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Population dynamics and epibiont associations of hermit crabs (Crustacea: Decapoda: Paguroidea) on Dog Island, Florida

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Abstract

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Periodic belt transects and daily shoreline surveys in January and in June–July over a 10-year period (1992–2001) were used to study the seven species of hermit crabs most common in the upper intertidal zone of a low energy bay with a 960 m shoreline at the east end of Dog Island, Florida, and their association with three common shell epibionts in the area: the Florida hermit-crab sponge, *Pseudospongosorites suberitoides*, the cloak anemone, *Calliactis tricolor*, and the hydrozoan *Hydractinia echinata*. Of 15,052 hermit crabs sampled, *Pagurus longicarpus*, *Pagurus pollicaris*, and *Pagurus impressus* were prevalent in January (88% of all animals) and *Clibanarius vittatus* dominated in the summer (86% of all animals). The following associations were highly significant: *P. impressus* with *P. suberitoides, P. pollicaris* with *H. echinata*, and *Petrochirus diogenes* with *C. tricolor. C. vittatus* rarely had anemones, and *P. impressus* were never found in shells with *H. echinata* and showed a significant tendency, whether in sponge or shell shelters, to become stranded compared to other pagurid species. Hermit crab sponges were commonly used as shelters by only two of the hermit crab species, *P. impressus* and *Paguristes hummi.* Together these two species accounted for 99% of the 1077 animals found in sponges. Hermit crab sponges varied yearly in abundance from plentiful to uncommon, and nearly half (1030 of 2107, or 49%) were empty.

Keywords Crustacea, Anomura, hermit crab, population dynamics, epibiont

Introduction

Studies of hermit crabs on Dog Island, Florida, a barrier island in the north-eastern corner of the Gulf of Mexico, over a 10 year period have shown the seven most common species encountered in intertidal waters surrounding the island to be as follows: *Pagurus longicarpus* Say, 1817, *Pagurus pollicaris* Say, 1817, *Pagurus impressus* (Benedict, 1892), *Pagurus stimpsoni* (A. Milne Edwards and Bouvier, 1893), *Paguristes hummi* Wass, 1955, *Petrochirus diogenes* (Linnaeus, 1758), and *Clibanarius vittatus* (Bosc, 1802). *Pagurus longicarpus* and *C. vittatus* are intertidal species (Strasser and Price, 1999; W. Herrnkind, pers. comm.). *Clibanarius vittatus* is a hardy species that often enters the upper intertidal and can spend days out of water (Rudloe, 1984). *Pagurus pollicaris* is primarily a shallow subtidal to lower intertidal species, and the other four are typically shallow to deep subtidal (Strasser and Price, 1999; Herrnkind, pers. comm.), although *P. impressus* moves into the intertidal zone during the winter months (Sandford and Brown, 1997). As is true for most hermit crabs, all seven species occupy gastropod shells but two, *P. impressus* and *P. hummi*, commonly use sponge shelters (Wass, 1955; Wells, 1969; Sandford and Kelly-Borges, 1997). The sponge, *Pseudospongosorites suberitoides* Diaz et al., 1993 (reclassified by McCormack and Kelly, 2002) is one of the compact and colourful hermit-crab sponges, a unique group of sponges (order Hadromerida, family Suberitidae) reported from many different locations worldwide (Sandford and Kelly-Borges, 1997). Hermit-crab sponges typically colonise a living or dead gastropod shell, although other substrates (e.g. other mollusc shells, inanimate objects such as floating docks or wharf pilings) are used (Sandford and Brown, 1997). The sponge eventually overgrows the shell which becomes increasingly more deeply enclosed within the sponge mass. If the shell is occupied by a hermit crab, the crab eventually vacates the shell and occupies a chamber within the sponge body, moving about in the sponge with only its anterior end visible through an opening maintained by the crab. Nearly all hermit-crab sponges worldwide are found in deep water, typically recovered by dredging, but on Dog Island such sponges are abundant in the intertidal zone in the winter months when *P. impressus* in sponge shelters bring sponges near shore. In the laboratory, *P. impressus* often switch from sponges into available shells, abandoning the sponges (Sandford, 1995). Because sponges are more easily affected by wave action than are shells, hermit crabs in sponges near shoreline are more likely to be affected by waves or beached by receding tides. During the month of January many sponges, both empty and occupied by hermit crabs, are found near the shoreline, or stranded and drying on shore (Sandford, 1995).

Two other commonly encountered shell epibionts in the area are the cloak anemone, *Calliactis tricolor* (Phylum Cnidaria, Class Anthozoa) and the "snail fur" hydrozoan *Hydractinia echinata* (Phylum Cnidaria, Class Hydrozoa).

To determine annual and seasonal population changes for the hermit crab species and to check for specificity in the three mentioned epibiont associations, a study was conducted on Dog Island for 10 consecutive years (1992–2001).

Methods

Study site. Studies were conducted on Dog Island, St George Sound, Florida (29°49.30´N, 84°34.30´W) annually since 1992, during the month of January (1992–2001) and during June–July for 4 years (1993, 1996, 1998, and 1999). Dog Island is the easternmost of a chain of barrier islands bounding the southern perimeter of Apalachicola Bay and St George Sound in the NE Gulf of Mexico. It is a true barrier island, made of unconsolidated sand overlying the SW-dipping limestone bedrock of the Florida platform. The island lies about 6 km offshore from the N. Florida panhandle, and is 11 km long and 1.2 km at its widest. All transect work was done in the intertidal zone of a north-facing bay at the east end of the island. The bay has a 960 m shoreline and a sandy and sand/mud bottom with scattered seagrass beds of manatee grass, *Syringodium filiforme* and turtle grass *Thallasia testudinum*. Water depth ranged from 0.3 to 1.3 m at mean low tide. At 1500 h in January water temperatures ranged from 12.5–18.5°C (normally 14–17°). January 2001 was atypical with temperatures as low as 11°C. Work consisted of periodic belt transect surveys, daily shoreline surveys, and shell/sponge switching experiments.

Shoreline surveying. Shoreline surveys were conducted once (0700–1000 h), and often twice (1400–1700 h), daily. All sponges and hermit crabs stranded on shore or in the water within 0.5 m from shoreline were collected and identified. Surveys included the shoreline of the 960 m low energy beach of the bay study site, in addition to two adjoining shores — a contiguous 700 m stretch of low energy bay beach on St George Sound up to the inlet of a tidal salt marsh and 2,300 m of high energy Gulf beach at the extreme east end of the island – a total of 3,960 m of shoreline. For the months of January 1992–2001 the surveys totalled 140 days and 338 h survey time; the summer surveys totalled 37 days and 59 h of survey time.

Belt transect surveying. In the belt transect surveys from one to four persons moved from one end of the bay to the other, collecting all hermit crabs stranded on shore and from shoreline into the intertidal zone to within 8 m from shoreline. All hermit crabs were identified to species, shell type and presence of epibionts noted, then released 200 m away in St George Sound. All sampling was done on a rising tide and usually from1600–1800 h. Sixty-six transects were taken: 46 from January 1993–2001, and 20 in the summer. Because no transect sampling was done the first year, all analyses of hermit crab populations were based on data from the last nine years of the study.

Testing for shelter preference and fidelity in Pagurus impressus. Previous studies in the laboratory (Sandford, 1995) showed that individuals of *P. impressus* prefer shell shelters. To determine shelter preference and shelter fidelity for recently field caught animals, shell/sponge switching experiments were conducted on Dog Island for three years, January 1994–1996. Shelter fidelity was measured by the tendency of animals to remain in their original shelters over the course of up to a 3 day testing and observation period.

Pagurus impressus in shell or sponge shelters collected during shoreline and belt transect surveys were isolated, then tested within 48–72 h of capture. Of 209 animals collected and used for testing, 126 were in sponges and 83 in shells of the gastropod *Strombus alatus*. All were juveniles or small adults with chela 4.5–10.0 mm long. To control for shell type preference, only animals found in *S. alatus* shells, a preferred shell for *P. impressus* (Table 4), were used in testing. Empty sponges and empty *Strombus alatus* shells were also collected. All shells and sponges used as shelter choices in the tests were field collected, either empty or previously occupied by individuals of *P. impressus*. All empty sponges were healthy (i.e. good colour with no bleaching and compact with a dense, non-flabby texture) and all empty *S. alatus* shells were undamaged and epibiont-free.

Initial Test. Each animal was placed between an empty *S. alatus* shell and an empty sponge at the center of a round (diameter 11.2 cm) plastic container, with a 1 cm depth of sand on the bottom and a 5 cm deep water column above the substrate surface. Water temperature ranged with outside temperature, from 12° to 19°C. Shelter choices were in the center of the chamber 1 cm apart with their opposite sides an equal distance from the walls of the chamber. Shelters were positioned with apertures or openings up and new sea water added after each trial. The choice shelter was of equal or slightly larger size than that occupied by the crab. The test lasted 30 minutes. Animals that switched into a new shelter were noted, then released and not tested again. It was noted whether the animal switched short-term (remained in the new shelter for <3 min) or long-term (remained in the new shelter for >3 min; crabs that remained in the new shelter for >3 min rarely returned to their original shelter).

Follow-up test. Any animal that did not switch into a new shelter during the initial test was immediately returned to its original container along with the two empty choice shelters and observed periodically for 72 h. All animals that switched into new shelters were noted; for such animals the test was considered ended if the animal remained in the new shelter for >24 h.

Data was analysed for significance using Minitab statistical software.

Results

Sponge abundance. Sponges varied in abundance by season and from year to year. A total of 2107 sponges were collected in ten years. Sponges were common in the winter (99.3% of all specimens) and uncommon in the summer, and approximately half were without a hermit crab occupant (Table 1). Sponge abundance in January varied on an annual basis and in a roughly cyclical way: sponges were abundant in 1994, common in 1992 and 1996, less common in 1993, 1995, 1997, 1999, and 2000, and uncommon in 1998 and 2001. In 1992, the first year of the study, hermit crab sponges were numerous and 358 were collected; 197 (55%) were occupied by a hermit crab, all of which were *Pagurus impressus*. But hermit crabs in sponges are more easily stranded on shore than those in shells and no transect sampling was done in 1992. To control for sampling bias, all analyses of associations between hermit crabs and sponges were restricted to the data gathered by both transect and shoreline sampling from 1993 to 2001.

Hermit crabs of Dog Island. A total of 15,052 hermit crabs, representing seven species, were surveyed over the ten year period. The four most common species (*P. impressus, P. pollicaris, P. longicarpus,* and *C. vittatus*) comprised over 98% of all hermit crabs sampled annually (Table 2). All species, with the exception of *C. vittatus*, were most prevalent during the winter. In January individuals of three species, *Pagurus impressus, P. longicarpus,* and *P. pollicaris*, constituted 96% of all animals sampled; the most prevalent species was the intertidal species *P. longicarpus* which comprised 41% of all animals sampled (Table 2). The typically subtidal species *P. diogenes, P. hummi,* and *P. stimpsoni* occurred sporadically. In the summer, individuals of *C. vittatus* dominated the intertidal zone, along with some individuals of *P. longicarpus* and *P. pollicaris*, whereas the other species were rare (Table 2).

Association of hermit crab species with sponge shelters. Two species, *Pagurus impressus* and *Paguristes hummi*, were commonly found in sponge shelters. Individuals of three other species, *P. longicarpus, P. pollicaris,* and *C. vittatus*, rarely used sponge shelters (< 0.5%) (Table 3). Over half of all *P. impressus* and nearly a third of all *P. hummi* found were in sponges. The difference in use of sponges as shelters between *P. impressus* and *P. hummi* compared to the other 3 species was highly significant ($\chi^2 = 9608$, df = 2, $P < 0.001$). Although individuals of both *P. impressus* and *P. hummi* were found in sponges, the greater association with sponges by *P. impressus* was significant (two sided test for equality of two proportions, $Z = 5.14$, $P < 0.001$). Individuals of *P. impressus* showed a highly significant association with sponge shelters compared to all other species and to *P. pollicaris*, the third most common species using sponges (Table 3). Of all 1494 *P. impressus* collected from 1993–2001, most (56%) were in sponges, compared to only 7 of 1,621 *P. pollicaris* found in sponges (two sided test for equality of two proportions, $Z = 42.6$, $P < 0.001$).

Most of the 1,077 occupied sponges in the study contained individuals of *Pagurus impressus* and most of the sponges collected in the study were found stranded on shore, but a noticeable association of *P. impressus* with sponge shelters is also evident for all animals collected in water during the belt transect surveys (Table 4). A total of 454 *P. impressus* individuals were collected in the surveys from 1993–2001. Of these 194 were in sponges (42.7%) and 260 were in shells (57.3%). Individuals of *P. impressus* used 15 shell types, but three, *Strombus alatus*, *Cantharus cancellarius*, and *Busycon contrarium*, were used by 72% of all individuals (Table 4). Because nearly all hermit crab-occupied sponges, whether collected in water or on shore, contained individuals of *P. impressus* and because the frequency with which empty sponges were found in January varied annually (from 87% in 1997 to 19% in 2000) the data for 1993–2001 were analyzed to see if the number of empty sponges sampled correlated with the number of *P. impressus* surveyed. Poor correlations were found for both (i) the total number of *P. impressus* surveyed (in both sponges and shells) ($R^2 = 0.44$) and (ii) only the *P. impressus* found in shells ($R^2 = 0.27$).

Table 1. Hermit crab sponge abundance on Dog Island, Florida, by season, over a ten-year period (1992–2001).

Time of year	Empty	With hermit crabs	Total
Winter (Jan 1992–2001)	1017	1075	2092
Summer (1993, 1996, 1998–1999)	13	2	15
Total	1030	1077	2107

Association of four hermit crab species with the hydroid Hydractinia echinata. For the four most common hermit crab species, 13,995 individuals were in shells, and of these, 1343 (9.6%) were covered with hydroids of *Hydractinia echinata* (Table 5). The association of the hydroid with the four hermit crab species was dramatically non-random. No individuals of P. *impressus* or of *C. vittatus* were associated with hydroids, whereas 66% of *P. pollicaris* and 8% of *P. longicarpus* were in hydroid-covered shells (Table 5). The differences between the three pagurids were all highly significant (two-sided tests for the equality of two proportions: *P. pollicaris* vs *P. impressus*, $Z = 55.5$, $P < 0.001$; *P. pollicaris* vs *P. longicarpus,* $Z = 44.9$, $P < 0.001$; *P. longicarpus* vs *P. impressus*, $Z = 17.6$, $P < 0.001$).

Hydroids of *H. echinata* were found on all gastropod shell types commonly used by hermit crabs on Dog Island. However, to check for the possible effects of shell substrate on hydroid growth, the association of *H. echinata* with only shells of the ribbed whelk, *Cantharus cancellarius,* was examined (Table 6). Younger animals of all three pagurid species commonly use *Cantharus cancellarius* shells. This was especially true for individuals of *P. pollicaris* as over half (56%) of all animals sampled were in *Cantharus* shells, and 92% of these were covered by *H. echinata*. *Cantharus* shells were more likely to be covered by hydroids than other shell types and as was the case with all shells (Table 5), the associations of the three pagurid species in hydroid-covered *Cantharus* shells are all significantly different from one another (two-sided tests for equality of two proportions: *P. pollicaris* vs *P. impressus*, $Z = 102.3$, $P < 0.001$; *P. pollicaris* vs *P. longicarpus*, $Z = 47.1$, $P < 0.001$; *P. longicarpus* vs *P. impressus*, $Z = 15.3$, $P < 0.001$). *Pagurus pollicaris* is commonly associated with hydroids, *P. longicarpus* significantly less so, and *P. impressus* never uses *Cantharus* shells with hydroids (Table 6).

Table 2. Summary of hermit crabs collected by belt transect and shoreline surveys for nine years, 1993–2001, by season.

		Winter			Summer		
Species	Total	Number	% of species	% of all animals	Number	% of species	% of all animals
Pagurus impressus	1,494	1,489	99.7	27.6	5	0.3	<0.1
Pagurus pollicaris	1,621	1,471	90.7	27.3	150	9.3	<1.5
Pagurus longicarpus	3,399	2,203	64.8	40.9	1,196	35.2	12.4
Clibanarius vittatus	8,323	13	0.2	0.2	8,310	99.8	86.0
Petrochirus diogenes	39	38	97.4	0.7	1	2.6	<0.1
Paguristes hummi	117	116	99.1	2.2	1	0.9	<0.1
Pagurus stimpsoni	54	54	100.0	1.0	0	0.0	0
unidentified	5	5	100.0	0.1	0	0.0	0
Totals	15,052	5,389		100.0	9,663		100.0

Table 3. Association of *Pagurus impressus* and *Paguristes hummi*, two species commonly found in sponges, with five other hermit crab species that rarely or never used sponge shelters for nine years (1993–2001).

Species	Numbers	% in sponges
Pagurus impressus	1,494	55.5
Paguristes hummi	117	32.5
Pagurus pollicaris	1,621	0.4
Pagurus longicarpus	3,399	0.1
Clibanarius vittatus	8,323	<0.1
Petrochirus diogenes	39	0
Pagurus stimpsoni	54	0
Unidentified	5	0
Total	15,052	5.85

Table 4. Shelters occupied by 454 individuals of *Pagurus impressus* collected in 66 belt transect surveys, 1993–2001.

Shelter	Numbers	% total	% of shell species
in sponges	194	42.7	
in shells:	260	57.3	
Strombus alatus	76		29.2
Cantharus cancellarius	62		23.9
Busycon contrarium	50		19.2
Busycon spiratum	20		7.7
Chicoreus dilectus	12		4.6
others (10 spp.)	40		15.4
Total	454	100.0	100.0

Table 5. Association of the four most common hermit crab species (for all individuals found in shells) with the hydroid *Hydractinia echinata* on Dog Island, Florida, for nine years, 1993–2001.

Species	Numbers in shells	Percent with *H. echinata*
Pagurus impressus	622	0
Pagurus pollicaris	1,614	65.6
Pagurus longicarpus	3,397	8.4
Clibanarius vittatus	8,322	0
Total	13,995	9.6

Table 6. Association of three pagurids with shells of C*antharus cancellarius*, with or without the hydroid, *Hydractinia echinata,* on Dog Island, Florida for nine years, 1993–2001.

Species	Numbers in Shells	% in *Cantharus*	% with *H. echinata*
Pagurus impressus	662	23.3	0.0
Pagurus pollicaris	1,614	56.4	92.0
Pagurus longicarpus	3,397	28.8	19.2
Total	5,673		

Table 7. Association of five hermit crab species found in shells with the cloak anemone, *Calliactis tricolor*, on Dog Island, Florida, for nine years, 1993–2001.

Species	Numbers in shells	% with *C. tricolor*
Pagurus impressus	662	7.3
Pagurus pollicaris	1,614	5.5
Pagurus longicarpus	3,397	0
Clibanarius vittatus	8,322	0.1
Petrochirus diogenes	39	66.7
Total	14,034	1.2

Table 8. Test of shelter preference for 126 individuals of *Pagurus impressus* captured in sponges. Initial test lasting 30 minutes, checking whether the crab switched into another sponge, into a *Strombus alatus* shell, into both sponge and shell, or did not switch. Two-tailed binomial probability test, H_o: $P_{sponge} = 0.5$, P = 0.0004, significant.

Switched from sponge into:	Numbers	%
Sponge	9	7.1
Shell	32	25.4
Both	4	3.2
no switch	81	64.3
Total	126	100.0

Table 9. Test of shelter preference for 83 individuals of *Pagurus impressus* in *Strombus alatus* shells. Initial test lasting 30 minutes testing whether the hermit crab switched from its shell into a sponge, into another *Strombus alatus* shell, into both sponge and shell, or did not switch. Two-tailed binomial probability test, H_o: $P_{shell} = 0.5$, $P = 0.0006$, significant.

Switched from sponge into:	Number	%
sponge	1	1.2
shell	15	18.1
both	1	1.2
no switch	66	79.5
Total	83	100.0

Association of five hermit crab species with the cloak anemone, Calliactis tricolor. The individuals of all four species present in shells that were checked for *H. echinata* (Table 5) were also examined for the presence of the cloak anemone, *Calliactis tricolor*. Data for a fifth species, *Petrochirus diogenes*, was also recorded; this species never used sponges (Table 3) or shells covered with *H. echinata*, but was commonly found carrying one or more anemones (Table 7). A total of 14,034 individuals of the five species was collected in shells, of which 173 had anemones, nearly all of large size (basal diameter >1 cm). Anemones were never found on shells occupied by *P. longicarpus* and only rarely (<1%) found on shells containing *C. vittatus*. Anemones occurred with individuals of *P. impressus* and *P. pollicaris* about 5–7% of the time and were commonly found on shells used by *P. diogenes*. Of 39 *P. diogenes* surveyed, 26 (67%) had anemones. Of these, anemone number ranged from one to eleven individuals (mean = 3.8).

The association of *P. impressus* with anemones was significantly less than *P. diogenes* and significantly greater than *C. vittatus* (two-sided tests for equality of two proportions: *P. impressus* vs *C. vittatus*, $Z = 7.07$, $P < 0.001$; *P. impressus* vs *P. diogenes*, $Z = 7.80$, $P < 0.001$). No significant difference was found between *P. impressus* and *P. pollicaris* in terms of their association with anemones ($Z = 1.50$, $P = 0.13$).

Incidence of stranding on shore. Clibanarius vittatus is a hardy species that often leaves the water and can remain on shore for days at a time (Rudloe, 1984). During the summer transects, many individuals of *C. vittatus*, the dominant species in the bay during the summer, were found on shore. For example, in the five belt transects conducted during June 1999, 1,218 *C. vittatus* individuals were collected, and 404 (33.3%) were on shore.

Individuals of *Pagurus impressus* in sponge shelters are commonly stranded on shore. However, hermit crabs in shells are also often stranded on shore in January, and such shells are often occupied by a *P. impressus*, sometimes *P. pollicaris*, and only rarely by another hermit crab species. To determine whether individuals of *P. impressus* in shells had a greater likelihood of becoming stranded than other species, the stranding of individuals of *P. impressus* in shells was compared with *P. pollicaris*, the other species often found on shore. During the five years, January 1997–2001, 1,124 *P. pollicaris* in shells were surveyed, 1,074 in the water and 54 (4.8 %) on shore. Over the same period 283 *P. impressus* in shells were surveyed, 126 in the water and 157 (55.5%) on shore. Compared to *P. pollicaris*, individuals of *P. impressus* in shells show a significantly greater likelihood of becoming stranded on shore (two-sided test for equality of two proportions, $Z = 16.8$, $P < 0.001$), and are even more likely to be found on shore than the hardy upper intertidal species *C. vittatus*.

Shelter preference and fidelity for Pagurus impressus. (i). Initial and follow-up test for animals in sponges. In the initial choice test lasting 30 minutes, of 126 *P. impressus* in sponges, 45 animals (36%) switched into a different shelter, showing a significant preference for shells ($P = 0.0004$) (Table 8). In the follow-up test for the 81 animals that did not switch in the initial test, 43 (53%) switched shelters; of these, 42 of 43 (97.7%) selected the shell ($P < 0.0001$). In summary, 88 of the 126 (70%) animals captured in sponges switched into a new shelter, showing a highly significant preference for shells over sponges.

(ii). Initial and follow-up test for animals in shells. In the initial choice test, of 83 animals captured in *S. alatus* shells, 17 animals (20%) switched into a new shelter, showing a significant preference for other *S. alatus* shells ($P = 0.0006$) (Table 9). In the follow-up test of the 66 animals that did not switch in the initial test, 25 (38%) switched into a new shelter, always choosing a shell ($P < 0.0001$). In summary, 42 of the 83 (51%) *P. impressus* captured in *S. alatus* shells switched into a new shelter, showing a highly significant preference for other shells, not sponges. Results show that individuals of *Pagurus impressus,* a species commonly found in hermit crab sponges in the Dog Island area, exhibit a significant preference for shell shelters. The likelihood with which animals switch shelters depends on shelter type. In the shelter preference tests shelter-fidelity was also significantly higher for animals in shells (31/83 or 37.3%) than for those in sponges (19/126 or 15.1%) ($\chi^2 = 13.63$, df 1, $P < 0.001$).

Nearly all switches in the follow-up tests were long-term and >24 h. Animals in shells that switched long-term (24–72 h), always switched into other shells, never sponges. Animals in sponges showed more variability in response and a greater incidence of switching. Most animals in sponges (59%) switched into a shell, and the majority (42/48 or 87.5%) remained long-term (24–72 h). Many more animals in sponges (16%, compared to 3%) switched into both shelter choices and many of these switched into and used all three available shelters during the follow-up test. Several animals switched from seven to nine times between all three shelters during a 48 h period.

Discussion

The fact that only one or two species of hermit crabs (i.e. *Pagurus impressus* in the intertidal zone and both *P. impressus* and *Paguristes hummi* in the subtidal zone) commonly use sponge shelters in the Gulf of Mexico is similar to situations in other locations where hermit crab sponges occur. In Hokkaido, Japan, nearly all hermit crab sponges are occupied by *Pagurus pectinatus* (Stimpson), 1858 and in southwest England and Scotland by *Pagurus cuanensis* Thompson, 1843 (H. Mukai, pers. comm.; Sandford, pers. obs.). In other localities with hermit crab sponges, however, up to nine or more species use sponge shelters (e.g. British Columbia (Kozloff, 1987), Mikawa Bay, Japan (Tanaka, 1995), and the Mediterranean (Vosmaer, 1933).

In nearly every location where hermit crab sponges have been reported, they occur in deep water and are only retrievable by scuba, trawling, dredging or other means (e.g. octopus traps). Dog Island is unusual in that hermit crab sponges are common near shore or on shore. This is partially due to the behaviour of *P. impressus*, a typically subtidal species that often uses sponge shelters, which migrates into the intertidal zone in the winter, bringing sponges closer to shore. When animals in sponges switch into available shells, the empty sponges are abandoned and easily washed on shore. Nearly half of all sponges collected in the surveys were empty. Although the presence of hermit crab sponges in the intertidal zone of Dog Island in the winter is largely due to individuals of *P. impressus* transporting them from the subtidal zone near to shore, the number of empty sponges found each year from 1993 to 2001 did not correlate with the number of *P. impressus* surveyed. This suggests that sponge abundance at the study site is not due solely to the behaviour of *P. impressus* but to other factors, such as weather and tides, or the biology and reproduction of the sponges.

Recently field-caught juvenile individuals of *P. impressus*, a majority in sponge shelters, exhibit significant shell preference. Animals in either shell or sponge shelters usually switch into shells, not into sponges, supporting results of previous studies on individuals maintained in the laboratory in mixed-species assemblages or in conspecific groups (Sandford, 1994, 1995). A shell preference was also indicated by differences in short-term versus long-term switching. Animals switching into shells from either shells or sponges, usually remained in shell shelters long-term (i.e. >5 minutes, and typically at least 24–48 h). Animals switching from one sponge into another typically exhibited no such long-term bias. Crabs in sponges showed significantly reduced shelter fidelity, and were more likely to switch shelters, usually into shells. In areas where they occur, hermit crab sponges are used as alternative shelters by shell-dwelling hermit crabs, although sponges are less preferred and are likely suboptimal shelters.

These results contradict the suggestion (Benedict, 1900; Vosmaer, 1933; Rabaud, 1937; Hart, 1971) that one possible benefit of use of a sponge shelter by a hermit crab is the advantage of a longer term association with a living, growing home and a reduced need to change shelters compared to hermit crabs in shells. Encrusting sponges and bryozoans are the only gastropod shell epibionts associated with hermit crabs which would allow the crab to retain a shell shelter for a longer period by constantly growing and effectively enlarging the volume of the shelter (Stachowitsch, 1980; Taylor, 1994). Although it has been suggested that encrusting symbionts growing on gastropod shells may reduce the frequency of switching, Taylor (1994) noted that this has never been documented by long-term observations of individual hermit crabs. This study confirms that individuals of *P. impressus* using sponge shelters do not typically exhibit long-term attachments. A similar tendency to leave sponges and enter shells occurs for *Paguristes hummi* (Sandford, unpubl. data), the only other hermit crab found in the area that commonly uses sponges (Wass, 1955; Wells, 1969; Williams, 1984).

Shell/sponge switching has not been studied in sponge/crab associations from elsewhere, but in many locales only certain hermit crab species occur as the typical sponge occupants (e.g. *Pagurus cuanensis* and *Paguristes eremita* in *Suberites domuncula* from the North Aegean Sea (Voultsiadou-Koukoura and Koukouras, 1993), *Pagurus cuanensis* in *Suberites* sp. from the Adriatic Sea (Stachowitsch, 1980), the Irish coast (Selbie, 1921) or south-western England and the western coast of Scotland (Allen, 1967; Sandford, pers. obs.), and *Pagurus pectinatus* in *Suberites ficus* from Hokkaido, Japan (Sandford, pers. obs.). Shell preference for sponge-using hermit crabs from these and other locations is not known.

Wilber (1990) speculated that hermit crabs change shells frequently and Abrams (1987), studying shell switching in five hermit crab species, found that the percentage of individuals that switched shells ranged from 40% in *Pagurus hemphilli* to 81% in *P. samuelis*. In this study 47/83 *P. impressus* (57%) switched from one *S. alatus* shell into another, a figure consistent with Abrams' (1987) findings.

Use of sponges as shelters can be costly. Sponges interfere with burying in the substrate, and are more easily influenced by tides and currents or beached by waves. On Dog Island hermit crabs in sponges are seen rolling about in the swash zone and are often washed ashore. The crabs often die from desiccation but the sponges rehydrate successfully when reimmersed.

Since use of sponge shelters is costly and *P. impressus* juveniles prefer shell shelters, why are so many found occupying sponges? Several possibilities exist. Juvenile *P. impressus* either use sponge shelters because (i) they confer some survival advantage, (ii) appropriate shells are scarce, or (iii) they are out-competed by more aggressive species such as *P. pollicaris*.

Sponges may confer survival advantages, especially to small or juvenile individuals of *P. impressus*, the typical occupants. Nybakken (1996) considered the sponge/hermit crab association an example of true mutualism, with the sponge deterring crab predators with its disagreeable taste. Taylor (1994) noted that shell-encrusting bryozoans may reduce predation because of shell thickening, chamber enlargement, and camouflage. These same arguments could apply for shell-overgrowing sponges, and there is some evidence to suggest that hermit crabs in sponges are less likely to be attacked or eaten by blue crabs, *Callinectes sapidus*, a typical predator, either because of a chemical, texture, or camouflage factor (Farley, pers. comm.; Sandford, pers. obs.).

In laboratory conditions, use of sponges by individuals of *P. impressus* increases as shells become less available (Sandford, 1995) so in the field crabs may use sponges in those habitats where shells are relatively scarce. Shell scarcity is a limiting factor for hermit crabs (Kellogg, 1976, 1977; Hazlett, 1981; Pace, 1993) and may be a major factor explaining the large number of *P. impressus* using sponge shelters in the Dog Island area.

Shell use and aggression in hermit crabs are linked (Hazlett,

1981) and it has been suggested (Rudloe, 1999) and there is some evidence (Kellogg, 1977; Hazlett, 1980; Sandford, pers. obs.) that individuals of *P. impressus* are less aggressive or less competitive than other hermit crab species. Sympatric hermit crab species can coexist in spite of shell competition by exhibiting different shell preferences, habitat preferences, or other biological differences (Hazlett, 1981). Kellogg (1977) in Beaufort Harbor, North Carolina, studied many of the same hermit crab species as in this study. He found that hermit crab populations there were shell-limited and that both *P. impressus* and *P. hummi* individuals were infrequently found in inshore areas, and were likely to be outcompeted by *P. pollicaris* and *P. longicarpus*. In the Dog Island area individuals of both *P. impressus* and *P. hummi* may use the sponges as less favoured alternative shelters as a consequence of such competition.

The possible benefits of sponge shelters remain undetermined, but it is now clear that sponges are suboptimal shelters that may affect locomotion and increase mortality risks from dehydration due to stranding. Although many juvenile and some adult individuals of *P. impressus* use sponges for extended periods, most switch into shells when available.

For the other two epibionts studied, *Calliactis tricolor* and *Hydractinia echinata*, the results clearly show a significant association of *P. pollicaris* with the hydroid *H. echinata* and a significant lack of association of both *P. impressus* and *C. vittatus* with the same hydroid. The cloak anemone *Calliactis* was associated with three species (*P. pollicaris, P. impressus*, and especially *P. diogenes*) and not associated with two others (*P. longicarpus* and *C. vittatus*). The common association of *Calliactis tricolor* with *P. diogenes* found in this study has been noted by Rudloe (1984) who has found *P. diogenes* individuals with as many as 20 anemones.

The association of anemones with *P. impressus*, *P. pollicaris*, and *P. diogenes* is to be expected, as they frequent subtidal hard bottom habitats more optimal for anemones. Conversely, the two intertidal species, *P. longicarpus* and *C. vittatus*, that live in sandy bottom habitats which are less optimal for anemones, lacked anemones. The deficiency of anemones on shells occupied by *C. vittatus* may also be related to the fact that *C. vittatus* is the hardiest of all hermit crab species in the Gulf of Mexico, and often leaves the water for days at a time (Rudloe, 1984, 1999). Under such circumstances, any anemones carried on the shells would desiccate. Any association of *C. vittatus* with *C. tricolor* is non-symbiotic in nature (Brooks et al., 1995). Individuals of *Calliactis tricolor* are found rarely attached to shells occupied by *C. vittatus* but it is not certain whether anemones do not discriminate (Brooks et. al., 1995; Sandford, pers. obs.) or actually avoid *C. vittatus* as reported by Rudloe (1984).

The lack of association of *P. longicarpus* with the anemone may also be due to this hermit crab's burying behaviour. Although features such as shell size or shell damage affect the switching behaviour and survival of species like *P. pollicaris* (McClintock, 1985), Kuhlmann (1992) concluded that for *P. longicarpus* burying behaviour is probably more important than shell features as an anti-predator factor. The burying behaviour of *P. longicarpus*, in addition to its intertidal zone habitat and smaller size relative to the other species examined for anemones, likely explains the absence of anemones on shells occupied by this species. Individuals of *P. pollicaris* also commonly bury in the substrate (McLean, 1974), commonly associate with *C. tricolor* (Rudloe, 1999), and were often found with anemones in this study, so their greater association with the anemone relative to *P. longicarpus* is most likely explained by their greater exposure to habitats in the subtidal zone where anemones more commonly occur.

A preferential association of *H. echinata* with certain hermit crab species was reported by Yund and Parker (1989). The complete absence of *H. echinata* on shells used by *C. vittatus* may be explained by this species' preference for the upper intertidal zone and/or its tendency to spend time on shore. The total lack of association of the hydroid with *P. impressus* is most likely due to the rejection of hydroid-covered shells by individuals of this species.

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