Shell utilization and morphometrics of the hermit crab *Diogenes brevirostris* Stimpson

W.D. Emmerson and M.D. Alexander
Department of Zoology, University of Port Elizabeth, Port Elizabeth

Fecundity, shell utilization, and crab and associated shell morphometrics were investigated for the hermit crab *Diogenes brevirostris* collected from three intertidal sites in the eastern Cape. The relationship between crab fresh mass and egg number was linear. *D. brevirostris* was found to occupy 33 gastropod shell species of which *Burnupena* predominated on the rocky shore (*B. lagenaria*, 35,9%; *B. cincta*, 17,5%; *B. pubescens*, 16,5%) while *Bullia* was more commonly used near sandy shores (*B. annulata*, 4%; *B. digitalis*, 2,7%; *B. rhodostoma*, 2,5%). Although *Oxystele* is common, it was hardly used by *D. brevirostris* (*O. sinensis*, 2,7%). Whereas shell type (*Burnupena lagenaria, B. cincta, B. pubescens* and *Bullia rhodostoma*) was found to have no significant influence on the crab length/mass relationships, significant differences were found between elevations but not slopes of the fresh mass/volume relationships ($p < 0,05$). *B. rhodostoma* was significantly different from all three species of *Burnupena* suggesting that small *D. brevirostris* occupy *Bullia* shells of a larger volume than a similar-sized crab occupying a *Burnupena* shell to compensate for the increased 'dead space' incurred with a high spire. Overall, there did not appear to be any selection towards low-spired (17 species, $n = 264$) or high-spired (15 species, $n = 262$) shell species, but there was when compared for each site ($p < 0,01$), indicating shell availability to be important. A good size correlation was found between *D. brevirostris* and its associated shell suggesting that selection of available material and/or mutualism may occur.

S. Afr. J. Zool. 1986, 21: 211 – 216

Vrugbaarheid, skulpbenutting asook krap- en skulpvormafmetings is bestudeer by die kluisenaarskrap *Diogenes brevirostris* wat versamel is by drie tussengetygebiede in die Oos-Kaap. 'n Lineêre verhouding bestaan tussen die vars massa en die eieraantal van die krap. Daar is ook gevind dat *D. brevirostris* skulpe benut van 33 spesies van Gastropoda waarvan *Burnupena* die hoogste persentasie op die rotsstrand uitgemaak het (*B. lagenaria*, 35,9%; *B. cincta*, 17,5%; *B. pubescens*, 16,5%), terwyl *Bullia* meer benut is in die sandstrandgebied (*B. annulata*, 4%; *B. digitalis*, 2,7%; *B. rhodostoma*, 2,5%). Alhoewel *Oxystele* algemeen voorgekom het, is dit nie baie benut deur *D. brevirostris* nie (*O. sinesis*, 2,7%). Alhoewel skulptipe (*Burnupena lagenaria, B. cincta, B. pubescens* en *Bullia rhodostoma*) geen betekenisvolle invloed op die krap se lengte-/massaverhouding gehad het nie, is daar wel verskille gevind tussen die vlakke maar nie die hellings van die varsmassa-/volumeverhoudings nie ($p < 0,05$). *B. rhodostoma* het betekenisvol verskil van al drie spesies van *Burnupena* wat daarop dui dat klein *D. brevirostris*, *Bullia*-skulpe met 'n groter volume betrek as 'n soortgelyke krap wat *Burnupena*-skulpe betrek. 'n Moontlike verklaring hiervoor is om te kompenseer vir die groter 'dooie ruimte' wat saamhang met 'n hoë spiraal. In sy geheel gesien wil dit nie voorkom asof daar enige seleksie is ten opsigte van skulpspesies met 'n lae spiraal (17 spesies; $n = 264$) of hoë spiraal (15 spesies; $n = 262$) nie, maar daar was wel seleksie wanneer die skulpspesies vir elke betrokke gebied vergelyk is ($p < 0,01$) wat daarop dui dat skulpbeskikbaarheid belangrik mag wees. 'n Goeie korrelasie is gevind tussen *D. brevirostris* en sy geassosieerde skulpe wat 'n aanduiding gee dat seleksie van beskikbare materiaal en/of mutualisme mag voorkom.

S.-Afr. Tydskr. Dierk. 1986, 21: 211 – 216

W.D. Emmerson*
Present address: Department of Zoology, University of Transkei,
Private Bag X5092, Umtata, Republic of Transkei

M.D. Alexander
Department of Zoology, University of Port Elizabeth,
P.O. Box 1600, Port Elizabeth, 6000 Republic of South Africa

*To whom correspondence should be addressed

Received 27 May 1985; accepted 18 March 1986

Diogenes brevirostris Stimpson occurs from Saldhana Bay to Durban (Day 1974), and is the most common hermit crab occurring in tidal pools and estuaries in the Eastern Cape. At Flat Rocks, Algoa Bay this anomuran is a major scavenger forming 1,4% of the total biomass (McLachlan, Lombard & Louwrens 1981), although it is also a filter feeder (Bolt 1961). Very little is known about its biology, however, especially when compared to the plethora of research which has been carried out on similar species elsewhere (Mitchell 1976; Hazlett 1981; Bertness 1982). Although the availability of empty gastropod shells has been shown to be a limiting factor to hermit crab populations (Kellogg 1976; Fotheringham 1976; Scully 1979), the sizes of shells occupied by hermit crabs in the field are, nevertheless, almost always well correlated with crab size owing to mechanisms such as 'mutual gain' shell exchange (Hazlett 1981, 1983). The aim of this work therefore, was to examine the fecundity, shell utilization and morphometrics of both crab and its associated shell, as well as to compare selected morphometric relationships of various shell species which predominate in crab populations in different localities in the eastern Cape.

Materials and Methods

The *D. brevirostris* used in this study were collected from tidal pools during spring low tide, mainly from Cape Recife, Algoa Bay (34°00'S/25°30'E), but also from the Quinera mouth (33°00'S/27°55'E) and Morgan Bay (32°42'S/28°20'E; Figure 1). To estimate fecundity a wide size range ($n = 35$) of ovigerous crabs was collected during breeding season (September to January), removed from their shells by immersion in warm (35°C) tap water, their eggs stripped using forceps, and the eggs measured and counted under a stereo microscope fitted with a calibrated ocular micrometer. Crab fresh mass (mg) was measured after blotting dry and carapace length and width (hard cephalothoracic shield; mm) was measured using Vernier calipers. To observe which shells were utilized by *D. brevirostris*, 527 crabs were collected and identified from Kilburn & Rippey (1982). For morphometric data, the following crab measurements were taken; fresh mass (mg), dry mass (mg, oven-dried for 24 h at 80°C), carapace length and width (mm) and right (large) chela length (propodus plus dactyl, mm) and width (propodus, mm). Crab sex was determined by pleopod examination (Barnard 1950). The various shell parameters measured were shell mass (mg, after oven-drying), aperture length and width (mm) and shell volume (to the nearest 0,01 mℓ). Shell volume was estimated by pouring fine dry sand into a pre-dried shell, tapping it to ensure proper sand penetration and compaction and weighing the filled sand. Sand

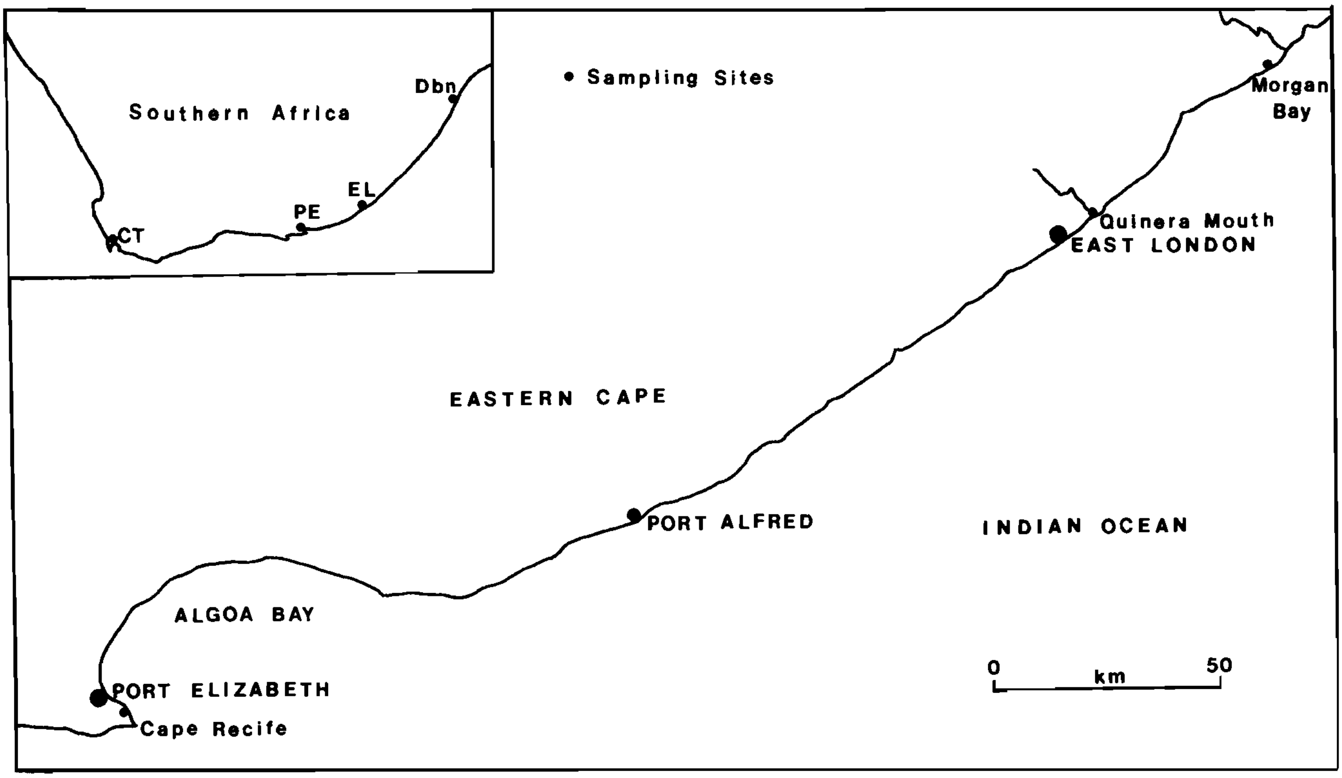

Figure 1 Locality map showing sampling sites.

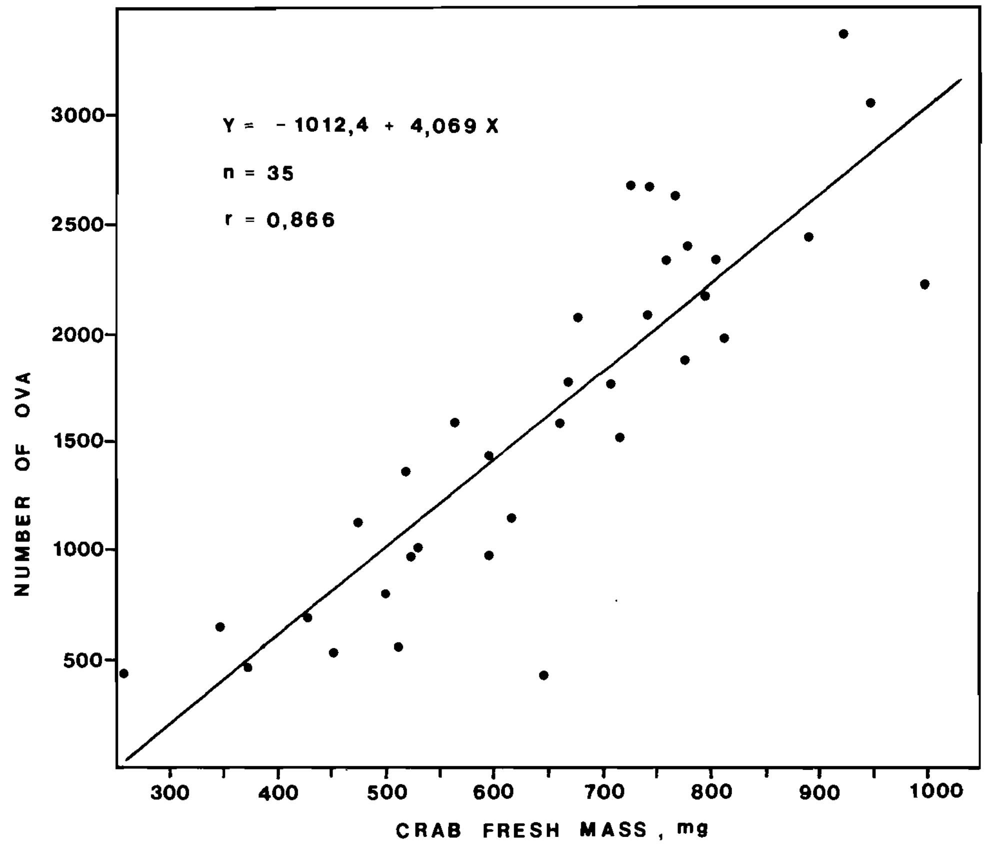

Figure 2 *Diogenes brevirostris*. Relationship between crab fresh mass and number of ova produced.

mass was then converted to volume using a regressed calibration line.

Results

D. brevirostris eggs were found to be relatively large with a mean diameter of 0,75 mm ($n = 85$; *S.E.* = 0,002; range 0,71 – 0,79 mm). The relationship between crab fresh mass and egg number was linear (Figure 2), as was the relationship between carapace length and egg number (Table 1). Ovigerous crab fresh mass ranged from 271 to 1620 mg, carapace length from

Table 1 Fecundity and morphometric relationships for *Diogenes brevirostris* and its associated shell (data pooled for all shell species. S**, highly significant)

Comparison						
X	Y	Formula	r	n	p	Significance
(a) crab fresh mass	*vs* egg no.	$Y = -1012,4 + 4,069X$	0,866	35	$< 0,01$	S**
(b) carapace length	*vs* egg no.	$Y = -4403,3 + 1371,318X$	0,820	35	$< 0,01$	S**
(c) carapace length	*vs* carapace width	$Y = 0,037 + 1,065X$	0,989	420	$< 0,01$	S**
(d) crab fresh mass	*vs* crab dry mass	$Y = 0,002 + 0,353X$	0,982	420	$< 0,01$	S**
(e) crab carapace length	*vs* crab fresh mass	$Y = 9,935X^{2,792}$	0,926	420	$< 0,01$	S**
(f) crab carapace length	*vs* crab dry mass	$Y = 2,007X^{2,977}$	0,940	420	$< 0,01$	S**
(g) crab fresh mass	*vs* shell volume	$Y = 0,001X^{1,051}$	0,948	420	$< 0,01$	S**
(h) crab dry mass	*vs* shell volume	$Y = 0,005X^{0,988}$	0,953	420	$< 0,01$	S**
(i) crab dry mass	*vs* shell mass	$Y = 24,029X^{0,841}$	0,930	420	$< 0,01$	S**
(j) chela width	*vs* shell aperture width	$Y = 2,083X^{0,797}$	0,877	420	$< 0,01$	S**
(k) chela length	*vs* shell aperture length	$Y = 3,636X^{0,728}$	0,878	420	$< 0,01$	S**

Table 2 Shell species utilized by *Diogenes brevirostris* at three sites (H, high-spired; L, low-spired)

		Site							
		Flat Rocks		Morgan Bay		Quinera Mouth		Combined	
Species	Spire	N	%	N	%	N	%	N	%
Afrocominella turtoni	H	–	–	1	0,4	–	–	1	0,2
Ancilla fasciata	L	1	0,4	–	–	–	–	1	0,2
Bullia annulata	H	–	–	20	8,5	1	3,3	21	4,0
Bullia callosa	H	–	–	–	–	4	13,3	4	0,8
Bullia digitalis	H	3	1,1	8	3,4	3	10,0	14	2,7
Bullia diluta	H	–	–	–	–	3	10,0	3	0,6
Bullia rhodostoma	H	–	–	–	–	13	43,3	13	2,5
Bullia tennuis	H	–	–	7	3,0	–	–	7	1,3
Burnupena cincta	H	17	6,5	73	31,2	2	6,7	92	17,5
Burnupena lagenaria	L	167	63,5	22	9,4	–	–	189	35,9
Burnupena pubescens	H	–	–	87	37,2	–	–	87	16,5
Clionella kraussi	H	6	2,3	1	0,4	–	–	7	1,3
Cymatium cutaceum dolarium	L	2	0,8	–	–	–	–	2	0,4
Cymatium tabulatum durbanese	L	2	0,8	–	–	–	–	2	0,4
Fusinus ocelliferus robustior	H	1	0,4	–	–	–	–	1	0,2
Gibbula cicer	L	3	1,1	–	–	–	–	3	0,6
Littorina knysnaensis	L	5	1,9	–	–	–	–	5	0,9
Nassarius capensis	H	1	0,4	–	–	–	–	1	0,2
Nassarius speciosus	H	–	–	3	1,3	–	–	3	0,6
Natica tecta	L	2	0,8	–	–	–	–	2	0,4
Natica sp.	–	–	–	–	–	1	3,3	1	0,2
Nerita albicilla	L	1	0,4	–	–	–	–	1	0,2
Nucella squamosa	L	1	0,4	10	4,3	–	–	11	2,1
Oxystele sinensis	L	14	5,3	–	–	–	–	14	2,7
Oxystele tigrina	L	8	3,0	–	–	–	–	8	1,5
Oxystele variegata	L	5	1,9	–	–	1	3,3	6	1,1
Phalium labiatum zeylanicum	L	1	0,4	–	–	–	–	1	0,2
Thais capensis	H	4	1,5	–	–	1	3,3	5	0,9
Tricolia capensis	L	1	0,4	–	–	–	–	1	0,2
Turbo cidaris cidaris	L	5	1,9	–	–	–	–	5	0,9
Turbo cidaris x natalensis	L	5	1,9	–	–	–	–	5	0,9
Turbo sarmaticus	L	6	2,3	–	–	–	–	6	1,1
Turritella carinifera	H	2	0,8	2	0,9	1	3,3	5	0,9
		263	100,2	234	100,0	30	99,8	527	100,1

3,8 to 6,2 mm and egg numbers from 540 to 3478 per brood. *D. brevirostris* was found to inhabit a large number of shell species. Thirty-three gastropod species were identified, of which *Burnupena lagenaria* formed the highest combined percentage (35,9%; Table 2) followed by *Burnupena cincta* (17,5%), *Burnupena pubescens* (16,5%), *Bullia annulata* (4,0%), *Bullia digitalis* (2,7%), *Oxystele sinensis* (2,7%) and *Bullia rhodostoma* (2,5%).

The principal shell species utilized by *D. brevirostris* also varied with locality and with substrate (rocky or sandy shore).

Burnupena was the dominant genus used on the rocky shore sites at Flat Rocks and Morgan Bay, while *Bullia* was utilized more at the sandy shore site of Quinera mouth. At Flat Rocks, *Burnupena lagenaria* was undisputably the species most utilized (63,5% of site sample), while at Morgan Bay, *B. pubescens* (37,2%) and *B. cincta* (31,2%) were more important (Table 2). The dominant species used at Quinera mouth was *Bullia rhodostoma* (43,3%).

Overall, there did not appear to be any selection towards low-spired (17 species; $n = 264$) or high-spired (15 species; $n = 262$) shell species, but there was when the localities were compared. The numbers of low and high-spired shell species used by *D. brevirostris* were compared for each site using a 2 × 3 chi-squared contingency table (Zar 1974). A highly significant difference was found ($\chi^2 = 13{,}86$; $d.f. = 2$; $p < 0{,}01$). Similarly when the number of low and high-spired individuals used by *D. brevirostris* were compared for each site, the difference was also highly significant ($\chi^2 = 293{,}2$; $d.f. = 2$; $p < 0{,}01$).

Male crabs grew substantially larger than females with approximate maximum fresh masses of 3000 mg and 1500 mg respectively. Crab carapace width showed a strong linear correlation with carapace length ($r = 0{,}989$; Table 1) as did crab fresh mass versus crab dry mass ($r = 0{,}982$). Carapace length was found to have a power correlation with crab dry mass ($r = 0{,}940$). Highly significant correlations were found between crab and its associated shell, such as crab fresh mass and shell volume ($r = 0{,}948$; Table 1) crab dry mass and shell volume ($r = 0{,}953$), crab dry mass and shell mass ($r = 0{,}930$), chela width and shell aperture width ($r = 0{,}877$) and chela length and shell aperture length ($r = 0{,}878$). This indicated a good fit between the shell and its hermit crab occupant.

The predominating shell species from the three sites, namely *Burnupena lagenaria, Burnupena pubescens, Burnupena cincta* and *Bullia rhodostoma* were then compared using analysis of co-variance (Zar 1974) to test if shell type had any influence on the crab length/mass relationships or alternatively on the crab fresh mass/shell volume inter-relationship. Carapace length and fresh mass regressions were $\log_{10}$ transformed and the slopes and elevations compared. Both slopes ($F = 1{,}142$; $d.f. = 3{:}171$; $p < 0{,}05$) and elevations ($F = 2{,}266$; $d.f. = 3{:}155$; $p > 0{,}05$) were not significantly different from one another suggesting that shell type had little to no influence on crab condition, using the crab length/mass relationship as an indicator.

However, as high-spired shells such as *Bullia rhodostoma* would tend to carry more 'dead space' or wasted volume in the unoccupied top of the spire, the slopes and elevations of the fresh mass/shell volume relationships for the same four dominant shell species were compared (Figure 3). Although the slopes were not significantly different from one another ($F = 0{,}986$; $d.f. = 3{:}175$; $p > 0{,}05$), the elevations were significantly different ($F = 2{,}940$; $d.f. = 3{:}157$; $p < 0{,}05$). Regressions were then compared in pairs to establish which was different (Table 3). The *Burnupena* species were not significantly different from each other whereas *Bullia rhodostoma* was highly significantly different from *Burnupena lagenaria* and *Burnupena cincta* and significantly different

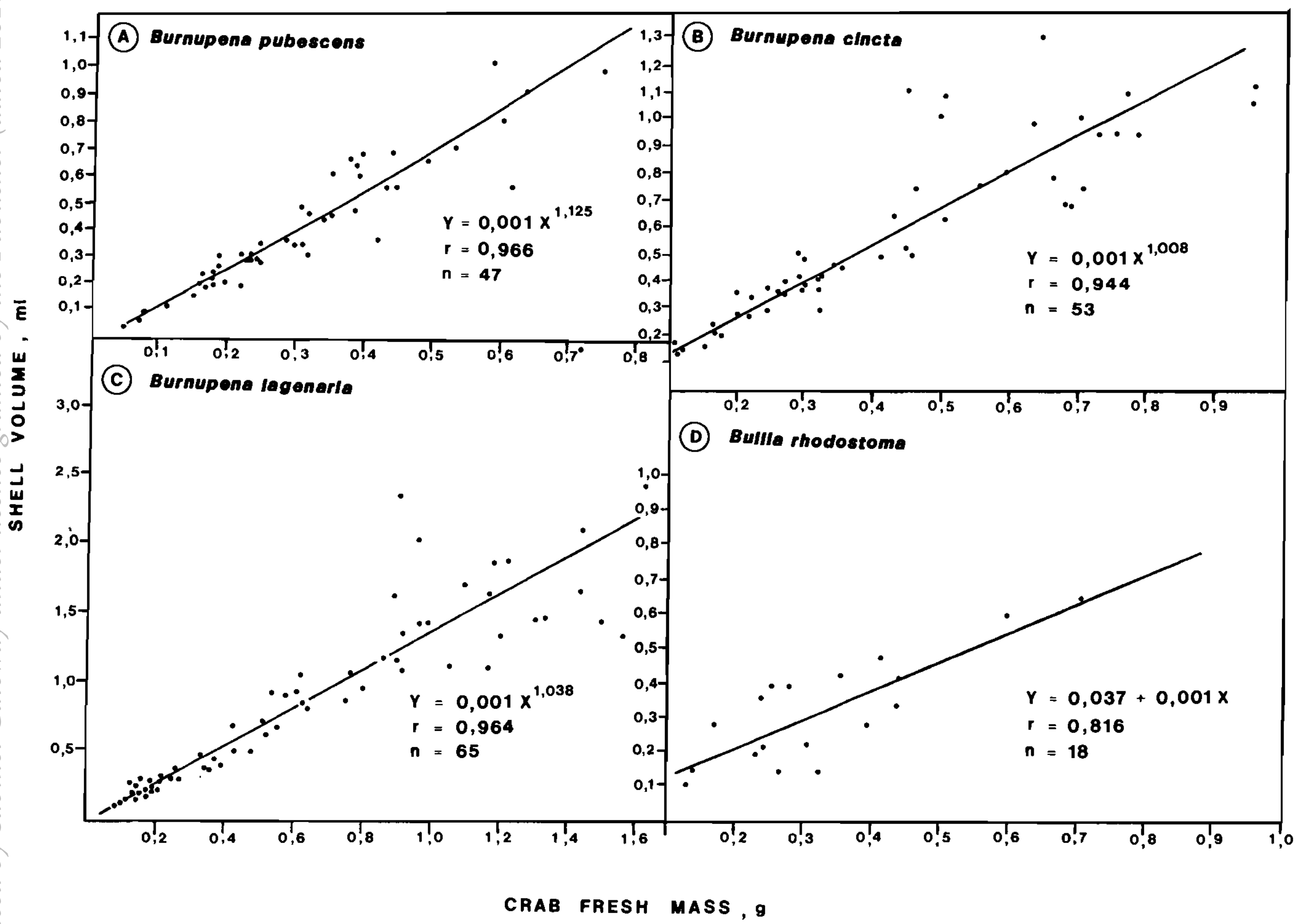

Figure 3 *Diogenes brevirostris.* Relationships between crab fresh mass and shell volume for four principal gastropod shell-species; A, *Burnupena pubescens*; B, *Burnupena cincta*; C, *Burnupena lagenaria*; D, *Bullia rhodostoma*.

Table 3 A paired comparison of elevations for the relationship between crab fresh mass and the shell volume of four species of gastropod selected by *Diogenes brevirostris*. A = *Bullia rhodostoma*, B = *Burnupena lagenaria*, C = *Burnupena cincta*, D = *Burnupena pubescens*

Comparison	*F*	*d.f.*	Significance	*p*
(1) A *vs* B	38,382	1 : 61	S**	< 0,01
(2) A *vs* C	18,416	1 : 67	S**	< 0,01
(3) A *vs* D	4,406	1 : 79	S	< 0,05
(4) B *vs* C	0,521	1 : 114	NS	> 0,05
(5) B *vs* D	0,004	1 : 108	NS	> 0,05
(6) C *vs* D	1,520	1 : 96	NS	> 0,05

from *Burnupena pubescens* (Table 3).

Discussion

The fecundity of *D. brevirostris* as described by expressions (a) and (b) in Table 1 is low when compared to brachyura of similar size ranges (*cf.* Baird 1978). This is due to ovigerous pleopods being limited to just one side of the abdomen (Hazlett 1981) and the limitation of shell volume (Bertness 1981a). These two factors could also possibly explain why the expressions for fecundity were linear and not power-related as is generally observed in crustacea (Emmerson 1980). Shell occupation, however, affords egg protection from predation and physical stress (Hazlett 1981) and although the shell adequacy index (Vance 1972) is generally lower for ovigerous hermit crabs (Bertness 1981a) owing to superior intraspecific competition from males and non-ovigerous females (Bertness 1981b), crabs in smaller shells reproduce more often (Bertness 1981a). It would appear that maturity in *D. brevirostris* females may be reached at about 270 mg fresh mass (3,8 mm CL) when approximately 540 ova are produced.

The 33 species of gastropod shell occupied by *D. brevirostris* compares well with those for other hermit crabs which have been shown to range from 4 to 34 (Hazlett 1981). Orians & King (1964) for example found that *Diogenes gardineri* occupied 16 species of gastropod. As the sampling areas only incorporated the Algoa marine province (Kilburn & Rippey 1982) and as *D. brevirostris* extends to Durban which would include the Algoa/Natal overlap in Transkei and the Natal marine province, it is certain that this species of hermit crab may be recorded occupying many more shell species, especially from these warmer marine zones which are particularly rich in molluscs (Kilburn & Rippey 1982).

Reese (1962), Scully (1979), Bertness (1980) and Wilber & Herrnkind (1982) have all shown that shell-species utilization by hermit crabs is related to availability. At the Flat Rocks site the single most important shell species utilized by *D. brevirostris* was *Burnupena lagenaria* (63,5%, $n = 167$; Table 2) with the other 23 species constituting the balance (eg. *Burnupena cincta*, 6,5%, $n = 17$; *Oxystele sinensis*, 5,3%, $n = 14$; *Oxystele tigrina*, 3,0%, $n = 8$; *Turbo sarmaticus*, 2,3%, $n = 6$ and *Clionella kraussi*, 2,3%, $n = 6$). In a survey of the fauna occurring at an adjacent intertidal site at Flat Rocks, Emmerson, McLachlan, Watling & Watling (1983) found that both *Burnupena lagenaria* (27,6%) and *Oxystele sinensis* (27,6%) were the most common gastropod species present, followed by *Turbo sarmaticus* (14,5%), *Gibbula cicer* (9,9%), *Burnupena cincta* (5,3%), *Clionella rosario* (2,6%) and *Anachis kraussii* (2,6%). The frequency of occurrence of the three most important shell species selected by *D. brevirostris* was then tested against their natural frequency of occurrence using a 2 × 3 chi-squared contingency table (Zar 1974). It was found to be highly significantly different ($\chi^2 = 61{,}6$, $d.f. = 2$; $p < 0{,}001$). Shell availability therefore does appear to be important in shell selection by *D. brevirostris*, but although *O. sinensis* was equally as common as *B. lagenaria*, its shells were utilized far less. This is probably related to shell strengths as *Burnupena* shells are robust compared to the thinner *Oxystele* shells which would be damaged more easily by wave action and consequently contribute less to the available shell pool. *Nerita albicilla* is a commonly occurring species both at Flat Rocks and Morgan Bay, but although it has a strong shell, it is hardly utilized by *D. brevirostris* because of its limpet-like shape. Similarly, shells of *Conus* spp. are common at Morgan Bay, yet are not utilized because of the slit-like aperture. Gastropod zonation and the redistribution of empty shells by water are other important factors which would affect shell availability to *D. brevirostris*. Of the shell species utilized by this hermit crab (Table 2), the major ones selected were from intertidal species, with infratidal species yielding low numbers of specimens. A notable exception was *Littorina* which is mainly supralittoral, but does extend into the intertidal zone (Kilburn & Rippey 1982). The Flat Rocks site is in a sheltered bay and it is interesting to compare this site with a high energy rocky shore such as Morgan Bay where a large contribution is made to the shell pool by subtidal species such as *Burnupena pubescens* and *Bullia annulata*, the shells of which are washed into gullies. *Burnupena pubescens* was not common at Flat Rocks and consequently was not available for utilization by *D. brevirostris* whereas *B. lagenaria* was and was heavily utilized. Quinera mouth is flanked on both sides by long sandy beaches where *Bullia* is common. Here five species of *Bullia* were utilized of which *Bullia rhodostoma* was the species most occupied, again emphasizing the importance of local shell availability. Many workers have examined the parameters which are used by hermit crabs in shell selection. Hazlett (1978) and Conover (1978) both found shell mass and internal volume to be critical (*cf.* Table 1; h and i), whereas Mitchell (1976) found aperture width to be important (*cf.* Table 1; j). Vance (1972) and Kellogg (1976) formulated a shell adequacy index (SAI) to explain shell selection while Reese (1962) used a weight index. Abrams (1978, 1982) found shell condition to be a criterion in shell selection while thermal stress (Bertness 1982) and predation pressure (Rossi & Parisi 1973; Bertness 1982) have also been found to be factors in shell selection. Gilchrist (1984), on re-evaluating hermit crab shell indices has since found them to be increasingly more unreliable with increasing crab size and suggests caution in their use and interpretation. Bertness (1982) observed that high-spired shells maximized protection from thermal stress, while low-spired shells enhanced resistance to predation. The major shell species utilized by *D. brevirostris* have both high and low spires (Table 2) suggesting that shell availability may be more important than both thermal stress and predation pressure.

In comparing crab fresh mass and shell volume (Table 3), *Bullia rhodostoma* was found to be significantly different from the three species of *Burnupena*. Although crab numbers in *B. rhodostoma* shells were low, the significant difference in elevation suggests that small *D. brevirostris* occupy shells of a larger volume than a similar-sized crab occupying a *Burnupena* shell to compensate for the increased 'dead space'. However, although the slopes were not significantly different, the lower b-value (slope) and significantly different elevation tends to suggest that larger crabs occupy *B. rhodostoma* shells of a smaller volume than their *Burnupena* counterparts. These larger crabs would then be relatively even more cramped as a higher proportion of this volume cannot be utilized because of the high spire.

Littorina knysnaensis, being a small species, was only occupied by juvenile *D. brevirostris*. Grant & Ulmer (1974) similarly observed that *Littorina* shells were only utilized by juvenile *Pagurus pubescens* and *P. acadianus*. Other small shell species utilized by juvenile *D. brevirostris* were *Ancilla fasciata, Gibbula cicer, Nassarius capensis, Natica tecta* and *Tricolia capensis*.

Personal observations in the laboratory have shown that *D. brevirostris* invariably inserts its larger chela into the shell aperture before entering an empty shell. This has also been documented for *Clibanarius virescens* (Branch & Branch 1983) and Reese (1962) has suggested that this is a shell selection mechanism. *D. brevirostris* may thus be able to assess the suitability of a shell and the chela ('operculum') fit before occupation of the shell, as well as to check for shell inhabitants. This piece of behaviour could possibly explain the good relationship between chela width and shell aperture width (Table 1; j). The weaker relationship between shell aperture length and chela length (Table 1; k) may be due to the wide range of aperture lengths found in different gastropod species.

In conclusion it may be stated that there is a good size correlation between *D. brevirostris* and its associated shell suggesting that selection and/or mutualism occurs. This is important as the occupation of inadequate shells reduces crab survival, growth and fecundity (Markham 1968; Hazlett 1981). Further work on *D. brevirostris* and other hermit crab species occurring in southern African waters is required in order to better understand the biology, ecology and behaviour of these interesting, and so far neglected, members of the littoral zone.

Acknowledgements

The authors thank D. Winter for his help in computing the data, Dr T. Lasiak-Dye and M. Bird for checking the shell species, Professor A. Dye for his critical appraisal of the manuscript and Mrs P. Dardis for preparing the typescript. Work was funded by a C.S.I.R. grant for which thanks are extended.

References

ABRAMS, P. 1978. Shell selection and utilization in a terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). *Oecologia* (Berl.) 34: 239 – 253.

ABRAMS, P. 1982. Intraspecific shell exchange in the hermit crab *Clibanarius virescens* (Krauss). *J. Exp. Mar. Biol. Ecol.* 59: 89 – 101.

BAIRD, D. 1978. Fecundity of *Sesarma catenata* Ortmann (Grapsidae: Crustacea) occurring in the saltmarshes of the Swartkops estuary, Port Elizabeth. *S. Afr. J. Sci.* 74: 31 – 32.

BARNARD, K.H. 1950. Descriptive catalogue of South African decapod Crustacea. *Ann. S. Afr. Mus.* 38: 1 – 837.

BERTNESS, M.D. 1980. Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *J. Exp. Mar. Biol. Ecol.* 48: 1 – 16.

BERTNESS, M.D. 1981a. Pattern and plasticity in tropical hermit crab growth and reproduction. *Am. Nat.* 117: 754 – 773.

BERTNESS, M.D. 1981b. Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage. *J. Exp. Mar. Biol. Ecol.* 49: 189 – 202.

BERTNESS, M.D. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. *J. Exp. Mar. Biol. Ecol.* 64: 159 – 187.

BOLTT, R.E. 1961. Antennary feeding of the hermit crab *Diogenes brevirostris* Stimpson. *Nature.* 192: 1099 – 1100.

BRANCH, G. & BRANCH, M. 1983. The living shores of southern Africa, C. Struik Publishers, Cape Town.

CONOVER, M.R. 1978. The importance of various shell characteristics to the shell-selection behaviour of hermit crabs. *J. Exp. Mar. Biol. Ecol.* 32: 131 – 142.

DAY, J.H. 1974. A guide to marine life on southern African shores, A.A. Balkema, Cape Town.

EMMERSON, W.D. 1980. Induced maturation of prawn *Penaeus indicus*. *Mar. Ecol. Prog. Ser.* 2: 121 – 131.

EMMERSON, W.D., McLACHLAN, A., WATLING, H.R. & WATLING, R.J. 1983. Some ecological effects of two sewage outfalls in Algoa Bay. *Water S.A.* 9: 23 – 30.

FOTHERINGHAM, N. 1976. Effects of shell stress on the growth of hermit crabs. *J. Exp. Mar. Biol. Ecol.* 23: 299 – 305.

GILCHRIST, S. 1984. Evaluation of hermit crab shell indices. *Mar. Biol.* 78: 147 – 151.

GRANT, W.C. & ULMER, K.M. 1974. Shell selection and aggressive behaviour in two sympatric species of hermit crabs. *Biol. Bull. mar. biol. Lab., Woods Hole.* 146: 32 – 43.

HAZLETT, B.A. 1978. Shell exchanges in hermit crabs: aggression, negotiation or both? *Anim. Behav.* 26: 1278 – 1279.

HAZLETT, B.A. 1981. The behavioural ecology of hermit crabs. *Ann. Rev. Ecol. Syst.* 12: 1 – 22.

HAZLETT, B.A. 1983. Interspecific negotiations: Mutual gain in exchanges of a limiting resource. *Anim. Behav.* 31: 160 – 163.

KELLOGG, C.W. 1976. Gastropod shells: a potentially limiting resource for hermit crabs. *J. Exp. Mar. Biol. Ecol.* 22: 101 – 111.

KILBURN, R. & RIPPEY, E. 1982. Sea shells of southern Africa, Macmillan, Johannesburg.

MARKHAM, J.C. 1968. Notes on growth patterns and shell utilizations of the hermit crab *Pagurus bernhardus* (L.). *Ophelia* 5: 189 – 205.

McLACHLAN, A., LOMBARD, H.W. & LOUWRENS, S. 1981. Trophic structure and biomass distribution on two East Cape rocky shores. *S. Afr. J. Zool.* 16: 85 – 89.

MITCHELL, K.A. 1976. Shell selection in the hermit crab, *Pagurus bernhardus*. *Mar. Biol.* 35: 335 – 343.

ORIANS, G.H. & KING, C.E. 1964. Shell selection and invasion rates of some Pacific hermit crabs. *Pac. Sci.* 18: 297 – 306.

REESE, E.S. 1962. Shell selection behaviour of hermit crabs. *Anim. Behav.* 10: 347 – 360.

ROSSI, A.C. & PARISI, V. 1973. Experimental studies of predation by the crab *Eriphia verrucosa* on both snail and hermit crab occupants of conspecific gastropod shells. *Boll. Zool.* 40: 117 – 135.

SCULLY, E.P. 1979. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab, *Pagurus longicarpus* Say. *J. Exp. Mar. Biol. Ecol.* 37: 139 – 157.

VANCE, R.R. 1972. The role of shell adequacy in behavioural interactions involving hermit crabs. *Ecology* 53: 1075 – 1083.

WILBER, T.P. & HERRNKIND, W. 1982. Rate of new shell acquisition by hermit crabs in a saltmarsh habitat. *J. Crust. Biol.* 2: 588 – 592.

ZAR, J.H. 1974. Biostatistical analysis, Prentice-Hall, Englewood Cliffs, New Jersey.