

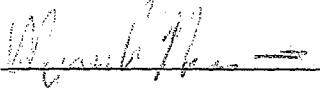
**Periwinkle Behavioral Modifications
Across a Wave-Exposure Gradient**

A Senior Project
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Advisor:



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Abstract

The physical forces associated with wave-swept intertidal shores are known to affect many aspects of an organism's ecology. Common periwinkles, *Littorina littorea*, on exposed shorelines travel less distance in periods between low tides than individuals on protected shorelines. This appears to be a plastic response to the increased probability of dislodgement associated with higher water velocities, as individuals transplanted to an exposed site moved less distance than individuals translated to a protected site. The distance an individual traveled did not correlate with individual size nor with location in the intertidal.

Introduction

The intertidal zone of wave-swept shores was one of the first environments to be scientifically scrutinized in the fields of marine biology and ecology due to its accessibility and to the highly visible zonation of plants and animals. The vertical zonation of intertidal areas is generically characterized by kelps and algae in the lower intertidal, mussels and snail grazers in intermediate areas, and barnacles in the highest point of the intertidal. This zonation also varies along a horizontal exposure gradient, with protected shores exhibiting highly different zonation patterns than exposed shores. Species composition (Menge 1976; Bertness 1999), species distribution (Hamilton 1978; Garrity 1984), and habitat utilization (Kohn and Leviten 1976; Gendron 1977; Raffaelli and Hughes 1978; Atkinson and Newbury 1984), are all clearly affected by wave-forces, as mussels and barnacles dominate wave-exposed shores while grazers and predators are limited to the protective confines of cracks and crevices. Organism morphology (Trussell *et al.* 1993; Vermeij 1972; Boulding and Van Alstyne 1993; Denny *et al.* 1985; Boulding *et al.* 1999) and life history characteristics (Etter 1989) are also known to be affected by the physical forces of a wave-swept environment.

Despite this large body of research, very few studies have looked at the possible behavioral adaptations of intertidal organisms in response to hydrodynamic forces. While many intertidal

organisms are sessile with few options for behavioral modifications, motile organisms can alter their location or tenacity in order to cope with wave stresses. Distribution differences of motile organisms in protected and exposed shorelines are obviously the result of modified behaviors or are an indication of differential survival. This investigation will examine *Littorina littorea* movement behavior modification in wave-swept and protected shores on the rocky intertidal coasts of Maine.

Littorina littorea, the common periwinkle, is a widely distributed herbivorous periwinkle found in most intertidal environments, from salt marshes and mud flats to the rocky intertidal. It is one of the most abundant motile organisms on the New England rocky shoreline, moving throughout the intertidal and subtidal to forage. There is no evidence that periwinkles home to specific scars and crevices in the substrate which is a behavior present in limpets (Cook *et al.* 1969; Raffaelli and Hughes 1976) although work done by Gendron (1977) revealed that *L. littorea* uses waves as an orientational cue. *Littorina littorea* distribution is clearly effected by wave forces as periwinkles are widely distributed at protected sites but are primarily found in cracks and crevices at exposed sites (Kohn and Leviten 1976; Garrity 1984; Boulding and Van Alstyne 1993; Trussell *et al.* 1993; Kidder 2001). *Littorina spp.* transplanted from a crevice to a horizontal rock face or area of high flow are easily dislodged (Boulding and Van Alstyne 1993) illustrating the importance of protective habitat on wave swept shores. Theory developed by Denny *et al.* (1985) reveals that the size-independent probability for dislodgment increases when organisms are actively moving. Boulding and Van Alstyne (1993) reported that gastropods placed in a flow tank remained still at very high water velocities. These findings suggest that stationary individuals can tolerate much higher water velocities than non-stationary individuals,

therefore, gastropods constantly exposed to high water velocities on exposed shorelines should be restricted to time periods when it is mechanically safe to move, while protected shores have larger windows of opportunity. While there is a lot of data demonstrating the increased risk of dislodgment when actively moving or when caught outside of a natural refuge, no studies have looked to see if this risk results in behavioral adaptations.

Research has also shown that wave-swept shores are characterized by periwinkles which attain smaller overall sizes than individuals on protected shores (Denny *et. al* 1985; Boulding and Van Alstyne 1993; Boulding *et. al* 1999) possibly due to the hydrodynamic stresses experienced by large individuals. Large periwinkles experience increased lift and drag coefficients which correspond to an increased risk of dislodgement over smaller periwinkles. It follows that large individuals may have their movement restricted to protective microhabitat, i.e. cracks and crevices, which lessen the effects of wave forces, and this habitat limitation may subsequently result in less distance traveled when compared to smaller individuals. This investigation also looked at distance traveled as a function of individual size in protected versus exposed environments.

In addition to examining trends between sites, I also examined the effects of submersion time on movement behavior of *L. littorea*. Desiccation has repeatedly been shown to be a stress on intertidal organisms (Kohn and Leviten 1976; Garrity 1984). *L. littorea* is active when wet or washed by rising and falling tides, but when dry, it retreats into its shell, seals off its operculum to retain moisture, and attaches itself to the substrate with a small amount of mucus (Vermeij 1972). Increased time out of water should limit the movement of an individual periwinkle and

this was examined by documenting distances moved at low intertidal areas and high intertidal areas.

By examining behavior modification on protected and exposed shorelines, the relationship between individual size and distance moved, and the effects of submersion time on distance moved – a combination of behavioral data, ecological data, and experimentation – I hope to develop a better understanding of the mechanical stresses on *L. littorea* and the resulting behavioral adaptations.

Methodology

This study was conducted along the shores of Mt. Desert Island, ME during the spring of 2001. Data was collected in April and May at several locations throughout the island that experience differing amounts of wave action. There were four study sites, two in areas protected from high wave action and two in high wave action areas. COA Beach (COA) and Indian Point (IP) are located on the Northern side of the island (Fig.1) in protected harbors and bays which experience low wave energy. In comparison, Otter Cliffs (OC) and Great Head (GH) are located on the eastern side of the island and are directly exposed to swell from the Gulf of Maine and the North Atlantic (Fig.1). The tides are mixed semi-diurnal and data was gathered during low tides. All sites could be characterized as rocky intertidal, but low wave action areas contained smaller rocks and cobble which were absent from high wave action areas.

Differences in exposure between sites was quantified by deploying plaster of Paris discs in the intertidal and measuring the percent of weight remaining due to dissolution. Dissolution of plaster of Paris indicates total water motion (Coyer and Whitman 1990) and plaster discs were

placed in each site for 24 hours (modification of Denny 1988). Plaster discs were made in paper cups with ice-fishing line coming through a small hole in the bottom of the cup and out the top. The dried plaster discs were weighed and then tied to the substrate in the intertidal at similar tidal heights. They were recollected during the next low tide, allowed to dry for four days and subsequently weighed again. Three discs were deployed at each site, although only 2 were recovered at Indian Point. It should be noted that these measurements were not quantified against a control but rather the dissolution rate was used to indicate differences between sites.

The study organism, *L. littorea*, was present in all study sites. To document the distance of gastropod travel over 24 hours, specific individuals were marked, their positions documented, and subsequent positions were recorded 24 hours later. Individual periwinkles were chosen haphazardly and nail polish was used to write an identifying number on the shell (Coyer and Witman 1990). The diameter of each periwinkle, corresponding to the longest linear dimension, was measured to a tenth of a millimeter using calipers. Periwinkles were not removed from the substrate during these procedures so as not to disturb behavioral patterns. Positions were recorded by setting up an axis line in the field and the Cartesian coordinate system was used to obtain a position for each individual. Thin, plastic knitting cord, approximately 1 meter in length, served as the physical axis and was oriented parallel to the tide line. The cord was tied or taped to the substrate and its beginning and end points were marked on the substrate with nail polish or paint. This allowed the cord to be replaced in the same position when the site was revisited 24 hours later to document periwinkle movement over time. Four samples were taken from each site, two high tide samples and two low tide samples. Each sample contained 20

marked snails giving a total of 80 marked snails at each site and approximately 320 snails marked at all 4 sites combined.

Once initial and subsequent coordinates for individual periwinkles were obtained, the Pythagorean Theorem was applied, giving the shortest distance traveled between the two points. Periwinkles may not have taken the shortest, most direct path between their two positions and this may be a source of error; however, as the same technique was applied to all sampled individuals, the consistency in sampling should eliminate substantial error.

Tag loss was quantified by marking 20 haphazardly chosen periwinkles and placing them in buckets for 24 hours in the intertidal and recovering the bucket at low tide. One bucket sample was placed in the lower intertidal and one bucket sample was placed in the high intertidal. The thin plastic buckets had slits along the top, bottom, and sides allowing water to flow in and out with the rising and falling tides. This mimicked natural conditions but kept the periwinkles contained so that tag loss could be documented.

One transplant experiment was performed to document the effects of wave forces on periwinkles between 10 and 20 cm in diameter. Sixty periwinkles were collected haphazardly from an intermediate area of Otter Cliffs. Thirty were marked and released further down the beach in a semi-protected area and 30 were marked and released in a highly exposed area on the other side of the cliffs. The distances they traveled over 24 hours was recorded using the previously described methodology. This transplant was performed to determine if periwinkles had immediate plastic behavioral responses when placed in more exposed environments.

Results

There was a significant difference among sites in the amount of plaster remaining on wave-exposure discs (ANOVA: $F_{(18,8)} = 23.58$, $p < 0.002$; Fig. 2). The sites chosen significantly differ in their degree of exposure and differ from each other when comparing dissolution rates of plaster discs. The amount of plaster remaining at protected sites was lower than the amount of plaster remaining at exposed sites (Bonferroni post hoc; COA and IP, $p = 1$; OC and GH, $p = 1$) illustrating that these sites are accurate relative representations of protected and exposed environments.

The distances periwinkles traveled differed among sites (ANOVA: $F_{(6,23)} = 20.44$, $p < 0.001$; Fig 3). Periwinkles from protected sites traveled significantly farther over 24 hours than periwinkles from wave-exposed sites ($\bar{x} = 79.2$ cm and 81.3 cm at the two protected sites, $\bar{x} = 23.4$ cm and 30.9 cm at the two exposed sites; Table 1). Periwinkle movement was not different between the two protected sites nor between the two exposed sites (Tukey post hoc; COA and IP, $p = 1$; OC and GH, $p = 1$).

Snails transplanted to the extremely exposed area moved significantly less distance than those transplanted to a more protected site ($t = 9.108$, $p < 0.001$). The mean distance traveled of snails transplanted to the semi-protected shore was 124.5 cm while snails transplanted to the exposed shore traveled less than one-sixth of this distance, $\bar{x} = 17.916$ cm.

Experiments quantifying tag loss showed that approximately 25% of tags were lost or damaged between the time when snails were initially tagged and the time when the distances they had traveled were measured. Approximately 56% of tagged snails were recovered, although

significantly more were recovered from exposed sites than from protected sites (Pearson chi-square, $\chi^2 = 12.545$, $p < 0.001$).

No correlation was found between periwinkle size and distance moved at three of the four sites (COA $r_s = 0.139$, $p > 0.05$; IP $r_s = -0.056$, $p > 0.05$; GH $r_s = 0.276$, $p > 0.05$). Individual size did appear to appear to be related to distance moved at Otter Cliffs (OC (r_s) = 0.426, $p < 0.05$) but it is not a strong relationship and size and distance are not correlated when sites are analyzed together (Pearson; $r = -0.048$, $p > 0.05$) There was extreme variation in the distance individuals moved (Fig. 4) giving a high standard deviation (SD = 92.544). Larger periwinkles do not move greater distances due to their larger size, nor did they move shorter distances, which was another possibility since their increased size theoretically increases the probability of dislodgement.

There was also no difference found in movement of periwinkles located in the low intertidal and periwinkles located in the high intertidal. Converse to what would be expected, the mean distance traveled by periwinkles in the high intertidal was greater ($x = 71.5$) than the mean distance of periwinkle travel in the low intertidal ($x = 55.48$); however, data were not significantly different ($t = 1.49$, $p > 0.05$). Longer submergence time does not result in greater distance traveled.

Discussion

Intertidal organisms on wave-exposed shores experience hydrodynamic forces which effect numerous aspects of their ecology. Motile organisms can modify behavior as a means of adapting to these stresses. Periwinkles on exposed shores exhibit such behavioral adaptations, moving less distance than periwinkles on protected shores. This finding is in agreement with the

literature where gastropods on exposed shorelines are known to be mainly found in cracks and crevices or other natural refuges. Kohn and Leviten (1976) increased the density and species composition of gastropods by drilling holes into the substrate of, illustrating the importance of protective microhabitat in tropical areas. Evidence suggests that snails exhibit randomized movement patterns and therefore encounter natural refuges by chance (Raffaelli and Hughes 1978). Snails traveling out of a protective refuge may not encounter another crevice before the tide returns and will be at greater risk of dislodgement due to wave action. Dislodgement probability also increases when snails are moving, and theoretical work done by Denny *et al.* (1985) shows that an actively moving snail cannot withstand water velocities greater than 5 m/s. Therefore, snails on exposed shorelines, where water velocities are often above 5 m/s, are movement restricted whereas snails on protected shores have more opportunity to move due to the lower water velocities.

Snails experience an increased risk of dislodgment on exposed shores due to large hydrodynamic forces. It has also been shown that snails on wave-exposed shores mature earlier and attain smaller overall size (Denny *et al.* 1985; Boulding and Van Alstyne 1993; Boulding *et al.* 1999), evidence that wave-exposure differentially effects small and large periwinkles. Both larger snails and snails at wave-exposed environments experience greater hydrodynamically induced dislodgement forces, but while this study found a correlation between distance moved and exposure of sample site, no correlation was found between size and distance moved. Size may not be a determinate of distance moved due to the fact that snail tenacity is already extremely low, and even the smallest individuals are unable to withstand the direct force of a

breaking wave (Denny *et al.* 1985). This appears to be the case as all size classes of periwinkles on exposed shores are found only in protective microhabitat where wave forces are lessened.

Only one transplant was performed but differences between snails transplanted to the exposed site and snails transplanted to the more protected site were readily apparent. Both groups of snails were taken from the same area yet those transplanted to the exposed site moved less distance. This indicates that distance moved is a plastic response to specific aspects of the site and is not an ingrained trait specific to populations of snails living in varying degrees of wave-exposed environments.

Fifty- six percent of tagged snails were recovered on subsequent visits to sample sites; 295 snails were tagged, 166 were recovered for distance data. Approximately 25% of snails not recovered can be attributed to tag loss or damage and the remaining amount were most likely not recoverable due to snails taking refuge in inaccessible places. The distances periwinkles traveled differed among sites (ANOVA: $F_{(6,23)} = 20.44$, $p < 0.001$; Fig 3). The distances periwinkles traveled differed among sites (ANOVA: $F_{(6,23)} = 20.44$, $p < 0.001$; Fig 3). More snails were recovered from exposed sites (66%) than protected sites (47%). This difference in recovery rate at exposed and protected shores may be due to the fact that periwinkles on protected shores were traveling greater distances and this greater dispersal hindered recovery efforts. Therefore, estimates of distance traveled on protected shores may be a conservative estimate and a higher recovery rate may have only reinforced results.

Intertidal ecology literature often cites dessication as one of the main stresses on an intertidal organism, a stress that intensifies with distance away from the mean tide line.

Periwinkles located in the high intertidal would be more likely to suffer from dessication due to

decreased submergence time. Garrity (1984) showed that gastropods exhibit behavioral adaptations to cope with heat stress and it would follow that a periwinkle could retain moisture by withdrawing into its shell and spending less time actively moving. However, the periwinkles in this study did not exhibit such behaviors as no correlation was found between the height the snail was located in the intertidal and distance moved. This finding is contradictory to what literature predicts, but many previous desiccation studies have taken place in the tropics where high temperatures are much more extreme and would consequently pose more of a problem. Desiccation may not be an important stress on intertidal organisms on the Maine coast during the months of April through May as temperatures are still fairly moderate. Desiccation may be more critical factor during the summer months.

Previous studies on the effects of wave-forces on gastropods have focused primarily on morphological adaptations and habitat preference. Although habitat preference indicates a behavioral adaptation, little attention has been paid to the behaviors which allow for this preference. Field data indicates that periwinkles move less distance in wave-exposed environments when compared to periwinkles in more protected environments and that this is a plastic response. It was already known that actively moving snails and snails located away from protective refuges risk a greater chance of dislodgement and this study offers evidence that these risks are reflected in periwinkle behavior. This reinforces the notion that wave-forces have profound impacts on intertidal organisms. Denny (1988) noted that the predatory sea star, *Pisaster ochraceus*, is prohibited from moving about due to dislodgement risk (Quinn 1979 as cited in Denny 1988) and that this pattern is very likely to exist in snails as well. This study

shows this to be the case and these modified behaviors likely affect other aspects of intertidal communities, such as predator/prey interactions and grazing intensity near crevices.

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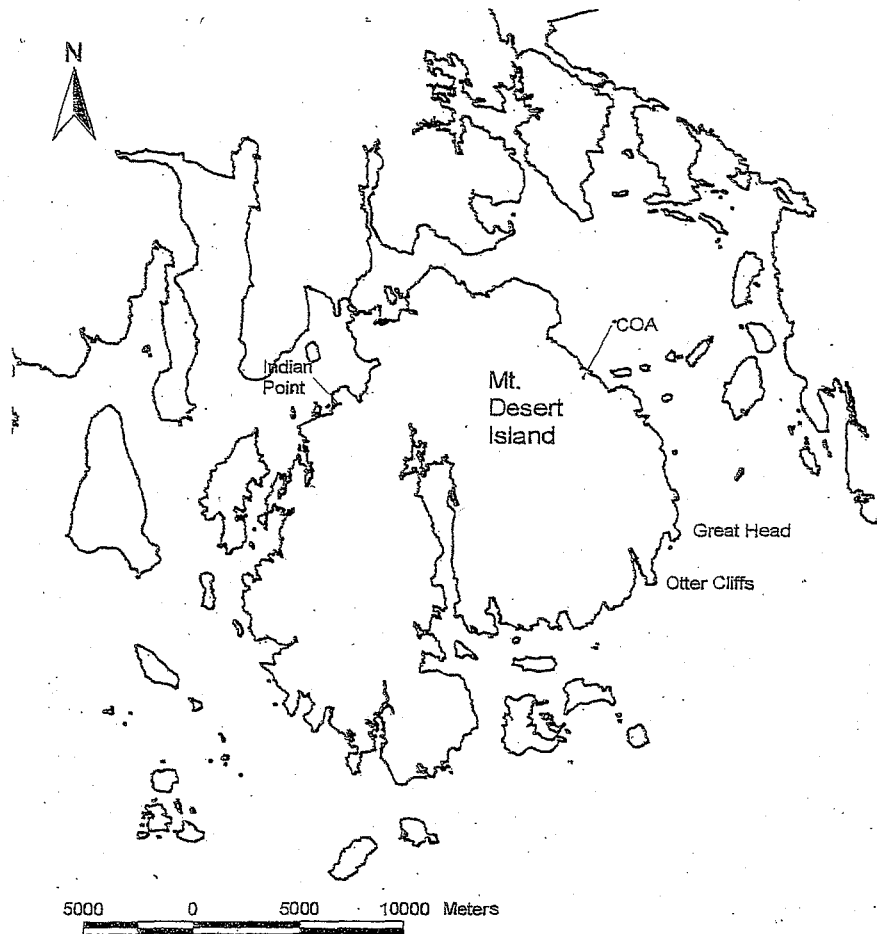


Figure 1. Location of four sample sites on Mt. Desert Island. COA and Indian Point are protected sites, Otter Cliffs and Great Head are exposed sites.

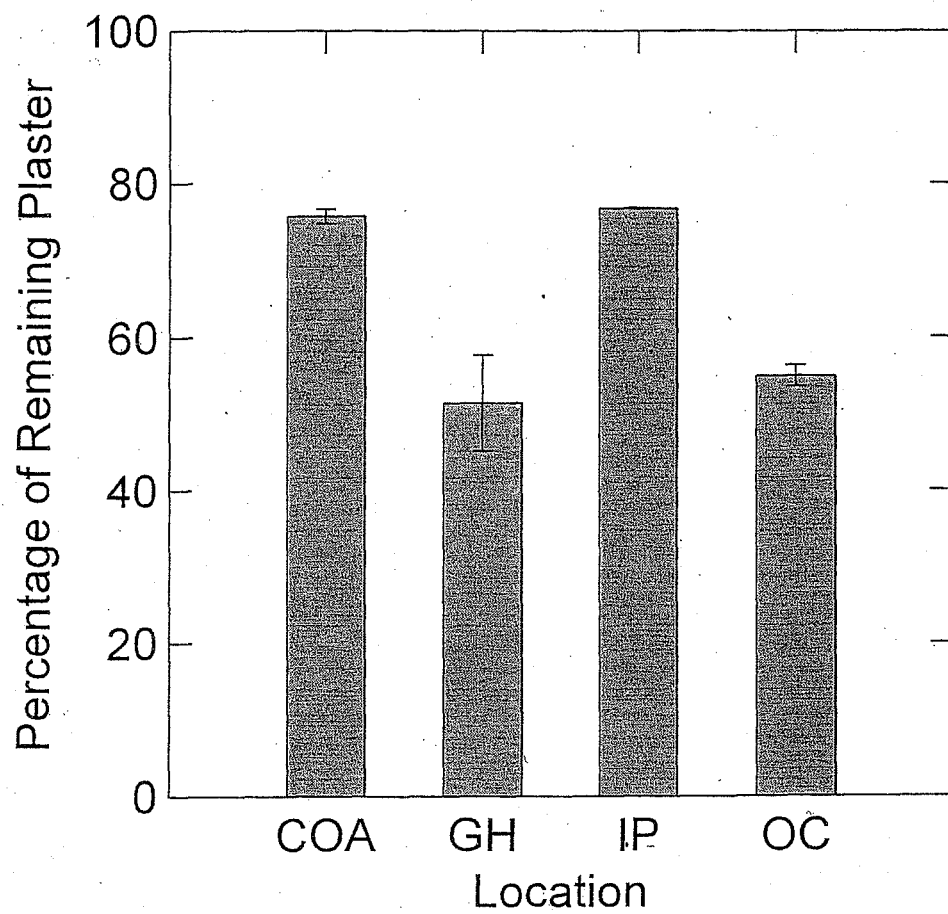


Figure 2. Mean remaining percentage of plaster discs, indicating total water motion. Only two discs were recovered from Indian Point so there is no standard error bar ($SE = \pm 1$). Protected sites have significantly more plaster remaining than exposed sites.

Table 1. Descriptive statistics for distance of periwinkle movement over 24 hours at four sample sites.

	COA	Indian Point	Otter Cliffs	Great Head
N of cases	49	26	35	56
Minimum Distance (cm)	1.443	14.206	1.562	1.442
Maximum Distance (cm)	241.924	214.223	81.022	151.327
Mean Distance (cm)	79.290	81.390	23.493	30.909
Standard Dev (cm)	61.800	50.547	20.818	25.104

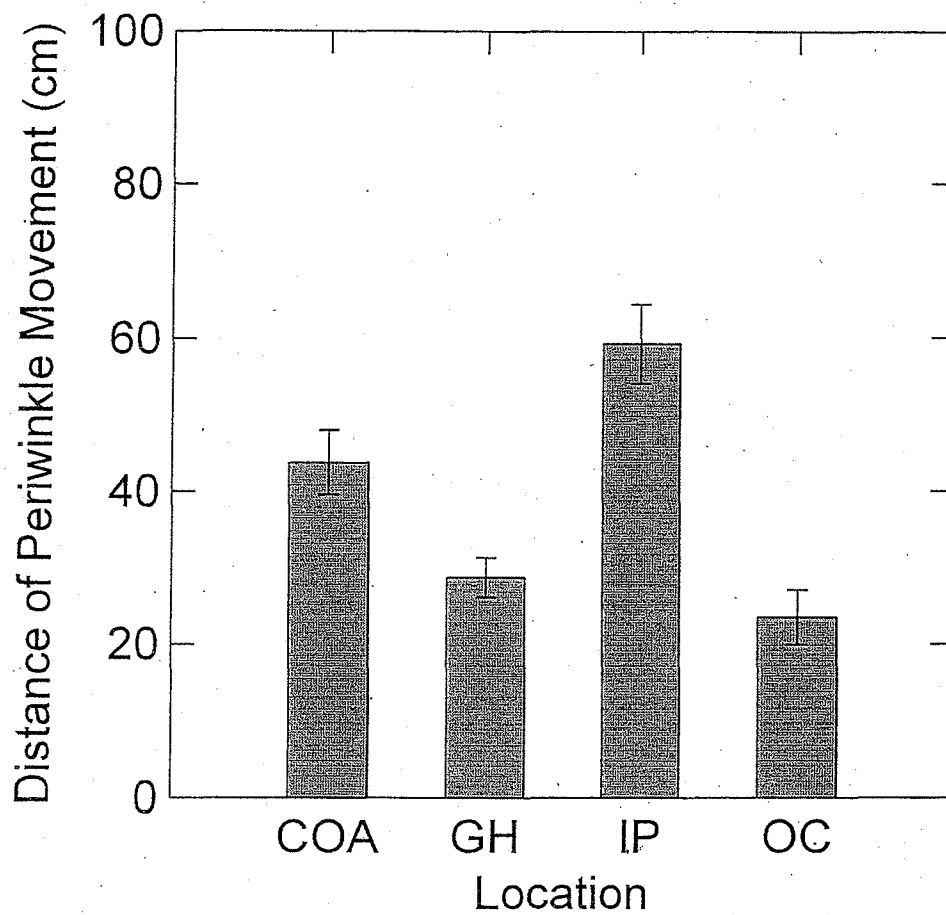


Figure 3. Mean distance traveled by individual periwinkles at four sample sites. Individuals traveled significantly farther in protected sites than exposed sites.

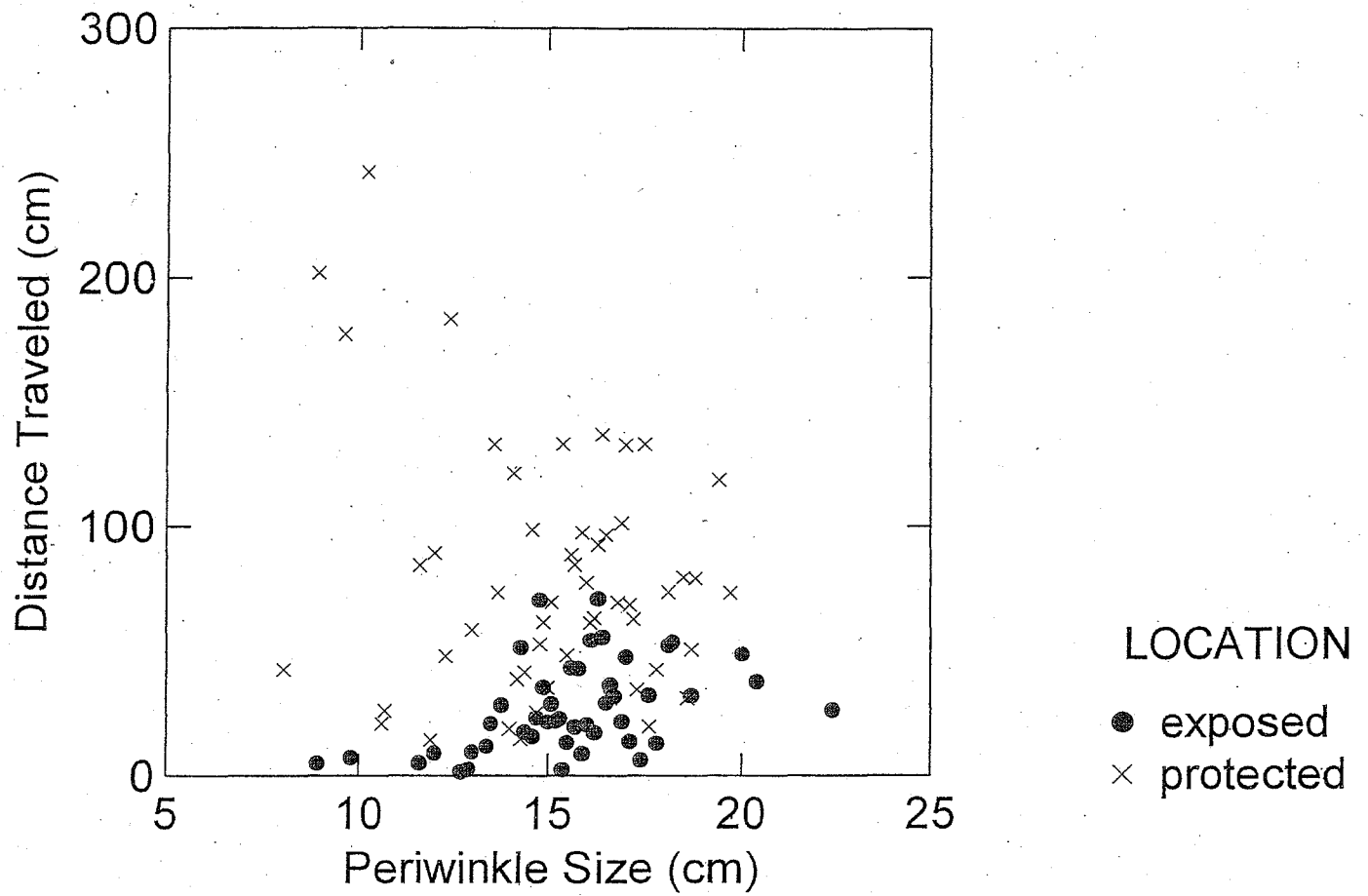


Figure 4. Individual size versus distance traveled at all sample sites. There was not a strong correlation between size and distance traveled although the pattern of distance traveled in exposed versus protected sites can be seen.