

# Ecology of tropical hermit crabs at Quirimba Island, Mozambique: shell characteristics and utilisation

David K. A. Barnes\*

Department of Zoology and Animal Ecology, University College Cork, Lee Maltings, Cork, Ireland\*\*  
and

Frontier, The Society for Environmental Exploration, 77 Leonard Street, London EC2A 4QS, United Kingdom

**ABSTRACT:** The use of gastropod shells by hermit crabs at Quirimba Island, Mozambique, was investigated. Particular attention was paid to the upper shore/supralittoral zone species *Clibanarius longitarsus*, *Coenobita cavipes* and *Coenobita rugosus*. The study area is characterised by a high diversity of gastropod species as well as hermit crabs. Supralittoral hermit crabs were little, if at all, resource restricted due to concentration of empty shells on the strandline and shell middens created by local people. The range of the 3 study species overlaps substantially and each uses a wide range of shell types. Shore habitat, shell abundance and availability were found to have little influence on shell use. With increased tidal emersion/terrestrial nature (for a given crab mass), total diversity of shells used increased, shell mass carried decreased, damaged shell use decreased and carried shell fit increased. The architecture and strength of shells used, however, followed more complex individual species characteristics and behaviour patterns. Species specific differences in behavioural patterns may be important for shell resource partitioning.

**KEY WORDS:** Hermit crab · Shell use · Mozambique · Resource partitioning

## INTRODUCTION

The characteristic and unique behaviour of hermit crabs selecting mollusc shells has been, and remains, a considerable source of interest to a diverse range of biologists for interpretation of competition, resource partitioning, behavioural and population ecology, evolution and predator/prey interactions. A wide variety of (shell) morphological influences have been found to influence choice, e.g. identity (Reese 1963, Young 1979), size (Reese 1963, Vance 1972), weight (Reese 1962), degree of damage (Conover 1978) and epibiosis (Jensen 1970). A variety of environmental factors are also considered to influence shell choice, e.g. shell abundance (Reese 1969), habitat tidal height (Bertness 1982) and latitude (Vermeij 1976). Investigations of the importance of environmental and shell factors on shells used have, to date, centered on intertidal or subtidal

species. The influence of predation and specialised nature of predators on gastropods increases towards the tropics (Vermeij 1976, Zipser & Vermeij 1978). Correspondingly, predation has been inferred to be an important influence on shell selection for tropical intertidal hermit crabs (Bertness 1982, Borjesson & Szelistowski 1989). However, supralittoral (semi-terrestrial) hermit crabs, by their nature, have very different behaviour, access to resources and face very different predation and physiological pressures (Burggren & McMahon 1988). Yet, to date, little more is known of shell use by tropical supralittoral species than the preliminary work of Völker (1967) on *Coenobita scalveola*.

The vast majority of studies and resultant knowledge on the ecology of both temperate and tropical hermit crabs stems from work in the Americas. This has included many of the most important contributions to advances in understanding Anomuran biology (e.g. Vance 1972, Conover 1978, Hazlett 1980, Bertness 1982, Abrams 1987, Wilber 1990). As in most fields the density and distribution of knowledge strongly reflects

\*E-mail: dkab@ucc.ie

\*\*Address for correspondence

that of academic institutes and researchers, and thus the ecology of hermit crabs in tropical Africa has been comparatively little studied. There is, however, a wide diversity of East African intertidal Anomura, which may locally be highly abundant and cluster spectacularly (Hilgendorf 1878, Vannini 1976, Lewinsohn 1982, Gherardi et al. 1991). The principal area of recent East African hermit crab studies has focused on populations of *Clibanarius laevimanus* in Kenyan mangrove habitats (Gherardi et al. 1991, 1994, Gherardi & Vannini 1992, 1993).

Hermit crabs are an extremely abundant, diverse and sometimes locally dominant component of the intertidal macrobenthos of the Quirimba Archipelago, tropical northern Mozambique (Barnes 1997a,b). There are at least 7 genera and 16 species of hermit crabs found between the subtidal and supralittoral zones within the archipelago. Quirimba Island, one of the larger islands at 6 by 3 km, has a particularly high diversity, not only of hermit crabs but also of gastropod molluscs amongst other taxa (Frontier Mozambique unpubl. data). Consequently, there is a diverse variety of gastropod shells potentially available to hermit crabs, of which the supply of some sizes outstrip demand. This is particularly the case for the larger shells as the living molluscs are removed to form an important dietary component of local and regional artisanal fisheries (Barnes et al. 1998). Two of the 3 supralittoral hermit crab species at Quirimba Island climb trees, a behavioural trait which may influence and be influenced by shell choice (Barnes 1997b).

In this paper the shells occupied by hermit crabs, principally those of the supralittoral zone, of Quirimba Island are examined in relation to a number of shell characteristics. The diversity of shells utilised across the shore, subtidal to supralittoral, is compared to the number of living gastropod species across the shore. Shell use of the supralittoral zone hermit crabs is compared between the 3 main habitats encompassed at Quirimba Island. Of the shells themselves the environmental characteristics of abundance and availability, and physical characteristics of size, architecture, mass, strength, fit and damage were examined. Symbionts/epibionts were not present on any of the supralittoral hermit crab shells investigated, so epibiotic influences, if present in the wider population, must be minor.

## METHODS

Characteristics of gastropod shells utilised by intertidal hermit crabs and of hermit crabs themselves were studied at Quirimba Island, northern Mozambique. The fieldwork was carried out from the Darwin/Frontier Mozambique station on Quirimba Island, between

May and July of 1996. The number of gastropod shells and the identity and proportion of each used by 10 hermit crab species, spanning the supralittoral zone to the subtidal zone margins, were recorded using multiple quadrat techniques at 10 m sample intervals along intertidal transects (5 quadrats, of area 1 m<sup>2</sup>, randomly placed every 10 m along 3 transects). Using this method the total number of mollusc species used by hermit crabs was compared to the total number available across the shore. The abundances of 15 species of mollusc were also estimated and ranked using this method, and the proportion of each mollusc shell used by hermit crabs and unused shells were calculated to estimate and rank shell availability. Three closely spaced supralittoral habitats and their hermit crab populations were studied in particular detail. The habitats were (1) open sandy scrub beach, (2) thin mangrove forest margin (approximately 100 m wide), and (3) mangrove forest (approximately 400 m wide), dominated by *Rhizophora* trees; for map and further details see Barnes (1997a).

The 3 species of supralittoral zone hermit crabs were *Clibanarius longitarsus*, *Coenobita rugosus* and *Coenobita cavipes*. From these species, 93, 176 and 187 individuals, respectively, were removed carefully from their shells. This was done by inserting a coiled cable tie into the shells and tickling the abdomen and claspers to encourage shell vacation. The advantage of this method, over the more traditional shell flaming (Fotheringham 1976), was that specimens could ultimately be returned to the environment alive and undamaged. The crabs and shells were then dried using tissue paper and a variety of measurements were made using a variety of spring balances (to a maximum accuracy of 0.25 g) and a micrometer. Measurements made included shell length and mass, shell aperture length and width, hermit crab mass and cephalothorax length, and major chela length and width. The gender of crabs was undetermined, but Abrams (1978) and Bertness (1980) found that sex did not alter shell selection.

The shell mass was compared to that of the carrying hermit crab for a sample of all 3 species and the proportion carrying damaged shells was compared for various mass size classes. Damage of shells was assessed visually: shells were scored as damaged if a complete hole was present in any of the whorls or if the edge of the main whorl was broken. The proportions of certain shell species used by *Coenobita rugosus* and *C. cavipes* were compared for various mass size classes between the supralittoral zone habitats in which each occurred. The strength of shells was measured by construction of a pivot lever, to which a variable force could be applied, following the method of Peck (1993). The force was applied to the outer whorl of each shell and the mass and lever distance calculated to give a



*Coenobita rugosus*, *Coenobita cavipes* and *Clibanarius longitarsus* had different and distinct patterns of shell use. Each crab species used 1 shell identity considerably more than any other: the mangrove whelk *Terebralia palustris* accounted for 46% of *C. cavipes* and 38% of *C. longitarsus* shell use, whilst *T. coronatus* accounted for 43% of *C. rugosus* shell use. The total number of shell identities used by hermit crabs at Quirimba Island decreased down the shore from around 20 in the supralittoral and upper shore zones to around 5 by the subtidal zone (Fig. 1). In contrast the total number of living gastropods and the source of shells increased downshore from 6 in the supralittoral zone to 29 by the extreme lower shore zone.

#### Habitat and crab size influences on shell identities used

Supralittoral hermit crabs at Quirimba Island occur in 3 broadly different habitats, sand/scrub (open shore), fringe mangrove (thin mangrove areas) and mangrove (dense trees). The species variation between these habitats and the habitats themselves are described in Barnes (1997a). Although *Coenobita cavipes* occurs in all 3 supralittoral zone habitats, only specimens with a mass > 2.5 g were recorded from the sand/scrub habitat. The pattern of shell use of *C.*

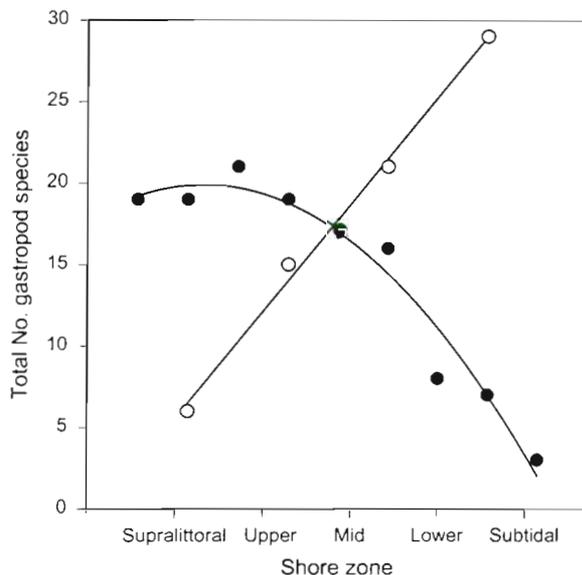


Fig. 1 Total number of gastropod shell species used with total number of living gastropod species for shore position at Quirimba Island. X-axis (shore zones) is by time period of emersion (e.g. lower shore exposed for 3 h, mid shore exposed for 6 h etc.) on an average shore. Supralittoral zone was ~15 m wide, other zones were ~300 m wide. (●) Total number of gastropod shell identities used by hermit crabs; (○) Total number of living gastropod species. Line and curve are fitted by eye

*cavipes* changed little between the 3 habitats: *C. cavipes* of 1 to 5 g mass mostly used the shell of *Terebralia palustris*. Mid-sized (5 to 10 g) individuals mainly used the shell of the predatory pear snail *Volema paradisica* in the sand/scrub and mangrove habitats. No one shell identity was principally used by *C. cavipes* of this size class in the fringe mangrove habitat. The large tulip shell *Fasciola trapezium* was used in increasing importance with *C. cavipes* size, forming the majority of the 28 g size class, in all 3 habitats.

*Coenobita rugosus* was only present in the sand/scrub and fringe mangrove habitats. As with the pattern of shell use of *C. cavipes* there was little difference in the shell identities used by *C. rugosus* between habitats. In contrast to *C. cavipes*, though, the shells of *Terebralia palustris* were only used by the smallest size class of *C. rugosus*. The shells of *Turbo coronatus* were used by every size class of *C. rugosus* and formed up to 60% of the choice of mid-sized individuals. In similar manner to *C. cavipes*, the shells of *Volema paradisica* and *Fasciola trapezium* were important to the larger size classes of *C. rugosus*. Individuals of the largest size class (18 g) of *C. rugosus* only occurred in the open sand/scrub habitat.

The proportions of each shell type used by *Coenobita rugosus* and *C. cavipes*, thus, changed dramatically with crab size. The sizes of crab using each shell type had a clear, but overlapping, sequence of size suitability. The most used shells of *C. rugosus* and *C. cavipes*, *Turbo coronatus* and *Terebralia palustris* respectively, have 2 of the widest size ranges of use. Shells with a narrower size range of crabs using them were generally less important, even within their particular size range. Interestingly, although the level of use of the shell *Volema paradisica* differed between *C. rugosus* and *C. cavipes*, the mean size, magnitude of size range and actual size ranges of crabs using them were very similar. This was similarly true for the shell of *T. coronatus*, used by a wide range of crab sizes, and the shell of *Thais svignyi*, used by a narrow range of crab sizes. So the difference in shell types used by *C. rugosus* and *C. cavipes* was not predominantly a result of size or habitat influences.

#### Shell abundance and availability

Fifteen of the most important shells used by supralittoral zone hermit crabs at Quirimba Island were ranked in order of their abundance in the supralittoral habitat (Table 2). The most important shell identity to *Clibanarius longitarsus* and *Coenobita cavipes* was *Terebralia palustris*. This was the most abundant gastropod species in the supralittoral zone samples at Quirimba Island. The most important shell identities to *Coenobita*

Table 2. Abundance and availability of shells to supralittoral zone hermit crabs of Quirimba Island. The abundance rankings for each of the 15 species of gastropod are based on transect surveys (most abundant shell = 1, least abundant = 15) and the source refers to the cause of their supralittoral presence (e.g. Mid shore = mid shore population of living snails, empty shells washed into supralittoral from there). The occupation values are percent of sample population and have 3 possible outcomes: crab occupied, mollusc occupied, or unoccupied (empty)

| Gastropod species            | Abundance |             | Occupation |         | Availability |      |
|------------------------------|-----------|-------------|------------|---------|--------------|------|
|                              | Rank      | Source      | Crab       | Mollusc | Empty        | Rank |
| <i>Terebralia palustris</i>  | 1         | Inhabitant  | 76.3       | 21.1    | 2.6          | 7    |
| <i>Peristernia forskalii</i> | 2         | Upper shore | 66.7       | 5.5     | 27.8         | 4    |
| <i>Fasciola trapezium</i>    | 3         | Collected   | 45.5       | 0       | 54.5         | 2    |
| <i>Chicoreus ramosus</i>     | 3         | Collected   | 30         | 0       | 70           | 1    |
| <i>Cerithidium decollata</i> | 5         | Inhabitant  | 28.6       | 57.1    | 14.3         | 3    |
| <i>Turbo coronatus</i>       | 6         | Upper shore | 91.6       | 2.6     | 2.6          | 12   |
| <i>Nerita plicata</i>        | 7         | Inhabitant  | 75.9       | 24.1    | 0            | 10   |
| <i>Planaxis sulcatus</i>     | 8         | Upper shore | 71.5       | 28.5    | 0            | 9    |
| <i>Volema paradisica</i>     | 9         | Collected   | 100        | 0       | 0            | 13   |
| <i>Nerita polita</i>         | 10        | Upper shore | 90.4       | 4.8     | 4.8          | 11   |
| <i>Polinices mamilla</i>     | 11        | Mid shore   | 100        | 0       | 0            | 13   |
| <i>Thais svignyi</i>         | 12        | Upper shore | 86.6       | 6.7     | 6.7          | 8    |
| <i>Strombus mutabilis</i>    | 13        | Collected   | 76.7       | 0       | 23.3         | 5    |
| <i>Nerita textilis</i>       | 14        | Upper shore | 88.9       | 0       | 11.1         | 6    |
| <i>Nassarius coronatus</i>   | 15        | Mid shore   | 100        | 0       | 0            | 13   |

*rugosus* were, in contrast, only mid ranked. Shell abundance rankings were positively correlated with shell usage rankings of *C. cavipes* (Spearman Rank Correlation Coefficient,  $r = 0.55$ ,  $p < 0.05$ ), but not with *C. rugosus* ( $r = -0.32$ ,  $p > 0.05$ ). The 3 top ranked shell identities all had different sources responsible for their supralittoral zone abundance. The living gastropod *T. palustris* occurred as a mangrove inhabitant, fringe mangrove and to a lesser extent lowest fringe of the open sand/scrub habitats of the supralittoral zone. The shells of *Peristernia forskalii* were washed up on spring tides from upper shore populations and the shells of *Fasciola trapezium* were discarded in piles on the shore by fishermen. The latter are an important source of food for islanders (Barnes et al. 1998).

The levels of abundance of each shell identity in many cases contrasted with their immediate availability. Although the gastropod *Terebralia palustris* was highly abundant in the supralittoral zone, most were occupied by hermit crabs and most of the remainder by the living molluscs, resulting in just 2.6% of the shells being empty (Table 2). The same proportion of shells of *Turbo coronatus* were unoccupied. However, in contrast to *T. palustris* the abundance of *T. coronatus* was much lower. Thus, the availability of *T. coronatus* shells, which were heavily used by *Coenobita rugosus* and *C. cavipes*, was equal to the lowest in Table 2. Conversely, the abundant and available shells of the gastropod *Cerithidium decollata* were little used by *C. cavipes* and unused by *C. rugosus*. Neither of the shell usage rankings of *C. rugosus* and *C. cavipes* were positively correlated with shell availability (Spearman

Rank Correlation Coefficients,  $r = 0.069$  and  $-0.788$ ). The lack of correlation to shell availability in *C. cavipes* gives some cause to doubt the biological significance of the correlation with shell abundance in this species. Shell size was an inevitable confounding factor as the most immediately available shell identities were *Chicoreus ramosus* and *Fasciola trapezium*, 2 of the largest types. The shells of *C. ramosus* and *F. trapezium* were unused by hermit crabs with a cephalothorax length smaller than 16.4 mm, the majority of the population.

The data suggest that, with the possible exception of the shell of *Terebralia palustris*, the abundance and/or availability of shell types had only minor possible influence on shell selection in the supralittoral habitat of Quirimba Island. In addition, the differences in abundance and availability of gastropod shell types would largely influence *Coenobita rugosus* and *C. cavipes* to a similar extent as their overlap in local distribution was large (Barnes 1997a,b,c). Thus, the differences in shell identity use of *C. rugosus* and *C. cavipes* shell type were unexplained by abundance or availability.

### Shell architecture, mass and strength

The majority of the gastropod shells used by hermit crabs at Quirimba Island were architecturally low spired. There were 2 abundant mid spired gastropods, *Thais svignyi* and *Chicoreus ramosus*, of which the former was particularly used by mid shore species. The most used shell of each of the supralittoral zone (with the exception

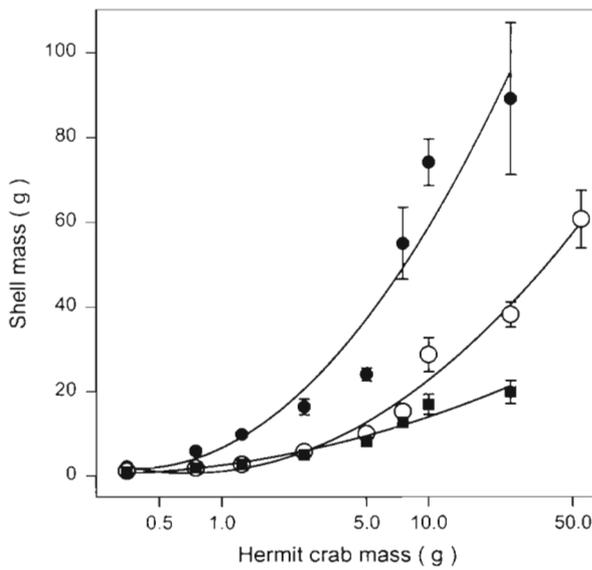


Fig. 2. Mass of shell (log) carried with crab mass (log) for 3 species of supralittoral hermit crab at Quirimba Island. The crab species are *Clibanarius longitarsus* (●), *Coenobita cavipes* (○) and *Coenobita rugosus* (■). The data are presented as mean with standard error. The regression equations are *C. longitarsus* ( $\log y = \log (0.904x) + 0.834$ ,  $r^2 = 0.97$ ), *C. cavipes* ( $\log y = \log (0.854x) + 0.405$ ,  $r^2 = 0.98$ ) and *C. rugosus* ( $\log y = \log (0.757x) + 0.371$ ,  $r^2 = 0.98$ )

of *Coenobita rugosus*), upper, mid and highest lower shore zone hermit crab species was high spired. These were principally the shells of *Terebralia palustris* or *Rhinoclavis sinensis*. Four of the 5 most abundant shell identities (in the supralittoral zone) were, however, high spired. Only 38.2% of shells occupied by *Coenobita cavipes* were low spired, compared to 95.2% of those occupied by *C. rugosus*. *C. rugosus* showed significant preference for squat low spired shells ( $\chi^2 = 31.3$ , df 3,  $p < 0.01$ ) irrespective of abundance and availability. Conversely, *C. cavipes* showed a significant preference for tall spired shells ( $\chi^2 = 47.9$ , df 3,  $p < 0.01$ ).

The mass of shell carried with respect to carrier mass increased in a log-log relationship between the 3 supralittoral zone hermit crab species (Fig. 2). Increase was similarly logarithmic in each species (slope of lines not significantly different, GLM, ANOVA,  $F = 0.62$ ,  $p = 0.5$ ) but across significantly different ranges of mass (intercepts significantly different, GLM, ANOVA,  $F = 712$ ,  $p < 0.001$ ). The mass of shell carried by *Coenobita cavipes* and *Coenobita rugosus* was only significantly different in the 2 largest comparable size classes (ANOVA, Tukey tests; 10 g size class:  $F = 5.8$ ,  $p < 0.05$  and 25 g size class:  $F = 13.9$ ,  $p < 0.001$ ). The comparative shell mass carried (at least in the larger size classes) increased upshore from *Clibanarius longitarsus*, through *C. cavipes* to *C. rugosus*.

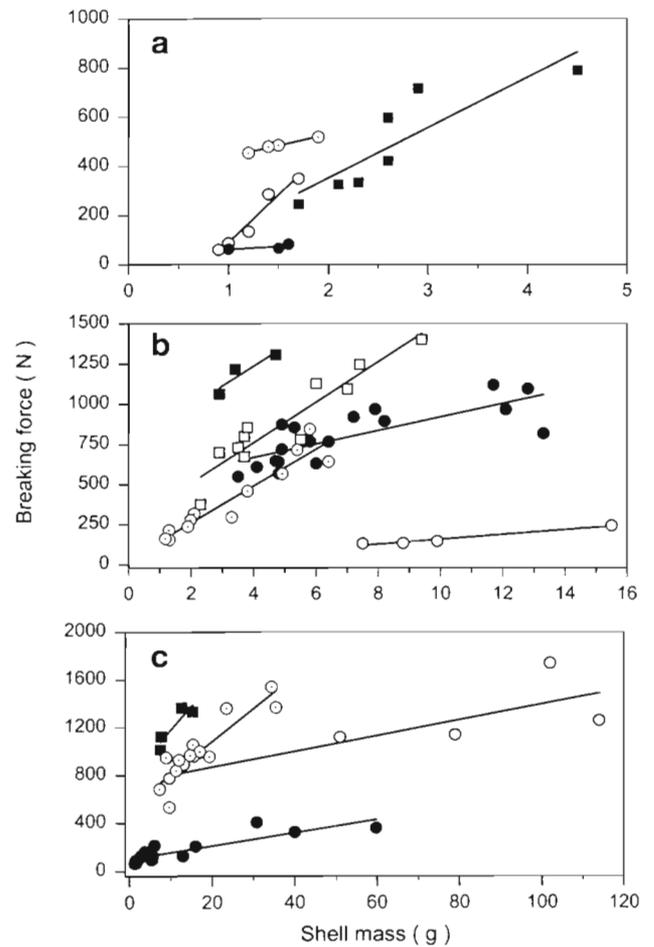


Fig. 3. Gastropod shell strength (cracking force) with mass. Data are presented as individual measurements with fitted regression lines. Note the different scales of mass: (a) shells in the range 0 to 5 g, (b) shells in the range 0 to 16 g and (c) shells in the range 0 to 120 g. The significance of the regressions are \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ . The shell types and regressions for (a) are (●) *Cerithidium decollata*,  $y = 25.2x + 35.6$ ,  $F = 1.4$ , (○) *Nerita albicilla*,  $y = 389x - 299$ ,  $F = 62$ \*\*, (◊) *Planaxis sulcatus*,  $y = 91.5x + 348$ ,  $F = 130.5$ \*\* and (■) *Thais svignyi*,  $y = 205x - 57$ ,  $F = 15.1$ \*. The shell types and regressions for (b) are (●) *Turbo coronatus*,  $y = 41.7x + 502$ ,  $F = 22.7$ \*\*\*, (○) *Strombus mutabilis*,  $y = 15x + 5.8$ ,  $F = 57.6$ \*, (◊) *Nerita plicata*,  $y = 115x + 28.2$ ,  $F = 90.9$ \*\*\*, (◻) *Nerita polita*,  $y = 125x + 260$ ,  $F = 64.3$ \*\*\* and (■) *Nassarius coronatus*,  $y = 116x + 762$ ,  $F = 18$ . The shell types and regressions for (c) are (●) *Terebralia palustris*,  $y = 5.51x + 100$ ,  $F = 52.4$ \*\*\*, (○) *Fasciola trapezium*,  $y = 6.62x + 736$ ,  $F = 5.2$ , (◊) *Volema paradisica*,  $y = 27.6x + 530$ ,  $F = 48.9$ \*\*\* and (■) *Polinices mamilla*,  $39.7x + 782$ ,  $F = 8.7$

The physical strength, measured as cracking force, of the gastropod shells used by the *Coenobita* species varied by more than an order of magnitude. The magnitude of increase in strength with size of shell was also highly variable between shell types (Fig. 3). Of the smaller (<2 g) shells, the littorinid snail *Planaxis sul-*

*catus* was the strongest by a considerable margin (Fig. 3a). This was nearly 7 times stronger than that of the weakest shell type, *Cerithidium decollata* (70 N cracking force). Above 2 g shell mass, the strongest shell was *Nassarius coronatus*, but above the maximum size of *N. coronatus* (5 g) the strongest shell then became *Nerita polita* (Fig. 3b). At comparative masses the shell of *N. polita* was weaker than that of *N. coronatus*, but at its maximum size (9 g) *N. polita* peaked at a similar absolute strength (about 1400 N). The strombid shell *Strombus mutabilis* was clearly unusual amongst the gastropods sampled in being of such weak construction (Fig. 3b). Above 9 g shell mass, a succession of *Polinices mamilla*, *Volema paradisica* and *Fasciola trapezium* were each the strongest shell type above their listed predecessor's maximum size respectively (Fig. 3c). The maximum absolute strength of these 3 shell types was similar, albeit at different masses, and were the highest of those sampled. The strength of shells carried by *Coenobita rugosus* were significantly stronger than those of *Coenobita cavipes* in all but the 2 largest size classes (ANOVA, Tukey test; all  $p < 0.01$ ).

Absolute strength of gastropod shells, however, must be put into perspective in terms of cost benefit by comparison to their respective masses. Table 3 shows the average mass of each shell type used by 5 size classes of *Coenobita* hermit crabs. The shell strength at each of these particular masses (interpreted from Fig. 3) is also shown in Table 3. As with absolute strength, the variation in values of strength per mass varies between shell types by more than an order of magnitude. Whilst the cracking force of a *Turbo coronatus* shell used by the 1 g *Coenobita* size class was 26% higher than that of *Planaxis sulcatus*, the mean shell mass of the latter was just 1.6 g compared to 3.9 g for *T. coronatus*. Thus,

the shell of *Planaxis sulcatus* was 45% stronger per gram than that of *T. coronatus*. In the smallest 3 and largest size classes, the absolute strongest shells were also those of greatest cost benefit in terms of strength per mass. Only in the 10 g size class was the strongest shell type per mass (*Nerita plicata*) one of the weaker shells in absolute strength.

The comparisons of shell strength per mass have illustrated a cost benefit standard between shell types (Table 3). Cost benefit of shell strength to mass for hermit crabs has another important perspective, shell strength per mass, per mass. The cost benefit (shell strength per gram) of the shells of *Turbo coronatus* and *Thais svignyi* to the 1 g *Coenobita* size class were similar (171 compared to 183 respectively). Their respective mean shell masses used by the 1 g size class were, however, quite different (3.9 compared to 2.5 g respectively). The shell of *T. svignyi* offered similar protection to that of *T. coronatus* per gram for  $\sim 1/2$  mass.

### Shell damage and fit

The proportion of damaged gastropod shells used by hermit crabs increased with crab body mass up to the mid-size categories, after which it declined (Fig. 4). The peak proportion of damaged shell users, at 7.5 to 10 g mass, was most striking in the *Coenobita* species. Up to a fifth of shells occupied by *Clibanarius longitarsus* were damaged to some extent. The number of damaged shells used by *C. longitarsus* was significantly higher than that used by *Coenobita cavipes* (Mann-Whitney *U*-test,  $W = 43.5$ ,  $p < 0.01$ ), which, in turn, was significantly higher than that used by *Coenobita rugosus* (Mann-Whitney *U*-test,  $W = 24$ ,  $p < 0.05$ ).

Table 3. Shell mass and strength for 13 shell types and 5 hermit crab size classes. The values are: ( ): mean shell mass used by hermit crab size classes, italics: strength measured as cracking force in newtons (from Fig. 3) and bold: strength per mass ( $N\ g^{-1}$ ). –: shell type unused by a particular size class, \*: only 1 individual used so data not presented

| Shell identity               | <i>Coenobita</i> sp. size class (g) |                       |                       |                        |                     |
|------------------------------|-------------------------------------|-----------------------|-----------------------|------------------------|---------------------|
|                              | 1                                   | 2.5                   | 5                     | 10                     | 25                  |
| <i>Cerithidium decollata</i> | 68 (1.3) <b>52</b>                  | –                     | –                     | –                      | –                   |
| <i>Planaxis sulcatus</i>     | 494 (1.6) <b>309</b>                | –                     | –                     | –                      | –                   |
| <i>Thais svignyi</i>         | 457 (2.5) <b>183</b>                | 764 (4) <b>191</b>    | –                     | –                      | –                   |
| <i>Nerita albicilla</i>      | 450 (2.0) <b>225</b>                | 625 (2.7) <b>231</b>  | –                     | –                      | –                   |
| <i>Nassarius coronatus</i>   | 875 (1.3) <b>673</b>                | 1000 (2.2) <b>454</b> | –                     | –                      | –                   |
| <i>Nerita polita</i>         | 573 (2.5) <b>229</b>                | 899 (5.1) <b>176</b>  | 1125 (6.9) <b>163</b> | –                      | –                   |
| <i>Nerita plicata</i>        | 225 (1.7) <b>132</b>                | 443 (3.6) <b>123</b>  | 593 (4.9) <b>121</b>  | 720 (6.0) <b>120</b>   | –                   |
| <i>Turbo coronatus</i>       | 665 (3.9) <b>171</b>                | 719 (5.2) <b>138</b>  | 861 (8.6) <b>100</b>  | 1049 (13.1) <b>80</b>  | *                   |
| <i>Terebralia palustris</i>  | 114 (2.6) <b>44</b>                 | 132 (5.8) <b>23</b>   | 165 (11.8) <b>14</b>  | 291 (34.5) <b>8</b>    | 417 (57.7) <b>7</b> |
| <i>Strombus mutabilis</i>    | –                                   | 122 (7.8) <b>16</b>   | 144 (9.3) <b>16</b>   | –                      | –                   |
| <i>Polinices mamilla</i>     | –                                   | 950 (6.0) <b>158</b>  | 1123 (8.6) <b>131</b> | 1191 (10.3) <b>116</b> | *                   |
| <i>Volema paradisica</i>     | –                                   | 600 (4.8) <b>125</b>  | 822 (10.6) <b>78</b>  | 1033 (18.2) <b>57</b>  | 1165 (23) <b>51</b> |
| <i>Fasciola trapezium</i>    | –                                   | –                     | –                     | 849 (17.2) <b>49</b>   | 1005 (41) <b>25</b> |

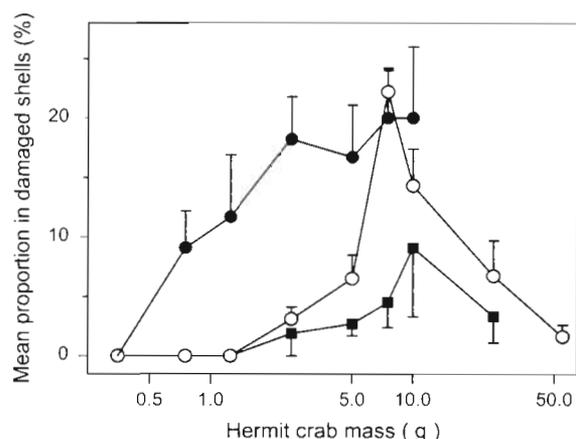


Fig. 4. Proportion of occupied shells damaged with crab mass for 3 species of supralittoral hermit crab at Quirimba Island. The crab species are (●) *Clibanarius longitarsus*, (○) *Coenobita cavipes* and (■) *Coenobita rugosus*. The data are presented as mean with standard error. Error bars are shown as either positive or negative with each plot to ease interpretation of overall patterns

There was a wide variation in degree of fit of shells to the hermit crabs *Coenobita cavipes* and *Coenobita rugosus*. Few individuals of either species forcibly protruded, but many carried oversize shells (Table 4). In only 1 lesser used shell identity, *Nassarius coronatus*, was there over 52% of *C. cavipes* individuals closely fitting the shell carried. Two shells, *Strombus mutabilis* and *Chicoreus ramosus*, had aperture shapes that completely precluded a good fit even if the crab was the appropriate size. In 7 of the 11 shell types 50% or more of *C. rugosus* individuals closely fitted the shells car-

ried. Both *S. mutabilis* and *C. ramosus* were not used by *C. rugosus*. There was a significant correlation between the rankings of shell fit with the usage rankings of *C. rugosus* ( $r = 0.653$ ,  $p < 0.05$ ). There was, however, no correlation between shell fit and use rankings in *C. cavipes*. Although the 2 *Coenobita* species were morphologically similar and used many shell types in common, there was no correlation between the degree of fit shell rankings of *C. cavipes* and those of *C. rugosus*.

## DISCUSSION

The wide intertidal zone surrounding Quirimba Island, Mozambique, is populated by an unusually high diversity of hermit crabs (Barnes 1997a). There is also a high diversity of local intertidal gastropods. Partly as a result of the use of such molluscs for food by local human inhabitants (Barnes et al. 1998), the hermit crab populations are only shell restricted at certain sizes. Furthermore, the 3 species of supralittoral hermit crabs present overlap widely in their range, use atypical food sources (Barnes 1997c) and are behaviourally unusual in undertaking extensive tree climbing and remaining *in arborecum* for protracted periods. The shell identity used by tree climbing hermit crabs has been found to significantly influence this behaviour at Quirimba Island (Barnes 1997b). The results of the present study show that actual shell use, in a field situation, is dictated by a diverse complexity of factors with very different levels of importance.

Approximately 40% of the shells used by each of the 3 supralittoral zone study species were of 1 identity, although a total of 42 shell identities were used. It is of

Table 4. Shell fit in the supralittoral zone hermit crabs *Coenobita cavipes* and *C. rugosus*. Values other than ranking scores are percent of sample population. Hidden, Flush and Protrude refer to the crabs chelae when maximum withdrawn into shell

|                              | <i>Coenobita cavipes</i> |       |          |      | <i>Coenobita rugosus</i> |       |          |      |
|------------------------------|--------------------------|-------|----------|------|--------------------------|-------|----------|------|
|                              | Hidden                   | Flush | Protrude | Rank | Hidden                   | Flush | Protrude | Rank |
| <i>Terebralia palustris</i>  | 79.8                     | 15.7  | 4.5      | 8    | –                        | –     | –        | –    |
| <i>Peristernia forskalii</i> | 66.7                     | 33.3  | 0        | 6    | 66.7                     | 33.3  | 0        | 9    |
| <i>Fasciola trapezium</i>    | 62.5                     | 12.5  | 25       | 9    | 71.4                     | 28.6  | 0        | 11   |
| <i>Chicoreus ramosus</i>     | 100                      | 0     | 0        | 11   | –                        | –     | –        | –    |
| <i>Cerithidium decollata</i> | 90.9                     | 9.1   | 0        | 10   | –                        | –     | –        | –    |
| <i>Turbo coronatus</i>       | 29.4                     | 29.4  | 41.2     | 7    | 29.9                     | 60.8  | 9.3      | 6    |
| <i>Nerita plicata</i>        | 24                       | 74    | 2        | 2    | 8                        | 84    | 8        | 1    |
| <i>Planaxis sulcatus</i>     | 48.3                     | 51.7  | 0        | 3    | 50                       | 50    | 0        | 7    |
| <i>Volema paradisica</i>     | 33.3                     | 38.9  | 27.8     | 5    | 36.4                     | 63.6  | 0        | 5    |
| <i>Nerita polita</i>         | –                        | –     | –        | –    | 17.4                     | 82.6  | 0        | 2    |
| <i>Polinices mamilla</i>     | –                        | –     | –        | –    | 18.1                     | 72.7  | 9.1      | 4    |
| <i>Thais svignyi</i>         | 51.7                     | 48.3  | 0        | 4    | 50                       | 50    | 0        | 7    |
| <i>Strombus mutabilis</i>    | 100                      | 0     | 0        | 11   | –                        | –     | –        | –    |
| <i>Nerita textilis</i>       | –                        | –     | –        | –    | 0                        | 11.1  | 88.9     | 6    |
| <i>Nassarius coronatus</i>   | 12.1                     | 78.8  | 9.1      | 1    | 66.7                     | 33.3  | 0        | 9    |

note that the number of shell identities decreases from the upper shore to the lower shore zones. This was the converse of the pattern of gastropod diversity on the Quirimba Island study shore. This rather surprising situation may result from empty shells being quickly carried upshore on the floodtide and deposited on the high water mark. Thus, the actual variety of available shell identities on the uppershore may be greater than on the lower, as most hermit crabs are unable to gain them from living gastropods (but see Rutherford 1977). Few studies have described as wide a range of shells being used within such an area, although Bertness (1982) describes a species of *Clibanarius* and *Calcinus* using 30 shell types at a Panamanian site. In contrast to the present study the usage of shell identities by hermit crabs was much more even (only 1 shell identity comprised more than 14%).

Each of the 3 study species had distinct shell identity use patterns. *Clibanarius longitarsus* carried significantly heavier shells at equivalent sizes than either *Coenobita cavipes* or *Coenobita rugosus*. This is energetically feasible when much of the mass of a heavier shell is supported by water, the period when *C. longitarsus* was active. Within the supralittoral zone of Quirimba Island, habitat had no significant influence on the shell identity used. Hermit crab mass certainly influenced shell use as a few shell identities could only be used by hermit crabs of a certain size. The size range of most shells, however, allowed use for all but extremes of hermit crab mass. The most abundant shell, that of *Terebralia palustris*, was the most important shell identity used by *C. longitarsus* and *C. cavipes*. The rankings of shell abundance, though, differed substantially from their availability rankings, and the shell use of neither *C. cavipes* nor *C. rugosus* were correlated with shell availability. There was locally a variety of shells partially buried at various depths. No hermit crabs of any species, however, were seen excavating these, as described from North Carolina (USA) by Kellogg (1976).

Various aspects of shell architecture have been investigated by a number of authors, including axis angle and centre of gravity (Conover 1978), sculpture and aperture characteristics (Vermeij 1976) and spire height (Bertness 1982). Hermit crabs may often predominantly be found in shells of less desired architecture or size, through restricted availability (Bertness 1980). The preference for particular architecture is, thus, not necessarily apparent from field observations. However, where 2 hermit crab species almost completely overlap in field distributions, shell availability should be similar and preference more easy to determine (Bertness 1982). At Quirimba Island the supralittoral zone distributions of *Coenobita cavipes* and *C. rugosus* overlap in all but the dense mangrove habitat

(Barnes 1997a,c). Bertness (1982) found that 2 hermit crab species living in similar environments had different architectural preferences partly as a result of crab behavioural differences. In contrast, Gherardi (1990) found that 2 species of hermit crabs occupying similar niches had no difference in architectural preferences. Of the 2 coenobitid species of hermit crabs at Quirimba Island, which heavily overlap in habitat, *C. cavipes* used mainly high spired shells and *C. rugosus* low spired shells. It has been suggested that high spired shells are preferentially used when resistance to desiccation is more important than predation because of the increased potential for carrying fluid (Bertness 1982). Both of the coenobitid species studied at Quirimba Island were, however, semi-terrestrial and, of the two, *C. rugosus*, which uses mostly low spired shells, lives furthest from water. A more likely explanation in this instance may be linked to their refuge behavioural differences. Shell identity has been found to have a significant influence on the tree climbing behaviour of coenobitids at Quirimba Island (Barnes 1997b). *C. rugosus* uses low spired shells and principally burrows rather than climbing trees, whilst *C. cavipes* is the converse. Covering low spired shells is probably easier when burrowing and the increased protection offered by squat shells may be of high priority (than desiccation resistance) for a mainly ground dwelling species.

The shells of lowest physical strength were rarely used by Quirimba Island hermit crabs, regardless of other characteristics, including abundance and availability. The strongest shell, by mass, *Nassarius coronatus*, was also rarely used, though it was rare as a living mollusc and no empty shells were seen. The shells mainly used by *Coenobita rugosus*, *Nerita albicilla*, *N. plicata*, *N. polita*, *Turbo coronatus* and *Volema paradisica* (Table 1), were strong, both outright and per mass (Table 3). The shell *Terebralia palustris* accounted for 43% of total use by *Coenobita cavipes*, but was one of the weakest both outright and per mass. So although *C. rugosus* and *C. cavipes* individuals of similar mass carried shells of similar mass, those of *C. rugosus* were about 6 times stronger. These findings support those suggested by considerations of shell architecture that the principal priorities of *C. cavipes* and *C. rugosus* are avoidance of desiccation and predation respectively. *Clibanarius longitarsus* is able to carry much heavier shells as it is only active when submerged and the mass is partly supported by water. The different shell architecture and strength requirements of these 3 species of hermit crab may be vital in resource partitioning.

Direct predation of the 3 study species was rarely observed during the experimental period. However, actual and potential predators as well as the relative

degrees of predation can be estimated from a combination of observations, relative predator abundance's and other reports of tropical studies in the literature. Two main groups of predators of occupiers of intertidal mollusc shells have been generally described, firstly puffer fish and secondly portunid and xanthid crabs (Bertness 1981, Borjesson & Szelistowski 1989). Observations using SCUBA (Frontier Mozambique unpubl. data) showed that representatives of the first group were comparatively rare locally. There was, however, a high diversity and abundance of both portunid and xanthid crab predators (Barnes & Hogarth unpubl. data). In contrast to studies at other locations, however, the majority of *Coenobita* specimens observed being eaten in the Quirimba Island supralittoral zone were being eaten by other coenobitids. Crows and mangrove kingfishers were also observed eating coenobitids on 2 occasions.

Damaged shells were observed to be frequently used by hermit crabs that were frequently water covered at Quirimba Island, including the supralittoral species *Clibanarius longitarsus* (Fig. 4). Damaged shells have even been shown to be preferentially chosen compared to shells of inappropriate size (Wilber 1990). Damaged shells were, however, rarely used by either semi-terrestrial coenobitid species, except for mid-sized individuals (Fig. 4). As both *Coenobita cavipes* and *Coenobita rugosus* are locally shell limited most at this size, this suggests use of damaged shells is a response to such limitation. Other authors have noted use of non size preferred shells (Vance 1972) or epibiotically encrusted shells (Wright 1973) in limiting situations.

Subtidal hermit crabs at Quirimba Island mostly occupied gastropod shells with very narrow apertures such as *Conus* or *Cypraea* species. All observed specimens of hermit crab species covered by water at some point were able to withdraw completely inside, including all observed specimens of the lower supralittoral species *Clibanarius longitarsus*. Occupying large shells has been found to confer advantages in avoiding predation (Vance 1972, Bertness & Cunningham 1981) and desiccation (Bertness 1981). In contrast, the American east coast intertidal species *Pagurus longicarpus* was found by Wilber (1990) to avoid large shells more than small. In this study, both the upper supralittoral coenobitid species were generally flush with the shell aperture when withdrawn, although there was no correlation between absolute shell fit and use by *Coenobita cavipes*. Only in the most terrestrial of the hermit crabs at Quirimba Island, *Coenobita rugosus*, was there a correlation between shell fit and use. This suggests, as might intuitively be expected, that the importance of shell fit increases with increasing terrestrial nature.

The abundant hermit crab assemblages at Quirimba Island not only show unusual diversity (Barnes 1997a) and behaviour patterns (Barnes 1997b,c), but also complex and novel shell use patterns. Neither habitat, shell abundance nor availability were suggested as major influences on gastropod shell use at Quirimba Island. Within an overlapping intertidal habitat, a sequence of shell use characteristics is suggested with decreased immersion. With increased terrestrial nature (for a given crab mass), the total number of shells used increased, carried shell mass decreased, damaged shells used decreased and shell fit increased. The architecture and strength of shells used followed individual species characteristics and behaviour patterns.

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