

# Utilization of partially predated snail shells by the hermit crab *Pagurus longicarpus* Say, 1817

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**Abstract** The hermit crab *Pagurus longicarpus* was shown to inhabit shells that were partially predated from intertidal areas of Long Island, New York. Among field collections of *P. longicarpus*, 2.13% of the hermit crabs (46 of 2155) were found with shells with snail tissue present. Over 90% of these partially predated snail shells were occupied by male hermit crabs. Although hermit crabs were in 8 species of snail shells, only *Littorina littorea* and *Nassarius obsoletus* were found occupied by hermit crabs and containing snail tissue. In the laboratory, we found that specimens of the spider crab *Libinia emarginata* were able to pull off the operculum of snails, leaving damage as found in field collections. In contrast, specimens of *P. longicarpus* were not able to prey on live, healthy snails. When specimens of *P. longicarpus* were placed in communal tanks, hermit crabs preferred partially predated snail shells to empty and original shells. However, original shells and empty shells were occupied with more frequency than partially predated shells when crabs were isolated. These findings indicate *P. longicarpus* actively seeks shells soon after attack and abandonment by snail predators, especially in the presence of competitors.

## Introduction

Most of the 850+ described species of hermit crabs (Paguroidea) inhabit empty gastropod shells and use these

mobile shelters for protection of their soft abdomens. In the marine realm, hermit crabs are found in a wide range of habitats from the intertidal to the deep sea. In addition, a small number of hermit crabs from tropical and subtropical areas are terrestrial. Regardless of adult habitats, all hermit crabs spawn in the sea where their larvae develop in the plankton before settling as megalopae and assuming the benthic life style, seeking out gastropod shells. Shells are thus an important resource for hermit crabs and are typically in limited supply within hermit crab populations (e.g., Provenzano 1960; Hazlett 1970; Kellogg 1976; Scully 1979; see Barnes 1999 for example where this is not true). The shells provide protection from predators, desiccation and supply a space to brood embryos attached to the female's pleopods (Lancaster 1988). Extensive research has been completed on shell selection by hermit crabs, particularly in reference to the factors that influence decisions to abandon an old shell and occupy a new one (e.g., see reviews in Hazlett 1981; Lancaster 1988; Elwood and Neil 1992; Williams and McDermott 2004). In contrast to this large body of literature, relatively few studies have shown how new shells become available to hermit crab populations.

Hermit crabs typically acquire shells through the following pathways: (1) empty shells may be found on the substrate when recently abandoned by a hermit crab (e.g., Vance 1972; Abrams 1980), (2) empty shells that are buried may be exhumed by hermit crabs or reworked as fossils (Walker 1989), (3) shells may be acquired from conspecifics or members of other species during shell switching or eviction events (e.g., Hazlett 1978, 1980; Bertness 1981), or (4) shells may be obtained immediately following snail death, typically after non-destructive predation events (McLean 1974; Scully 1979; Wilber and Herrnkind 1984; McClintock 1985; Pechenik et al. 2001;

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Gilchrist 2003; Rittschof 1980a, b; Rittschof et al. 1992; Tricarico et al. 2009; see Table 1). In regard to predation events, hermit crabs often aggregate where gastropods have been preyed upon, orienting to these sites by chemical and visual cues (Rittschof 1980a, b; Hazlett and Herrnkind 1980; Gilchrist 1984; Rittschof et al. 1990, 1992, 1995; Kratt and Rittschof 1991; Rittschof 1992; Diaz et al. 1994; Hazlett 1996; Rittschof and Hazlett 1997; Chiussi et al. 2001; Pezzuti et al. 2002; Gherardi and Tiedemann 2004; Gherardi and Atema 2005; Tricarico and Gherardi 2006; Tricarico et al. 2009). Shell exchanges can occur at these predation sites, often down a hierarchical vacancy chain once the dominant hermit crab switches shells (see Lewis and Rotjan 2009). For example, the Mediterranean hermit crab *Clibanarius erythropus* (Latreille, 1818) is attracted to gastropod predation sites simulated in the field that serve as “shell exchange markets” (Tricarico et al. 2009). Although *Pagurus longicarpus* is also attracted to gastropod predation sites, extensive movements by this hermit crab may be a more important tactic in locating new shells, especially in populations where predation on gastropods is low (Tricarico and Gherardi 2006).

Predatory gastropods and octopuses have been shown to provide shells for hermit crabs to inhabit (Wilber and Herrnkind 1984; Gilchrist 2003). However, the shell-boring process of some of these predators leaves suboptimal shells for hermit crabs, which will actively seek out more suitable homes (Wilber 1990; Pechenik and Lewis 2000; Pechenik et al. 2001). Decapod crustaceans are a dominant group that supplies empty shells for hermit crabs (e.g., Shoup 1968; Vermeij 1977, 1978, 1987; Seed and Hughes 1995; Hughes 2000; Turra et al. 2005). Although some of these crabs crack the shell extensively during feeding, and thus make them unsuitable for hermit crabs, others chip away the shell only slightly prior to extraction of the snail tissue. For example, the green crab *Carcinus maenas* (Linnaeus, 1758) preys on snails such as *Littorina littorea* (Linnaeus, 1758) by cracking the shells with its chelipeds or by chipping the aperture until the operculum is exposed and the snail can be pulled out (Hadlock 1980). Elner and Raffaelli (1980) found that *C. maenas* inserts its pincer claw into the aperture to extract the snail and in this way allows for future use by hermit crabs. Turra et al. (2005) found that the hermit crab *Pagurus criniticornis* (Dana, 1852) inhabits shells exhibiting damage similar to that caused by *Callinectes danae* Smith, 1869 and other decapod predators of gastropods.

Vertebrates also prey on snails but often do not leave usable shells for hermit crabs (Vermeij 1987). For example, shell-crushing predators such as diamondback terrapins *Malaclemys terrapin* (Schoepff, 1793) prey on gastropods, particularly *Littorina* spp. (Tucker et al. 1995). Birds that drop shells to gain access to the flesh also

typically leave the shells useless for occupation by hermit crabs (Brightwell 1951, 1953; Nyblade 1974).

Some hermit crabs have been documented to attack snails directly for their shells, but this appears to be rare (Table 2). For example, field observations in Japan showed that *Pagurus geminus* McLaughlin, 1976 and potentially the hermit crabs *Diogenes spinifrons* (De Haan, 1849) and *D. edwardsii* (De Haan, 1849) will attack healthy snails and inhabit shells with soft tissue still present (Imafuku 1983; Imafuku and Nakamura 1995). More often, hermit crabs have been shown to remove sick, dead or recently killed snails from shells. In Europe, Brightwell (1951) documented that the hermit crab *Pagurus bernhardus* (Linnaeus, 1758) removed unhealthy whelks from their shells and then inhabited the shell. Similarly, some hermit crabs are known to remove other organisms that occupy gastropod shells. For example, *P. longicarpus* removes sipunculids that inhabit empty gastropod shells and in some cases, enters the shell without removing the sipunculid (Kellogg 1976).

Although some hermit crabs appear to be able to attack live snails to obtain shells, this has not been documented in hermit crabs from the east or west coasts of North America, in spite of extensive ecological studies on hermit crabs in these regions. In addition, field data on hermit crabs occupying shells attacked by other predators is limited. However, our preliminary research along the south shore of Long Island, NY showed specimens of the hermit crab *P. longicarpus* inhabiting shells of *L. littorea* that still had soft tissue of the snail present. In most cases, the snails appeared to be recently attacked and had their opercula removed. At the study sites, the spider crab *Libinia emarginata* Leach, 1815 was the most common crab found in the areas where *L. littorea* was abundant. Based on these novel findings, we investigated the use of partially predated snails by *P. longicarpus* and sought to determine the species responsible for attacking *L. littorea*. Specifically, we focused on the following questions: (1) What is the prevalence of partially predated snail shells in the field? (2) What is the fate of the snail tissue in these shells? (3) Does *P. longicarpus* directly attack snails or are they attacked by the spider crab *L. emarginata*? and (4) Does *P. longicarpus* prefer partially predated snail shells over originally occupied shells or empty shells?

## Materials and methods

### Collection sites

*Pagurus longicarpus* occupying different species of gastropod shells were collected randomly by hand from May 2004 to November 2006 (hermit crabs were not sampled

**Table 1** Documented cases of predators that leave potential gastropod shells for hermit crabs to inhabit

Predator	Prey	Hermit crabs that use shell resource	Source
<b>Gastropoda</b>			
<i>Euspira heros</i> (Say, 1822)	<i>Littorina littorea</i> (Linnaeus, 1758)	<i>Pagurus longicarpus</i> (Say, 1817)	Pechenik and Lewis (2000)
<i>Melongena corona</i> (Gmelin, 1791)	<i>Littorina irrorata</i> (Say, 1822)	<i>Pagurus longicarpus</i> (Say, 1817)	Wilber and Herrnkind (1984)
<i>Pleuroploca gigantea</i> (Kiener, 1840)	<i>Fasciolaria hunteria</i> (Perry, 1811)	<i>Pagurus pollicaris</i> Say, 1817	McLean (1974)
<b>Cephalopoda</b>			
<i>Octopus vulgaris</i> Cuvier, 1797, <i>Octopus briareus</i> Robson, 1929	12 species of gastropods including members of the genera: <i>Cerithium</i> , <i>Cyphoma</i> , <i>Leucozonia</i> , <i>Natica</i> , and <i>Oliva</i>	<i>Pagurus brevidactylus</i> (Stimpson, 1858), <i>Pagurus criniticornis</i> (Dana, 1852) and 6 others	Gilchrist (2003)
<b>Brachyura</b>			
<i>Callinectes danae</i> Smith, 1869, <i>Eriphia gonagra</i> (Fabricius, 1781), <i>Menippe nodifrons</i> Stimpson, 1859, <i>Panopeus occidentalis</i> de Saussure, 1857 <i>Cancer productus</i> Randall, 1840 <i>Carcinus maenas</i> (Linnaeus, 1758)	<i>Cerithium atratum</i> Born, 1778	<i>Pagurus criniticornis</i> (Dana, 1852)	Turra et al. (2005)
<i>Eriphia squamata</i> Stimpson, 1859	<i>Cerastostoma foliatum</i> (Gmelin, 1791) <i>Littorina rudis</i> (Maton, 1797), <i>Littorina nigrolineata</i> Gray, 1839, <i>Littorina saxatilis</i> (Olivier, 1792), <i>Littorina littorea</i> (Linnaeus, 1758) <i>Nerita funiculata</i> Menke, 1851, <i>Anachis fluctuata</i> (Sowerby, 1832), <i>Cerithium stercusmuscarum</i> Valenciennes, 1833	Not specified Not specified Not specified	Donovan et al. (1999) Elner and Raffaelli (1980), Ekendahl (1998), Grosholz and Ruiz (1996), Hadlock (1980), Hamilton and Heithaus (2001) and Naczek et al. (2004) Bertness and Cunningham (1981)
<i>Menippe adina</i> Williams and Felder, 1986 <i>Neopanope texana</i> (Stimpson, 1859) <i>Ozius verreauxii</i> Saussure, 1853	<i>Strammonita haenastoma</i> (Linnaeus, 1758) <i>Littorina</i> spp. Ferussac, 1822 <i>Nerita funiculata</i> Menke, 1851, <i>Anachis fluctuata</i> (Sowerby, 1832), <i>Cerithium stercusmuscarum</i> Valenciennes, 1833	Not specified <i>Pagurus longicarpus</i> (Say, 1817) Not specified	Richardson and Brown (1992) Scully (1979) Bertness and Cunningham (1981)
<b>Echinodermata</b>			
<i>Pycnopodia helianthoides</i> (Brandt, 1835)	<i>Cerastostoma foliatum</i> (Gmelin, 1791)	Not specified	Donovan et al. (1999)
<b>Diodontidae</b>			
<i>Diodon</i> sp.	<i>Thais kioskiformis</i> (Duclos, 1832), <i>Thais biserialis</i> Blainville, 1832	Not specified	Palmer (1979)
<b>Carchariaformes</b>			
<i>Scyllorhinus caniculus</i> Linnaeus, 1758	<i>Buccinum undatum</i> (Linnaeus, 1758)	Not specified	Eales (1949)

Some of these predators chip, crush, crack, and/or drill holes into the gastropod shells, leaving suboptimal shells. Although there are many other gastropod predators (e.g., see Vermeij 1987), those listed above represent cases where the predators have been shown to supply shells to hermit crabs

**Table 2** Documented cases of hermit crabs directly attacking gastropods or occupying shells with snail tissue present

Hermit crab	Shell	Direct attack or tissue present	Source
<i>Clibanarius tricolor</i> (Gibbes, 1850)	<i>Batillaria minima</i> (Gmelin, 1791)	Tissue present	McDermott (2002)
<i>Clibanarius vittatus</i> (Bosc, 1802) &/or <i>Pagurus pollicaris</i> Say, 1817	Busyconine whelks	Attack snails <sup>a</sup>	Magalhaes (1948)
<i>Dardanus crassimanus</i> (H. Milne Edwards, 1836)	<i>Pleuroploca trapezium paeteli</i> (Strebel, 1912)	Attack snails	Imafuku in Imafuku and Nakamura (1995)
<i>Diogenes edwardsii</i> (De Haan, 1849) & <i>Diogenes spinifrons</i> (De Haan, 1849)	<i>Glassaulax didyma</i> Roding, 1798	Tissue present/attack snails?	Imafuku and Nakamura (1995)
<i>Paguristes turdigus</i> (Stimpson, 1957)	<i>Busycotypus canaliculatus</i> (Linnaeus, 1758)	Attack snails <sup>a</sup>	Rutherford (1977)
<i>Pagurus bernhardus</i> (Linnaeus, 1758)	<i>Buccinum undatum</i> (Linnaeus, 1758)	Attack snails <sup>a</sup>	Brightwell (1953)
<i>Pagurus criniticornus</i> (Dana, 1852) and others	Not specified	Tissue present	Gilchrist (2003)
<i>Pagurus geminus</i> McLaughlin, 1976	<i>Lunella coronata coreensis</i> Récluz, 1853 and <i>Ergalatax contractus</i> Reeve, 1846	Attack snails	Imafuku (1983)
<i>Pagurus longicarpus</i> (Say, 1817)	<i>Littorina littorea</i> Linnaeus, 1758	Tissue present <sup>b</sup>	Tricarico and Gherardi (2006)
<i>Pagurus longicarpus</i> (Say, 1817)	<i>Nassarius obsoletus</i> (Say, 1822)	Tissue present	McDermott (unpublished data)
<i>Pagurus pollicaris</i> Say, 1817	<i>Fasciolaria hunteria</i> (Perry, 1811)	Tissue present <sup>b</sup>	McLean (1974)
<i>Petrochirus diogenes</i> (Linnaeus, 1758)	<i>Eustrombus gigas</i> (Linnaeus, 1758)	Attack snails <sup>a</sup>	Randall (1964)

Hermit crab species known to attack snails directly are distinguished from those inhabiting shells with some soft tissue of snail present that was left by other snail predators. In addition to the scientific reports summarized above, Kurata (1968) and Purtymun (1971) supplied notes in popular journals of direct shell acquisition by hermit crabs

<sup>a</sup> Not certain whether these hermit crabs can attack and kill healthy whelks; hermit crabs may attack dead or dying snails

<sup>b</sup> Occupation of recently predated snail shell, remains of soft tissue not confirmed

during the winter months) from intertidal zones at three sites along the north shore [Tappan Beach (40° 51.8'; 73° 39.3'), Oyster Bay (40° 53'; 73° 32'), and Cedar Creek (41° 04'; 72° 25')] and four sites along the south shore [Jones Beach (40° 35.2', 73° 34.7'), Fishing Pier at Jones Beach (40° 37.2', 73° 31.4'), Tobay Beach (40° 37.2', 73° 23.7'), and Oak Beach (40° 38.5'; 73° 17.2')] of Long Island, NY. The shoreline was walked and all visible hermit crabs were collected. The crabs were isolated in the field to avoid shell exchanges during transport by placement in compartmentalized plastic containers (24 compartments of 50 × 50 × 50 mm) filled with seawater. The crabs were kept alive in the laboratory in their containers by placing them in a temperature-controlled refrigerator (18°C) and feeding them *Ulva* sp. and shrimp pellets. The seawater in the plastic boxes was changed every day until the hermit crabs were examined.

#### Measurements of specimens

The gastropod shell species were identified, and measurements of their aperture and total length were taken using vernier calipers. The shells were examined for external evidence of predation (e.g., chipped aperture, missing apex, or drill holes). The sex, size (shield length, SL), and absence or presence of eggs of hermit crabs were recorded

after inducing the hermit crabs to move out of their shells by cracking the shell in a vise.

#### Predation trials with *Littorina littorea*

Observations made while collecting hermit crabs showed the spider crab *L. emarginata* was prevalent in the field at Oak Beach where partially predated snails were found. Therefore, trials were set up from August 2005 to November 2006 to determine whether this decapod was attacking and removing the opercula of *L. littorea*. In these predation trials and shell choice trials described in the following paragraphs, we chose to focus on *L. littorea* because it was the most frequent gastropod species found to be inhabited by hermit crabs with snail tissue still present. Twelve live intact *L. littorea* and one *L. emarginata* collected from Oak Beach were placed into each of four 37.9-L tanks lined with sand and rocks connected with a seawater filtration system (these numbers per tank approximated the density of *L. emarginata* and *L. littorea* in the field). Tanks for this and all subsequent experiments were maintained at ambient temperatures (21.1°C) and light conditions (12 light:12 dark). Specimens of *L. emarginata* used in these experiments were of average carapace size (40–50 mm) compared to those observed in the field. Interactions between spider crabs and live snails were

monitored daily for 2 weeks. The spider crabs and snails were fed *Ulva* sp. and shrimp pellets three times a week. New crab and snail specimens were collected for each of four replicates of the predation trials (16 total trials were completed with new crabs in each).

Separate trials were conducted to test whether *P. longicarpus* would prey on snails. Twelve live intact *L. littorea* and four *P. longicarpus* were placed into each of four 37.9-L tanks identical to those described in the first experiment (these numbers per tank approximated the density of *P. longicarpus* and *L. littorea* in the field). The tanks were monitored for 2 weeks from August 2005 to November 2005; hermit crabs and snails were fed as described earlier. Because no evidence of hermit crab predation on gastropods was found, only four total trials were run.

Once a predation event occurred, the snail shells were evaluated. Special attention was used when evaluating the aperture of the shell and operculum. The shell was then cracked to observe the damage to the snails' soft tissue. Damage to *L. littorea* during predation events was compared to partially predated shells collected from the field to assess the identity of the predator.

#### Shell choice experiments

Between June 2005 to November 2005, we determined whether *P. longicarpus* prefer empty gastropod shells or partially predated gastropod shells. *P. longicarpus* and live *L. littorea* were collected from Oak Beach. To avoid influence of symbionts and reproductive condition on shell choice, no hermit crabs with observable epibionts on shells and no ovigerous female hermit crabs were used. Four separate 37.9-L tanks lined with sand and rocks connected with a seawater filtration system contained four hermit crabs in their natural shells, *Ilyanassa trivittata* (Say, 1822) or *Nassarius obsoletus* (Say, 1822), and twelve *L. littorea* shells. The twelve shells were composed of six empty gastropod shells and six live snail shells with the opercula removed with forceps, mimicking predation observed in the field-collected specimens. During this procedure, the snail showed no evidence of blood loss and none were killed in the process. The shells were marked with nail polish for identification. To obtain the empty gastropod shells, live *L. littorea* were boiled and the soft tissue was removed so there was no potential for symbionts to be influencing shell choice. Interactions between hermits and live snails were monitored daily for 2 weeks. The hermit crabs and snails were fed *Ulva* sp. and shrimp pellets three times a week. New hermit crab and snail specimens were collected for each of 4 replicates of the shell choice trials

(32 total trials; shell choice of 128 individual hermit crabs recorded).

Between June 2006 and August 2006, a second set of shell choice experiments were completed with hermit crabs in isolation to remove influence of competition from conspecifics. Again, *P. longicarpus* and live *L. littorea* were collected from Oak Beach, and no hermit crabs in shells with observable epibionts were used. Eight 37.9-L tanks were sectioned off into three compartments using perforated plastic dividers. The tanks were lined with sand and rocks connected with a seawater filtration system. One hermit crab in its original *N. obsoletus* shell with two empty shells and two partially predated *L. littorea* shells were placed into each compartment. Nail polish was used for shell identification. As in the above-mentioned experiment, empty shells were obtained by boiling and partially predated snails were mimicked by removing the opercula using forceps. Hermit crabs were fed as indicated earlier; the interactions were monitored daily for 2 weeks. New hermit crab and snail specimens were collected for each of 3 replicates of the shell choice trials (67 total trials; shell choice of 67 individual hermit crabs recorded).

After the 2-week monitoring period, all shells (excluding live snails) were cracked and examined for the amount of soft tissue still present. The hermit crabs' original shells were cracked and evaluated for external damage and evidence of symbionts. The hermit crabs' sex, shield length, and presence of eggs were measured and recorded.

#### Use of partially predated shells and fate of snail tissue

Preliminary observations showed that all tissue in partially predated snail shells was missing after hermit crabs occupied the shells for a period of 2 weeks. To determine more precisely how long it takes the hermit crabs to remove all the snails' soft tissue, we set up a series of containers (30 cm × 19 cm × 20 cm) with hermit crabs and partially predated snail shells of *L. littorina* from August 2006 to November 2006. Hermit crabs were removed from their original shells and placed with one snail with its operculum removed in plastic containers with seawater. The hermit crabs and snails were not fed during the experiment. One snail shell occupied by a hermit crab was cracked and evaluated daily until there was no evidence of snail tissue still present in the shells (6 trials were completed; in total 46 hermit crabs were sampled over the 2-week period). Any evidence of hermit crabs feeding on the snail tissue was recorded. A control tank was set up with 14 live *L. littorea* with opercula removed as described earlier. Each day for 2 weeks, a snail was removed and cracked to observe the amount of decay with no hermit crabs present.



## Statistics

Data on the number of male and female hermit crabs found at each site along the north and south shores as well as for each of the shell species were tabulated and percentages were calculated. The abundance and percentage of gastropod shell species from each site was determined. Chi-square tests were used to determine whether the distribution of shell species was different from expected values of equal distribution of shell species along each shore and whether the sex distribution was different from the expected values of equal distribution. Chi-square tests were also used in experiments with three shells types (original, empty, and partially predated) for both those in presence of conspecifics and those in isolation. The impacts of hermit crab shield length on sex and shell type (original, empty, and partially predated) were tested using ANOVAs for hermit crabs in the presence of conspecifics and hermit crabs in isolation; a post hoc test (Tukey's HSD) was run to determine significant differences between shell types chosen. To determine if the social condition of hermit crabs (in presence of conspecifics versus in isolation) impacted shell choice, a random sample of individuals of hermit crabs with conspecifics were taken ensure the two conditions had the same sample size. The social condition of hermit crabs was coded, and impact of shield length and shell size (shell length and aperture) on social condition, sex, and shell type were tested using ANOVAs. Descriptive statistics were reported as mean  $\pm$  standard deviation.

## Results

### Shell use by *Pagurus longicarpus*

Among all sites combined, *P. longicarpus* ( $N = 2,155$ ) occupied eight different species of gastropod shells. Seven hermit crabs (0.3%) were found lacking shells (one and six from the north and south shores, respectively). The shells used by hermit crabs were significantly different between the north and south shores ( $\chi^2_8 = 923.1$ ,  $N = 2,155$ ,  $P < 0.001$ ). At three sites along the north shore, hermit crabs inhabited six gastropod shell species: *Crepidula fornicata* (Linnaeus, 1758), *I. trivittata*, *Lunatia heros* (Say, 1822), *L. littorea*, *N. obsoletus*, and *Urosalpinx cinerea* (Say, 1822), but over 92% of hermit crabs from the north shore occupied shells of *N. obsoletus* (Fig. 1). Tappan Beach hermit crabs inhabited all six gastropod shell species, Cedar Creek hermit crabs utilized four different gastropod shell species (none found in *C. fornicata* or *L. heros*), and those from Oyster Bay only inhabited *N. obsoletus* shells.

At four sites along the south shore, hermit crabs inhabited seven gastropod shell species: *Busycotypus canaliculatum* (Linnaeus, 1758), *Eupleura caudata* (Say, 1822), *I. trivittata*, *L. heros*, *L. littorea*, *N. obsoletus*, and *U. cinerea* (Fig. 1). The most abundant gastropod shell inhabited by hermit crabs was *I. trivittata* (49.5%) for all sites except the fishing pier, in which *N. obsoletus* was the most abundant shell used by the hermit crabs (94%). Oak Beach hermit crabs utilized all seven shell species. Hermit crabs used five different shell species at Jones Beach (*B. canaliculatum* and *E. caudata* not inhabited). Hermit crabs from the fishing pier used five different gastropod shells: *I. trivittata*, *L. heros*, *L. littorea*, *N. obsoletus*, and *U. cinerea*. Tobay Beach hermit crabs utilized three shell species: *I. trivittata*, *L. heros*, and *N. obsoletus* (Fig. 1).

Sex ratios of hermit crabs were similar between north and south shore sites. Males dominated at all sites and male to female sex ratios were approximately 3:1 and 5:1 for the north and south shores, respectively. There was a significant difference between male and female samples on the North Shore of Long Island ( $\chi^2_1 = 125.2$ ,  $N = 649$ ,  $P < 0.001$ ). There was also a significant difference between male and female samples on the South Shore of Long Island ( $\chi^2_1 = 653.4$ ,  $N = 1,506$ ,  $P < 0.001$ ). Ovigerous females were collected from May through September on both shores, with the majority being collected in June. Collectively during the spring and summer months sampled, nearly 44% of the females from the north shore were ovigerous, whereas 16% of the females collected from south shore were ovigerous.

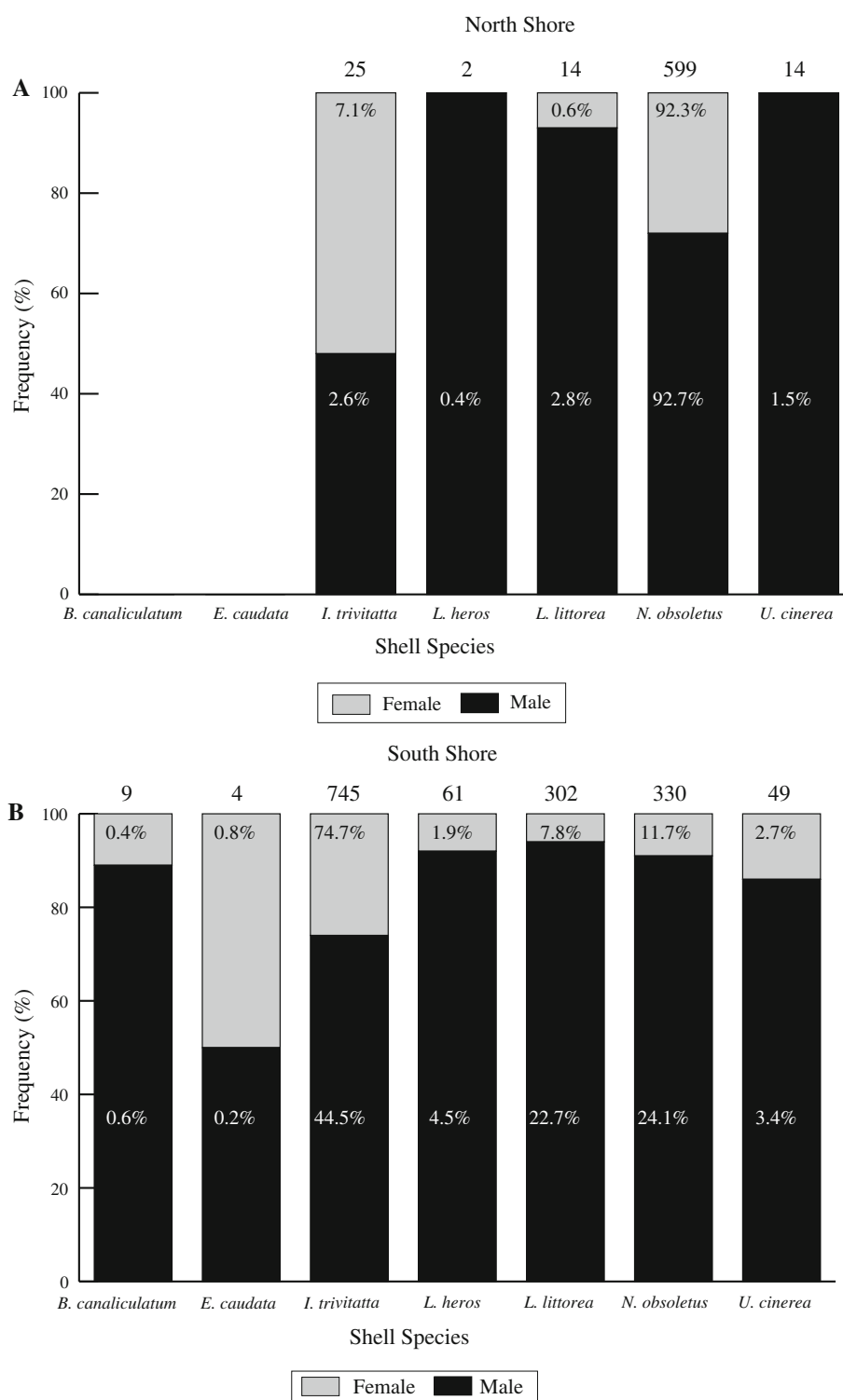
Forty-six hermit crabs inhabited shells with snail tissue still present (overall prevalence = 2.13% of 2,155). Of the partially predated snail shells, 8.7% ( $N = 4$ ) were occupied by females and 91.3% ( $N = 42$ ) were occupied by males ( $\chi^2_1 = 31.42$ ,  $N = 46$ ,  $P < 0.001$ ). Use of partially predated snail shells occurred on both shores, at four of the seven sites: Oyster Bay, Tappan Beach, Jones Beach, and Oak Beach. Snail tissue presence was only found in two snail species, *N. obsoletus* and *L. littorea*. The highest prevalence of hermit crabs in shells with tissue present was found at Oak Beach where 31 hermit crabs (all males) inhabited *L. littorea* shells (3.6%) during 2005. A male occupied the only partially predated *L. littorea* shell found at Tappan Beach, whereas three females and seven males inhabited *N. obsoletus* shells from this site. Males occupied three partially predated *N. obsoletus* shells from Jones Beach. One female hermit crab occupied a partially predated *N. obsoletus* at Oyster Bay.

In almost all cases, the snail appeared dead with tissue partially intact (half to nearly a whole snail still in the shell). In the instances with nearly a whole snail was present, the snail was missing its operculum. There was no

**Fig. 1** The percentage of male and female *Pagurus longicarpus* utilizing different gastropod shell species found along the north and south shores of Long Island, NY.

**a** *P. longicarpus* found along the north shore.

**b** *P. longicarpus* found along the south shore. Numbers above bars indicate total number of shells sampled; percentages indicate proportion of total number of males and females using each shell species. Individuals in *C. fornicata* and those lacking shells were removed from the analysis



evidence of shell cracking, or scrapes on the shell or around the operculum. In one case, a partially predated snail was alive and infested with a trematode parasite (metacercarial stage), identified as *Himasthla quissetensis* (Miller and Northrup, 1926).

#### Predation trials

All experimental *L. emarginata* were observed attacking *L. littorea* and four out of the sixteen (25%) crabs removed the opercula of the snails. In total, these four spider crabs

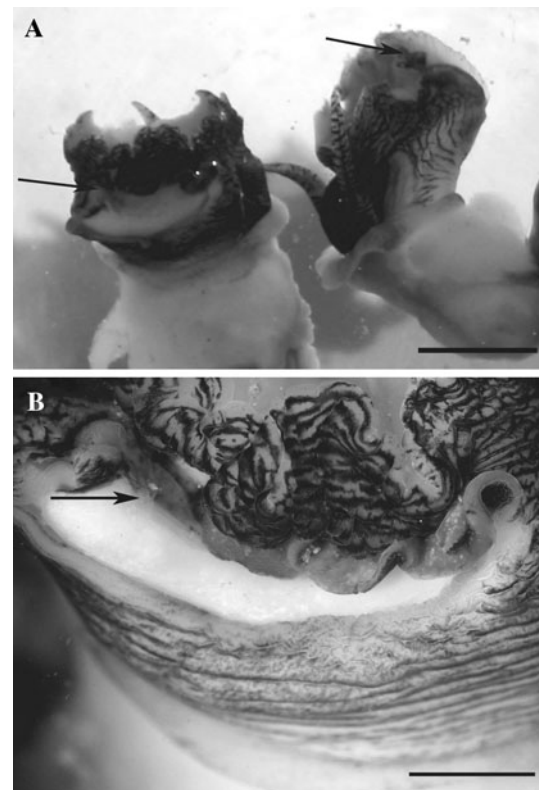
removed the opercula from eight snails and then abandoned the soft tissue. The average aperture size of the predated snail shells was  $11.3 \pm 2.6$  mm ( $N = 8$ ), and the length was  $18.7 \pm 4.1$  mm ( $N = 8$ ).

When attacking *L. littorea*, the spider crab used one cheliped to hold the shell and the other cheliped was inserted into the aperture to grasp the operculum or snail soft tissue. The spider crab inserted its claw as far into the aperture as possible. If unsuccessful in grasping the operculum, the crab released the snail and moved away. If successful, the crab continued pulling until the operculum was removed. After the removal of the operculum, the crab was largely unsuccessful in extracting soft tissue. Removed opercula were never found in the tanks. During laboratory predation, the crab left no observable chips or scrapes on the aperture or the rest of the shells. Upon completion of predation trials, the gastropod shells were cracked to assess damage to the soft tissue and all snails were found to be alive and relatively unharmed (little to no tissue removed) with the exception of the removal of the operculum. In one case, part of the operculum was not completely removed. All snails used in these trials lacked trematode parasites. Shell condition following predation events in the laboratory was consistent with the predated snails found in the field (Fig. 2).

*P. longicarpus* was not successful in preying on live *L. littorea* in the laboratory trials. The hermit crabs explored and examined the snails. However, it appeared that once they determined that the shells were still inhabited by snails, they did not further evaluate the shell or attempt to prey on the snails. No *L. littorea* lacked opercula at the end of trials with hermit crabs or exhibited any other damage.

#### Shell choice and partially predated snail shells

In the presence of conspecifics, *P. longicarpus* started searching and examining the new potential shells. The hermit crabs displayed normal shell choice behavior, evaluating potential shells with their chelipeds before switching shells. Shell fights occurred in low numbers. The majority of the hermit crabs (70%; 90 of 128) stayed in their chosen shell. However, a few hermit crabs kept switching shells during the last few (<3) days of the experiment. Sex of the hermit crabs had a significant effect on shell choice. Males had a preference for partially predated snail shells (58%) over original shells (24%) and empty shells (18%) ( $\chi^2_2 = 26.7$ ,  $N = 99$ ,  $P < 0.001$ ) (Fig. 3a). Females either stayed in their original shells (48%) or switched into partially predated snail shells (45%); only 7% of the female hermit crabs switched into empty shells (18%) ( $\chi^2_2 = 9.2$ ,  $N = 29$ ,  $P = 0.01$ ) (Fig. 3a). Shield lengths of hermit crabs used in the experiment were significantly different between sexes



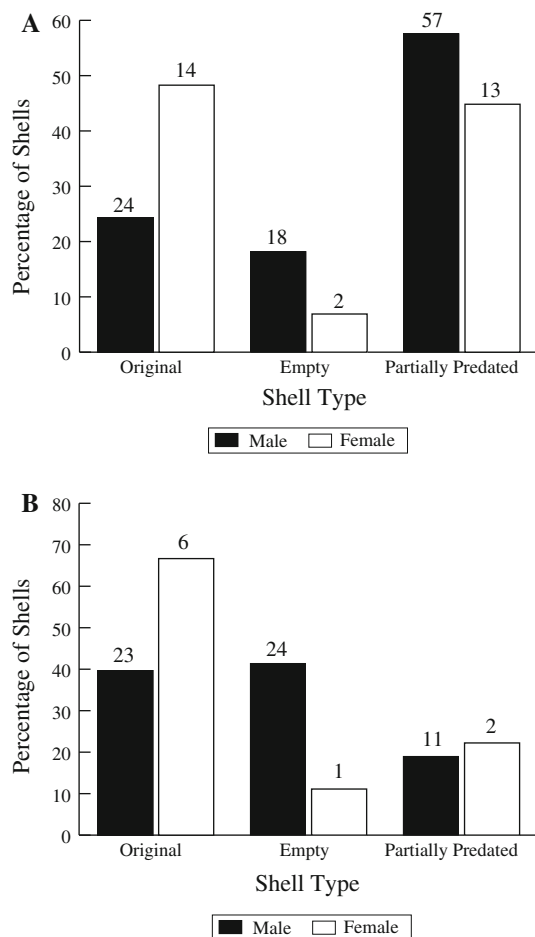
**Fig. 2** Examples of *Littorina littorea* preyed upon by *Libinia emarginata* during laboratory trials. **a** *L. littorea* without operculum on left and *L. littorea* with operculum on right. Arrows indicate operculum attachment point. **b** Close-up of *L. littorea* with operculum removed, arrow indicates operculum remnant. Scale bars, **a** = 5.0 mm, **b** = 2.5 mm

( $F_{(1,127)} = 42.2$ ,  $P < 0.001$ ) and among shell types ( $F_{(2,127)} = 17.5$ ,  $P < 0.001$ ). Tukey's HSD test showed there was a significant difference between empty and original shells ( $P < 0.001$ ) and between original and predated shells ( $P < 0.001$ ). The average male shield length was  $3.35 \pm 0.32$  mm ( $N = 99$ ) and the average female shield length was  $2.89 \pm 0.23$  mm ( $N = 29$ ).

All shells were cracked after 2 weeks to observe the amount of soft tissue still present. Most shells contained no snail soft tissue. No pieces of tissue were found in the tanks or filters and although the hermit crabs were not directly observed eating the snail tissue, it is likely that the hermit crabs ingested the material during unobserved periods. Once the shells were cracked, many exhibited a foul odor of recent decay. However, the 2-week period is too short for complete snail tissue decay in the absence of hermit crabs (see the following section on fate of snail tissue), supporting the conclusion that hermit crabs ate the soft tissue.

When the hermit crabs were offered shells in isolation, they were not as active as the hermit crabs in the presence of conspecifics and stayed near the dividers of the tanks.





**Fig. 3** Shell choice of male and female *Pagurus longicarpus* between original, partially predated snail, and empty shells. **a** Shell choice of hermit crabs when placed in tanks with four conspecifics. **b** Shell choice of hermit crabs in isolation. Percentages indicate proportion of hermit crabs using each shell type; the observed number of hermit crabs found in each shell type are shown above each bar

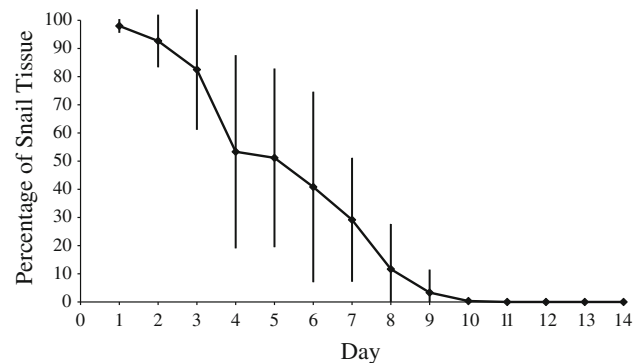
In isolation, the sex of the hermit crabs did not have a significant effect on shell choice ( $\chi^2_2 = 4.7$ ,  $N = 9$ ,  $P = 0.09$  for females;  $\chi^2_2 = 5.4$ ,  $N = 58$ ,  $P = 0.07$  for males) (Fig. 3b). The majority of the males either switched into empty shells or stayed in their original shells, 41 and 40%, respectively; 19% of the male population switched into predated snail shells. The majority of females stayed in their original shell (67%), when compared to predated snail shells (22%) and empty shells (11%). Shield lengths of hermit crabs were significantly different between sexes ( $F_{(1,66)} = 27.4$ ,  $P < 0.001$ ) but not shell type ( $F_{(2,66)} = 2.7$ ,  $P = 0.07$ ). The average male shield length was  $3.60 \pm 0.32$  mm ( $N = 58$ ), and the average female shield length was  $2.98 \pm 0.30$  mm ( $N = 9$ ). Predated snail shells that were inhabited by hermit crabs did not possess any snail tissue at the end of the experiment.

Social condition (presence or absence of conspecifics) did impact shell choice for male but not female hermit

crabs ( $\chi^2_2 = 10.8$ ,  $N = 91$ ,  $P = 0.005$  and  $\chi^2_2 = 0.52$ ,  $N = 26$ ,  $P = 0.77$ , respectively). However, impact of social condition on shell choice was confounded by that fact that males from the isolated tanks were significantly larger than those in the conspecific tanks ( $F_{(1,122)} = 49.1$ ,  $P < 0.001$ ); females from the conspecific tanks were not significantly larger than those from the isolated tanks. In addition, original shells were significantly smaller in shell length ( $F_{(2,122)} = 4.2$ ,  $P < 0.02$ ) and shell aperture ( $F_{(2,122)} = 36.4$ ,  $P < 0.001$ ) for both the experiments with isolated hermit crabs and random sample of hermit crabs in presence of conspecifics.

#### Use of partially predated shells and fate of snail tissue

When a shell-less hermit crab and one partially predated *L. littorea* was placed in a tank, complete tissue removal occurred within 10 days from the beginning of the trials (Fig. 4). In total, 46 hermit crabs (43 males and 3 females) with an average shield length of  $3.4 \pm 0.3$  mm ( $N = 46$ ) were allowed to inhabit partially predated shells that had an average total length of  $19.5 \pm 1.4$  mm ( $N = 46$ ) and an average aperture of  $10.6 \pm 0.8$  mm ( $N = 46$ ). All 46 hermit crabs moved into the shells within 1–2 days. On average, hermit crabs needed  $8.5 \pm 1.6$  days to completely remove the snail tissue. During the first few days of the trial, there was usually a nearly whole snail still present. The snails appeared to be dead and did not move or retract if touched. As the trial progressed, there was a steady decrease in the amount of snail tissue present in the shells until the tissue was completely gone. There was no evidence of snail tissue in the tanks. Shells exhibited an odor of decay that lasted about 2–3 days after the tissue had been removed. The snails in the control tank (absence of hermit crabs) exhibited no appreciable decay over the 2-week period.



**Fig. 4** Percentage of tissue of *Littorina littorea* remaining in shells inhabited by *Pagurus longicarpus* over a 2-week period. Error bars show standard deviation

## Discussion

Although the prevalence of occupation of partially predated snails was relatively low (<3% overall) in the field, our findings are most likely conservative estimates of the availability of this resource in hermit crab populations. Decapod predators are certainly supplying shells to the hermit crabs and shells that have been partially predated are an important resource to hermit crabs, supplying two resources—a new home and food (Imafuku and Nakamura 1995). Similar results have been found at octopus middens where hermit crabs feed on the flesh remaining in predated snail shells and will use these shells as a new home (Gilchrist 2003). There are a variety of predators that leave empty gastropod shells for hermit crab use, ranging from invertebrates such as predatory snails and crabs to vertebrates such as fishes and sharks (Table 1). Although some snail predators leave empty gastropod shells suitable for hermit crabs, many predators crack or chip the shell (*Carcinus maenas*) or drill holes (*Melongena corona* (Gmelin 1791)) leaving suboptimal shells. Crabs usually do not pull the soft tissue completely from the aperture. Juvenile and small *C. maenas* from Maces Bay, Canada, were able to remove gastropod tissue from the aperture without damage to the shell, but the mechanism was not recorded (Randeley and Thomas 1987). However, larger *C. maenas* crush or chip the shell to gain access to the soft tissue (Hadlock 1980), damaging the shell too much for mature hermit crabs to occupy. Newly settled hermit crab recruits and juveniles may use shell apices left by predators (Gilchrist 2003; Turra et al. 2005).

Based on appearance of shells and lack of damage, large *C. maenas* do not appear to be supplying partially predated shells to the Long Island hermit crab populations we studied. Instead, the non-destructive gastropod predator *L. emarginata* was mostly likely supplying hermit crab populations with these shells. Ropes (1989) found that *L. emarginata* ate gastropods under laboratory conditions; unfortunately, the species of gastropods were not identified and the mechanism by which the spider crab acquired the snail tissue was not described. Similarly, Schenk and Wainwright (2001) showed that *L. emarginata* ate gastropods but ingested more vegetation. The high abundance of spider crabs at sites such as Oak Beach (McGuire pers. obs.) appeared to have led to the novel findings of their predation attempts leaving shells for hermit crabs. Although unsuccessful in ingesting large amounts of the soft tissue of *L. littorea* (at least in the laboratory), the spider crabs removed the opercula of shells. Since the opercula were never found in the tanks after a predation event, this material may have been ingested by *L. emarginata*. Other crabs attack gastropods in a similar manner, leaving shells for hermit crabs to inhabit. For example,

*Callinectes danae* from Brazil was found to insert its sharp, thin claws into gastropod shell apertures, damaging the operculum and consuming the snail tissue (Turra et al. 2005). The size of the brachyuran crabs may also affect snail predation and shell use by hermit crabs. Larger adult crabs (e.g., *Callinectes* spp.) could crack the snail shells and leave them uninhabitable but juveniles might remove the opercula and hence not damage the shells in the process.

Hermit crabs were not able to predate on the snail shells in the laboratory. Their claws were too small and not powerful enough to grasp the operculum and hold the snail shell in place at the same time. In fact, there have been only a few documented cases in which hermit crabs were shown to prey on live snails (Table 2). In Japan, Imafuku (1983) observed 26 shell acquisition events by *Pagurus geminus* in the field and found that in 4 cases (15%) this species directly attacked snails for their shells. Rutherford's (1977) snail predation experiments with *Paguristes turdigus* showed that this species was able to prey on *Busycotypus canaliculatus* under laboratory conditions by pulling on the siphon and foot. However, *P. turdigus* does not naturally encounter *B. canaliculatus* (observations were made in tanks) and the snails may have been unhealthy. Similarly, Brightwell (1953) found that the European hermit crab *Pagurus bernhardus* was able to remove *Buccinum undatum* (Linnaeus, 1758) from shells, likely because they were dead or dying.

Empty shells in good condition are a major limiting factor in many hermit crab populations (Kellogg 1976; Scully 1979), and thus partially predated snail shells provide a valuable resource. The limited availability of optimal shells may be due to low gastropod death rates, low predation rates on snails and rapid occupation of empty shells (Mantelatto and Meireles 2004). When optimal shells are limited, hermit crabs will occupy suboptimal shells, e.g., damaged or ill-fitting shells. In the present study, the larger males were more often found in the partially predated shells, suggesting they may outcompete females for this resource that provides both a new home and food. Similarly, Asakura (1995) found that males of *Diogenes nitidimanus* (Terao, 1913) were better competitors than females in shell acquisition. In contrast, Turra (2003) found that ovigerous females used undamaged, non-encrusted shells more often than non-ovigerous females and males. Also, males showed no preference between encrusted and non-encrusted shells (Turra 2003). Although partially predated snail shells are clearly in high demand by hermit crabs, it should be noted that the fit of these shells may not be optimal both when initially occupied (due to the presence of the snail tissue) and after the tissue is removed (shells may be bigger than optimal size).

Hermit crabs usually inhabit shells as soon as they become available; otherwise, the shells will be buried by sediment, damaged by abrasion, or inhabited by other organisms (Wilber and Herrnkind 1984). As a result, empty shells typically do not last long in the field. Studies have shown that abrasion was the highest within the first few months after snail death; within 9 months, the shells were too worn for hermit crab use (Walker and Carlton 1995). Since most hermit crabs do not appear able to prey on live snails, they must wait for other gastropod predators to supply new shells and occupy shells after death of the snail. This is why it is believed that new shells are supplied to the hermit crab populations slowly (Walker and Carlton 1995). Areas that have higher abundance of gastropod predators and snails tend to have higher abundance of hermit crabs (Wilber and Herrnkind 1984).

Chemical cues (e.g., peptides or hemolymph) released from injured gastropods are used by hermit crabs to find freshly predated shells (Rittschof 1980a, b; Gilchrist 1984; Rittschof et al. 1990, 1992, 1995; Kratt and Rittschof 1991; Rittschof 1992; Diaz et al. 1994; Hazlett 1996; Rittschof and Hazlett 1997; Chiuissi et al. 2001; Pezzuti et al. 2002; Gherardi and Tiedemann 2004; Gherardi and Atema 2005; Tricarico and Gherardi 2006; Tricarico et al. 2009). *Pagurus longicarpus* is known to quickly form small aggregations at gastropod predation sites and exchange shells (Tricarico and Gherardi 2006 but see Gilchrist 1984 and Rittschof 1980a). Detection of shells by chemical cues from snail tissue allows *P. longicarpus* to locate shells over 10 m away (Rittschof et al. 1992), thus insuring that most partially predated snail shells will be found and occupied (in contrast to shells without tissue present that typically must be found by sight or contact). *P. longicarpus* has also been shown to be attracted to odors of dead conspecifics (Gilchrist 1984; Rittschof et al. 1992; Hazlett 1996). Since hemolymph is released when a hermit crab is injured, hermit crabs appear to seek shells at these sites. However, Gherardi and Atema (2005) found *P. longicarpus* remained motionless in the presence of conspecifics, presumably to avoid predation by remaining inconspicuous. Hermit crabs can directly detect effluents from predators and under such conditions will hide for longer periods (e.g., Rosen et al. 2009).

In contrast to optimal shells, hermit crabs in some populations encounter a high number of damaged shells. Damage to shells can result from predation events or following natural death of the snails. Damage from predation includes broken or chipped shells from brachyuran crabs (e.g., *Cancer* spp.) and drill holes from predatory snails (e.g., *U. cinerea* and *M. corona*). Wilber (1990) showed that damage to the apex affected the hermit crab decision more than aperture damage in shell choice experiments with *P. longicarpus*. He also found that *P. longicarpus*

prefers apex or aperture damaged shells to shells that exhibit both types of damage. *P. longicarpus* prefers apex or aperture damaged shells to large shells, showing that the ill effects of damaged shells outweigh the energy expense of carrying large shells (Wilber 1990). However, shells with a drill hole may not adequately protect against desiccation due to the inability to hold water. Drilled shells expose hermit crabs to decapod predators and allow easier eviction by conspecifics during shell fights (Pechenik et al. 2001). The type of damage to the shell also influences shell choice. Shells with drill holes appear to be more detrimental than shells with apex and aperture damage or small intact shells (Wilber 1990; Pechenik and Lewis 2000; Pechenik et al. 2001).

Hermit crabs may have preferred partially predated snail shells to their original shells due to the potential food source provided. Hermit crabs spend much of their time foraging for food and thus using partially predated shells would be a great benefit. The means by which the hermit crabs feed on the snail tissue remains unknown. It is possible that the hermit crabs leave the shell for short periods of time to feed on the snail tissue. Another possibility is that the hermit crab fed on the tissue from a partially predated shell while still in their chosen shell by withdrawing into the shell and consuming small portions of tissue. The hermit crabs may also use their posterior walking legs to pull tissue forward or pump their bodies in the shell to transfer decaying tissue forward. In addition to a food source, hermit crabs gained shells that were in good condition since snails have the ability to repair the shell and have an anti-fouling mechanism (Wahl 1989). Once the snail dies, the shells start to deteriorate. Shell strength decreases and epibionts start to settle on the shell (LaBarbera and Merz 1992).

The present study showed that in the presence of conspecifics, *P. longicarpus* preferentially moved into partially predated and empty shells. Under conditions where competition with conspecifics was present, there appeared to be greater motivation for the hermit crabs to inhabit optimal shells. Gherardi and Atema (2005) found that odors from live conspecifics induced *P. longicarpus* to engage in shell investigation behaviors. In addition, research has shown that *P. longicarpus* engages in fights based on the shell adequacy of occupied shells, regardless of the quality of shells inhabited by conspecifics (Gherardi 2006; Tricarico and Gherardi 2007a, b). In the present study, even though the partially predated shells were slightly (but not significantly) smaller, hermit crabs still switched to these shells. Shells in good condition and with a food source appear to outweigh the impacts of smaller size in shell choice.

In contrast to shell choice in the presence of conspecifics where the hermit crabs often took both resources (new shell and food), *P. longicarpus* in isolation did not switch shells

as much and, when they did, the majority switched into empty shells. Such differences in shell choice of hermit crabs based on the presence or absence of conspecifics have been found in previous studies (e.g., Gherardi and Atema 2005). However, the findings in the present study are difficult to interpret because of the partially predated snail shells acting as both a new home and a potential food source and due to the confounding factors that males from the isolated tanks were significantly larger than those with conspecifics and original shells were significantly smaller. If the isolated hermit crabs were using the snail as a food source, they would not need to switch into the shell; instead they may have stayed in their original shells and fed on the tissue of the partially predated snails. Since there were no competitors, there was no need to occupy the shell in order to protect the food source from being stolen. Further experimental studies are needed to control for factors of hermit and shell size and to determine the influence of the food resource of partially predated snail shells in the motivation of hermit crabs to switch shells. The impact of the motivational state (occupation of suboptimal or damaged shells) and hunger state of the hermit crabs (Gherardi and Atema 2005) should also be considered in these future studies. Due to the lack of optimal shells, hermit crabs will often engage in agonistic behaviors to obtain desired shells when there is a low abundance of optimal shells. This type of behavior typically occurs between two hermit crabs of different sizes and results in shell exchange. Hazlett (1980) found that males predominantly were both the initiators and non-initiators of the shell fights behavior. Females (ovigerous or not) normally do not engage in shell fighting behavior.

*P. longicarpus* appeared to be consuming the snail tissue after they inhabited the shell, as has been found in previous studies (Imafuku and Nakamura 1995). The lack of tissue pieces in the tank and the fact that all the tissue had been removed suggested that the hermit crabs were eating the tissue. Other evidence that the hermit crabs consumed the snail tissue was that complete decay takes longer than 2 weeks. Although natural decay following snail death is certainly occurring, this decay takes longer than the time frame for snail tissue removal that was determined in the laboratory (<10 days). The shells that were found in the field with snail tissue still present showed that the hermit crabs recently (within approximately 1 week) moved into the shell and had not completely eaten the tissue yet. In the laboratory, the snails appeared to be dead approximately 1 day after the hermit crabs inhabited the shells. The one instance in the field where a snail was found alive after hermit crab inhabitation suggests that the hermit crab recently moved in (within 24 h); remarkably, the snail harbored parasitic trematodes. If these parasites weakened the snail, it is possible that this hermit crab

directly attacked the snail (as found in other reports; see Table 2).

In the field, the different amounts of snail tissue found in the shells was mostly likely due to the variation in time that had passed since the hermit crab moved in and the amount of feeding that had taken place. Tissue decay odor was detected in the laboratory while the hermit crabs inhabited the shells even when only a small piece of tissue remained and even when there was no detectable tissue left in the shell. Similar cases of odoriferous shells were found in the field, providing evidence that the snail had died recently (or had been attacked by a predator) and the hermit crab subsequently inhabited the shell. These shells were not counted as hermit crabs inhabiting partially predated snail shells, but this odor is indicative of a recent snail death. Thus, hermit crab occupation of recently predated snails appears to be more prevalent than previously acknowledged. Evidence for this also comes from studies showing that hermit crabs readily switched into shells with snail tissue remaining when experimentally provided in the field (Imafuku 1984). Future studies should examine the prevalence of partially predated snail shells in other hermit crab populations and the potential dual function of such shells as new homes and food sources.

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