Intra- and interspecific variability in the distribution patterns and diet of the two most common catsharks caught in demersal trawls off the West and South coasts of South Africa: Evidence for habitat and resource partitioning?

By

Grant Mark van der Heever

A thesis submitted in fulfilment of the requirements for the degree of

Magister Scientiae in the Department of Biodiversity and Conservation Biology,

University of the Western Cape.

July 2017

Intra- and interspecific variability in the distribution patterns and diet of the two most common catsharks caught in demersal trawls off the West and South coasts of South Africa: Evidence for habitat and resource partitioning?

Grant Mark van der Heever

Keywords:

By-catch

Catsharks

Competition

Demersal

Diet

Distribution

Intraspecific

Interspecific

Resource

Stable isotope analysis

Abstract

Intra- and interspecific variability in the distribution patterns and diet of the two most common catsharks caught in demersal trawls off the West and South coasts of South Africa: Evidence for habitat and resource partitioning?

G.M van der Heever

MSc Thesis, Department of Biodiversity and Conservation Biology, University of the Western Cape.

The objective of this thesis was to elucidate intra- and interspecific variability in the distribution patterns and diet of the two most common demersal catsharks taken as by-catch by the commercial trawling industry targeting the two Cape hake species off the West and South coasts of South Africa. Samples and data were collected during routine demersal hake biomass surveys conducted by DAFF, with distribution data collected from 1994 to 2015 and stomach content and stable isotope data collected from 2014 to 2015. On examination of the distribution data, *Holohalaelurus regani* was found to be more abundant on the West Coast and *Scyliorhinus capensis* was found to be more abundant on the South Coast. Both catsharks were observed to display size-based segregations, with catshark size increasing with depth in both species. Differences in the distribution patterns of male and female *H. regani* were also noted, with female catsharks inhabiting inshore areas and male catsharks inhabiting offshore areas. The two catsharks appeared to display high levels of dietary overlap, with individuals feeding on the most abundant crustaceans and cephalopods caught as by-catch in the trawl on each coast. However, although both catsharks consumed similar prey groups across the coast, the abundances of the individual prey species in their diets appeared to differ. Ontogenetic shifts in the diets of both catshark species were also noted, with small catsharks being observed to primarily feed on small prey items, and large catsharks being observed to primarily feed on large prey items. A similar trend was noted for stable isotope data, with $\delta^{15}N$ isotope values increasing with catshark size in both species. Differences in $\delta^{15}N$ isotope values were noted between coasts as well, with both catshark species displaying significantly higher $\delta^{15}N$ values on the West Coast than on the South Coast. The results appear to indicate a strong relationship between habitat and diet, with food separation appearing to be largely a reflection of habitat separation. Based on this, I argue that these morphologically similar catshark species partition their habitat and food resources to limit co-existence, and thus reduce the intensity of intra-and interspecific competition between them. Alternatively, these differences may also be a reflection of differences in environmental tolerance owing the unique environmental and biological factors evident off each coast; or they may simply be due to size-based changes in habitat use that may be associated with parturition or nursery grounds, changes in the habitat of their preferred diet items, or a means to prevent predation by larger sharks.

DECLARATION

I declare that: ***Intra- and interspecific variability in the distribution patterns and diet of the two most common catsharks caught in demersal trawls off the West and South coasts of South Africa: Evidence for habitat and resource partitioning?*** is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Grant Mark van der Heever July 2017

Signed:

Acknowledgements

Firstly, I would like to express my sincere gratitude to my supervisor, Professor Mark John Gibbons, for his continuous support and patience throughout this thesis. He gave me the opportunity to fulfil my childhood dream, and I am forever grateful. I would also like to express my thanks to my co-supervisors, Dr Carl van der Lingen and Dr Rob Leslie, for their insightful comments, knowledge and guidance. Their expertise and passion for marine science most certainly increased my love for marine life. Besides my supervisors, I would like to acknowledge and thank the Department of Agriculture, Forestry and Fisheries (DAFF) demersal team, which includes; Dr Deon Durholtz, Robert Cooper, George Julius, George Kant, Clifford Hart, James Peterson and Joe Mhlongo. Their support and guidance, and enthusiasm and humour made the month long research surveys something to look forward to. Special thanks are also due to the captain, officers and crew of *FV Andromeda*; thanks for your hospitality and safe ventures.

Additionally, I would like to thank Tracey Fairweather (DAFF) for her technical support with GIS, as well as Ian Newton and John Lanham from the light stable isotope unit at the University of Cape Town, for processing my muscle tissue samples. I am also grateful to Dr Lara Atkinson (SAEON) for encouraging me to persevere and write. Special thanks are also due to DAFF and NRF for financial support.

Most of all, I would like to thank my family, Joy, Mark and Tammy for their love and support. They gave me the opportunity to achieve my life-long dream of

becoming a marine biologist, and I will forever be indebted to them. Last but not least, I would like to thank my partner, friend and ad-hoc research assistant, Danielle Laubscher, for her love and patience. Thank you for the encouragement, motivation and for putting up with my constant “does this sentence make sense to you” question. It really meant a lot, and I thank you for that.

Table of Contents

List of Figures

List of Tables

List of Appendices

Chapter One

General Introduction

The Class Chondrichthyes, which contains the Family Scyliorhinidae (catsharks), are distinguished from bony fish (Osteichthyes) by a number of characters, including: internal skeletons made of cartilage instead of bone; a set of true upper and lower jaws; a sensory snout that extends over the mouth; and nostrils that are positioned below the snout. Instead of overlapping scales, they have a thick layer of skin covered with minute dermal denticles (except for some batoid fish), and teeth either visible in longitudinal rows or fused tooth plates (Didier *et al*. 2012, Ebert 2013).

Chondrichthyans can be placed in one of two subclasses, namely: Holocephalii and Elasmobranchii (Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013). The subclass Holocephalii consists of chimaeras and elephant fish, and contains about 50 species worldwide (Walovich *et al*. 2017). They can be identified by a single gill opening on either side of the head, an upper jaw that is attached to the cranium, and teeth in the form of solid dermal plates (Didier *et al*. 2012, Walovich *et al*. 2017). The subclass Elasmobranchii is by far the larger of the two subclasses, comprising of *c.* 1200 extant species worldwide (Didier *et al*. 2012, Ebert and Stehmann 2013, Ebert and van Hees 2015). This subclass includes all fossil shark groups, as well as the Subcohort Neoselachii, which contains all modern sharks and rays (Didier *et al*. 2012, Ebert and Stehmann 2013, Ebert and van Hees 2015). Elasmobranchs can be identified by the presence of five to seven gill openings on either side of the head, an articulated upper jaw and cranium, and separate teeth that are constantly being replaced (Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013).

The Elasmobranchii contain more than 500 shark species, all of which are characterised by cartilaginous skeletons, bodies that are either flat or cylindrical, and up to eight fins: a pair of pectoral fins that are not connected to the head, two pelvic fins, one or two dorsal fins, long caudal fins, and an anal fin that is present in some species and absent in others (Nelson 2006, Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013). They have an average size of about one metre, but sizes can range from 21 cm in smalleye pygmy sharks (*Squaliolus aliae*) and cylindrical lantern sharks (*Etmopterus carteri*) to up to 20 m in whale sharks (*Rhincodon typus*) (Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013).

Sharks reproduce by means of internal fertilisation, with males using paired, external sexual structures, named claspers, located at the posterior base of their pelvic fins to insert sperm directly into the female’s oviduct (Didier *et al*. 2012, Ebert 2013). Over millions of years sharks have developed three distinct reproductive strategies: (1) oviparous or egg-laying, where the female carries the eggs for a few days or weeks, and once the eggs are ready to hatch she lays them [e.g. as in the Izak catshark (*Holohalaelurus regani*) that produces pairs of eggs throughout the year]; (2) placental or yolk sac viviparity, where the female carries the eggs until they hatch inside her, thus giving birth to live young [e.g. as in the Shortspine spiny dogshark (*Squalus mitsukurii*) that produces between 4-9 pups/litter]; and (3) viviparous or live-bearing, where, as the name suggests, the embryo develops in a “placenta” and the females give birth to live young [e.g. as in the bluntnose sixgill shark (*Hexanchus griseus*) that produces between 22-108 pups/litter] (Didier *et al*. 2012, Musick and Ellis 2005, Ebert *et al.* 2006, Ebert 2013). Although sharks exhibit a wide range of life-history characteristics, most shark populations are known to increase at a relatively slow rate (Dulvy *et al*. 2008, Musick and Ellis 2005, Kyne and Simpfendorfer 2007, Ebert 2013, Ebert and Stehmann 2013).

All sharks are carnivorous, and have, over the years, developed a variety of different teeth types suited to their diets (Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013). These include: (1) broad compressed teeth such as the large, triangular teeth of the white shark (*Carcharodon carcharias)* and cockscomb shaped teeth of the tiger shark (*Galeocurdo cuvier*) suited for taking large chunks of meat from prey; (2) long slender teeth, such as in the ragged tooth shark (*Carcharias taurus*), suited for catching slippery squid or swallowing fish whole; (3) blunt molariform teeth, such as in the smooth hound shark (*Mustelus palumbes*), suited for grinding the hard shells of molluscs and crustaceans; and (4) dagger-like upper teeth and saw-like lower teeth such as in the cookiecutter shark (*Isistius brasiliensis*), suited for slicing out circular chunks of meat from large pelagic fish and marine mammals (Didier *et al*. 2012, Ebert 2013 and 2014).

To remain the specialist hunters that they are, sharks not only had to develop different teeth types, but they also had to develop different hunting strategies in order to successfully catch their prey (Didier *et al*. 2012, Ebert 2013). Some sharks are specialist ambush predators that lie camouflaged on the seabed to catch unsuspecting prey (Didier *et al*. 2012, Ebert 2013 and 2014). For example, catsharks have been observed to use their reticulated patterns to blend in among bottom features; a type of camouflage known as disruptive colouration (Ebert 1994, Didier *et al*. 2012). Other species such as thresher sharks (Alopiidae) and sawsharks (Pristiophoridae) use their specialised appendages (long tail in thresher sharks and tooth-studded rostra in sawsharks) to stun schools of fish (Didier *et al*. 2012, Ebert and Stehmann 2013). Some, such as lantern sharks (*Etmopterus sp.*) and white tip reef sharks (*Triaenodon obesus*), are even known to hunt in packs, allowing them to dismember large prey items and catch fast moving prey (Didier *et al*. 2012, Ebert and Stehmann 2013).

Sharks are known to occupy an array of habitats, from shallow, intertidal and coastal waters, to continental and insular shelves and slopes that can range to over 2000 m in depth (Didier *et al*. 2012, Simpfendorfer and Heupel 2012, Ebert 2013 and 2014). They can be pelagic in nature, solely occupying the water column, or display a demersal lifestyle, and live on the seafloor (Ebert 2013). Although a number of sharks have been observed in estuarine and freshwater habitats, only the bull shark (*Carcharhinus leucas*) and rare river shark species (*Glyphis* sp.) are capable of inhabiting these freshwater habitats for extended periods (Ebert 2013, Ebert and Stehmann 2013).

In South Africa, sharks inhabit the entire coast, occurring from the Orange River in the west to the border of Mozambique in the east. This region is home to over 100 shark species, with 16% being endemic to the region (Ebert 2013, Ebert and van Hees 2015). Here, the Family Scyliorhinidae forms a diverse component of the shark assemblage (Richardson *et al*. 2000b), and of the 160 species documented worldwide (Ebert and van Hees 2015), 17 occur in South Africa, with 13 (>75%) being endemic to the region (Ebert *et al*. 2006, Human 2006, Ebert and van Hees 2015).

The Scyliorhinidae is one of the largest shark families, made up of approximately 17 genera with 160 species, occupying the temperate, tropical and Arctic regions of the world's oceans (Ebert 2013, Ebert and van Hees 2015). They occur from subtidal waters to depths of over 2000 m, and are among the deepest living sharks (Escobar-Porras 2009, Ebert 2013, Ebert and Stehmann 2013). Catsharks are rather small (most adults < 1 m long), sluggish sharks that can be recognised by their catlike eyes with nictitating eyelids and two dorsal fins, the first of which originates over or behind the origin of the pelvic fin (Didier *et al*. 2012, Ebert 2013, Ebert and Stehmann 2013). They have several rows of multi-cuspid teeth, and primarily feed on fish, cephalopods and crustaceans, depending on opportunity, locality and season (Ebert *et al*. 1996, Wetherbee and Cortés 2004, Pethybridge *et al*. 2011).

Their predominant mode of reproduction is single oviparity, with most gestation periods lasting up to 12 months (Ebert *et al*. 2006, Ebert and Stehmann 2013). During this time, one fertilised egg enters each oviduct. In single oviparity, embryonic development primarily occurs outside the female with eggs taking up to two years or more to hatch. In areas of intense predation, however, multiple oviparity and viviparity may also be common; with shark hatchlings being produced after only one month in the former (Ebert *et al.* 2006, Ebert 2013, Ebert and Stehmann 2013). Unlike most viviparous sharks, catshark males usually mature at sizes greater than or equal to that of the females (Ebert *et al.* 2006). Similar to most sharks, catshark populations increase at a relatively slow rate, thus making them particularly vulnerable to over-exploitation (Frisk *et al.* 2005, Kyne and Simpfendorfer 2007, Dulvy *et al.* 2008, Ebert 2013).

Since the onset of commercial fishing there has been a world-wide decline in shark numbers, with millions of sharks being removed from the ocean every year (Clarke *et al*. 2006 and 2012, Dulvy *et al*. 2008). A study by Clarke *et al*. (2006), investigating the global estimates of shark catches using trade records from commercial markets, estimated that the fins of between 26 and 73 million sharks end up in the fin trade annually, with the authors projecting a global average of 38 million. A more recent study by Dulvy *et al*. (2008) estimated the global threat status of 21 pelagic shark and ray species based on the IUCN-Red List Criteria, and classified 16 of these species as Threatened or Near Threatened, with 11 being globally threatened and at risk of extinction.

Catsharks in particular are taken in large numbers as by-catch, especially in South Africa, where they form a big component of the by-catch of sports fishers and commercial trawlers (Ebert 2013, Ebert and Stehmann 2013). Although the majority of catsharks are not commercially important, some are readily used for fishmeal and oil, while others, such as the spotted catsharks (*Scyliorhinus*), are also used for human consumption (Didier *et al*. 2012, Ebert *et al*. 2006, Ebert 2013, Ebert and Stehmann 2013).

Despite the growing concern that South African catshark species are being caught at an unsustainable rate, there is still a lack of catch and trend data for a number of species (Compagno *et al*. 2004, Human 2006). This is the case for the *Holohalaelurus regani* (Izak catshark) (Gilchrist 1922) and *Scyliorhinus capensis* (yellow-spotted catshark) (Müller and Henle 1838), perhaps the most common catsharks caught as by-catch by the demersal trawling industry targeting the two Cape hake species (*Merluccius capensis* and *M. paradoxus*) on the West and South coasts of South Africa (Richardson *et al.* 2000b, Petersen *et al*. 2008). In spite of commonly occurring in trawls, species specific studies on their general biology still seem to be lacking, with only a few known studies being conducted on them thus far (Ebert *et al.* 1996, Richardson *et al*. 2000b, Ebert *et al*. 2006, Human 2006).

Holohalaelurus regani is endemic to southern Africa and a near endemic of South Africa, and occurs from Lüderitz in Namibia to central Kwazulu-Natal (Richardson *et al*. 2000b, Human 2006). This species occupies both the continental shelf and upper slope between depths of approximately 40-1075 m, but are most common between depths of around 150-300 m (Human 2006). They are the largest species of the genus *Holohalaelurus*, and can be recognised by their broad head, long mouth, rounded snout and yellow body covered in a “horse-shoe” shaped pattern of black lines (Human 2006, Ebert 2013). Notably, this “horse-shoe” shaped pattern only develops in *H. regani* at a much larger size; with the dorsal patterning in juvenile *H. regani* being large, irregularly shaped, solid brown spots (Human 2006).

Holohalaelurus regani has a diet that consists primarily of (listed in decreasing importance) teleosts, crustaceans and cephalopods (Ebert *et al*. 1996, Richardson *et al*. 2000b, Human 2006, Ebert 2013 and 2015). They can grow up to 63 cm TL, with females maturing at 42-50 cm TL and males maturing at 60-63 cm TL (Human 2006). Oviparity is their only mode of reproduction, laying pairs of eggs year round. Seasonal and size-based aggregations are common within this species, with most of the population migrating inshore in autumn and juveniles occurring in shallower water than the adults (Human 2006, Ebert 2013). Although *H. regani* forms a frequent by-catch of bottom trawlers they have no commercial use as yet (Richardson *et al*. 2000b).

Scyliorhinus capensis is also endemic to southern Africa and can be found from Lüderitz in Namibia to central Kwazulu-Natal between depths of approximately 26-530 m (Didier *et al*. 2012, Ebert 2013). They can be identified by the distinctive yellow spots on their grey bodies and a second dorsal fin that is much smaller than the first (Didier *et al*. 2012, Ebert 2013). Similar to *H. regani*, they are thought to be generalist feeders, mainly feeding on (in order of importance) teleosts, crustaceans, cephalopods and polychaetes (Ebert 2013). *Scyliorhinus capensis* can grow up to a length of 1.2 m TL, with females maturing at 72-83 cm TL and males at 75-80 cm TL (Ebert 2013). They are oviparous, producing pairs of eggs year round (Didier *et al*. 2012, Ebert 2013). The IUCN Red List of Threatened Species regards *S. capensis* as near threatened (Compagno *et al*. 2004) due to their frequency of capture by ski-boat anglers and trawlers that target the hake (*M. capensis* and *M. paradoxus*) fishing grounds (Didier *et al*. 2012, Ebert 2013).

A thorough understanding of the biology and life-history patterns of sharks is required for the effective conservation of sharks and their environment (Estrada *et al*. 2003, Hussey *et al*. 2012). However, the implementation of such strategies has long been hindered by a lack of research addressing these gaps (Shiffman *et al.* 2012). Consequently, Simpfendorfer *et al.* (2011) recognized 26 'research needs' necessary for the effective conservation of elasmobranchs, one of them being diet and trophic structure, specifically ontogenetic change in diet and the most suitable method to examine diet and trophic linkage.

In the past, investigations into size, sex, habitat and seasonally related shifts in the feeding habits of sharks have mainly employed the use of stomach content analyses (Cortés 1997, Wetherbee and Cortés 2004, Matich *et al*. 2010). For example, Lucifora *et al*. (2009) used stomach content analysis to examine ontogenetic diet shifts in copper sharks (*Carcharhinus brachyurus*), and White *et al*. (2004) used the same method to determine the effect of resource partitioning and competitive exclusion on the distribution and diet of four carcharhinid shark species. Similar dietary studies on small meso-predatory catshark species have been conducted by Lyle (1983) and Olaso *et al*. (2005), with the former examining the diet of the lesser-spotted catshark (*Scyliorhinus canicula*) in the Irish Sea and the latter examining trophic ecology of the lesser-spotted catshark (*Scyliorhinus canicula*) and black mouth catshark (*Galeus melastomus*) in the Cantabrian Sea. Studies on the diets of catsharks off the coasts of South Africa include a study by Ebert *et al*. (1996) who used stomach content analysis to investigate the diets of six co-occurring catshark species (*Apristurus microps*, *A. saldanha*, *A.* spp., *Galeus polli*, *Scyliorhinus capensis* and *Holohalaelurus regani*) along the West Coast, and another by Richardson *et al*. (2000b) who used the same method to determine the feeding habits of *H. regani* off the West and South coasts of South Africa.

Although the diets and feeding behaviours of many shark species have been determined using stomach content analysis (Stillwell and Kohler 1982, Richardson *et al*. 2000b, White *et al* 2004, Lucifora *et al.* 2009), it still remains a time-consuming process that requires the removal of the sharks stomach and the identification of individual prey items to the lowest taxon (Vander Zanden *et al*. 1997, Richardson *et al*. 2000b, Pinnegar *et al*. 2001, Renones *et al*. 2002). Moreover, owing to the effects of digestion, this method only provides data on recently consumed prey items, and is further hampered by the occurrence of unidentifiable prey items following digestion (Vander Zanden *et al*. 1997, Richardson *et al*. 2000b, Pinnegar *et al*. 2001, Renones *et al*. 2002). There is also a tendency to over-estimate the importance of prey items that take longer to digest and under-estimate prey items that are rapidly digested. Furthermore obtaining large enough sample sizes from which significant conclusions can be drawn is often difficult, and requires a large number of sharks to be sacrificed (Vander Zanden *et al*. 1997, Pinnegar *et al*. 2001, Renones *et al*. 2002, MacNeil *et al*. 2005, Matich *et al*. 2010).

In recent times, however, stable isotope analysis (SIA), has grown as an alternative or complementary method that can be used by ecologist to obtain information on the diet and trophic interactions of animals (Fisk *et al.* 2002, MacNeil *et al.* 2005, Martinez del Rio *et al*. 2009, Matich *et al.* 2010). Unlike stomach content analysis, SIA gives information on the consumer and its assimilated prey, and is able to provide researchers with information on the origin of the consumer and its prey (i.e. whether it is benthic, pelagic, marine or freshwater), as well as the importance of the consumer and its prey in the food web (DeNiro and Epstein 1978, Thomas and Cahoon 1993, Hussey *et al.* 2012). Consequently, stable isotope analysis allows ecologists to answer more intricate questions in marine ecosystems, including identifying specialist and generalist-feeding behaviours, seasonal and ontogenetic dietary shifts, spatial variability in feeding habits and intra- and interspecific partitioning of resources (Matich *et al.* 2010, Hussey *et al*. 2012, van der Lingen and Miller 2014).

Stable isotope analysis is based on the premise that the stable isotope ratios present in the tissue of the prey item are also reflected in the tissue of the consumer (Post 2002, Bearhop *et al.* 2004, Martínez del Rio *et al.* 2009, Matich *et al.* 2010, Hussey *et al.* 2012). Using the stable isotope ratios of carbon (^{13}C:^{12}C) and nitrogen

(^{15}N:^{14}N), ecologists can obtain information on the movement and migration patterns of marine organisms as well as information on their trophic position and overall food web structure. Owing to metabolic processes (fractionation), consumers are known to preferentially assimilate the heavier isotopes ($\delta^{13}C$ and $\delta^{15}N$) and expel the lighter isotopes ($\delta^{12}C$ and $\delta^{14}N$), resulting in a known stepwise enrichment from prey to consumer (Peterson and Fry 1987). This stepwise enrichment is low in $\delta^{13}C$, averaging at 0.4‰ (1 SD = 1.3‰) per trophic level, but high in $\delta^{15}N$, averaging at 3.4‰ (1 SD = 1‰) per trophic level (Minagawa and Wada 1984, Post 2002). Due to the fact that $\delta^{13}C$ remains relatively constant as it moves from prey to consumer, but varies between primary producers (C_3 vs C_4 plants, pelagic plankton vs seagrasses), it can be used to provide insight into source production at the base of the food-web (DeNiro and Epstein 1978, Peterson and Fry 1987, Shiffman *et al*. 2012). Whereas the relatively large increase of $\delta^{15}N$ from prey to consumer allows for a comparative estimation of an organism's trophic position within a food-web, and relative to that of others (DeNiro and Epstein 1978, Peterson and Fry 1987, Shiffman *et al*. 2012).

In recent times, numerous studies have successfully utilised SIA to identify the diets and trophic pathways of marine taxa (MacAvoy *et al.* 2001, Jardine *et al.* 2005, Haramis *et al.* 2007, Matich *et al.* 2010). For example, Graham *et al.* (2010) used SIA to assess ontogenetic dietary shifts and trophic positions of the yellowfin tuna (*Thunnus albacares*), and Estrada *et al.* (2005) used a similar method to uncover ontogenetic dietary shifts and trophic positions of the Atlantic Bluefin tuna (*Thunnus thynnus*). In South Africa, Parkins (1993) used stable nitrogen and carbon isotope ratios to explain the variability in the trophic ecology of the commercially important shallow water Cape hake, *Merluccius capensis*. More recently, van der

Lingen and Miller (2014) also used SIA to assess intra-and interspecific variability in the trophic ecology of the two co-occurring Cape hake species (*M. capensis* and *M. paradoxus*).

To date, SIA has been used to estimate size, sex, habitat and seasonally related shifts in the feeding habits of several large, commercially important shark species (Estrada *et al*. 2003, MacNeil *et al*. 2005, Hussey *et al*. 2012). Owing to its slow incorporation rate, white muscle tissue is perhaps the most frequently sampled tissue used to examine interspecies variation in the feeding habits, trophic positions and habitat use patterns of sharks (Estrada *et al*. 2003, MacNeil *et al*. 2005, Hussey *et al*. 2012). For example, MacNeil *et al*. (2005) undertook a SIA study using white muscle tissue sampled from blue sharks (*Prionace glauca*), shortfin mako sharks (*Isurus oxyrinchus*) and thresher sharks (*Alopias vulpinus*) to determine whether their diets changed over time. The results from this study showed a dietary shift from cephalopods to *Pomatomus saltatrix* (known as “bluefish” in the USA, “elf” in Cape Town and “shad” in Kwazulu-Natal) in the shortfin mako in spring, whereas blue sharks and thresher sharks were found to display a rather constant diet throughout the year. Similarly, Matich *et al.* (2010) used muscle tissue to determine the feeding behaviours of tiger sharks (*Galeocerdo cuvier*) and bull sharks (*Carcharhinus leucas*) inhabiting two distinct ecosystems. The results from that study showed variation in the isotope ratios of tiger sharks, thus indicating generalist feeding behaviours, whereas the rather constant isotope ratios of bull sharks through time is suggestive of specialist feeding behaviour within this species of shark.

More recently, there seems to be an increase in the number of studies utilising stomach content analysis and SIA to examine size, sex, habitat and seasonal shifts in the diets and trophic ecologies of the more charismatic and commercially important shark species (e.g. Laminids and Carcharhinids) (Estrada *et al.* 2003, MacNeil *et al.* 2005, Hussey *et al.* 2012). However, similar studies on sharks with no commercial or aesthetic value (e.g. Scyliorhinidae) are almost non-existent. This is particularly true in South Africa, where research on the two most common demersal catsharks, namely *H. regani* and *S. capensis*, caught as by-catch by the demersal trawling industry operating on the West and South coasts of South Africa is limited to only two known dietary studies (Ebert *et al*. 1996, Richardson *et al*. 2000b), both of which focused on stomach content analyses. There seems to be an even greater paucity in studies evaluating the habitat use patterns of these co-occurring shark species, with currently no research having been conducted on possible habitat competition between these abundant catsharks. Moreover, to my knowledge, studies using SIA to understand the trophic ecology of South African catshark species have yet to be conducted.

This study is a first attempt at understanding the habitat use patterns, diet and trophic ecology of *H. regani* and *S. capensis* by investigating intra-and interspecific variability in their habitat use and trophic ecology, and how these variables change with location, depth, size and sex. I begin in Chapter 3, where I investigate intra-and interspecific variability in the habitat use patterns of these catshark species, with a specific focus on changes in habitat use with depth, size and sex, and an interspecific comparison of habitat use around the coasts of South Africa. In Chapter 4 I focus on their feeding ecology, using stomach content data to evaluate changes in the prey items consumed by species, coast, depth, and size. Similarly in Chapter 5, I use stable isotope analysis to describe changes in their trophic ecology by species, coast, depth and size. This information will be compared with the results described in the previous Chapters, and will form the first record of the stable isotope signatures of these catsharks around South Africa.

Chapter Two

Methods

General Methods

Study location

Samples were collected using a demersal trawl net deployed during routine hake biomass surveys conducted by the Department of Agriculture, Forestry and Fisheries (DAFF) on the West and South coasts of South Africa. West Coast surveys were conducted between the international border with Namibia (*c.* 29° 30’ S) and Cape Agulhas (20° E), and South Coast surveys were conducted between Cape Agulhas (20° E) and Port Alfred (27° E) (Figure 1). For the purpose of this study, Cape Agulhas (20° E) formed the border between the two coasts (Figure 1). This border was established due to the different coastal, oceanographic and environmental conditions present on the West and South coasts of South Africa (Hutchings *et al*. 2009, van der Lingen and Miller 2014).

Survey design

West Coast surveys were conducted annually during summer (January and February), whereas South Coast surveys were conducted bi-annually during autumn (March, April, May and June) and spring (September and October). Notably, no West Coast surveys were conducted in 1998 and 2012. South Coast autumn surveys were not conducted in 1998, 2002, 2012 and 2013, and South Coast spring surveys were not conducted from 1996 to 2002, 2005 and from 2009-2015 (Appendix 1). All surveys occurred from the coast to the 500 m isobath, except for some spring surveys, that only extended to the 200 m isobath. From 2003 onwards spring surveys extended out to the 500 m isobath, and all surveys were extended out to the 1000 m isobaths from 2011 onwards.

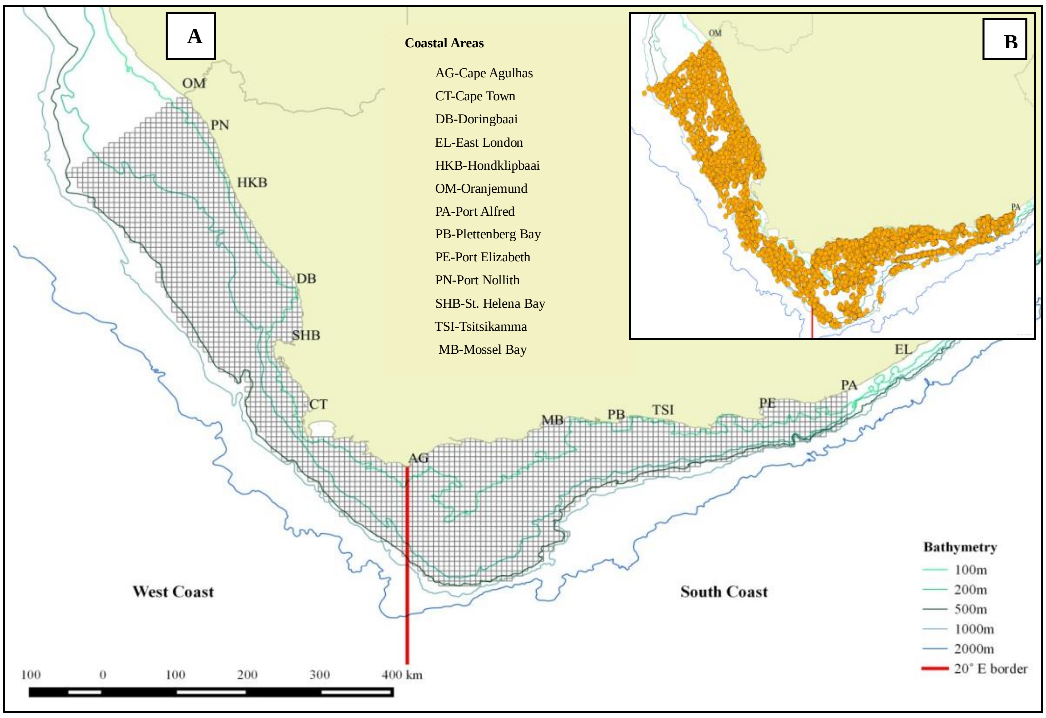


Figure 1: Map of South Africa, illustrating the demersal survey grid (grids indicate selected areas for trawling) (**A**) and locations of all stations trawled from 1994-2015 (**B**). Red line indicates 20˚ E meridian, the border between the West and South coasts.

Trawls were conducted during daylight hours, using a pseudo-random, depth-stratified sampling design, with the number of stations per depth and latitude (West Coast) or longitude (South Coast) stratum being directly proportional to the area of each stratum (Payne *et al*. 1985). Until 2003, the trawl gear consisted of a 2-panel 180-foot German trawl net with a rope-wrapped chain footrope and 50 m sweeps, 32 mm diameter trawl warp and a 1.5 t WV otter boards (old gear). This was subsequently changed to a 4-panel 180-foot German trawl net with a modified rockhopper footrope and 9 m sweeps, 28 mm diameter trawl warps and 1.5 t multipurpose Mogere otter boards (new gear). The higher net opening of the new gear allows for more pelagic catches and the shorter sweeps reduces the effect of herding (R. Leslie, DAFF, pers comm.). To aid the calibration of the gears and to provide overlap between the time series with the two gear types, the old gear was used again in 2006 and 2010 (Leslie and Glazer 2011).

Analyses

Based on catshark length at birth and maturity (Richardson *et al*. 2000b, Compagno *et al*. 2005, Human 2006, Ebert 2013), three respective size classes were defined. For *H. regani*, individuals ranging from 15-30 cm in size were regarded as juvenile; 31-45 cm as maturing; and 46-80 cm as mature. For *S. capensis*, individuals ranging from 15-30 cm in size were regarded as juvenile; 31-70 cm as maturing; and 71-100 cm as mature. Here, the terms small, medium and large are used as alternatives for juvenile, maturing and mature, respectively. Depth-of-capture data were grouped into six 100 m depth strata: 0-100 m; 101-200 m; 201-300 m; 301-400 m; 401-500 m and 501-600 m. Throughout this thesis the depth strata are referenced by the mid-point of the depth bin, e.g. the 101-200 m depth stratum is referred to as the 150 m depth stratum.

Distribution Chapter Methods

Study location and data collection

Samples were collected using a demersal trawl net deployed during routine hake biomass surveys conducted by DAFF on the West and South coasts of South Africa from 1994-2015 using the methods described by Payne *et al*. (1985) (see General Methods).

Data analysis

From 1994-2015, a total of 6 948 research stations were trawled along the West and South coasts of South Africa. Totals of 4 279 and 2 669 trawls were completed on the West and South coasts respectively (Figure 1B). At each station, the total length, sex and total weight were obtained from all *H. regani* and *S. capensis* individuals caught. Distribution maps were generated using Quantum GIS Valmiera 2.2.0, and contour maps based on observed densities were plotted in Surfer 9.0 (Golden Software Inc., U.S.A).

To analyse intra- and interspecific patterns of habitat use by depth, depth-frequency histograms were plotted for each coast, by species, size and sex. Patterns in the size distribution, by depth stratum, both within and between taxa, were then tested using X^2 contingency tables, separately for the West and South coasts (Zar 2010). To test for differences in the observed densities of *H. regani* and *S. capensis* between coasts a Mann-Whitney *U*-test was used, while differences in the observed densities of *H. regani* and *S. capensis* between depths, separately for the West and South coasts, were tested for using a Kruskal-Wallis *H*- test. Data were analysed separately for males and females as well as collectively for male, female and unsexed catsharks.

All data are based on observed and average densities (average density: number of sharks caught per trawl/total number of trawls x 100), and expressed as mean densities per square nautical mile (nm^{-2}). This was calculated by dividing the number of individuals caught at each station by the area swept at that station; the area swept was calculated as the product of the width (mouth opening of the net) and length of the trawl track (Richardson *et al*. 2000b). The width of the trawl track, taken as the distance between the wing tips (wingspread) was measured by transducers placed at the wing tips or estimated from the distance between the trawl doors (doorspread) using a relationship developed from stations where both doorspread and wingspread data were available (DAFF, unpublished data). For historic data, the length of the trawl track was estimated as the product of the towing speed and the trawl duration, but with the advent of accurate GPS navigation, it was calculated from start and end positions of the trawl track.

Diet Chapter Methods

Study location

Samples were collected using a demersal trawl net deployed during routine hake biomass surveys conducted by DAFF on the West and South coasts of South Africa from 2014-2015 using the methods described by Payne *et al*. (1985) (see General Methods). West and South coasts surveys were conducted during late summer (January and February) and autumn (March and April) respectively, and spanned the width of the shelf to the 1000 m isobath.

Sample collection

Once the net was on board the vessel, all *H. regani* and *S. capensis* were collected, individually weighed (g) and measured to the nearest 0.5 cm, TL. A median ventral incision was then made through the abdominal wall of each individual, excising the stomach by separating it from the oesophagus and the duodenum. Stomachs were weighed (to the nearest 0.1 g), transferred to containers and frozen until return to the laboratory.

Prey identification

In the laboratory, stomachs were allowed to thaw and were subsequently examined for food remains. Recovered material was fixed in 10% formalin for 48 hours. Prey items were then soaked in water, and later preserved in 70% ethanol for processing. All prey items were identified (where possible) and counted, and then blotted dry and weighed to the nearest 0.01 g. Intact prey items were measured (TL, 0.1 mm) using a ruler. When the size at ingestion could not be directly measured (prey items that were broken or well digested), identifiable anatomical parts such as cephalopod beaks, crustacean chelipeds or eye stalks or teleost otoliths were measured using a graticule at 16x magnification, and length-weight regression equations were used to estimate original prey size (Richardson *et al*. 2000a, Froese and Pauly 2016). Prey items were identified to the lowest possible taxonomic level using taxonomic keys (e.g. Smith and Heemstra 1986), unpublished field guides and information from specialists. Five major prey groups were established: Cephalopoda, Crustacea, Teleostei, unidentified and other; the last comprising of algae, Chondrichthyes, Gastropoda, Polychaeta, Porifera and Urochordata. This group was set up to avoid misinterpretation, as including many groups of uncommon prey items could skew the results.

Analysis of diet

Maps representing the location and number of stomachs sampled from *H. regani* and *S. capensis* for dietary analysis were plotted in Surfer 9.0 (Golden Software Inc., U.S.A). Intra- and interspecific differences in diet were assessed by coast, depth stratum and size class. Notably, small sample sizes in some depth strata and size classes may not be sufficient to completely describe diets.

Dietary composition was estimated based on the percent number (%N), percent weight (%W) and percent frequency of occurrence (%FO) of prey items (Hyslop 1980). These three measures were then used to calculate the Index of Relative Importance (IRI) (Hyslop 1980).

Percent by number

Percent by number (%N) was calculated by dividing the total number of prey items from a prey group by the total number of all prey items from all prey groups, multiplied by 100 (Hyslop 1980). The advantage of the numerical method is that it is simple, provided all prey items can be identified (Hyslop 1980). The disadvantage of this method is that the importance of small prey items can be overestimated if they are present in large numbers (Hyslop 1980, Bizzaro *et al*. 2007). Hyslop (1980) suggested that this method should not be used in isolation to determine dietary composition.

Percent by weight

Percent by weight (%W) was calculated by dividing the total weight of all prey items from a prey group by the total weight of all prey items from all prey groups, multiplied by 100 (Bizzaro *et al*. 2007, Dale *et al*. 2011). Factors to consider when using percent by weight are the digestion rate of prey items, the order of ingestion, water that may be trapped inside prey items, and anatomical remains that cannot be used to establish the ingested weight of prey. This method also overemphasizes rare, heavy prey items and discounts the importance of abundant, small prey items that are rapidly digested. These underlying factors can cause large errors in the estimate (Hyslop 1980, Bizzarro *et al*. 2007, Baker *et al*. 2014).

Percent frequency of occurrence

Percent frequency of occurrence (%FO) was calculated by dividing the total number of stomachs that contained a prey item from a specific prey group by the total number of stomachs that contained prey, multiplied by 100 (Hyslop 1980, Bizzarro *et al*. 2007, Dale *et al*. 2011). The frequency of occurrence method is dependent on the positive identification of any prey item or its remains (Hyslop 1980). All prey items are recorded as present from the time of ingestion until the last identifiable remains of the prey item is gone. When compared to the other two measures of prey quantity (i.e. %N and %W), the frequency of occurrence method provides the most robust measure of dietary composition, with the most interpretable data (Baker *et al*. 2014). This method does however tend to overemphasise the importance of prey groups that contain species with hard parts that are slow to digest.

Index of relative importance

The importance of each prey group in the diet of the two catshark species was further estimated using the Index of Relative Importance (IRI), which was calculated as: IRI = (%N + %W)*%FO (Cortés 1997, Bizzarro *et al*. 2007, Dale *et al*. 2011). The IRI values were converted to a percentage (IRI%) to allow comparisons between prey taxon (Cortés 1997, Dale *et al*. 2011):

$$\left(\frac{IRI_i}{\sum IRI}\right) \times 100$$

The IRI% incorporates all three measures of prey quantity into a single metric, and allows for easy comparisons of fish diets between published work (Cortés 1997, Cortés 1998, Baker *et al*. 2014). However, differences in taxonomic resolution and the unquantifiable errors associated with each individual measure of prey quantity makes comparisons between studies impossible at times (Hannsson 1998, Baker *et al*. 2014).

Statistical analyses

To analyse intra- and interspecific patterns in diet, histograms based on IRI% and tables based on %FO, %N, %W and IRI% were constructed for each species, by coast, depth stratum and size class. Prey items were considered noteworthy if they were recorded in more than 10% of the stomachs analysed (%FO > 10%) or if IRI%

was > 10%. I have focussed on %FO and IRI% because the former provides robust, reliable data and the latter is a standardised method that is easily compared with other studies (Baker *et al*. 2014). To analyse whether prey weight increased with predator size, histograms displaying average prey weight by predator size class was plotted for each species by coast. To test for intraspecific differences in catshark size between coasts independent samples *t*-tests were performed.

In the present study most individual sharks only had a small number of prey items in their stomachs, with several prey groups not represented. Throughout this thesis, data for each species was firstly pooled by coast, and then by depth stratum and size class, separately for each coast. This was done to overcome the analytical problems associated with analysing the diet of individual shark species with only a limited number of prey taxa in their stomach (Linke *et al*. 2001, Platell and Potter 2001).

Using X^2 contingency tables, intraspecific differences in diet were tested for by coast, and then by depth stratum and size class (Zar 2010). Interspecific differences in diet were then collectively tested for by coast, depth stratum and size class using multivariate analyses that were performed using the statistical package Primer V6 (Clarke and Gorley 2001). All data were square root transformed, to achieve normality, and the Bray-Curtis coefficient was used to calculate similarity matrices (Clarke and Gorley 2001). Using a two-way ANOSIM (analysis of similarity), based on two factors (factor 1: size class and factor 2: depth stratum), differences in dietary composition were then tested for on the West and South coasts respectively. ANOSIM creates a pair-wise similarity matrix between all data points to generate a Global R statistic ($0 > R < 1$) and a p value (Clarke and Gorley 2001).

R values close to unity indicate differences in dietary composition between factors, whereas values close to zero demonstrate similarity. Factors were considered significantly different from each other when $p < 0.05$ and R was close to one. Non-metric multidimensional scaling analysis (NMDS) and hierarchical cluster analysis were used to graphically demonstrate any differences.

All significance testing were based on FO data only, and factors with sample sizes of less than five were removed from the analyses.

Stable Isotope Chapter Methods

Study location

Samples were collected using a demersal trawl net deployed during routine hake biomass surveys conducted by DAFF on the West and South coasts of South Africa from 2014 to 2015, using the methods described by Payne *et al*. (1985) (see General Methods). West and South coast surveys were conducted during late summer (January and February) and autumn (March and April) respectively, and spanned the width of the continental shelf to the 1000 m isobath.

Data collection

Once the net was on board the vessel, all *H. regani* and *S. capensis* were collected and individually weighed (g) and measured (cm, TL). From each shark, approximately 2 grams of white dorsal muscle tissue was excised from below the anterior end of the first dorsal fin and above the fifth gill slit. Tissue samples were placed in appropriately labelled vials, and frozen at -20˚C until return to the laboratory.

Laboratory analysis

In the laboratory, muscle tissue samples were partially thawed, before removing the epidermal layer of skin and rinsing with distilled water to expose a clean piece of white muscle tissue. Tissue samples were re-frozen for 24 hours, freeze-dried for 48-72 hours and then homogenised using a mortar and pestle. Homogenised samples were transferred to labelled vials and sent to the Stable Light Isotope Unit based at the University of Cape Town, South Africa, for processing. Here, aliquots of approximately 0.5 mg were weighed into tin cups on a Sartorius M2P micro balance. The cups were then squashed to enclose the sample. Samples were combusted in a Flash 2000 organic elemental analyser (Thermo Scientific, Bremen, Germany) coupled to a Delta V $^{\text{Plus}}$ isotope ratio mass spectrometer (IRMS) (Thermo Scientific, Bremen, Germany), via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). Nitrogen and carbon data are expressed in delta (δ) notation using the equation:

$$\delta X\ ‰ = [(R_{sample}/R_{standard}) - 1] \times 1\,000,$$

where δX denotes the standardised isotope signature ($\delta^{13}C$ and $\delta^{15}N$) in parts per thousand (‰) and R represents the ratio of the light to heavy isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$) in the sample and standard respectively. Recognised in-house standards were used for comparison with sample units, with carbon being expressed relative to Vienna Pee-Dee Belemnite (PDB) and nitrogen being expressed relative to atmospheric nitrogen. Based on replicates of Choc (commercial chocolate/egg mixture), Seal (crushed seal bone) and Valine, analytical errors (S.D.) were calculated to be 0.12‰ for carbon and 0.07‰ for nitrogen. Analytical errors were obtained by averaging the largest standard error values across all runs for carbon and nitrogen respectively (Ian Newton, Light Stable Isotope Unit, pers comm.).

In SIA analyses it is standard procedure to apply a lipid normalisation equation to samples that have a C:N ratio > 3.5. High C:N ratios are usually indicative of high lipid content, and the correction is applied because lipids are depleted in $\delta^{13}C$ relative to other biochemical compounds (McConnaughey and McRoy 1979). In the present study however, normalisation was not necessary because the C:N ratio was below 3.5 for all samples analysed.

Analysis of stable isotope data

Maps representing the location and number of *H. regani* and *S. capensis* sampled for stable isotope analysis were plotted in Surfer 9.0 (Golden Software Inc., U.S.A). Following Chapter 3, *H. regani* and *S. capensis* individuals were classed by coast, depth stratum and size class.

Statistical analyses

Intraspecific differences in catshark size between coasts were tested for using a one way ANOVA. To analyse the range of $\delta^{15}N$ and $\delta^{13}C$ isotope values, raw isotopic data were used to construct bi-plots of $\delta^{13}C$ against $\delta^{15}N$ and mean isotopic data were used to construct boxplots and histograms for each species, by coast, depth stratum and size class.

General Linear Model (GLM) analysis was used to assess intra-and interspecific differences in isotope data, with $\delta^{15}N$ or $\delta^{13}C$ set as the dependent variable, species, coast, depth stratum and size class as the independent categorical variables, and size (TL) as a covariate. Size class was added as an independent variable to allow for multiple comparisons (i.e. interaction terms and *post-hoc*-Tukey test) between categories. Interaction terms were used to test for intraspecific differences in isotope data between coast*depth stratum and coast*size class, and interspecific differences between species*coast, species*depth stratum and species*size class. Non-significant interactions were excluded from the analyses, and where significant differences were noted, a *post-hoc* Tukey test was used to perform multiple comparisons. Statistical tests were not conducted on categories with samples sizes of < 2.

In total, six GLMs were conducted, respectively analysing carbon and nitrogen for each species, by coast, size and depth. Both intra-and interspecific tests were performed, as it is possible that intraspecific patterns could be masked when analysing data on an interspecific level alone.

Using linear regression analysis, δ^{15}N and δ^{13}C were plotted against size (TL) to assess the relationship between catshark size and isotope ratios. Correlation coefficients were used to determine the strength of the relationship and p-values used to determine significance.

All statistical tests were conducted using the statistical package IBM SPSS Statistics 21, and normality was assessed using a Kolmogorov-Smirnov-Lilliefors test. Results were considered significant at an alpha level of 0.05.

Chapter Three

Spatial and ontogenetic variability in the distribution patterns of two co-occurring catsharks (Scyliorhinidae) caught around the coasts of South Africa: Evidence for habitat partitioning?

Abstract

Holohalaelurus regani and *S. capensis* are similar sized catsharks, occupying rather similar geographic and bathymetric distributions. Despite this, no studies currently exist on their habitat use patterns. Through analysing data collected on research surveys on the West and South coasts of South Africa from 1994-2015, this study provides a first attempt at understanding the habitat use patterns of these co-occurring catsharks. The results indicate an inverse relationship in their distribution, with an increase in the abundance of *H. regani* and a decrease in the abundance of *S. capensis* when moving from the South Coast to the West Coast. Both species also displayed size-based segregations by depth, with catshark size increasing with depth for *H. regani* on the West Coast and for *S. capensis* on the West and South coasts. Segregation by sex was noted for *H. regani* only, with males inhabiting significantly deeper depths than females on both coasts. This study supports the findings of previous studies that have found sharks with similar morphologies and lifestyles to partition their habitat on an intra- and interspecific level to reduce the intensity of competition between them. The intra- and interspecific size and sex-based segregations noted in the two catshark species in the present study was assumed to be suggestive of either: morphological changes associated with ontogeny, size-based changes in habitat use that may be associated with parturition or nursery grounds,

changes in the habitat of their preferred diet items, or a means to prevent predation by larger sharks.

Introduction

In order to successfully conserve and manage sharks and the environments they form part of, a good understanding of their habitat use patterns is required (Heithaus *et al*. 2002, Petersen *et al*. 2008, Simpfendorfer *et al*. 2011, Bizzarro *et al*. 2014). This is particularly true for mesopredators such as small bodied sharks since meso-predatory sharks are both predator and prey in the food-web and play an important role in linking upper and lower trophic levels (Ritchie and Johnson 2009, Ferretti *et al*. 2010, Vaudo and Heithaus 2011, Yick *et al*. 2011). Despite this, most shark habitat-use studies have been focussed on top predators such as large sharks (Heithaus *et al.* 2010, Matich *et al*. 2010, Yick *et al*. 2011, Caut *et al*. 2013), and the few studies that have investigated habitat use by small bodied sharks have mainly focussed on activities such as mating, pupping, and foraging (Simpfendorfer and Heupel 2004, Heithaus *et al*. 2010, Flammang *et al*. 2011, Yick *et al*. 2011).

Understanding competition and predation among shark species is critical to understanding their habitat use patterns (Demirhan *et al*. 2007, Marshall *et al.* 2008, Flammang *et al*. 2011, Guttridge *et al*. 2012). This is because sharks, like other elasmobranchs, partition their habitat by size, sex or species to reduce the intensity of intra- and interspecific competition and predation (Springer 1967, Platell *et al*. 1998, Kinney and Simpfendorfer 2009, Speed *et al*. 2010). Thus when different shark species co-exist there may be partitioning of the physical environment, with sharks segregating by depth (Olaso *et al*. 2005) or habitat (White *et al*. 2004); or the partitioning of resources, with sharks consuming resources at different times or in differing proportions (Ebert *et al*. 1992, Laptikhovsky *et al*. 2001, Lucifora *et al.* 2009). Partitioning of the environment also occurs on an intra-specific level, with sharks segregating according to size, sex or life-history stage (Richardson *et al*. 2000b, Olaso *et al*. 2005, Papastamatiou *et al*. 2006).

Numerous studies have examined and reported on the influence that competition and predation has on shark distributions (Heithaus *et al*. 2002, Lowe *et* al. 2006, Papastamatiou *et al*. 2006, Heithaus 2007, Meyer *et al*. 2009). However, as with most studies on sharks, they are mainly focussed on upper trophic level species such as blacktip sharks (*Carcharhinus melanopterus)*, bull sharks (*C. leucas*), lemon sharks (*Negaprion brevirostris*) and tiger sharks (*Galeocerdo cuvier*) (Heithaus 2007, Kinney *et al*. 2011, Guttridge *et al*. 2012, Hammerschlag *et al*. 2012, Matich 2014), with only a few being focussed on small, meso-predatory shark species (Olaso *et al*. 2005, Ebert and Ebert 2005, Escobar-Porras 2009). For example, a study investigating resource partitioning and competitive exclusion among the most common carcharhinid shark species in the Hawaiian Islands found that shark species with the lowest dietary overlap co-occurred whereas those with the highest dietary overlap did not co-occur (Papastamatiou *et al*. 2006). A more recent study investigating intraspecific predation by adult lemon sharks on juveniles in the Bimini Islands, Bahamas, found that juveniles occurred in shallower waters than adults to avoid predation (Guttridge *et al.* 2012). A similar study by Escobar-Porras (2009), investigating movement patterns of four inshore catshark species in South Africa, showed that when pyjama sharks (*Poroderma africanum*) are very abundant they may limit the abundance of smaller catshark species. Pyjama sharks are known to feed on smaller sharks and elasmobranch egg cases (Compagno *et al*. 2004).

Although studies investigating the influences that competition and predation have on coastal sharks are well-documented, similar studies on small-bodied, deeper water and more benthic sharks are few (Matich *et al*. 2010, Caut *et al*. 2013).

In South Africa, small meso-predatory catsharks form one of the most diverse components of the demersal shark assemblage (Richardson *et al*. 2000b), with *H. regani* and *S. capensis* perhaps being the most common (Petersen *et al*. 2008). These two catsharks occupy rather similar geographic and bathymetric distributions, occurring from Lüderitz in Namibia to central Kwazulu-Natal and between depths of approximately 50-900 m (Compagno *et al.* 1989, Compagno *et al*. 2005). In addition to occurring in common habitats, these two species are known to have rather similar feeding habits, with diets comprising mainly of teleosts, cephalopods and other invertebrates (Compagno 1984, Ebert *et al.* 1996, Ebert 2013). In spite of their similar distribution patterns and feeding habits, no detailed study has yet been conducted to explore possible habitat and feeding competition between the different species and size classes of these sharks.

This chapter gives an overview of the distribution patterns (including patterns by size and sex) of *H. regani* and *S. capensis*, around the West and South coasts of South Africa using data collected from 1994 to 2015. This information will be used to assess how intra- and interspecific competition might shape the distribution of these two species around South Africa, and will form the basis for a first attempt to understand habitat partitioning within and between these co-occurring catsharks.

Results

Intraspecific segregation

Holohalaelurus regani

Holohalaelurus regani were caught in 9.5% of the 6 948 trawls conducted on the West and South coasts from 1994 to 2015, occurring in 11.4% of all trawls conducted on the West Coast and in 6.5% of all trawls on the South Coast. When present, *H. regani* revealed significantly (Mann-Whitney: U= 2385; $p < 0.05$) higher densities on the West Coast (640 individuals.nm^{-2}, SE= ± 33.82) compared to the South Coast (211 individuals.nm^{-2}, SE= ± 17.49) (Figure 2). Highest densities were recorded between Oranjemund and Cape Agulhas, with some localized patches of moderate density between Plettenberg Bay and Port Elizabeth (Figure 3).

In terms of depth, *H. regani* were recorded between 80-584 m on the West Coast and 58-440 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for *H. regani* on the West (Chi-square: X^2= 121.64, $p < 0.05$) and South (Chi-square: X^2= 147.45, $p < 0.05$) coasts (Figure 4). Highest densities were 5 047.2 individuals.nm^{-2} in the 250 m depth stratum on the West Coast and 1 668.8 individuals.nm^{-2} in the 150 m depth stratum on the South Coast (Table 1).

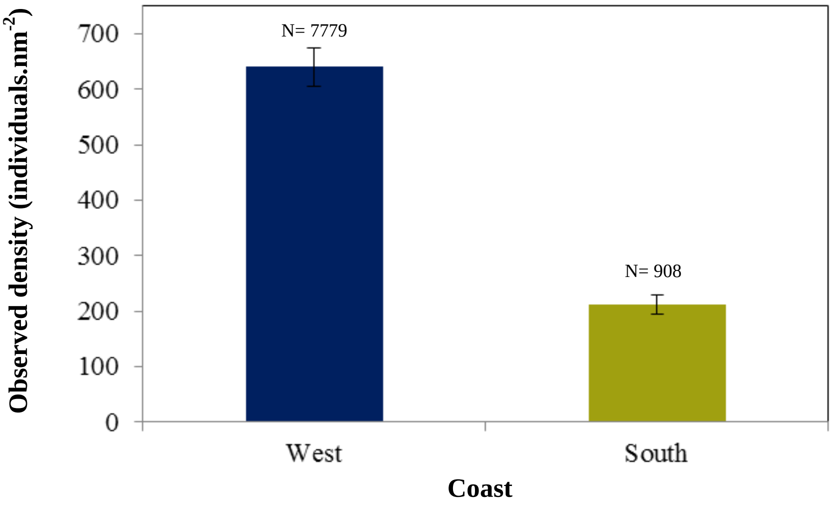


Figure 2: Catch data for *H. regani* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

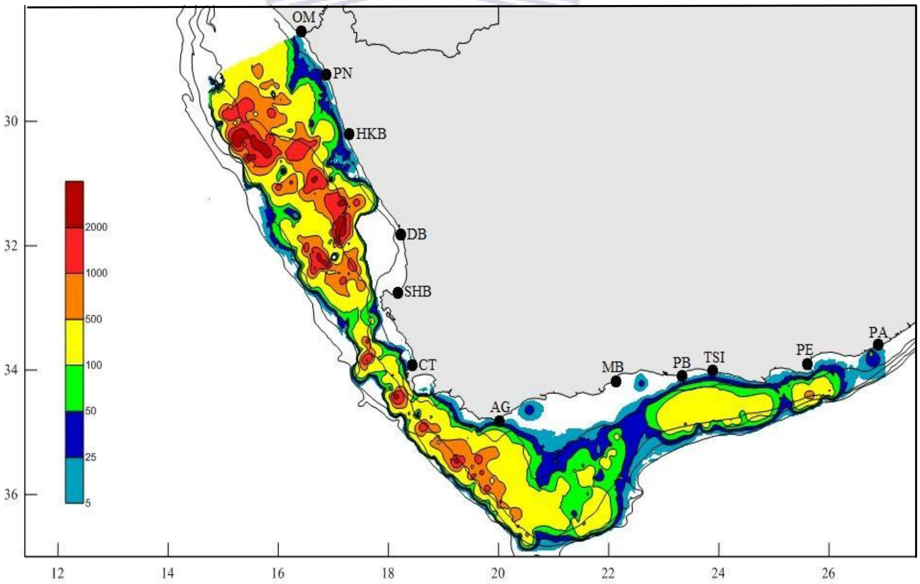


Figure 3: Observed densities (individuals.nm^{-2}) of all *H. regani* caught on the West and South coasts from 1994-2015. See Figure 1 for key to place names and depth contours.

There were significant differences in the observed densities of *H. regani* between depths on the West Coast only (Kruskal Wallis: H= 72.75, $p < 0.05$, df= 5), with differences between the 150 and 250 m and 150 and 450 m depth strata, between the 250 and 450 m depth strata, as well as between the 350 and 450 m depth strata (Figure 5**A**).

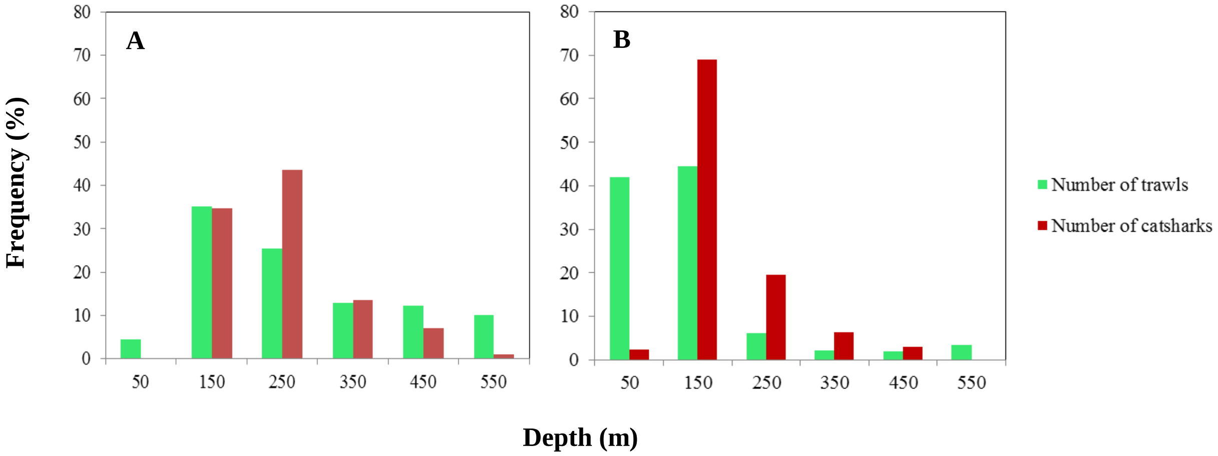
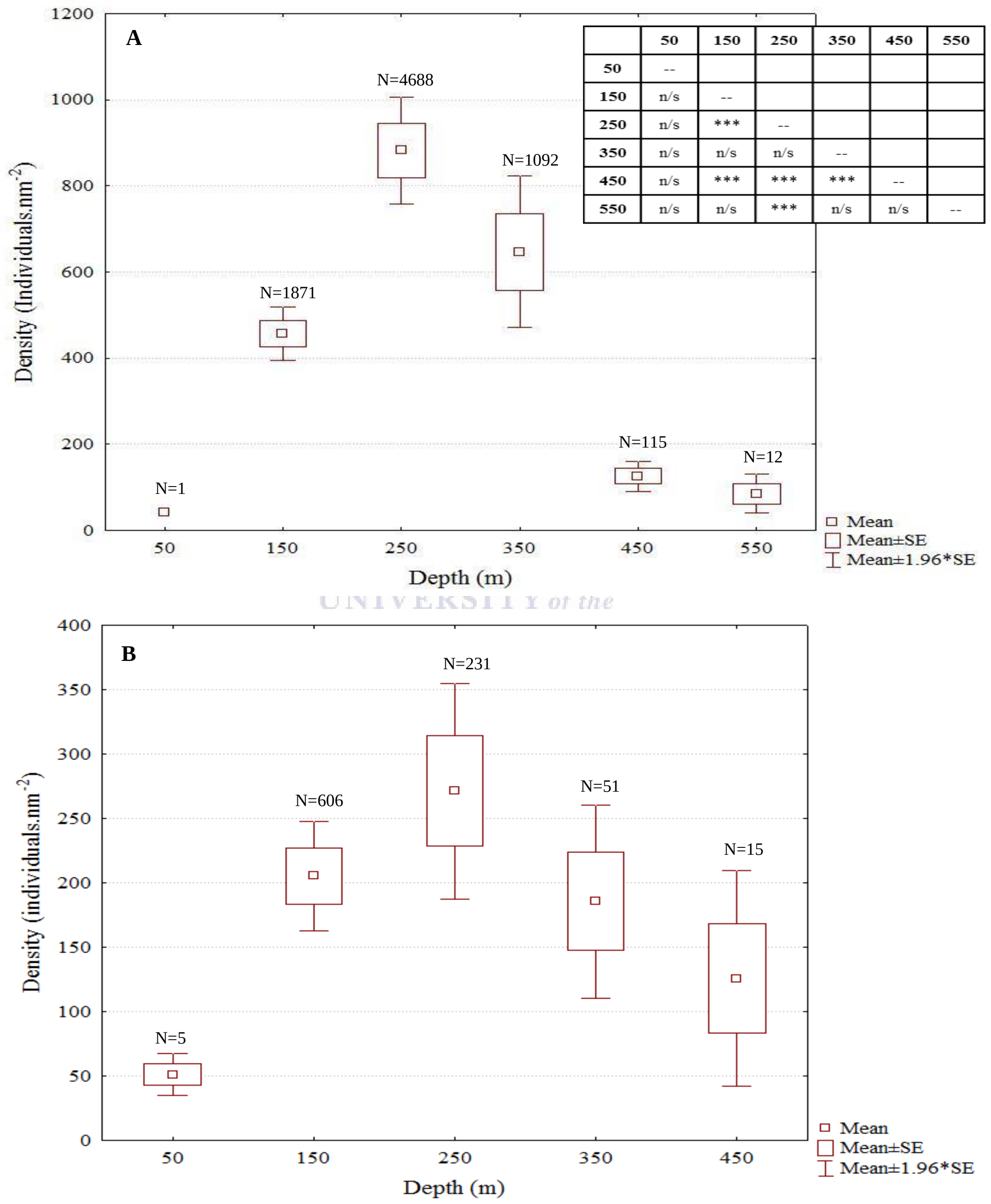


Figure 4: Histograms illustrating the distribution of fishing effort and the depth of capture for *H. regani* on the West (**A**) and South (**B**) coasts.

Table 1: Average densities of *H. regani*, expressed as the mean number of catsharks (individuals.nm^{-2}, ±SE) caught within each depth stratum on the West and South coasts from 1994-2015. Table includes the observed maximum densities (individuals.nm^{-2}) for each depth strata. "-" denotes to null/zero values

Coast	**West**			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	0.2	0.2	42.1	0.2	0.1	75.6
150	51.2	5.1	1990.2	20.7	2.8	1668.8
250	172.4	16.3	5047.2	56.9	12.4	936.2
350	78.0	14.0	3866.8	35.2	11.9	437.1
450	8.2	1.8	381.8	12.3	6.5	244.2
550	1.7	0.9	152.5	-	-	0

The bathymetric patterns of abundance for *H. regani* showed intraspecific segregation by depth among size classes on the West Coast only (X^2=52.23; $p < 0.05$) (Table 2). Here, there was a peak in the mean densities of small, medium and large individuals in the 150-250 m, 250 m and the 250-350 m depth strata respectively (Figure 6**A**). On the South Coast all life stages of *H. regani* appeared to display their peak density in the 250 m depth stratum (Figure 6**B**).



	50	150	250	350	450	550
50	--					
150	n/s	--				
250	n/s	***	--			
350	n/s	n/s	n/s	--		
450	n/s	***	***	***	--	
550	n/s	n/s	***	n/s	n/s	--

Figure 5: Boxplot illustrating the observed densities of *H. regani* on the West (**A**) and South (**B**) coasts. Table represents multiple comparison Kruskal-Wallis tests, with significant values ($p < 0.05$) being denoted by ***, and non-significant values being denoted by n/s. Data labels indicate number of individuals caught.

Table 2: Average densities of *H. regani*, expressed as the mean number of catsharks (individuals.nm^{-2}, ±SE) caught on the West and South coasts. Table includes the observed maximum densities (indviduals.nm^{-2}), as well as X^2 values for the patterns in size distribution by depth on each coast. Significant chi-square values are denoted by: ** $p < 0.05$, * $p > 0.05$

Coast	**Mean**	**±SE**	**Max density**	**X^2**
West	73.0	4.9	5047.2	52.23**
South	13.8	1.5	1668.8	7.97*

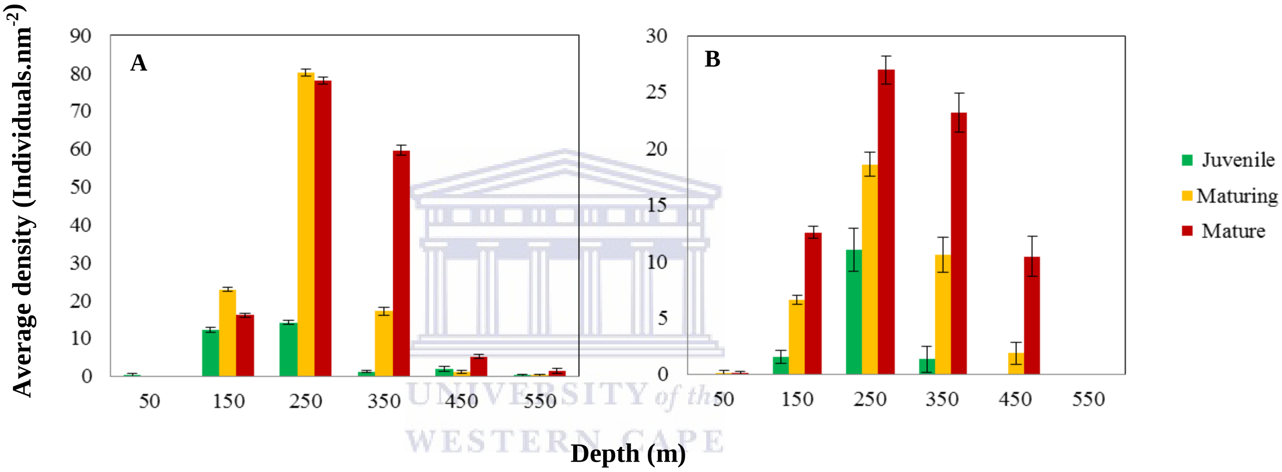


Figure 6: Bathymetric patterns of distribution for all *H. regani* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught in each depth stratum.Error bars indicate standard error.

One small *H. regani* was caught in the 50 m depth stratum on the West Coast, making up 100% of the catch (Figure 7**A**). Medium *H. regani* dominated catches in the 150 and 250 m depth strata, and constituted 45 and 47% of the catch respectively (Figure 7**A**). Large *H. regani* dominated catches in the 350, 450 and 550 m depth strata, and contributed > 50% to the catch in each depth (Figure 7**A**). Notably on the West Coast, medium and large *H. regani* were caught in higher densities than small *H. regani* in the 250, 350, 450 and 550 m depth strata (Figure 7**A**).

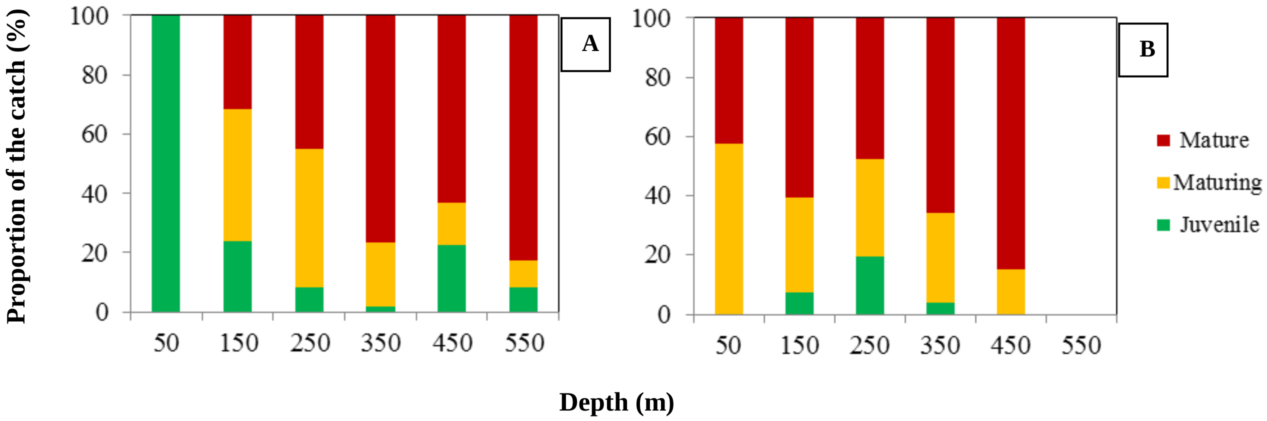


Figure 7: Bathymetric patterns of distribution for all *H. regani* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

Catches per size class in each depth on the South Coast revealed that medium *H. regani* dominated catches in the 50 m depth stratum, with 57% of the catch composed of medium individuals (Figure 7**B**). Large *H. regani* dominated catches in the 150, 250, 350 and 450 m depth strata, and contributed >50% to the catch in each depth (Figure 7**B**). Small *H. regani* did not dominate catches in any depth and made the greatest contribution (20%) to the catch in the 250 m depth stratum (Figure 7**B**). On the South Coast, large individuals were caught in higher densities than small and medium individuals in most depth strata, except for the 50 m depth stratum where medium individuals contributed more (Figure 7**B**).

Scyliorhinus capensis

Scyliorhinus capensis were recorded in 4.6% of the 6 948 trawls conducted on the West and South coasts from 1994 to 2015, occurring in 2.8% of all trawls conducted on the West Coast and 7.6% of all trawls conducted on the South Coast. When present, *S. capensis* revealed no significant difference (Mann Whitney: U= 1170, p= 0.61) in their average densities between the West (273 individuals.nm^{-2}, SE= ± 50.94) and South (201 individuals.nm^{-2}, SE= ± 33.41) coasts (Figure 8). Highest densities were recorded between Cape Agulhas and Tsitsikamma, with localized patches of high densities between Port Nolloth and Hondeklipbaai (Figure 9).

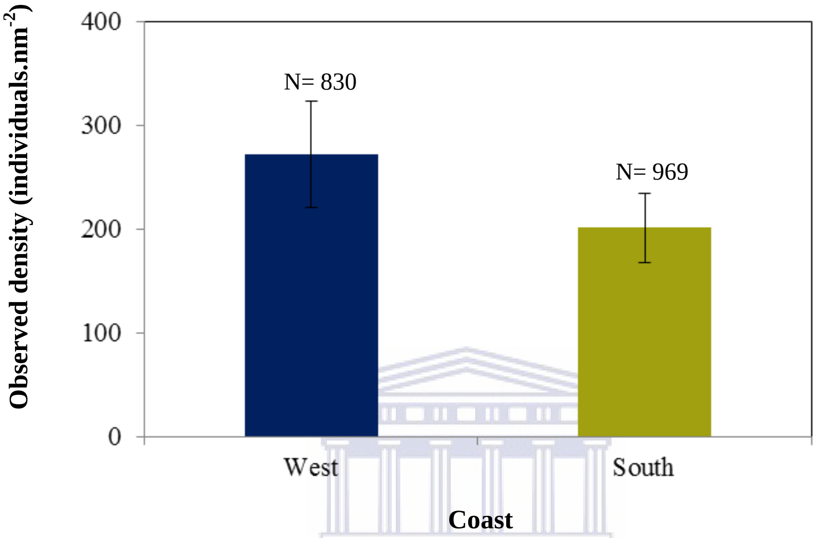


Figure 8: Catch data for *S. capensis* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

Scyliorhinus capensis were recorded between 145-555 m on the West Coast and 80-556 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for *S. capensis* on the West (Chi-square: X^2= 75.23, $p < 0.05$) and South (Chi-square: X^2= 116.63, $p < 0.05$) coasts (Figure 10).

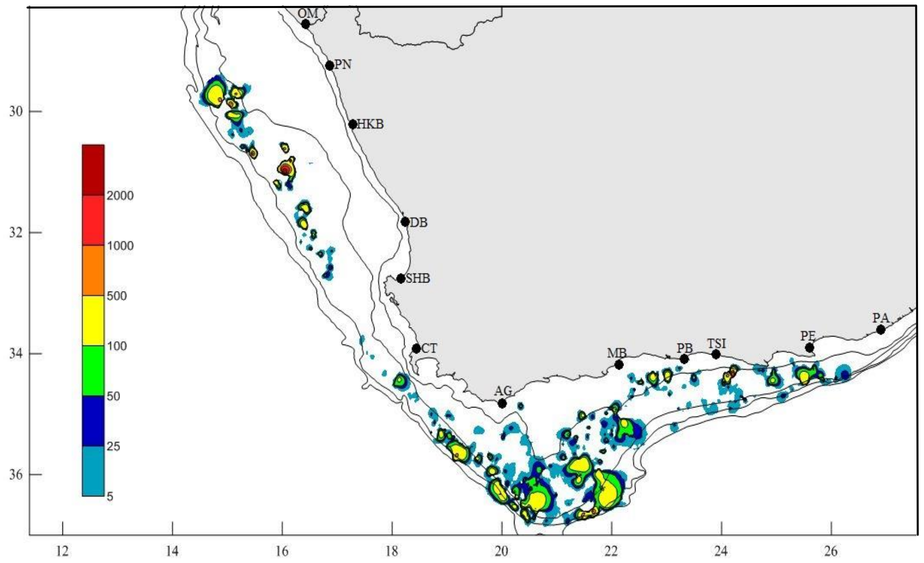


Figure 9: Observed densities (individuals.nm^{-2}) of all *S. capensis* caught on the West and South coasts from 1994-2015. See Figure 1 for key to place names and depth contours.

Highest densities were 4 127.4 individuals.nm^{-2} in the 350 m depth stratum on the West Coast and 5 779.9 individuals.nm^{-2} in the 150 m depth stratum on the South Coast (Table 3). There were no significant differences in the observed densities of *S. capensis* between depths on either coast ($p > 0.05$) (Figure 11). The bathymetric patterns of abundance for *S. capensis* showed intraspecific segregation by depth among size classes on the West (Chi-square: X^2=26.00; $p < 0.05$) and South (Chi square: X^2=22.52; $p < 0.05$) coasts (Table 4).

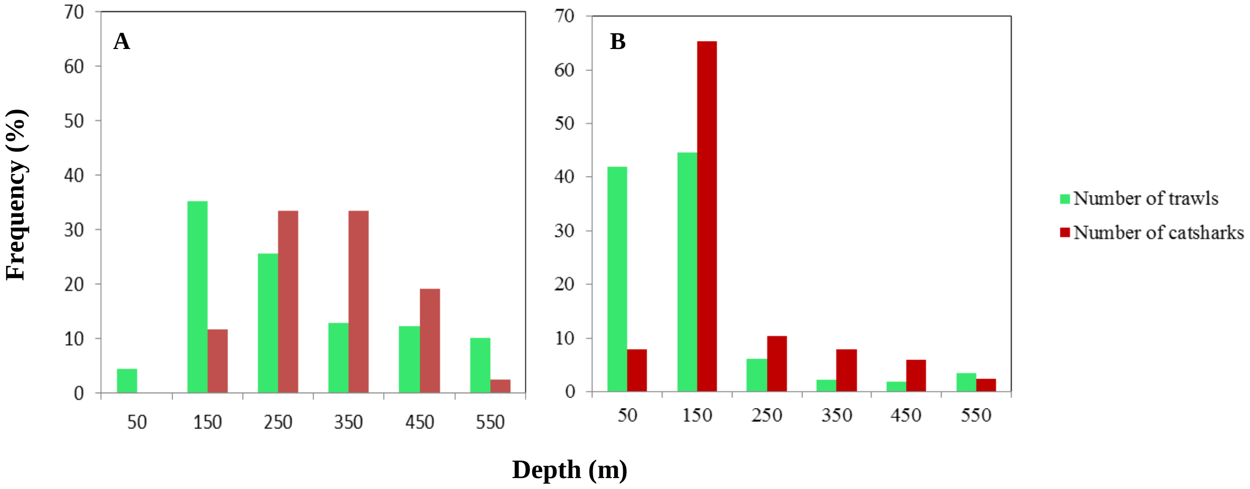


Figure 10: Histograms illustrating the distribution of fishing effort and the depth of capture for *S. capensis* on the West (**A**) and South (**B**) coasts.

Table 3: Average densities of *S. capensis*, expressed as the mean number of catsharks (individuals.nm^{-2}, ±SE) caught in each depth stratum on the West and South coasts from 1994-2015. Table includes the observed maximum densities (individuals.nm^{-2}) for each depth. “-“ denotes to null/zero values

Coast	**West**			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	-	-	0	2.2	0.7	485.2
150	0.7	0.2	245.2	21.4	5.4	5779.9
250	7.6	2.5	2181.7	15.2	4.4	470.3
350	33.0	10.9	4127.4	108.4	40.1	1527.1
450	8.5	2.6	975.1	74.8	40.7	1942.7
550	3.4	3.2	801.9	3.9	1.7	60.2

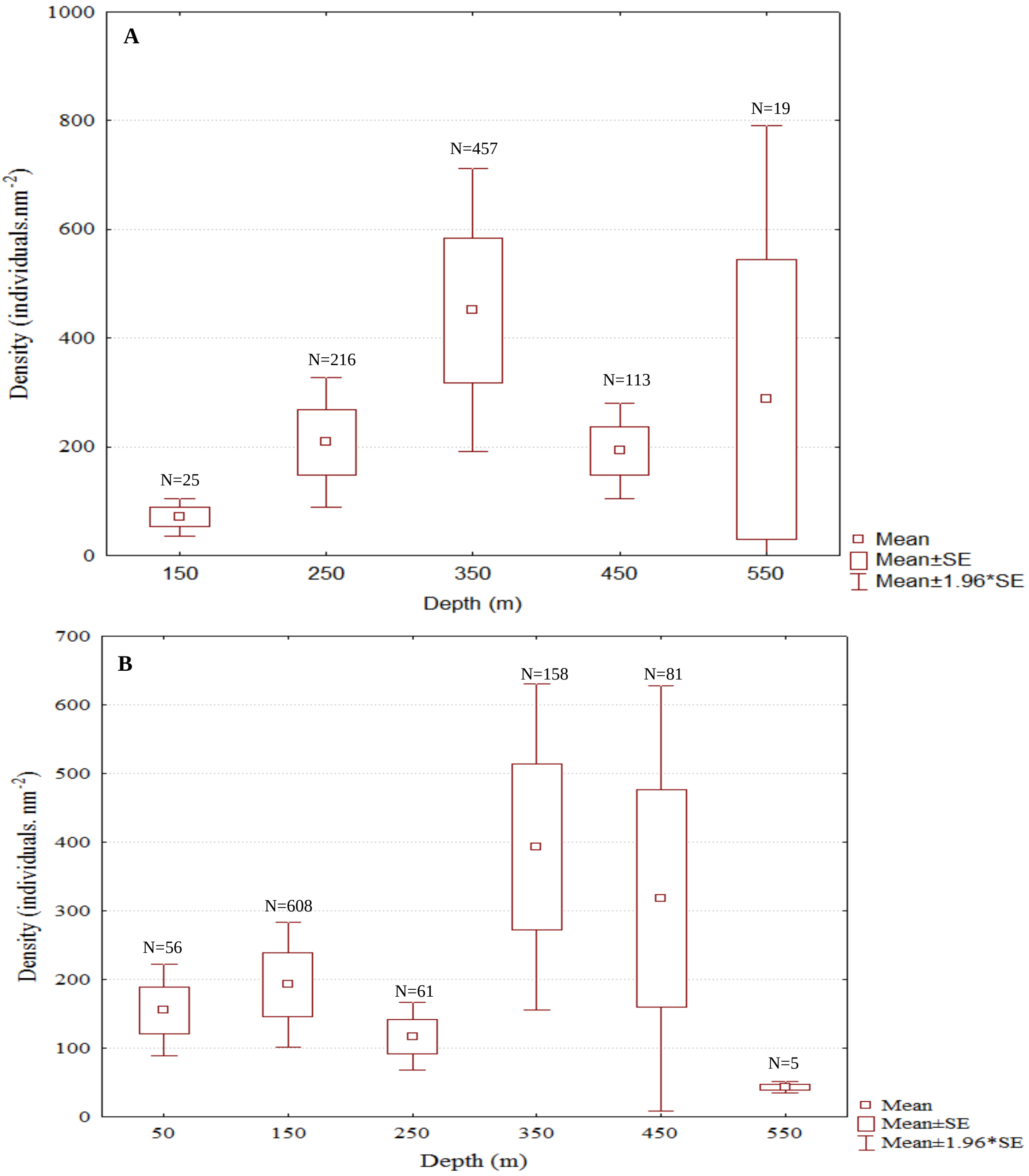


Figure 11: Boxplot illustrating the observed densities of *S. capensis* on the West (**A**) and South (**B**) coasts. Data labels indicate number of individuals caught.

On the West Coast there was a peak in the mean densities of small, medium and large individuals in the 250 m, 350 m and both the 350 and 450 m depth strata, respectively (Figure 12**A**). On the South Coast, a peak in the mean densities of small, medium and large individuals were recorded in the 150 m, 350 m and 450 m depth strata, respectively (Figure 12**B**).

Table 4: Average densities of *S. capensis*, expressed as the mean number of catsharks (individuals.nm^{-2}, ±SE) caught on the West and South coasts. Table includes the observed maximum densities (indviduals.nm^{-2}), as well as X^2 values for the patterns in size distribution by depth on each coast. Significant chi-square values are denoted by: ** p < 0.05, * p > 0.05

Coast	**Mean**	**±SE**	**Max density**	**X^2**
West	7.6	1.6	4127.4	26.00**
South	15.2	2.7	5779.9	22.52**

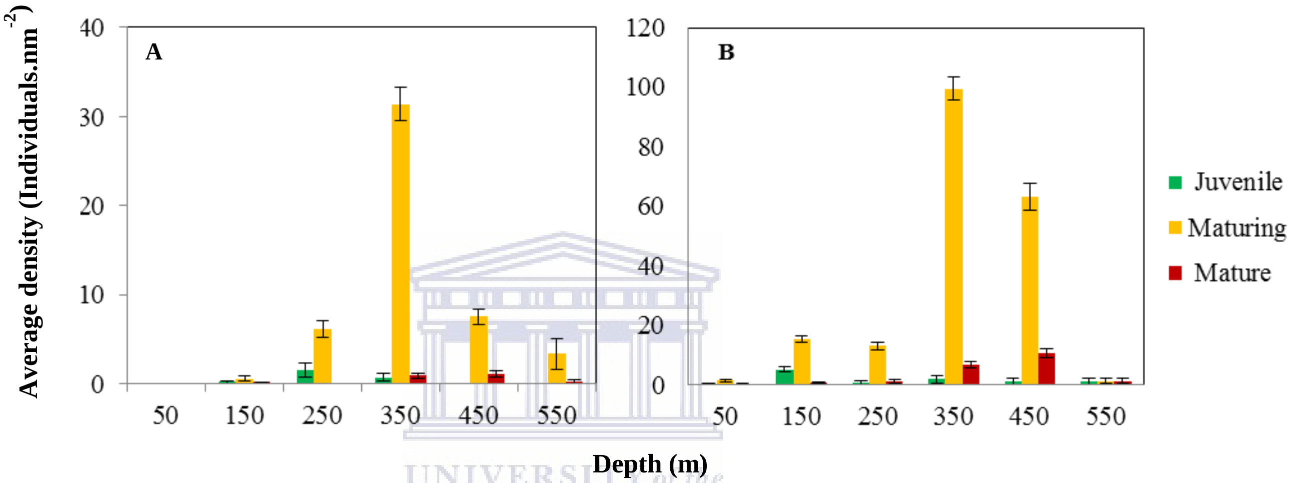


Figure 12: Bathymetric patterns of distribution for all *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught in each depth stratum. Error bars indicate standard error.

Catches per size class in each depth on the West Coast revealed that medium *S. capensis* dominated catches in all depth strata, constituting >50% of the catch across all depths (Figure 13**A**). Small and large *S. capensis* were caught in their highest proportions in the 250 and 450 m depth strata respectively (Figure 13**A**). Similarly on the South Coast, medium *S. capensis* dominated most depths and constituted >50% of the catch in the 50-450 m depth strata (Figure 13**B**). Notably, catch rates appeared to be equal among all life stages of *S. capensis* in the 550 m depth stratum (Figure 13**B**), but this may be an artefact of small sample size (n=5) at that depth.

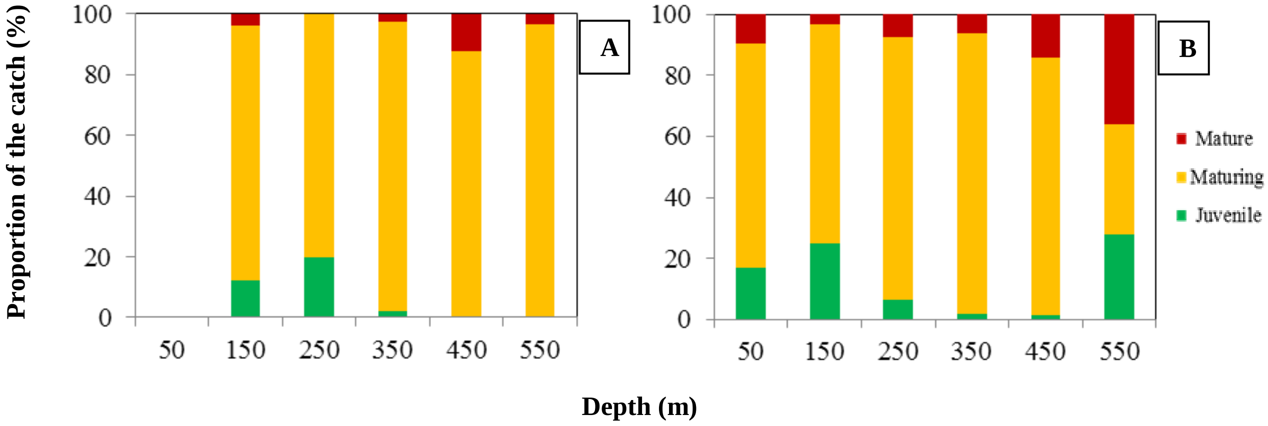


Figure 13: Bathymetric patterns of distribution for all *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

Intraspecific segregation by sex

Holohalaelurus regani

Males

Male *H. regani* occurred in 5.7% of all trawls conducted on the West Coast and 1.6% of all trawls conducted on the South Coast. Where present, male *H. regani* revealed significantly (Mann-Whitney: U= 2913, p < 0.05) higher densities on the West Coast (709 individuals.nm^{-2}, SE= ± 56.61) compared to the South Coast (174 individuals.nm^{-2}, SE= ± 25.75) (Figure 14). Highest densities were recorded between Oranjemund and Saldanha Bay, with patches of high density off Cape Town and the western Agulhas Bank (Figure 15).

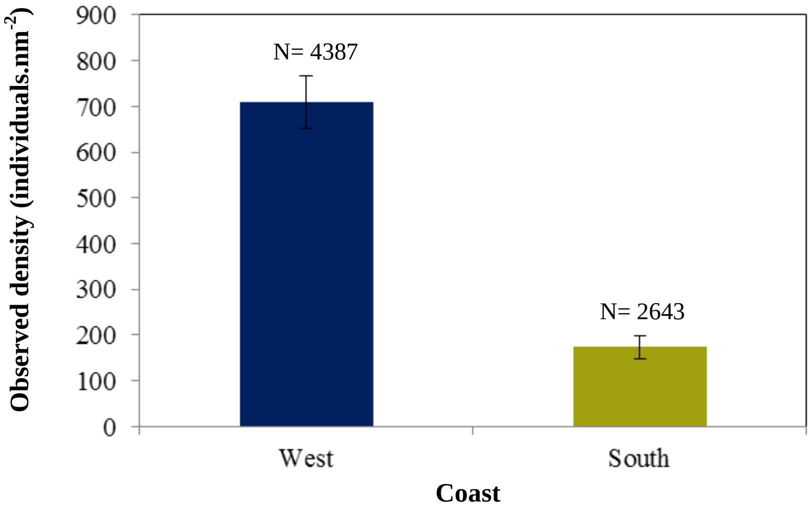


Figure 14: Catch data for male *H. regani* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

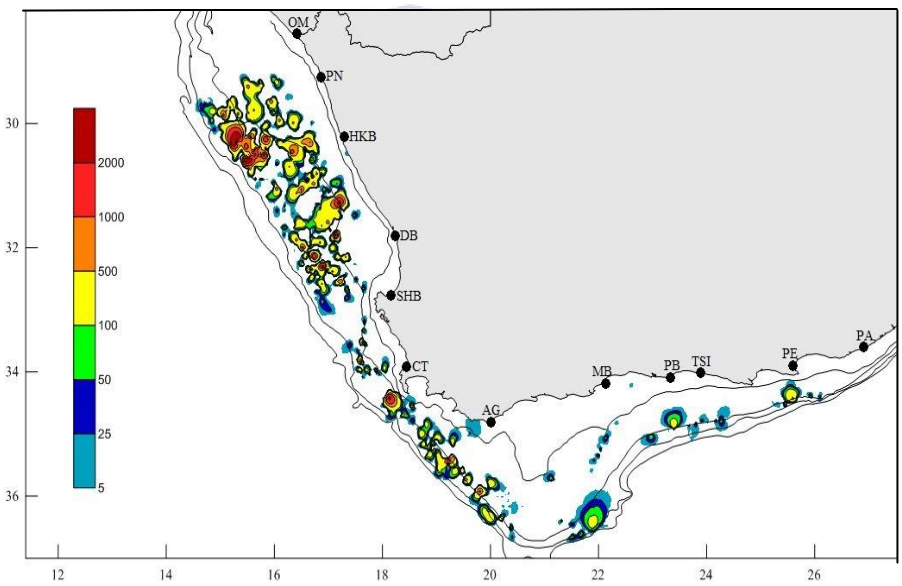


Figure 15: Observed densities (individuals.nm^{-2}) of male *H. regani* caught on the West and South coasts from 1994-2015. See Figure 1 for place names and depth contours.

Male *H. regani* were caught between 112-584 m on the West Coast and 73-439 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for male *H. regani* on the West (Chi square: $X^2= 27.83$, $p < 0.05$) and South (Chi square: $X^2= 60.08$, $p < 0.05$) coasts

(Figure 16).

Highest densities were 5 047.2 and 732.7 individuals.nm^{-2} in the 250 m depth stratum on the West and South coasts respectively (Table 5). There were significant differences in the observed densities of male *H. regani* between depths on the West Coast only (Kruskal Wallis: H= 45.78, $p < 0.05$, df= 4), with differences between the 150 and 450 m, 250 and 450 m and 350 and 450 m depth strata (Figure 17**A**).

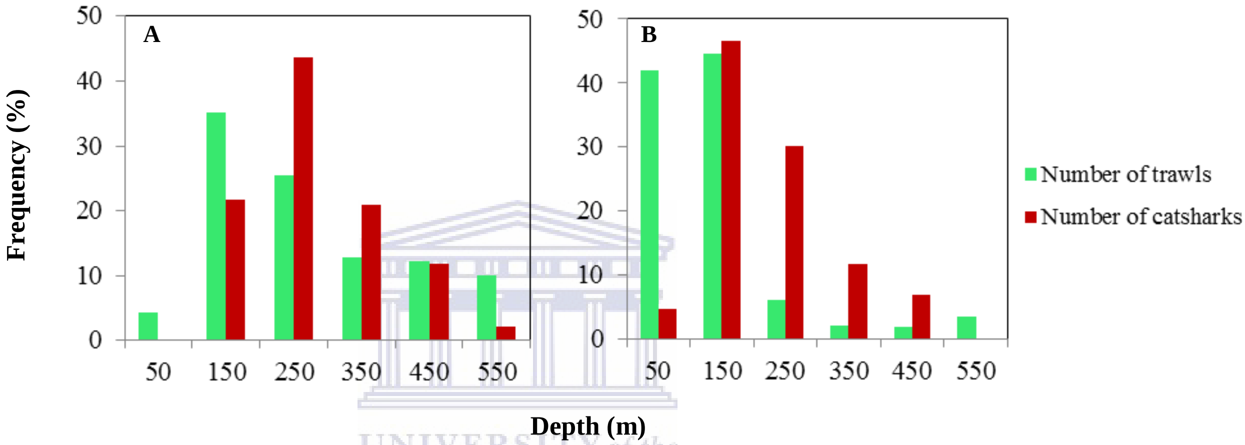


Figure 16: Histograms illustrating the distribution of fishing effort and the depth of capture for male *H. regani* on the West (**A**) and South (**B**) coasts.

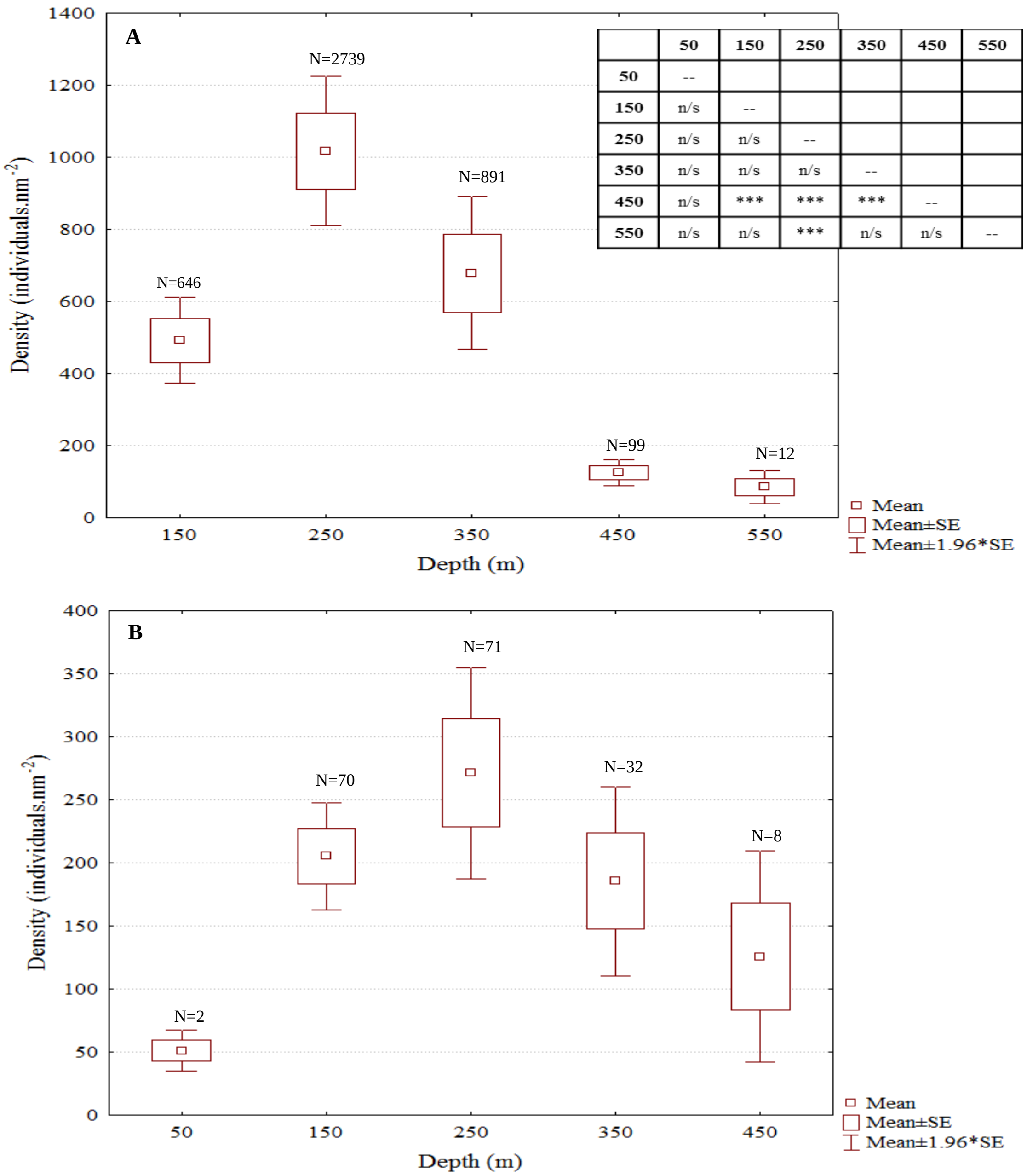
The bathymetric patterns of abundance for male *H. regani* showed intraspecific segregation by depth among size classes on the West Coast only (Chi-square: X^2= 41.22; $p < 0.05$). On this coast, there was a peak in the mean densities of small and medium males in the 150-250 m, and 250 m depth strata, respectively.

Table 5: Average densities of male *H. regani*, expressed as the mean number of male catsharks (individuals.nm^{-2}, ±SE) caught in each depth stratum on the West and South coasts. Table includes the observed maximum densities (individuals.nm^{-2}) for each depth. “-“ denotes to null/zero values

	West			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	-	-	0	0.1	0.1	41.7
150	18.7	3.4	1913.1	2.7	0.8	607.6
250	110.7	15.3	5047.2	20.5	7.8	732.7
350	65	13.5	3866.8	24.3	12.1	437.1
450	7.1	1.6	337.5	7.1	4.7	203.1
550	1.7	0.9	152.5	-	-	0

The mean density of large males peaked in the 250 and 350 m depth strata (Figure 18**A**). Although not significant, on the South Coast, the mean densities of small, medium and large males appeared to peak in the 250 m, 250-350 m and 350 m depth strata respectively (Figure 18**B**).

Catches per size class in each depth on the West Coast showed that the contribution to the catch per depth range by small males was highest (20%) in the 150 m depth stratum (Figure 19**A**). The highest contribution by medium-sized males (49%) was also in the 150 m depth stratum. Large males contributed >50% to the catch in each of the 350, 450 and 550 m depth strata (Figure 19**A**).



	50	150	250	350	450	550
50	--					
150	n/s	--				
250	n/s	n/s	--			
350	n/s	n/s	n/s	--		
450	n/s	***	***	***	--	
550	n/s	n/s	***	n/s	n/s	--

Figure 17: Boxplot illustrating the observed densities of male *H. regani* on the West (**A**) and South (**B**) coasts. Table represents multiple comparisons Kruskal-Wallis tests, with significant values ($p < 0.05$) being denoted by ***. Data labels indicate number of individuals caught.

Catches per size class in each depth on the South Coast showed that the 31% of males caught in the 150 m depth stratum were small. Medium and large males were caught in similar proportions (50%) in the 50 m depth stratum (Figure 19**B)**. Large males also contributed >50% to the catch in each of the 350 and 450 m depth strata (Figure 19**B).**

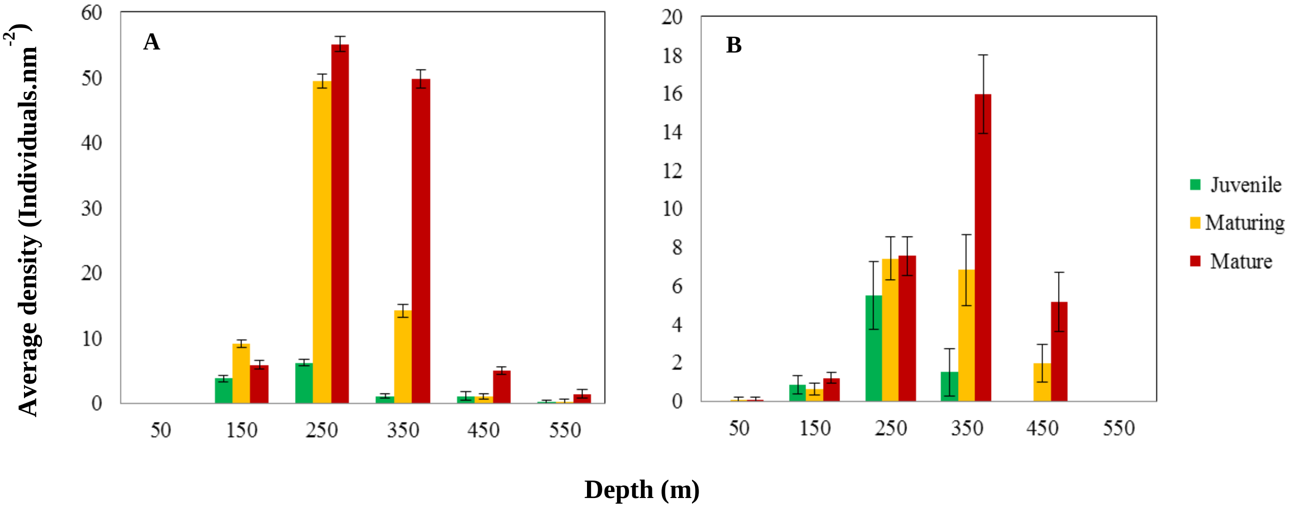


Figure 18: Bathymetric patterns of distribution for male *H. regani* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught at each depth stratum. Error bars indicate standard error.

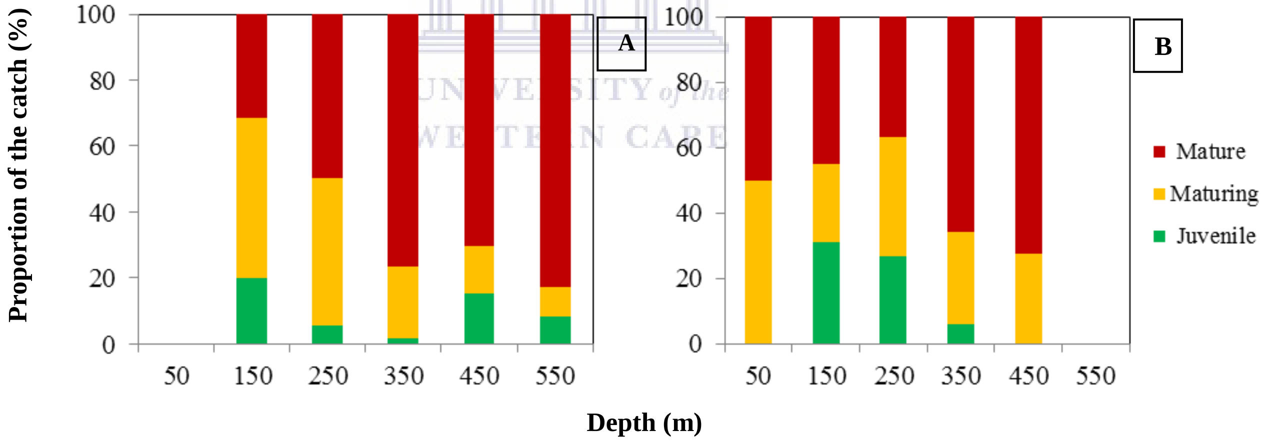


Figure 19: Bathymetric patterns of distribution for male *H. regani* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

Females

Female *H. regani* occurred in 4.6 and 3.9% of all trawls conducted on the West and South coasts respectively. Where present, female *H. regani* revealed significantly (Mann-Whitney: U= 5667, $p < 0.05$) higher average densities on the

West Coast (534 individuals.nm^{-2}, SE= ± 36.98) compared to the South Coast (196 individuals.nm^{-2}, SE= ± 17.99) (Figure 20). Highest densities were observed between Oranjemund and Doringbaai (Figure 21). Patches of high density were also noted east of Cape Town and off the western Agulhas Bank (Figure 21).

Female *H. regani* were caught between 138-486 m on the West Coast and 64-366 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for female *H. regani* on the West (Chi-square: X^2= 45.02, $p < 0.05$) and South (Chi-square: X^2= 55.86, $p < 0.05$) coasts (Figure 22).

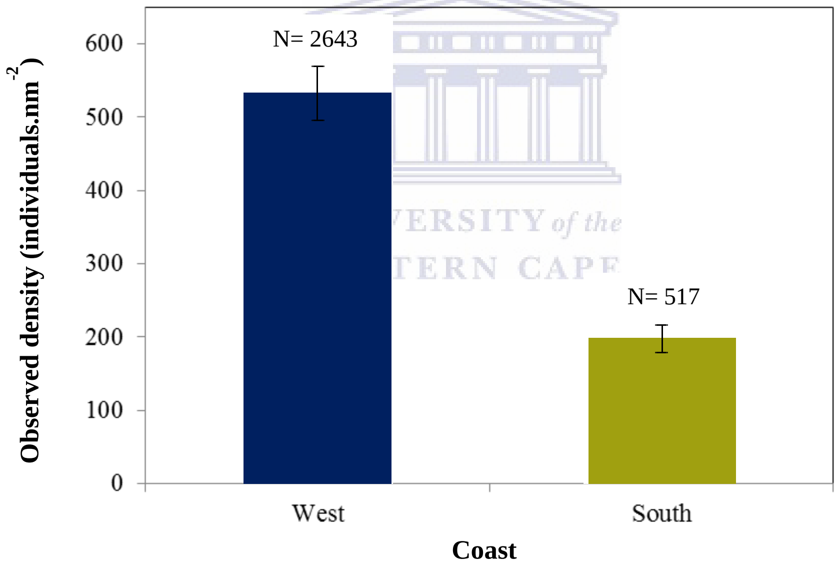


Figure 20: Catch data for female *H. regani* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

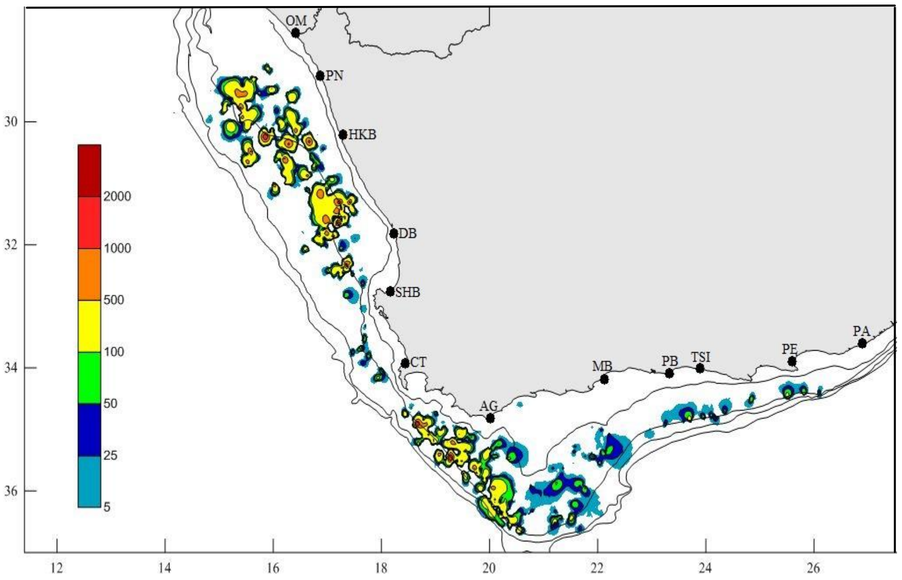


Figure 21: Observed densities (individuals.nm^{-2}) of female *H. regani* caught on the West and South coasts from 1994-2015. See Figure 1 for key to place names and depth contours.

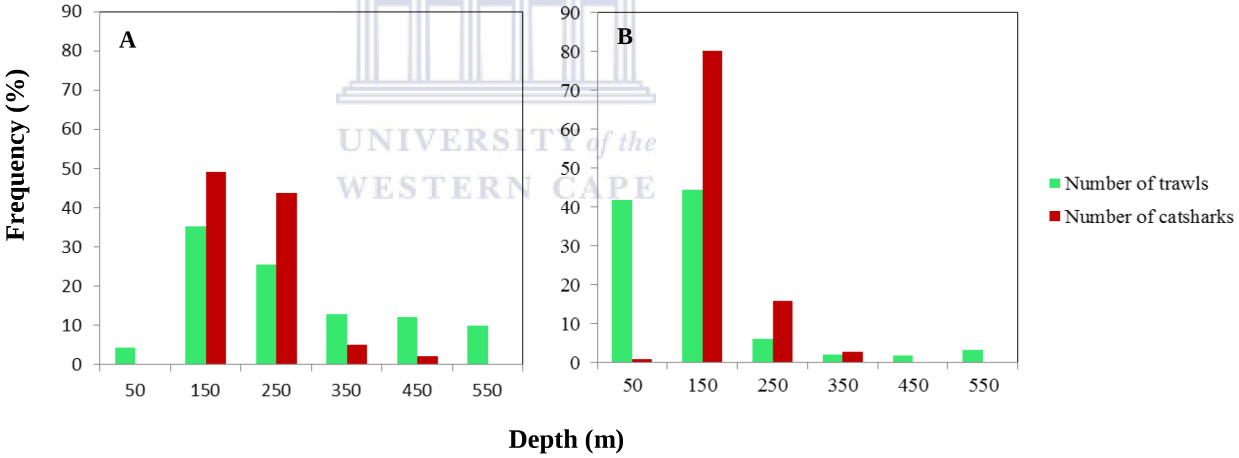


Figure 22: Histograms illustrating the distribution of fishing effort and the depth of capture for female *H. regani* on the West (**A**) and South (**B**) coasts.

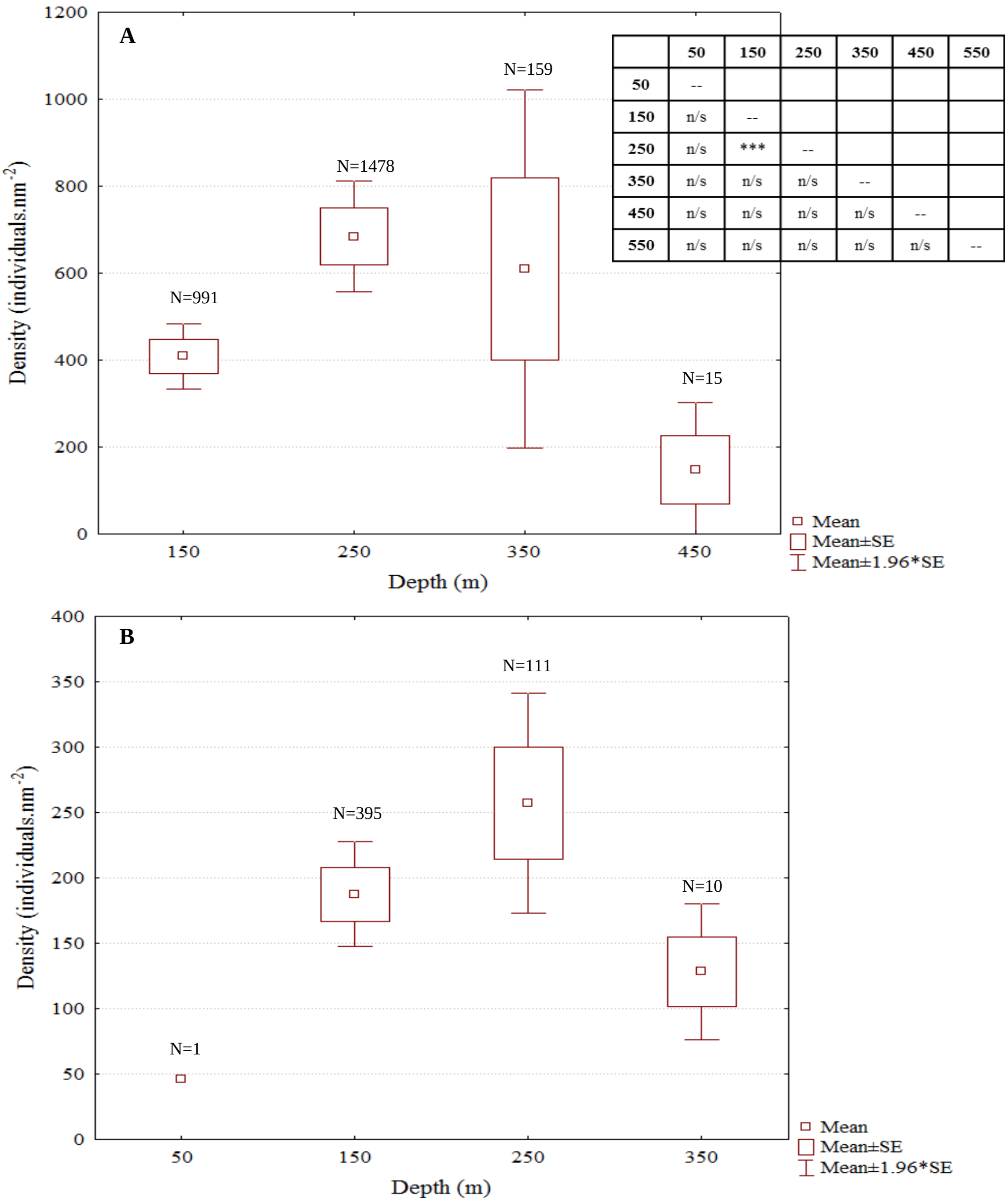
Highest densities of female *H. regani* were 2 376.3 individuals.nm^{-2} in the 250 m depth stratum on the West Coast and 895.5 individuals.nm^{-2} in the 150 m depth stratum on the South Coast (Table 6). There were significant differences in the observed densities of female *H. regani* between depths on the West Coast only (Kruskal Wallis: H= 15.08, $p < 0.05$, df= 3), with differences between the 150 and

250 m depth strata (Figure 23**A**).

Table 6: Average densities of female *H. regani*, expressed as the mean number of male catsharks (individuals.nm^{-2}, ±SE) caught in each depth stratum on the West and South coasts. Table includes the observed maximum densities (individuals.nm^{-2}) for each depth. “-“ denotes to null/zero values

Coast	**West**			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	-	-	0	0.04	0.04	45.7
150	27.6	3.7	1990.2	13.8	2.1	895.5
250	61.1	8.5	2376.3	30.2	8.5	693.4
350	12.4	5.6	2198	7.7	4.6	163.1
450	1.2	0.8	381.8	-	-	0
550	-	-	0	-	-	0

The bathymetric patterns of abundance for female *H. regani* showed no intraspecific segregation by depth among size classes ($p > 0.05$). On the West Coast, there appeared to be a peak in the mean densities of all female *H. regani* in the 250 m depth stratum (Figure 24**A**). Notably, females were absent from the shallowest (50 m) and deepest (550 m) depths of capture (Figure 24**A**). Similarly on the South Coast, there appeared to be a peak in the mean densities of all female *H. regani* in the 250 m depth stratum, and an absence of females from the deeper depths (450 and 550 m) (Figure 24**B)**.



	50	**150**	**250**	**350**	**450**	**550**
50	--					
150	n/s	--				
250	n/s	***	--			
350	n/s	n/s	n/s	--		
450	n/s	n/s	n/s	n/s	--	
550	n/s	n/s	n/s	n/s	n/s	--

Figure 23: Boxplot illustrating the observed densities of female *H. regani* on the West (**A**) and South (**B**) coasts. Table represents multiple comparisons Kruskal-Wallis tests, with significant values ($p < 0.05$) being denoted by ***. Data labels indicate number of individuals caught.

Catches per size class in each depth on the West Coast revealed that small females constituted 64% of the catch in the 450 m depth stratum, while medium and large females constituted 52 and 73% of the catch in the 250 and 350 m depth strata, respectively (Figure 25**A**). Catches per size class in each depth on the South Coast revealed that large females constituted >50% of the catch in all depths (Figure 25**B**). The highest proportions of small and medium females were recorded in the 250 and 350 m depth strata, respectively (Figure 25**B**).

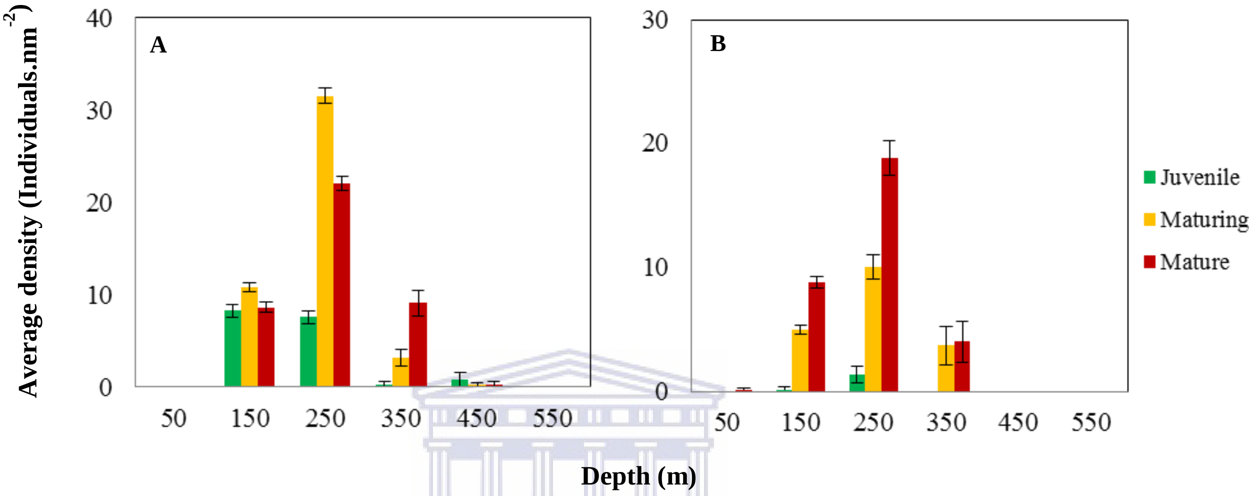


Figure 24: Bathymetric patterns of distribution for female *H. regani* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught in each depth stratum. Error bars indicate standard error.

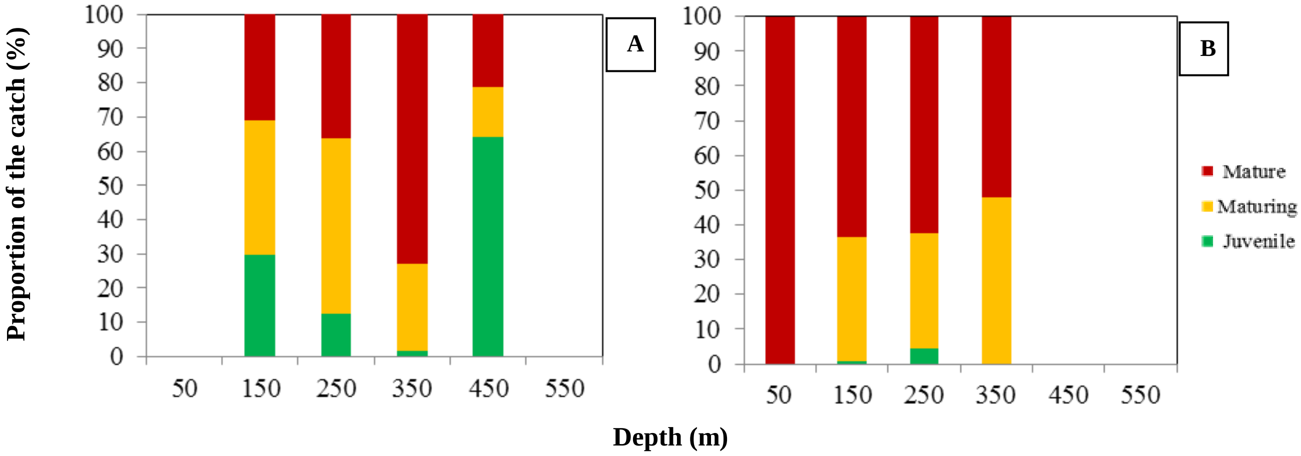


Figure 25: Bathymetric patterns of distribution for female *H. regani* caught along the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

Scyliorhinus capensis

Males

Male *S. capensis* occurred in 3.5 and 1.1% of all trawls conducted on the South and West coasts, respectively. Where present, male *S. capensis* revealed no significant difference (Mann-Whitney: U= 2079, p= 0.34) in their densities on the West (244 individuals.nm^{-2}, SE= ± 62.2) and South (202 individuals.nm^{-2}, SE= ± 27.1) coasts (Figure 26). Highest densities were recorded between Cape Agulhas and Mossel Bay, with small patches of high density off Hondeklipbaai (Figure 27).

Male *S. capensis* were caught between 80-451 m on the West Coast and 145-515 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for male *S. capensis* on the West (Chi-square: X^2= 27.83, p < 0.05) and South (Chi-square: X^2= 60.08, p < 0.05) coasts (Figure 28).

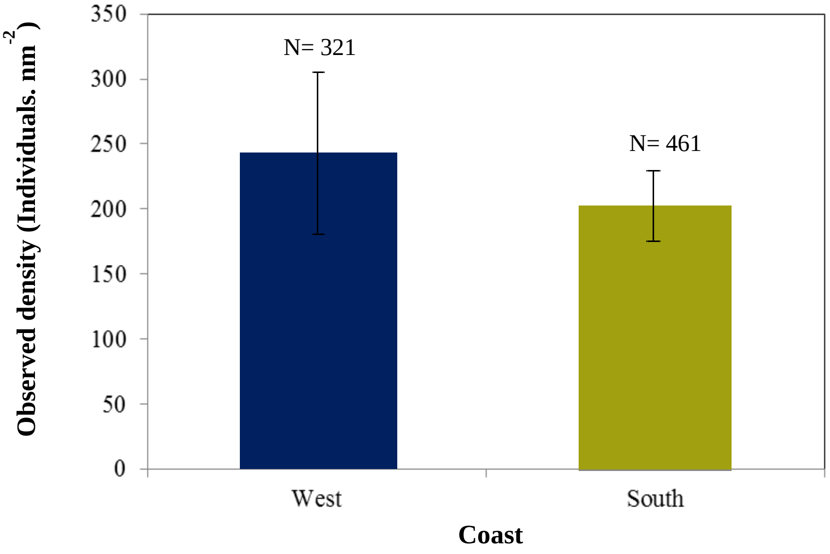


Figure 26: Catch data for male *S. capensis* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

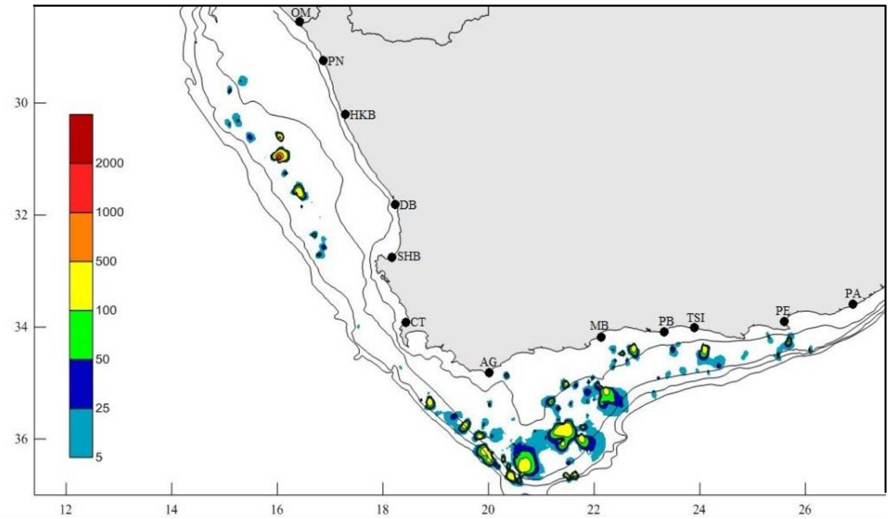


Figure 27: Observed densities (individuals.nm^{-2}) of male *S. capensis* caught on the West and South coasts from 1994-2015. See Figure 1 for key to place names and depth contours.

Highest densities were recorded in the 350 m depth stratum on both coasts, with 2 754.7 individuals.nm^{-2} logged on the West Coast and 1527.1 individuals.nm^{-2} logged on the South Coast (Table 7). There were significant differences in the observed densities of male *S. capensis* between depths on the West (Kruskal Wallis: H= 12.46, $p < 0.05$, df= 4) and South (Kruskal Wallis: H= 10.59, $p < 0.05$, df= 4) coasts, with differences between the 150 and 350 m depth stratum on both coasts (Figure 29**A** and **B**).

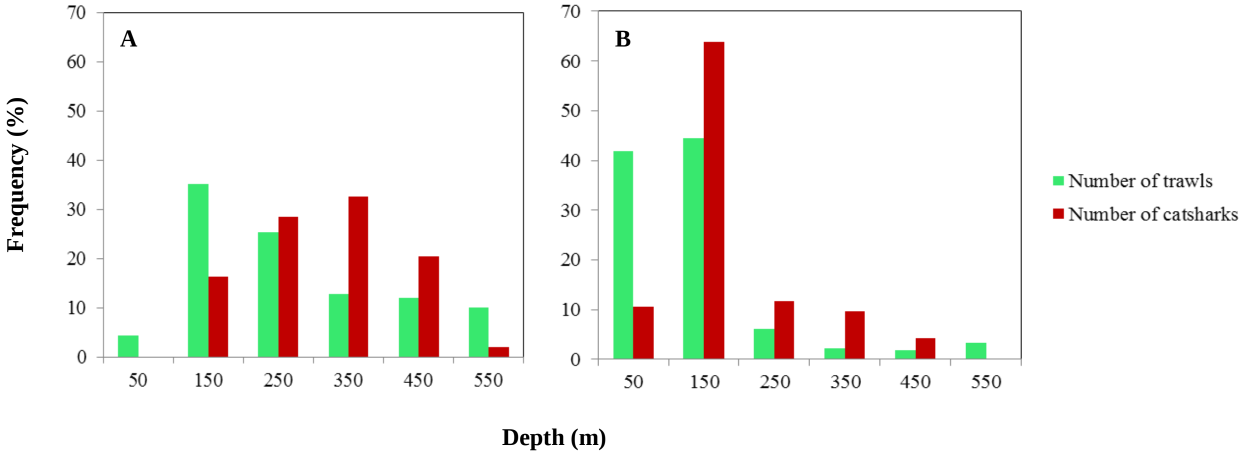


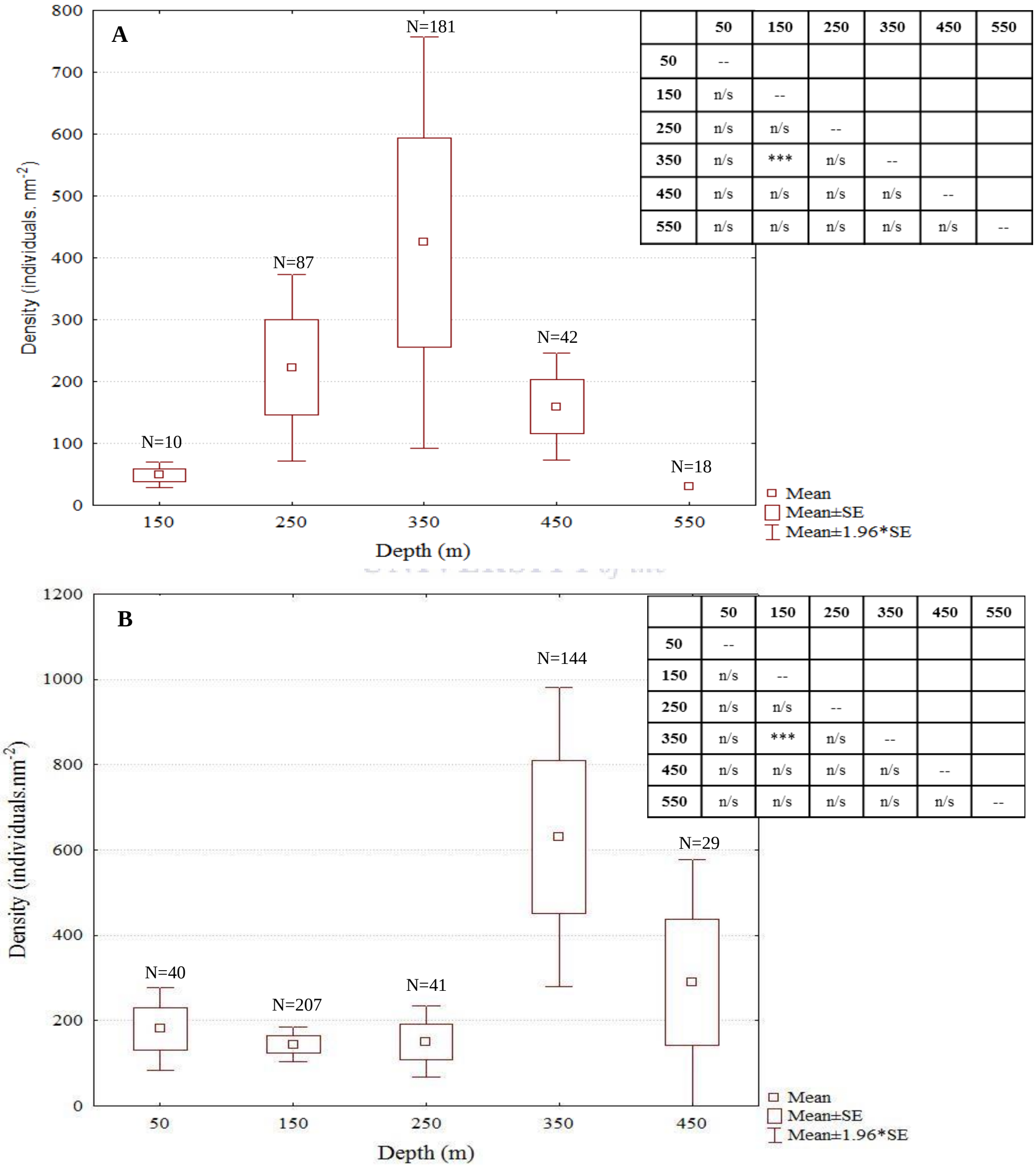
Figure 28: Histograms illustrating the distribution of fishing effort and the depth of capture for male *S. capensis* on the West (**A**) and South (**B**) coasts.

The bathymetric patterns of abundance for male *S. capensis* showed intraspecific segregation by depth among size classes on the West (Chi square: $X^2 = 18.78$, $p < 0.05$) and South (Chi square: $X^2 = 19.43$, $p < 0.05$) coasts. On the West Coast, there was a peak in the mean densities of small, medium and large males in the 250 m, 350 m and 450 m depth strata respectively (Figure 30**A**). On the South Coast, there was a peak in the mean densities of small and medium males in the 350 m depth stratum, and a peak in the mean density of large males in the 450 m depth stratum (Figure 30**B**).

Table 7: Average densities of male *S. capensis*, expressed as the mean number of male catsharks (individuals.nm^{-2}, ±SE) caught within each depth stratum on the West and South coasts from 1994-2015. Table includes the observed maximum densities (individuals. nm^{-2}) for each depth stratum. “-“ denotes to null/zero values

Coast	**West**			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	-	-	0	1.6	0.7	485.2
150	0.3	0.1	121.6	7.8	1.5	975.6
250	2.9	1.2	1094.1	10.9	4.3	470.3
350	13.0	6.0	2754.7	111.2	45.4	1527.1
450	3.2	1.3	488.4	26.9	17.7	714.7
550	0.1	0.1	30.7	-	-	0

Catches per size class in each depth on the West Coast revealed that 38% of the males caught in the 250 m depth stratum were small (Figure 31**A**). Medium-sized males contributed >50% to the catch in each of the 150, 250, 350 and 450 m depth strata (Figure 31**A**). The highest contribution by large males was in the 500 m depth stratum, where they contributed 100% to the catch (Figure 31**A**). Catches per size class in each depth on the South Coast revealed that medium-sized males contributed >50% to the catch in all depth strata (Figure 31**B**). The highest proportions of small and large males were caught in the 50 and 450 m depth strata, respectively (Figure 31**B**).



A

	50	**150**	**250**	**350**	**450**	**550**
50	--					
150	n/s	--				
250	n/s	n/s	--			
350	n/s	***	n/s	--		
450	n/s	n/s	n/s	n/s	--	
550	n/s	n/s	n/s	n/s	n/s	--

B

	50	**150**	**250**	**350**	**450**	**550**
50	--					
150	n/s	--				
250	n/s	n/s	--			
350	n/s	***	n/s	--		
450	n/s	n/s	n/s	n/s	--	
550	n/s	n/s	n/s	n/s	n/s	--

Figure 29: Boxplot illustrating the observed densities of male *S. capensis* on the West (**A**) and South (**B**) coasts. Table represents multiple comparisons Kruskal-Wallis tests, with significant ($p < 0.05$) values being denoted by ***. Data labels indicate number of individuals caught.

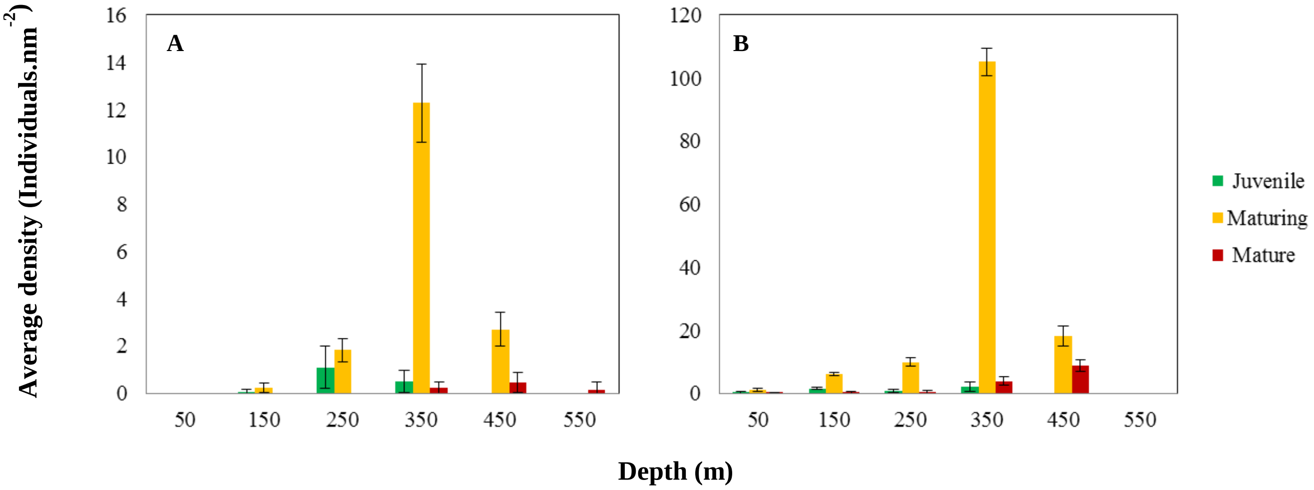


Figure 30: Bathymetric patterns of distribution for male *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught in each depth stratum. Error bars indicate standard error.

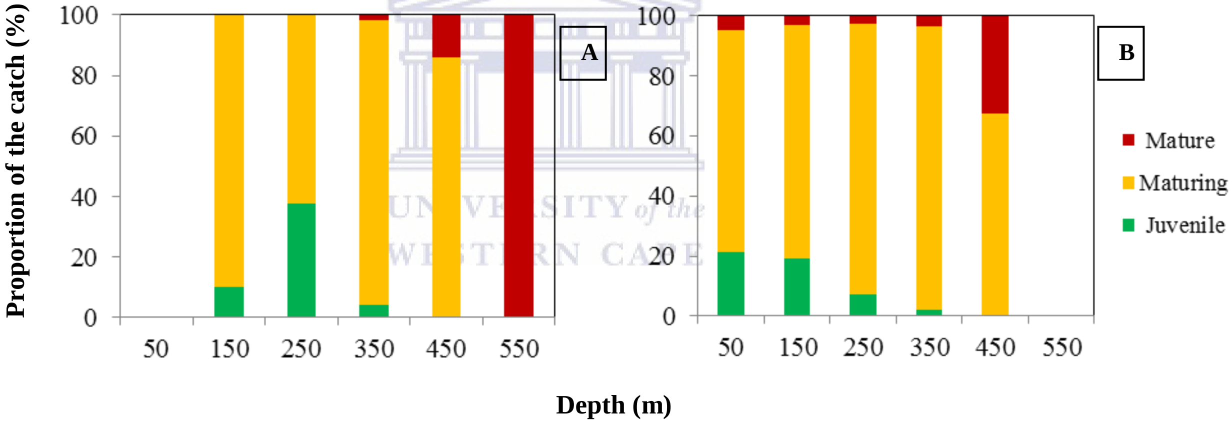


Figure 31: Bathymetric patterns of distribution for male *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

<u>Females</u>

Female *S. capensis* occurred in 1.6% of all trawls conducted on the West Coast and in 3.2% of the all trawls conducted on the South Coast. Where present, no significant difference (Mann-Whitney: U= 2836, p= 0.967) in the densities of female *S. capensis* was noted on the West (280 individuals.nm^{-2}, SE= ± 75.99) or South (148 individuals.nm^{-2}, SE= ± 27.41) coasts (Figure 32). Highest densities were recorded between Cape Agulhas and Mossel Bay, with patches of high density off the coast of Hondeklipbaai (Figure 33).

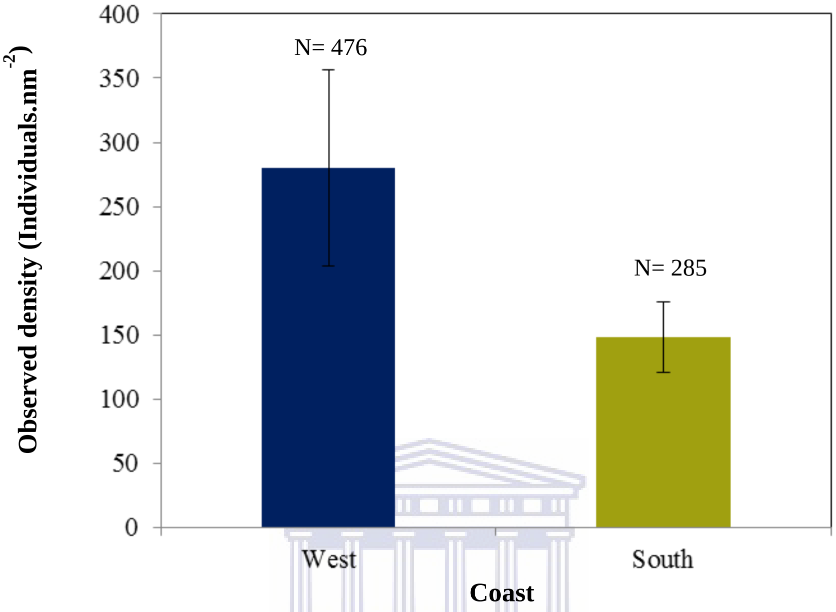


Figure 32: Catch data for female *S. capensis* on the West and South coasts. Bars represent observed densities (individuals.nm^{-2}, ± SE). Data labels indicate number of individuals caught.

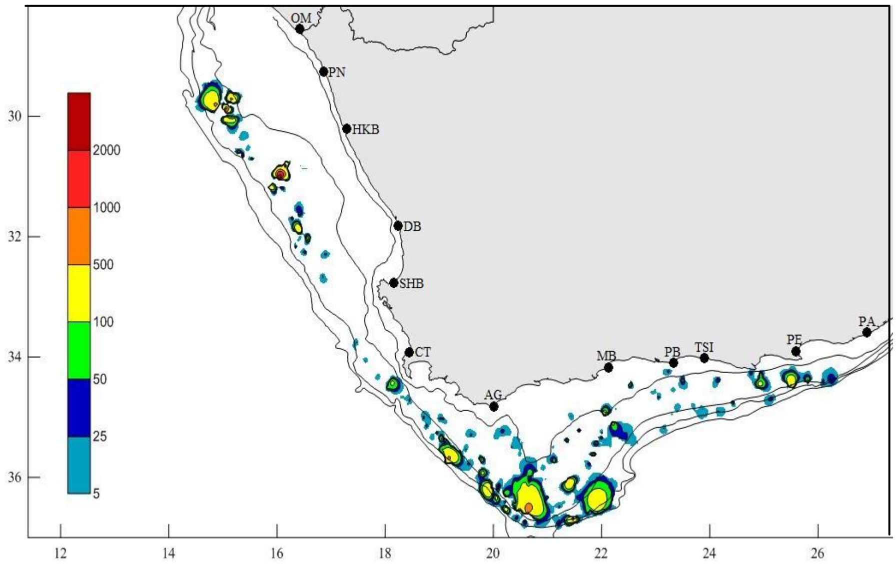


Figure 33: Observed densities (individuals.nm^{-2}) of female *S. capensis* caught on the West and South coasts from 1994-2015. See Figure 1 for key to place names and depth contours.

Female *S. capensis* were caught between 161-515 m on the West Coast and 87-556 m on the South Coast. There were significant differences between the distribution of fishing effort and the depth of capture for female *S. capensis* on the West (Chi-square: $X^2 = 45.02$, $p < 0.05$) and South (Chi-square: $X^2 = 55.86$, $p < 0.05$) coasts (Figure 34). Highest densities were 4 127.4 individuals.nm^{-2} in the 350 m depth stratum on the West Coast and 1 942.7 individuals.nm^{-2} in the 450 m depth stratum on the South Coast (Table 8). There were no significant differences in the observed densities of female *S. capensis* between depths on either coast ($p > 0.05$) (Figure 35).

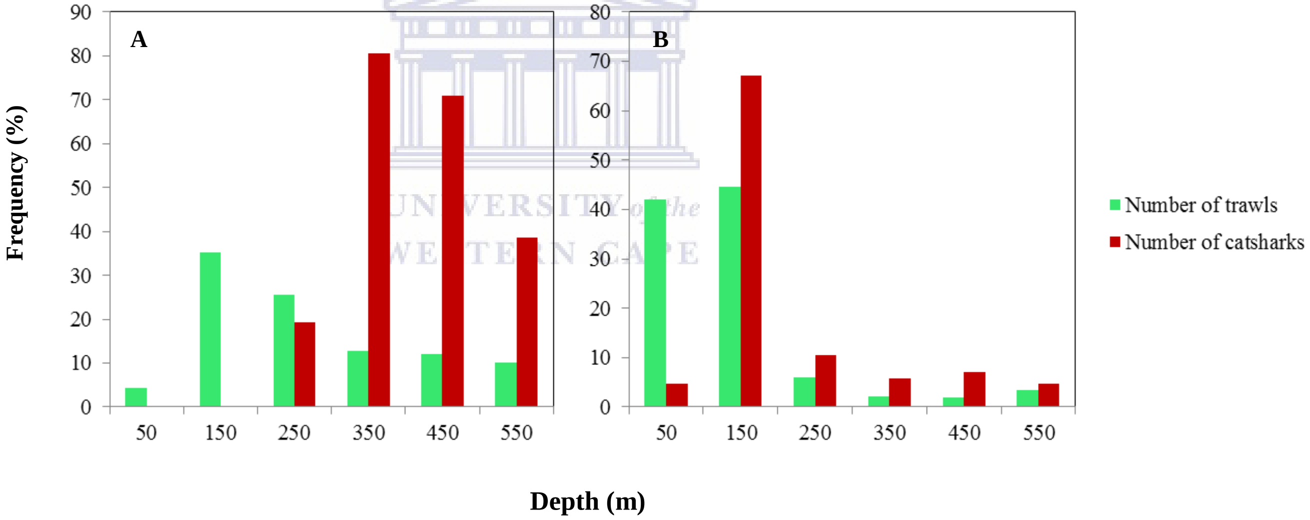


Figure 34: Histograms illustrating the distribution of fishing effort and the depth of capture for female *S. capensis* on the West (**A**) and South (**B**) coasts.

The bathymetric patterns of abundance for female *S. capensis* showed intraspecific segregation by depth among size classes on the West Coast only (Chi square: $X^2=20.97$, $p < 0.05$). On the West Coast, there was a peak in the mean densities of small females in the 250 m depth stratum, while the mean densities of medium and large females peaked in the 350 m depth stratum (Figure 36**A**).

Table 8: Average densities of female *S. capensis*, expressed as the mean number of female catsharks (individuals.nm^{-2}, ±SE) caught within each depth stratum on the West and South coasts from 1994-2015.Table includes the observed maximum densities (individuals.nm^{-2}) for each depth stratum. “-“ denotes to null/zero values

Coast	**West**			**South**		
Depth (m)	**Mean**	**±SE**	**Max density**	**Mean**	**±SE**	**Max density**
50	-	-	0	0.4	0.2	258.9
150	0.4	0.2	245.2	7.3	1.5	1083.4
250	4.8	2.2	2181.7	5.1	2.1	231.5
350	17.9	9	4127.4	10.6	6.5	292.4
450	5.3	2.3	975.1	57.2	43.6	1942.7
550	3.3	3.2	802.0	3.3	1.6	60.2

On the South Coast, there was a peak in the mean densities of small females in the 150 m depth stratum, while the mean densities of medium and large females appeared to peak in the 450 m depth stratum (Figure 36**B**).

Catches per size class in each depth on the West Coast revealed that medium females constituted >50% of the catch in all depth strata (Figure 37**A**). The highest proportions of small and large females were caught in the 150 and 450 m depth strata, respectively (Figure 37**A**). Similarly on the South Coast, medium females constituted >50% of the catch across all depths, except the deepest (550 m), where small and large females made up 34 and 44% of the catch, respectively (Figure 37**B**).

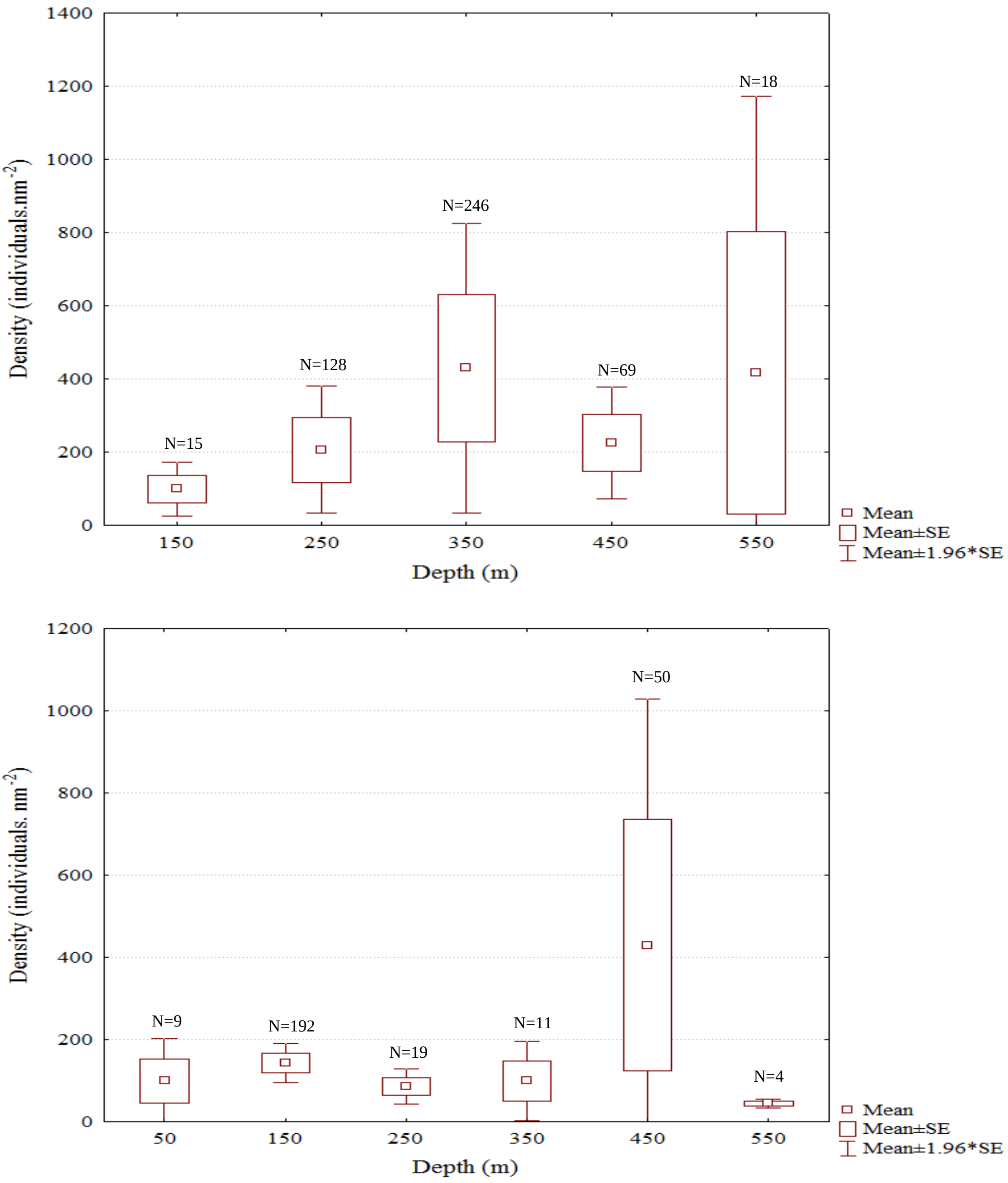


Figure 35: Boxplot illustrating the observed densities of female *S. capensis* on the West (**A**) and South (**B**) coasts. Data labels indicate number of individuals caught.

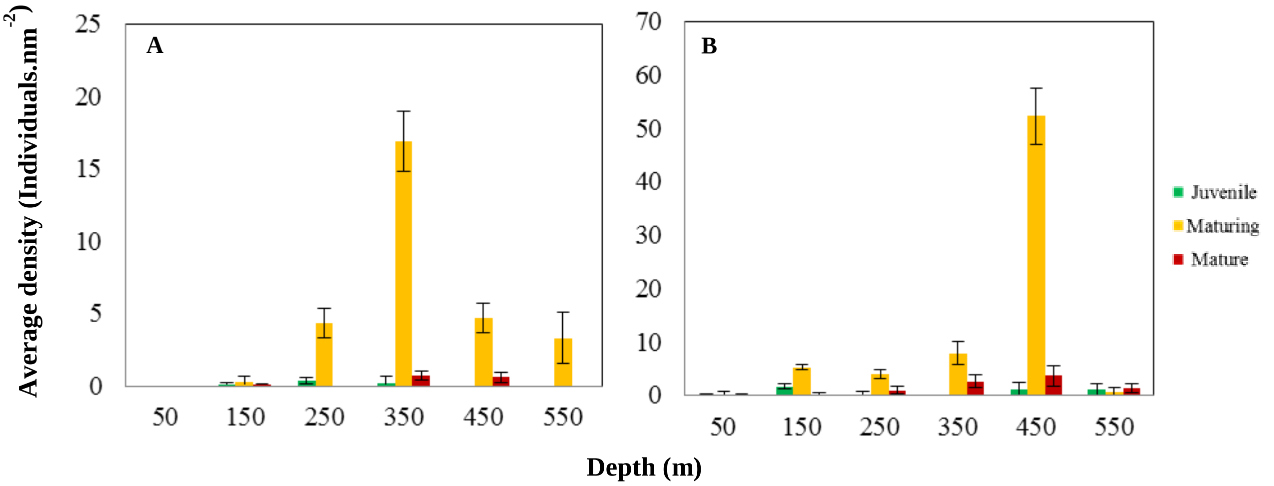


Figure 36: Bathymetric patterns of distribution for female *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the average densities (individuals.nm^{-2}) of all juvenile, maturing and mature individuals caught in each depth stratum. Error bars indicate standard error.

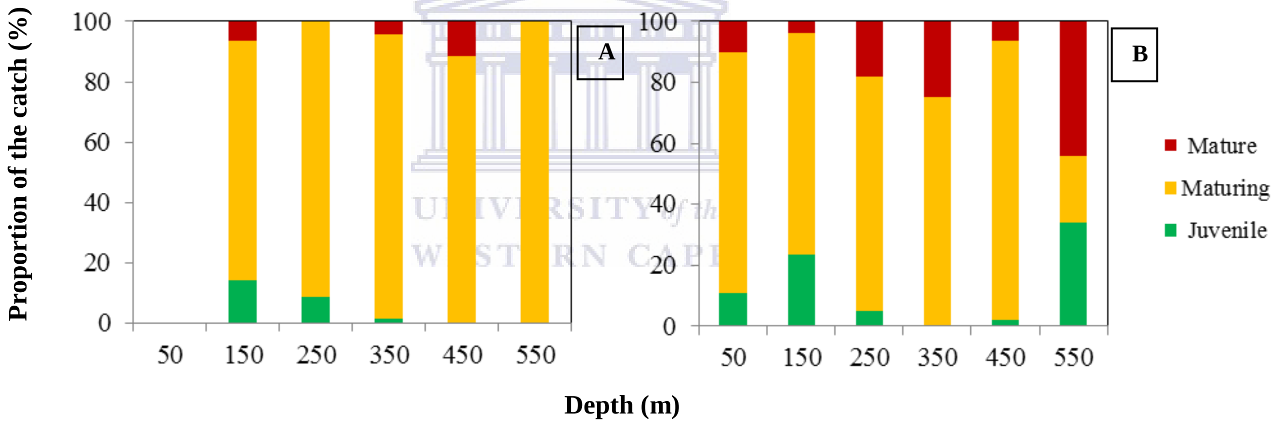


Figure 37: Bathymetric patterns of distribution for female *S. capensis* caught on the West (**A**) and South (**B**) coasts from 1994-2015. Bars represent the proportion of the catch for each size class in each depth stratum.

Intraspecific segregation between sexes

Holohalaelurus regani

Male and female *H. regani* displayed intraspecific segregation by depth among size classes on both coasts. Significant differences in the size of co-occurring male and female *H. regani* was noted in the 250 (Chi square: $X^2 = 47.93$, $p < 0.05$) and 350 m depth strata (Chi square: $X^2 = 35.32$, $p < 0.05$) on the West Coast and in the 150 m depth strata (Chi square: $X^2 = 92.01$, $p < 0.05$) on the South Coast. Male *H. regani* were caught further offshore than female *H. regani* on both coasts (Figure 15 and 21). Males were caught in greater densities than females between Oranjemund and Saldanha Bay, while females were caught in greater densities than males over the western Agulhas Bank (Figure 15 and 21).

Scyliorhinus capensis

For *S. capensis,* no significant differences were noted in the size of co-occurring males and females on either coast ($p > 0.05$). However, female *S. capensis* appear to have been caught in greater densities than males off Oranjemund and Cape Town (Figure 27 and 33). Both male and female *S. capensis* display notable patches of high density off Hondeklipbaai, and between Cape Agulhas and Mossel Bay (Figure 27 and 33).

Interspecific segregation between catsharks

Where present, *H. regani* and *S. capensis* revealed significant differences in their observed densities on the West (Mann Whitney: U= 14 372.50, $p < 0.05$) and South (Mann Whitney: U= 13 499.50, $p < 0.05$) coasts. *H. regani* appears to be more widely distributed than *S. capensis* throughout the study area (Figures 3 and 9). *Holohalelurus regani* also displays a less patchy distribution than *S. capensis*. Significant differences in the size of co-occurring *H. regani* and *S. capensis* was noted on the West and South coasts, with interspecific segregation by depth among size classes observed in the 250 (Chi square: $X^2 = 47.93$, $p < 0.05$) and 350 m depth strata (Chi square: $X^2 = 35.32$, $p < 0.05$) on the West Coast and in the 150 m depth stratum (Chi square: $X^2 = 92.9$, $p < 0.05$) on the South Coast.

Discussion

In the present study, the two catshark species were caught across the entire study area. This overlaps their known distribution range which extends from Lüderitz in Namibia to central Kwazulu-Natal (Compagno *et al*. 1991, Richardson *et al*. 2000b, Human 2006). The two species displayed an inverse relationship in their distributions, with *H. regani* being predominantly caught on the West Coast whereas *S. capensis* was predominantly caught on the South Coast (Appendix 2). Catshark distributions are known to be influenced by location, environmental characteristics and faunal composition (Bass *et al*. 1975, Escobar-Porras 2009, Flammang *et al*. 2011). The different physical and biological factors evident off South Africa's West and South coasts (Hutchings *et al*. 2009, Teske *et al*. 2011, van der Lingen and Miller 2014) thus offers a suitable explanation for the spatial separation evident between the two catsharks. This pattern of spatial separation between two similar shark species is also consistent with the findings of other studies, showing how sharks with similar morphologies and lifestyles partition their environment to possibly reduce the intensity of interspecific competition between them (Bethea *et al*. 2004, White *et al*. 2004, Papastamatiou *et al*. 2006).

Bottom trawl survey data revealed that *H. regani* was the most common catshark caught throughout the study area. This could be a reflection of different availability of these species to the research trawl; Compagno *et al*. (2004) and

Petersen *et al*. (2008) found that *S. capensis* frequent rough grounds where demersal trawling does not occur. Alternatively this could reflect real differences in abundance between these two species. *Scyliorhinus capensis* breed once a year (winter) and females produce a maximum of only two eggs per year, one egg from each of the paired oviducts (Compagno 1984, Ebert *et al*. 2006, Ebert 2013). Given this low reproductive output they are therefore particularly vulnerable to over exploitation, hence it is not surprising that *S. capensis* was classified as Near Threatened by the IUCN Red List of Threatened Species (Compagno *et al*. 2004, Ebert 2013). The paucity of large *S. capensis* in the present study possibly also supports the hypothesis that the population of this species is depleted.

In contrast *H. regani* produces pairs of eggs year round, making this species more resilient and possibly less susceptible to overexploitation by the demersal long-line and trawl fisheries (Richardson *et al*. 2000b). The IUCN Red List of Threatened species has classified *H. regani* as a species of least concern following their continued increase in spite of commercial fishing pressure (Compagno *et al*. 2004). The study by Richardson *et al*. (2000b) attributed this increase in *H. regani* population size to the decrease in fishing effort in inshore areas, where female and juvenile *H. regani* are abundant, following the reduction in effort by the commercial demersal fishing fleet on the South Coast, and the absence of a commercial demersal fishing fleet inshore on the West Coast. These inshore areas possibly function as a refuge for *H. regani* from trawling, and allow for a balance between mortality and production.

Depth-of-capture data for the two catsharks caught in this study showed substantial overlap with their known depth range. Both catsharks appeared to be predominantly caught between 101-500 m, and were rare shallower than 100 m (Richardson *et al*. 2000b, Human 2006, Petersen *et al*. 2008, Ebert 2013). The two catsharks also displayed distinct depth zonation, with interspecific size-based segregations at their most commonly used depths. Such size-based segregations are common in deep-sea benthic sharks, reducing competition for resources through segregating by depth (Carrassón *et al.* 1992, Olaso *et al*. 2005, Flammang *et al*. 2011).

The bathymetric patterns of abundance for *H. regani* showed intraspecific segregation by depth on the West Coast only, whereas *S. capensis* showed intraspecific segregation by depth on both the West and South coasts. The general trend observed for the two catshark species was higher abundances of small individuals in shallow waters and higher abundances of medium and large individuals in deep waters. This “bigger-deeper” pattern has been observed in numerous fish species (Yokota and Lessa 2006, Davis 2010, Flammang *et al*. 2011). Since visual acuity and gape of catsharks are known to increase with age (Bozzano *et al*. 2001, Olaso *et al*. 2005), the distributional changes noted in these catshark species could be attributed to the morphological changes associated with growth and diet preference (Olaso *et al*. 2005). A plausible explanation for these size-based segregations could therefore be an ontogenetic shift in diet, with the smaller catsharks inhabiting shallow areas to obtain a greater encounter rate with small prey, and the larger catsharks inhabiting deep areas to obtain a greater encounter rate with large prey (Sims 2003, Speed *et al*. 2010, see Chapter 4).

Predator avoidance has also been shown to influence habitat selection by juvenile sharks (Heupel and Heuter 2002, DeAngelis *et al*. 2008, Davis 2010). By inhabiting shallow areas, small catsharks possibly decrease their encounter rate with large sharks, which tend to inhabit deep waters. However, other factors such as resource exclusion, physiological development and water parameters (i.e. temperature, salinity, depth, benthos type) (Springer 1967, Weng *et al.* 2007, Carlisle and Starr 2009, Meyer *et al*. 2009, Speed *et al*. 2010) may also play a role in the size-based segregations evident among these catshark species.

Although distinct depth zonation was noted, co-occurrence of different sized individuals within a depth band was still apparent. A study by Ebert and Ebert (2005) in Humboldt Bay, California, found that adult leopard sharks (*Triakis semifasciata*) co-occurred with juveniles in nursery areas, but that they feed on different prey items. It might therefore be plausible that when different sized individuals co-occur they would feed on different prey items and when they do not co-occur they would feed on similar prey items. In the presence of abundant resources, however, different sized individuals inhabiting the same depth band may also be found to feed on the same prey (Vaudo and Heithaus 2011).

Notably, small catsharks were caught in lower densities than medium and large catsharks at their most commonly-used depths on both coasts (150-450 m depth strata). A possible explanation for this might be different substrate preferences; with small individuals migrating up into the water column or into rocky-reef habitats after birth, where trawling does not occur. For example, previous work on brown catsharks (*Apristurus brunneus*) and filetail catsharks (*Parmaturus xaniurus*) have reported ontogenetic migrations, with juveniles inhabiting the mid-water column after birth and shifting to a more demersal lifestyle with growth (Ebert *et al*. 2006). Moreover, small sharks have also been shown to have greater mobility than large sharks (Scacco *et al*. 2002, Rey *et al*. 2005), perhaps enabling them to avoid capture by the trawl net. Conversely, the preponderance of larger individuals at all depths may be attributed to their greater size, broader environmental tolerance or overall competitive dominance (Ferretti *et al*. 2010).

On comparing the distribution of the two catshark species by sex, differences were noted in the distribution of male and female *H. regani*. Male *H. regani* appeared to inhabit deeper depths than females on both coasts. The use of inshore areas as nursery grounds by pregnant females is a common trait among sharks (Springer 1967, Richardson *et al*. 2000b). Since male *H. regani* are known to attain larger sizes than females (Bass *et al*. 1975, Compagno 1984, Richardson *et al.* 2000b), the partial segregation evident between them could also be attributed to sexual dimorphism and the morphological changes associated with ontogeny. However, an alternative explanation could be the avoidance of aggressive males and the associated energy required for mating activities (Klimley 1987, Hight and Lowe 2007, Sims 2003, Papastamatiou 2008, Speed *et al*. 2011).

Catch data for *S. capensis* showed no difference in the distribution of males and females. A study on *Scyliorhinus canicula* reported a similar pattern, with the authors attributing the lack of sexual segregation to the relatively similar life-history traits observed in oviparous shark species (Klimley 1987, Rodríguez-Cabello *et al*. 2007).

This study supports the hypothesis that sharks with similar morphologies and lifestyles partition their habitat on intra- and interspecific levels to reduce the intensity of competition between them. The catsharks under study here displayed both intra- and interspecific size-based segregations, which could be assumed to arise from either morphological changes associated with ontogeny, changes in the habitat of their preferred diet items, a means to prevent predation by larger sharks, or size-based changes in habitat use that may be associated with parturition or nursery grounds (Springer 1967, Olaso *et al*. 2005, Escobar-Porras 2009, Flammang *et al*. 2011). This study has also revealed possible differences in the vulnerability of the two species to trawling. Further investigation of commercial by-catch is thus necessary, as it will improve our understanding of the impacts of trawling on the different sex and age classes of these catshark species. Such information will be important in developing strategies to mitigate the impact of trawling, especially on *S. capensis*.

In future, studies evaluating the distributional patterns of catsharks should aim to combine sampling by trawling and long-line. Long-line fishing can occur over rough grounds that are not available to the trawl, but typically selects larger individuals than trawling. Therefore combining both fishing methods may reduce the biases associated with each method. Using one method assumes that the abundance of *H. regani* and *S. capensis* are similar on both untrawlable (rocky-reef habitats) and trawlable grounds, as long-lining may indirectly target large individuals that prefer rocky-reef habitats whereas trawling may target individuals who prefer sandy habitats. The use of baited camera traps on rough grounds is also recommended to get unbiased estimates of the size-structure in catshark populations on rough grounds.

Also, because the sex ratios were collected over different seasons the data presented here may not be sufficient to conclusively infer any form of sexual segregation, as any observed differences may simply be attributed to bias in sampling. Further investigation which includes data from commercial trawlers, that are operational throughout the year, is suggested for future studies, as it could provide further insights into how the reproductive behaviours of these species influence their distributional patterns at different times of the year.

This distributional data should also be combined with diet data to test whether the diets of the two species reflect this observed habitat separation. This information will contribute to a better understanding of how size and sex based changes in their distributional patterns are influenced by competitive interactions for food resources. This will be discussed further in Chapter 4.

Chapter Four

Spatial and ontogenetic variability in the feeding habits of two co-occurring catsharks (Scyliorhinidae) caught around the coasts of South Africa: Evidence for resource partitioning?

Abstract

Understanding the feeding habits of sharks is important for the formation of conservation strategies as it provides vital information on habitat preference and food-web structure. In South Africa, *H. regani* and *S. capensis* are perhaps the most common demersal catsharks caught in trawls on the West and South coasts. In spite of their abundance in trawls, dietary information on these benthic catsharks is limited to only two studies. By analysing samples collected on research surveys on the West and South coasts of South Africa from 2014 to 2015, this study provides the first comprehensive attempt at understanding the diets of these co-occurring catsharks by coast, depth stratum and size class. In both catsharks, the most important prey items consumed were: (1) crustaceans, (2) cephalopods and (3) teleosts, with prey items such as chondrichthyans, poriferans, polychaetes, gastropods and urochordates contributing less to their diet. On comparison, crustaceans and cephalopods were observed to be of equal importance in the diet of *H. regani*, while crustaceans appeared to be more important in the diet of *S. capensis*. The results indicated a relatively uniform feeding behaviour, with no significant difference in the major prey groups consumed between coasts and across depths for either species. However, in terms of the individual prey species consumed, a significant difference was noted between coasts for both species, and between depth strata for *S. capensis* on the

South Coast. It was argued that this difference possibly indicates spatial differences in prey availability, owing to the different patterns of habitat use (around coasts and between depths) observed in the two catshark species. A significant ontogenetic dietary shift was noted in the diet of *H. regani* on the West Coast, with individuals consuming larger prey items with increasing size. Although no significant ontogenetic shift was noted in the diet of *S. capensis*, a similar pattern appeared to be apparent on both coasts, with individuals also consuming larger prey items with increasing size. These ontogenetic dietary shifts can be attributed to changes in morphology (gape size) or metabolic requirements with growth, or to the "bigger-deeper pattern", with large individuals inhabiting deeper waters and thus increasing their encounter rate with large prey.

Introduction

Understanding the trophic ecology of a species through dietary analysis provides important information on food web dynamics (Krebs 1989, Rinewalt 2007, Vaudo and Heithaus 2011). Knowledge of diet is also important in evaluating ecological requirements, as it gives vital information on habitat preference, resource partitioning, predation, competition and trophic ecology (Talent 1976, Stillwell and Kohler 1982, Newman 2003, Fanelli *et al*. 2009). Such ecological information is particularly important in the formation of conservation strategies, and thus plays a key role in the protection of species and ecosystems (Hoggarth *et al*. 2005, Simpfendorfer *et al*. 2011, Braga *et al*. 2012).

In shark ecology, diet is perhaps one of the most thoroughly researched areas (Cortés 1999, Simpfendorfer *et al.* 2011, Ferretti *et al*. 2010, Bornatowski *et al*.

2014). This is because sharks, through predation, play a vital part in the structure and functioning of marine environments (Wetherbee and Cortés 2004, Myers *et al*. 2007, Braccini 2008). Although the popular view of sharks is as large (> 3 m) top predators, the majority of sharks are small, meso-predatory species (Olaso *et al.* 2005, Ferretti *et al*. 2010, Caut *et al*. 2013). Meso-predatory sharks are mid-trophic level species that range from 0.2 to < 1.5 m in size (Ferretti *et al*. 2010). Owing to their position in the food web, meso-predators play an important role in linking upper and lower trophic levels, and thus contribute significantly to ecosystem dynamics and stability (Ritchie and Johnson 2009, Vaudo and Heithaus 2011).

Following substantial declines in the numbers of large sharks, due to direct and indirect fishing pressure (Baum *et al*. 2003, Dulvy *et al*. 2008, Ferretti *et al*. 2010), there has been an increase in dietary studies on large sharks and on the influences their declines have on the regulation of their prey populations (Heithaus *et al*. 2008, Ferretti *et al*. 2010). In recent times however, commercial fishing pressure has shifted further offshore into deeper waters (Aldebert 1997, Klaer 2001, Sink *et al*. 2012), where communities are largely composed of small, less-resilient, meso-predatory shark species (Rogers and Ellis 2000, Graham *et al*. 2001, Ferretti *et al*. 2010). Despite this shift, studies evaluating the diet and feeding habits of deep-sea, mid-trophic level sharks are few when compared to similar studies on the more coastal, upper-trophic level shark species (Heithaus *et al*. 2010, Vaudo and Heithaus 2011, Caut *et al*. 2013).

Catsharks are intermediate sized, mid-trophic level species that are both predators and prey in the food web. Through linking different trophic levels, catsharks contribute substantially to the stability and functioning of marine ecosystems (Vaudo and Heithaus 2011). Catsharks are particularly vulnerable to overexploitation, with many species forming frequent by-catch of sports fishers and commercial trawlers (Richardson *et al.* 2000b, Myers & Worm 2003, Ebert *et al.* 2006, Didier *et al*. 2012). An understanding of the trophic ecology of catsharks is thus crucial, as it allows us to predict the possible effects that their removal may have on an ecosystem (Navia *et al*. 2010, Braga *et al*. 2012, Bornatowski *et al*. 2014).

Although literature does exist on the feeding habits of catshark species (Fariña and Ojeda 1993, Ebert *et al*. 1996, Olaso *et al*. 2005, Escobar-Porras 2009) studies are fragmented, with quantitative dietary studies lacking for a number of species. This is particularly true for the small meso-predatory catsharks, *H. regani* and *S. capensis*. These catsharks frequent the South African coastline, occupying rather similar geographic and bathymetric distributions and feeding on similar prey items (Compagno 1984, Ebert *et al.* 1996, Didier *et al*. 2012, Ebert 2013). They are also the most common catsharks taken as by-catch by the demersal trawling industry that targets the two Cape hake species (*M. capensis* and *M. paradoxus*) on the West and South coasts of South Africa (Richardson *et al*. 2000b, Petersen *et al*. 2008).

In spite of their abundance, similar feeding habits and frequency of capture in trawls, dietary information on these demersal catsharks is limited to only two studies (Ebert *et al*. 1996, Richardson *et al*. 2000b). The initial study by Ebert *et al.* (1996) was a preliminary study on the diet of all catsharks caught in demersal trawls on the West Coast of South Africa, whereas the study by Richardson *et al*. (2000b) focused on the basic biology of *H. regani*.

Knowledge of the diet of these catshark species, that are so closely associated with the commercial trawling industry, is crucial to their management and conservation as it provides important information of their ecology and their influence on the demersal food web. Thus in an attempt to better understand the feeding habits of *H. regani* and *S. capensis* this chapter gives an overview of the diet of these two catshark species, with a specific focus on intra-and interspecific changes in diet with coast, depth stratum and size class. This information will be used to describe how intra- and interspecific competition might shape the diet of *H. regani* and *S. capensis* around South Africa, and will form the basis for a first attempt to understand resource partitioning within and between these co-occurring species.

Results

The stomachs of 179 *H. regani* and 162 *S. capensis* were examined, with 111 *H. regani* and 74 *S. capensis* stomachs examined from the West Coast and 68 *H. regani* and 88 *S. capensis* stomachs examined from the South Coast (Table 9). One large *H. regani* and two large *S. capensis*, each sampled at 350 m depth on the West Coast (Tables 9, 10 and 11), were recorded with empty stomachs.

The *H. regani* specimens sampled on the West Coast covered a wider size range than those on the South Coast, and although the mean size for the South Coast sample was greater than for the West Coast (Table 9), the difference was not significant (df= 104, p > 0.05). Of the *H. regani* stomachs analyzed, on both coasts, more large individuals were sampled than small and medium individuals combined (Table 10).

Table 9: Illustrates the number (n), size range and mean size (± SE) of *H. regani* and *S. capensis* sampled on the West and South coasts. In column n, the number in brackets denotes to the number of empty stomachs

	H. regani				***S. capensis***			
Coast	***n***	**Size range (cm, TL)**	**Mean size (cm, TL)**	**±SE**	***n***	**Size range (cm, TL)**	**Mean size (cm, TL)**	**±SE**
West Coast	111(1)	19.0-65.0	50.1	9.6	74(2)	34.0-90.0	56.5	1.5
South Coast	68	40.0-63.0	51.1	0.9	88	28.0-92.0	46.4	1.3

Table 10: Illustrates the number (n) and mean size (± SE) of *H. regani* and *S. capensis* sampled for each size class on the West and South coasts. In column *n*, the number in brackets denotes the number of empty stomachs. “+” is where values are greater than 0 but less than the minimum displayable value and “-“ denotes to null/unknown values

	H. regani						***S. capensis***					
Coast	**West Coast**			**South Coast**			**West Coast**			**South Coast**		
Size	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**
Small	16	28.7	1.2	-	-	-	1	34.5	-	6	31.2	0.3
Medium	39	40.8	0.4	20	43.2	0.3	61	50.1	0.1	76	47.4	+
Large	56 (1)	55.3	0.8	48	52.7	0.9	12 (2)	76.7	0.2	6	86.3	0.4

The most *H. regani* individuals were sampled at 250 m depth on the West Coast and at 150 m depth on the South Coast, with an apparent increase in mean size with increasing depth observed on the West Coast only (Table 11). Notable is the absence of small *H. regani* individuals on the South Coast, and the rather small sample sizes at 450 m depth on the West Coast and at 350 m depth on the South Coast (Tables 10 and 11).

The *S. capensis* specimens sampled on the South Coast covered a wider size range than those on the West Coast, and although the mean size on the West Coast was greater than for the South Coast, the difference was not significant (df= 101, $p > 0.05$) (Table 9). On both coasts, more medium *S. capensis* were sampled than small and large individuals combined (Table 10). Notable is the low number of small individuals sampled on the West Coast (Table 10). The most *S. capensis* individuals were sampled at 350 m depth on the West Coast and at 150 m depth on the South Coast (Table 11), with an apparent increase in mean size with increasing depth observed on the West Coast, as well as on the South Coast up until 350 m depth (Table 11).

Table 11: Illustrates the number (n) and mean size (± SE) of *H. regani* and *S. capensis* sampled in each depth stratum on the West and South coasts. In column *n*, the number in brackets denotes the number of empty stomachs. "-" denotes to null/unknown values

	H. regani						***S. capensis***					
Coast	**West Coast**			**South Coast**			**West Coast**			**South Coast**		
Depth	***N***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**
150	29	38.0	2.3	41	47.9	1.0	10	47.1	2.3	52	42.6	1.2
250	52	47.7	1.3	20	52.1	1.7	10	51.0	3.2	12	53.0	4.8
350	29 (1)	48.7	1.6	2	44.5	3.5	37 (2)	52.8	2.4	18	61.9	3.3
450	1	58.0	-	5	52.2	4.1	17	60.9	2.3	6	51.5	2.6

For *H. regani*, most individuals were collected between Hondeklipbaai and Doringbaai, off Cape Town and off Cape Agulhas (Figure 38). Similarly, large numbers of *S. capensis* were collected off Hondeklipbaai, and between Cape Agulhas and Mossel Bay (Figure 38).

In total, 10 prey groups were identified in the diets of the two catshark species, including algae, Cephalopoda, Chondrichthyes, Crustacea, Gastropoda, Polychaeta, Porifera, Teleostei, Urochordata and unidentified. Within these prey groups 36 individual prey species were identified, including one alga, five cephalopods, one chondrichthyan, 15 crustaceans, one sponge, one polychaete, one gastropod, 10 teleosts and one urochordate (Appendices 1 and 6). Throughout this chapter, the prey classes are referred to as ‘prey groups’.

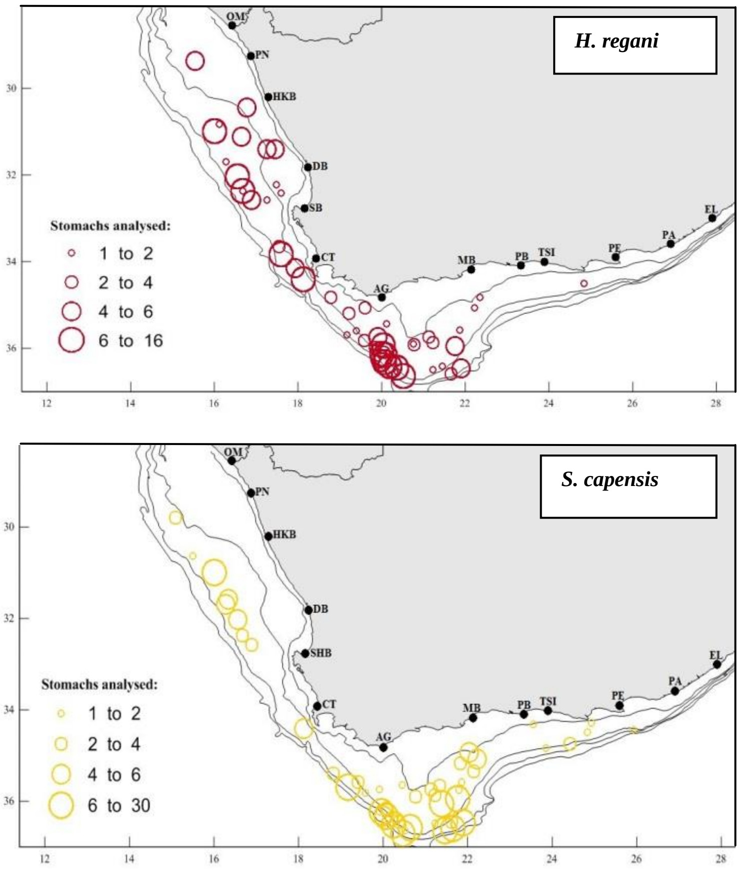


Figure 38: Location and number of *H. regani* and *S. capensis* sampled on the West and South coasts whose stomachs were used in the diet analysis. See Figure 1 for key to place names and depth contours.

Diet of *Holohalaelurus regani*

Frequency of occurrence data for prey groups indicated no significant difference in the diet of *H. regani* between coasts ($p > 0.05$). On both coasts, crustaceans and cephalopods were the most important prey groups consumed (IRI%), and constituted the majority of prey by %FO, %N and %W (Figure 38, Table 12). Unidentified and “other” prey items contributed the least to all four measures of prey abundance (Figure 38, Table 12). Notably, the weights of the teleost and “other” prey group were underestimated owing to the lack of anatomical remains that could be used to establish original fish size.

There was a significant difference in the frequency of occurrence of the prey species in the diet of *H. regani* between coasts (X^2= 54.48, df= 25, p < 0.05). Of the identifiable prey species, the shallow-water hermit crab *Sympagurus dimorphus*, was the most important prey (IRI%) item consumed on both coasts, occurring in > 50% of stomachs and contributing the most in terms of %N and %W (Appendix 3). The lesser-flying squid *Todaropses eblanae,* was of secondary importance, and occurred in > 30% of catsharks stomachs on both coasts (Appendix 3).

Table 12: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of *H. regani* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable valuable and "-" denotes to null/unknown values

	West Coast				**South Coast**			
Prey Groups	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Cephalopoda	82.7	58.3	27.6	43.9	89.7	59.5	37.9	50.3
Crustacea	84.5	27.9	72.3	52.4	88.2	32.2	62.0	47.9
Teleostei	50.0	11.3	+	3.5	42.6	6.3	0.1	1.5
Other	0.9	0.8	+	+	7.3	0.9	-	+
Unidentified	10.9	1.6	-	0.1	7.3	1.1	-	0.1

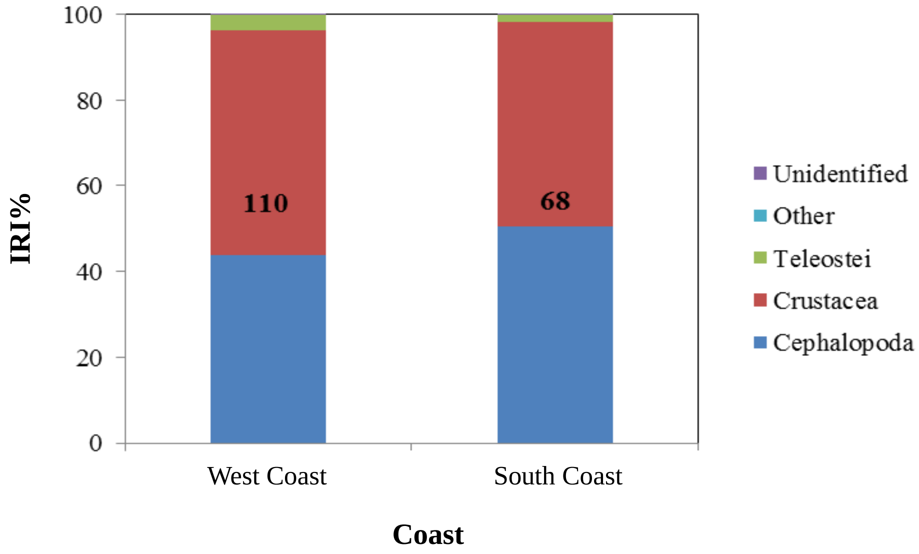


Figure 39: Major prey groups (IRI%) identified in the stomachs of *H. regani* on the West and South coasts. Data labels represent number of stomachs containing food.

Other frequently consumed prey species of *H. regani* on the West Coast were hagfish egg case remains, lightfish *Maurolicus walvisensis*, Southern-cuttlefish *Sepia australis*, and mantis shrimp *Pterygosquilla armata capensis* (Appendix 3). Whereas on the South Coast, other frequently consumed prey species in the diet of *H. regani* were red spotted crabs, *Mursia cristiata*, *P. a. capensis*, *S. australis*, *Lycoteuthis lorigera* (squid), *Loligo reynaudii* (chokka squid), and unidentified gammarid amphipods (Appendix 3). Several other species of crustaceans, cephalopods, teleosts, sponges, elasmobranch egg case remains and algal material were also observed in the diet of *H. regani*, but were of minor importance (IRI%) (Appendix 3). Notably, unidentified cephalopods and teleost were frequently observed in the diet of *H. regani* on both coasts (Appendix 3).

Diet of *Holohalaelurus regani* by depth

Frequency of occurrence data indicated no significant difference in the prey groups identified in the diet of *H. regani* between depth strata on either coast ($p > 0.05$). Cephalopods and crustaceans were the most important (IRI%) prey groups in the diet of *H. regani* across all depth strata on the West and South coasts, and contributed the most to the diet in terms of %FO, %N and %W (Figure 39, Table 13). Teleosts were also frequently consumed in all depth strata, but contributed less in terms %N and %W (Table 13). No statistical analyses were conducted for the 450 m depth stratum on the West Coast and the 350 m depth stratum on the South Coast due to small sample sizes at these depths.

Table 13: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of *H. regani* at different depths on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (%IRI) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

	Coast	**West Coast**				**South Coast**			
Depth (m)	**Prey Groups**	**% FO**	**% N**	**% W**	**IRI%**	**% FO**	**% N**	**% W**	**IRI%**
150	Cephalopoda	75.9	58.1	21.7	39	85.4	55.9	31.3	43.3
	Crustacea	82.8	31.9	78.3	58.7	90.2	37.1	68.7	55.6
	Teleostei	41.4	8.8	-	2.3	36.6	4.8	-	1.0
	Other	3.4	0.6	-	+	7.3	1.0	-	+
	Unidentified	3.4	0.6	-	+	7.3	1.3	-	0.1
250	Cephalopoda	86.5	54.4	30.3	44.4	100.0	66.5	52.2	64.6
	Crustacea	86.5	29.5	69.5	51.9	85.0	24.2	47.4	33.1
	Teleostei	46.2	12.6	0.1	3.5	45.0	8.7	0.4	2.2
	Other	1.9	1.2	+	+	-	-	-	-
	Unidentified	15.4	2.3	-	0.2	5.0	0.6	-	+
350	Cephalopoda	82.1	65.9	27.4	47.6	100.0	42.9	55.4	65.9
	Crustacea	82.1	21.5	72.6	48	50.0	42.9	44.6	29.3
	Teleostei	64.3	10.8	-	4.3	50.0	14.3	-	4.8
	Other	7.1	0.4	-	+	-	-	-	-
	Unidentified	10.7	1.3	-	0.1	-	-	-	-
450	Cephalopoda	100.0	22.2	-	11.1	80.0	61.4	29.8	41.1
	Crustacea	100.0	55.6	100.0	77.8	100.0	27.1	70.2	54.9
	Teleostei	100.0	22.2	-	11.1	80.0	7.1	-	3.2
	Other	-	-	-	-	40.0	2.9	-	0.6
	Unidentified	-	-	-	-	20.0	1.4	-	0.2

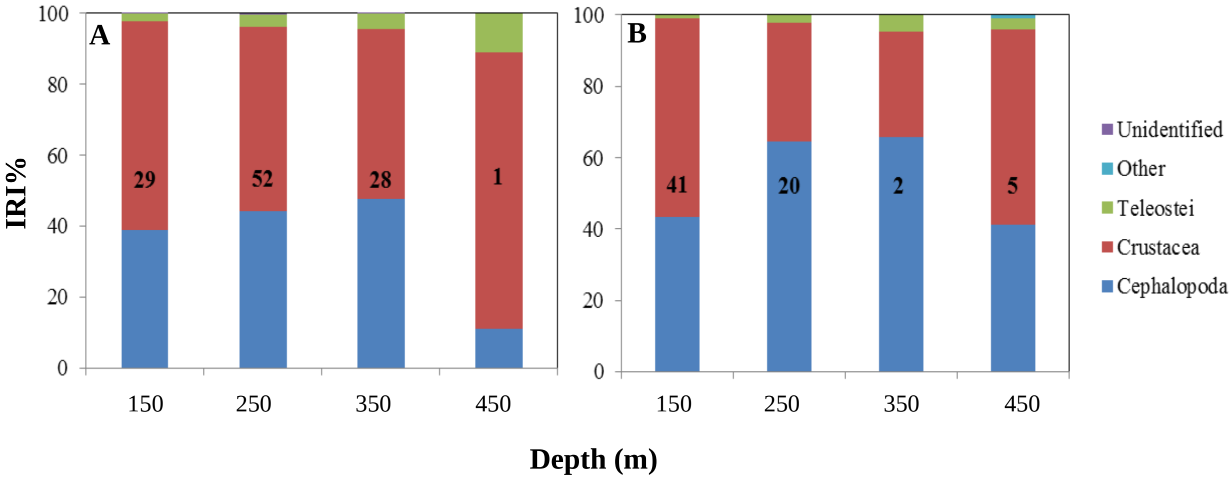


Figure 40: Major prey groups (IRI%) identified in the stomachs of *H. regani* at different depths on the West (**A**) and South (**B**) coasts. Data labels represent number of stomachs containing food in each depth stratum.

On analysis, frequency of occurrence data indicated no significant difference in the prey species identified in the diet of *H. regani* by depth. Of the identifiable prey species, *Sympagurus dimorphus* was the most important (IRI%) prey item consumed across all depth strata on the West and South coasts (Appendices 4 and 5). *Todaropses eblanae* was almost as prevalent, and primarily consumed in the 250 and 350 m depth strata on the West Coast and in the 150 and 250 m depth strata on the South Coast (Appendices 4 and 5). Other frequently consumed prey species in the diet of *H. regani* on the West Coast were *Pterygosquilla armata capensis* and unidentified gammarid amphipods in the 150 m depth stratum, and hagfish egg remains, *Sepia australis* and *Maurolicus walvisensis* in the 250 and 350 m depth strata (Appendix 4). *Pterygosquilla armata capensis* was also frequently consumed by *H. regani* in the 350 m depth stratum, along with *Lycoteuthis lorigera*, *Mursia cristiata* and the deep-water hermit crab *Parapagurus bouvieri* (Appendix 4).

On the South Coast, frequently consumed prey species in the diet of *H. regani* in the 150 m depth stratum were *Pterygosquilla armata capensis*, *Sepia australis*, *Mursia cristiata,* unidentified gammarid amphipods and *Loligo reynaudii* (Appendix 5). In the 250 m depth stratum, *Lycoteuthis lorigera*, *S. australis* and *Maurolicus walvisensis* typified the diet of *H. regani* (Appendix 5). *Lycoteuthis lorigera* also frequented the diet of *H. regani* in the 450 m depth stratum, along with *M. cristiata*, green algae, elasmobranch egg case remains, *Parapagurus bouvieri*, and two Caridae shrimp species, *Acanthephyra pelagica* and *Glyphocrangon* sp (Appendix 5).

Diet of *Holohalaelurus regani* by size

Frequency of occurrence data indicated no significant difference in the prey groups consumed by *H. regani* between size classes on either coast (p > 0.05). Cephalopods and crustaceans were the most commonly consumed prey groups across all size classes on the West and South coasts, as indicated by their high %FO and %N (Table 14). Teleosts were also commonly consumed by all size classes on both coasts, with their frequency of occurrence appearing to increase with increasing predator size on the West Coast only (Table 14). There appeared to be a notable increase in the %W of cephalopod prey consumed with increasing *H. regani* size on both coasts, with no such trend noted for teleosts (Table 14). Notably, the average weight of crustaceans increased with increasing *H. regani* size (Figure 41).

Considering IRI%, crustaceans appeared to be more important than cephalopods in the diet of small *H. regani* on the West Coast, owing to their comparatively high %W (Figures 40 and 41, Table 14). In the diet of medium and large *H. regani*, cephalopods and crustaceans appeared to be of approximately equal importance (Figure 40, Table 14).

Table 14: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of small, medium and large *H. regani* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “+” is where values are greater than 0 but less than the minimum displayable value and “-“ denotes to null/unknown values

	Coast	**West Coast**				**South Coast**			
Size	**Prey Group**	**% FO**	**% N**	**% W**	**IRI %**	**% FO**	**% N**	**% W**	**IRI %**
Small	Cephalopoda	56.3	31.0	1.1	14.3	-	-	-	-
	Crustacea	68.8	50.0	97.0	80.3	-	-	-	-
	Teleostei	37.5	14.3	2.0	4.8	-	-	-	-
	Other	-	-	-	-	-	-	-	-
	Unidentified	12.5	4.8	-	0.5	-	-	-	-
Medium	Cephalopoda	84.6	60.6	15.6	41.1	90.0	49.5	37.8	49.5
	Crustacea	79.5	25.9	84.4	55.9	75.0	36.4	62.2	46.6
	Teleostei	38.5	12.0	-	3.0	50.0	12.1	-	3.8
	Other	5.1	1.4	0.1	+	-	-	-	+
	Unidentified	-	-	-	-	10.0	1.9	-	0.1
Large	Cephalopoda	89.1	59.7	31.1	45.8	89.6	61.9	37.9	50.0
	Crustacea	92.7	26.9	68.9	50.3	93.8	31.2	62.0	48.8
	Teleostei	61.8	10.7	-	3.8	39.6	4.9	0.1	1.1
	Other	5.5	0.6	-	+	10.4	1.1	-	0.1
	Unidentified	10.9	2.1	-	0.1	6.3	0.9	-	+

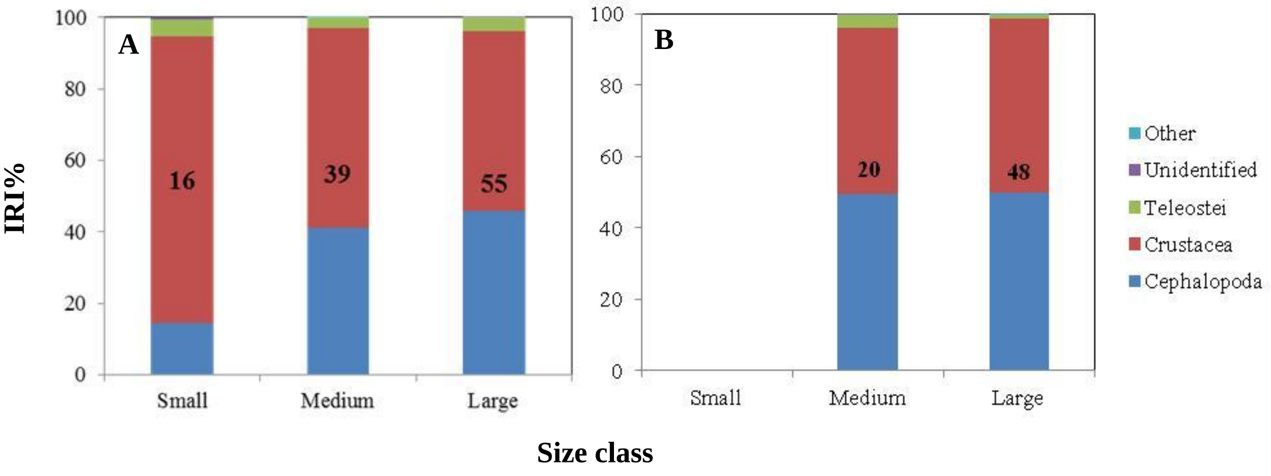


Figure 41: Major prey groups (IRI%) identified in the stomachs of small, medium and large *H. regani* on the West (**A**) and South (**B**) coasts. Data labels represent number of stomachs containing food for each size class.

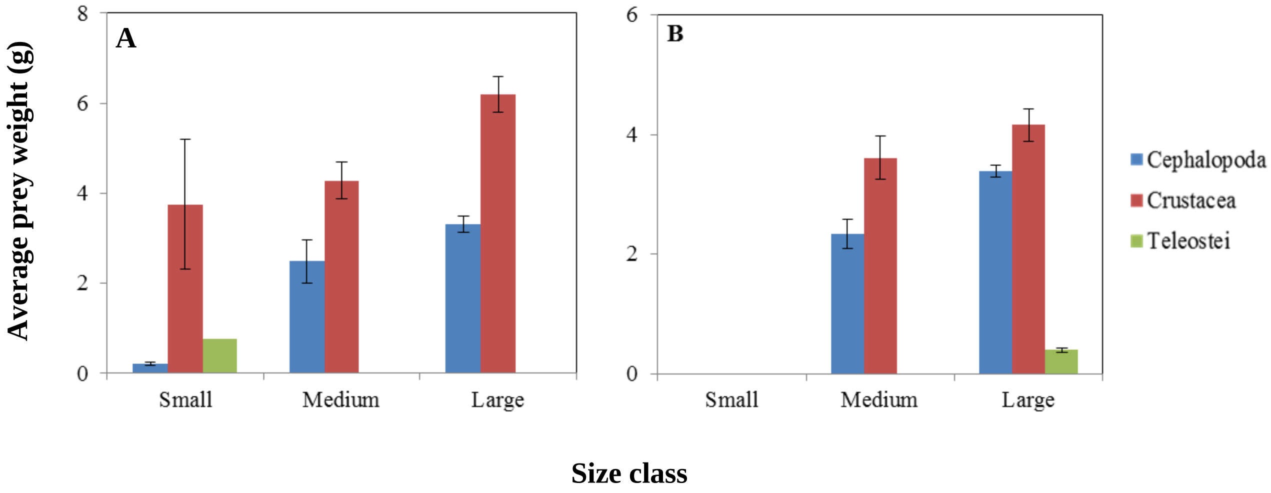


Figure 42: Illustrating the average weights (g) of the major prey groups (± SE) consumed by small, medium and large *H. regani* on the West (**A**) and South (**B**) coasts.

There were significant differences in the frequency of occurrence of the individual prey species consumed by *H. regani* between size classes on the West Coast (X^2= 91.79, df= 38, $p < 0.05$). On both coasts, *Sympagurus dimorphus* was the single most important (IRI%) identifiable prey item in the diet of small, medium and large *H. regani*, and contributed the most in terms of %FO, %N and %W (Appendices 6 and 7). In the diet of small *H. regani* on the West Coast, *Pterygosquilla armata capensis* was the second most frequent prey item consumed, followed by amphipods and *Sepia australis* (Appendix 6). *Pterygosquilla armata capensis* and *S. australis* were also frequently consumed by medium *H. regani* on the West Coast, along with *Todaropses eblanae*, *Mursia cristiata* and *Maurolicus walvisensis* (Appendix 6). The diet of large *H. regani* on the West Coast was supplemented by hagfish egg case remains, *Parapagurus bouvieri* and *Lycoteuthis lorigera* (Appendix 6).

Other prevalent prey items in the diet of medium *H. regani* on the South Coast were *Todaropses eblanae*, *Loligo reynaudii*, *Lycoteuthis lorigera*, *Sepia australis*, *Pterygosquilla armata capensis* and *Mursia cristiata* (Appendix 7).

With the exception of *Loligo reynaudii* and the addition of unidentified gammarid amphipods and *Parapagurus bouvieri*, all the above mentioned prey items were also frequently consumed by large *H. regani* on the South Coast (Appendix 7).

Diet of *Scyliorhinus capensis*

Frequency of occurrence data indicated no significant difference in the prey groups consumed by *S. capensis* between coasts ($p > 0.05$). Crustaceans were the most important prey group (IRI%) consumed on both coasts, and contributed the most in terms of %FO, %N and %W (Figure 42, Table 15). Cephalopods were the second most common prey group (IRI% and %FO) consumed by *S. capensis*, followed by teleosts, “other” and unidentified prey (Figure 42, Table 15).

There was a significant difference in the frequency of occurrence of the prey species in the diet of *S. capensis* between coasts ($X^2 = 72.29$, df= 28, $p < 0.05$). *Sympagurus dimorphus* was the most important (IRI%) identifiable prey item consumed on both coasts, and contributed the most in terms of %FO, %N and %W (Appendix 8). The second most frequently consumed prey item was *Todaropses eblanae* on the West Coast whereas in contrast *Mursia cristiata* was more frequently consumed on the South Coast (Appendix 8).

Table 15: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of *S. capensis* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “-“ denotes to null/zero values

	West Coast				South Coast			
Prey Items	**% FO**	**% N**	**% W**	**IRI %**	**% FO**	**% N**	**% W**	**IRI %**
Cephalopoda	56.7	30.5	16.3	24.1	42.1	20.4	15.2	10.9
Crustacea	60.8	48.9	79.0	70.3	81.8	68.3	78.2	87.3
Teleostei	29.7	11.7	4.6	4.4	13.6	7.2	6.41	1.3
Other	16.2	5. 2	-	0. 7	22.7	2.3	0.2	0.4
Unidentified	10.8	3. 4	-	0. 3	7.9	1.8	-	0.1

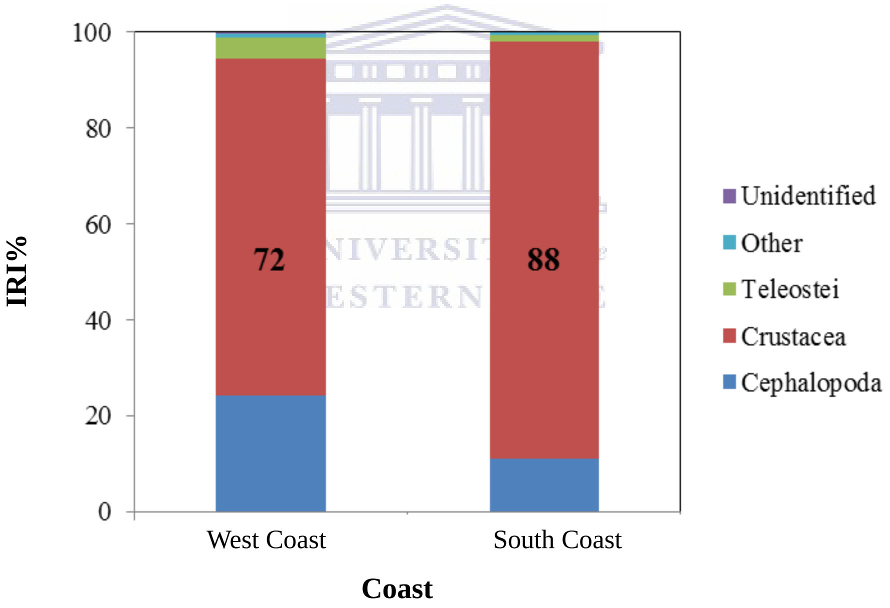


Figure 43: Major prey groups (IRI%) identified in the stomachs of *S. capensis* on the West and South coasts. Data labels represent number of stomachs containing food.

Other common prey items in the diet of *S. capensis* on the South Coast were *Callianasa* sp. (mud shrimp), *Pterygosquilla armata capensis*, *Todaropses eblanae*, unidentified gammarid amphipods and *Dyspanopeus* sp. (choc tip crab) (Appendix 8). Data on prey items of lesser importance (%IRI) are presented in Appendix 8.

Notably, unidentified cephalopods and teleosts were also frequently consumed by *S. capensis* on both coasts (Appendix 8).

Diet of *Scyliorhinus capensis* by depth

Frequency of occurrence data indicated no significant difference in the prey groups consumed by *S. capensis* between depth strata on the West and South coasts ($p > 0.05$). On both coasts, crustaceans appeared to be the most important (IRI%) prey group identified in the diet of *S. capensis* across all depth strata, and contributed the most in terms of %FO and %W (Figure 43, Table 16). This is with the exception of the 350 m depth stratum on the South Coast, where cephalopods appeared to be more important (Figure 43, Table 16). Cephalopods were almost as prevalent (in terms of %FO and %N), but appeared to contribute less in terms of %W (Figure 43, Table 16). Teleosts were most frequently encountered in the 350 m depth stratum on both coasts, whereas "other" prey items were most frequently encountered in the 350 m depth stratum on the West Coast, and in the 250 m depth stratum on the South Coast (Figure 43, Table 16). There was a significant difference in the FO of the individual prey species consumed in each depth stratum on the South Coast only ($X^2 = 104.07$, df= 60, $p < 0.05$). *Sympagurus dimorphus* constituted the majority of prey items in the diet of *Scyliorhinus capensis* across all depths on the West Coast, but only in the 250 and 450 m depth strata on the South Coast (Appendices 9 and 10).

Table 16: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of *S. capensis* at different depths on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

	Coast	**West Coast**				**South Coast**			
Depth (m)	**Prey Groups**	**% FO**	**% N**	**% W**	**IRI %**	**% FO**	**% N**	**% W**	**IRI %**
150 m	Cephalopoda	50.0	32.0	12.1	17.8	26.9	16.2	4.7	3.9
	Crustacea	70.0	48.0	87.9	76.7	86.5	76.6	82.0	94.5
	Teleostei	-	-	-	-	15.4	3.8	9.2	1.4
	Other	10.0	4.0	-	0.3	3.8	0.9	0.5	+
	Unidentified	40.0	16.0	-	5.2	11.5	2.6	-	0.2
250 m	Cephalopoda	60.0	50.0	28.9	41.0	41.7	15.4	6.5	5.6
	Crustacea	70.0	25.0	57.2	49.8	91.7	71.8	93.5	93.2
	Teleostei	30.0	16.7	13.9	8.0	16.7	5.1	-	0.5
	Other	20.0	5.6	-	1.0	16.7	5.1	-	0.5
	Unidentified	10.0	2.8	-	0.2	8.3	2.6	-	0.1
350 m	Cephalopoda	60.0	33.3	28.4	35.3	72.2	36.6	43.6	54.3
	Crustacea	54.3	37.8	68.8	55.1	55.6	36.6	46.4	43.2
	Teleostei	40.0	16.7	2.7	7.4	77.8	19.7	10.0	-
	Other	22.9	8.9	-	1.9	+	+	-	2.6
	Unidentified	8.6	3.3	-	0.3	38.9	7.0	-	-
450 m	Cephalopoda	58.8	17.9	4.6	10.0	83.3	20.9	9.9	13.5
	Crustacea	70.6	73.1	90.6	87.2	100.0	72.1	89.9	85.3
	Teleostei	29.4	7.7	4.8	2.8	33.3	7.0	-	1.2
	Other	5.9	1.3	-	0.1	-	-	-	-
	Unidentified	-	-	-	-	-	-	-	-

The brachuryan crab *Mursia cristiata* was the primary prey item in the diet of *S. capensis* in the 150 and 350 m depth strata on the South Coast. These crabs were also frequently consumed in the 350 and 450 m depth strata on the West Coast (Appendices 9 and 10). *Todaropses eblanae* was also frequently consumed between the 250 and 450 m depth strata on the West Coast, and in the 350 and 450 m depth strata on the South Coast (Appendices 9 and 10).

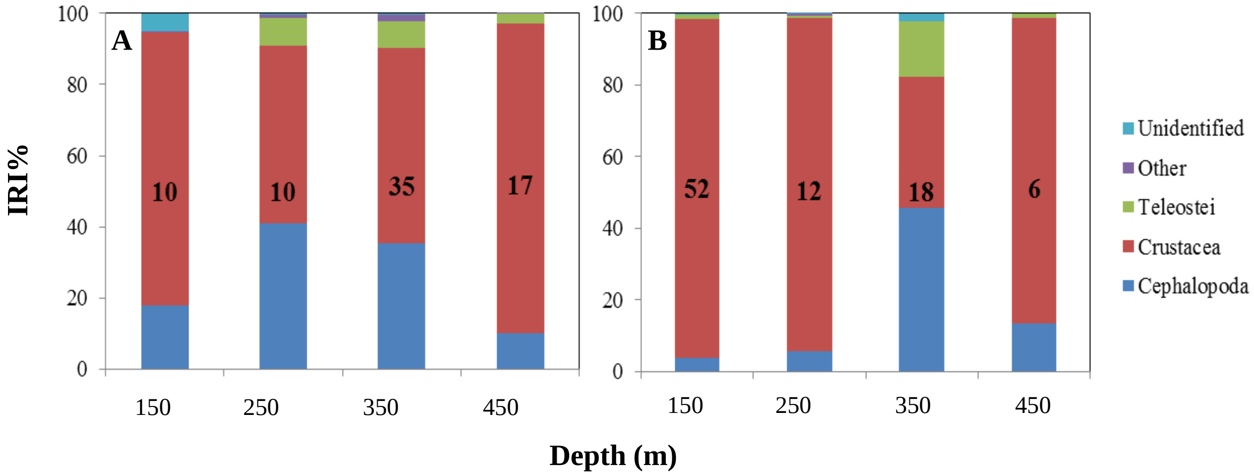


Figure 44: Major prey groups (IRI%) identified in the stomachs of *S. capensis* at different depths on the West (**A**) and South (**B**) coasts. Data labels represent number of stomachs containing food in each depth stratum.

Other frequently consumed prey items in the diet of *Scyliorhinus capensis* on the West Coast were Polychaete species in the 350 m depth stratum, and *Parapagurus bouvieri* and *Solonocera africana* (Caridae shrimp) in the 450 m depth stratum (Appendix 9). On the South Coast, other frequently consumed prey items were unidentified gammarid amphipods and *Pterygosquilla armata capensis* in the 150 and 250 m depth strata and Polychaete species in the 250 and 350 m depth strata (Appendix 10). *Pterygosquilla armata capensis* and *Lycoteuthis lorigera* were also frequently consumed in the 350 m depth stratum, and *P. bouvieri*, *Dyspanopeus* sp., *Acanthephyra pelagica*, unidentified isopods and *Solonocera africana* in the 450 m depth stratum (Appendix 10).

In terms of IRI%, *Sympagurus dimorphus* was the most important prey species consumed across all depths on the West Coast (Appendix 9). On the South Coast, the most important prey species consumed in the different depth strata were *Mursia cristiata* in the 150 m depth stratum, *Todaraopses eblanae* in the 350 m depth stratum and *Sympagurus dimorphus* in the 250 and 450 m depth strata

(Appendix 10).

Diet of *Scyliorhinus capensis* by size

Frequency of occurrence data for prey groups indicated no significant difference in the diet of *S. capensis* between predator size classes on either coast (p > 0.05). Small and medium *S. capensis* predominantly fed on crustaceans (in terms of %FO and IRI%), and to a lesser extent on cephalopods and teleosts (Figure 44, Table 17). The prevalence of cephalopods appeared to increase with increasing size on both coasts, as indicated by the notable increase in %FO, %N and IRI% from medium to large individuals (Figure 44, Table 17). Teleosts also appeared to increase in frequency with increasing size, occurring > 50% of large *S. capensis* stomachs on both coasts (Figure 44, Table 17). Prey items in the "other" category were frequently consumed by medium *S. capensis* on the South Coast, and by medium and large *S. capensis* on the West Coast (Figure 44, Table 17). Notable was the apparent increase in the average weight of cephalopod and crustacean prey with increasing catshark size on both coasts, as well as the increase in teleost weight with increasing catshark size on the West Coast (Figure 45).

On the West Coast, *Sympagurus dimorphus* dominated the diet of medium *S. capensis*, while *Todaropses eblanae* dominated the diet of large *S. capensis* (Appendix 11). Other prevalent prey species in the diet of large *Scyliorhinus capensis* on the West Coast were *Mursia cristiata*, *Parapagurus bouvieri* and elasmobranch egg case remains (Appendix 11). Unidentified gammarid amphipods constituted the majority of prey items in the diet of small *S. capensis* on the South Coast, followed by *Sympagurus dimorphus*, *Mursia cristiata*, *Callianassa* sp., *Sepia australis* and *Dyspanopeus* sp. (Appendix 12).

Table 17: Percentage frequency (%FO), percentage number (%N), percentage weight (%W) and percentage IRI (IRI%) data for the five major prey groups found in the stomachs of small, medium and large *S. capensis* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “-“ denotes to null/unknown values

	Coast	**West Coast**				**South Coast**			
Size	**Prey Category**	**% FO**	**% N**	**% W**	**IRI %**	**% FO**	**% N**	**% W**	**IRI %**
Small	Cephalopoda	100.0	50.0	34.2	42.1	33.3	3.8	14.0	3.2
	Crustacea	100.0	50.0	65.8	57.9	100.0	96.2	86.0	96.8
	Teleostei	-	-	-	-	-	-	-	-
	Other	-	-	-	-	-	-	-	-
	Unidentified	-	-	-	-	-	-	-	-
Medium	Cephalopoda	52.5	25.0	10.7	17.3	42.1	23.0	15.2	11.6
	Crustacea	60.7	53.5	85.7	77.8	82.9	65.2	77.4	85.3
	Teleostei	26.2	12.2	3.6	3.8	26.3	7.5	7.2	2.8
	Other	13.1	4.7	-	0.6	10.5	2.8	0.3	0.2
	Unidentified	13.1	4.7	-	0.6	6.6	1.6	-	0.1
Large	Cephalopoda	75.0	47.3	28.2	45.0	50.0	21.4	16.0	18.3
	Crustacea	58.3	34.5	64.3	45.8	50.0	35.7	84.0	58.5
	Teleostei	50.0	10.9	7.4	7.3	66.7	28.6	-	18.6
	Other	33.3	7.3	-	1.9	-	-	-	-
	Unidentified	-	-	-	-	33.3	14.3	-	4.7

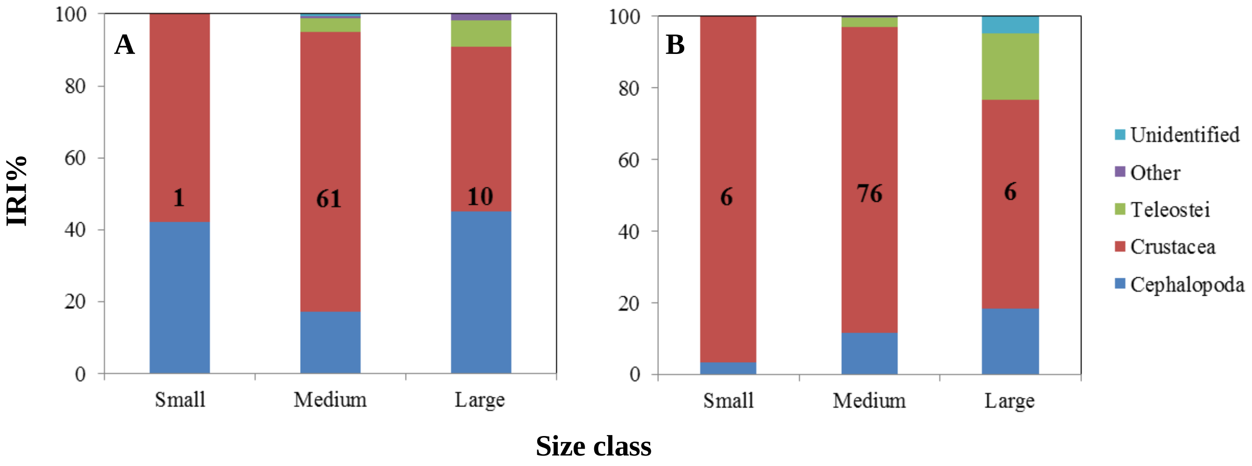


Figure 45: Major prey groups (IRI%) identified in the stomachs of small, medium and large *S. capensis* on the West (**A**) and South (**B**) coasts. Data labels represent number of stomachs containing food for each size class.

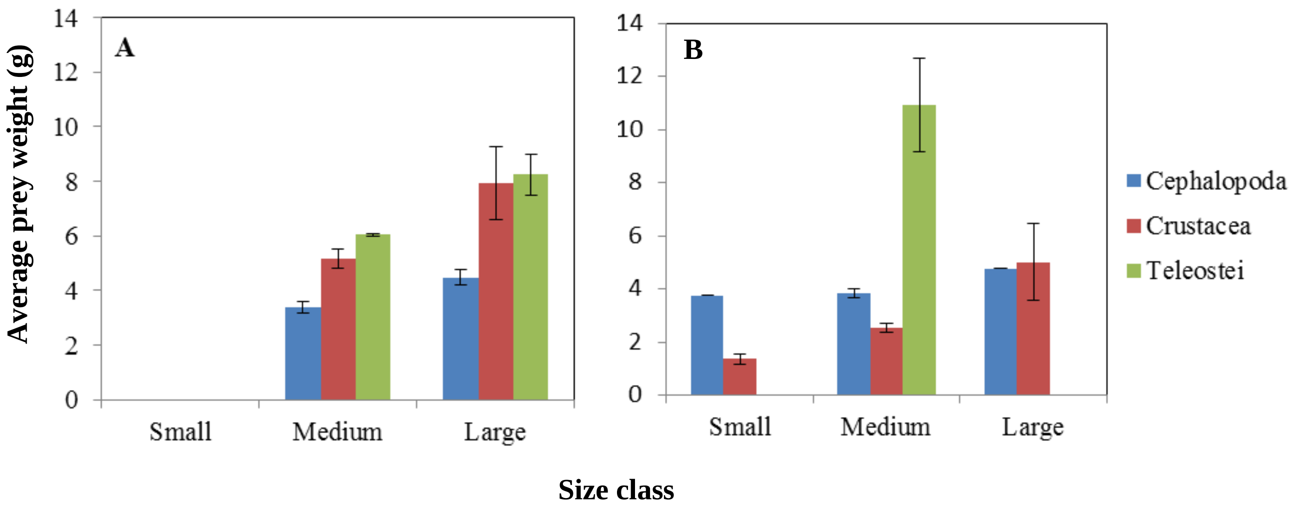


Figure 46: Illustrating the average weights (g) of the major prey groups (± SE) consumed by small, medium and large *S. capensis* on the West (**A**) and South (**B**) coasts.

The diet of medium and large *Scyliorhinus capensis* on the South Coast was dominated by *Sympagurus dimorphus* (Appendix 12). Other frequently encountered prey items in the diet of medium *Scyliorhinus capensis* on the South Coast were *M. cristiata*, *Callianassa* sp., *Pterygosquilla armata capensis*, *Todaropses eblanae* and *Dyspanopeus* sp. *Pterygosquilla armata capensis* and *Lycoteuthis lorigera* supplemented the diet of large *Scyliorhinus capensis* on the South Coast (Appendix 12).

Interspecific differences in diet by size and depth

Examination of the NMDS ordination plots (Figure 46) and hierarchical cluster analysis plots (Appendices 13 and 14) for each coast and factor (depth strata and size class) revealed a high degree of dietary overlap between the two catsharks, with cluster analysis revealing > 70% similarity between sample units. An ANOSIM test run on each of the factors also illustrated no significant difference in the diet of *H. regani* and *S. capensis* on the West ($R_{size\,=}$ - 0.164, R_{depth} = - 0.271) or South

(R_{size} = 0.2, R_{depth} = 0.556) coasts. Similarly, chi-square tests on the prey species consumed by the two catshark species revealed no significant differences by depth stratum and size class on either coast ($p > 0.05$). However, although the majority of catsharks preyed on similar prey items, there was some variability, with separate clusters forming on the West (i.e. medium *S. capensis* at 150 and 350 m and large *H. regani* at 250 and 350 m) and South (small *S. capensis* at 150 m and medium *S. capensis* at 250 and 450 m) coasts (Figure 46). This may either be suggestive of differences in their habitat-use on a micro-scale and/or individual specialization in their feeding habits.

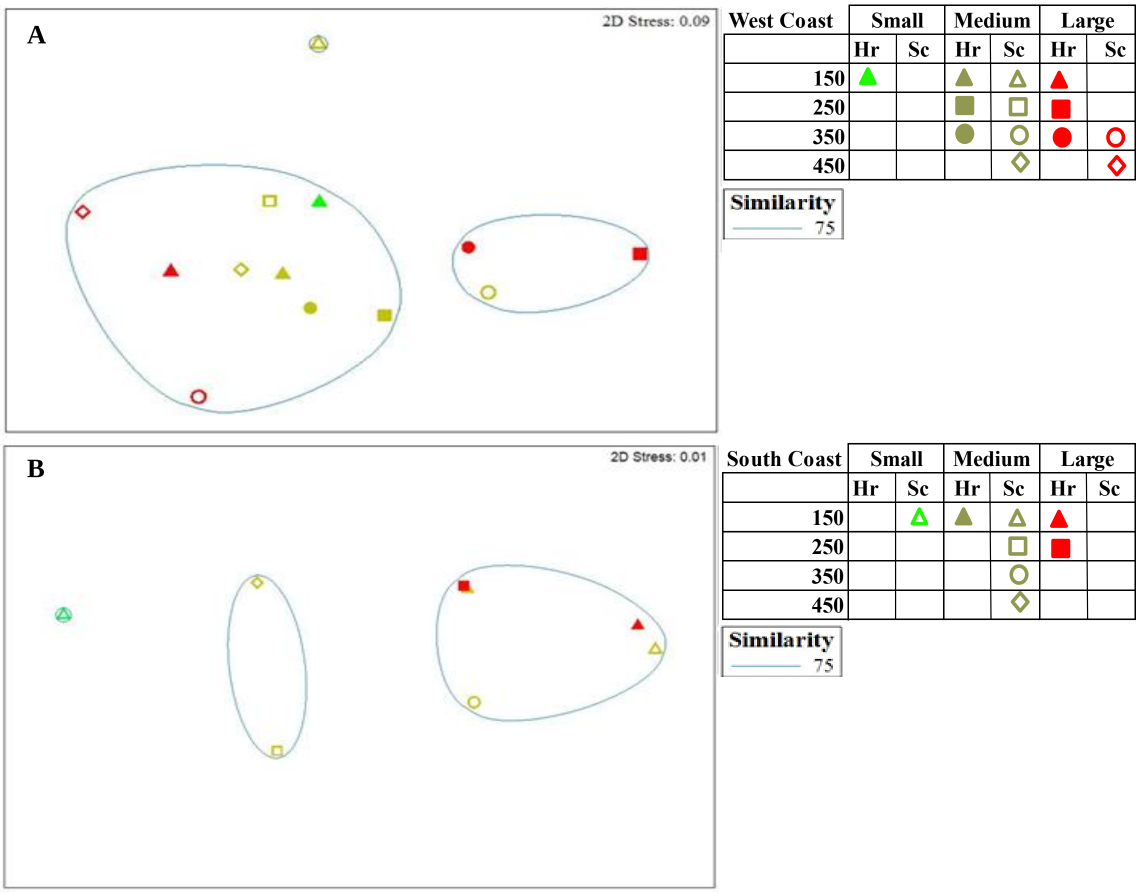


Figure 47: Non-metric multidimensional scaling ordination of the stomach contents of *H. regani* (Hr, solid symbols) and *S. capensis* (Sc, open symbols) pooled by size and depth on the West (**A**) and South (**B**) coasts.

Discussion

The present study is the first comprehensive attempt at understanding intra- and interspecific variability in the feeding habits of *H. regani* and *S. capensis* by coast, depth stratum and size class. Previous studies reporting on the diets of *H. regani* and *S. capensis* off the coasts of South Africa have described them as generalist feeders that consume a wide variety of teleosts, crustaceans and cephalopods (Ebert *et al*. 1996, Richardson *et al*. 2000b). Crustaceans, cephalopods and teleosts were also the most prevalent prey items recorded in the diet of *H. regani* and *S. capensis* in the current study. Crustaceans appeared to be the most important prey item consumed by *S. capensis*, whereas cephalopods and crustaceans appeared to be of equal importance in the diet of *H. regani*. This study is in agreement with that of Carrassón *et al*. (1992), reporting on the diet and distribution of the benthic catshark, *Galeus melastomus*, in the Western Mediterranean, who also found crustaceans to be the most important prey item consumed by this catshark. Notably, *H. regani* appeared to consume cephalopods in greater abundances than did *S. capensis* on both coasts. Likewise the study by Ebert *et al*. (1996), on the diet of catsharks off the West Coast of South Africa, also found *H. regani* to consume cephalopods in greater quantities than *S. capensis*.

Notably, the studies by Ebert *et al*. (1996) and Richardson *et al.* (2000b) observed teleosts to be the most important prey item consumed by the two catshark species. In the present study, however, crustaceans and cephalopods were observed to be the most important prey items consumed. This discrepancy may be due to the fact that the previous studies did not use the anatomical remains of crustaceans and cephalopods to establish ingested prey weight. Owing to this, the authors may possibly have under-estimated the importance of these numerically abundant prey species in the diet of *H. regani* and *S. capensis*.

Eleven crustacean, four cephalopod, three teleost, one chondrichthyan, one poriferan and one algal species were identified in the diet of *H. regani* (21 prey items in total), whilst 13 crustacean, five cephalopod, seven teleost, one chondrichthyan, one gastropod, one polychaete and one urochordate species were identified in the diet of *S. capensis* (29 prey items in total). This study presents the first record of a number of prey items that have not previously been identified in the diet of these catsharks (Ebert *et al*. 1996, Richardson *et al*. 2000b), including: seven crustaceans, one cephalopod and two teleosts in the diet of *H. regani*, and seven crustaceans, one cephalopod, six teleosts and one gastropod in the diet of *S. capensis*. These differences in the prey items observed between studies may be attributed to differences in sample sizes, with the number of catshark stomachs sampled in previous studies perhaps being insufficiently large to completely describe their diets. Alternatively, the studies may have been conducted in different localities with the diets possibly being reflective of the most abundant prey in those areas (Payne 1987, Meyer and Smale 1991, Smale 1992). For example, the study by Ebert *et al*. (1996) was focused off the West Coast, whereas the study by Richardson *et al*. (2000b) gave a general description of the diet of *H. regani*, not indicating along which coast the catsharks stomachs were sampled. It is also important to consider when the data were collected, as it is possible that prey abundance could change seasonally and annually (Serrano *et al*. 2003).

The results illustrate that although there is no difference in the relative importance of the major dietary groups consumed by the two catsharks between coasts, there appeared to be a marked difference in the species composition of the groups. Such differences have been reported in a number of studies on marine predators (Payne 1987, Meyer and Smale 1991, Smale 1992), and can be linked to opportunistic feeding and the influence of locality and season on prey availability. Both species appeared to consume a wider variety of prey items on the South Coast than on the West Coast. This higher diversity in the Indian Ocean compared to the Atlantic Ocean has previously been reported (Eckman 1967, Smale 1992). For example, *H. regani* and *S. capensis* showed a pronounced consumption of the crustacean *Sympagurus dimorphus* on the West Coast, and the crustaceans *S. dimorphus, Pterygosquilla armata capensis, Mursia cristiata*, as well as unidentified gammarid amphipods, on the South Coast. *Sympagurus dimorphus* is known to be abundant on both coasts (Branch *et al*. 2010), whereas amphipods and *M. cristiata* are more commonly observed in trawls conducted on the South Coast (pers. obs.; Branch *et al*. 2010).

Similarly, there were also apparent differences in the relative consumption of cephalopods between coasts. For example, *H. regani* primarily fed on *Todaropses eblanae* and *Sepia australis* on the West Coast, and on *T. eblanae, S. australis, Lycoteuthis lorigera* and *Loligo reynaudii* on the South Coast. In accordance with these findings, a study by Lipiński *et al*. (1992), reporting on the importance of cephalopods as prey in hake and other groundfish, also found the shallow-water Cape hake (*M. capensis*) to mainly prey on *S. australis* and *T. eblanae* on the West Coast, and on *S. australis* and *L. reynaudii* on the South Coast. *Todaropses eblanae*, which is abundant on both coasts and commonly taken as by-catch in trawls (Sauer and Smale 1991, Jereb and Roper 2010), was the most frequently consumed cephalopod in the diet of *S. capensis* on both coasts as well.

As found in previous studies (Ebert *et al*. 1996, Richardson *et al*. 2000b), common teleosts recorded in the diet of *H. regani* were *Lampanyctodes hectoris* (myctophid), *Maurolicus walvisensis* and hagfish eggs. The only teleosts identified in the diet of *S. capensis* on the West Coast were *M. walvisensis*, *Champsodon capensis* (lizardfish) and *Lepidopus caudatus* (ribbonfish). These species are all very abundant on the West Coast (Smith and Heemstra 1986, Armstrong and Prosch 1991). Teleosts consumed by *S. capensis* on the South Coast were *Paracallionymus costatus* (dragonette), *Trachurus capensis* (Cape horse mackerel), *Symbolophurus barnardii* (myctophid) and an unidentified myctophid. These teleosts are all widely distributed across the South African coastline (Smith and Heemstra 1986).

The presence of both mesopelagic and benthic teleosts in the diet of the two catshark species is suggestive of benthopelagic feeding habits, with *H. regani* and *S. capensis* possibly carrying out occasional migrations into the water column to feed. Such feeding habits have previously been reported in benthic catsharks (Lyle 1983, Bozzano *et al*. 2001, Olaso *et al*. 2005). For example, a study Olaso *et al*. (2005) reporting on the trophic relations of blackmouth catsharks (*Galeus melastomus*) in the Cantabrian sea, found that this species carries out vertical migrations to feed on pelagic and mesopelagic teleosts. Alternatively, the mesopelagic teleost species found in the stomachs of catsharks in this study may have been predated on during the day when they are close to the seabed. However, it is also possible that *H. regani* and *S. capensis* scavenge these mesopelagic teleost from the seafloor, as the lantern fish *Lampanyctodes hectoris* and lightfish

Maurolicus muelleri are known to be common discards of commercial trawling (Alldredge and King 1980).

To my knowledge, this study presents the first record of chondrichthyans, sponges and algae in the diet of *H. regani* (Ebert *et al*. 1996, Richardson *et al*. 2000b). Pyjama catsharks (*Poroderma africanum*) along the coast of South Africa have however been reported to consume smaller sharks and their egg cases (Compagno *et al*. 2004, Escobar-Porras 2009), while redspotted catsharks (*Schroederichthys chilensis*) along the coast of Chile have been reported to feed on algal material (Fariña and Ojeda 1993). Chondrichthyans were also recorded in the diet of *S. capensis*, along with polychaetes, gastropods and urochordates. Consistent with these findings are those by Ebert *et al*. (1996), who reported the presence of polychaetes in the diet of *S. capensis* on the West Coast. Although there have been no previous reports of gastropods and urochordates in the diet of *S. capensis*, they have been recorded in the diet of other catsharks inhabiting the coast of South Africa. For example, Richardson *et al*. (2000b) observed unidentified gastropods in the diet of *H. regani*, while Ebert *et al*. (1996) noted the occurrence of the urochordate *Pyrosoma* sp. in the diet of the small eye catshark (*Apristurus microps*).

Although there were no statistical differences between the prey groups consumed at each depth stratum for both species and coasts, there were changes in the individual prey species consumed. Such changes in the diets of sharks with depth have been reported in a number of studies, and have been related to changes in the abundances of prey with depth (Carrassón *et al*. 1992, Smale and Compagno 1997, Olaso *et al*. 2005, Fanelli *et al*. 2009, Valls *et al*. 2011). The results of the present study could possibly be suggestive of such changes. In the present study, *Sympagurus dimorphus* and *Todaropses eblanae* appeared to dominate the diet of *H. regani* and *Scyliorhinus capensis* throughout the bathymetric range explored. Both these species are common on the South African coast, with *Sympagurus dimorphus* inhabiting depths of between 200-600 m and *T. eblanae* inhabiting depths of between 20-850 m (Nesis 1987, Sanchez 1988, Jereb and Roper 2010). Notably, *Mursia cristiata* dominated the diet of *Scyliorhinus capensis* on the South Coast at 150 and 350 m depth, overlapping their known depth of range which has been reported to be up to 400 m depth (Branch *et al*. 2010). Furthermore, catsharks sampled between 150-250 m depth appeared to primarily consume shallow-water prey such as *Pterygosquilla armata capensis* and *Sepia australis*. Distributional studies on *P. a. capensis* and *Sepia australis* have reported them to be most common at depths < 200 m (Griffiths and Blaine 1988, Lemaitre 1989, Augustyn *et al*. 1995, Jereb and Roper 2005). *Loligo reynaudii* appeared to be most frequently consumed by *H. regani* in shallow waters on the South Coast, where these squid commonly aggregate to spawn (Augustyn *et al*. 1992). In accordance with this, a study by Sauer and Smale (1991), reporting on the predation of *L. reynaudii*, also found these squid to commonly be consumed by sharks and teleosts on their spawning grounds. Similarly, *Trachurus capensis* was identified in the diet of *S. capensis* at 105 m depth on the South Coast. This teleost species is known to recruit in shallow waters on this coast (Hecht 1990, Barange *et al*. 1998, Mc Laverty 2012). Catsharks sampled in deeper waters (>250 m) appeared to primarily consume deep-water prey such as *Lycoteuthis lorigera*, *Bathypolypus valdiviae* (boxer octopus), and the deep-water hermit crab *Parapagurus bouvieri*; *L. lorigera* is known to be common between 300-900 m (Roeleveld *et al*. 1992), *B. valdiviae* at depths > 450 m (Roper *et al*. 1984) and *P. bouvieri* between 400-1400 m depth (Lemaitre 1989).

Demersal trawling has been shown to increase the availability of infaunal prey, such as polychaetes, to fish and other benthic predators because of habitat alteration (Ramsay *et al*. 1997). For example, a study by Rijnsdorp and Vingerhoed (2001) linked the increasing growth rate of commercially important flatfish (*Pleuronectes platessa* and *Solea solea*), that primarily feed on polychaetes (Braber and de Groot 1973), in the NE Atlantic to increases in the abundances of small polychaetes in trawled areas. Similarly, a study by Olaso *et al*. (1998), on the lesser spotted catshark (*S. canicula*) in the Cantabrian Sea, noted that the physical effects of trawling increases the exposure of endobenthic prey items such as polychaetes to predation. Since trawling effort remains relatively consistent spatially, it could be assumed that fishing grounds are productive feeding areas for demersal predators scavenging the sea-floor. In the present study, *S. capensis* consumed polychaetes between 350-450 m depth on the West Coast and between 150-350 m depth on the South Coast. The presence of these endobenthic prey items in the diet of *S. capensis* at these depths overlaps with the highest commercial trawling effort around South Africa, occurring at depths of between 200-600 m (Sink *et al*. 2012). The presence of polychaetes in the diet of *S. capensis* could thus be attributed to their opportunistic feeding behaviour, possibly responding to the high abundances of polychaetes at these depths following a trawling disturbance. The absence of polychaetes in the diet of *H. regani*, however, could possibly indicate a level of dietary preference. However, differences in micro-habitat use might also be responsible for the absence of polychaetes in the diet of *H. regani*, with *H. regani* possibly not occurring in areas where polychaetes are abundant.

Ontogenetic shifts in diet have been observed in a wide variety of shark species (Lyle 1983, Smale 1991, Smale and Compagno 1997, Richardson *et al*. 2000b, Olaso *et al*. 2005). For example a study by Fanelli *et al*. (2009), reporting on the diet of blackmouth catsharks (*G. melastomus*) and velvet belly lantern sharks (*Etmopterus spinax*) in the Western Mediterranean, reported the preferential selection of small crustaceans and cephalopods by small catsharks and the preferential selection of large crustaceans and cephalopods by large catsharks. In accordance with the study by Fanelli *et al*. (2009), the %W of the crustaceans and cephalopods consumed in the present study also increased with increasing catshark size. This pattern of higher %W with increasing catshark size was also noted for teleost in the diet of *S. capensis* on the West Coast.

In terms of %FO data, only *H. regani* on the West Coast showed a significant size-related change in their dietary composition, with a shift from small crustaceans and cephalopods, such as amphipods and *Sepia australis* in small individuals, to big crustaceans and cephalopods, such as *Parapagurus bouvieri, Lycoteuthis lorigera* and *Todaropses eblanae* in large individuals. Although there were no significant ontogenetic dietary shifts in *S. capensis*, cephalopods and teleost appeared to increase in frequency with increasing catshark size on both coasts. The consumption of bigger and faster prey items by large catsharks is possibly as a consequence of their increased metabolic requirements, or their better prey handling abilities due to their increased gape size and speed (Smale and Compagno 1997, Bozzano *et al*. 2001, Sims 2003, Olaso *et al*. 2005). However, the consumption of bigger prey items by large sharks may also be related to the “bigger-deeper pattern”, with large individuals inhabiting deeper waters, and thus increasing their encounter rate with large, deep water prey (see Chapter 3; Yokota and Lessa 2006, Flammang *et al*. 2011). Accordingly, deep-water prey species such as *Parapagurus bouvieri* was frequently consumed by large catsharks, while shallow-water prey such as *Pterygosquilla armata capensis* and *S. australis* was commonly consumed by small catsharks.

Overall, *H. regani* and *S. capensis* can be described as euryphagous and opportunistic predators that primarily feed on, in order of descending importance, crustaceans, cephalopods and teleosts. The catsharks seem to spend most of their time on or near the sea floor, opportunistically feeding on abundant benthic prey items such as hermit crabs (Paguridae), mantis shrimp (Stomatopoda), brachuryan crabs and polychaetes. These catsharks also appeared to carry out vertical migrations to feed on pelagic (*T. capensis*) and mesopelagic (*L. hectoris* and *M. walvensis*) teleost species. However, these mesopelagic prey items may have been predated on during the day when they are close to the seabed, or they may have been scavenged from the sea floor in areas of high trawling effort, where they are possibly discarded as by-catch.

Both catsharks displayed a relatively uniform feeding behaviour across depth strata and size classes, opportunistically feeding on the most abundant prey. However, some dietary differences were noted, and are possibly indicative spatial differences in prey availability owing to the different patterns of habitat use (around coasts and between depths) observed in the two catshark species (see Chapter 3).

Ontogenetic shifts in the diet of these catsharks were also noted, with individuals consuming larger prey items with increasing size. These ontogenetic shifts in diet could be attributed to changes in morphology (i.e. gape size) or metabolic requirements with growth, or to the “bigger-deeper pattern”, with large individuals inhabiting deeper waters and thus increasing their encounter rate with large, deep water prey.

The current study has filled in important gaps in catshark feeding ecology around the coast of South Africa. Given their abundance, these demersal catshark species can exert an important influence on the regulation of benthic communities, and are probably, through feeding on the most abundant prey items, indirectly controlling the relative abundance of a number of demersal species that would possibly proliferate in their absence (i.e. *Sympagurus dimorphus* and *Todaropses eblanae*).

In future, studies evaluating the diet of these catshark species should aim to combine sampling by trawling and long-line. Long-line fishing can occur over rough grounds that are not available to the trawl. Since locality influences prey availability, we could assume that the catsharks sampled by each respective sampling method will feed on different prey items. Additionally, collaborations with the commercial trawling industry should also be initiated so that samples can be collected throughout the year. This will allow for the elucidation of catshark diets on a larger spatial and temporal scale. The collection of such information will most certainly increase our understanding of trophic dynamics and food web structure in these under-studied shelf and shelf-edge environments.

Chapter Five

Using the stable isotopes of carbon and nitrogen to elucidate spatial and ontogenetic variability in the trophic ecology of two co-occurring catsharks (Scyliorhinidae) caught off South Africa

Abstract

The present study is the first attempt using stable isotope analysis to understand the trophic ecology of the two most common demersal catsharks caught as by-catch off the West and South coasts of South Africa. Stable isotopes (SI) of carbon (δ^{13}C) and nitrogen (δ^{15}N) recorded for the two species were used to describe spatial and ontogenetic variability in their trophic ecology, with General Linear Models used to assess intra-and interspecific changes in their SI ratios between coasts, depth strata and size classes. The effect of coast on δ^{15}N was observed to be significant for both species ($p < 0.05$), with a general pattern of higher δ^{15}N values recorded for individuals sampled on the West Coast than on the South Coast and inter-coast differences of 0.29 and 0.23‰ noted for *H. regani* and *S. capensis*, respectively. A significant effect of depth on δ^{15}N was noted for *H. regani*, with a trend of decreasing δ^{15}N values with increasing depth noted on the South Coast only. Size class was found to be a significant parameter as well, with the δ^{15}N values recorded for both species increasing with increasing size. For *S. capensis*, significant interactions between coast and depth stratum and coast and size class was noted for δ^{15}N, indicating that the pattern of SI with depth stratum and size class differs between the two coasts. The effect of depth stratum and size class on δ^{13}C was found to be significant for *S. capensis* only ($p < 0.05$), with the δ^{13}C values recorded for

S. capensis decreasing with increasing depth stratum and size class. Interspecifically, size class accounted for the most variation in both δ^{15}N and δ^{13}C, followed by coast, species and depth stratum for δ^{15}N, and by depth stratum for δ^{13}C. The interaction between species and size class was found to be significant for both isotopes as well. Based on these findings I conclude that the variability in δ^{15}N and δ^{13}C are largely as a result of the differences in source production off each coast. However, it is also possible that differences in trophic levels, owing to spatial and ontogenetic changes in habitat use, resource availability and prey items consumed, play a key role in the distinct isotopic values observed within and between these catshark species.

Introduction

Owing to their position in the food-web sharks play an important role in the structure and function of marine ecosystems (Heithaus *et al*. 2008, Matich *et al*. 2010, Hussey *et al*. 2012). Understanding their diet and trophic position is thus crucial, as it provides important information on food-web dynamics and community structure (Kitchell *et al*. 2002, Andrews *et al*. 2010, Hussey *et al*. 2012).

In recent times, over-fishing has resulted in substantial declines in shark numbers (Andrews *et al*. 2010, Worm *et al*. 2013). Despite this, little is known about the effects of fishing-related shark mortality on trophic interactions in marine ecosystems (Worm *et al*. 2013). There is thus an increased need for ecologists to understand the diet and trophic position of sharks, as their declines may be causing significant changes in marine food-webs (Heithaus *et al.* 2008, Baum and Worm 2009, Hussey *et al*. 2012, Worm *et al*. 2013).

In the past, investigations into the trophic ecology of sharks and other fish have mainly employed the use of stomach content analyses (Cortés 1997, McQueen and Griffiths 2004, Wetherbee and Cortés 2004, Matich *et al*. 2010, Iitembu and Richoux 2015). However, stomach content analysis requires stomachs containing food, contents that are in a relatively undigested and identifiable state, and large sample sizes on which significant conclusions can be based (James 1988, van der Bank 2010, Iitembu and Richoux 2015). This is particularly true when conducting spatio-temporal studies on opportunistic predators that feed relative to prey availability (McQueen and Griffiths 2004). For example, a study by McQueen and Griffiths (2004) quantitatively described the diet of *Thyrsites atun* (snoek) in the Benguela ecosystem, and found that a minimum of 70 snoek stomachs, containing food, should be sampled per sampling event in order to obtain an accurate description of their diet. Furthermore, stomach content analysis only provides dietary information on recently consumed prey, and has the tendency to under-estimate the importance of prey items that are consumed first or digested the fastest (Vander Zanden *et al*. 1997, Pinnegar *et al*. 2001, Renones *et al*. 2002, MacNeil *et al*. 2005, Matich *et al*. 2010, Baker *et al*. 2014).

In recent times, stable isotope analysis (SIA) has become an alternative or complementary method to stomach content analysis that can be used by ecologists to examine the trophic interactions between organisms, including sharks (Fisk *et al*. 2002, MacNeil *et al*. 2005, Martinez del Rio *et al*. 2009, Matich *et al*. 2010). Unlike stomach content analysis, SIA is able to provide trophic information on the shark and its prey (when in an undigested state), thus allowing researchers to determine the position of the shark and its prey in the food-web. In addition, through the use of known isotopic baseline signatures, SIA can also provide spatial information (whether benthic or pelagic, marine or freshwater) of the shark and its prey (DeNiro and Epstein 1978, Thomas and Cahoon 1993, Hussey *et al*. 2012). Since SI ratios reflect assimilated diet, ecologists can, from one sampling event, obtain a time-integrated measure of diet that can be used understand size, sex and seasonal based changes in the trophic positions and habitat-use patterns of sharks (Bearhop *et al*. 2004, Matich *et al*. 2010, Hussey *et al*. 2012).

When considering carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N), consumers are known to differentially assimilate the heavier isotopes (^{13}C and $\delta^{15}N$) and expel the lighter isotopes (^{12}C and ^{14}N), resulting in a predictable stepwise enrichment from prey to consumer (Peterson and Fry 1987). Using SIA, information on trophic position can be obtained through the examination of nitrogen isotopes, as $\delta^{15}N$ displays a known stepwise enrichment of around 3.4‰ (1 SD = 1‰) per trophic level (Minagawa and Wada 1984, Post 2002). This predictable enrichment allows for a comparative estimation of an organisms' trophic position in relation to that of others (Minagawa and Wada 1984, Peterson and Fry 1987, Post 2002). Information on foraging ecology and movement/migration patterns can be obtained through the examination of carbon isotopes, as $\delta^{13}C$ values varies between primary producers (C_3 vs C_4 plants, pelagic vs benthic sources of production) but displays less change when moving from prey to predator up the food chain, averaging at 0.4‰ (1 SD = 1.3‰) per trophic level (Peterson and Fry 1987, Post 2002, Shiffman *et al*. 2012).

Over the past two decades, numerous studies on sharks have utilised SIA, with the majority of these studies using the stable isotopes of carbon and nitrogen to describe food-web linkages, trophic structure and movement/migration patterns (Fisk *et al.* 2002, MacNeil *et al.* 2005, Matich *et al.* 2010, Hussey *et al.* 2012, Shiffman *et* *al*. 2012). However, as with most studies on sharks, research has been mainly focused on the large, charismatic shark species, with comparatively fewer studies being conducted on small, meso-predatory sharks (Heithaus *et al*. 2010, Vaudo and Heithaus 2011, Caut *et al*. 2013).

This is particularly true in South Africa, where small meso-predatory catsharks form one of the most diverse components of the demersal shark assemblage (Richardson *et al*. 2000b). Despite their abundance and diversity, however, little is known about their trophic ecology, and to my knowledge studies using SIA to evaluate the trophic ecology of these sharks has not previously been conducted in South Africa.

This study is a first attempt to understand the trophic ecology of South African catsharks using SIA. It aims to explore intra-and interspecific resource use around the coast using carbon and nitrogen isotope analyses of white muscle tissue. White muscle tissue samples were collected from the two most common demersal catsharks caught as by-catch by the demersal trawling industry operating on the West and South coasts of South Africa, namely *H. regani* and *S. capensis*. In this Chapter stable isotope data is used to describe intra- and interspecific changes in the feeding habits of these catshark species between coasts, and across depth strata and size classes.

Results

Sample Distribution

A total of 172 *H. regani* and 155 *S. capensis* were sampled, with 110

H. regani and 70 *S. capensis* sampled on the West Coast and 62 *H. regani* and 85 *S. capensis* sampled on the South Coast (Table 18). Most *H. regani* were collected between Hondeklipbaai and Doringbaai, and off Cape Town and Cape Agulhas (Figure 47). Similarly, large numbers of *S. capensis* were collected between Hondeklipbaai and Doringbaai, and between Cape Agulhas and Mossel Bay (Figure 47).

Table 18: Number (n), size range and mean size (± SE) of *H. regani* and *S. capensis* sampled on the West and South coasts for SI analysis

	H. regani				*S. capensis*			
Coast	***N***	**Size range (cm, TL)**	**Mean size (cm, TL)**	**±SE**	***N***	**Size range (cm, TL)**	**Mean size (cm, TL)**	**±SE**
West Coast	110	19.0-65.0	45.7	1. 0	70	34.0-90.0	53. 5	1.5
South Coast	62	40.0-63.0	49.9	0.9	85	28.0-92.0	48. 9	1.5

A significant difference was noted between size (TL) and coast for *H. regani* ($F_{1,\ 170} = 7.381$, $p < 0.05$) (Figure 48, Appendix 15), with both smaller and larger individuals collected off the West Coast than off the South Coast (Figure 48, Appendix 1). Notable is the absence of small *H. regani* and the large number of intermediate sized *H. regani* collected off the South Coast (Figure 48, Appendix 15). Conversely, *S. capensis* were found to cover a similar size range (TL) on both coasts ($F_{1,\ 153} = 4.655$, $p > 0.05$) (Table 18, Figure 48, Appendix 15).

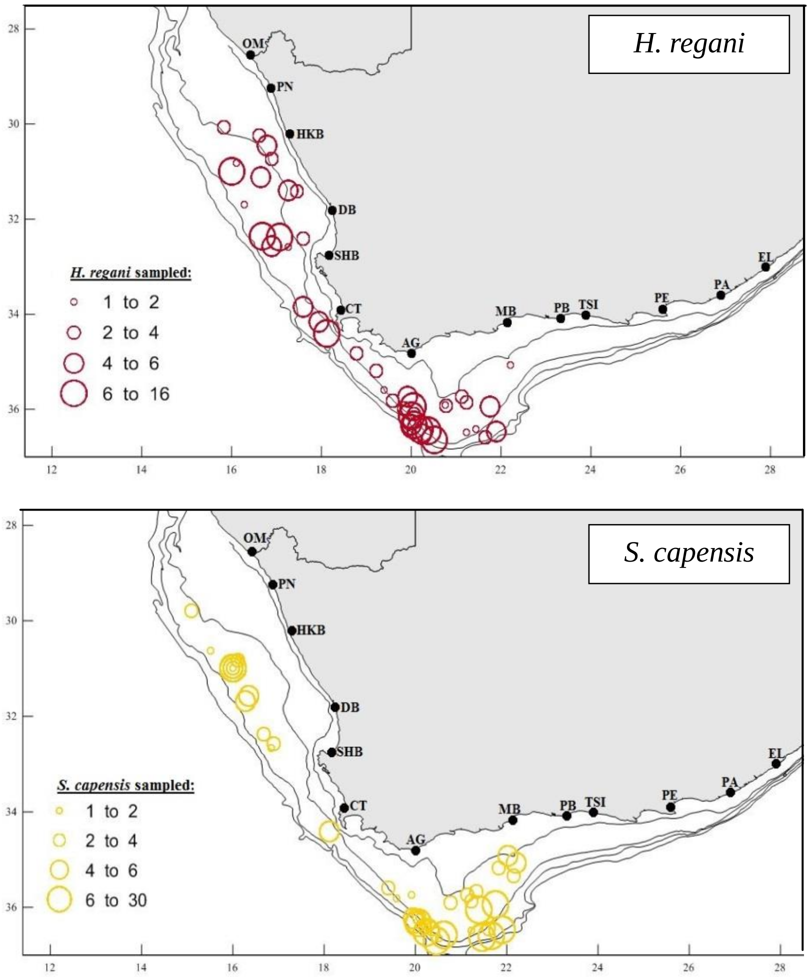


Figure 48: Location and number of *H. regani* and *S. capensis* collected for stable isotope analysis on the West and South coasts. See Figure 1 for key to place names and depth contours.

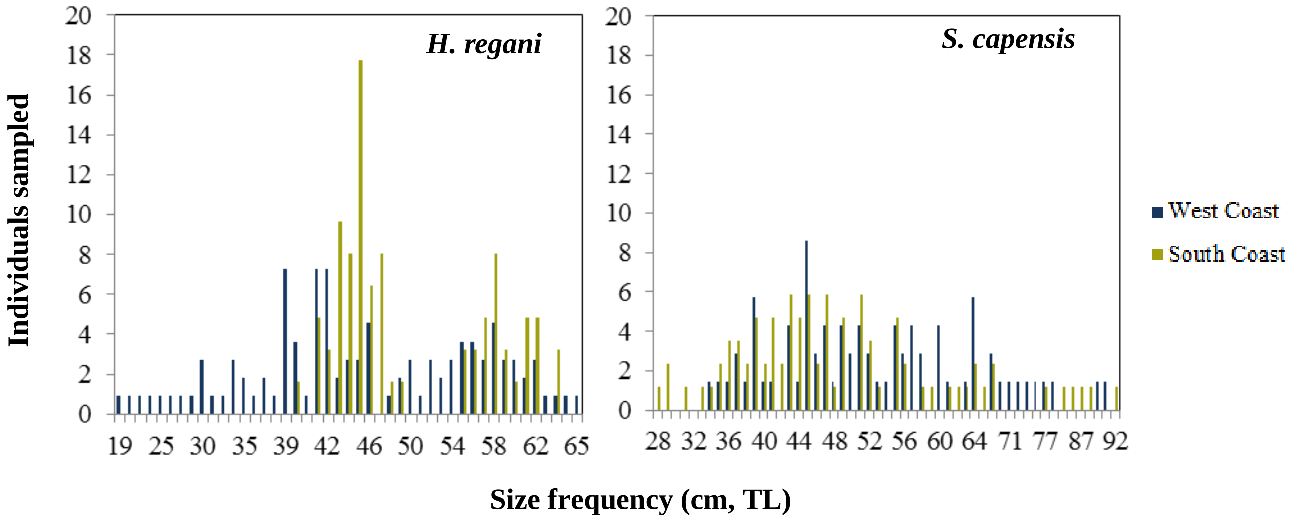


Figure 49: Illustrates the number of individuals sampled by size for *H. regani* and *S. capensis* on the West and South coasts.

For *H. regani*, most individuals were sampled between the 150-350 m depth stratum on the West Coast and between the 150-250 m depth stratum on the South Coast. Whereas for *S. capensis*, most individuals were sampled between the 350-450 m depth stratum on the West Coast and at the 150 and 350 m depth stratum on the South Coast (Figure 49, Appendix 16). Notably, both species appeared to display an increase in mean size with increasing depth on the West Coast only (Appendix 16).

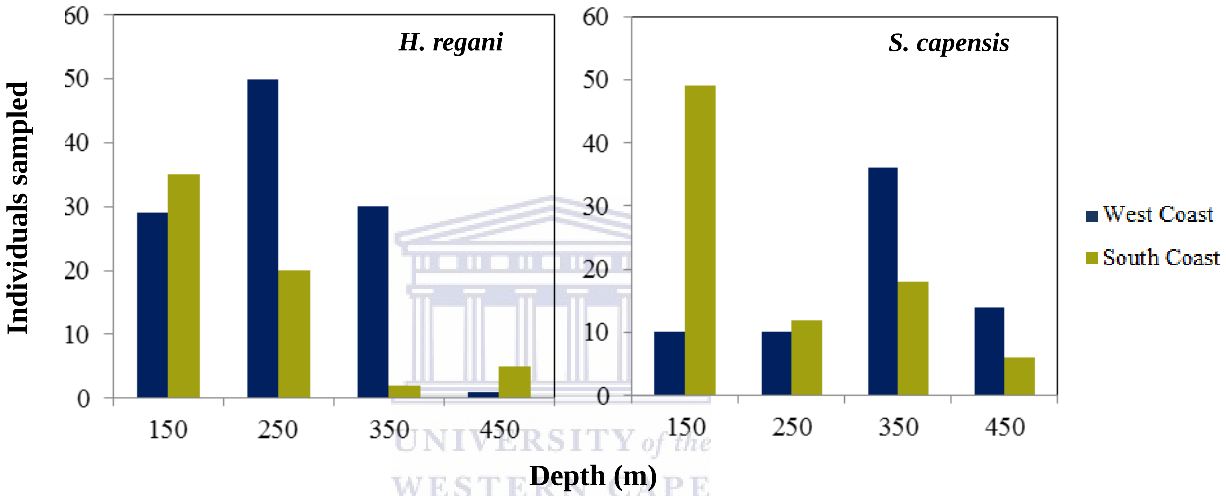


Figure 50: Illustrates the number of individuals sampled at each depth stratum for *H. regani* and *S. capensis* on the West and South coasts.

Variation in δ^{15}N and δ^{13}C values of *H. regani*

For *H. regani*, the results obtained from the GLMs indicated significant differences for δ^{15}N only, with coast accounting for the most variance in δ^{15}N, followed by size class and then depth stratum (Table 19).

The isotopic bi-plot of δ^{15}N and δ^{13}C values recorded for *H. regani* between coasts displayed a high degree of overlap, with only some spatial difference being apparent, particularly in δ^{15}N (Figure 50). GLMs indicated a significant effect of coast on δ^{15}N ($F_1 = 25.11$, $p < 0.05$) (Table 19), with higher mean values recorded for

H. regani on the West Coast (14.49‰, SE ± 0.38) than on the South Coast (14.20‰, SE ± 0.49) (Figure 51, Appendix 17). Conversely, no significant effect of coast on $\delta^{13}C$ was noted for *H. regani* off either coast ($F_1 = 0.0002$, $p > 0.05$) (Table 19), with rather similar mean values being recorded for *H. regani* on both the West (-15.67‰, SE ± 0.04) and South (-15.60‰, SE ± 0.04) coasts (Figure 51, Appendix 17). Neither depth nor size was significant for $\delta^{13}C$ (Table 19).

Table 19: Summary of results obtained from univariate tests of significance testing for variation in the $\delta^{15}N$ and $\delta^{13}C$ values of *H. regani* between coasts, depth strata and size (TL). Significant P-values ($p < 0.05$) are indicated in bold. Interaction terms were omitted from this table due to their lack of significance

$\delta\ ^{15}N$

Parameters	**Df**	**SS**	**MS**	**F**	**Sig.**
Model	5	9.624	1.925	15.894	**P < 0.05**
Intercept	1	1014.895	1014.895	8380.334	**P < 0.05**
Coast	1	3.041	3.041	25.111	**P < 0.05**
Size (TL)	1	2.480	2.480	20.475	**P < 0.05**
Depth	3	2.348	0.783	6.464	**P < 0.05**
Error	166	20.103	0.121		

$\delta^{13}C$

Parameters	**Df**	**SS**	**MS**	**F**	**Sig.**
Model	5	1.121	0.224	1.614	P > 0.05
Intercept	1	1396.767	1396.767	10048.690	**P < 0.05**
Size (TL)	1	0.849	0.849	6.106	P > 0.05
Depth	3	0.267	0.089	0.640	P > 0.05
Coast	1	0.0002	0.0002	0.002	P > 0.05
Error	166	23.074	0.139		

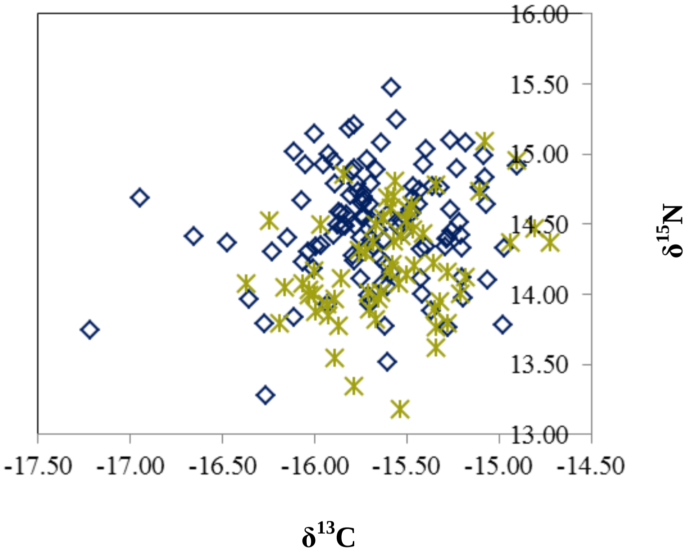


Figure 51: Isotopic bi-plot illustrating δ^{15}N and δ^{13}C values of *H. regani* on the West (◇) and South (✳) coasts.

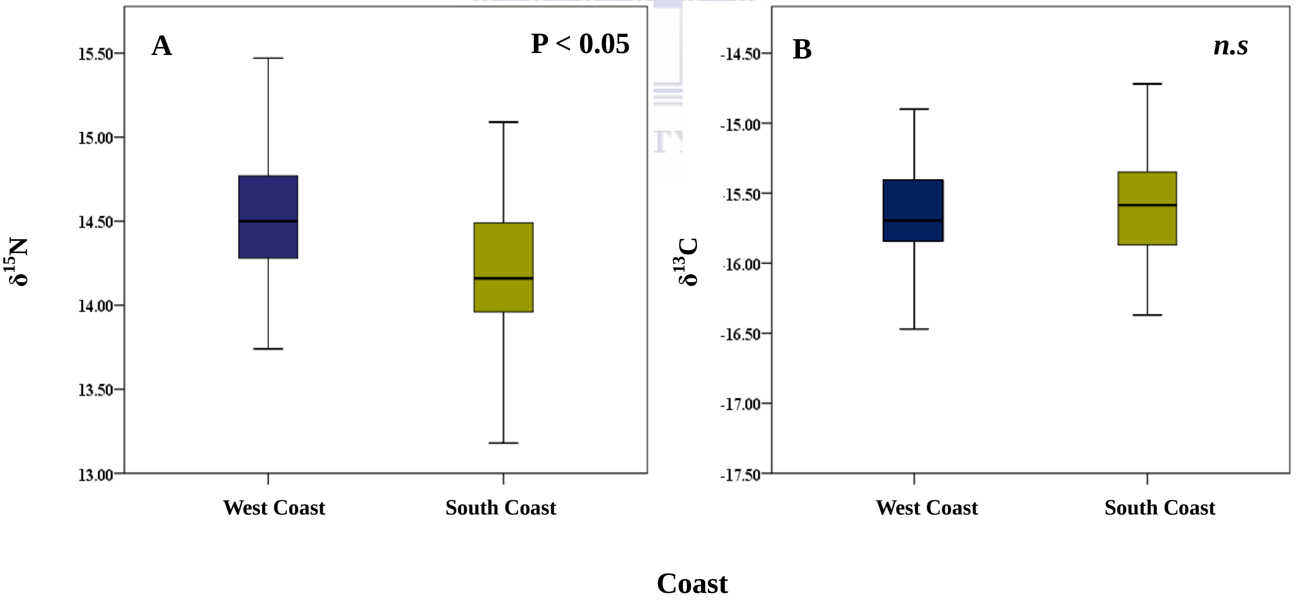


Figure 52: Boxplot illustrating mean δ^{15}N (**A**) and δ^{13}C (**B**) values (±SE) of *H. regani* on each coast. $P < 0.05$ indicates a significant difference between mean values.

The isotopic bi-plots displaying δ^{15}N and δ^{13}C values by depth strata appear to display a clear spatial separation by depth on both coasts (Figures 52**A** and **B**). The GLM showed a significant effect of depth on δ^{15}N ($F_3 = 6.464$, $p < 0.05$) (Table

19), with a *post-hoc* Tukey test indicating differences in the δ^{15}N values recorded for *H. regani* between the 150 and 250 m and 250 and 350 m depth strata on the West Coast, and between the 150 and 250 m and 250 and 450 m depth strata on the South Coast (Figures 53**A** and **B**). Notably, there was no significant effect of depth on δ^{13}C ($F_3 = 0.640$, $p > 0.05$) (Table 19), with similar mean δ^{13}C values being observed across all depth strata on both coasts (Figures 54**A** and **B**, Appendix 18).

For δ^{15}N, the lowest mean values were recorded for *H. regani* at 150 m on the West Coast and at 450 m on the South Coast, while the highest mean δ^{15}N values were observed at 250 m on both coasts (Figures 53**A** and **B**, Appendix 18). For δ^{13}C, the lowest mean values were recorded for *H. regani* at 150 m on the West Coast and at 350 m on the South Coast, while the highest mean values were recorded at 250 m on the West Coast and at 150 m on the South Coast (Figures 54**A** and **B**, Appendix 18).

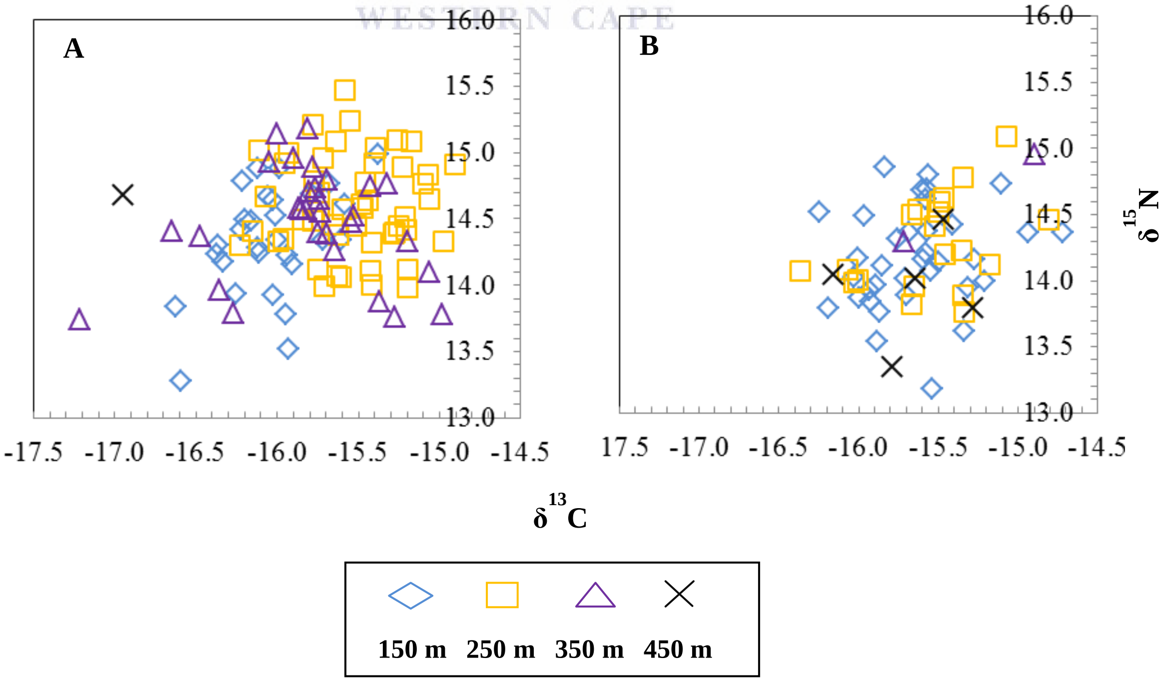
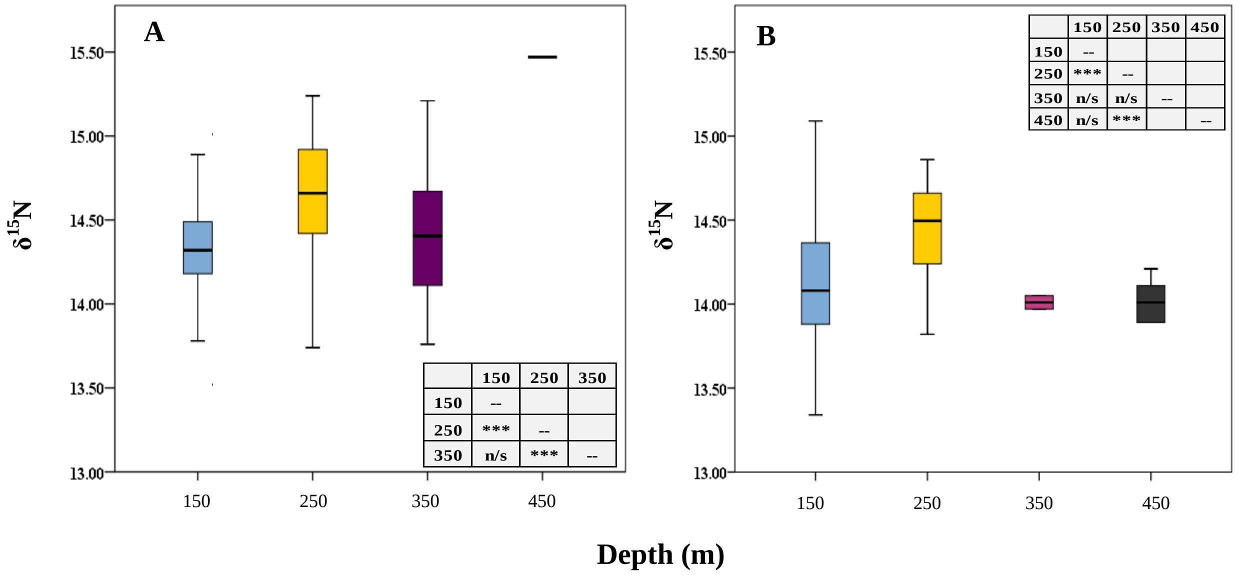


Figure 53: Isotopic bi-plot illustrating the δ^{15}N and δ^{13}C values of *H. regani* at each depth stratum on the West (**A**) and South (**B**) coasts.



A

	150	250	350
150	--		
250	***	--	
350	n/s	***	--

B

	150	250	350	450
150	--			
250	***	--		
350	n/s	n/s	--	
450	n/s	***		--

Figure 54: Boxplot illustrating mean δ^{15}N values (±SE) of *H. regani* at each depth stratum on the West (**A**) and South (**B**) coasts. Tables represent *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

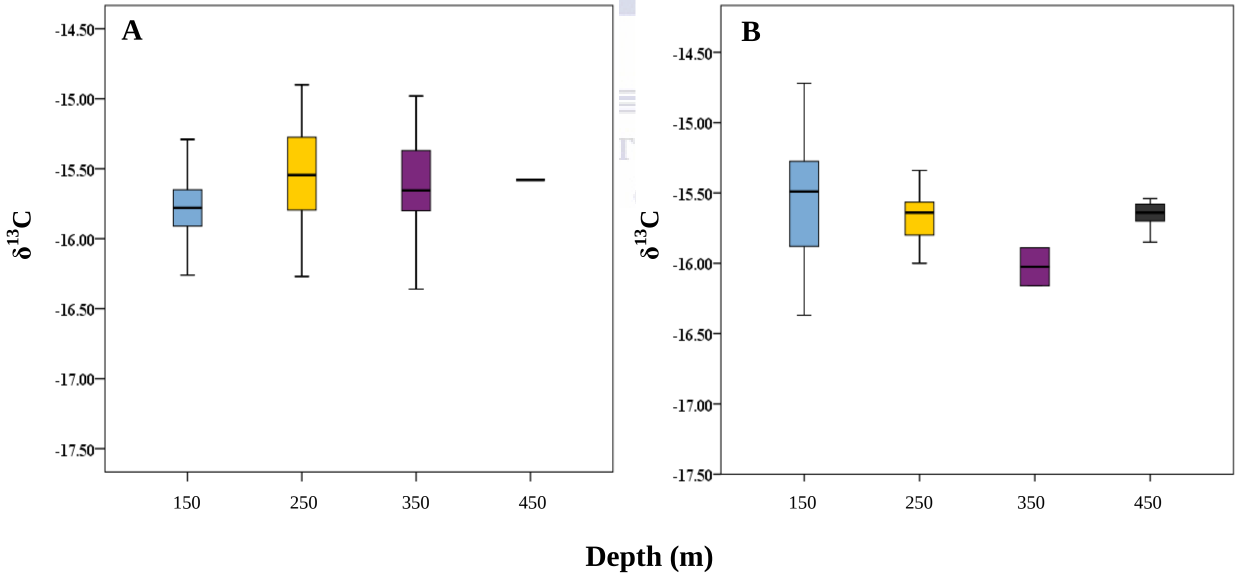


Figure 55: Boxplot illustrating mean δ^{13}C values (±SE) of *H. regani* at each depth stratum on the West (**A**) and South (**B**) coasts.

The δ^{15}N and δ^{13}C values observed among size classes appear to show a high degree of overlap (Figures 55**A** and **B**). Some separation can however be noted, particularly between small and medium, and small and large individuals (Figures 55**A** and **B**). Results from the GLMs indicated a significant effect of size class on $\delta^{15}N$ ($F_1 = 20.475$, $p < 0.05$) (Table 19), with scatterplots displaying a positive correlation between $\delta^{15}N$ and size on the West Coast only ($R^2 = 0.1935$, $p < 0.01$) (Figures 56**A** and **B**).

On further analysis, a *post-hoc* Tukey test indicated significant differences between the $\delta^{15}N$ values recorded in small and large *H. regani* sampled on the West Coast, with $\delta^{15}N$ values increasing with increasing size (Figure 57**A**, Appendix 18). There was no significant effect of size on $\delta^{15}N$ on the South Coast (Figure 57**B**), possibly due to the absence of samples of small individuals from this coast. For $\delta^{13}C$, there was no significant effect of size on either coast (Figures 58 and 59, Table 19).

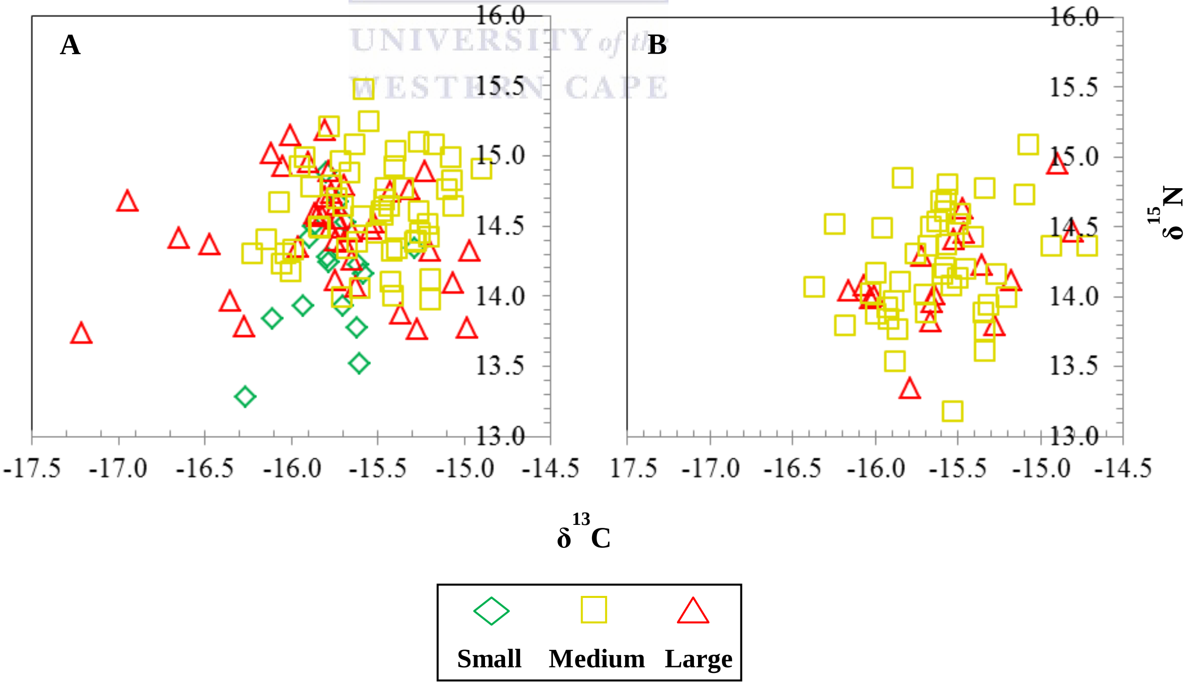


Figure 56: Isotopic bi-plot illustrating the $\delta^{15}N$ and $\delta^{13}C$ values of *H. regani* for each size class on the West (**A**) and South (**B**) coasts.

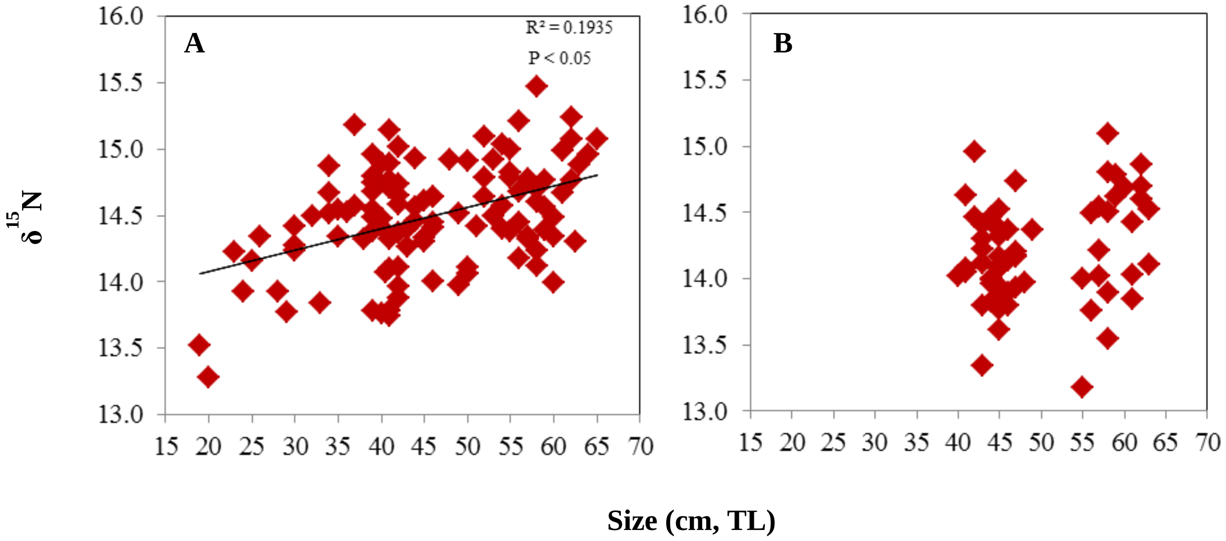
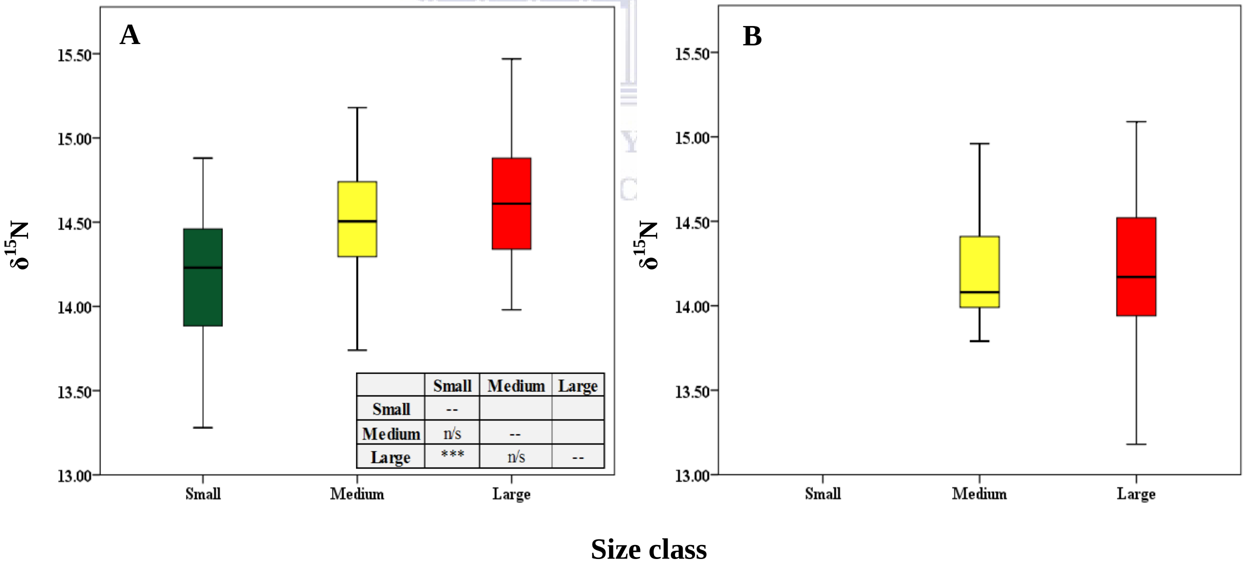


Figure 57: Scatterplots of δ^{15}N and size for *H. regani* on the West (**A**) and South (**B**) coasts. Graphs include linear trendlines, R^2 values and P- values where significant relationships are noted.



	Small	Medium	Large
Small	--		
Medium	n/s	--	
Large	***	n/s	--

Figure 58: Boxplot illustrating mean values (±SE) of *H. regani* for each size class on the West (**A**) and South (**B**) coasts. Table represents *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

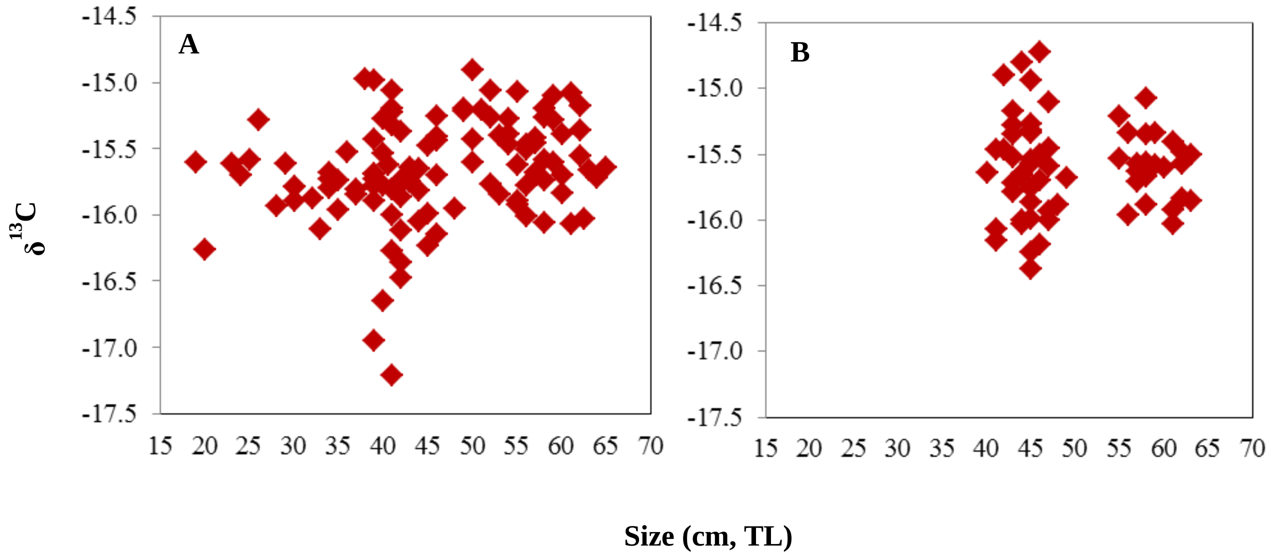


Figure 59: Scatterplots of δ^{13}C and size for *H. regani* on the West (**A**) and South (**B**) coasts.

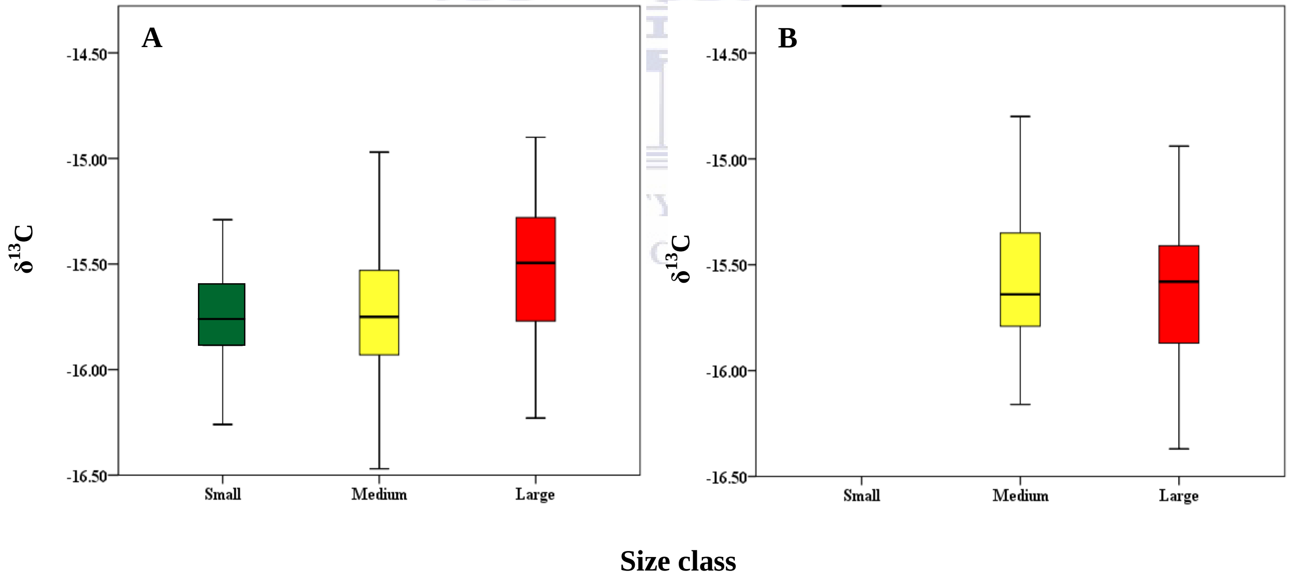


Figure 60: Boxplot illustrating mean δ^{13}C values (±SE) of *H. regani* for each size class on the West (**A**) and South (**B**) coasts.

Variation in δ^{15}N and δ^{13}C of *S. capensis*

The GLM for *S. capensis* indicated significant effects for both isotopes, with size accounting for the most variance in both δ^{15}N and δ^{13}C. This was followed by depth for δ^{13}C, and coast for δ^{15}N.

The isotopic bi-plot of δ^{15}N and δ^{13}C values displays some spatial separation between coasts (Figure 60). For δ^{15}N, the GLM indicated a significant difference between coasts ($F_1 = 7.321$, $p < 0.05$) (Table 20), with higher mean values recorded for *S. capensis* on the West Coast (14.22‰, SE ± 0.06) than on the South Coast (13.99‰, SE ± 0.05) (Figure 61**A**, Appendix 19). There was no significant effect of coast on δ^{13}C ($F_1 = 0.378$, $p > 0.05$) (Table 20), with similar mean values being recorded in *S. capensis* on both the West (-15.92 ± 0.05) and South (-15.64 ± 0.06) coasts (Figure 61**B**, Appendix 19).

Table 20: Summary of results obtained from univariate tests of significance testing for variation in the δ^{15}N and δ^{13}C values of *S. capensis* between coasts, depth stratum and size (TL). Significant interaction terms are included in the table and significant P-values ($p < 0.05$) are indicated in bold

δ^{15}N

Parameters	**Df**	**SS**	**MS**	**F**	**Sig.**
Model	12	20.294	1.691	16.644	**$P < 0.05$**
Intercept	1	368.724	368.724	3628.817	**$P < 0.05$**
Size (TL)	1	3.283	3.283	32.306	**$P < 0.05$**
Coast	1	1.462	1.462	14.392	**$P < 0.05$**
Depth	3	0.923	0.308	3.029	$P > 0.05$
Coast*Size class	4	1.869	0.467	4.597	**$P < 0.05$**
Coast*Depth	3	1.310	0.437	4.297	**$P < 0.05$**
Error	142	14.429	0.102		

δ^{13}C

Parameters	**Df**	**SS**	**MS**	**F**	**Sig.**
Model	5	13.053	2.611	13.558	**$P < 0.05$**
Intercept	1	1745.268	1745.268	9064.406	**$P < 0.05$**
Size (TL)	1	1.748	1.748	9.079	**$P < 0.05$**
Depth	3	4.229	1.410	7.321	**$P < 0.05$**
Coast	1	0.073	0.073	0.378	$P > 0.05$
Error	149	28.689	0.193		

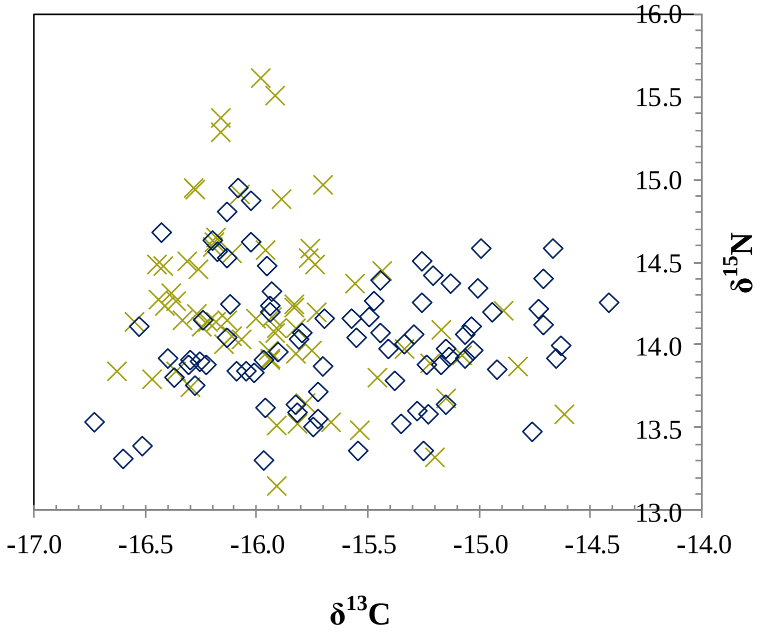


Figure 61: Isotopic bi-plot illustrating δ^{15}N and δ^{13}C values of *S. capensis* on the West (◇) and South (X) coasts.

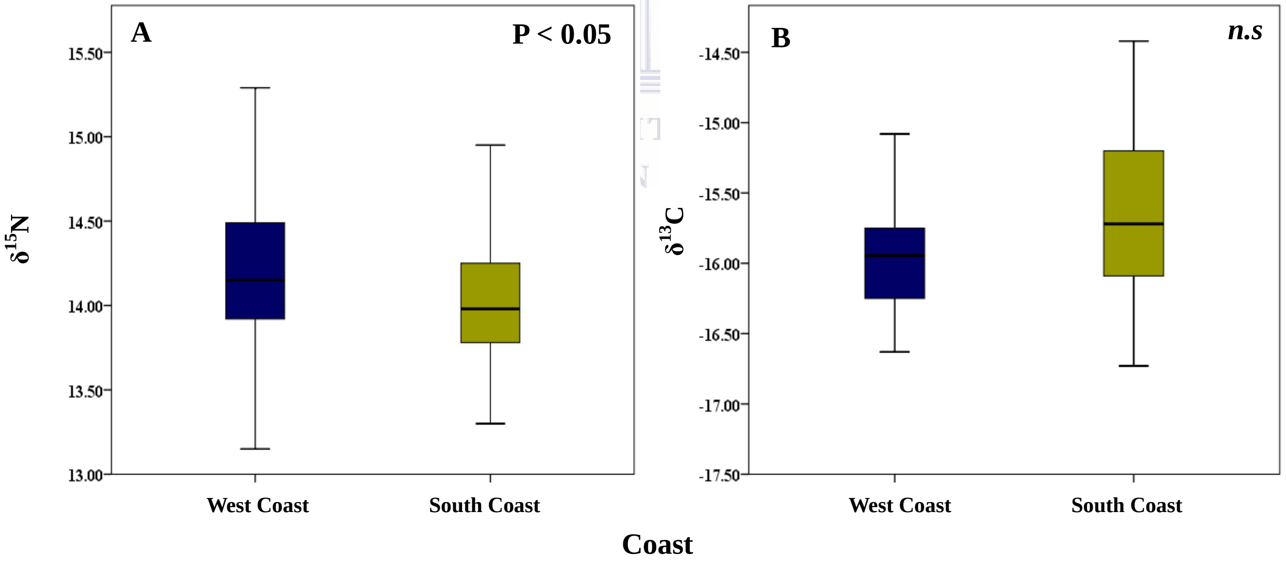


Figure 62: Boxplot illustrating mean δ^{15}N (**A**) and δ^{13}C (**B**) values (±SE) of *S. capensis* on each coast. $P < 0.05$ indicates a significant difference between mean values.

Isotopic bi-plots displaying δ^{15}N and δ^{13}C values by depth stratum shows separation on both coasts (Figures 62**A** and **B**). For δ^{15}N, results obtained from the GLM indicated a significant coast*depth strata interaction ($F_3 = 4.297$, $p < 0.05$)

(Table 20), indicating that the pattern of δ^{15}N with depth is not the same on both coasts (Figure 63, Appendix 20). Although no significant difference was noted for depth itself, δ^{15}N values recorded in *S. capensis* appear to increase with increasing depth on the West Coast (Figure 63**A**).

For δ^{13}C, no significant interaction between coast and depth strata was noted (Table 20). However, after removing the interaction term, the GLM indicated a significant effect of depth on δ^{13}C ($F_3 = 7.321$, $p < 0.05$) (Table 20), with a *post-hoc* Tukey test indicating differences in the δ^{13}C values recorded for *S. capensis* between the 150 and 350 m and 150 and 450 m depth strata on the South Coast only (Figure 64**B**). Although a *post-hoc* Tukey test indicated no significant difference in the δ^{13}C values recorded in *S. capensis* between depth strata on the West Coast, a decrease in δ^{13}C with increasing depth is apparent (Figure 64**A**, Appendix 20).

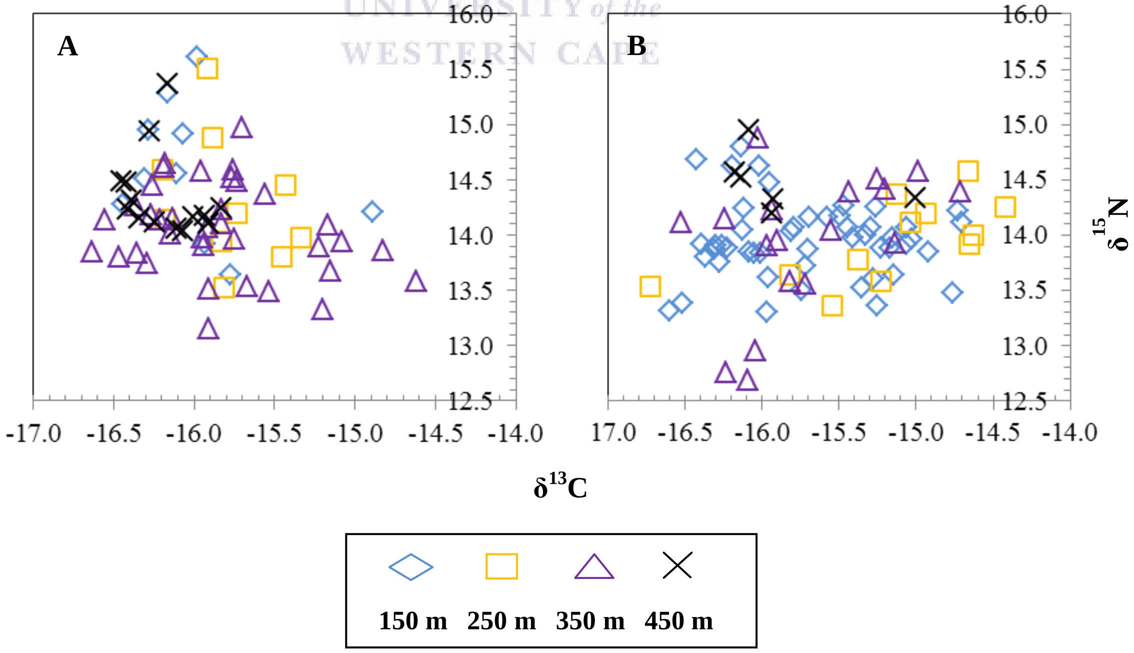


Figure 63: Isotopic bi-plot illustrating the δ^{15}N and δ^{13}C values of *S. capensis* at each depth stratum on the West (**A**) and South (**B**) coasts.

The lowest mean $\delta^{15}N$ values were recorded from *S. capensis* sampled at 150 m on the West Coast and at 450 m on the South Coast, while highest mean $\delta^{15}N$ values were recorded at 450 m on the West Coast and at 250 m on the South Coast (Figures 63**A** and **B**, Appendix 20). The highest mean $\delta^{13}C$ values were observed in *S. capensis* sampled at 250 m on the West Coast and at 150 m on the South Coast, while lowest mean $\delta^{13}C$ values were observed at 450 m on both coasts (Figures 64**A** and **B**, Appendix 20).

In terms of catshark size class, the $\delta^{15}N$ and $\delta^{13}C$ values appear to be clearly separated in isospace on both coasts (Figures 65**A** and **B**). Results obtained from the GLM indicated a significant effect of size on $\delta^{15}N$ ($F_1 = 32.306$, $p < 0.05$) (Table 20), with scatterplots displaying a strong positive correlation between $\delta^{15}N$ and size on the West ($R^2 = 0.5867$, $p < 0.05$) and South ($R^2 = 0.3168$, $p < 0.05$) coasts (Figures 66**A** and **B**).

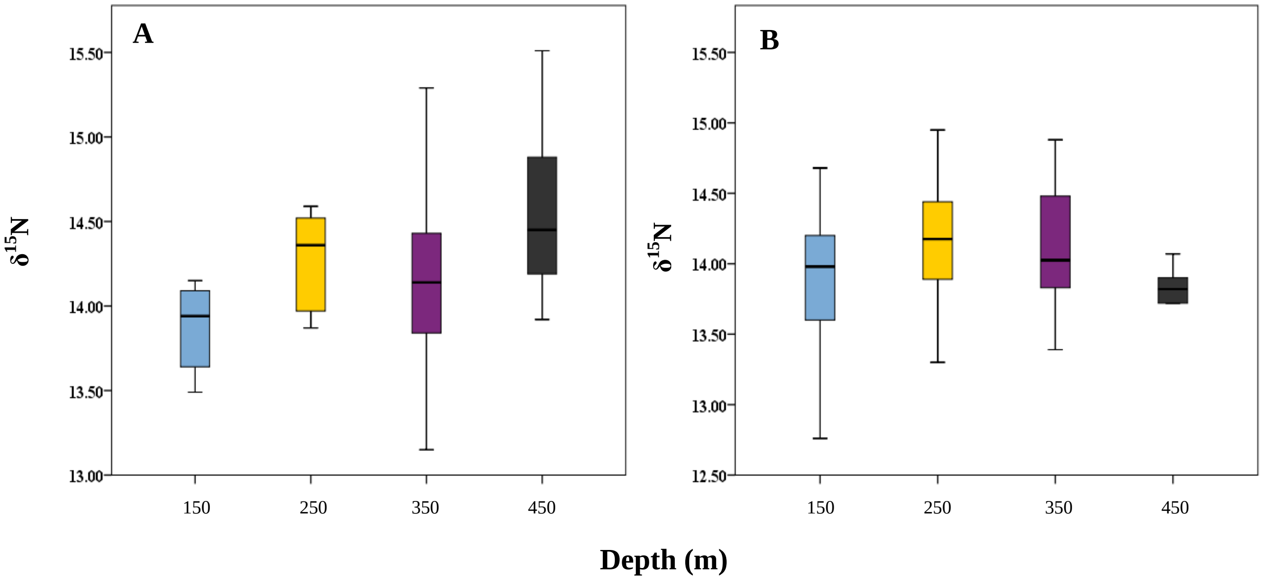
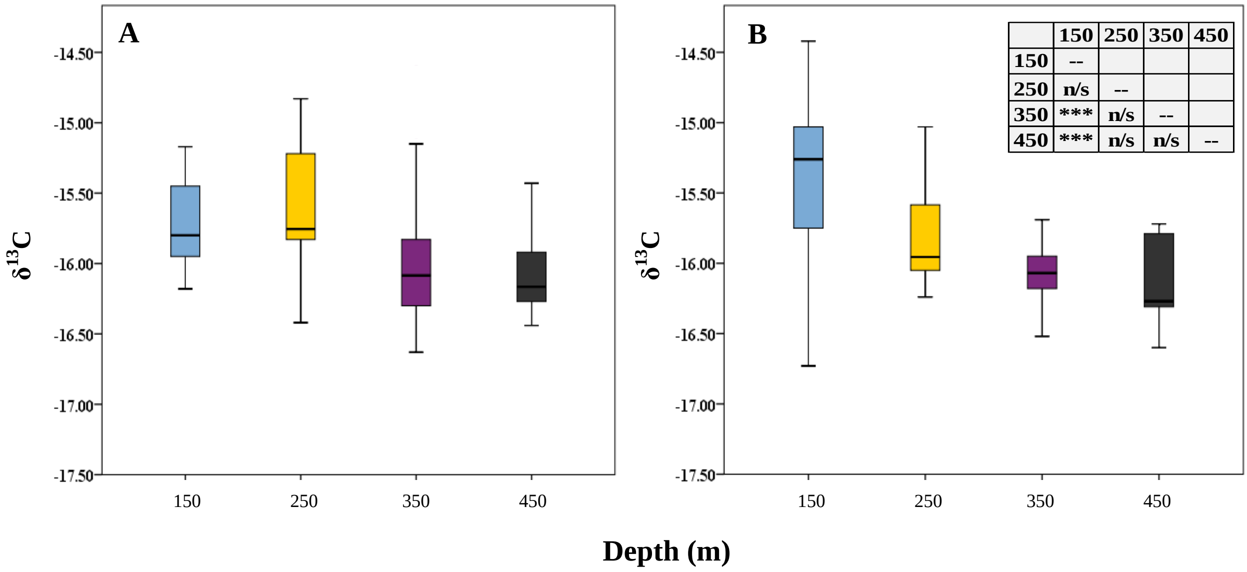


Figure 64: Boxplot illustrating mean $\delta^{15}N$ values (±SE) of *S. capensis* at each depth stratum on the West (**A**) and South (**B**) coasts.



	150	250	350	450
150	--			
250	n/s	--		
350	***	n/s	--	
450	***	n/s	n/s	--

Figure 65: Boxplot illustrating mean $\delta^{13}C$ values (±SE) of *S. capensis* at each depth stratum on the West (**A**) and South (**B**) coasts. Table represents *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

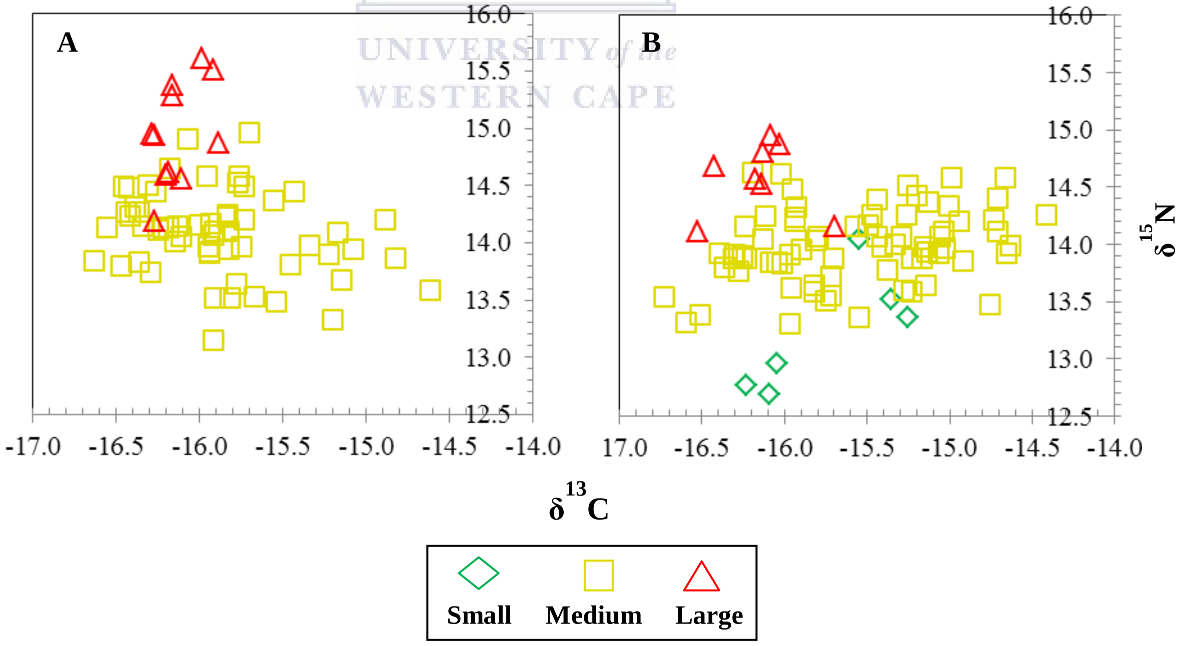


Figure 66: Isotopic bi-plot illustrating the $\delta^{15}N$ and $\delta^{13}C$ values of *S. capensis* for each size class on the West (**A**) and South (**B**) coasts.

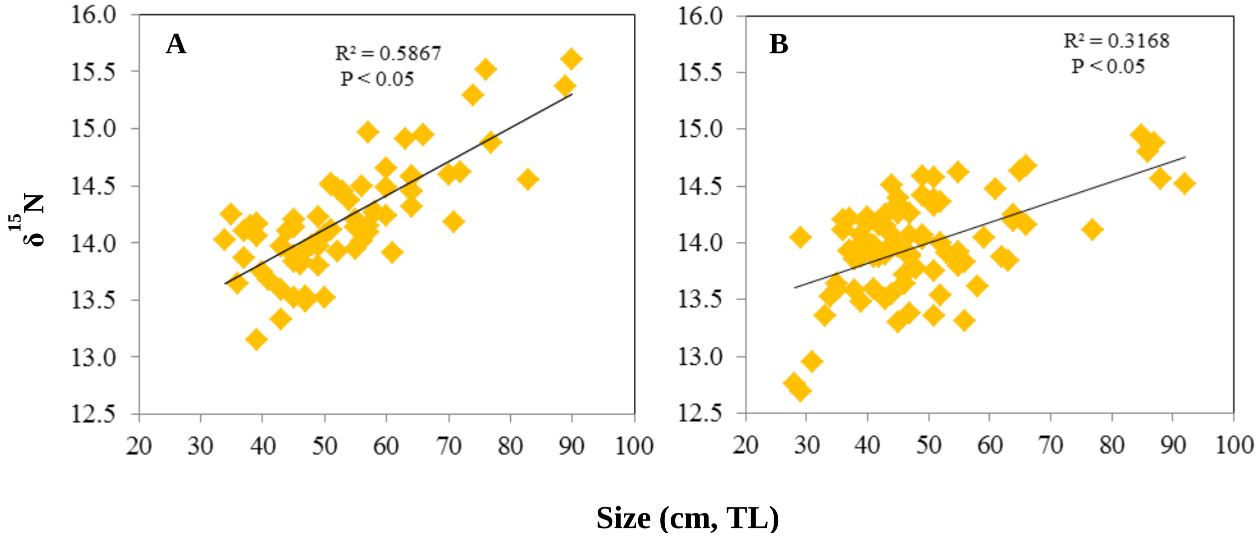
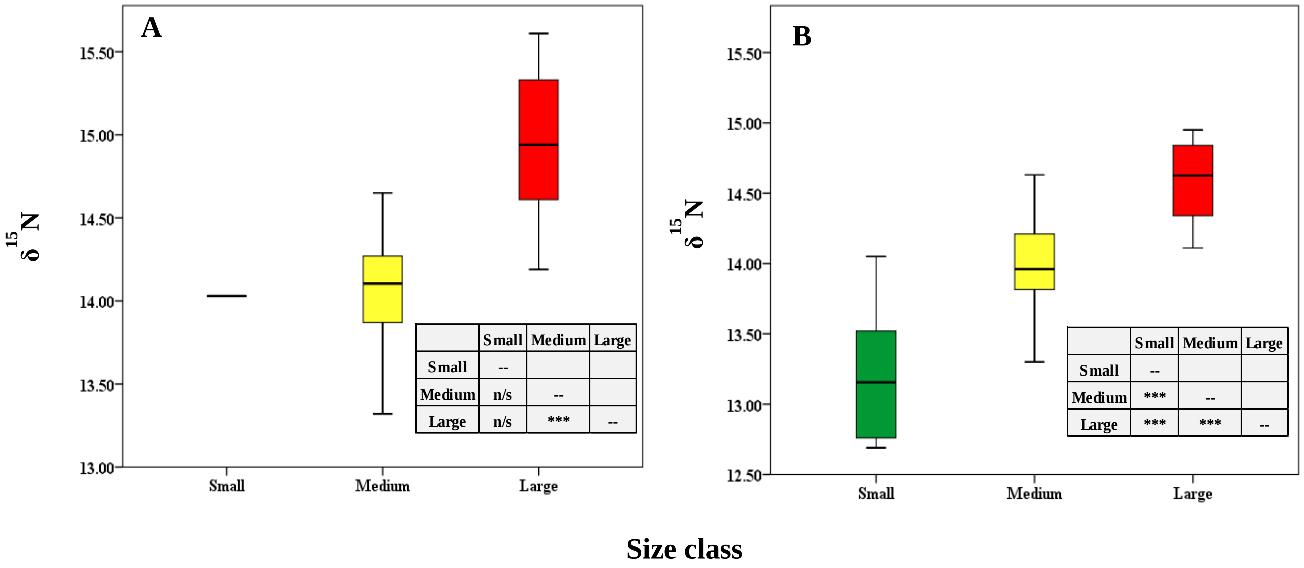


Figure 67: Scatterplots of δ^{15}N and size for *S. capensis* on the West (**A**) and South (**B**) coasts. Graphs include linear trendlines, R^2 values and P- values where significant relationships ($p < 0.05$) are noted.

On further analysis, a *post-hoc* Tukey test indicated a significant difference between the δ^{15}N values recorded in medium and large individuals on the West Coast (Figure 67**A**), and between small and medium, small and large, and medium and large individuals on the South Coast (Figure 67**B**); with mean δ^{15}N values increasing with increasing *S. capensis* size on both coasts (Figures 67**A** and **B**). For δ^{15}N, a significant coast*size class interaction was noted as well ($F_4 = 4.597$, $p < 0.05$) (Table 20), with higher mean values observed across size classes on the West Coast than on the South Coast (Appendix 20). Notably, the relationship between δ^{15}N and size class is steeper on the West Coast as well (Figures 66 and 67).



	Small	Medium	Large
Small	--		
Medium	n/s	--	
Large	n/s	***	--

	Small	Medium	Large
Small	--		
Medium	***	--	
Large	***	***	--

Figure 68: Boxplot illustrating mean $\delta^{15}N$ values (±SE) of *S. capensis* for each size class on the West (**A**) and South (**B**) coasts. Table represents *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

The results of the GLM indicated a significant effect of size on $\delta^{13}C$ ($F_1 = 9.079$, $p < 0.05$) (Table 20), with scatterplots displaying a significant negative correlation between $\delta^{13}C$ and size on the South Coast only ($R^2 = 0.2008$, $p < 0.05$) (Figure 68**B**). A *post-hoc* Tukey test indicated a significant difference between the $\delta^{13}C$ values recorded in medium and large individuals on the South Coast (Figure 69**B**), with mean $\delta^{13}C$ values decreasing with increasing size (Figure 69**B**). Non-significant relationships between coast*depth strata and coast*size class indicates similar relationships off both coasts (Table 20).

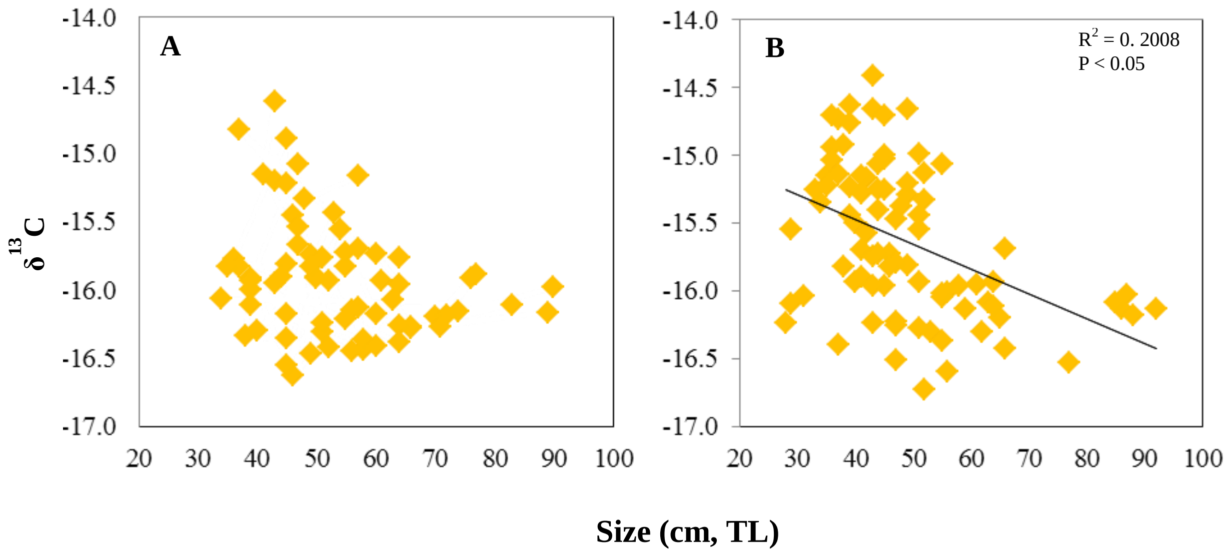
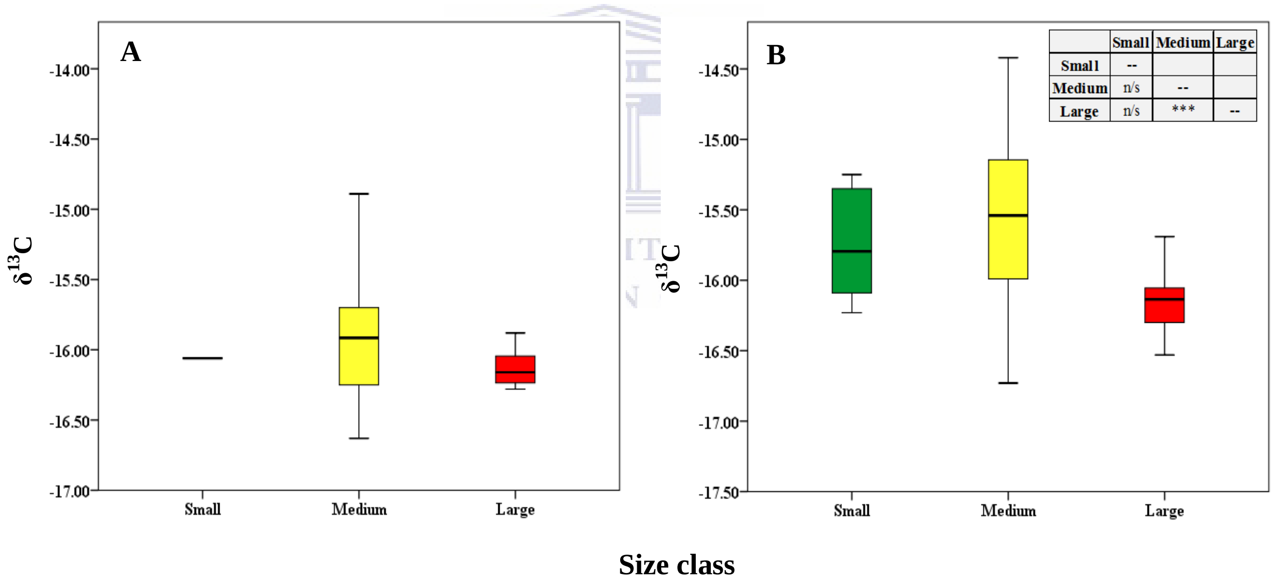


Figure 69: Scatterplots of δ^{13}C and size for *S. capensis* on the West (**A**) and South (**B**) coasts. Graphs include linear trendlines, R^2 values and P- values where significant relationships ($p < 0.05$) are noted.



	Small	Medium	Large
Small	--		
Medium	n/s	--	
Large	n/s	***	--

Figure 70: Boxplot illustrating mean δ^{13}C values (±SE) of *S. capensis* for each size class on the West (**A**) and South (**B**) coasts. Table represents *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

Interspecific variation in δ^{15}N and δ^{13}C

The isotopic bi-plot displaying δ^{15}N and δ^{13}C values of *H. regani* and *S. capensis* shows a high degree of overlap between species and between coasts (Figure 70). Despite this, significant interspecific differences were noted for δ^{15}N, but not for δ^{13}C (Table 21). Size accounted for most of the variance in δ^{15}N and δ^{13}C, followed by coast, species and depth strata for δ^{15}N, and depth strata for δ^{13}C (Table 21). A significant interaction between species and size class was noted for both isotopes as well, indicating that the size effects on δ^{15}N and δ^{13}C differ between the two species (Table 21).

For both species there was a decrease in δ^{15}N values when moving from west to south, with *H. regani* displaying significantly higher mean δ^{15}N values than *S. capensis* on the West (*H. regani*: 14.49 ± 0.38; *S. capensis*: 14.20 ± 0.49) and South (*H. regani*: 14.22 ± 0.59; *S. capensis*: 13.99 ± 0.05) ($F_1 = 29.085$, $p < 0.05$) coasts (Figure 71**A**, Appendices 17 and 19). No significant difference was noted between δ^{13}C and coast ($F_1 = 0.306$, $p > 0.05$) (Figure 71**B,** Table 21).

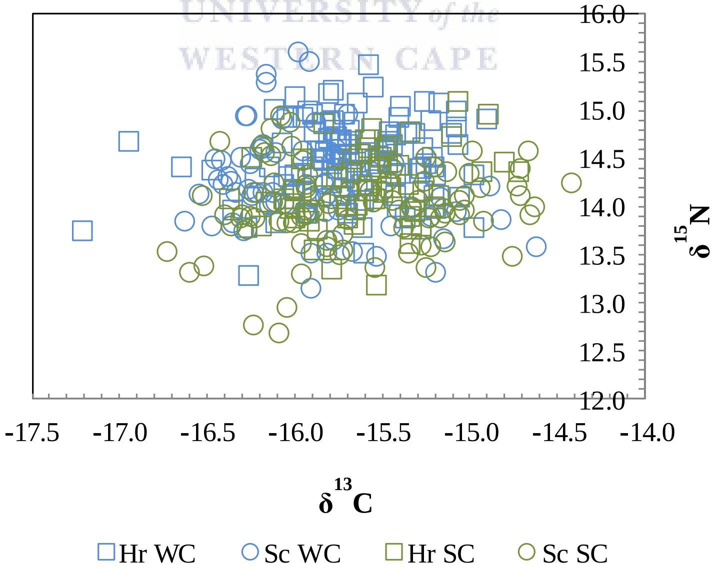


Figure 71: Isotopic bi-plot illustrating the δ^{15}N and δ^{13}C values of *H. regani* (Hr) and *S. capensis* (Sc) on the West (WC) and South (SC) coasts.

Table 21: Summary of results obtained from univariate tests of significance testing for variation in the $\delta^{15}N$ and $\delta^{13}C$ values between species, coasts, depth stratum and size (TL). Significant interaction terms are included in the table and significant P-values ($p < 0.05$) are indicated in bold

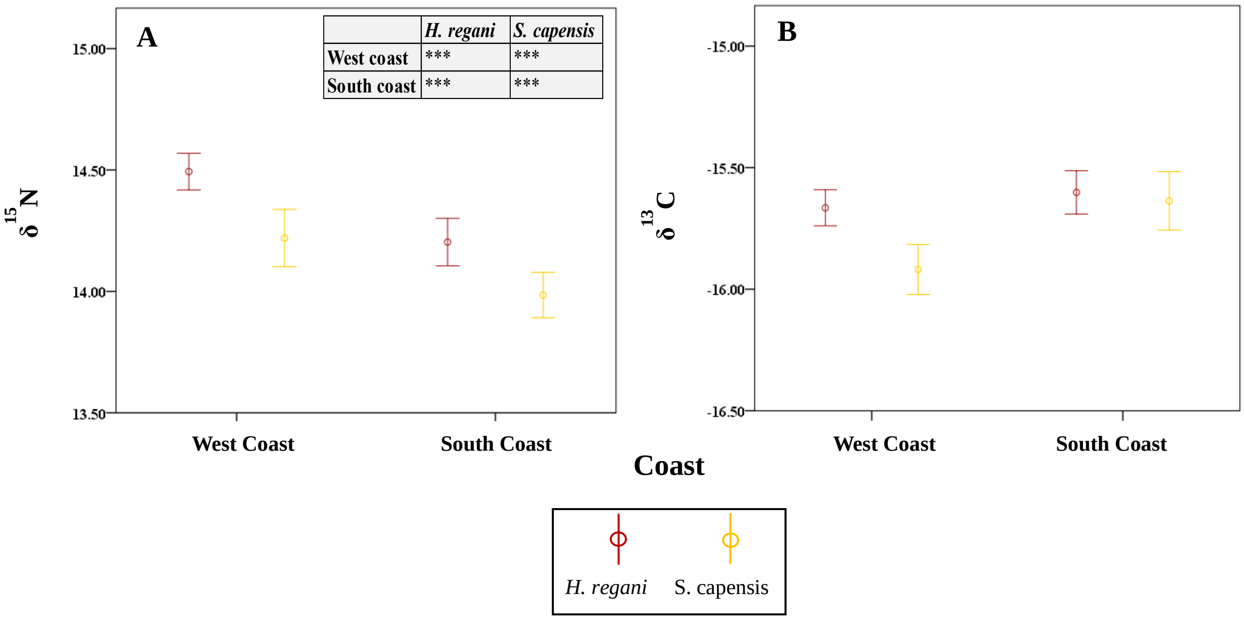
$\delta^{15}N$

Parameters	**df**	**SS**	**MS**	**F**	**Sig.**
Model	10	34.171	3.417	28.794	**P < 0.05**
Intercept	1	973.175	973.175	8200.325	**P < 0.05**
Size (TL)	1	3.849	3.849	32.432	**P < 0.05**
Coast	1	3.452	3.452	29.085	**P < 0.05**
Species	1	2.102	2.102	17.710	**P < 0.05**
Depth	3	3.070	1.023	8.622	**P < 0.05**
Species*Size class	4	2.460	0.615	5.181	**P < 0.05**
Error	316	37.501	0.119		

$\delta^{13}C$

Parameters	**df**	**SS**	**MS**	**F**	**Sig.**
Model	10	14.235	1.424	8.502	**P < 0.05**
Intercept	1	1284.986	1284.986	7076.508	**P < 0.05**
Size (TL)	1	1.480	1.480	8.837	**P < 0.05**
Depth	3	4.181	1.394	8.324	**P < 0.05**
Coast	1	0.051	0.051	0.306	P > 0.01
Species	1	0.009	0.009	0.056	P > 0.01
Species*Size class	4	4.221	1.055	6.302	**P < 0.05**
Error	316	52.912	0. 167		

With the exception of the 350 m depth stratum on the South Coast, significantly higher mean $\delta^{15}N$ values were recorded for *H. regani* than for *S. capensis* across all depths on both coasts (Figures 72**A** and **B**) ($F_3 = 8.622$, $p < 0.05$). For $\delta^{13}C$, both species had rather similar mean values, except at the 350 and 450 m depth strata on the West Coast and at the 450 m depth stratum on the South Coast, where *S. capensis* displayed lower mean $\delta^{13}C$ values than *H. regani* (Figures 73**A** and **B**).



	H. regani	*S. capensis*
West coast	***	***
South coast	***	***

Figure 72: Boxplot illustrating mean δ^{15}N (**A**) and δ^{13}C (**B**) values (± SE) for *H. regani* and *S. capensis* on the West and South coasts. Table represents *post-hoc* tests, with significant interactions ($p < 0.05$) being denoted by ***.

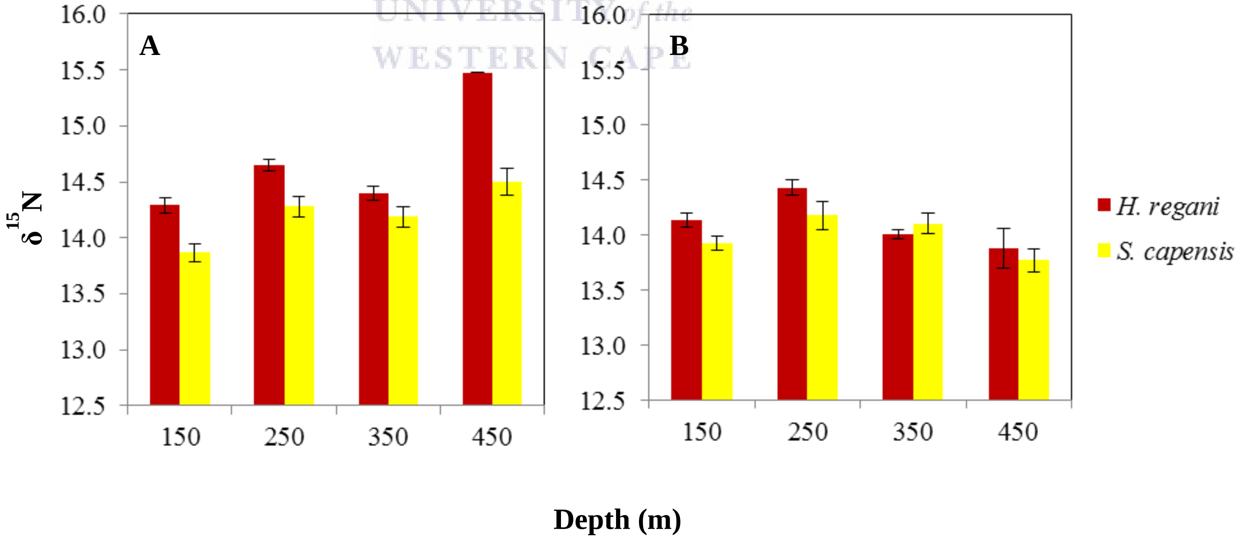


Figure 73: Mean δ^{15}N values (± SE) of *H. regani* and *S. capensis* at each depth stratum on the West (**A**) and South (**B**) coasts.

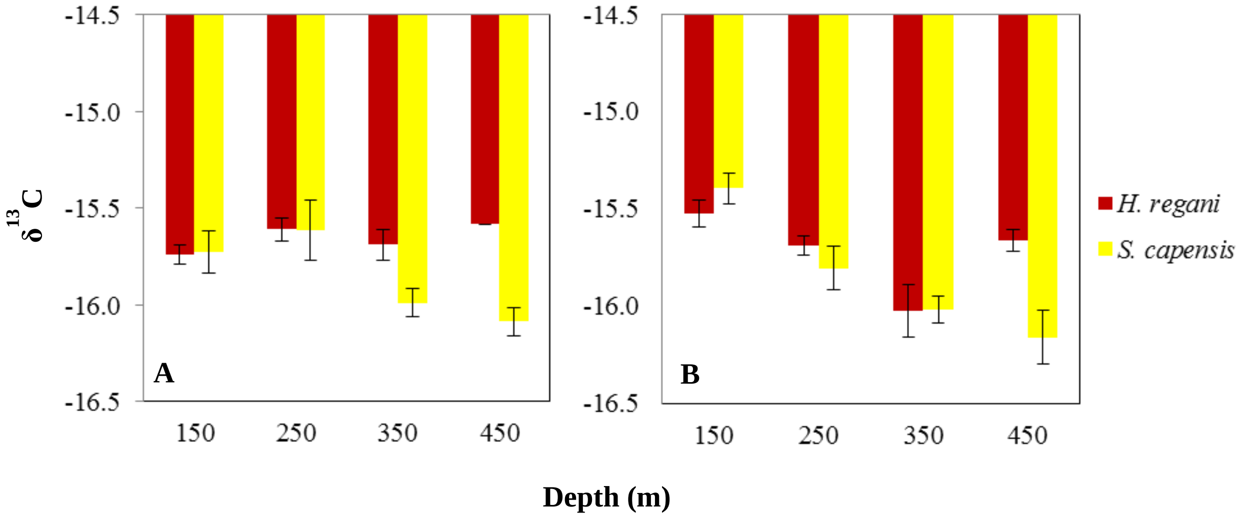


Figure 74: Mean δ^{13}C values (± SE) of *H. regani* and *S. capensis* at each depth stratum on the West (**A**) and South (**B**) coasts.

Size was significantly correlated with δ^{15}N and δ^{13}C for both species (Table 21). On the West Coast, higher mean δ^{15}N values were recorded for small and medium *H. regani* than for small and medium *S. capensis*, whereas higher mean δ^{15}N values were recorded for large *S. capensis* than for large *H. regani* (Figure 74**A**). Similarly on the South Coast, higher mean δ^{15}N values were recorded for medium *H. regani* than for medium *S. capensis*, whereas large *S. capensis* were recorded to display higher mean δ^{15}N values than large *H. regani* (Figure 74**B**). Lower mean δ^{13}C values were recorded for *S. capensis* than for *H. regani* across all size classes on both coasts (Figures 75**A** and **B**).

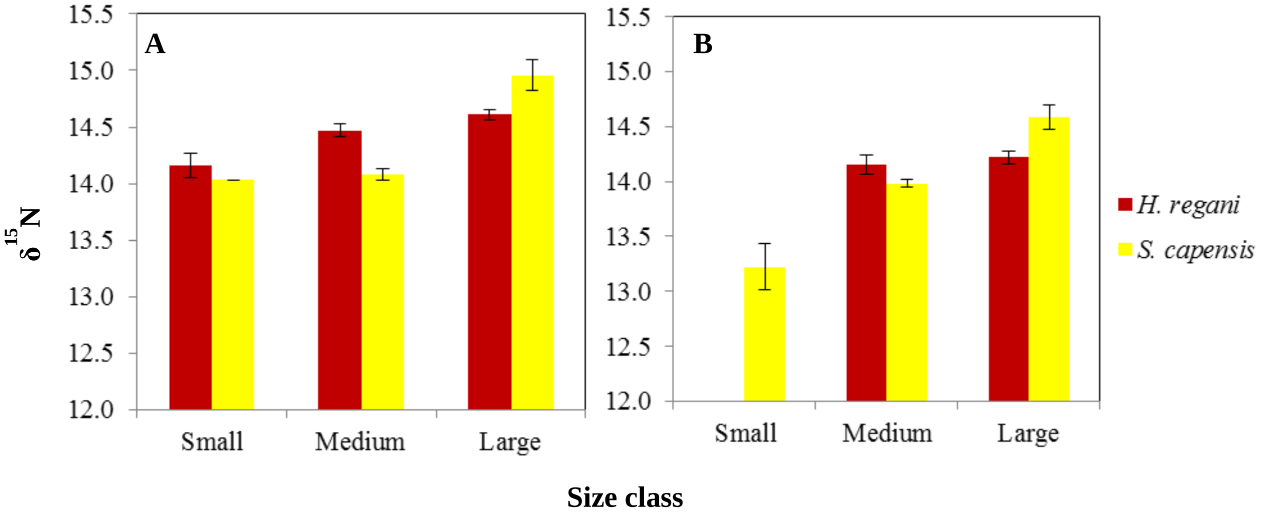


Figure 75: Mean δ^{15}N values (± SE) of *H. regani* and *S. capensis* at each size class on the West (**A**) and South (**B**) coasts.

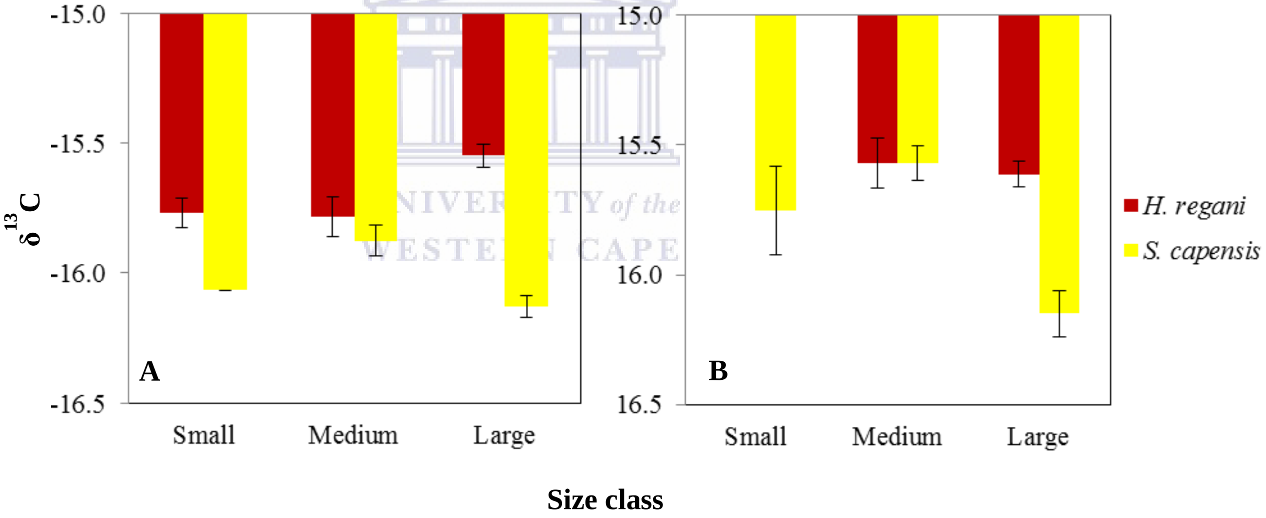


Figure 76: Mean δ^{13}C values (± SE) of *H. regani* and *S. capensis* at each size class on the West (**A**) and South (**B**) coasts.

Discussion

Spatial variability

In the present study both catshark species were recorded to display significantly higher δ^{15}N values on the West Coast than on the South Coast. These findings are consistent with those of other studies conducted around the coasts of South Africa, which have also reported significantly higher $\delta^{15}N$ values in marine organisms sampled on the West Coast as opposed to the $\delta^{15}N$ values found in marine organisms sampled on the South Coast (Parkins 1993, shallow-water Cape hake; Hill *et al*. 2006, intertidal mussels; Kohler *et al*. 2011, African black oyster catcher; van der Lingen and Miller 2014, shallow and deep-water Cape hakes). For example, van der Lingen and Miller (2014) noted that the two Cape hake species (*M. capensis* and *M. paradoxus*) sampled on the West Coast had $\delta^{15}N$ values that were about 1.4‰ higher than those sampled on the South Coast. Those authors attributed this spatial variability in $\delta^{15}N$ to differences in isotopic baselines owing to the different current systems (Benguela and Agulhas Currents) and environmental factors evident off the West and South coasts of South Africa.

This seems to be the case in the present study as well, with the shift in $\delta^{15}N$ values appearing to be reflective of the isotopic gradient from the West Coast to the South Coast. The West Coast is a region characterised by cold, eutrophic waters, with high chlorophyll *a* levels, diatom dominated phytoplankton communities, and a reliance on upwelled nitrate that is enriched in nitrogen, as the primary source of nitrogen. In contrast, the South Coast is a region characterised by temperate, seasonally oligotrophic waters, with low chlorophyll *a* levels, flagellate-dominated phytoplankton communities and a reliance on recycled nitrogen and N-fixed nitrogen, both of which are depleted in nitrogen, as the primary source of nitrogen (Demarcq *et al*. 2007, Hutchings *et al*. 2009, van der Lingen and Miller 2014). Consistent with these findings is a study by Mullin *et al*. (1984), on geographic and temporal variations in the stable nitrogen isotopes of copepods and chaetognaths in the North Pacific, who reported significantly higher $\delta^{15}N$ values in zooplankton reliant on upwelled nitrate as their primary source of nitrogen, and lower $\delta^{15}N$ levels in zooplankton reliant on recycled nitrogen as their primary source of nitrogen.

Notably, the differences in the $\delta^{15}N$ values between the West and South coasts in the present study (0.2 to 0.3‰) was much smaller than the difference (1.4‰) noted in the study on Cape hakes by van der Lingen and Miller (2014). This difference could be due to the fact that the study by van der Lingen and Miller (2014) collected samples across a wider geographic range than the present study; van der Lingen and Miller (2014) obtained samples from the Orange River mouth to Port Alfred (ca. 1600 kms) while the present study only obtained samples from Port Nolloth to Mossel Bay (ca. 900 kms). Nevertheless, the spatial variability in $\delta^{15}N$ in the present study can still be considered significant due to the fact that the difference in $\delta^{15}N$ isotope values between coasts was greater than the analytical error for $\delta^{15}N$, which was calculated to be 0.07‰.

Alternatively, these differences in $\delta^{15}N$ values may also be attributed to spatial variability in dietary composition, with catsharks possibly consuming higher trophic level species on the West Coast than on the South Coast. Numerous marine organisms have been shown to be capable of changing their trophic position in response to localised changes in available resources, particularly changes in food availability (Meyer and Smale 1991, Thomas and Cahoon 1993, Pillar and Wilkinson 1995, Rinewalt 2007). For example, a study by Thomas and Cahoon (1993) used stable isotope analysis to describe the trophic ecology of rocky-reef fish, and linked changes in their isotopic ratios to changes in food availability between study locations. Similarly, a study by Pillar and Wilkinson (1995), on the diet of the shallow-water Cape hake (*M. capensis*) on the South Coast of South Africa, reported that *M. capensis* consumed different prey items on each coast. A similar pattern was noted in the present study, with high trophic level species such as teleosts and cephalopods being abundant in the diet of *H. regani* and *S. capensis* on the West Coast, while low trophic level crustaceans were more abundant in their diet on the South Coast (see Chapter 4). It is thus possible that the spatial variability in their diets also contributes to the comparatively higher δ^{15}N values observed on the West Coast.

Notably, the effect of coast on δ^{13}C was not significant for both species.

Variability with depth

Previous studies evaluating changes in δ^{15}N and δ^{13}C with depth have attributed the variability in isotope ratios to the characteristic baseline values and trophic pathways present in inshore and offshore environments (Parkins 1993, Andrews *et al.* 2010, Abrantes and Barnett 2011, Hussey *et al*. 2012). Benthic organisms in inshore marine environments are reliant on microphytobenthic sources of production which are enriched in δ^{15}N and δ^{13}C, while benthic organisms in offshore environments are reliant on phytoplanktonic sources of production that are depleted in these isotopes (McConnaughey and McRoy 1979, France 1995). Furthermore, benthic sources of production in inshore waters have been reported to have more trophic links, which allows for additional fractionation and thus higher isotopic values in organisms inhabiting these environments (McConnaughey and McRoy 1979, France 1995, Nerot *et al*. 2012, van der Lingen and Miller 2014). For example, a study by Abrantes and Barnett (2011) on intrapopulation variation in the diet and habitat use of the broadnose sevengill shark (*Notorynchus cepedianus*) off Tasmania, Australia, found that δ^{15}N and δ^{13}C values decreased with distance from shore, with the authors attributing this variability to lower baseline values and shorter food-webs in offshore environments. Similarly, a study by Andrews *et al.* (2010), using carbon and nitrogen isotopes to describe the trophic ecology of spiny dogfish (*Squalus acanthias*) inhabiting the northeastern Pacific Ocean, linked variability in δ^{15}N and δ^{13}C values to differences in inshore and offshore feeding habits, with enriched isotopic values being related to inshore feeding and depleted isotopic values to offshore feeding.

In the present study, a significant effect of depth on δ^{15}N was noted for *H. regani* on both coasts. Although no obvious trend was noted on the West Coast, the δ^{15}N values of *H. regani* on the South Coast displayed a decrease from 250 m to 450 m. This commonly described trend of decreasing isotope values with increasing depth held true for the δ^{13}C values of *S. capensis* on the South Coast as well, with a consistent decrease in δ^{13}C values with increasing depth. A similar pattern was noted for the δ^{13}C values of *S.capensis* on the West Coast, albeit not significant.

For *S. capensis*, a significant coast*depth strata interaction was noted for δ^{15}N. In contrast to *H. regani, S. capensis* individuals on the West Coast can be seen to display a trend of increasing δ^{15}N values with increasing depth, while no obvious trend can be noted on the South Coast. This trend observed on the West Coast could possibly be attributed to the “bigger-deeper pattern” (see Chapter 3) and the associated shift in prey items consumed at each depth. Such changes in the diets of sharks have previously been reported (Carrassón *et al*. 1992, Smale and Compagno 1997, Olaso *et al*. 2005, Fanelli *et al.* 2009, Valls *et al*. 2011), and have been linked to changes in the abundance, diversity and size of prey items with changing depth (see Chapter 4).

Variability with size

In the present study clear ontogenetic shifts were noted, with the general pattern being an increase in $\delta^{15}N$ values with increasing catshark size. Such changes in $\delta^{15}N$ values have been observed in numerous elasmobranch species, and have been linked to ontogenetic dietary shifts associated with changes in morphology, physiology or lifestyle with growth (Wetherbee and Cortés 2004, Andrews *et al.* 2010, Dale *et al*. 2011). For example, a study by Dale *et al*. (2011), on the distribution and diet of the brown stingray (*Dasyatis lata*) in Kane'ohe Bay, Hawaii, attributed increases in $\delta^{15}N$ values with increasing size to a known dietary shift from lower level trophic species such as alpheids and polychaetes in small individuals to higher trophic level species such as portunids and gobies in large individuals. Similarly, Andrews *et al.* (2010) attributed increases in $\delta^{15}N$ values with increasing spiny dogfish (*Squalus acanthias*) length to ontogenetic shifts in their diets, with small dogfish observed to consume smaller and a less diverse range of prey than large dogfish.

The results of this study support these findings; with both catsharks having been found to change their diets with increasing size (see Chapter 4). Although crustaceans appeared to be the primary prey item consumed across all size classes, cephalopods became increasingly important with increasing size for *H. regani* on the West Coast, and cephalopods as well as teleosts in the diet of *S. capensis* on the West and South coasts (see Chapter 4). There were also changes in the size of prey items consumed and average weight of individual prey items, with the %W of crustaceans and cephalopods increasing with increasing catshark size on both coasts (see Chapter 4). Similar to previous studies, it appears that *H. regani* and *S. capensis* are not only consuming larger prey items, but also preying on higher trophic level species such as cephalopods and teleosts, with increasing size. The strong correlation between δ^{15}N and size is thus not surprising, with the higher δ^{15}N values possibly being as a result of the higher proportion of cephalopods and teleosts in the diets of large individuals.

The lack of a relationship between δ^{15}N and size for *H. regani* on the South Coast, however, could be explained by the absence of small individuals on this coast (see Chapter 4). The rather similar δ^{15}N values observed in medium and large *H. regani* on the South Coast are possibly as a result of their similar size and metabolic requirements, with both size classes probably feeding on prey from the same trophic level. Furthermore, the turnover rate of tissue in small sharks has been reported to be faster than in large sharks that retain their isotopic signatures for a longer period (Barnes *et al*. 2007). Small sharks can therefore be expected to display more variable isotope signatures than medium and large sharks.

A significant effect of size on δ^{13}C was noted for *S. capensis*, with δ^{13}C values being lowest in large individuals. Since δ^{13}C values are known to be high in organisms inhabiting inshore environments and low in organisms inhabiting offshore environments (McConnaughey and McRoy 1979, France 1995), it is not surprising that large *S. capensis*, that are known to inhabit deeper waters than small and medium *S. capensis* (see Chapter 3), display lower δ^{13}C values than their smaller counterparts.

Conversely, no significant effect of size on δ^{13}C was noted for *H. regani* on either coast. Similarly a study by Parkins (1993), on the isotope ratios of the shallow-water Cape hake (*M. capensis*) off the West and South coasts of South Africa, also reported no change in δ^{13}C values with increasing fish length. This possibly indicates that trophic level rather than source production is having a greater influence on the stable isotope values of *H. regani* by size.

Interspecific variability

There were significant interspecific differences in δ^{15}N values between the two species, with *H. regani* feeding at a higher trophic level than *S. capensis* on both the West and South coast. This corroborates the findings of the previous chapter, based on diet analysis, which reported *H. regani* to feed on a greater proportion of higher trophic level species such as cephalopods and teleosts than *S. capensis,* which appeared to be more dependent on lower trophic level crustaceans (see Chapter 4). A similar pattern was noted in the two Cape hake species, with *M. capensis* being found to display higher δ^{15}N values than *M. paradoxus* owing to the fact that *M. capensis* consumed more teleosts than *M. paradoxus* (van der Lingen and Miller 2014).

Although the pattern of higher δ^{15}N values for *H. regani* than *S. capensis* was commonly observed between depths and size classes, large *S. capensis* were however found to display higher δ^{15}N values than large *H. regani* on both coasts. This could possibly be attributed to their larger size (maximum TL, 92 cm) and thus their ability to consume larger and possibly higher trophic level prey items, than large *H. regani* (maximum TL, 65 cm). A similar pattern was noted in a study by Vaudo and Heithaus (2011), describing dietary overlap in meso-predatory elasmobranchs in Shark Bay, Western Australia, who attributed the lower δ^{15}N values, observed in *Neotrygon* spp. (Maskray), when compared to larger batoids in the same system, to their comparatively smaller size. Those authors concluded that their small size limits them to comparatively smaller, lower trophic level prey items than their larger counterparts.

This is the first study using δ^{13}C and δ^{15}N isotopes to compare spatial and ontogenetic variability in the trophic ecology of *H. regani* and *S. capensis* on the West and South coasts of South Africa.

Based on the findings of the present study it appears that the spatial and ontogenetic variability in δ^{13}C and δ^{15}N values are reflective of spatially different isotopic baseline values, owing to regional differences in carbon and nitrogen production, and the spatially distinct phytoplankton and zooplankton communities evident off each coast. However, it is also possible that differences in trophic levels, owing to spatial and ontogenetic changes in habitat use, resource availability and prey items consumed, also play a role in the distinct isotopic values observed within and between these catshark species.

Although the present Chapter describes the trophic ecology of these demersal catsharks, I suggest that future studies attempt to collect samples over a wider geographic range in order to gain a more extensive understanding of the distinct isotopic differences observed on the West and South coasts. Additionally, samples should be collected from small areas to determine whether changes in isotope ratios with size and depth are due to a depth effect, a size effect or a combination of depth and size. Furthermore, samples should also be collected over different seasons to elucidate temporal differences in the physical and biological processes operating off each coast. I recommend that isotope data be collected from their ingested prey as well, when prey items are in an identifiable and undigested state, in order to gain a better understanding of the role these abundant catsharks in the demersal food-web.

Chapter Six

General Conclusions

The objectives of this thesis were to examine the distribution patterns and trophic ecology of the two most common catsharks, *H. regani* and *S. capensis*, caught as by-catch by the commercial demersal trawling industry targeting the two Cape hake species (*M. capensis* and *M. paradoxus*) off the West and South coasts of South Africa. To do this distribution data collected during research surveys conducted from 1994 to 2015 and stomach content and stable isotope data collected from 2014 to 2015 were analysed. Methods of sample collection and processing, and data analyses conducted, are given in Chapter 2.

On examination of the distribution data, I found that although both species occurred around the coastline, they displayed different centres of distribution, with *H. regani* being more abundant on the West Coast and *S. capensis* being more abundant on the South Coast. In addition, both catsharks were also observed to display size-based segregations, with catshark size increasing with depth in both species. Based on these patterns of distribution, it was argued that these morphologically similar catshark species partition their habitat to limit co-existence, and thus reduce the intensity of intra-and interspecific competition between them. This argument is in agreement with the findings of several other studies that have also found competitive interactions between morphologically similar species to result in different patterns of habitat use and hence distribution (Schoener 1974, Gascon and Leggett 1977, Hodgson *et al*. 1997). However, as noted in a study by Pianka (1981), overlap only results in competition when resources are limiting. In the case of abundant resources, a number of alternative explanations for the observed patterns of habitat use could therefore also hold true. These include: (1) size-based changes in habitat use that may be associated with parturition or nursery grounds, (2) changes in the habitat of their preferred diet items, or (3) a means to prevent predation by larger sharks.

Numerous studies have also reported on the strong influence that geographical location, environmental characteristics and faunal composition has on catshark distributions (Bass *et al*. 1975, Escobar-Porras 2009, Flammang *et al*. 2011). It is therefore also plausible that the distribution patterns of the two catshark species are influenced by the different oceanographic, coastal and trophic environments experienced off South Africa's West and South coasts. If this is the case, then it could be argued that the observed differences in catshark distributions are as a result of differences in environmental tolerance rather than a result of competition.

In terms of their diet, both catsharks appeared to display high levels of dietary overlap, with individuals feeding on the most abundant crustaceans (*Sympagurus dimorphus* and *Mursia cristiata*) and cephalopods (*Todaropsis eblanae* and *Sepia australis*) caught as by-catch in the trawl on each coast (based on pers. obs of trawl by-catch). This is in agreement with previous studies that have described *H. regani* and *S. capensis* as euryphagous and opportunistic predators that feed relative to prey availability (Ebert *et al*. 1996, Richardson *et al*. 2000b). In addition, numerous studies have reported dietary breadth to be inversely related to prey abundance, with dietary overlap being greatest in the presence of abundant prey species (Zaret and Rand 1971, Croxall *et al*. 1999, Tinker *et al*. 2008). This seems to be the case in the present study as well.

However, although both catsharks consumed similar prey categories off both the West and South coasts, the abundances of the individual prey species in their diets appeared to differ. It was argued that this difference possibly indicates spatial differences in prey availability, owing to the different patterns of habitat use (around coasts and between depths) observed in the two catshark species. It therefore appears that food separation is largely a reflection of habitat separation. In agreement with this argument is a study by Schoener (1974), on resource partitioning in ecological communities, who reported habitat partitioning to be more effective than resource partitioning in reducing ecological overlap. Likewise, a number of studies on deep-sea benthic sharks have also reported sharks to display habitat segregation to reduce competition for food resources (Carrason *et al.* 1992, Olaso *et al*. 2005, Flammang *et al*. 2011).

In terms of the stable isotope data, differences in δ^{15}N isotope values were noted between coasts, with both catshark species displaying significantly higher δ^{15}N values on the West Coast than on the South Coast. This pattern of higher δ^{15}N values on the West Coast than on the South Coast has previously been reported in a number of studies (Parkins 1993, Hill *et al*. 2006, Kohler *et al*. 2011, van der Lingen and Miller 2014), and has been attributed to the characteristic environmental and biological factors evident off each coast that affect isotopic baselines. For example, the study by van der Lingen and Miller (2014) attributed the higher δ^{15}N values observed in *Merluccius* sp. sampled on the West Coast to their reliance on upwelled nitrate, that is high in nitrogen, as their primary source of nitrogen, while *Merluccius* sp. sampled on the South Coast relied on recycled and N-fixed nitrogen, both of which are depleted in nitrogen, as their primary source of nitrogen.

Alternatively, these differences in δ^{15}N values may be attributed to spatial variability in dietary composition, as both catsharks were observed to feed at a comparatively higher trophic level on the West Coast than on the South Coast. Diet data indicated that higher trophic level species such as teleosts and cephalopods were abundant in the diet of *H. regani* and *S. capensis* on the West Coast, while lower trophic level crustaceans were more abundant in their diets on the South Coast. Such changes in trophic position in response to localised changes in available resources, particularly changes in food availability, has been reported in a number of studies on marine organisms (Meyer and Smale 1991, Thomas and Cahoon 1993, Pillar and Wilkinson 1995, Rinewalt 2007, Brown *et al*. 2012).

The “bigger-deeper” pattern observed within the two catshark species was further supported by diet data, with small catsharks being observed to primarily feed on small prey items that inhabit shallow water, and large catsharks being observed to primarily feed on large prey items that inhabit deep water. In addition to feeding on larger prey items with increasing size, both catsharks also consumed a greater proportion of higher trophic level species, such as cephalopods and teleosts, with increasing size. The results obtained from stable isotope data support these observations, with the general trend being an increase in δ^{15}N values with increasing catshark size in both species. This adds further support to the argument that differences in habitat use and the associated changes in food resources are largely responsible for influencing the variability in the feeding habits of the two catshark species.

Differences in the distribution patterns of male and female *H. regani* were also noted, with female catsharks inhabiting inshore areas and male catsharks inhabiting offshore areas. It was argued that this spatial separation could possibly be attributed to the fact that male *H. regani* grow larger than female *H. regani.* In relation to the “bigger-deeper” pattern, males can therefore be expected to inhabit deeper water than female catsharks. However, this is not conclusive as the data presented here were not collected through a full seasonal cycle, and seasonality is known to have a strong influence on catshark distributions (Ellis and Shackley 1997, Richardson *et al.* 2000b, Ebert *et al*. 2006). Combining these data with data collected by fishing vessels operating throughout the year could possibly provide a more conclusive overview of intra-and interspecific sexual segregations in the two catshark species.

Overall *H. regani* appeared to be more abundant than *S. capensis* throughout the study area. This is in agreement with data provided by the IUCN Red List of Threatened Species, which regards *S. capensis* as near threatened while *H. regani* is regarded as a species of least concern. Moreover, a study by Petersen *et al*. (2008) on chondrichthyan by-catch in demersal long-line and trawl fisheries off South Africa, noted a 44% decrease in *S. capensis* numbers on the West Coast and a 50% decrease in their numbers on the South Coast from 2000-2007. No such decrease was noted for *H. regani* (Petersen *et al*. 2008). Despite the different statuses of these similar catshark species, studies evaluating their habitat use patterns are limited to a handful of studies (Ebert *et al*. 1996, Richardson *et al*. 2000b, Petersen *et al*. 2008).

Essentially, we need more detailed studies on the distribution of these catshark species to determine whether their numbers are depleted or whether the results of the present study is simply due to sampling biases (i.e. data based on trawling only). If so, it would be beneficial to form collaborations with both the commercial trawling and long-line industry, as combining these data will most certainly reduce the biases associated with each method, as well as providing a comprehensive overview of their habitat use patterns across a wider spatial and temporal scale. However, using commercial data also has its associated biases, as efforts will be concentrated in areas where commercial fish are most abundant and less frequent where fishing is not as lucrative.

With the recent advances in deep-water camera systems (baited camera traps, ROV's and towed cameras) and their use in understudied benthic ecosystems, it is now possible to observe these catsharks in areas that they have not been observed before. Data collected in this way can most certainly increase our understanding of these catshark species, and also allow for a more focussed level of sampling.

Numerous studies have reported on the cascading effects changes in elasmobranch populations can have on marine food-webs (van der Elst 1979, Yamaguchi *et al*. 2005, Myers *et al*. 2007). For example, a study by Yamaguchi *et al*. (2005) on the life-history patterns of the longheaded eagle ray (*Aetobatus flagellum*) in the northwest Pacific Ocean, reported substantial declines in shellfish numbers following the subsequent increase of meso-predatory longheaded eagle rays. More recently, a study by Myers *et al*. (2007) on the cascading effects of the loss of apex predatory sharks from a coastal ocean, reported that the forced closure of a century-old scallop fishery in North Carolina was largely due to increased predation of bay scallops (*Argopectin irradians*) by cownose rays (*Rhinoptera bonasu*), following the subsequent population increase of this meso-predatory ray species.

Similarly in the present study, we could assume that changes in the abundance of these meso-predatory catshark species can cause significant changes in the benthic food web, which in turn may have significant influences on South Africa's commercial fishing industry as a whole. Approximately 55% of South Africa's demersal trawl catches are exported, with the hake fishery amounting to approximately 50% of the total value of the fisheries (DAFF 2013). Although catsharks are not of direct economic importance, they play an indirect role in supporting our valuable fishing resources (through food-web effects). The dietary data provided by this study emphasizes the potentially important structuring role these catsharks play in benthic communities, and how they, through feeding on the most abundant crustaceans and cephalopods, indirectly control the relative abundance of a number of species that would possibly proliferate or decline in their absence.

Owing to the current lack of data, and in the face of increasing commercial fishing pressure, I strongly recommend further studies on available catches and monitoring of population trends, as well as plans for the establishment of marine protected areas where these species are abundant. At present, none of their habitat is protected and they appear to have no refuge from commercial fishing.

This thesis forms the first comprehensive attempt at understanding intra- and interspecific variability in the distribution patterns and diet of these two catsharks, with a specific focus on how these variables change with species, location, size and depth. In the present study, both catshark species were observed to partition their habitat between coasts and across depths and size classes. The general trend was high abundances of *H. regani* on the West Coast and high abundances of *S. capensis* on the South Coast, as well as a pattern of increasing catshark size with increasing depth. Segregation by sex was noted for *H. regani* only, with males inhabiting significantly deeper depths than females on both coasts. In terms of their diet, both catsharks were observed to display a relatively uniform feeding behaviour, primarily consuming (in order of importance) crustaceans, cephalopods and teleosts. On a species level, however, significant differences were noted, with catsharks displaying spatial and ontogenetic differences in prey species consumed. Generally, higher trophic level prey species were consumed on the West Coast, with prey size and prey weight being found to increase with catshark size in both species. Stable isotope data was in agreement with the dietary data, with the effect of coast, depth and size being significant for $\delta^{15}N$; $\delta^{15}N$ values of both species were higher on the West Coast and found to increase with catshark size. The effect of depth and size class on $\delta^{13}C$ was found to be significant for *S. capensis* only, with $\delta^{13}C$ values decreasing with increasing depth and size class.

These results obtained fill in important gaps in catshark distribution patterns and trophic ecology around the coast of South Africa, as well as creating a number of new questions and ideas for future studies. I believe it is time for us to develop a better understanding of our understudied benthic communities, as they form the base of the demersal fishing industry, and it is possible that any losses or additions to this dynamic environment could have significant implications for fisheries management as a whole.

References

Abrantes KG and Barnett A. 2011. Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark *Notorynchus cepedianus*. *Marine Ecology Progress Series* 442: 133-148.

Aldebert Y. 1997. Demersal resources of the Gulf of Lions (NW Mediterranean). Impact of exploitation on fish diversity. *Vie et Milieu* 47: 275–285.

Alldredge AL and King JM. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology* 44: 133-156.

Andrews III AG, Kruse GH, Wooller MJ, Hillgruber N, Foy RJ, Sutton TM, Castellini MA, Duffy LK. 2010. Variation in the trophic position of spiny dogfish (*Squalus acanthias*) in the northeastern Pacific Ocean: An approach using carbon and nitrogen stable isotopes. *Unpublished masters dissertation, University of Alaska Fairbanks, Alaska*.

Armstrong MJ and Prosch RM. 1991. Abundance and distribution of the mesopelagic fish *Maurolicus muelleri* in the southern Benguela system. *South African Journal of Marine Science* 10: 13-28.

Augustyn CJ, Lipiński MR, Sauer WHH. 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *South African Journal of Marine Science* 12: 903-918.

Augustyn CJ, Lipinski MR, Roeleveld MAC. 1995. Distribution and abundance of Sepioidea off South Africa. *South African Journal of Marine Science* 16: 69-83.

Baker R, Buckland A, Sheaves M. 2014. Fish gut content analysis: robust measures of diet composition. *Fish and Fisheries* 15: 170-177.

Barange M, Pillar SC, Hampton I. 1998. Distribution patterns, stock size and life-history strategies of Cape horse mackerel *Trachurus trachurus capensis,* based on bottom trawl and acoustic surveys. *South African Journal of Marine Science* 19: 433-447.

Bass AJ, D'Aubrey JD, Kistnasamy N. 1975. Sharks of the east coast of southern Africa II. The families Scyliorhinidae and Pseudotriakidae. *Investigational Report of the Oceanographic Research Institute* 37: 1–64.

Barnes C, Sweeting CJ, Jennings S, Barry JT, Polunin NVC. 2007. Effects of temperature and ration size on carbon and nitrogen stable isotope fractionation. *Functional Ecology* 21: 356-362.

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299: 389-392.

Baum JK and Worm B. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* 78: 699-714.

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007-1012.

Bethea DM, Buckel JA, Carlson JK. 2004. Foraging ecology of the early life stages of four sympatric shark species. *Marine Ecology Progress Series* 268: 245–264.

Bizzarro JJ, Broms KM, Logsdon MG, Ebert DA, Yoklavich MM, Kuhnz LA, Summers AP. 2014. Spatial Segregation in Eastern North Pacific Skate Assemblages. *PLoS ONE* 9: e109907. doi:10.1371/journal.pone.0109907.

Bornatowski H, Wosnick N, Do Carmo WPD, Corrêa MFM, Abilhoa V. 2014. Feeding comparisons of four batoids (Elasmobranchii) in coastal waters of southern Brazil.

Journal of the Marine Biological Association of the United Kingdom 94: 1491-1499.

Bozzano A, Murgia AR, Vallerga S, Hirano J, Archer S. 2001. The photoreceptor system in the retinae of two dogfishes, *Scyliorhinus canicula* and *Galeus melastomus*: possible relationship with depth distribution and predatory lifestyle. *Journal of Fish Biology* 59: 1258–1278.

Braber L and de Groot SJ. 1973. The food of five flatfish species (Pleuronectiformes) in the southern North Sea. *Netherlands Journal of Sea Research* 6: 163-172.

Braccini JM. 2008. Feeding ecology of two high-order predators from south-eastern Australia: the coastal broadnose and the deepwater sharpnose sevengill sharks. *Marine Ecology Progress Series* 371: 273-284.

Braga RR, Bornatowski H, Vitule JRS. 2012. Feeding ecology of fishes: an overview of worldwide publications. *Reviews in Fish Biology and Fisheries* 22: 915-929.

Branch GM, Griffiths CL, Branch ML, Beckley LE. 2010. *Two Oceans: A Guide to the marine life of southern Africa*. Cape Town, South Africa: Random House Struik (Pty) Ltd. 456 pp.

Brown SC, Bizzarro JJ, Cailliet GM, Ebert DA. 2012. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian Skate (*Bathyraja aleutica* Gilbert, 1986). *Environmental Biology of Fishes* 95: 3-20.

Carlisle AB and Starr RM. 2009. Habitat use, residency and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough California. *Marine Ecology Progress Series* 380: 213-228.

Carrassón, M, Stefanescu C, Cartes JE.1992. Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean). *Marine Ecology Progress Series* 82: 21–30.

Caut S, Jowers MJ, Michel L, Lepoint G, Fisk AT. 2013. Diet- and tissue-specific incorporation of isotopes in the shark *Scyliorhinus stellaris*, a North Sea mesopredator. *Marine Ecology Progress Series* 492: 185-198.

Clarke KR and Gorley RN. 2001. *PRIMER Version 5.02: User Manual/Tutorial*. Primer E, Plymouth, England. 91 pp.

Clarke SC, McAllister MK, Milner-Gulland EJ, Kirkwood GP, Michielsens CGJ, Agnew DJ, Pikitch EK, Nakano H, Shivji MS. 2006. Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* 9: 1115-1126.

Clarke SC, Harley SJ, Hoyle SD, Rice JS. 2012. Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. *Conservation Biology* 27: 197-209.

Compagno LJV. 1984. *FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1 – Hexanchiformes to Lamniformes*. Food and Agriculture Organisation of the United Nations Fisheries, Rome. Synopsis 125: 1–249.

Compagno LJV, Ebert DA, Cowley PD. 1991. Distribution of offshore demersal cartilaginous fish (Class Chondrichthyes) off the west coast of southern Africa, with notes on their systematics. *South African Journal of Marine Science* 11: 43-139.

Compagno LJV, Dando M, Fowler SL. 2004. *A field guide to the Sharks of the world*. London UK: Collins. 370 pp.

Cortés E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 726–738.

Cortés E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56: 707–717.

Croxall JP, Reid K, Prince PA. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series* 177: 115–131.

Dale JJ, Wallsgrove NJ, Popp BN, Holland KN. 2011. Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. *Marine Ecology Progress Series* 433: 221-236.

Davis C. 2010. Prey selection by young lemon sharks (*Negaprion brevirostris*) at Chandeleur Island nursery habitats with a comparison to three other co-occurring shark species. *University of New Orleans Theses and Dissertations* 1281.

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB. 2008. First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. *Marine Ecology Progress Series* 358: 257–271.

Demarcq H, Barlow R, Hutchings L. 2007. Application of a chlorophyll index derived from satellite data to investigate the variability of phytoplankton in the Benguela ecosystem. *African Journal of Marine Science* 29: 271–282.

Demirhan SA, Seyhan K, Basuta N. 2007. Dietary overlap in spiny dogfish (*Squalus acanthias*) and thornback ray (*Raja clavata*) in the southeastern Black Sea. *Ekoloji* 62: 1-8.

DeNiro MJ and Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495-506.

Department of Agriculture, Forestry and Fisheries. 2013. Strategic plan for the Department of Agriculture, Forestry and Fisheries 2013/2014 to 2017/2018. Department of Agriculture, Forestry and Fisheries. Available at:

http://www.daff.gov.za/doaDev/topMenu/DAFF%20Strategic%20Plan%202013.pdf.

Didier DA, Kemper JM, Ebert DA. 2012. Phylogeny, biology and classification of extant Holocephalans. *In*: Carrier JC, Musick JA, Heithaus MR (eds), *Biology of Sharks and their relatives II*. Florida: CRC Press. pp 97-122.

Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortés E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* 18: 459-482.

Dunn OJ. 1961. Multiple comparisons among means. *Journal of the American Statistical Association* 56: 52-64.

Ebert DA. 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. *South African Journal of Marine Science* 14: 213-218.

Ebert DA. 2003. *The Sharks, Rays and Chimaeras of California*. Berkeley, CA: University of California Press. 284 pp.

Ebert DA. 2013. *FAO Species Catalogue. Vol. 1. Deep sea cartilaginous fishes of the Indian Ocean*. Food and Agriculture Organisation of the United Nations Fisheries, Rome. Synopsis 8: 1-256 pp.

Ebert DA. 2015. *FAO Species Catalogue*. *Deep-sea cartilaginous fishes of the Southeastern Atlantic Ocean.* Food and Agriculture Organisation of the United Nations Fisheries, Rome. Synopsis 9: 1-251 pp.

Ebert DA, Compagno LJV, Cowley PD. 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. *South African Journal of Marine Science* 12: 601-609.

Ebert DA, Cowley PD, Compagno LJV. 1996. A preliminary investigation of the feeding ecology of catsharks (Scyliorhinidae) off the west coast of southern Africa. *South African Journal of Marine Science* 17: 233-240.

Ebert DA and Ebert TB. 2005. Reproduction, diet, and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California,USA. *Marine and Freshwater Research* 56: 1089-1098.

Ebert DA, Compagno LJV, Cowley PD. 2006. Reproductive biology of catsharks (Chondrichthyes: Scyliorhinidae) from off the west coast of southern Africa. *ICES Journal of Marine Science* 63: 1053–1065.

Ebert DA and Stehmann M. 2013. *FAO Species Catalogue for Fishery Purposes*. *No. 7. Sharks, batoids and chimaeras of the North Atlantic*. Food and Agriculture Organisation of the United Nations Fisheries, Rome. 1-523 pp.

Ebert DA and van Hees KE. 2015. Beyond Jaws: rediscovering the ‘lost’ sharks of southern Africa. *African Journal of Marine Science* 37: 141-156.

Ekman S. 1967. *Zoogeography of the sea*. London: Sidgwick and Jackson. 417 pp.

Elliott JM. 2002. A quantitative study of day-night changes in the spatial distribution of insects in a stony stream. *Journal of Animal Ecology* 71: 112–122.

Ellis JR and Shackley SE. 1997. The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, UK. *Journal of Fish Biology* 51: 361-372.

Escobar-Porras J. 2009. Movement patterns and population dynamics of four catsharks endemic to South Africa. *Unpublished masters dissertation, Rhodes University, South Africa*.

Estrada JA, Rice AN, Lutcavage ME, Skomal GB. 2003. Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *Journal of the*

Marine Biological Association of the United Kingdom 83: 1347−1350.

Estrada JA, Lutcavage M, Thorrold SR. 2005. Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. *Marine Biology* 147: 37-45.

Fanelli E, Rey J, Torres P, Gil de Sola L. 2009. Feeding habits of blackmouth catshark *Galeus melastomus* Rafinesque, 1810 and velvet belly lantern shark *Etmopterus spinax* (Linnaeus, 1758) in the western Mediterranean. *Journal of Applied Ichthyology* 25: 83-93.

Fariña JM and Ojeda FP. 1993. Abundance and trophic patterns of the redspotted catshark *Shroederichthys chilensis*, on the Pacific Temperate coast of Chile. *Copeia* 1993: 545-549.

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13: 1055−1071.

Fisk AT, Tittlemier JL, Pranschke JL, Norstrom RJ. 2002. Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of the Greenland shark. *Ecology* 83: 2162-2172.

Flammang BE, Ebert DA, Cailliet GM. 2011. Intraspecific and interspecific spatial distribution of three eastern North Pacific catshark species and their egg cases (chondrichthyes: Scyliorhinidae). *Breviora* 525: 1-18.

France RL. 1995. Differentiation between littoral and pelagic foodwebs in lakes using stable carbon isotopes. *Limnology and Oceanography* 40: 1310–1313.

Frisk MG, Miller TJ, Dulvy NK. 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analysis. *Journal of Northwest Atlantic Fishery Science* 35: 27-45.

Froese R and Pauly D. 2016. *Fishbase*. World Wide Web electronic publication. www.fishbase.org, (06/2016).

Gascon D and Leggett WC. 1977. Distribution, abundance, and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. *Journal of the Fisheries Board of Canada* 34: 1105-1117.

Graham KJ, Andrew, Hodgson KE. 2001. Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine Freshwater Research* 52: 549–561.

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D. 2010. Using isoscapes to trace the movements and foraging behaviour of top predators in oceanic ecosystems. *In*: West JB, Bowen GJ, Dawson TE, Tu K (eds), *Isoscapes: understanding movement, patterns and processes on earth through isotope mapping*. New York: Springer. pp 299-318.

Griffiths CL and Blaine ML. 1988. Distribution, population structure and biology of stomatopod Crustacea off the west coast of South Africa. *South African Journal of Marine Science* 7: 45-50.

Guttridge TL, Gruber SH, Franks BR, Kessel ST, Gledhill KS, Uphill J, Krause J, Sims DW. 2012. Deep danger: inter-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series* 445: 279-291.

Hammerschlag N, Luo J, Irschick DJ, Ault JS. 2012. A Comparison of Spatial and Movement Patterns between Sympatric Predators: Bull Sharks (*Carcharhinus leucas*) and Atlantic Tarpon (*Megalops atlanticus*). *PLoS ONE* 7: e45958. doi:10.1371/journal.pone.0045958.

Hannsson S. 1998. Methods of studying fish feeding: a comment. *Canadian Journal of Fisheries and Aquatic Science* 55: 2706-2707.

Haramis GM, Link WA, Osenton PC, Carter DB, Weber RG, Clark NA, Teece MA, Mizrahi DS. 2007. Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. *Journal of Avian Biology* 38: 367-376.

Hecht T.1990. On the life history of Cape horse mackerel *Trachurus trachurus capensis* off the south-east coast of South Africa. *South African Journal of Marine Science* 9: 317-326.

Heupel MR and Hueter RE. 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine and Freshwater Research* 53: 543-550.

Heithaus MR, Dill LM, Marshall GJ, Buhleier BM. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology* 140: 237–248.

Heithaus MR. 2007. Nursery areas as essential shark habitats: A theoretical perspective. *American Fisheries Society Symposium* 50: 3-13.

Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in ecology and evolution* 23: 202-210.

Heithaus MR, Frid A, Vaudo JJ, Worm B, Wirsing AJ. 2010. Unraveling the ecological importance of elasmobranchs. *In*: Carrier JC, Musick JA, Heithaus MR (eds), *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation*. Florida: CRC Press. pp 607–633.

Hight BV and Lowe CG. 2007. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioural thermoregulation? *Journal of Experimental Marine Biology and Ecology* 352:114–128.

Hill JM, McQuaid CD, Kaehler S. 2006. Biogeographic and nearshore-offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. *Marine Ecology Progress Series* 318: 63-73.

Hill JM and McQuaid CD. 2008. δ^{13}C and δ^{15}N biogeographic trends in rocky intertidal communities along the coast of South Africa: evidence for strong environmental signatures. *Estuarine and Coastal Shelf Science* 80: 261–268.

Hodgson JR, He X, Schindler DE, Kitchell JF. 1997. Diet overlap in a piscivore community. *Ecology of freshwater fish* 6: 144-149.

Hoggarth DD, Mees CC, O'Neill C, Hindson J, Krishna M. 2005. A guide to fisheries stock assessment using the FMSP tools. Marine Resource Assessment Group, London. ISBN 81-86385-99-1.

Human BA. 2006. A taxonomic revision of the catshark genus *Holohalaelurus* Fowler 1934 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae), with descriptions of two new species. *Zootaxa* 1315: 1-56.

Hussey NE, MacNeil MA, Olin JA, McMeans BC, Kinney MJ, Chapman DD, Fisk T. 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *Journal of Fish Biology* 80: 1449-1484.

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS. 2009. The Benguela Current: an ecosystem of four components. *Progress in Oceanography* 83:

15–32.

Hyslop EJ. 1980. Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17: 411–429.

James AG. 1988. Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *South African Journal of Marine Science* 7: 161-177.

Jardine TD, Gray MA, McWilliam SM, Cunjak RA. 2005. Stable isotope variability in tissues of temperate stream fishes. *Transactions of the American Fisheries Society* 134: 1103-1110.

Jereb P and Roper CFE. 2005. *Cephalopods of the World. An annotated and illustrated catalogue of cephalopod species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes 4: 1-262 pp.

Jereb P and Roper CFE. 2010. *Cephalopods of the World. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid squids*. FAO Species Catalogue for Fishery Purposes 4: 1-605 pp.

Kinney MJ and Simpfendorfer CA. 2009. Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters* 2 (2): 53–60.

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA. 2011. Communal or competitive: stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. *Marine Ecology Progress Series* 439: 263–276.

Kitchell JF, Essington TE, Boggs CH, Schindler DE, Walters CJ. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. *Ecosystems* 5: 202-216.

Klaer NL. 2001. Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine Freshwater Research* 52: 399–410.

Klimley PA. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* 18: 27-40.

Kohler SA, Connan M, Hill JM, Mablouké C, Bonnevie B, Ludynia K, Kemper J, Huisamen J, Underhill LG, Cherel Y, McQuaid CD, Jaquemet S. 2011. Geographic variation in the trophic ecology of an avian rocky shore predator, the African black oystercatcher, along the southern African coastline. *Marine Ecology Progress Series* 435: 235–249.

Krebs CJ. 1989. *Ecological methodology*. New York: Harper and Row: 654 pp.

Kyne PM and Simpfendorfer CA. 2007. *A Collation and summarization of available data on deepwater Chondrichthyans*: *biodiversity, life histories and fisheries*. A report prepared by the IUCN SSC Shark Specialist Group for the Marine Conservation Biology Institute.

Laptikhovsky VV, Arkhipkin AI, Henderson AC. 2001. Feeding habits and dietary overlap in spiny dogfish *Squalus acanthias* (Squalidae) and narrowmouth catshark *Schroederichthys bivius* (Scyliorhinidae). *Journal of the Marine Biological Associated of the United Kingdom* 8: 1015-1018.

Lemaitre R. 1989. Revision of the genus *Parapagurus* (Anomura: Paguroidea: Parapaguridae), including redescriptions of the western Atlantic species. *Rijksmuseum van Natuurlijke Historie*.

Linke TE, Platell ME, Potter IC. 2001. Factors influencing the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. *Journal of Experimental Marine Biology and Ecology* 266:193–217.

Lipinski MR, Payne AIL, Rose B. 1992. The importance of cephalopods as prey for hake and other groundfish in South African waters. *In*: Payne AIL, Brink KH, Mann KH, Hillborn R (eds), Benguela trophic functioning. *South African Journal of Marine Science* 12: 651-662.

Iitembu JA and Richoux NB. 2015. Trophic relationships of hake (*Merluccius capensis* and *M. paradoxus*) and sharks (*Centrophorus squamosus*, *Deania calcea* and *D. profundorum*) in the Northern (Namibia) Benguela Current region. *African Zoology* 2015: 1-7.

Lowe CG, Wetherbee BM, Meyer CG. 2006. Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French Frigate Shoals and Midway Atoll. *Atoll Research Bulletin* 543: 281–303.

Lucifora LO, García VB, Menni RC, Escalante AH, Hozbor NM. 2009. Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* 24: 109–118.

Lyle JM. 1983. Food and feeding habits of the lesser spotted dogfish, *Scyliorhinus canicula* (L.), in Isle of Man waters. *Journal of Fish Biology* 23: 725–737.

MacAvoy SE, Macko SA, Garman GC. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 923-932.

MacNeil MA, Skomal GB, Fisk AT. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Marine Ecology Progress Series*. 302: 199-206.

Marshall AD, Kyne PM, Bennett MB. 2008. Comparing the diet of two sympatric urolophid elasmobranchs (*Trygonoptera testacea* Müller & Henle and *Urolophus kapalensis* Yearsley & Last): evidence of ontogenetic shifts and possible resource partitioning.

Journal of Fish Biology 72: 883-898.

Martinez del Rio C, Wolf N, Carleton SA, Gannes LZ. 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews* 84: 91-111.

Matich P. 2014. Environmental and individual factors shaping the habitat use and trophic interactions of juvenile bull sharks (*Carcharhinus leucas*) in a subtropical estuary. *FIU Electronic Theses and Dissertations* 1236.

Matich P, Heithaus MR, Layman CA. 2010. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal of Animal Ecology* 80: 294-305.

McConnaughey T and McRoy CP. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology* 53: 257–262.

Mc Laverty KJ. 2012. A re-evaluation of the life history strategy of Cape horse mackerel, *Trachurus capensis* in the southern Benguela. *Unpublished masters dissertation, University of Cape Town, South Africa.*

McQueen N and Griffiths MH. 2004. Influence of sample size and sampling frequency on the quantitative dietary descriptions of a predatory fish in the Benguela ecosystem. *African Journal of Marine Science* 26: 205-217.

Meyer M and Smale MJ. 1991. Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 1. Pelagic predators. *South African Journal of Marine Science* 10: 173-191.

Meyer CG, Clark TB, Papastamatiou YP, Whitney NM, Holland KN. 2009. Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. *Marine Ecology Progress Series* 381:223–235.

Minagawa M and Wada E. 1984. Stepwise enrichment of ^{15}N along foodchains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et cosmochimica acta* 48: 1135-1140.

Mullin MM, Rau GH, Eppley RW. 1984. Stable nitrogen isotopes in zooplankton: some geographic and temporal variations in the North Pacific. *Limnology and Oceanography* 29: 1267-1273.

Musick JA and Ellis JK. 2005. Reproductive evolution of chondrichthyans. *In* Hamlett WC (eds), *Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras.* Enfield, New Hampshire: Science Publishers, Inc. 45-79 pp.

Myers RA and Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280–283.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315: 1846-1850.

Navia AF, Cortés E, Mejía-Falla PA. 2010. Topological analysis of the ecological importance of elasmobranch fishes: the Gulf of Tortugas food web, Colombian Pacific Ocean, as a case study. *Ecological Modelling* 221: 2918–2926.

Nelson JS. 2006. *Fishes of the World* (4th ed.). New York: John Wiley and Sons. 601 pp.

Nerot C, Lorrain A, Grall J, Gillikin DP, Munaron JM, Le Bris H, Paulet YM. 2012. Stable isotope variations in benthic filter feeders across a large depth gradient on the continental shelf. *Estuarine, Coastal and Shelf Science* 96: 228–235.

Nesis KN.1987. *Cephalopods of the World: squids, cuttlefishes, octopuses, and allies*. Multipet, Durban. 351pp.

Newman SP. 2003. Spatial and temporal variation in diet and prey preference of nursery-bound juvenile lemon sharks (*Negaprion brevirostris*) at Bimini, Bahamas. *Unpublished doctors dissertation, University of Plymouth, England.*

Olaso I, Velasco F, Pérez N. 1998. Importance of discarded blue whiting (*Micromesistius poutassou*) in the diet of lesser spotted dogfish (*Scyliorhinus canicula*) in the Cantabrian Sea. *ICES Journal of Marine Science* 55: 331–341.

Olaso I, Velasco F, Sánchez F, Serrano A, Rodríguez-Cabello C, Cendrero O. 2005. Trophic relations of lesser-spotted catshark (*Scyliorhinus canicula*) and blackmouth catshark (*Galeus melastomus*) in the Cantabrian Sea. *Journal of Northwest Atlantic Fishery Science* 35: 481–494.

Papastamatiou YP. 2008. Movement patterns, foraging ecology and digestive physiology of blacktip reef sharks, *Carcharhinus melanopterus*, at Palmyra Atoll: a predator dominated ecosystem. *Unpublished doctors dissertation, University of Hawaii.*

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL. 2006. Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series* 320: 239–251.

Parkins CA. 1993. Stable carbon and nitrogen isotope ratios in the shallow-water Cape hake, *Merluccius capensis* (Castelnau) as indicators of trophic position and diet on the west and south coasts of South Africa. *Unpublished masters dissertation, University of Cape Town, South Africa.*

Payne AIL, Augustyn CJ, Leslie RW. 1985. Biomass index and catch of Cape hake from random stratified sampling cruises in Division 1.6 during 1984. *International Commission for the Southeast Atlantic Fisheries.* 12: 99-123.

Payne AIL, Rose B, Leslie RW. 1987. Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. *South African Journal of Marine Science* 5: 471-501.

Peterson BJ and Fry B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320.

Petersen SL, Honig MB, Ryan PG, Underhill LG, Compagno LJV. 2008. Chondrichthyan bycatch in demersal longline and trawl fisheries off southern Africa. *In*: Petersen SL, Nel DC, Ryan PG, Underhill LG (eds), Understanding and mitigating vulnerable bycatch in southern African trawl and longline fisheries. *WWF South Africa Report Series* -2008/Marine/002.

Pethybridge H, Daley RK, Nichols PD. 2011. Diet of demersal sharks and chimaeras inferred by fatty acids profiles and stomach content analysis. *Journal of Experimental Marine Biology and Ecology* 409: 290-299.

Pianka ER. 1981. Competition and niche theory. *Theoretical ecology principles and applications* 8:167-196.

Pillar and Wilkinson. 1995. The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. *South African Journal of Marine Science* 15: 225-239.

Pinnegar JK, Cambell N, Polunin NVC. 2001. Unusual stable isotope fractionation patterns observed for fish host-parasite trophic relationships. *Journal of Fish Biology* 59: 494-503.

Platell ME, Potter IC, Clarke KR. 1998. Resource partitioning by four species of elasmobranch (Batoidea: Urolophidae) in coastal waters of temperate Australia. *Marine Biology* 131: 719-734.

Platell ME and Potter IC. 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. *Journal of Experimental Biology and Ecology* 261: 31-54.

Post DM. 2002. Using stable isotopes to estimate trophic positions: methods, models, and assumptions. *Ecology* 83: 703-718.

Ramsay K, Michel J, Kaiser MJ, Moore PG, Hughes RN. 1997. Consumption of fisheries discards by benthic scavangers: Utilization of energy subsidies in different marine habitats. *Journal of Animal Ecology* 66: 884-896.

Renones O, Polunin NVC, Goni R. 2002. Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. *Journal of Fish Biology* 61: 122-137.

Rey JL, De Sola G, Massutí E. 2005. Distribution and Biology of the Blackmouth Catshark *Galeus melastomus* in the Alboran Sea (Southwestern Mediterranean). *Journal of Northwest Atlantic Fishery Science* 35: 215-223.

Richardson AJ, Lamberts C, Isaacs G, Moloney CL, Gibbons MJ. 2000a. Length-weight relationship of some important forage crustaceans. *Naga, The International Centre for Living Aquatic Resource Management* 23: 2.

Richardson AJ, Maharaj G, Compagno LJV, Leslie RW, Ebert DA, Gibbons MJ. 2000b. Abundance, distribution, morphometrics, reproduction and diet of the Izak catshark. *Journal of Fish Biology* 56: 552-576.

Rijnsdorp AD and Vingerhoed B. 2001. Feeding of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal of Sea Research* 45: 219-229.

Rinewalt CS. 2007. Diet and Ecomorphology of the Sandpaper Skate, *Bathyraja kincaidii* (Garman, 1908) from the Eastern North Pacific. *Unpublished masters dissertation, Moss Landing Marine Laboratories and California State University, Monterey Bay*.

Ritchie EG and Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12: 982–998.

Rodríguez-Cabello C, Sanchez F, Olaso I. 2007. Distribution patterns and sexual segregations of *Scyliorhinus canicula* (L.) in the Cantabrian Sea. *Journal of Fish Biology* 70:1568-1586.

Roeleveld MAC, Lipiński MR, Augustyn CJ, Stewart BA. 1992. The distribution and abundance of cephalopods on the continental slope of the eastern South Atlantic. *South African Journal of Marine Science* 12: 739-752.

Rogers SI and Ellis JR. 2001. Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science* 57: 866–881.

Roper CFE, Sweeney MJ, Nauen CE. 1984. *Cephalopods of the world*. FAO Fisheries Synopsis 12: 1-277 pp.

Sanchez P. 1988. Systematics and distribution of the cephalopods of Namibia. *Monografias de Zoologia Marina* 3: 205-266.

Sauer WHH and Smale MJ. 1991. Predation patterns on the inshore spawning grounds of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) off the south-eastern Cape, South Africa. *South African Journal of Marine Science* 11: 513-523.

Scacco UG, La Mesa G, Vacchi M. 2002. Changes of swimming ability with length in a small benthic elasmobranch, *Galeus melastomus*: a work hypothesis. *In*: Vacchi M, La Mesa G, Serena F and Seret B (eds), Proceedings of the 4th European Elasmobranch Association, Livorno, Italy, 2000. ICRAM, ARPAT & SFI, 2002: 127–134.

Serrano A, Velasco F, Olaso I, Sánchez F. 2003. Macrobenthic crustaceans in the diet of demersal fish in the Bay of Biscay in relation to abundance in the environment. *Sarsia* 88: 36–48.

Shiffman DS, Gallagher AJ, Boyle MD, Hammerschlag-Peyer CM, Hammerschlag N. 2012.

Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. *Marine and Freshwater Research* 63: 635-643.

Simpfendorfer CA, Goodreid AB, McAuley RB. 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Environmental Biology of Fishes* 61: 37-46.

Simpfendorfer CA and Heupel MR. 2004. Methods for studying habitat use in elasmobranchs: 553–572. *In*: Carrier JC, Musick JA, Heithaus MR, editors. *The biology of sharks and their relatives*. Boca Raton, Florida: CRC Press.

Simpfendorfer CA, Heupel MR, White WT, Dulvy NK. 2011. The importance of public opinion to conservation and management of sharks and rays: a synthesis. *Marine and Freshwater Research* 62: 518-527.

Simpfendorfer CA and Heupel MR. 2012. Assessing habitat use and movement. *In*: Carrier JC, Musick JA, Heithaus MR (eds.), *Biology of Sharks and their Relatives*. UK, London: CRC Press. 576-601 pp.

Sims DW. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of fish biology* 63: 53-73.

Sink KJ, Wilkinson S, Atkinson LJ, Sims PF, Leslie RW, Attwood CG. 2012. The potential impacts of South Africa’s demersal hake trawl fishery on benthic habitats: historical perspectives, spatial analyses, current review and potential management actions. *Unpublished report, South African National Biodiversity Institute.*

Smale MJ. 1991. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena* on the Eastern Cape coast of South Africa. *South African Journal of Marine Science* 11: 31-42.

Smale MJ 1992. Predatory fish and their prey- An overview of trophic interactions in the fish communities of the west and south coasts of South Africa. *South African Journal of Marine Science* 12: 803-821.

Smale MJ and Compagno LJV. 1997. Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* (Smith, 1957) (Pisces: Triakidae). *South African Journal of Marine Science* 18: 229-248.

Smith MM and Heemstra PC. 1986. *Smith's Sea Fishes* (1st ed.). Johannesburg, South Africa: Southern Book Publication. 1048 pp.

Speed CW, Field IC, Meekan MG, Bradshaw CJA. 2010. Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series* 408: 275–293.

Speed CW, Meekan MG, Field IC, McMahon CR, Stevens JD, McGregor F, Huveneers C, Berger Y, Bradshaw CJA. 2011. Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Marine Ecology Progress Series* 429: 261-275.

Springer S. 1967. Social organization of shark populations. *In*: Matherson RF, Gilbert PW, Ralls DP (eds), *Sharks, Skates, and Rays*. Baltimore, Maryland: The Johns Hopkins University Press.

Stillwell CE and Kohler NE. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Science* 39: 407-414.

Talent LG. 1976. Food habits of the leopard shark, *Triakis simifasciata*, in the Elkhorn Slough, Monterey Bay. *California Fish Game* 62: 286-298.

Teske PR, Von der Heyden S, McQuaid CD, Barker NP. 2011. A review of marine phylogeography in southern Africa. *South African Journal of Marine Science* 107: 5-6.

Thomas CJ and Cahoon LB. 1993. Stable isotope analysis differentiates between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress-Series* 95: 19-24.

Tinker MT, Bentall GB, Estes JA. 2008. Food limitation leads to behavioural diversification and dietary specialisation in sea otters. *Proceedings of the Natural Academy of Sciences of the United States of America* 105: 560–565.

Valls M, Quetglas A, Ordines F, Moranta J. 2011. Feeding ecology of demersal elasmobranchs from the shelf and slope of the Balearic Sea (western Mediterranean). *Scientia Marina* 75: 633-639.

van der Bank MG. 2010. Studies on the integrated feeding of *Sufflogobius bibarbatus* (von Bonde, 1923) in the Northern Benguela ecosystem using fatty acid biomarkers and stable isotopes (δ^{13}C, δ^{15}N, δ^{34}S). *Unpublished masters dissertation, University of the Western Cape, South Africa.*

van der Elst RP. 1979. A proliferation of small sharks in the shore-based Natal shark fishery. *Environmental Biology of Fishes* 4: 349–362.

van der Lingen CD and Miller TW. 2014. Spatial, ontogenetic and interspecific variability in stable isotope ratios of nitrogen and carbon of *Merluccius capensis* and *Merluccius paradoxus* off South Africa. *Journal of Fish Biology* 85: 456-472.

Vander Zanden MJ, Cabana G, Rasmussen JB. 1997. Comparing the trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1142-1158.

Vaudo JJ and Heithaus MR. 2011. Dietary niche overlap in a nearshore elasmobranch mesopredator community. *Marine Ecology Progress Series* 425: 247-260.

Walovich K. 2017. Taxonomic revision of the Short Nose Chimaeras (Genus *Hydrolagus*) from the Southern African region. *Unpublished masters dissertation*, *San José State University, California.*

Weng KC, O'Sullivan JB, Lowe CG, Winkler CE, Dewar H, Block BA. 2007. Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series* 338: 211–224.

Wetherbee BM and Cortés. 2004. Food consumption and feeding habits. *In*: Carrier JC, Musick JA, Heithaus MR (eds), *The biology of sharks and their relatives*. Boca Raton, Florida: CRC Press. 225-246 pp.

White W, Platell M, Potter I. 2004. Comparisons between the diets of four abundant species of elasmobranchs in a subtropical embayment: implications for resource partitioning. *Marine Biology* 144:439-448.

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy* 40: 194-204.

Yamaguchi A, Kawahara I, Ito S. 2005. Occurrence, growth and food of longheaded eagle ray, *Aetobatus flagellum*, in Ariake Sound, Kyushu, Japan. *Environmental biology of fishes* 74: 229-238.

Yick J, Tracey S, White R. 2011. Niche overlap and trophic resource partitioning of two sympatric batoids co inhabiting an estuarine system in southeast Australia. *Journal of Applied Ichthyology* 27.5: 1272-1277.

Yokota L and Lessa RP. 2006. A nursery area for sharks and rays in Northeastern Brazil.

Environmental Biology of Fishes 75: 349–360.

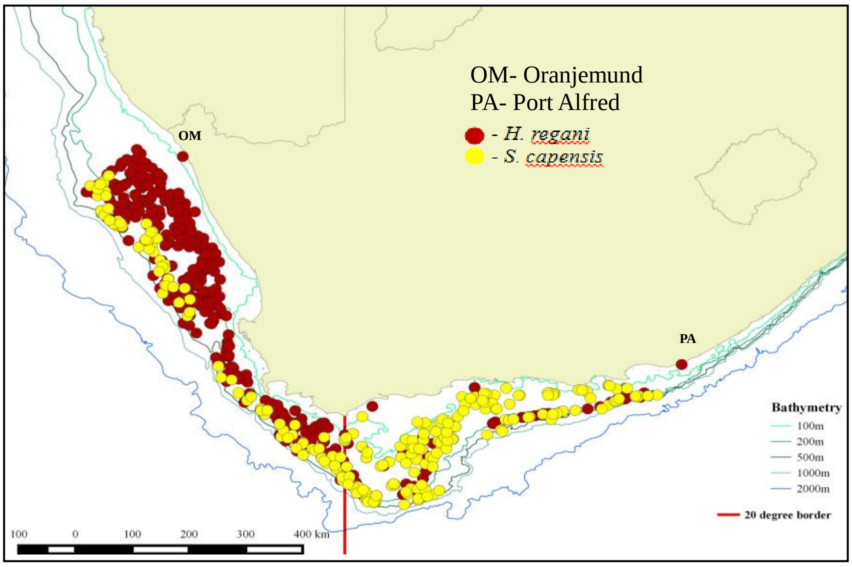
Zar JH. 2010. *Biostatistical Analysis* (5th ed). New Jersey: Pearson Prentice Hall International Editions. 944 pp.

Zaret TM and Rand AS. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52: 336-342.

Appendices

Appendix 1: Illustrating all trawls conducted on the West and South Coasts from 1994-2015. “+” denotes to where trawls were conducted.

	WEST COAST	SOUTH COAST	
Year	**Summer**	**Autumn**	**Spring**
1994	+	+	+
1995	+	+	+
1996	+	+	
1997	+	+	
1998			
1999	+	+	
2000	+	+	
2001	+	+	
2002	+		
2003	+	+	+
2004	+	+	+
2005	+	+	
2006	+	+	+
2007	+	+	+
2008	+	+	+
2009	+	+	
2010		+	
2011	+	+	
2012			
2013	+		
2014	+	+	
2015	+	+	



Appendix 2: Map illustrating the distribution records of both *H. regani* and *S. capensis* around the coasts of South Africa from 1994-2015.

Appendix 3: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *H. regani* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

	West Coast				South Coast			
	%FO	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae								
Green algae	-	-	-	-	4.4	0.5	-	+
Cephalopoda								
Bathypolypus valdiviae	-	-	-	-	-	-	-	-
Loligo reynaudii	4.5	0.7	1.6	0.1	10.3	2.0	3.6	0.6
Lycoteuthis lorigera	7.3	1.5	1.4	0.2	23.5	4.0	5.4	2.4
Todaropses eblanae	35.5	9.9	23.7	12.5	41.2	12.3	26.7	17.3
Sepia australis	14.5	3.5	0.9	0.7	25.0	5.1	2.2	2.0
Unidentified cephalopods	68.2	42.6	-	30.4	77.9	36.2	-	30.4
Chondrichtyes								
Elasmobranchii egg case	4.5	0.7	-	+	2.9	0.4	-	+
Crustacea								
Acanthephyra pelagica	-	-	-	-	1.5	0.2	-	0.0
Amphipoda (unid)	5.5	1.8	0.1	0.1	10.3	1.8	0.1	0.2
Callianassa sp.	0.9	0.1	0.1	+	-	-	-	-
Dyspanopeus sp.	1.8	0.3	0.1	+	2.9	0.4	0.4	+
Euphasiids (unid)	-	-	-	-	1.5	0.2	-	+
Glyphocrangon sp.	-	-	-	-	1.5	0.2	0.1	+
Goneplax angulata	0.9	0.1	0.3	+	1.5	0.2	+	+
Isopoda (unid)	-	-	-	-	-	-	-	-
Mursia cristiata	5.5	1.2	1.7	0.2	26.5	6.0	11.7	5.0
Parapagurus pilosimanus	9.1	1.8	9.7	1.1	7.4	2.4	4.7	0.6
Pseudodromiidae sp.	0.9	0.1	0.4	0.0	-	-	-	-
Pterygosquilla a. capensis	13.6	2.0	1.4	0.5	26.5	3.3	3.2	1.8
Shrimp (unid)	0.9	0.1	-	0.0	-	-	-	-
Solonocera africana	0.9	0.1	0.1	0.0	5.9	1.1	2.0	0.2
Sympagurus dimorphus	62.7	19.8	58.4	51.3	61.8	16.3	39.7	37.3
Unidentified crustaceans	2.7	0.4	-	+	2.9	0.4	-	+
Porifera								
Polymastia litoralis	0.9	0.1	+	+	-	-	-	-
Polychaeta								
Polychaete sp.	-	-	-	-	-	-	-	-
Gastropoda								
Gastropod (unid)	-	-	-	-	-	-	-	-
Teleostei								
Hagfish eggs	16.4	2.5	-	0.4	1.5	0.2	-	+
Champsodon capensis	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	1.5	0.2	-	+
Lampanyctodes hectoris	0.9	0.1	0.1	+	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-
Maurolicus walvensis	14.5	3.7	-	0.6	4.4	1.3	0.1	0.1
Myctophid (unid)	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-
Unidentified teleost	30.9	5.0	-	1.6	36.8	4.7	-	1.9
Urochordata								
Pyrosoma sp.	-	-	-	-	-	-	-	-
Unidentified	10.9	1.6	-	0.2	7.4	1.1	-	0.1

Appendix 4: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *H. regani* at different depths on the West Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “+” is where values are greater than 0 but less than the minimum displayable value and “-“ denotes to null/unknown values

Depth (m)	**150**				**250**				**350**				**450**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae																
Green algae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda																
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loligo reynaudii	6.9	1.3	3.7	0.4	3.8	0.6	1.2	0.1	3.6	0.4	1.3	0.1	-	-	-	-
Lycoteuthis lorigera	3.4	0.6	1.8	0.1	3.8	0.9	0.5	+	17.9	3.1	3.2	1.2	-	-	-	-
Todaropses eblanae	17.2	4.4	15.9	4.1	48.1	14.3	27.7	19.1	32.1	7.6	21.5	10.1	-	-	-	-
Sepia australis	6.9	1.3	0.2	0.1	21.2	4.4	1.0	1.1	10.7	4.0	1.3	0.6	-	-	-	-
Unidentified cephalopods	69.0	50.6	-	40.7	67.3	34.2	-	21.8	67.9	50.7	-	37.2	100.0	11.1	-	7.4
Chondrichtyes																
Elasmobranchii egg case	3.4	0.6	-	+	5.8	0.9	-	+	3.6	0.4	-	+	-	-	-	-
Crustacea																
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda (unid)	17.2	5.6	0.4	1.2	1.9	1.2	0.1	+	-	-	-	-	-	-	-	-
Callianassa sp.	-	-	-	-	1.9	0.3	0.2	+	-	-	-	-	-	-	-	-
Dyspanopeus sp.	-	-	-	-	3.8	0.6	0.2	+	-	-	-	-	-	-	-	-
Euphasiids (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	3.4	0.6	2.3	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mursia cristiata	-	-	-	-	3.8	0.6	0.7	+	14.3	3.1	4.9	1.2	-	-	-	-
Parapagurus pilosimanus	3.4	0.6	5.5	0.2	9.6	2.3	7.8	0.9	14.3	1.8	17.0	2.9	-	-	-	-
Pseudodromiidae sp.	-	-	-	-	-	-	-	-	3.6	0.4	1.4	0.1	-	-	-	-
Pterygosquilla a. capensis	24.1	4.4	2.2	1.9	5.8	0.9	0.8	0.1	17.9	2.2	2.5	0.9	-	-	-	-
Shrimp (unid)	-	-	-	-	1.9	0.3	-	0.0	-	-	-	-	-	-	-	-
Solonocera africana	3.4	0.6	0.7	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Sympagurus dimorphus	48.3	20.0	67.2	49.0	69.2	22.5	59.9	54.0	64.3	13.9	46.8	42.2	100.0	27.8	100.0	85.2
Unidentified crustaceans	-	-	-	-	5.8	0.9	-	+	-	-	-	-	-	-	-	-
Porifera																
Polymastia litoralis	-	-	-	-	1.9	0.3	+	+	-	-	-	-	-	-	-	-
Polychaeta																
Polychaete sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda																
Gastropod (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei																
Hagfish eggs	6.9	1.3	-	0.1	21.2	3.2	+	0.6	17.9	2.2	-	0.4	-	-	-	-
Champsodon capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	1.9	0.3	0.1	+	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maurolicus walvensis	13.8	2.5	-	0.4	13.5	4.7	-	0.6	17.9	3.1	-	0.6	-	-	-	-
Myctophid (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	27.6	5.0	-	1.6	26.9	4.4	-	1.1	39.3	5.4	-	2.3	100.0	11.1	-	7.4
Urochordata																
Pyrosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	3.4	0.6	-	+	15.4	2.3	-	0.3	10.7	1.3	-	0.2	-	-	-	-

Appendix 5: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *H. regani* at different depths on the South Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “+” is where values are greater than 0 but less than the minimum displayable value and “-“ denotes to null/unknown values

Depth (m)	**150**				**250**				**350**				**450**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae																
Green algae	4.9	0.6	-	+	-	-	-	-	-	-	-	-	20.0	1.4	-	0.2
Cephalopoda																
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loligo reynaudii	12.2	1.9	3.4	0.8	10.0	3.1	5.3	0.7	-	-	-	-	-	-	-	-
Lycoteuthis lorigera	9.8	1.9	3.1	0.6	35.0	5.6	5.9	3.4	50.0	28.6	55.4	42.0	80.0	7.1	12.4	12.0
Todaropses eblanae	36.6	11.1	21.8	14.4	55.0	18.0	40.9	27.2	-	-	-	-	40.0	5.7	17.4	7.1
Sepia australis	34.1	7.6	3.6	4.6	15.0	2.5	0.6	0.4	-	-	-	-	-	-	-	-
Unidentified cephalopods	75.6	33.3	-	30.2	90.0	37.3	-	28.1	50.0	14.3	-	7.1	60.0	48.6	-	22.4
Chondrichtyes																
Elasmobranchii egg case	2.4	0.3	-	+	-	-	-	-	-	-	-	-	20.0	1.4	-	0.2
Crustacea																
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-	20.0	1.4	-	0.2
Amphipoda (unid)	17.1	3.2	0.3	0.7	-	-	-	-	-	-	-	-	-	-	-	-
Callianassa sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dyspanopeus sp.	4.9	0.6	0.6	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Euphasiids (unid)	2.4	0.3	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-	20.0	1.4	0.7	0.3
Goneplax angulata	2.4	0.3	0.1	+	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mursia cristiata	26.8	7.3	15.3	7.3	25.0	4.3	7.5	2.5	-	-	-	-	40.0	4.3	6.5	3.3
Parapagurus pilosimanus	9.8	3.8	8.2	1.4	-	-	-	-	-	-	-	-	20.0	1.4	0.4	0.3
Pseudodromiidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterygosquilla a. capensis	36.6	4.8	4.9	4.2	10.0	1.2	0.6	0.2	50.0	14.3	8.9	11.6	-	-	-	-
Shrimp (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solonocera africana	7.3	1.6	1.9	0.3	-	-	-	-	-	-	-	-	20.0	1.4	0.2	0.3
Sympagurus dimorphus	53.7	14.9	37.0	33.4	75.0	18.0	39.2	36.0	50.0	28.6	35.7	32.1	80.0	17.1	62.5	49.0
Unidentified crustaceans	2.4	0.3	-	+	5.0	0.6	-	+	-	-	-	-	-	-	-	-
Porifera																
Polymastia litoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta																
Polychaete sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda																
Gastropod (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei																
Hagfish eggs	2.4	0.3	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Champsodon capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	5.0	0.6	-	+	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maurolicus walvensis	-	-	-	-	15.0	4.3	0.4	0.6	-	-	-	-	-	-	-	-
Myctophid (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	34.1	4.4	-	1.8	30.0	3.7	-	0.9	50.0	14.3	-	7.1	80.0	7.1	-	4.4
Urochordata																
Pyrosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	7.3	1.3	-	0.1	5.0	0.6	-	+	-	-	-	-	20.0	1.4	-	0.2

Appendix 6: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of small, medium and large *H. regani* on the West Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

Size classes	**Small**				**Medium**				**Large**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae												
Green algae	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda												
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	-	-	-	-
Loligo reynaudii	-	-	-	-	2.6	0.5	1.6	+	7.3	0.8	1.6	0.2
Lycoteuthis lorigera	-	-	-	-	5.1	0.9	0.8	0.1	10.9	1.9	1.6	0.3
Todaropses eblanae	-	-	-	-	15.4	3.2	14.5	2.6	60.0	13.9	26.6	21.3
Sepia australis	12.5	4.8	1.1	1.1	10.3	1.9	0.6	0.2	18.2	4.2	1.0	0.8
Unidentified cephalopods	50.0	26.2	-	20.6	76.9	54.2	-	39.6	67.3	38.9	-	22.9
Chondrichtyes												
Elasmobranchii egg case	-	-	-	-	5.1	0.9	-	+	5.5	0.6	-	+
Crustacea												
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda (unid)	18.8	16.7	1.6	5.4	5.1	0.9	0.1	+	1.8	0.8	0.1	+
Callianassa sp.	6.3	2.4	2.9	0.5	-	-	-	-	-	-	-	-
Dyspanopeus sp.	-	-	-	-	-	-	-	-	3.6	0.4	0.2	+
Euphasiids (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	-	-	-	-	2.6	0.5	1.9	0.1	-	-	-	-
Isopoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Mursia cristiata	-	-	-	-	12.8	3.7	8.5	1.5	1.8	0.2	0.3	+
Parapagurus pilosimanus	-	-	-	-	2.6	0.5	2.8	0.1	16.4	2.5	11.6	2.0
Pseudodromiidae sp.	-	-	-	-	-	-	-	-	1.8	0.2	0.5	+
Pterygosquilla a. capensis	25.0	9.5	5.1	5.7	17.9	3.7	5.3	1.5	7.3	0.6	0.5	0.1
Shrimp (unid)	-	-	-	-	-	-	-	-	1.8	0.2	-	+
Solonocera africana	6.3	2.4	3.4	0.6	-	-	-	-	-	-	-	-
Sympagurus dimorphus	37.5	19.0	84.0	60.7	53.8	15.3	86.8	52.2	76.4	21.8	51.4	49.1
Unidentified crustaceans	-	-	-	-	7.7	1.4	-	0.1	-	-	-	-
Porifera												
Polymastia litoralis	-	-	-	-	2.6	0.5	0.1	+	-	-	-	-
Polychaeta												
Polychaete sp.	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda												
Gastropod (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei												
Hagfish eggs	-	-	-	-	7.7	1.4	-	0.1	27.3	3.2	-	0.8
Champsodon capensis	-	-	-	-	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	6.3	2.4	2.0	0.4	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-	-	-	-	-
Maurolicus walvensis	6.3	2.4	-	0.2	12.8	6.5	-	0.8	18.2	2.5	-	0.4
Myctophid (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	25.0	9.5	-	3.7	23.1	4.2	-	0.9	38.2	5.0	-	1.7
Urochordata												
Pyrosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	12.5	4.8	-	0.9	-	-	-	-	18.2	2.1	-	0.3

Appendix 7: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of medium and large *H. regani* on the South Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). “+” is where values are greater than 0 but less than the minimum displayable value and “-“ denotes to null/unknown values

Size classes	**Medium**				**Large**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae								
Green algae	-	-	-	-	6.3	0.7	-	+
Cephalopoda	-	-	-	-	-	-	-	-
Bathypolypus valdiviae	-	-	-	-	-	-	-	-
Loligo reynaudii	25.0	6.5	9.0	5.2	4.2	0.9	2.3	0.1
Lycoteuthis lorigera	25.0	6.5	8.8	5.1	22.9	3.4	4.6	1.8
Todaropses eblanae	30.0	10.3	18.4	11.5	45.8	12.8	29.1	18.9
Sepia australis	25.0	7.5	1.7	3.1	25.0	4.5	2.4	1.7
Unidentified cephalopods	65.0	18.7	-	16.2	83.3	40.4	-	33.1
Chondrichtyes								
Elasmobranchii egg case	-	-	-	-	4.2	0.4	-	+
Crustacea								
Acanthephyra pelagica	-	-	-	-	2.1	0.2	-	-
Amphipoda (unid)	10.0	1.9	0.1	0.3	10.4	1.8	0.1	0.2
Callianassa sp.	-	-	-	-	-	-	-	-
Dyspanopeus sp.	-	-	-	-	4.2	0.4	0.4	+
Euphasiids (unid)	5.0	0.9	-	0.1	-	-	-	-
Glyphocrangon sp.	-	-	-	-	2.1	0.2	0.1	+
Goneplax angulata	-	-	-	-	2.1	0.2	0.1	+
Isopoda (unid)	-	-	-	-	-	-	-	-
Mursia cristiata	20.0	6.5	15.1	5.8	29.2	5.8	11.0	4.8
Parapagurus pilosimanus	-	-	-	-	10.4	2.9	5.9	0.9
Pseudodromiidae sp.	-	-	-	-	-	-	-	-
Pterygosquilla a. capensis	25.0	4.7	3.9	2.9	27.1	2.9	2.9	1.6
Shrimp (unid)	-	-	-	-	-	-	-	-
Solonocera africana	10.0	2.8	1.2	0.5	4.2	0.7	1.1	0.1
Sympagurus dimorphus	55.0	19.6	41.9	45.0	64.6	15.5	39.8	35.1
Unidentified crustaceans	-	-	-	-	4.2	0.4	-	+
Porifera								
Polymastia litoralis	-	-	-	-	-	-	-	-
Polychaeta								
Polychaete sp.	-	-	-	-	-	-	-	-
Gastropoda								
Gastropod (unid)	-	-	-	-	-	-	-	-
Teleostei								
Hagfish eggs	5.0	0.9	-	0.1	-	-	-	-
Champsodon capensis	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	2.1	0.2	-	+
Lampanyctodes hectoris	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-
Maurolicus walvensis	5.0	3.7	-	0.2	4.2	0.7	0.1	+
Myctophid (unid)	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-
Unidentified teleost	40.0	7.5	-	4.0	35.4	4.0	-	1.4
Urochordata								
Pyrosoma sp.	-	-	-	-	-	-	-	-
Unidentified	10.0	1.9	-	0.2	6.3	0.9	-	0.1

Appendix 8: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *S. capensis* on the West and South coasts. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

	West Coast				**South Coast**			
	%FO	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae								
Green algae	-	-	-	-	-	-	-	-
Cephalopoda								
Bathypolypus valdiviae	1.4	0.4	0.5	+	1.1	0.3	0.5	+
Loligo reynaudii	2.7	0.9	1.0	0.1	-	-	-	-
Lycoteuthis lorigera	4.1	1.3	1.4	0.2	5.7	1.3	3.3	0.7
Todaropses eblanae	18.9	9.6	13.3	7.0	12.5	3.4	10.1	4.4
Sepia australis	5.4	1.7	0.2	0.2	3.4	0.8	1.3	0.2
Unidentified cephalopods	23.0	16.6	-	6.2	26.1	14.7	+	10.0
Chondrichtyes								
Elasmobranchii egg case	8.1	2.6	-	0.3	-	-	-	-
Crustacea								
Acanthephyra pelagica	-	-	-	-	1.1	0.3	0.3	+
Amphipoda (unid)	1.4	0.4	+	+	10.2	14.7	1.1	4.2
Callianassa sp.	-	-	-	-	15.9	4.6	7.1	4.9
Dyspanopeus sp.	-	-	-	-	10.2	3.6	4.1	2.0
Euphasiids (unid)	-	-	-	-	1.1	0.3	-	+
Glyphocrangon sp.	-	-	-	-	-	-	-	-
Goneplax angulata	-	-	-	-	3.4	1.0	3.4	0.4
Isopoda (unid)	-	-	-	-	2.3	8.2	1.4	0.6
Mursia cristiata	9.5	3.1	2.3	0.8	29.5	12.1	20.3	24.9
Parapagurus pilosimanus	8.1	3.1	12.6	2.1	3.4	1.3	3.9	0.5
Pseudodromiidae sp.	-	-	-	-	6.8	1.5	2.4	0.7
Pterygosquilla a. capensis	4.1	0.9	1.1	0.1	15.9	5.2	7.0	5.0
Shrimp (unid)	-	-	-	-	-	-	-	-
Solonocera africana	2.7	0.9	0.1	+	5.7	1.3	0.4	0.2
Sympagurus dimorphus	45.9	39.3	63.0	76.1	35.2	10.8	26.7	34.4
Unidentified crustaceans	20.3	1.3	-	0.4	11.4	2.8	-	0.8
Porifera								
Polymastia litoralis	-	-	-	-	-	-	-	-
Polychaeta								
Polychaete sp.	6.8	2.2	-	0.2	8.0	2.1	-	0.4
Gastropoda								
Gastropod (unid)	1.4	0.4	-	+	-	-	-	-
Teleostei								
Hagfish eggs	-	-	-	-	-	-	-	-
Champsodon capensis	1.4	0.9	1.6	0.1	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-
Lepidopus caudatus	1.4	0.4	-	+	-	-	-	-
Maurolicus walvensis	4.1	1.3	-	0.1	-	-	-	-
Myctophid (unid)	-	-	-	-	1.1	0.3	1.3	+
Paracallionymus costatus	-	-	-	-	1.1	0.3	-	+
Trachurus capensis	-	-	-	-	1.1	0.3	4.1	0.1
Symbolophurus barnardii	-	-	-	-	1.1	0.3	1.1	+
Unidentified teleost	27.0	9.2	3.1	5.4	28.4	6.7	-	5.0
Urochordata								
Pyrosoma sp.	-	-	-	-	1.1	0.3	0.2	+
Unidentified	10.8	3.5	-	0.6	8.0	1.8	-	0.4

Appendix 9: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *S. capensis* at different depths on the West Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

Depth (m)	**150**				**250**				**350**				**450**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae																
Green algae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda																
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	1.0	0.2
Loligo reynaudii	-	-	-	-	-	-	-	-	5.7	2.2	2.9	0.5	-	-	-	-
Lycoteuthis lorigera	10.0	4.0	4.8	1.1	10.0	2.8	4.0	1.1	-	-	-	-	5.9	1.3	1.0	0.2
Todaropses eblanae	10.0	4.0	6.6	1.3	30.0	13.9	24.9	19.7	22.9	15.6	25.2	14.8	11.8	2.6	2.6	0.9
Sepia australis	10.0	4.0	0.7	0.6	-	-	-	-	8.6	3.3	0.3	0.5	-	-	-	-
Unidentified cephalopods	40.0	20.0	-	9.9	30.0	33.3	-	16.9	11.4	12.2	-	2.2	35.3	12.8	-	6.5
Chondrichtyes																
Elasmobranchii egg case	10.0	4.0	-	0.5	20.0	5.6	-	1.9	8.6	3.3	-	0.5	-	-	-	-
Crustacea																
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda (unid)	-	-	-	-	-	-	-	-	2.9	1.1	0.1	0.1	-	-	-	-
Callianassa sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dyspanopeus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphasiids (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mursia cristiata	10.0	4.0	2.3	0.8	-	-	-	-	11.4	4.4	4.4	1.6	11.8	2.6	1.3	0.7
Parapagurus pilosimanus	-	-	-	-	10.0	2.8	17.9	3.5	2.9	1.1	2.3	0.2	23.5	6.4	21.9	9.6
Pseudodromiidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterygosquilla a. capensis	-	-	-	-	10.0	-	2.5	0.4	5.7	2.2	2.2	0.4	-	-	-	-
Shrimp (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solonocera africana	-	-	-	-	-	-	-	-	-	-	-	-	11.8	2.6	0.3	0.5
Sympagurus dimorphus	50.0	40.0	85.6	77.5	50.0	19.4	36.9	47.6	48.6	28.9	59.9	68.7	41.2	60.3	67.1	75.9
Unidentified crustaceans	10.0	4.0	-	0.5	10.0	2.8	-	0.5	-	-	-	-	5.9	1.3	-	0.1
Porifera																
Polymastia litoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta																
Polychaete sp.	-	-	-	-	-	-	-	-	11.4	4.4	-	0.8	5.9	1.3	-	0.1
Gastropoda																
Gastropod (unid)	-	-	-	-	-	-	-	-	2.9	1.1	-	0.1	-	-	-	-
Teleostei																
Hagfish eggs	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Champsodon capensis	-	-	-	-	10.0	5.6	13.9	3.3	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	10.0	2.8	-	0.5	-	-	-	-	-	-	-	-
Maurolicus walvensis	-	-	-	-	-	-	-	-	8.6	3.3	-	0.5	-	-	-	-
Myctophid (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	-	-	-	-	30.0	8.3	-	4.2	34.3	13.3	2.7	8.8	29.4	7.7	4.8	5.3
Urochordata																
Pyrosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	40.0	16.0	-	7.9	10.0	2.8	-	0.5	8.6	3.3	-	0.5	-	-	-	-

Appendix 10: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of *S. capensis* at different depths on the South Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

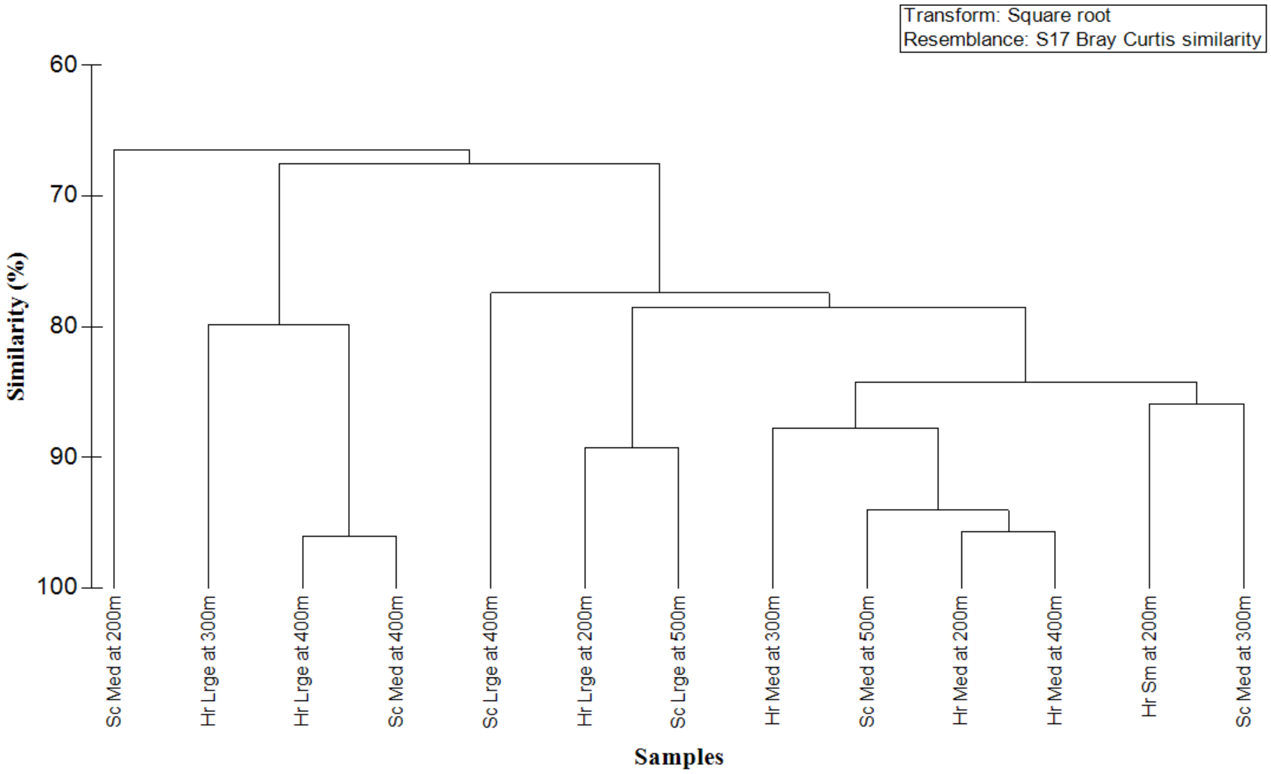
Depth (m)	**150**				**250**				**350**				**450**			
Prey Items	**%FO**	**%N**	**%W**	**%IRI**	**%FO**	**%N**	**%W**	**%IRI**	**%FO**	**%N**	**%W**	**%IRI**	**%FO**	**%N**	**%W**	**%IRI**
Algae					-	-	-	-								
Green algae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda																
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	5.6	1.4	2.3	0.3	-	-	-	-
Loligo reynaudii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lycoteuthis lorigera	-	-	-	-	2.5	8.3	6.5	0.8	16.7	4.2	8.9	3.4	16.7	2.3	2.5	0.7
Todaropses eblanae	3.8	0.9	1.9	0.3	-	-	-	-	38.9	12.7	32.4	27.3	33.3	4.7	7.3	3.4
Sepia australis	5.8	1.3	2.8	0.8	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified cephalopods	17.3	14.4	-	7.8	12.5	41.7	-	5.6	27.8	18.3	-	7.9	66.7	14.0	-	7.8
Chondrichtyes																
Elasmobranchii egg case	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crustacea																
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-	16.7	2.3	1.4	0.5
Amphipoda (unid)	13.5	24.0	2.3	11.1	5.0	16.7	0.9	1.1	-	-	-	-	-	-	-	-
Callianassa sp.	25.0	7.9	16.1	18.9	2.5	8.3	-	0.2	-	-	-	-	-	-	-	-
Dyspanopeus sp.	13.5	4.4	7.1	4.9	2.5	8.3	-	0.2	-	-	-	-	33.3	7.0	4.2	3.1
Euphasiids (unid)	1.9	0.4	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	5.8	1.7	7.6	1.7	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda (unid)	1.9	12.7	0.7	0.8	-	-	-	-	-	-	-	-	16.7	7.0	4.8	1.7
Mursia cristiata	26.9	9.6	24.3	28.7	10.0	16.7	2.8	2.3	38.9	18.3	13.1	19.0	50.0	18.6	27.8	19.6
Parapagurus pilosimanus	-	-	-	-	-	-	-	-	-	-	-	-	50.0	11.6	17.2	12.2
Pseudodromiidae sp.	9.6	2.2	3.3	1.7	-	-	-	-	5.6	1.4	4.1	0.5	-	-	-	-
Pterygosquilla a. capensis	13.5	5.7	9.0	6.2	12.5	41.7	22.1	15.5	11.1	2.8	3.9	1.2	-	-	-	-
Shrimp (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solonocera africana	3.8	0.9	0.6	0.2	2.5	8.3	0.5	0.3	5.6	1.4	0.2	0.1	16.7	2.3	0.2	0.4
Sympagurus dimorphus	21.2	5.2	14.5	13.1	30.0	66.7	67.2	69.9	33.3	11.3	25.1	18.9	100.0	23.3	34.5	48.7
Unidentified crustaceans	13.5	3.5	-	1.5	5.0	16.7	-	0.9	5.6	1.4	-	0.1	-	-	-	-
Porifera																
Polymastia litoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta																
Polychaete sp.	1.9	0.4	-	+	5.0	16.7	-	0.9	22.2	7.0	-	2.4	-	-	-	-
Mollusca																
Gastropoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei																
Hagfish eggs	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Champsodon capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maurolicus walvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myctophid (unid)	-	-	-	-	-	-	-	-	5.6	1.4	5.4	0.6	-	-	-	-
Paracallionymus costatus	1.9	0.4	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	1.9	0.4	9.2	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	5.6	1.4	4.6	0.5	-	-	-	-
Unidentified teleost	15.4	3.5	-	1.7	7.5	25.0	-	2.0	66.7	16.9	-	17.6	33.3	7.0	-	2.0
Urochordata																
Pyrosoma sp.	1.9	0.4	0.5	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	2.5	8.3	-	0.2	-	-	-	-	-	-	-	-

Appendix 11: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of small, medium and large *S. capensis* on the West Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

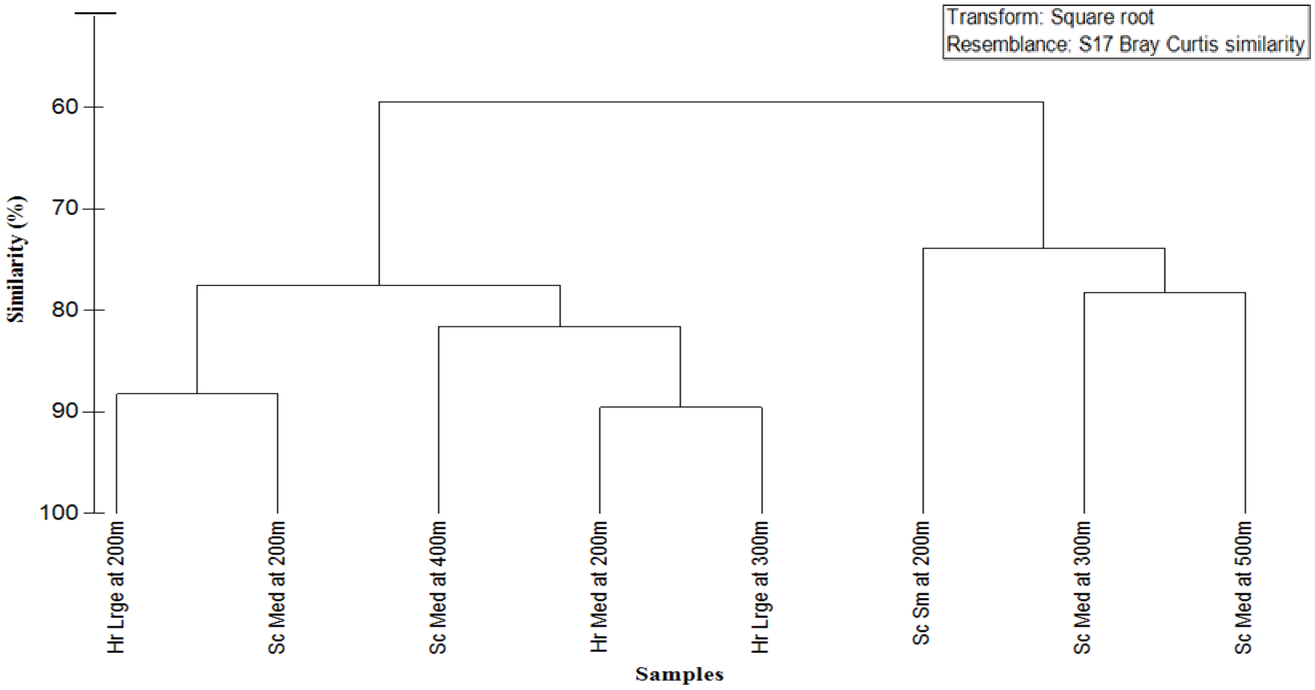
Size classes	**Small**				**Medium**				**Large**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae												
Green algae	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda												
Bathypolypus valdiviae	-	-	-	-	-	-	-	-	10.0	1.8	1.5	0.4
Loligo reynaudii	100.0	50.0	34.2	42.1	1.6	0.6	0.8	+	-	-	-	-
Lycoteuthis lorigera	-	-	-	-	4.9	1.7	2.0	0.3	-	-	-	-
Todaropses eblanae	-	-	-	-	13.1	5.8	7.7	2.6	60.0	21.8	26.7	32.9
Sepia australis	-	-	-	-	4.9	1.7	0.2	0.1	10.0	1.8	0.1	0.2
Unidentified cephalopods	-	-	-	-	19.7	15.1	-	4.4	50.0	21.8	-	12.3
Chondrichtyes												
Elasmobranchii egg case	-	-	-	-	6.6	2.3	-	0.2	20.0	3.6	-	0.8
Crustacea												
Acanthephyra pelagica	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda (unid)	-	-	-	-	1.6	0.6	0.0	+	-	-	-	-
Callianassa sp.	-	-	-	-	-	-	-	-	-	-	-	-
Dyspanopeus sp.	-	-	-	-	-	-	-	-	-	-	-	-
Euphasiids (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Mursia crisiata	-	-	-	-	4.9	1.7	1.3	0.2	40.0	7.3	4.5	5.3
Parapagurus pilosimanus	-	-	-	-	4.9	1.7	8.2	0.7	30.0	7.3	23.2	10.3
Pseudodromiidae sp.	-	-	-	-	-	-	-	-	-	-	-	-
Pterygosquilla a. capensis	-	-	-	-	4.9	1.2	1.5	0.2	-	-	-	-
Shrimp (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Solonocera africana	-	-	-	-	1.6	0.6	0.1	0.0	10.0	1.8	0.1	0.2
Sympagurus dimorphus	100.0	50.0	65.8	57.9	47.5	45.9	74.5	85.6	40.0	18.2	36.5	24.7
Unidentified crustaceans	-	-	-	-	24.6	1.7	-	0.6	-	-	-	-
Porifera												
Polymastia litoralis	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta												
Polychaete sp.	-	-	-	-	6.6	2.3	-	0.2	10.0	1.8	-	0.2
Gastropoda												
Gastropod (unid)	-	-	-	-	-	-	-	-	10.0	1.8	-	0.2
Teleostei												
Hagfish eggs	-	-	-	-	-	-	-	-	-	-	-	-
Champsodon capensis	-	-	-	-	1.6	1.2	2.3	0.1	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	1.6	0.6	-	+	-	-	-	-
Maurolicus walvensis	-	-	-	-	4.9	1.7	-	0.1	-	-	-	-
Myctophid (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Paracallionymus costatus	-	-	-	-	-	-	-	-	-	-	-	-
Trachurus capensis	-	-	-	-	-	-	-	-	-	-	-	-
Symbolophurus barnardii	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	-	-	-	-	23.0	8.7	1.2	3.4	60.0	10.9	7.4	12.4
Urochordata												
Pyrosoma sp.	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	13.1	4.7	-	0.9	-	-	-	-

Appendix 12: Percentage frequency (%FO), percentage number (%N) percentage weight (%W) and percentage IRI (IRI%) data for prey items found in the stomachs of small, medium and large *S. capensis* on the South Coast. Values in red denote frequently occurring (%FO)/important taxa (IRI%) (>10%). "+" is where values are greater than 0 but less than the minimum displayable value and "-" denotes to null/unknown values

Size classes	**Small**				**Medium**				**Large**			
Prey Items	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**	**%FO**	**%N**	**%W**	**IRI%**
Algae												
Green algae	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda												
Bathypolypus valdiviae	-	-	-	-	1.3	0.3	0.6	+	-	-	-	-
Loligo reynaudii	-	-	-	-	-	-	-	-	-	-	-	-
Lycoteuthis lorigera	-	-	-	-	5.3	1.2	2.7	0.5	16.7	7.1	16.0	5.3
Todaropses eblanae	-	-	-	-	14.5	4.0	11.3	5.5	-	-	-	-
Sepia australis	16.7	1.9	14.0	3.7	2.6	0.6	0.6	0.1	-	-	-	-
Unidentified cephalopods	16.7	1.9	-	0.4	26.3	16.8	-	11.0	33.3	14.3	-	6.6
Chondrichtyes												
Elasmobranchii (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Crustacea												
Acanthephyra pelagica	-	-	-	-	1.3	0.3	0.4	+	-	-	-	-
Amphipoda (unid)	50.0	80.8	15.2	66.7	7.9	4.7	0.3	1.0	-	-	-	-
Callianassa sp.	16.7	5.8	33.1	9.0	17.1	4.7	6.1	4.6	-	-	-	-
Dyspanopeus sp.	16.7	1.9	6.0	1.8	10.5	4.0	4.2	2.2	-	-	-	-
Euphasiids (unid)	-	-	-	-	1.3	0.3	-	+	-	-	-	-
Glyphocrangon sp.	-	-	-	-	-	-	-	-	-	-	-	-
Goneplax angulata	-	-	-	-	3.9	1.2	3.8	0.5	-	-	-	-
Isopoda (unid)	-	-	-	-	2.6	9.9	1.6	0.8	-	-	-	-
Mursia cristiata	33.3	3.8	11.8	7.3	31.6	14.0	22.1	28.4	-	-	-	-
Parapagurus pilosimanus	-	-	-	-	3.9	1.6	4.4	0.6	-	-	-	-
Pseudodromiidae sp.	-	-	-	-	7.9	1.9	2.7	0.9	-	-	-	-
Pterygosquilla a. capensis	-	-	-	-	15.8	5.6	6.9	4.9	33.3	14.3	15.4	13.7
Shrimp (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Solonocera africana	-	-	-	-	6.6	1.6	0.4	0.3	-	-	-	-
Sympagurus dimorphus	33.3	3.8	19.9	11.0	35.5	11.5	24.4	31.8	33.3	21.4	68.6	41.5
Unidentified crustaceans	-	-	-	-	13.2	3.4	-	1.1	-	-	-	-
Porifera												
Polymastia litoralis	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta												
Polychaete sp.	-	-	-	-	9.2	2.5	-	0.6	-	-	-	-
Gastropoda												
Gastropod (unid)	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei												
Myxinidae	-	-	-	-	-	-	-	-	-	-	-	-
Champsodon capensis	-	-	-	-	-	-	-	-	-	-	-	-
Chelidonichthys capensis	-	-	-	-	-	-	-	-	-	-	-	-
Lampanyctodes hectoris	-	-	-	-	-	-	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-	-	-	-	-	-	-
Maurolicus walvensis	-	-	-	-	-	-	-	-	-	-	-	-
Myctophid (unid)	-	-	-	-	1.3	0.3	1.4	0.1	-	-	-	-
Paracallionymus costatus	-	-	-	-	1.3	0.3	-	+	-	-	-	-
Trachurus capensis	-	-	-	-	1.3	0.3	4.6	0.2	-	-	-	-
Symbolophurus barnardii	-	-	-	-	1.3	0.3	1.2	+	-	-	-	-
Unidentified teleost	-	-	-	-	27.6	6.8	-	4.7	66.7	28.6	-	26.3
Urochordata												
Pyrosoma sp.	-	-	-	-	1.3	0.3	0.3	+	-	-	-	-
Unidentified	-	-	-	-	6.6	1.6	-	0.3	33.3	14.3	-	6.6



Appendix 13: Dendogram illustrating the % similarity of the diets of *H. regani* (Hr) and *S. capensis* (Sc) pooled by size and depth on the West Coast.



Appendix 14: Dendogram illustrating the % similarity of the diets of *H. regani* (Hr) and *S. capensis* (Sc) pooled by size and depth on the South Coast.

Appendix 15: Illustrates the number (n) and mean size (± SE) of *H. regani* and *S. capensis* sampled for each size class on the West and South coasts. “-“ Denotes to null/unknown values

	H. regani						*S. capensis*					
Coast	**West Coast**			**South Coast**			**West Coast**			**South Coast**		
Size	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**
Small	16	28.7	1.2	-	-	-	1	34.5	-	6	31.1	0.9
Medium	40	40.8	0.3	17	43.1	0.3	58	50.1	1.0	71	47.3	0.9
Large	54	55.3	0.7	45	53.1	1.0	11	76.3	2.5	8	81.3	3.5

Appendix 16: Illustrates the number (n) and mean size (± SE) of *H. regani* and *S. capensis* sampled at each depth on the West and South coasts. “-“ Denotes to null/unknown values

	H. regani						*S. capensis*					
Coast	**West Coast**			**South Coast**			**West Coast**			**South Coast**		
Depth (m)	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**	***n***	**Mean size (cm, TL)**	**±SE**
150	29	38.5	2.3	35	49.1	1.1	10	49.0	2.4	49	43.3	1.2
250	50	49.0	1.3	20	52.5	1.7	10	50.7	3.2	12	53.5	4.7
350	30	48.3	1.4	2	45.0	3.5	36	52.5	2.3	18	62.4	3.2
450	1	58.5	-	5	52.7	4.0	14	63.7	2.1	6	52.0	2.5

Appendix 17: Mean values (± SE) and ranges of δ^{15}N and δ^{13}C for *H. regani* on the West and South coasts

Coast	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**
West	14.49 (± 0.38)	13.28 to 15.47	-15.67 (± 0.04)	-17.21 to -14.90
South	14.20 (± 0.49)	13.18 to 15.09	-15.60 (± 0.04)	-16.37 to -14.72

Appendix 18: Mean values (± SE) and ranges of δ^{15}N and δ^{13}C for *H. regani* at each depth and size class on the West and South coasts. “-“ Denotes to null/unknown values

	West Coast				**South Coast**			
Depth	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**
150 m	14.29 (± 0.07)	13.28 to 14.88	-15.74 (± 0.05)	-16.26 to -14.97	14.12 (± 0.06)	13.34 to 15.09	-15.52 (± 0.07)	-16.37 to -14.72
250 m	14.65 (± 0.05)	13.74 to 15.18	-15.61 (± 0.06)	-17.21 to -14.90	14.43 (± 0.07)	13.82 to 14.85	-15.69 (± 0.05)	-16. 24 to -15.34
350 m	14.39 (± 0.06)	13.98 to 15.47	-15.67 (± 0.08)	-16.95 to -14.98	14.01 (± 0.04)	13.97 to 14.04	-16.02 (± 0.14)	-16.16 to -15.89
450 m	15.47	-	-15.58	-	13.88 (± 0.18)	13.18 to 14.21	-15.66 (± 0.06)	-15.85 to -15.54
Size	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**
Small	14.16 (± 0.11)	13.28 to 14.88	-15.77 (± 0.06)	-16.27 to -15.29	-	-	-	-
Medium	14.47 (± 0.06)	13.74 to 15.18	-15.78 (± 0.08)	-17.21 to -14.97	14.15 (± 0.09)	13.34 to 14.96	-15.57 (± 0.09)	-16.16 to -14.80
Large	14. 61 (± 0.05)	13.98 to 15.47	-15.55 (± 0.04)	-16.23 to -14.90	14.22 (± 0.06)	13.18 to 15.09	-15.61 (± 0.05)	-16.37 to -14.72

Appendix 19: Mean values (± SE) and ranges of δ^{15}N and δ^{13}C for *S. capensis* on the West and South coasts

Coast	**δ^{15}N (± SE)**	**Range**	**δ^{13}C (± SE)**	**Range**
West	14.22 (± 0.06)	13.15 to 15.61	-15.92 (± 0.05)	-16.63 to -14.62
South	13.99 (± 0.05)	12.69 to 14.95	-15.64 (± 0.06)	-16.73 to -14.42

Appendix 20: Mean values (± SE) and ranges of $\delta^{15}N$ and $\delta^{13}C$ for *S. capensis* at each depth and size class on the West and South coasts. “-“ Denotes to null/unknown values

	West Coast				**South Coast**			
Depth	**$\delta^{15}N$ (± SE)**	**Range**	**$\delta^{13}C$ (± SE)**	**Range**	**$\delta^{15}N$ (± SE)**	**Range**	**$\delta^{13}C$ (± SE)**	**Range**
150 m	13.87 (± 0.08)	13.49 to 14.15	-15.73 (± 0.11)	-16.18 to -15.17	13.92 (± 0.06)	12.69 to 14.68	-15.39 (± 0.08)	-16.73 to -14.42
250 m	14.28 (± 0.09)	13.87 to 14.59	-15.62 (± 0.16)	-16.42 to -14.83	14.18 (± 0.13)	13.29 to 14.95	-15.80 (± 0.11)	-16.24 to -15.03
350 m	14.19 (± 0.09)	13.15 to 15.61	-15.99 (± 0.07)	-16.63 to -14.62	14.10 (± 0.09)	13.39 to 14.88	-16.01 (± 0.07)	-16.52 to -15.33
450 m	14.50 (± 0.12)	13.92 to 15.51	- 16.09 (± 0.07)	-16.44 to -15.43	13.77 (± 0.11)	13.31 to 14.07	- 16.16 (± 0.14)	-16.60 to -15.72
Size	**$\delta^{15}N$ (± SE)**	**Range**	**$\delta^{13}C$ (± SE)**	**Range**	**$\delta^{15}N$ (± SE)**	**Range**	**$\delta^{13}C$ (± SE)**	**Range**
Small	14.03	-	-16.06	-	13.22 (± 0.21)	12.69 to 14.04	-15.75 (± 0.17)	-16.23 to -15.25
Medium	14.08 (± 0.05)	13.15 to 14.97	-15. 88 (± 0.06)	-16.63 to -14.62	13.98 (±0.04)	13.29 to 14.63	-15.57 (± 0.07)	-16.73 to -14.42
Large	14.96 (± 0.14)	14.19 to 15.61	-16. 13 (± 0.04)	-16.28 to -15.88	14.58 (±0.11)	14.11 to 14.95	-16.15 (± 0.09)	-16.53 to -15.69