allowed for a detailed analysis of *T. testudinalis* movement. Even though there was significantly more movement during the night than the day, this difference would have been even more drastic if the first half hour of the day had been discounted. Since over half of the daytime movement occurred within the first half hour, this movement was analyzed more closely. Almost exclusively, the movements at the beginning of the day were off of the two species of encrusting algae, off of horizontal surfaces, and onto vertical surfaces (Fig. 10). This rapid movement resulted in the highest overall movement rate of the 24-hour cycle as individuals scrambled to move onto the preferred vertical surfaces. There are several possible reasons for this daytime preference for vertical surfaces, all of which will be discussed later in the context of overall movement patterns.

While movement increased dramatically at the beginning of the night, as would be expected since individuals were beginning to feed and search for food, the decline in movement

towards the end of the night was more gradual (Fig. 7). Presumably because they had eaten their fill or because they knew that daylight was coming, there was a marked decline in movement beginning around 2 AM. The continuation of this decline until daybreak indicates that *T. testudinalis* is well adapted or evolved to feed just during the nighttime hours. The spike in movement around daybreak was a result of the rapid retreat to a vertical surface by those individuals that had not done so already as the night wound down. There are a variety of possible explanations for the movement to vertical surfaces while not feeding or searching, though it is probably related to some sort of risk. Being on a vertical surface could reduce the risk of getting knocked off by waves or eaten by predators such as crabs or gulls. It is also possible that the vertical orientation exposes them less to sunlight that could heat them up too much or potentially desiccate them if they were out of the water. Either way, this behavior does not seem to vary by individual, so is likely innate. It is possible that a preference for vertical surfaces was selected for at some point in *T. testudinalis* evolutionary history or that it is advantageous at some stage of their life history.

Factors such as shell length and shell color were not found to be correlated with substrate switching or movement rate in any of the experiments. Species such as *Acmaea digitalis* and *L. gigantea* have been shown to have different behaviors based on coloration and size, respectively (Geisel 1970, Stimson 1970, Mercurio et al. 1985). Since neither coloration nor size had any effect on movement, it is likely that all the colorations and sizes of this species have similar feeding, searching and resting site preferences.

A factor that did influence feeding, searching, and movement rate was the discovery of a food source. In the five-day substrate choice experiments, individuals moved significantly and drastically less after discovering the location of either *H. rubra* or *C. circumscriptum* (Fig. 13).



This is a result of the relatively high rate of movement while searching for food compared to feeding. Individuals that had discovered a food source rarely searched, although they did leave the encrusting algae for a vertical daytime resting site. In contrast, those limpets that had found neither of the encrusting algae continued to move at a relatively quick rate until they located a potential food source (Fig. 12). This makes it likely that in the field, individuals that are in pools with low amounts of *C. circumscriptum* and *H. rubra* would move around more than those in pools with an abundance of encrusting algae. Since individuals that had already discovered *C. circumscriptum* in the lab were unlikely to explore the area and search for more food, the limpets that moved into the quadrats in the intra-tide pool movement experiments were likely individuals that were yet to discover an adequate food source. Unless shifted around by waves, it is unlikely that a limpet with sufficient access to a high-quality food source would move a great deal around the pool.

The results from the field and laboratory experiments largely corroborated each other, providing convincing evidence for nocturnal movement, a lack of homing behavior, and daytime preference for vertical surfaces by *T. testudinalis*. A movement model is put forth for this species that is characterized by low site fidelity and a preference for vertical resting sites, with a feeding preference for *C. circumscriptum*. This behavioral pattern likely reduces risk of wave-bashing or predation during the day and is solidly supported for the mid-intertidal zone of mid-coast Maine. The selection by *T. testudinalis* of impermanent resting sites that are not on the preferred food source is markedly similar to behavior displayed by *T. scutum* (Kitting 1980).

Unlike in previous studies, *T. testudinalis* was not found to home to or prefer *C. circumscriptum* while not feeding (Steneck 1982). The rank preference of different food sources is a new contribution to the body of knowledge on this species and has widespread implications.

For one, it is possible that *T. testudinalis* has evolved or adapted to feed on different substrates as the abundances of encrusting algae species fluctuate. Another possibility raised by the relatively high amounts of grazing on *H. rubra* is that *T. testudinalis* attempts to maintain a mixed diet, as does its western North American relative, *T. scutum* (Kitting 1980). By showing an inclination towards multiple food sources, it is possible that this species could avoid having an adverse impact on the amounts of different types of encrusting algae in tide pools. Limpet species have been shown to alter the algal composition of the pools in which they reside (Connell 1972, Dungan 1986, Fletcher 1987, Johnson et al., 1997), so a mixed diet could be an adaptation designed to preserve their preferred food source, *C. circumscriptum*. However, it is entirely possible that *H. rubra* is only consumed in the absence of a better alternative, making it a backup plan as algal compositions change spatially or temporally.

The preference for vertical resting sites displayed by this species is an entirely new concept that has not been shown for any other known species of limpet and warrants further investigation. This pattern has interesting implications in intertidal communities, as most species that move to a safer area move to crevices where they are more protected. Because of their shell morphology, limpets are well-suited to withstand the pounding of waves and the pull of predators such as crabs or sea stars. Therefore, a vertical surface provides *T. testudinalis* with many of the same advantages that crevices provide to other species, as it allows them to avoid severe wave bashing, exposure to the sun, and predation by gulls and crabs. This study has provided a great deal of understanding of the movement patterns and feeding preferences of *T. testudinalis*. However, there are many questions that have been raised by this work as well.

Future work on the nocturnal movement of *T. testudinalis* in the field would be an important contribution to the knowledge about this species, though nighttime work in the

intertidal zone is extremely challenging. In addition, since these experiments were conducted during the winter months, simply repeating the field experiments during the warmer summer months would provide an interesting comparison. It would also be instructive to examine the exact locations of individuals in the field from day-to-day. Photo quadrats and any type of marking were found to be impractical, so this would likely need to involve measurement and triangulation from fixed points as has been done by Gray and Naylor (1996). Long-term studies would also be useful, as they would allow researchers to see if the movement and behavior of *T. testudinalis* changes over the course of its lifetime. In the laboratory, it would be interesting to manipulate things such as the position of the light and the temperature of the water in order to determine if these factors have an impact on behavior. All of this future work would enhance the knowledge of patterns discovered by this study, notably the rank preference for a variety of food sources, nocturnal feeding behavior, and the preference for vertical resting sites by *T. testudinalis*.

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