Hermit crab population ecology on a shallow coral reef (Bailey's Cay, Roatan, Honduras): octopus predation and hermit crab shell use

SANDRA L. GILCHRIST

New College of Florida, 5700 N. Tamiami Trail, Sarasota, Florida 34243, USA (gilchrist@ncf.edu)

Abstract

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Shells can be a limiting factor in allowing hermit crab populations to increase. Predators of gastropod molluscs and of hermit crabs release shells into reef environments where hermit crabs find and cycle them within their populations. Predators also play a role in distributing shells among hermit crab species. To highlight how octopuses influence shell availability to hermit crabs, observations were made on members of *Octopus vulgaris* Cuvier, 1797 and *O. briareus* Robson, 1929 at Bailey's Cay Reef (Roatan, Honduras) during July and August each of three years, 1999–2001. In addition to feeding while foraging, *Octopus vulgaris* and *O. briareus* individuals create shell and debris middens outside of their temporary dens. These middens concentrate shells and food for hermit crabs in the reef environment where locating an empty shell could be difficult. However, because hermit crabs are prey items for octopuses, hermit crabs using the middens risk predation from the den occupant. Relatively small hermit crab species such as *Pagurus brevidactylus* (Stimpson, 1858) and *P. criniticornis* (Dana, 1852) were found commonly in dens and among middens, opening the possibility that the den functions as a refugium for some species as well.

Keywords   Crustacea, Anomura, hermit crab, predation, shell use, octopus

Introduction

Hermit crabs generally do not procure shells directly from live molluscs (Hazlett, 1981; for an exception see Rutherford, 1977). Recycling of postmortem shells from gastropods and from live or postmortem hermit crabs is common (Bertness, 1982; Wilber and Herrnkind, 1984). Because shell availability has been shown to be important in determining hermit crab population size, hermit crab shell use has been widely investigated both in the lab and in the field (Benvenuto and Gherardi, 2001; Elwood et al., 1979; Garcia and Mantelatto, 2001; Hahn, 1998; Hazlett, 1996; Osorno et al., 1998; Siu and Lee, 1992; Vance, 1972 inter alia). Predators on gastropods and hermit crabs provide a variety of shells for habitation by hermit crabs (Carikker, 1981; Mather, 1991; Tirelli et al., 2000). Sustainable recycling requires hermit crabs to assess continually the quality of resources within the recycle pool. Some predators leave shells intact with little apparent damage (Gilchrist, 1984; Jory and Iversen, 1983; Ray and Stoner, 1995) while other predators crush or smash the shells beyond use for hermit crabs (Brown et al., 1979; Hsueh et al., 1992; Hughes, 2000; Seed and Hughes, 1995; Vermeij, 1977; Yamada and Boulding, 1998). However, LaBarbera and Merz (1992) noted decreases in shell strength after removal of the living gastropod, suggesting that even intact shells begin deterioration upon entering the hermit crab use cycle.

The cycle of shells among gastropods and hermit crabs is not well known in coral reef environments. Octopuses consume both crustaceans and molluscs, making their potential impact on hermit crab shell cycling complex. They can prey upon hermit crabs as well as crustaceans that are hermit crab predators. In addition, they not only consume gastropods that can provide shells for hermit crabs, they also carry prey from various parts of the reef back to a den location. Mather et al. (1997) speculated that hermit crabs are sometimes associated with octopus dens as scavengers opportunistically feeding on remains of prey left in middens and dens. Some workers have indicated hermit crabs as prey items for octopuses in field studies (Iribarne et al., 1993) while other researchers have used hermit crab zoeae as prey in food searching studies of octopus paralarvae (Navarro and Villanueva, 2000; Villanueva et al., 1996). Octopuses can crush or drill their prey. They may also extract gastropod or hermit crab prey through shell apertures, leaving a relatively intact shell. The fact that octopuses not only feed on hermit crabs, but can also concentrate shell and food resources in middens formed outside of their dens suggested that their role in the cycling process should be examined more

closely in the reef system. The types of shells entering the hermit crab shell cycle for this study were noted at Bailey's Cay reef by observing octopuses in the field to determine their role in the hermit crab shell cycle.

Methods

Description of sampling area. The eastern reef area surrounding Bailey's Cay provides an opportunity to examine the hermit crab shell cycle under field conditions. The Cay is located within the Roatan Marine Preserve, so no spearfishing is allowed in the area and only artisanal line fishing from traditional canoes is permitted. Bailey's Cay is part of a collapsed volcanic ridge surrounded by patch reefs to the east ending with a reef wall that drops nearly vertically to about 30 m. There is a wall that drops vertically to 35 m with a narrow shelf to the north. A boat channel about 15 m deep between Bailey's Cay and Roatan bounds the southern part of the reef. Thus, because of the water depth surrounding the reefs of the cay, once hermit crabs and molluscs metamorphose from the plankton, they are surrounded by deeper water, restricting movements from the area.

General octopus foraging observations. Octopuses were active both day and night. They were observed using focal animal and focal area techniques (Altman, 1974) during July and August of 1999–2001 at the same area of the eastern reef of Bailey's Cay. The sampling area was approximately 5000 m^2, extending from shallow seagrass through the top of the forereef.

Though observations were made on octopuses and their dens in the same area for three years, it is unlikely that the octopuses were the same individuals each year. The life span of these animals is limited and they grow rapidly (Hanlon, 1983). The size of each octopus observed was small (3–5 cm head diameter; estimated using the methods described by Aronson, 1982), suggesting that they were juveniles. To facilitate observations, dens of octopuses in the sampling area were identified and marked discreetly. Observation areas were chosen where the minimum distance between conspecific dens was 5 m while minimum distance for different species was approximately 12 m for octopuses observed in 1999–2001. Observers using SCUBA or snorkeling remained at 2–3 m from foraging octopuses. Only animals that habituated to presence of observers were used for collecting foraging data. (The area is frequented during the day by recreational snorkelers and swimmers, thus octopuses are not in an isolated habitat). Colour changes and movements of octopuses were clearly visible from 3 m. The visibility was determined by horizontal and vertical secchi measurements.

In July–August of each year, 5–7 octopuses were identified for behavioural observations. However, only data for 3 individuals of *O. vulgaris* were analyzed each year because some octopuses were eaten by moray eels or were injured during the sampling period. Each year, 3 individuals were each followed for at least 20 minutes for each of three consecutive days (60 minutes total for each) as they emerged from their dens, generally in late afternoon or early evening. Individuals of *O. briareus* (one in 1999 and two each in 2000 and 2001 which survived the entire sampling period without injury; 5 total) were observed most often in early evening and at night; they were rarely active outside of the den during daylight hours. Each animal was observed for a minimum of 20 minutes and a maximum of 30 minutes as it emerged from the den and proceeded with foraging for each of 3 consecutive days. Civil dusk in the area occurs around 7:30 CST during July and August. Lights were used after civil dusk. These lights were not directly applied to octopuses as they foraged. Indirect lighting did not result in colour changes by the octopuses and the animals continued to forage for several hours. The observations of foraging allowed establishment of general feeding areas, feeding duration and habitats visited. Remains discarded by foraging *O. vulgaris* and *O. briareus* individuals were collected and categorised by shell type, organism consumed. Characteristic behaviours exhibited by octopuses described by Hanlon and Messenger (1996) and Mather (1991) were used to suggest items eaten away from the den, though specific numbers from foraging were not determined over the entire foraging time of octopuses in this study. Postmortem gastropod shells were identified by remains of muscles or flesh attached to shells. Gastropod shells recovered with no remaining flesh were categorised as formerly occupied by hermit crabs. Gastropod shell fragments were noted separately because former occupant could not be determined clearly for most fragments. A shell was considered a fragment for this study if at least two whorls beyond the protoconch were intact.

Hermit crab observations at octopus dens. After establishing den areas and general foraging patterns for *O. vulgaris*, remains in middens were collected and catalogued daily for seven consecutive days. *Octopus briareus* individuals generally consumed prey while hunting (about 80% eaten away from the den), however, the small middens formed by these animals were also sampled for seven consecutive days. Two active dens of *O. vulgaris* and one of *O. briareus* were selected in August 2001 for more focused hermit crab observations.

Active den sites for both octopus species were observed for hermit crab activity every 30 minutes for a two-hour period starting an hour before sunset. A circular area of one-metre diameter was outlined around each den using plastic tent pegs driven into the substrate. The 1-m area was considered the den area while the den was the physical shelter used by the octopus. As background information, two circles with 1 m diameters were marked elsewhere in the seagrass and in the coral rubble to examine hermit crab activity independent of the den sites. Hermit crabs found in the den area and around octopus dens were removed after the octopus left for a foraging bout. The background areas were sampled for hermit crabs around the same time. Live gastropods and postmortem shells were also collected within the den, den area, and background sites. Hermit crabs were removed from the den sites for seven consecutive days. Marked crabs in marked shells were returned to their original collection areas each day. Dactyls were clip-coded (Gilchrist, 1984) to allow recognition of returned hermit crabs. Hermit crab species were identified and individuals with their shells were measured using plastic calipers (precision 0.01 mm) and marked. Postmortem gastropod shells and live gastropods were marked.

In a previous study (Gilchrist, 2000), shield length was found to have the highest correlation (0.78) with shell width (an indicator of shell size) for all hermit crab species combined, so shield length is used to indicate hermit crab size in this study. Gastropod shell length, shell width from center axis, shell aperture length and shell aperture width were measured for all intact shells (those used by hermit crabs, live gastropods, and post mortem gastropod shells). In addition, number of disassociated gastropod opercula at the site was determined and these opercula were removed.

Other researchers have noted that field observations of octopuses generally yield few data (Forsythe and Hanlon, 1997), confining short-term studies to descriptive analyses. Thus, data were collected to show general trends in contributions to the hermit crab shell cycle for this study.

Results

General observations. Dens of *Octopus vulgaris* were mainly among isolated coral heads or dead coral within the grassbed while those of *O. briareus* were sometimes found in isolated coral heads but were most often located in crevices within the forereef. The average water depth for the dens of *O. vulgaris* sampled in this study was 20±3 cm while the average for those of *O. briareus* was 41±5 cm. Mather et al. (1997) and Forsythe and Hanlon (1997) noted that some octopuses modify habitats in den construction. Dens in the grassbeds were modified by the octopuses that placed rubble, large shells, and other materials around the den opening. Typically, a shell or other object was held by the octopus resident to block the den opening partially. Some excavation was also observed for *O. vulgaris* individuals. Dens of *O. briareus* did not show similar modifications; individuals of this species seemed to find a crevice and to use this area with little modification. Individuals of *O. vulgaris* were observed clearing their dens of materials frequently while individuals of *O. briareus* were not noted for removing items from the dens. During the sampling periods each year, members of *O. vulgaris* showed den fidelity, returning repeatedly to the same dens (it is unclear whether the same octopus returned to the den, but an animal of similar size returned to the den) while *O. briareus* individuals used a single den primarily, but also sheltered periodically at secondary den sites, returning to the primary den after a few days. Because of differences in den use, data for *O. briareus* were more difficult to obtain.

Visibility at the site as measured by horizontal and vertical secchi was in excess of 30 m each of the sampling days.

Octopus foraging observations. Feeding ranges for the *O. vulgaris* individuals each year were generally ovoid, encompassing seagrass areas, isolated coral heads, and patch reefs. The majority (70–80%) of foraging time was spent in seagrass and coral rubble. At least one octopus each year was eaten or injured by an eel (green moray *Gymnothorax funebris*, Ranzani, 1840) when foraging in the forereef while no deaths or major injuries (such as loss of an arm) were observed for octopuses foraging in seagrass and coral rubble. Descriptions

of feeding behaviours are modified from those made by Mather (1991). The most common feeding behaviours in the seagrass were "webover" (body web and arms spread out to form sac over part of the environment, typically accompanied by a blanching of web if prey captured) and "crawl-poke" (moving while exploring substrate with one or more arms, stopping periodically to probe among seagrasses, into holes or around objects). When foraging away from the den in the seagrasses and surrounding rubble, individuals of *O. vulgaris* concentrated feeding on *Calappa flammea* (Herbst, 1794), *Hepatus epheliticus* (Linnaeus, 1763), *Cataleptodius floridanus* (Gibbes, 1850), *Eurypanopeus dissimilis* (Benedict and Rathbun, 1891), *Mithraculus forceps* (A. Milne Edwards, 1875), *Oliva* sp., chitons (including *Tonicia elegans* (Frembley, 1827) and *Craspedochiton hemphilli* (Pillsbry, 1893)), a variety of clams such as *Macrocallista maculata* Linnaeus, 1758 and *Nucula proxima* Say 1822, and gastropods such as *Modulus modulus* (Linnaeus, 1758), *Natica livida* Pfeiffer, 1840 and *Cerithium atratum* (Born, 1778) based on observations of prey struggling beneath the web and remains observed. As noted by Forsythe and Hanlon (1997) for another octopus species, individuals of *O. vulgaris* were followed by wrasses (*Thalassoma bifasciatum* (Bloch, 1791) and *Halichoeres bivitattus* (Bloch, 1791)) during foraging, with fish snapping at material around the octopus and the octopuses seemingly ignoring the fish. Octopuses were not observed eating fish while foraging.

On the coral heads and patch reefs, crawl-poke and webover were commonly observed behaviours of individuals of *O. vulgaris*. Chitons (primarily *Acanthochitona spiculosa* Reeve, 1847, *Chiton tuberculatus* Linnaeus, 1758 and *Acanthopleura granulata* (Gmelin, 1791)) and individuals of *Mithraculus forceps* were typical prey. "Tuck-hold" behaviour where the octopus held a large prey item under the web (evidenced by one or two arms folded at their bases and a bulge or movement under the web), was more frequent near den sites while "pull-tuck-consume" where the animal is using the suckers at the base of the arms to pull apart a clam or to hold a prey while tearing or drilling (evidenced by shortening of arms, blanching of web, and remains jettisoned; see description given in Nixon and Maconnachie, 1988) was observed away from the den. Only two *O. vulgaris* individuals were directly observed eating hermit crabs while foraging among coral. In both instances (occurring during August 2000), the hermit crabs were *Paguristes puncticeps* Benedict 1901 (confirmed from examining discarded appendages and shields) in shells of juvenile (less than 45 mm shell length; Stoner et al., 1998) *Strombus gigas* Linnaeus, 1758. One octopus consumed a mean of 8 hermit crabs/foraging bout and the other ate a mean of 14/foraging bout. Other prey items were captured by *O. vulgaris* individuals and returned to their dens for consumption. Table 1 shows the observed numbers of hermit crabs eaten by octopuses while foraging along with the relative condition of the shell released during the observation periods. By far, the most common method used by the octopuses for feeding on hermit crabs was removal through the shell aperture, resulting in a shell with little visible damage.

Table 1. Numbers of shells from hermit crab (HC) and gastropod (G) prey after predation by octopuses for 1999-2001 foraging observations in seagrass, patch reef, reef and forereef areas combined. The number of octopuses included in the observations is given in parentheses. Shell fragments (F) that contain the apex are noted. Numbers of predators are given in parentheses. For octopuses, data reflect only prey not returned to dens. Category 1 – no damage, category 2 – aperture chipped, category 3 – body whorl peeled, and category 4 – apex removed or shell crushed. Shells reused by hermit crabs (RS) are given for each category. Two hermit crabs escaped from an individual of *O. vulgaris*.

Predator species	Shell condition by category												
	1			2			3			4			F
	HC	G	RS	HC	G	RS	HC	G	RS	HC	G	RS	
Octopus vulgaris (9)	35	11	21	0	3	3	0	0	–	9	3	1	2
Octopus briareus (5)	22	51	47	36	18	45	33	0	0	0	3	0	8

Table 2. Middens formed by *Octopus* species (where prey is at least 5% by number of midden content for all dens combined; listed with most common item first; modeled after Mather, 1991) returning from foraging. Hermit crab species are indicated by an asterisk.

1999	2000	2001
OCTOPUS VULGARIS		
Crustaceans		
Pitho sp.	*Pitho* sp.	*Pitho* sp
Mithraculus forceps	*Mithraculus forceps*	*Mithraculus forceps*
Calappa flammea	*Cataleptodius floridanus*	*Calappa gallus*
Calappa gallus	*Calappa gallus*	*Calcinus tibicen*
Hepatus epheliticus	*Paguristes puncticeps*	*Paguristes puncticeps*
Cataleptodius floridanus	*Calcinus tibicen*	
Eurypanopeus dissimilis	*Paguristes cadenati*	
Dardanus venosus		
Paguristes puncticeps		
Molluscs		
Nucula proxima	*Macrocallista maculata*	*Macrocallista maculata*
Natica livida	*Acanthochitona spiculosa*	*Natica livida*
Macrocallista maculata	*Natica livida*	*Oliva* sp.
Oliva circinata	*Leucozonia nassa*	*Leucozonia nassa*
Acanthochitona spiculosa	*Cerithium atratum*	*Cerithium atratum*
Modulus modulus	*Oliva* sp.	*Oliva* sp.
Echinoderms		
		Echinometra lucunter
OCTOPUS BRIAREUS		
Crustaceans		
Mithraculus forceps	*Mithraculus forceps*	*Mithraculus forceps*
Calappa flammea		*Eurypanopeus sp.*
Paguristes puncticeps		*Calappa flammea*
		Calappa gallus
Molluscs		
Macrocallista maculata	*Acantochitona spinculosa*	*Macrocallista maculata*
Conus mindanus	*Cyphoma gibbosum*	*Acanthochitona spinculosa*
Echinoderms		
	Tripneustes ventricosis	*Tripneustes ventricosis*
	Echinometra sp.	*Echinometra* sp.

Individuals of *O. briareus* also exhibited an ovoid feeding range each year, overlapping the areas where *O. vulgaris* individuals had dens and did their foraging. However, *O. briareus* individuals concentrated their feeding among the patch reef corals and forereef areas using crawl-poke behaviour. When moving between seagrass and coral patches, these octopuses swam short distances, blended with the substrate, and swam again, repeating this until reaching the seagrass. Rarely did individuals crawl on the open substrate between patch reef corals and the seagrass. Snake eels (*Ophichthus cruentifer* (Goode and Bean, (1896)) and green morays (*Gymnothorax funebris*) were observed eating *O. briareus* individuals as well as biting off arms both in dens and while foraging. Some foraging occurred in seagrasses where the webover was most common behaviour, and *Calappa flammea* and *C. gallus* (Herbst, 1903) were most often consumed. Appendages from *Mithraculus* species and *Pitho* species were also found after octopuses captured prey, as were shells and remains from *Strombus gigas* and *Leucozonia nassa* (Gmelin, 1791). Individuals of *O. briareus* were observed consuming hermit crabs each year. One octopus in the 2001 sampling season was seen eating 3 hermit crabs during a single feeding bout. All of

the hermit crabs eaten were *Paguristes puncticeps* in *Strombus gigas* shells. Each hermit crab consumed was eaten away from the den, apparently being extracted through the shell aperture (Table 1). Appendages were jettisoned as the hermit crabs were consumed and the shells were left behind. Postmortem shells were used by hermit crabs (Table 1) which sometimes brought the shells liberated from octopus foraging back to the den site.

Observations at octopus dens. Octopuses at dens had postmortem gastropod shells (from hermit crabs or from gastropods) comprise least 40% (by number) of their midden and den area contents for each of the three years surveyed in this study. It was difficult to determine how many hermit crabs were consumed at dens because remains were primarily appendages and a few shields. Table 2 lists the types of remains recovered in the octopus middens and den areas. During 2001, only one *O. briareus* individual accumulated a large amount of hermit crab material in its midden and den area (72% by weight). One of the shells in its midden had been marked from a den in the 2000 sampling year, presumably worn by a hermit crab that had been eaten or that had exchanged a shell at the midden in 2001. The octopus had a small head diameter (about 3 cm) and was the smallest specimen observed in the area. However, this individual was eaten before the end of the observation period and was not considered in the final analyses of den materials.

Live hermit crabs were found in dens and around middens (Table 3) of *O. vulgaris* and *O. briareus*. Two hermit crab species, *Pagurus criniticornis* and *P. brevidactylus*, were found in and around dens commonly. These species are considered den associates. Individuals of *P. criniticornis* (mean shield length 3.1±0.6 mm) were found most often within *O. vulgaris* dens and middens. Individuals of *P. criniticornis* represented the largest group of hermit crabs associated with dens (Table 3). Some individuals exchanged shells for those discarded by an octopus in a midden (Table 4). Individuals of *P. criniticornis* were observed feeding on remains of prey left by octopuses both in the den and at the middens. Some individuals of *P. criniticornis* remained in the den and midden area for all seven sampling days. Individuals of *P. brevidactylus* (mean shield length 4.2±0.3 mm) were also found inside dens of *O. vulgaris* within the seagrass area. These species of hermit crab occupied dens and middens primarily found in seagrass areas, however, dens in coral were difficult to observe fully. Individuals of *P. brevidactylus* observed in and around dens of both octopus species did use shells procured by the octopuses (Table 4). Only about 23% of the crabs occupying shells and fragments were new to the den sites over the entire time period sampled.

Four other hermit crab species, *Paguristes puncticeps*, *Paguristes cadenati* Forest, 1954, *Calcinus tibicen* (Herbst, 1791), and *Phimochirus holthuisi* (Provenzano, 1961), were visitors to dens and middens, but were considered den/midden transients. They did not remain at the den sites or middens for more than 1–2 days. *Paguristes puncticeps* (mean shield length 13.3±3 mm) and *C. tibicen* (mean shield length 13.7±4 mm) individuals were found almost exclusively in den and midden areas of *O. vulgaris* individuals located on patch reefs and in the fore reef. However, there was a difference in the sizes of

Table 3. Median number per day of live hermit crabs, mollusc shells, and opercula found at den sites of *Octopus vulgaris* (two den areas observed seven days), *O. briareus* (one den area observed seven days) and two background areas in August 2001. Opercula were also counted, marked and returned because muscle still attached that could serve as a hermit crab attractant. D = den, M = midden, B = background.

| | *O. vulgaris* | | *O. briarius* | | |
	D	M	D	M	B
Hermit crabs					
Calcinus tibicen	12	3	5	7	2
Paguristes cadenati	8	9	0	1	2
Paguristes puncticeps	8	23	0	11	1
Phimochirus holthuisi	0	0	3	18	1
Dardanus venosus	0	0	0	2	1
Petrochirus diogenes		0	0	0	2
Pagurus criniticornis	57	7	8	5	2
Pagurus brevidactylus	22	54	0	3	1
Mollusc shells					
Macrocallista maculata	0	17	0	2	0
Acanthochitona spinculosa	0	7	0	11	4
Cyphoma gibbosum	0	5	0	23	1
Natica livida	0	12	0	2	1
Nucula proxima	0	7	0	0	0
Oliva sp.	2	10	1	2	2
Oliva circinata	5	17	0	0	1
Modulus modulus	5	3	0	0	1
Glyphoturris rugima	2	3	1	1	4
Polinices lateus	2	5	0	0	1
Leucozonia nassa	2	12	1	1	0
Astraea tecta	0	3	0	2	0
Cymatium partenopeum	0	5	0	0	1
Cerithium atratum	8	9	0	0	5
Strombus gigas	0	2	0	1	1
Trignostoma pulchra	0	2	0	2	1
Opercula	29	63	11	14	3

Table 4. Hermit crabs occupying shells and fragments returned to three octopus dens (two *O. vulgaris* and one *O. briareus*) over a seven day period in August 2001. The total includes cumulative number of hermit crabs each day, thus some individuals are counted more than one time in the total. Hermit crabs counted more than once are indicated in parentheses. A = total observed around dens and middens, B = in shells from middens, C = in fragments from middens

	A	B	C
Calcinus tibicen	43 (7)	9 (2)	2
Dardanus venosus	7 (2)	0	0
Paguristes cadenati	31 (3)	4 (1)	0
Paguristes puncticeps	87 (11)	12 (1)	2 (1)
Pagurus brevidactylus	238 (71)	27 (4)	9 (6)
Pagurus criniticornis	371 (112)	52 (15)	35 (11)
Petrochirus diogenes	9	0	0
Phimochirus holthuisi	39 (3)	3	7 (1)

hermit crabs inside the dens and in the den/midden area. The *P. puncticeps* individuals collected from inside the dens of the *O. vulgaris* individuals were all relatively small (mean shield length <5 mm) while those found in the middens and

surrounding areas were larger (mean shield length >17 mm). Most hermit crabs found with *O. briareus* were collected from the middens, rarely within the dens. Dens were generally within coral crevices and were hard to access. *Phimochirus holthuisi* (mean shield length 6.5±2 mm) and *Paguristes puncticeps* individuals were observed feeding on prey remains from both species of octopuses as well as taking shells from the middens. Individuals of *Petrochirus diogenes* (Linnaeus, 1758) and *Dardanus venosus* (H. Milne Edwards, 1848) were not observed taking shells or fragments from the sites.

Transient hermit crab species commonly removed shells from middens of both octopus species, but did not change shells at the midden site. Thus, a shell was not deposited back into the midden if a shell exchange occurred.

The control areas sampled near the dens yielded small numbers of live gastropods, gastropod shells and hermit crabs. The controls were in seagrass and patch reef/rubble/reef areas. The largest number of gastropods found per square m was seven while the largest number of hermit crabs collected per square m was eight. Consistently, control area in seagrass beds yielded hermit crabs and gastropods while the one located in patch reef/coral rubble/reef had few, if any, hermit crabs or gastropods visible. In sandy areas among the rubble and patch reefs, both hermit crabs and gastropods tended to bury. The highest number of empty shells per square m in either of the control areas was 13; these were mostly small specimens (<0.5 cm) of *Cyphoma gibbosum* (Linnaeus, 1758) (a shell not often occupied by hermit crabs at this site), *Conus mindanas* Hwass, 1792, *Glyphoturris rugirima* (Dall, 1889), and *Cerithium atratum* (Table 2).

Discussion

Octopus vulgaris and *O. briareus* individuals feed opportunistically, consuming some prey while foraging and other prey at their dens. Hermit crabs formed a part of the diet both during foraging and at the dens. Some octopuses in the present study seemed to specialise on molluscs while others most frequently discarded remains of crustaceans. Octopuses reared in the laboratory feed preferentially on crustaceans (Boletzky and Hanlon, 1983), though molluscs and other prey also are consumed readily. Some species of octopods use the radulae and beak to rasp holes in mollusc shells or operculum (Arnold and Arnold 1969; Wodinsky, 1969) and crustacean prey (Boyle and Knobloch, 1981). Octopuses that drill take much longer to handle prey than those that pull open shells (Fiorito and Gherardi, 1999). The differences in handling time for prey items varies, typically with crustaceans requiring less handling than molluscs. Some crustaceans and gastropods are crushed by octopus beaks (Ambrose, 1986; Voight, 2000) while others are envenomated. Crustaceans may be envenomated through the eye (Grisley et al., 1996) or other less chitinous body regions, making it difficult to determine cause of death from remains. However, in the present study, some crustaceans also escaped from octopuses, suggesting a trade-off for octopuses in consumption and handling. Hermit crabs occupying thick shells into which they could withdraw completely posed a challenge for the octopuses, requiring drilling of the shells to access the

hermit crabs. Some hermit crabs were abandoned by the foraging octopuses as prey in this study, although hermit crabs in thick shells such as *Strombus* were also pulled out through the shell apertures as well. Other researchers have noted that removal of both hermit crabs and gastropods through the aperture is a common feeding strategy for octopuses (Brooks and Mariscal, 1985; Fawcet, 1984).

Postmortem shells from both molluscs and hermit crabs released by individuals of *O. vulgaris* and *O. briareus* observed foraging around Bailey's Cay were typically not drilled, though drilling is a well-documented feeding strategy for these species of octopuses (Nixon, 1987). Drilling often takes more time than other feeding strategies. For some species of hermit crabs (Pechenik and Lewis, 2000), drilled shells might have been avoided when possible. LaBarbera and Merz (1992) recognised that postmortem gastropod shells do change in strength not only from major breaks but also from microfractures. Octopuses observed in present study removed the gastropod or hermit crab through the shell aperture primarily, leaving intact shells that were available to hermit crabs. There was little or no visible damage to shell apertures. Several authors have shown that many factors, including shell thickness and epibionts, are important in resistance to predation by crabs and other duraphagous predators (Dietl and Alexander, 1995; Kamat et al., 2000; Palmer 1979, 1985 and 1990; Voight, 2000) that include octopuses. These same shell features are important in hermit crab choices of shells. Researchers (Elwood and Neal, 1992; Hazlett et al., 1996; Imafuku, 1994; McLean, 1974, inter alia) have found that hermit crabs transferring shells can experience decreases in shell quality from erosion, epibionts and change of fit. There was little evidence that hermit crabs using postmortem shells from predation by octopuses experienced decreases in overall shell quality. Shells liberated by octopuses in the present study had few epibionts with the exception of hydroids and no erosion of shells was observed for the shells recycled (Table 1). However, change of fit was not examined in the field experiments.

Gastropod and bivalve shells with flesh attached are discarded as the octopuses move through their foraging ranges. It is difficult to quantify how much the post mortem gastropod shells contribute to the shell economy of hermit crabs over time with a series of short observations. However, it is clear that large, intact shells are made available and that chemical cues from degrading flesh may attract hermit crabs to the resource (Chiussi et al., 2001; Hazlett and Rittschof, 1997; Rittschof, 1980; Rittschof et al., 1992). Postmortem shells from gastropods in the present study generally contained some remaining flesh. Rittschof (1992) noted that several aspects of hermit crab activities can be modulated by degradation products from gastropod flesh including feeding, alarm, shell selection, and aggregation. In a highly three dimensional habitat like a seagrass-reef system, finding gastropod shells visually may be difficult. Empty gastropod shells are not a common commodity in benthic environments as shown in the background values in the present study (Table 3) as well as noted by other researchers (Leite et al., 1998; Scully, 1983; Vance, 1972) observing different habitats. The chemical signal from degrading gastropod flesh could give additional information to guide

crabs to shells. Even if the signal is not displayed over long distances, the information could be important to a hermit crab in determining whether to investigate a shell. Weissburg and Zimmer-Faust (1993) and Moore and Atema (1991) showed how crustaceans use chemical signals to derive fine-scale information about prey. Several authors (Benoit et al., 1997; Hazlett, 1996; Small and Thacker, 1994) have shown the importance of chemoreceptive stimuli for shell seeking by different species of hermit crabs. Hermit crabs investigating shells in the present study were observed eating and removing flesh from shells, though only two transfers of hermit crabs from old shells were observed for shells deposited by foraging octopuses. However, marked shells redeposited in the sampling area were removed and shells were left behind in the same general area. Some hermit crabs in marked shells that were deposited after foraging by octopuses also were found at middens, indicating that shells were exchanged by hermit crabs.

Interestingly, though individuals of both species had overlapping foraging ranges, members of *O. briareus* concentrated their feeding activities in the forereef and coral rubble/patch reef areas while individuals of *O. vulgaris* concentrated efforts in seagrass and patch reef corals. Octopuses are highly mobile predators, foraging once or twice a day at Bailey's Cay. Individuals of *O. vulgaris* almost always made two foraging trips while members of *O. briareus* rarely ventured forth twice. This difference may be related to the growth rates of the two species. *Octopus vulgaris* has a more rapid growth rate and food conversion ratio than *O. briareus*, suggesting that additional forays are necessary for maintaining growth and development (Mangold and Boletzky, 1973). This could have contributed to the larger middens found outside *O. vulgaris* dens. Ambrose (1984) and Forsythe and Hanlon (1997) have shown that octopuses may also learn the distributions of some prey, choosing their foraging areas and prey species accordingly. In addition to learning the prey distribution through mapping of an area, octopuses likely learn to avoid predators as well. Mather and O'Dor (1991) noted that foraging strategies and predation risk can influence feeding choices of octopuses. Predators such as eels were common at Bailey's Cay, not only killing octopuses but also removing arms. Loss of arms could lead to infections as well as decreased foraging or mating abilities. There were switches in prey exploitation during the three years of sampling. In 2000 and 2001 sampling seasons, there was a decline in live coral at the sampling site, with algal growth increasing. This may account for chitons and echinoderms (*Echinometra lucunter* (Linnaeus, 1758) and *Tripneustes ventricosis* (Lamarck, 1916)) becoming a more important part of the diets for both species of octopuses (Table 2) in the coral rubble/patch reef areas and the forereef.

Though foraging octopuses may offer a widely dispersed resource for hermit crab use, the dens and middens provide a stationary source of food and shells for hermit crabs. Crustaceans dominated the number of prey remains deposited in middens for both octopus species (approximately 55%, 63% and 33% for 1999-2001, respectively, of total prey observed in middens for *O. vulgaris* and 62%, 45% and 29% for 1999-2001, respectively, of prey in middens for *O. briareus*). Examining remains at middens and dens more closely reveals

that the foraging behaviours of the two octopuses offer different degrees of potential resources for hermit crabs. In this sampling area at Bailey's Cay, hermit crabs were more closely associated with dens of *Octopus vulgaris* both as prey and as recyclers at middens and dens. Neither of the octopus species had hermit crabs as significant parts of their diets during the observation periods, though for some octopuses, hermit crabs may be a preferred item. In the items noted for Table 2, hermit crabs did not constitute more than 19% of the midden remains by number for any year. It is unclear from other field studies what the consumption rates of hermit crabs in the field might be because middens are sampled for prey remains only (Anderson et al.,1999). Given that close examination of shells at a midden is required to determine whether a gastropod or hermit crab may have occupied the shell most recently, it is likely that hermit crabs have been underestimated in diets of octopuses determined only from prey remains at middens in other studies.

Shell resources at middens are available to a range of hermit crab sizes. Some shells were left intact while others were peeled or crushed, leaving a shell apex suitable for smaller crabs. Hermit crabs attracted to the middens sometimes remained for several days. For *Calcinus tibicen*, Brown et al. (1993) noted that presence of potential competitors for shells lengthened the time of shell assessment. This suggests that individuals of *C. tibicen* at middens and dens may have remained at the sites manipulating shells longer than if other hermit crabs were not present. When members only of *C. tibicen* were present at predation sites, researchers noted that shell assessment time was not significantly shorter than when other species of hermit crabs were present. However, variation in assessment time did occur between genera of shells, as Brown et al. (1993) also reported. Few direct aggressive interactions were observed at the den or midden sites in the present study for individuals of *C. tibicen*, especially between crabs of different sizes. For larger crabs, movement around an occupied octopus den could elicit a feeding response from the octopus. On one occasion, an *O. vulgaris* individual was observed to dart from a den during mid-day, pounce on and consume an individual of *Paguristes cadenati* Forest, 1954 and *Paguristes puncticeps* engaged in an aggressive encounter at a midden. Shells and appendages from both individuals were jettisoned into the midden after about 10 minutes. In laboratory experiments, Kobayashi (1986) found that octopuses presented with three different size classes of hermit crabs in ideal shells selected the largest hermit crabs in 90% of the trials.

Individuals of *Pagurus criniticornis* and *P. brevidactylus* may use the sites for refugia as well as for finding shells and for feeding. These hermit crabs may associate with occupied octopus dens and surrounding middens to decrease risk of consumption by other predators. *Octopus vulgaris* individuals have been shown to ignore small hermit crabs in experimental conditions (Tirelli et al., 2000), suggesting that they have a minimal prey size. The small hermit crabs within the dens are not accessible to other duraphagous predators while the octopus is in residence. *Pagurus criniticornis* and *P. brevidactylus* individuals in dens were observed feeding on remains left attached to shells by octopuses. Most often in middens, members of

P. criniticornis and *P. brevidactylus* were found consuming remains from bivalves and echinoderms. Fish bones within dens were also cleaned of flesh. In addition to protection from predation and access to food at the dens, the smaller crabs also selected shells from nearby middens. Shells used from middens were sometimes so large that the hermit crabs were unable to move them. One individual of *P. punciceps* (shield length 4.1 mm) was observed occupying a *Strombus gigas* shell (shell length 17.4 mm) in the same location over a seven day period. For hermit crabs found commonly around dens in grassbeds, octopuses bringing shells back from over the entire reef may give access to new resources not commonly available in the grassbeds.

Ramsay et al. (1997) noted that individuals of *Pagurus bernhardus* (Linnaeus, 1758) attracted to small patches of food showed increased numbers of aggressive interactions. These researchers found that size frequency of visitors at carrion sites in the field varied relative to patch size with larger hermit crabs being prevalent at smaller patches. They suggested that these larger individuals were superior intraspecific competitors for the resource. In the present study, individuals of *O. vulgaris* and *O. briareus* created different sizes of middens outside of their dens, offering hermit crabs of different species relatively varying patches of food and types of shells. Regardless of patch size, however, smaller hermit crabs did not flee the area as described by Ramsay et al. (1997) for *P. bernhardus* when confronted by either a larger conspecific or a larger hermit crab of another species. Smaller hermit crabs in the present study retreated into the openings of the octopus dens or plunged into the midden mound. Movement into the middens likely allowed the hermit crabs not only to avoid larger hermit crabs but also to shift shells in middens, potentially encountering new shells for assessment.

All of the shells within the middens were not necessarily from octopus predation. Hermit crabs selecting shells from middens could contribute a shell back to the middens. When another hermit crab uses the shell left behind, this is referred to as indirect shell transfer. Hazlett et al. (1996) showed that indirect transfer of shells between hermit crab species at predation sites (areas where predators consume prey) does occur. The middens function as predation sites, attracting hermit crabs to shells and food by chemical cues. Crustacean predators (i.e. *Menippe mercenaria* (Say, 1918)) also visited the middens. These predators smashed empty gastropod shells, removing flesh remnants from them as well as feeding on predatory gastropods such as *Nassarius vibex* (Say, 1822) and *Cancellaria nodulifera* Sowerby, 1825 attracted to prey remains at the middens. Thus, these crustacean predators also contributed to the shell middens of the octopuses. Shells that were smashed still yielded category 4 shells with the apices intact. These shells were readily taken by small hermit crabs. Morton and Yuen (2000) showed that interspecific competition for carrion does occur between hermit crabs and gastropods. However, no direct interference was noted at the midden sites in this study.

Three parts of the methodology used for the current study may have affected the observations at dens and middens. First, hermit crab species that are consumed by octopuses may approach dens and middens when the predators are not in resi-

dence to obtain shells and to feed on flesh remaining in shells. The present study did not focus on an ethogram of activities at unoccupied dens. Brooks (1989) indicated that at least two species of hermit crabs, including *Dardanus venosus* that is found at Bailey's Cay, could detect octopuses through chemical cues. Further experiments may indicate that other hermit crab species at Bailey's Cay also have this ability, allowing them to reduce risk of predation by octopuses yet take advantage of the shells available in middens and dens. Second, the method of removing shells from the site each day may have influenced the numbers, sizes and types of hermit crabs (Gilchrist, 1984; Rittschof, 1980) and other attendants (Rahman et al., 2000) attracted to the middens and dens by decreasing the amount and types of flesh degradation products over time. This could decrease the number of hermit crabs available to octopuses as prey at middens in this study and could have influenced the removal of shells from middens and dens. However, the octopuses are known to do housecleaning of the dens and middens (Mather, 1991, 1994), removing debris from the area on a regular basis. Finally, by sampling over a short time period during the same time of year, a full picture of potential contributions of octopuses to hermit crab shell cycling is not possible.

Cycling of shells within the Bailey's Cay system is complex. Octopus dens and middens provide a concentrated resource of shells as well as food for hermit crabs, augmenting opportunities for both intra- and interspecific shell exchanges in the reef system. Species such as *P. criniticornis* and *P. brevidactylus* also have individuals that shelter within octopus dens without being eaten.

Acknowledgements

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