Resource utilization and reproduction of the hermit crab *Clibanarius virescens* (Crustacea: Decapoda: Anomura) in South Africa.

by

Michelle Wait

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Co-promoter: Prof. D. Baird

Abstract

Clibanarius virescens (Krauss) is a common and abundant hermit crab along the East coast of South Africa. Despite this, its biology is poorly known, both in South Africa and throughout the rest of its range in the West Indo-Pacific region.

This study focuses on the descriptive analysis of the shell resource used by *C. virescens* and of the effects of this resource on crab populations. The underlying hypothesis of the study is that biogeographically imposed gradients in the morphology of intertidal gastropod shells used by hermit crabs affect hermit crab population parameters. The gradient of potential change in the shell resource was captured by sampling at 12 localities, encompassing the range of *C. virescens* in South Africa.

Seasonal changes in shell use, population structure and reproduction at a single locality (Cape Recife) were recorded over a period of 13 months. The breeding season of C. virescens at the southern extreme of its range extended from December to June. The population structure shows some seasonal change, but no clear trends emerge.

The shell resource changed substantially in nature over the region studied. Based on shell use, localities clustered into separate southern and northern groups with a break occurring between Dwesa and Coffee Bay. Southern localities were characterised by use of *Burnupena cincta*, *B. lagenaria* and *B. pubescens*. Northern localities were characterised by the use of *Morula granulata*, *M. nodosa* and *Peristernia forskalii*. Intertidal shells used by *C. virescens* show fewer adaptations to predation in southern localities than shells from northern localities. Southern shells

are relatively large, light and have wider apertures than those from northern localities which are generally smaller, heavier and have decreased aperture widths.

Shell parameters affect population size-distributions as southern crabs were larger and heavier than northern crabs. *C. virescens* show sexual size dimorphism in which male crabs uniformly dominate the larger size classes at all localities. Differences in the sex ratio between males and females show more variable patterns. Most southern localities show no difference in the number of male and female crabs, but most northern localities show a skewed sex ratio in favour of females. Shell use and population size distributions of females affect reproductive output. Southern females produced significantly larger clutches than northern females. Reproductive output was related to crab mass and shell volume.

Shell use patterns conform to the biogeographical regions in the range of the study and have a clear effect on both the population size distributions and reproductive output of *Clibanarius virescens*.

Key words:
Biogeographical gradient

Clibanarius virescens

Hermit crab

Reproductive output

Shell use

Size-frequency distribution

South Africa

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Chapter 1: General introduction

Hermit crabs provide a fascinating glimpse into interdependencies in rocky shore marine habitats and provide the opportunity for population-level processes to be understood through interaction with a single resource (Hazlett 1981). There are approximately 1062 known species of hermit crabs in 143 genera (De Grave *et al.* 2009), and most of them are obligatory users of gastropod shells during some phase of their lifetime (Hazlett 1981). Among the exceptions are those, such as *Discorsopagurus schmitti* (Gherardi and Cassidy 1995) or *Calcinus tubularis* (Gherardi 2004), which use the stationary tubes of polychaete worms as shelters, or *Birgus latro*, the coconut crab, which carries a shell during early development, but becomes fully carcinized as an adult (Reese and Kinzie1968). Hermit crabs require shells to protect their uncalcified abdomens and those inhabiting the intertidal zone also use shells as mobile microclimates (Reese 1969). The use of a shell has allowed members of the Coenobetidae, or land hermits, to lead almost fully terrestrial lives. All aspects of hermit crab biology, from larval settlement (Worcester and Gaines 1997) to mating success and fecundity (Hazlett 1989) are affected by the gastropod shell resource. This relationship is one of the few systems in nature where a single, unmodified biological structure acts as protection for two different animals: the original mollusc and the hermit crab (LaBarbera and Merz 1992).

It is therefore not surprising that most studies on hermit crabs centre on their use of shells. Many such studies either describe the shell resource used in the field, or report on shell selection experiments which aim to determine whether the shells used by hermits crabs are their preferred shells. Often intra- or interspecific competitive interactions are reported upon. An entire school of behavioural research has grown out of investigating motivation, signalling behaviour, negotiation (rather than

"fighting") and decision-making during interactions involving shell exchange (for a review of early work see Elwood and Neill 1992). More is probably known about the shell selection behaviour of many species than about their role in the ecology of marine ecosystems.

Almost all studies of hermit crab population structure and reproduction centre on the effect of the shell resource on these parameters, as does this study. The main focus of this study will be a descriptive analysis of the shell resource used by *Clibanarius virescens* and of the effects of this resource on the crab populations sampled. Comment on shell preference or competitive interaction among and within species will not be explored beyond occasional speculation and reference to the literature on experimentally established preferences and competitive outcomes. Questions framed within the descriptive analysis will be driven by the underlying hypothesis that the biogeographical gradient in the morphology of the intertidal gastropod shells used by hermit crabs affects hermit crab population parameters. Hermit crabs are at the sharp end of a cascade of physical, environmental and ecological effects that combine to shape their primary resource.

1.1 Overview of selected literature

There exists a wealth of literature on hermit crabs. This overview does not seek to be an exhaustive review of information, but rather an introduction to some of the concepts important to this study, as well as an overview of work on hermit crabs done in Africa. Chapter introductions will further examine literature relevant to their contents.

The independent life of a hermit crab begins as a planktotrophic larva. Even at the point of larval release, the shell resource used by the female crab affects the larva. Zeigler and Forward (2006) described larval release behaviours in *Clibanarius vittatus*, and showed that females in damaged shells did not display stereotypical release behaviours, and that often the larvae released by such females were not viable. Much of the work on larval hermit crabs has focussed on describing larval developmental stages in the laboratory (for example, Bartilotti *et al.* 2008). Complete larval development consists of 4 zoeal and one megalopal (also called a glaucothoë) stage. The megalopa is able to swim, and it is this stage that is responsible for finding small shells in which to settle (Hazlett and Provenzano 1965, Gherardi and Cassidy 1995). Megalopae are able to delay metamorphosis when no shells are available (Harvey 1996), and the lack of small shells may be the first limiting interaction between a hermit crab population and its shell resource (Halpern 2004, Oba and Goshima 2004). In *Clibanarius vittatus*, larvae settle away from adults as adults feed by disturbing the sediment. This pattern is unlikely in *Clibanarius virescens*, which lives on rocky substrates.

Early work on the effect of shells on growth rates was conducted by Fotheringham (1976a, 1976b) and Bertness (1981a, 1981c, 1981d). Fotheringham (1976a) conducted laboratory rearing experiments with *Pagurus longicarpus* and *P. pollicaris* to measure the effect on the growth rates of small shells compared to preferred shells. He concluded that growth rates were significantly reduced in sub-optimal shells. Bertness (1981a) also conducted laboratory rearing experiments on *Clibanarius albidigitus*, and tested the effect of modified shells (additional weight) on growth in male crabs. In the same study Bertness (1981a) examined the effect of shell type on clutch size by comparison of clutch sizes in the different shell types

used by females. He found that light-weight shells with high volumes allowed higher growth rates and larger clutch sizes than heavier, low volume shells. Shells that are too small can affect growth rates to the extent that crabs experienced no growth (Angel 2000) or even experienced negative growth (Asakura 1992), an unusual situation for most crustaceans (Hartnol 1982). Wada *et al.* (1997) also conducted laboratory rearing experiments and found that hermit crabs could not only assess shell availability and alter their shell preference according to their prospective growth rate, but that they could also alter their growth rate based on assessment of the shells available. This indicates that hermits use a complex model of shell assessment.

The population structure of hermit crabs tends to show numerical dominance by females, but size dominance by males. The sex ratio is skewed towards females for entire populations (Fransozo and Mantelatto 1998, Turra and Leite 1999, Turra and Leite 2000, Litulo and Tudge 2005, Mantelatto *et al.* 2005), but within the same species, populations may show differences between localities (Benvenuto and Gherardi 2001), while in some populations there is no difference in the sex ratio between males and females (Garcia and Mantelatto 2001). There may also be seasonal differences in the sex ratio (Fransozo and Mantelatto 1998, Benvenuto and Gherardi 2001).

Hermit crab populations tend to display sexual dimorphism with males generally becoming larger than females (Harvey 1990, Wada 1999, Mantelatto and Martinelli 2001, Contreras-Garduño and Córdoba-Aguilar 2006). Proximally, this is probably due to differences in growth patterns between the sexes (Mantelatto *et al.* 2007), as males have faster growth rates than females, especially when suitable large shells

are available (Wada *et al.* 1997). Ultimately sexual size dimorphism in hermit crabs could be due to increased mating success with increased size (Asakura 1995, Osorno *et al.* 1998, Wada 1999), either through male-male competition or through increased ability of large males to copulate successfully with smaller females (Hazlett 1989). It could also be driven by female mate choice, but this is as yet unproved in hermit crabs (Contreras-Garduño and Córdoba-Aguilar 2006). Although sexual size dimorphism is common, examples can be found where congeneric species in the same environment show different size-distribution patterns (MacPherson and Raventos 2004).

The reproductive biology of hermit crabs has also been fertile ground for research. Childress (1972) sought to link reproductive biology and fitness theory by assessing shell effects on the biology of *Clibanarius albidigitus*. He attempted to construct fitness sets by combining reproductive fitness and aggressive dominance into a measurement of behavioural fitness. He found that hermit crabs use optimal ratios strategies in order to select shells with optimum mass, which would allow maximised reproductive fitness (Childress 1972).

Early work in Africa, conducted by Ameyaw-Akumfi (1975), catalogued the reproductive output of two African *Clibanarius* species. Most work on hermit crab reproduction compares clutch size or mass to various measures of crab size and shell size in order to determine which factors most affect a particular hermit crab species in a particular environment (for example Fotheringham 1976a, 1980, Bertness 1981a, 1981b, 1981d, Elwood *et al.* 1995, Shih and Mok 2000). A number of studies have determined the breeding season of crabs (for a recent summary see Litulo and Tudge 2005). Carlon and Ebersole (1995) included a rare glimpse of the

patterns of larval abundance in relation to breeding season in their study of three *Pagurus* species. Manjón-Cabeza and García Raso (2000) examined ovarian structure of *Diogenes pugilator* and also compared clutch size to female size.

Most reproductive studies have found that clutch size is closely correlated to crab size but may (Mantelatto *et al.* 2002, Hazlett *et al.* 2005) or may not (Hazlett 1989) be correlated to shell dimensions or type depending on the crab species investigated. Egg size is most often related to the size reached by a particular species of crab rather than to individual female size (Manjón-Cabeza and García Raso 2000).

Little work has been done on hermit crab biology in Africa. Ameyaw-Akumfi (1975) worked in Ghana and quantified reproductive output in *Clibanarius chapini* and *C. senegalensis*. Between 1997 and 2000, Barnes produced a series of papers on the ecology of tropical hermit crabs at Quirimba Island, Mozambique, in which he investigated many aspects of hermit crab ecology and hermit-human interactions. The most relevant to this study was research on the distribution, abundance and activity of 16 species of hermit crabs (Barnes 1997), and the shell characteristics and shell use by 10 species of hermit crabs in 42 shell types (Barnes 1999). He also analysed niche width in which shell use, habitat use and the exploitation of gastropod shells from human-made shell middens was investigated (Barnes and de Grave 2000). More recently, Litulo, working in southern Mozambique has produced work on the basic biology of *Diogenes brevirostris* (Litulo 2004, Litulo and Tudge 2005), *Clibanarius longitarsus* (Litulo 2005a), *Calcinus gaimardi* (2005d), and *Dardanus deformis* (Litulo 2005b, 2005c).

In South Africa there have been few studies of hermit crabs. Emmerson and Alexander (1986) investigated shell used and morphometrics of *Diogenes brevirostris* on the East coast, while Walters and Griffiths (1987) investigated distribution, abundance and shell use in the same species, but in a very different habitat on the West coast of South Africa. Reddy and Biseswar (1993) and Nakin and Somers (2007) all worked on *Clibanarius virescens* and their work is discussed below. McLaughlin and Forest (1999) published on *Pagurus* spp., most of which occur sub-tidally off the coast of South Africa.

1.2 *Clibanarius virescens*

Clibanarius virescens (Krauss) is commonly known as the yellow-banded hermit crab. It is one of the most common hermits crabs along the eastern shore of Southern Africa and is easily distinguished from co-occurring species by its sub-equal chelipeds, dark greenish-brown to black colour and yellow bands on the dactyls of its walking legs (McLaughlin 1997), although the pattern of these can differ within populations (Morgan 1988).

The type locality of the species is Durban on the east coast of South Africa (Lewinsohn 1982, Gerhardi and McLaughlin 1994). It is a reptant decapod crustacean classified into the Infraorder Anomura, Super Family Paguriodea and Family Diogeniade (De Grave *et al.* 2009). The pagurid hermit crabs are viewed as a polyphyletic group based on cladistic analysis of gross morphological features (McLaughlin 1983) and on analysis of the ultrastructure of the spermatozoa and morphological features of the spermatophores (Tudge 1997). Tudge (1997) examined 24 species of hermit crabs, and grouped *Clibanarius* with the Family

Diogenidae based on an analysis of spermatophore and spermatozoal characteristics. *Clibanarius* forms a distinct clade within the Diogenidae when using these characteristics. The classification of the Anomura, however, is contentious and the focus of on-going revision of both morphological and molecular evidence (De Grave *et al.* 2009)

Only two members of the genus *Clibanarius*, namely *Clibanarius virescens* and *C. longitarsus*, occur in South Africa, but several cogenerics are noted from Mozambique, including *C. padavensis*, *C. striolatus* and *C. eurysternus* (Barnard 1950). The distribution of *C. virescens* in Southern Africa is noted by Barnard (1950), and described by Day (1974) who gives its distribution as extending from Port Elizabeth to Moçambique Island. Port Elizabeth, on the south coast of South Africa, can be considered the western-most edge of its range in Africa and thus of the Indo-West Pacific region. Its distribution continues through Mozambique (MacNae and Kalk 1962), Tanzania, Kenya, the Comoros Islands and Madagascar (Reay and Haig 1990), and into Somalia (Lewinsohn 1982). Hogarth *et al.* (1998) note its presence in the Maldives. Lewinsohn (1982) describes *C. virescens* as the most frequently encountered hermit crab in the Indo-West Pacific region, extending from East Africa to Japan and the Fiji Islands. He notes that it had not been found in the Red Sea, in contrast to Barnard (1950), who includes the Red Sea in its distribution. Simões *et al.* (2001) describe it as common on Socotra Island, off the horn of Africa. C*libanarius virescens* is also reported from the Gulf of Oman by Moradmand and Sari (2007). In the Pacific Ocean, *C. virescens* occurs on Guam (Abrams 1981), and on One Tree Island in eastern Australia (Abrams, 1982). In a report from the Faculty of Fisheries, Kasetsart University, Wisespongpand *et al.* (2007) include *Clibanarius virescens* as a rare species and a new record for Mu Ko Surin National Park in the

Andaman Sea off Thailand. Imazu and Asakura (1994) and Wada *et al.* (2005) studied population dynamics and shell use by *C. virescens* at two sites in Japan.

The only published studies on *C. virescens* in South Africa are by Reddy and Biseswar (1993) and more recently by Nakin and Somers (2007). Both these studies examine shell use by *C. virescens*. Reddy and Biseswar (1993) compared the shell use of *C. virescens* and *Calcinus laevimanus* occurring sympatrically at two sites, most likely Isipingo Beach and Park Rynie (Biseswar, pers com.) in KwaZulu-Natal on the east coast. They also noted the effect of shell weight and volume on clutch sizes in both crab species. Nakin and Somers (2007) examined patterns of shell use compared to shell availability and intertidal gastropod abundance at three localities (Dwesa, Nqabara and Mendwana) in the Eastern Cape Province on the southeast coast. These studies are difficult to compare because they occur in two different biogeographic provinces and have only two shell species in common. The findings of these studies will be discussed in relation to the current study in the relevant chapters.

Elsewhere in the world, *Clibanarius virescens* has not been as extensively studied as some other hermit crab species. In the Quirimba Archipelago of Mozambique, Barnes described the distribution, abundance and activity of tropical hermit crabs (Barnes 1997) as well as the characteristics of shells used by hermit crabs, among which *Clibanarius virescens* (Barnes 1999). At Quirimba he found 7 genera comprising 16 species of hermit crabs of which three species, *Clibanarius laevimanus*, *C. virescens* and *Calcinus laevimanus* accounted for 75% of the intertidal hermit crab abundance. He noted that *C. virescens* was found mainly in the mid-littoral zone and that it was super-abundant (> 10 m^{-2}) to common (1 – 0.1 m^{-2})

on the islands of the archipelago. He also noted that *C. virescens* tended to cluster on the lower mid-shore mainly on high points on the shore and that it also occurred in sea-grass beds (Barnes 1997). He inferred that the crabs clustered to become dormant as this activity took place at low tide. He found that *C. virescens* was a heavy user of (> 5% of usage) of 5 shell species, out of a total of 18 shell species used by it. He noted that *Clibanarius* and *Calcinus* species show similar shell use patterns.

In Kenya, Reay and Haig (1990) reported that on intertidal hard substrates *Clibanarius virescens* and *Calcinus laevimanus* appeared to be co-dominant in the upper littoral zone and were particularly common and conspicuous. At low tide in Kenya *Clibanarius virescens* often formed dense clusters at the edges of rock pools and could also be found in aggregations under rocks.

In Japan Imazu and Asakura (1994) sampled a single site on the Bozo Peninsula and described the distribution, reproduction and shell utilization patterns of three species of intertidal hermits crabs, namely *Pagurus geminus*, *P. lanuginisus* and *Clibanarius virescens*. *C. virescens* accounted for 26.4 % of the crabs collected during the sampling period. Numbers of *C. virescens* varied monthly and ovigerous females were only present between June and November, with numbers peaking in August. Juveniles were collected throughout the year, with peaks in mid-winter and spring. Males were generally found further from the mean low water spring-tide mark than females, but *C. virescens* generally occupied the mid-litoral zone. Males did not differ significantly in size from non-ovigerous females, but were larger than ovigerous females. Generally more females were found than males, except in size classes with large crabs, where males dominated. Shell utilization was found to be different

between the three crab species, with *C. virescens* using the largest number of shell species. Differences in shell utilization between the sexes were also seen for two out of four size classes in *C. virescens*. This is likely due to the differences in size, and therefore shell requirements, between large males and smaller, ovigerous females.

Wada *et al.* (2005) sampled further southwest, in Tosa Bay on southern Shikoku Island, Japan. Although their study concentrated on four species of *Pagurus*, they also determined the reproductive seasons of nine other species of hermit crab, among them *C. virescens*. They found that *C. virescens* was the third most abundant hermit crab in the sample. Wada *et al.* (2005) found that the average size for ovigerous females was larger than the average size females overall, but still smaller than the average size of males. Ovigerous females were found only between March and September. It is interesting to note that a difference of less than 2° latitude shifts the breeding pattern of this species (Bozo Penisula is at 35°0' N while Tosa Bay is at 33°18' N).

Abrams (1981) refers to *C. virescens* sampled on Guam as part of a study on competition in Indo-Pacific hermit crabs. He mentions that it was about an order of magnitude less abundant than *Clibanarius humilis*, which was abundant on Guam. *C. virescens* formed part of the inner reef-flat community. *C. virescens* was able to out-compete *C. humilis* for shells, but was evenly matched against *Calcinus laevimanus*, although the results were not statistically significant. *Clibanarius virescens* also suffered the greatest total competitive effect, but this was not discussed. In another study, Abrams (1982) examined intraspecific shell exchange in *C. virescens* on One Tree Island at the southern end of the Great Barrier Reef in Australia. *C. virescens* was very abundant, with densities of up to 150 crabs per m^2

during peak times of activity (dusk with an incoming tide). At this locality all *C. virescens* individuals were collected in only one shell species.

Hazlett (1996) sampled in Queensland, Australia, to study the pre-copulatory behaviour of both *C. virescens* and *Diogenes avarus*. The study concentrated on *D. avarus*. It was assumed that the type of shell occupied by male *Clibanarius virescens* would influence success in mating, but this could not be directly observed as all the males that mated were in the same shell type.

Dunbar, Coates and Kay (2003) also sampled extensively in Queensland to determine whether hermit crabs could be used as indicators of freshwater inundation on tropical shores. They compared the freshwater tolerance of *Clibanarius taeniatus* and *Clibanarius virescens* and found that *C. virescens* was intolerant of fresh water. A survey showed that sites with no freshwater influence maintained higher percentages of *C. virescens* than of *C. taeniatus*. This work was followed by a study (Dunbar and Coates 2004) which showed that the different responses to freshwater by the two crab species were not due to differences in ionic or osmotic regulation, but rather to a higher tolerance to dilution of body fluids by *C. taeniatus* than by *C. virescens*.

Knowledge of *Clibanarius virescens* worldwide consists of a patchwork of information that does not provide a good picture of the species and its adaptations to habitat differences. Nothing is known about the population structure or reproductive period of *Clibanarius virescens* in Africa, despite it being a very common crab in this region.

1.3 Biogeography

Clibanarius virescens occurs in at least two South African biogeographic regions and depends on the shells of gastropod species that occur within these regions. While very little work has been done specifically on gastropod biogeography on the South African coast, it is accepted that gastropod species distributions change markedly within the South and East coast regions of South Africa. This change probably, in turn, affects *C. virescens* populations occurring within the regions.

The South and East coasts of South Africa are the main focus of this study and therefore this overview will focus on the biogeographical divisions within these areas. South African biogeographic regions were first defined by Stephenson (1939, 1944, 1948). During the late 1930's Stephenson surveyed 39 localities along the South African coastline and collected information for approximately 1200 species of intertidal animals and algae. The information from these surveys, the bulk of which was published in Stephenson (1939), Stephenson, (1944) and Stephenson (1948), together with existing literature, was qualitatively analysed and used to classify the South African coastline into five sections: the Natal section (Umpangazi to Port Edward), the south coast section (Port Elizabeth to Cape Agulhas), the west coast section (Port Nolloth to Kommetje), the eastern overlap (Port Edward to Port Elizabeth) and the western overlap (Cape Agulhas to Kommetje). Stephenson (1944) acknowledged that this classification applied mainly to the fauna of open rock surfaces. However, Stephenson's sections have since been applied broadly to many taxa, even to those not occurring in the intertidal zone. The boundaries of these sections have been questioned by several authors with regard to specific taxonomic groups (for discussion see Brown and Jarman 1978). Brown and Jarman (1978) divide the coast into the subtropical east coast (between 26°and 31°S – roughly

from Maputo Bay to Port Edward), the warm-temperate south coast (the area affected by the presence of the continental shelf), a south-coast overlap region, and False Bay.

Finer quantitative resolution of the biogeographic regions of the intertidal zone by Emanuel *et al.* (1992), and Bustamante and Branch (1996) has yielded slightly different patterns. Emanuel *et al.* (1992) analysed all major intertidal and subtidal (down to 15 m) taxa within 48, 100 km-long sections of coastline, from the Cunene River at the southern border of Angola to Ponta da Barra Falsa in mid-Mozambique. Using Bray-Curtis similarity matrixes they were able to classify the coast into four provinces. Most relevant to this study are the warm-temperate south coast (Agulhas province), extending from Agulhas to East London, and a sub-tropical east coast (Natal province), extending from East London to Ponta da Barra Falsa. Emanuel *et al.* (1992) indicate a break in invertebrate distribution around Durban (Figure 1.1). Bustamante and Branch (1996) sampled 231 intertidal species in15 different localities, focussing mainly on the west coast. Their classification, also using Bray-Curtis similarity matrixes, indicates a break between the south coast and east coast regions occurring between Dwesa on the southeast coast and Balito Bay, close to Durban, on the east coast (Figure 1.1).

The studies discussed above have concentrated on the west coast regions, and have not achieved consensus regarding the eastern limits of the Agulhas province (Lombard *et al.*, 2004). From the work of Stephenson (1944), Emanuel *et al.* (1992), and Bustamate and Branch (1996), it would seem that there is a change between the warm, temperate south coast (Agulhas province) and the sub-tropical east coast (Natal province) fauna and flora somewhere between East London and Durban.

Lombard *et al.* (2004) divide the entire South African marine environment into 43 biozones based on a number of geological and ecological criteria derived from existent research and expertise on biogeographic patterns in South Africa. Based on their synthesis they identify five inshore bioregions and classify an Agulhas bioregion as extending from Cape Point to the Mbashe River (near Dwesa), and a Natal bioregion extending from the Mbashe River to Cape Vidal (Figure 1.1).

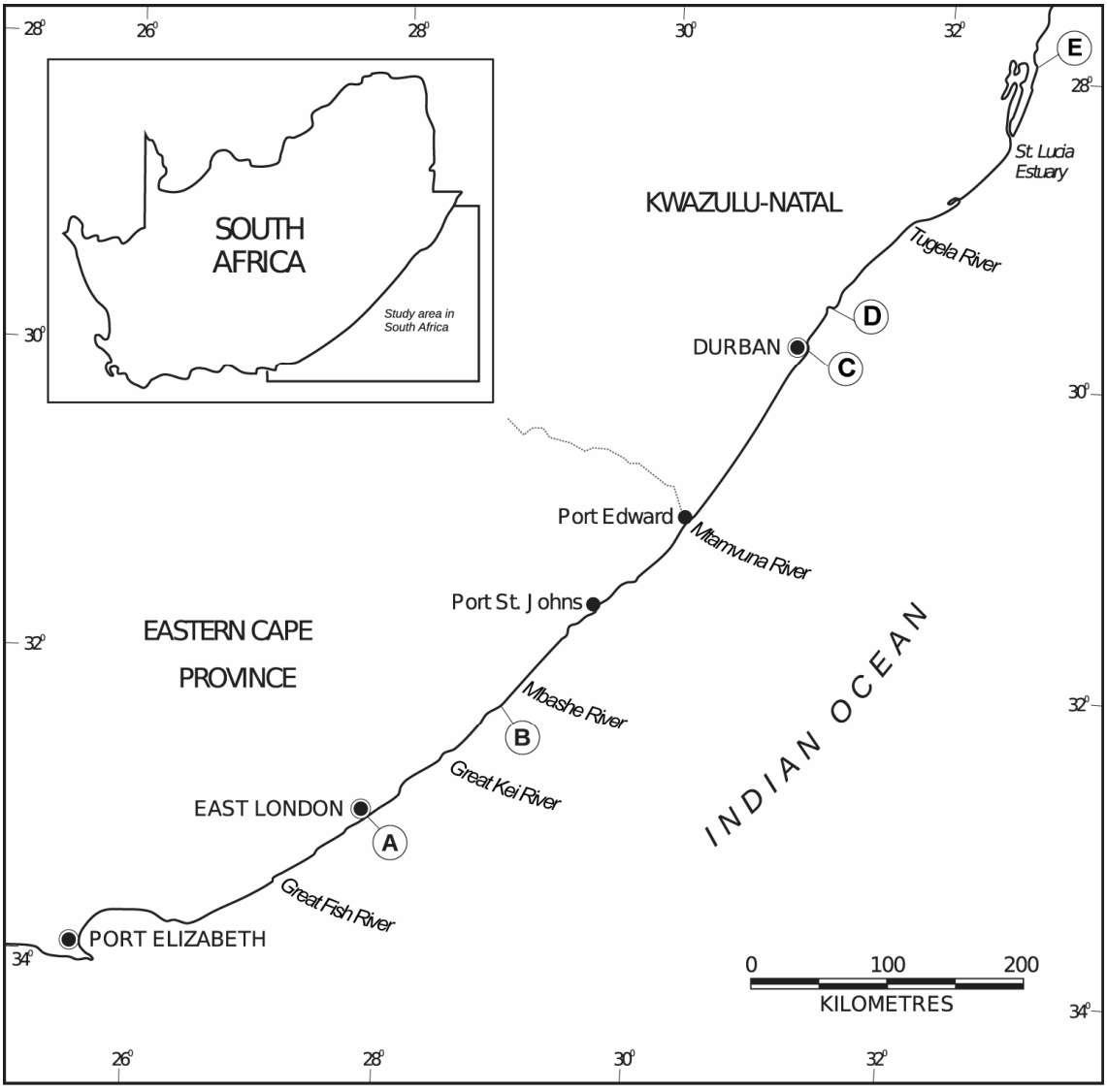

Figure 1.1: Important breaks in the boundaries between southern and eastern biogeographic zones as proposed by various recent authors occur over a large area. Emanuel *et al.* (1992) suggested that the Natal province extended from East London (A) to Ponta da Barra Falsa (off the map to the north-east), with a clear break in invertebrate distribution at Durban (C). Bustamante and Branch (1996) proposed breaks in the south and east coast regions occurring at Dwesa (B) and Balito Bay (D). Lombard *et al.* (2004) proposed that the break between the Agulhas and Natal bioregions occurs at the Mbashe River, while the Natal region extends to Cape Vidal (E).

Most relevant for this study is the change in gastropod mollusc species, as *Clibanarius virescens* exclusively uses gastropod shells as protection for its poorly calcified abdomen. According to Stephenson and Stephenson (1972), the east coast section boasts a large "snail population" of at least 19 intertidal species of gastropod, but not much other information is supplied on the distribution of gastropod molluscs. Kilburn and Rippey (1982) discuss the distribution of mollusc species and divide the coast into 4 marine provinces. The Namaqua province comprises most of the Atlantic coast, analogous to Stephenson's west coast. The Algoa province stretches from Still Bay to the Great Kei river mouth. This corresponds with Stephenson's south coast population, but extends it further eastwards by a few hundred kilometres. Kilburn and Rippey's (1982) Natal Province extends from the Great Kei river mouth to roughly the Tugela River. The area north of the Tugela they view as part of a larger Indo-Pacific province.

The mollusc fauna of the Algoa Province (Kilburn and Rippey 1982) comprises over 70% warm-temperate, endemic molluscs. Most of the remainder represent either Natal province or Indo-Pacific species that can be considered to be at the limits of their range. These warmer-water intertidal species begin to make their appearance at Port Alfred. Kilburn and Rippey (1982) propose an area of overlap between the Algoa and Natal Provinces that extends from the Great Kei River to an arbitrary boundary at the Umtata River. They acknowledge that there is little agreement regarding the exact boundaries of faunal provinces along the south-east coast, but remark that there are distinct changes in the number of Natal and Indo-Pacific species between the western and eastern boundaries of the overlap.

The east coast of South Africa is an area in which many communities change from a warm-temperate fauna to a subtropical fauna. It appears that this shift is not a clear, discrete transition, but that different groups change in response to different environmental variables, leading to a large, rich transition zone.

1.4 Thesis structure and aims

This study will provide the first comprehensive description of shell use, population structure and reproduction of *Clibanarius virescens* in Africa, where it is both common and abundant. The aim is to describe its shell use, population structure and reproduction in relation to biogeographical change in the shell resource over its range in South Africa.

The chapters on population structure and reproduction rely on the description of shell use, but each chapter is intended to stand on its own. The sampling localities, sampling method and laboratory methods are discussed in Chapter 2.

Chapter 3 investigates temporal changes in shell use, population structure and reproduction at a single locality (Cape Recife) over a period of 13 months, and provides a template for some of the methods used in the following chapters.

A basic premise of this study is that biogeographic change in the nature of the shell resource used by *C. virescens* underlies patterns in population structure and reproduction across the range studied. In order to capture the gradient of potential changes in the shell resource, 12 localities, from Cape Recife to Mission Rocks, were sampled.

In Chapter 4, patterns in resource use are investigated and related to the biogeographical areas in which the 12 localities are situated. It is expected that there will be a transition in resource characteristics, but it is not known where this transition will be or whether it will be clear or gradual. Morphological differences in the shell resource are examined as a prelude to understanding their effect on population structure and reproduction.

Chapter 5 examines the population structure of *C. virescens* at all localities sampled. Size distribution patterns are described, the sex ratios investigated and sexual size dimorphism is examined. Shell use is related to the population characteristics and to variation in characteristics that may occur among localities.

Chapter 6 examines reproduction at 10 localities at which ovigerous females were recorded. Clutch size, clutch mass and egg size are used as indicators of female fecundity. It is expected that resource-induced changes in the population structure of females will have consequences for reproduction.

Chapter 7 will provide a short general conclusion and explore ways in which future research, based on the current study might be structured.

Chapter 2: General method and sampling localities

2.1 Introduction

Twelve localities were sampled for this study (Figure 2.1). Localities were chosen for accessibility as only a limited time around spring tides offered ideal sampling conditions and it was essential to cover maximum ground in as short a time as possible. Easy accessibility for researchers also made the localities accessible for holidaymakers and fishers so that none of the localities visited may be described as pristine. The only locality in a marine protected area was at Dwesa. Sampling could be undertaken only during holiday periods, but took place at the start of each holiday period in order to minimize the effect of recreational beach usage on the populations sampled.

All localities were located on rocky shorelines. *Clibanarius virescens* was not found in sandy areas or in estuary mouths. Localities can be viewed on mapping websites using the coordinates listed (Table 2.1). At all localities *Clibanarius virescens* was collected in intertidal pools or crevices in the mid to low tide level.

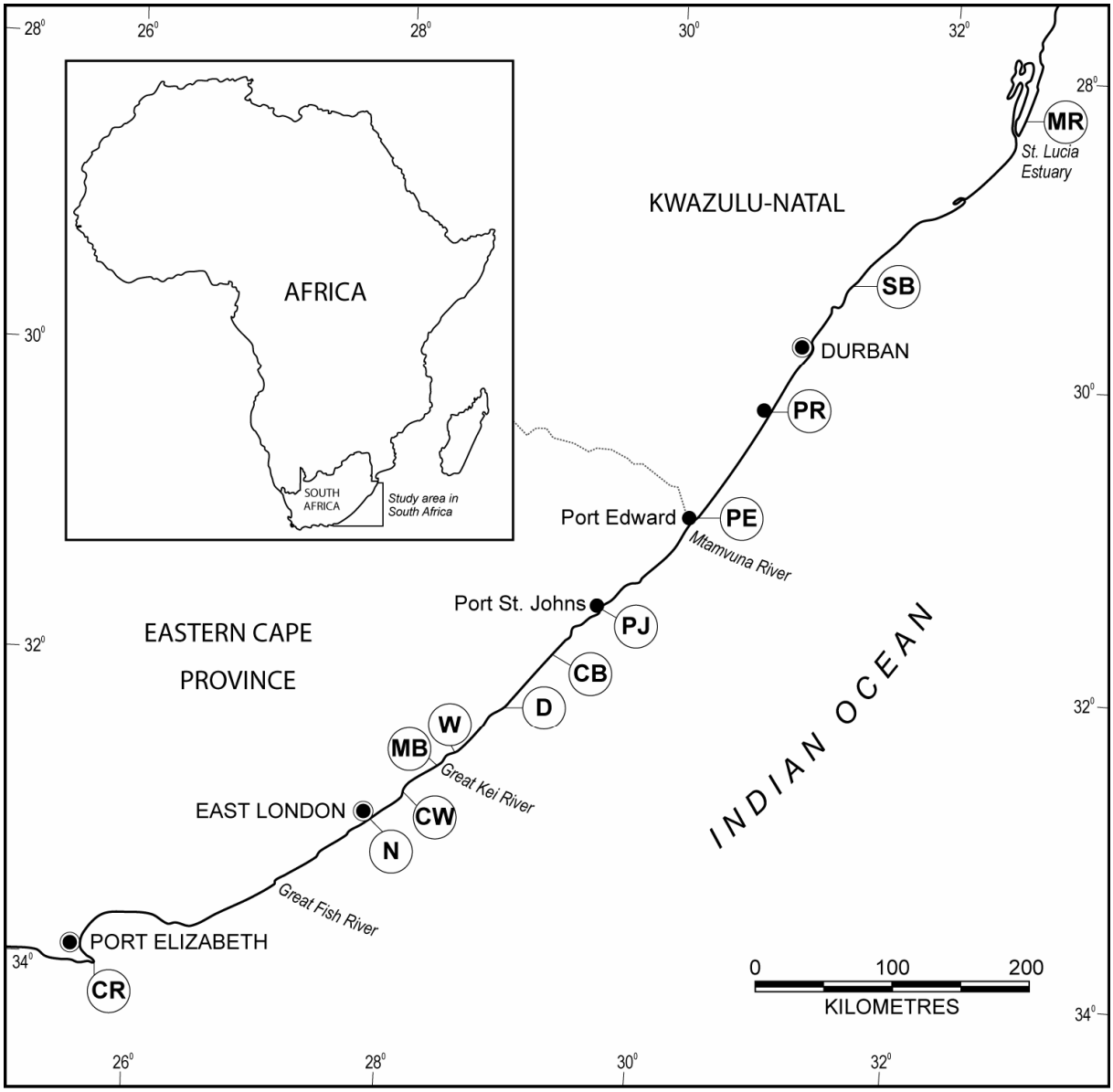

Figure 2.1: The 12 localities sampled as part of this study ranged from Port Elizabeth in the southwest to St Lucia in the northeast. Localities are as follows: CR = Cape Recife, N = Nahoon Beach, CW = Cintsa West Beach, MB = Morgan Bay, W = Wavecrest, D = Dwesa, CB = Coffee Bay, PJ = Port St Johns, PE = Port Edward, PR = Park Rynie, SB = Sheffield Beach, and MR = Mission Rocks.

Table 2.1: Coordinates, sample sizes and dates sampled for localities included as part of this study.

Localities	Co-ordinates	*n*	Dates Sampled
Cape Recife	34°01'48" S, 25°42'18" E	1185	On spring tides from 1 Nov 2001 to 3 Oct 2002
Nahoon Beach	32°59'10" S, 27°57'10" E	205	29 September 2000
Cintsa West Beach	32°50'14" S, 28°07'00" E	110	29 September 2000
Morgan Bay	32°42'35" S, 28°20'31" E	200	2 December 2002
Wavecrest	32°34'24" S, 28°32'50" E	200	4 December 2002
Dwesa	32°18'38" S, 28°49'42" E	200	5 December 2002
Coffee Bay	31°59'01" S, 29°08'59" E	200	6 December 2002
Port St Johns	31°39'22" S, 29°30'26" E	200	7 December 2002
Port Edward	31°03'44" S, 30°13'27" E	200	8 December 2002
Park Rynie	30°19'35" S, 30°44'18" E	200	9 December 2002
Sheffield Beach	29°29'03" S, 31°15'31" E	200	24 November 2003
Mission Rocks	28°16'91" S, 32°29'09" E	183	18 October 2002

2.2 Sampling localities

The Cape Recife locality (Figure 2.1, CR) was situated on the north side of the cape and hermit crabs were sampled in proximity to a man-made breakwater. The locality had several large, shallow rock pools in the mid-tidal zone. None of the pools had foliose algae growing in them. The beach was occasionally covered by red-algae wrack, particularly after storms. The locality was frequently visited by bait collectors and fishers, both permit holding and illegal. Although situated in the Cape Recife Nature Reserve, the marine section of the reserve did not enjoy protection. The beach often had empty shells washed up at the high-tide mark. *Diloma* spp., especially *D. sinensis* were very common both as empty shells and as live gastropods. The man-made breakwater allowed an unusually high number of *Burnupena lagenaria* to occur at the locality. These whelks were often seen clustered on the more shaded southern side, at the base of the wall. The sampling area was also home to large numbers of another species of hermit crab, *Diogenes brevirostris*. *D. brevirostris* occurred further up the shore, was always associated with sandy substrates and occurred in far greater numbers than *Clibanarius virescens* at this locality.

At the Nahoon River mouth (Figure 2.1, N), hermit crabs were collected on rock outcrops both north and south of the river mouth. More crabs were found in the southern section than in the northern section. Hermit crabs were collected on a rocky outcrop south of the Cintsa River (Figure 2.1, CW). *Diogenes brevirostris* was found at both Nahoon Beach and Cintsa West Beach in similar numbers to *Clibanarius virescens*. Hermit crabs were collected on a rocky shore in front of the hotel at Morgan Bay (Figure 2.1, MB). The collection locality was south of the river mouth. The beach and rocky areas around the Kei River mouth were searched but no hermit crabs were found at the time of sampling.

At Wavecrest (Figure 2.1, W), hermit crabs were found north of the river mouth on a small rocky promontory isolated by small beaches on both sides. No hermit crabs were found on the rocks south of the river mouth. A few, large *Diogenes brevirostris* were observed on the same outcrop, but were not as numerous as *Clibanarius virescens*. This was the northern-most locality at which *C. virescens* co-occurred with *D. brevirostris* at sampling localities visited for this study. At Dwesa (Figure 2.1, D), the rocky shore directly opposite the gatehouse was sampled. This area had distinct gullies, and hermit crabs were sampled from the pools left in the gullies by the retreating tide. Dwesa is a marine protected area and the collection was carefully monitored by a conservation official. A few *Calcinus laevimanus* were observed sharing pools with *Clibanarius virescens*.

The Coffee Bay collection locality (Figure 2.1, CB) was on rocks near the river mouth. A large number of hermit crabs were collected very quickly with the help of a group of local children. *Calcinus laevimanus* was once again observed in the same area as

Clibanarius virescens. Hermit crabs were found at Third Beach at Port St. Johns (Figure 2.1, PJ). They were collected off the rocks in front of the parking area. At Port Edward (Figure 2.1, PE), the shore south of North Sand Bluff was sampled and *Calcinus laevimanus* was present.

Park Rynie (Figure 2.1, PR) has two man-made tidal pools. The area between the tidal pools was sampled for hermit crabs. There were several large natural mid-tidal pools with large numbers of both *Clibanarius virescens* and *Calcinus laevimanus*. The shore at the Sheffield Beach locality (Figure 2.1, SB) was fronted by houses. The shore had several large rock pools and rock outcrops of up to 1 m high creating sheltered areas. Both *Clibanarius virescens* and *Calcinus laevimanus* were plentiful. *Calcinus gaimardii* was also present, but in very small numbers. At Mission rocks (Figure 2.1, MR) the rocky shore sloped sharply down towards the sea, compressing the intertidal zone. Rock pools were small and situated in the mid to upper tidal zone. Both *Clibanarius virescens* and *Calcinus laevimanus* were plentiful.

2.3 Sampling

All sampling events were planned to take place within 4 days of a spring tide. Sampling periods were intended to correspond to the breeding season of *Clibanarius virescens*. It was assumed that *C. virescens* would breed by September. The only information that could be obtained was a mention that Reddy and Biseswar (1993) had sampled *C. virescens* in KwaZulu-Natal in September (out of 4 sampling events) and that they had also done reproductive work on the species. Imazu and Asakura (1994), working at higher latitudes in the northern hemisphere, reported ovigerous females as early as April. Initial sampling, from Port Elizabeth to Cintsa West Beach,

was undertaken during late September 2000. It was assumed that at lower latitudes in South Africa, the start of the breeding season for *C. virescens* would be at or before the spring equinox. This proved to be too early for the Eastern Cape as only 1 crab out of 316 crabs analysed had eggs. Hermit crabs from this sampling trip were included in the analysis of shell resource use by *C. virescens*. The next sampling trip took place during December 2002 and covered localities from Morgan Bay and the Kei River mouth north-eastwards towards Durban. All localities had reproducing crabs at this time. Two additional "spot" samples could be made during an academic field trip to Cape St. Lucia (Mission Rocks sample) during October 2002 and at Sheffield Beach during November 2003. Cape Recife, the western-most distribution limit for *C. virescens*, was sampled at every spring tide from the 1st of November 2001 to the 3rd of October 2002. A total of 1183 crabs were sampled at Cape Recife, but only crabs sampled between 31 December 2000 and 28 January 2001 were used in the analyses in Chapters 4 and 5 to avoid greatly uneven sample sizes among localities.

Clibanarius virescens tends to cluster around tidal pools in sheltered crevices in the mid to low tidal region (Barnes, 1999, Reay and Haig, 1990, and Imazu and Asakura, 1994). This study does not concentrate on the spatial distribution of *C. virescens* on the shore, nor does it concentrate on relative population densities between localities. Crabs were therefore sampled by collecting all visible crabs, irrespective of size, by hand until a required number had been found. This method of collection is adequate as the research questions are considered independent of the sampling method (Ritschoff *et al.*1995). Care was taken to collect all crabs in a cluster and care was taken not to overlook small crabs. Cape Recife had a smaller population of *C. virescens* than encountered at other sampling localities and the population had to

sustain sampling at every spring tide over an annual cycle. To prevent depletion of the population, approximately 50 crabs were collected at each spring tide. At all other sampling localities, collection continued until 200 crabs had been collected or until the tide came in. This number was deemed suitable to sample the range of shell types used by each sample population (Reddy and Biseswar 1993). Crabs from Cape Recife and Sheffield Beach were frozen. Crabs from all other localities were preserved in 70% ethyl alcohol.

Crabs from a single locality were placed together in a single container for transport back to the laboratory or field base where they were frozen or fixed. The transport period seldom exceeded 30 minutes. It is possible, but unlikely that some shell exchange took place during this period. At each locality, empty shells found in the vicinity of the crabs were also collected. Empty shells were collected in a separate container.

2.4 Laboratory analysis

In the laboratory, each crab was extracted from its shell and its cephalothoracic shield length was measured under a dissecting microscope using an ocular micrometer and converted to the nearest 0.01 mm using constants derived from the calibration of the micrometer. The anterior part of the cephalothorax is the only part that is calcified (McLaughlin 1980) and is used as a standard reference measurement in many studies (Manjón-Cabeza and García-Raso 1999). Cephalothoracic shield length, hereafter referred to as shield length, is measured from the tip of the rostrum to the cervical groove (McLaughlin 1980). Crabs were sexed as male or female using gonopore position. Gonopores are found on the coxae of the third pereopods

of females and on the coxae of the fifth periopods of males (McLaughlin 1980). Where no gonopores could be clearly distinguished, the crabs were classed as juvenile. Where one or two of both male and female gonopores were clearly present, the individual was classed as intersex (Turra 2004). After taking measurements and staging the eggs, crabs and eggs were dried at 60 °C until a constant mass was achieved and were weighed on an electronic balance to 0.0001 g. This method was chosen as it minimises the volatilisation of lipids from the drying samples (Hines 1982).

Ovigerous crabs had their eggs carefully stripped off the pleopods with forceps. The eggs were counted. If the eggs were in excellent condition, a maximum of 10 eggs per female was measured (Fotheringham 1980). The diameters of both the egg envelope and the yolk mass were measured across the greatest diameter of the egg. Only undistorted eggs with unbroken egg envelopes were measured. Eggs were classified into 5 developmental stages derived from the methods of (Boolootian *et al.* 1959). Stage 1 shows no sign of development. Stage 2 has small crescent-shaped eyes and some chromatophore development. Stage 3 has larger, oval eyes, some limb development, but retains some yolk. Stage 4 has no yolk but is not completely developed, while Stage 5 eggs have fully developed larvae. Stages 4 and 5 are very close in appearance and were grouped for many analyses, but Stage 5 is indicative of hatching and was useful to note.

Shells were identified to species wherever possible using shell guides by Kilburn and Rippey (1982) and Steyn and Lussi (1998), and their tidal habitat was identified using Kilburn and Rippey (1982) and data from the Ocean Biogeographic Information System (OBIS, http://www.iobis.org). The most commonly used shell types in this

study were *Burnupena lagenaria*, *Burnupena cincta*, *Burnupena pubescens*, *Morula granulata*, *Morula nodosa* and *Peristernia forskalii*. Also used frequently were *Clionella bornii*, *C. kraussii*, *Cominella elongata*, *Diloma tigrina*, *D. sinensis*, Turbo *cidaris* and *Thais capensis* (Figure 2.2).

Shell length, width and aperture width were measured to the nearest 0.02 mm with vernier callipers. Shell length was measured as the columellar length and shell width as the maximum width of the body whorl perpendicular to the aperture opening (*sensu* Kellog 1976). Shells were allowed to air-dry before being weighed to 0.0001 g. Internal shell volume was determined using acid-washed sand (grain diameter 0.1 – 0.3 mm, 50 to 150 mesh), based on the methods of Fotheringham (1976a) and Brown *et al.* (1993). In cases where crabs could not be extracted from their shells, the shells were measured and then carefully cracked open in a bench vice so as not to damage the crab. The dry shell shards were weighed.

Shells that were too worn to be accurately identified, or that were very badly broken were classed as “fragments”. The damage to each shell was recorded. Lip breakage, the condition of the nacreous layer and the periostracum, the extent of encrusting organisms, the number, type and position of holes in the shell, and the state of the shell apex were noted and coded (Table 2.2).

Figure 2.2: Shells used by *Clibanarius virescens* in southern localities included *Burnupena cincta* (A), *B. lagenaria* (B), *B. pubescens* (C), *Clionella bornii* (D), *C. kraussii* (E) and *Cominella elongata* (F). Shell types commonly used in northen localities included *Morula granulata* (G), *M. nodosa* (H) and *Peristernia forskalii* (I). *Thais capensis* (J) was used at most localities. *Turbo cidaris* (K), *Diloma sinensis* (L) and *D. tigrina* (M) are examples of low-spired shells, while shell types A to J are all high-spired shells

2.5 Data analysis

All statistical analyses were carried out using R version 2.10.1 (2009-12-14) (R Development Core Team 2009). R is both a language and environment for statistical computing and graphics, as well as a suite of software allowing data manipulation and graphing. The specific statistical methods used will be mentioned in the relevant chapters.

Table 2.2: Shell damage was assessed and the most common types of damage were assigned values according to the classification given here.

Lip Breakage	Code
Light / None	0
Apparent	1
Heavy	2

Nacreous Layer	Code
Shiny	0
Dull but smooth	1
Eroded	2

Encrusting organisms	Code
Inside	
None	0
Few	1
Heavy	2
Outside	
None	0
Few	1
Changes outline of shell	2
Covers shell	3

Periostracum/outer shell layer	Code
Full coverage (except apex tip)	0
Full cover to 80% present	1
80% to 60% present	2
60% to 40% present	3
40% to 20% present	4
Worn off	5

Holes (counts recorded)		Code
Body whorl:	whelk-drilled holes	BWW: 0 →
	bigger/irregularly shaped holes	BWB: 0 →
Second whorl:	whelk-drilled holes	SWW: 0 →
	bigger/irregularly shaped holes	SWB: 0 →
Third whorl:	whelk-drilled holes	TWW: 0 →
	bigger/irregularly shaped holes	TWB: 0 →

Apex condition	Code
Apex intact	0
Apex open	1
Top few whorls missing	2

Chapter 3: Population structure and reproduction of *Clibanarius virescens* during an annual cycle at Cape Recife

3.1 Introduction

Cape Recife (34°01’48” S, 25°42’18" E) forms the we stern headland of Algoa Bay, a log-spiral shaped bay typical of the southern coast of South Africa. Sea water temperature is mainly affected by the predominantly south-westerly wind regime, but occasionally current meanders from the warm Agulhas current enter the bay (Goschen and Schumann 1994). Sea surface temperatures vary by about 5 ℃ from 22 ℃ in summer to 16 ℃ winter (Lutjeharms 1998). This is a greater change than occurs further north, where the temperature regime is more constant (Lutjeharms 1998). The continental shelf narrows near East London and allows the Agulhas current to have a year-long moderating effect on the climate of the east coast of South Africa (Lutjeharms, 1998).

The sampling locality at Cape Recife is described in Chapter 2. More generally, the area consists of outcrops of eroded Table Mountain sandstone interspersed with sandy patches. Because of the shelter provided by a man-made concrete groyne, the sampling locality has what seems to be an artificially large population of a whelk, *Burnupena lagenaria*. Its congeneric, *B. cincta*, is also common. McLachlan *et al.* (1981) studied the trophic structure and biomass of two localities (Flat Rocks and Schoenmakerskop) on either side of Cape Recife, and found that *B. cincta* made up 2.5 % of the biomass at Schoenmakerskop, while *Burnupena lagenaria* is described as the most common of its genus on the eastern shore of South Africa (Kilburn and Rippey 1982). It lives high up the shore, between high- and low-water neaps. Its

distribution on the shore may intergrade with *B. cincta*, which inhabits rock pools and lives lower on the shore than *B. lagenaria* (Kilburn and Rippey 1982). The abundance of *B. lagenaria* and *B. cincta* ensured that most of the hermit crabs collected at this locality were found in the shells of these two whelk species. The dominance of these two shell types may affect the population structure of *Clibanarius virescens* at this locality.

McLachlan *et al.* (1981) did not record *Clibanarius virescens* at either Flat Rocks or Schoenmakerskop during their study. This attests to the patchy distribution and possible habitat preferences of *C. virescens*. However, they did record that *Diogenes brevirostris*, a sand-loving or psammophylic species of hermit crab that co-occurs with *C. virescens* at Cape Recife, made up 1.4% of the total intertidal biomass at Flat Rocks. *C. virescens* was less abundant than *D. brevirostris* at Cape Recife, indicating that on this shore, at the edge of its range, it does not make a large contribution to the intertidal fauna.

Cape Recife represents the south-western distribution limit of *C. virescens* in the Indo-Pacific region. The characteristics of this population provide a picture of adaptation at its distribution limit and provides a baseline against which to compare other localities for plasticity in population structure. The only other population data for *C. virescens* is from 33 ºN (Wada *et al.* 2005) and 35 ºN (Imazu and Asakura 1994), probably the northern-most limit of its distribution in the Indo-Pacific region. While climate regimes may differ considerably between the Japanese localities and the South African locality, the studies by Imazu and Asakura (1994) and Wada *et al.* (2005) will form a basis against which the Cape Recife locality will be compared.

A large proportion of the crabs were collected in the shells of *Burnupena lagenaria* and *B. cincta*. Preliminary analysis showed that *Burnupena lagenaria* and *B. cincta* have among largest volume-to-mass ratios of the high-spired shells used by crabs in this study (see Chapter 4). The population structure of *C. virescens* will therefore be an interesting baseline for comparison against other localities (see Chapter 5) as almost all members of the *C. virescens* population at Cape Recife have access to shells close to the theoretical ideal. The availability of shells with large volumes at this locality may also affect the reproductive output of females when compared to localities where females do not have access to voluminous shells (see Chapter 6).

The aims of this chapter are to examine shell-use patterns, to describe the population structure and to determine the reproductive pattern and output of *Clibanarius virescens* at Cape Recife. Three sets of comparisons regarding shell use will be made: seasonal or monthly changes will be investigated, the differences between male and female crabs will be noted and lastly, differences between ovigerous and non-ovigerous females will be examined.

There is often clear partitioning of the shell resource between male and female hermit crabs (Benvenuto and Gherardi 2001, Turra and Leite 2001a), usually with males and females using different shell types or using different sizes of the same shell type (Rodrigues *et al.* 2000). Male fitness is increased by obtaining shell types that increase mating success (Hazlett 1989, 1996). Obtaining larger shells also allows faster growth rates (Angel 2000), and larger males are better able to guard females until copulation takes place (Yoshino *et al.* 2002), thus ensuring their paternity. Shells with high internal volumes and light weight are known to allow higher growth rates and larger clutch sizes than in heavier, low-volume shells

(Bertness 1981a). Shell volume directly affects female fecundity as the volume of eggs that can be brooded by a female hermit crab is limited by the volume of the shell inhabited (Hazlett 1981), and in some hermit crab species shell size determines whether females will reproduce or not (Hazlett *et al.* 2005). The volume-to-mass ratios of commonly used shells will be compared and related to shell use by males and females to determine whether they show partitioning of the shell resource by using different shell types with different volume-to-mass ratios. Examination of the shell-use patterns by ovigerous females and non-ovigerous females will provide a comparison between females that have successfully produced eggs and those that are large enough to produce eggs but were not carrying eggs when sampled.

It is expected that males will attain larger sizes than females and therefore use shells with larger absolute sizes than those used by females. Males within the same size range as females are expected to use larger shells than females, as males of any size should attempt to obtain shells that are large enough to allow growth. If non-ovigerous females persue the same strategy of attempting to maximise growth, it is expected that they will occupy relatively larger shells than ovigerous females of the same size, which will have opted to invest in immediate rather than deferred reproduction. Alternatively, if non-ovigerous females are simply those females that have failed to reproduce because they have not obtained suitable shells, it would be expected that non-ovigerous females would be in smaller shells than ovigerous females. There may be a mix of these two options for non-ovigerous females, which might be difficult to tease apart and which might lead to no difference in mean shell size between ovigerous and non-ovigerous females within the same size classes.

Crab population structure will be described. Monthly changes in size-frequency distribution will be tracked to determine whether any clear recruitment pulses can be detected (Lowery and Nelson 1988, Turra and Leite 1999). Hermit crabs are known to depart from an equal male-to-female sex ratio (Imazu and Asakura 1994, Asakura 1995, Fransozo and Mantelatto 1998, Manjon-Cabeza and Garcia-Raso 1998, Turra and Leite 2000). The sex ratio for *C. virescens* will be examined for the sampling period to determine whether it is affected by time of year. Hermit crab populations often display distinct size dimorphism with males becoming much larger than females (Harvey 1990, Wada 1999, Turra and Leite 2000, Mantelatto and Martinelli 2001, Contreras-Garduño and Córdoba-Aguilar 2006). The Cape Recife population will be examined to determine whether sexual size dimorphism exists and whether it can be related to shell use patterns between males and females.

The reproductive period for *C. virescens* at Cape Recife will be described and the occurrence of juveniles in the population noted. Clutch size in crabs is often described as highly correlated to crab size (Fotheringham 1976a, Mantelatto & Garcia 1999, Turra & Leite 1999), and can be affected by shell weight and internal volume (Fotheringham 1976a. There is a trade-off between shell features chosen by the crabs and the fitness conferred by the particular shell feature, for example, a heavy shell may reduce predation, but may have a cost in terms of energy available for growth or reproduction (Bertness 1981a). The degree to which the number of eggs produced relates to crab size (shield length and mass) and to mass and volume of the shells used by ovigerous females will be examined.

3.2 Methods

The sampling locality, collection methods and laboratory analyses are described in Chapter 2.

Shell use by the crab population was analysed according to the following groupings: all sampled crabs, males, all females, juveniles, intersex individuals, ovigerous females, all non-ovigerous females (collected throughout the year) and non-ovigerous females collected during the breeding season and within the same size range as ovigerous females (hereafter referred to as BS non-ovigerous females).

The most commonly used shell types were identified. Shell type is used as an abbreviation indicating the shell of a particular gastropod species. A log-likelihood ratio test (G-test) was used to determine whether there was a difference in the frequency of use of different shell types within the categories sex, month and female reproductive state. Mean and standard error of shell dimensions (length, width, aperture width, mass and volume) were calculated for each month and for each crab grouping. Analysis of covariance was used to determine the effect of discrete factors (month, sex and female reproductive state) on the relationship of shell width, aperture width, mass and volume to shell length. The relationships of shell mass and volume to shell length, the data were linearised through a logarithmic transformation. The relationship of volume-to-mass was determined for the 5 most commonly used shell types (*Clionella bornii* and *Clionella kraussii* were grouped together) as well as for the combined group of the *Turbo* and *Diloma* spp.

Statements regarding differences in shell dimensions between sexes and among months, as well as crab dimensions among months were further examined by means

of analyses of variance and post-hoc tests using Tukey's honest significant difference (HSD) test. Tukey's HSD test is based on a studentised range distribution and is used for multiple comparisons of means to determine which are significantly different to each other (Zar 1999).

Mean and standard error of crab dimensions (crab shield length and dry mass) were calculated for each month and for all crab groupings. A log-likelihood ratio test (G-test) was used to determine whether the frequency of males and females was dependent on month. A Chi-squared goodness of fit test was used to determine whether the numbers of males and females departed significantly from a ratio of 1:1. The effect of factors (month, sex and female reproductive state) on the relationship between crab shield length and crab dry mass was tested using ANCOVA.

The duration of the reproductive period was determined by noting the first and last sample dates at which ovigerous females occurred. The proportions of ovigerous females in the monthly samples were plotted together with sea-surface temperatures for the same period. Sea surface temperatures for Algoa Bay were obtained from the South African Weather Services. The relationship between the proportion of ovigerous females and sea surface temperature was described by linear regression and the significance of the relationship was determined by ANOVA. The relationship of ovigery to sea surface temperature was compared both for the month in which the sample was taken (i.e. January's proportion of ovigerous females compared to January's sea temperature) as well as with a temperature lag of one month (i.e. January's proportion of ovigerous females compared to December's sea temperature). It was predicted that if sea surface temperature is a causal factor of ovigery, then the relationship of temperature in the month preceding the sample

would have a closer relationship to the proportion of ovigerous females than the temperature in the month of the sample.

The proportions of eggs in different stages of development were determined for each month. The effect of egg stage on the relationship of egg number to crab shield length, crab mass, shell mass or shell volume was determined in order to examine the feasibility of grouping eggs stages which might improve the sample size for subsequent analyses. It was expected that crab shield length, crab mass, shell mass or shell volume would be reliable predictors of egg number. Therefore the number of eggs produced was regressed against crab and shell dimensions. The number of eggs produced by a female may show a heterogenous response to any of the measured predictors (such as crab or shell dimensions) or may be a response to unmeasured factors or combinations of the measured factors (Cade *et al.* 1999). In such cases, quantile regression is particularly useful (Cade and Noon 2003) and was used to determine the upper limit of the relationship between the number of eggs produced and the predictor variables.

Egg size was analysed to determine whether there was a relationship between egg size and crab shield length, crab mass, shell mass, shell volume and egg number. Visual inspection of Normal Q-Q plots for each relationship indicated that, despite a small sample size of 101 eggs obtained from 11 females, the data were normally distributed. ANOVA was used to test whether mean egg size varied among the 11 samples. Only measurements from undamaged Stage 1 eggs were used. Egg size at the inner egg membrane was measured across the widest part of the egg, as described in Chapter 2. A maximum of 10 eggs from a single brood were measured.

3.3 Results

Clibanarius virescens used 17 shell types at Cape Recife. The five most commonly used shell types were *Burnupena cincta* (6.0% of total shells used), *B. lagenaria* (74.3%), *Clionella bornii* (6.7%), *C. kraussii* (2.6%) and *Cominella elongata* (4.0%). These five shell types made up 93.6% of all shells used. The use of *Burnupena lagenaria* dominated during all months (Figure 3.1).

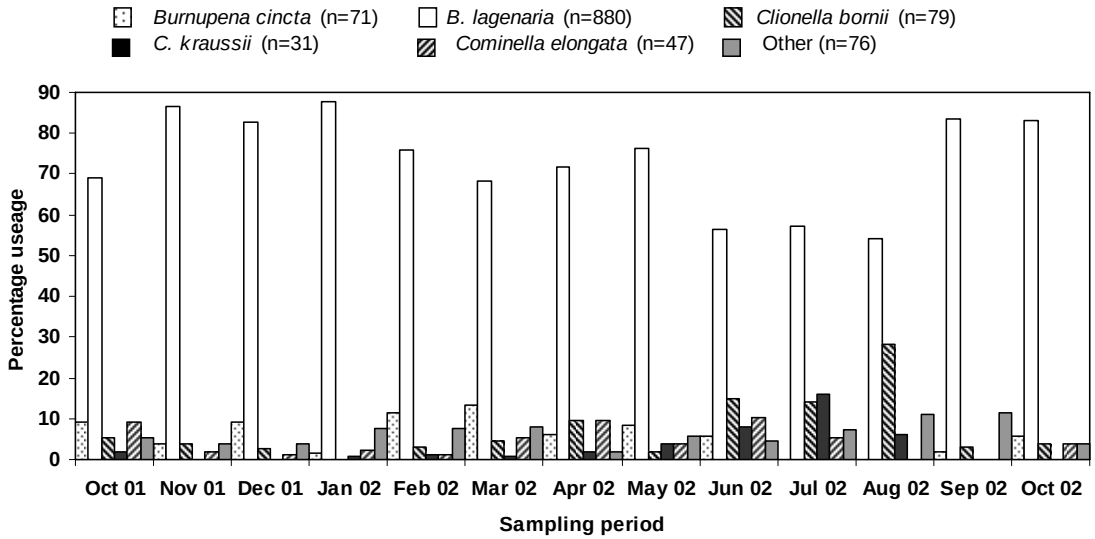

Figure 3.1: Of 17 shell types used by *Clibanarius virescens* during the sampling period, the five most commonly used types were *Burnupena cincta*, *B. lagenaria*, *Clionella bornii*, *C. kraussii* and *Cominella elongata*. The use of *Burnupena lagenaria* dominated during all months. Only 76 out of a total of 1184 crabs were found in shell types other than the five most commonly used types.

A log-likelihood ratio test (G-test) was used to compare variables (the five most common shell types) across all categories (sex and, month and female reproductive state). The tests showed that the frequency of use of the five most commonly used shell types was not independent of month ($G = 225.99$, $P < 0.001$, $DF = 48$). Similarly, the frequency of shell use was not independent of sex ($G = 30.02$,

P<0.001, DF = 4), even when males and females in the same size range were compared (G = 22.17, P<0.001, DF = 4).

Differences in shell use by month seem to be caused by the increased use of *Clionella* spp. and *Cominella elongata* during the winter months (June, July and August) (Figure 3.1). Male and female *Clibanarius virescens* used the same five shell types, but in different proportions (Figure 3.2). Both male and female *C. virescens* used mainly *Burnupena lagenaria*, despite it having the lowest volume-to-mass ratio of the five most commonly used shells (Figure 3.3). Of the shells used by female hermit crabs a larger proportion (16.4%) consisted of high-spired *Clionella* and *Cominella* shells, than was used by males (6.0%). Large males occasionally (4.3%) used low-spired, high-volume shells (Figure 3.3) such as *Diloma tigrina*, *D. sinensis* and *Turbo cidaris*, while females rarely (0.7%) used them.
Twenty-five juvenile crabs were collected. Of the shell types used by juveniles *Burnupena lagenaria* comprised 32.0%, *Clionella bornii*, 16.0%; *C. kraussii*, 24.0%; *Colina pinguis*, 12.0% and two juveniles (8.0%) were found in damaged fragments. Seven intersex crabs were collected during the sampling period; one was found in *Burnupena cincta* (14.3%), five were in *B. lagenaria* (71.4%) and one was in a shell fragment (14.3%).

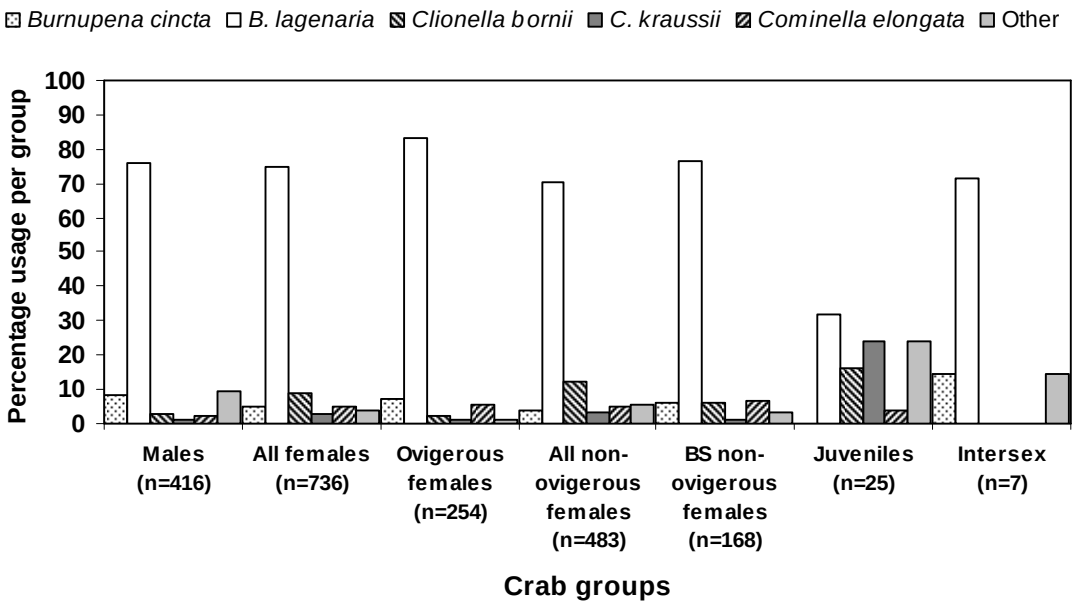

Figure 3.2: Crab groups showed different patterns of shell use. All groups used mainly *Burnupena lagenaria*, but a higher proportion of the shells used by females were high-spired *Clionella* and *Cominella* shells. *Clionella* and *Cominella* shells also formed a large proportion of shells used by juveniles

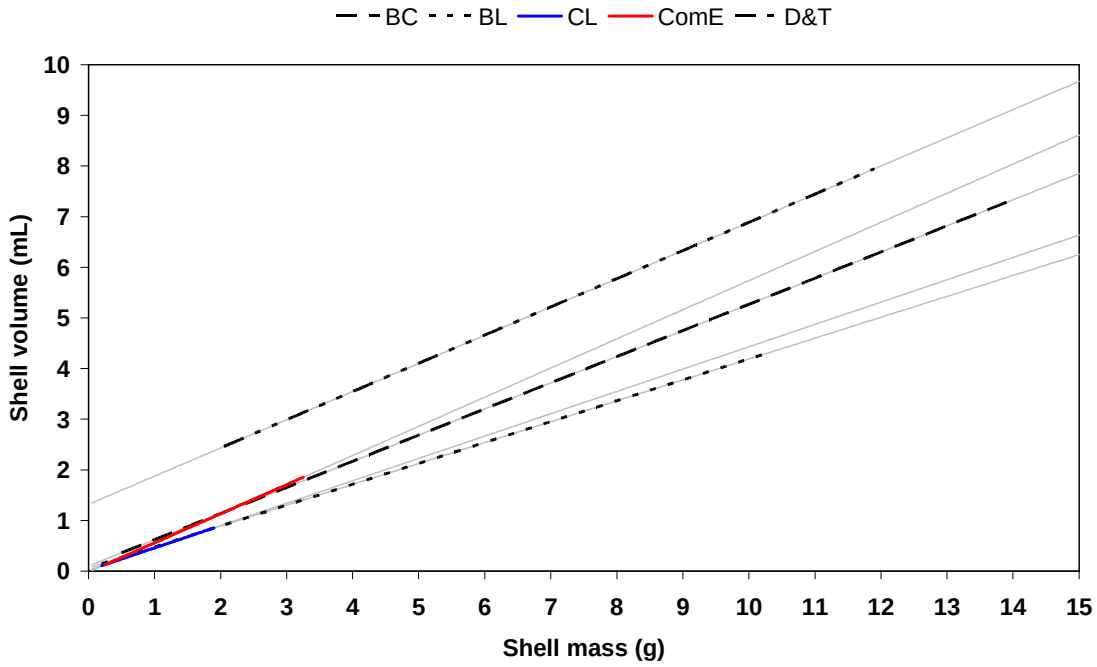

Figure 3.3: The relationship between mass and volume for the shells used by *C. virescens.* The spread of observed data are shown by the black and coloured lines while the light grey lines are extrapolations of the relationships. *Diloma* and *Turbo* spp. (D&T) are not commonly used, but do have a far greater volume in relation to mass than any of the other shell types used, followed in order by *Cominella elongata* (ComE), *Burnupena cincta* (BC), the grouped *Clionella* spp. (CL) and *Burnupena lagenaria* (BL).

ANCOVA was used to test the relationship of volume to mass by shell type of the most commonly used shell types, including the *Diloma* and *Turbo* spp. Both slopes and intercepts varied significantly among shell types ($F = 17.744$, $DF = 1$ on 1004, $P < 0.001$). Data for *Clionella bornii* and *Clionella kraussii* were grouped for analyses as these shell types showed no significant difference when compared by species for the relationship of shell width ($F = 1.5268$, $DF = 1$ on 85, $P = 0.2200$), aperture width ($F = 0.9319$, $DF = 1$ on 85, $P = 0.3371$), mass ($F = 0.1377$, $DF = 1$ on 85, $P = 0.7115$) or volume ($F = 0.7242$, $DF = 1$ on 39, $P = 0.4000$) to shell length. Where their shell sizes overlap, *Cominella elongata* has a larger volume-to-mass ratio than *Burnupena cincta* and the grouped *Clionella* spp. have greater volume-to-mass ratios than *B. lagenaria,* but *C. elongata* and the *Clionella* spp. do not attain the large sizes reached by *B. cincta* and *B. lagenaria*.

Male crabs used shells with larger mean dimensions than females for all shell dimensions (Table 3.1). Analysis of variance showed that the differences between all males and all females were significant for shell length ($F = 17.01$, $DF = 1$ on 1147, $P < 0.001$), width ($F = 54.27$, $DF = 1$ on 1147, $P < 0.001$), aperture width ($F = 66.57$, $DF = 1$ on 1147, $P < 0.001$), mass ($F = 56.44$, $DF = 1$ on 1147, $P < 0.001$) and volume ($F=81.72$, $DF = 1$ on 1022). Between males and females of the same size, shell width ($F = 12.15$, $DF = 1$ on 1108, $P < 0.001$), aperture width ($F = 24.61$, $DF = 1$ on 1108, $P < 0.001$), mass ($F = 15.74$, $DF = 1$ on 1108, $P < 0.001$) and volume differed ($F = 26.38$, $DF = 1$ on 986, $P < 0.001$), while shell length did not ($F = 0.56$, $DF = 1$ on 1108, $P = 0.456$). Even within the same size range males used shells with larger dimensions than females.

Similarly, ANOVA showed that there were significant differences in shell dimensions among months (shell length: $F = 9.64$, DF = 12 on 1136, $P < 0.001$, width: $F = 7.15$, DF = 12 on 1136, $P < 0.001$, aperture width: $F=18.96$, DF = 12 on 1136, $P < 0.001$, mass: $F=10.87$, DF = 12 on 1136, $P < 0.001$ and volume: $F=9.05$, DF = 12 on 1011). *C. virescens* used larger shells during December, January and February than at other times of the year, as shown by Tukey's honest significant difference test (Figure 3.4). Shell width, aperture width, mass and volume show similar results as shell length.

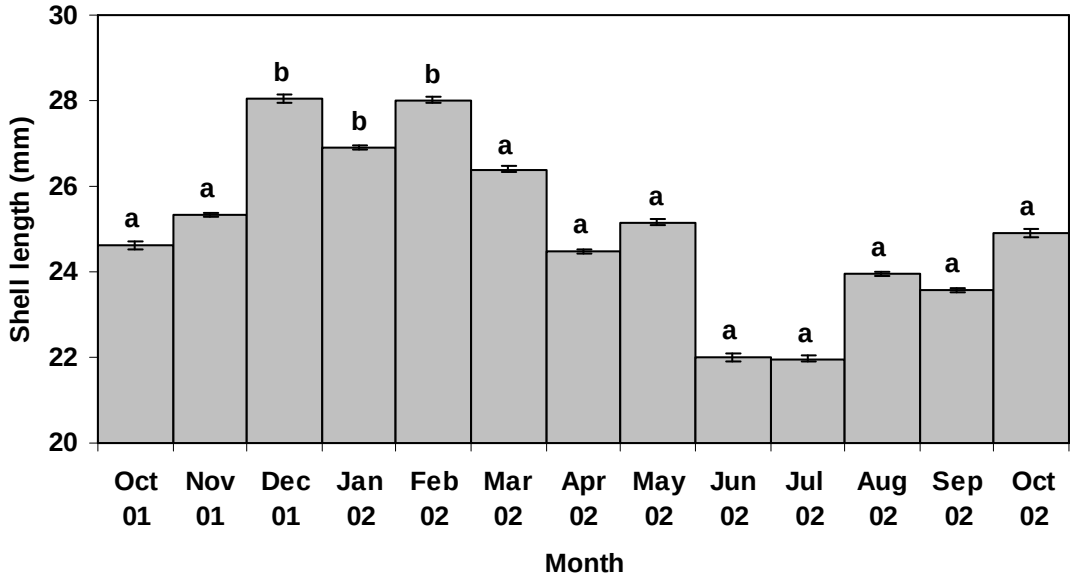

Figure 3.4: Mean lengths of shells used by *C. virescens* varied throughout the sampling period, but were significantly larger during December, January and February. Shell width, aperture width, mass and volume followed the same pattern. Bars with the same letters are not significantly different to each other. Error bars indicate standard error.

Shell use by ovigerous and BS non-ovigerous females (collected during the breeding season and in the same size range as ovigerous females) showed that the shell type used was independent of reproductive state of female crabs ($G = 5.22$, $P > 0.5$, $DF = 4$) (Figure 3.2).

Relationships among shell dimensions for *Burnupena cincta*, grouped *Clionella* spp. and *Cominella elongata* did not differ significantly when compared by month (Table 3.2). Only *Burnupena lagenaria* showed significant differences in all relationships among shell dimensions compared by month. This could be due to the increased power of the test owing to large sample sizes available for *B. lagenaria*. Combined *Clionella* data showed significant differences only in comparisons of shell length to shell width by month (Table 3.2)

Table 3.1: Dimensions of shells used by different groups of crabs and by month. Data for shell volume has smaller sample sizes as some shells were crushed to extract the crabs. (All NOF* = All non-ovigerous females, including the non-breeding season, BS NOF* = non-ovigerous females in the breeding season and in the same size range as ovigerous females, OvigFem* = ovigerous females)

	Length (mm)			Width (mm)			Aperture width (mm)			Mass (g)			Volume (ml)		
	n	**Mean**	**Std Err**	***n***	**Mean**	**Std Err**	***n***	**Mean**	**Std Err**	***n***	**Mean**	**Std Err**	***n***	**Mean**	**Std Err**
By crab grouping															
All crabs	1184	25.21	0.005	1185	13.13	0.003	1184	6.72	0.002	1185	2.31	0.001	1040	1.14	0.001
Males	416	26.33	0.018	416	14.25	0.011	416	7.50	0.007	416	2.83	0.005	377	1.47	0.003
All females	736	24.91	0.006	737	12.69	0.004	736	6.39	0.002	737	2.08	0.002	648	0.96	0.001
All NOF*	483	23.74	0.010	483	11.98	0.006	482	5.92	0.004	483	1.78	0.002	408	0.82	0.001
BS NOF*	168	24.26	0.030	168	12.54	0.016	168	6.35	0.010	168	1.98	0.007	155	0.89	0.004
OvigFem*	253	27.15	0.016	254	14.05	0.008	254	7.30	0.006	254	2.65	0.004	240	1.2	0.002
Juveniles	25	14.39	0.114	25	6.95	0.077	25	2.95	0.035	25	0.33	0.008	8	0.17	0.008
Intersex	7	28.20	1.397	7	14.29	0.505	7	7.39	0.336	7	3.18	0.296	7	1.46	0.213
By Month															
Oct 2001	55	24.60	0.098	55	12.66	0.053	55	6.29	0.035	55	1.9920	0.0210	53	0.94	0.011
Nov 2001	104	25.34	0.045	104	13.39	0.025	104	6.82	0.016	104	2.2725	0.0114	98	1.05	0.006
Dec 2001	76	28.06	0.090	76	14.76	0.040	76	7.94	0.034	76	3.1394	0.0279	67	1.45	0.016
Jan 2002	128	26.90	0.036	129	15.07	0.028	128	7.92	0.018	129	2.8682	0.0099	123	1.45	0.008
Feb 2002	104	28.02	0.058	104	15.35	0.042	104	8.07	0.025	104	3.1611	0.0191	100	1.61	0.012
Mar 2002	114	26.40	0.064	114	13.77	0.038	114	7.17	0.023	114	2.7301	0.0203	103	1.34	0.012
Apr 2002	116	24.49	0.055	116	12.25	0.029	116	6.18	0.017	116	2.0674	0.0161	104	0.96	0.008
May 2002	105	25.16	0.065	105	12.94	0.035	105	6.64	0.021	105	2.2389	0.0163	95	1.14	0.010
Jun 2002	88	22.00	0.078	88	10.87	0.041	88	5.42	0.028	88	1.5837	0.0185	72	0.84	0.010
Jul 2002	56	21.97	0.069	56	10.46	0.039	56	5.02	0.027	56	1.2758	0.0129	42	0.59	0.007
Aug 2002	81	23.94	0.049	81	11.37	0.031	81	5.29	0.019	81	1.5923	0.0116	53	0.75	0.007
Sep 2002	104	23.56	0.047	104	12.41	0.026	104	6.37	0.015	104	2.0610	0.0109	82	0.89	0.006
Oct 2002	53	24.89	0.104	53	13.21	0.056	53	6.82	0.035	53	2.2463	0.0247	48	1.13	0.014

Table 3.2: The effect of the factor "Month" on shell dimensions. Most shells do not show a change in shell dimension by month, with the exception of *Burnupena lagenaria*. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
Burnupena lagenaria					
Width (mm) by length (mm)	Differ	Differ	1.909	12 on 827	P = 0.030
Aperture width (mm) by length (mm)	Differ	Differ	2.069	12 on 827	P = 0.017
Mass (g) by length (mm)*	Differ	Differ	1.828	12 on 827	P = 0.040
Volume (mL) by length (mm)*	Do not differ	Differ	2.002	12 on 801	P = 0.003
Burnupena cincta					
Width (mm) by length (mm)	Do not differ	Do not differ	0.667	9 on 54	P = 0.057
Aperture width (mm) by length (mm)	Do not differ	Do not differ	1.179	9 on 54	P = 0.327
Mass (g) by length (mm)*	Do not differ	Do not differ	1.543	9 on 54	P = 0.157
Volume (mL) by length (mm)*	Do not differ	Do not differ	1.029	9 on 45	P = 0.433
***Clionella* spp. (*Clionella bornii* and *Clionella kraussii* combined)**					
Width (mm) by length (mm)	Differ	Differ	2.750	7 on 72	P = 0.014
Aperture width (mm) by length (mm)	Do not differ	Do not differ	1.774	7 on 79	P = 0.104
Mass (g) by length (mm)*	Do not differ	Do not differ	0.641	7 on 79	P = 0.721
Volume (mL) by length (mm)*	Do not differ	Do not differ	2.331	5 on 35	P = 0.073
Cominella elongata					
Width (mm) by length (mm)	Do not differ	Do not differ	0.527	6 on 32	P = 0.783
Aperture width (mm) by length (mm)	Do not differ	Do not differ	1.077	6 on 32	P = 0.397
Mass (g) by length (mm)*	Do not differ	Do not differ	0.568	6 on 32	P = 0.752
Volume (mL) by length (mm)*	Do not differ	Do not differ	0.802	6 on 26	P = 0.557

Similarly, there was little variation in shell dimensions within shell types used by male and female *C. virescens* (Table 3.3). Ovigerous females and BS non-ovigerous females showed significantly different intercepts for all shell dimensions when the five most commonly-used shell types were grouped and compared by female reproductive state (Table 3.4). However, these shell types have different morphologies, which could explain the differences. When comparing shell dimensions for only one shell type, *Burnupena lagenaria*, it appears that the intercepts of the relationships of shell width to shell length, and shell volume to shell length differ significantly (Table 3.4) between ovigerous and BS non-ovigerous females, with ovigerous females again occupying shells with a slightly larger width and volume than BS non-ovigerous females.

The crab population sampled at Cape Recife comprised 35.1% males, 62.2% females, 2.1% juveniles and 0.6% intersex individuals. The largest size classes (7.0

to 7.9 and 8.0 to 8.9 mm) contained males, except for one intersex individual in size class 7.0 to 7.9 mm (Figure 3.5). During the breeding season 56.3% of females were ovigerous. The size-frequency distribution for the entire sampled population (Figure 3.5), as well as size-frequency distributions by month (Figure 3.6) showed no evidence of recruitment pulses as size distributions are unimodal.

Table 3.3: The effect of crab sex on shell dimensions. Within a shell type shell dimensions do not show a change between male and female crabs. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
All Shells					
Width (mm) by length (mm)	Do not differ	Differ	41.892	1 on 1146	P < 0.001
Aperture width (mm) by length (mm)	Do not differ	Differ	52.252	1 on 1146	P < 0.001
Mass (g) by length (mm)*	Do not differ	Differ	13.530	1 on 1146	P < 0.001
Volume (mL) by length (mm)*	Do not differ	Differ	32.380	1 on 1021	P < 0.001
Burnupena lagenaria					
Width (mm) by length (mm)	Do not differ	Do not differ	0.171	1 on 850	P = 0.679
Aperture width (mm) by length (mm)	Do not differ	Do not differ	1.523	1 on 850	P = 0.218
Mass (g) by length (mm)*	Do not differ	Differ	8.518	1 on 850	P = 0.004
Volume (mL) by length (mm)*	Do not differ	Do not differ	3.613	1 on 812	P = 0.058
Burnupena cincta					
Width (mm) by length (mm)	Do not differ	Do not differ	0.002	1 on 62	P = 0.969
Aperture width (mm) by length (mm)	Do not differ	Do not differ	0.035	1 on 62	P = 0.853
Mass (g) by length (mm)*	Do not differ	Do not differ	0.259	1 on 62	P = 0.613
Volume (mL) by length (mm)*	Do not differ	Do not differ	1.623	1 on 53	P = 0.208
***Clionella* spp. (*Clionella bornii* and *Clionella kraussii* combined)**					
Width (mm) by length (mm)	Do not differ	Do not differ	0.279	1 on 85	P = 0.599
Aperture width (mm) by length (mm)	Do not differ	Do not differ	0.954	1 on 85	P = 0.331
Mass (g) by length (mm)*	Do not differ	Do not differ	0.208	1 on 85	P = 0.649
Volume (mL) by length (mm)*	Do not differ	Do not differ	3.138	1 on 39	P = 0.843
Cominella elongata					
Width (mm) by length (mm)	Differ	Differ	5.295	1 on 36	P = 0.027
Aperture width (mm) by length (mm)	Do not differ	Do not differ	0.001	1 on 37	P = 0.976
Mass (g) by length (mm)*	Do not differ	Do not differ	0.211	1 on 37	P = 0.649
Volume (mL) by length (mm)*	Do not differ	Do not differ	0.872	1 on 31	P = 0.358

A G-test found that the frequency of males to females was not independent of month ($G = 41.5$, $DF = 12$, $p < 0.001$). A Chi-squared goodness of fit test showed that males and females departed significantly from a 1:1 ratio except during May ($\chi^2 = 0.08$, $DF = 1$), June ($\chi^2 = 1.76$, $DF = 1$) and September 2002 ($\chi^2 = 0.55$, $DF = 1$) (Figure 3.7). Males and females departed significantly from a 1:1 ratio for all size

classes except 1.0 to 1.9 mm ($\chi 2 = 0.06$, DF = 1), the smallest size class in which they both occur. The overall sex ratio for the population over the entire sampling period was 1:1.77 in favour of females.

Table 3.4: The effect of reproductive status (ovigerous or BS non-ovigerous) of female crabs on shell dimensions for all shells used and for *Burnupena lagenaria* only. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
All shells used by ovigerous females and BS non-ovigerous females.					
Width (mm) by length (mm)	Do not differ	Differ	15.052	1 on 410	P < 0.001
Aperture width (mm) by length (mm)	Do not differ	Differ	13.725	1 on 410	P = 0.002
Mass (g) by length (mm)*	Do not differ	Differ	7.447	1 on 410	P = 0.007
Volume (mL) by length (mm)*	Do not differ	Differ	9.364	1 on 388	P = 0.002
***Burnupena lagenaria* used by ovigerous females and BS non-ovigerous females.**					
Width (mm) by length (mm)	Do not differ	Differ	5.601	1 on 336	P = 0.019
Aperture width (mm) by length (mm)	Do not differ	Do not differ	3.216	1 on 336	P = 0.074
Mass (g) by length (mm)*	Do not differ	Do not differ	0.048	1 on 336	P = 0.826
Volume (mL) by length (mm)*	Do not differ	Differ	7.230	1 on 327	P = 0.007

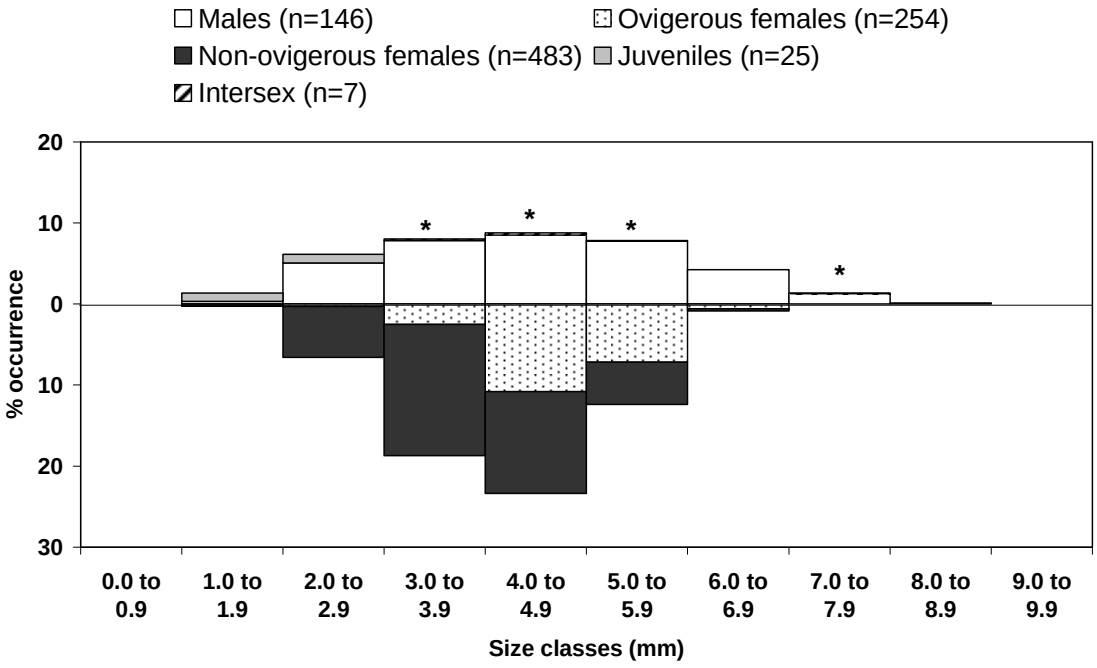

Figure 3.5: Males dominate the larger size classes, but females show a greater frequency of occurrence in smaller size classes. Intersex individuals formed too small a percentage to show clearly on the graph, so the size classes in which they occur are indicated by asterisks.

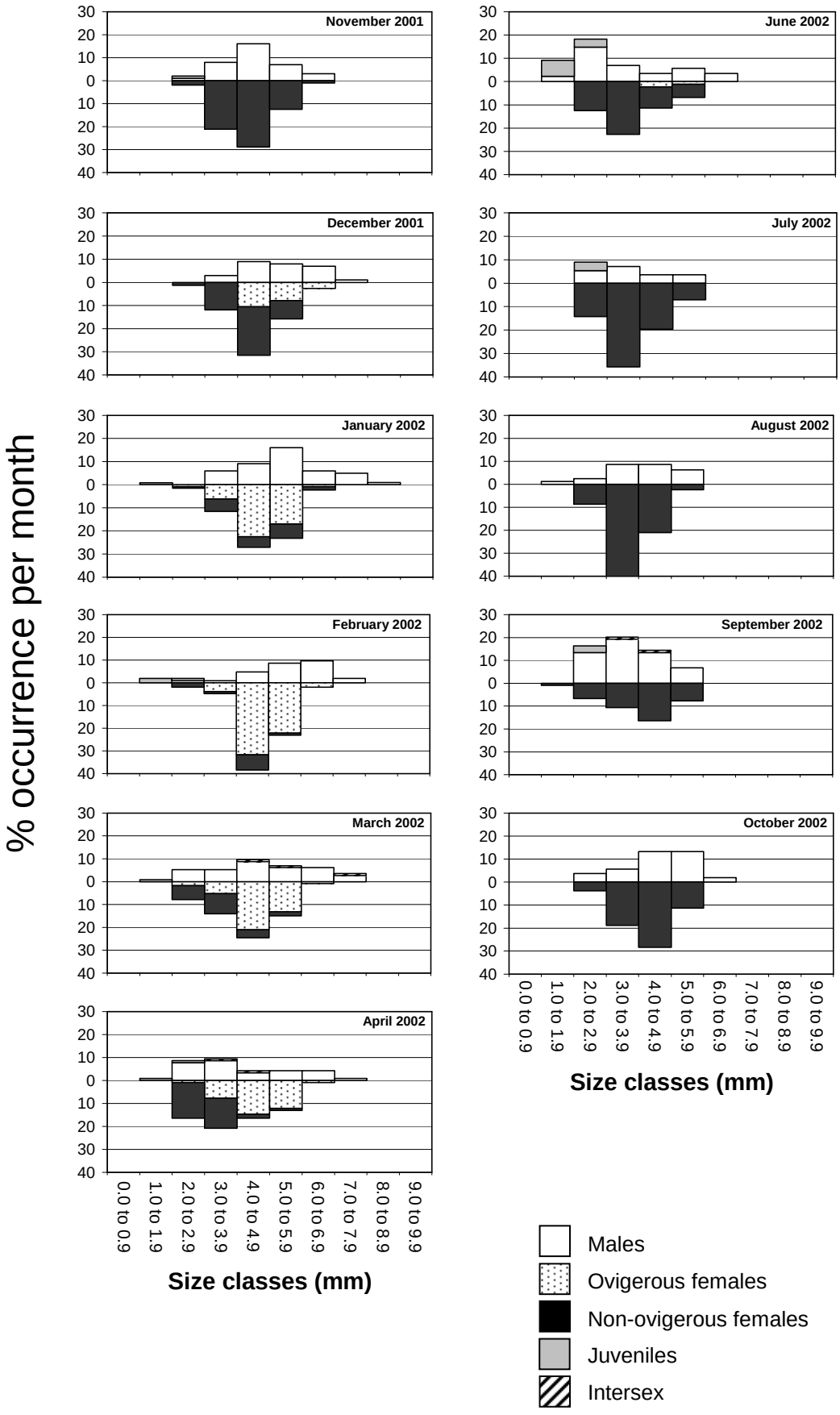

Figure 3.6: Size-frequency distributions by month. Both males and females show mainly unimodal distributions

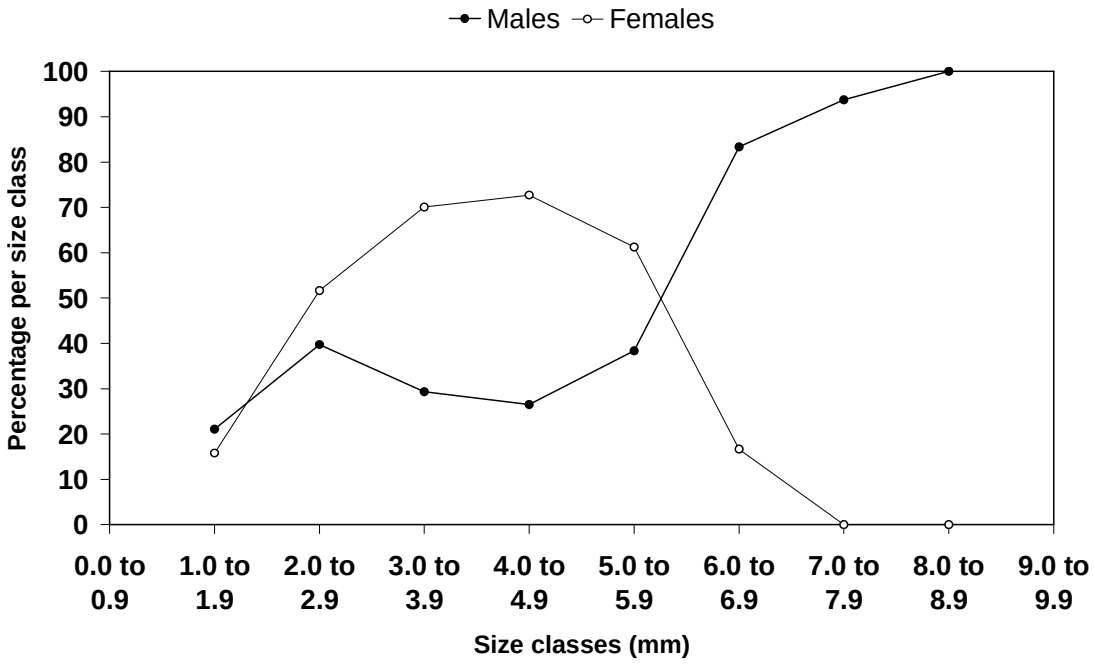

Figure 3.7: Males and females depart significantly from a 1:1 ratio for all size classes except the smallest one. The population also shows clear sexual dimorphism as males dominate large size classes.

Mean crab shield length and mass were determined for all crab groupings (Table 3.5). Analysis of variance showed that there was a significant difference in the shield lengths of males, all females, all non-ovigerous females, BS non-ovigerous females and ovigerous females ($F = 41.81$, $DF = 4$ on 2053, $P < 0.01$). Post-hoc multiple comparisons among these crab groups using Tukey's "honest significant difference" test showed that males had a significantly larger mean shield length than all females, all non-ovigerous females and BS non-ovigerous females (Figure 3.8). However the mean shield length of males was not different to that of ovigerous females.

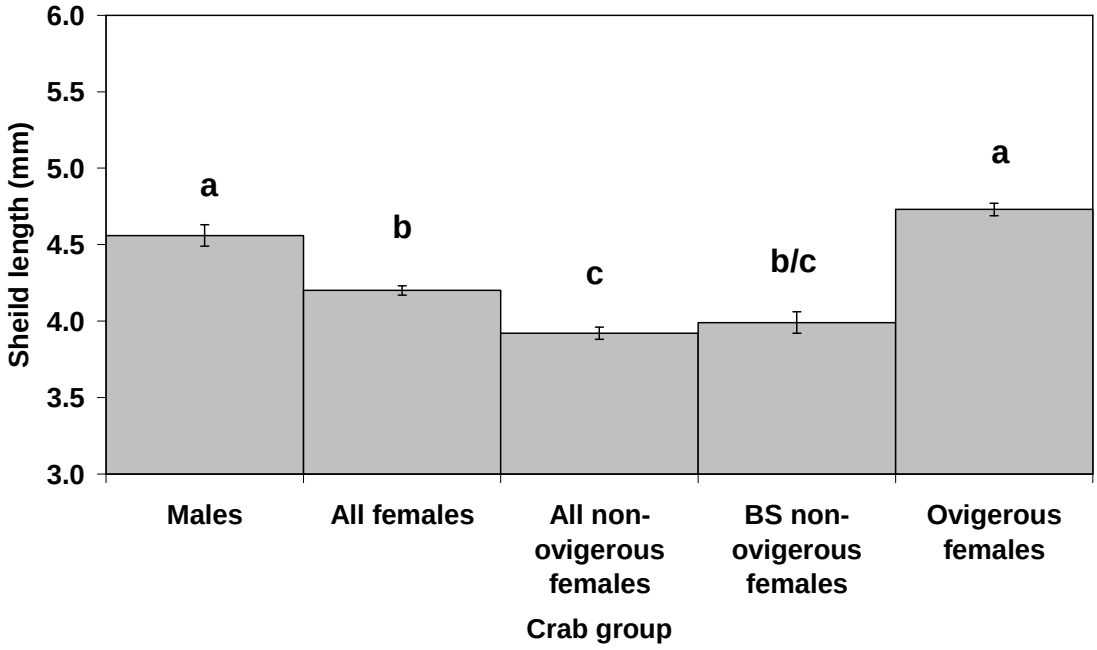

Figure 3.8: Mean shield length of males does not differ to that of ovigerous females. The group comprising all non-ovigerous females differs from all females. Bars with the same letter are not significantly different to each other. Error bars indicate standard error.

Except for the group comprising all non-ovigerous females, all crab groupings reach maximum sizes (mass and shield length) during December, January and February. For the group comprising all non-ovigerous females, maximum sizes occurred during November, December and January (Table 3.5). The maximum size reached was by a male crab (8.50 mm). The smallest size recorded was for a juvenile (1.19 mm), and the smallest ovigerous female had a shield length of 2.80 mm.

ANOVA also showed that mean shield lengths differed among months for all crabs ($F = 16.27$, $DF = 12$ on 1136, $P < 0.001$), males ($F = 8.96$, $DF = 12$ on 403, $P < 0.001$), all females ($F=10.18$, $DF = 12$ on 724, $P < 0.001$), all non-ovigerous females ($F = 9.00$, $DF = 12$ on 470, $P < 0.01$) and BS non-ovigerous females ($F = 7.89$, $DF = 6$ on 161, $P < 0.01$). Mean shield lengths of ovigerous females did not show significant

differences (F = 1.58, DF = 6 on 247, P = 0.16) among months. Means of intersex and juvenile crabs were not compared owing to small sample sizes.

Post-hoc multiple comparisons using Tukey's "honest significant difference" test showed that crab shield lengths were significantly different during summer (December, January and February) and winter months, particularly June and July, for groups comprising all crabs, males, all females and BS females (Figure 3.9). The group of all non-ovigerous females showed no significant differences during spring and summer, but had significantly smaller shield lengths during autumn and winter (Figure 3.9).

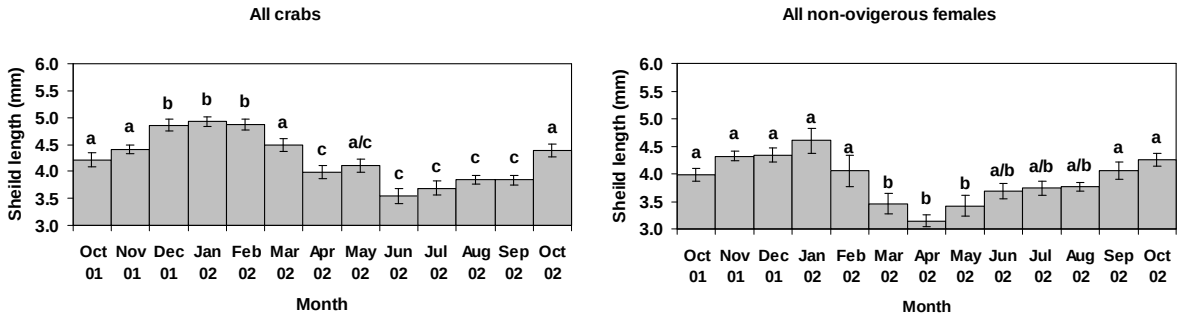

Figure 3.9: There are significant differences in shield length between summer and winter. The patterns for males, all females and BS females are similar to that shown for all crabs. While non-ovigerous females show largest shield lengths during November, December and January, these months do not form a discrete group as found in other crab groups. Bars with the same letters are not significantly different to each other. Error bars indicate standard error.

Analysis of covariance was used to test the effect of the factors sex and month on the relationship between crab shield length and dry mass. While the relationship differs among months, it does not differ significantly between males and females (Table 3.6).

Table 3.5: Mean crab shield lengths and masses for all crab grouping per month and for the entire sampling period.

		Shield length (mm)		Mass (g)	
Sampling period	***n***	**Mean**	**Std error**	**Mean**	**Std error**
All Crabs					
Entire period	1185	4.28	0.34	0.1490	0.0038
October 2001	55	4.21	0.13	0.1230	0.0114
November 2001	104	4.40	0.08	0.1477	0.0096
December 2001	76	4.86	0.11	0.2235	0.0170
January 2002	129	4.93	0.09	0.2322	0.0139
February 2002	104	4.88	0.10	0.1934	0.0113
March 2002	114	4.49	0.12	0.1862	0.0161
April 2002	116	3.98	0.12	0.1255	0.0131
May 2002	105	4.11	0.12	0.1429	0.0144
June 2002	88	3.55	0.14	0.0936	0.0112
July 2002	56	3.69	0.13	0.0664	0.0062
August 2002	76	3.85	0.08	0.0819	0.0066
September 2002	104	3.84	0.09	0.1235	0.0075
October 2002	53	4.39	0.12	0.1173	0.0105
Males					
Entire period	416	4.56	0.07	0.1893	0.0085
October 2001	16	4.76	0.32	0.1798	0.0284
November 2001	35	4.61	0.16	0.1790	0.0192
December 2001	28	5.28	0.21	0.2781	0.0354
January 2002	43	5.51	0.19	0.3204	0.0316
February 2002	28	5.64	0.21	0.2842	0.0260
March 2002	39	4.85	0.25	0.2518	0.0373
April 2002	34	4.18	0.28	0.1560	0.0346
May 2002	53	4.39	0.18	0.1746	0.0252
June 2002	32	3.73	0.27	0.1156	0.0242
July 2002	11	3.77	0.35	0.0781	0.0195
August 2002	22	4.09	0.21	0.1150	0.0175
September 2002	55	3.76	0.12	0.1148	0.0097
October 2002	20	4.61	0.23	0.1465	0.0215
All females					
Entire period	737	4.20	0.03	0.1308	0.0034
October 2001	39	3.98	0.11	0.0997	0.0088
November 2001	68	4.32	0.09	0.1315	0.0102
December 2001	48	4.61	0.11	0.1916	0.0158
January 2002	85	4.68	0.09	0.1903	0.0108
February 2002	73	4.68	0.08	0.1662	0.0095
March 2002	71	4.29	0.12	0.1473	0.0117
April 2002	78	3.95	0.12	0.1172	0.0120
May 2002	49	3.93	0.14	0.1169	0.0125
June 2002	47	3.75	0.14	0.0954	0.0117
July 2002	43	3.74	0.13	0.0660	0.0061
August 2002	54	3.76	0.08	0.0696	0.0057
September 2002	44	4.06	0.14	0.1422	0.0121
October 2002	33	4.25	0.18	0.0997	0.0097

Table 3.5: continued

		Shield length (mm)		Mass (g)	
Sampling period	***n***	**Mean**	**Std error**	**Mean**	**Std error**
All non-ovigerous females					
Entire period	483	3.92	0.04		
October 2001	39	3.98	0.11	0.0997	0.0088
November 2001	68	4.32	0.09	0.1276	0.0088
December 2001	32	4.34	0.13	0.1537	0.0169
January 2002	24	4.60	0.22	0.1879	0.0272
February 2002	11	4.05	0.28	0.0785	0.0165
March 2002	23	3.46	0.19	0.0727	0.0158
April 2002	36	3.14	0.11	0.0474	0.0096
May 2002	27	3.42	0.18	0.0811	0.0164
June 2002	44	3.68	0.14	0.0905	0.0121
July 2002	43	3.74	0.13	0.0660	0.0061
August 2002	59	3.76	0.08	0.0696	0.0057
September 2002	44	4.06	0.15	0.1422	0.0121
October 2002	33	4.25	0.12	0.0997	0.0097
Non-ovigerous females collected during the breeding season and within the same size range as ovigerous females (BS non-ovigerous female).					
Entire period	168	3.99	0.07	0.1151	0.0076
December 2001	32	4.34	0.13	0.1537	0.0169
January 2002	23	4.71	0.20	0.1958	0.0271
February 2002	10	4.24	0.23	0.0849	0.0168
March 2002	18	3.75	0.20	0.0882	0.0187
April 2002	25	3.37	0.14	0.0580	0.0133
May 2002	23	3.66	0.16	0.0938	0.0180
June 2002	37	3.92	0.13	0.1045	0.0132
Ovigerous females					
Entire period	254	4.73	0.04	0.1869	0.0055
December 2001	16	5.15	0.15	0.2673	0.0240
January 2002	61	4.71	0.09	0.1913	0.0108
February 2002	62	4.79	0.07	0.1818	0.0095
March 2002	48	4.69	0.11	0.1831	0.0127
April 2002	42	4.65	0.11	0.1771	0.0158
May 2002	22	4.57	0.12	0.1608	0.0147
June 2002	3	4.84	0.23	0.1674	0.0190
Juveniles					
Entire period	25	1.95	0.07	0.0079	0.0012
November 2001	1	2.00		0.0078	
January 2002	1	1.61		0.0041	
February 2002	3	2.19	0.26	0.0071	0.0079
March 2002	1	1.42		0.0021	
April 2002	2	1.91	0.22	0.0052	0.0023
May 2002	3	2.07	0.44	0.0091	0.0144
June 2002	9	1.83	0.08	0.0055	0.0107
July 2002	2	2.09	0.06	0.0089	0.0137
September 2002	3	2.15	0.07	0.0189	0.0144
Intersex					
Entire period	7	4.48	0.51	0.1814	0.0916
March 2002	3	5.50	0.86	0.3155	0.2048
April 2002	2	3.54	0.49	0.0526	0.0208
September 2002	2	3.89	0.52	0.1093	0.0362

Table 3.6: The effect of the factors "Month" and "Sex" on crab dimensions. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
By month					
Crab mass (g) by shield length (mm)*	Differ	Differ	6.378	12 on 1127	P < 0.001
By Sex					
Crab mass (g) by shield length (mm)*	Do not differ	Do not differ	0.159	1 on 1150	P = 0.689

Recruitment of juveniles into the population occurs throughout the summer and winter from February to September, with the largest proportion of juveniles recorded in June (Figure 3.10 and Table 3.5).

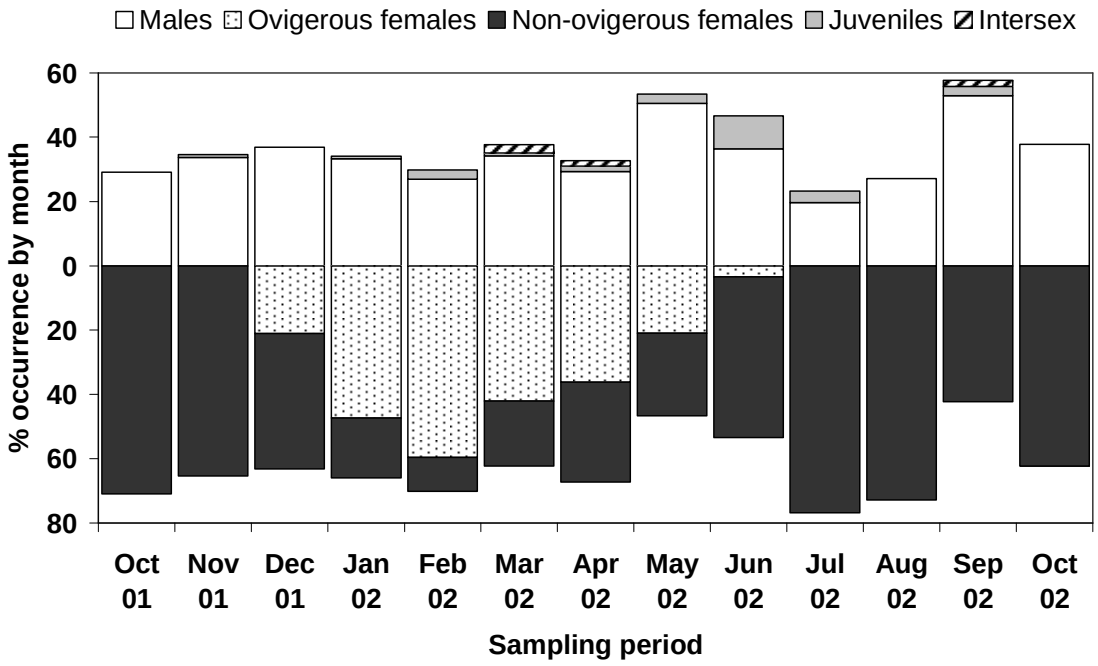

Figure 3.10: Ovigerous females occurred from December to June. Females outnumbered males in all months except May, June and September, when numbers of males and females did not depart from a 1:1 ratio (statistics reported in text).

Crabs were collected twice a month on each spring tide. No ovigerous females were obtained from the first December sample (14 December 2001), but were noted in the second sample for December 2001 (31 December 2001). At the end of the breeding period, ovigerous females were collected during the first June sample (12 June 2002), but none were found in the second June sample (24 June 2002). The *C. virescens* population at Cape Recife can therefore be described as seasonal breeders that breed during summer and autumn, between mid-December and mid-June (Figure 3.10).

The proportion of ovigerous females in the population mirrored changes in sea-surface temperatures, with about a month's delay between changes in temperature and changes in the proportion of ovigerous females (Figure 3.11). There is a significant relationship between the proportion of ovigerous females and sea surface temperature both in the month in which the sample was taken ($r^2 = 0.47$, $F = 7.16$ on 1 and 6 DF, $P = 0.037$), i.e. January's proportion of ovigerous females compared to January's sea temperature. This relationship is even stronger ($r^2 = 0.98$, $F = 569.4$ on 1 and 6 DF, $P < 0.001$) when the proportion of ovigerous females is compared to the sea temperature in the month previous to the sample (i.e. January's proportion of ovigerous females compared to December's sea temperature).

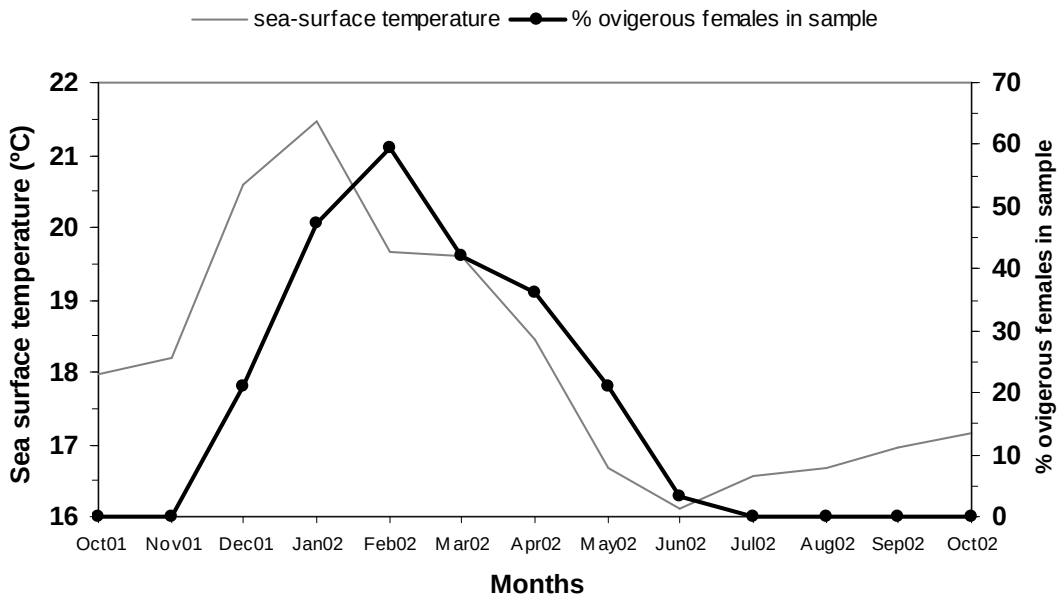

Figure 3.11: The breeding period for *Clibanarius virescens* at Cape Recife starts in December and ends at the beginning of June. The proportion of ovigerous females in the samples closely matches and lags the patterns in sea surface temperature. (Sea surface temperature data supplied by the South African Weather Services.)

Eggs were classified into 5 different stages (described in Chapter 2). All eggs carried within a single brood were at the same stage of development. Broods with Stage 1 eggs made up 78.7%, broods with stage 2 eggs made up 7.6%, broods with Stage 3 eggs made up 8.8%, broods with Stage 4 eggs made up 4.0% and broods with Stage 5 eggs made up 0.8% of the total number of broods. For most graphs stages 4 and 5 are combined. Stage 1 eggs predominate during all months of the breeding season with the exception of June (Figure 3.12).

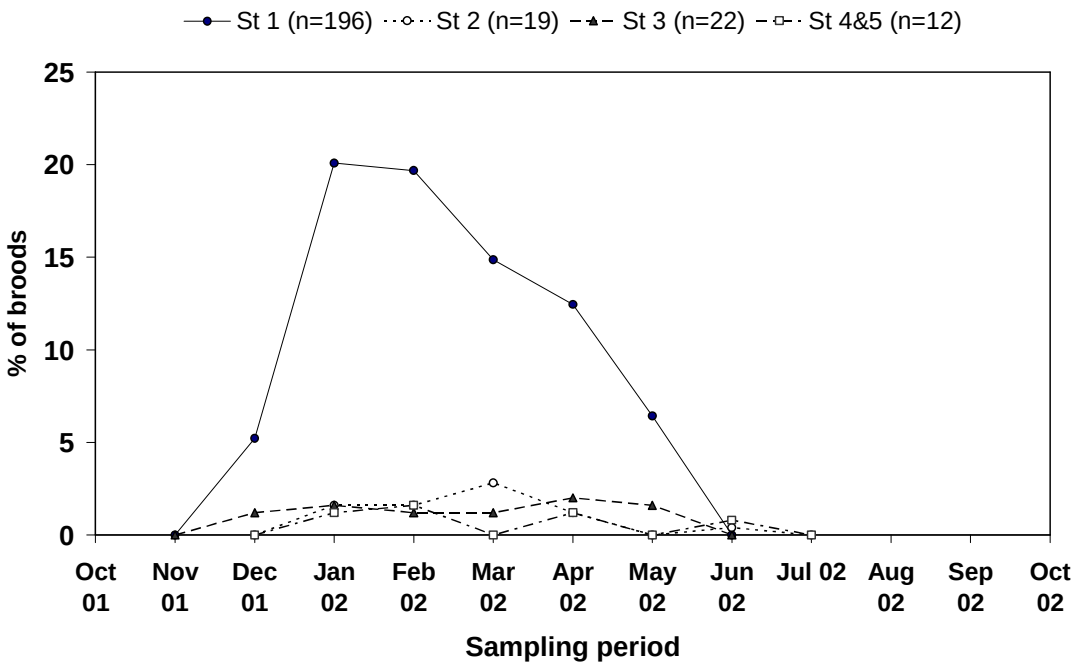

Figure 3.12: Stage 1 eggs make up the largest proportion of the total number of broods (249 broods) in all months except June 2002. The proportion of Stage 2 eggs peaks in March, while Stage 3 eggs show peaks in January and April 2002. Stages 4 and 5 are combined and show peaks in February, April and June.

Egg stage did not significantly affect the relationship of egg number to crab shield length, crab mass, shell mass or shell volume (Table 3.7). Therefore all eggs stages were grouped together for further analyses. While there was a significant positive relationship between the number of eggs produced and each crab and shell dimension tested (Table 3.7), for all relationships the coefficients of determination (r^2) produced by linear regressions demonstrated that there was a great deal of variability in the number of eggs, even when the data were transformed (Table 3.8). The shell type used by female crabs did not affect the number of eggs produced (Table 3.9).

Table 3.7: The effect of egg stage on the relationship between the number of eggs and crab shield length, crab mass, shell mass and shell volume.

	Slopes	Intercepts	F	DF	P
Number of eggs by crab shield length (mm)	Do not differ	Do not differ	0.668	3 on 243	P = 0.572
Number of eggs by crab mass (g)	Do not differ	Do not differ	1.567	3 on 243	P = 0.198
Number of eggs by shell mass (g)	Do not differ	Do not differ	1.198	3 on 243	P = 0.311
Number of eggs by shell volume (mL)	Do not differ	Do not differ	1.147	3 on 230	P = 0.331

Table 3.8: Regression coefficients for the relationships between number of eggs and crab shield length, crab mass, shell mass and shell volume. (* indicates transformation of both variables by taking the natural logarithm.)

	r^2	RSE	F	DF	P
Number of eggs by crab shield length (mm)	0.21	589.9	67.14	246	P<0.001
Number of eggs by crab mass (g)	0.11	625.5	32.53	246	P<0.001
Number of eggs by shell mass (g)	0.15	611.8	45.15	246	P<0.001
Number of eggs by shell volume (mL)	0.12	624.7	32.68	233	P<0.001
Number of eggs by crab shield length (mm)*	0.07	0.908	20.96	246	P<0.001
Number of eggs by crab mass (g)*	0.04	0.926	11.24	246	P<0.001
Number of eggs by shell mass (g)*	0.05	0.919	14.58	246	P<0.001
Number of eggs by shell volume (mL)*	0.05	0.937	13.23	233	P<0.001

Table 3.9: The effect of shell type on the relationship between the number of eggs and crab shield length, crab mass, shell mass and shell volume.

	Slopes	Intercepts	F	DF	P
Number of eggs by crab shield length (mm)	Do not differ	Do not differ	0.751	1 on 5	P = 0.586
Number of eggs by crab mass (g)	Do not differ	Do not differ	0.429	1 on 5	P = 0.828
Number of eggs by shell mass (g)	Do not differ	Do not differ	0.329	1 on 5	P = 0.895
Number of eggs by shell volume (mL)	Do not differ	Do not differ	0.445	1 on 5	P = 0.897

Despite the variability in the number of eggs produced, there appeared to be an upper limit to the number of eggs produced at a given crab or shell dimension (Figure 3.13). Because of the heterogenous distribution of the response variable (number of eggs) to the predictor variable (crab shield length, crab mass, shell mass and shell volume), a traditional regression model did not give an ecologically useful description of the relationship. Quantile regression was used to determine the relationship between number of eggs produced and predictor variables at the 98th, 90th, 75th, 50th (median) and 25th quantiles. The upper limit of the relationship between the number of eggs produced and the predictor variables was best described by

regression of the 98th quantile (Figure 3.14). While female crabs can produce fewer eggs than described by these relationships (Table 3.10), they are unlikely to produce more.

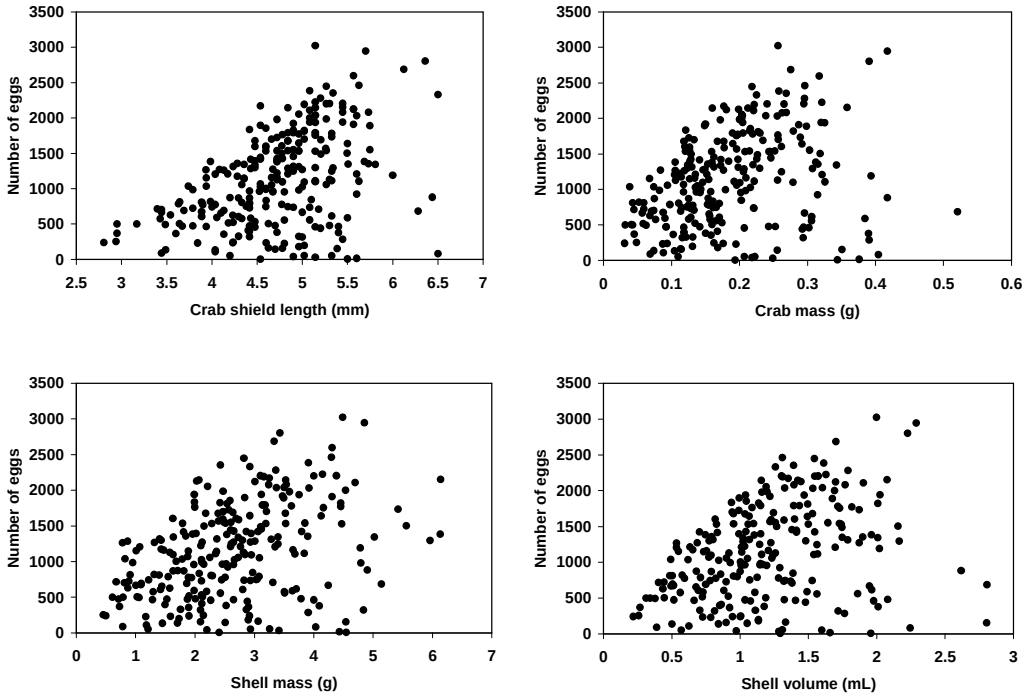

Figure 3.13: The relationships of the number of eggs produced to crab shield length, crab mass, shell mass and shell volume all seem to have upper boundary limits that indicate that there is a maximum number of eggs that can be produced by a crab of a certain size in a shell of a certain size.

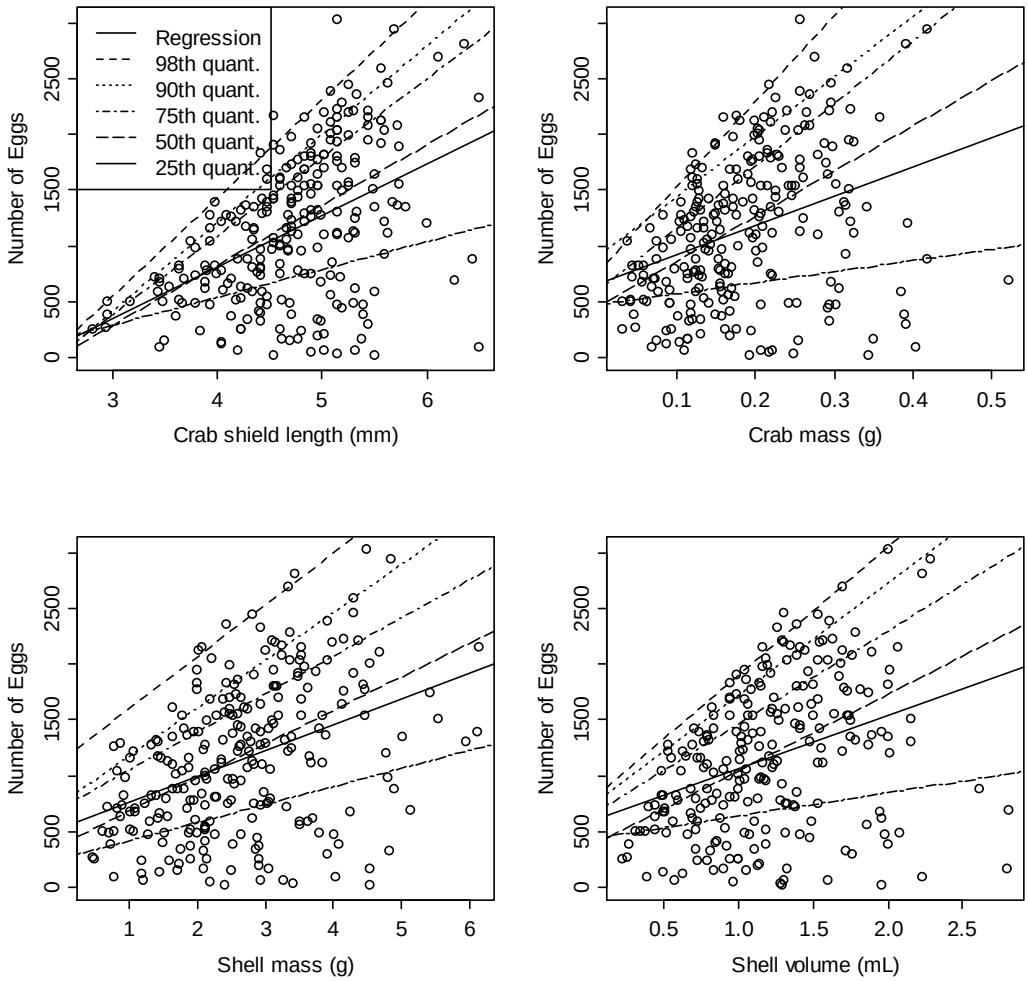

Figure 3.14: There is no clear relationship between the predictor variables and the number of eggs produced. The maximum number of eggs produced at a given predictor is best described by regression of the 98th quantile.

Table 3.10: The upper limit for the number of eggs produced at a given crab shield length, crab mass, shell mass and shell volume at the 98th quantile.

		Value	SE	t	DF	P
Number of eggs by crab shield length	Slope	884.98	81.55	10.85	246	P<0.001
	Intercept	-2112.45	240.74	-8.77	246	P<0.001
Number of eggs by crab mass	Slope	7727.73	920.07	8.39	246	P<0.001
	Intercept	762.26	80.88	9.42	246	P<0.001
Number of eggs by shell mass	Slope	467.77	62.00	7.54	246	P<0.001
	Intercept	1128.98	192.73	5.86	246	P<0.001
Number of eggs by shell volume	Slope	1151.11	97.36	11.82	233	P<0.001
	Intercept	752.95	51.60	14.59	233	P<0.001

Although egg stage does not have a significant effect on the relationship of egg number to crab shield length, crab mass, shell mass or shell volume (Table 3.7), from a Kruskal-Wallis rank sum test it appears that there is a significant difference (KW $\chi 2$= 8.48, DF=3, P=0.0370) in the number of eggs among stages (Table 3.11).

Table 3.11: Clutch sizes for broods with eggs in different stages. There is a great deal of variability in the number of eggs per brood for all egg stages.

Egg stage	Minimum	Maximum	Mean	*n*	SE
Stage 1	5	3024	1169.6	201	3.25
Stage 2	138	2463	1211.9	19	37.34
Stage 3	146	2597	961.2	22	32.42
Stages 4 & 5	15	1835	648.2	12	48.25

A limited number of eggs (101 from 11 females) were in suitable condition to provide accurate measurements of egg size. The relationships of mean egg size to crab and shell dimensions were compared by linear regression and the significance of the regressions was tested by analysis of variance. Visual inspection of Normal Q-Q plots indicated that the untransformed data were normally distributed and thus transformation of data was not required. Mean egg size did not have a strong relationship with any of the crab or shell predictors and the regressions were not significant for crab shield length (r^2 = 0.01, F = 2.76, DF = 99, P = 0.09), crab mass (r^2 = 0.008, F = 1.88, DF = 99, P = 0.17), shell mass (r^2 = -0.006, F = 0.46, DF = 99, P = 0.50) or shell volume (r^2 = -0.009, F = 0.1564, DF = 99, P = 0.69). Mean egg size did show a weak but significant relationship with number of eggs (r^2 = 0.053, F = 6.64, DF = 99, P = 0.01), with a decrease in egg size as egg number increased.

3.4 Discussion

Data from studies on *C. virescens* in Japan by Imazu and Asakura (1994) and Wada *et al.* (2005) are comparable to data from Cape Recife. On the Bozo peninsula (Imazu and Asakura 1994) *C. virescens* used 10 shell types, a larger number than other species of hermit crabs (*Pagurus geminus* and *P. lanuginosus*) that co-occurred with it. However, none of these shell types dominated shell use as *Burnupena lagenaria* does at Cape Recife.

At Hane-Cape (Wada *et al.* 2005) males reach a mean shield length of 4.3 mm ± 1.01 (SD) and females a mean of 3.62 mm ± 0.76 (SD). The minimum size for an ovigerous female is 2.48 mm, while ovigerous females reach a mean shield length of 3.96 mm ± 0.59 (SD). The Cape Recife population showed slightly larger sizes with males attaining a mean shield length of 4.56 mm ± 1.39 (SD) and females reaching a mean of 4.20 mm ± 0.91 (SD). The minimum size for an ovigerous female was 2.80 mm, while the mean size was 4.73 mm ± 0.66 (SD). Imazu and Asakura (1994) report the maximum sizes for the *C. virescens* population at Bozo peninsula. Males reach a maximum of 8.70 mm while females grow to 6.65 mm. At Cape Recife the maximum male shield length is 8.50 mm, while the largest female reaches 6.50 mm. At Bozo peninsula males were significantly larger than ovigerous females, but not significantly larger than non-ovigerous females (Imazu and Asakura 1994). At Cape Recife the opposite occurred. Males had a larger mean shield length than any of the female groupings (all females, all non-ovigerous females and BS non-ovigerous females), but were not significantly different to ovigerous females.

At Cape Recife (34°01’ S), the breeding period of *Clibanarius virescens* starts in mid-December (summer) and ends at the beginning of June (winter). This period is

reflects the breeding period of *C. virescens* in Japan, which extends from May (late spring) to September (autumn) at Hane-Cape (33°18' N) (Wada *et al.* 2005), and from April (spring) to November (early winter) on the Bozo peninsula (35°0' N) (Imazu and Asakura 1994). In all three cases, *C. virescens* presents a seasonal breeding pattern with crabs breeding over 5 to 6 months during summer.

At Bozo peninsula, juvenile *C. virescens* were collected during all 13 months of the study, while at Cape Recife, juveniles were collected between January and July 2002. Juveniles were also collected in low numbers in November 2001, before the start of the breeding season, and in September 2002, two months after the last ovigerous females were recorded. No information could be found on the duration of brooding, larval development or settlement behaviour of *C. virescens*, so attempting to explain the appearance of juveniles before the breeding season would involve some speculation. Imazu and Asakura (1994) suggest that the early recruitment peak may result from juveniles over-wintering in the subtidal zone, out of reach of winter storms, and then migrating into the intertidal at the start of spring. Migration of adults has been found in *Clibanarius vittatus* off the coast of Texas (Fotheringham 1975), but is not mentioned in a study from Sao Paulo State, Brazil (Sant' Anna *et al.* 2006). While fewer and smaller *C. virescens* were collected at Cape Recife during the winter months, it did not appear as though a substantial seasonal migration had taken place. *C. vittatus* takes between 33 and 51 days to reach the megalopa stage at 25 ℃ in the laboratory (Lang and Young 1977), a nd 24 days to hatch at 25 ℃ (Turra and Leite 2007). If *C. virescens* has a similar or longer developmental period (likely in the colder water at Cape Recife), recruitment two months after the breeding season may be explained. From Imazu and Asakura (1994) and Wada *et al.* (2005) it appears that the population dynamics of *Clibanarius virescens* is similar at similar latitudes.

Clibanarius virescens at Cape Recife predominantly used the shells of one mollusc species, *Burnupena lagenaria*, even through shell use patterns indicated that there were at least 17 shell types available to them. This suggests that *C. virescens* has a preference for a particular shell type, an observation supported by Nakin and Somers (2007), who, at three localities on the East Coast of South Africa, found that *C. virescens* also appeared to show preferences. They found that the frequencies of shell types used differed from the availability of empty shells and the presence of live animals in the vicinity of the crabs sampled. In their study, *C. virescens* showed a strong preference for shells of *Burnupena cincta* and *B. pubescens*. Crabs at Cape Recife were found in a larger number of shell types than in Nakin and Somers' (2007) study, yet used a larger proportion of a single shell type, which may support the idea that *C. virescens* at Cape Recife prefer shells of *B. lagenaria* over other shell types. However, shell use by a population is primarily determined by shell availability and not always by preference (Botelho and Costa 2000, Barnes 2005) as crabs can only select from the pool of available shells. At Quirimba Island in Mozambique, Barnes (1999) found that *C. virescens* used 18 shell types out of a potential 42 shell types available but showed only a small degree of shell usage segregation. *C. virescens* at Qurimba Island used a unique combination of shell types but its usage pattern did not demonstrate preferences as clear as those in some other hermit crab species at the same locality.

At Cape Recife male and female *C. virescens* used significantly different frequencies of shell types, even when compared within the same size range. Males in the same size range as females also used larger shells for all shell dimensions (except shell length) than females. The difference can therefore not simply be ascribed to males

using a different suite of shells because they become much larger than females. Males within the same size range as females must be selecting a different suite of shells for a different purpose to females. Male hermits at Cape Recife may be selecting shell types that allow them to increase their growth rate and thus achieve larger sizes than females. Obtaining larger shells of suitable shell types and reaching larger sizes than females may increase fitness in male crabs as large males can obtain more matings than smaller males (Harvey 1990) and can guard larger females (Yoshino *et al.* 2004), which are capable of producing more eggs (Fotheringham 1976a). These patterns are known from several hermit crab populations (Harvey 1990, Wada 1999, Turra and Leite 2000, Mantelatto and Martinelli 2001, Garcia and Mantelatto 2002) and very likely explain both the differences in shell use and sexual size dimorphism at Cape Recife. Sexual size dimorphism in invertebrates usually involves large females and small males (Blanckenhorn 2005), but in hermit crabs the opposite is usually true. Size dimorphism in hermits may be maintained in the population by increased mating success of large males (Blanckenhorn 2005), but is unlikely to be the result of female choice (Contreras-Garduño and Córdoba-Aguilar 2006), or may rather be weak selection for fecundity in females (Harvey 1990).

The population at Cape Recife shows not only shows size dimorphism, but the population also departs from a 1:1 ratio for the number of males to females for all size classes except the smallest class. The equality of males and females in the smallest size ratio is expected from Fischers' (1930 in Wenner 1972) hypothesis that most populations produce equal numbers of male and female offspring, but departures from the expected sex ratio require further explanation. At Cape Recife the proportion of females in the population increases and then declines with size in a bell-shaped curve. The proportion of males dips in the classes 3.0 to 3.9 mm and 4.0

to 4.9 mm before climbing steadily to reach 100% in the largest size class. This pattern of sex ratio agrees with Wenners' (1972) "anomalous pattern", also found for the hermit crab *Calcinus laevimanus*. Wenner (1972) offers several explanations for this kind of pattern, but the suggestion that it is caused by differential growth rates between males and females best fits what has since been discovered about growth rates in hermit crabs (Fotheringham 1975, Branco *et al.* 2002, Turra and Leite 2000, Biagi *et al.* 2006, but see Fransozo and Mantelatto 1998). At a given size, males may grow more rapidly than females, causing a smaller number to be found within those size classes.

Females use a higher proportion of *Cominella elongata* and *Clionella* spp. shells than males. *Cominella elongata* has a higher volume-to-mass ratio than *B. lagenaria*, while *Clionella* spp. has a similar, but potentiall larger volume-to-mass ratio than *B. lagenaria*. However both these shell types reach smaller absolute sizes than *B. lagenaria* and this, coupled with the small proportion of these shell types used by ovigerous females (8.6%), must limit their importance to the average reproductive output of females. Both ovigerous and BS non-ovigerous females used mainly *Burnupena lagenaria*, and there was no significant difference in the frequency of use of shell types between these two groups. There was a significant difference in the sizes of shells used by ovigerous and BS non-ovigerous females. Ovigerous females used larger shells and attained greater average sizes than non-breeding females within the potentially fertile size range. Even within a single shell type, *B. lagenaria*, ovigerous females obtain wider, more voluminous shells than non-ovigerous females. This indicates that non-breeding females within the potentially fertile size range might not breed because they inhabit small shells.

There are several factors that affect fecundity in female hermit crabs. These aspects will be discussed in detail in Chapter 6. Briefly, females reach larger sizes if allowed access to large shells, and larger females are capable of producing more eggs than small females (Fotheringham 1976a). In particular, females in light weight, high volume shells are capable of producing more eggs than females in less suitable shells (Bertness 1981a). However, female crabs have to make considerable trade-offs between growth and reproductive output, which may limit their size. These trade-offs may form part of the explanation for sexual size dimorphism in hermit crabs.

At Cape Recife, *Clibanarius virescens* breeds during summer and autumn (mid-December to early June). There was a significant positive relationship between the number of eggs produced and female size (shield length and mass) and the number of eggs and shell size (mass and volume). This pattern is expected because the cost of a large adult brooding a large clutch does not increase significantly compared to a small individual brooding a smaller clutch (Heino and Kaitala 1999). In a review of the literature Contreras-Garduño and Córdoba-Aguilar (2006) found that the reported percentage of correlation between clutch size and female body size obtained from regression equations ranged from 20% to 90% in the different studies surveyed by them. At Cape Recife, the percentage correlation is in the lower part of the range. However, there was a clear upper limit for the number of eggs that could be produced, but many females produced fewer eggs than the upper limit. Crab and shell size were not good predictors of the number of eggs produced, but rather were predictors of the maximum number of eggs that could be produced. The variation in the number of eggs suggests that the fecundity of female hermit crabs at Cape Recife is possibly limited by more than one factor (Cade and Noon 2003). This

variation was not caused by egg loss during sampling or laboratory analysis and so must represent reproductive decisions by, or constraints acting on, female crabs. By using quantile analysis the parameters of the upper limit of fecundity could be obtained. This will be a useful measure to compare maximum realised fecundity at different localities (see Chapter 6) rather than using the more variable mean fecundity estimates produced by linear regression.

Maternal investment generally involves a trade-off between fedundity and the size of the eggs produced (Ramirez Llodra 2002). At Cape Recife there is a decrease in egg size with increasing egg number, although the relationship is weak. Any reason for this relationship will be speculative at best. This may represent a balance between investment into each offspring and the number of eggs that can be brooded within the shell. Both strategies, either producing fewer, larger eggs or producing more small eggs may increase the fitness of a female crab within the population as either strategy results in each female maximising the number of surviving offspring produced.

In summary, the population of *Clibanarius virescens* at Cape Recife is comparable to other populations of *C. virescens* at similar latitudes. The population uses mainly one shell type, that of *Burnupena lagenaria*. The shell resource changes through the year and *C. virescens* appears to partition the shell resource between males and females. The population shows sexual size dimorphism as only males reach large size classes. The ratio of males to females, however, is skewed towards females. Reproduction is seasonal and occurs during summer and autumn. Juveniles are found throughout the breeding season, with a strong peak towards the end of the breeding season. It appears that ovigerous females obtain slightly, but significantly

more voluminous shells than non-ovigerous females. Females show variable fecundity with increasing size, and although egg production relates positively to crab size and shell mass and volume, these variables are better predictors of the maximum fecundity than of the mean fecundity.

Chapter 4: Trends in shell use by *Clibanarius virescens* along the east coast of South Africa

4.1 Introduction

Shells available to, and used by hermit crabs often closely match gastropod species in the intertidal and shallow subtidal zones (Barnes 1999, Turra and Leite 2001a), but even within the choice available crabs may show some degree of preference (Nakin and Somers 2007). The latitude at which the gastropods live ultimately affects the shells available to hermit crabs, as both the gastropod species diversity (Roy *et al.* 1998) and shell morphology (Vermeij and Currey 1980) change with latitude. The South African coastline is divided into several biogeographic zones (as discussed in Chapter 1) and the intertidal shell resource changes accordingly. *Clibanarius virescens* occurs within the Agulhas bioregion, from Cape Point to the Mbashe River, and the Natal bioregion, from the Mbashe River to Cape Vidal (Lombard *et al.* 2004). It shows a change in the shell resource used in warm-temperate higher latitudes through to subtropical lower latitudes within this range.

The paradigm that the tropics harbour a greater diversity of species than temperate regions has long been accepted (Wallace 1878 in Fischer 1960). This general trend also applies to prosobranch gastropods (Thorson 1952, 1957 in Fischer 1960, Roy *et al.* 1998) in the northern hemisphere. Gray (2001), however, cautions that Roy *et al.* (1998) extrapolate their findings to the southern hemisphere although they have no data from the area. He (Gray 2001) proposes that in the southern hemisphere trends in diversity are more variable and that there is not a clear increase in species richness with decreasing latitude. Although there is no literature specifically on latitudinal tends in gastropods in southern Africa, Barnes (2003) notes that the genus

Clibanarius uses more shell types with decreasing latitude on both sides of the equator. This trend holds within Africa for *Clibanarius virescens*, as it uses more shell types in Madagascar than in Mozambique, and more there than in South Africa. It does seem, therefore, that this pattern of diversity in shell use, and by inference gastropod diversity, is comparable to trends in the northern hemisphere.

Roy *et al.* (1998) found that there are strong latitudinal gradients in the diversity of prosobranch gastropods in the northern hemisphere for both the western Atlantic and eastern Pacific oceans. This pattern of diversity is thought to be dependent on the total amount of available energy, generally taken to be the amount of incoming solar radiation, which correlates strongly to sea surface temperature (Roy *et al.* 1998). Mean sea surface temperature seems to be an important correlate of increasing mollusc species diversity with decreasing latitude.

Sea surface temperature is one of the factors that contributes to the morphology of gastropod shells, as the calcification index, or the ease with which calcium carbonate precipitates out of solution (Graus 1974), shows a linear relationship with an increase in water temperature. Graus (1974) found a weak latitudinal trend in shell characteristics that can be explained by the relative ease of building a shell in warmer waters. These characteristics include heavier ornamentation or increased sculpting towards the tropics. Tropical shells, especially in the Indian and Pacific Oceans, are thicker and heavier than shells from temperate regions (Vermeij and Currey 1980).

Thicker shells have costs to the gastropods that include the cost of making the shell (depositional costs), the cost of carrying a heavier shell (transport costs) and a growth cost as growth is constrained by the rate at which the shell can be deposited

(Palmer 1981). The maximum rate of deposition seems independent of energy intake and rather seems to have a maximum limit at the sustainable rate at which calcium carbonate can be precipitated out of the biological medium (Palmer 1981). For a constant calcium carbonate deposition rate, shells that grow fast may incorporate more organic matter into the shell than shells that grow more slowly (Kemp and Bertness 1984). Fast growth thus leads to a relatively lighter, weaker shell. Organisms with thicker calcium carbonate skeletons have slower rates of body growth, and therefore smaller total size than those of the same species with lighter skeletons (Vermeij and Curry 1980, Palmer 1981). Sculpturing may also selectively reduce growth rates though the same mechanism.

While the ability to increase shell thickness towards the tropics is related to the ability to deposit calcium carbonate, the need for shell thickening and for shell ornamentation is greatly influenced by predation rates. These characteristics make the shells stronger and more resistant to crushing by predators (Vermeij and Curry 1980). The advantages of increasing thickening and ornamentation to avoid or resist predation offset the costs of building a thicker shell (Palmer 1992). Two main types of predation on gastropods occur: crushing predators include many kinds of fish, while peeling predators include crabs and lobsters. Gastropods adapt to peeling predators by forming elongate, narrow, or dentate apertures, by developing shorter spires and by increasing external shell sculpturing (Vermeij 1976). Gastropods can selectively increase shell thickening in the presence of predators (Appleton and Palmer 1988). For example, *Thais* (or *Nucella*) *lamellosa* develops thicker apertural teeth in the presence of water-soluble chemical cues produced when *Cancer productus*, a major crab predator of *T. lamellosa*, feeds on conspecific gastropods. The influence of predation on shell morphology may supersede localised

environmental factors. Boulding, Holst and Pilon (1999) showed that shell morphology differs on wave-exposed and wave sheltered localities, not because of the action of waves, but because of different types of predation that occur at these localities.

Different types of predation on gastropods ultimately have consequences for hermit crabs as they rely on shells made available by mortality within local gastropod populations (Vance 1972, Barnes 1997). The quality of shells available to hermit crabs will be affected by the manner in which the shells are made available. If the gastropods are victims of crab predation, the primary shell supply may be shells that are damaged. The types of damage will depend on the size of the shell and the nature of the predator (Turra *et al.* 2005). Predation of gastropods by whelks is also important. *Pagurus longicarpus*, a hermit crab from North America, actively avoids shells that have been drilled by whelks, as the damaged shells provide less shelter from predation by *Carcinus maenas*, the principle crab predator in the area (Pechenik *et al.* 2001). By contrast, if gastropods die from desiccation (Scully 1979) the shell supply may consist of pristine shells.

Other factors that influence the nature of the shell resource available to hermit crabs include gastropod population size and food availability (Kemp and Bertness 1984). This is illustrated by *Littorina littorea* in New England, which develops thin, globose shells when the snail population is small and food is not limiting. The globose shape indicates maximum growth as a rounder shell maximises internal volume which in turn houses a larger body mass.

It can therefore be expected that patterns of shell usage by hermit crabs will be closely affected by the availability and quality of shells from the immediate vicinity (Conover 1978, Barnes 1999, Floeter *et al.* 2000). Shells are generally considered limiting (Vance 1972, Kellogg 1976, Raimondi and Lively 1986, Rittschof *et al.* 1995, Worcester and Gaines 1997, Shih and Mok 2000), but there are exceptions (Spight 1977, Siu and Lee 1992, Turra and Leite 2001a).

In the natural environment shell strength decreases once the gastropods have died (LaBarbera and Merz 1992). Although some hermit crabs can modify shells externally by encouraging the growth of epibionts (McLean 1983) the crabs cannot repair broken shells. Shells constantly lose small amounts of calcium, and this calcium leaching seems to be the way in which crabs can locate suitable shells (Mesce 1982). However calcium loss leads to a loss in mechanical strength of shells (LaBarbera and Merz 1992). If hermit crabs inhabit shells that are weaker than those inhabited by living snails, one would expect predators to prefer eating hermit crabs, as they would be easier to extract from their shells. Bertness and Cunningham (1981) however, found that there was no significant difference in choice between hermit crabs and snails in tropical crab predators. Where a preference has been established (Rossi and Parisi 1973) it is not clear whether hermit crabs were preferred to snails because the behaviour of the hermits attracted the predatory crab, or because of the decrease in shell strength.

Hermit crabs choose to avoid damaged shells wherever possible (Pechenick and Lewis 2000, Rotjan *et al.* 2004), but the factors that lead a hermit crab to make a specific choice of shell are diverse. There is a trade-off between shell features chosen by the crabs and the fitness conferred by the particular shell feature, for

example, heavy shells may reduce predation, but may have a cost in terms of energy available for growth or reproduction (Bertness and Cunningham 1981). Choices are limited by the available shells, and by the particular needs of the hermit crab. The effects of shell choice on hermit crab population biology (Chapter 5) and reproduction (Chapter 6) will be discussed later.

While Kuris and Brody (1976) suggest that hermit crabs use a "gestalt" picture of the shell being examined rather than a single shell characteristic, it would seem that hermit crabs tend to select shells that offer maximum internal volume compared to mass. On tropical shores, hermit crabs choose shells with high internal volume in order to optimise retention of water during low tide (Bertness 1981b). Conover (1978) suggests that weight and volume are the two most important considerations when choosing shells, but that the centre of gravity and the angle of the axis of the shell are also important considerations. He remarks further that shells must be light enough to carry yet heavy enough to provide protection and that in small shells, volume may be more important to the hermit crab, but in large shells, the weight of the shell becomes an issue. Floeter *et al.* (2000), working in Brazil found that for both *Clibanarius antillensis* and *Calcinus tibicen*, shell internal volume was more important than weight, even though the two species preferred different types of shell and inhabited different zones of the shore. Terossi *et al.* (2006), also working in Brazil, obtained similar results for *Pagurus exilis*, a subtidal species. In Hong Kong, Siu and Lee (1992) found that *Pagurus trigonocheirus* and *Clibanarius bimaculatus* chose shells with the highest internal volume to weight ratio.

This chapter aims to describe the shell resource used by *Clibanarius virescens* in South Africa as well as to test certain predictions. The shell resource will be

described mainly in terms of the shell types (shell type is used as an abbreviation for the shell of a gastropod species) used by *Clibanarius virescens*. Shells found close to hermit crabs at the sampling localities, and presumed available to the hermit crabs, will be listed. Emphasis will be placed on the shells used rather than on the shells presumed available, as this study does not aim to examine shell preferences or choices made by *Clibanarius virescens*. An overview of the morphology of the shells used by *Clibanarius* will be given. The dimensions of the most commonly used shells will be analysed by species.

The diversity of the shell resource will be examined and related to latitude. Barnes' (2003) findings that *Clibanarius virescens* uses more shell types with decreasing latitude will be examined to determine if the trend continues further south, or whether the trend is variable (Gray 2001). Patterns in the distribution of the resource will be examined to determine whether the localities sampled can be grouped according to biogeographic province.

Several predictions can be made about changes in resource with locality. These predictions arise from slower body growth (and therefore smaller size) in intertidal gastropods as a result of adaptations to predation (thicker, more sculptured shells and smaller apertures) expected with decreasing latitude. It is predicted that the shells used by *Clibanarius virescens* will become smaller from south to north. Variation in the resource with locality will be examined, with emphasis on the most commonly used shells. If gastropods have sufficient morphological plasticity to adapt their shell dimensions to the change in the physical and biological environment associated with decreasing latitude, it is predicted that these changes will become apparent at the species level. This prediction is coupled to the prediction that the

mass-to-volume ratio of shells used will increase from south to north. It is also predicted that aperture sizes will decrease from south to north.

If gastropods are expected to adapt their shell morphologies in response to predation, it would also be useful to investigate whether any evidence of predation occurs. Damage to the shells used by *C. virescens* will be examined for evidence of peeling and crushing predation. Predation caused by whelks will not be examined as in most cases in it impossible to determine whether whelk-drilled holes in the shells were caused by predation or whether the damage was inflicted post mortem by scavenging whelks. Chapter 5 will investigate the effect of shell damage on the populations characteristics of *Clibanarius virescens*.

4.2 Methods

Sampling localities, collection methods and laboratory analyses are described in Chapter 2. Only crabs sampled between 31 December 2000 and 28 January 2001 at Cape Recife were used to avoid greatly uneven sample sizes among localities. Shell types used by *Clibanarius virescens*, as well as empty shells found at the different sampling localities, were identified to species level (Chapter 2). The data were analysed to determine the most commonly used shells and to determine which shell types were prevalent at different sites. The habitats of the gastropod species of all shell types, both empty and in use by *C. virescens*, were identified using Kilburn and Rippey (1982) and the Ocean Biogeographic Information System (OBIS, http://www.iobis.org).

For each locality, the Shannon-Weiner Index (H') and the Evenness Index (J') were calculated. Indices were plotted against the latitudes of the sites to examine whether a trend could be determined, and the indices were regressed against latitude to determine the nature of the relationship.

The dimensions (shell length, width of the body whorl, aperture width, mass and volume) of the shells used by *Clibanarius virescens* grouped clearly into 2 categories: high-spired shells and low-spired shells (Figure 4.1). Because these groups displayed such distinct morphological relationships, data could not be pooled for analysis and each group had to be analysed separately. Groupings were made after exploratory graphing and were partially based on the methods of Floeter *et al.* (2000), who consider shells as high-spired if they have 4 whorls or more, and the work of

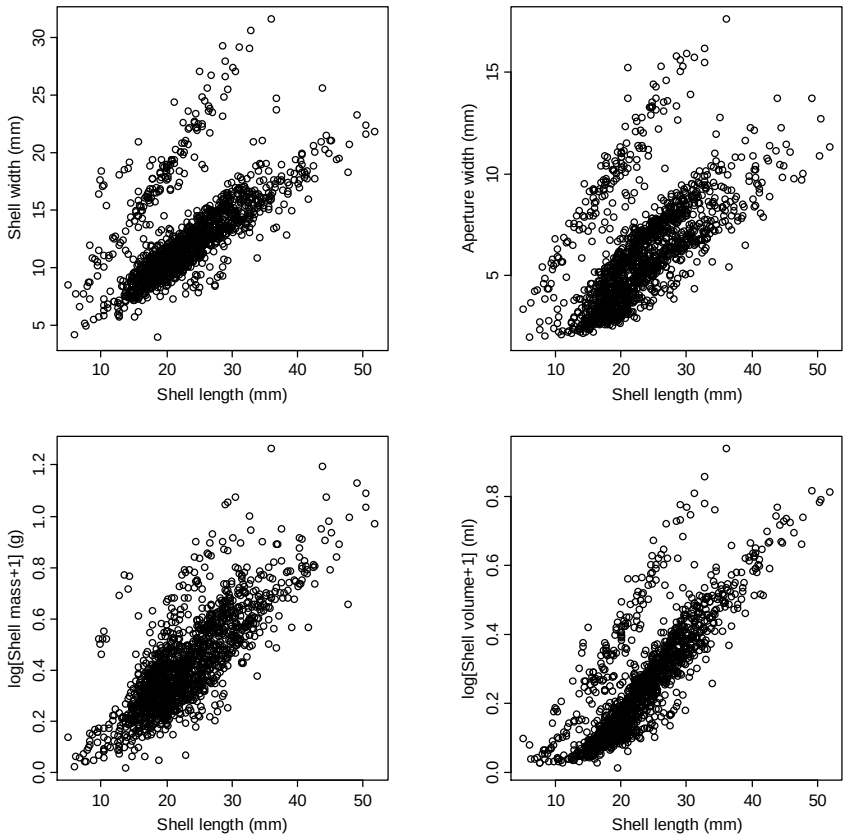

Figure 4.1: The shell dimension data clearly display two distinct patterns, the upper grouping representing low-spired shells and the lower, much larger grouping representing high-spired shells.

Vermeij and Currey (1980), who classify the acuteness of the shell as the ratio between length and breadth (width). Shells were classified as high or low spired by species rather than on the shell parameters of individual shells. Badly damaged shells were excluded from the analysis. Shell dimensions of high-spired shells and low-spired shells were regressed against shell length to describe the morphometric relationships of the shells.

Dimensions of the six most commonly used shell types were regressed against shell length to describe the morphometric relationships of the shells. Shell volume could not be determined for all shells, as some shells were crushed in order to extract the crabs, but for shell length, width, aperture width and mass, larger sample numbers

were available. In all cases data for shell mass and volume were transformed so that linear regression models could be used.

To examine the patterns of shell distribution across the geographic range sampled, the shell types used by *Clibanarius virescens* at each locality were compiled into a presence/absence matrix. A dissimilarity index was calculated using Jaccard's coefficient, as this is a suitable similarity measure for binary variables (Everitt 1993). Data for shell fragments were discarded as fragments are a ubiquitous component and are not representative of a single shell type. Hierarchical clustering with "average" linking was employed to generate a diagram showing locality clusters. Nonmetric multidimensional scaling was applied to the presence/absence data, again using Jaccard's coefficient, in order to generate an ordination plot showing both shell types and localities. This kind of exploratory analysis is useful in order to present distance matrices graphically (Everitt 1993).

It was expected that shells would become smaller with decreasing latitude. Analysis of covariance (ANCOVA) was used to determine whether shell dimensions varied by locality. The model tests the hypothesis that the regression lines generated for a pair of shell dimensions are completely separate for each locality, i.e. that both the slopes and the intercepts vary. If the interaction term (regression slope × locality) was not significant, the data were refitted to a model that tested whether parallel intercepts of the regressions varied among localities. While ANCOVA can test whether differences exist, it cannot determine the nature of the differences. To better visualise the nature of the differences, boxplots of shell dimensions at the 12 localities sampled were constructed for all the shells used by *Clibanarius virescens*. ANCOVA was used to test whether high-spired shells and low-spired shells varied by

locality. Intraspecific differences were also tested by locality. The six most common shell types were available in sufficient numbers to allow comparison of shell dimensions among most localities where the shell types were used.

It was predicted that, for a given mass, shells in northern localities would have smaller volumes than in southern localities. This increase in the mass-to-volume ratio with decreasing latitude would also indicate that shells would have thicker walls (Vermeij and Curry 1980), with decreasing latitude. To see the general nature of the relationship, boxplots of the mass-to-volume ratio were plotted against locality. To test the prediction, the regressions of mass-to-volume of the six most commonly used shells were compared by locality using ANCOVA. While general changes in mass-to-volume ratios with locality might be explained by a change in species composition at the different localities, it was felt that the prediction that individual species would adapt their morphology to increasing predation with decreasing latitude could be tested by intraspecific comparisons. To further examine intraspecific changes, the regression lines of volume against mass were plotted to graphically examine the relationship between volume and mass of the six most commonly used shell types.

It was also predicted that shells would show smaller apertures with decreasing latitude. The same method as used above was employed to test this prediction. Data were explored generally and graphically, and ANCOVA was used to determine intraspecific differences by locality. The regressions were plotted to further examine the nature of any differences found.

The effect of shell peeling and apex crushing predation was examined by determining the proportions of shells that suffered damage that could reasonably be

attributed to predators. Damage was classified as described in Chapter 2 (Table 2.2). Lip breakage coded as “2” was classified as shell peeling damage, while apex damage coded as “2” was classified as apex crushing damage.

4.3 Results

Among the 2281 *Clibanarius virescens* sampled across 12 localities, 75 shell types were used. The six most commonly used shell types (71.3%) by percentage use for pooled data at all sites were *Burnupena lagenaria* (18.1%), *Morula granulata* (16.4%), *Peristernia forskalii* (11.1%), *Burnupena pubescens* (10.9%), *Burnupena cincta* (8.2%) and *Morula nodosa* (6.6%).

Fragments made up 3.6% of the total number of shells used. *Burnupena lagenaria* and *Thais capensis* were used at nine of the twelve sites, while *B. pubescens*, *B. cincta*, *M. granulata* and *P. forskalii* were used at eight of the twelve sites, and *M. nodosa*, *Diloma tabularis* and *Nucella squamosa* (the latter two in low numbers) were used at six of the twelve sites. *Turbo cidaris* showed a high percentage use at Cintsa West Beach, but was used in low numbers at other sites (Figure 4.2).

The shells of 98 gastropod species were recorded at the 12 localities sampled (Appendix 1). This total includes shell types used by *Clibanarius virescens* as well as those found as empty shells in the vicinity of the crabs (Table 4.1). Of the 98 gastropod shells recorded, 75 species (76.5%) were recorded as living in the intertidal zone, and all six of the most commonly used shells were from intertidal gastropods.

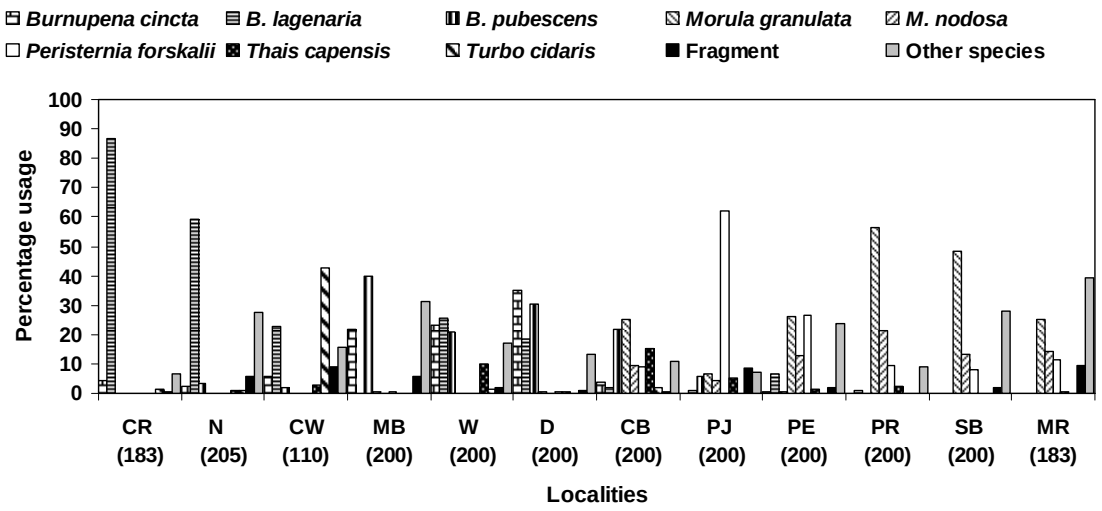

Figure 4.2: Shell use by *Clibanarius virescens*. *Burnupena* spp. dominate southern localities, while *Morula* spp. are more commonly used at northern sites. Shells used at Coffee Bay seem to show a zone of overlap with both *Burnupena* spp and *Morula* spp. used by crabs. *Thais capensis*, while used in low numbers, occurs at most sites. *Turbo cidaris* shows a strong peak at Cintsa West Beach, which is likely a reflection of its availability at this locality. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR). Sample sizes at each locality are shown in parentheses.

Table 4.1: The number of shell types used at the various localities compared to the number of shell types found in the vicinity of the crabs while sampling. (For details see Appendix 1.)

Locality	Used by crabs	Empty shell types found near crabs	Empty shells of types not used by crabs	Used but not found empty	Total number at locality
Cape Recife	8	23	16	1	24
Nahoon Beach	24	29	5	0	29
Cintsa West Beach	14	28	19	4	33
Morgan Bay	16	34	24	6	40
Wavecrest	21	6	3	18	25
Dwesa	21	22	12	11	33
Coffee Bay	21	0	0	21	21
Port St Johns	12	2	2	12	14
Port Edward	21	11	5	15	26
Park Rynie	15	0	0	15	15
Sheffield Beach	25	6	0	18	25
Mission Rocks	23	0	0	23	23

Both the Shannon-Weiner Index (H') and the Evenness Index (J') for shells used by *C. virescens* were plotted against the latitudes of the localities sampled (Figure 4.3). Both indices showed an increase in diversity with decreasing latitude, although the trends were not significant. The regression of H' against latitude shows a marginally stronger trend ($r^2 = 0.22$, F = 4.05, DF = 10, P = 0.072) than the regression of J' against latitude ($r^2 = 0.20$, F = 3.79, DF = 10, P = 0.079).

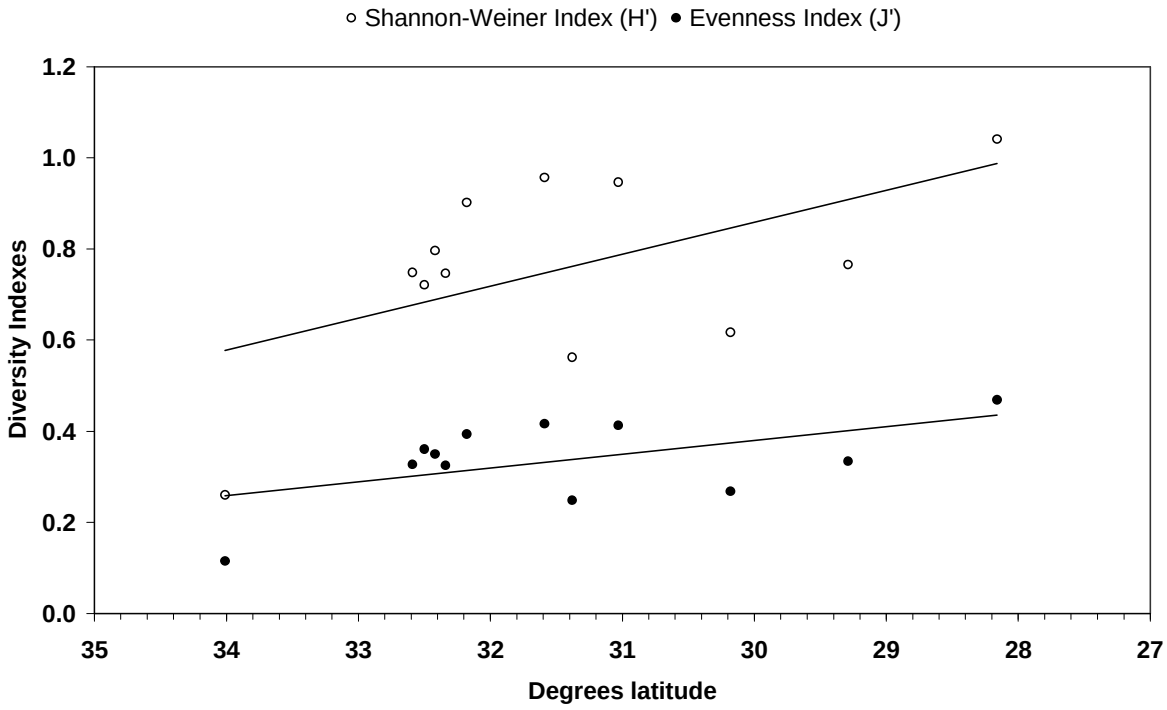

Figure 4.3: Both the Shannon-Weiner Index and the Evenness index indicate an increase in shell diversity decreasing latitude.

Cluster analysis divides the localities into two main groups of six localities each (Figure 4.4). Cape Recife, Dwesa, Morgan Bay, Nahoon Beach, Cintsa West Beach and Wavecrest form a distinct group of southern localities. Within this group Cintsa West Beach and Wavecrest are the most similar while Cape Recife is distinct from the rest of the localities in the group. Coffee Bay and Port St John's form a sub-group of the second cluster that includes the northern localities of Sheffield Beach,

Mission Rocks, Port Edward and Park Rynie. Park Rynie and Sheffield Beach are the least dissimilar localities within the northern cluster. Port Edward and Mission Rocks cluster together based on the shell types used by *C. virescens* even though they are geographically separated.

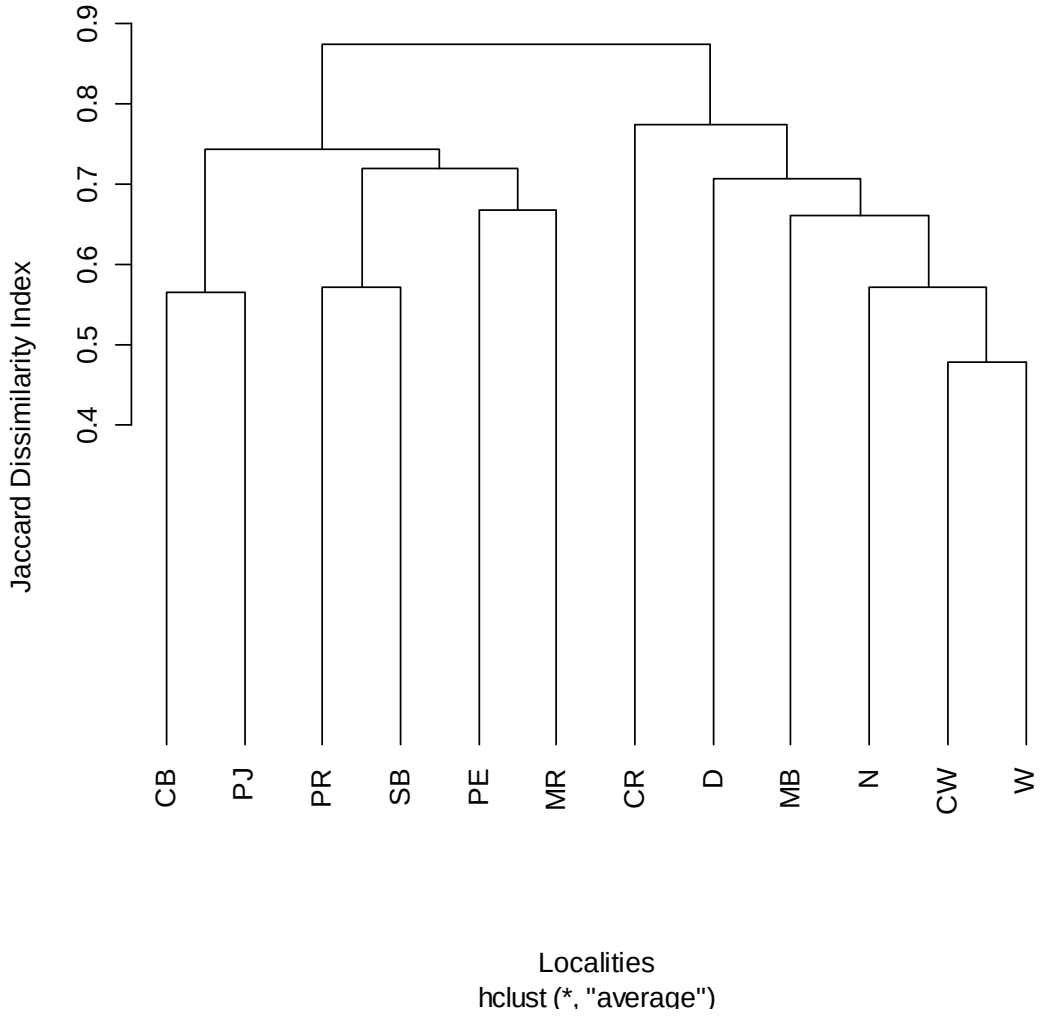

Figure 4.4: Localities cluster together based on a dissimilarity matrix. Two main locality clusters can be determined. Cape Recife (CR), Dwesa (D), Morgan Bay (MB), Nahoon Beach (N), Cintsa West Beach (CW) and Wavecrest (W) form a distinct group of localities. Coffee Bay (CB) and Port St John's (PJ) form a sub-group of a cluster which includes Park Rynie (PR), Sheffield Beach (SB), Port Edward (PE) and Mission Rocks (MR).

An ordination plot derived from nonmetric multidimensional scaling of the shell presence/absence data shows Cape Recife and Sheffield Beach to be the most dissimilar localities (Figure 4.5). The spatial distribution of sites on the ordination plot reflects the distribution of sites on the cluster diagram.

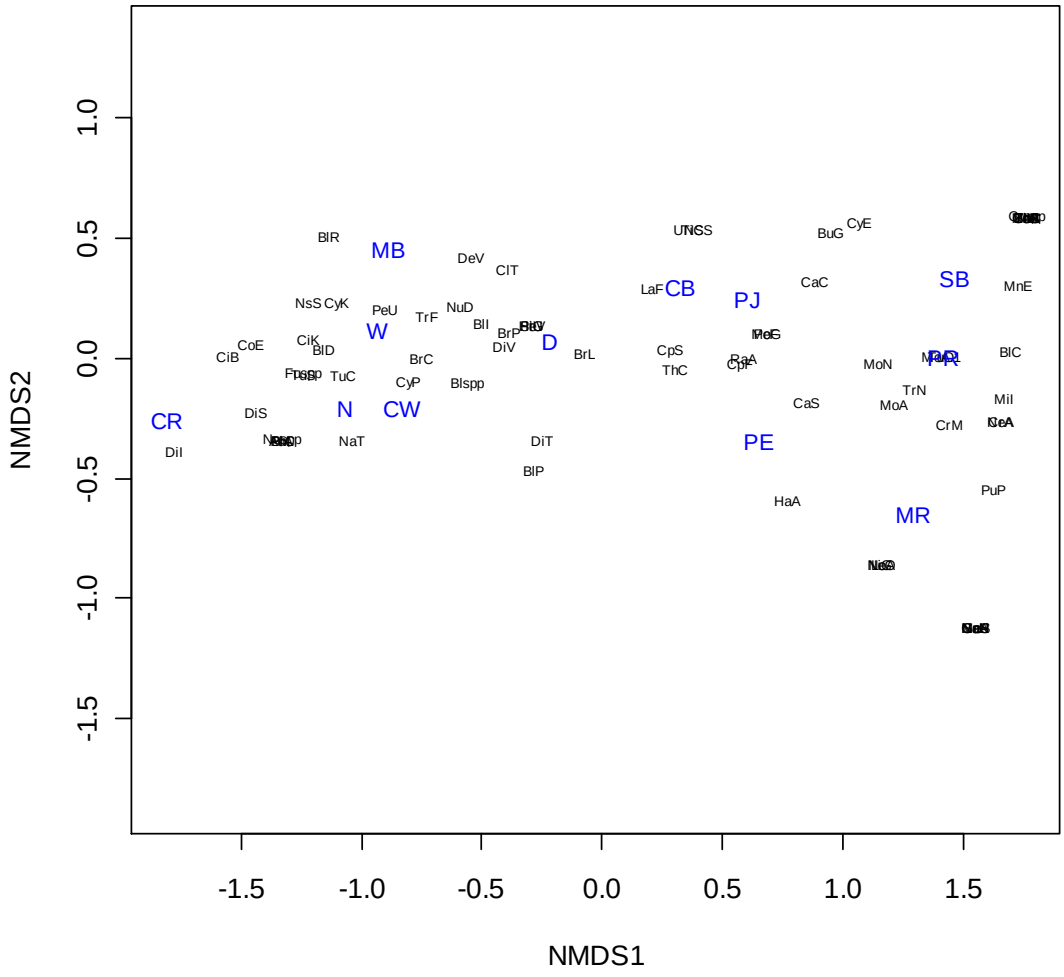

Figure 4.5: An ordination plot derived from nonmetric multidimensional scaling of the presence/absence data for all shells used by *Clibanarius virescens*. Cape Recife (CR) and Sheffield Beach (SB) are the most dissimilar localities. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR). Full names and abbreviations of shell types are given in Appendix 1.

The shells used by *Clibanarius virescens* were grouped into high-spired and low-spired shells as the two groups showed very different morphological relationships (Figure 4.1). Shell width, aperture width, shell mass, and shell volume were regressed against shell length to describe the morphological relationships (Table 4.2). Fewer low-spired shells *(n*=142) were used by *Clibanarius virescens* than high-spired shells (*n*=1236). The length-to-width ratio of high-spired shells ranged between 1.29 and 3.00, while the ratio for low-spired shells ranged between 0.75 and 1.28. All of the six most commonly used shell types were high-spired shells. For these six shell types, shell width, aperture width, shell mass and shell volume were regressed against shell length. It is interesting to note that the relationship of volume to shell length has a steeper slope for high-spired shells than for low-spired shells, while the relationship of mass to length has a steeper slope for low-spired shells than for high-spired shells. This indicates that volume increases faster with length for high-spired shells than for low-spired shells, while low-spired shells become heavier with length than high-spired shells.

Table 4.2: Relationships between shell length and other shell dimensions for high-spired and low-spired shells. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slope	Intercept	r^2	DF	RSE	F	P
High-spired shells							
Width (mm) by length (mm)	0.404	2.385	0.88	1234	1.138	7038	P<0.001
Aperture width (mm) by length (mm)	0.281	-1.044	0.75	1234	1.084	3738	P<0.001
Mass (g) by length (mm)*	2.137	-6.293	0.77	1234	0.317	4140	P<0.001
Volume (mL) by length (mm)*	3.005	-9.922	0.90	1234	0.273	11070	P<0.001
Low-spired shells							
Width (mm) by length (mm)	0.843	1.649	0.93	140	1.307	1991	P<0.001
Aperture width (mm) by length (mm)	0.465	1.003	0.87	140	1.035	964	P<0.001
Mass (g) by length (mm)*	2.701	-7.162	0.92	140	0.268	1629	P<0.001
Volume (mL) by length (mm)*	2.699	-7.715	0.95	140	0.199	2957	P<0.001

For high-spired shells both slopes and intercepts of regressions of shell width, aperture width, mass and volume vary by locality. For low-spired shells the same pattern holds, except for shell mass, where only the intercepts vary (Table 4.3).

Table 4.3: Results from an analysis of covariance of shell dimensions by locality for high-spired shells and low-spired shells. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	DF	F	P
High-spired shells					
Width (mm) by length (mm)	Differ	Differ	11 on 1212	3.525	P<0.001
Aperture width (mm) by length (mm)	Differ	Differ	11 on 1212	9.120	P<0.001
Mass (g) by length (mm)*	Differ	Differ	11 on 1212	8.212	P<0.001
Volume (mL) by length (mm)*	Differ	Differ	11 on 1212	5.852	P<0.001
Low-spired shells					
Width (mm) by length (mm)	Differ	Differ	9 on 122	2.403	P<0.015
Aperture width (mm) by length (mm)	Differ	Differ	9 on 122	3.096	P<0.002
Mass (g) by length (mm)*	Do not differ	Differ	9 on133	11.822	P<0.001
Volume (mL) by length (mm)*	Differ	Differ	9 on 122	5.279	P<0.001

When examining shell dimensions in relation to locality it appears that the largest shells (for all shell dimensions) are found at the southern-most locality and the smallest shells are found at the northern-most locality (Figure 4.6). The trend is not smooth for any of the shell dimensions and there is a large range within shell dimensions for any particular locality. The means of all shell dimensions differ among localities for all shells and for grouped data for the six most commonly used shells (Table 4.4). *Post hoc* analyses were conducted using Tukey's honest significant difference (HSD) test. Shell aperture width, mass and volume of all shell types as well as the six most commonly used shells were compared among localities to determine which localities differed from one other (Figure 4.7). As predicted, shell apertures were narrower northern localities than in southern localities, while shell masses and volumes were larger in most southern localities when compared to northern localities. Although shell species composition at Nahoon and Morgan Bay

places them among the southern localities, shell dimensions seem similar to those found at the northern localities.

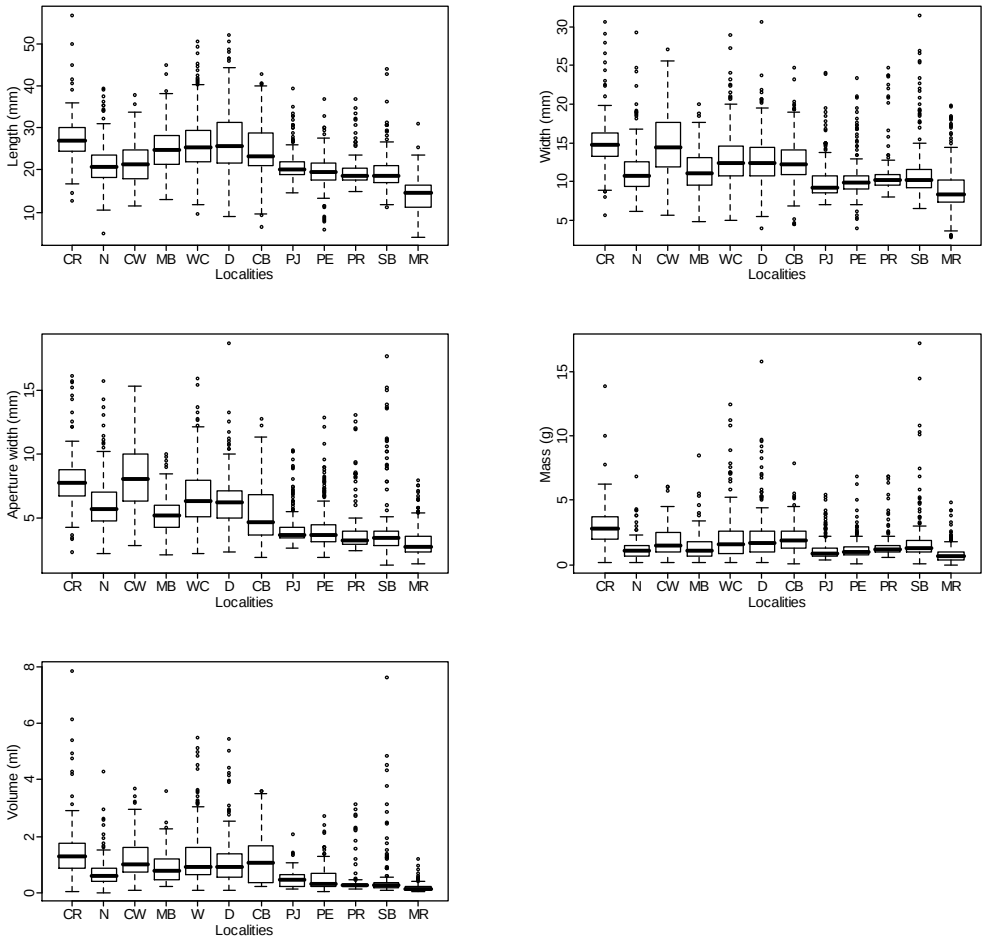

Figure 4.6: Boxplots of the shell dimensions of length, width, aperture width, mass and volume for all shells used at the 12 localities sampled indicate a great degree of variation in the dimensions of the shells used by *Clibanarius virescens*, both within and between localities. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

Table 4.4: Mean shell dimensions for all shells as well as for each of the six most commonly used shells were compared among localities. Analysis of variance shows that mean shell dimensions differ among localities.

Shell type	F	DF	P
Length (mm)			
All shells	99.45	11 on 2268	P<0.01
Combined data for the 6 most commonly used shells	112.91	11 on 1612	P<0.01
Width (mm)			
All shells	53.42	11 on 2269	P<0.01
Combined data for the 6 most commonly used shells	123.47	11 on 1613	P<0.01
Aperture width (mm)			
All shells	109.20	11 on 2268	P<0.01
Combined data for the 6 most commonly used shells	253.40	11 on 1613	P<0.01
Mass (g)			
All shells	34.97	11 on 2264	P<0.01
Combined data for the 6 most commonly used shells	56.78	11 on 1609	P<0.01
Volume (mL)			
All shells	32.85	11 on 1477	P<0.01
Combined data for the 6 most commonly used shells	52.43	11 on 1056	P<0.01

For all six shell types and for all shell dimensions there was a significant relationship between the shell dimension (width, aperture width, mass and volume) and shell length (Table 4.5). Thus shell length (the predictor) was significant in terms of explaining the response (other shell dimensions).

Burnupena cincta, *B. lagenaria* and *B. pubescens* reach larger sizes than *Peristernia forskalii*, *Morula granulata* or *M. nodosa* (Figure 4.8). When compared to the *Burnupena* spp., *Morula granulata*, *M. nodosa* and *P. forskalii* show comparatively poor relationships between aperture width and shell length, as indicated by the low coefficients of determination (Table 4.5). These three species also show lower coefficients of variation for the relationships of shell width mass and volume to shell length than those of the *Burnupena* spp., indicating that they are more morphologically variable than the *Burnupena* spp. (Table 4.5). For almost all combinations of shell dimensions for the six most commonly used shells, the intercepts of regressions of shell width, aperture width, mass and volume against shell length vary by locality (Table 4.6). The only exception is *Burnupena pubescens*, where shell volumes regressed against shell lengths show no significant differences

in either slope or intercept among localities. Differences in the slopes of the regressions i.e. the rate of change of shell dimensions in relation to shell length, show no clear trend among shell types.

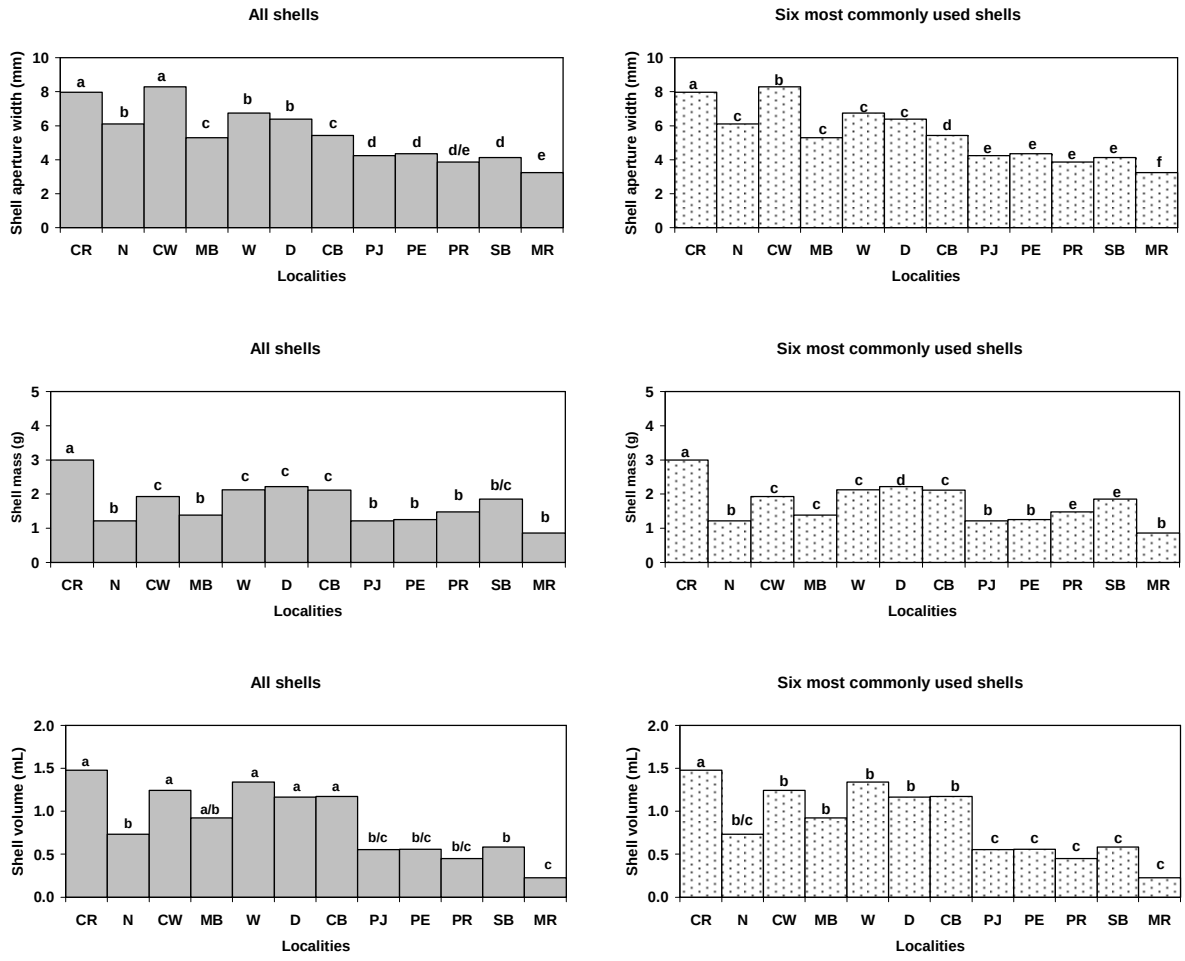

Figure 4.7: Aperture widths and shell volumes decrease in size from southern to northern localities. The trend is still present but less marked for shell mass. Nahoon and Morgan Bay show smaller shell dimensions than surrounding southern localities, but the northern localities show similar shell dimensions. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

Table 4.5: Relationships between shell length and other shell dimensions for the six most commonly used shells. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slope	Intercept	r^2	DF	RSE	F	P
Burnupena lagenaria							
Width (mm) by length (mm)	0.529	-0.044	0.92	401	0.656	4977	P<0.001
Aperture width (mm) by length (mm)	0.305	-0.534	0.87	401	0.051	2774	P<0.001
Mass (g) by length (mm)*	2.947	-8.792	0.91	401	0.174	4044	P<0.001
Volume (mL) by length (mm)*	2.913	-9.396	0.95	381	0.126	6619	P<0.001
Volume (mL) by mass (g)	0.913	-0.665	0.88	381	0.186	2816	P<0.001
Burnupena cincta							
Width (mm) by length (mm)	0.401	1.824	0.94	185	0.773	2866	P<0.001
Aperture width (mm) by length (mm)	0.221	0.176	0.92	185	0.443	2150	P<0.001
Mass (g) by length (mm)*	2.732	-8.508	0.93	185	0.175	2669	P<0.001
Volume (mL) by length (mm)*	2.712	-8.956	0.94	134	0.159	2294	P<0.001
Volume (mL) by mass (g)	0.972	-0.492	0.92	134	0.191	1563	P<0.001
Burnupena pubescens							
Width (mm) by length (mm)	0.402	1.300	0.93	235	0.559	2913	P<0.001
Aperture width (mm) by length (mm)	0.196	0.452	0.92	235	0.290	2572	P<0.001
Mass (g) by length (mm)*	2.753	-8.662	0.92	235	0.157	2835	P<0.001
Volume (mL) by length (mm)*	2.742	-9.183	0.96	144	0.112	3637	P<0.001
Volume (mL) by mass (g)	0.946	-0.540	0.92	144	0.160	1702	P<0.001
Morula granulata							
Width (mm) by length (mm)	0.770	0.096	0.74	364	0.062	1049	P<0.001
Aperture width (mm) by length (mm)	0.565	-0.535	0.25	364	0.131	125	P<0.001
Mass (g) by length (mm)*	2.605	-7.320	0.83	364	0.158	1823	P<0.001
Volume (mL) by length (mm)*	2.455	-8.403	0.79	223	0.149	823	P<0.001
Volume (mL) by mass (g)	0.827	-1.483	0.76	223	0.156	725	P<0.001
***Morula* nodosa**							
Width (mm) by length (mm)	0.910	-0.399	0.83	145	0.054	724	P<0.001
Aperture width (mm) by length (mm)	0.874	-1.218	0.45	145	0.125	123	P<0.001
Mass (g) by length (mm)*	2.949	-8.521	0.90	145	0.123	1447	P<0.001
Volume (mL) by length (mm)*	2.813	-9.588	0.81	88	0.814	386	P<0.001
Volume (mL) by mass (g)	0.888	-1.462	0.82	88	0.142	404	P<0.001
Peristernia forskalii							
Width (mm) by length (mm)	0.707	0.069	0.72	247	0.049	651	P<0.001
Aperture width (mm) by length (mm)	0.841	-1.246	0.59	247	0.079	358	P<0.001
Mass (g) by length (mm)*	2.170	-6.699	0.72	247	0.152	634	P<0.001
Volume (mL) by length (mm)*	2.790	-9.829	0.79	51	0.178	195	P<0.001
Volume (mL) by mass (g)	1.070	-1.311	0.70	51	0.212	122	P<0.001

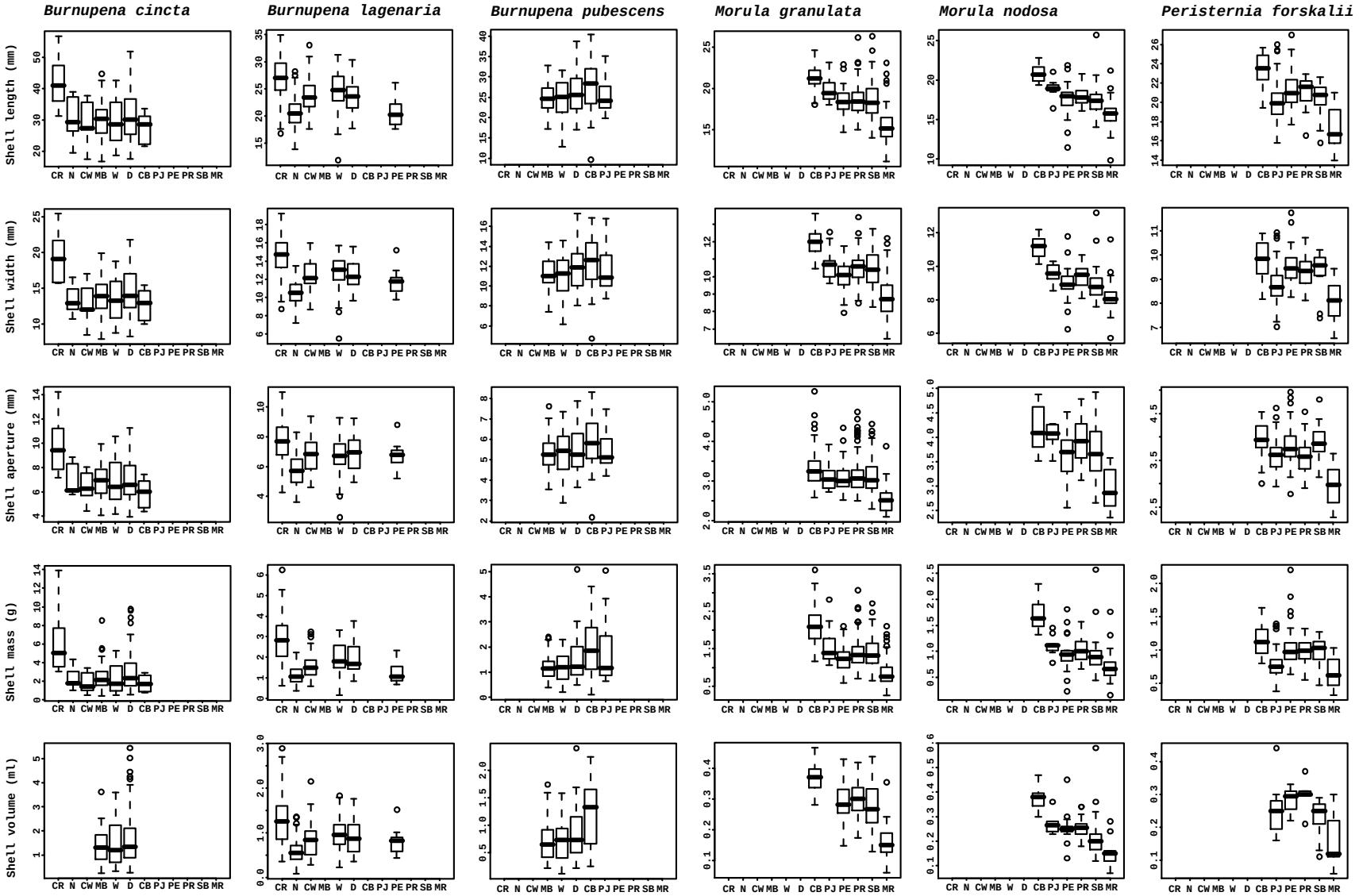

Figure 4.8: Shell dimensions for the six most commonly used shells across all localities at which they occurred. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

Table 4.6: Analysis of covariance of shell dimensions by locality for the six most commonly used shell types. Regressions lines for shell dimensions regressed against shell length are compared by locality to determine whether the relationships differ among localities. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	DF	F	P
Burnupena lagenaria					
Width (mm) by length (mm)	Differ	Differ	5 on 391	3.837	P=0.002
Aperture width (mm) by length (mm)	Do not differ	Differ	5 on 396	18.994	P<0.001
Mass (g) by length (mm)*	Differ	Differ	5 on 391	4.821	P<0.001
Volume (mL) by length (mm)*	Differ	Differ	5 on 373	2.273	P=0.046
Volume (mL) by mass (g)	Differ	Differ	5 on 373	4.162	P=0.001
Burnupena cincta					
Width (mm) by length (mm)	Do not differ	Differ	6 on 179	3.200	P=0.005
Aperture width (mm) by length (mm)	Differ	Differ	6 on 173	4.633	P<0.001
Mass (g) by length (mm)*	Do not differ	Differ	6 on 179	6.091	P<0.001
Volume (mL) by length (mm)*	Differ	Differ	2 on 117	3.705	P=0.027
Volume (mL) by mass (g)	Differ	Differ	2 on 117	11.043	P<0.001
Burnupena pubescens					
Width (mm) by length (mm)	Differ	Differ	4 on 227	2.844	P=0.025
Aperture width (mm) by length (mm)	Do not differ	Differ	4 on 231	2.578	P=0.038
Mass (g) by length (mm)*	Differ	Differ	4 on 227	9.535	P<0.001
Volume (mL) by length (mm)*	Do not differ	Do not differ	3 on 137	0.037	P=0.991
Volume (mL) by mass (g)	Differ	Differ	3 on 134	4.724	P=0.003
Morula granulata					
Width (mm) by length (mm)	Differ	Differ	5 on 354	3.363	P=0.005
Aperture width (mm) by length (mm)	Do not differ	Differ	5 on 359	5.685	P<0.001
Mass (g) by length (mm)*	Do not differ	Differ	5 on 359	6.696	P<0.001
Volume (mL) by length (mm)*	Do not differ	Differ	4 on 220	18.360	P<0.001
Volume (mL) by mass (g)	Differ	Differ	4 on 216	2.904	P=0.023
***Morula* nodosa**					
Width (mm) by length (mm)	Do not differ	Differ	5 on 140	7.123	P<0.001
Aperture width (mm) by length (mm)	Do not differ	Differ	5 on 140	7.447	P<0.001
Mass (g) by length (mm)*	Do not differ	Differ	5 on 140	9.258	P<0.001
Volume (mL) by length (mm)*	Differ	Differ	5 on 81	3.479	P=0.006
Volume (mL) by mass (g)	Differ	Differ	5 on 81	3.034	P=0.014
Peristernia forskalii					
Width (mm) by length (mm)	Do not differ	Differ	5 on 242	9.727	P<0.001
Aperture width (mm) by length (mm)	Do not differ	Differ	5 on 242	9.498	P<0.001
Mass (g) by length (mm)*	Do not differ	Differ	5 on 242	15.016	P<0.001
Volume (mL) by length (mm)*	Do not differ	Differ	4 on 47	2.595	P=0.048
Volume (mL) by mass (g)	Do not differ	Differ	4 on 47	3.906	P=0.008

There is a general increase in the mass-to-volume ratio from south to north (Figure 4.9), which indicates that shells offer less internal volume for the same unit of mass and have thicker walls from south to north. This general picture is in part explained by the change in the shell types used by hermit crabs as one moves from south to north (Figure 4.2). The change in mass-to-volume ratio, as explained by change in species composition, is seen even more clearly if one examines the regressions of mass against volume for the six most commonly used shell types. *Burnupena cincta*,

B. lagenaria and *B. pubescens* have higher volumes per unit mass than *Peristernia forskalii*, *Morula granulata* or *M. nodosa* (Figure 4.10).

When the relationships of mass-to-volume for each species are tested by locality (Table 4.6), it can be seen that for almost all shell types both the slopes and intercepts of regressions of mass against volume differ by locality, indicating that the form of growth within a shell type is different among localities. *P. forskalii* is the only exception where only the intercepts of the regressions differ by locality, while the slopes of the relationships do not differ. While the volumes of *P. forskalii* differ at different localities, the parallel slopes indicate that the form of growth, or the way in which volume increases with mass is the same at all localities. Upon closer examination of the regressions by locality, no clear trend emerges of steeper slopes in southern localities compared to northern localities (Figure 4.11).

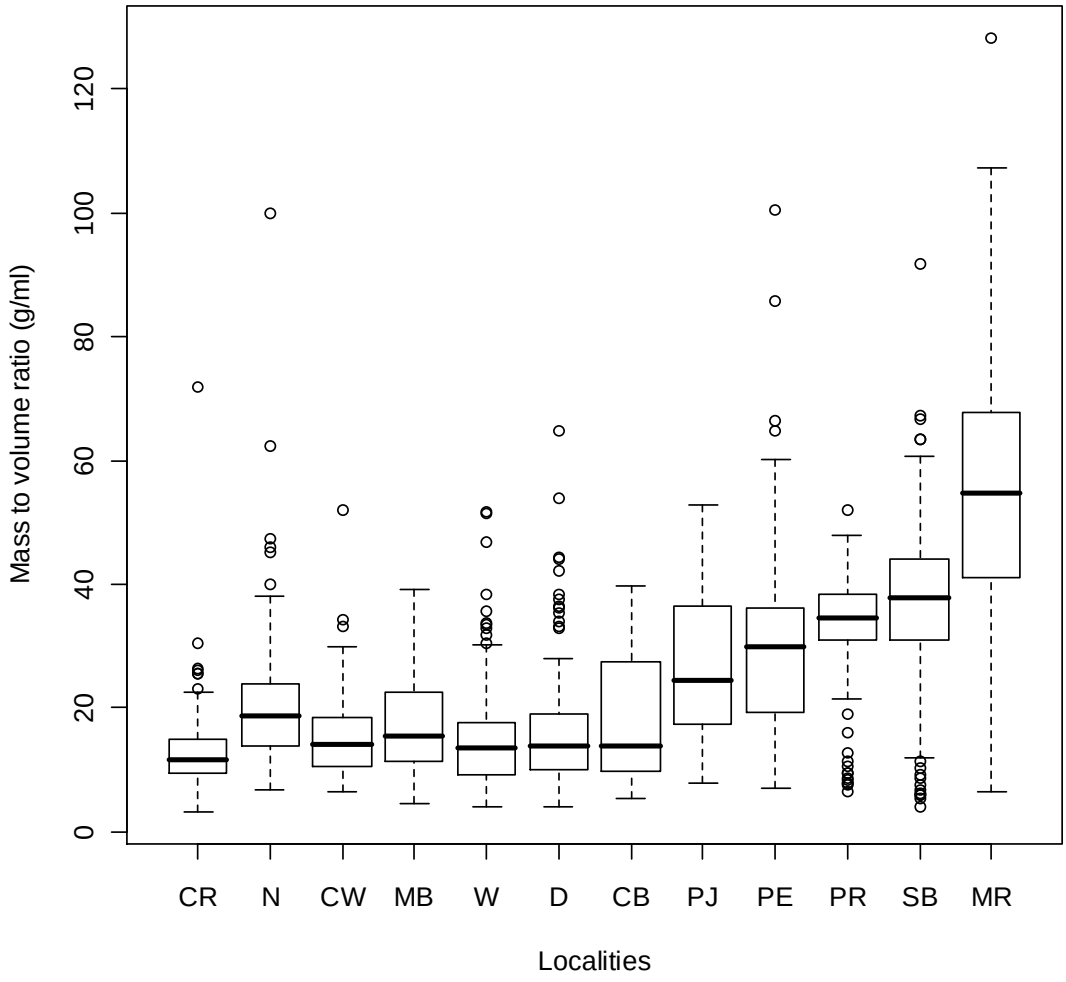

Figure 4.9: The mass-to-volume ratios of all shells used at each locality. Generally there seems to be a trend of increasing mass-to-volume ratio from southern to northern localities. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

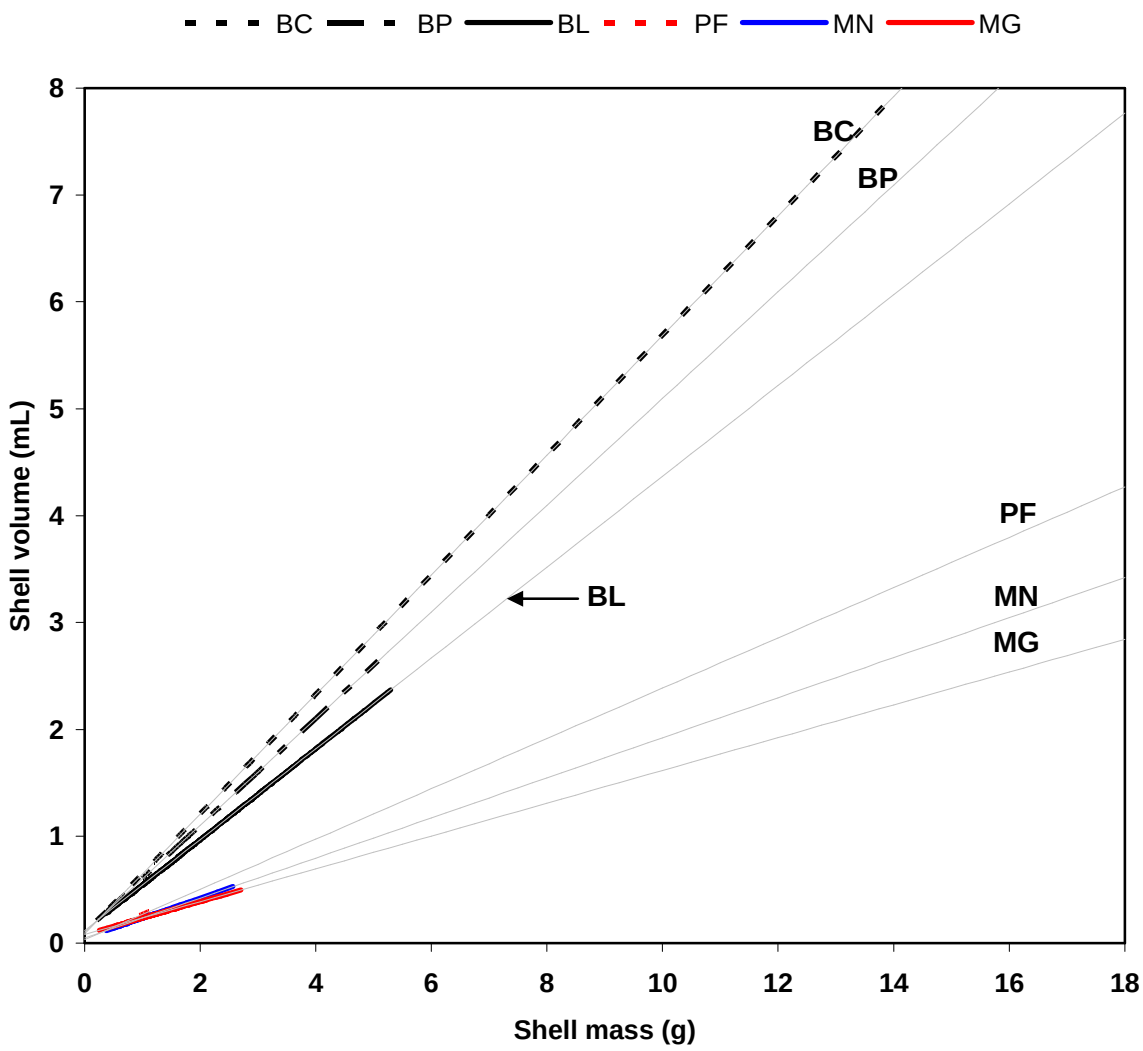

Figure 4.10: The regressions of mass against volume for the six most commonly used shells group clearly into the *Burnupena* spp. and *Morula* spp. and *Peristernia forskalii*. The steepest line is that of *Burnupena cincta* (BC) followed in order by *B. pubescens* (BP) and *B. lagenaria* (BL). Of the lower three lines *P. forskalii* (PF) has the steepest slope, followed by *M. nodosa* (MN) and then by *M. granulata* (MG) with the lowest volume per unit mass. The light grey lines are extrapolations of the relationships.

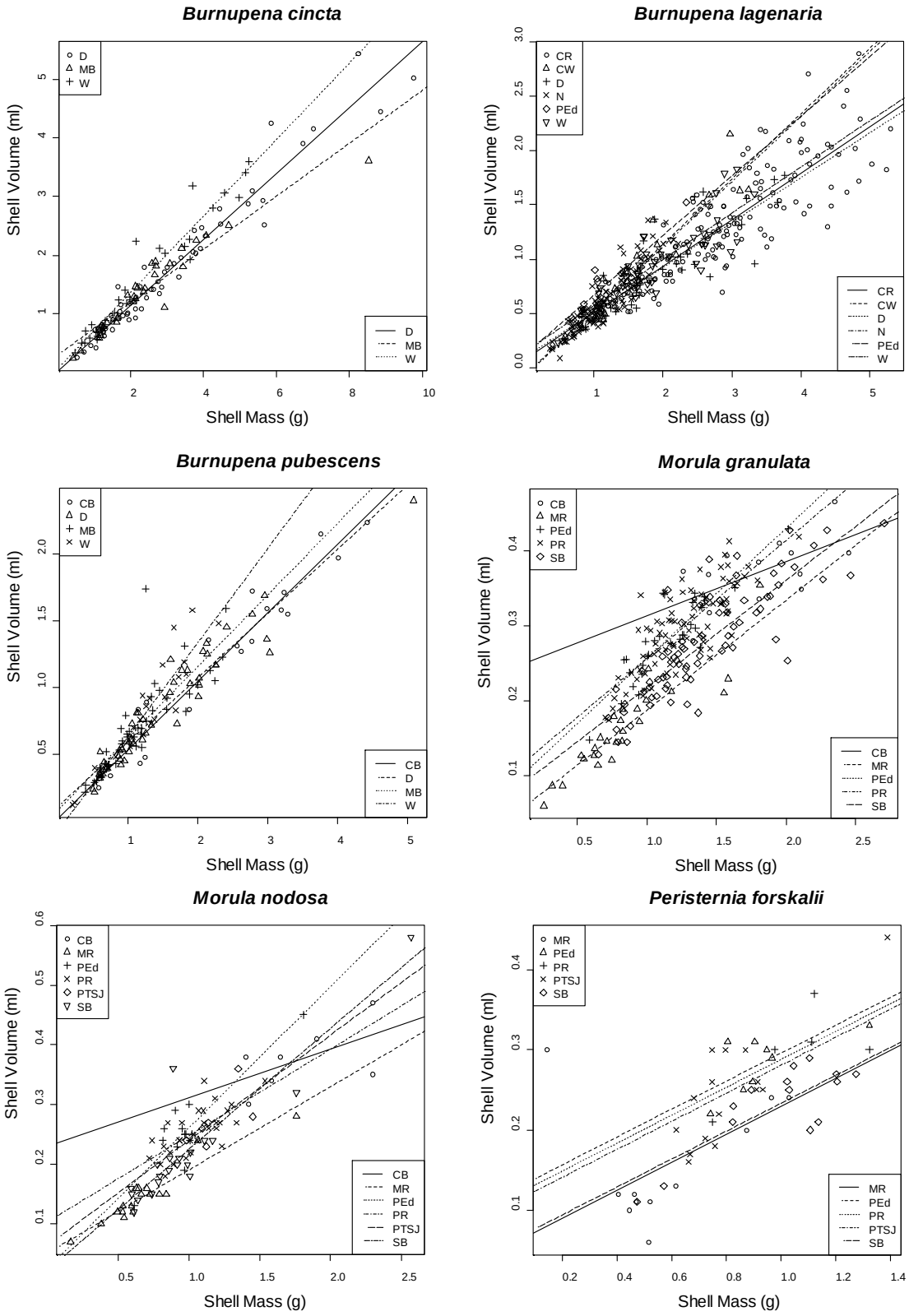

Figure 4.11: The regressions of shell volume against shell mass by locality show lines with differing slopes and intercepts for all shell types but *Peristernia forskalii*, where only the intercepts differ. There is no clear intraspecific trend of increasing mass-to-volume ratio from southern localities to northern localities. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

There is a decrease in aperture width from southern to northern localities when looking at data for all shells (Figure 4.6). Again, this general trend could be a reflection of the change in species composition from south to north (Figure 4.2). When comparing the aperture widths of the six most commonly used shells by locality, it can be seen that aperture width seems to show a different pattern to other shell dimensions (Table 4.5) as, for all species but *Burnupena cincta*, only the intercepts of the regressions lines of aperture width against length differ while the slopes remain the same. There is no clear trend of an intraspecific decrease in aperture size as a function of shell length from south to north (Figure 4.12), although the absolute sizes of the apertures seem to show this pattern for *Burnupena cincta* and *Morula* spp. (Figure 4.8).

There is no clear trend of damage type with decreasing latitude (Figure 4.12). Shells at all sites suffer some shell peeling and apex crushing damage and when analysing the frequency of lip breakage and apex damage, damage is not independent of locality ($G = 106.2$, $DF = 11$, $P < 0.001$). Shells at Park Rynie suffer slightly more apex crushing damage compared to peeling damage than at other localities, which show more peeling damage than crushing damage. Shells at Wavecrest suffer the least predator-inflicted damage, while those at Mission Rocks suffer the most damage by predators. Lip breakage and apex crushing damage are not independent of shell type for the six most commonly used types ($G = 50.7$, $DF = 7$, $P < 0.001$). A clear trend emerges when comparing these shell types (Figure 4.14). *Burnupena* spp. suffers a higher rate of peeling damage than *Morula* spp. or *Peristernia forskalii*. *Burnupena* spp. have larger apertures (Figure 4.8) and thinner shells as indicated by the relationship of mass-to-volume (Figure 4.9), which make them vulnerable to peeling predators.

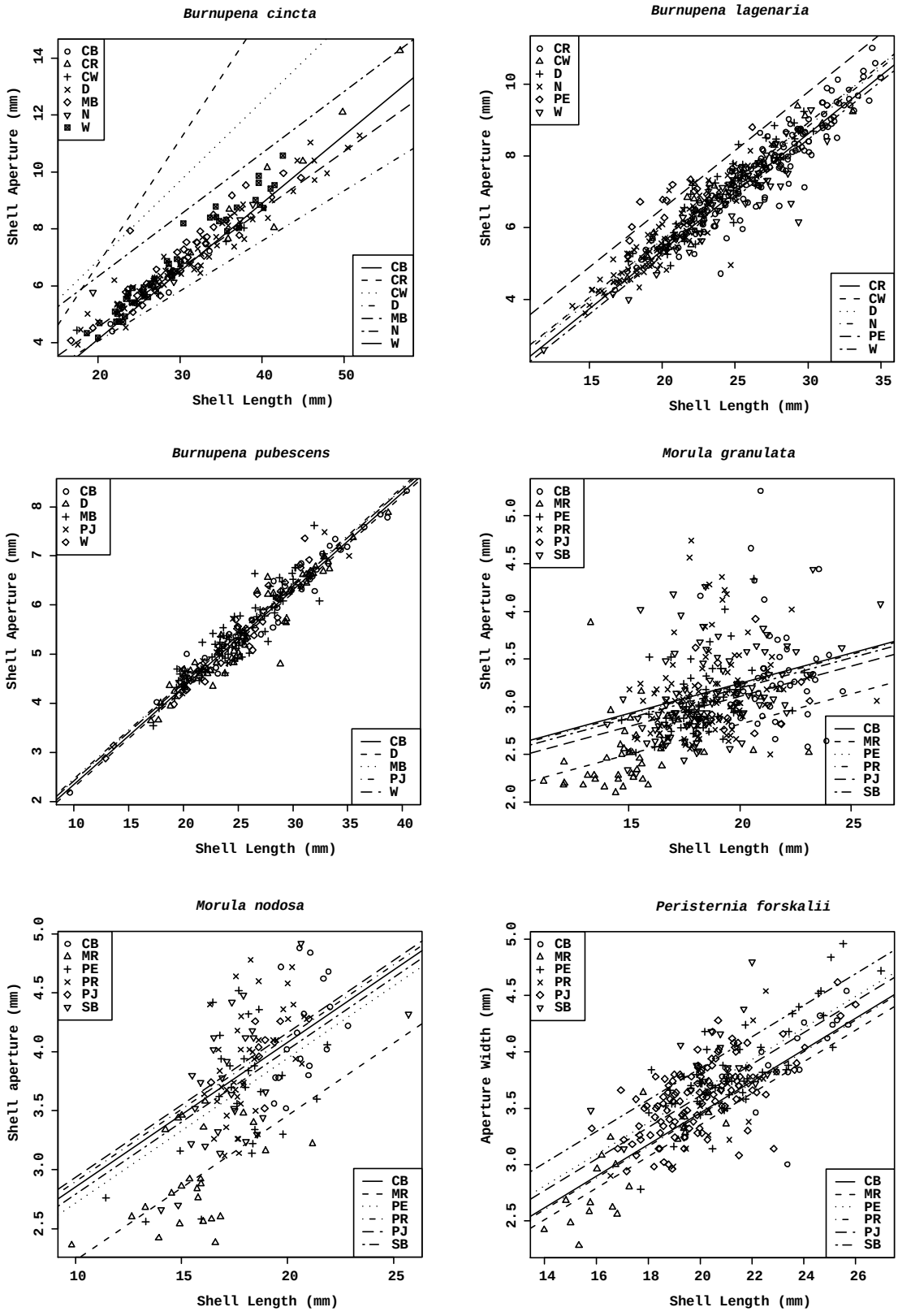

Figure 4.12: The regressions of shell aperture width against shell length by locality show lines with differing intercepts for all shell types but *Burnupena cincta*, where both the intercepts and the slopes differ. From south to north the localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

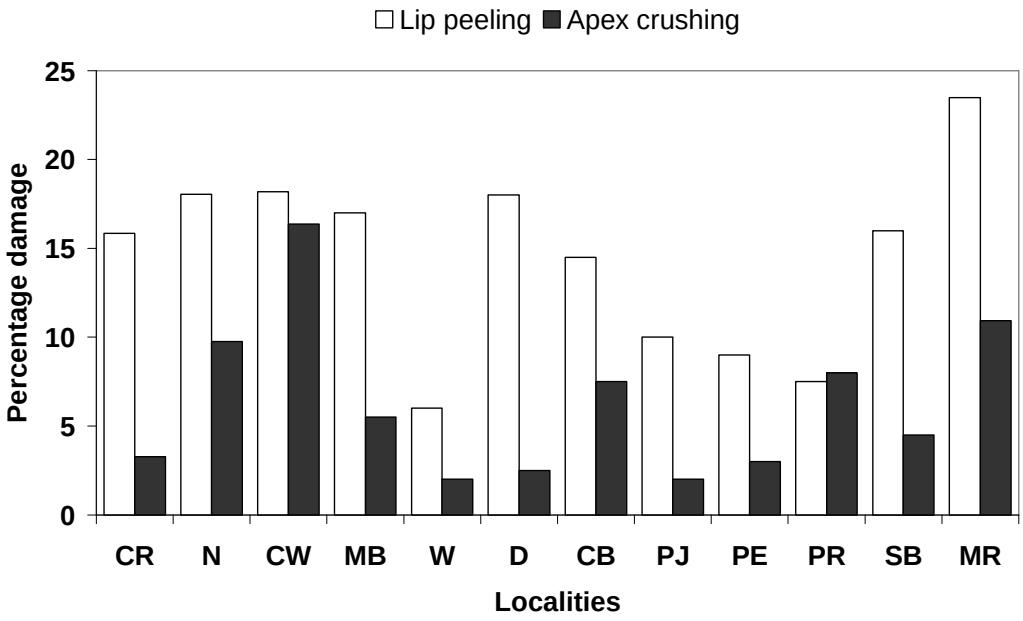

Figure 4.13: Shell peeling and apex crushing damage show no clear trend across localities. Shells from Wavecrest (W) show the least damage, while those from Mission Rocks (MR) show the most damage that can be attributed to predators. The localities are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

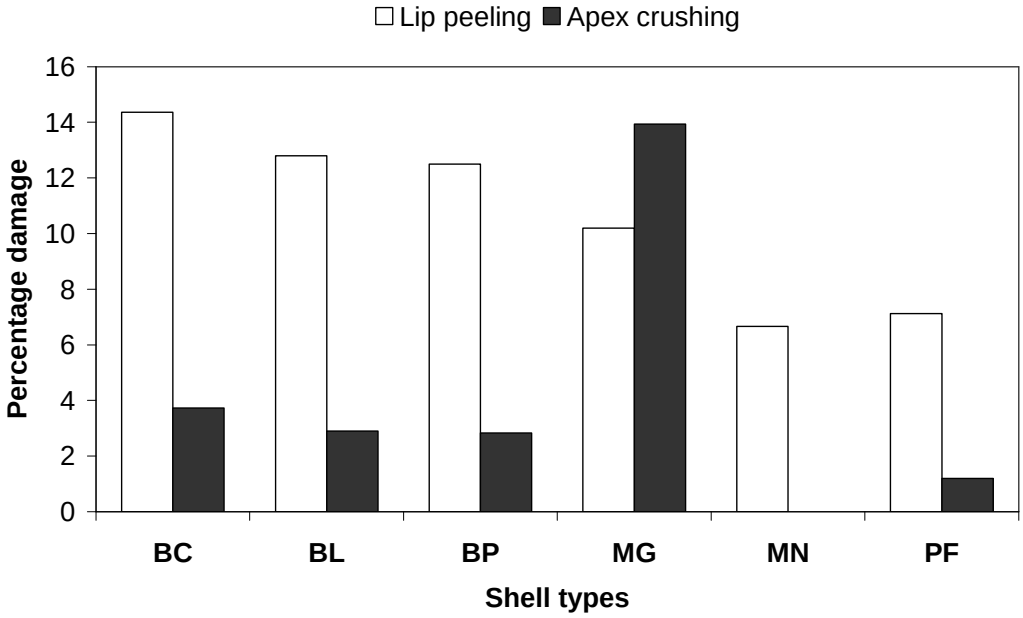

Figure 4.14: *Burnupena cincta* (BC), *B. lagenaria* (BL) and *B. pubescens* (BP) show more lip peeling than *Morula granulata* (MG), *M. nodosa* (MN) and *Peristernia forskalii* (PF). The last three species may be modified against such predation by virtue of their smaller apertures and thicker shells compared to the *Burnupena* spp. *Morula granulata* often shows irregularly shaped shells that may make it more vulnerable to apex crushing damage.

4.4 Discussion

In this study 2281 *Clibanarius virescens* used 75 shell types across the 12 localities sampled, and the highest number of shell types used at a single site was 25 shell types. *Clibanarius virescens* is dependent on intertidal shells as most of the shell types used were from intertidal gastropod species. When compared to other studies of shell use by *C. virescens* (Reddy and Biseswar 1993, Nakin and Somers 2007), a few similarities are apparent. Reddy and Biseswar (1993) found that 400 *C. virescens* used 23 gastropod species at 2 sites, probably Park Rynie and Isipingo Beach, near Durban (Biseswar pers. com.). Nakin and Somers (2007) recorded 11 shell types used by 193 *C. virescens* at Dwesa. In this study, 200 *C. virescens* used 15 shell types at Park Rynie, while 22 shell types were used by 200 hermit crabs at Dwesa. In this study there were 12 shell types in common with Reddy and Biseswar's research at Park Rynie, and 8 shell types in common with Nakin and Somers' study at Dwesa. It appears that the diversity data for these three studies are somewhat comparable, but allowances must be made for differences in annual and seasonal weather patterns that make shells available to hermit crabs. Although the number of shell types used by *C. virescens* may vary, the nature of the resource available at a given locality remains roughly stable. At Quirimba Island in Mozambique, *C. virescens* uses 18 shell types (Barnes 1999) while in Japan, Imazu and Asakura (1994) note that *C. virescens* uses more shell types (33 types) than co-occurring hermit crabs. It can be concluded that shell use by *C. virescens* in this study is not atypical, and that the species tends to use a large variety of shell types when these are available. *C. virescens* uses some shell types disproportionately to their availability (Nakin and Somers 2007), which seems to indicate that *C. virescens* has preferences, although these may be less stringent than in other species of hermit crab.

Barnes' (2003) findings that *C. virescens* uses fewer shell types with increasing latitude does seem to be supported by the trend in diversity indices for this study, although the trends found here are not statistically significant. Very generally, fewer shell types are used at high latitudes than at lower latitudes, but the lack of a clear pattern may be due to the changes in gastropod species composition between biogeographic provinces. In Barnes' (2003) study, region emerged as one of the most important influences on the variability in hermit crab shell use, but he concedes that the relationships between resource and resource users have many complexities and may elude simple answers.

The localities sampled in this study can be grouped into two main regions based on shell resource use by hermit crabs, with a zone of overlap occurring between them. The suite of shells used by hermit crabs may be a better representation of the shells available at a locality than a "snapshot" sample of empty shells available on a beach, as hermit crabs may preserve shells that have a short retention time in the intertidal zone (Spight 1977). This representation of the resource available is tempered by hermit crab preferences. Nevertheless it has been established that *C. virescens* uses a larger range of shell types than most other mid-littoral hermit crab species (Imazu and Asakura 1994), and this makes the shells in used by *C. virescens* a good reflection of the resource available.

Based on shell use patterns, the first main region to emerge includes Cape Recife, Nahoon Beach, Cintsa West Beach, Morgan Bay and Wavecrest. These southern localities are characterised by the high proportion of use of *Burnupena* spp. The second clear group to emerge include the northern localities of Port Edward, Park Rynie, Sheffield Beach and Mission Rocks. These sites are characterised by the

high proportion of use of *Morula* spp. The transition zone includes Dwesa, Coffee Bay and Port St Johns. These localities show affinities with the northern localities as *Morula* spp. are used, but also with the southern localities as some use is made of *Burnupena* spp. Coffee Bay and Port St Johns group together because of a high proportion of use of *Peristernia forskalii*. The southern grouping agrees with the regions proposed by Bustamante and Branch (1996), who suggest that a break between the south coast and east coast regions occurs somewhere between Dwesa and Balito Bay. Shell use patterns in this study indicate that a change occurs at Dwesa, but it seems that the northern break occurs south of Balito Bay, between Port Edward and Park Rynie, which is closer to the break at Durban as suggested by Emanuel *et al.* (1992).

In describing the morphological relationships and shell dimensions of the shell resource it immediately becomes apparent that the resource groups into high-spired shells and low-spired shells. Hermit crabs use more high-spired shells than low-spired shells in this study as well as in the studies of Reddy and Biseswar (1993) and Nakin and Somers (2007). This study classifies high-spired shells differently to the classification used in Nakin and Somers (2007), but the system used in this study is supported by and reflects the patterns that occur in the data. It is predictable that shell dimensions correlate well for grouped data and correlate better within single shell types. Gastropods are commonly recognised and classified on the appearance of their shells, and for most species the relationships between shell dimensions can be expected to remain constant within a species. Shell length generally shows a linear relationship to shell width and to aperture, while mass and volume show an allometric relationship to length. This pattern is repeated for *Burnupena* spp., but deviates for *Morula* spp. and *Peristernia forskalii*. Kilburn and Rippey (1982) state

that *M. granulata* shells are often eroded and malformed and that members of the Family Muricidae are known for their variable shells. This was apparent in the shells used by crabs in this study, as *Morula* spp. showed weaker relationships between shell dimensions than *Burnupena* spp.

It was predicted that the shells making up the resource would decrease in size, display higher mass-to-volume ratios and would have smaller apertures with decreasing latitude. These predictions have been confirmed by the grouped data for all shell types. The shell resource does change with decreasing latitude. These changes are caused by changes in gastropod species composition with latitude. *Burnupena* spp., dominantly used in the southern localities, are generally much larger than the suite of shells, including *Morula* spp. and Peristernia forskalli, used in the northern localities.

The question was asked whether the six most commonly used shell types exhibited sufficient morphological plasticity to adapt their shell dimensions to the change in environment, both biotic and abiotic, associated with decreasing latitude. To answer this question, the six most commonly used species were analysed to see whether shell dimensions showed any significant differences among localities. The shell dimensions of all six shell types did show statistical differences among localities, but the nature of the differences did not reflect the expected trend. There was no adaptive trend that matched the change in latitude, i.e., shells of single species did not become smaller, increase their mass-to-volume ratio or decrease their aperture size with a decrease in latitude.

This means that either the sample sizes were too small to adequately represent the variation in the gastropod population, or that hermit crab shell use did not represent the gastropod population, or that gastropods adapt closely to local conditions, which may not always agree with larger regional trends. It must be concluded that large-scale morphological changes in the shell resource with latitude depend on changes in the gastropod species composition rather than on morphological plasticity within gastropod species.

Changes in mass-to-volume ratio and aperture size are in part adaptations to increased predation by shell peeling predators such as large decapod crustaceans. No clear latitudinal trend emerged for the expected increase in shell damage with decreasing latitude, but this may be precisely because shells further north are better adapted to the expected increase in predation by shell peeling and apex crushing predators. All of the three most commonly used species at northern localities inhabit the upper to mid-tidal range, making them less accessible to decapod predators. All three species also have small apertures and thick shells as evinced by their high mass-to-volume ratios. All three northern shell types showed lower proportions of lip peeling damage than *Burnupena* spp. *Morula granulata* shows a high proportion of apex crushing damage, and this may be directly related to irregular shell morphology, which could make it more vulnerable to apex crushing predators.

The changes in shell size, mass-to-volume ratio, and aperture size, as well as types of shell damage all have implications for *C. virescens* and will affect its population structure and reproduction. These changes will be discussed in the following chapters.

Chapter 5: Effects of the shell resource on population structure

5.1. Introduction

The shells used by hermit crabs constitute a resource that is not consumed, is used temporarily (Spight 1985), and cannot be substantially modified by the crabs themselves (LaBarbera and Merz 1992), except by the addition or encouragement of epibionts (McLean 1983). By carrying a shell, hermit crabs obtain a mobile microclimate that ensures their survival in the intertidal zone (Reese 1969). Mobility is important as it allows them to distribute themselves spatially and temporally to avoid extremes in temperature, wave action, osmotic changes and, to some degree, to avoid predation. When mobility is limited, the shell as microclimate still offers shelter from desiccation and thermal stress (Bertness 1981b) and osmotic changes (Pechenick *et al.* 2001). The use of shells has allowed hermit crabs to successfully exploit the intertidal zone and to become one of the most conspicuous groups of organisms on temperate rocky littoral environments, on reef flats and in mangrove swamps (Reese 1969). From the point of view of the researcher, shells represent a discrete and easily quantifiable resource (Lively 1988).

There is consensus that shell types available to hermit crabs shape their populations. Reese (1969) regarded hermit crabs as forming a guild of shell-users within benthic communities and proposed that shell use is important in the social structures of hermit populations as shell availability might constrain the maximum size, and thus sex ratio for dimorphic species. This has been confirmed in subsequent work by several authors (for example, Harvey 1990, Wada 1999, Turra and Leite 2000). The availability and suitability of available shells affects hermit crab population size

(Vance 1972, Spight 1977), growth (Fotheringham 1976b, Bertness and Cunningham 1981, Blackstone 1985, Wada *et al.* 1997, Osorno *et al.* 1998, Turra and Leite 2003), reproduction in both males (Hazlett 1989) and females (Elwood *et al.* 1995, Hazlett *et al.* 2005), larval release (Ziegler and Forward 2006) and recruitment (Worcester and Gaines 1997).

This chapter attempts the first exploration of the effect of shell resource on population size-structure of a single species of hermit crab across biogeographical provinces in South Africa. Despite the wealth of literature available on comparisons of population biology of geographically sympatric species of hermit crab at a single site (Reese 1968, Reddy and Biseswar 1993, Floeter *et al.* 2000, Turra and Leite 2000, 2001b, 2004, Wada *et al.* 2000, 2005, Turra and Denadai 2002, Turra 2003, Macpherson and Raventos 2004, Oba and Goshima 2004, Sant'Anna *et al.* 2006, Oba *et al.* 2008), comparisons of a single species across several sites are less common (Leite *et al.* 1998, Botelho and Costa 2000, Benvenuto and Gherardi 2001, Nakin and Somers 2007, Mantelatto *et al.* 2010). Comparisons of any aspect of the biology of hermit crabs among several geographically distant localities are rare (Blackstone 1985, 1989, Young *et al.* 2002).

Blackstone (1985) tested the "moulding hypothesis" that hermit crabs adapt their morphology to that of the shells available to them. He sampled crabs from four localities ranging from Massachusetts to South Carolina. He concentrated mainly on how allometric growth of chelipeds in males and females is affected by shell type, but also mentions changes in body size. Both crab shield length and shell size (calculated as ½(length + width)) increased from south to north, with smaller crabs and shells in warmer areas and larger crabs in more temperate localities. From field

data he concluded that although shell type can have a profound effect on morphology in *Pagurus longicarpus*, morphological differences between different populations are more likely to have a genetic basis than an environmental one. He also reared crabs in low-spired and high-spired shells and found that crabs in large, low-spired shells attained larger sizes than those in high-spired shells. Blackstone (1989) also examined two subspecies of *Pagurus hirsutiusculus* at seven localities ranging from Alaska to southern California to test whether carcinization, size of crabs and reduced shell-living differed between the two subspecies. He found that the northern crabs, particularly males, were larger, more carcinized and made use of smaller shells that protected proportionally less of the body, that these changes were possibly due to environmental influence and that carcinization was favoured at high northern latitudes.

Young *et al.* (2002) compared nine populations of *Pagurus longicarpus* from the Gulf of Mexico and the Atlantic seaboard of the USA in order to determine whether small morphological differences between the Gulf of Mexico populations and Atlantic populations might have been due to major vicariance events separating populations, as had been found for a variety of marine taxa with similar distributions. They concluded that the northern populations may have survived in distinct refugia during the last glacial maximum, explaining the genetic divergence between the northern and southern populations.

Of more relevance to this study is the recent work of Mantelatto *et al.* (2010) in which they compare population traits between geographically distant populations of *Clibanarius vittatus* in Brazil. Although only two localities are sampled they are separated by 21 degrees of latitude and comprise a tropical locality (02°05’ 12.5” S,

41°35’ 19.0” W) and a sub-tropical locality (23°4 8’ 78.1” S, 45°24’ 46.9” W). Fewer shell types were used at the lower latitude (6) than at the higher latitude (9). They noted sexual size dimorphism in both populations, with males becoming larger than females. They also noted that the frequency of shell use differed between males and females at both localities. At the northern locality ovigerous and non-ovigerous females did not differ in size, but in the southern locality ovigerous females were significantly smaller than non-ovigerous ones. At the northern locality, the ratio of females to males did not depart from a 1:1 ratio, while at the southern locality males significantly outnumbered females. Mantelatto *et al.* (2010) note that the southern locality in their study is situated at a biogeographical border between tropical and temperate zones. Unfortunately the gastropod populations in these areas, and thus the shell resources available to hermit crabs, are poorly studied.

Other studies comparing a single crab species over two or more localities tend to either be geographically small-scale studies, with sampling localities less than a degree of latitude apart, or compare only two populations. This study is comparable to that of Blackstone (1985) as he describes a gradient of change in the population in one species of hermit crab over several degrees of latitude. A gradient of change may also be observed in South Africa as the range of *Clibanarius virescens* encompasses two biogeographic provinces and the transition zone between them.

The localities in this study can be grouped according to the shell suites used by *C. virescens* in different areas (see Chapter 4). While Chapter 4 describes in detail shell-use patterns and shell morphology at the 12 localities studied, this chapter will determine what shell types are used by different crab size groups and sexes. It is hypothesised that crab population size-structure will follow the shell size trends and

that the northern and southern localities identified in Chapter 4 will show clear differences in crab population size-structure. The use of damaged shells by different crab size classes and sexes will be described. The crab populations at each locality will be described in terms of population size-structure, changes in size structure between localities, sexual size dimorphism and the ratio of males to females. The proportion of damaged crabs for different localities and sexes will be determined.

5.2. Methods

Sampling localities, collection methods and laboratory analyses are described in Chapter 2. Only crabs sampled between 31 December 2000 and 28 January 2001 at Cape Recife were used to avoid greatly uneven sample sizes among localities. Shell morphometric parameters for the six most commonly used shell types were obtained and described in Chapter 4. Twelve shell types were included for discussion in this chapter and only pertinent analyses on the additional shell types were included. Not all of the additional shell types are included in statistical analyses owing to small sample sizes.

Shell volume was related to shell mass by linear regression for the 10 most commonly used shell types. These relationships were compared using analysis of covariance with shell type as the covariate. This analysis determined whether there were significant differences in the volume-to-mass relationship among the shell types. Frequency of shell use was compared graphically within different size classes, sexes and female reproductive states (ovigerous and non-ovigerous). The frequency of shell use by size class or could not be compared statistically among all localities because non-overlapping use of shell types among localities led to “missing data” within a contingency table when using a log-likelihood ratio test (G test). Shell types could not be sensibly coded into smaller groups to make up for the missing data.

Shell damage was examined by size class, sex and female reproductive state. Log-likelihood ratio tests (G tests) were used to determine whether sex, female reproductive state (ovigerous or non-ovigerous) and size class were independent of each other in terms of the frequency of damage type.

Crab dimensions (shield length and dry mass) were regressed against shell dimensions (length, width, aperture width, mass and volume) to determine which shell dimension related best to either shield length or dry mass.

Average crab dimensions (shield length and mass) with standard errors were determined for crab groupings (all crabs, males, all females, ovigerous females, non-ovigerous females and BS non-ovigerous females) at each locality. Whether differences in mean crab shield lengths among localities existed was determined by analysis of variance. *Post hoc* analysis using Tukey's honest significant difference (HSD) was conducted to pin-point how average shield lengths differed among localities. Local differences in the relationship of shield length to dry mass were determined by running ANCOVA with locality as the covariate factor.

Log-likelihood ratio (G test) tests were used to determine whether sex was independent of locality in the populations sampled. The sex ratios for individual localities were compared using chi-squared goodness of fit to determine whether the sex ratio departed from a 1:1 relationship. Sex ratios for each size class were compared graphically at each locality to determine the pattern.

5.3. Results

This section is divided into two parts. The first part deals with shell use and shell damage patterns by different crab groups at different localities. The second part describes the crab population structure.

In Chapter 4 the six most commonly used shell types were analysed for morphological relationships across the 12 localities sampled. The six most commonly used shell types were *Burnupena lagenaria* (18.1%), *Morula granulata* (16.4%), *Peristernia forskalii* (11.1%), *Burnupena pubescens* (10.9%), *Burnupena cincta* (8.2%) and *Morula nodosa* (6.6%). In this chapter, the use of 12 shell types by *C. virescens* will briefly be discussed (Table 5.1) in order to better relate shell use to crab population parameters. The additional six shell types increase the representation of shell types used by juveniles and males. Of the six most commonly used shell types, *Morula granulata*, *M. nodosa* and *Peristernia forskalii* are predominantly used by females, and in the greatest proportion by ovigerous females (Figure 5.1). These shells also have the lowest volume-to-mass ratios of the 12 shells types commonly used (Figure 5.2).

Table 5.1: Numbers and proportional usage of the 12 most commonly used shell types across all localities.

Shell type	***n***	**Percentage of total shell use**
Burnupena lagenaria	414	18.1
Morula granulata	373	16.4
Peristernia forskalii	253	11.1
Burnupena pubescens	248	10.9
Burnupena cincta	188	8.2
Morula nodosa	150	6.6
Thais capensis	75	3.3
Diloma spp.	61	2.7
Turbo cidaris	59	2.6
Trochus nigropunctatus	23	1.0
Nodilittorina spp.	19	0.8
Turbo coronatus	17	0.7
Total of commonly used shell types	1835	80.4
Total of all shells types used across all localities	2281	100.0

Burnupena cincta, *Diloma* spp., *Thais capensis*, *Turbo cidaris*, and *T. coronatus* are used mainly by males. These shell types have high volume-to-mass ratios (Figure 5.2). The six intersex individuals use *Burnupena lagenaria*, *B. cincta* and *Thais capensis*. Juveniles are found in small shells of *Burnupena lagenaria*, *B. pubescens*, *Morula* spp., *Peristernia forskalii*, *Trochus nigropunctatus* and a large proportion of juveniles occur in shells of *Nodilittorina* spp (Figure 5.1). However, not all of these shell types were included in all statistical analyses as especially *Trochus nigropunctatus*, and *Nodilittorina* spp. were used in low numbers.

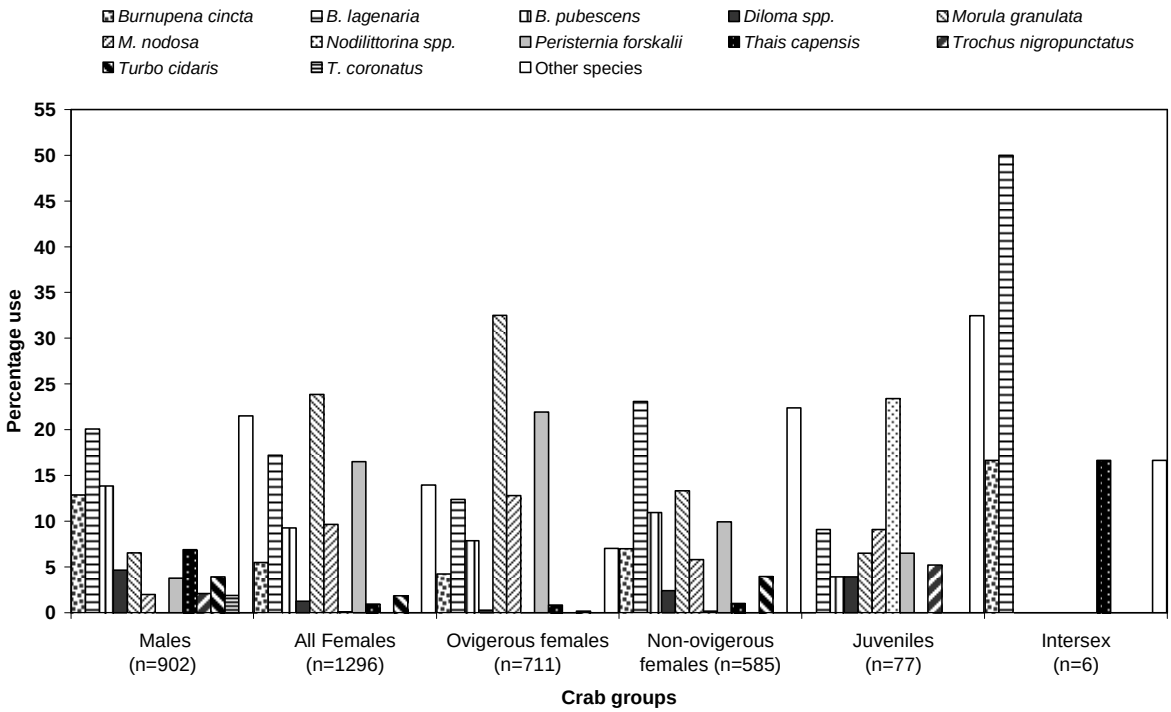

Figure 5.1: Shell use by crab group shows that while there is considerable overlap in the shell types used among groupings, each crab group shows its own combination of shell use.

When compared using ANCOVA, slopes and intercepts of the relationship of volume to mass differed significantly ($F = 39.333$, $DF = 9$ on 1223, $P<0.001$) among the ten shell types for which sufficient data were available. The relationship of volume to mass shows that *Diloma* spp., *Turbo* spp., *Burnupena* spp. and *Thais capensis* have high volume-to-mass ratios. These are larger shell types than *Morula* spp. and *Peristernia forskalii*, which have low volumes compared to mass and remain small (Figure 5.2).

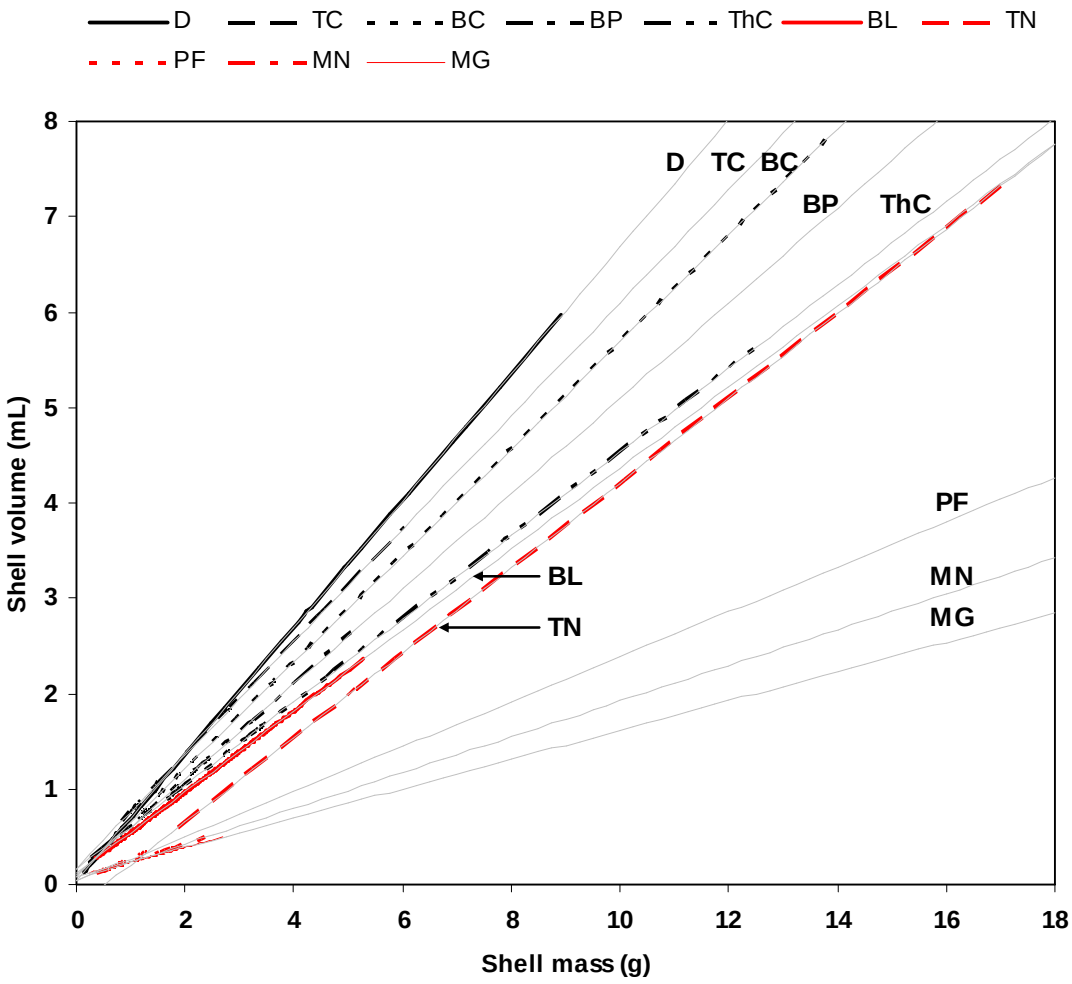

Figure 5.2: The relationship of mass to volume is plotted for the shell sizes used by hermit crabs. The light grey lines are extrapolations of the regressions of volume to mass and are given to aid comparison. (Shell types are *Diloma* spp. (D), *Turbo cidaris* (TC), *Burnupena cincta* (BC), *B. pubescens* (BP), *Thais capensis* (ThC), *B. lagenaria* (BL), *Turbo coronatus* (TN), *Peristernia forskalii* (PF), *Morula granulata* (MG) and *M. nodosa* (MN)

Sex and size are closely linked as males attain larger sizes than females at almost all sites in this study. Unsurprisingly shell use is also linked to crab size (Figure 5.3). The maximum size for a female crab in this study is 6.5 mm, showing that crabs larger than 7 mm, i.e. males, use *Burnupena cincta*, *B. lagenaria*, *Thais capensis*, and low-spired shells such as *Diloma* spp. and *Turbo* spp. The smallest individual (0.99 mm) was found in *Nodilittorina africana*.

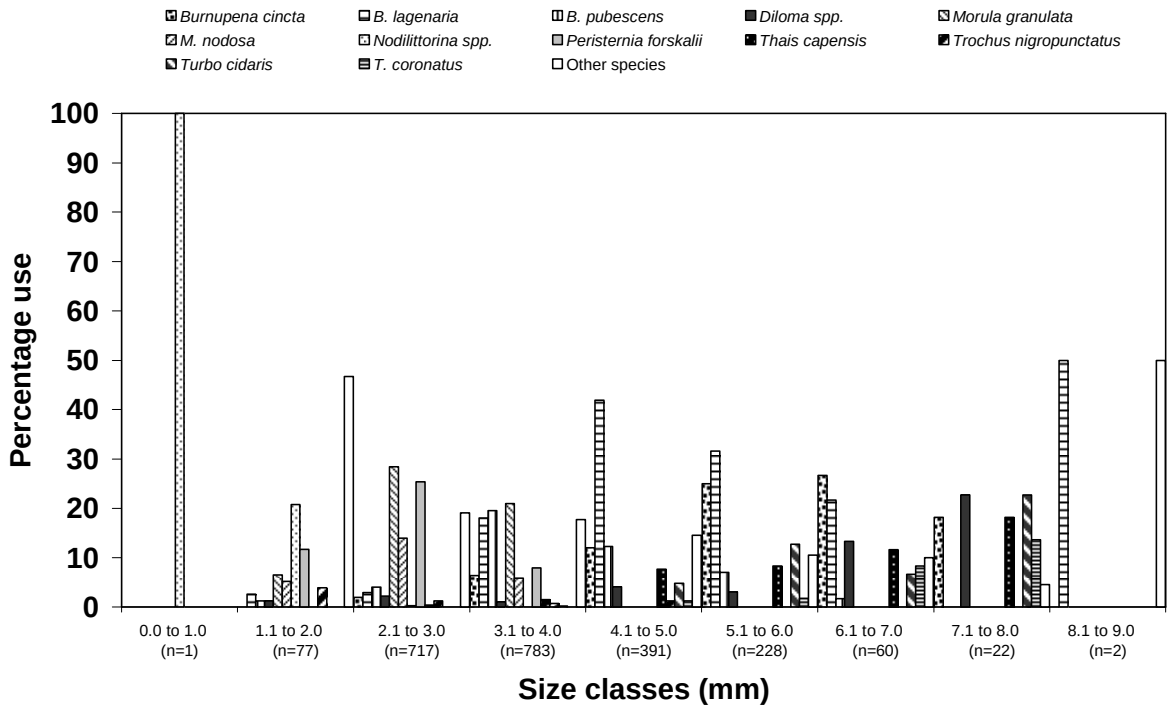

Figure 5.3: Shell use by crab size classes shows that smaller size classes use mainly *Morula* spp. and *Peristernia forskalii*, while larger size classes use *Diloma* spp., *Thais capensis*, and *Turbo* spp. At localities where it occurs, *Burnupena* spp. is used by all size classes except the very smallest.

As discussed in Chapter 4, shell use varies by locality. At all localities specific size classes of crabs also use characteristic shells suites (Figure 5.4). The populations at Cape Recife and Nahoon Beach are dominated by the use of *Burnupena lagenaria*, but Nahoon Beach and Cintsa West Beach show large crabs in low-spired *Turbo cidaris* and *Diloma* spp. Morgan Bay and Dwesa show high usage of *Burnupena* spp, particularly *B. cincta*. At Wavecrest, the site between them, crabs supplement the use of *Burnupena* spp. with *Thais capensis*. From Coffee Bay northwards the use of *Morula* spp. and *Peristernia forskalii* increases, especially in the smaller size classes. From Port Edward northwards low-spired *Turbo coronatus* is used by large crabs, except at Mission Rocks, where large size classes of crabs are absent from the population. *Trochus nigropunctatus*, also a low-spired shell, appears at Port Edward (Figure 5.4) and is used exclusively by males and juvenile crabs (Figure 5.1).

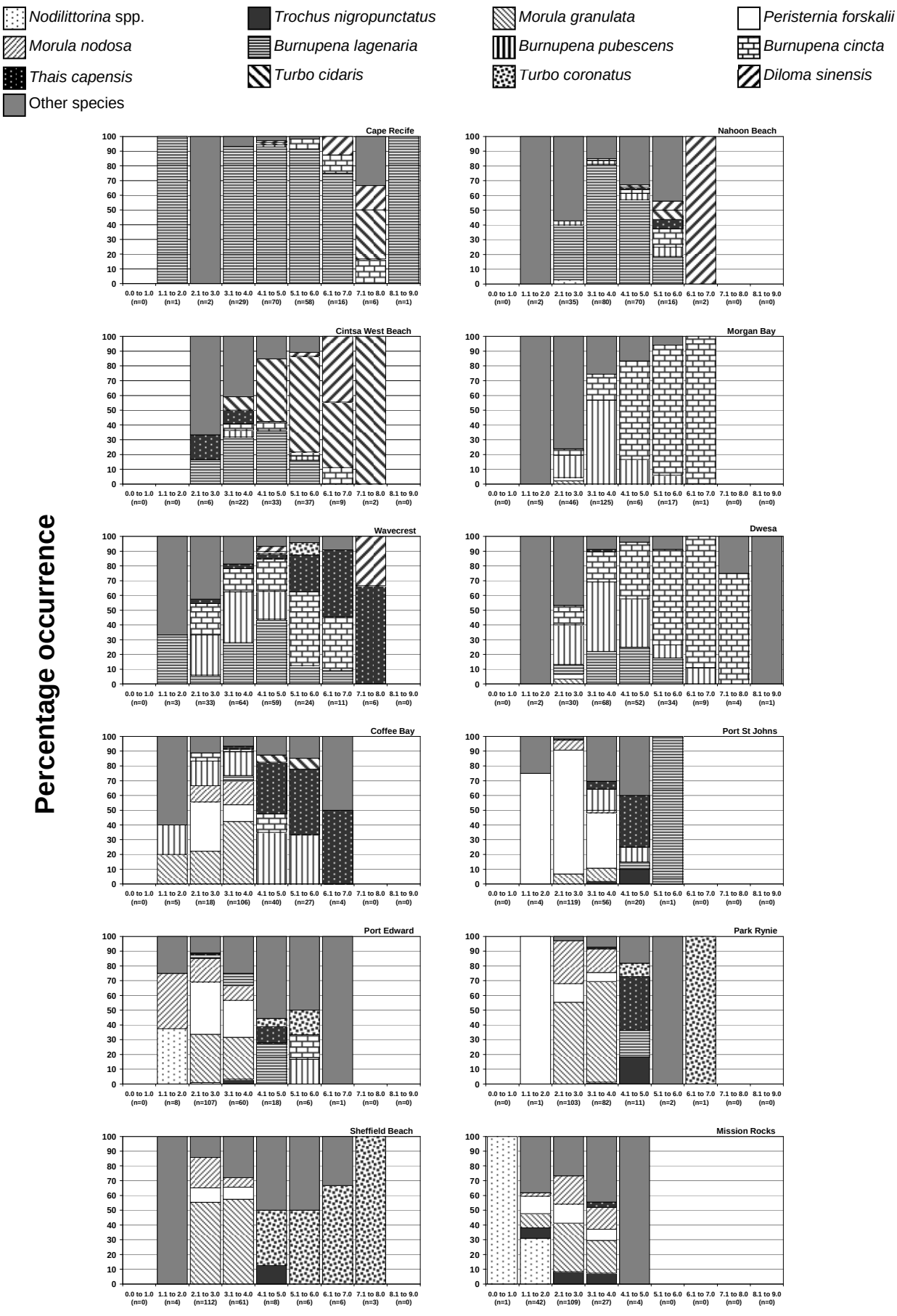

Figure 5.4: Shell use by size class. Each locality and each size class within a locality uses a specific suite of shells. For a map of localities, see Chapter 2.

Damage to shells was recorded as described in Chapter 2. A log-likelihood ratio test (G-test) was used to compare frequency of shell-damage characteristics across categories of crab sex, reproductive state and size class. Categories were compared for the number of shells that showed some kind of damage for each damage type. Most of the shells (99.2%) inhabited by *C. virescens* in this study showed some kind of damage (Figure 5.5), and most shells had multiple types of damage. When comparing frequency of damage types between males and females, a log-likelihood ratio test showed that damage type was not independent of sex ($G = 43.7$, $DF = 11$, $P<0.001$). Damage type was also not independent of reproductive state ($G = 45.6$, $DF = 11$, $P<0.001$) when comparing frequency of damage types between ovigerous and non-ovigerous females. Juveniles and intersex individuals were excluded because of small sample sizes within damage type variables.

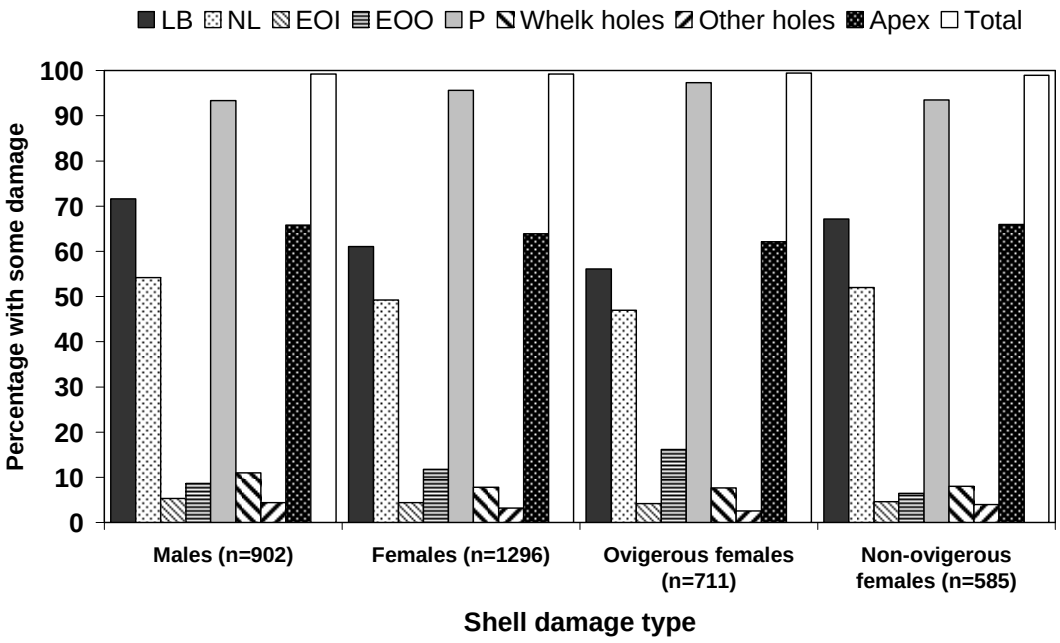

Figure 5.5: Most shells showed some damage (Total), and wear to the outer layer. Males carry shells with more holes than other groups, while ovigerous females use shells with less lip breakage and nacreous layer wear. Damage types are: lip breakage (LB), nacreous layer wear (NL), encrusting organisms on the inside (EOI) and on the outside (EOO) of the shell, wear to the outer layer of the shell (P), and apex damage (Apex).

All crab groupings show a high total percentage damage, and almost all crabs occupy shells that show some wear to the outer layer of the shell. The least common forms of damage are encrusting organisms and holes. Males more frequently occupy shells with whelk holes than females, while females more frequently occupy shells with external encrustation than males. This difference is particularly noticeable when comparing non-ovigerous females, which have fewer encrusting organisms, and ovigerous females, which have the highest percentage (16.2%) of encrusting organisms. Ovigerous females also inhabit shells with more external wear than any other crab grouping.

Damage type is not independent of size class ($G = 152.6$, $DF = 66$, $P<0.001$). Damage patterns across crab size classes show that, excluding the smallest and largest size classes, there is an increase in damage in most damage types from small to medium-sized crabs, after which the percentage breakage declines again (Figure 5.6). This bell-shaped pattern is particularly clear for lip breakage and apex damage, but can also be seen for whelk holes. Larger crabs, in larger shells, show more encrusting organisms on the outside of the shell than smaller crabs with smaller shells.

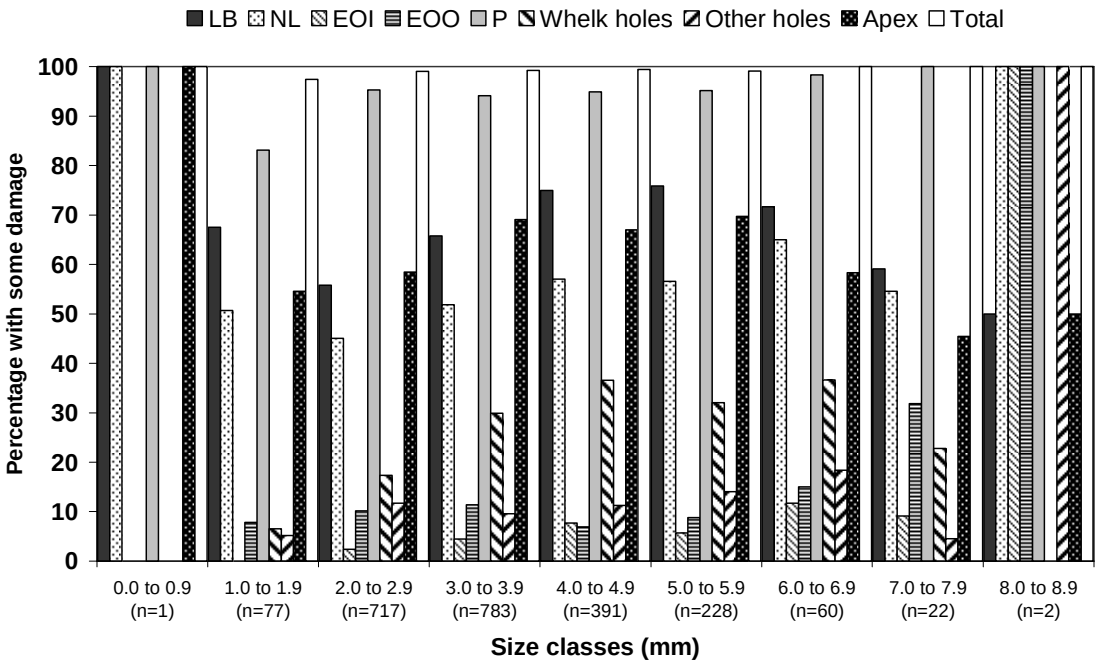

Figure 5.6: The proportion of shells with lip breakage and apex damage increases towards the middle size classes and then decreases towards the larger size classes. Damage types are: lip breakage (LB), nacreous layer wear (NL), encrusting organisms on the inside (EOI) and on the outside (EOO) of the shell, wear to the outer layer of the shell (P), and apex damage (Apex).

Crab dimensions were regressed against shell dimensions to determine which shell dimension best relates to either crab shield length or crab dry mass (Table 5.2). In all comparisons there was a significant relationship between either crab shield length or crab dry mass and shell variables. As discussed in Chapter 4, the shell resource was divided into high-spired shells and low-spired shells. Shield length showed a strong relationship to shell volume for both high-spired and low-spired shells. Dry mass related best to shell width for high-spired shells and equally well to shell length, width and volume for low-spired shells.

Table 5.2: The relationship of crab dimensions were compared to shell dimensions for high-spired and low-spired shells by linear regressions. The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slope	Intercept	r^2	DF	RSE	F	P
For all high-spired shells							
Crab shield length (mm) by:							
Shell length (mm)	5.354	3.055	0.78	1229	3.067	4343	P<0.001
Shell width (mm)	2.386	2.755	0.83	1229	1.160	6061	P<0.001
Shell aperture width (mm)	1.779	-1.245	0.81	1229	0.920	5331	P<0.001
Shell mass (g)*	1.975	-2.203	0.68	1229	0.382	2558	P<0.001
Shell volume (mL)*	2.830	-4.225	0.86	1229	0.313	7813	P<0.001
Crab mass (g) by:							
Shell length (mm)*	0.255	3.843	0.77	1229	0.130	4052	P<0.001
Shell width (mm)*	0.235	3.111	0.85	1229	0.091	6903	P<0.001
Shell aperture width (mm)*	0.367	2.679	0.73	1229	0.208	3256	P<0.001
Shell mass (g)*	0.627	2.143	0.74	1229	0.340	3549	P<0.001
Shell volume (mL)*	0.835	1.821	0.82	1229	0.358	5675	P<0.001
For all low-spired shells							
Crab shield length by:							
Shell length (mm)	3.833	0.207	0.83	137	2.384	700	P<0.001
Shell width (mm)	1.431	3.297	0.82	137	2.169	625	P<0.001
Shell aperture width (mm)	1.848	0.777	0.80	137	1.298	548	P<0.001
Shell mass (g)*	2.668	-3.513	0.79	137	0.431	538	P<0.001
Shell volume (mL)*	2.764	-4.174	0.89	137	0.317	1071	P<0.001
Crab mass (g) by:							
Shell length (mm)*	0.297	3.573	0.88	137	0.117	1024	P<0.001
Shell width (mm)*	0.266	3.435	0.88	137	0.105	1025	P<0.001
Shell aperture width (mm)*	0.269	2.858	0.83	137	0.131	675	P<0.001
Shell mass (g)*	0.810	2.461	0.83	137	0.392	680	P<0.001
Shell volume (mL)*	0.821	1.980	0.89	137	0.318	1061	P<0.001

Individuals sampled in this study range from 0.99 mm to 8.50 mm shield length. Pooled data for all crabs show that most crabs sampled occur in the range of 2 to 6 mm (Figure 5.7). Male crabs attained larger mean shield lengths overall than females (Table 5.3). The populations sampled are sexually dimorphic and large size classes are composed of only male crabs at most localities (Figure 5.8 and Table 5.3), irrespective of the maximum sizes reached by males, i.e. even when the largest size classes in the population are small (e.g. Mission Rocks) relative to other populations, the largest size classes are still dominated by males. The largest females were ovigerous, reached 6.50 mm shield length and were both recorded at Cape Recife, while the smallest ovigerous female, recorded at Coffee Bay, measured 1.89 mm shield length. Intersex individuals were recorded only at Nahoon Beach

and at Wavecrest, making up 1.4% and1.5%, respectively, of the population (3 individuals) at each locality. Juveniles were recorded at all localities except Cape Recife and Dwesa. At Mission Rocks, juveniles made up 20% of the sample. At the remaining localities juveniles made up less than 3 % of the sample.

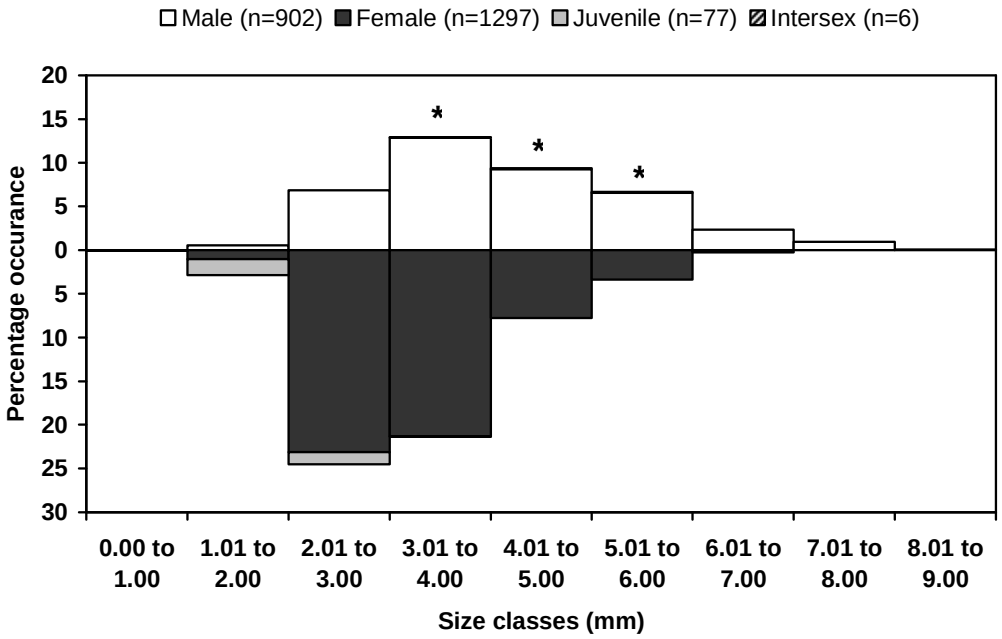

Figure 5.7: Crab shield lengths range from 0.99 mm to 8.50 mm. Only one juvenile occurs in the smallest size class and two males occur in the largest size class. There are too few intersex individuals (<0.1% of the population) to show clearly on the graph, so size classes in which intersex individuals occur are marked with an asterisk.

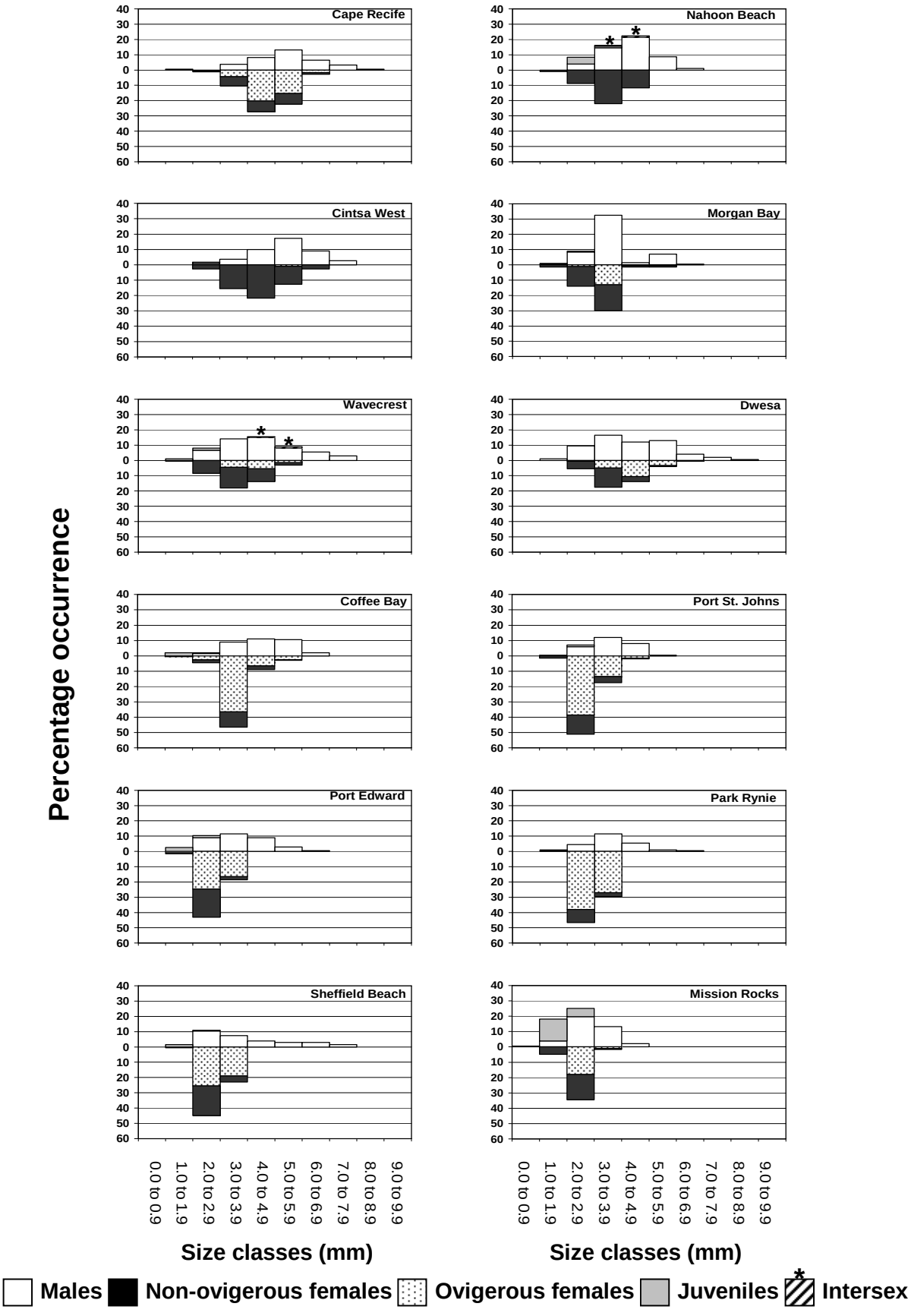

Figure 5.8: Size frequency distributions within localities show that males dominate large size classes at all localities. Size classes in which intersex individuals occur are marked with an asterisk.

Table 5.3: Mean shield length for each crab grouping for each locality. (*BS non-ovigerous refers to non-ovigerous females in the same size range as ovigerous females.)

Crab Shield Length (mm)		All	Males	All females	Ovigerous females	Non-ovigerous females	*BS non-ovigerous females	Juveniles	Intersex
All sites	Mean	3.62	4.17	3.34	3.36	3.31	3.35	1.91	4.59
	n	2281	902	1296	711	585	570	77	6
	SE	0.02	0.04	0.02	0.03	0.04	0.04	0.06	0.35
Cape Recife	Mean	4.99	5.51	4.72	4.85	4.57	4.64	2.27	
	n	183	65	117	75	40	39	1	
	SE	0.08	0.14	0.07	0.07	0.15	0.14		
Nahoon Beach	Mean	3.84	4.25	3.49				2.77	4.04
	n	205	102	89				11	3
	SE	0.06	0.09	0.07				0.13	0.40
Cintsa West Beach	Mean	4.80	5.37	4.39	5.20	4.38		2.27	
	n	110	48	61	1	60		1	
	SE	0.10	0.15	0.11		0.11			
Morgan Bay	Mean	3.42	3.65	3.21	3.56	3.05	3.32	1.85	
	n	200	101	97	30	67	43	2	
	SE	0.06	0.09	0.07	0.08	0.09	0.05	0.41	
Wave-crest	Mean	4.15	4.55	3.75	4.27	3.57	3.99	2.05	5.13
	n	200	104	88	23	65	45	5	3
	SE	0.09	0.13	0.09	0.15	0.11	0.10	0.26	0.39
Dwesa	Mean	4.15	4.34	3.87	4.39	3.39	3.53		
	n	200	117	83	40	43	37		
	SE	0.08	0.12	0.09	0.11	0.09	0.08		
Coffee Bay	Mean	3.84	4.59	3.53	3.56	3.44	3.44	1.60	
	n	200	68	127	97	30	30	5	
	SE	0.07	0.11	0.06	0.07	0.11	0.11	0.12	
Port St Johns	Mean	3.04	3.61	2.84	2.90	2.65	2.72	2.25	
	n	200	54	144	107	37	30	2	
	SE	0.05	0.10	0.04	0.04	0.09	0.06	0.03	
Port Edward	Mean	3.09	3.72	2.83	2.94	2.63	2.73	1.89	
	n	200	66	126	82	44	38	8	
	SE	0.06	0.12	0.03	0.03	0.05	0.04	0.17	
Park Rynie	Mean	3.10	3.63	2.94	2.96	2.85	2.94	2.03	
	n	200	47	152	130	22	19	1	
	SE	0.04	0.13	0.02	0.02	0.07	0.05		
Sheffield Beach	Mean	3.19	4.04	2.87	2.97	2.68	2.71	1.66	
	n	200	59	137	89	48	44	4	
	SE	0.07	0.20	0.03	0.03	0.05	0.04	0.15	
Mission Rocks	Mean	2.39	2.85	2.31	2.47	2.17	2.26	1.69	
	n	183	71	75	35	40	28	37	
	SE	0.05	0.07	0.04	0.05	0.05	0.03	0.07	

Table 5.3 continued: Mean dry mass for each crab grouping for each locality. (*BS non-ovigerous refers to non-ovigerous females in the same size range as ovigerous females.)

Crab mass (g)		All	Males	All females	Ovigerous females	Non-ovigerous females	*BS non-ovigerous females	Juveniles	Intersex
All sites	Mean	3.62	0.11	0.06	0.06	0.05	0.05	0.01	0.11
	n	2281	902	1295	710	585	570	76	6
	SE	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Cape Recife	Mean	0.24	0.32	0.20	0.21	0.19	0.20	0.02	
	n	183	65	117	75	40	39	1	
	SE	0.01	0.02	0.01	0.01	0.02	0.02		
Nahoon Beach	Mean	0.07	0.09	0.05				0.02	0.07
	n	205	102	89				11	3
	SE	0.00	0.00	0.00				0.00	0.02
Cintsa West Beach	Mean	0.11	0.15	0.08	0.10	0.08		0.02	
	n	110	48	61	1	60		1	
	SE	0.01	0.01	0.29		0.01			
Morgan Bay	Mean	0.06	0.07	0.05	0.06	0.04	0.05	0.01	
	n	200	101	97	30	67	43	2	
	SE	0.00	0.01	0.00	0.00	0.00	0.00	0.00	
Wave-crest	Mean	0.10	0.13	0.06	0.09	0.06	0.07	0.01	0.14
	n	200	104	88	23	65	45	5	3
	SE	0.01	0.24	0.00	0.01	0.01	0.01	0.00	0.02
Dwesa	Mean	0.09	0.11	0.07	0.10	0.04	0.05		
	n	200	117	83	40	43	37		
	SE	0.01	0.01	0.01	0.01	0.00	0.00		
Coffee Bay	Mean	0.08	0.13	0.06	0.06	0.06	0.06	0.00	
	n	199	68	126	96	30	30	5	
	SE	0.005	0.01	0.00	0.00	0.01	0.01	0.00	
Port St Johns	Mean	0.034	0.06	0.03	0.03	0.02	0.02	0.01	
	n	200	54	144	107	37	30	2	
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Port Edward	Mean	0.04	0.06	0.02	0.03	0.02	0.02	0.01	
	n	200	66	126	82	44	38	8	
	SE	0.00	0.01	0.00	0.00	0.00	0.00	0.00	
Park Rynie	Mean	0.04	0.07	0.03	0.03	0.03	0.03	0.01	
	n	200	47	152	130	22	19	1	
	SE	0.00	0.01	0.00	0.00	0.00	0.00	#DIV/0!	
Sheffield Beach	Mean	0.07	0.15	0.04	0.04	0.03	0.03	0.00	
	n	200	59	137	89	48	44	4	
	SE	0.01	0.02	0.00	0.00	0.00	0.00	0.00	
Mission Rocks	Mean	0.02	0.03	0.01	0.02	0.01	0.01	0.01	
	n	182	71	75	35	40	28	36	
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

ANOVA and post-hoc tests (Tukey's honest significant difference (HSD)) were used to compare shield lengths among localities. Groups comprising all crabs, males, all females, ovigerous females, non-ovigerous females and BS non-ovigerous females were tested. ANOVA showed that mean shield length varied among localities for all groups tested (Table 5.4). Tukey's HSD showed which localities were similar to each other (Figure 5.9). When all crabs were compared among localities, crabs at Cape Recife and Cintsa West reach a large average size. Results for all crabs and males show that crabs at Sheffield beach have larger shield lengths than at other northern localities. Crabs at northern localities generally have larger shield lengths than crabs at southern localities, with the exception of Nahoon Beach and Morgan Bay, which show size affinities with southern localities (Figure 5.9). Crab mass reflects the trend found for shield length.

There was a strong exponential relationship between crab shield length and dry mass ($r^2 = 0.92$, DF = 2275, F = 25970, $P<0.001$). When the relationship of shield length to dry mass was compared by localities using ANCOVA, it was found that both the slopes and intercepts differed among localities (F = 5.6229, DF = 11 on 2253, $P<0.001$).

Table 5.4: Analysis of variance shows significant differences in mean shield length (mm) among localities for each group tested.

Group	F	DF	P
All crabs	118.87	11 on 2269	P < 0.001
Males	32.34	11 on 890	P < 0.001
All females	141.07	11 on 1284	P < 0.001
Ovigerous females	155.45	10 on 700	P < 0.001
Non-ovigerous females	57.15	10 on 485	P < 0.001
BS non-ovigerous females	43.52	9 on 411	P < 0.001

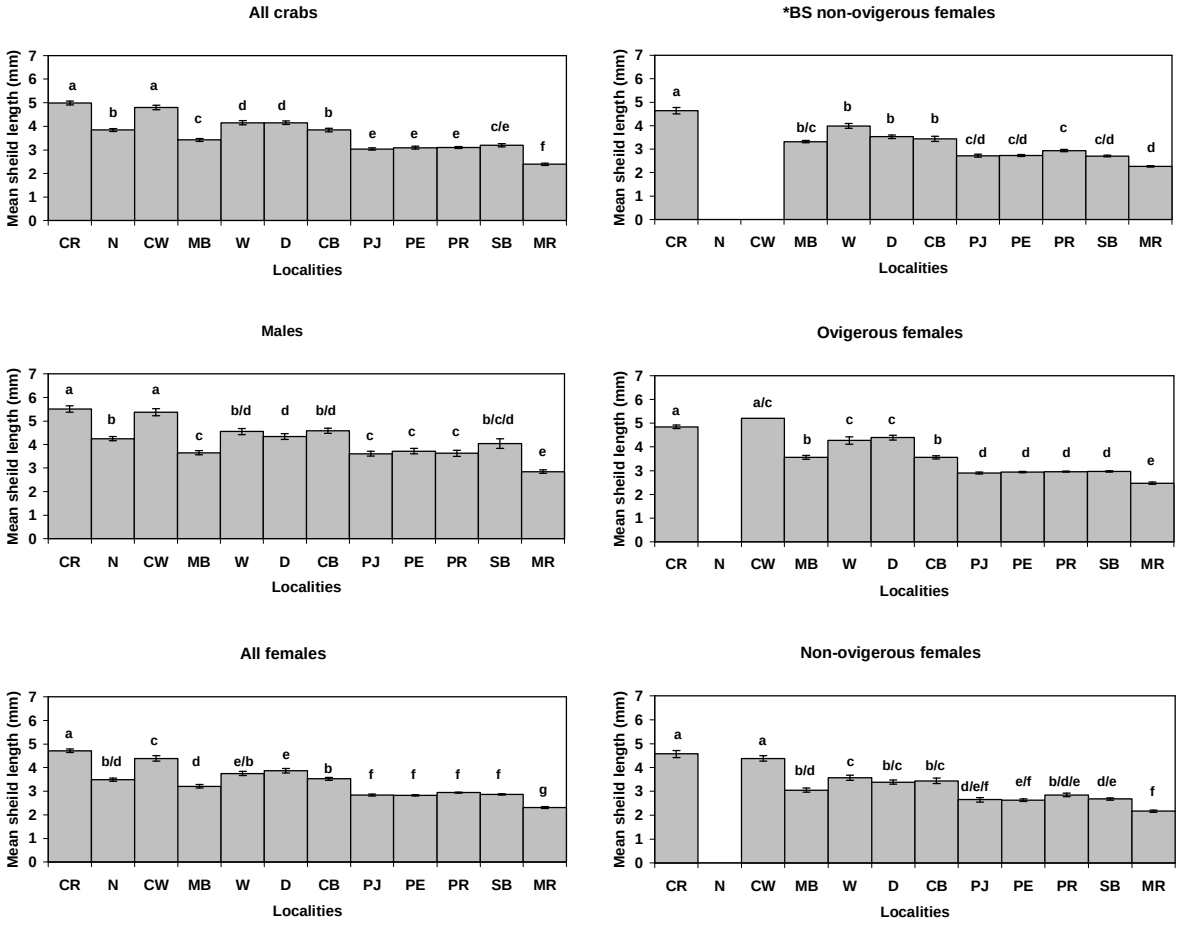

Figure 5.9: Tukey's HSD shows which localities are have crabs of similar average shield lengths. Southern localities tend to have crabs with larger average shield lengths than northern localities, a trend most clearly seen for the groups comprising males and ovigerous females. Localities with the same letters are not significantly different to each other. Error bars indicate SE. Localities from South to North are: Cape Recife (CR), Nahoon Beach (N), Cintsa West Beach (CW), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

The sex ratios of males to females in the sampled populations were compared using a contingency table and a log-likelihood ratio test (G test) with the null hypothesis that the frequency of occurrence of males and females in the populations sampled was independent of the locality. The null hypothesis was rejected ($\chi^2 = 27.69$, $\nu = 11$, $P < 0.005$), indicating that different localities have different sex ratios. When the numbers of males and females at individual localities were compared using Chi-square goodness of fit, it was found that 7 of the 12 sites departed from the expected 1:1 ratio for males to females (Table 5.5).

The ratio of males to females changed with size class (Figure 5.10). Females dominated mid-sizes at all sites, while males made up 100% of the larger size classes.

Table 5.5: Comparison of male and female numbers using Chi-square goodness of fit to determine whether the numbers departed from a 1:1 ratio.

Locality	No. Males	No. Females	Ratio (M:F)	χ^2 statistic	Result
Cape Recife	65	117	1:1.80	14.86	Departs from 1:1 ratio
Nahoon Beach	102	89	1:0.87	0.88	1:1 ratio
Cintsa West Beach	48	61	1:1.27	1.55	1:1 ratio
Morgan Bay	101	97	1:0.96	0.08	1:1 ratio
Wavecrest	104	88	1:0.85	1.33	1:1 ratio
Dwesa	117	83	1:0.71	5.78	Departs from 1:1 ratio
Coffee Bay	68	127	1:1.87	17.85	Departs from 1:1 ratio
Port St. Johns	54	144	1:2.67	40.91	Departs from 1:1 ratio
Port Edward	66	126	1:1.91	18.75	Departs from 1:1 ratio
Park Rynie	47	152	1:3.23	55.40	Departs from 1:1 ratio
Sheffield Beach	59	137	1:2.32	31.04	Departs from 1:1 ratio
Mission Rocks	71	75	1:1.05	0.11	1:1 ratio

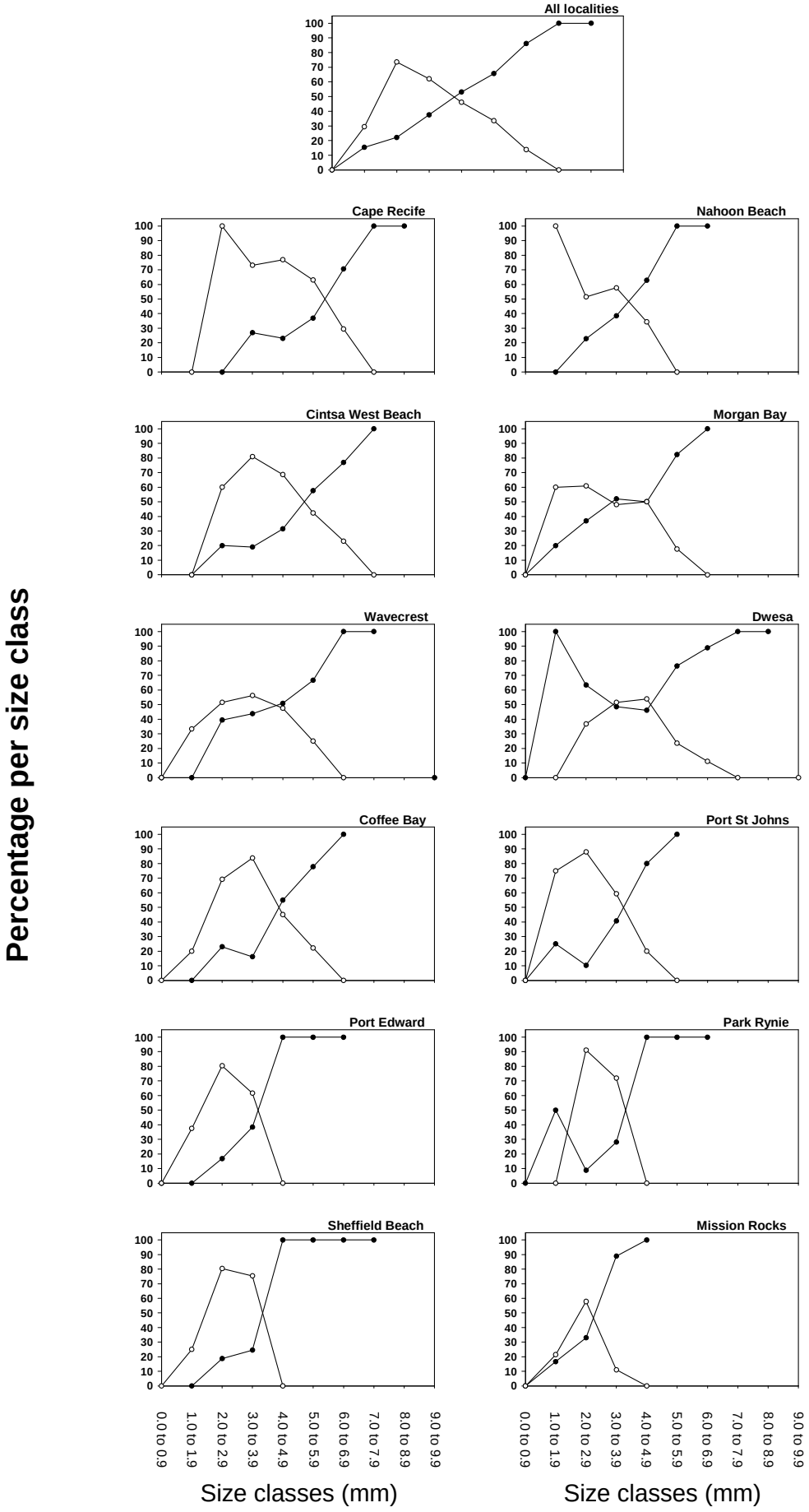

Figure: 5.10: The ratio of males to females changes with size class, but the pattern of males making up 100% of larger size classes holds regardless of the sizes reached by the males.

The relationship between shield length and dry mass for the entire population was determined by linear regression after transformation of the data. In Crustacea change of mass with increasing length normally takes the form of an allometric relationship where mass increases at a greater rate relative to length (Hartnol 1982). In this case, transformation of both variables by taking the natural logarithm (*e*) provided the best fit of a linear regression to the data (Table 5.6) and a pattern of residuals indicating homoscedastic variance (Zar 1999) (Figure 5.11).

Table 5.6: The effects of transformation on the relationship between crab mass and shield length.

Transformation	r^2	DF	RSE	F	P
Untransformed	0.729	2275	0.049	6138	P < 0.001
Log transformed	0.684	2275	0.019	4938	P < 0.001
LN transformed	0.919	2275	0.295	25970	P < 0.001

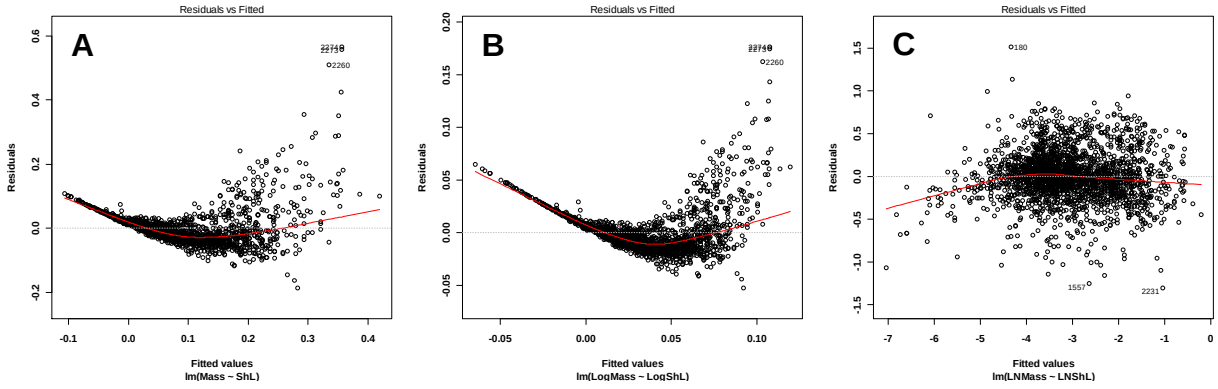

Figure 5.11: Pattern of residuals generated from a linear regression of crab mass (g) against shield length (mm) for (A) untransformed data, (B) log transformed data and (C) LN transformed data. LN transformed data (C) yield a pattern of residuals that best indicate homoscedastic variance.

ANCOVA was used to compare the relationship between shield length and dry mass for males and females at each locality (Table 5.7). Results showed that at all localities except Nahoon Beach there was no significant difference in either the intercepts or the slopes of the relationships. At Nahoon Beach the slopes did not

differ between males and females, but the intercepts did. When data for all localities were pooled to improve the power of the test, the result showed a significant difference for intercepts but not for slopes of the relationships between all males and all females (Table 5.7). Student's t-tests were used to compare mean male and female shield length at each locality (Table 5.8), and at all localities there was a significant difference between the mean shield lengths for males and females, with males uniformly achieving larger mean shield lengths than females (Table 5.3).

Table 5.7: The effect of crab sex on the relationship between shield length and dry mass. Males and females show the same relationship between length and mass.

Dimensions	Slopes	Intercepts	F	DF	P
Cape Recife	Do not differ	Do not differ	0.054	1 on 179	P=0.469
Nahoon Beach	Do not differ	Differ	5.085	1 on 187	P=0.026
Cintsa West Beach	Do not differ	Do not differ	3.311	1 on 106	P=0.072
Morgan Bay	Do not differ	Do not differ	0.289	1 on 195	P=0.592
Wavecrest	Do not differ	Do not differ	0.070	1 on 189	P=0.791
Dwesa	Do not differ	Do not differ	2.656	1 on 197	P=0.105
Coffee Bay	Do not differ	Do not differ	3.546	1 on 189	P=0.061
Port St Johns	Do not differ	Do not differ	1.428	1 on 195	P=0.234
Port Edward	Do not differ	Do not differ	0.447	1 on 188	P=0.505
Park Rynie	Do not differ	Do not differ	1.937	1 on 196	P=0.166
Sheffield Beach	Do not differ	Do not differ	3.475	1 on 193	P=0.064
Mission Rocks	Do not differ	Do not differ	0.969	1 on 141	P=0.327
Grouped for all localities	Do not differ	Differ	13.779	1 on 2186	P<0.001

Table 5.8: Comparisons of mean shield lengths indicate a significant difference between males and females at different localities.

Locality	t-statistic	DF	P
Cape Recife	4.91	98.45	P<0.001
Nahoon Beach	6.74	184.71	P<0.001
Cintsa West Beach	5.29	93.09	P<0.001
Morgan Bay	3.96	190.54	P<0.001
Wavecrest	4.95	178.50	P<0.001
Dwesa	3.10	192.53	P=0.002
Coffee Bay	8.09	101.66	P<0.001
Port St Johns	7.09	66.41	P<0.001
Port Edward	7.22	72.47	P<0.001
Park Rynie	5.13	47.89	P<0.001
Sheffield Beach	5.73	60.34	P<0.001
Mission Rocks	6.33	104.27	P<0.001

Very few crabs with damage (1.18% of the population) were recorded. Damage varied among localities (Table 5.9). Cintsa West Beach shows the highest proportion of crabs with damage with 14.5% of the sample showing damage to either the chelipeds or ambulatory legs. Males and females show the same frequency of damage (14 occurrences each), but males show 12 occurrences of damage to the chelipeds compared to 9 occurrences in females. While moulting is not strictly damage, it also leaves crabs vulnerable. Dwesa showed the highest proportion of "soft shelled" crabs with 6 out of 200 (3%) of the sample moulting. None of the six intersex individuals showed any damage.

Table 5.9: Damage and moulting in crabs at the localities sampled. Damage to males (M), females (F) and juveniles (J) is recorded.

Locality	Type of damage											Damage Totals		Moulting crabs
	Left cheliped missing			Right cheliped missing			Both chelipeds missing		Ambulatory limbs missing			No.	%	
	n	**M**	**F**	**J**	**M**	**F**	**J**	**M**	**F**	**M**	**F**			
Cape Recife	183											0	0	
Nahoon Beach	205											0	0	
Cintsa West Beach	110		3		4	4			2	1	2	16	14.5	
Morgan Bay	200				1							1	0.5	
Wavecrest	200				1							1	0.5	2
Dwesa	200											0	0	6
Coffee Bay	200	1			1							1	0.5	
Port St Johns	200											0	0	
Port Edward	200	2										0	0	1
Park Rynie	200											0	0	
Sheffield Beach	200										2	2	1	
Mission Rocks	183	2		1			1			1	1	6	3.3	
Total	2281	5	3	1	7	4	1	0	2	2	5	27	1.18	9

5.4 Discussion

Shell use by *Clibanarius virescens* across the 12 localities sampled must be seen in the light of the change in the nature of the shell resource from Cape Recife, within the Agulhas bioregion, to Mission Rocks, which is close to the northern margin of the Natal bioregion (Lombard *et al.* 2004). In Chapter 4 the frequency of shell use was used to differentiate two main areas in which crabs had access to similar suites of shells. These areas formed the southern localities (Cape Recife to Dwesa), the northern localities (Port Edward to Mission Rocks) and a transition zone (Coffee Bay and Port St Johns). The transition localities show greater similarities to the northern localities than to the southern localities, but still group clearly. Despite the geographical range (*ca.* 950 km) encompassed by these localities and the large number (75) of shell types used, relatively few shell types emerged as being frequently used. The southern shell suite comprised mainly *Burnupena* spp., with *Turbo cidaris* also being used. The northern shell suite was made up of mainly *Morula* spp. and *Peristernia forskalii*, while *Turbo coronatus* and *Trochus nigropunctatus* were also used. *Thais capensis*, *Diloma* spp. and *Nodilittorina* spp. were used throughout the range. The transition localities used a mixture of shell types from both South and North. The nature of these shell suites might have a large role in influencing the population size-structure and degree of sexual dimorphism at the different localities.

Male crabs have faster growth rates than female crabs (Asakura 1995) and low-spired shells seem to allow faster growth rates than high-spired shells (Turra and Leite 2003). In this study low-spired shells of the genera *Diloma* and *Turbo* were most frequently used by males. These shell types also had high volume to mass ratios which might promote faster growth by being energetically less costly to carry

(Herreid and Full 1986, Turra 2003) even though this cost is somewhat ameliorated by *C. virescens* spending most of its time immersed (Barnes 2005). The potential advantage conferred on male crabs by using the shells of *Diloma* spp. or *Turbo* spp. was especially noticeable in the southern suite of shells where *Diloma* spp. and *Turbo cidaris* had the highest volume to mass ratios of the ten most commonly used shells. Low-spired, *Turbo coronatus*, found exclusively in northern sites, was heavily armoured and was much heavier than the southern *Turbo* spp., but was still the largest, lightest shell commonly available to male crabs at the northern localities. At southern localities *Diloma* spp. (particularly *Diloma sinensis* and *Diloma tigrina*), *Turbo cidaris* and *Burnupena cincta* were the largest shells, in all dimensions, that hermit crabs were likely to encounter. This might remove them from the purview of smaller, female crabs.

The lack of light, large shells at the northern localities might be causally related to the lack of large male crabs in these areas. Asakura (1995) found that male *Diogenes nitidimanus* maintain high growth rates even when shells of adequate size were lacking. If a crab outgrows its shell and is unable to procure a suitable new one, it becomes vulnerable to predation and environmental stress. If *Clibanarius virescens* had a similar growth pattern to *D. nitidimanus*, it could explain the lack of large males at sites such as Mission Rocks; males might experience high mortality once they outgrow the local supply of large shells. In contrast, if *C. virescens* were able to anticipate shell availability and adapt its growth accordingly, as found in *Pagurus middendorffii* by Wada *et al.* (1997), the populations in areas where few large shells are available might simply not generate large males. Both these scenarios could explain the lack of large males in the northern localities. Of the northern localities

only Sheffield Beach had crabs in the 7.0 to 7.9 mm size class, all of which were male and all of which inhabited *Turbo coronatus*.

Females, on the other hand, have several trade-offs to make between reproduction (present and future) and growth (Stearns 1992). Some decisions may be forced by environmental factors; for example, females may be forced to devote energy to reproduction if they cannot acquire large enough shells to allow growth (Heino and Keitala 1999). While there is a benefit to growth, as larger females produce more eggs, obtaining larger shells may involve competitive interactions with males, which may result in damage (Briffa and Dallaway 2007). Females coming into ovigery need shells that are voluminous enough to shelter their clutch before they produce eggs as there is a danger of egg loss (Neil and Elwood 1985) should they attempt to obtain new shells once carrying eggs. With the exception of Cintsa West Beach, which had only 1 ovigerous female in the sample, all ovigerous females in the southern localities were found in shells of *Burnupena* spp. The transition localities showed a shift from *Burnupena* spp. to *Morula* spp. and *Peristernia forskalii*, the use of which by ovigerous females predominated at the northern localities.

Cape Recife and Mission Rocks, at the edges of the range sampled, provided extreme contrasts in shell use and consequently crab population structure. At Cape Recife crabs had access to large shells with high volume to mass ratios. The average crab shield length at Cape Recife was 4.99 mm, while at Mission Rocks the average shield length was 2.39 mm. In Chapter 4 it was established that the shells used by *C. virescens* decrease in size, decrease in volume to mass ratio and have smaller apertures with decreasing latitude. These trends were mirrored in the decreasing average crab shield length from southern localities to northern localities.

Crab dimensions all related strongly to all shell dimensions, but shield length related most strongly to volume in both high-spired and low-spired shells. Turra and Leite (2004) suggest that low r^2 values for the relationship between crab and shell dimensions, found in several crab populations, indicate that the crabs inhabit shells with poor fit. Results with high r^2 values from this study seem to indicate that *C. virescens* in South Africa generally inhabit adequate shells.

All the transition localities and the northern localities (excluding Mission Rocks) had significantly more females than males. As females used only small shells, and reached small sizes, the population size-structure at these localities was skewed towards small crabs. Southern localities, with the exception of Cape Recife, showed no significant difference between the numbers of males and females and in these localities females were able to obtain large shells, and reach larger sizes. The implications that this holds for crab fecundity will be discussed in Chapter 6. Notwithstanding differences in the ratio of males to females, most localities showed what Wenner (1972) describes as an “anomalous” pattern, where large size classes are composed entirely of males. This pattern may be described as anomalous because the population departs from an equal sex ratio. It is also anomalous as, in many terrestrial invertebrate taxa, females become much larger than males (Fairbairn 1997), as well as in some marine Crustacea (Wenner 1972). The anomalous pattern of sex distribution occurred at all localities regardless of the size of the largest males in the population, which indicated that the same processes were at work in establishing this pattern. The distribution of males and females in small size classes differed from the expected ratio. Ideally small size classes should show equal numbers of male and female offspring, so as to conform to Fisher’s (1930 in Wenner 1972) sex ratio which predicts that a population will produce an equal number of

male and female offspring when the costs of either sex is equal. At most of the localities sampled, small size classes did not conform to an equal ratio of males to females, but this could be due to unrepresentative sampling rather than bias in the production of male and female offspring. Small crabs were very difficult to see in rock pools. Although every effort was made to avoid sampling bias, small crabs might have been under-sampled.

Apart from body size dimorphism, the genus *Clibanarius* does not display any other common form of sexual dimorphism (MacLaughlin 1980), such as difference in the relative growth of chelipeds between males and females found in other genera like *Calcinus* and *Diogenes*. From the data for females across the distribution range it appeared that maximum female size was plastic. Asakura (1995) noted that female growth in *Diogenes nitidimanus* was restricted by the size of available shells, while that of males is not. That females did not reach the same sizes as males could be due entirely to reduced competitive ability (Briffa and Dalloway 2007) leading to the inability to obtain larger shells and the need to divert energy from growth into reproduction (Heino and Kaitala 1999).

Different groups also had to contend with different kinds of damage to shells. In Chapter 4 it was proposed and demonstrated that shell morphology changed from the southern to northern localities, due in part to predation pressure on gastropods. Northern shells had smaller apertures that might prevent shell peeling by large decapod Crustacea, but some northern shells, particularly *Morula* spp., suffered a high proportion of apex-crushing damage. The southern suite of shells were not similarly reinforced against predation, and peeling damage was observed in especially *Burnupena* spp. Predation damage to gastropods necessarily affects

hermit crabs as they have no way of repairing their shell resource. When testing the frequency of damage variables for all types of damage across each category (crab size class, sex and reproductive state) it was found that none of the categories were independent of damage type. This means that crabs within each category must deal with particular damage types. Male crabs seemed to more frequently inhabit shells with holes, particularly holes made by whelks and the occurrence of whelk holes peaked in the middle to large size classes. Male crabs wear larger shells than female crabs. Larger gastropods may reach a size refuge from crushing and peeling predators, only to succumb to predation by whelks, explaining the large number of whelk holes in the shells of males. Among females, ovigerous females occupy shells with more external wear and external encrustation than non-ovigerous females. One possible cause of this is that ovigerous females do not readily acquire new shells (Neil and Elwood 1985), which may lead to them keeping the same shell for the ovigerous period during which it progressively becomes more encrusted and worn. There seems to be an almost Gaussian distribution of shell damage peaking in the shells inhabited by medium-sized crabs, similar to the damage pattern described by Barnes (1999). This damage pattern is particularly clear for lip breakage and apex damage and may reflect handling efficiencies of predatory crabs. Very few crabs are able to obtain shells that are not damaged in some way. Patterns of damage seem better explained by investigating predation on gastropods (Turra *et al.* 2005). With such a high rate of damage it does not appear that *C. virescens* does or is able to select shells to avoid particular damage types. However, this can only be conclusively tested by experiment.

Scully (1983) found that in populations where there were few empty shells available the incidence of crab injury increased, most likely due to agonistic interaction

between hermits engaged in shell exchange. In shell-stressed populations the right cheliped is most frequently lost. Cintsa West Beach (14.5%) and Mission Rocks (3.3%) showed the highest proportion of damaged crabs from all localities. This would suggest the *C. virescens* is not severely shell stressed at most localities, which is supported by the good fit between crab dimensions and shell dimensions. Male crabs showed the highest number of cheliped injuries (12) compared to female damage (9 incidents).

In summary, *Clibanarius virescens* was a heavy user of a small selection of the shell types available to it. All shell dimensions showed strong relationships to crab size, which indicated that crabs were able to obtain shells with good fit and were not shell-stressed. Low proportions of crabs with injuries characteristic of shell fights supported this conclusion. Shell volume showed the best relationship to crab size demonstrating that it was probably the most important shell characteristic for crabs. Most crabs used shells with some degree of damage and damage patterns reflected predation on the original gastropods. Southern localities had larger crabs than northern localities. Males and females showed the same patterns of growth (length-to-mass relationship), but males reached larger absolute sizes than females. Large males used different shell suites to females. This difference might have contributed to the strong sexual size dimorphism observed at all localities. Females outnumbered males at most of the northern localities, while most southern localities showed an equal sex ratio. It was hypothesised that crab population size-structure would follow the shell size trends and that the northern and southern localities identified in Chapter 4 would show clear differences in crab population size-structure. This hypothesis has been clearly upheld by the results of this chapter.

Chapter 6: Effects of the shell resource on reproduction

6.1 Introduction

Evolutionary fitness is a very broad term that is used in different ways by different authors, possibly because it "is something everyone understands, but no one can define precisely" (Stearns 1976: 4), although in general terms it involves the rate of increase in a population brought about by reproduction during the (variable) lifespan of an organism (Bell 1980). Individual fitness is a phenotypic condition that is determined by demographic traits, and these demographic traits are elucidated by studying the life history of organisms (Stearns 1992). Brommer (2000) defines life history as the way in which an organism apportions its reproduction throughout its lifetime, and states that reproduction is intrinsic to all definitions of fitness. Measures of fitness have included the intrinsic rate of increase (r), the ratio of multiplication per generation (R_0) and reproductive value (υ) (Brommer 2000). Reproductive value encompasses the consequences to population growth of decisions regarding when and what pattern reproduction should follow. These decisions include how many times in the lifespan to reproduce, the number of offspring to produce per reproductive event, when to start reproducing, and what size the offspring should be (Stearns 1976), and is influenced by the environment and resources available to the organism. In the life of a hermit crab, reproductive decisions involve how many clutches to brood (per season and per lifetime), how many eggs to produce in a clutch, at what size to start reproducing and what size offspring, as mediated through the size of the eggs, should be produced.

Reproductive strategies are important to the population dynamics and biogeography of an organism (Ramirez Llodra 2002). Reproduction is often measured through fecundity, which in the most general terms refers to the total number of offspring produced by a female during her lifetime (Ramirez Llodra 2002). However, many studies are only able to catch a snap-shot of female fecundity during one breeding season or in a single clutch of eggs. These kinds of fecundity data are best described as apparent fecundity, or the number of eggs produced in a single breeding season (Scheltema 1994 in Ramirez Llodra 2002) and realised fecundity, or the number of eggs carried on the abdomen of a single female (Anger and Moreira 1998, but not in the same sense as Brommer 2000). Realised fecundity equates to brood size, probably the most common measurement of fecundity for hermit crabs.

Longevity relates directly to fitness through the total lifetime fecundity, and has been estimated for a few hermit crab species. It is very difficult to determine age in hermit crabs (and crustaceans in general) as they have no physical structures that record age-related increments (Hartnoll 2001). Longevity for a Brazilian hermit crab, *Clibanarius vittatus*, has been calculated at 66 months for females, 60 months for males (Sant'Anna *et al.* 2008) and at 42 months for the population studied (Turra end Leite 2000). Mantelatto *et al.* (2005), calculated longevity for another Brazillian species, *Pagurus brevidactylus*, at 24 months for males and 18 months for females. In this species, females showed a more rapid growth rate than males, which allowed intense reproduction, but a shorter estimated lifespan than males. *Dardanus insignis*, also from Brazil, is estimated to live for 20-62 months (Branco *et al.* 2002). In the north-Atlantic, Manjón-Cabesa and García-Raso (1998) estimated the maximum lifespan of *Diogenes pugilator* to be 2 years, but the authors state that the animals live for about 1 year at their study site.

The number of clutches produced per breeding season varies. Wada *et al.* (2000) compared conspecifics from the same geographic area (Hakodate Bay, Japan) and showed that they displayed considerable differences in the duration of incubation and the number of clutches carried within one breeding season. For example, *Pagurus nigrofascia* and *P. middendorffii* each spawned a single clutch per breeding season and incubated their eggs for 9 months and 3.5 months respectively. In contrast, *P. filholi* spawned several times and *P. langinosus* spawned two or more clutches with incubation periods of 16 days (at 21.5 ℃) and 1.5 months respectively. Wada *et al.* (2008) found that *Pagurus nigrivittatus* could breed more than once in a breeding season and that some females had a long interval between producing clutches, while others had a much shorter interval. There is no information available regarding the number of clutches per breeding season for *Clibanarius* species.

The number of eggs produced per clutch varies among *Clibanarius* species (Table 6.1). Reddy and Biseswar (1993) converted egg mass to an estimate of egg number and determined that the mean clutch size for *Clibanarius virescens* in KwaZulu-Natal, South Africa, is 372 eggs, with some females producing a maximum of approximately 800 eggs. This rather small reported clutch size is matched only by *Clibanarius zebra*, from Hawaii (Hazlett 1989). Other species of *Clibanarius* show much larger clutch sizes (Table 6.1), the largest clutch size being measured for *Clibanarius vittatus* at Galveston (Fotheringham 1976a). Observations from Brazil (Turra and Leite 2001b) showed that clutch size varied within the same species for geographically distant populations, as *C. vittatus* in Brazil had smaller clutch sizes (Table 6.1) than found in at Galveston. Clutch size also varies between populations that were situated close to each other as demonstrated by *Clibanarius antillensis* in Brazil. This example also demonstrates the degree to which clutch sizes can vary in

a relatively short period of time as the earlier samples were collected during 1993 to 1994 (Turra and Leite 1999), while sampling for the second study took place during 1995 to 1996 (Turra and Leite 2001b). From Fotheringham (1980), it would not appear that there is a trend of increasing clutch size with increasing latitude, and it is far more likely that clutch size is influenced by local factors such as the shell types available and possibly by egg predation (Williams 2002).

Table 6.1: Comparison of clutch sizes for *Clibanarius* spp. at various localities.

Species	Locality	Clutch size		Reference
		Maximum	Mean ± SD	
C. antillensis	Praia Grande, São Sebastião, Brazil (23°49'S, 45°24'W)		637.1 ± 762.0	Turra and Leite (1999)
C. antillensis	Pernambuco Islet, São Sebastião, Brazil (23°49' S, 45°24' W)	6 083	2 149.9 ± 1 581.2	(Turra and Leite 2001b).
C. chapini	Prampram, Ghana, (5°43' N, 0°5' E)	1 353	745.5 ± 285.2	Ameyaw-Akumfi (1975)
C. sclopetarius	Pernambuco Islet, São Sebastião, Brazil (23°49' S, 45°24' W)	11 802	6 722.1 ± 2 153.3	(Turra and Leite 2001b).
C. senegalensis	Prampram, Ghana, (5°43' N, 0°5' E)	1 484	618.9 ± 268.5	Ameyaw-Akumfi (1975)
C. virescens	KwaZulu-Natal, South Africa (30°19' S, 30°44' E)	ca. 800	372.0	Reddy and Biseswar (1993)
C. vittatus	Pernambuco Islet, São Sebastião, Brazil (23°49' S, 45°24' W)	11 293	5 579.2 ± 2 283.9	(Turra and Leite 2001b).
C. vittatus,	Galveston, USA 29°14' N, 94°53' W	30 520	9 291 ± 784.0	(Fotheringham 1976a)
C. zebra	Kaneohe Bay, Ohau, Hawaii (21°26' N, 157°47' W)	712	349 ± 166.0	Hazlett (1989)

Size at first reproduction is an important life-history trait, as current reproductive output generally has consequences for future reproductive allocation (Stearns 1992). This means that the size at first reproduction may vary temporally and geographically, even within the same species. An example is the mole crab, *Emerita analoga*, sampled across three degrees of latitude in Chile (Brazeiro 2005). Length

at sexual maturity varied from 14 to 21 mm and was positively correlated with variables affecting the swash zone, such as mean grain size, mean effluent-line crossing rate and mean swash frequency. Minimum ovigerous size for the hermit crab, *Loxopagurus loxochelis*, has been found to vary over time. In 2001 the minimum ovigerous size was determined to be 4.6 mm shield length by Mantelatto and Martinelli (2001), but was recorded as 3.5 mm shield length by Bertini *et al.* (2004) even though both sampled populations came from the same area.

Egg size, another important life-history component, has been found to be proportional to larval size (Fotheringham and Bagnall 1976, Turra and Leite 2007), as well as to duration of larval development (Turra and Leite 2007), thus implicating egg size in the number of clutches that can be brooded within a single breeding season. Egg sizes mentioned in the following section are reported as mean ± standard deviation. Within the Brazilian *Clibanarius* species, egg size varies from 0.354 ± 0.011 mm for *C. antillensis* to 0.479 ± 0.039 mm for *C. sclopetarius* (Turra and Leite 2007). It appears that eggs size does not vary much within a single species as *C. vittatus* egg diameters were similar in Texas in 1972 to 1973 (0.455 ± 0.0056 mm) (Fotheringham 1976a), Brazil in 1995 to 1996 (0.441 ± 0.021 mm) (Turra and Leite 2001b) and again in Brazil in 2001 (0.444 ± 0.019 mm) (Turra and Leite 2007).

Life-history traits such as longevity, size at first reproduction, number of clutches, size of clutches and egg size are affected by the resources available to the organism. In hermit crabs the shells used represent a vital, yet easily quantifiable resource (Lively 1988) that affects almost every part of the crabs' lives (Hazlett 1981). Hermit crabs show a great deal of variation of life-history traits in response to shell parameters. Some studies suggest that internal shell volume plays an important part in

determining clutch size (Bertness 1981a, Hazlett 1989). Other studies have found shell mass to be a more important criterion (Turra and Leite 2001b, Iossi *et al.* 2005), but realized fecundity may also be affected by overall shell size (Yoshino *et al.* 2002). Shell size is mediated by shell type and therefore shell type may affect fecundity through the relative masses and volumes of different kinds of shells used by ovigerous females. However, shell type is not the overriding influence on fecundity, as shell type may have little effect on fecundity once female size is taken into account (Hazlett 1989). In some cases it has been found that females in shells that are too small or too big are not ovigerous, prompting researchers to conclude that females will not breed in inadequate shells (Hazlett *et al.* 2005). Clearly these studies indicate that there are complex relationships between hermit crabs and their shell resource.

This chapter aims to understand how the change in the shell resource affects the fitness of *Clibanarius virescens* across its range in South Africa. Chapters 4 and 5 discussed the change in the nature of the shell resource with latitude and how that change affected *Clibanarius virescens* populations. This chapter investigates reproduction of *C. virescens* in terms of differences in realized fecundity or clutch size among the different localities. This will be related to female size, shell parameters and shell types used by ovigerous females. Egg size will be investigated to determine whether it is affected by clutch size, i.e. whether there is a trade-off between the number of eggs and the size of eggs among different localities.

6.2 Methods

The sampling locality, collection methods and laboratory analyses are described in Chapter 2.

Comparisons between ovigerous and non-ovigerous females in this chapter used only non-ovigerous females in the same size range as ovigerous females. These females have been labelled in Chapter 3 and 5 as BS (breeding season) non-ovigerous. Data from only 15 small females were omitted. The proportion of each sampled population that comprised ovigerous females was calculated and the size distribution of ovigerous and non-ovigerous groups was determined. A log-likelihood ratio test (G-test) was used to compare size frequency distributions between ovigerous and non-ovigerous females. The minimum ovigerous shield length at each locality was established.

The shell types most commonly used by females were identified. The frequency of shell use between ovigerous and non-ovigerous females at each locality was compared by means of a log-likelihood ratio test.

Linear regressions on transformed data were performed to determine the strength of relationships between descriptors of crab size (crab shield length (mm) and crab dry mass (g)) and descriptors of shell size (shell length (mm), shell width (mm), shell aperture width (mm), shell mass (g) and shell internal volume (mL)). Where necessary, data were linearized by taking the natural logarithm of both variables concerned. The rationale for using this form of transformation is discussed in Chapter 5. The significance of the relationships was tested by ANOVA. Where high coefficients of determination were found they were taken to describe a good shell fit

(Turra and Leite 2004). Analysis of covariance was used to test the effect of qualitative factors such as female reproductive state, shell type, locality and egg stage on the relationships among variables measuring shell, crab and clutch characterisitcs.

Kruskal-Wallace rank sum tests were used to determine whether the frequency distribution of variables was the same within each group or sample. This method is robust when the data may not come from normally distributed populations and when the variances may be heterogeneous (Zar 1999). Nonparametric multiple comparisons were used to determine whether differences existed among localities for crab shield lengths (mm), crab dry masses (g), clutch sizes (number of eggs per clutch) and clutch masses (g). Nonparametric multiple comparisons used Steel-type test procedures to provide simultaneous rank test procedures for a one-way analysis (Munzel and Hothorn 2001).

Quantile regressions (Cade *et al.* 1999) were used to establish the upper boundaries of relationships between clutch size and crab or shell dimensions. Being able to examine relationships other than estimates of the mean are very useful when response variables show a great deal of variability relative to predictor variables (Cade and Noon 2003). Being able to describe a boundary relationship is ecologically more useful in the investigation of potential maximum realised fecundity than the description of the mean relationship, as given by linear regression. ANCOVA was used to determine whether the relationships between crab mass, shell mass and clutch size and mass differed by locality. Quantile regression lines for each of the northern and southern localities were individually compared to the relevant quantile of the combined data set.

Ovigerous females were not recorded at all the localities used in Chapters 4 and 5. Nahoon Beach and Cintsa West Beach were sampled during September 2000 (Table 6.2). No ovigerous females were found at Nahoon Beach, while only one ovigerous female was found at Cintsa West Beach. These localities were therefore omitted from use in this chapter. Cape Recife was sampled twice a month (on each Spring tide) from 31 October 2001 to 3 October 2002 and 1185 crabs were collected. This sample size was larger than the number of crabs sampled at other localities (Table 6.2). Using all the ovigerous females from Cape Recife would result in extremely unequal sample sizes which would affect some of the statistical tests used. It was therefore appropriate to sub-sample from the Cape Recife data.

Table 6.2: Samples sizes of ovigerous females (OF) and dates at which samples were collected at the different localities.

Localities	***n* (OF)**	**Dates Sampled**
Cape Recife (used in this chapter)	141	28 January, 12 and 28 February, and 14 and 28 March 2002
Morgan Bay	30	2 December 2002
Wavecrest	22	4 December 2002
Dwesa	40	5 December 2002
Coffee Bay	94	6 December 2002
Port St Johns	107	7 December 2002
Port Edward	82	8 December 2002
Park Rynie	128	9 December 2002
Sheffield Beach	88	24 November 2003
Mission Rocks	35	18 October 2002

Other localities from which ovigerous females were recorded were sampled during October (Mission Rocks), November (Sheffield Beach) and December (Morgan Bay, Wavecrest, Dwesa, Coffee Bay, Port St Johns, Port Edward and Park Rynie). The breeding season at Cape Recife started in mid-December, and it would have been appropriate to use data from the same months as the bulk of the other samples. However, the egg dry mass data from Cape Recife for 31 December 2001 and 14 January 2002 presented a problematic set of outlying data points (Figure 6.1). It was possible that a processing error led to the anomalous pattern for these two samples; and they were therefore omitted. The combined samples collected on 28 January, 12 and 28 February, and 14 and 28 March 2002 added up to 181 female crabs, of which 144 were ovigerous (Table 6.2). This sample size was comparable to sample sizes at other localities and was used throughout this chapter as the sub-sample of data from Cape Recife.

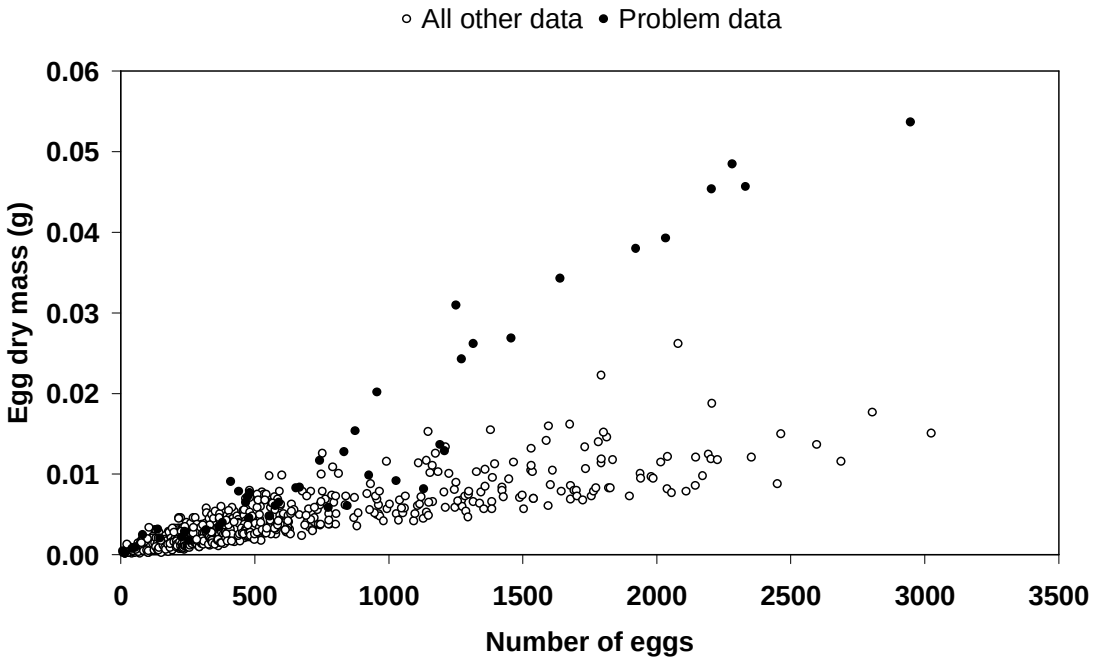

Figure 6.1: Data from 31 December 2001 and 14 January 2002 (problem data) showed an anomalous pattern, possibly as a result of an error in processing, and were omitted from the data set entirely.

6.3 Results

Data from 1188 females, of which 64.5% were ovigerous, were used in this chapter. Ovigerous females ranged in size from 1.90 mm to 6.44 mm, while non-ovigerous females ranged in size from 1.90 mm to 5.96 mm. While only non-ovigerous females in the same size range as ovigerous females were used in analyses, all data were skewed towards the smaller size classes (Figure 6.2). There were higher proportions of non-ovigerous females than ovigerous females in the two smallest size classes, skewing the distribution for non-ovigerous females even further. The mean shield length of ovigerous females was 3.46 ± 0.01 mm, while that of non-ovigerous females was 3.09 ± 0.02 mm. A log-likelihood ratio test (G-test) showed that frequency of occurrence per size class was not independent of female reproductive status ($G = 144.65$, $DF = 9$, $P<0.001$).

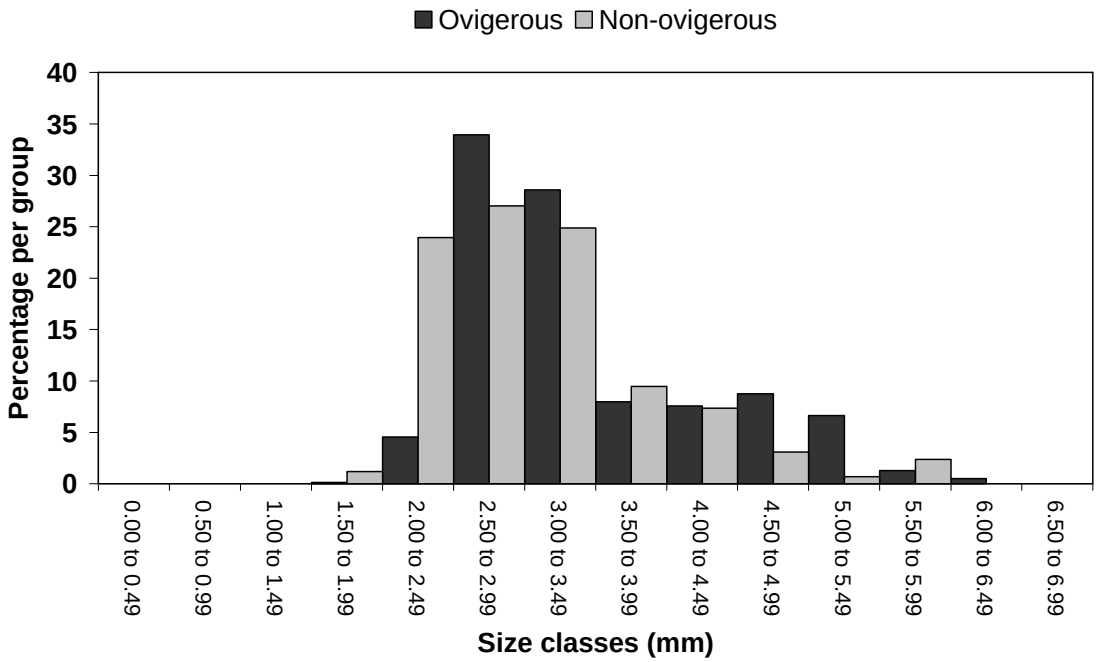

Figure 6.2: Size-frequency distributions for ovigerous and non-ovigerous females show that more small females than large females were recorded, and that there were more small, non-ovigerous females than small ovigerous females.

Minimum ovigerous shield length ranged from 1.90 mm at Coffee Bay to 3.16 mm at Wavecrest (Table 6.3). The proportion of females that were ovigerous ranged from 25.3 % at Wavecrest to 85.3 % of females at Park Rynie.

Table 6.3: Both minimum ovigerous shield length and proportion of ovigerous females vary among localities.

Locality	Minimum ovigerous shield length (mm)	Proportion of females that were ovigerous (%)
Cape Recife	2.80	77.3
Morgan Bay	2.73	31.9
Wavecrest	3.16	25.3
Dwesa	2.84	48.2
Coffee Bay	1.90	75.8
Port St Johns	2.19	75.4
Port Edward	2.30	66.7
Park Rynie	2.46	85.3
Sheffield Beach	2.14	64.7
Mission Rocks	2.03	51.5

Female crabs used a total of 46 shell types at the localities and within the periods sampled. The six most commonly used shell types were *Burnupena cincta* (6.7%), *B. lagenaria* (15.6%), *B. pubescens* (9.7%), *Morula granulata* (25.4%), *M. nodosa* (10.3%) and *Peristernia forskalii* (17.6%). A log-likelihood ratio test (G-test) determined that shell type was not independent of reproductive status ($G = 44.98$, $P < 0.001$, $DF = 5$). Ovigerous females used a larger percentage of *Burnupena lagenaria*, *Morula granulata*, *M. nodosa* and *Peristernia forskalii* than non-ovigerous females, which used more *Burnupena cincta* and *B. pubescens* (Figure 6.3). Non-ovigerous females used more shell types (37) than ovigerous females (29 types).

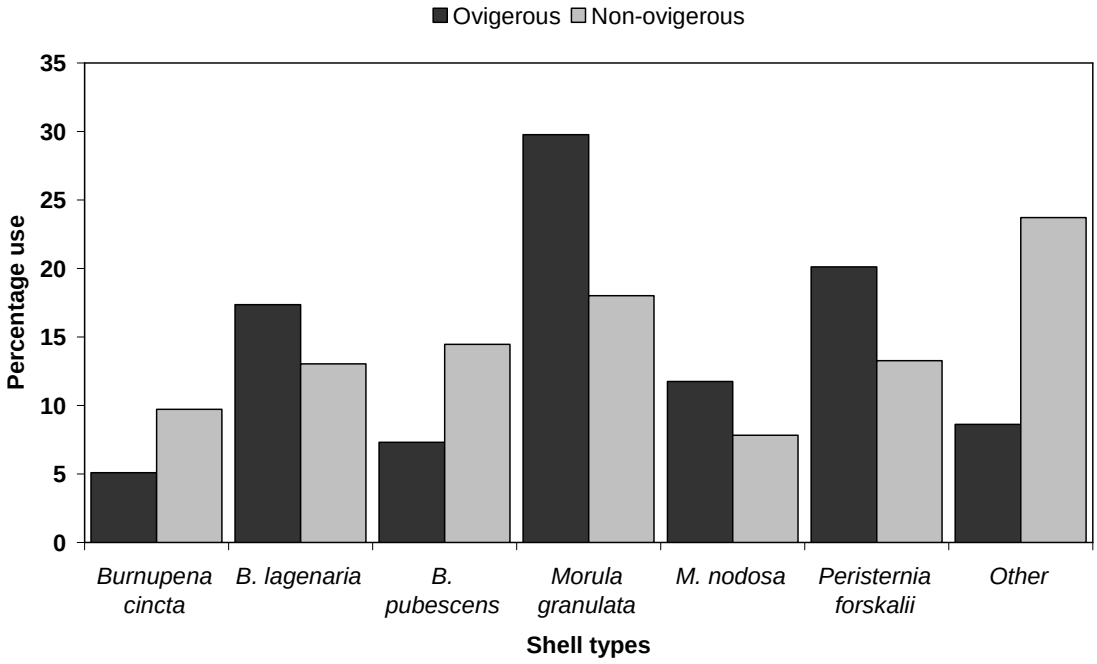

Figure 6.3: Ovigerous and non-ovigerous females use different proportions of the most commonly used shell types, and non-ovigerous females use many more shell types than ovigerous females.

A comparison of frequency of shell use between ovigerous and non-ovigerous females per locality (Table 6.4) showed that at most localities the frequency of use of different shell types was independent of female reproductive state. This result indicated that frequency of use of different shell types did not differ between ovigerous and non-ovigerous females at most localities. *Burnupena* spp. was used frequently at southern localities, while *Morula* spp. and *Peristernia forskalii* were favoured at northern localities (Figure 6.4).

The relationship of shell dimensions (length, width, aperture width, mass and volume) to crab shield length was compared by regression (Table 6.5). The relationship between crab and shell dimensions differed considerably among localities, but at all localities shell volume showed either a strong or the strongest relationship of all shell dimensions to crab shield length, despite lower sample sizes. Shell volumes could not be obtained for all shells as some shells were crushed during the removal of the

crabs. A high coefficient of determination (r^2) indicates the strength of the relationship between the two variables being compared (Zar 1999). Populations at localities where a high coefficient of determination between crab dimensions and shell dimensions were found were considered to be less shell-stressed than those at localities where the relationship was not strong.

Table 6.4: Comparison of frequency of shell use between ovigerous and non-ovigerous females at each of the localities sampled.

Locality	No. shell types used	G	DF	P
Cape Recife	3	106.99	2	P < 0.001
Morgan Bay	5	4.62	4	P > 0.05
Wavecrest	4	2.13	3	P > 0.05
Dwesa	5	3.94	4	P > 0.05
Coffee Bay	7	11.34	6	P > 0.05
Port St Johns	5	9.42	4	P > 0.05
Port Edward	4	0.92	3	P > 0.05
Park Rynie	4	12.11	3	P < 0.01
Sheffield Beach	4	3.00	3	P > 0.05
Mission Rocks	4	7.05	3	P > 0.05

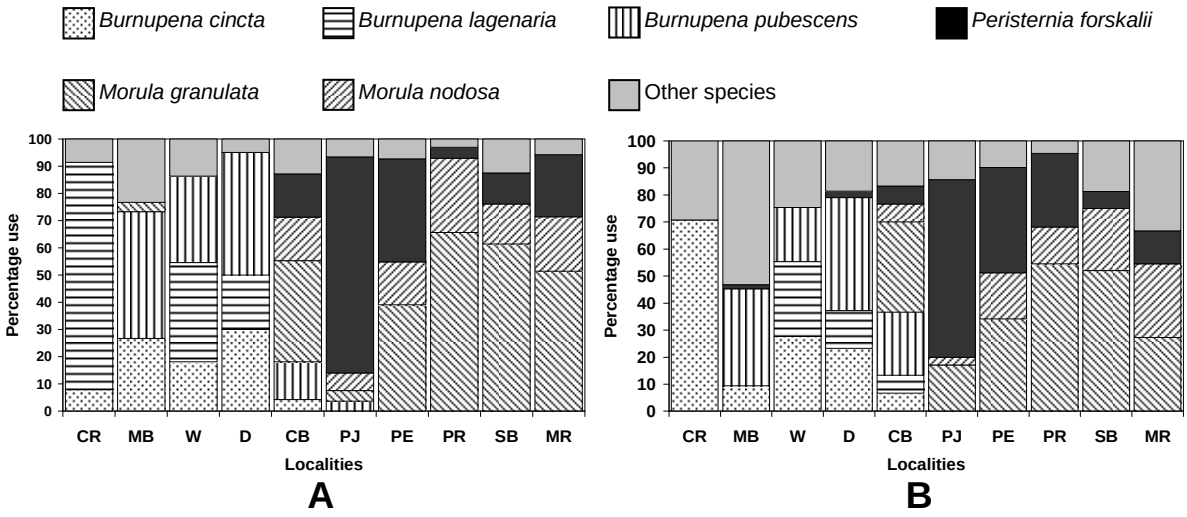

Figure 6.4: Shell use by ovigerous females (A) and non-ovigerous females (B). *Burnupena* spp. dominate the southern localities, while *Morula* spp. dominate the northern localities. From south to north the localities are: Cape Recife (CR), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR).

Table 6.5: Relationships of grouped shell dimensions of the six most commonly used shells to crab shield length (CSL) (mm). Comparisons were done by linear regression of variables at each locality. The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slope	Intercept	r^2	DF	RSE	F	P
Cape Recife							
Shell length (mm) by CSL	3.598	4.977	0.70	159	2.467	382.3	P<0.001
Shell width (mm) by CSL	2.227	2.569	0.81	159	0.939	701.0	P<0.001
Shell aperture width (mm) by CSL	0.478	1.491	0.75	159	0.651	492.5	P<0.001
Shell mass (g)* by CSL	-2.723	2.383	0.76	159	0.249	514.7	P<0.001
Shell volume (mL)* by CSL	-3.876	2.589	0.86	151	0.194	931.1	P<0.001
Morgan Bay							
Shell length (mm) by CSL	9.343	4.592	0.47	49	2.817	46.1	P<0.001
Shell width (mm) by CSL	3.877	2.224	0.57	49	1.128	47.4	P<0.001
Shell aperture width (mm) by CSL	1.333	1.228	0.54	49	0.666	58.9	P<0.001
Shell mass (g)* by CSL	-2.484	2.165	0.49	49	0.322	48.61	P<0.001
Shell volume (mL)* by CSL	-1.193	0.559	0.79	29	0.193	116.0	P<0.001
Wavecrest							
Shell length (mm) by CSL	9.139	4.192	0.69	65	2.242	150.1	P<0.001
Shell width (mm) by CSL	4.431	1.972	0.73	65	0.975	175.5	P<0.001
Shell aperture width (mm) by CSL	1.241	1.248	0.71	65	0.650	158.7	P<0.001
Shell mass (g)* by CSL	-2.548	2.172	0.72	65	0.277	170.3	P<0.001
Shell volume (mL)* by CSL	-3.238	2.229	0.80	48	0.218	202.2	P<0.001
Dwesa							
Shell length (mm) by CSL	6.639	4.889	0.64	66	2.485	120.5	P<0.001
Shell width (mm) by CSL	3.256	2.249	0.79	66	0.789	253.1	P<0.001
Shell aperture width (mm) by CSL	1.445	1.138	0.54	66	0.712	77.9	P<0.001
Shell mass (g)* by CSL	-2.712	2.319	0.75	66	0.237	203.8	P<0.001
Shell volume (mL)* by CSL	-3.147	2.169	0.75	54	0.211	162.1	P<0.001
Coffee Bay							
Shell length (mm) by CSL	3.678	5.616	0.62	100	2.308	168.5	P<0.001
Shell width (mm) by CSL	4.750	1.974	0.49	100	1.054	99.9	P<0.001
Shell aperture width (mm) by CSL	-1.267	1.588	0.50	100	0.839	101.9	P<0.001
Shell mass (g)* by CSL	-0.950	1.193	0.19	100	0.342	24.3	P<0.001
Shell volume (mL)* by CSL	-4.832	3.244	0.84	24	0.255	137.1	P<0.001
Port St Johns							
Shell length (mm) by CSL	7.223	4.621	0.54	126	1.425	149.3	P<0.001
Shell width (mm) by CSL	2.879	2.213	0.47	126	0.782	113.8	P<0.001
Shell aperture width (mm) by CSL	1.037	0.938	0.35	126	0.427	68.8	P<0.001
Shell mass (g)* by CSL	-1.916	1.710	0.34	126	0.279	65.92	P<0.001
Shell volume (mL)* by CSL	-3.821	2.407	0.52	19	0.261	22.4	P<0.001
Port Edward							
Shell length (mm) by CSL	7.435	4.272	0.25	110	1.989	38.7	P<0.001
Shell width (mm) by CSL	4.631	1.777	0.37	110	0.626	67.5	P<0.001
Shell aperture width (mm) by CSL	1.605	0.679	0.11	110	0.508	14.9	P<0.001
Shell mass (g)* by CSL	-1.642	1.643	0.37	110	0.203	67.6	P<0.001
Shell volume (mL)* by CSL	-3.362	1.984	0.61	41	0.145	66.3	P<0.001
Park Rynie							
Shell length (mm) by CSL	7.652	3.663	0.22	141	1.506	40.5	P<0.001
Shell width (mm) by CSL	3.279	2.309	0.32	141	0.730	68.6	P<0.001
Shell aperture width (mm) by CSL	2.463	0.316	0.01	141	0.569	2.11	P=0.148
Shell mass (g)* by CSL	-1.839	1.860	0.26	141	0.231	51.9	P<0.001
Shell volume (mL)* by CSL	-3.365	1.929	0.42	102	0.149	75.5	P<0.001
Sheffield Beach							
Shell length (mm) by CSL	6.743	4.099	0.36	144	1.780	65.6	P<0.001
Shell width (mm) by CSL	2.946	9.455	0.48	114	0.835	106.7	P<0.001
Shell aperture width (mm) by CSL	2.015	0.449	0.06	114	0.554	8.09	P=0.005
Shell mass (g)* by CSL	-1.932	1.986	0.31	114	0.342	53.3	P<0.001
Shell volume (mL)* by CSL	-3.381	1.879	0.56	89	0.197	113.6	P<0.001

Table 6.5 continued: Relationships of grouped shell dimensions of the six most commonly used shells to crab shield length (CSL) (mm). Comparisons were done by linear regression of variables at each locality. The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slope	Intercept	r^2	DF	RSE	F	P
Mission Rocks							
Shell length (mm) by CSL	3.525	5.001	0.47	50	1.427	46.7	P<0.001
Shell width (mm) by CSL	2.590	2.383	0.65	50	0.479	94.2	P<0.001
Shell aperture width (mm) by CSL	1.310	0.581	0.12	50	0.408	7.73	P=0.007
Shell mass (g)* by CSL	-2.111	1.970	0.57	50	0.185	69.0	P<0.001
Shell volume (mL)* by CSL	-3.431	1.678	0.69	31	0.122	71.0	P<0.001

In Chapter 4 it was established that *Morula* spp. had a less rigid morphology than other shell types making it possible that females might use shells with slightly different morphologies within the same shell type. ANCOVA was used to determine whether there was a difference in the relationship of crab shield length to shell dimensions between ovigerous and non-ovigerous females for grouped data of the six most commonly used shell types for each locality (Table 6.6).

At localities where *Burnupena* spp dominate (Figure 6.2), there was little difference in either slopes or intercepts of the relationships between shell and crab dimensions when compared by female reproductive state. Ovigerous and non-ovigerous females used shells with similar morphologies and sizes. However, at Park Rynie and Cape Recife, ovigerous and non-ovigerous females did not use the same frequencies of shell types (Table 6.4) and also used shells with different lengths (at Cape Recife), and masses and volumes (at Park Rynie) (Table 6.6). At Port Edward, Sheffield Beach and Mission Rocks, where the use of morphologically irregular *Morula* spp. dominated, it did not appear that ovigerous and non-ovigerous females used shells with significantly different shapes. Port St Johns showed several differences in the relationship between crab shield length and shell dimensions. Females at Port St Johns used a high percentage of *Peristernia forskalii* compared to other localities (Figure 6.4), which may be implicated in the differences noted.

Table 6.6: The effect of female reproductive state on the relationship of grouped shell dimensions of the six most commonly used shells to crab shield length (CSL) (mm). The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
Cape Recife					
Shell length (mm) by CSL	Do not differ	Differ	8.582	1 on 158	P = 0.004
Shell width (mm) by CSL	Do not differ	Do not differ	3.258	1 on 158	P = 0.073
Shell aperture width (mm) by CSL	Do not differ	Do not differ	0.953	1 on 158	P = 0.331
Shell mass (g)* by CSL	Do not differ	Do not differ	3.316	1 on 158	P = 0.071
Shell volume (mL)* by CSL	Do not differ	Differ	9.105	1 on 150	P = 0.003
Morgan Bay					
Shell length (mm) by CSL	Do not differ	Do not differ	1.629	1 on 48	P = 0.208
Shell width (mm) by CSL	Do not differ	Do not differ	1.996	1 on 48	P = 0.323
Shell aperture width (mm) by CSL	Do not differ	Do not differ	2.615	1 on 48	P = 0.112
Shell mass (g)* by CSL	Do not differ	Do not differ	1.241	1 on 48	P = 0.271
Shell volume (mL)* by CSL	Do not differ	Do not differ	3.162	1 on 28	P = 0.086
Wavecrest					
Shell length (mm) by CSL	Do not differ	Do not differ	0.594	1 on 64	P = 0.444
Shell width (mm) by CSL	Do not differ	Do not differ	0.132	1 on 64	P = 0.718
Shell aperture width (mm) by CSL	Do not differ	Do not differ	1.535	1 on 64	P = 0.219
Shell mass (g)* by CSL	Do not differ	Do not differ	0.685	1 on 64	P = 0.411
Shell volume (mL)* by CSL	Do not differ	Do not differ	0.949	1 on 47	P = 0.335
Dwesa					
Shell length (mm) by CSL	Do not differ	Do not differ	0.266	1 on 65	P = 0.608
Shell width (mm) by CSL	Do not differ	Do not differ	0.387	1 on 65	P = 0.536
Shell aperture width (mm) by CSL	Do not differ	Do not differ	0.000	1 on 65	P = 0.996
Shell mass (g)* by CSL	Do not differ	Do not differ	0.002	1 on 65	P = 0.969
Shell volume (mL)* by CSL	Do not differ	Do not differ	0.816	1 on 53	P = 0.370
Coffee Bay					
Shell length (mm) by CSL	Do not differ	Do not differ	0.332	1 on 99	P = 0.566
Shell width (mm) by CSL	Do not differ	Do not differ	0.412	1 on 99	P = 0.523
Shell aperture width (mm) by CSL	Do not differ	Differ	11.478	1 on 99	P = 0.001
Shell mass (g)* by CSL	Do not differ	Do not differ	0.887	1 on 99	P = 0.349
Shell volume (mL)* by CSL	Do not differ	Do not differ	2.383	1 on 23	P = 0.136
Port St Johns					
Shell length (mm) by CSL	Differ	Differ	5.219	1 on 124	P = 0.024
Shell width (mm) by CSL	Do not differ	Differ	10.672	1 on 125	P = 0.001
Shell aperture width (mm) by CSL	Differ	Differ	22.633	1 on 124	P < 0.001
Shell mass (g)* by CSL	Do not differ	Differ	42.850	1 on 125	P < 0.001
Shell volume (mL)* by CSL	Do not differ	Do not differ	0.075	1 on 18	P = 0.788
Port Edward					
Shell length (mm) by CSL	Do not differ	Do not differ	2.124	1 on 109	P = 0.139
Shell width (mm) by CSL	Do not differ	Do not differ	1.165	1 on 109	P = 0.283
Shell aperture width (mm) by CSL	Do not differ	Do not differ	2.354	1 on 109	P = 0.128
Shell mass (g)* by CSL	Do not differ	Do not differ	1.633	1 on 109	P = 0.204
Shell volume (mL)* by CSL	Do not differ	Do not differ	0.112	1 on 40	P = 0.740
Park Rynie					
Shell length (mm) by CSL	Do not differ	Do not differ	0.599	1 on 140	P = 0.208
Shell width (mm) by CSL	Do not differ	Do not differ	2.996	1 on 140	P = 0.086
Shell aperture width (mm) by CSL	Do not differ	Do not differ	0.248	1 on 140	P = 0.619
Shell mass (g)* by CSL	Differ	Differ	5.663	1 on 139	P = 0.019
Shell volume (mL)* by CSL	Do not differ	Differ	7.924	1 on 101	P = 0.006
Sheffield Beach					
Shell length (mm) by CSL	Do not differ	Do not differ	1.835	1 on 113	P = 0.178
Shell width (mm) by CSL	Do not differ	Do not differ	3.255	1 on 113	P = 0.074
Shell aperture width (mm) by CSL	Do not differ	Do not differ	0.316	1 on 113	P = 0.575
Shell mass (g)* by CSL	Do not differ	Do not differ	2.223	1 on 113	P = 0.139
Shell volume (mL)* by CSL	Do not differ	Do not differ	2.384	1 on 88	P = 0.126

Table 6.6 continued: The effect of female reproductive state on the relationship of grouped shell dimensions of the six most commonly used shells to crab shield length (CSL) (mm). The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

Dimensions	Slopes	Intercepts	F	DF	P
Mission Rocks					
Shell length (mm) by CSL	Do not differ	Do not differ	0.136	1 on 49	P = 0.714
Shell width (mm) by CSL	Do not differ	Do not differ	0.498	1 on 49	P = 0.484
Shell aperture width (mm) by CSL	Do not differ	Do not differ	0.053	1 on 49	P = 0.819
Shell mass (g)* by CSL	Do not differ	Do not differ	0.041	1 on 49	P = 0.841
Shell volume (mL)* by CSL	Do not differ	Do not differ	0.621	1 on 30	P = 0.437

In Chapter 5 it was established that average crab size decreased from southern to northern localities. This trend was reflected by the shield lengths and masses of both ovigerous and non-ovigerous females (Figure 6.5). Non-parametric multiple comparisons showed that two localities stand out from the others. Ovigerous females at Cape Recife were significantly larger and heavier than at other localities, while both ovigerous and non-ovigerous females at Mission Rocks were significantly smaller and lighter than at other localities.

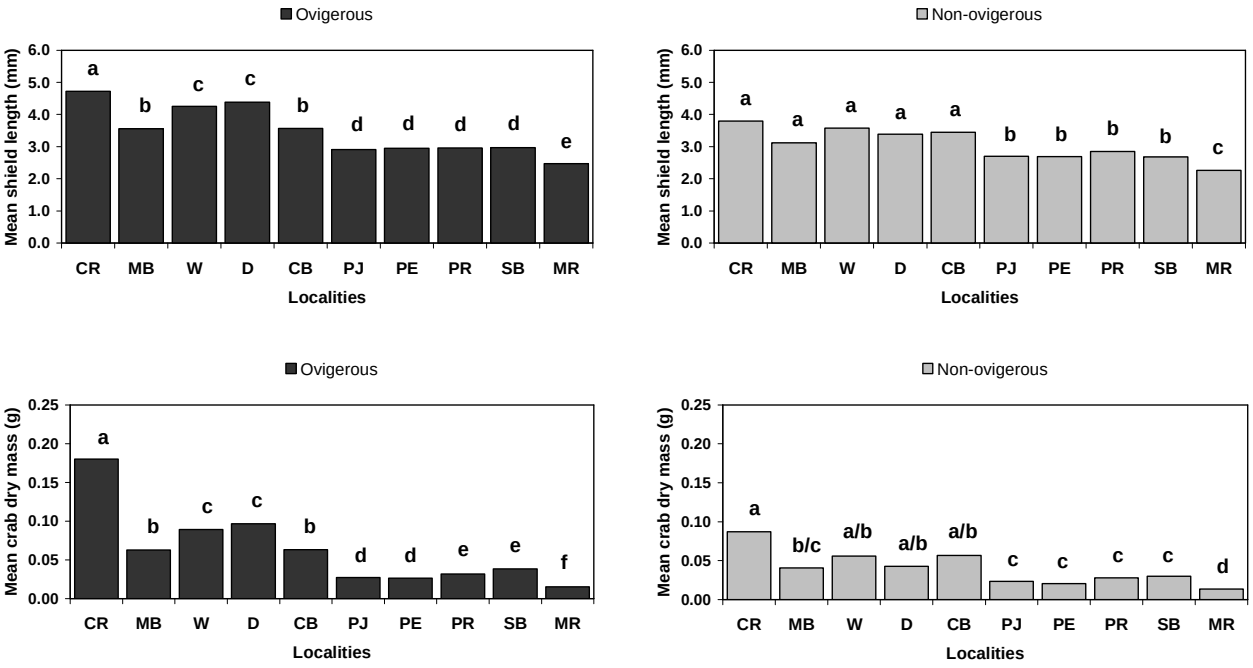

Figure 6.5: Average shield lengths and dry masses vary among localities. Ovigerous females at Cape Recife form a distinct group. However, the southern localities, Cape Recife (CR), Morgan Bay (MB), Wavecrest (W), Dwesa (D) and Coffee Bay (CB) show similarities, as do the northern localities, Port St Johns (PJ), Port Edward (PE), Park Rynie (PR) and Sheffield Beach (SB). In all cases Mission Rocks (MR) is significantly different to other localities. (In each graph, columns with the same letter are not significantly different to each other).

Within localities, significant differences in shield length and dry mass between ovigerous and non-ovigerous females were recorded in a few instances (Table 6.7). Localities at which there was no significant difference in mean shield length were Coffee Bay and Park Rynie, while no significant difference in mean dry mass was recorded at Coffee Bay, Port St Johns, Park Rynie and Mission Rocks. While ovigerous and non-ovigerous females analysed in this chapter were all within the same size range (1.90 mm to 6.44 mm), mean lengths and masses for ovigerous females were consistently larger for ovigerous females than for non-ovigerous females.

Table 6.7: Comparisons of mean shield lengths and dry masses between ovigerous and non-ovigerous females at each locality.

Locality	Shield length (mm)			Dry Mass (g)		
	t	DF	P	t	DF	P
Cape Recife	5.32	48	P < 0.001	6.44	62.89	P < 0.001
Morgan Bay	3.69	81	P < 0.001	3.44	73.86	P < 0.001
Wavecrest	3.70	42	P < 0.001	3.06	35.58	P < 0.001
Dwesa	7.24	77	P < 0.001	6.39	54.46	P < 0.001
Coffee Bay	0.90	52	P = 0.369	0.82	52.67	P = 0.414
Port St Johns	2.21	47	P < 0.001	1.24	45.16	P = 0.221
Port Edward	4.80	72	P < 0.001	3.92	69.57	P < 0.001
Park Rynie	1.62	25	P = 0.118	1.63	24.68	P = 0.115
Sheffield Beach	4.99	82	P < 0.001	2.89	97.86	P = 0.005
Mission Rocks	2.98	66	P = 0.004	1.01	57.36	P = 3.17

Clutch sizes ranged from 9 eggs to 3024 eggs (Table 6.8). Eggs in all stages of development except Stage 5 (see Chapter 2) were found in the samples. At most localities and for grouped data, Stage 1 eggs make up the largest proportion of the total number of clutches (Table 6.8).

When all eggs were grouped, clutch size decreased in each progressive developmental stage for both mean and maximum number of eggs, but this difference was not significant when tested by a Kruskall-Wallace rank sum test (χ^2 = 3.88, DF = 3, P = 0.274). However, there was a significant difference in mean clutch mass among stages (χ^2 = 21.5465, DF= 3, P < 0.001) as clutch mass also decreased with developmental stage. There was a significant positive relationship between clutch mass and number of eggs per clutch (r^2 = 0.74, DF = 759, P < 0.001), although both slopes and intercepts of this relationship differed when ANCOVA was used to compare the relationship by stage (F = 6.3865, DF = 3 on 753, P < 0.001).

There was a stronger relationship between untransformed data for crab shield length, crab mass, shell mass and shell volume compared to clutch size than between transformed data (Table 6.9). However, when data were transformed by taking the

natural logarithm of all variables, a better distribution of residuals against fitted values resulted, indicating that transformation had homogenised data variance (Figure 6.6). When ANCOVA was used on transformed data to compare the relationship of crab shield length, crab mass, shell mass and shell volume to clutch size by developmental stage, it was shown that stage affected the slopes of the relationship of all variables except shell volume, to clutch size (Table 6.10). To remove the potentially confounding effect of egg stage, only Stage 1 eggs were used in subsequent analyses involving clutch size or clutch mass.

Table 6.8: Clutch sizes for broods with eggs in different stages. There is a great deal of variability in the number of eggs per brood for all egg stages.

	Minimum	Maximum	Mean	*n*	SE
All Localities					
Stage 1	15	3024	566.61	537	0.99
Stage 2	85	2463	512.95	115	3.92
Stage 3	9	2597	480.04	79	5.53
Stage 4	20	1835	401.69	32	13.35
Cape Recife					
Stage 1	32	3024	1296.14	112	5.56
Stage 2	154	2463	1295.50	14	47.59
Stage 3	232	2597	1166.78	9	78.76
Stage 4	356	1835	975.60	5	132.28
Morgan Bay					
Stage 1	78	1154	301.52	27	8.35
Stage 2					
Stage 3			9.00	1	
Stage 4			25.00	1	
Wavecrest					
Stage 1	15	965	413.40	20	14.58
Stage 2			216.00	1	
Stage 3			57.00	1	
Stage 4					
Dwesa					
Stage 1	15	2040	760.47	30	17.92
Stage 2	115	1387	550.50	6	76.01
Stage 3	109	2015	742.00	4	219.15
Stage 4					
Coffee Bay					
Stage 1	117	1801	620.94	52	7.36
Stage 2	238	1731	598.05	22	18.43
Stage 3	185	1532	547.09	11	36.53
Stage 4	150	1245	485.63	8	46.04
Port St Johns					
Stage 1	78	929	284.09	63	2.56
Stage 2	140	624	296.88	25	5.53
Stage 3	28	523	343.25	16	7.18
Stage 4	69	383	261.33	3	56.17
Port Edward					
Stage 1	41	715	279.11	53	2.62
Stage 2	128	617	350.46	13	12.06
Stage 3	177	633	355.08	13	10.52
Stage 4	99	442	213.67	3	65.91
Park Rynie					
Stage 1	55	747	342.79	76	1.92
Stage 2	156	777	413.79	24	6.60
Stage 3	48	709	365.50	20	8.36
Stage 4	20	581	308.38	8	24.70
Sheffield Beach					
Stage 1	66	803	303.53	80	1.71
Stage 2	85	394	239.50	2	109.25
Stage 3	234	335	279.67	3	17.06
Stage 4	45	100	63.67	3	10.49
Mission Rocks					
Stage 1	64	384	190.21	24	2.92
Stage 2	127	480	223.50	8	15.56
Stage 3			113.00	1	
Stage 4	65	274	169.50	2	73.89

Table 6.9: The effect of data transformation on the relationship between crab shield length, crab mass, shell mass and shell volume and clutch size for eggs in all developmental stages. (* indicates transformation of both variables by taking the natural logarithm.)

	r^2	RSE	F	DF	P
Clutch size by crab shield length (mm)	0.61	318.1	1196	759	P < 0.001
Clutch size by crab mass (g)	0.63	311.6	1277	759	P < 0.001
Clutch size by shell mass (g)	0.47	372.8	664	759	P < 0.001
Clutch size by shell volume (mL)	0.48	419.1	432	469	P < 0.001
Clutch size by crab shield length (mm)*	0.45	0.650	621	759	P < 0.001
Clutch size by crab mass (g)*	0.45	0.647	363	759	P < 0.001
Clutch size by shell mass (g)*	0.32	0.722	361	759	P < 0.001
Clutch size by shell volume (mL)*	0.38	0.726	289	469	P < 0.001

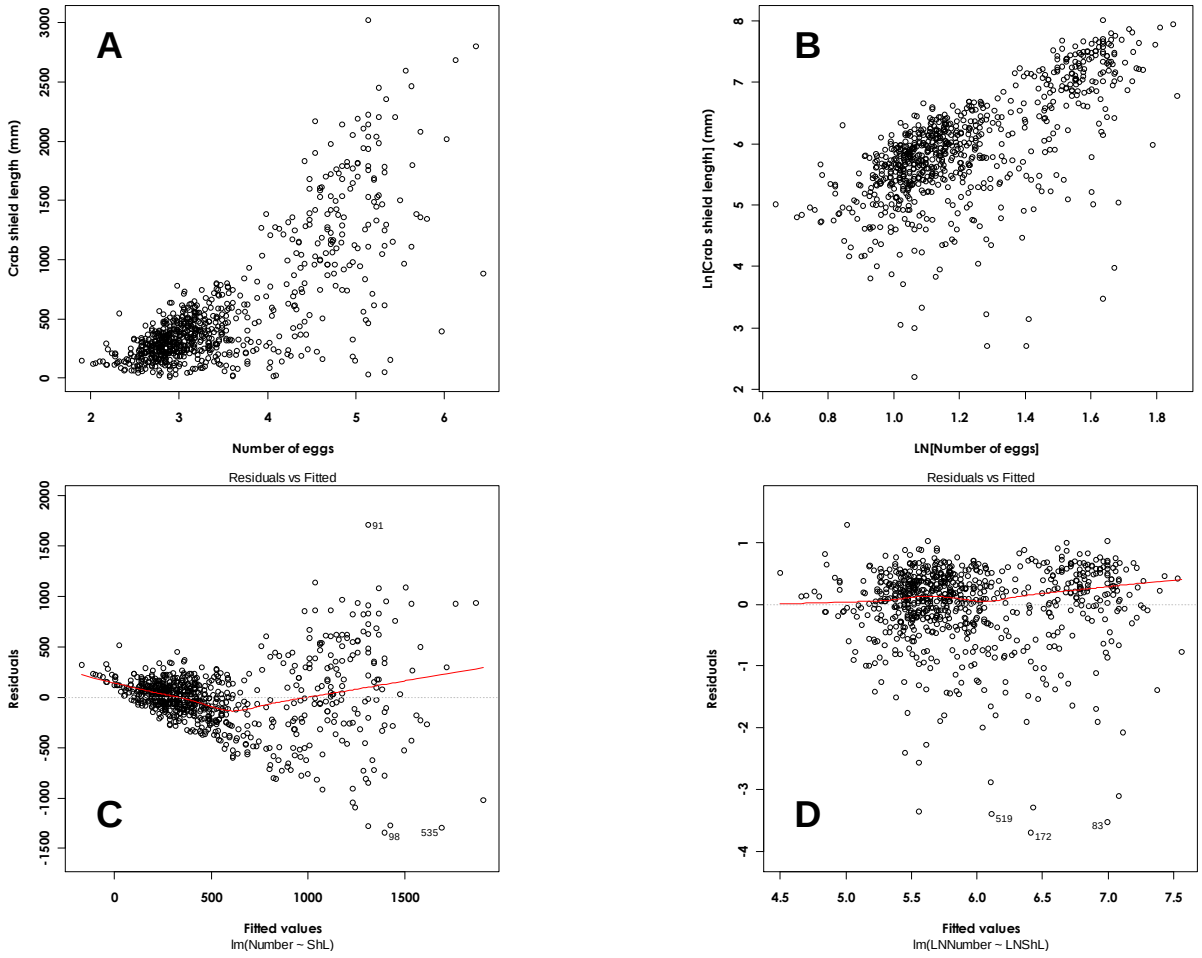

Figure 6.6: The relationship of crab shield length to the number of eggs (A) is used as an example to show how transformation of the data (B) affects the distribution of residuals from indicating heteroscedasticity (C) to a more homoscedastic distribution (D).

Table 6.10: The effect of egg developmental stage on the relationship between the number of eggs and crab shield length, crab mass, shell mass and shell volume. (* indicates transformation of both variables by taking the natural logarithm.)

	Slopes	Intercepts	F	DF	P
Number of eggs by crab shield length (mm)*	Do not differ	Differ	4.54	3 on 756	P=0.004
Number of eggs by crab mass (g)*	Do not differ	Differ	8.04	3 on 756	P<0.001
Number of eggs by shell mass (g)*	Do not differ	Differ	6.36	3 on 756	P<0.001
Number of eggs by shell volume (mL)*	Do not differ	Do not differ	0.39	3 on 463	P<0.763

The strength of the relationships between crab dimensions (shield length and mass) and shell dimensions (mass and volume) to clutch size and mass for Stage 1 eggs (Table 6.11) indicated that clutch size and mass were more sensitive to crab size than to shell dimensions. The relationships were all positive and showed that large females had larger clutches than smaller females, and that heavier, therefore larger, and more voluminous shells could accommodate larger clutches.

Multiple regression techniques were applied to estimate the contribution of predictor variables to clutch size and mass. A multiple regression of crab shield length, crab mass and shell volume to clutch size accounted for 51.2% of the variability in clutch size, slightly improving upon the explanatory ability of individual predictors (Table 6.11). Crab mass, shell volume and crab shield length influenced clutch size in descending order, while shell mass proved to be a non-significant relationship in the comparison. Clutch mass, however, was only significantly affected by crab mass and not by any of the other predictor variables when all predictor variables were included in a multiple regression.

Table 6.11: The relationships between crab shield length, crab mass, shell mass and shell volume and clutch size for Stage 1 eggs. The significance of the regressions was tested by analysis of variance. (* indicates transformation of both variables by taking the natural logarithm.)

	r^2	RSE	F	DF	P
Clutch size by crab shield length (mm)*	0.47	0.639	479.5	533	P < 0.001
Clutch size by crab mass (g)*	0.50	0.622	534.3	533	P < 0.001
Clutch size by shell mass (g)*	0.35	0.712	282.3	533	P < 0.001
Clutch size by shell volume (mL)*	0.43	0.696	241.2	354	P < 0.001
Clutch size by shield length, shell mass and shell volume*	0.51	0.664	124.7	3 & 351	P < 0.001
Clutch mass by crab shield length (mm)*	0.38	0.657	322.1	533	P < 0.001
Clutch mass by crab mass (g)*	0.39	0.652	335.7	533	P < 0.001
Clutch mass by shell mass (g)*	0.29	0.701	218.0	533	P < 0.001
Clutch mass by shell volume (mL)*	0.36	0.682	0.682	354	P < 0.001

ANCOVA was used to test the effect of locality on the relationship of crab shield length, crab mass, shell mass and shell volume to clutch size and clutch mass of Stage 1 eggs. For crab dimensions both the slopes and intercepts of the relationships differ by locality, but for shell dimensions the slopes remain constant, while the intercepts differ (Table 6.12), indicating that the relationship between crab dimensions and clutch size is more easily affected by locality than the relationship between shell dimensions and clutch size.

Table 6.12: The effect of locality on the relationship between clutch size and clutch mass, and crab shield length, crab mass, shell mass and shell volume for Stage 1 eggs. (* indicates transformation of both variables by taking the natural logarithm.)

	Slopes	Intercepts	F	DF	P
Clutch size by crab shield length (mm)*	Differ	Differ	2.11	9 on 515	P=0.027
Clutch size by crab mass (g)*	Differ	Differ	3.58	9 on 515	P<0.001
Clutch size by shell mass (g)*	Do not differ	Differ	18.09	9 on 524	P<0.001
Clutch size by shell volume (mL)*	Do not differ	Differ	11.59	9 on 345	P<0.001
Clutch mass by crab shield length (mm)*	Differ	Differ	156.58	9 on 515	P=0.027
Clutch mass by crab mass (g)*	Differ	Differ	3.88	9 on 515	P<0.001
Clutch mass by shell mass (g)*	Do not differ	Differ	23.05	9 on 524	P<0.001
Clutch mass by shell volume (mL)*	Do not differ	Differ	14.21	9 on 345	P<0.001

Nonparametric multiple comparisons showed that there were significant differences among localities for both clutch size and clutch mass (Figure 6.7). The number of eggs per clutch closely mirrors ovigerous female mass (Figure 6.5). The southern group of localities (Cape Recife, Morgan Bay, Wavecrest and Dwesa) as defined by shell use (see Chapter 4), tend to have larger and markedly heavier clutches than the northern localities (Coffee Bay, Port St Johns, Port Edward, Park Rynie, Sheffield Beach and Mission Rocks). Although shell use at Coffee Bay has more in common with the northern localities, clutch size and mass are similar to those found at the southern localities. As with shield length and mass of ovigerous females, Cape Recife again stands out with much larger and heavier clutches than other localities.

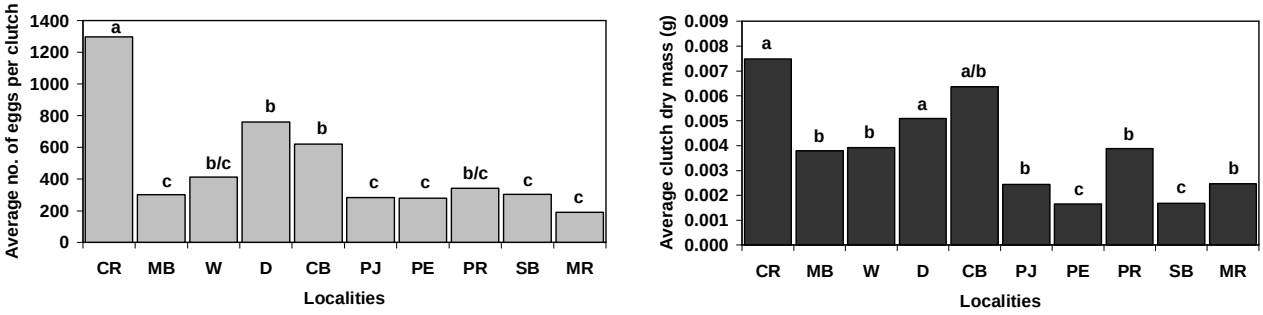

Figure 6.7: Patterns of clutch size and clutch mass among localities indicate that southern localities have larger, and particularly heavier, clutches than northern localities. The localities from South to North are Cape Recife (CR), Morgan Bay (MB), Wavecrest (W), Dwesa (D), Coffee Bay (CB), Port St Johns (PJ), Port Edward (PE), Park Rynie (PR), Sheffield Beach (SB) and Mission Rocks (MR). In each graph, columns with the same letter are not significantly different to each other.

In Chapters 4 and 5 it was demonstrated that *Burnupena* spp. have greater volume-to-mass ratios than *Morula* spp and *Peristernia forskalii*. These shell groups were also representative of shells most commonly used in southern (*Burnupena* spp.) and northern (*Morula* spp. and *Peristernia forskalii*) localities. Given that both shell

volume and shell mass might affect clutch size, ANCOVA was used to compare the relationships between clutch size and clutch mass to shell volume and shell mass by shell type for the six most commonly used shell types (Table 6.13). The relationships of clutch size to both shell mass and volume were influenced by shell type, but the relationship of clutch mass to shell dimensions was more sensitive to shell type, as both slopes and intercepts of the interactions varied. These results indicated that the type of shell used by ovigerous females affected the size and mass of clutches through the interplay of shell mass and volume.

Nonparametric multiple comparisons of clutch sizes in each shell type showed that clutch sizes in *Burnupena* spp. were not significantly different to each other, while clutch sizes in *Morula* spp. and *Peristernia forskalii* showed no significant difference to each other (Figure 6.8). Clutch sizes in *Burnupena* spp. were, however, significantly different from those in *Morula* spp. and *Peristernia forskalii*.

Table 6.13: The effect of shell type on the relationship between clutch variables (size and mass) and shell dimensions (mass and volume). (* indicates transformation of both variables by taking the natural logarithm.)

	Slopes	**Intercepts**	**F**	**DF**	**P**
Clutch size by shell mass (g)*	Do not differ	Differ	6.19	5 on 478	P < 0.001
Clutch size by shell volume (mL)*	Do not differ	Differ	6.37	5 on 314	P < 0.001
Clutch mass by shell mass (g)*	Differ	Differ	1.20	5 on 473	P = 0.308
Clutch mass by shell volume (mL)*	Differ	Differ	1.07	5 on 309	P = 0.378

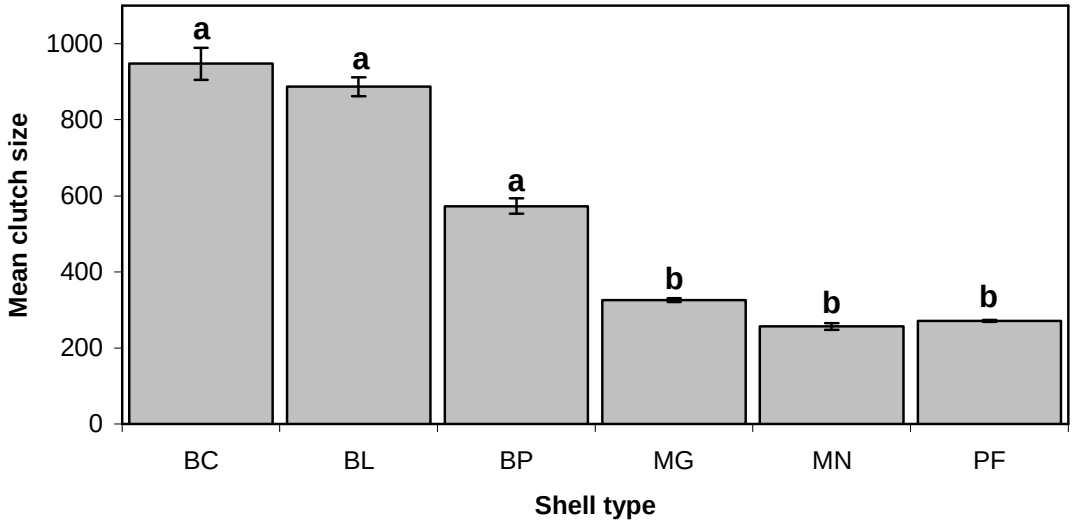

Figure 6.8: There is a significant difference in the mean clutch sizes produced by females in different shell types. Shells of *Burnupena* spp., characteristic of southern localities, house similar clutch sizes as do shells of *Morula* spp. and *Peristernia forskalii*, which are characteristic of northern localities. Shell types are *Burnupena cincta* (BC), *B. lagenaria* (BL), *B. pubescens* (BP), *Morula granulata* (MG), *Morula nodosa* (MN) and *Peristernia forskalii* (PF). Columns with the same letter are not significantly different to each other. Error bars indicate the standard error.

Notwithstanding the significantly positive relationships between crab dimensions, shell dimensions and clutch variables (Table 6.11), there was great deal of variation in the number of eggs, and consequently the mass of clutches produced by female hermit crabs (Figure 6.9). Even large, heavy females in large (heavy) and voluminous shells could produce very small clutches, leading to relatively low coefficients of determination (r^2) in the relationships of crab and shell dimensions to clutch size and mass. A linear regression through transformed data could, at best, describe the nature of the relationship, but could not give ecologically useful information about the upper limits of clutch size that might be predicted by crab and shell dimensions. There clearly were upper limits as indicated by the sharp upper boundary to clutch size when plotted against crab and shell dimensions (Figure 6.9).

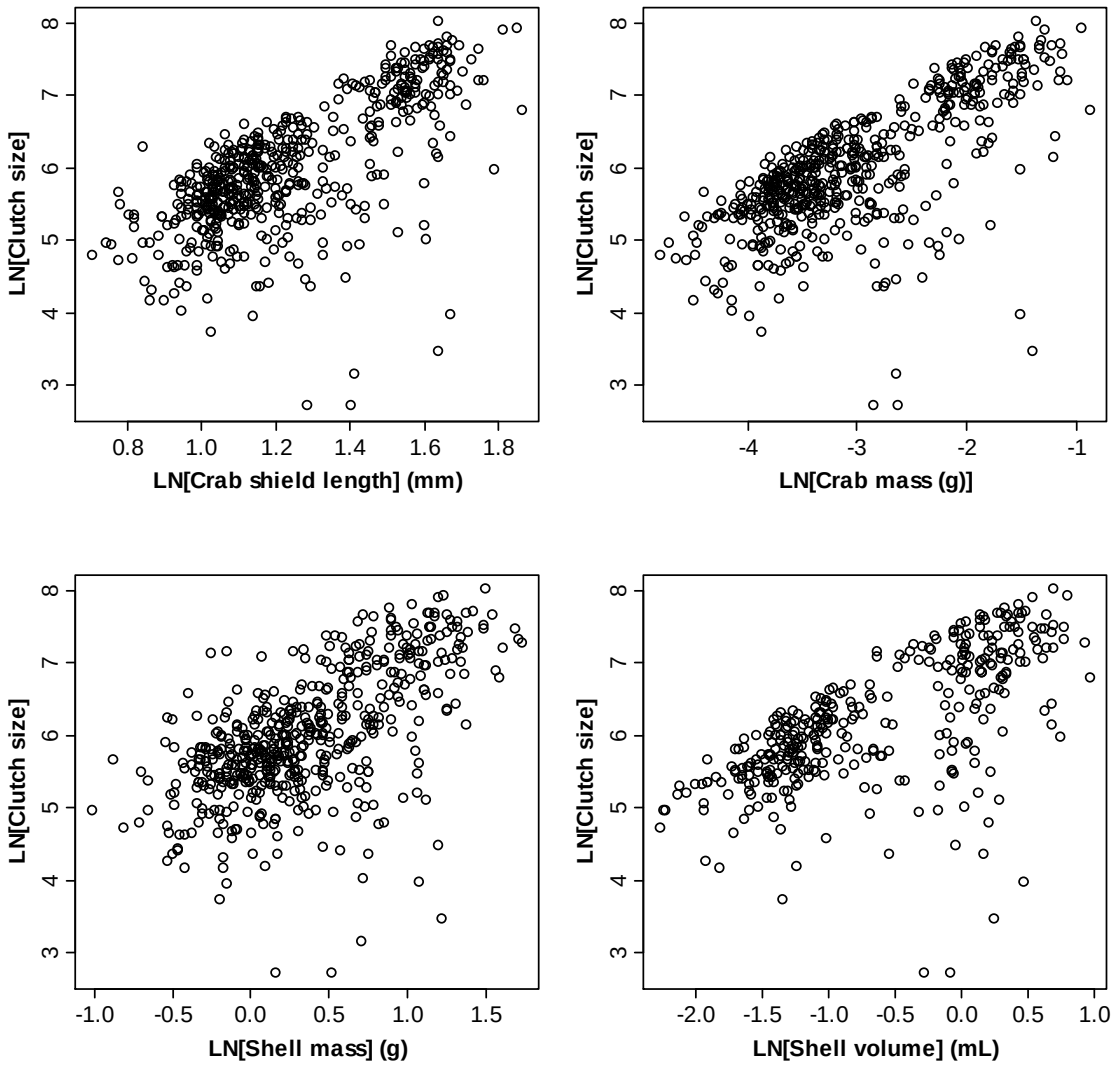

Figure 6.9: There was a great deal of variability in clutch size as some large, heavy females in large (heavy), voluminous shells had small clutches. There was, however, an upper boundary for clutch size, most clearly seen in the relationships of crab mass and shell volume to clutch size.

Quantile regressions at the 95th percentile were used to describe the upper boundaries for these relationships (Figure 6.10). Just as multiple linear regressions can be compared, multiple quantile regressions can also be compared. Attempting comparison by individual locality proved unsuccessful because of small sample sizes at some localities. Data were therefore grouped into southern and northern localities according to shell use patterns (See Chapter 4) and regressions of the 95th percentiles of the relationship between crab dry mass and clutch size, and

regressions of shell volume to clutch size were compared to determine whether there was a difference in the upper boundary of clutch size between southern and northern localities.

Only quantile regressions for crab dry mass by clutch size, and shell volume by clutch size were compared between northern and southern localities because it seemed that crab dry mass and shell volume were the best predictors of the upper boundary of clutch size among the crab dimensions and shell dimensions, respectively. This assessment was based on examination of both coefficients of determination (r^2) (Table 6.11), and from visual inspection of the crispness of the upper boundary of clutch size (Figure 6.9)

Slopes and intercepts of the separate quantile regression models for data from northern and southern localities were compared to a quantile regression model of the pooled data. For the relationship between clutch size and dry mass the slopes and intercepts of the separate quantile regressions for data from northern and southern localities did not differ from that of the pooled data. However for the relationship between clutch size and shell volume, both slopes and intercepts differed, indicating that the relationship of clutch size to shell volume does not remain constant between northern and southern localities (Table 6.14).

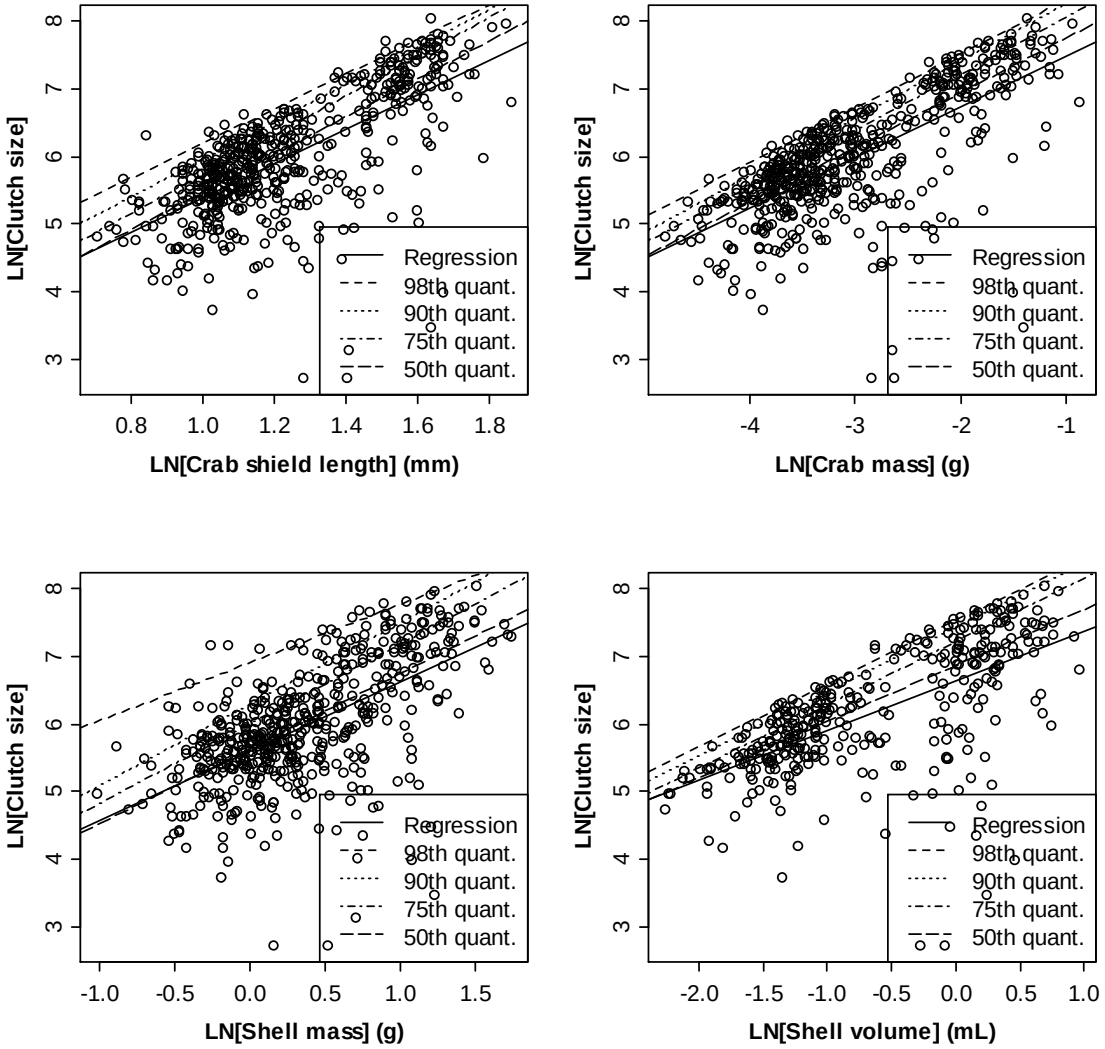

Figure 6.10: Quantile ranges between 98th to the 90th quantiles were considered good estimates of the upper boundary of clutch size.

Table 6.14: The effect of locality (northern vs. southern localities) on regressions of the 95th quantiles of the relationships of clutch size to crab mass and shell volume. (* indicates transformation of both variables by taking the natural logarithm.)

	Slopes	Intercepts	t	DF	P
Clutch size by crab mass (g)*	Do not differ	Do not differ	0.1966	534	P = 0.196
Clutch size by shell volume (mL)*	Differ	Differ	-3.6258	352	P < 0.001

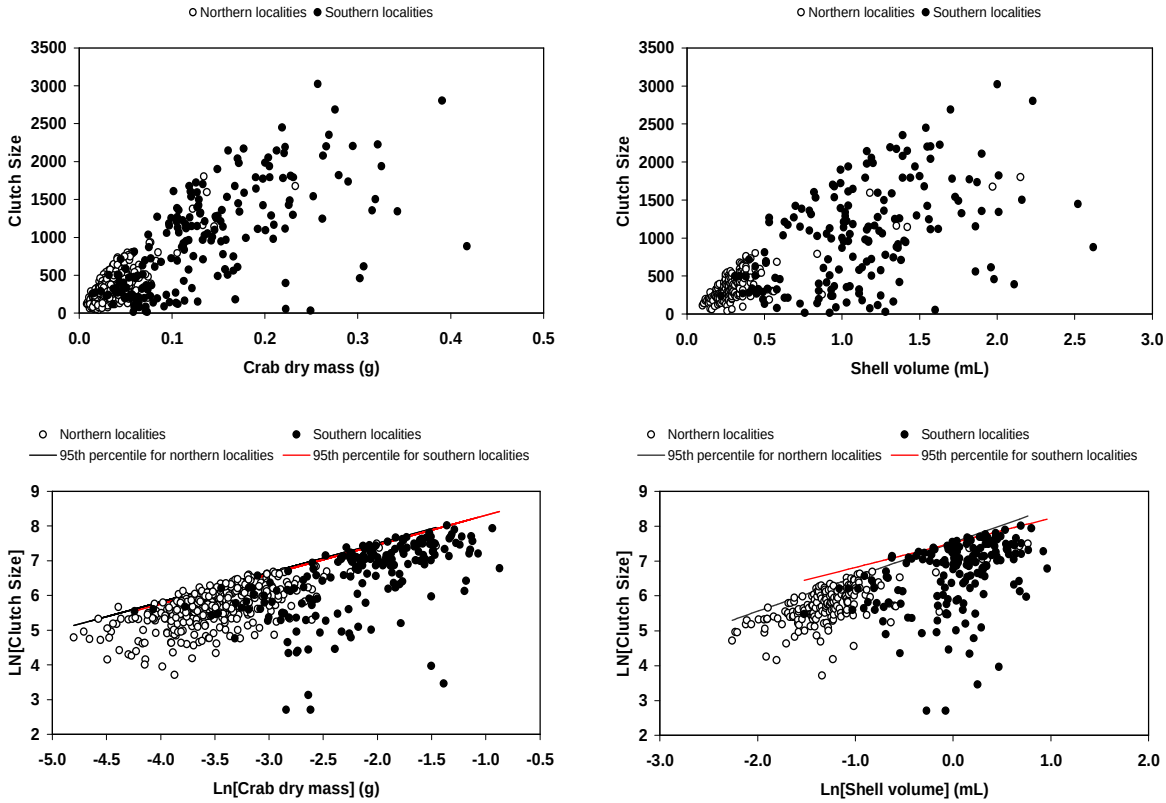

Figure 6.11: Female crabs of the same masses are able to produce the same number of eggs at a given mass regardless of locality, but clutch sizes are affected by shell volumes between localities.

The egg diameters of 1708 eggs from 217 females were measured (see Chapter 2 for method), and the average egg diameter per female was determined. It has been demonstrated that females in northern localities produce smaller clutches than females in southern localities.

It is hypothesised that females in northern localities might maximize their reproductive output by producing smaller eggs, thus being able to fit more eggs into shells with smaller volume relative to southern females. If northern females had smaller eggs than southern females it would mean that although they had smaller clutch sizes, they produced more eggs relative to southern females and thus had greater potential fitness than southern females. The relationships of potential

predictors of egg size (clutch size, clutch mass, crab shield length, crab mass, shell weight and shell volume) were compared to average egg diameters. Data for eggs in all developmental stages as well as for Stage 1 eggs were used in the comparisons to determine whether egg diameter was affected by egg stage, as found for clutch size and clutch mass.

When the predictor variables (clutch size, clutch mass, crab shield length, crab mass, shell weight and shell volume) were compared to egg diameter for grouped data of eggs in all developmental stages, weak but significant relationships were found for all comparisons (Table 6.15). The strongest relationships were clutch mass, crab shield length and shell volume to average egg diameter (Table 6.15). Egg diameter shows a positive relationship to developmental stage ($r^2 = 0.71$, DF = 216, F = 524.9, $P < 0.001$). This means that eggs in late developmental stages are bigger than in earlier stages. If egg diameters are compared among localities, a locality with a high proportion of eggs in late developmental stages (for example Port St Johns or Park Rynie, Table 6.8) will give misleading results. This effect is demonstrated by the significant differences in mean egg diameter among different localities when all developmental stages are compared ($\chi^2 = 18.57$, DF = 5, P = 0.002) by a Kruskall-Wallace rank sum test. These differences once again make it prudent to use only Stage 1 eggs in comparisons of predictor variables to egg diameters, especially if the relationships are compared among localities.

Diameters of Stage 1 eggs showed only one significant relationship (crab shield length) with any of the potential predictors (Table 6.15). Egg diameter decreased slightly with increasing shield length. Egg diameters showed no significant differences when Stage 1 eggs were compared among localities ($\chi^2 = 5.774$, DF = 5,

P = 0.329). This indicates that females at different localities do not produce eggs with different mean sizes and that northern females do not maximize their reproductive output by producing smaller eggs.

Table 6.15: The relationship of predictors of egg diameter and egg diameter show only one significant relationship for Stage 1 eggs, while grouped data for eggs in all developmental stages show weak but significant relationships of all predictors to egg diameter.

	r^2	RSE	F	DF	P
All developmental stages					
Egg diameter (mm) by clutch size (mm)*	0.029	0.145	7.419	216	P = 0.007
Egg diameter (mm) by clutch mass (g)*	0.092	0.146	23.050	216	P < 0.001
Egg diameter (mm) by shield length (mm)*	0.081	0.141	20.190	216	P < 0.001
Egg diameter (mm) by crab mass (g)*	0.034	0.145	8.681	216	P = 0.004
Egg diameter (mm) by shell mass (g)*	0.019	0.146	5.303	216	P = 0.022
Egg diameter (mm) by shell volume (mL)*	0.119	0.128	15.380	105	P = 0.002
Developmental Stage 1					
Egg diameter (mm) by clutch size (mm)*	0.002	0.083	1.288	153	P = 0.258
Egg diameter (mm) by clutch mass (g)*	<0.001	0.083	1.031	153	P = 0.311
Egg diameter (mm) by shield length (mm)*	0.022	0.082	4.470	153	P = 0.036
Egg diameter (mm) by crab mass (g)*	0.004	0.082	1.586	153	P = 0.209
Egg diameter (mm) by shell mass (g)*	0.012	0.082	2.829	153	P = 0.095
Egg diameter (mm) by shell volume (mL)*	-0.007	0.071	0.419	79	P = 0.519

6.4 Discussion

Many hermit crab life-history traits are closely bound to the shell resource available to them. This chapter demonstrates that, at localities where females were unable to obtain large shells, the size of ovigerous females was reduced and clutch sizes were consequently reduced. This is in sharp contrast to localities where females had access to larger shells, attained larger sizes and produced significantly larger clutches.

At most localities there were significant differences in the mean shield length between ovigerous and non-ovigerous females, and ovigerous females were larger than non-ovigerous females. At most localities ovigerous females made up a large proportion of the females sampled. Fecundity is related to female size and it may benefit small females to grow before reproducing. Yoshino *et al.* (2002) found that small *Pagurus filholi* females breed later than larger females. This strategy represents a trade-off between future and current reproduction. Small females have smaller clutches than larger females, but by breeding late in the season they maximise growth while still ensuring that they will reproduce at least once during their lives. It is difficult to determine why large non-ovigerous females have no eggs. By the argument presented above, large females may breed earlier than small females and at least some of the large non-ovigerous females sampled may have been between clutches. Non-ovigerous females may also not be in their preferred shells. Elwood *et al.* (1995) found that large *Pagurus bernhardus* females in preferred shells produced two clutches per breeding season, while those in less preferred shells produced only one clutch, often with reduced clutch size. In this study, non-ovigerous *Clibanarius virescens* used more shell types than ovigerous females, and it

is possible that some of those shell types represent less preferred shells for *C. virescens*.

Female reproduction may also be affected by the fit of the shells used. The coefficient of determination (r^2) for relationships of shell dimensions to crab dimensions has been used as an indicator of shell adequacy, especially in hermit crabs taken from the field (Scully 1983, Turra and Leite 2002, Turra and Leite 2004). Females from most of the southern localities (Cape Recife, Wavecrest and Dwesa) showed a good fit between crab shield length and shell dimensions. At these localities the use of *Burnupena* spp. dominated, and few other shell types are used. In contrast to this, at another southern locality, Morgan Bay, females used more shell types than at other southern localities. Paradoxically it would seem that greater choice did not lead to better shell fit in this instance. It may be that at Cape Recife, Wavecrest and Dwesa *Burnupena* shells were available in sufficient quantities for females to use shells that fitted well despite potential competition from males, while at Morgan Bay males out-competed females and monopolised access to the best shells. "Best shells" for females seemed to be the most voluminous shells as females from all localities showed the strongest relationship between shield length and shell volume. This parameter seemed to be the defining characteristic of an adequate shell. Shells of *Burnupena* spp. were larger, and relatively lighter and more voluminous than shells of *Morula* spp. and of *Peristernia forskalii*. This was reflected strongly in female size. At Cape Recife, Wavecrest and Dwesa females were significantly larger and heavier than at either Morgan Bay or northern localities.

Females from northern localities were found almost exclusively in the shells of *Morula* spp. and *Peristernia forskalii*. These small, relatively heavy shells offered far smaller

volumes than the *Burnupena* spp. The transition in shell use occurred between Coffee Bay, where females used both northern and southern shell suites, and Port St Johns, where females uniquely use mainly *Peristernia forskalii*. At Coffee Bay females had access to all six of the most commonly used shell types and the shell fit pattern at Coffee Bay was intermediate between the southern localities and the northern localities.

Shells of *Morula* spp. had variable morphologies which could lead to differential selection of particular shell characteristics, such as shell volume, between ovigerous and non-ovigerous females. It was expected that, at localities where *Morula* spp. were extensively used, there might be differences between ovigerous and non-ovigerous females in the relationship of shell dimensions to crab shield length. This was not the case, as female reproductive state had no influence on the relationship between shell dimensions and crab dimensions for these shell types. At some localities where differences in the relationship of shell dimensions to crab shield length were found, the differences in shell fit could be explained by the significant differences in frequency of use of shell types by ovigerous and non-ovigerous females. For example, non-ovigerous females at Cape Recife used a high proportion of *Burnupena cincta* shells. These shells were both longer and more voluminous than shells of *B. lagenaria*, used by most ovigerous females. Similarly at Park Rynie, non-ovigerous females used more *Peristernia forskalii* than did ovigerous females (which used mostly *Morula* spp.) and again the differences in shell morphologies among rather than within shell types could explain differences in shell fit.

The shell types used by hermit crabs affect their growth rates and hermit crabs that are unable to access large shells have reduced growth rates (Asakura 1995, Hazlett

1981). This effect is very clearly demonstrated by ovigerous female *Clibanarius virescens* in this study. Females show significant differences in average shield length and dry mass among localities. These differences again relate closely to the different shell suites used in northern and southern localities.

Female size is the most important determinant of clutch size (Hazlett 1989), and shell volume is an important determinant of shell choice (Hazlett 1987, 1989). The shell type used by females affects body size, which in turn affects clutch size. Ultimately realised fecundity depends on the shell resource available to females.

Stage 1 eggs were used for most analyses as clutches in early developmental stages are the best representatives of realized fecundity. Both clutch size and clutch mass decreased with increasing developmental stage. Egg loss may be due to egg predation (Williams 2002), but may also be related to the increase in egg diameter as larval development takes place. Reduction in clutch mass is related to egg loss. Clutch sizes in northern localities were smaller than in southern localities, following the pattern of female size and shell size. It is important to note, however, that females did not compensate for differences in locality or shell resource as the relationship of maximum clutch size to female size did not vary between northern and southern localities.

Small *C. virescens* females did not produce relatively larger clutches in relation to body mass than larger females. Small crab females are restricted by the amount of somatic investment that they can re-direct into reproduction by the physical constraints of the number of eggs that they can develop in their ovaries at any one time (Hines 1982, Hartnoll 2006). Similarly they are constrained by the volume

available in their shells in which to brood eggs (Hazlett 1981). Small *C. virescens* females did not produce smaller eggs than large females (the converse occurred), so they could not increase their realized fecundity by producing more, smaller eggs.

The only way that small *C. virescens* females might compensate for small clutches is by producing more clutches per season. *C. virescens* shows a great deal of variability in the number of eggs produced at a given size. This may indicate the production multiple clutches within a single breeding season (Mantelatto *et al.* 2002). Multiple clutches, if present, might depend on locality. In Chapter 3 it was demonstrated that the breeding season in *Clibanarius virescens* is closely linked to water temperature. It is possible to speculate that as average water temperature increases from southern to northern localities the breeding season increases in length and the duration of larval development decreases (Young and Hazlett 1978). The possibility of the extension of the breeding season has been recently demonstrated in *Clibanarius vittatus* occurring in Brazil (Mantelatto *et al.* 2010). *C. vittatus* shows continuous breeding in warmer northern localities (02°05' S) while the breeding season in cooler southern localities (23° 48' S) is shorter and seasonal. Breeding seasons of *Clibanarius virescens* in Japan also vary in duration with a two-degree change in latitude (Imazu and Asakura 1994, Wada *et al.* 2005). The breeding season of *C. virescens* in Japan extends from May to September at Hane-Cape (33°18' N) (Wada *et al.* 2005), and from April to November on the Bozo peninsula (35°0' N) (Imazu and Asakura 1994). Alt hough it is somewhat counter-intuitive that populations further north should have longer breeding seasons than those in the (assumed) warmer south, it is an indication that the duration of the breeding season of *C. virescens* shows plasticity.

Plasticity in the length of the breeding season might also be found in South Africa. At the southern edge of its range at Cape Recife, the breeding season of *Clibanarius virescens* starts in mid December. While only 1 ovigerous female was recorded at Cintsa West (ca. 400 km north-east of Cape Recife) during September, the presence of an ovigerous female is an indication that onset of the breeding season can shift considerably over short distances. Further north at Sheffield Beach, 64.7 % of the female population were ovigerous by November, while at the northern-most locality in this study (Mission Rocks), more than half of the female population carried eggs as early as October and ovigerous females were found on casual inspection during early September. If *C. virescens* shows similar rates of larval development to *C. vittatus* (Turra and Leite 2007), it could be quite possible for a single female *C. virescens* to produce more than one clutch per breeding season. At temperatures of 25 ℃ and salinities of 34 ‰ *C. vittatus* eggs take 25 days to hatch. Turra and Leite (2007) propose that different incubation periods among hermit crab species might be affected by yolk composition, as indicated by the differences in colour of newly laid eggs. In their study (Turra and Leite 2007), both *Clibanarius vittatus* and *C. sclopetarius* produced dark-red to purple eggs and these species showed the longest incubation periods (27 days for *C. sclopetarius* and 25 days for *C. vittatus*). *Clibanarius virescens* produces eggs of similar colour, possibly with similar yolk composition, which allows speculation that *C. virescens* has an incubation period similar to those of its South American congenerics. Although Cape Recife experiences lower maximum water temperatures than in the study above, it would be possible for females even at this southern-most locality to produce two clutches per breeding season and it is very likely that females in warmer waters could produce two clutches of eggs, or more, per breeding season.

This study has introduced information on a few of the life history traits of *Clibanarius virescens* in South Africa. Size at first reproduction varied among localities, but females larger than 1.90 mm should be able to produce eggs. The number of clutches per season could not be established from these data, but it may be safe to speculate that populations in northern localities may produce more than one clutch per season. It was demonstrated that clutch size varied considerably, but was most strongly related to female mass and to shell volume. Egg diameter of Stage 1 eggs did not vary among localities nor did it vary with crab mass or shell mass or volume. There was a weak but significant negative relationship between egg diameter and female shield length.

Chapter 7: General Conclusion

The underlying premise of this study was that the shell resource changes with the biogeography of the region and that this change in shell resource affects both the population structure and reproduction of *Clibanarius virescens* within its range in South Africa. It was hypothesised that the shell resource used by *C. virescens* would increase in diversity from south to north and that shell size would decrease, aperture width would decrease and that shell thickness, as indicated by the mass to volume ratio would increase from south to north. Based on the outcomes of these hypotheses it was predicted that crab size would decrease from south to north and that this would affect reproductive output by females.

The biogeographical regions used in this study were based primarily on the scheme developed by Lombard *et al.* (2004). *Clibanarius virescens* occurs in the Agulhas bioregion (Cape Point to the Mbashe River) and the Natal bioregion (Mbashe River to Cape Vidal). The boundary between the two regions, however, is contentious as other general biogeographic studies place the transition as far South as East London (Bustamante and Branch 1996) and as far North as Balito Bay (Emanuel *et al.* 1992). In the context of this study, the northern boundary of the Agulhas bioregion is the Mbashe River, just North of Dwesa.

It was found that the shell resource did change along the biogeographical gradient between Cape Recife and Mission Rocks. There was a distinct change in the nature of the resource among the 12 localities sampled. Cluster analysis showed that the localities formed two separate groups with a clear break occurring between Dwesa and Coffee Bay. The southern localities, identified from shell use patterns, were

(from South to North) Cape Recife, Nahoon Beach, Cintsa West Beach, Morgan Bay, Wavecrest and Dwesa, all situated within the Agulhas bioregion. The northern localities were Coffee Bay, Port St Johns, Port Edward, Park Rynie, Sheffield Beach and Mission Rocks, all situated within the Natal bioregion as defined by Lombard *et al.* (2004). Within the northern section Coffee Bay and Port St Johns clustered out separately. Coffee Bay represented a transition locality in which shells from both regions were used. At Port St Johns, the shells used by *C. virescens* were characteristic of the northern localities, but were dominated by use of a single shell type (*Peristernia forskalii*).

Southern localities were characterised by use of *Burnupena cincta*, *B. lagenaria* and *B. pubescens*. These species constituted a shell resource that had larger, relatively lighter and more voluminous shells than the resource used in the northern localities. Southern localities show less partitioning of shell types between males and females, while in the northern localities females are confined to smaller, relatively heavier and less voluminous shell types than either northern males or their southern female counterparts. Northern localities were characterised by the use of *Morula granulata*, *M. nodosa* and *Peristernia forskalii*.

These distinct differences had knock-on effects that not only affected crab population structure but also the reproductive output and ultimately the life history strategies of *Clibanarius virescens* in different areas within its range. It was hypothesised that northern crabs (both males and females) would be smaller than southern crabs, and generally they were, except in localities where males were able to obtain large shells (Sheffield Beach) and consequently were able to reach similar sizes to males in southern localities. This ability of northern crabs to reach large sizes given a suitable

shell resource demonstrated that the small sizes reached in northern localities were dictated by the shell resource rather than by any intrinsic (genetic) characteristics of the crabs.

The shell resource used by *Clibanarius virescens* in this study showed some differences to the shell use recorded in two other studies on shell use by *C. virescens* in South Africa. Comparisons of South Africa gastropod species among studies is complicated by differences in nomenclature in early gastropod studies (Kensley 1973). Almost every shell guidebook for South African shells uses a different classification system and set of generic names, but the use of several sources of information allows for comparison. At Park Rynie, crabs in this study used 15 shell types while Reddy and Biseswar (1993) recorded use of 23 shell types. At Dwesa, Nakin and Somers (2007) recorded use of 11 shell types, while this study recorded the use of 22 shell types at Dwesa. There were 12 shell types in common at Park Rynie and 8 at Dwesa. Although the number of shell types used by *C. virescens* varied, the nature of the resource available remained roughly stable.

Clibanarius virescens followed the population structure patterns of most other *Clibanarius* species. *C. virescens* showed sexual size dimorphism as male crabs uniformly dominated the larger size classes at all localities. Similar patterns have been found for geographically separated populations of *Clibanarius vittatus* in Brazil (Mantelatto *et al.* 2010), for *Clibanarius antillensis*, also in Brazil (Turra and Leite 2000) and for *Clibanarius erythropus* in Portugal (Benvenuto and Gherardi (2001).

Differences in the sex ratio between males and females show more variable patterns. In this study most of the southern localities showed no difference in the number of

male and females crabs, but most northern localities showed a skewed sex ratio in favour of females. This is in contrast to *Clibanarius vittatus* which, at a northern site in Brazil showed no difference in overall sex ratio between males and females, while a southern site did show a difference, but in favour of males (Mantelatto *et al.* 2010). It would appear that the sex ratio is highly variable between localities in most hermit crab species. It has been suggested that the sex ratio depends on differential growth rates between males and females, both of which are closely affected by the shell resource available to them (Wada 1997, Turra and Leite 2000).

Shell use had consequences for reproductive output which followed hypothesised trends. In southern localities females became larger and produced larger clutches than in northern localities. It was postulated that northern females could compensate for small clutch sizes by decreasing individual eggs size, but egg sizes did not differ significantly between crabs in southern and northern localities. Instead, it was speculated that females in northern localities were likely to produce more than one clutch per breeding season. Temperature data from Cape Recife showed that ovigery was coupled to sea temperature. The breeding season started earlier in the year (September) at northern localities than at Cape Recife, where the breeding season extended from December to June. Differences in reproductive output could lead to local effects on recruitment and population maintenance in these different zones.

7.1 Scope for future research

Understanding of the life-history of *Clibanarius virescens* is far from complete. Over much of its range in South Africa, *C. virescens* co-occurs with other species of hermit crabs. In the southern localities identified by this study it co-occurs with *Diogenes brevirostris* (pers. obs.), while from Dwesa northwards, and throughout the East coast of Africa, it co-occurs with *Calcinus laevimanus* (Reay and Haig 1990). Both *D. brevirostris* and *C. laevimanus* are morphologically distinct from *Clibanarius virescens* in that their left chelae form a large claw that is used to block their shell apertures when they are threatened. *Clibanarius virescens* has sub-equal chelae and tends to withdraw completely into its shell. The shells used by *C. virescens* used in this study may reflect the part of the shell resource that it can acquire through interspecific competitive interaction with either *D. brevirostris* or *Calcinus laevimanus*. There is great scope for the study of resource partitioning within these species. Experimental work to firstly establish shell preferences, and then to examine competitive interactions between species would be interesting.

Clibanarius virescens has the entire Indo-West Pacific as its range. The entire population could be considered a metapopulation, or a system of interacting demes (Levin 1992), where demes are local populations of interbreeding organisms (Krebs 1985). It would be ideal to be able to take samples from within a single deme when trying to establish the characteristics of a population, but this is not always possible. The pragmatic approach is simply to define a population as the group of individuals that the biologist chooses to study. In this study, it was assumed that a single locality comprised a single population. Whether *Clibanarius virescens* comprises a single, graded interbreeding population within southern Africa is not known. Patterns of larval distribution may contribute to genetic mixing among, or at least between,

localities. Teske *et al.* (2006) found that there were clear genetic differences in populations of *Upogebia africana*, an estuarine thalassinid mud-prawn with a marine larval stage lasting *ca.* 27 days at 11 ℃ (Newman *et al.* 2006). There appear to be only two populations (northern and southern) of *U. africana* in South Africa, with population overlap occurring in the transition zone between the Agulhas and Natal bioregions. Teske *et al.* (2006) postulate that the genetic differences in *Upogebia* are related to the deflection of the Agulhas current by the widening of the continental shelf in this area, which acts as a barrier to the larval dispersal of temperate species northward.

Clibanarius virescens occurs across this break. Although nothing is known about the distribution and potential longevity of *C. virescens* larvae in the plankton, it is possible that southern populations may receive occasional genetic input from northern localities, as surface waters from the Agulhas current often move over the continental shelf as far south as Port Elizabeth (Lutjeharms 1998), but it is unlikely that the reverse occurs. Mantelatto *et al.* (2010) have used genetic analysis to show that *Clibanarius vittatus* populations separated by 21 degrees of latitude in Brazil have low interpopulational variability, although they are still the same species. It would be interesting to determine whether the southern African *Clibanarius* population shows such variability, and this might have implications for its status as a single species throughout its range. Experimental work to determine whether genetic variability (if it exists) affects shell choice and growth, especially in female hermit crabs would answer questions regarding the effect of apparent shell limitation in northern females. How plastic are shell preferences, particularly in shell-naive recruits from different populations?

In final conclusion, this study has been a first glance at the biology of *Clibanarius virescens* in South Africa. There remains much work to be done to understand its role in intertidal marine ecology.

Chapter 8: Literature cited

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Appendix 1: Shell types used by *Clibanarius virescens* and found empty at the 12 localities sampled. Classification is according to Steyn and Lussi (1989) who based their system on that of Millard (1997). Shells occupied by hermit crabs are in columns headed by "HC", empty shells in columns headed by "E" and "P" indicates where the species is present.

Order	Family	Species	Code	Cape Recife		Nahoon Beach		Cintsa West Beach		Morgan Bay		Wavecrest		Dwesa		Coffee Bay		Port St Johns		Port Edward		Park Rynie		Sheffield Beach		Mission Rocks	
				HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E
Caenogastropoda	Bursidae	*Bursa granularis*	BuG	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	P	–	–	–
	Cassidae	*Phalium labiatum zeylanicum*	PhL	–	P	P	P	–	P	–	P	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Epitoniidae	*Gyroscala lamellosa*	GyL	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Eulimidae	*Melanella cumingii*	MeC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Lamellariidae	*Trivia* spp.	Trspp	–	P	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Littorinidae	*Litoraria glabrata*	LiG	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	P	–
	Littorinidae	*Nodilittorina africana*	NoA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	P	–
	Littorinidae	*Nodilittorina natalensis*	NoN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–
	Littorinidae	*Nodilittorina* spp.	Nospp	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Naticidae	*Natica tecta*	NaT	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Naticidae	*Tanea euzona*	TaE	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Planaxidae	*Supplanaxis acutus*	SuA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–
	Ranellidae	*Cabestana cutacea*	CaC	–	P	–	P	–	P	–	P	–	P	P	P	P	–	–	P	–	–	P	–	P	–	–	–
	Ranellidae	*Charonia lampas pustulata*	ChL	–	P	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Ranellidae	*Cymatium exaratum dubanense*	CyE	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	P	–	–	–
	Ranellidae	*Cymatium klenei*	CyK	–	–	–	–	P	–	P	–	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Ranellidae	*Cymatium labiosum*	CyL	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Ranellidae	*Cymatium parthenopeum*	CyP	–	–	P	P	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
	Ranellidae	*Ranella australasia gemmifera*	RaA	–	–	–	–	–	P	–	P	–	–	P	P	P	–	P	–	–	–	–	–	–	–	P	–
	Strombidae	*Strombus mutabilis*	StM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Turritellidae	*Turritella carinifera*	TrC	–	P	–	–	–	P	–	P	–	P	–	P	–	–	–	–	–	P	–	–	–	–	–	–
Heterostropha	Architectonicidae	*Heliacus variegatus*	HeV	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
Neogastropoda	Buccinidae	*Burnupena cincta*	BrC	P	P	P	P	P	P	P	P	P	P	P	P	P	–	–	–	P	–	–	–	–	–	–	–
	Buccinidae	*Burnupena lagenaria*	BrL	P	P	P	P	P	P	–	P	P	–	P	P	P	–	P	–	P	–	P	–	P	–	–	–
	Buccinidae	*Burnupena pubescens*	BrP	–	P	P	P	P	P	P	P	P	–	P	P	P	–	P	–	P	–	–	–	–	–	–	–
	Buccinidae	*Cantharus subcostatus*	CaS	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	P	–	–	–	–	–	P	–
	Buccinidae	*Cantharus undosus*	CaU	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–
	Buccinidae	*Cominella elongata*	CoE	P	P	P	P	–	P	P	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Buccinidae	*Cominella turtoni*	CoT	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Cancellaridae	*Trigonostoma foveolata*	TrF	–	–	–	–	–	P	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
	Conidae	*Conus coronatus*	CoC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Conidae	*Conus sp*	Cospp	–	P	–	P	–	P	–	P	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Coralliophilidae	*Corraliophila fritschi*	CpF	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	P	–	–	–	–	–	–	–
	Coralliophilidae	*Corraliophila squamosissima*	CpS	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	P	–	–	–	–	–	–	–
	Fasciolariidae	*Fusinus* spp.	Fuspp	–	–	P	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Fasciolariidae	*Latirus filmerae*	LaF	–	–	–	–	–	–	–	–	–	–	P	P	–	–	P	–	–	–	–	–	–	–	–	–
	Fasciolariidae	*Peristernia forskalii*	PeF	–	–	–	–	–	–	P	–	–	–	P	–	P	–	P	–	P	–	P	–	P	P	P	–
	Fasciolariidae	*Peristernia fuscotincta*	PeU	–	–	–	–	P	–	P	P	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
	Fasciolariidae	*Peristernia nassatula*	PeN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–	–
	Marginellidae	*Fasciolaria lugubris heynemanni*	FaL	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Marginellidae	*Fusinus ocelliferus*	FuO	–	P	–	P	–	–	–	P	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Marginellidae	*Marginella piperata*	MaP	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Marginellidae	*Marginella rosea*	MaR	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Mitridae	*Austromitre capensis*	AuC	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Mitridae	*Mitra latruncularia*	MiL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Mitridae	*Mitra litterata*	MiI	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	P	–
	Mitridae	*Pyrene obtusa*	PyO	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Muricidae	*Cronia margariticola*	CrM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	P	–	P	–

Appendix 1: Continued.

Order	Family	Species	Code	Cape Recife		Nahoon Beach		Cintsa West Beach		Morgan Bay		Wavecrest		Dwesa		Coffee Bay		Port St Johns		Port Edward		Park Rynie		Sheffield Beach		Mission Rocks	
				HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E	HC	E
Neogastropoda	Muricidae	*Cronia marginatra*	CrA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–
	Muricidae	*Cronia* spp.	Crspp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Muricidae	*Maculotriton serriale fm. digitale*	MaS	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–
	Muricidae	*Mancinella echinulata*	MnE	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–
	Muricidae	*Morula aspera*	MoA	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	P	–	–	–	P	–
	Muricidae	*Morula granulata*	MoG	–	–	–	–	–	–	P	–	–	–	P	–	P	–	P	–	P	P	P	–	P	P	P	–
	Muricidae	*Morula nodosa*	MoN	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	P	P	P	–	P	–	P	–
	Muricidae	*Morula squamilirata*	MoS	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–
	Muricidae	*Nucella dubia*	NuD	–	–	P	P	P	P	P	P	P	P	–	P	P	–	P	–	–	–	–	–	–	–	–	–
	Muricidae	*Pteropurpura graagae*	PtG	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
	Muricidae	*Purpura panama*	PuP	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	P	–
	Muricidae	*Thais bufo*	ThB	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Muricidae	*Thais capensis*	ThC	–	P	P	P	P	P	–	P	P	P	P	P	P	–	P	–	P	–	P	–	P	–	P	–
	Muricidae	*Thais sacellum*	ThS	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–
	Muricidae	*Thais savignyi*	ThA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–	–
	Nassariidae	*Bullia annulata*	BlA	–	–	P	P	–	P	–	P	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–
	Nassariidae	*Bullia callosa*	BlC	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–
	Nassariidae	*Bullia digitalis*	BlD	–	–	P	P	P	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Nassariidae	*Bullia diluta*	BlI	–	–	–	–	–	–	P	P	P	–	–	P	–	–	–	–	P	–	–	–	–	–	–	–
	Nassariidae	*Bullia pura*	BlP	–	–	P	P	–	–	–	P	–	–	–	–	–	–	–	–	P	P	–	–	–	–	–	–
	Nassariidae	*Bullia rhodostoma*	BlR	–	P	–	–	–	–	P	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Nassariidae	*Bullia* spp	Blspp	–	–	P	P	P	P	P	–	P	–	P	–	–	–	–	–	–	P	–	–	–	–	P	–
	Nassariidae	*Demoulia ventricosa*	DeV	–	–	–	P	–	P	P	P	P	–	P	P	P	–	–	–	–	–	–	–	–	–	–	–
	Nassariidae	*Nassarius capensis*	NsC	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Nassariidae	*Nassarius speciosus*	NsS	–	–	P	P	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Olividae	*Melapium lineatum*	MlL	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Terebridae	*Hastula albula natalensis*	HaA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–
	Turridae	*Clavatula tripartita*	ClT	–	–	–	–	–	–	–	–	P	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella bornii*	CiB	P	P	P	P	–	P	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella krausii*	CiK	P	–	P	P	–	P	P	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella rosaria*	CiR	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella semicostata*	CiS	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella sinuata*	CiI	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella* spp	Cispp	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Turridae	*Clionella subventricosa*	SiU	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
Vetigastropoda	Neritidae	*Nerita albicila*	NeA	–	P	–	–	–	–	–	P	–	–	–	–	–	–	–	P	–	–	–	–	P	–	P	–
	Neritidae	*Nerita plicata*	NeP	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–
	Neritidae	*Nerita polita*	NeO	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	P	–
	Trochidae	*Diloma sinensis*	DiS	P	P	P	P	P	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Trochidae	*Diloma tabularis*	DiT	–	–	P	P	P	–	–	P	P	–	P	P	–	–	–	–	P	P	–	–	–	–	P	–
	Trochidae	*Diloma tigrina*	DiI	P	P	P	P	–	P	–	P	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–
	Trochidae	*Diloma vareigata*	DiV	–	P	P	P	P	–	–	–	P	–	P	–	–	–	–	–	–	P	–	–	P	–	–	–
	Trochidae	*Monodonta australis*	MoA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	P	–	P	P	–	–
	Trochidae	*Trochus nigropunctatus*	TrN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	P	P	–	P	–	P	–
	Turbinidae	*Tricolia capensis*	TiC	–	P	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–
	Turbinidae	*Turbo cidaris*	TuC	P	P	P	P	P	P	–	P	P	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–
	Turbinidae	*Turbo coronatus*	TuO	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	P	P	–	–
	Turbinidae	*Turbo sarmaticus*	TuS	–	P	P	P	–	P	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		Land snail	LS	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		Unknown small shell	UNSS	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–