# Deep water parapagurid hermit crabs: their distribution, abundance, population structure and associations in the Southern Benguela

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"It is a dangerous business, Frodo, going out your door..." It's an adventurous business to be sure, to set off on an adventure like an MSc by dissertation, working on animals very few people have studied before, and none of which I would see alive. And what sort of adventure would it be without a little danger, a little rain and a little fire? I could not have gone there and back again without the guidance, support, humour and wisdom of my ever patient supervisor, Emeritus Professor Charles Griffiths. I am forever grateful for your lessons on science, life and joy. To my merry band of fellow Team Hermit conspirators – Jannes, Arno, Jackson and Robyn – thank you for your hard work and enthusiasm for interesting questions, zoanthid "goo" and decapods in general. Hats off to Lara Atkinson for her organisation and advice, to Tracey Fairweather for data, proof reads and guidance, and to the collection team from DAFF, who go to sea come-what-may and who started collecting "monkey nuts" all those years ago. Thanks to my fellow detainees in the postgraduate lab, especially Jess and Mark, who kept me sane and challenged me in equal measure. Since this thesis would have remained but a dream without the support of my funders, I must thank the NRF, the Marine Research Institute of UCT and the Cape Tercentenary Foundation. I am especially grateful to my parents, for their support, love and enthusiasm for my dreams, and to the rest of the family, for listening to two solid years of hermit talk. And finally, to Hilton – thank you for your boundless love, your endless humour and your patient support.

## **Plagiarism Declaration**

I, Amy Grace Wright, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever. I confirm that the uploaded files are the correct versions for the Library/ OpenUCT.

A supporting paper is included in Appendix 2 for consideration by the examiner. As a co-supervisor of the project undertaken by TPA Botha, I participated in all of the laboratory work involved, and played a role in the conceptualisation and management of the project.

Signature: Signed by candidate

Date: \_\_\_\_2017-02-16\_\_\_\_\_

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### Abstract

The parapagurids Sympagurus dimorphus (Studer, 1883) and Parapagurus bouvieri (Stebbing, 1910) dominate South African deeper-water benthic invertebrate communities. Samples from the 2016 DAFF bi-annual hake demersal research trawl surveys provided data on population structure and morphology. Since these species forego the use of "traditional" gastropod shells in favour of symbiotically-associated Epizoanthus pseudoshells, these data were also used to investigate parameters of pseudoshell association. S. dimorphus to have a female-biased sex ratio of 1:1.5, and P. bouvieri of 1:1. The proportion of males in both species increased with cephalothoracic shield (CL) length. S. dimorphus males had positive allometric major right chelipeds, while P. bouvieri cheliped lengths were positively allometric in males, and negatively allometric in females. All collected P. bouvieri occurred in pseudoshells, but S. dimorphus showed a real shell occupancy rate of 3.39% (n = 38). A positive relationship was found between CL size and real shell occupation frequency ( $r^2$  = 0.96). S. dimorphus pseudoshell zoanthid polyps increased in number as a function of both total shell volume ( $R^2 = 0.73$ ) and colony height ( $R^2 = 0.61$ ), with polyps present on every available part of the shell. No such relationship was found for *P. bouvieri*, presumably because the polyps are distributed in a linear pattern around the back and outside of the pseudoshell. Juvenile parapagurids appear to select for Naticidae original shells, with Euspira napus being the dominant original shell species for both S. dimorphus (45.45 %) and P. bouvieri (39.00 %). Questions are raised about whether these hermits exist along an evolutionary continuum of traditional shell reliance, whereby the species utilise their pseudoshells differently - P. bouvieri appears to show a stronger mutualistic symbiosis with its exclusive pseudoshell species than S. dimorphus, and may have lost the ability to change shelters entirely, utilising the pseudoshell as a brood pouch covering only the abdomen, rather than as a shell in which to retract to escape predation. Data from 1987 – 2014 surveys were used to map the distribution patterns and densities of these species in the southern Benguela, and to investigate changes in the populations over time. As it stands, no correction factor need be applied to South African parapagurid catches as a result of the 2003-2004 change in survey gear. However, further work is needed. S. dimorphus occurred at a significantly greater mean sample mass (287.88 kg.km<sup>-2</sup>) than *P. bouvieri* (31.37 kg.km<sup>-2</sup>). The bulk of sample mass occurred within the West Coast Benguela upwelling region, with very few parapagurids caught over the Agulhas Bank, which may be too shallow for either species, given that S. dimorphus showed a preferential depth range of 200 – 299 m (range 30 - 814 m) and P. bouvieri of 400 - 499 m (range 62 - 700 m). The highest mean sample masses occurred on muddy sand (61.00 kg.km<sup>-2</sup>) and sandy sediments (45.68 kg.km<sup>-2</sup>). Overall catchability (mean = 43.35%) has remained constant over the 23 years ( $R^2 = 0.13$ ) with a slight trend towards increasing catchability over time, which may correspond to a change in survey design.

# Chapter 1

# Hermit crabs, their shelters and their associates: a review of gastropod shell use and Cnidarian associations



Dorsal view of two parapagurid cloaked hermit crabs, Sympagurus dimorphus (Studer, 1883). Image: CL Griffiths (2015)

#### Hermit crabs and their associations with other biota

Hermit crabs are decapod crustaceans of the infra-order Anomura, within the superfamily Paguroidea (Latreille, 1802) and the suborder Pleocyemata (Burkenroad, 1963). Amongst the Anomura, hermit crabs are unique in having an unsegmented, twisted abdomen (twisted predominantly to the right in healthy individuals) that lacks the protection of a rigid exoskeleton (Lancaster, 1988). As a result of this "naked abdomen", almost all hermit crabs occupy various forms of "ready-made accommodation" i.e. shelters that are not produced by the crabs themselves (Von Frisch and Von Frisch, 1974; Hazlett, 1981; Lancaster, 1988). Without a shelter, most hermit crabs are vulnerable to predation and physical stresses, such as desiccation, as shown by Reese (1968), and osmotic stress, as demonstrated by Shumway (1978) - see Elwood and Neil (1992) for a review. The most common types of shelters occupied are empty gastropod shells (Schejter and Mantelatto, 2011), but scaphopod shells (Hazlett, 1966), bivalve shells, hollowed stones, pieces of wood, calcareous polychaete tubes (Schejter and Mantelatto, 2011), hollow bamboo tubes (Rabaud, 1941) and corals have all been recorded as hermit crab homes (Lancaster, 1988; Williams and McDermott, 2004). This occupation of ready-made shelters influences life history, behaviour and physiology of the hermit crabs (Hazlett, 1980; Williams and McDermott, 2004). For example, when a hermit crab glaucothöe (the final larval stage) settles and becomes a benthic adult crab, its metamorphosis produces the necessary physiological asymmetries (such as the aforementioned twisted abdomen) required to inhabit a shell as an adult (Hazlett, 1981). Hazlett (1981) highlights that almost all 800 hermit crab species tend to adopt shelters that allow mobility during occupation, and it is thus hypothesised that it is the combination of the protection offered by the adopted shelters, and the mobility afforded by these same shelters that has led to the high abundances of hermit crabs in most of the world's oceans (Hazlett, 1981).

Within these "ready-made" shelters, there are a host of fauna that live in symbiotic association with hermit crabs. Coined by Anton de Bary (1879), "symbiosis" initially described any association between different species, but has become to describe the continuum of biotic interactions occurring between two organisms that live in close association with each other (Antoniadou, Vafeiadou, and Chintiroglou, 2012). The known hermit crab symbiotic associates were reviewed by Williams and McDermott (2004). Over 550 invertebrate species from 16 phyla were found to be associated with more than 180 species of hermit crabs, with 232 species being incidental associates, 114 obligate commensals and 215 facultative commensals (Williams and McDermott, 2004). There are numerous ways in which these species can be associated with hermit crabs - some are epibiotic species (species found on the shells occupied by hermit crabs), or endolithic species (species that bore into the shell). Other species live within the lumen of the shell (either free-living or attached to

the shell), are attached to the hermit crabs themselves, or are hypersymbionts (Williams and McDermott, 2004). Some hermit crab species may have multiple associated symbionts. For example, *Sympagurus burkenroadi* (Thompson, 1943) live in association with the large zoanthid "pseudoshells" they inhabit, but also have a number of additional symbionts, such as hydroids, copepods and turbellarian worms (Lemaitre, 2004). Of the hermit crab associates examined, Williams and McDermott (2004) noted that the taxa exhibiting the highest number of associates were arthropods (126), followed by polychaetes (105), and cnidarians (100). Of the three, the cnidarians, both solitary and communal, are among the most well-studied associates of hermit crabs, especially in terms of associate - host interactions (Williams and McDermott, 2004). Some 32 of the cnidarian associates were described as obligate commensals, existing in complex and often mutualistic symbiotic relationships with their hermit crab hosts (Williams and McDermott, 2004).

It is this diversity in hermit crab associates and associations that renders hermit crabs allogenic ecosystem engineers i.e. organisms able to transfer biotic/abiotic substances from one physical form to another (Gutiérrez, 2007). This is because hermit crabs and their shelters shape and maintain invertebrate biodiversity in certain environments (Reiss *et al.*, 2003). For example, in soft sediment benthic marine ecosystems, the occupation of gastropod shells by hermit crabs prevents the burial of such shells (Conover, 1975 and 1979). These inhabited gastropod shells, as the only hard substrate available in the system, may in turn provide space for the settlement of epifauna (Stachowitsch, 1979; Reiss *et al.*, 2003) that would otherwise be absent from the community. Thus, the abundance of hermit crabs may directly influence the abundance and density of the epifaunal community in a system (Hazlett, 1981; Reiss *et al.*, 2003).

The aim of this first chapter is to review the current state of knowledge of three common hermit crab shelter associations: that of empty gastropod shells, and that of two epibiont taxa, namely Actiniaria (anemones) and Zoantharia (zoanthids). The hermit crab - zoanthid association remains understudied and poorly understood with limited work, and no live studies available, this being due in part to the difficulties of collecting and keeping such deep-water animals (Schejter and Mantelatto, 2011). As such, an important starting point to gaining insight into this association is to conduct a review of the widely-studied field of hermit crab - gastropod shell associations and the mechanistically, taxonomically similar association between hermit crabs and anemones. This is because many of the concepts discussed in the latter two associations apply to the former, and because the theory behind well-understood associations may lend insight into the complexities of poorly-understood associations.

#### Hermit crab – gastropod shell associations

A large variety of shell species and shell sizes are inhabited opportunistically by hermit crabs (Orians and King, 1964; Hazlett, 1981). Since hermit crabs will generally select the shell of "best fit" for their body size at a given time (if there is an abundance of shells to select from), there is a general correlation between shell size and hermit crab size (Arce and Alcaraz, 2012). It is rare, however, for each individual crab to occupy a "perfect fit" shell, or a "perfect condition" shell free of erosion or breakages because, in general, empty shells are rare in areas inhabited by hermit crabs, such as the intertidal (Abrams, 1978; Abrams, 1980; Bertness, 1980). It is also rare for the whole population of a hermit crab species to occupy a single shell species, but this may occur when there is a very low shell diversity available in the area inhabited by the crab (Hazlett, 1981).

There appears to be some degree of flexibility in shell selection, even if shells are freely available (Abrams, 1978). For example, Grant and Ulmer (1974) showed that larger Pagurus pubescens and P. acadianus adults are found only in Buccinum and Polinices shells, whilst smaller individuals are found in Littorina and Thais shells because the latter simply do not get large enough to accommodate larger crabs. In addition, though primarily dictated by the preference of the hermit crab, shell species selection in the field can also be influenced by the relative abundance of shells available i.e. the more abundant a shell species in an area, the greater the proportion of the hermit crab population occupying that shell species (Turra and Leite, 2003; Alcaraz and Kruesi, 2009). Arce and Alcaraz (2012) give some weight to this hypothesis, by showing that the shell species selection patterns of Calcinus californiensis in laboratory conditions matched the sequence of shell selection in the field (as measured by Arce and Alcaraz, 2011). Predation pressure may also influence shell selection, which in turns affects survival (and thus fitness). In experimental studies by Arce and Alcaraz (2013), C. californiensis changed their shell selection patterns in the presence of a predator (an octopus) – when a predator was present, the hermit crabs selected larger shells that allowed full retraction and protection of the appendages, which in turn improved survival rates. Ayres-Peres, Quadros, and Mantelatto (2012) concluded, after comparing the shell-use patterns of multiple independent Loxopagurus loxochelis populations, that there are numerous interacting factors that influence how hermit crabs select their shells, including shell abundance, shell morphology, environmental conditions, and both inter- and intraspecific competition. For a review of the behavioural mechanisms that underlie shell selection by hermit crabs, see Reese (1963).

In addition to physical protection provided to the hermit crab itself, the occupation of gastropod shells by hermit crabs provides direct protection of any eggs carried by the female. Hazlett (1981) noted with respect to eggs, that "their protection from predation or physical stress is as good (or

bad) as that offered by the shell". The occupation of external shells by hermit crabs offers both egg protection and mobility, in contrast to the situation in other Anomurans, which typically carry their eggs in a bunch under the abdomen, often resulting in impaired mobility (Hazlett, 1981). The inhabited shell has been shown to influence both the probability of a female being berried (see Fotheringham, 1981 and Bach *et al.*, 1976), and the size of clutch she carries (Bertness, 1981a) because the volume of eggs that can be carried is restricted by the size of the occupied shell (Hazlett, 1981). Since shell size is correlated to hermit crab size, a female hermit occupying a larger shell is thus able to carry a larger volume of protected eggs (Hazlett, 1981).

The primary cost incurred by hermit crabs as a result of their occupation of external shelters is that as old shells become outgrown, worn down or broken, hermit crabs need to move into new gastropod shell homes continuously throughout their life cycle (Hazlett, 1981). If shells are limited, and there is a high level of competition for the available shells, it is unlikely that each individual hermit crab will find a shell of "perfect fit". Hermit crabs must often therefore "make do" with illfitting shell homes. This mismatch in crab and shell size (the shelter being either too large or too small) negatively impacts the fitness of the individual crab occupying the shell (Alcaraz, Chávez-Solís and Kruesi, 2014), and thus has a negative impact on population growth. For example, Vance (1972) showed that predation rates were higher on crabs in too-small shells, because the shell size prevented the crab from withdrawing far enough into the shell to escape predation. Angel (2000) also demonstrated that the hermit crab *Pagurus longicarpus* was significantly more susceptible to predation when inhabiting a non-ideal fitting shell.

In addition, poorly-fitted shells negatively impact hermit crab fecundity and growth. Various authors have shown that, even if food is not limited, the growth rate will be slowed if the shell occupied is too small (Markham, 1968; Fotheringham, 1976a, 1976b). Angel (2000) showed that the hermit crab *P. longicarpus* that occupied shells that were too large or small had slower growth rates than those inhabiting shells of the correct fit, even though feeding rates were not significantly affected by the occupation of an ill-fitting shelter. There is a significant cost to hermit crabs associated with a decline in growth rate because hermit crab size and fecundity are positively correlated (Gassell, 1937; Ameyaw-Akumfi, 1975; Bach *et al.*, 1976; Fotheringham, 1976; Bertness, 1981a), larger crabs have a decreased risk of predation, due in part to increased strength of the selected shell (Bertness and Cunningham, 1981), larger females tend to produce more eggs than smaller females, and larger males often have better access to females (Osorno, Fernández-Casillas and Rodríguez-Juárez, 1998). Overall, there is a correlation between clutch size and shell size – a smaller shell resulting in a lower volume of eggs, even after body size is taken into account (Childress, 1972; Fotheringham, 1976).

While smaller crabs are more likely to occupy shells of the preferred size (Vance, 1972), the larger the crab grows, the more difficult is becomes to find a shelter of the correct size (Hazlett, 1981).

There is a lower selective pressure for marine hermit crabs to carry a lighter shell when compared to terrestrial hermits due to the buoyancy provided by the water (Osorno *et al.*, 1998; Laidre, 2012). However, some hermit species in high water flow or high wave environments may actively select for heavier shell homes in order to "weigh themselves down" (Hahn, 1998). However, Alcaraz *et al.* (2014) showed that *C. californiensis* in shell species with the highest IV/M ratio (i.e. the lightest shells) had higher growth rates compared to those in heavy shells (with comparatively low IV/M ratios). There is thus a trade-off between having a light, thin shell (with the associated benefit of a faster growth rate that comes with having a lighter shell to carry) and an increase in predation associated with thinner, less protective shells homes (Alcaraz *et al.*, 2014).

#### Hermit crab - actiniaria associations

The association between hermit crabs and their anemone symbionts is one of the best described types of mutualism in the marine system (Vafeiadou, Antoniadou, and Chintiroglou, 2012) and one of the most studied interactions involving marine decapods (Ross, 1983). There are multiple families of hermit crabs involved. While most of these associations involve the attachment of the anemone to a pre-inhabited gastropod shell occupied by the hermit crab, some anemones (such as the genera *Adamsia* and *Stylobates*) form a chitinous living cloak (a carcinoecium) that expands the available living space offered by the gastropod shell (Gusmão and Daly, 2010).

The hermit crab - anemone association is most often initiated by the hermit crab, which actively detaches and places anemones onto its shell (Gusmão and Daly, 2010). However, this association also involves one of the most complex behaviours exhibit by cnidarians (Ross, 1974b), whereby an anemone actively transfers itself onto the gastropod shell occupied by the hermit crab (Ross and Sutton, 1961; Davenport *et al.*, 1961; Ross, 1959, 1965). This is rare, however, only occurring in three species of *Calliactis* and one species of *Paracalliactis* (Ross, 1974b).

Since shallow-water Actiniaria are relatively easy to collect and keep, the bulk of the work on hermit crab – cnidarian symbioses has been focused on these anemone associations. This can be used to inform our understanding of the under-studied and poorly understood zoanthid associations discussed below. A detailed summary of the costs and benefits of this association are shown in Table 1.1, which is adapted from Gusmão and Daly (2010).

Table 1.1: Overview of the benefits and costs of hermit crab - anemone symbiosis for the hermit crab host and the anemone associate (adapted from Gusmão and Daly, 2010).

Advantages		Source	Disadvantages	Source
He	rmit Crab			
•	Improved protection from predators (through anemone's nematocysts). Some hermit crab species actively place anemones (of the genera Adamsia Calliactis and	Antoniadou <i>et al.</i> (2012) Ross (1970) Gusmão and Daly (2010)	<ul> <li>Increased energy costs of carrying heavier shells.</li> </ul>	Antoniadou <i>et al.</i> (2012)
	Paracalliactis), onto the gastropod shell they inhabit; shown to collect/gather more anemones (theft from other crabs may occur when under increased predation pressure).			
•	<ol> <li>Increased shell strength:</li> <li>Expansion of anemone over shell as a "living cloak" that strengthens the shells and improves shell defences.</li> </ol>	Ross (1984)	<ul> <li>Increased competition:         <ol> <li>Inter- and Intraspecific i.e. stealing of anemones from the shells of other hermit crabs.</li> </ol> </li> </ul>	Ross (1979) Giraud (2011)
	<ol> <li>Anemones of genus Adamsia forms a chitin shell-like structure ('carcinoecium") which may improve protection of the hermit crab as it grows; does not require switching of shells as the crab grows.</li> <li>(2) also reported in Stylobates</li> </ol>	Gusmão and Daly (2010) Dunn and Lieberman		
	genus in tropical seas.	(1983)		
•	Some cases of host preying on anemone in times of starvation.	Antoniadou <i>et al.</i> (2012)		
Anemone				
•	Protection from predators (via active defence by host).	Brocks and Gwaltney (1993)	<ul> <li>Predation by host (only in specific cases).</li> </ul>	Antoniadou <i>et al.</i> (2012)
•	Substratum availability, especially in sandy areas with little other solid substrata available for settlement.	Riemann-Zórneck (1994)		

Table 1.1 continued: Overview of the benefits and costs of hermit crab - anemone symbiosis for the hermit crab host and the anemone associate (adapted from Gusmão and Daly, 2010).

Ac	dvantages	Source	Disadvantages	Source
Ar	nemone			
•	Improved feeding capacity: 1. Due to increased mobility (because hermit crab "substratum" is mobile).	Stachowitsch (1997; 1980)		
	<ol> <li>Due to increased food availability because of host feeding/mastication/handling of food, and resultant residual food particles available for anemone consumption.</li> </ol>	Fautin (1992)		
	<ol> <li>Due to direct feeding by host (remains controversial).</li> </ol>	Wortley (1963) Fox (1965) Ross (1974a)		
	Anemones placed closer to the aperture of the shell received more benefit from hermit crab feeding; anemones placed on the top of the shell experienced increased accessibility to suspended organic particulate matter in the water column.	Brooks (1989)		
•	Increased dispersal, due to hermit crab (i.e. substratum) mobility.	Balss (1924)		

#### Hermit crab - zoantharia associations

There is a severe deficienty in knowledge about hermit crab – zoanthid associations on a global scale, with most studies only reporting the presence of such a relationship (Herberts 1972a, 1972b; Muirhead, Tyler and Thurston, 1986; Zhadan, 1999). Ates (2003) provided the first, and the most recent, world-wide review on hermit crab – zoanthid associations, even though most of the zoanthid associates in this review were identified only to the level of the genus *Epizoanthus* (Gray, 1867) (Cnidaria, Anthozoa), or simply listed as "a zoanthid". Previous reviews on hermit crab symbionts (such as Hazlett, 1981 and Ross, 1983) have either ignored zoanthid associates completely, or barely discussed them at all. The taxonomic work on the zoanthid symbionts exists (Williams and McDermott, 2004), but remains incomplete. Lemaitre (i.e. 1986, 1989, 1990 and 2004) has done much to complete the taxonomy of the hermit crabs involved, and further work is currently underway (J. Landschoff, Pers. Comm., 2016).

Ates (2003) tentatively designated three types of hermit crab - zoanthid associations. The first is the growth of a zoanthid colony on a gastropod shell that is already inhabited by a hermit crab. While the only current example of zoanthid species involved in this association "type" is *Epizoanthus arenaceus*, which covers 7% of shells occupied by *Paguristes eremits* and *P. cuanensis* in the Adriatic Sea (Stachowitsch, 1980), Ates (2003) hypothesised that there may be more than one zoanthid species involved in this association. The second association "type" defined by Ates (2003) is one whereby an Epizoanthid species "covers most of a gastropod shell occupied by a hermit crab to form a carcinoecium" i.e. *E. incrustatus* (Ates, 2003). Ates (2003) hypothesised that there may be behavioural adaptations of the crab to allow the possession of a carcinoecium, and that the zoanthid species involved in this association "type" may have different polyp orientation organisation patterns, but fails to elaborate on the implications of either statement any further. Due to a paucity of knowledge, assigning a specific hermit crab – zoanthid association to either type 1 or type 2 may not be possible (Ates, 2003).

The third type of association is more distinct that the previous two. Here, the zoanthid species is described by Ates (2003) as held by the hermit-crab directly, covering the abdomen as would a gastropod shell. Instead of the "traditional occupation" of empty gastropod shell homes, these "pseudoshells" are built by the zoanthid after settlement on the small, "original" shell occupied by the juvenile hermit crab (Schejter and Mantelatto, 2011), and grow to form a protective, living "cloak" within which the hermit crab dwells. This potentially negates the need to periodically replace the inhabited shell completely, and the problems associated with this process as described above (Muirhead *et al.*, 1986; Schejter and Mantelatto, 2011). These pseudoshells appear "gastropod shell-like" in appearance, with their growth appearing to follow the "pattern" defined by the initial gastropod shells inhabited by the juvenile crab (Schejter and Mantelatto, 2011) i.e. the pseudoshell retains a similar shape as that of the "original" shell. This sack-like pseudoshell structure is held and carried by the hermit crab through various behavioural and physical adaptations, such as modified pereopods and uropods, such as those of *Paguropsis typica* used to carry its *Epizoanthus paguropsides* pseudoshell (Balss, 1924; Schäfer *et al.*, 1983).

This third association type is generally understood to be a symbiotic relationship between hermit crabs of the family Parapaguridae (Smith, 1882) and pseudoshell-building *Epizoanthus* species. There are ten genera currently included within the Parapaguridae: *Bivalvopagurus* (Lemaitre, 1993); *Oncopagurus* (Lemaitre, 1996); *Paragiopagurus* (Lemaitre, 1996); *Parapagurus* (Smith, 1879); *Probeebei* (Boone, 1926); *Strobopagurus* (Lemaitre, 1989); *Sympagurus* (Smith, 1883); *Tsunogaipagurus* (Osawa, 1995); *Tylaspis* (Henderson, 1885) and *Typhlopagurus* (de Saint Laurent, 1972). Hermit crabs involved in the first or second type associations described by Ates (2003) may or

may not fall within the family Parapaguridae. Many species of Parapaguridae have been described as "deep-sea inhabitants" (e.g. Filhol, 1885a, b; Menzies *et al.*, 1973), as they are found at depths of 55 - 5000 m (Lemaitre, 1989). As such, little work has been conducted on these species. Addressing some of the deficit in this knowledge is of importance, due to the high biomass and ubiquity of parapagurid hermit crabs on a global scale. The genera *Parapagurus* (Smith, 1879), for example, has been described as constituting some of the most conspicuous and abundant groups of organisms in the continental slope region ( $200 - 3\ 000\ m$ ) around the world (Lemaitre, 1986; Lemaitre, 2004). Addressing the knowledge deficient is also of importance in relation to the impact some fishing industries may have on parapagurid species as these may form a significant component of the invertebrate by-catch in demersal trawl operations (Lange and Griffiths, 2014; T. Fairweather, Pers., Comm., 2016).

The construction of these living pseudoshells appears to be dependent on the *Epizoanthus* species involved. For example, Muirhead *et al.* (1986) found that, after settlement on the shell, the zoanthid *E. paguriphilus* begins to form multiple polyps (up to 10) around a cavity (shaped by the movement of the crab) into which the hermit crab grows. Other zoanthid species, such as *E. abyssorum*, consist of multiple polyps (Williams and McDermott, 2004), of which the ventral polyps are hypothesised to occur in areas of the shell where they can best take advantage of and gain access to food dropped/torn by the hermit crab host (Muirhead *et al.*, 1986). However, there does not appear to be a species-specific association between hermit crab host and zoanthid associate i.e. several zoanthid associates may occur in symbiosis with a single hermit crab species, and vice versa. Table 1.2 shows that some *Epizoanthus* species are found in association with multiple crab hosts, and that many hermit crab species are known to associate with multiple zoanthid species. Invariably, the "better known" Parapaguridae, such as *Parapagurus pilosimanus*, have been recorded with multiple zoanthid associates.

In such an association, the hermit crab does not have to change shells as it grows (Schejter and Mantelatto, 2011). It has been inferred that the enlargement of the gastropod shell by a pseudoshell-building zoanthid is of major benefit to the hermit crab host – a "build your own home" approach would negate the costs of having to find new shell homes to accommodate growth, as well as the fitness costs to survival, reproduction and growth rate incurred through the use of substandard shells (as the host and zoanthid presumably interact to ensure the shell is enlarged at the appropriate rate). However, unlike the well-understood benefits that the hermit crab host derives from living in association with an anemone (Table 1.1), such a benefit remains unproven and unquantified in parapagurid – zoanthid associations (Ates, 2003). Pseudoshell construction would be especially beneficial in environments where gastropod shells are rare or absent (Balss, 1924). As

such, it has been hypothesised that this arrangement has allowed the establishment (and persistence) of dense populations of parapagurid hermit crabs at greater depths, where there may be a paucity of usable gastropod shell homes available (Schejter and Mantelatto, 2011). This is certainly supported by the high biomass at which some species are found (Lemaitre, 1986; Lemaitre, 2004; Lange and Griffiths, 2014).

Schejter and Mantelatto (2011) first detailed the morphometric relationship between the hermit crab *S. dimorphus* and the associated pseudoshell building zoanthid *E. paguricola* in the Argentine Sea (85 - 131 m depth). They found that the zoanthid colonies created soft pseudoshells modelled on the shape of the initial gastropod shell (of which 12 different species were described) and which were almost all completely covered by *E. paguricola* colonies. They also showed that the number of epizoanthid polyps per colony increased in relation to the weight of the colony and the size of the hermit crab (Schejter and Mantelatto, 2011). The authors hypothesised that the initial association of *S. dimporphus*, *E. paguricola* and the associated initial gastropod shell begins during the hermit crabs' juvenile phase, when the crab occupies a small shell and the zoanthid settles on it (Schejter and Mantelatto, 2011).

Ates (2003) listed at least 13 *Epizoanthus* species involved in this type of association (Table 1.2), and most of these live below 150 m depth. Globally, there are over 20 recorded species of zoantharia of the genus *Epizoanthus* that live in association with hermit crabs (Table 1.2). See Balss (1924) and Ates (2003) for full reference lists and possible further hermit crab – zoanthid associations.

Hermit Crab Species and General Distribution	Associated Epizoanthus Species	Sources
Parapagurus pilosimanus* Smith (1879)	E. abyssorum (Verrill, 1885)	Verrill (1885b); Carlgren (1913); Carlgren (1923); Muirhead <i>et al</i> . (1986)
Eastern Atlantic: Bay of Biscay to the Gulf of Guinea; South Atlantic: Tristan da Cunha; South Africa; North Atlantic: southwest of Iceland and the Faeroe Islands to west of Ireland; Western Atlantic: from off Nova Scotia to Guyana.	E. carcinophilus (Carlgren, 1923)	Carlgren (1938)
	<i>E. paguriphilus</i> (Verrill, 1883) = <i>E. hirondellei</i> (Jourdan, 1891) = <i>E. parasiticus</i> (Hertwig, 1882)	Verrill (1882); Verrill (1885a); Smith (1886); Jourdan (1891 and 1895); Milne Edwards and Bouvier (1893); Carlgren (1913); Lwowsky (1913); Carlgren (1923); Boone (1930); Carlgren (1934b); Muirhead <i>et al.</i> (1986)
Paguropsis typica*	E. paguropsidis (Boas, 1926)	Boas (1926); Schäfer <i>et al.</i> (1983)
(Henderson, 1888)		
South Western Indian Ocean: Madagascar; Mozambique.		
Sympagurus dimorphus*	E. studeri (Carlgren, 1923)	Jourdan (1895); Carlgren (1938); Lwowsky
(Studer, 1883)	<i>= Sidisia cancrisocia</i> (Studer, 1879)	(1913)
Southern hemisphere between latitudes 22°S and 57°S.		
	E. paguricola (Roule, 1900)	Schejter and Mantelatto (2011)
	<i>Epizoanthus</i> sp. (probably)	Lemaitre (1996); Forest <i>et al.</i> (2000)
	? (actinians or zoanthids [Epizoanthus?]) South western Atlantic specimens have been found in gastropod shells with one or more anthozoan polyps (actinians or zoanthids) attached to the shells. Specimens from the eastern Atlantic are commonly found living in colonies of Epizoanthus species. Young individuals are sometimes found living in scaphopod shells (Zhadan, 1999).	Lemaitre (1989)

Hermit Crab Species and General Distribution	Associated Epizoanthus Species	Sources
Parapagurus bouvieri*	E. carcinophilus (Carlgren, 1923)	Carlgren (1938)
(Stebbing, 1910) South Eastern Atlantic: from Namibia to South Africa; South Western Indian Ocean: from off Natal to South Africa.	Epizoanthus sp.	Stebbing (1910); Lemaitre (1990); Lemaitre (1999); Forest <i>et al.</i> (2000)
Parapagurus abyssorum*	Epizoanthus sp.	Lemaitre (1989); Forest <i>et al.</i> (2000)
(Filhol, 1885)		
Eastern Atlantic: from the Azores to Cape Verde Islands; North Atlantic, including the north-eastern coast of the United States.		
Parapagurus andreui*	<i>Epizoanthus</i> sp.	Lemaitre (1990; 1999)
(MacPherson, 1984)		
South Eastern Atlantic: from off the southern coast of Angola to Namibia, including the Valdivia Bank; South Western Indian Ocean: south of Madagascar.		
	E. frenzeli (Pax, 1937)	Pax (1937)
	E. steueri (Pax, 1937)	Pax (1937)
	<i>E. vatovai</i> (Pax, 1937)	Pax and Lochter (1935); Pax (1937)
Sympagurus acinops*	? Actinians or zoanthids	Lemaitre (1989)
(Lemaitre, 1989)		
North Eastern Atlantic: Canary Islands; Western Atlantic: Tongue of the Ocean (Bahamas).		
Sympagurus dofleini*	? Zoanthid	Lemaitre (1994)
(Balss, 1912)		
Japan, Indonesia (Borneo), Mariana Islands (Guam), Australia, New Caledonia, Wallis and Futuna, Samoa, Tonga, Hawaiian Islands, French Polynesia, Nazca, and Sala y Gomez ridges, Zanzibar, Mozambique Channel, Madagascar and Reunion.		
Sympagurus villosus*	Epizoanthus sp.	Lemaitre (1996)
(Lemaitre, 1996)		
South Pacific Ocean: Wallis and Futuna; New Caledonia.		

Hermit Crab Species and General Distribution	Associated Epizoanthus Species	Sources
Pagurus pubescens	E. parasiticus (Verrill, 1861)	Verrill (1866)
(Kröyer, 1839)		
North Western Atlantic Ocean: Bay of Fundy and Gulf of Saint Lawrence (USA); Cobscook Bay (Canada); Iceland; North Eastern Atlantic: Saguenay Fjord (France); Irish Sea; Belgium; Scotland; Norway.		
Sympagurus papposus	<i>Epizoanthus</i> sp.	Lemaitre (1996); Forest <i>et al.</i> (2000)
(Lemaitre, 1996) = S. burkenroadi* (Thompson, 1943)		
Indian Ocean: Mozambique Channel; Indian/Pacific: Eastern and Western Australia.		
Pagurus bernhardus	E. incrustatus (Von Düben and Koren, 1847)	Ates (1985); Ates (2003)
(Linnaeus, 1758)		
North Atlantic: European waters (France, Portugal, Ireland, UK, Belgium, Holland); Azores; Mediterranean Sea: Eastern Basin.		
Pagurus cuanensis	E. arenaceus (Delle Chiaje, 1823)	Milne Edwards and Bouvier (1900); Pax
(Bell, 1846)		(1937); Stachowitsch (1980)
North Atlantic; Mediterranean Sea; South Africa.		
	E. paguricola (Roule, 1900)	Roule (1900a, 1900b); Herberts (1972a, 1972b)
Anapagurus laevis	E. incrustatus (Von Düben and Koren, 1847)	Crawshay (1912); Carlgren (1913); Bull
(Thompson, 1844)	= E. americanus (Verrill, 1864); E. papillosus (Gray,	(1939); Manuel (1981); Cranmer <i>et al.</i>
North Atlantic, Mediterranean Sea; North Sea.	1867)	(1983); Dyer <i>et al</i> . (1983); Muirhead <i>et</i> <i>al.</i> (1986)
Oncopagurus monstrosus	E. paguricola (Roule, 1900)	Roule (1900a, 1900b); Herberts (1972a,
(Alcock, 1894)		1972b)
= Sympagurus arcuatus var. monstrosus (Alcock, 1894)		
= ? Eupagurus brevimanus (Yokoya, 1933)		
Bay of Bengal, Gulf of Aden, Australia, Indonesia, Philippine Islands, Taiwan, Japan.		

Hermit Crab Species and General Distribution	Associated Epizoanthus Species	Sources
Paguristes puniceus	Epizoanthus sp.	Alcock (1905)
(Henderson, 1896)		
Eastern Indian Ocean: Andaman Sea; Northern Australia; Bay of Bengal; Indonesia; South Western Indian Ocean: Réunion; Madagascar; South Western Pacific: New Caledonia.		
Oncopagurus minutus	Epizoanthus sp.	Alcock (1905); Lemaitre (2003)
(Henderson, 1896)		
Indo-Pacific: Banda Sea and Celebes Sea (Indonesia).		
Anapagurus chiroacanthus	E. paguricola (Roule, 1900)	Roule (1900a, 1900b); Herberts (1972a,
(Lilljeborg, 1856)		1972b)
North Eastern Atlantic.		
Paguristes balanophilus	Epizoanthus sp.	Alcock (1905)
(Alcock, 1905)		
North Western Indian Ocean: Andaman Sea.		
Nematopagurus muricatus (Henderson, 1896)	<i>Epizoanthus</i> sp.	Alcock (1905)
Western Indian Ocean and the Arabian Sea: Red Sea (Eritrea); Maledives; Seychelles.		
Paguristes eremita	E. arenaceus (Delle Chiaje, 1823)	Bell (1846); Milne Edwards and Bouvier
(Linnaeus, 1767)		(1900); Pax (1937); Stachowitsch (1980)
Mediterranean Sea and North East Atlantic.	E. frenzeli (Pax, 1937)	Pax (1937)
	E. steueri (Pax, 1937)	Pax (1937)
	<i>E. vatovai</i> (Pax, 1937)	Pax and Lochter (1935); Pax (1937)
Anapagurus pusillus	Epizoanthus sp.	Henderson (1888)
(Henderson, 1888)		
North Atlantic Ocean: Azores; European Waters; Faial Island (Portugal); Canary Islands (Spain).		
Parapagurus latimanus	<i>Epizoanthus</i> sp. (probably)	Lemaitre and McLaughlin (1992)
(Henderson, 1888)		
South Pacific Ocean: Wallis and Futuna; New Caledonia; New Zealand.		

Hermit Crab Species and General Distribution	Known Associated Epizoanthus Species	Sources Recording the Association
Iridopagurus globulus	Unknown zoanthid family	García-Gómez (1983)
(de Saint Laurent-Dechancé, 1966 )		
North Western Atlantic Ocean: Gulf of Mexico; Caribbean Sea.		
Oncopagurus indicus	Unknown zoanthid family (anthozoan polyp)	Lemaitre (1996)
(Alcock, 1905)		
Western Pacific Ocean: Solomon Sea; Indonesia; Southern Japan; Australia; Eastern Indian Ocean: Australia.		
Oncopagurus orientalis	?	Lemaitre (1997)
(De Saint Laurent, 1972)		
Pacific Ocean: Philippines.		
Possibly Paguristes sp.	E. ramosus (Carlgren, 1934)	Carlgren (1934a)
Pagurus?	E. senegambiensis (Carter, 1882)	Carter (1882); Pax and Müller (1956)
Diogenes ovatus (Miers, 1879)		
Paguristes palythophilus	E. sagaminensis (Pax, nomen nudum?)	Balss, 1924
(Ortmann,1892)		
Pacific Ocean: Indonesia; Japan; Taiwan; New Caledonia; Indian Ocean; Madagascar; Mozambique Channel.		
Oncopagurus bicristatus	? Actinians or zoanthids	Lemaitre (1989)
(Milne Edwards, 1880)		
Eastern Atlantic: from the Canary Islands and Cape Verde Islands to the Gulf of Guinea; Western Atlantic: from the Straits of Florida and the Gulf of Mexico to off the coast of Maranhao, Brazil.		
Parapagurus alaminos	? Actinians or zoanthids	Lemaitre (1989)
(Lemaitre, 1986)		
W Atlantic: off eastern USA; Bahamas Islands; Florida Straights; Gulf of Mexico; Caribbean Sea; E. Atlantic: Canary Islands; Cape Verde Islands; Gulf of Guinea		
Parapagurus richeri	? Anthozoan polyp	Lemaitre (1999); Forest <i>et al.</i> (2000)
(Lemaitre, 1999)		
South Pacific Ocean: Wallis and Futuna; New Caledonia; New Zealand.		

Hermit Crab Species and General Distribution	Known Associated Epizoanthus Species	Sources Recording the Association
Parapagurus nudus	Epizoanthus sp.	Lemaitre (1989)
(Milne Edwards, 1891)		
Eastern Atlantic: the Azores and Canary Islands to the Gulf of Guinea. Western Atlantic: off Nantucket Island to Guyana.		
Eupagurus sp.?	E. similis (Carlgren, 1938)	Carlgren (1938)
Parapagurus saintlaurentae	?	Lemaitre (1999)
(Lemaitre, 1999)		
Indian Ocean: Mozambique Channel.		
Oncopagurus gracilis	? Actinians or zoanthids	Lemaitre (1989; 2003)
(Henderson, 1888)		
Eastern Atlantic: Gulf of Guinea; Western Atlantic: from the Straits of Florida to off Pernambuco, Brazil.		
Sympagurus andersoni (Henderson, 1896)	<i>Epizoanthus</i> sp.	Lemaitre (2004)
Gulf of Aden, Maldives, Laccadive Sea, off eastern Africa from Somalia to Mozambique, Madagascar, Seychelles and Straits of Malacca.		
Parapagurus armatus var monstrosus ?	E. valdiviae (Carlgren, 1923)	Carlgren (1923)

Work on hermit crab – anemone associations lends insight to understanding hermit crab – zoanthid associations, but it remains unclear if hermit crabs compete for their pseudoshellbuilding symbionts, or if there is any competition between Zoantharia for settlement on hermit crab hosts (Ates, 2003). Schäfer *et al.* (1983) described how the adult *P. typica* is associated with a zoanthid associate, while the glaucothöe stage is associated with an anemone, but it remains unknown how many hermit crab species can switch between the two cnidarian partners, or whether they are able to do so at all (Ates, 2003). While the benefits derived by anemone associates are relatively well known (Table 1.1), there is almost nothing known about the benefits to the *Epizoanthus* species by being associated with hermit crabs (Ates, 2003). Some hypothesised advantages of the relationship include the availability of hard substrate for *Epizoanthus* polyp settlement in otherwise sandy or muddy environments (Stachowitsch, 1980), and that their mobile hermit crab hosts generate currents that bring nutrients etc. to the filter-feeding zoanthid (Ates, 2003).

It is almost impossible to know the true advantages and disadvantages of the relationship for both associates when the conditions of the association and the environments in which it occurs remain unknown (Ates, 2003). This study will thus serve to provide much-needed baseline data on two South African deep water cloaked hermit crab (parapagurid) species, Sympagurus dimorphus and Parapagurus bouvieri. Specimens of both species collected from demersal trawl surveys in 2016 are examined to provide data on basic biology, such as sex ratios, age at first reproduction and fecundity and this is presented in Chapter 2. The distribution and abundance of zoanthid polyps on the shell is also included in Chapter 2 to investigate whether zoanthids settle in such a way as to take advantage the hermit crab feeding/mastication, as anemones have been documented to do i.e. positioned directly above the head of the hermit crab to take advantage of suspended organic particulate matter in the water column. The hermit crab - zoanthid relationships is further investigated using these collected samples to answer questions pertaining to pseudoshell use, fit and potential benefits, as outlined above in a supporting paper (Appendix 2), and whether similar benefits exist to hermit crabs with zoanthid associates as those with anemone symbionts. To this end, questions to be answered include whether females in berry inhabit larger "made to order" pseudoshells than non-ovigerous females of the same size, whether pseudoshells provide a "better fit" than gastropod shells, and whether pseudoshells offer physical protection comparable to "real shells". Using historical demersal trawl survey data, Chapter 3 of this thesis provides data on the depth distributions of the two populations and their habitat range, both in terms of geographical distribution and preferred benthic habitat type. Changes

in the population over decadal time scales is assessed using these data in Chapter 4, and the interactions of these populations with and impacts of commercial trawl fisheries are discussed. This is the first long-term study of its kind globally.

This dissertation builds on the work conducted on *S. dimorphus* in Argentina by Schejter and Mantelatto (2011; 2015), but in a South African context and based on much larger sample sizes and a long historical data set. It is also the first work of its kind globally to be conducted on the biology of *P. bouvieri*.

# Chapter 2

# Population structure and morphology of South African deep-water parapagurid hermit crabs



A live Sympagurus dimorphus (Studer, 1883) together with its open zoanthid polyps. Image: CL Griffiths (2015)

#### Introduction

Parapagurid hermit crabs are widely distributed on the continental shelves and slopes of many of the world's oceans, where they often dominate deeper-water benthic invertebrate communities (Lemaitre, 1989; Lemaitre, 1996; Lange and Griffiths, 2014). They also form a component of the invertebrate by-catch of many demersal fishery operations, including in Argentina, Austrialia and South Africa (Lemaitre, 2004; Schejter, Bremec and Hernández, 2008; Floerl, Hewitt and Bowden, 2012; Lange and Griffiths, 2014; Schejter and Mantelatto, 2015; McLaughlin, 2015).

Parapagurid hermit crabs form symbiotic relationships with anthozoans of the genus *Epizoanthus* (Grey, 1867), the zoanthids forming a 'pseudoshell' or 'cloak', within which the crab dwells (Balss, 1924; Ates, 2003; Schejter and Mantelatto, 2011; 2015). The symbiotic zoanthids eventually entirely replace the gastropod shells traditionally used as protection for the uncalcified abdomen of hermit crabs (Ates, 2003), and it is hypothesised that this association has allowed parapagurid hermit crab populations to attain high abundances in areas where there is a paucity of suitable gastropod shells (Schejter and Mantelatto, 2011). This association type exists in many parapagurid genera, and multiple *Epizoanthus* species can be associated with a single hermit crab species (Ates, 2003). The pseudoshell is built by the zoanthid after it settles on the initial shell inhabited by the juvenile hermit crab, and it often preserves the shape dictated by the "original" shell, including a columelar axis (Schejter and Mantelatto, 2011). It is also hypothesised that the association of the hermit crab with its zoanthid pseudoshell negates the need for the continual replacement of gastropod shells as the hermit grows (Schejter and Mantelatto, 2011), conferring fitness benefits associated with having a living shell that continuously expands to provides a "perfect fit".

*Sympagurus* (Smith, 1883) and *Parapagurus* (Smith, 1879) are among the best-known genera within the family Parapaguridae. Five *Sympagurus* and four *Parapagurus* species are known to associate with pseudoshell-forming zoanthids (see Chapter 1 for list). Two of these, *Sympagurus dimorphus* (Studer, 1883) and *Parapagurus bouvieri* (Stebbing, 1910), are the most abundant parapagurid species on the continental shelf and slope around South Africa (Lange and Griffiths, 2014). Colloquially referred to by fishermen as "monkey nuts", *S. dimorphus* and *P. bouvieri* associate with the zoanthid species *Epizoanthus paguricolai* (Carlgren, 1923) and *E. carcinophilus* (Carlgren, 1923) respectively. Globally *S. dimorphus* has a reported depth range of 91 - 1 995 m, while *P. bouvieri* is reportedly found at depths of 249 - 810 m (Lemaitre, 1989, 2004; Lemaitre and McLaughlin, 1992), but within South African

waters the reported depth ranges are 30 – 814 m and as 62 – 700 m respectively (Chapter 2). *S. dimorphus* has a broad distribution in the southern hemisphere between latitudes 22°S and 57° (Lemaitre 1989, 2004; Lemaitre and McLaughlin, 1992), while *P. bouvieri* has a more limited distribution in the south-eastern Atlantic, ranging from Namibia to KwaZulu-Natal (Lemaitre, 1990). Nothing is known about the life history or biology of either species in South African waters, and while some work has been conducted on South American populations of *S. dimorphus* (Schejter and Mantelatto, 2011, 2015), *P. bouvieri* is known only from taxonomic work (Lemaitre, 1986; Lemaitre, 1989; Lemaitre, 1990) and its biology remains entirely undescribed.

The hermit crab – zoanthid symbiosis is not obligate for all parapaguid hermit crabs. For example Schejter and Mantelatto (2011) found that although the vast majority of adult *S. dimorphus* lived in symbiosis with *Epizoanthus* pseudoshells, a small proportion occupied "real" gastropod shells. It is unknown whether a similar pattern is present for *P. bouvieri*. Typically, larger hermit crabs have an advantage when it comes to competing for the limited numbers of gastropod shells avaliable in most systems (Bertness and Cunningham, 1981). Therefore, it is hypothesised that larger, male, parapagurid hermit crabs may preferentially occupy any real shells found at depth, since Schejter and Mantelatto (2011, 2015) showed that male *S. dimoprhus* are typically larger than females. Furthermore, since shell volume limits the number of eggs that can be carried (Hazlett, 1981), and since pseudoshell shape and size may be controlled in some way by the hermit crab (an assumption as yet unproved), it is hypothesised that ovigerous female parapagurid hermit crabs may occupy larger, "custom made" pseudoshells than non-ovigerous individuals.

While the probable benefits derived by parapagurid hermit crabs in this "grow your own home" association with zoanthid pseudoshells have been explored in Chapter 1, the benefits derived by the Epizoanthus pseudoshells in this symbiotic arrangement remain unknown (Ates, 2003). Work on hermit crab - anemone symbioses may provide insight into the benefits derived by the zoanthid, which may include increased substrate availability in sandy or muddy areas, where few other solid substrata are available for settlement (Riemann-Zórneck, 1994), and increased mobility (Stachowitsch, 1997, 1980). A further, as yet unproven, benefit to the zoanthid increased food availability, may be as a result of the host feeding/mastication/handling of food (see Fautin, 1992) for similar work on anemones). Muirhead et al. (1986) for example, hypothesised that the ventral polyps of E. abyssorum take advantage of, and gain access to, food dropped by the hermit crab host. If the zoanthid is deriving food benefit from its hermit crab partner, it might be expected that the zoanthid polyps would be distributed close to, or around, the aperture of the shell, to take maximum advantage of increased residual food particles generated during host food handing.

Despite their ubiquity, their fascinating symbiotic relationships with *Epizoanthus* pseudoshells, and their interactions with commercial fishing operations, almost nothing is known about the basic biological parameters and life-history traits of parapagurid hermit crabs (Lemaitre, 1989), this largely being due to the high costs and logistical difficulties typically involved in obtaining adequate samples from deeper waters. Therefore, the objectives of the present study are to document the sex ratio, sexual dimorphism, size frequency and depth distributions, relative growth and population structures of the two parapagurid hermit crab species, *S. dimorphus* and *P. bouvieri*, which dominate the South African benthic invertebrate fauna. This work examines many more specimens, collected from a far greater geographical distribution and depth range than those sampled by Schejter and Mantelatto (2015), and will be the first of its kind globally for any species of the genus *Parapagurus*. Also presented is the first work on the distribution of the zoanthid polyps that make up the *Epizoanthus* pseudoshells of these two species.

#### Methods

#### Survey methods

Parapagurid hermit crabs were collected during the 2016 bi-annual demersal research trawl surveys conducted by the South African Government's Department of Agriculture, Forestry and Fisheries (DAFF) aboard the vessel *Compass Challenger*, using the same gear as previous DAFF surveys (for details of sampling methods, see Chapter 3). Two surveys were conducted, the first during late summer (February/March) of 2016 on the West Coast of South Africa, and the second on the South Coast during autumn (May) of 2016. The parapagurid samples collected on these two survey cruise (51 hauls in total) were pooled to provide a larger sample size, thus forming a large representative sample of the South African parapagurid population. If less than 100 parapagurid hermit crabs were found in a sample, these were all retained and frozen for later examination, but if samples contained more than 100 individuals, a random sub-sample of 100 of these was retained and the remainder discarded.

In the laboratory, hermit crabs were initially sorted into the two known species, the "shallow water" *Sympagurus dimorphus* and the "deep water" *Parapagurus bouvieri*. Each hermit crab was then removed from its shell and sexed using taxonomic characteristics outlined by

Lemaitre (1986, 1989, 1996, 2004). Size was estimated by measuring the cephalothoracic shield length (CL) (total n = 1 670) and the length of the propodus of the major (right) cheliped (CHL) (total n = 826), as per Schejter and Mantelatto (2015). Fewer chelipeds were measured because many specimens had lost their protruding cheliped during capture, storage or transportation. Shell size was estimated by measuring the pseudoshell/real shell aperture width (n = 959) and colony height (n = 473) (some pseudoshells were deformed, and colony height was thus considered too inaccurate a measure, hence the difference the number of measurements taken for aperture width and colony height). All measurements were taken using a vernier caliper to a precision of 1 mm. Ovigerous females were noted.

#### Sex ratios and size distributions

The relationships between size class and M:F sex ratio for both species were analysed, with sex ratio plotted by size class as per Wenner (1972). To test if the sex ratio differed significantly from 1:1, a hypothesis test for a binomial distribution (at the 95% confidence interval) was conducted for the number of males counted for each species. Size at 50% maturity was calculated for females of both species. The size distributions of both species were plotted, and two sample Kolmogorov–Smirnov (KS) tests were performed to verify whether the two samples come from the same distribution. Rank-Sum Kruskal-Wallis K-way tests were used to compare the sizes of males, females and ovigerous females for both *S. dimorphus* and *P. bouvieri*, followed by a post-hoc Dunn (1964) Test (as per Dinno, 2015). All statistical analyses were conducted in either *Statistica* 10 (Statsoft Inc. 2011), or the Real Statistics Data Analytics Add-in for Microsoft Excel (2015).

#### Sexual dimorphism

The morphometric relationship between CHL and CL was compared for both species, and the pattern of allometry, as the power function  $y = ax^b$  established, based on the b value (where b = 1 represents isometry; b < 1 negative allometry and b > 1 positive allometry) (as per Schejter and Mantelatto, 2015). Isometry was indicated by 0.9 < b < 1.1 as a 'conservative definition' indicated by Clayton (1990) and Schejter and Mantelatto (2015).

#### Population structure across depth

The mean CL (mm) for both male and female populations of *P. bouvieri* and *S. dimorphus* were calculated per 100 m and per 50 m depth class respectively. The CL length data were transformed via  $y = \log(x + 1)$  to account for unequal variances. Rank-Sum Kruskal-Wallis K-way tests, and where appropriate, post-hoc Dunn's Tests, were conducted to determine

influence of depth on mean parapagurid size. A polynomial line of best fit was constructed for both species. In addition, the percentages of males to females across the depth classes were calculated for both species, and polynomial regression curves constructed to determine the significance of these relationships.

#### Pseudoshell occupancy and structure

Each hermit crab was assessed as having either a "real shell" or a pseudoshell, a "real" shell being defined as one entirely free of *E. carcinophilus* (Carlgren, 1923) or *E. paguricola* (Roule, 1900) polyps. To investigate whether larger hermit crabs tend to occupy real shells rather than pseudoshells, the proportion of *S. dimorphus* occupying real shells was plotted against the cephalothoracic shield length (CL), and the CL of male *S. dimorphus* occupying real shells were compared to those occupying pseudoshells with a Mann-Whitney U Test.

To determine whether ovigerous females occupy larger shells than non-ovigerous females, pseudoshell volume measurements were taken for 11 non-ovigerous and 11 ovigerous female *S. dimorphus*, and for 9 non-ovigerous and 9 ovigerous female *P. bouvieri*. Linear least-squares regressions were constructed for each non-ovigerous and ovigerous female hermit crabs measured for both CL and pseudoshell volume.

To compare pseudoshell morphology, the total number of zoanthid polyps visible on the external surfaces of the pseudoshells were counted for 50 *P. bouvieri* and 50 *S. dimorphus*. Least-squares regressions for the relationship between the total number of polyps and the colony height (mm) and volume of the shell (ml) were constructed for both species.

Zoanthid polyp distribution around the circumference of the pseudoshell was plotted by placing each pseudoshell onto a 360° protractor, and dividing it, as viewed from directly above, into four 90° quadrants (Figure 2.1), then counting the number of polyps within each. Results were expressed as percentages, in order to account for increasing polyp numbers with size. Rank-Sum Kruskal-Wallis K-way tests and post-hoc Dunn's Test were conducted to determine if there were significant groupings of zoanthid polyps on the pseudoshells of each species.

To determine which species of shell were originally colonised by juvenile hermits the original shells contained within the pseudoshells of adult hermits were extracted for randomly selected samples of *S. dimorphus* (n = 45) and *P. bouvieri* (n = 41) and identified to species or genus level based on Barnard (1958) and Steyn and Lussi (2005). The aperture width of each shell was measured, and the mean calculated.





Figure 2.1: The division of the pseudoshell of both parapagurid species into the four equal quadrants, based on a 360° protractor: Quadrant I (behind the shell aperture); Quadrant II (behind the shell aperture); Quadrant III (adjacent to the shell aperture); Quadrant IV (over the shell aperture / mouth). The number of zoanthid polyps within each quadrant was recorded.

#### Results

A total of 51 trawl samples were collected during the two 2016 surveys, trawl depths ranging from 74 – 667 m. From these samples 1 671 parapagurid hermit crabs were collected, comprising 1 122 *Sympagurus dimorphus* and 549 *Parapagurus bouvieri*. The shallowest station containing *S. dimorphus* was at 147 m, and the deepest at 563 m, with a mean successful depth of 282 m ( $\pm$  82.89 m SD). *P. bouvieri* were caught across a depth range 242 -604 m, with a mean depth of 413 m ( $\pm$  99.13 m SD).

#### Sympagurus dimorphus

#### Sex Ratios and size distributions

*S. dimorphus* had a female-biased sex ratio of 1:1.5, with 452 males (40.29%) and 670 females (59.71%), of which 397 (59.25% of all females) were ovigerous. The sex ratio differed significantly from a 1:1 ratio (p < 0.01).

Figure 2.2 shows the relationship between sex and size. The proportion of *S. dimorphus* males in the population increasing as cephalothoracic shield (CL) length increases - all *S. dimorphus* over the size of 12.1 mm (CL) being males (Figure 2.2). The percentage of ovigerous *S. dimorphus* females as a function of CL length is also shown in Figure 2.2. Length at which 50% of females were ovigerous occurred at a relatively small CL length, within the class size 5.1-6.0 mm (Figure 2.2) and the CL length at which 50% of *S. dimorphus* females were ovigerous can be approximated as 5.30 mm. The proportion of ovigerous females present remained relatively constant across the size classes (approximately 60%), increasing to 100% ovigerous within the largest class size of 11.1-12.0 mm CL (Figure 2.2).

While the overall *S. dimorphus* population showed a relatively normal size distribution (Figure 4.2), female frequencies were skewed right, towards smaller/intermediate size classes (K-S distribution = 0.276; p < 0.01). Female frequency peaked at class size 9.0 - 9.9 mm CL (both ovigerous and non-ovigerous females) (Figure 2.2). There were no females larger than the size class 12.0-12.9 mm, and the largest female present (size class 12.0-12.9 mm CL) was ovigerous (Figure 2.2). There was an unequal sex ratio in almost all size classes, with an increased ratio of males in larger size classes. Male *S. dimorphus* frequency peaked over the two class sizes, 7.0 - 7.9 mm CL and 8.0-8.9 mm CL and all individuals larger than 13 mm were male (Figure 2.2).

Male *S. dimorphus* (9.31  $\pm$  2.04 SD mm mean CL, range 4.30 – 16.60 mm) were significantly larger (Hs = 66.40; df1 = 2, df2 = 878; p < 0.01) than both females (8.02  $\pm$  1.46 SD mm mean

CL, range 4.70 – 10.70 mm) and ovigerous females (8.27  $\pm$  1.40 mm SD mean CL, range 4.40 – 12.00 mm), which were not significantly different to each other. The smallest ovigerous *S. dimorphus* female caught was 4.40 mm CL.



Figure 2.2: Size frequency distribution (CL = cephalothoracic shield length) for *S. dimorphus* males and females (ovigerous females indicated).

#### Sexual dimorphism

The relationships between cheliped length and shield length for both male and female *S*. *dimorphus* are shown in Figure 2.3. As the species name suggests, male *S*. *dimorphus* had much larger mean CHL lengths (mean CHL =  $46.43 \pm 15.71$  SD; range 13.3 - 75.9 mm) than females (mean CHL =  $26.22 \pm 3.60$  SD; range = 16.10 - 36.20 mm) across all but the smallest size classes (Figure 2.3). Cheliped length was positively allometric in both male and females (Table 2.1). Male *S*. *dimorphus* showed a larger range of CHL sizes for a given CL than females, and males had a stronger relationship between CL and CHL (R<sup>2</sup> = 0.73) than females (R<sup>2</sup> = 0.63) (Figure 2.3).

Table 2.1: Regression equations for parapagurids <i>S. dimorphus</i> and <i>P. bouvieri</i> . CL: cephalothoracic shield length;
CHL: major cheliped length; r <sup>2</sup> : coefficient of determination; A: allometry – (=) isometry, (-) negative, (+) positive; n
= number of individuals examined.

Species	Sex	n	Relationship	Power Function $y = ax^b$	Linear Function y = lna + blnx	R <sup>2</sup>	А
S. dimorphus	Male	184	CHL x CL	$CHL = 1.9986(CL)^{1.367}$	$CHL = \ln(0.69) + 1.37\ln(CL)$	0.73	+
	Female	268	CHL x CL	$CHL = 7.0219(CL)^{0.617}$	$CHL = \ln(1.95) + 0.62ln(CL)$	0.63	+
P. bouvieri	Male	75	CHL x CL	$CHL = 1.8(CL)^{1.355}$	$CHL = \ln(0.75) + 1.36\ln(CL)$	0.72	+
	Female	76	CHL x CL	$CHL = 6.05(CL)^{0.7862}$	$CHL = \ln(2.20) + 0.80ln(CL)$	0.71	-



Figure 2.3: Relative growth of major cheliped length (CHL) in relation to cephalothoracic shield length (CL) in male and female *S. dimorphus*. Regression equations and coefficients of determination shown.

#### Mean size and sex ratio across depth

The mean sampled depth of all hauls containing *S. dimorphus* was 282.73 m. Figure 2.4 shows that male CL was consistently larger than that of females across all depth classes, and that there was a significant relationship between size and depth: CL length increased with depth, peaking at 250-299 m before declining again for both males ( $R^2 = 0.72$ ) and females ( $R^2 = 0.94$ ). The smallest mean CL occurred in depth class 100-149 m for both males (mean = 8.60 mm) and females (mean = 6.38 mm), while the largest males (mean = 10.49 mm) and females (mean = 8.91 mm) both occurred in depth class 250-299 m (Figure 2.4). There was a

significant influence of depth on size for female *S. dimorphus* (H = 186.57; df1 = 5; df = 669; p < 0.01), with three depth classes significantly different for female CL length: 200-299 m; 150-199 m and 300-399 m; as well as the deepest and shallowest depth classes of 100-149 and 400+ m (Figure 2.4). Depth also had a significant influence on male *S. dimorphus* size (H =60.38; df1 = 5; df = 452; p < 0.01), with two distinct CL groupings with depth: 200-399 m; as well as the shallowest (100-199 m) and deepest (400+ m) depth classes (Figure 2.4).

There was also significant relationship between depth and *S. dimorphus* sex ratio (Figure 2.4)  $(R^2 = 0.72)$ , this being skewed towards females in shallower depth classes, with the proportion of males increasing with depth until a 1:1 sex ratio was reached at the deepest depth classes of 350-399 m (47.62% male) and 400+ m (53.33% male) (Figure 2.4).


Figure 2.4: *S. dimorphus* CL (mm) size and sex ratio (frequency) – depth distributions for all collected males and females.  $\pm$ SD. Asterisk (\*) indicates significance (p < 0.05). Regression equations and coefficients shown.

The proportion of *S. dimorphus* individuals occupying real shells was 3.39% (n = 38). CHL sizes of male *S. dimorphus* in real shells were larger (mean CHL = 51.84  $\pm$  12.96 SD) than for males in pseudoshells, and *S. dimorphus* occupying real shells (mean CL (mm) = 11.33;  $\pm$  2.33 SD) were significantly larger (U = 1767.5; p < 0.01) than males found in pseudoshells (mean CL (mm) = 9.35  $\pm$  1.90 SD).

There is also a positive significant increasing relationship ( $r^2 = 0.96$ ) between the proportion of *S. dimorphus* individuals found in real shells and the CL size of those animals (Figure 2.5).



Figure 2.5: The relationship between the size of *S. dimorphus* hermits (CL class size (mm)) and the percentage of those hermits occupying real shells. The regression equation and coefficient of determination for a linear function is shown.

Figure 2.6 indicates that there were positive, but non-significant, relationships between pseudoshell volume and CL length for both ovigerous ( $R^2 = 0.55$ ) and non-ovigerous ( $R^2 = 0.38$ ) females. The number of *S. dimorphus* pseudoshell polyps increased as a semi-asymptotic function of both colony height ( $R^2 = 0.62$ ), and total shell volume ( $R^2 = 0.78$ ) (Figure 2.7).



Figure 2.6: Relative size of the hermit crab (CL length) and the volume (ml) of its occupied pseudoshell between ovigerous and non-ovigerous female *S. dimorphus*. Regression equations and coefficients of determination shown.



Figure 2.7: Pseudoshell polyp count as a function of colony height (mm) and shell volume (ml) for *S. dimorphus*. Regression equations and coefficients of determination for a potential function are shown.

There were two significant (H = 135.25; df1 = 3; df2 = 200; p < 0.01) groupings of zoanthid polyps on *S. dimorphus* pseudoshells (Figure 2.8). Most polyps were found on the body/length of the pseudoshell (i.e. quadrant I), followed by the block closest to the aperture (quadrant IV) (Figure 2.8). However, whilst also close to the aperture of the shell, quadrant III had the fewest polyps (Figure 2.8).



Figure 2.8: *S. dimorphus* zoanthid polyp distribution around the pseudoshell.  $\pm$ SD. Asterisks (\*) indicates significance (p < 0.05); brackets indicate significant groupings as per the post-hoc test.

Nine different species of basal ("original") gastropod shells were recorded within *S. dimorphus* pseudoshells, as listed in Table 2.2. The most common (45.45%) original shells identified were *Euspira napus*, followed by *Bullia* species (20.45%) (Table 2.2). The average aperture width of the original shells present within the pseudoshell matrix was 5.29 mm ( $\pm$  1.75 mm SD). Both the largest (11.20 mm) and smallest (3.10 mm) of the original shells was identified as *Comitas saldanhae* (Table 2.2). The average original shell aperture width for *S. dimorphus* was 4.10 - 5.00 mm (Figure 2.9).

Original Shell Genus/Species	Frequency	Mean Aperture Width (mm)	Aperture Width Range (mm)	
Athleta disparilis (Rehder, 1969)	3	4.70 (± 0.71)	4.20 - 5.20	
Bullia sp. (Griffith, 1834)	9	6.29 (± 1.02)	4.30 - 7.30	
Coluzea radiale (Watson, 1882)	2	5.40 (± 0.42)	5.10 - 5.70	
Comitas sp. (Finlay, 1926)	1	7.90		
<i>Comitas saldanhae</i> (Barnard, 1958)	7	5.11 (± 2.79)	3.10 - 11.20	
Euspira napus (Smith, 1904)	20	4.57 (± 1.00)	3.30 - 7.30	
Fusivoluta sp. (Martens, 1902)	1	7.20		
Marginella musica (Hinds, 1844)	1	10.10		
Mitra sp. (Lamarck, 1798)	1	3.70		

Table 2.2: Identified "original" gastropod shells dissected out of the pseudoshells inhabited by *S. dimorphus* and the frequency at which the shell species occurred. Aperture width (mm) means (±SD) and size ranges (mm) are reported.



Figure 2.9: Frequency distribution of original shell aperture width (mm) of *S. dimorphus* and *P. bouvieri*.

## Parapagurus bouvieri

#### Sex ratios and size distributions

*P. bouvieri* displayed parity in sex ratio, with 262 males (47.72%) and 287 females (52.28%), of which 231 (80.49% of all females) were ovigerous. The binomial distribution test indicates that the sex ratio did not differ significantly from 1:1 (p = 0.15).

At all CL sizes sampled, more than 60% of females were ovigerous, so CL length at 50% maturity could not be estimated and must lie in size classes smaller than those sampled. All *P. bouvieri* females (100%) larger than 13.10-16.00 mm CL were ovigerous, and all *P. bouvieri* larger than 18.10 mm (CL) were males (Figure 2.10). The size class frequencies for *P. bouvieri* show a non-normal, bimodal distribution for both males and females (K-S distribution = 0.46; p < 0.01), with a size class modal peak of 9.10 – 10.00 mm CL for ovigerous females (Figure 2.10) and of 13.00 – 14.0 0mm CL for males (Figure 2.10).

There were significant differences in size between male, female and ovigerous female *P*. *bouvieri* (Hs = 82.11; df1 = 2, df2 = 660; p < 0.01), with males (11.86  $\pm$  2.15 SD mm mean CL, range 2.20 – 19.00 mm) larger than both females (9.57  $\pm$  1.56 SD mm mean CL, range 6.60 – 13.00 mm) and ovigerous females (10.12  $\pm$  1.62 SD mm mean CL, range 4.20 – 17.30 mm), which also differed significantly from each other. The smallest ovigerous *P. bouvieri* female was 4.20 mm CL.



Figure 2.10: Size frequency distribution (CL = cephalothoracic shield length) for *P. bouvieri* males and females (proportion of ovigerous females also indicated).

#### Sexual dimorphism

The relationships between cheliped length and shield length for both male and female *P. bouvieri* are shown in Figure 2.11. The relationships between size of the animal (shield length CL) and length of the major cheliped (CHL) were significant for both males ( $R^2 = 0.72$ ) and females ( $R^2 = 0.71$ ). While the major right cheliped (CHL) of male *P. bouvieri* were longer (mean CHL = 46.43 ± 15.71 SD; range 25.80 – 86.10 mm) on average than those of females (mean CHL = 38.96 ± 4.97 SD; range 28.00 – 52.80 mm), this difference became apparent only above a carapace length of approximately 10 mm CL (Figure 2.11). Male *P. bouvieri* also showed greater variability in CHL length compared to females. *P. bouvieri* cheliped length was positively allometric in males, and negatively allometric in females (Table 2.1; Figure 2.11).



Figure 2.11: Relative growth of major cheliped length (CHL) in relation to cephalothoracic shield length (CL) in male and female *P. bouvieri*. Regression equations and coefficients of determination shown.

#### Mean size and sex ratio across depth

The mean depth for hauls containing *P. bouvieri* was 373 m. Figure 2.12 shows that there was a significant increase in mean size with depth for both males ( $R^2 = 0.55$ ) and females ( $R^2 = 0.68$ ). Male CL was consistently larger than that of females across all depth classes (Figure 2.12). The smallest mean CL occurred within the depth class 100-199 m for both males (mean

= 7.92 mm) and females (mean = 6.73 mm), while the largest males occurred in the depth class 200-299 m (mean = 12.01 mm) and largest females in the depth class 400 – 499 m (mean = 9.77 mm) (Figure 2.12). There was a significant influence of depth on size for both female (H = 131.13; df1 = 5; df = 404; p < 0.01) and male *P. bouvieri* (H =80.56; df1 = 5; df = 364; p < 0.01), with this significance explained by the CL length of females and males within the shallowest depth class of 100-199 m. There is a significant relationship between depth and *P. bouvieri* sex ratio (Figure 2.12) (R<sup>2</sup> = 0.77), this being skewed towards females in the shallowest (100-199 m) depth classes, as well as the deepest (500-600+ m), but attaining a 1:1 ratio between 300-400 m depth (Figure 2.12). The depth class 400-499 m attains the closest parity at 51.34% male (Figure 2.12).



Figure 2.12: *P. bouvieri* CL (mm) size and sex ratio (frequency) – depth distributions for all collected males and females.  $\pm$ SD. Asterisk (\*) indicates significance (p < 0.05). Regression equations and coefficients of determination for a potential function are shown.

#### Pseudoshell occupancy and structure

All *P. bouvieri* individuals collected occurred in pseudoshells – it appears that *P. bouvieri* do not utilise real gastropod shells during adult life.

The pseudoshell volume of both ovigerous ( $R^2 = 0.78$ ) and non-ovigerous ( $R^2 = 0.67$ ) females increased significantly with CL. Figure 2.13 shows that non-ovigerous females occupied larger volume pseudoshells for their size up to CL  $\approx$  11.25 mm, beyond which ovigerous females had larger pseudoshells. Figure 2.14 shows that there was no relationship between number of zoanthid polyps on *P. bouvieri* pseudoshells relative to either pseudoshell volume ( $R^2 =$ 0.42) or colony height ( $R^2 = 0.36$ ).



Figure 2.13: Relative size of the hermit crab (CL length) and the volume (ml) of its occupied pseudoshell between ovigerous and non-ovigerous female *P. bouvieri*. Regression equations and coefficients of determination shown.



Figure 2.14: Pseudoshell polyp count as a function of colony height (mm) and shell volume (ml) for P. bouvieri.

There was a significant pattern in the distribution of the polyps around the pseudoshell (Figure 2.15) for *P. bouvieri* (H = 101.14; df1 = 2; df2 = 147; p < 0.01), with the majority of polyps located around the "outside" of the shell, and none found directly over the aperture (quadrant I).



Figure 2.15: *P. bouvieri* zoanthid polyp distribution around the pseudoshell.  $\pm$ SD. Asterisk (\*) indicates significance (p < 0.05).

Ten species of original gastropod shells were recorded within *P. bouvieri* pseudoshells, as listed in Table 2.2. The most common (39.00 %) original shells identified were *Euspira napus*, followed by *Turricula* sp. 1 (ridged) (14.63 %) and *Calliostoma* sp. 1 (ridged) (12.20 %) (Table 2.3). The average aperture width of the original shells present within the pseudoshell matrix was 5.18 mm (± 1.34 mm SD.), while the largest shell measured 8.10 mm and the smallest measured aperture width of 2.10 mm (Table 2.3). Figure 2.9 shows that majority of original shell aperture widths falling within the range 4.10 - 5.00 mm.

Table 2.3: Identified "original" gastropod shells dissected out of the pseudoshells inhabited by P. bouvieri and the
frequency at which the shell species occurred. Aperture width (mm) means (±SD) and size ranges (mm) are
reported.

Original Shell Genus/Species	Frequency	Mean Aperture Width (mm)	Aperture Width Range (mm)
Amalda sp. (Adams and Adams, 1853)	4	6.73 (± 1.19)	5.50 - 8.10
Athleta disparilis (Rehder, 1969)	1	4.70	
Calliostoma (Swainson, 1840) sp. 1 (ridged)	5	6.23 (± 1.67)	2.10 - 5.00
Calliostoma (Swainson, 1840) sp. 2 (criss-cross)	2	5.40 (± 0.91)	3.20 – 4.50
Calliostoma (Swainson, 1840) sp. 3 (jagged)	1	7.90	
Euspira napus (Smith, 1904)	16	5.11 (± 1.24)	3.00 - 8.10
Fusinus sp. (Rafinesque, 1815)	2	4.57 (± 0.49)	4.70 – 5.40
Fusivoluta sp. (Martens, 1902)	1	7.20	
Turricula (Schumacher, 1817) sp. 1 (ridged)	6	10.10 (± 1.56)	3.40 - 6.60
Turricula (Schumacher, 1817) sp. 2 (smooth)	3	3.70 (± 1.78)	4.30 – 7.60

# Discussion

The preferred depth range for *S. dimorphus* reported here was 147 - 563 m (mean 282.73 m ± 82.89 m SD), and that for *P. bouvieri* 242 - 604 m (mean 413.87 m ± 99.13 m SD). Chapter 4 reports preferential depth ranges of 200 – 299 m for *S. dimorphus* and 400 – 499 m for *P. bouvieri* in South African waters.

## Sex ratios and size distributions

The M:F sex ratio of 1:1.5 for *S. dimorphus* reported here differs from the 1:1 ratio reported by Schejter and Mantelatto (2015) from Argentinian waters. This discrepancy may be real, or an artefact of differences in sampling method, or sampling depth. The samples examined here were collected via trawl, which probably selects for larger individuals. Since male *S. dimorphus* are significantly larger than females, one would thus expect males to be preferentially selected for in trawl surveys, suggesting that the smaller females are even more abundant in South Africa that indicated by the 1:1.5 sex ratio obtained. Sampling depth ranges may also influence sex ratio, and the sampling sites for *S. dimorphus* in Argentina overlapped with the Patagonian scallop (*Zygochlamys patagonica*) fishery at depths of only

81 – 141 m (Schejter and Mantelatto, 2015), compared to the South African samples, which were collected at 74 – 667 m. However, our data (Figure 2.4) suggest that females are, if anything, more abundant in shallower waters, whereas the shallow Argentinian samples are poorer in females than the South African ones. Deviation of the expected Fisher's 1:1 sex ratio (Fisher, 1930; Kolman, 1960), as reported here, is common among marine decapod crustaceans (Wenner, 1972) including for hermit crab species such as *Calcinus latens* (Wenner, 1972), *Pagurus brevidactylus* (Mantelatto, Christofoletti and Valenti, 2005), *P. calliopsis* (Biagi, Meireles and Mantelatto, 2006), *P. criniticornis* (Mantelatto, *et al.*, 2007), *Clibanarius antillensis* (Turra and Leite, 1999) and *Dardanus insignis* (Frameschi *et al.*, 2013).

In contrast, *P. bouvieri* had an observed sex ratio of 1:1. While equal sex ratios have been reported in other hermit crabs species, such as *Paguristes erythrops* (Garcia and Mantelatto, 2001) and *Clibanarius vittatus* (Fotheringham, 1975) amongst others, the fact that almost all individuals in the smaller size classes were females, the vast majority of which were mature and ovigerous, suggests that smaller females were under-sampled, meaning that in reality females are probably considerably more common that our samples suggest.

The patterns corresponding to the sex ratio size class analysis established by Wenner (1972) for both *S. dimorphus* and *P. bouvieri* (Figure 2.3) corresponds to a Type III or intermediate sex ratio probability of curve (Wenner, 1972), where the majority of small animals were female, while all animals in the largest class sizes were male. The lack of small male individuals for both *S. dimorphus* and *P. bouvieri* is likely a result of the aforementioned selection bias of the gear towards larger animals, and larger males in particular. A Type III sex ratio probability curve has also been reported by Wenner (1972) for the hermit crab *Calcinus latens* and the king crab *Paralithodes camntschatica*. It is hypothesised that the pattern observed here is a result of the overlapping bi-modal size class distribution for males and females for both *P. bouvieri* and *S. dimorphus* (see Schejter and Mantelatto, 2015). As such, the "dip" in the probability curve at intermediate CL sizes for *S. dimorphus* can be explained by the "accumulation of females at these sizes" (as per Schejter and Mantelatto, 2015). As hypothesised by Schejter and Mantelatto (2015), the most probable cause for this is differences in growth rates between males and females, although this remains untested and requires future work.

Female *S. dimorphus* were 50% ovigerous at 5.30 mm CL length, and the smallest ovigerous female measured 4.40 mm CL. Both of these measurements are smaller than the smallest ovigerous female found by Schejter and Mantelatto (2015), which had a CL of 6.00 mm. The

size of *S. dimorphus* juveniles in South African waters can thus be defined as  $\leq$ 4.44 mm. The smallest ovigerous *P. bouvieri* female measured 4.20 mm CL, but since all size classes caught had more than 50% of females ovigerous, size at 50% maturity cannot be estimated, but can be assumed to be < 4.20 mm CL. Both species show a high ratio of ovigerous females in both summer and autumn, and while this may suggest continuous reproduction, as observed in species such as *Pagurus brevidactylus* (Mantelatto, Christofoletti, and Valenti, 2005) and *Clibanarius antillensis* (Turra and Leite, 1999), the lack of winter samples does not allow definitive conclusions to be formulated - other species such as *Calcinus tibicen* (Fransozo and Mantelatto, 1998) and *Paguristes erythrops* (Garcia and Mantelatto, 2001) show discontinuity in reproduction, with an absence of ovigerous females during winter, and a spawning period from spring to autumn. Therefore, collection of winter specimens is required to determine if the high ratio of ovigerous parapagurid females is linked to seasonality in reproduction.

## Sexual dimorphism

Males of both S. dimorphus and P. bouvieri have far larger major right chelipeds than females. In many decapods, there is isometric growth of the chelae in males and females until maturation, after which there is a rapid increase in relative size of male chelae and a subsequent increase in allometry between males and females (Mariappan, Balasundaram and Schmitz, 2000). Hermit crabs show a complete range of dimorphic chelipeds, from positive allometry in Pagurus longicarpus males (Blackstone, 1985), Paguristes erythrops males (Biagi and Mantelatto, 2006) and S. dimorphus males (Schejter and Mantelatto, 2015) to isometric or arithmetic growth in Paguristes erythrops females (Biagi and Mantelatto, 2006) and S. dimorphus juveniles (Schejter and Mantelatto, 2015) to negative allometry in S. dimorphus females (Schejter and Mantelatto, 2015). Such dimorphism has been reported in other hermit crabs, such as Loxopagurus loxochelis (Mantelatto and Martinelli, 2001) and Paguristes erythrops (Biagi and Mantelatto, 2006), both of which have similar body size dimensions to S. dimorphus and P. bouvieri. S. dimorphus appears to fall on the extreme end of the dimorphic spectrum, with the mean male S. dimorphus cheliped (mean = 46.43  $mm \pm 15.71$  SD) double the length of female chelipeds (mean CHL = 26.22 mm  $\pm$  3.60 SD) on average, and showing an extreme range of CHL sizes from 13.30 – 75.90 mm, compared to the female range of 16.10 – 36.20 mm. Thus, like Schejter and Mantelatto (2015), this work found that S. dimorphus males had positive allometric growth of major right chelipeds. This work reports for the first time that P. bouvieri cheliped lengths are positively allometric in males, and negatively allometric in females. P. bouvieri showed a less extreme dimorphism in cheliped lengths than S. dimorphus, however, with male chelipeds larger (mean CHL = 46.43 mm  $\pm$ 

15.71 SD) than those of females (mean CHL =  $38.96 mm \pm 4.97$  SD) and a less extreme range in CHL sizes between males (range 25.8 - 86.1 mm) and females (range 28.00 - 52.80 mm).

While male *S. dimorphus* occupied pseudoshells of a similar size to females, the length of the male *S. dimorphus* cheliped often exceeded the total length of the pseudoshell, rendering these males unable to fully retract into the protective pseudoshell, unlike females, which were regularly found drawn fully into the shell (Pers. Obs., 2016). Although female *S. dimorphus* also presented positive allometric major right cheliped growth, the chelipeds were in general far smaller, and more likely to be used as an operculum (Pers. Obs., 2016; Schejter and Mantelatto, 2011). Therefore, a trade-off may result between the territorial defence, courtship and intra-specific fighting linked to the larger size of the male cheliped (Hartnoll, 1974; Gherardi and Nardone 1997; Schejter and Mantelatto; 2011) and increased vulnerability to predation, which may also account for the sex ratio skewed in favour of females. Further work on differences in mortality rates between males and females is required to test this hypothesis.

## Population structure across depth

There is little work on changes in hermit crab size with depth, and this work represents the first description of changes in parapagurid size with depth. For both *S. dimorphus* and *P. bouvieri*, slightly larger individuals were found within the preferential depth range, with a slight drop to smaller individuals in the shallower and deeper extremes of the range. This may indicate that larger, most competitive individuals occupy preferrential niche space, while smaller less competetive individuals (particularly smaller males), are pushed to peripheral habitats. Since the sex ratio of *S. dimorphus* was skewed towards females, smaller, less competitive males would be pushed into deeper waters, thus accounting for the increase in the proportion of males with increasing depth. Likewise, smaller *P. bouvieri* females dominate the shallowest and deepest depth classes, while the larger males increased in abundance, and thus increased the overall size, in the "preferential" intermediate depth classes.

## Pseudoshell occupancy and structure

The vast majority of *S. dimorphus* (97.34%) occupied pseudoshells, as reported by Schejter and Mantelatto (2011) for *S. dimorphus* in Argentinian waters (92.3%). In contrast, none of the sampled *P. bouvieri* utilised real gastropod shells, all exclusively inhabiting *Epizoanthus* pseudoshells. While there were no hermit crab juveniles present in the sample that were still within their "original shell", these "original" gastropod shells were still present and visible within the greater pseudoshell structure, further supporting the hypothesis by Schejter and Mantelatto (2011, 2015) that the zoanthid settles on this initial shell and develops from there. This was particularly evident for *P. bouvieri*, where the small original shell appeared entirely detached from the hermit crabs abdomen and "suspended" in the pseudoshell matrix, while some small *S. dimorphus* individuals were still gripping their original shells with the last pair of pereiopods.

In soft sediment benthic marine ecosystems unoccupied shells are quickly buried (Conover, 1975 and 1979), and it can be inferred that there is a shortage of usable gastropod shells in deep water soft sediment environments, which parapagurids preferentially inhabit (Chapter 2). This study showed that male S. dimorphus dominated real shell occupancies (occupying 79.17% of all real shells sampled), a finding supported by Schejter and Mantelatto (2011), who found that all real shells sampled contained males. The larger male S. dimorphus cheliped and larger overall size may result in males outcompeting females for access to real shell shelters, which may offer better levels of physical protection than the softer pseudoshells (see Appendix 2). This may suggest that real shells are indeed preferred over pseudoshells - indeed even though many of the real shells examined were broken or damaged, parapagurids were still using them. Support for this hypothesis comes from the fact that males inhabiting real shells were significantly larger than males in pseudoshells, and that size and real shell occupation were positively correlated (Figure 2.5) – larger size being a known determinate of preferential access to better shelters for hermit crabs (Hazlett, 1981; Dowds and Elwood, 1983). The lack of real shell occupation among P. bouvieri raises questions however, given that the two species show a large degree of spatial overlap (Chapter 4). Possibly S. dimorphus and P. bouvieri exist along an evolutionary spectrum of independence from traditional gastropod shelters, and potentially even utilise the shells in different ways and for different purposes - P. bouvieri may exist within a stronger mutualistic symbiosis with its exclusive pseudoshell species, with the pseudoshell acting more as a "brood pouch" type structure for protecting only the abdomen, rather than as a traditional shell home, and may have lost the ability to change shelters entirely. In contrast, S. dimorphus utilised the pseudoshells much like a traditional gastropod shell home, being able to pull the entire body into the shelter. Questions remain as to how the juvenile crabs obtain and inhabit their original shells, why these are not buried, and whether the availability of these original shells limits the population. Sampling with a finer mesh trawl or dredge is required to resolve these questions

Pseudoshell volume of both ovigerous and non-ovigerous female *P. bouvieri* increased significantly with increasing CL, but no such relationship was present for *S. dimorphus* (the

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relationships for between males and ovigerous females for both species are explored further in Appendix 2). It does appear that ovigerous female parapagurid hermit crabs occupy larger pseudoshells than non-ovigerous hermits, the benefits of which include that larger shell volumes are associated with larger clutch sizes (Hazlett, 1981). However, while these results show that small, non-ovigerous *P. bouvieri* females occupy larger volume pseudoshells for their size compared to ovigerous females, the small sample size (n = 9) requires these results to be interpreted with caution, and further work is required to determine if this is a consistent pattern.

There are two *Epizoanthus* species known to be pseudoshell associates to *S. dimorphus*, namely *E. studeri* (Carlgren, 1923) and *E. paguricola* (Roule, 1900), the latter being associated with both Argentinian (Schejter and Mantelatto, 2011) and South African populations. The pseudoshells of *S. dimorphus* were flexible and tough, but far more rigid and easier to tear than those of *P. bouvieri* (Pers. Obs.). In addition, the zoanthid polyps were present on every available surface of the pseudoshell, and increased in number as the pseudoshell grew and its surface area increased. The surface area available (and thus the number of zoanthid polyps that can grow on the pseudoshell) increases as the volume increases, which explains the typical SA: V graph produced for *S. dimorphus*. The polyps also appeared to be relatively consistent in size, regardless of the pseudoshell size, but further work is required to test this. The polyps of *S. dimorphus* pseudoshells appeared concentrated around the aperture of the pseudoshell. This may suggest that the zoanthid pseudoshell is receiving some benefit, such as increased food availability, by its symbiosis with the hermit crab. The larger count of polyps found within Quadrant II of the shell may due to the typical triangular shape of the pseudoshell, which meant that the largest portion of the shell fell within this Quadrant.

The *Epizoanthus* pseudoshells occupied by *P. bouvieri* have been identified as *E. carcinophilus* (Carlgren, 1923). These zoanthid pseudoshells were flexible, but tough to tear or break compared to those of *S. dimorphus* (Pers. Obs.). In contrast to *S. dimorphus*, no polyps were found directly over the mouth of the shell (and very few adjacent to the shell aperture), and it is therefore unlikely that the zoanthid is obtaining much benefit from its *P. bouvieri* partner in terms of increased food availability. There appears to be some regularity in the number of polyps found on the shell, with no significant increase in numbers with increased pseudoshell size. This is likely due to the arrangement of the polyps, which were arranged in a linear pattern around the back and outside of the pseudoshell, with none present on the top of the shell outside of this line.

It is evident that juvenile parapagurids inhabit small gastropod shells of a variety of species – both S. dimorphus and P. bouvieri occupy about the same number of "original shell" species (n = 9 and n = 10 respectively) a count similar to the 12 gastropod species identified by Schejter and Mantelatto (2011). Euspira napus was the dominant original shell species for both S. dimorphus (45.45 %) and P. bouvieri (39.00 %) in this study, a species within the family Naticidae which also formed the bulk of S. dimorphus original shells identified by Schejter and Mantelatto (2011) in Argentinian waters. The abundance of naticid shells available in the South African benthic system is not known, but Steyn and Lussi (2005) list Euspira napus as "Uncommon". It is unknown whether there is selection of the original shell, but given the similar results to those by Schejter and Mantelatto (2011), it is likely that there is some level of original shell selection by South African parapagurids. Both S. dimorphus and P. bouvieri inhabit original shells of similar mean aperture widths (5.29 mm (± 1.75 mm SD) and 5.18 mm (± 1.34 mm SD) respectively), and the majority of original shell aperture widths of these original shells fall within the same 4.10 – 5.00 mm group (Figure 2.9), although both parapagurids inhabit shells smaller than this (Table 2.2; 2.3). Therefore, we can conclude that parapagurid hermit crabs inhabit their original gastropod shells as juveniles capable of fitting within a shell of aperture width of approximately  $\leq$  5.00 mm, since the size of juvenile S. *dimorphus* and *P. bouvieri* in South African waters can thus be defined as  $\leq$ 4.44 mm CL and <4.20 mm CL respectively. However, some larger original shells were found (the largest being a *Comitas saldanhae* of 11.20 mm aperture width), indicating that the parapagurid juveniles may switch to larger gastropod shell homes if the opportunity arises.

The differences noted between *P. bouvieri* and *S. dimorphus* in terms of real shell utilisation, polyp distribution and general interaction with their pseudoshell *Epizoanthus* partners raises questions about whether *P. bouvieri* and *S. dimorphus* utilise their pseudoshell shelters in different ways – it would appear that *S. dimorphus* readily switches to real shell occupation should the opportunity arise, and that the larger cheliped of males allow them to dominate real shell utilisation over females, while *P. bouvieri* do not utilise real shells as adults, perhaps because they have lost their ability to switch shelters completely. Currently, pseudoshell utilisation by hermit crabs is understood as a mutualistic symbiotic relationship (Williams and McDermott, 2004), but perhaps such evidence as presented here points to a closer, more obligate symbioisis between *P. bouvieri* and its pseudoshell *Epizoanthus carcinophilus*. While some work has been conducted on the growth patterns of zoanthids associated with pagurids (Muirhead *et al.*, 1986; Schejter and Mantelatto, 2011), behavioural studies are crucial to

understanding how these deep water hermits interact with and affect the growth of their pseudoshells, but such studies remain conspicuously absent from the literature.

# Chapter 3

Distribution and abundance patterns of deep water Parapaguridae hermit crabs (Crustacea: Decapoda: Anomura) along the west and south coasts of South Africa



Two Sympagurus dimorphus (Studer, 1883) hermits. Image: CL Griffiths (2015)

## Introduction

The family Parapaguridae (Smith, 1882) (infraorder Anomura) consists of ten genera of deepwater hermit crabs (McLaughlin, 2015a) that are found at depths of 55 - 5000 m (Lemaitre, 1989). Many Parapaguridae species forego the use of traditional gastropod shell homes and instead carry colonies of cnidarian anthozoans (Poore, 2004), while some genera do not inhabit shells at all, such as *Bivalvopagurus* (Lemaitre, 1993) and *Tylaspis* (Henderson, 1885) (McLaughlin and Lemaitre, 1997). *Parapagurus* (Smith, 1879) and *Sympagurus* (Smith, 1883) are among the best known genera within the family Parapaguridae, and constitute some of the most conspicuous and abundant organisms found on continental and upper slope regions in the southern hemisphere (Lemaitre, 1989; Lemaitre, 1996). The 51 described *Parapagurus* species form the majority of species within the family Parapaguridae (Lemaitre, 1989) and are found mostly at depths of 200 – 3000 m, although some records are from depths exceeding this range (Lemaitre, 1986). There are 17 recognised species within the genus *Sympagurus* (Schejter and Mantelatto, 2011), some of which grow to be the largest of the Parapaguridae (Lemaitre, 2004) and these are typically distributed between depths of 500 - 1000 m, but have a known range of 80 – 2537 m (Lemaitre, 2004).

Hermit crabs in the genera Parapagurus and Sympagurus have been of interest to zoologists since early times (Lemaitre, 1989) due to their associations with zoanthid symbionts that are either carried on an inhabited gastropod shell, or replace the shell entirely, forming a "pseudoshell". The first type of association accounts for the majority of the recorded zoanthid associations within the genus Parapagurus, such as in P. latimanus (Henderson, 1888), P. alaminos (Lemaitre, 1986), P. richeri (Lemaitre, 1999), P. saintlaurentae (Lemaitre, 1999) and P. nudus (Milne Edwards, 1891), but appears to be less common in Sympagurus, occurring only in S. andersoni (Henderson, 1896). The latter "pseudoshell" association involves zoanthid species encasing the hermit crabs to form living, cloak-like shells, hence the common name of "cloaked hermit crabs". From the current literature (Balss, 1924; Muirhead, Tyler, and Thurston, 1986; Ates, 2003; Williams and McDermott, 2004), all zoanthids associated commensally with these hermit crabs belong to the genus Epizoanthus (Grey, 1867). Approximately 22 Epizoanthus species are known hermit crab symbionts (Ates, 2003), but many more associates have been identified simply as "Epizoanthus sp." or "Unknown zoanthid" in the review by Ates (2003). Some hermit crab species exhibit both association "types", and in some cases multiple *Epizoanthus* species are known to associate with a single parapagurid species (Table 3.1). The four recorded Parapagurus, and five recorded

*Sympagurus* species associated with *Epizoanthus* pseudoshells and the *Epizoanthus* species with which each is associated are listed in Table 3.1.

Table 3.1: List of parapagurid – zoanthid associations involving "pseudoshell" Epizoanthus species encasing species of *Parapagurus* and *Sympagurus* (adapted from Ates, 2003).

Host Genus	Host Species	Associated Epizoanthus Species	References
Parapagurus	<i>P. pilosimanus</i> (Smith,1879)	E. abyssorum (Verrill, 1885) E. carcinophilus (Carlgren, 1923) E. paguriphilus (Verrill, 1883)	Verrill (1882); Verrill (1885a); Verrill (1885b); Smith (1886); Jourdan (1891 and 1895); Milne Edwards and Bouvier (1893); Carlgren (1913); Carlgren (1923); Carlgren (1938); Muirhead <i>et al.</i> (1986); Carlgren (1913); Lwowsky (1913); Boone (1930); Carlgren (1934b)
	P. andreui (Filhol, 1885)	Epizoanthus sp.	Lemaitre (1989); Forest <i>et al.</i> (2000)
	P. abyssorum (Filhol, 1885)	Epizoanthus sp.	Lemaitre (1989); Forest <i>et al.</i> (2000)
	<i>P. bouvieri</i> (Stebbing, 1910)	<i>E. carcinophilus</i> (Carlgren, 1923) <i>E. paguricola</i> (Roule, 1900) <i>Epizoanthus</i> sp.	Carlgren (1938); Stebbing (1910); Lemaitre (1990); Lemaitre (1999); Forest <i>et al.</i> (2000)
Sympagurus	<i>S. dimorphus</i> (Studer, 1883)	E. studeri (Carlgren, 1923) E. paguricola (Roule, 1900) Epizoanthus sp.	Jourdan (1895); Lwowsky (1913); Carlgren (1938); Lemaitre (1989); Lemaitre (1996); Forest <i>et al.</i> (2000); Schejter and Mantelatto (2011)
	<i>S. acinops</i> (Lemaitre, 1989)	<i>Epizoanthus</i> sp.	Lemaitre (1989)
	S. dofleini (Balss, 1912)	Epizoanthus sp.	Lemaitre (1994)
	<i>S. villosus</i> (Lemaitre, 1996)	Epizoanthus sp.	Lemaitre (1996)
	<i>S. burkenroadi</i> (Thompson, 1943)	Epizoanthus sp.	Lemaitre (1996); Forest <i>et al.</i> (2000)

Despite the ubiquity and intriguing aspects of the biology of these crabs and their relationships with associated zoanthids, almost nothing is known about the ecology and biology of the hermit crab species themselves (Ates, 2003 and Schejter and Mantelatto, 2011), or indeed about the nature of the association and its benefits to either hermit or zoanthid. As with many other deep-water invertebrates (Day *et al.*, 1989; Constable, 1999; Koslow *et al.*, 2001; Lange, 2010;), the majority of research on cloaked hermits to date has been taxonomic (Lemaitre, 1986; Lemaitre, 2004) and there is a lack of data sets that are sufficiently intensive or broad-scale to enable even the distribution patterns, densities or size distributions of these species to be reliably plotted. Schejter and Mantelatto (2015)

investigated the distribution patterns of *S. dimorphus* on the Argentinean shelf in the south western Atlantic, and found that the species exists in a "patchy distribution along the shelf break". However, further work is required to fully assess even this species, since this study was limited to the southernmost distribution limit for the species investigated (Schejter and Mantelatto, 2015), and because the samples were obtained as by-catch from dredge assessments of the commercial Patagonian scallop stock fishery (668 dredged sample sites).

This chapter takes advantage of data from a regular series of large-scale demersal research trawl surveys off the South African shelf in order to map the biogeographical distribution and abundance patterns, as well as the influence of season on sample mass, of two species of Parapaguridae hermit crabs, *Parapagurus bouvieri* (Stebbing, 1910) and *Sympagurus dimorphus* (Studer, 1883). These data provide by far the most comprehensive data set that has been used to describe the population structure of these or any other parapagurid species to date.

## Methods

## Survey methods

The data analysed here were obtained from a series of bi-annual, demersal research trawl surveys conducted by the South African government's Department of Agriculture, Forestry and Fisheries (DAFF) from 1987 to 2014. Sampling occurred within the Exclusive Economic Zone (EEZ) of South Africa, along a stretch of approximately 1 400 km of coast from the South African border with Namibia (28°36' S, 16°26' E) in the Atlantic Ocean to east of Port Elizabeth (33° 39' S, 27°00' E) in the Indian Ocean and spanning a depth range of 17 - 1 400 m (Figure 3.1). Pre-2008 demersal research trawls focused on sampling from the coast to the 500 m isobath, and trawls deeper than 500 m were only completed on an ad hoc basis, as opportunities arose. Post 2011, demersal research trawls were routinely completed below 500 m. Although catch biomass (i.e. sample mass) and length (or number) data were recorded for all species and biological information for selected species; the primary purpose of the surveys was to monitor the commercially important Cape hakes (Merluccius capensis and M. paradoxus). Thus all demersal research trawls were conducted during the day to avoid nocturnal vertical migrations of the target hake species (DAFF, 2014). The entire catch of most demersal research trawls was brought on board (Atkinson et al., 2011b), and sorted to species for processing. The cloaked hermit crabs caught were sorted visually into "deep water" (Parapagurus bouvieri) or "shallow water" (Sympagurus dimorphus) species and the

total mass of each weighted. If demersal research trawl catches were too large to be fully sorted on deck (> 4t), a known proportion of the catch was subsampled and sorted and the weights scaled up to calculate the total catch weight (kg). Sampling was conducted during the austral summer/winter on the West Coast (west of ~20° E, Figure 3.1), and during the austral spring/autumn on the South Coast (east of ~20° E, Figure 3.1).



Figure 3.1: Map of the sample area within the EEZ of South Africa. The lines of bathymetry are indicated, as is the 5'x5' survey grid (DAFF, 2015). The dark grey blocks indicate 5'x5' survey blocks that were sampled between 1987 and 2014 (n = 1 794), while the light grey blocks indicate survey grid blocks that were not sampled between 1987 and 2014 (n = 1 874). The boundary used to delimit 'West' and 'South' Coasts is indicated in red.

#### Survey vessel and demersal research trawl gear

Surveys were conducted aboard the *FRS Africana* from 1987 to 2012 (inclusive), except that this vessel did not conduct surveys in the summer of 1989, or in 2000 and 2001, because of technical problems. The 2002 data were excluded because the hard copy data were lost. The 2000 and 2001 surveys were conducted aboard the Norwegian *RV Dr Fridtjof Nansen*, but those data were excluded from this analysis due to vessel and demersal research trawl gear differences. Due to unavailability of the *FRS Africana*, surveys were conducted in 2013 and

2014 aboard the *FV Andromeda*, and are included because of the continuation of the random stratified survey design and the similarity in gear and vessels.

From 1986 to 2003 (inclusive) and in 2006 and 2010, the demersal research trawl gear consisted of a two-panel 180 ft German otter trawl, 50 m sweeps and 1.5 t WV otter boards (as per Atkinson *et al.*, 2011b). Door spread was approximated 120 m, with a 2 m vertical and 26 m horizontal mouth opening, and a rope-wrapped chain footrope (Atkinson *et al.*, 2011b). The demersal research trawl gear configuration was altered in May 2003, and from 2004 to 2014 (excluding 2006 and 2010 when the 'old' gear was used), the 'new' gear consisted of a four-panel 180 ft German otter trawl, 9 m sweeps and 1.5 t Morgere multipurpose otter boards (Atkinson *et al.*, 2011b). Door spread was 60 - 75 m, mouth opening 3 - 4 m vertical and 20 - 29 m horizontal, and the footrope was constructed from rubber discs (rock hoppers) (Atkinson *et al.*, 2011b). According to Atkinson *et al.* (2011b), these changes in gear resulted in a greater portion of the water column being sampled, a reduction in herding and the reduced sampling of flatfish and batoids. Mesh size was 110 mm wings, a 75 mm cod end with a 25mm mesh liner (Hutchings and Griffiths, 2005; Atkinson *et al.*, 2011a; K. Hutchings, Pers. Comm., 2017).

#### <u>Survey design</u>

Sampling was conducted via a pseudo-random stratified survey design (DAFF, 2014). A predetermined 5'x5' grid was projected onto the total survey area, with one sample (one demersal research trawl) taken randomly within each preselected grid block cell (Figure 3.1). The start point co-ordinates of each demersal research trawl were used to confirm whether the trawl had been conducted on the West or South Coast, and to determine the grid identification of the 5'x5' block surveyed. No grid block was sampled twice in one cruise, but subsequent cruises occasionally surveyed the same grid block again. Between 1987 and 2014, the annual demersal research surveys (as indicated in Appendix 1) covered 48.91% of the predetermined 5' x 5' survey grid squares available (Figure 3.1).

Equal numbers of stations within each depth class were sampled during each survey cruise, with the number of stations sampled within each depth stratum being proportional to the total area of that stratum (DAFF, 2014). This sampling design means each sample demersal research trawl was taken independently of the others, and thus the data were considered to meet the assumption for independence. Areas of rough ground were excluded from the station selections (DAFF, 2014).

A target of 100 demersal research trawls was set for each cruise pre-2011 and an increased target of 120 from 2011 to adequately sample the extended depth range. Demersal research trawl duration (30 minutes, but occasionally reduced because of rough ground), ship speed (3.5 knots) and the mouth width of the demersal research trawl net (mean = 26 m) were used to calculate swept area for each tow, using the following equation (as per Atkinson *et al.*, 2011b):

Swept Area (ha) = 
$$\frac{\frac{Trawl Duration [min]}{60} \times Speed of the Trawl [nm.h^{-1}] \times \frac{Trawl Mouth Width [m]}{1852}}{342.99}$$

This measurement was converted first to  $nm^2$  (1  $ha = 0.002915 nm^2$ ) and then to  $km^2$  (1  $nm^2 = 3.4299 km^2$ ). The mean swept area per demersal research trawl was 0.024 nautical miles<sup>2</sup>.

## Calculating sample mass

To obtain a measure of hermit crab density within each grid block, hereafter referred to as sample mass (in units of kg.km<sup>-2</sup>); the catch sample mass (in kg) was divided by the area swept within the grid block in question. When a grid block was sampled twice, the average sample mass for that block was calculated as follows:

Sample mass per block 
$$(kg. km^{-2}) = \frac{\sum total \ catch \ weight \ (kg)}{\sum total \ area \ swept \ (km^{2})}$$

If required, the sample mass data were transformed by  $y = \log(x + 1)$  to rectify nonhomogeneity of variances. All statistical analyses were conducted in either *Statistica* 10 (Statsoft Inc., 2011) or the Real Statistics Data Analytics Add-in for Microsoft Excel (2015).

The term "sample mass" was used in favour of "relative biomass" because sample trawling for commercial species is never fully effient, either with regards to catching invertebrates, or the yaregt species themselves. As only a portion of the possible catch is retained, we do not know the proportion of the caught species (particularly in the case of by-catch) represent of the population of the entuire area (see Caddy, 1968; Iribarne *et al.*, 1991; Rago *et al.*, 2006; Somerton *et al.*, 2007; Hennen *et al.*, 2012).

## Implications of gear changes to catches

DAFF (2014) notes that time-series abundance indices for both *Merluccius* hake and Agulhas sole (*Austroglossus pectoralis*) are not comparable between the 'old' and 'new' gears. Therefore, to test whether the change in gear affected the "catchability" of parapagurid hermit crabs, the mean sample mass (kg.km<sup>-2</sup>) of catches for the West Coast during summer

for the five years preceding (1997, 1999, 2003, 2006) and following (2005, 2007, 2008, 2009) the change in gear were compared using a Mann–Whitney Rank Sum test. The data were averaged per grid block sampled.

To determine whether the change in gear affected the success of the demersal research trawls in catching cloaked hermit crabs, both the frequency of "successful" hauls in which defined sample mass "ranges" of 100 kg.km<sup>-2</sup> each were caught, and the frequency of "unsuccessful" 0 kg.km<sup>-2</sup> hauls, were calculated for the "new" and "old" gears. The percentage of total effort represented by those frequencies was calculated for the 0 kg.km<sup>-2</sup> hauls for the old and new gear as follows:

% of total effort =  $\frac{Frequency of haul = 0}{Total number of hauls}$ 

A Rank-Sum Kruskal-Wallis K-way test was conducted to determine if there was a significant difference for the catch frequencies between the "old" and "new" gear for the defined sample mass ranges.

In addition, the percentages of successful hauls (demersal research trawls containing cloaked hermit crabs) relative to the total number of demersal research trawls conducted in each of the 25 sampled years was plotted, and a curve of best fit plotted to determine if the change in gear affected the "catchability" of parapagurid hermit crabs over time.

## Sample mass, spatial and depth distributions

#### Geographical distribution of sample mass

A Mann–Whitney Rank Sum test was used to compare the total mean sample masses on each coast for *Parapagurus bouvieri* and *Sympagurus dimorphus*. A presence/absence model mapped the start co-ordinates of every demersal research trawl in which any parapagurid hermit crabs were caught ("presence") and every demersal research trawl in which none were caught ("absence") to determine the true distributions of both hermit crab species. Alteryx Designer 9.5 (Alteryx Pty. Ltd., 2015) was used for the blending of data and QGIS (Open Source Geospatial Foundation, 2016) for the final map visualisation.

#### Latitudinal and longitudinal distribution

Since the West Coast of South Africa essentially represents a linear gradient north to south and the South Coast a linear gradient west to east, latitude and longitude were used to represent linear changes in distributions along these coasts. To examine the relationships between latitude and longitude and parapagurid sample mass, the total mean sample mass for both *S. dimorphus* and *P. bouvieri* for each degree of latitude and longitude was calculated and plotted against degree of latitude along the West Coast, and degree of longitude for the South Coast (using the start point latitude and longitude for each demersal research trawl). A Rank-Sum Kruskal-Wallis K-way test was used to determine the significance of latitude and longitude on sample mass, and a post-hoc Dunn (1964) Test was conducted (as per Dinno, 2015). A Dunn/Sidák correction was utilized to reduce experiment-wise Type I error.

#### Depth range and depth distribution

To determine the depth distributions of the cloaked hermit crab species within their range, the continental slope was divided into 50 m depth strata from 0 - 899 m and the number of demersal research trawls (n) in which each hermit crabs were found relative to the total number of demersal research trawls conducted within that depth class calculated as percentages for both South and West Coasts. Although seemingly more useful, the exceedingly large variation within the sample mass data prohibited the use of sample mass itself as a reliable measure of distribution with depth, and thus the proxy measurement of demersal research trawl "success" was deemed more appropriate for these purposes. The demersal research trawl depth was based on the "start depth" (m) measurement taken for each trawl. To determine if there was a significance overlap in mean depth distribution for the two species on each of the coasts, a Mann–Whitney Rank Sum test was conducted on y = log(x) transformed start depth data for each species.

## The influence of sediment and seasonality on catches

#### Association with sediment type

The sediment type for 5 954 demersal research trawls was extracted from sediment texture coverage of the South African continental shelf, as provided by the Council for Geoscience, Cape Town (Geological Survey, 1986). Texture classes included mud (silt and clay-sized sediment particles less than 63 microns in diameter), sand (mineral particles 0.6 -2.0 mm in diameter) and gravel (unconsolidated sediments composed of rock fragments > 2 mm). Eight further combinations of classes are provided by Pidwirny (2000), and are defined by the proportion of mud, sand or gravel contained in the sediment. The sediment type was matched to the start co-ordinates of each demersal research trawl using the Join Data Tool in ArcGIS (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). A Rank-Sum Kruskal-Wallis K-way test evaluated the influence of sediment type on mean relative parapagurid sample mass (kg.km<sup>2</sup>).

#### Seasonal relationships

Seasonal changes in sample mass of parapagurid hermit crabs were compared between summer and winter for the West Coast for the preselected 5'x5' grid blocks, as per Figure 3.2 (using Mann–Whitney Rank Sum tests; sample mass data for S. dimorphus was not transformed, while the data for P. bouvieri were transformed to ensure homogeneity of variances). The pre-selected grid was selected at random to encompasses the full parapagurid depth range of 100 – 1 000 m depth, south of Cape Columbine (33°S) and includes both areas trawled for demersal research, and avoided, by the commercial fishery. South Coast data were excluded from this analysis because of inconsistencies in the sampling process of the demersal research trawls conducted on the South Coast during spring i.e. the spring surveys were predominantly used to intensify sampling in waters shallower than 150 m depth, specifically to better sample the inshore benthic fishery biomass. Catches north of Cape Columbine (33°S) were excluded as it has been found that demersal fish assemblages differ across a latitudinal gradient in the region (Roel, 1987; Atkinson et al., 2011b), and it is as yet unknown if such a latitudinal difference is also present for parapagurid hermit crabs. Due to the high levels of variance, the standard error of the mean ( $SEM = \frac{Standard Deviation}{\sqrt{Count}}$ ) was calculated in addition to the standard deviation. The SEM is used to determine how precisely the mean measured reflected the true mean of the population.



Figure 3.2: Map of the pre-selected 20'x20' grid blocks within cloaked hermit crab habitat selected as a proxy to measure cloaked hermit crab sample mass seasonality on the West Coast of South Africa. The grey shaded areas indicate the commercial trawl fishery footprint, whilst the red shaded area indicates the selected grid blocks included in seasonality calculations.

# Results

## Implications of gear changes for pooling of catch data

A total of 491 hauls were conducted during the four years preceding the gear change (1997, 1999, 2003 and 2006), while 322 hauls were conducted during the four years following gear change (2005, 2007, 2008 and 2009). Figure 3.3 shows that a larger mean sample mass was caught using the "old gear" (123.48 kg.km<sup>-2</sup>) than that with "new gear" (67.56 kg.km<sup>-2</sup>), but this difference was not statistically significant (U = 74550; Z = 1.374; p = 0.133).



Figure 3.2: Total relative mean sample mass (kg.km<sup>-2</sup>) of the old and new demersal research trawl gear configurations for four years preceding and following the change in gear. Data taken from the West Coast demersal research trawls conducting during summer for all parapagurid hermit crabs ± SD

Similarly, there was no significant difference in the frequency distribution of catch sample mass between the "old" and "new" gear for the defined sample mass ranges (H = 156; df1 = 1; df2 = 44; p = 0.21). The new gear produced 18.83 % fewer (n = 181) "unsuccessful" hauls (0 kg.km<sup>-2</sup> hermit crabs) compared to the old (n = 265) (Figure 3.4). However, these "unsuccessful" hauls represented a larger portion of the total demersal research trawl effort for the new gear (56.04%) compared to the old (53.64 % of the total old gear demersal research trawl effort). There was a decline of 10.47 % in hauls <100 kg.km<sup>-2</sup> when the new gear (n = 116) was used compared to the old (n = 94) (Figure 3.4). The new gear (n = 3) produced almost 3 times fewer catches > 1 000 kg.km<sup>-2</sup> than the old gear (n = 10) (Figure 3.4).



Figure 3.3: Frequency of mean sample mass (kg.km<sup>-2</sup>) classes caught with the old gear (years 1997, 1999, 2003 and 2006) and the new gear (years 2005, 2007, 2008 and 2009) on the West Coast during summer.

Overall, then, there is no evidence of a change in "catchability" of cloaked hermit crabs over the 25 years sampled (Figure 3.5), and while a declining linear trend is shown for the years in which the "old gear" was used and an increasing linear trend is shown for the years in which the "new gear" was used, these trends are not significant ( $R^2 = 0.07$  and  $R^2 = 0.19$ respectively).

The available evidence thus suggests that there is no statistical difference in the catches of parapagurid hermit crabs between the old and new gears, and thus no correction factor is required and the data are pooled for further analyses in the following sections.



Figure 3.4: Proportion of successful hauls relative to the total number of demersal research trawls conducted with the old and new gears for all years sampled.

## Sample mass, spatial and depth distributions

The mean demersal research trawl start depths on the West and South Coasts were 253.05 m and 124.67 m respectively. In total, 486.63 km<sup>2</sup> of sea floor was sampled, and this was relatively evenly distributed between the two coasts (237.03 km<sup>2</sup> on the West Coast and 249.60 km<sup>2</sup> on the South Coast). A larger area was sampled on the West Coast in summer (192.17 km<sup>2</sup>) relative to winter (44.86 km<sup>2</sup>); and a larger area in autumn (158.44 km<sup>2</sup>) relative to spring (91.96 km<sup>2</sup>) on the South Coast. A summary of the year, season, demersal research trawl number, swept area and gear used on each survey is given in Appendix 1.

### Geographical distribution of sample mass

The total mean sample mass (kg.km<sup>-2</sup>) of both cloaked hermit crab species was much higher on the West than on the South Coast (Table 3.2), these differences were significant for both *P. bouvieri* (U = 9 038; p < 0.01) and *S. dimorphus* (U = 5 483; p < 0.01). The West Coast grid blocks W2246 (32°53'24"S; 17°29'34"S) and W3281 (32°28'12"S; 17°12'36"S) contained both the largest mean sample mass *P. bouvieri* (912.59 kg.km<sup>-2</sup>, during the summer of 1999), and of *S. dimorphus* (1 780.08 kg.km<sup>-2</sup>, during the summer of 2006) over the 25 years of sampling. Of the demersal research trawls on the West Coast, 44.34% contained parapagurids, with *S. dimorphus* recorded in 30.59% of demersal research trawls, and *P. bouvieri* present in 13.76% (Table 3.2). On the South Coast, parapagurids were found in 9.39% of demersal research trawls, with *S. dimorphus* present in 5.81% and *P. bouvieri* caught in 3.58%, (Table 3.2). Both cloaked hermit crab species were present in 44.25% and 8.77% of demersal research trawls on the West and South Coasts respectively.

Species	Coast	% of demersal research trawls containing parapagurids	Average Sample Mass (kg.km <sup>-2</sup> )	Range (kg.km <sup>-2</sup> )
S. dimorphus	West Coast	30.59	287.88	0 - 1 780.08
	South Coast	5.81	31.37	0-712.03
P. bouvieri	West Coast	13.76	38.56	0-912.59
	South Coast	3.58	16.32	0-205.30

Table 3.2: Mean sample masses (kg.km<sup>-2</sup>) for each parapagurid hermit crab species on the West and South Coasts; ranges of sample mass catch value per grid blocks at all sites and for all years are also shown.

The spatial distribution of all samples (Figure 3.6) clearly show that shallow water stations on both coasts were almost devoid of parapagurids. This is particularly obvious on the South Coast, where the shallow Agulhas Bank creates a wide swathe virtually devoid of parapagurids. The wide shelf North of Cape Columbine on the west coast was also virtually free of these species. The stations where hermits where captured also show a fairly clear apparent separation of "shallower water" Sympagurus dimorphus and the "deep water" Parapagurus bouvieri cloaked hermit crab species. This is especially evident on the West Coast, where the "deep water" hermit crabs appear to cluster further offshore than the "shallow water" species, although there is some overlap (8.89% of grids surveys contained both species). Most of the "presence" dots (64.80%) fall within the footprint of the commercial trawl fishery on the West Coast, especially south of Cape Columbine (33° S), while there appear to be more cloaked hermits found outside of the commercial trawl fishery footprint north of Cape Columbine, but still deeper than 100 m (Figure 3.6). On the South Coast, there was a notable absence of parapagurid hermit crabs on the Agulhas Bank, despite the large number of demersal research trawls conducted there and the commercial inshore trawl fishery operations in that area. While some "shallow" water stations over the Bank contained parapagurids, most of the cloaked hermit crabs on the South Coast were found further offshore, off Port Elizabeth along the 200 m isobath and following the western flank of the Agulhas Bank offshore of Cape Agulhas. It is notable how many more demersal research trawls were "positive" for cloaked hermit crabs on the West Coast (n = 1265) relative to the South (n = 310), and that the West Coast hermits appeared to occupy a larger, "broader" area of continental shelf and slope relative to those on the South Coast, which appeared to be narrowly concentrated around regions of the shelf break beyond the Agulhas Bank (Figure 3.6).



Figure 3.5: Presence/absence distribution map of the two suggested cloaked hermit crab species around the South African coastline based on all survey years combined. The blue dots indicate demersal research trawls where no cloaked hermit crabs were found ("unsuccessful" hauls), the red dots indicate demersal research trawls where the "shallow water" S. dimorphus was recorded and the yellow dots indicate demersal research trawls the "deep water" *P. bouvieri* was reported. The commercial demersal trawl footprint (both 'inshore' and 'offshore'), the 5'x5' demersal survey grid blocks, and the lines are bathymetry are indicated.

#### Latitudinal and longitudinal distribution

On the West Coast, the majority of demersal research trawls (n = 1 453) were conducted between 30° S and 32° S (Figure 3.7). There was a significant effect of latitude on *S. dimorphus* sample mass (H = 62.46; df1 = 6; df2 = 481; p < 0.01), with a significant increase in sample mass ( $R^2 = 0.89$ ) from north to south and a peak in average sample mass between 33°S and 35° S (Figure 3.7). Dunn's test indicates two distinct groupings of sample mass: a lower *S. dimorphus* sample mass north of 32°S, while a higher sample mass was found south of this boundary. While there was a significant effect of latitude on *P. bouvieri* sample mass (H = 16.72; df1 = 6; df2 = 315; p = 0.01), there was no apparent trend in sample mass from north to south (Figure 3.7), and Dunn's test detected no distinct latitudinal grouping of sample mass for *P. bouvieri* (Figure 3.7).

There is also a significant effect of longitude on *S. dimorphus* sample mass along the South coast (H = 23.23; df1 = 5; df2 = 144; p < 0.01), with a higher sample mass ( $R^2$  = 0.80) in the West than the East (Figure 3.7) with a separation of the sample mass occurring at 23°W. As with latitude, there was a significant effect of longitude on *P. bouvieri* sample mass (H = 13.09; df1 = 5; df2 = 93; p = 0.02), but again no trend in sample mass from west to east (Figure 3.7), and no post-hoc longitudinal grouping of *P. bouvieri* sample mass.



Figure 3.6: Mean sample mass (kg.km<sup>-2</sup>) of parapagurid hermit crabs (trend line) and the total number of demersal research (the 'count' shown as histogram bars) for each degree of longitude for the West Coast and for each degree of latitude for the South Coast. Regression equations and coefficients of determination for a potential function are shown.

#### Depth range and depth distribution

Table 3.3 shows the depth distributions of all samples taken and of those that contained parapagurid hermits. The shallowest sample was at 17 m and the deepest at 1 550 m, with a

median depth of 145.50 m. Overall 68.51% of demersal research trawls were conducted below 150 m depth, with 22.62% between 50 - 99 m and 23.37% within the depth class 100 - 149 m. By contrast only 3.39% of demersal research trawls were conducted deeper than 500 m, and only 0.16% deeper than 1 000 m (data not shown). While almost no parapagurid hermit crabs were caught in depths shallower than 150 m (Table 3.3), the proportion of "successful" hauls increased with depth (Table 3.3), with the highest proportion of successful trawls occurring between 200 – 499 m (Table 3.3) before declining again. No parapagurids were found deeper than 850 m (Table 3.3). The number of trawls containing both *S. dimorphus* and *P. bouvieri* increased with depth, and while > 50 % of trawls conducted at 200 – 299 m contained *S. dimorphus* (Table 3.3), *P. bouvieri* were predominantly found in deeper trawls, with > 50% of trawls conducted between 400 – 449 m containing *P. bouvieri*.

Table 3.3: Depth class frequencies for trawls conducted down to 1 049m depth, and the proportion of those	trawls
that contained no parapagurids, S. dimorphus and P. bouvieri. The red figures indicate depths where more	e than
50% of trawls contained parapagurids.	

Denth Class (m)	Number of bauls	% Trawls Containing:		
Depth class (III)	Number of flauis	No hermits	S. dimorphus	P. bouvieri
0-49	314	99.36	0.64	0.00
50-99	1 376	99.20	0.65	0.15
100-149	1 421	97.19	2.32	0.49
150-199	1 057	62.54	32.17	5.30
200-249	613	37.19	54.32	8.48
250-299	347	32.85	50.43	16.71
300-349	230	30.00	32.61	37.39
350-399	188	36.17	23.94	39.89
400-449	195	30.77	17.95	51.28
450-499	137	46.72	10.22	43.07
500-549	56	76.79	3.57	19.64
550-599	38	78.95	13.16	7.89
600-649	31	87.10	6.45	6.45
650-699	14	85.71	7.14	7.14
700-749	11	90.91	0.00	9.09
750-799	6	100.00	0.00	0.00
800-849	17	94.12	5.88	0.00
850-899	7	100.00	0.00	0.00
900-949	12	100.00	0.00	0.00
950-999	4	100.00	0.00	0.00
1000-1049	4	100.00	0.00	0.00

The depth distribution patterns of both species on the West Coast (Figures 3.8) show the same separation in depth distribution between the "shallower water" *S. dimorphus* and the
"deep water" *P. bouvieri*, although the two species do share a broad area of overlap in the depth range of 100 - 700 m. Again, both species show a bimodal distribution pattern, with *S. dimorphus* peaking at 200 - 249 m and *P. bouvieri* at 450 - 499 m. *P. bouvieri* were present at significantly (U = 23469.50; Z = -10.8381; p < 0.01) deeper mean "successful" trawl depths (mean depth = 336.36 m; median depth = 334.00 m) compared to *S. dimorphus* (mean depth = 247.36 m; median depth = 222.75 m) on the West Coast (Figures 3.8). However, the deepest trawl in which *S. dimorphus* was present on the West Coast was within the depth range of 800 - 849 m (total trawl n = 15), while the deepest *P. bouvieri* catch was obtained at 650 - 699 m (total trawl n = 2) (Figures 3.8).

On the South Coast there also appears to be a separation of two species by depth (Figure 3.9) where *S. dimorphus* showed a broad peak over the range 200 - 449 m. The "deep water" *P. bouvieri* peaked between 400 - 449 m (48.28%) and 450 - 499 m (47.37%), then showed a secondary peak at 700 - 749 m, but in fact this was based on just two trawls, one with *P. bouvieri* present and one without. However, there was no significant difference in the mean "successful" trawl depths (U = 2091.00; Z = -1.70357; p = 0.09) between *S. dimorphus* (mean depth = 217.95 m; median depth = 190.50 m) and *P. bouvieri* (mean depth = 276.04 m; median depth = 205.00 m) on the South Coast (Figure 3.9).



Figure 3.7: Depth distribution of each of the two cloaked hermit species on the West Coast expressed as % of positive trawls within each depth range.



Figure 3.8: Depth distribution of each of the two cloaked hermit species on the South Coast range of distribution expressed as % of positive trawls within each depth range.

### The influence of sediment and seasonality

#### Association with sediment type

Parapagurid hermit crabs were found across a variety of sediment types on both West and South Coasts (Table 3.4). There was a significant difference in sample mass for different sediment types (H = 62.36; df1 = 6; df2 = 1 864; p < 0.01). More trawls were conducted overall on sandy or muddy substrata, rather than rocky or gravel-based sediments. The highest mean parapagurid sample mass was found on muddy-sand (61.00 kg.km<sup>-2</sup>) and sand (45.68 kg.km<sup>-2</sup>) sediment types (Table 3.4). On the West Coast, most trawls were conducted on sand (45.53%), followed by muddy-sand (37.41%) (Table 3.4), while 75.52% of trawls conducted on the South Coast were taken on sandy substratum (Table 3.4). Trawls conducted on muddy-sand and sand were less successful (fewer trawls caught hermit crabs) than those conducted on gravel, or sandy gravel sediments (Table 3.4). However, 83.52% of trawls were conducted on muddy sand (n = 1 352) and sand (n = 3 621), far more than those conducted on gravel (n = 8) and sandy gravel (n = 72) or gravelly mud (n = 57). No parapagurids were found on gravelly mud sediment (Table 3.4). Table 3.4: Numbers of total and successful trawls, the proportion of successful trawls (i.e. trawls in which parapagurids were caught), the distribution of those trawls between the two coasts, and mean relative parapagurid sample mass (kg.km<sup>-2</sup>) for each sediment type.

Sediment Type	Total Trawls Conducted	Trawls Containing Hermit Crabs	Percentage Successful Trawls	Number of Trawls on each Coast		Mean Sample	Standard
				West	South	Mass (kg.km <sup>-2</sup> )	Deviation
Gravel	8	4	50.00	2	6	0.65	0.90
Gravelly Mud	57	0	0.00	0	57	0.00	0.00
Mud	320	24	7.50	186	134	3.29	35.34
Muddy Sand	1 352	442	32.69	1 092	260	61.00	215.03
Sand	3 621	1 176	32.48	1 329	2 292	45.68	187.90
Sandy Gravel	72	32	44.44	0	72	6.80	29.07
Sandy Mud	524	100	19.08	310	214	39.80	162.28
TOTAL	5 954	1 778	29.86	2 919	3 035		

#### Seasonal relationships

Within the preselected grid block (Figure 3.2), a total of 328 trawls were conducted and 27.94 km<sup>2</sup> was surveyed during the summer cruises, while during the winter cruises, 141 trawls were conducted and 15.40 km<sup>2</sup> was surveyed. In total, parapagurid hermit crabs were present in 263 trawls conducted during summer and 119 trawls conducted during winter. *P. bouvieri* was present in 74 of the trawls conducted during summer and in 32 trawls conducted during the winter, indicating that the percentage of successful hauls remained constant across seasons (22.56% during summer and 22.70% during winter). *S. dimorphus* was present in 189 and 87 trawls conducted in summer and winter respectively, with a slightly higher overall catchability during winter (61.70%) compared to summer (57.62%). *S. dimorphus* was thus caught more often than *P. bouvieri*, and was present in more trawls overall within the area (Figure 3.2).

Figure 3.10 shows that the sample mass of *S. dimorphus* was significantly (U = 2287; Z = 5.13; p < 0.01) higher in summer (243.58 kg.km<sup>-2</sup>) compared to winter (89.29 kg.km<sup>-2</sup>). *P. bouvieri* showed a similar pattern with a significantly (U = 3.124.5; 2.75; p < 0.01) higher sample mass in summer (27.77 kg.km<sup>-2</sup>) relative to winter (3.66 kg.km<sup>-2</sup>).



Figure 3.9: Mean sample mass (kg.km<sup>-2</sup>) for each species for the selected grid area on the West Coast in both summer and winter (±SEM).

# Discussion

### Implications of gear changes to catches

Before pooling the data used in this analysis, it was important to establish whether the new survey gear used by the demersal research trawls influenced the "catchability" of cloaked hermit crabs. Overall, there was no evidence that the change in gear made any substantial difference to the cloaked hermit crab catch, and thus no correction factor need be applied. Any influence of the change in gear is less likely due to any changes in mesh size as it is to the type and configuratuiion of the footrope used – the gear was changed from a chain wrapped around a rope to a chain with rubber rollers (i.e. the old gear sat directly against the sediment, compared to a chain with rolelrs). Therefore, it would be expected that there would be higher catches of parapagurid hermit crabs with the old gear comared to the new gear with rolelrs that sits higher above the sediment. This would explain why a greater csample mass caught in years with the old gear compared to those with the new (Figure 3.3).

However, there was a higher proportion of "successful" demersal research trawls with the new gear relative to the old, and this can be attributed to changes in survey design. Prior to 2008, surveys were limited to demersal research trawls shallow than 500 m depth, but from 2008 to 2011, demersal research trawls were occasionally conducted below the 500 m isobath on an opportunistic basis (T. Fairweather, Pers. Comm., 2016) even though they

occurred within survey grid blocks listed as < 500 m. This increase in successful demersal research trawls is a result of this change, since trawling deeper would skew the data in favour of deeper-living species, such as cloaked hermit crabs, and particularly *P. bouvieri*. From 2012 onwards, it was logistically feasible for demersal research trawls to routinely trawl deeper than 500 m, and this was accounted for within the data.

It must be noted however that, within the literature, it is somewhat rare (and is generally not recommended) to pool data from different sample siources (as the different gear, in this case). This must be bourne in mind when examining the data presented here, and conclusins interpreted as such.

#### Sample mass, spatial and depth distributions

#### Geographical distribution of sample mass

Both species of cloaked hermits occurred across the entire geographica range over which sampling was conducted. However, there were significant differences in Sympagurus dimorphus and Parapagurus bouvieri sample masses between the two sampled coasts: the average sample mass of S. dimorphus was almost 10 times higher on the West Coast compared to the South, while catches of P. bouvieri were twice as large on the West Coast relative to the South. The actual numerical sample masses reported here are almost certainly conservative underestimates of actual abundances of both species, given that the demersal research trawl gear used is designed primarily to target fish species for stock assessments, and may be ineffective at sampling benthic invertebrates, thus probably retaining only a proportion of parapagurids within the trawled area. The sample masses presented here are likely to be good measures of the relative population levels, but almost certainly exclude juvenile parapagurids (further explored in Chapter 4). The higher parapagurid sample masses reported on the West Coast follows the well-established pattern of higher productivity, higher sample mass and lower diversity on the West coast (due to the higher productivity and food availability of the Benguela upwelling system), relative to the east (Bustamante et al., 1995; Gyory et al. 2004; Griffiths et al., 2010; Lange and Griffiths, 2014). Parapagurids also occurred over a greater area on the West Coast (i.e. were more evenly distributed across the shelf and slope), due to differing bathymetry patterns. The broad, gently sloping West Coast shelf narrows south of the St Helena Bay headland (32° S) and broadens again to 20° E, while the relatively shallow Agulhas Bank (mean depth of slightly over 100 m, Gyory et al., 2004), which is virtually devoid of parapagurids, extends up to 250 km from the coast on the South Coast, before dropping off steeply after the 200 m shelf break (Atkinson et al., 2011b) - the

Bank may be too shallow for parapagurids, given that the mean sampled sample masses of both *S. dimorphus* and *P. bouvieri* occurred below 200 m depth. The broader continental slope of the West Coast may afford more suitable depth niche space than the wide continental shelf narrow and steep slope of the Agulhas Bank, which restricts habitat for parapagurids at their respective preferred depths. The bathymetry may also influence the bimodal partitioning of the "deep water" and "shallow water" cloaked hermit crab niches on the South Coast, which may explain why the average depths of *S. dimorphus* and *P. bouvieri* occurrence on the South Coast were non-significant, whilst a significant effect was found between the two species on the West Coast, where the slope is less steep, and the cloaked hermit crabs have more space to occupy their preferred depth niche.

Both S. dimorphus and P. bouvieri are broadly distributed on the continental slope regions of South Africa, as is the case in the other areas where they are found (Forest and McLay, 2001; Schejter and Mantelatto, 2015). S. dimorphus has a broad global distribution, and is found in all Southern Hemisphere waters between latitudes 22°S and 57°S (Lemaitre, 2004). This species is noted in the literature as occurring off Tristan da Cuna, on the Agulhas Bank, off Marion Island and Patagonia (Henderson, 1888), in the Southern Ocean (Hale, 1941), in New Zealand (Probert et al., 1979; Schembri, 1982; Schembri and McLay, 1983; Forest and McLay, 2001), in Argentina (Schejter and Mantelatto, 2011, 2015), off Namibia (Macpherson, 1983a) and off the western and southern coasts of South Africa (Lemaitre, 2004). There does not appear to be any record of S. dimorphus further north into Angolan waters. In contrast, P. bouvieri appears to have a more limited range – Lemaitre (1990) lists the species distribution as off south western Africa from Namibia, around the south coast of South Africa and into KwaZulu-Natal (Lemaitre, 1990). However, the Australian Department of the Environment Appendix B2.6 list of non-commercial species caught by fishery independent surveys (2004) lists P. *bouvieri* as a by-catch species, so there appears to be some taxonomic uncertainty that requires resolution before it can be confirmed that P. bouvieri is restricted to the current "Southern African" distribution as described by Lemaitre (2004). Therefore, this study covers the known range of S. dimorphus in South African waters, but excludes the known distribution of the species northwards into Namibia (Macpherson, 1983a; Lemaitre, 2004) and includes the known south and western distribution of P. bouvieri in South African waters, but again excludes the known northward distribution in Namibian waters (Lemaitre, 1990). It appears unlikely that this study, given that the eastern boundary of the survey samples were conducted offshore of Port Elizabeth, covers the full range distribution of P. bouvieri in South African waters, because of the reported presence of P. bouvieri further eastward on the

KwaZulu-Natal Coast (Lemaitre, 1990). It must also be noted that, in addition to *S. dimorphus* (Lemaitre, 1989) and P. *bouvieri* (Lemaitre, 1990; 1999), seven other known parapagurid hermit crab species occur on the South African continental shelf: *Sympagurus trispinosus* (Lemaitre, 2004), *Parapagurus andreui* (Lemaitre, 1999), *Parapagurus richeri* (Lemaitre, 1999), *Oncopagurus africanus* (Lemaitre, 1990 as *Sympagurus*), *Strobopagurus sibogae* (Kensley, 1981) and *Paragiopagurus* n. sp. (Landschoff and Lemaitre, in prep., 2016).

#### Latitudinal and longitudinal distribution

Plotting of parapagurid sample mass in relation to latitude (west coast) and longitude (south coast) showed that the highest parapagurid sample masses occurred in the south western portion of the South African continental shelf, south of Cape Columbine and west of Cape Agulhas. The majority of demersal research trawls were conducted between 30° S and 32° S, which may be a function of shelf size – the shelf between 30° S and 32° S being well sampled because it encompasses the largest shelf area on the West Coast. Both species are very common invertebrate species on the West Coast of South Africa. For example Lange and Griffiths (2014) showed S. dimorphus as representing 11.43% of the total benthic invertebrate sample mass of the shelf, while P. bouvieri represents 2.34%. . In their survey these species were the 3<sup>rd</sup> and 6<sup>th</sup> most abundant benthic invertebrates on the South African shelf respectively (Lange and Griffiths, 2014). S. dimorphus was also shown to occur in a broad distribution across the shelf between 200 - 500 m (Lange and Griffiths, 2014). In this study, S. dimorphus represents 85.33% of the total parapagurid sample mass off the coast of South Africa, whilst P. bouvieri comprises only 14.67%. The separation of S. dimorphus sample mass into two "groups" to the north and south of 32°S appears to follow the West Coast latitudinal gradient described in demersal fish assemblages by Roel (1987) and Atkinson et al. (2011b), although those assemblages were separated at Cape Columbine (33°S) on West Coast, since the shelf north of 33° S is generally wider than that to the south. Why such trends were not obtained for P. bouvieri remains unknown.

#### Depth range and depth distribution

This study provides the first firm evidence (Figure 3.12; Table 3.3) to support the long-held anecdotal division between "deeper water" and "shallow water" cloaked hermit crabs, as reported by commercial trawl fishermen, with the "deeper water" *P. bouvieri* occurring at deeper depths than the "shallow water" *S. dimorphus*, although the two species do show substantial overlaps in depth range. Lemaitre (1989; 2004) and Lemaitre and McLaughlin (1992) noted the depth range of *S. dimorphus* to be 91 - 1 995 m and of *P. bouvieri* as 249 -

810 m. In New Zealand waters, *S. dimorphus* is common at depths 200 - 1 000, and *P. bouvieri* typically occurs below 250 m to almost 1 000 m (Forest and McLay, 2001). This work presents the depth ranges of *S. dimorphus* as 30 - 814 m (with a preferential depth range of 200 - 299 m) and of *P. bouvieri* as 62 - 700 m (preferential depth range 400 - 499 m) in South African waters. The difference in range between this study and those in the literature may be due to a greater sampling effort at shallower depths in the present study, and the paucity of demersal research trawls below 500 m depth (and very few below 1 000 m) due to the survey design and the primary purpose of the demersal research trawls, which was to monitor the commercially-targeted South African Cape hake population. Despite these differences, however, the description as "typical inhabitants of deep waters" by Lemaitre (1989) is warranted, given both species' preferential distribution in waters deeper than 150 m and given that cloaked hermit crab are caught more often in deeper demersal research trawls, whilst being conspicuously absent in demersal research trawls shallower than 150 m, despite the many demersal research trawls conducted in this depth range.

#### The influence of sediment and seasonality

#### Association with sediment type

The highest average parapagurid sample masses were found on muddy sand (61.00 kg.km<sup>-2</sup>) and sand (45.68 kg.km<sup>-2</sup>). Prior taxonomic work (such as Henderson, 1888) has reported the occurrence of *S. dimorphus* on similar sediments, such as sand, volcanic sand and "blue mud". It would thus appear that parapagurids prefer sandy/muddy sediments, even though such habitats do not allow for the retention of useable gastropod shells - shells tend to be buried quickly in such sediments, and thus removed from the pool of useable hermit crab homes (see Conover, 1975 and Parsons-Hubbard *et al.*, 1999). This raises questions about the life history of these animals and their relationships to their zoanthid pseudoshell homes. Schejter and Mantelatto (2011, 2015) hypothesised that parapagurid juveniles settle out of their larval phase and immediately inhabit very small gastropod shells, upon which the *Epizoanthus* polyps settle and grow into the shell-replacing pseudoshell symbiont. Furthur work is required to collect and examine juvenile parapagurids to determine how this process occurs (using finer mesh sampling gear than the demersal research trawl gear utilsed in this work), and assessments as to the avaliablity of empty, usable gastropod shells on deep water sandy and muddy sediments need to be conducted.

While higher average sample masses were reported for sandy/muddy sediments, these sediments accounted for the vast majority of sites sampled (83.52%). In addition, while demersal research trawls conducted on gravel-type sediments had a higher success rate in catching parapagurids than those conducted on sandy-type sediments, rough ground tends to damage nets, and rocky and gravel-type substrates are thus avoided by demersal research trawl operations in general and thus samples taken on "gravel-type" sediments accounted for only 0.02% of trawls conducted. Given this evidence, therefore, it can be hypothesised that parapagurids show habitat preference towards sandy/muddy sediments, but more data are required, particularly experimental data, pertaining to the life history, diet and behaviour of parapagurid to determine their true habitat preferences.

#### Seasonal relationships

There appears to be a significant influence of season on parapagurid sample mass, with a higher sample mass on the West Coast in summer compared to winter, for both the deep and shallow water species. This is expected, given that the distinct seasonal oceanographic drivers in the Benguela system, specifically the wind-driven inshore summer upwelling, and the subsequent increase in nutrients and associated productivity (Lutjeharms and Meeuwis, 1987; Brown *et al.*, 1991; Barlow *et al.*, 2005; Pitcher *et al.*, 2008; Hugget *et al.*, 2009 amongst others). As yet, seasonal sample mass variations for cloaked hermit crabs as a whole have not been established, but the findings appear to be consistent with literature detailing the sensitivity of demersal crustacean biomass to seasonal factors (Sardà, Cartes and Company, 1994). For example, Branco, Turra and Souto (2002) showed that *Dardanus insignis* presents a seasonal reproductive peak from September to November (i.e. spring/summer) with commencement of recruitment during September i.e. spring (Branco *et al.*, 2002). *Pagurus longicarpus* and *P. pollicaris* also present a larval peak over the summer months (Carlon and Ebersole, 1995), with the highest proportion of ovigerous females occurring in summer (Carlon and Ebersole, 1995).

However, life-history traits, such as longevity and migration, may also result in a higher summer parapagurid sample mass, and require further exploration. Hermit crabs such as *Clibanarius vittatus, Pagurus longicarpus* (Rebach, 1978; 1981) and *Diogenes nitidimanus* (Asakura, 1987) appear to undertake seasonal migrations from shallow to deeper waters (Branco, Turra and Souto, 2002), with marked changes in abundances at a given site between seasons (Branco *et al.*, 2002). However, these seasonal migrations appear to be short range (i.e. from the intertidal to the shallow subtidal) and whilst little is known about migratory

movement of Parapaguridae, it seems unlikely that hermits which occupy such a broad range across the continental shelf would be able to migrate to and from deeper waters on a seasonal basis. While no estimates of longevity for parapagurid hermit crabs exist within the current literature, it is known that other hermit crab species may be relatively long lived -Pagurus brevidactylus (Stimpson, 1859) has been reported to have a longevity of 24 months for males and 18 months for females (Mantelatto, Christofoletti and Valenti, 2005), while Branco, Turra and Souto (2002) estimated that *Dardanus insignis* (which can live down to 500 m depth) has a longevity of 20 - 62 months. It can be hypothesised that parapagurids show similar or potentially even greater longevity, based on their larger size (Lemaitre, 2004) and preferred "deeper water" depth range - larger crustacean individuals are generally assumed to be older individuals (but this remains speculation, given the difficulties in aging Crustacea; see Wenner, Fusaro and Oaten, 1974) and in general, deep living species attain greater longevity than shallower water species (Gage and Tyler, 1992). Since parapagurid hermit crabs can thus be hypothesised to be relatively long-lived rather than annual, the differences in oberved sample mass between seasons is likely not the result of differing avalaibility to capture – in annual species, the "juvenile phase" presents as a lower overall sample masses because smaller, juvenile, individuals are not retained by the demersal research trawl net mesh. This does not appear to be the case for parapagurids (see Chapter 4). However, with work on the life history of parapagurids sorely lacking, more investigations into the fecundity and growth rates etc. is required to determine the reason for the observed increase in summer sample mass.

No work has yet been conducted to conclusively demonstrate the movement of parapagurids into trawl lanes to scavenge off the dead or destroyed organic material damaged by the passing trawl gear. However, given the anecdotes from fishermen and fisheries researchers in both the North Sea (R. Knust, Pers. Comm., 2015) and the Benguela system (D. Japp, Pers. Comm., 2016) futhur questions remain. Furthermore, there appears to be a significant observed overlap between parapagurid hermit crab presence and commercial trawl fishery operations around the South African coastline, questions must be asked regarding the impact of trawl operations on parapagurid populations.

# **Chapter 4**

Long-term changes in distribution and abundance of South African hermit crabs of the family Parapaguridae (Crustacea: Decapoda: Anomura)



Parapagurus bouvieri (Stebbing, 1910). Image: CL Griffiths (2015)

## Introduction

The paucity of knowledge of the ecology and biology of hermit crabs of the family Parapaguridae (Latreille, 1802) is of particular concern (Ates, 2003; Schejter and Mantelatto, 2011), given their dominance within many deeper-water benthic invertebrate communities (Lemaitre, 1989; Lemaitre, 1996; Lange and Griffiths, 2014). In particular, both *Parapagurus bouvieri* (Stebbing, 1910) (misidentified in earlier references as *P. pilosimanus* - see Lemaitre, 1999) and *Sympagurus dimorphus* (Studer, 1883) occupy broad distributional ranges within the southern hemisphere (Stebbing, 1910; Lemaitre, 1989; Lemaitre, 1990; Lemaitre and McLaughlin, 1992; Lemaitre, 2004; McLaughlin, 2015a, b).

Examining the change in biomass of a species over time allows the initiation of investigations into anthropogenic impacts on that species. In this case, the predominant anthropogenic impacts faced by parapagurid hermit crabs is presumed to be that of demersal trawling operations - some data on by-catches of these species by commercial or experimental trawl fisheries are available in the published literature (Schejter, Bremec and Hernández, 2008; Floerl, Hewitt and Bowden, 2012; Lange, 2010; Lange and Griffiths, 2014; Schejter and Mantelatto, 2015), while other records can be found within the 'grey literature'. For example, the Australian Department of the Environment Appendix B2.6 list of non-commercial species caught by fishery independent surveys using ocean fish and prawn trawl gear (2004) shows that P. bouvieri has a frequency of occurrence of 18.8% across all trawls. Also, the 1997 summer Namibian Hake Stock Survey (Cruise Report No 1/97) reported parapagurid catches of 52 kg at 472 m depth; 96 kg at 426 m depth; 36.63 kg at 221 m depth, amongst other records (Annex III: Records of Fishing Stations). On the South African continental shelf, P. bouvieri and S. dimorphus are regularly caught in large numbers as invertebrate by-catch of demersal survey operations (Lange and Griffiths, 2014) which sample both the trawl lanes and untralwed grounds, and noted incidentally by observer programmes of commercial trawl operations (T. Fairweather, Pers. Comm., 2016) which is, at least in part, reflective of the programmes' focus on fish by-catch species. South Africa's commercial deep-sea hake fishery (Merluccius species) has historically operated on the shelf edge off the West Coast of the South Africa (Rademeyer, Butterworth and Plagányi, 2008; Atkinson et al., 2011b; DAFF, 2014), within the known depth ranges of both P. bouvieri and S. dimorphus, in waters from ca 300 - 600 m deep (Wilkinson and Japp, 2005), although recent technological advances in fishing and vessel equipment have extended fishing down to 1 000 m (Griffiths et al., 2004; Fairweather et al., 2006). No work has been conducted thus far on the impacts of trawling

activity on parapagurid hermit crabs, either in South Africa, or any other fishery where parapagurids form a component of by-catch.

In a wider context the impacts of commercial trawl fisheries on demersal faunal assemblages are relatively well understood, both as they relate to invertebrate by-catches (De Groot, 1984; Collie, Escanero, and Valentine, 1997; McConnaughey, Mier and Drew, 2000; Koslow *et al.*, 2001; Thrush and Dayton, 2002; Hiddink *et al.*, 2006; Pusceddu *et al.*, 2014), and in terms of their impacts on fish populations themselves (Rijnsdorp *et al.*, 1998; Atkinson, Leslie, Field, and Jarre, 2011). The impacts of trawl fishery operations on deep sea invertebrate communities include lowered species richness and diversity; declines in benthic faunal sample mass and changes in species composition, particularly declines in larger, slower-growing species (Jones, 1992; Collie *et al.*, 1997; Koslow *et al.*, 2001; Widdicombe *et al.*, 2004; Tillin *et al.*, 2006; Hiddink *et al.*, 2008; Durán Muñoz *et al.*, 2012; see Clark *et al.*, 2016 for a review).

As these parapagurid hermit crabs are abundant, large and easily identified, they are good indicator species that can be used to reflect changes in the benthic community over time, particularly with regards to anthropogenic impacts such as trawling. Benthic invertebrates have been used as indicators of environmental change or deterioration across multiple systems (Lenant, 1988; Harvey *et al.*, 1998; Ogbeibu and Oribhabor, 2002; Wildsmith *et al.*, 2011). The availability of long-term data on the sample mass of parapagurids captured during 23 years of standardised demersal research trawling surveys along the west and south coast of South Africa provide an opportunity to provide a baseline for future work by determining long-term trends in the mean sample mass – has it increased, declined or remained stable over this period, and speculating the causes of these changes. This chapter sets up the work for future analysis to determine any relationships between long-term changes in the abundances of *S. dimorphus* and *P. bouvieri* and commercial trawl fishery operations on the west coast over the period.

The signal is complicated however, because while the direct impacts of trawling on parapagurid species have not been measured, it has been speculated that, as scavengers, these hermit crabs may be drawn to trawl lanes from elsewhere to feed on the organic matter left/crushed by the trawl net. This alteration of benthic food webs by trawling activities (Caddy, 1973; Medcof and Caddy, 1971; Auster and Langton, 1998), and specifically the hypothesis that demersal scavengers actively move into trawl tracks to feed on damaged

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organic matter, is well documented for fish, such as the gurnards *Aspitrigla cuculus* and *Eutrigla gurnardus*, lesser-spotted dogfish *Scyliorhinus canicula* and whiting *Merlangius merlangus* (Kaiser and Spencer, 1994), as well as for invertebrates such as the sand crab *Portunus pelagicus* (Wassenberg and Hill, 1987), shrimps *Pandalus* sp. (Kaiser and Spencer, 1994), hermit crab *Pagurus bernhardus*, sea star *Asterias rubens*, whelk *Buccinum undatum*, swimming crabs *Liocarcinus* sp. (Ramsay *et al.*, 1997), and Norway lobster *Nephrops norvegicus* (Hiddink *et al.*, 2016). Ramsay *et al.* (1997) showed that the hermit crab *P. bernhardus* was attracted to "trawl resultant" carrion in greatest abundance of all scavengers assessed, aggregating at densities of up to 330 m<sup>2</sup>.

In general, the ability of scavengers to take advantage of the increased food source within trawled areas is dependent on their behaviour, mobility (Kaiser and Spencer, 1996b) and ability to remain within the trawled area. The latter is either the result of surviving capture by being immediately discarded as by-catch, or by passing over or through gear (Meyer et al., 1981; Fonds, 1994; Rumhor et al., 1994; Santbrink and Bergman, 1994; Kaiser and Spencer, 1995). Scavenging opportunities can potentially lead to longer-term increases in the abundances of scavenging species, due to increased food supply (Kaiser and Ramsay, 1997), and the removal of predators and competitors (Kaiser and Ramsay, 1997), which in turn influences the fitness and reproductive success of the scavenging species. For example, increase in abundance of common dab Limanda limanda in the North Sea has been attributed to increased food available to the species through scavenging on trawl grounds (Kaiser and Ramsay, 1997). Similarly, Wassenberg and Hill (1987) hypothesised that scavenging of trawl discards and detritus has allowed the sand crab Portunus pelagicus to occur in far greater abundances than would otherwise be the case. Shephard et al. (2013) showed that increased trawl intensity resulted in lower measured trophic level of two fish species, because the fish were substituting their usual prey fish with lower-trophic level invertebrates scavenged in more intensively trawled areas. Groenewold and Fonds (2000) listed the hermit crab Pagurus bernhardus (Linnaeus, 1758) as one of the main active scavengers attracted to experimental baited traps within trawl grounds in the southern North Sea.

It is, therefore, hypothesised that high abundance and by-catch of parapagurid hermit crabs during demersal survey operations may be at least partially due to their moving into deep water trawl lanes to scavenge, taking advantage of increased food supply and the removal of their predators. If that is the case, a positive correlation between commercial trawling intensity and mean relative parapagurid hermit crab sample mass might be expected.

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Alternatively, if the hermits are relatively long-lived and/or are not benefiting from increased scavenging opportunities as a result of commercial trawling, one might expect consistent trawling activities over their preferred habitat to result in declines in density (such as found by Kruger *et al.*, 2005). In general, longer-lived species are more susceptible to anthropogenic disturbance than annual species (Jones, 1992; Rumohr and Kujawski, 2000), and parapagurid hermit crabs are hypothesised to be relatively long-lived decapods (see Chapter 2), given their size (Lemaitre, 2004), preferred "deeper water" habitat (Gage and Tyler, 1992) and because other hermit crab species (such as *Pagurus brevidactylus* and *Dardanus insignis*, which can live down to 500 m depth) are known to be relatively long-lived (Mantelatto, Christofoletti and Valenti, 2005; Branco, Turra and Souto, 2002).

# Methods

The data analysed here were derived from the west coast summer demersal research trawl surveys conducted by the South African Government's Department of Agriculture, Forestry and Fisheries (DAFF) from 1987 - 2014. Full descriptions of the survey methods, gear used and methods employed in the calculation of mean sample mass are found in Chapter 3. Only data for the West Coast were analysed, as parapagurids were much more abundant there than on the South Coast (Chapter 3), and because any impacts of trawling activity are more likely to be detected on the West Coast, given the higher trawl intensity on the West Coast relative to the South (Rademeyer, Butterworth and Plagányi, 2008). In addition, ad hoc trawls that were conducted on the West Coast during specified South Coast surveys were excluded.

Inter-annual changes in parapagurid hermit crab populations (in terms of "catchability" and mean sample mass trends) were investigated by plotting the proportion of "successful hauls" (the proportion of trawls containing parapagurid hermit crabs). A least squares regression was fitted to both trend lines. To examine the relationships between the mean sample masses of each parapagurid species over time, the mean sample mass (kg.km<sup>-2</sup>) per year for *S. dimorphus* and *P. bouvieri* were plotted for two periods of time in the trawl survey period – between 1987 and 2002, and post-2002. The mean trawl start depth for each year was also plotted. Least squares regressions were fitted to all trend lines, and the coefficient of determination for the function noted. To investigate whether the trends noted were due to competition between the two species, a reciprocal was conducted between the mean sample mass of *S. dimorphus* and *P. bouvieri* for each year, and grouped depending on whether that year utilised the "new" or the "old" gear (see Chapter 2 for details). To account for the

change in survey design (pre-2011 the surveys were limited to 500 m depth, with some deeper trawls occurring on an opportunistic basis, with some deeper trawls occurring 2008 – 2010), "deeper" trawls (i.e. trawls deeper than 500 m) were excluded from these analyses. Due to the high levels of variance within the mean sample mass, the standard error of the mean ( $SEM = \frac{Standard Deviation}{\sqrt{Count}}$ ) was calculated in addition to the standard deviation.

Any changes in the mean sample mass of both S. dimorphus and P. bouvieri over the entire West Coast shelf were analysed by plotting the data for all seasons and across all depths on a decadal time scale (in order to remove 'noise' caused by random interannual fluctuations in catch). The average mean sample mass per survey 5' x 5' block was combined into 20' x 20' grid blocks for each decade (1980's, 1990', 2000's and 2010's). Use of larger block sizes minimised the number of blocks with no hermit crabs present, allowing for better comparison of sample mass changes over time. The nominal change in sample mass was then calculated using Alteryx Designer 9.5 (Alteryx Pty. Ltd., 2015) for each decade, relative to the mean sample mass of the preceding decade, and mapped via QGIS (Open Source Geospatial Foundation, 2016). The percentage changes between decades in each mapped 20' x 20' grid block were indicted via a colour key, as calculated by the Alteryx Designer 9.5 Smart Bins tile method. This method creates 'tiles' (i.e. discrete grid colour key ranges) using the standard deviations of the values, where the tiles assigned indicate whether record values fall within the average range (= 0 SD), above the average (+ 1 SD), or below the average (- 1 SD). This method is considered better for visualisation purposes, and more appropriate than assigning equal range values, due to the large variability in the percentage changes in grids, and because the calculation is based on the change in mean sample mass between decades, rather than the actual mass. The Alteryx Designer 9.5 Smart Bins tile method created bin values indicting a "Large Increase" (*Decade*  $x_2 - Decade x_1 \ge 125$ ), a "Small Increase" (Decade  $x_2$  – Decade  $x_1$  < 125), a "No Change" (Decade  $x_2$  – Decade  $x_1$  < 53), a "Small Decrease" (Decade  $x_2$  – Decade  $x_1$  < 19.25) and a "Large Decrease" (Decade  $x_2$  – Decade  $x_1 < -92$ ), and nulls (blanks, or if the block was only sampled during one of the two decades being compared).

Finally, a correlation between the relationship between mean relative hermit crab sample mass and trawl intensity was constructed. Data on total commercial demersal trawl fishery effort, expressed as trawl counts per 20' x 20' block were obtained from DAFF. Using the start co-ordinates for each trawl, the spatial trawl count data were overlain with the West Coast parapagurid survey trawl sample masses using Alteryx Designer 9.5 (Alteryx Pty. Ltd., 2015).

The relative parapagurid sample mass was averaged for each "commercial trawl block", and for each year of operation. A linear regression curve was constructed between the trawl intensity (counts per year across all grid blocks) and mean relative parapagurid sample masses (kg.km<sup>-2</sup>) for all grid blocks for all 23 years sampled.

# Results

There has been no significant change in the catchability (proportion of successful trawls) of parapagurids ( $R^2 = 0.13$ ) on the West Coast over the 23 sampled years (Figure 4.1), with an overall mean catchability of 43.35%. Although not statistically significant, there was a slight trend towards increasing catchability over time, with years of highest parapagurid catchability tending to occur post-2008. Highest catchability occurred in 2011, when 74% of all trawls conducted on the West Coast contained parapagurids and lowest catchability of 19% in 1987 (Figure 4.1). The total survey trawl count per year remained relatively constant over the time period, with a mean of 106.88, although there were three years with exceptionally high numbers of trawl samples – 1995, 2004 and 2011 (Figure 4.1).



Figure 4.10: Percentage of all trawls containing parapagurid hermit crabs (black dots) and the total number of trawls conducted each year ('trawl count' - histogram bars) over the 25 sampled years. The regression equation and coefficient of determination are for the relationship between catchability and time.

When these data are divided to show the two species separately different trends are observed. The mean sample mass of *S. dimorphus* ranged from 1.87 kg.km<sup>-2</sup> in 2014 to 713.35 kg.km<sup>-2</sup> in 1999 (and 0 kg.km<sup>-2</sup> caught in 2005), with an overall mean of 261.60 kg.km<sup>-2</sup>. Figure 4.2 shows that over the 23 years sampled, *S. dimorphus* mean sample mass shows a non-significant decline ( $R^2 = 0.45$ ), with the mean sample mass increasing from 1989, peaking in 1999 before declining to 2014. The largest declines occurred between 2007 and 2008, where the mean sample mass sampled declined from 337.41 kg.km<sup>-2</sup> in 2007 to 34.40 kg.km<sup>-2</sup> in 2008. For *P. bouvieri*, the mean sample mass ranges from 0.85 kg.km<sup>-2</sup> in 1994 to 188.20 kg.km<sup>-2</sup> in 2003 (with 0 kg.km<sup>-2</sup> caught in 1987), with an overall mean of 41.34 kg.km<sup>-2</sup> (Figure 4.2), and no trend in sample mass over time ( $R^2 < 0.01$ ) (Figure 4.2).



Figure 4.11: Total mean sample mass (kg.km<sup>-2</sup>) of *S. dimorphus* and *P. bouvieri* catches on the West Coast over the 25 sampled years (±SEM). Regression equations and coefficients of determination for a potential function are shown.

There appear to be distinct, apparent "groupings" of catch data – the earlier years (pre-2003), and the later years (post-2002, including the years of highest parapagurid catchability occurred, as per Figure 4.1). These two time periods are separated out in Figure 4.3. There was an increase in the in the mean sample mass caught over the first 11 years of the survey trawls, but was not significant trend for either *S. dimorphus* ( $R^2 = 0.24$ ) or *P. bouvieri* ( $R^2 = 0.44$ ). There was also no change in mean trawl depth sampled over this time period (mean = 239.43 m;  $R^2 = 0.08$ ) (Figure 4.3a). There was a non-significant decline in both *S. dimorphus* ( $R^2$ 

= 0.31) and *P. bouvieri* ( $R^2$  = 0.01) mean sample masses over the last 12 sampled years (Figure 4.3b). *S. dimorphus* mean sample mass caught peaked in 2006, before a sharp decline to 2014 (Figure 4.3b). No significant change in mean trawl depth was noted for this period (( $R^2$  = 0.03), although the mean trawl depth peaked in 2003 at 275.43 m (Figure 4.3b).



Figure 4.12: Total mean sample mass (kg.km<sup>-2</sup>) of *S. dimorphus* and *P. bouvieri* catches on the West Coast over a) the first 11 years of sampling and b) the last 12 years of sampling (±SEM). The mean trawl start depth (m) is also shown for each year (grey bars). Regression equations and coefficients of determination for a potential function are shown.

Figure 4.4 plots the sample masses of the two parapagurid species recorded in each year against one another. The results show no significant reciprocal relationship between the mean sample masses of *S. dimorphus* and *P. bouvieri* ( $R^2 = 0.03$ ) (Figure 4.4). All the years where "new gear" (grey dots) was utilised (see Chapter 3 for details) resulted in fewer *S. dimorphus* caught relative to *P. bouvieri*, compared to when the "old gear" was used (black dots) (Figure 4.4), except in 2005 and 2007 (white dots).



Figure 4.4: Reciprocal trend between the mean sample masses of *S. dimorphus* and *P. bouvieri* grouped by gear – years in which the old gear was used are indicated by black dots, while the years in which the new gear as used are indicated in grey dots. The white dots indicate 2005 and 2007, years in which the new gear was used but which resulted in more *S. dimorphus* caught relative to *P. bouvieri*. The least square regression line is given.

The decadal changes in mean sample mass (% changes) per grid square are shown in Figure 3.5. A total of 732 trawls were conducted in the 1980's; 2 398 in the 1990's; 2 037 in the 2000's and 923 in the 2010's. The majority of 20' x 20' blocks show either no change in mean sample mass between decades (grey), or are "null" values. Overall, the decadal percentage change from the 1980's to the 1990's showed a slight tendency towards increase (25 red or increase blocks, 7 blue or decrease blocks), while between the 1990's and the 2000's there appeared to be a slight trend towards decreases in mean sample mass (15 increase blocks, 31 decrease). Between the 2000's and the 2010's, considerably more blocks showed a decrease (30) vs only 5 showing an increase (Figure 4.5). The overall pattern thus appears to be a slight trend towards early in the series to more decrease blocks later, although in

all decades the great majority of blocks showed no change (grey blocks) and both increase and decrease blocks were present over each decade.



Figure 4.5: Decadal percentage change in mean sample mass of parapagurid hermit crabs (kg.km<sup>-2</sup>) as calculated for combined 20' x 20' grid blocks.

There appears to be a slight positive correlation between commercial trawl intensity per commercial grid block per year and mean relative parapagurid sample mass (Figure 4.6), but the relationship is not significant ( $R^2 = 0.42$ ).



Figure 4.6: Correlation between commercial trawl intensity and mean West Coast parapagurid hermit crab sample mass (kg.km<sup>-2</sup>) averaged per commercial trawl 20'x20' grid square.

# Discussion

The catchability of parapagurid hermit crabs (i.e. the proportion of survey trawl hauls with hermit crabs present relative to the total number of trawls conducted) has remained relatively constant over the 23 years sampled. Although a non-significant increasing trend is noted in Figure 3.1, this can be attributed to changes in survey design (see detail in Chapter 3). Prior to 2008, surveys were limited to demersal research trawls shallow than 500 m depth, but from 2008 to 2011, demersal research trawls were occasionally conducted below the 500 m isobath on an opportunistic basis (T. Fairweather, Pers. Comm., 2016) even though they occurred within survey grid blocks listed as < 500 m. This increase in successful demersal research trawls is a result of this change, since trawling deeper would skew the data in favour of deeper-living species, such as cloaked hermit crabs, and particularly *P. bouvieri*. From 2012 onwards, it was logistically feasible for demersal research trawls to routinely trawl deeper than 500 m, and this was accounted for within the data. It must be noted however that, within the literature, it is somewhat rare (and is generally not recommended) to pool data

from different sample sources (as the different gear, in this case). This must be borne in mind when examining the data presented here, and conclusions interpreted as such. The only prior study detailing parapagurid sample mass over time also noted no change in density, although that study only spanned a five-year sampling period within the area of commercial Patagonian scallop fishery activity (Schejter and Mantelatto, 2015).

Any influence of the change in gear is less likely due to any changes in mesh size as it is to the type and configuration of the footrope used – the gear was changed from a chain wrapped around a rope to a chain with rubber rollers (i.e. the old gear sat directly against the sediment, compared to a chain with rollers). Therefore, it would be expected that there would be higher catches of parapagurid hermit crabs with the old gear compared to the new gear with rollers that sits higher above the sediment. This would explain why a greater sample mass caught in years with the old gear compared to those with the new (Chapter 3), and potentially why the highest S. dimorphus mean sample mass was caught in 1999 (a year in which the old gear was used) and the largest decline in S. dimorphus mean sample mass occurring between 2007 and 2008, successive years in which the new gear was used. Indeed, the new gear resulted in lower sample mass caught, compared to the old (see Chapter 3), with a significant decline in S. dimorphus mean sample mass caught in the trawl surveys using the new gear. It may be that parapagurid sample masses in the field are declining, and catches are only maintained because of the new, more successful gear. However, these effects are difficult to unravel, given that such trawl gear is not ideal for the capture of benthic invertebrates, and the total parapagurid sample mass is thus certainly undersampled. Therefore, the figures given here represent only a relative index of sample mass comprising only larger individuals, since smaller parapagurids are liable to pass through the trawl mesh. Total sample mass figures should thus be interpreted with such bias in mind. Since permit conditions for the commercial deep water hake fishery stipulate a minimum stretched mesh size of 110 mm (DAFF, 2010), small parapagurid individuals are likely to also pass through the commercial trawl gear unharmed, thus reducing any direct impact of the commercial fishery on parapagurid populations, despite overlap in their distributions with the areas of operation of the commercial trawl fishery (Chapter 3). Work is required to test such a hypothesis, and could include comparing the size distributions of parapagurids caught in heavily-trawled areas to those caught in pristine areas, as well as determining the survival rates of Parapaguridae that encounter trawl gear.

While that there is no significant trend in mean trawl depth over the sampled period, there was an increase in mean trawl depth between 2007 and 2011 (peaking at a mean of 266.49

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m) before this trend declined for 2012 - 2014. The new gear does appear to catch a higher proportion of *P. bouvieri* than *S. dimorphus* in general (Figure 4.4), which is expected, given that Chapter 3 established that *P. bouvieri* generally occur deeper than *S. dimorphus*, but there is no reciprocal relationship noted (Figure 4.4) between the species, where deeper trawls would be expected to result in a decline in *S. dimorphus* mean sample mass, and an increase in *P. bouvieri* mean sample mass. In addition, the deepest mean trawl depth over the 24 years occurred in 2003, and there was no evidence of a decline in *S. dimorphus* mean sample mass in the following years. Therefore, it seems unlikely that an increase in mean survey trawl depth is the only contributing factor to a decrease in sample mass.

When the total mean sample mass data are plotted by decade (Figure 4.5), most of the 20'x20' grid blocks showed "no change" in hermit crab mean sample masses between decades. There is a slight trend towards increase in parapagurid hermit crab sample mass (in 25 of the 20'x20' grid blocks) between the 1980's and 1990's, but this may be a reflection of a learning curve, as the demersal survey was expanded to include and collect benthic invertebrate fauna, in addition to the targeted hake resource, over this period and the survey crews became better at identifying and collecting cloaked hermit crabs (T. Fairweather, Pers. Comm., 2016). There was a slight tendency towards decreases in mean sample mass between the 1990's and the 2000's (15 increasing blocks, 31 decreasing blocks) and a general decline between the 2000's and the 2010's (30 decreasing blocks, 5 increasing blocks). The apparent decline in mean relative mean sample mass of one of the most abundant species on the shelf (Lange and Griffiths, 2014) raises questions about the impact of trawling, which remains the most widespread and most regular anthropogenic disturbance in the system. Interestingly there appears to be a tentative positive relationship between commercial trawl intensity and parapagurid sample mass (Figure 4.6). However, since this result is non-significant, this result could simply indicate that habitat preferences of parapagurids (Chapter 3) overlap with the preferred substratum of the trawl fishery, which avoids rocky ground so as to avoid trawl net damage. The signal is complicated, however, by anecdotal evidence that suggests parapagurid hermit crabs become more common with subsequent repeat trawls (R. Knust, Pers. Comm., 2015 and R. Leslie, Pers. Comm., 2016), and more work involving monitoring of parapagurid catches following repeat trawls of the same lane is required to determine whether this apparent increase in parapagurid catches is the result of animals moving into trawl lanes to scavenge. The parapagurid mortality in the commercial trawl fishery is not known at this stage – the commercial trawlers do appear to catch the hermits (T. Fairweather, Pers. Comm., 2016), but the large mesh size would result in the hermits passing

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through the mesh and thus surviving. The parapagurids that are caught and brought up in the net may also survive, if discarded back into the sea, but the survival rate of hermit crabs passing through nets or being discarded is currently unknown.

The overall decline in parapagurid hermit crab catches over time correlate, to a degree, with the Total Allowable Catch (TAC) set for the commercial hake fishery, since a higher TAC would, in general, result in a higher intensity of trawl operations. The TAC increased slowly between 1987 and 2000, peaking in 2002 at 166 000 t (DAFF, 2014), while precautionary management measures subsequently reduced the TAC gradually by 27% between 2003 and 2009 (Atkinson et al., 2011b), after which there was an increase in TAC in 2010, which was set at 155 280 t in 2014 (DAFF, 2014). It would appear that the steady (slightly increasing) TAC between the 1980's and 1990's mirrors the decline in parapagurid survey mean sample mass over the same time period, with the high catches in 2006 appearing to coincide with the reduction in TAC over this time. However, since the effort limitation system was introduced (vessels are allocated a number of sea days in which to catch their guota based on their vessel specifications) (T. Fairweather, Pers., Comm., 2016), post-2000 TAC's do not correlate directly with a higher intensity of trawl operations. In addition, given that almost nothing is known of the biology or life history of these animals, more work is needed to untangle the potential influences of trawling on parapagurid hermit crab populations. Further work investigating whether the hermit crabs are being attracted by, and actively moving into, trawl fishing lanes is required. Given the there is evidence for crustaceans (including hermit crabs see Ramsay et al., 1997) benefiting from scavenging off trawl detritus, it seems likely that parapagurid hermit crabs would engage in similar behaviour, especially when their high reported sample mass is considered (Lange and Griffiths, 2014) (Chapter 3).

A scavenging species may benefit from trawl operations if the trawl mortality experienced by the species is balanced by the fitness benefits of increased food supply left by the trawl gear and the removal of predators (Lindeboom and de Groot, 1998). Despite the difficulties in the identification of Crustacea in stomach contents, we can be fairly confident that parapagurids are not a major component of the diets of predators such as hake (*Merluccius* sp. - Payne, Rose and Leslie, 1987; Punt, Leslie and Du Plessis, 1992; Pillar and Wilkinson, 1995; Pillar and Barange, 1997), kingklip (Macpherson, 1983b), blue stingray (*Dasyatis chrysonta*; Ebert and Cowley, 2003) or smoothhound sharks (*Mustelus* sp., Smale and Compagno, 1997). However, it cannot be ruled out that parapagurids are not being preyed upon by other non-commercial fish species. Longevity also plays a role, since a longer-lived species would be impacted more by disturbance than a shorter-lived species (Jones, 1992; Rumohr and Kujawski, 2000). We

currently have very little information about the mortality or longevity of parapagurids. We do not know what the actual mortality (as opposed to capture) of hermits is as a result of trawling, nor do we know what proportion of the actual population is caught (or how many pass though the gear entirely), or the survival of these animals that pass through the net, or the survival of those landed and subsequently discarded. An experimental tag/recapture study, comparison of samples from within and outside of the commercial trawl footprint, as well as experimental deep-water camera surveys within the trawl lanes (L. Atwood, Pers., Comm., 2016) would help in answering these questions.

# Conclusions



Sympagurus dimorphus (Studer, 1883). Image: J Landschoff (2016)

Aside from the taxonomy, almost nothing was known about the distributions, abundances, population biology or morphology of two parapagurid species that dominate deeper-water benthic invertebrate communities off the South African coast, and form a major component of the invertebrate by-catch in DAFF demersal research trawl survey operations: the parapagurid cloaked hermit crabs *Sympagurus dimorphus* (Studer, 1883) and *Parapagurus bouvieri* (Stebbing, 1910). This thesis provided the baseline data on the two deep water hermit crabs, building on the work on *S. dimorphus* by Schejter and Mantelatto (2011; 2015), and providing the first work of its kind for *P. bouvieri*.

The first chapter reviewed the current state of knowledge of three common hermit crab shelter associations: that of empty gastropod shells, and that Actiniaria (anemones) and Zoantharia (zoanthids). Since hermit crab – zoanthid associations remain poorly understood, investigations into hermit crab – anemone associations provided an important starting point in identifying potential benefits and burdens of the relationship for both host and symbiont. Three types of hermit crab – zoanthid associations were noted, including two that involved zoanthid settlement onto already inhabited gastropod shells as an adult crab, and one that involves the development of the zoanthid into a living "cloak" within which the hermit crab dwells, replacing the shell almost entirely as a "pseudoshell". In this association, the zoanthid is assumed to settle on small gastropod shells inhabited by juvenile crabs, and grow into the pseudoshell from there, potentially growing "with" the hermit crab to form a perfectly-fitted home, and negating the need for the growing crab to find new shelters to accommodate its growth. This association is generally understood to be a symbiotic relationship between hermit crabs of the family Parapaguridae (Smith, 1882) and Epizoanthus species, with ten genera currently included within the Parapaguridae, including Sympagurus (Smith, 1883) and Parapagurus (Smith, 1879).

The second chapter provided much needed basic biological parameters and life-history traits of *S. dimorphus* and *P. bouvieri* in a South African context, investigating the sex ratio, dimorphism, size frequency and depth distribution, relative growth and population structure of these two parapagurid hermit crabs, as well as some parameters of pseudoshell association, such as the distribution of the zoanthid polyps that make up the *Epizoanthus* pseudoshells. Male *S. dimorphus* (9.31  $\pm$  2.04 SD mm mean CL, range 4.30 – 16.60 mm) were significantly larger (Hs = 66.40; df1 = 2, df2 = 878; p < 0.01) than both females (8.02  $\pm$  1.46 SD mm mean CL, range 4.70 – 10.70 mm) and ovigerous females (8.27  $\pm$  1.40 SD mm mean CL, range 4.40 – 12.00 mm), which were not significantly different to each other. Male *P. bouvieri* (11.86  $\pm$  2.15 mm SD mean CL, range 2.20 – 19.00 mm) were significantly larger than both

females (9.57  $\pm$  1.56 SD mm mean CL, range 6.60 – 13.00 mm) and ovigerous females (10.12  $\pm$  1.62 SD mm mean CL, range 4.20 – 17.30 mm). S. dimorphus had a female-biased sex ratio of 1:1.5, while P. bouvieri had a sex ratio of 1:1. The proportion of males in both parapagurid populations increases as cephalothoracic shield length increases - all S. dimorphus over the size of 12.10 mm (CL) and all P. bouvieri larger than 18.10 mm (CL) were males. Both S. dimorphus and P. bouvieri correspond to a Type III or intermediate sex ratio probability of curve, where the majority of animals in the small class sizes were female, while all animals in the largest class sizes were male. Size (CL length) at which 50% ovigerous of S. dimorphus females were ovigerous can be approximated as 5.30 mm, and while at no size class were fewer than 60% of female *P. bouvieri* ovigerous, the smallest ovigerous female measured 4.20 mm CL. S. dimorphus males had positive allometric major right chelipeds. This work reports for the first time that P. bouvieri cheliped lengths are positively allometric in males, and negatively allometric in females. There was also a significant relationship between mean size and depth for both S. dimorphus and P. bouvieri, and a significant relationship between depth and sex ratio for both species. There was a real shell occupancy rate of 3.39% (n = 38) for S. dimorphus individuals, while all collected P. bouvieri individuals occurred in pseudoshells. Parapagurid hermit crab males that occupied real shells (mean CL (mm) = 11.33;  $\pm$  2.33 SD) were significantly larger (U = 1767.5; p < 0.01) than males of the same species found in pseudoshells (mean CL (mm) =  $9.35 \pm 1.90$  SD), and a positive relationship was found between CL size and real shell occupation ( $r^2 = 0.64$ ). While no such relationship was found for S. dimorphus, the pseudoshell volume of both ovigerous ( $R^2 = 0.78$ ) and non-ovigerous ( $R^2$ = 0.67) female P. bouvieri increased significantly with increasing CL length. In addition, S. dimorphus pseudoshell zoanthid polyps increased in number as a function of both total shell volume ( $R^2 = 0.73$ ) and colony height ( $R^2 = 0.61$ ), and these polyps were present on every available surface of the pseudoshell, and thus became more numerous as the pseudoshell grew and the surface area increased. In contrast, no relationship was found between the polyp count on *P. bouvieri* pseudoshells relative to either the colony height and pseudoshell volume, presumably as a result of the distribution of polyps in a linear pattern around the back and outside of the pseudoshell, with none present on the top of the shell outside of this line, or over the "mouth" of the shell, indicating that it is unlikely that the zoanthid is obtaining much benefit from its P. bouvieri partner in terms of increased food availability. Juvenile parapagurids inhabit small gastropod shells of a variety of species of a similar aperture width, but appear to select for original shells of the family Naticidae, given that

*Euspira napus* was the dominant original shell species for both *S. dimorphus* (45.45 %) and *P. bouvieri* (39.00 %) in this study.

Chapter 3 presented the largest and most comprehensive spatial and temporal mapping of the distribution and abundance of S. dimorphus and P. bouvieri currently available, encompassing a coastline distance of approximately 1 400 km and sampling 486.63 km<sup>2</sup> of sea floor over 24 years. This analysis was the first of its kind for both species in South African waters, and the first measure of P. bouvieri sample mass and distribution world-wide. Importantly, this work presented evidence that no correction factor need be applied to parapagurid catches in South African waters as a result of the 2003-2004 change in survey gear at this stage, meaning that the data can be pooled for future analysis. S. dimorphus dominated the parapagurid sample mass on the continental shelf of South Africa, being captured at a mean sample mass of 287.88 kg.km<sup>-2</sup> on the West Coast, significantly greater than the mean relative *P. bouvieri* sample mass of 31.37 kg.km<sup>-2</sup>. Both species are broadly distributed over the shelf, with the bulk of sample mass occurring on the nutrient-rich Benguela upwelling region of the West coast, and very few parapagurids caught over the Agulhas Bank, which at a mean depth of just over 100 m may be too shallow for either species, given that S. dimorphus showed a preferential depth range of 200 – 299 m (range 30 - 814 m) and P. bouvieri of 400 - 499 m (range 62 - 700 m) in South African waters. There was a latitudinal and longitudinal effect on parapagurid sample mass, specifically on S. dimorphus, with the highest parapagurid sample masses occurring south of Cape Columbine and west of Cape Agulhas. The parapagurids show a preference for muddy sand and sandy sediments, with the highest mean sample masses occurring on these sediment types (61.00 kg.km<sup>-2</sup> and 45.68 kg.km<sup>-2</sup> respectively).

The fourth and final chapter comprised the first investigation into the changes in the mean parapagurid sample mass over 24 years of standardised demersal research trawl surveys off the West Coast of South Africa. The overall catchability of parapagurids (mean = 43.35%) has remained constant over the 24 years under investigation ( $R^2 = 0.13$ ) with slight trend towards increasing catchability over time, which probably corresponds to the changes in demersal research survey design (i.e. prior to 2008, surveys were limited to demersal research trawls shallow than 500 m depth, but from 2008 to 2011, demersal research trawls were occasionally conducted below the 500 m isobath on an opportunistic basis (T. Fairweather, Pers. Comm., 2016) even though they occurred within survey grid blocks listed as < 500 m. This increase in successful demersal research trawls is a result of this change, since trawling

deeper would skew the data in favour of deeper-living species, such as cloaked hermit crabs. From 2012 onwards, it was demersal research trawls routinely trawled deeper than 500 m.

When separated by species, *S. dimorphus* shows a non-significant decline in mean sample mass (mean = 261.60 kg.km<sup>-2</sup>) over time ( $R^2 = 0.45$ ), whilst *P. bouvieri* (mean = 41.34 kg.km<sup>-2</sup>) shows no trend in mean sample mass ( $R^2 < 0.01$ ) over 24 years. There was no significant change in the depth of demersal research trawls occurring in the latter part of the time series (2003 – 2014), and no significant reciprocal relationship ( $R^2 = 0.03$ ) between *S. dimorphus* and *P. bouvieri*, indicating the one species was not increasing as the other decreased, although the new gear tended to catch more *P. bouvieri* than *S. dimorphus*, probably as a result of the aforementioned change in sample design. The increase in successful demersal research trawls is a result of this change, since trawling deeper would skew the data in favour of deeper-living species, such as cloaked hermit crabs, and particularly *P. bouvieri*. From 2012 onwards, it was logistically feasible for demersal research trawls to routinely trawl deeper than 500 m, and this was accounted for within the data. This may also indicate a decline in *S. dimorphus* populations, but more work is required to untangle these influences.

Mean relative parapagurid sample mass appeared to increase slightly between 1980's - 1990's, possibly due to the learning curve of the demersal research trawls beginning to collect demersal invertebrates in addition to the target fish species. In subsequent decades there was a slight tendency towards declines in captured sample mass, possibly as a result of a link between increases in TAC and effort of the commercial trawl fishery and decline in the mean sample mass of parapagurids. A positive relationship between commercial trawl intensity (the number of trawls per 20'x20' commercial grid block) and parapagurid catches (mapped via starting trawl co-ordinates and averaged by the same 20'x20' commercial grid blocks) was found, suggesting that these hermit crabs may be scavengers taking advantage of the increased food source provided by trawl operations. However, this result was not significant ( $R^2 = 0.42$ ), and may simply indicate that parapagurids prefer sandy and muddy substratum, corresponding with the preferred trawling grounds of the commercial trawl fishery, which avoids rocky ground so as to avoid trawl net damage.

Questions remain as to the influence of the fascinating symbiotic relationship these animals have with their *Epizoanthus* pseudoshells on these distribution and abundance patterns, and more life history and behavioural data, particularly experimental data, are needed for parapagurid hermit crabs in general. There are also concerns regarding the long-term impacts of commercial trawl operations on these hermit crabs, given that more than half of all

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parapagurid catches occurred within the South African deep water commercial trawl fishery operation "footprint". More work is required into the biology and life-history of these animals, especially mortality rates and longevity, to determine the impacts of commercial trawling on parapagurid populations, and whether these hermit crabs are utilising and benefiting from trawl detritus as a food source, especially since anecdotal evidence suggests that they are drawn into to trawl lanes to scavenge on the organic matter and detritus left by the trawl gear. Questions are also raised about whether these two parapagurid species utilise their pseudoshell shelters in different ways, perhaps existing along an evolutionary continuum of traditional shell reliance, whereby the species utilise their pseudoshells differently - *P. bouvieri* may exist within a stronger mutualistic symbiosis with its exclusive pseudoshell species than *S. dimorphus*, and may have lost the ability to change shelters entirely, utilising the pseudoshell as a brood pouch covering only the abdomen, rather than as a shell in which to retract to escape predation.

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## Appendices

## Appendix 1: Trawl survey cruise summary by year

Data	Coast			Trawls Containing Cloaked Hermits	Total Area Swept	Gear
Date	Coast	Season	Number of Trawis		(km <sup>*</sup> )	Used
1987	West	Winter	97	47	8.96	OLD
1988	West	Summer	119	67	11.45	OLD
	West	Winter	103	44	9.44	OLD
	South	Autumn	94	1	7.50	OLD
1989	West	Summer	67	26	5.40	OLD
	West	Winter	105	43	8.36	OLD
1990	West	Summer	119	68	9.36	OLD
	West	Winter	109	53	8.69	OLD
	South	Spring	91	3	6.43	OLD
1991	West	Winter	116	46	9.40	OLD
	South	Spring	82	2	6.40	OLD
	South	Autumn	96	7	7.69	OLD
1992	West	Summer	118	39	9.66	OLD
	South	Autumn	84	6	6.89	OLD
1993	West	Summer	90	30	7.52	OLD
	South	Spring	123	3	9.43	OLD
	South	Autumn	112	13	8.44	OLD
1994	West	Summer	107	42	8.59	OLD
	South	Spring	105	2	8.25	OLD
	South	Autumn	110	10	7.18	OLD
1995	West	Summer	132	44	10.72	OLD
	South	Spring	97	5	7.38	OLD
	South	Autumn	95	19	7.35	OLD
1996	West	Summer	101	34	7.66	OLD
	South	Autumn	80	8	6.19	OLD
1997	West	Summer	104	47	7.67	OLD
	South	Autumn	98	10	7.56	OLD
1999	West	Summer	91	37	7.47	OLD
	South	Autumn	80	14	6.35	OLD
2003	West	Summer	103	40	8.72	OLD
	South	Spring	94	14	7.63	NEW
	South	Autumn	88	14	7.25	OLD
2004	South	Spring	109	5	8.97	NEW
	South	Autumn	92	3	7.44	NEW
2005	West	Summer	114	26	9.46	NEW
	South	Autumn	105	10	8.65	NEW
2006	West	Summer	99	23	8.40	OLD
	South	Spring	147	7	11.89	OLD

TOTAL			6 013	1 575	486.63	
	South	Autumn	110	20	8.68	NEW
2014	West	Summer	134	66	11.19	NEW
2013	West	Summer	129	58	9.91	NEW
2012	West	Summer	130	76	10.77	NEW
	South	Autumn	105	23	8.54	NEW
2011	West	Summer	142	96	11.93	NEW
	South	Autumn	67	12	5.40	OLD
2010	West	Summer	106	57	8.88	OLD
	South	Autumn	94	26	7.61	NEW
2009	West	Summer	114	72	9.58	NEW
	South	Autumn	138	20	11.26	NEW
	South	Spring	135	18	11.09	NEW
2008	West	Summer	109	64	9.16	NEW
	South	Autumn	138	21	11.12	NEW
	South	Spring	82	9	6.79	NEW
2007	West	Summer	103	20	8.66	NEW
	South	Autumn	93	5	7.71	OLD

### **Appendix 2: Supporting Paper**

# Build or rent? Advantages and disadvantages of pseudoshells to two deep-water hermit crab species

**Student: Thomas Petrus Arnoldus Botha** 

Supervisors: Emeritus Professor Charles Griffiths & Amy Wright

Project submitted to the University of Cape Town, in partial fulfillment of the requirements to graduate with a B.Sc. (Hons) Degree in Marine Biology

University of Cape Town

Department of Biological Sciences

November 2016



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#### **Plagiarism Declaration**

- 1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.
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Date: 11 November 2016

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#### Abstract

Hermit crabs typically occupy empty gastropod shells to protect their soft, vulnerable abdomens. However, some species have evolved symbiotic associations with zoanthids that then form a 'pseudoshell', within which the hermit crab lives. In this study, the advantages and disadvantages of occupying a pseudoshell, as opposed to a conventional gastropod shell, are considered. This was done by comparing the weight, fit and compressive strengths of shells and pseudoshells occupied by two deep-water hermit crab species, Sympagurus dimorphus and Parapagurus bouvieri, whose fecundity was also compared. Pseudoshells occupied by P. bouvieri weighed almost 93% less than gastropod shells, and almost 72.63% less than pseudoshells occupied by S. dimorphus, presumably allowing more energy to be invested in growth and reproduction, and increasing the efficiency of locomotion. For a given cephalothoracic length, S. dimorphus occupied pseudoshells with a volume 14.23% smaller than gastropod shells and 111.75% bigger than pseudoshells occupied by P. bouvieri, possibly due to pseudoshell size limitations and different shell use strategies. Moreover, ovigerous *P. bouvieri* females were significantly more fecund than similar sized S. dimorphus, as they occupied shells with a higher volume/weight ratio, thus allowing more space in the shell for eggs and more energy for reproduction. On average, pseudoshells could withstand forces between 87.55 - 93.95% less than could gastropod shells, providing weaker physical protection. In compensation, there is a possibility that pseudoshells provide chemical protection to their occupants. Pseudoshell-occupation may well also permit these hermit crabs to occur at greater abundances, since pseudoshells are not likely a limiting resource, while empty gastropod shells are scarce. Occupying a pseudoshell may thus confer significant advantages, which could become even more evident if a chemical analysis of the pseudoshell demonstrates chemical protection.

#### Introduction

Hermit crabs are crustaceans of the Order Decapoda. The majority of species inhabit empty gastropod shells, within which they protect their vulnerable, non-calcified abdomens (Schejter & Mantelatto, 2011). The shells are also important in preventing desiccation in intertidal species (Reese, 1969). Throughout life, hermit crabs periodically switch to larger shells that adequately protect the growing crab and that provide enough space for the female's brood (Angel, 2000). Limitations in the availability of shells of appropriate size, volume or quality often force hermit crabs to occupy shells of inappropriate size, negatively affecting individual survival, growth, development and reproduction (Angel, 2000; Meireles *et al.*, 2003; Mantelatto & Meireles, 2004). Furthermore, empty gastropod shells that are not quickly utilised by hermit crabs are likely to become buried in the substrate due to wave action (Hazlett, 1981), causing further shortage of shells, especially in deeper waters (Pretterebner, 2011). Thus, gastropod shells are an important and often limiting resource for hermit crabs and shell selection has an important influence on individual growth, survival and fecundity (Angel, 2000; Williams & McDermott, 2004).

However, not all hermit crabs occupy empty gastropod shells. Some species are also known to inhabit pieces of wood, calcareous polychaete tubes, corals, etc. (see Williams & McDermott, 2004; Schejter & Mantelatto, 2011). Furthermore, some hermit crabs of the genera Parapagurus Smith, 1879 and Sympagurus Smith, 1883 form symbiotic associations with anthozoans, specifically Zoantharia and Actinaria (Lemaitre, 1989, 1990, 2004). These species are often referred to as 'cloaked' hermits, as the anthozoans construct a living cloak that act as a substitute shell or 'pseudoshell' for the hermit crab. Most studies on symbiotic relationships between hermit crabs and anthozoans have involved actinians, as they are shallow-water species and are easy to collect (Ates, 2003). Only a handful of studies exist on the relationship between zoanthids and hermit crabs, which tend to occur in deep-water species. Most available literature on hermit crab-zoanthid associations deals only with records of this phenomenon and does not provide detailed information of the nature of the relationship, or its potential benefits to either hermit crab or zooanthid. Schejter & Mantelatto (2011, 2015) were the first to describe the relationship between shell-like colonies of the zoanthid Epizoanthus paguricola Roule, 1900 and the hermit crab Sympagurus dimorphus (Studer, 1883). Pseudoshells are formed by a zoanthid polyp

after its settlement on a small shell inhabited by a juvenile hermit crab (Schejter & Mantelatto, 2011; Cardoso & Lemaitre, 2012). The polyp then divides and grows to form a carcinoecium (the inter-polyp tissue), which ultimately creates the shell-like structure the hermit crab inhabits. The pseudoshell generally preserves the coiled morphology of the gastropod shell that the zoanthid settled on (Schejter & Mantelatto, 2011) and the initial shell the zoanthid settled on remains lodged in the apical section of the pseudoshell. The associations between hermit crabs and anthozoans enable these hermit crabs to grow without switching shells and it is believed such associations evolved due to the lack of shells in deeper parts of the ocean (Schejter & Mantelatto, 2011).

A problem often faced by hermit crabs is that of finding a shell of the appropriate size, as this is a limited resource (Angel, 2000). Thus, a shortage of gastropod shells restricts population size, as shells are fundamental to hermit crab survival. More often than not, the shell is either too big or too small, and both these scenarios have negative implications for the hermit crab. If a shell is too small, the hermit crab is not able to retract fully into the shell, and the appendages that are protruding are at risk from predators. Moreover, small shells often do not have enough space for the female's brood or for the hermit crab itself, thus fecundity and growth may be constrained (Bertness, 1981; Angel, 2000). If a shell is too large, energy that could have been invested towards growth or reproduction is wasted by carrying a heavy shell. Therefore, not only is locating a shell difficult, but finding one of the correct size is even more arduous, as larger gastropod shells are exceptionally scarce (Walters & Griffiths, 1987). Therefore, pseudoshells can be advantageous to hermit crabs that live in environments constrained by shell availability. As the hermit crab grows bigger, so does the pseudoshell, as it is a 'living cloak', thus negating the need to regularly find bigger shells. This is especially beneficial for deeper water hermit crabs, as in this environment gastropod shells are thought to be a particularly limiting resource (Schejter & Mantelatto, 2011). Use of pseudoshells may allow these species to become far more common that otherwise would be the case.

The coasts of Southern Africa hosts approximately 63 species of hermit crabs, mostly occurring in the intertidal zone (Landschoff, pers. comm.). Most species occur on the East Coast, and fewer on the South and especially West Coasts (Kensley, 1981). This is a common trend for invertebrates on the coasts of South Africa that has been

observed for multiple taxa (Awad, Griffiths & Turpie, 2002). The majority of South African hermit crab species occur only in gastropod shells, although some (e.g. *Dardanus pedunculatus* & *Dardanus cuanensis*) also have an association with anemones that live on the shell, further protecting the hermit crab (Williams & McDermott, 2004). Two deep-water species known from South Africa are instead known to have a symbiotic association with a zoanthid, although a third is currently being described (Landschoff, pers. comm.). The two well-known species, namely *Sympagurus dimorphus* and *Parapagurus bouvieri* will be the focus of this study.

*Sympagurus dimorphus* is found in the Southern Hemisphere from  $22^{\circ}$  -  $57^{\circ}$  with a possibility to be found as far north as Ascension Island (Lemaitre, 2004). It is a deepwater species found at depths between 91 - 1995 m (Lemaitre, 2004), although mostly below 150 m in South African waters (Wright, pers. comm.). Two studies have been published on *S. dimorphus* and its symbionts, describing its relationship with a zoanthid (*E. paguricola*) in the western Atlantic (Schejter & Mantelatto, 2011, 2015). *Sympagurus dimorphus* occupy both pseudoshells and gastropod shells (Figure 1a & 1b respectively).

*Parapagurus bouvieri* generally occurs in the Southwestern Atlantic from Namibia to South Africa, as well as in the Southwestern Indian Ocean from KwaZulu-Natal to Australia (Lemaitre, 1990). This is a deeper water species, found at depths between 55 - 5000 m (Lemaitre, 1986). *Parapagurus bouvieri* has only been described in taxonomic literature (Lemaitre 1989, 1990) and very little is known about its biology. From previous studies (Ates, 2003) it has been noted that one of the zoanthids in association with *P. bouvieri* is *Epizoanthus carcinophilus* Carlgren, 1923, but it is uncertain whether this is the species found in association with South African populations. *Parapagurus bouvieri* occupies pseudoshells exclusively (Figure 1c).



Apart from being listed as a prominent by-catch species in the hake trawl survey catches (Lange & Griffiths, 2014), little is known about South African *S. dimorphus* and no previous research has been conducted on the association between either hermit crab species and its zoanthid pseudoshell. There are several interesting aspects that can be compared between these pseudoshells and gastropod shells. Perhaps the most obvious are comparisons between the weight and fit of the hermit crab in these respective shelters, and between the compressive loads required to fracture shells and pseudoshells.

This study will focus on the advantages and disadvantages of occupying a pseudoshell, as opposed to an empty gastropod shell. Shell aspects that will be compared between pseudoshells and empty gastropod shells are the weight of the shells in seawater, the fit of hermit crabs in shells and the maximum compressive loads they withstand. It is hypothesised that pseudoshells are lighter, as they are not made of calcium carbonate, unlike gastropod shells. Furthermore, it is hypothesised that as the hermit crab grows, the pseudoshell grows with it and that some form of communication exists between the hermit crab and the zoanthid. Therefore, the fit of hermit crabs is expected to be better for hermit crabs occupying pseudoshells than for those in empty gastropod shells. Physical protection is the key reason hermit crabs occupy shells and a stronger shell will provide superior physical protection. Empty gastropod shells are hypothesised to be stronger, as they are less malleable than their pseudoshell counterparts. The availability of real shells relative to pseudoshells and how this might affect the population density and structure of hermit crabs in the deep sea will also be speculated upon.

This study thus aims to contribute to existing knowledge concerning deep-water hermit crabs and their association with their zoanthid symbionts, and is the first of its kind in South Africa.

#### Methods

Specimens of *S. dimorphus* and *P. bouvieri* were collected during the February-March and May-June 2016 demersal research surveys. These surveys were conducted by The Department of Agriculture, Forestry and Fisheries (DAFF) off the west (west of  $20^{\circ}$  E) and south (east of  $20^{\circ}$  E) coasts of South Africa, respectively. The research survey was primarily done to estimate the abundances of the two Cape hake species (*Merluccius sp.*) and the fish by-catch associated with them. The surveys ranged between 17 - 1550 m in depth and all sampling occurred within South Africa's Exclusive Economic Zone (EEZ). A few other individuals were collected in the Cape Canyons.

Sampling was conducted using the research vessel *Compass Challenger*. The gear used consisted of a four-panel 180 ft German otter trawl, as well as 9 m sweeps and 1.5-t Morgere multipurpose otter boards. The door spread was roughly 60 - 75 m and the mouth opening was 3 - 4 m vertical and 20 - 29 m horizontal. Lastly, the footrope was constructed from rubber discs (Atkinson *et al.*, 2011b).

Specimens were frozen on board ship, then transferred to the laboratory at the University of Cape Town (UCT), where they were thawed and examined. For each specimen of both species, it was noted whether they occurred in a gastropod shell or a pseudoshell and percentage zoanthid cover was estimated for pseudoshells.

In total, 189 *P. bouvieri* and 521 *S. dimorphus* individuals were examined. All *P. bouvieri* individuals were found in pseudoshells. Of the 521 *S. dimorphus* individuals, 485 were found in pseudoshells and 36 in empty gastropod shells. All individuals were sexed, randomly sub-sampled (except those in gastropod shells) and divided into three

sampling groups to be used in analyses. The first was *P. bouvieri* in pseudoshells (n = 50), the second was *S. dimorphus* in pseudoshells (n = 50) and lastly *S. dimorphus* in gastropod shells (n = 36). Various physical properties of the pseudoshells or gastropod shells and hermit crabs were measured, including the weight of the shells in seawater, the volume of the shell and the fecundity of female crabs, as well as the compression strength of the shells. The cephalothoracic length of each hermit crab was measured using a vernier caliper with a precision of 0.01 mm and was used as a proxy for body size.

#### Shell weight

The weight of the shells in seawater was weighed with a precision of 0.01 g using a balance scale. A cylinder was placed on the scale, with a rod through it. Fishing line was fastened on either end of the rod and both ends of the string attached to a hook (Figure 2). The shell was attached to the hook and placed in seawater, subsequently it was rotated to ensure all air was expelled and weighed. For this analysis, the pseudoshells of all 50 specimens of both species that were randomly sub-sampled were weighed. All 36 gastropod shells occupied by *S. dimorphus* were also included.

#### Shell volume

The volume was taken by submerging the shell in seawater and then rotating it to ensure all air was out of the shell. The water inside the shell was then transferred to a volumetric cylinder (50 ml or 10 ml), ensuring all water was out of the shell. For both pseudoshell groups, 36 pseudoshells were randomly sub-sampled from the original sub-sample of 50 shells. All 36 gastropod shells were used. This was to ensure the three groups had equal sample sizes, with the gastropod shell group limiting the sample size.

#### Fecundity

The egg counts of 17 and 11 randomly sub-sampled ovigerous females in pseudoshells were estimated of *P. bouvieri* and *S.* dimorphus respectively. Too few ovigerous females in gastropod shells were found to be able to include them in this analysis. The two species had different cephalothoracic lengths and only individuals that had a cephalothoracic length that occurred within the area of overlap (between 8 - 13 mm) of the two species were considered. Eggs were counted by collecting them in a petri dish and counting them using a calibrated pipette (see Dando, 2016). The volume/weight

ratio was obtained for all 50 sub-sampled pseudoshells occupied by both species as well as for all 36 gastropod shells occupied by *S. dimorphus*.

#### Shell strength

The maximum compressive loads of the shells were measured in collaboration with the Department of Engineering Materials Laboratory at UCT, using a Zwick 1484 hydraulic press with the test Xpert II software. A 200 kN loading cell was used to test each shell's maximum compression strength with a resolution of  $\pm 1\%$ . The shells were tested individually by first placing them in a standardised position, with the aperture facing downwards, between the load cell and bottom plate. The bottom plate was manually moved just so the shell touched the loading cell. This plate was then moved upwards at a speed of 2.5 mm per minute until the shell was fractured to the point at which the hermit crab would have been compromised. For gastropod shells the maximum force required to fracture the shell was used. Similarly, for pseudoshells the maximum compression strength was used prior to the pseudoshell compressing on itself, which increases the force applied on the pseudoshell in an exponential manner. The pseudoshells occupied by S. dimorphus are made of a granular structure, with a rough surface and are flexible to a degree, but can withstand some force when applied. Conversely, the pseudoshells occupied by P. bouvieri are smooth and thick, but they are extremely flexible and offer negligible resistance when force is applied. Therefore, when the maximum compressive loads were measured, only pseudoshells and gastropod shells occupied by S. dimorphus were measured and none occupied by P. bouvieri. All 50 pseudoshells occupied by S. dimorphus were used and 20 gastropod shells were used to test their maximum compressive loads.



Figure 2: Illustration of the scale used to weigh the shells and pseudoshells in seawater.

#### **Statistical analyses**

To detect differences between the weights of the respective shells in seawater, the nonparametric Kruskal-Wallis test (Zar, 2010) was used and subsequently a post-hoc test was done. To estimate the fit of the hermit crab in their respective shells an appropriate regression between volume of shell and cephalothorax length was used. Regressions between the cephalothoracic length and volume were also performed for ovigerous females and males of both species occupying pseudoshells. To compare mean fecundity between ovigerous females of both species occupying pseudoshells, a Welch's t-test was performed. Two more non-parametric Kruskal-Wallis tests were used to detect differences in the volume/weight ratios of the three groups of shells, as well as between the maximum compressive loads between pseudoshells and three genera of gastropod shells. Subsequently two post-hoc tests were conducted to identify specific differences. All statistical analyses were performed using R Software (R Core Team, 2016). The "pgirmess" package (Giraudoux, 2016) was used to perform all Kruskal-Wallis tests.

#### Results

#### Shell weight

In total, 189 *P. bouvieri* and 521 *S. dimorphus* individuals were examined. All *P. bouvieri* individuals (3.2 - 19.3 mm cephalothoracic length) were found in pseudoshells. Conversely, of the 521 *S. dimorphus* individuals, 485 were found in pseudoshells (1.6 - 17.9 mm cephalothoracic length) and 36 in empty gastropod shells (2.4 - 15.1 mm cephalothoracic length). The weight of the shells in seawater amongst the three groups differed significantly (Kruskal-Wallis; H = 85.85; df = 2; p < 0.01). The pseudoshells (mean weight  $\pm$  SD) occupied by *P. bouvieri* (0.26 g  $\pm$  0.162) were significantly lighter than pseudoshells occupied by *S. dimorphus* (0.95 g  $\pm$  0.555; p < 0.05) and almost 92.86% lighter than gastropod shells occupied by *S. dimorphus* (3.64 g  $\pm$  2.806; p < 0.05; Figure 3). The latter two groups were also significantly different from one another (p < 0.05), with the gastropod shells being heaviest (Figure 3).



Figure 3: Mean weight in grams ( $\pm$ SD) in seawater of pseudoshells occupied by *Parapagurus bouvieri* (n = 50) and *Sympagurus dimorphus* in pseudoshells (n = 50) and gastropod shells (n = 36). Only hermit crabs with a cephalothoracic length between 8 - 12 mm were considered.

#### Shell volume

A positive relationship exists between the volume of the shells and the cephalothoracic length of the hermit crabs for all three groups of shells (Figure 4). A perpendicular was placed at 10 mm (logged value is 2.3 mm) as this was well within the cephalothoracic size range of all three groups (7.1 - 15.1 mm for *P. bouvieri*, 5.6 - 13.3 mm for *S. dimorphus* in pseudoshells and 2.4 - 15.1 mm for those in gastropod shells). The volumes of the shells occupied by this standard sized individual show that there are major differences in shell volume between groups. *Parapagurus bouvieri* occupied the tightest fitting shell (3.32 ml), *S. dimorphus* in pseudoshells have an intermediate volume (7.03 ml) and *S. dimorphus* in gastropod shells occupied by *S. dimorphus* had a volume almost 14.23% less than gastropod shells and 111.75% bigger than pseudoshells occupied by the same-sized *P. bouvieri* individual. Furthermore, gastropod shell volume was most closely correlated with cephalothoracic length and had an R<sup>2</sup> value of 0.76, followed by *S. dimorphus* in pseudoshells R<sup>2</sup> = 0.74 and lastly *P. bouvieri* R<sup>2</sup> = 0.64 (Figure 4).



Figure 4: Relationships between pseudoshell/shell volume and cephalothoracic length for three groups of hermit crabs; *Parapagurus bouvieri* in pseudoshells (n = 36), *Sympagurus dimorphus* in pseudoshells (n = 36) and in gastropod shells (n = 36).

Both males and females of *S. dimorphus* showed a positive relationship between pseudoshell volume and cephalothoracic length (Figure 5). Small males occupied marginally smaller pseudoshells than females, but bigger males occupied bigger shells than females (Figure 5). Males had an  $R^2$  value of 0.73 and females of 0.58 (Figure 5).



Figure 5: Relationship between the pseudoshell volume and cephalothoracic length of *Sympagurus dimorphus* males (n = 36) and ovigerous females (n = 36).

Small females occupied smaller pseudoshells than males, while bigger females occupied bigger shells than males (Figure 6). The relationship between pseudoshell volume and cephalothoracic length for males had an  $R^2$  value of 0.54 and for females of 0.77 (Figure 6).



Figure 6: Relationship between the pseudoshell volume and cephalothoracic length of *Parapagurus* bouvieri males (n = 36) and ovigerous females (n = 36).

#### Fecundity

The fecundity of similar sized ovigerous females of both species were found to be significantly different (t = 2.12; df = 25; p < 0.05). Ovigerous females of *P. bouvieri* had significantly more eggs (1381 ± 971 eggs) than those of *S. dimorphus* in pseudoshells (796 ± 481 eggs). The three groups of shells had significantly different volume/weight ratios (H = 91.85; df = 2; p < 0.01). Pseudoshells occupied by *P. bouvieri* had a significantly (p < 0.05) higher volume/weight ratio (25.99 ± 14.34) than both *S. dimorphus* in pseudoshells (6.37 ± 2.04) and in gastropod shells (4.35 ± 3.86). Also, pseudoshells occupied by *S. dimorphus* had a significantly higher volume/weight ratio compared to those in gastropod shells (p < 0.05).

#### Shell strength

*Sympagurus dimorphus* differs from *P. bouvieri* in that they are not only found in pseudoshells, but also in gastropod shells. The pseudoshells occupied by the two species are dissimilar, as they are made by different zoanthid species (*S. dimorphus* associates with *E. paguricola* and *P. bouvieri* associates with *E. carcinophilus*). The maximum compressive loads were measured for pseudoshells occupied by *S. dimorphus* and three genera of gastropod shells - *Fusitriton* Cossman, 1903, *Coluzea* Finlay, 1926 and *Athleta* Conrad, 1853. The maximum compressive loads for these four groups differed significantly (H = 42.16; df = 3; p < 0.01). The post-hoc test showed that all three gastropod shell genera differed significantly from the pseudoshell group (all showed p < 0.05), but did not significantly differ from each other. Figure 7 shows that *Athleta* shells had the highest compressive load (300.96 N  $\pm$  88.44), followed by *Coluzea* shells (261.55 N  $\pm$  195.35) and *Fusitriton* (146.22 N  $\pm$  71.72). Pseudoshells had a far lower maximum compressive load (18.21 N  $\pm$  11.51), as expected, and they could only withstand forces 87.55 - 93.95% less than gastropod shells (Figure 7).



Figure 7: Mean maximum compressive loads and standard deviation for pseudoshells (n=50) and three genera of gastropod shells (*Fusitriton*, n = 12; *Coluzea*, n = 5; *Athleta*, n = 3) occupied by *Sympagurus dimorphus*.

#### Discussion

This study examined the relationships between hermit crab and gastropod shell/pseudoshell characteristics such as shell weight, shell volume, fecundity and shell strength to understand the advantages and disadvantages of occupying a pseudoshell. This is the first study in South Africa to examine these characteristics, and the first globally to examine the advantages and disadvantages associated with the occupation of a pseudoshell.

#### Shell weight

As expected pseudoshells occupied by both species were significantly lighter in seawater than gastropod shells. However, pseudoshells occupied by *S. dimorphus* were significantly heavier than those occupied by *P. bouvieri*. Occupying a lighter shell is

advantageous to hermit crabs as it will conserve critical resources and allow for more efficient locomotion compared to those in gastropod shells, thus improving their scavenging ability. Therefore, carrying a heavy shell is energetically costly for hermit crabs, as it wastes resources that could have been invested in reproduction and growth (Fotheringham, 1976; Angel, 2000; & Mantelatto & Meireles, 2004). An increased growth rate is favourable for several reasons. Firstly, attaining a larger size reduces predation risk (Bertness & Cunningham, 1981). Secondly, larger-sized females are positively correlated with fecundity (Osorno, Fernández-Casillas & Rodríguez-Juárez, 1998) and larger males perform more favourably in male-male interactions (Hazlett, 1981).

The three groups sampled in this study represent a continuum of zoanthid cover. Gastropod shells essentially had little or no zoanthid cover, whereas pseudoshells occupied by *S. dimorphus* were almost completely covered, but in most cases the original gastropod shell was still visible. However, most pseudoshells occupied by *P. bouvieri* were completely covered by the zoanthid and only in few cases was the original gastropod shell visible. Therefore, it is unsurprising that pseudoshells occupied by *P. bouvieri* weighed the least, as they had a larger coverage of zoanthid, which is composed of a lighter material than calcium carbonate. The current understanding is that hermit crabs do not change their pseudoshells, but that these grow with the hermit crab (Schejter & Mantelatto, 2011). Thus, by occupying a pseudoshell, not only is there more energy available for growth and/or reproduction, it is also unnecessary to locate new shells, which in an environment where shells are a limiting resource (Schejter & Mantelatto, 2011), is greatly advantageous.

#### Shell volume

Gastropod shells occupied by *S. dimorphus* were found to be larger than pseudoshells occupied by a similar-sized individual. This could mean that the pseudoshell has an upper size limit to which it grows, and subsequently *S. dimorphus* become too big and are forced to seek alternative shelters such as gastropod shells. However, gastropod shells are most likely a limiting resource in deep-water ecosystems, as Schejter & Mantelatto (2011) found in the western Atlantic and thus few gastropod shells of an adequate size will be available. This study found that 93% of *S. dimorphus* occurred in pseudoshells and 7% in gastropod shells, similar to Schejter & Mantelatto (2011), who

found 92% in pseudoshells and only 8% in gastropod shells, suggesting that the trend in the western Atlantic is also present here. Furthermore, Lange & Griffiths (2014), found that with depth gastropods decline substantially and since *S. dimorphus* is a deep-water species, gastropod shells on South Africa's West Coast are most likely a limiting resource. This could be why *S. dimorphus* had a marginally better fit in gastropod shells rather than in pseudoshells, as only few were able to find gastropod shells and the majority was forced to occupy smaller, worse fitting pseudoshells.

The two pseudoshell types differed significantly, with those occupied by *S. dimorphus* having the largest volume for a standard sized hermit crab. This may be due to the different ways in which the two hermit crab species utilise the shells they occupy. As Schejter & Mantelatto (2011) noted, *S. dimorphus* use their cheliped as a gastropod operculum to essentially close the shell aperture like a 'door'. These individuals are able to fully retract into their shells (be it a gastropod shell or pseudoshell) when confronted by predators. Therefore, they require large shells that allow them to shelter their entire bodies. Conversely, almost no *P. bouvieri* individuals were able to retract back into their shells, nor could they use their cheliped as a 'door'. Those individuals able to retract into their shells were not able to fit their appendages, as the shells were too small, potentially leaving them vulnerable to predators (Figure 8).



Figure 8: *Parapagurus bouvieri* in a pseudoshell, with long protruding appendages, unable to retract fully (a) and *Sympagurus dimorphus*, with shorter appendages, able to fit its whole body into the pseudoshell (b).

Visual stimuli are important for hermit crabs occurring in the photic zone, as this is how they identify threats and respond by fully retracting into their shell (Ping *et al.*, 2015). However, since deep-water hermit crabs such as *S. dimorphus* and *P. bouvieri* mostly occur either in the aphotic zone, or low-light environments, visual stimuli become less important in darker environments and the hiding response of hermit crabs is not triggered via these stimuli. Furthermore, a trend has been noted that with increasing depth, megafauna biomass declines (Levin & Gooday, 2003). Thus, a lower biomass would be accompanied by fewer predators compared to intertidal areas and therefore there will be less predation on deep-water hermit crabs. Therefore, large shells are not required, as is the case for intertidal hermit crabs, since there may be less of a need to fully retract into their shell. This could possibly be the reason why *P. bouvieri* occupied the smallest shells, as they are found at greater abundance with depth (Wright, 2016) compared to *S. dimorphus* that are likely subject to greater predation rates. The need for smaller, lighter shells along with the lack of predation
pressure and adequate light might be the reason why *P. bouvieri* were found in smaller pseudoshells.

There could be several reasons as to why the fit of *P. bouvieri* in pseudoshells appear to be worse than *S. dimorphus*. It is general convention when measuring hermit crab size to use the cephalothoracic length as a proxy (Bertness, 1981; Osorno, Fernández-Casillas & Rodríguez-Juárez, 1998; Schejter & Mantelatto, 2011, 2015). However, since the cephalothorax of *P. bouvieri* rarely fits into the pseudoshell (Figure 8), this measure might not be the most appropriate to correlate with shell size for this species. This is most likely why the fit of *P. bouvieri* appeared to be the worst. In contrast, the abdomen, as well as the cephalothorax, and in most instances the appendages of *S. dimorphus* were able to fit into the pseudoshell. Therefore, rather than using the cephalothoracic length as a proxy of hermit crab size, a more representative measure of both species (perhaps the weight or a measure of the abdomen) might be more appropriate to estimate the fit of the hermit crabs in their shells.

Male and female hermit crabs have different uses for their shells. Females require more space inside their shells than males to accommodate their eggs (Angel, 2000). Therefore, males are expected to occupy smaller shells than females of a similar size. Thus, it was proposed to rather estimate the fit separately for males and females, suggesting that grouping them together might be the reason for the poor fit. However, there was no difference observed between the shells occupied by males and females of *S. dimorphus*, nor those of *P. bouvieri*. Hence the poor fit of both species in their pseudoshells may not be due to the different requirements of males and females, but rather as suggested, the difficulties with estimating hermit crab size.

# Fecundity

Bertness (1981) and Osorno, Fernández-Casillas & Rodríguez-Juárez (1998) suggested that the volume/weight ratio has an important influence on hermit crab fecundity. Pseudoshells occupied by *P. bouvieri* had the highest volume/weight ratio, and these females had significantly more eggs than similar sized *S. dimorphus* females that were found in pseudoshells with a low volume/weight ratio. This is similar to Bertness (1981), who found that females occupying shells with a higher volume/weight ratio had twice as many eggs per clutch as those in shells with a low volume/weight ratio. By occupying a pseudoshell with a high volume/weight ratio, there is more space,

allowing for more eggs, and the shell is light, so more energy is available for reproduction. Investing more energy into reproduction will increase the hermit crab's probability of successfully passing its genes on to the following generation. Although this analysis was not able to include *S. dimorphus* in gastropod shells, as not enough ovigerous females were found occupying these shells, the volume/weight ratio suggests that females occupying those shells will be less fecund than those in pseudoshells.

### Shell strength

Most hermit crabs rely on hard calcium carbonate gastropod shells for protection from predators (Hazlett, 1981), which struggle to break these shells and are in a constant evolutionary arms race with gastropod shells (Bertness & Cunningham, 1981). However, when adequate force is applied, the brittle gastropod shells may crack and subsequently break. Conversely, the pseudoshell is a more malleable structure, which is disfigured when force is applied, but still returns to its original shape. As expected, the gastropod shells could withstand much greater forces than the pseudoshells. The trade-off that hermit crabs face is between a lighter shell that allows more resources to be available for growth and reproduction, and a stronger shell that provides better physical protection.

Pseudoshells may not provide the same physical protection as a gastropod shell, but they may not be completely defenseless against predators. Cnidarians are known to have nematocysts, which are secreted by nematocytes (Weber, 1990). Cnidarians use nematocysts to either capture their prey or to defend themselves (or associated organisms) from predators (Kass-Simon & Scappaticci, 2002). Few studies have assessed the toxic nature of zoanthids, however Moore & Scheuer (1971) made the first discovery of palytoxin in a Hawaiian zoanthid species called "limu-make-o-hana", which means deadly seaweed of Hana. Palytoxin is one of the most toxic non-protein substances known and has been known to cause human death (Moore & Scheuer, 1971). Therefore, it is feasible that the zoanthids associated with hermit crabs might offer some form of chemical defense, rather than a physical one.

# Future Studies

An interesting question raised in this study is how the zoanthid and hermit crab communicate to ensure that the pseudoshell remains the correct shape and fit by growing along with its host. To answer both these questions, a study would have to be done on live animals, and seeing as both are deep-water species, this could be challenging. Another question is whether the hermit crabs are chemically, rather than physically protected by their pseudoshells. A chemical analysis is underway to investigate this, but unfortunately the results were not ready by the time of submission. It would also be valuable to do choice experiments to see if *S. dimorphus* actively prefer gastropod shells to pseudoshells, as well as recording the numbers of empty gastropod shells found in the samples.

### Concluding remarks

It is interesting to note that the two species of pseudoshells are not similar structures. The literature on pseudoshell-forming zoanthids is incredibly scarce and thus far there has been no mention that pseudoshells might not all have a similar function. In this study it was found that pseudoshells not only differ with regard to weight and volume as stated earlier, but also with regard to shape (Figure 8). The pseudoshell occupied by *S. dimorphus* acts as a substitute shell for a gastropod shell and retains the coiled, shell-like shape. However, the pseudoshell occupied by *P. bouvieri* does not act as a substitute shell, as it does not protect the entire animal. It only protects the abdomen and the eggs of ovigerous females, and is essentially a brood pouch for females. Therefore, the two pseudoshell types seem to represent an evolutionary continuum, where the pseudoshell occupied by *S. dimorphus* has the original shell shape and those occupied by *P. bouvieri* exhibit a more specialised structure.

Based on this study, there are mostly advantages associated with the occupation of a pseudoshell. According to Lange & Griffiths (2014), *S. dimorphus* was the most abundant invertebrate found in their survey of South Africa's West Coast and made up ~47% of the total number of individuals sampled. Thus, pseudoshells allow hermit crabs to occur in great abundance in areas where, without them, this would not be possible. This provides further evidence that pseudoshells are mostly advantageous for hermit crabs and without them hermit crabs would not occur in such great abundance. While this study set out to compare pseudoshells and gastropod shells, the differences between the two types of pseudoshells is an interesting finding, and like with much of science the interesting finding has little to do with the original aims of this study. We look forward to more research regarding comparisons of pseudoshells.

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