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## Behavior and microhabitat selection of the tortoiseshell limpet *Testudinalia testudinalis* in the northwest Atlantic intertidal zone

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## ABSTRACT

*Testudinalia testudinalis*, the only species of intertidal limpet in the northwest Atlantic, feeds on the encrusting coralline alga *Clathromorphum circumscriptum*. We explored the behavior and habitat preference of this limpet in the intertidal zone of southern Maine and in laboratory experiments. We found *T. testudinalis* to be almost exclusively nocturnal, moving approximately 30-fold more during the night. This limpet did not home or display a consistent preference for any substrate as a resting site or preferred non-feeding habitat. However, they did show a significant preference for horizontal surfaces during feeding at night and vertical surfaces during the day. This behavior was observed at three intertidal sites along the Maine coast and in laboratory experiments, indicating a preference for a vertical resting site where heat stress, desiccation or predation may be less likely.

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### 1. Introduction

The tortoiseshell limpet *Testudinalia testudinalis* Müller is a common inhabitant of the rocky intertidal and subtidal zones along the northeastern coast of North America (Steneck, 1982). Like other limpet species, *T. testudinalis* is limited by desiccation (Wolcott, 1973) to the lower and mid-intertidal zones (Branch, 1981; Wallace, 1972; Williams and Morrill, 1995). These limpets are typically found in or near tide pools and are rarely seen on fully exposed rock surfaces (Wallace, 1972; pers. obs.). Though little work has focused specifically on *T. testudinalis*, these limpets are ideal study organisms because of their abundance, limited home range, and role as dominant grazers and structuring agents in marine communities (Steneck, 1982).

The existence of *T. testudinalis* in the intertidal zone demonstrates its ability to withstand the stress and environmental variability of that habitat. The physical and biotic stresses of the intertidal zone (desiccation, osmotic stress, marine and terrestrial predation) are the driving forces behind habitat selection in intertidal gastropods (Branch, 1981; Denny et al., 2006; Frank, 1965; Garrity, 1984; Gendron, 1977). These pressures force some species of limpets to select microhabitats such as crevices or vertical surfaces to avoid potentially deadly conditions (Branch et al., 1988; Frank, 1965; Garrity, 1984; Sutherland, 1970; Williams and Morrill, 1995; Wolcott, 1973).

Several limpet species respond to these stresses by homing to a specific location on the substratum when not feeding or foraging (Jakob et al., 2001; Santana, 1993; Shanks, 2002; Steneck, 1982; Villee and Groody, 1940). Tightly attaching to a home scar serves as a means of predator avoidance and protects limpets from desiccation stress and wave activity (Wallace, 1972). Species that home, such as *Patella rustica*, spend most of their time on a home scar, with short feeding excursions (Evans and Williams, 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 (Santana, 1993). This homing instinct is extremely strong in some limpet species such as *Lottia gigantea* and *P. rustica* but is weaker in others such as *Cellana toreuma*, which only displays strong site fidelity when there is a high amount of food or predation (Iwasaki, 1992).

*T. testudinalis* has been reported to display some homing behavior both in subtidal environments and in the laboratory (Steneck, 1982). However, since this species was not observed by Steneck (1982) in the intertidal zone and homing was not shown conclusively in laboratory or field studies, these findings warrant further investigation. Unlike some strictly homing limpets that create a sunken indentation in the rock, *T. testudinalis* does not make a sunken home scar (Cook et al., 1969; Hewatt, 1940). A former sister species to *T. testudinalis*, *Lottia scutum*, does not home to a precise location following feeding excursions but has been shown to return to a general area or habitat (Kitting, 1980). Kitting (1980) termed this general area a “resting site” and this same terminology will be used throughout this paper since homing has not been shown conclusively for *T. testudinalis* (Steneck, 1982).

Although *T. testudinalis* feeds on diatoms as well as several species of encrusting algae, it prefers the encrusting coralline alga *Clathromorphum*

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*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). The feeding preference for *C. circumscriptum* could play a significant role in the movement and behavioral patterns of *T. testudinalis*.

Like feeding and homing behavior, limpet movement patterns vary by species and are heavily influenced by diurnal, seasonal, interspecific and intraspecific cues. For example, most limpet species prefer to feed and search for food at high tide, when they are covered with water and thus protected against desiccation stress (Black, 1979; Branch, 1975b, 1981). However, *T. testudinalis* differs from most limpet species in that most individuals of this species live in pools and thus are submerged even at low tide (Steneck, 1982; Wallace, 1972). This behavior could lessen the influence of tides on the movement patterns of this species and could allow it to feed at both high and low tides. Light cycles also influence limpet movement, as *Patella flexuosa* moves only during the day, while *Fissurella crassa* moves exclusively at night (Branch, 1981; Serra et al., 2001).

In this contribution we explore microhabitat selection, movement, and feeding behavior of *T. testudinalis*. Specifically, we examine pool, substrate, and surface orientation preferences of this species as well as feeding preferences and movement periodicity. Use of three sites and corroborative laboratory studies allow for robust inferences on limpet habitat selection on the Maine coast as related to environmental variability and the prevailing stresses at each site. By analyzing this field and laboratory research, we describe the heretofore poorly known behavior, movement patterns, and feeding preferences that enable *T. testudinalis* to survive the challenges of the Maine intertidal zone.

## 2. Materials and methods

### 2.1. Surveys

Data on *T. testudinalis* density and resting site preference were collected at three sites along the mid-Maine coast. Pemaquid Point

(44°30'N, 69°32'W), the Outer Head and Little River Ledges of Reid State Park (43°47'N, 69°43'W), and Owl's Head State Park (44°5'N, 69°2'W) (Fig. 1) are rocky intertidal sites that support populations of *T. testudinalis*.

Surveys were conducted at all three sites in February–March 2008 during the daytime low tide. Limpet density and overall percent cover of algae and substrate were measured using line transects. Transects were extended from low water (0.0 m tidal level) to the lower barnacle/bare rock zone in the high intertidal, above the upper limit of *T. testudinalis*. High shore limits were at approximately three vertical meters above the mean low water level, though this varied widely by site and exposure.

Transect locations were randomly chosen at each site. Substrate percent cover was obtained by recording the presence and identity of rock or algae every 25 cm along the transect. The tide zone in which each point occurred as well as the presence or absence of a tide pool was recorded. Limpet densities were found by counting the number of limpets in a 30-cm wide swath along these transects perpendicular to the shoreline. Because of the difficulty of finding and accurately counting very small limpets, all surveys and experiments included only limpets greater than 5 mm in length. Individuals of this size were not very common and their abundance and behavior were not addressed in this study.

A second component of the field survey focused on the substrates ecologically relevant as either a resting surface or a food source for *T. testudinalis*. Limpet substrate choice was examined in areas of observed high limpet density ( $>48/m^2$ ) during low tide. Substrate, surface orientation (vertical or horizontal) and limpet shell color were recorded for each limpet within a  $1/16 m^2$  quadrat. Limpets were classified into one of three color categories based on the amount of white on their shell: light (71–100% white), mottled (31–70% white), and dark (0–30% white). This classification was done in order to determine whether or not habitat preference varied with limpet color. Percent cover estimates of the major substrates (rock, *C. circumscriptum*, and *Hildenbrandia rubra*) in each quadrat were also obtained. Visual estimates of percent cover were used instead of more time-consuming

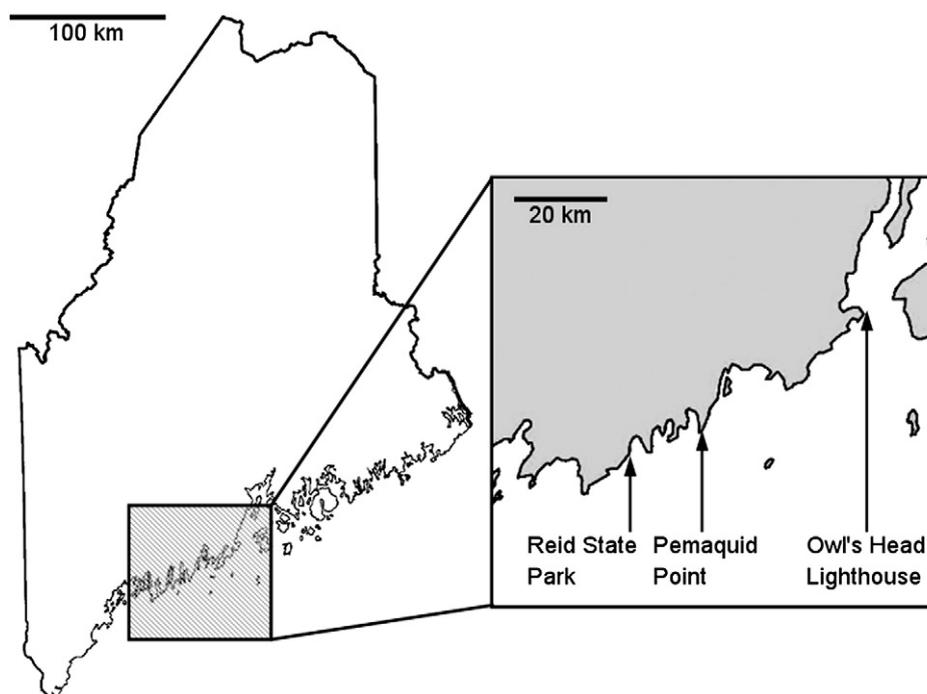


Fig. 1. Survey sites along the Maine coast at Reid State Park, Pemaquid Point, and Owl's Head Lighthouse. The full map shows all of the state of Maine, while the blowup focuses on the study sites.

methods such as a dot-quadrat, because exact percent cover was not needed and practiced visual percent cover estimates are not significantly less accurate than other methods (Dethier, 1984).

## 2.2. Field experiments

To determine in situ limpet microhabitat preference and movement patterns, several field experiments were performed in January 2008 during the daytime low tides at Pemaquid Point. Removal experiments were conducted in eight randomly chosen small ( $<1\text{ m}^2$ ) pools. All limpets in these pools were removed and labeled, then relocated to the low water level (0.0 m tidal level). Labels were permanently marked numbers cut from a vinyl sheet and super-glued to the back of the shell of each limpet. Pools were checked for the presence of marked limpets once daily for 5 days and then periodically for two more weeks.

Addition experiments were also conducted. Individual *T. testudinalis* were collected from a variety of pools and substrates at Pemaquid Point and were tagged in the lab. They were kept overnight in flowing seawater tanks at the University of Maine Darling Marine Center in Walpole, Maine, where length was measured and color was observed. Twelve small ( $<1\text{ m}^2$ ) tide pools were selected for the additions. In each pool, four of the previously collected limpets per  $1/16\text{ m}^2$  of tide pool area were placed in the center of the pool. These limpets came from each substrate (rock, *C. circumscriptum*, *H. rubra*) and surface orientation (vertical or horizontal). A control pool, in which limpets were removed, labeled, and put back in their original location, was also established. All pools were examined at daytime low tide every day for 7 days, with substrate and vertical/horizontal orientation noted each day for all numbered limpets. This was done in order to assess the fidelity of *T. testudinalis* to a specific substrate. Visual substrate and surface orientation percent cover estimates were made of these pools to accurately assess the limpets' substrate choices.

Intra-tide pool movement experiments were performed in large ( $>1\text{ m}^2$ ) pools at Pemaquid. Within each pool, between one and four  $1/16\text{ m}^2$  quadrats were placed in areas of high limpet density. Limpets in each quadrat were removed, measured, and labeled, and their original substrate was noted. Each quadrat was randomly assigned one of four treatments (control, 0 m, 0.5 m, 1 m) and the limpets 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 m outside the quadrat, respectively. A total of 24 of these experiments were conducted, six for each treatment. Quadrats were checked every day for 6 days and then periodically for two additional weeks. The number of limpets in each quadrat as well as the substrates on which they rested was recorded. In addition to labeled limpets, any unlabeled limpets that moved into a quadrat were also categorized. The quadrats used for these experiments were not permanent, but rather were  $1/16\text{ m}^2$  PVC pipe quadrats that were placed in the same location every time the experiments were checked. Exact quadrat locations were triangulated by measuring distances from two permanent marks on rocks next to each tide pool.

## 2.3. Laboratory experiments

Laboratory experiments to further explore *T. testudinalis* movement, behavior, and substrate choice were conducted in February and March 2008 in the laboratory at Colby College in Waterville, Maine. Limpets and seawater were collected from Pemaquid Point and maintained in a cold room at  $4.4\text{ }^\circ\text{C}$ . The limpets were stored in multiple five-gallon aquaria with flowing water, rocks, and lamps set for a 10/14 light/dark cycle. Five-day substrate choice experiments were conducted in this room, with pictures taken automatically every 5 min with a digital camera and The Time Machine™

photo timer. For this experiment, randomly selected limpets were placed in an artificial pool, a shallow enamel-coated pan filled with seawater. This artificial tide pool 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 (rock, *H. rubra*, *C. circumscriptum*, surface of the artificial pool). Three trials were run for 5 days each on a timed day–night light cycle.

After the trials, photos were analyzed using accurate digital marking and measuring tools in Adobe Photoshop™. Movements of every limpet were marked on the photos and then digitized, producing a track showing the detailed movements of each individual. The distance traveled and rate of movement for each individual were calculated and recorded. The following aspects of movement were computed for each limpet: (1) total distance traveled 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, and (5) movement rates before and after discovering food source. This protocol not only enabled an in-depth analysis of limpet movement and substrate choice, but also served as a more controlled and closely monitored version of the field addition experiments.

Student's t-tests were used to test for differences between two populations (different sites) as long as the data were normally distributed. Analyses of variance were used to test for differences among three or more populations, followed by pair-wise Tukey HSD tests. When the data departed from normality, Mann–Whitney *U*-tests were used instead. To test for differences in proportions, Pearson's correlation analyses were used to test for statistically significant relationships between two variables. For all statistical tests,  $p=0.05$  was used as the critical value.

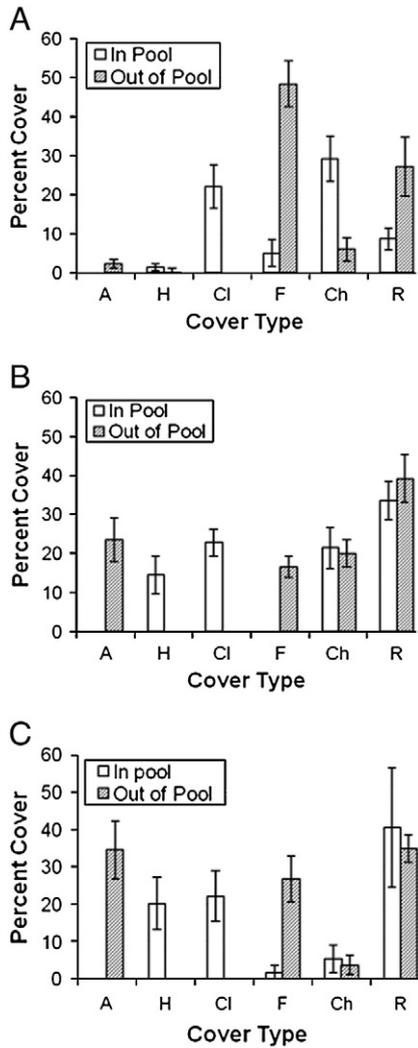
## 3. Results

### 3.1. Surveys

Based on line transect data, the overall density of *T. testudinalis* in the intertidal zone at Owl's Head Lighthouse was  $4.8\text{ limpets/m}^2$ , with a density of  $34.8/\text{m}^2$  in tide pools. At Pemaquid Point there were  $2.0\text{ limpets/m}^2$  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  $9.7/\text{m}^2$ . The predominant algae at all three sites were *Fucus distichus*, *Fucus vesiculosus*, *Ascophyllum nodosum*, and two encrusting algae, *H. rubra* and *C. circumscriptum*. There were significant differences between algal composition in tide pools and on emergent substrata (Fig. 2). While upright algae such as *Fucus* spp. and *A. nodosum* were largely found out of pools, *H. rubra*, *C. circumscriptum* and bare rock were the primary substrates in tide pools.

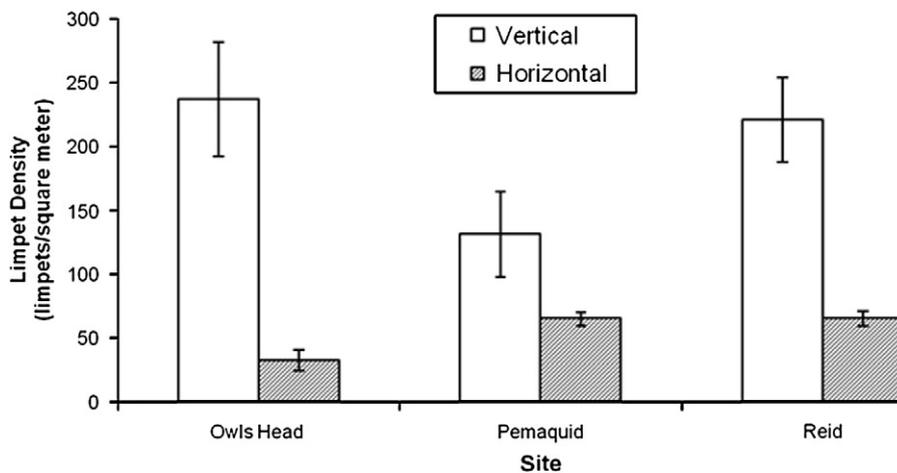
At all three sites the density of *T. testudinalis* did not differ significantly between the three predominant substrates in the tide pools: rock, *H. rubra*, and *C. circumscriptum*. Densities of *T. testudinalis* were significantly higher on vertical than horizontal surfaces at all three sites, regardless of substrate (Fig. 3). Differences in limpet density on vertical and horizontal substrata were observed during daytime low tide at Pemaquid ( $t=2.4$ ,  $df=89$ ,  $p<0.01$ ), Owl's Head ( $t=4.3$ ,  $df=59$ ,  $p<0.0001$ ), and Reid State Park ( $t=6.1$ ,  $df=44$ ,  $p<0.0001$ ).

Substrate cover and algal composition did not differ significantly between vertical and horizontal surfaces at any of the three sites. At each location, bare rock was the most common substrate on both vertical and horizontal surfaces. At Pemaquid, areas of high limpet density (surveyed with  $1/16\text{ m}^2$  quadrats,  $n=36$ ) had a significantly higher percent cover of *C. circumscriptum* (21.3%) than the same pools did overall (14.2%) (paired t-test,  $t=2.62$ ,  $df=35$ ,  $p<0.01$ ). The same was found at Reid State Park ( $n=16$ ), as areas of high limpet density had 34.3% cover of *C. circumscriptum*, while the pools overall had



**Fig. 2.** Algal and rock percent cover ( $\pm$  SE), as determined by line transect, in versus out of tide pools at (A) Reid State Park, (B) Pemaquid, and (C) Owl's Head, ME. Abbreviations: A—*A. nodosum*, H—*H. rubra*, Cl—*C. circumscriptum*, F—*Fucus* spp., Ch—*C. crispus*, and R—rock.

27.2% cover (paired t-test,  $t = -1.85$ ,  $df = 15$ ,  $p < 0.05$ ). The algal makeup at Owl's Head did not differ significantly between the high density and lower density areas within the tide pools.



**Fig. 3.** Average limpet density ( $\pm$  SE) on vertical versus horizontal surfaces at Owl's Head, Pemaquid, and Reid State Park, ME. All densities on vertical surfaces were significantly higher than horizontal surfaces.

### 3.2. Field experiments

In removal experiments conducted at Pemaquid, none of the 78 limpets that were removed from their tide pools and placed in the low intertidal returned to the original pool. To ensure the accuracy of these results, durability of the limpet tags was tested in the laboratory and the field. The tags were found to stay on even after high pressure water spraying in lab and after at least 2 months in the field.

Intra-tide pool movement experiments ( $1/16 \text{ m}^2$  removals) showed a high level of day-to-day *T. testudinialis* movement within the pools. At least 120 different unlabeled limpets moved into the  $24 \text{ } 1/16 \text{ m}^2$  quadrats for at least 1 day, an average of 5.3 per quadrat. Of the 120 limpets, 63 remained in a quadrat for more than 1 day. Since only limpets inside each quadrat were labeled at the beginning of the experiment, these unlabeled limpets had moved into the quadrat from elsewhere in the pool.

In transplant experiments, no limpets that were placed 1.0 m away from their initial location (quadrat) returned over the two-week monitoring period, but they remained in the same tide pools, so loss of tags was not a problem. Only 7.1% of *T. testudinialis* placed 0.5 m away and 10.0% of limpets placed 0.0 m away from the initial quadrat returned during the experiment. In the controls where limpets were picked up and placed exactly where they were before, 43.5% of the limpets remained in the initial quadrat over the two-week duration of the experiment. From 1 day to the next, the labeled and unlabeled limpets combined switched substrates 30.6% of the time. The number of substrate switches from day-to-day did not vary significantly based on the original substrate of each individual. Limpets originally in the quadrat were significantly more likely to remain there than individuals that moved into the quadrat over the course of the experiment ( $t_{15} = -2.08$ ,  $p < 0.05$ ).

In the addition experiments, *T. testudinialis* switched substrates from 1 day to the next a similar 29.0% of the time. There was no relationship between substrate choice or 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,  $r = 0.129$ ,  $p = 0.12$ ).

### 3.3. Laboratory experiments

Five-day behavioral experiments in artificial tide pools showed a striking diel difference in *T. testudinialis* movement and feeding behavior. Individual limpets moved significantly more during the night than the day in these trials ( $t = -4.6$ ,  $df = 46$ ,  $p < 0.0001$ ). They moved an average of 3.1% of the time during the day and 22.6% of the time during the night. 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 were analyzed for preference.

Rapid increases in activity occurred when lights went off at the beginning of the night and when they came back on in the morning, with much greater movement rates occurring at night (Fig. 4). The half-hour in which the most movement occurred was from 7:00 to 7:30 AM, which immediately followed the lights turning on and accounted for 59.9% of the movement for the entire daytime. During this time, individuals were observed to move quickly to a vertical surface. After this initial spike, movement rates were consistently low during daylight hours, with night movement rates approximately 30 times higher than those during the day, measured in distance traveled per hour (Fig. 4).

In addition to moving more at night, *T. testudinalis* individuals spent much more time on the two types of encrusting algae at night than during the day. Of the time limpets spent on *H. rubra*, 91% was during the night, with 69% of the time on *C. circumscriptum* occurring at night as well. Limpets were observed on rock 50% of the time during the day, significantly more often than they were observed on either *H. rubra* (1.4%) or *C. circumscriptum* (13.0%) (Tukey HSD,  $p < 0.05$ ). In addition, individuals stayed on vertical surfaces during the day 77% of the time, significantly more than the 18% of the time they spent on horizontal surfaces (ANOVA,  $F_{1,41} = 44.8$ ,  $p < 0.001$ ). Limpets spent significantly more time on horizontal surfaces at night (40%) than during the day (18%) (ANOVA,  $F_{1,41} = 4.7$ ,  $p < 0.04$ ).

From measurements of the distance each limpet moved every 10 min, movement rates on each substrate were calculated, with the greatest rate occurring on the surface of the artificial pool. Rates were successively lower on the rock, *H. rubra*, and *C. circumscriptum*, respectively (Fig. 5). All the differences in rates between substrates were highly significant (Mann–Whitney *U*-test, all  $p$  values  $< 0.0001$ ).

In these multiple-substrate artificial pool experiments, limpets that had discovered both *C. circumscriptum* and *H. rubra* returned to *C. circumscriptum* 100% of the time. While several limpets did feed on *H. rubra*, no individual that subsequently discovered *C. circumscriptum* returned to feed on the other species of encrusting algae. The rate of movement for individual limpets dropped significantly and drastically after the limpet discovered *C. circumscriptum* or *H. rubra* (pair-wise Mann–Whitney *U*-test,  $U_A = 11$ ,  $z = 3.2$ ,  $p < 0.001$ ).

Feeding behavior is characterized by slow movement and the sweeping back and forth of antennae, while searching movement is relatively quick, unidirectional movement. These definitions were used to identify the amount of time spent feeding versus searching for food on each of the different substrates. Slow, multidirectional

movements were classified as feeding behavior, while relatively fast, unidirectional movements were classified as searching movements. Only 1% of searching movements (over 15 days of time-lapse photos) occurred on *C. circumscriptum* and only 2% on *H. rubra*. Most of the searching (82%) occurred on the artificial pool surface, where no algae or other forms of food were present.

Over the course of the three 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 day (out of 120 opportunities) and these two individuals returned only once each.

#### 4. Discussion

Densities of *T. testudinalis* were much higher in tide pools than out at all three sites. This pattern, also observed by Wallace (1972), is different than the behavior of many other limpet species that tend to live on exposed rock surfaces (Branch, 1975a,b; Garrity, 1984; Giesel, 1970). Thermal tolerance is one of the primary determinants of habitat selection in marine organisms (Bates et al., 2005) and is likely a driving factor in the observed pattern. Because this study took place during winter, the tendency of limpets to favor pools is likely due to the avoidance of the sub-freezing air temperatures to which they would have been exposed on open rock surfaces. Limpets exposed during early-morning low tides were sometimes frozen (pers. obs.), causing death or loss of grip on the substrate. Preference by *T. testudinalis* for tide pools may also be due to the significantly higher abundance of their preferred food source, *C. circumscriptum*, in these pools (Fig. 2).

No evidence of *T. testudinalis* homing behavior was found at any of the three sites included in this study (Fig. 1) or in laboratory experiments. Homing has been defined by several sources as the return of an individual to a precise location on the substratum while not feeding (Jakob et al., 2001; Santina, 1993; Shanks, 2002; Steneck, 1982). Because the current study and others have shown that this species moves and feeds at night (Fig. 4), individuals are stationary during the day. Therefore, if *T. testudinalis* did display homing behavior, individuals should be found in the exact same location each day. However, only two of 120 limpets returned to the same location 2 days in a row in the artificial tide pool experiment. In addition, transplant experiments showed that *T. testudinalis* individuals did not return to and remain in the same 1/16 m<sup>2</sup> quadrat in which they were initially found. The low return rate is not

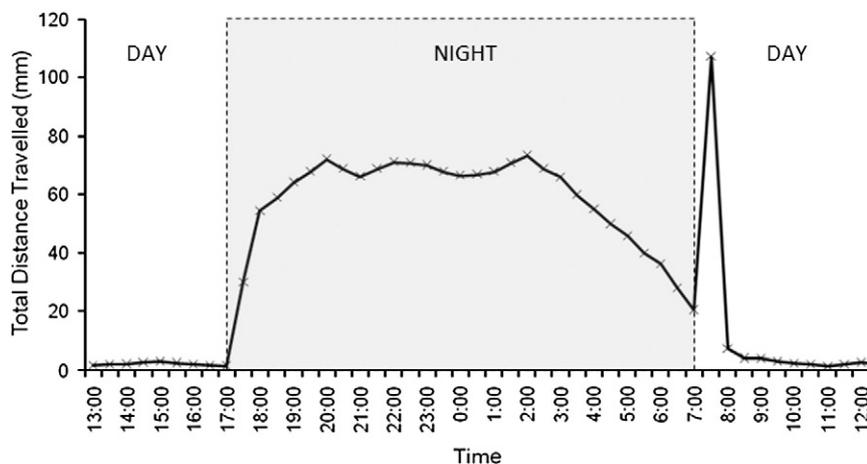
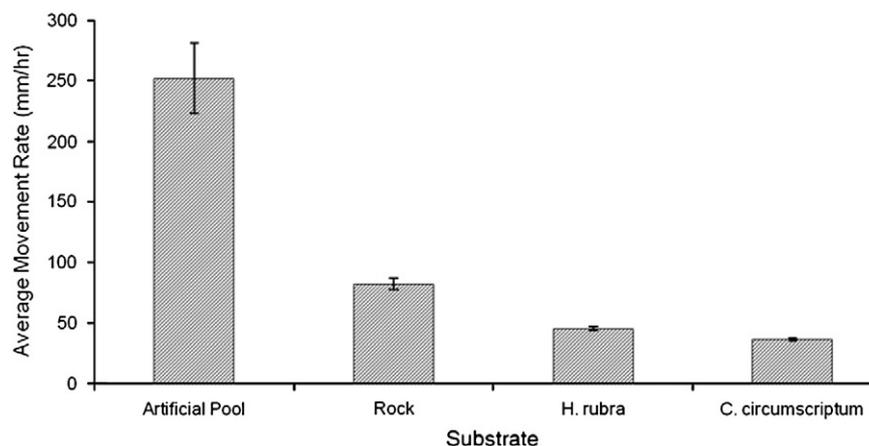


Fig. 4. Average amount of movement of individual limpets over a 24-hour cycle (divided into half hour increments). Each point is the average distance traveled by 24 limpets each day for 5 days ( $N = 120$ ). Movement distances are consistently low during the day with the exception of a spike immediately after the lights came on at 7 AM. Since the same limpets were used 5 nights in a row, this graph highlights obvious movement patterns but does not draw statistical comparisons with error bars. Day–night movement was statistically analyzed separately in the text of the results.



**Fig. 5.** 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.

remarkable in itself, since homing limpets follow mucous trails back to their original position (Santina, 1993) and these experimental individuals were moved manually. However, 55% of limpets that were not moved still left the quadrat over the course of the experiment, while different unmarked limpets moved in and out of the quadrats each day. These results indicate a low level of site fidelity and do not support any form of homing behavior.

The lack of homing by intertidal *T. testudinialis* is further supported by the amount of substrate switching that occurred between days. Individuals were found to be on different substrates from 1 day to the next 30% of the time in intra-tide pool movement experiments and 29% of the time in addition experiments. This pattern illustrates that these limpets do not return consistently to the same substrate as a resting site and thus could not have returned to the same precise location every day. Previous studies have suggested that *C. circumscriptum* is the preferred holding surface for *T. testudinialis* because of its consistently smooth, planar surface (Dethier and Steneck, 2001; Steneck, 1982). If holding surface quality was the most important factor driving substrate selection, individuals should have been found primarily on *C. circumscriptum* during the day. However, *T. testudinialis* showed no significant preference for any substrate as a resting site at any of the three sites in this study or in the laboratory experiments. This finding seemingly contradicts the work by Steneck (1982), who found limpets to reside in the highest density on *C. circumscriptum*. However, Steneck's work was mostly subtidal, where *T. testudinialis* may exhibit major differences in behavior.

Steneck (1982) proposed that limpets in the subtidal zone did not always remain on *C. circumscriptum* because of the low abundance of this substrate and the high density of limpets. However, this conclusion does not apply to the mid-intertidal zone, since *T. testudinialis* did not display any resting site preference, despite an abundance of *C. circumscriptum*. *C. circumscriptum* was the preferred food source of *T. testudinialis*, followed by *H. rubra* and then bare rock, as indicated by slow feeding movements in the artificial tide pool experiments (Fig. 5). This species of limpet has evolved to feed on *C. circumscriptum* (Steneck, 1982) and its radular morphology is well equipped for dealing with this calcareous crust, but *H. rubra* appears to be a less attractive but viable alternative food source. Since feeding occurs on these substrates at night, it is clear that many limpets leave the encrusting algae during the day when they select a resting site. Limpets in the field did not return to a precise location on the substratum or display significant substrate fidelity, indicating a total lack of homing behavior by *T. testudinialis*.

Despite the lack of homing behavior or resting site substrate preference, limpets at all three sites and in laboratory experiments were found at higher densities on vertical than horizontal surfaces (Fig. 3). This pattern was observed despite the fact that percent cover

of each substrate did not differ between the two surface orientations, indicating that the observed preference is indeed for the vertical orientation. Preference for vertical surfaces has been shown in gastropods (Garrity, 1984) including other limpet species such as *Cellana grata* (Williams and Morritt, 1995). Limpets that are on exposed surfaces in the field lose water more quickly on horizontal surfaces than on vertical surfaces or in crevices (Williams and Morritt, 1995). Solar heating, which increases the temperature of exposed surfaces and the internal temperature of individual limpets, is one explanation for the tendency of limpets to rest on shaded vertical surfaces (Denny et al., 2006). However, this species of limpet occurs mostly in tide pools, where desiccation is not a factor and temperature fluctuations are not as extreme as on exposed substrata. Therefore, the preference of *T. testudinialis* for vertical surfaces is probably not a result of desiccation or extreme temperature avoidance and is more likely due to other risk factors such as predation or wave action.

Most limpet species are preyed upon by birds such as gulls or oystercatchers (Frank, 1965; Giesel, 1970; Wootton, 1992), sea stars (Feder, 1963; Hewatt, 1937), crabs (Lowell, 1986) and predatory fishes (Parry, 1982). Gulls (Steneck, pers. comm.) and sea stars of the genus *Asterias* (Steneck, 1990) are known to feed on *T. testudinialis*, and crab and fish predation are likely as well. Residence on vertical surfaces 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). With a vertical resting site, limpets are able to decrease their visibility to visual predators as well as prevent birds and crabs from achieving an efficient angle of attack. Selection of vertical surfaces by *T. testudinialis* to avoid visual predators could also explain the lack of preference for vertical surfaces during the nighttime when visual predators would not be a risk. The vertical resting site allows limpets to avoid predation during the day when they are not moving and the nearby food source minimizes the amount of energy spent foraging and feeding during the night.

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