Shell Selection Behavior of the Hermit Crab, *Pagurus longicarpus*

Julie M. Giannelli

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Arts in Biological Sciences

Central Connecticut State University

New Britain, Connecticut

May 2004

Thesis Advisor

Dr. Jeremiah Jarrett

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Abstract

Hermit crabs are marine crustaceans that must inhabit empty gastropod shells for shelter and protection from predation, desiccation and osmotic stress. In New England, the hermit crab (*Pagurus longicarpus*) commonly occupies two different types of gastropod shells: the mud snail (*Nassarius obsoletus*) and the periwinkle (*Littorina littorea*). We conducted several laboratory experiments in which we examined the preference of hermit crabs for intact and damaged shells of the mud snail (*N. obsoletus*) and of the periwinkle (*L. littorea*). Our results suggest that the hermit crab, *Pagurus longicarpus*, does not show a preference for shells of either snail species when offered shells of similarly adequate size but that *P. longicarpus* strongly avoids damaged shells of either species when given a choice of an adequately sized, damaged shell of one species and an adequately sized, intact shell of the alternative snail species. In addition, hermit crabs chose shells of smaller than adequate size when given a choice of damaged adequately sized shells and smaller, intact shells of the mud snail (*N. obsoletus*).

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Finally, I would like to dedicate this thesis writing to my mother, Maureen, who passed away in the midst of my research and whose courage was and will always be an inspiration to me.

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Introduction

Hermit crabs are common crustaceans (Childress, 1972), existing in almost all marine environments around the world (Vermeij, 1977; Hazlett, 1981). Specifically, they are classified in the infraorder Anomura of the order Decapoda in the subphylum Crustacea (Hazlett, 1981). Hermit crabs are not true crabs and can be differentiated from true crabs by their reduced rear legs (Hazlett, 1981). All of the 700 plus species of hermit crabs lack calcification of the exoskeleton of their lower abdomen, leaving them vulnerable to predatory attack (Angel, 2000). This trait drives them to seek a protective shelter which, in almost all cases, is a gastropod shell (Hazlett, 1981; Angel, 2000; Barnes, 2003). The empty shells of gastropods, which are univalved molluscs whose shells are typically coiled at the apex, are suitable shelters as they provide the hermit crab with a hard, protective mobile shelter (Haas, 1950; Cote et al., 1998).

The hermit crab, *Pagurus longicarpus*, exists from Nova Scotia to Texas and Florida, inhabiting the intertidal range of the marine environment and congregating in areas of shallow water (Angel, 2000; Pechenik and Lewis, 2000). Hermit crabs are omnivorous scavengers usually feeding on scraps of food on the ocean floor but are also capable of filter feeding (Allee and Douglas, 1945; Reese, 1969; Kurta, 1982; Ruesink, 1998). *P. longicarpus* is gray in color, has an enlarged right cheliped, and has a soft, coiled abdomen with reduced appendages. Their abdomen is twisted asymmetrically and their small abdominal appendages are modified to allow them to hold onto the inside of the gastropod shell. *P. longicarpus* is one of the most abundant hermit crabs in Atlantic waters and, in New England, most often occupies shells of two different types: the mud snail, *Nassarius obsoletus* and the periwinkle, *Littorina littorea* (Williams, 1984).

Gastropod shells provide effective protection to hermit crabs from environmental factors such as osmotic stress, desiccation and water turbulence and biotic threats including competition and predation (Fotheringham, 1976; Bertness, 1981e; Pechenik and Lewis, 2000; Garcia and Mantelatyo, 2001). Hermit crabs have thus evolved to become specialized in their shell selection behavior and seek the optimal shell (Bertness, 1981b; Lively, 1988; Pechenik and Lewis, 2000). Characteristics that define the optimal shell vary among species and habitats (Pechenik and Lewis, 2000). However, an optimally sized shell for *Pagurus longicarpus* can be defined as the shell that is the preferred size and shape for an individual hermit crab of a specific size. Both in the laboratory and field, *P. longicarpus* discriminates among shells when searching for the best fitting shell (Pechenik and Lewis, 2000). In studies done with several species of hermit crab that use the same species of shell, shell size, aperture length and width, weight, internal volume and shell condition all influence choice of shell (Garcia and Mantelatyo, 2001). Shells that offer greater internal volume, or are deepest, provide the greatest protection from both predators and desiccation (Lively, 1988). Deeper shells also allow hermit crabs to retract all body parts into the shell and away from danger (Lively, 1988). Shells that are too small can leave walking legs and chelipeds exposed. The exposed hermit crab is at high risk from predation, as the predator is more able to pull the hermit crab out of its shelter (Angel, 2000). Studies in the laboratory reveal that shells that do not fit properly expose hermit crabs to greater risk of predation (Angel, 2000). Small shells also reduce brood space for females; therefore, decreasing fecundity (Vance, 1972a; Asakura, 1995). At the other extreme, larger shells may be disadvantageous because they are heavier and more energetically costly to the hermit crab when they are carried. Heavy shells may reduce a crab's mobility and therefore limit food access and possibly decrease reproductive opportunities (Fotheringham, 1976). These factors are almost irrelevant as large shells are rare in nature (Asakura, 1995; Garcia and Mantelatyo, 2001). All but very small empty shells are uncommon in the field (Vance, 1972b; Asakura, 1995).

In addition to shell size and weight, overall shell integrity influences a hermit crab's choice of shell. Predators of gastropods (i.e., moon snails) attack their prey by creating a drill hole in the snail's shell (Pechenik and Lewis, 2000). This empty shell, now available for hermit crab occupation, is generally avoided if intact shells are available. The drill hole weakens the shells, making breakage by predators easier, and allows small carnivorous worms to enter a shell more easily (Pechenik and Lewis, 2000; Pechenik et al., 2001). The hole may also increase chances of desiccation and eviction by another hermit crab (Pechenik and Lewis, 2000). The hermit crab, *Pagurus longicarpus* avoided drilled shells of the periwinkle *Littorina littorea* when presented with the choice of an optimally sized intact shell and optimally sized shell with a drill hole (Pechenik and Lewis, 2000; Pechenik et al., 2001). This avoidance is demonstrated in the field where shells with drill holes are utilized significantly less often than their availability (Pechenik and Lewis, 2000). Thus the activity of predatory snails can significantly change the dynamics of a population of hermit crabs. The competition for intact shells is very high, therefore predatory gastropods increase competition for shells (Bach et al., 1976; Bertness, 1981c; Pechenik and Lewis, 2000). Interestingly, shells that are damaged in other ways (cracked aperture, apex broken off) are not avoided (Pechenik and Lewis, 2000).

As stated, optimally sized, intact, empty shells are the limiting factor in most habitats suitable for hermit crabs. This factor modifies hermit crab behavior, leading populations to evolve towards aggressive action (Vance, 1972a; Fotheringham, 1976). Competition for the ideal shell can be severe and finding or fighting for the best shell is opportunistic (Fotheringham, 1976; Dowds and Elwood, 1983; Leite et al., 1998; Pechenik and Lewis, 2000). Since hermit crabs grow continuously, they are constantly searching for gastropod shells that are larger to better accommodate their increasing size (Reese, 1969; Barnes, 2003). In addition, shells also start to weaken over time and need to be replaced (LaBarbear and Merz, 1992).

In some hermit crab habitats there may be three or four gastropod shell species for hermit crabs to choose from (Hazlett, 1981). Certain species of hermit crabs favor particular species of shells while some hermit crab species simply favor shells that are the most abundant (Reese, 1969; Garcia and Mantelatyo, 2001). *Pagurus samuelis* and *P. granosimanus* are two species of hermit crab that show different preferences for shell species in the lab than in the field (Garcia and Mantelatyo, 2001). The shell species preferred in the laboratory was not available in the field or was not as abundant as the shell species that was selected in the field. Thus, hermit crabs can demonstrate behavioral plasticity when faced with a limited selection of shell species (Garcia and Mantelatyo, 2001).

In New England, the shell choices for the hermit crab, *Pagurus longicarpus* are not extensive. The most abundant gastropod shells available for shelter are the periwinkle, *Littorina littorea*, and the mud snail, *Nassarius obsoletus*. There are sites that contain exclusively periwinkle shells or mud snail shells depending on habitat type (personal observation). In addition, some sites have shells of both species available.

Pagurus longicarpus favors *Littorina littorea* shells that are intact and are of optimal size and weight (Angel, 2000; Pechenik and Lewis, 2000; Pechenik et al., 2001). When these shells are not available in the field they will choose damaged, drilled and suboptimal periwinkle shells for protection (Pechenik and Lewis, 2000; Angel, 2000; Pechenik et al., 2001). In areas of New England where mud snails are the predominate gastropod, there is the obvious tendency for hermit crabs to inhabit mud snail shells as they are most abundant. What is not known is if mud snail shells are chosen based on the same characteristics that periwinkle shells are chosen. Furthermore, it is not known if choice of shell, *Nassarius obsoletus* or *L. littorea*, is due to hermit crab preferences or simply due to the varying availability of shells of the two species.

I examined the shell characteristics that influence *Pagurus longicarpus* choice of mud snail shells and investigated the shell species (periwinkle or mud snail) preference of *P. longicarpus* in the laboratory.

Research Methods

Collection of hermit crabs

The hermit crab, *Pagurus longicarpus,* was collected from various sites in New England, including Scituate, MA, New Haven, CT, Madison, CT, and Point Judith, RI. Crabs were collected haphazardly with no preference given to sex or species of shell inhabited. All hermit crabs were placed in 20 L aquaria (1.2 μm filtered seawater, 20^{o} C). Living mud snails (*Nassarius obsoletus*) and periwinkles (*Littorina littorea*) of various sizes were also collected in the same areas that the hermit crabs were collected. In the laboratory, snails of both species were boiled to facilitate removal before using the shells in experiments. For all experiments, sample sizes varied depending on the successful extraction of hermit crabs from their shells. Replicate experiments were conducted on different dates and so are presented as Experiment A, Experiment B, etc.

Relationship between hermit crab mass and mud snail shell size (Shell Adequacy Index)

Optimal shell fit for the mud snail shells was determined by recording shell characteristics in relation to hermit crab mass. Fifty-one hermit crabs were extracted from the shells they were collected in and placed in a 10 L aquarium (1.2 μm filtered seawater, 20^{o} C). Hermit crabs were then given a choice of approximately 100 empty mud snail shells of various sizes. Two days later the hermit crabs were re-sampled, removed from the shells they selected and the following information was recorded: hermit crab mass (mg), internal shell volume (ml), shell mass (mg), shell length (mm) and aperture width (mm). Crab and shell mass were measured to the nearest 0.1 mg. Shell length, aperture length, and aperture width were all measured to the nearest 0.1 mm using calipers. Internal volume was measured by adding approximately 15 ml of deionized water to a 25 ml graduated cylinder and submerging a shell with the internal cavity filled with wax. After recording the change in volume, the wax was removed and the shell resubmerged to get a second measurement. The second measurement was subtracted from the first to determine the internal shell volume. Least squares linear regression was used to determine that aperture length and internal volume were the best predictors of the mass of the inhabiting hermit crab (Figure 1). With this information, I was then able to estimate the optimal mud snail shell for a given size hermit crab (shell adequacy index = 1.0) as well as estimate the optimal shell size for a crab of ¾ (a shell adequacy index of 0.75) and ½ (a shell adequacy index of 0.5) the mass of the given crab (Angel, 2000).

Selection between optimal and suboptimal mud snail shells

Hermit crabs were given the choice between mud snail shells of optimal size (shell adequacy index = 1.0) and a suboptimal mud snail shell of one of the following indexes: 0.25, 0.50, and 0.75. Although the research focused on suboptimal shells smaller than the optimally sized shell, one experiment examined the response by crabs to suboptimal shells that were larger than optimal size but only with shells with an index of 1.50. For each index, hermit crabs were gently removed from their shells, blotted dry with a paper towel and weighed to the nearest 0.1 mg. The hermit crabs were placed in individual 500 ml plastic cups filled with approximately 300 ml of seawater (room temperature ≈ 23° C; 12L:12D) containing two shells, an optimal shell (shell adequacy index = 1.0) and either a 0.25, 0.50, 0.75 or 1.50 index shell, based on the hermit crab's mass. Shell choice was recorded after 24 hours of exposure to both shells.

Selection between intact mud snail shells and mud snail shells with drill holes

Hermit crabs were given a choice of either a 1.0, 0.75, 0.50 or 0.25 intact mud snail shell or an optimally (shell adequacy index = 1.0) sized damaged mud snail shell to determine if hermit crabs avoid shells with drill holes. Holes of approximately 3.5 mm diameter (approximately equal to the diameter of a predators drill hole) were drilled near the lower right side of each shell's aperture (Figure 1).

For each index, hermit crabs were gently removed from their shells, blotted dry and weighed to the nearest 0.1 mg. The hermit crabs were placed in individual 500 ml plastic cups filled with approximately 300 ml of seawater (room temperature ≈ 23°C; 12L:12D) containing two choices of shells, an intact shell and a shell with a drill hole. The various shell indexes (0.25, 0.50, 0.75 and 1.50) were used based on the hermit crab's weight. Shell choice was recorded after 24 hours of exposure to both shells.

Mud snail shells versus periwinkle shells

Hermit crabs were presented with an optimally sized mud snail shell and an optimally sized periwinkle shell to determine if there is any shell species preference. Hermit crabs were gently removed from their shells, blotted dry and weighed to the nearest 0.1 mg. The hermit crabs were placed in individual 500 ml plastic cups that were filled with approximately 300 ml of seawater (room temperature ≈ 23°C; 12L:12D) containing two choices of shells, a 1.0 periwinkle shell and a 1.0 mud snail shell, based on the hermit crab's weight. In all three experiments shell mass was used as the shell adequacy indicator for periwinkle shells and shell internal volume was used as the shell adequacy indicator for mud snail shells based on regression models suggesting that these parameters best determine the optimal size shell for each species (Figures 2 & 3). Shell choice was recorded after 24 hours of exposure to both shells.

To determine if shell species preference is influenced by shell damage, hermit crabs were presented with an intact, optimally sized shell of one species and a damaged, optimally sized shell of the other species.

Data Analysis

The data collected for this research were analyzed using the chi-square significance test (Zar, 1999). The chi-square statistical test was used to determine if hermit crabs shell selection was due to chance.

Results

Selection between optimally (1.0) and suboptimally (0.75, 0.50, 0.25 & 1.50) sized mud snail shells

In general, *Pagurus longicarpus* preferred optimal (1.0) mud snail shells to smaller, suboptimal shells.

Optimal (1.0) versus suboptimal (0.75)

Hermit crabs showed a significant preference for optimal (1.0) mud snail shells, when given suboptimal (0.75) shells as an alternate choice. Thirty-one of thirty-nine hermit crabs (79%) chose the optimal (1.0) shell ($\chi^2 = 13.56$, p = 0.001) (Figure 4).

Optimal (1.0) versus suboptimal (0.50)

When given a choice between optimal (1.0) and suboptimal (0.50) shells, thirty-four of forty (85%) hermit crabs chose the optimal (1.0) shell ($\chi^2 = 19.60$, p = 0.001) (Figure 5).

Optimal (1.0) versus suboptimal (0.25)

Hermit crabs showed a significant preference for optimal (1.0) mud snail shells in one of two replicate experiments where the alternate shell was a 0.25 suboptimal shell. In Experiment A, seventeen of nineteen hermit crabs (89%) chose the optimal (1.0) shell while in Experiment B, twelve of seventeen hermit crabs (70.5%) also chose optimal (1.0) shells over suboptimal (0.25) shells but this difference was not statistically significant ($\chi^2 = 2.88$, p = 0.10) (Figure 6).

Optimal (1.0) versus suboptimal (1.50)

Hermit crabs showed no preference when given a choice between optimal (1.0) and suboptimal (1.50) mud snail shells in either replicate experiment. In Experiment A, only nine of twenty hermit crabs chose the optimal (1.0) shell ($\chi^2 = 0.20$, $p = 0.90$). Seven of eighteen hermit crabs chose the optimal (1.0) shell ($\chi^2 = 0.88$, $p = 0.90$) in Experiment B, (Figure 7).

Selection between intact and damaged mud snail shells

Overall, *Pagurus longicarpus* preferred intact mud snail shells to damaged shells. Intact and optimal (1.0) shells were chosen more often over intact and suboptimal (0.75, 0.50 or 0.25) mud snail shells.

Intact and optimal (1.0) versus damaged and optimal (1.0)

Hermit crabs preferred intact and optimal (1.0) mud snail shells to damaged optimally sized shells in both replicate experiments. In Experiment A, fourteen of nineteen (74%) hermit crabs chose intact and optimal (1.0) shells ($\chi^2 = 4.26$, $p = 0.01$) while eighteen of nineteen (93%) hermit crabs chose the intact and optimal (1.0) shell in Experiment B ($\chi^2 = 15.2$, $p = 0.001$) (Figure 8).

Intact and suboptimal (0.75) versus damaged and optimal (1.0)

In Experiment A sixteen of nineteen hermit crabs (84.2%) chose the intact suboptimal (0.75) mud snail shells to the damaged optimally sized shells ($\chi^2 = 8.89$, $p = 0.005$) (Figure 9). In Experiment B, although fourteen of twenty (79%) hermit crabs chose intact and suboptimal (0.75) mud snail shells over the damaged and optimal (1.0) shells, this difference was not statistically significant ($\chi^2 = 3.20$, $p = 0.10$).

Intact and suboptimal (0.50) versus damaged and optimal (1.0)

Hermit crabs showed no preference for either intact and suboptimal (0.50) or damaged and optimal (1.0) mud snail shells in two replicate experiments. Twelve of twenty hermit crabs (60%) chose intact and suboptimal (0.50) mud snail shells over damaged and optimal (1.0) mud snail shells in experiment A ($\chi^2 = 0.05$, $p = 0.90$) while in experiment B, ten of nineteen hermit crabs (53%) chose the intact and suboptimal (0.50) mud snail shells over the damaged and optimal (1.0) shell ($\chi^2 = 0.80$, $p = 0.90$) (Figure 10).

Intact and suboptimal (0.25) versus damaged and optimal (1.0)

Hermit crabs showed no significant preference for intact and suboptimal (0.25) or damaged and optimal (1.0) mud snail shells. Twelve of twenty hermit crabs (60%) chose the intact and suboptimal (0.25) shell while eight chose the damaged and optimal (1.0) shells ($\chi^2 = 0.80$, $p = 0.90$) (Figure 11).

Selection between periwinkle and mud snail shells

Optimal (1.0) periwinkle shells versus optimal (1.0) mud snail shells

Hermit crabs showed no significant preference for periwinkle shells or mud snail shells in three replicate experiments ($\chi^2 = 0.39$, $p = 0.90$) ($\chi^2 = 1.80$, $p = 0.10$) ($\chi^2 = 3.50$, $p = 0.10$) (Figure 12).

Intact and optimal (1.0) periwinkle shells versus damaged and optimal (1.0) mud snail shells

Hermit crabs preferred intact and optimal (1.0) periwinkle shells over damaged and optimal (1.0) mud snail shells in two replicate experiments. Eight of eight (100%) hermit crabs choose intact and optimal (1.0) periwinkle shells over damaged and optimal (1.0) mud snail shells in experiment A ($\chi^2 = 8.0$, $p = 0.005$). In Experiment B, nineteen of twenty hermit crabs (95%) chose the intact and optimal (1.0) periwinkle shells over the damaged and optimal (1.0) mud snail shells ($\chi^2 = 16.2$, $p = 0.001$) (Figure 13).

Damaged and optimal (1.0) periwinkle shells versus intact and optimal (1.0) mud snail shells

Hermit crabs preferred intact and optimal (1.0) mud snail shells over damaged and optimal (1.0) periwinkle shells in both experiments. Seventeen of twenty hermit crabs (85%) selected intact and optimal (1.0) mud snail shells over damaged and optimal (1.0) periwinkle shells in experiment A ($\chi^2 = 9.8$, $p = 0.005$). In Experiment B, all ten hermit crabs selected intact and optimal (1.0) mud snail shells over damaged and optimal (1.0) periwinkle shells ($\chi^2 = 10.0$, $p = 0.005$) (Figure 14).

Discussion

This study reports results of experiments designed to examine mud snail shell preferences with regard to size and quality of shell and to determine if *Pagurus longicarpus* shows a preference for shells of either periwinkles or mud snails. Recent studies have focused on periwinkle (*Littorina littorea*) shell utilization of *P. longicarpus* and have revealed that selection of periwinkle shells by *P. longicarpus* is size specific and that *P. longicarpus* prefer non-damaged shells (Angel, 2000; Pechenik and Lewis, 2000; Pechenik et al., 2001). Although *P. longicarpus* also routinely inhabit shells of the mud snail*, Nassarius obsoletus*, the degree of preference, if any, for shells of either snail species has not been reported.

Furthermore, little is known of the selection behavior of *P. longicarpus* in response to mud snail shells.

This study reveals that hermit crabs (*Pagurus longicarpus*) exhibit size specificity in choice of mud snail shells and that they avoid shells that are less than optimal size. These results are consistent with previous studies of *P. longicarpus* preferences using *Littorina littorea* shells. Hermit crabs did not discriminate between intact shells of optimal size (1.0) and shells larger than optimal size (1.50).

Hermit crabs in this study also preferred intact mud snail shells over damaged (drill hole) mud snail shells. In all experiments, greater than 50% of the hermit crabs chose intact shells over the alternative drilled shells. A significant preference was found when hermit crabs were given choices of intact optimal (1.0) and damaged optimal (1.0) or intact suboptimal (0.75) and damaged optimal (1.0).

These results suggest that there may be some critical shell size threshold below which hermit crabs will select damaged, optimally sized shells over intact suboptimal shells. Interestingly, even at shell sizes of 0.25, more hermit crabs still choose intact suboptimal shells (0.25) over damaged optimal (1.0) shells.

If shell size and quality are the most important shell selection factors influencing hermit crab shell utilization there must be a limiting factor keeping hermit crabs from occupying these ideal shelters in nature, as hermit crabs are often found in damaged and/or suboptimal shells. The most prominent factor affecting shell utilization in the field is shell supply (Vance, 1972b). A decreased amount of shells available in a community not only affects what shells are being utilized but also population size (Bertness, 1981e). In most communities, large shells are quickly taken by the males who grow faster (Harvey, 1990; Asakura, 1995). The medium size shells are the least common but most likely the optimal shell sought (Asakura, 1995). What determines shell supply is habitat and the biology of the gastropod species that inhabit the area (Busato et al., 1998). Predators influence shell supply by damaging the shells and making them either unavailable for use or unpopular (Busato et al., 1998). The importance of shell supply is apparent, since when shell availability increases so does reproduction, population density, and growth rate of hermit crabs (Bertness, 1981e; Mesce, 1982). A positive relationship between shell supply and hermit crab population size was found in Puget Sound (Bertness, 1981e).

With the supply of ideal shells being limited, inter and intraspecific competition for the shells that are optimal must be high. Competition can be manifested in shell fighting, resource distribution or niche separation (Bach et al., 1976). Hermit crabs fight for shells, use different shells than other species or spatially distribute themselves to eliminate the need for shell fighting. As hermit crabs spread themselves out, the proportion of fights decided by physical contact are reduced (Hazlett, 1968). *Pagurus longicarpus* occupies the sub-littoral zone where other hermit crabs species do not exist. For example, the larger flat claw hermit crab *P. pollicaris* prefers sandier areas (Grant, 1963). Therefore, interspecific competition is essentially nonexistent. Competition among conspecifics can be severe depending on the supply of shells available in the particular habitat (Bertness, 1981e). The benefit gained by competing for and obtaining a suitable shell is better protection, which directly influences growth and reproduction. In highly populated areas the benefit of competing exceeds the cost. Costs of competing are injury, death and high energy expenditure (Bertness, 1981e).

In this study, hermit crabs showed no preference for optimally sized shells over shells that were larger than optimal. The benefits of having a large shell are resistance to predation, thermal stress and desiccation stress (Bertness, 1981a,b). Large shell size can increase the chances of rearing a large clutch and, therefore, increase fecundity although crabs that have large shells tend to put more energy into growth while crabs in smaller shells concentrate on reproductive success (Bertness, 1981b,d). It is possible that choice of larger shell is linked to sex. In nature, male hermit crabs grow larger so they can compete for shells with more success. Gaining access to larger shells gives them security in obtaining access to reproducing females (Asakura, 1995). Larger shells are also selected when molting is occurring or about to occur (Wada et al., 1997). Large shells entering a hermit crab community tend to pass through the population rather quickly with larger crabs landing the best shells within two to four days (Bertness, 1981a). The large shells are a retreat from predators and are a definite benefit if they can be obtained in nature (Lively, 1988). Vance (1972a) found that hermit crabs in small shells were preyed upon first in fifteen out of sixteen trials. The downside to the pursuit of large shells is that they are heavy and can pose a greater energy deficit to the occupant. Large shells are also very rare in nature (Vance, 1972a; Asakura, 1995). Hermit crab populations can compensate for this dearth by delaying growth and reproducing more frequently. The high reproductive output increases the population and with small shells being the most abundant the offspring are able to find a shelter with relative ease (Bertness, 1981b). A population can be affected by the number of vacant shells that are of optimal size, therefore adapting with high reproductive output and decreased growth rate is advantageous (Asukura, 1995).

Predation, physical stresses, competition, population density and shell supply are all selective pressures influencing hermit crab shell choice. All of the above selection pressures affect shell utilization patterns (Bertness, 1981c). The types of shells that are inhabited might point to a particular selective force. For example, a hermit crab under duress from desiccation will be less choosy and perhaps select a small shell. While a hermit crab may choose a large shell if there is a high predation risk (Cote et al., 1998). The type of shell that a hermit crab ultimately chooses reflects an evaluation in ever-shifting priorities.

Pagurus longicarpus showed a tendency to prefer intact shells over damaged shells under laboratory conditions even when the intact shell was smaller than optimal size (0.75). However, no preference was shown when given choice of damaged optimal and either intact 0.50 or intact 0.25 shells. Hermit crabs must weigh the costs and benefits of inhabiting an intact but suboptimally sized shell versus a damaged but optimally sized shell. Damaged shells are abundant in the field (personal observation) so this laboratory choice is most likely a common choice in nature. Damaged shells should be avoided as they increase predation risk, osmotic stress and the chance of eviction by a competitor (Pechenik and Lewis, 2000; Pechenick et al., 2001). Shell quality also affects growth and reproduction. Relating this information back to the field, we know that *P. longicarpus* prefers shells that are intact and of optimal size but these shells are not always available. Hermit crabs not finding their ideal shell will choose shells that are either damaged, too large or too small (suboptimal) or a combination of damaged and suboptimal. Thus, shell selection is greatly influenced by the availability of intact, optimally sized shells at specific locations.

Pagurus longicarpus showed no preference for shell species when given the choice of optimally sized periwinkle (*Littorina littorea*) shells and optimally sized mud snail (*Nassarius obsoletus*) shells. However, hermit crabs consistently chose intact shells over damaged shells, regardless of shell species.

This study provides evidence that shell selection by *Pagurus longicarpus* is influenced by shell size and the degree of damage. This study also demonstrates how hermit crabs have become the ubiquitous creatures they are. Hermit crabs are able to live and prosper in different habitats due to their adaptability in choosing the shells that offer them protection and survival. It is possible that hermit crabs choose a species of shell over another based on the availability in the habitat they are in. Hermit crabs collected for this study were from different locations yet they all prefer shells based on specific size threshold and shell integrity. The results also showed hermit crabs have no preference for shell species. Also, in the field hermit crabs occupy the species of shell that is found in the area they inhabit (personal observation). However, Worcester and Gaines (1997) found that settling larvae of *Pagurus* species have definite shell species preferences and this influences shell utilization as adults. The long-lived planktonic larvae are able to disperse over extensive distances and settle in the most suitable area (Folino and Yund, 1998; Pessani and Chiara, 1998). Perhaps juveniles do prefer a particular species but that was not tested in this research. In contrast, Turra and Leite (2002) noted that the size of the shell directs the size of the crab that will inhabit it and not the species of shell. It seems that as the shell is the limiting resource in a community, occupying the optimal species, size and quality shell would be a luxury permitted only after a shelter of any sort is found. Cote et al. (1998) observed that hermit crabs under stress spent less time investigating shells before occupying them. Hermit crabs are able to assess size and quality of shell using tactile clues relatively quickly (Briffa and Elwood, 2000, 2001). Experiments examining shell species selection as a function of age/size and experiments examining the influence of predator presence on shell species selection would provide useful information.

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Figure 1: Mud snail shell (A) and periwinkle shell (B) with drill holes.

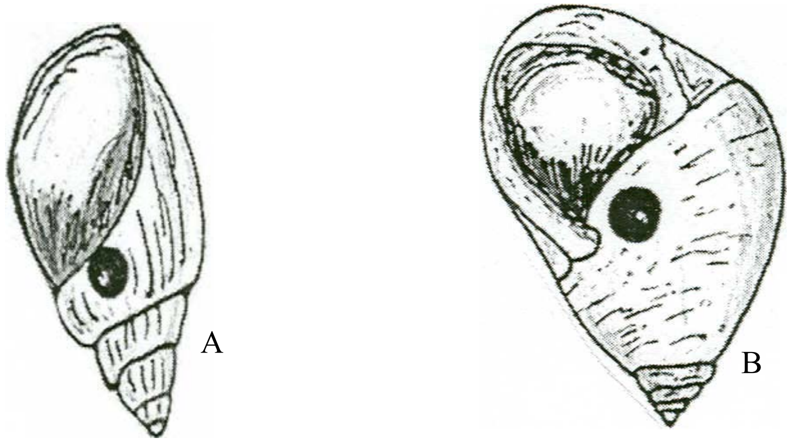


Figure 2: Regression graph for mud snail shells. Aperture length as a function of hermit crab mass.

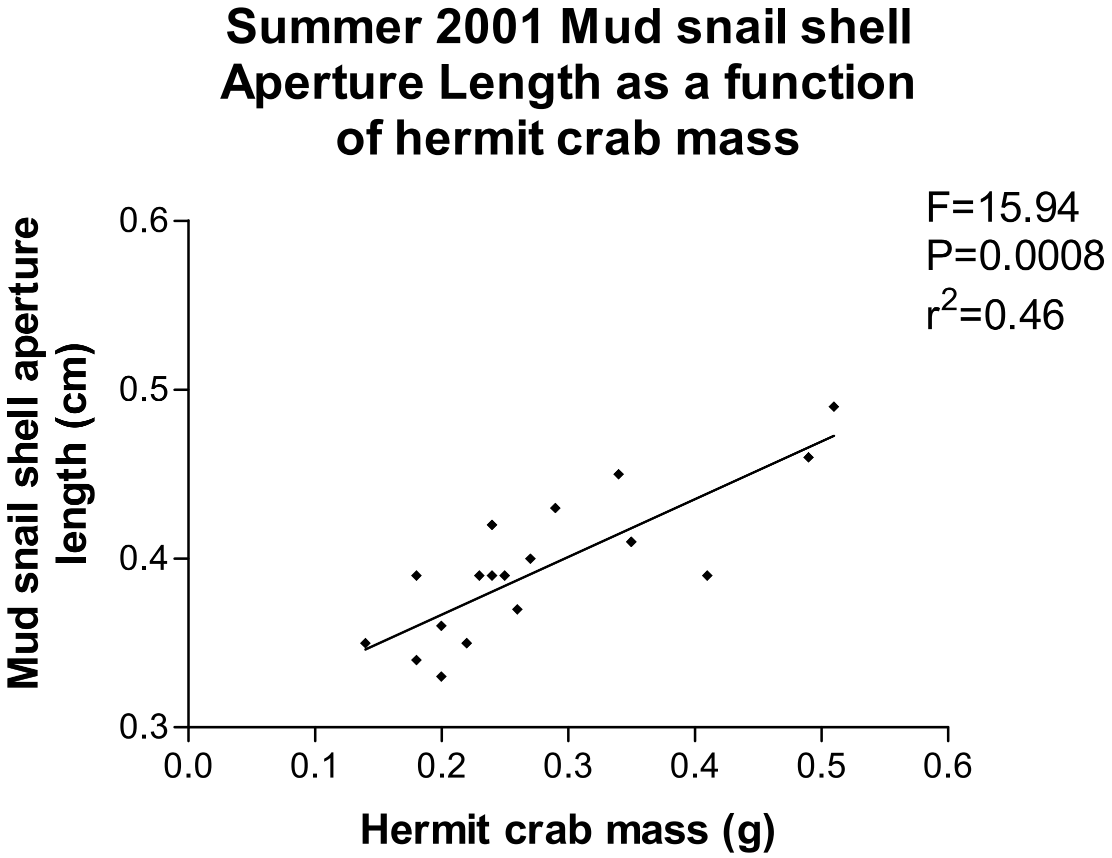


Figure 3: Regression graph for periwinkle shells. Shell mass as a function of hermit crab mass.

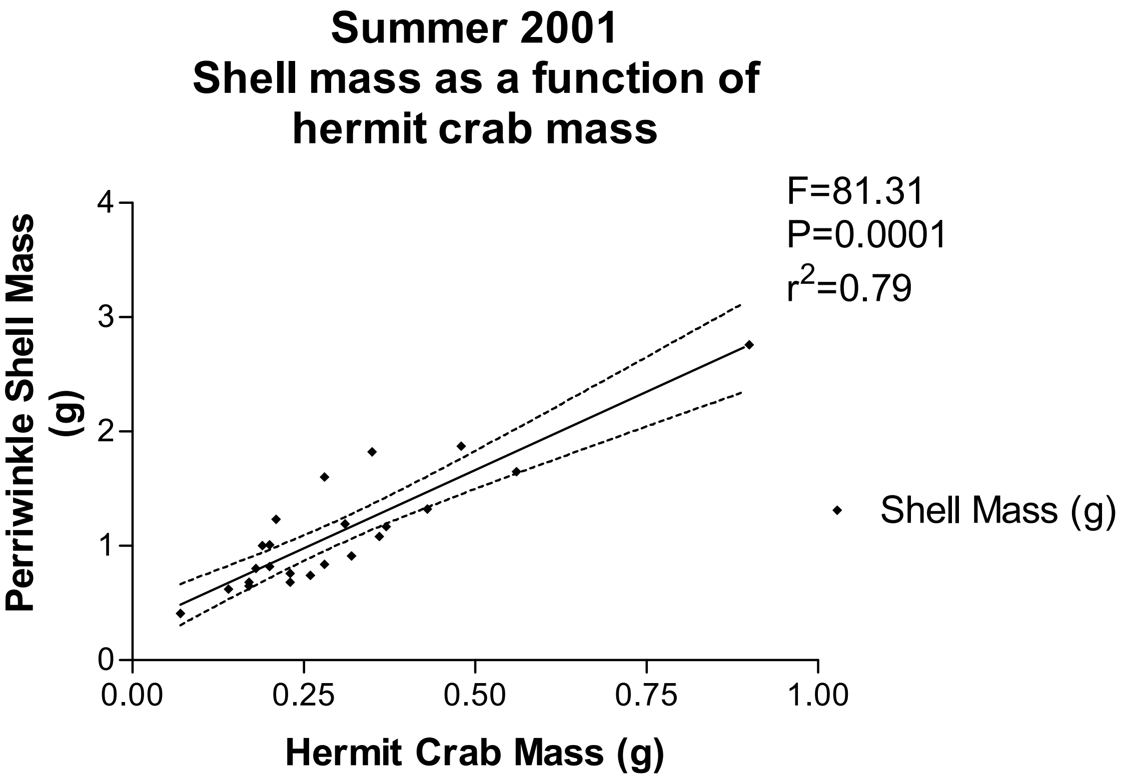


Figure 4: Hermit crab shell selection when given a choice of optimally (shell adequacy index=1.0) and suboptimally (shell adequacy index=0.75) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

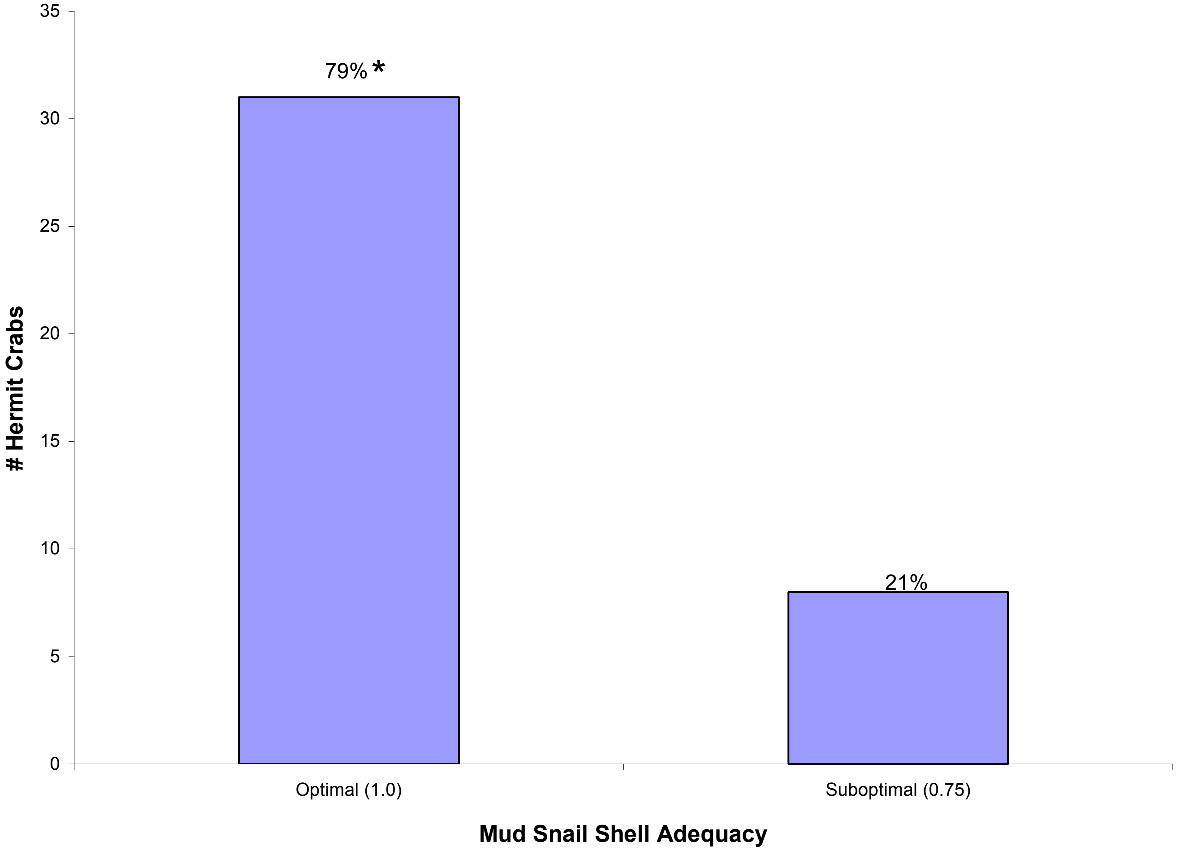


Figure 5: Hermit crab shell selection when given a choice of optimally (shell adequacy index=1.0) and suboptimally (shell adequacy index=0.50) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

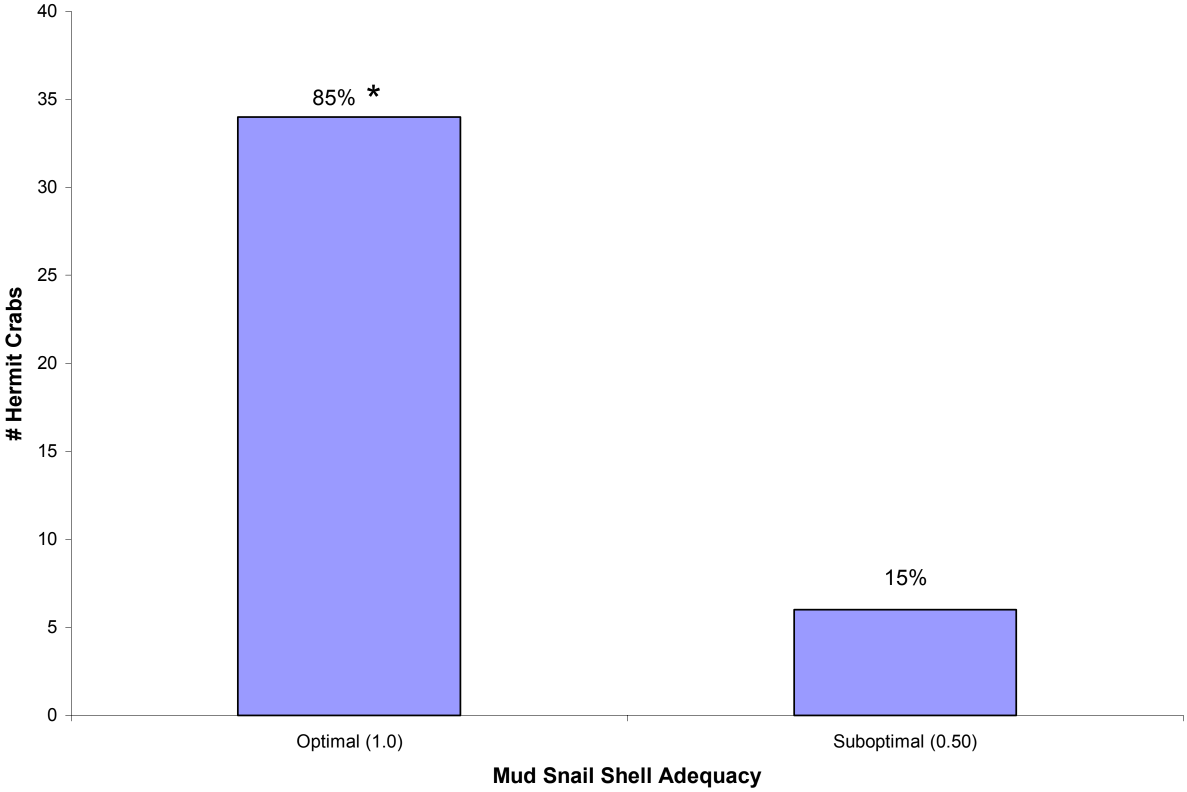


Figure 6: Hermit crab shell selection when given a choice of optimally (shell adequacy index=1.0) and suboptimally (shell adequacy index=0.25) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

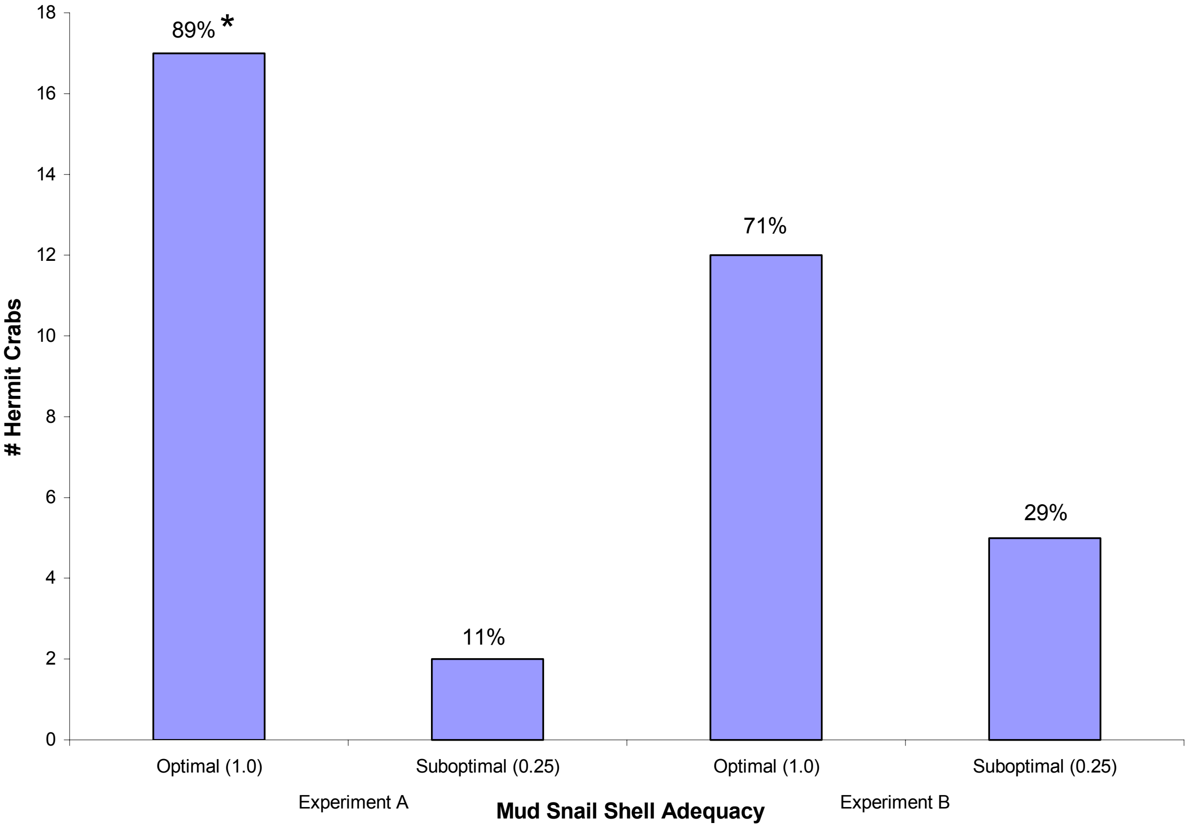


Figure 7: Hermit crab shell selection when given a choice of optimally (shell adequacy index=1.0) and suboptimally (shell adequacy index=1.50) mud snail shell (χ^2, $p \leq 0.05$).

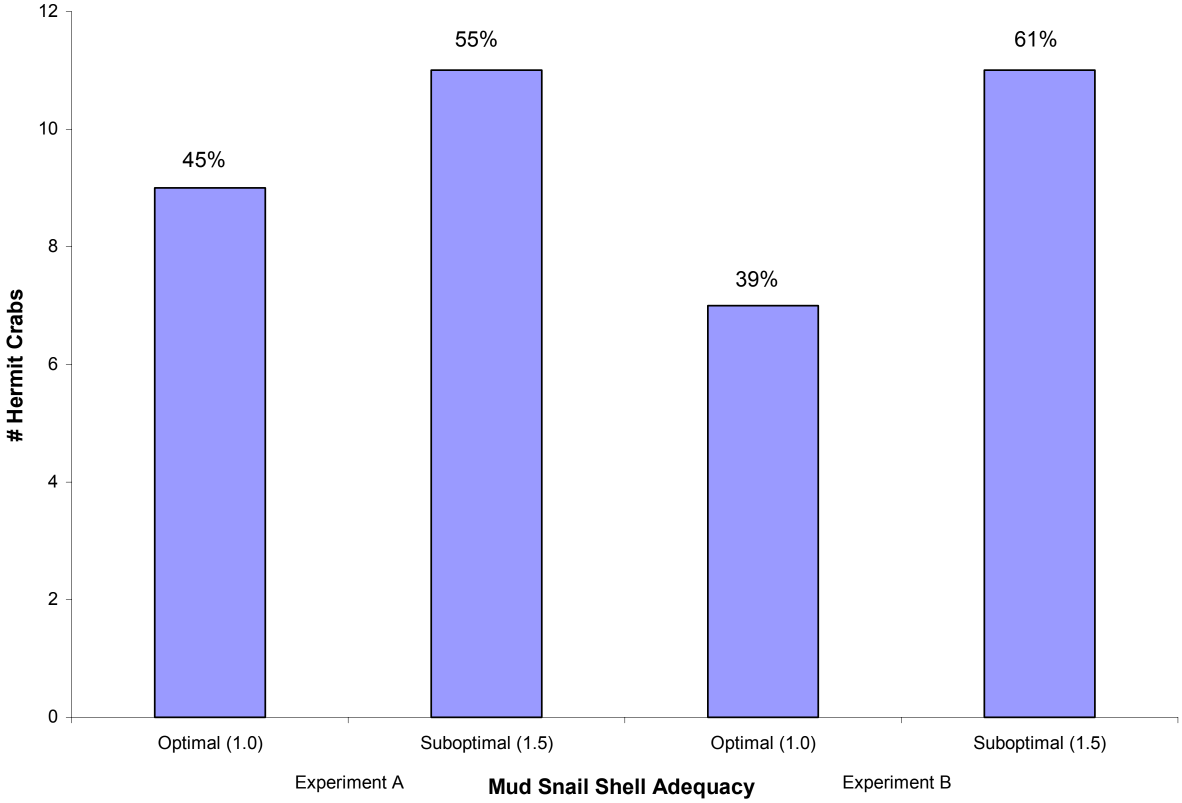


Figure 8: Hermit crab shell selection when given a choice of intact and optimally (shell adequacy index=1.0) and damaged and optimally (shell adequacy index=1.0) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

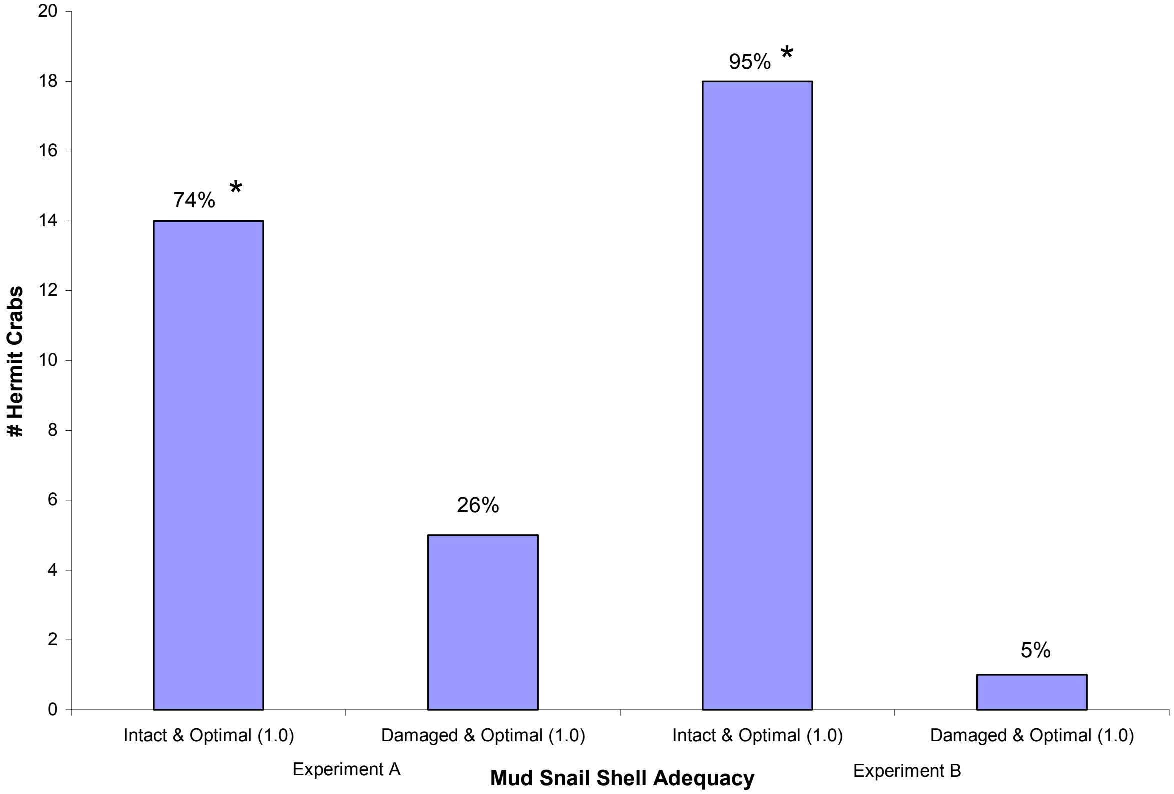


Figure 9: Hermit crab shell selection when given a choice of intact and suboptimally (shell adequacy index=0.75) and damaged and optimally (shell adequacy index=1.0) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

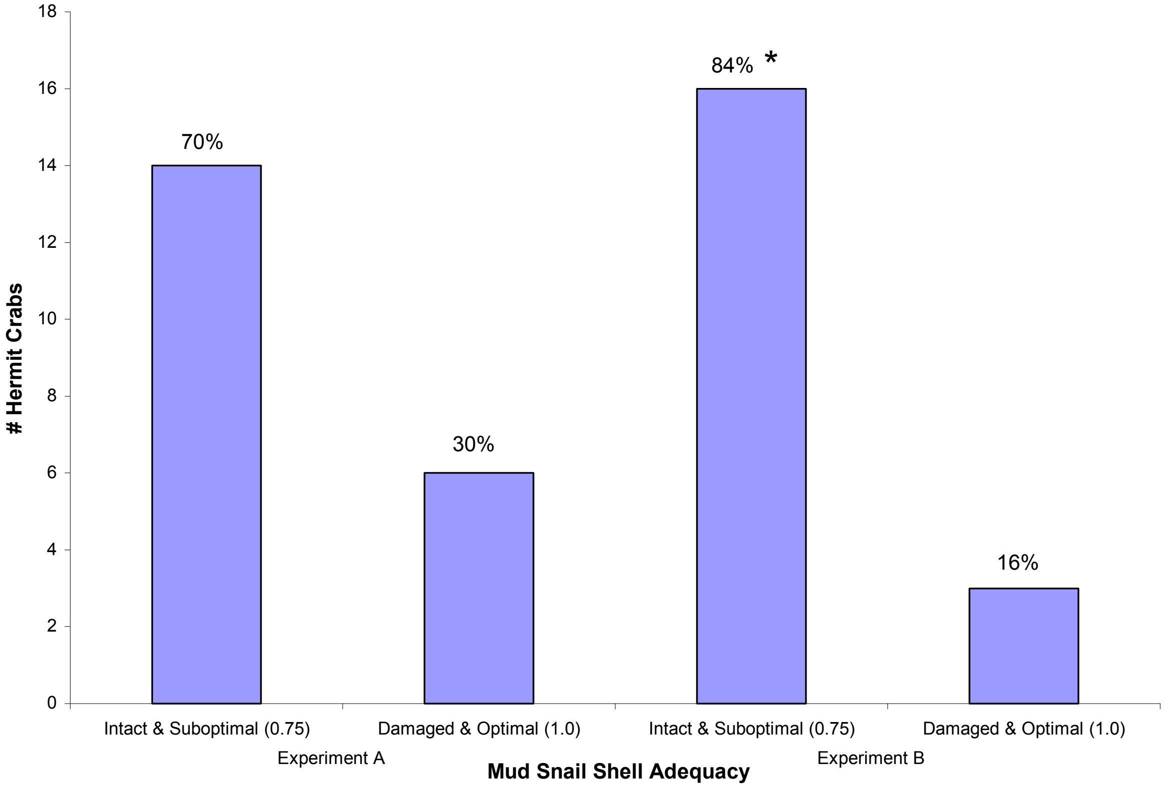


Figure 10: Hermit crab shell selection when given a choice of intact and suboptimally (shell adequacy index=0.50) mud snail shell and damaged and optimally (shell adequacy index=1.0) mud snail shell (χ^2, $p \leq 0.05$).

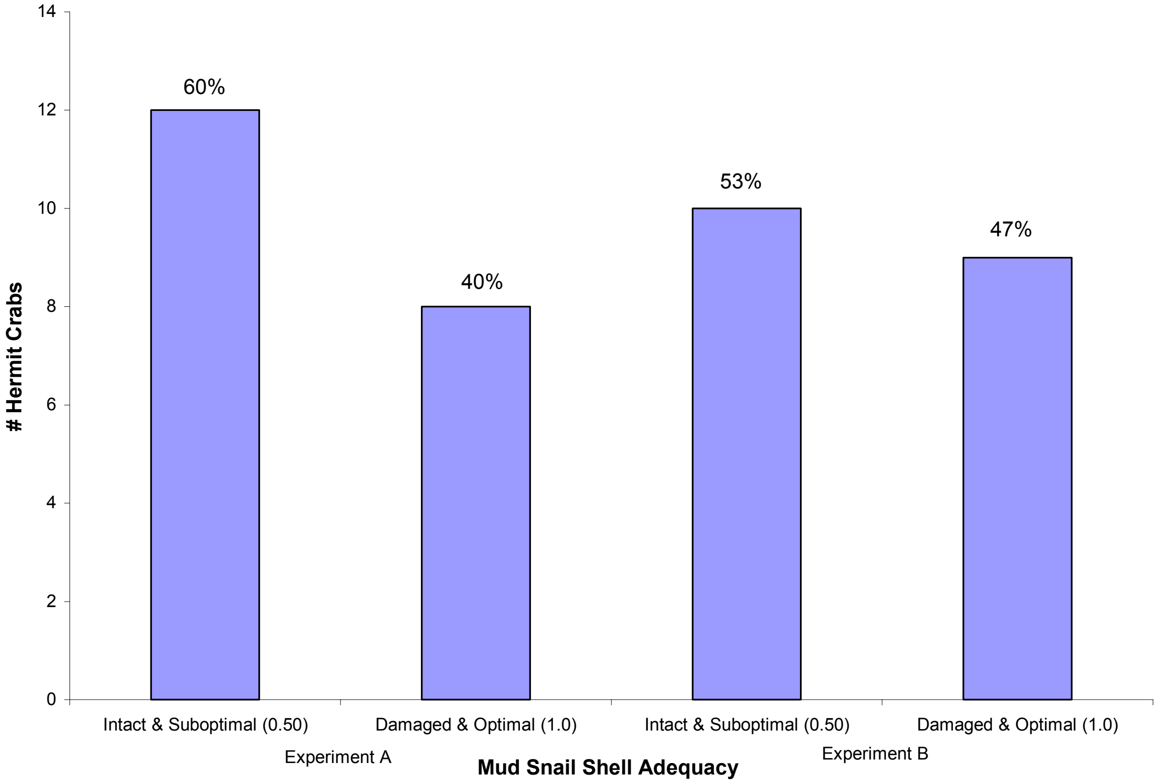


Figure 11: Hermit crab shell selection when given a choice of intact and suboptimally (shell adequacy index=0.25) mud snail shell and damaged and optimally (shell adequacy index=1.0) mud snail shell (χ^2, $p \leq 0.05$).

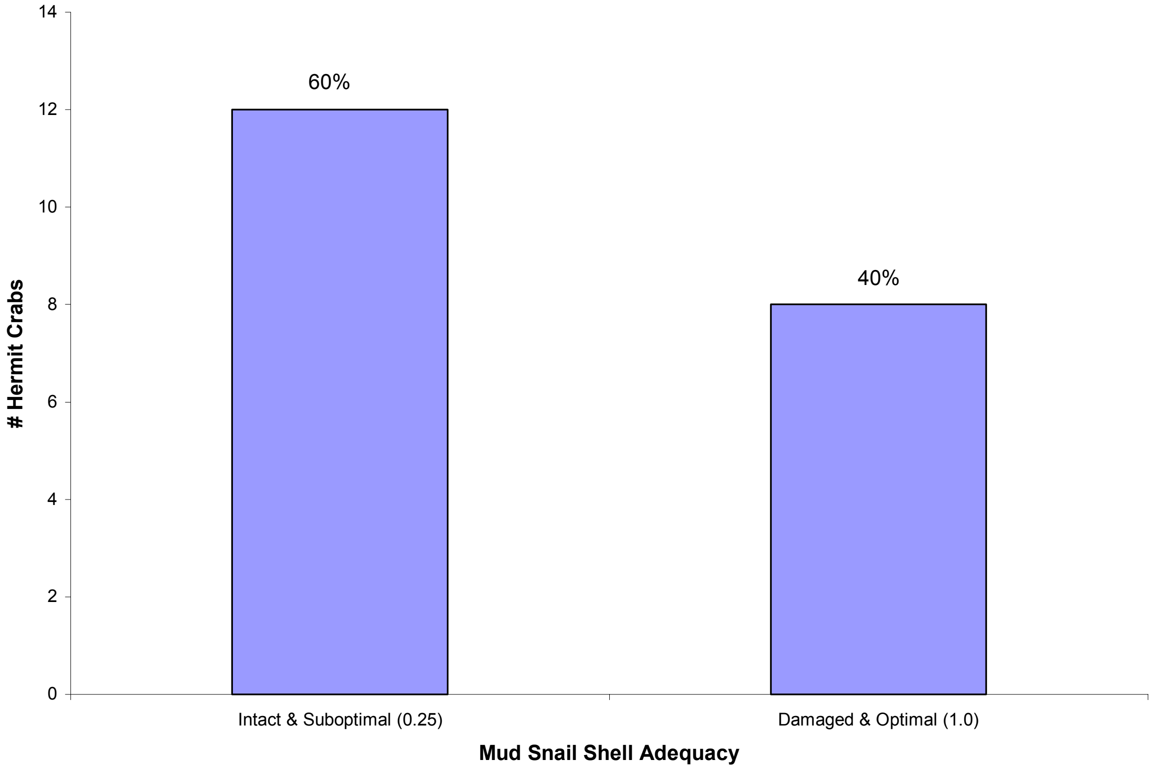


Figure 12: Hermit crab shell selection when given a choice of optimally (shell adequacy index=1.0) periwinkle shell or optimally (shell adequacy index=1.0) mud snail shell (χ^2, $p \leq 0.05$).

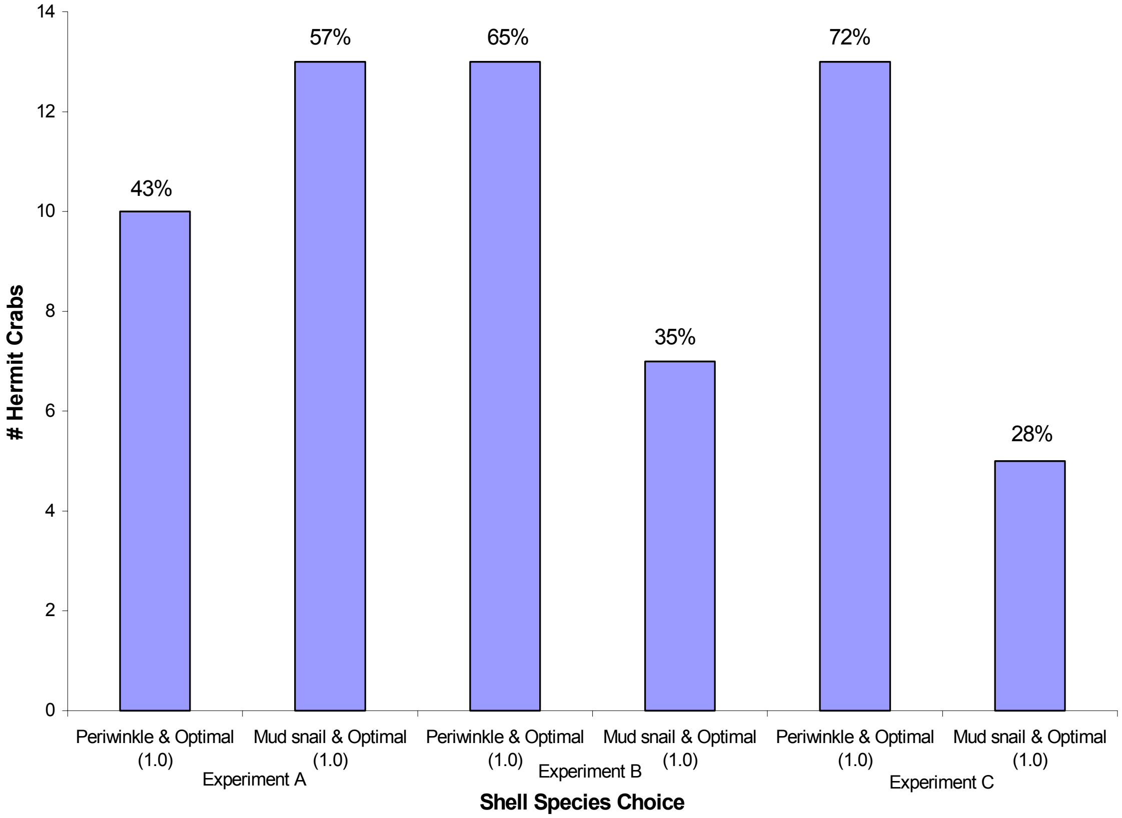


Figure 13: Hermit crab shell selection when given a choice of intact and optimally (shell adequacy index=1.0) periwinkle shell and damaged and optimally (shell adequacy index=1.0) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).

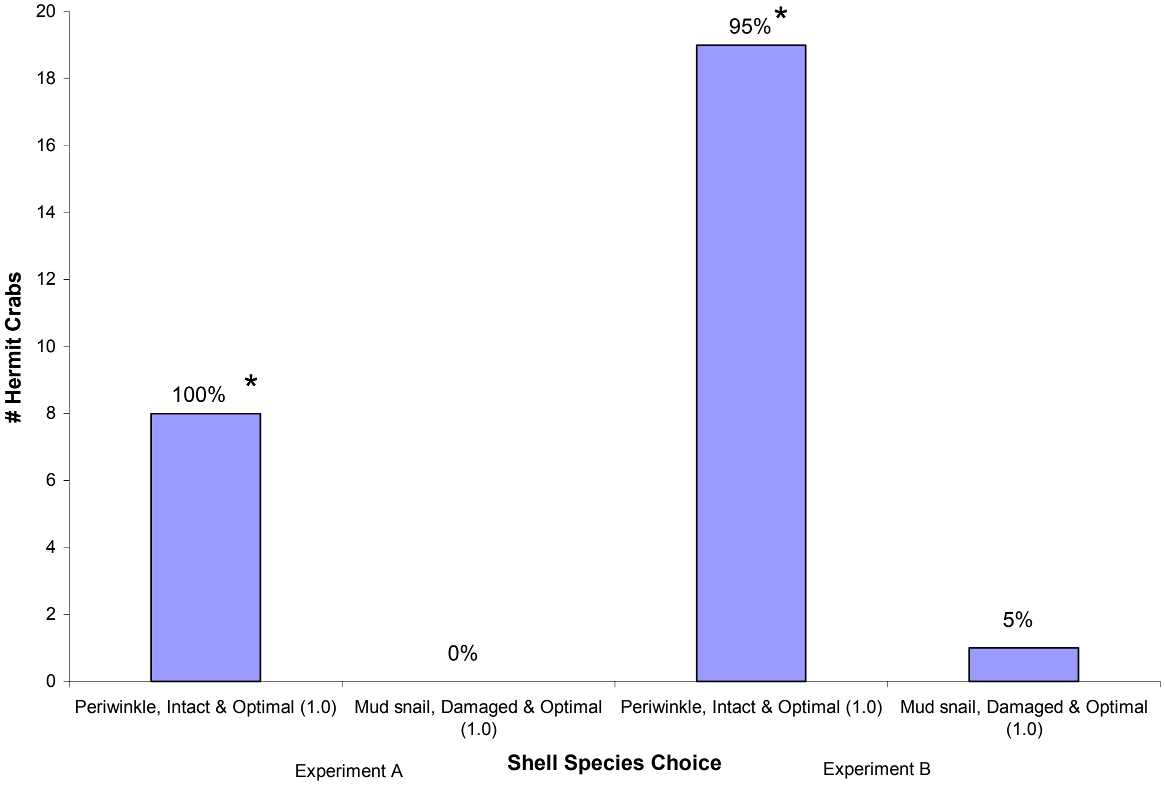
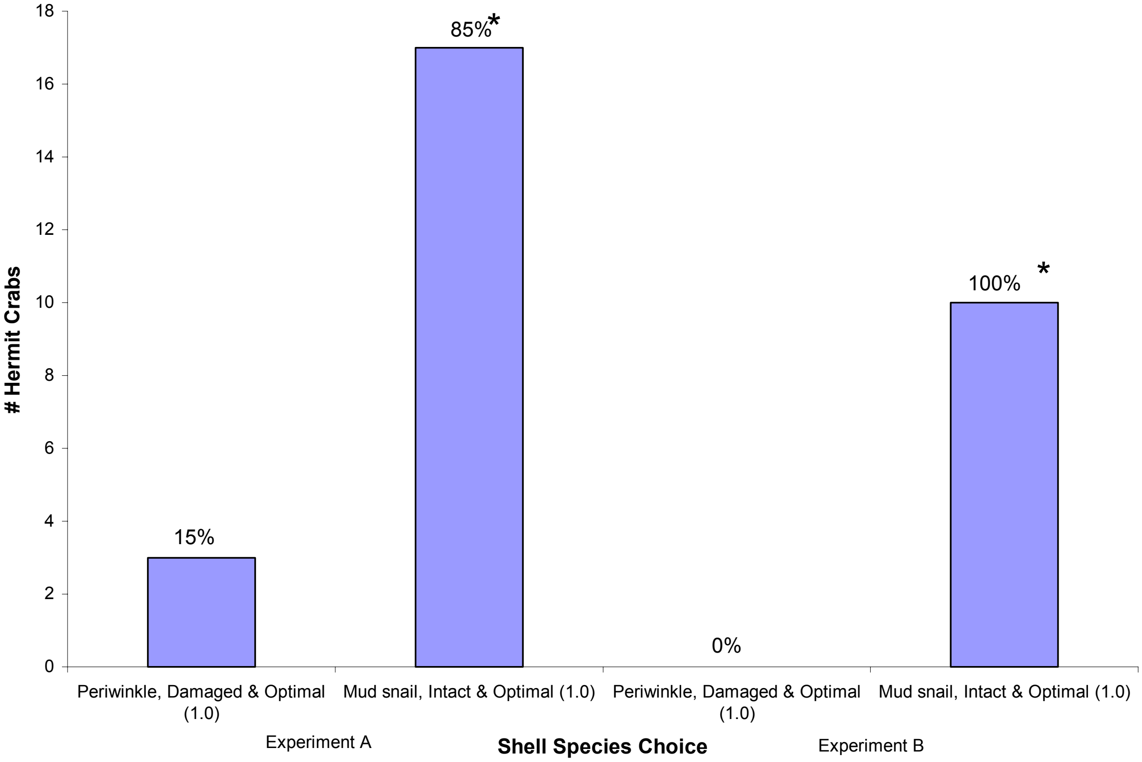


Figure 14: Hermit crab shell selection when given a choice of damaged and optimally (shell adequacy index=1.0) periwinkle shell and intact and optimally (shell adequacy index=1.0) mud snail shell. (*) indicates statistically significant difference (χ^2, $p \leq 0.05$).



Biographical Note

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Julie received her Bachelor of Science degree from Eastern Connecticut State University in 1994. Before pursuing her Master's degree, she held various jobs working with animals, including positions at a dairy farm and a humane society. Julie currently lives in Andover, Connecticut with her husband, Michael, their daughter, Sage and their multiple dogs, cats, chickens, guinea hens, geese and peafowl.