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INTRODUCTION

Most species of hermit crabs rely on gastropod shells to protect their uncalcified abdomens, and these mobile shelters help guard against predation, desiccation, and physical stresses (Hazlett, 1981). Shells are so essential that their availability has been considered a limiting factor for populations (Vance, 1972; Spight, 1977). The types of gastropod shells available also determine the size of hermit crabs present in an area (Markham, 1968). In shell-limited environments crabs are often forced to occupy inadequate shells, which in turn restricts not only their growth and fecundity but also increases their risk of predation (Sripathi et al., 1977). There is considerable evidence that hermit crabs do not enter gastropod shells at random, but select shells according to shell species and their associated characteristics of shape, epibionts, dimension, and weight (Grant & Ulmer, 1974). This differential shell preference may lead to a form of habitat partitioning that increases the likelihood of coexistence between similar hermit crabs (Vance, 1972).

*Pagurus hartae* (McLaughlin & Jensen, 1996) is a tiny species (maximum carapace length 6 mm) found from the Queen Charlotte Islands, Canada to the Mexican border. It occurs subtidally under rocks and in crevices at depths of 6-635 m, and large assemblages can be found in parts of Barkley Sound on Vancouver Island, British Columbia, Canada (Jensen, 1995). The present experiment was undertaken to determine what types of shells this newly described species occupies in natural surroundings and whether they exhibit any preference for shell species.

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MATERIALS AND METHODS

One hundred thirteen *Pagurus hartae* were captured on 15 and 23 August 2002 by dredge in Satellite Passage near the north shore of Helby Island (51°01′N 125°11′W) in Barkley Sound, British Columbia, Canada. The crabs were brought back to the Bamfield Marine Sciences Centre where they were held in an open circuit seawater system, and the species of shell used by each was identified.

To test for shell preference, 21 adult crabs were anaesthetized and extracted from their shells. Crabs were anaesthetized using a drop of oil of cloves diluted in 25 ml of seawater; after 10-15 minutes of immersion they were gently removed from their shells. Visibly parasitized (e.g., rhizocephalan externae) and ovigerous crabs were not used, nor were any that were damaged in the process. The naked crabs were isolated in ice cube trays immersed in an ambient (10°C) open circuit seawater system and allowed to recover for at least twelve hours.

Living and dead *Homalopoma luridum* (Dall, 1885), *Calliostoma ligatum* (Gould, 1849), *Amphissa columbiana* Dall, 1916, *Nassarius mendicus* (Gould, 1850), and *Alia carinata* (Hinds, 1844) shells were collected from Barkley Sound beaches. Shells were boiled in fresh water for 20 minutes to kill any associated organisms and to aid in removing tissues. Hermits can recognize and select their own previously inhabited shell by means of chemical cues; boiling destroys the cues left behind by previous occupants (Benoit et al., 1996).

Shells were categorized into three types based on their shape: (a) *Homalopoma* (short, globose structure), (b) *Calliostoma* (conical or top-shaped), or (c) *Alia, Amphissa*, and *Nassarius* (elongated). *Alia, Amphissa*, and *Nassarius* were used interchangeably, since they are very similar morphologically. Undamaged shells with aperture measurements similar to the individual crab’s original shell were used in the trials.

Naked crabs were placed singly into large glass preparation dishes (10 cm in diameter, with a volume of 350 ml) provided with running seawater and a substratum of washed sand and gravel. Each trial consisted of four shells each of *Homalopoma, Calliostoma*, and a mix of *Alia, Amphissa*, and *Nassarius*, randomly dispersed into the dish. Each trial ran for 12 hours and shell occupancy was noted at the end of that time; each crab was used only once. Some shells were boiled and reused in later trials. Shell choice was analysed using a Chi-square test.

RESULTS

The gastropod shells occupied by *Pagurus hartae* in the field consisted of 9 genera (fig. 1). Shells of *Calliostoma ligatum* were most frequently utilized (41.6%)
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Fig. 1. Proportions of shell types used by Pagurus hartae (McLaughlin & Jensen, 1996) in the field (n = 113). followed by Amphissa columbiana (26.5%), Alia carinata (9.7%), Nassarius mendicus (8.0%), and Homalopoma luridum (5.3%). Lacuna variegata Carpenter, 1864, Oenopota fidicula (Gould, 1849), Trichotropis cancellata Hinds, 1843, and Trophonopsis spp. were each used by fewer than 3% of the crabs collected. Two had severely worn and damaged shells that could not be identified.

Of the 21 P. hartae used in the shell selection experiment, 13 selected Homalopoma, five selected Alia, Amphissa, or Nassarius, and three selected Calliostoma (fig. 2). Of those that chose Homalopoma, four were originally housed in Alia, Amphissa, or Nassarius, six in Calliostoma, and three retained the same species of shell. Of five crabs that chose one of Alia, Amphissa, or Nassarius, three were originally housed in Calliostoma. The three crabs that selected Calliostoma were originally housed in that species. P. hartae did not randomly choose their new shells ($\chi^2 = 8.00$, d.f. = 2, 0.01 < p < 0.025) inhabiting Homalopoma significantly more often than the other types of shells offered.

DISCUSSION

Most field-collected Pagurus hartae were found utilizing shells of Calliostoma ligatum, yet this species was clearly not preferred when the crabs were given
a choice. In the laboratory, *P. hartae* selected *Homalopoma luridum*, a species used by only 5.3% of the *P. hartae* collected in the field. This suggests that shell utilization by *P. hartae* at that time and location depended on factors other than preference, such as shell availability or interspecific competition. The latter seems unlikely, however, given the very low numbers of other species that were present in the catch.

Hermit crabs show a tendency to use the shells of the most abundant coexisting gastropods, revealing the importance of shell availability in shaping their shell utilization patterns (Reese, 1969). Given the high proportion of *P. hartae* in *C. ligatum* shells, it can be inferred that this species was common in the *P. hartae* habitat and indeed, it was by far the most abundant snail caught in the dredge along with *P. hartae*. Elwood et al. (1979) found that *Pagurus bernhardus* (Linnaeus, 1758) with prior experience using a shell species were more likely to choose that same species when given a choice. In our experiment, shell selection by *P. hartae* was independent from the type of shell in which the crab was originally found.

Hermit crabs choose shells based on a wide variety of features, including shell configuration, aperture size, and shell weight/crab weight and shell weight/shell volume indices (Reese, 1963; Grant & Ulmer, 1974). From a physiological and anti-predator standpoint, shell shape can have important implications for intertidal and terrestrial hermits. In general, highly spiraled shells may hold water, thus protecting hermit crabs from temperature extremes (due to the high specific heat of
water), while low spiraled shells confer better protection from predation (Bertness, 1982). Since _P. hartae_ are strictly subtidal, thermal considerations are not a factor and protection from predators is probably the most important function of the shell. The thick, globose shell of _Homalopoma_ had the lowest spire of any of the species tested and presumably offers the greatest protection.

Another intriguing possibility is that _P. hartae_ could be selecting shells based in part on their durability. _Calliostoma_ shells decay at a remarkably fast rate following the death of the snail, causing the shell to lose about half of its original strength in compression tests after only three days (LaBarbera & Merz, 1992; Vermeij, 1993). In contrast, dead _Tegula_ shells withstood 12-15 months of use by intertidal hermits before becoming too worn and damaged to use (Kuris et al., 1979). Such rapid deterioration of _Calliostoma_ shells would necessitate frequent replacement. Since it has been demonstrated that some hermit crabs chemically recognize shells by their calcium (Mesce, 1993a, b) it is conceivable that they could also recognize and avoid shells that are dissolving at an excessive rate. This could be experimentally tested using shells modified to slow their dissolution rate. Alternatively, choice could be influenced by prior experience with rapidly dissolving shells; this would require testing captive-reared crabs to see if it is a learned response.

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**REFERENCES**


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