TROPHIC RELATIONSHIPS OF SHALLOW WATER CAPE HAKE

(*MERLUCCIUS CAPENSIS*) AND CAPE HORSE MACKEREL (*TRACHURUS*

CAPENSIS) IN THE NORTHERN BENGUELA ECOSYSTEM

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ABSTRACT

Shallow water Cape hake (*Merluccius capensis*) and Cape horse mackerel (*Trachurus capensis*) are ecologically and commercially important species in the northern Benguela ecosystem (Namibia). The understanding of their trophic relationships is however still limited. In this study stable isotope measurements [carbon (δ^{13}C) and nitrogen (δ^{15}N)] of their muscles and stomach contents were used to investigate their feeding interactions. Understanding the feeding interactions of these two species is vital, in order to consider trophic dynamics in their fisheries management strategies. Muscle tissues (n = 404) and stomach contents (n = 404), were collected during November 2017 bottom trawl survey in Namibian waters. Results indicated that krill (Euphausiids) was a dominant prey in the diet of *T. capensis* and *M. capensis*. The diet compositions of *T. capensis* remained the same with both total length and latitude but not for *M. capensis*, an indication of the influence of prey availability. A potential for interspecific feeding competitions between the two species was observed as krill and anchovy were found as their common prey species. The feeding interactions of the two species appear to have not changed much over time. Significant differences were found in both δ^{15}N values and δ^{13}C values of the two species. Although niche overlap was observed, a wider niche for *M. capensis* than *T. capensis* was observed; an indication of *M. capensis* broader trophic diversity and a more specialized niche of *T. capensis*. This is the first study that has combined stable isotopes and stomach content analysis methodologies, to understand the feeding interaction of *M. capensis* and *T. capensis*.

Keywords: Stable isotopes, Stomach content, Trophic relationship, Northern Benguela Ecosystem, Shallow water Cape hake, Cape horse mackerel.

LIST OF PUBLICATIONS AND CONFERENCES PROCEEDINGS

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LIST OF ABBREVIATIONS AND / OR ACRONYMS

ABFZ   Angola benguela frontal zone

BCE   Benguela current ecosystem

C: N   Mass ratio of carbon and nitrogen

FAO   Food and agriculture organisation

IRI   Index of relative importance

MFMR   Ministry of fisheries and marine resources

NBC   Northern benguela Current

NBE   Northern benguela ecosystem

SCA   Stomach content analysis

SEAC   Standard ellipse area

SIA   Stable isotopes analysis

TA   Total area of the convex hull

$\delta^{13}C$ Carbon isotopes

$\delta^{13}CR$ Carbon isotope range

$\delta^{15}N$ Nitrogen isotopes

$\delta^{15}NR$ Nitrogen isotope range

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Thank you all!

DEDICATION

I dedicated this work to the memories of my late father (+Nicanola Kadila) and my late brother (+Lukas Kadila).

_____Continue to rest in eternal peace until we meet again_____

DECLARATIONS

I, Hendrina Kapawanwa Kadila, hereby declare that this study is my own work and is a true reflection of my research, and that this work, or any part thereof has not been submitted for a degree at any other institution.

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Hendrina K Kadila   Date: 25 / 03 / 2019

CHAPTER 1

1. Introduction

1.1 Background of the study

Shallow water Cape hake (*Merluccius capensis*) and Cape horse mackerel (*Trachurus capensis*) are commercially exploited fish species and key secondary consumers in the Northern Benguela Ecosystem (Namibia). The two species are referred as *M. capensis* and *T. capensis* herein. The two species have overlapping depth distributions (Boyer and Hampton 2001) with *M. capensis* living in waters of 100 – 450 m (Burmeister 2001; Jansen et al. 2015), while *T. capensis* can live up to the depth of 400 m (Axelsen et al. 2004). Both species have diurnal movements between the pelagic and demersal components of the Benguela ecosystem (Pillar and Barange 1998; Bianchi et al. 1999; Iilende et al. 2001). The two species have similar prey in their diet, particularly with large *T. capensis* that are feeding deeper in midwater and their diet is similar to that of *M. capensis* of similar size (Krzeptowski 1982). *Merluccius capensis* and *T. capensis* are both predators of small fishes and crustaceans (Krzeptowski 1982; Konchina 1986).

Merluccius capensis and *T. capensis* have been exploited for decades. The two species are commercially valuable and the subject of targeted fisheries. Fishing of commercial species is thought to have many consequences on the functioning of marine ecosystems (Cooke and Cowx 2006; Perry et al. 2010). One of the direct effects of fishing commercial species being the reduction of large predators, due to the declining of prey they feed on (Pinnegar et al. 2000). The two species have been important predators in the Benguela current system for decades, but major changes

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have occurred in the system (Heymans et al. 2004). The observed changes in the Benguela current system include spatial changes in the distribution of small pelagic fish (Cury and Shannon 2004; Heymans et al. 2004), and increases in biomass of other species such as jellyfish (Flynn et al. 2012; Roux et al. 2013) and gobies (Utne-Palm et al. 2010; Van Der Bank et al. 2011). These two species have been managed through a single-species approach to fisheries management. Single-species management approach is the management that is based on very specific information about that species (individual species), without considering species interaction (Block et al. 1995). However, fisheries management through single-species approach is not effective at ecosystem level; because fish species serves as a prey or predator for other species in the ecosystem. A multispecies management approach to fisheries management is now increasingly being recommended, as fish species have complex linkages and interactions (Botsford et al. 1997; Mohanraj and Prabhu 2012). Multispecies management approach is the management that is based on numerous species by considering species interactions in the ecosystem (Hunter 1991; Block et al. 1995). The trophic linkages and interactions among species play a role in structuring marine fish communities and can significantly impact the dynamics of marine fish populations (Rothschild 1991). For example, predation of piscivorous fish influence population and community level dynamics (Bax 1998; Juanes et al. 2002). Predation and cannibalism have been suggested as a source of mortality which can regulate recruitment, and so population size of several fish species (Neuenfeldt and Köster 2000; Wespestad et al. 2000; Tsou and Collie 2001). For these commercial species to continue to be managed sustainably at ecosystem level their trophic relationships need to be understood. Trophic relationships are fundamental to the understandings of biological interaction of fish species in the ecosystem (Fanelli

2007). Trophic relationships include a component of diet, which is a significant component in understanding the ecology of a species. Therefore, increased understanding of trophic relationships among fish species can aid the application of multispecies consideration in fisheries management. This thesis discusses the trophic relationships of *T capensis* and *M. capensis*.

Trophic relationships have been studied using various methods such as food web models (Roux and Shannon 2004; Watermeyer et al. 2008), faecal analysis, radio tracer, immunological approaches (Trites 2001), fatty acid biomarkers analysis (Schukat et al. 2013; Iitembu and Richoux 2016), lipid content (Fernandez-Jover et al. 2007), stomach content (Iitembu 2014) and stable isotopes (Erasmus 2015; Luis-Varela et al. 2018). Although, these methods have helped to shed light and resolve food web structure, each of the methods has its own disadvantages. Researchers have used a combination of two or more methods to analyse the trophic structures and it proved to be the most useful way to study food webs (Budge et al. 2008). In this study a combination of stomach content and stable isotope analyses were used to investigate the trophic relationships of *M. capensis* and *T. capensis*.

Stomach content analysis (SCA) entails direct observation of stomach contents, providing an immediate record of what a fish has consumed and the quantity of the prey items (Costa et al. 1992; Elliott and Hemingway 2002; Van Der Lingen and Miller 2011; Carrasco et al. 2012; Iitembu 2014). Stomach content data can provide information on taxonomic, size composition of diets and predator – prey interactions in complex systems where species consume a variety of items that may be problematic to identify from stable isotope ratios alone (Layman et al. 2005). The

interpretation of stomach content result is however, limited spatially and temporally because they represent only snapshots of recent feeding, and are quantitatively biased due to differences in the digestion rates of diverse prey (Hyslop 1980; Cortés 1997; Vander Zanden et al. 1997; Hussey et al. 2011; Iitembu 2014). Several indices quantitatively express the relative importance of various prey in fish diets (Berg 1979; Hyslop 1980). In this study, the following indices were used: percentages of frequency of occurrence (% F), composition by number (% N), composition by weight (% W); and Index of relative importance (IRI) expressed in percentage (% IRI).

Another method used in this study to understand the trophic relationships of *M. capensis* and *T. capensis* is stable isotopes analysis (SIA). The usage of stable isotopes (nitrogen and carbon) provide temporally and spatially integrated view of an assimilated diet and can detect trophic interactions not observed through stomach content analyses (Pitt et al. 2007; Van der Bank et al. 2011; Iitembu et al. 2012; Van der Lingen and Miller 2014; Erasmus 2015). In addition, stable isotope analysis is also being progressively used to elucidate ontogenetic dietary shifts in fishes (Davis et al. 2012; Iitembu et al. 2012). However, stable isotope analysis does not give a detailed picture of an organism's prey items (Hüne et al. 2018). Stable isotope ratios of nitrogen ($\delta^{15}N$) are used to estimate the trophic position of a consumer, with each trophic level accounting for an approximate enrichment of 3.4 ‰ relative to it is diet (Minagawa and Wada 1984; Post 2002a). In addition, $\delta^{15}N$ are frequently used to examine dietary shifts and trophic relationships in food webs (Post 2002a; Hussey et al. 2011). Whereas the ratio of carbon stable isotopes ($\delta^{13}C$), which increases at a much slower rate than $\delta^{15}N$ as carbon moves through food webs (Post 2002a), have

been used in assessing the origin of carbon source production for an organism (Post 2002a; Fry 2006; Van der Lingen and Miller 2014). Lately, stable isotope compositions were also discovered as a potent tool for assessing the trophic niche width of species, as well as for identifying trophic specialists from generalists (Bearhop et al. 2004; Jackson et al. 2011).

The usage of the combination of stomach content analysis and stable isotope analysis, as done in this study, have been observed to present a better understanding of trophic interactions of fish species (Vander Zanden et al. 1997; Woodward and Hildrew 2002; Stowasser et al. 2006; Fanelli and Cartes 2010; Miller et al. 2010; Soares et al. 2018). Therefore, this project aimed at investigating the trophic relationships of *M. capensis* and *T. capensis* off Namibia using stomach content and stable isotopes methodologies.

1.2 Statement of the problem

Merluccius capensis and *T. capensis* are ecologically and commercially important species in the marine waters of Namibia. The two species have overlapping depth distribution and have diurnal movements between the pelagic and demersal components of the Benguela ecosystem. These two species are abundant predators, their predation may play an important role in the population dynamics of other economically important fish species, as well as of forage species. These species have been managed through a single-species approach to fisheries management respectively, but the focus in many fisheries has shifted to multi-species fisheries management. For multi-species fisheries management to be implemented, one need a comprehensive understanding of factors like their trophic relationships. The trophic

relationships of *M. capensis* and *T. capensis* is however, still not well understood to the extent that it can be considered in fisheries management.

1.3 Objective of the study

The main aim of this study was to investigate the trophic relationships of *M. capensis* and *T. capensis* in the northern Benguela ecosystem using stomach content and stable isotopes analyses.

The specific objectives were:

1. To compare the diet compositions of *M. capensis* and *T. capensis* using stomach content analysis.

2. To determine if there is significant difference in the stable isotopes (δ^{15}N and δ^{13}C) of *M. capensis* and *T. capensis*.

3. To determine if there are differences in the trophic niches of the two-species using their isotopic niche.

1.4 Hypotheses of the study

1. H_0: There are no differences in the dietary compositions of *M. capensis* and *T. capensis*.

2. H_0: There are no significant differences in the stable isotopes (δ^{15}N and δ^{13}C) of *M. capensis* and *T. capensis*.

3. H_0: There are no differences between the trophic niches of *M. capensis* and *T. capensis*.

1.5 Significance of the study

Merluccius capensis and *T. capensis* are important commercial species in Namibia. Both species are managed as single species; but they are not living in isolation in the ecosystem, necessitating the need for multispecies management approach of these fisheries. However, multispecies management approach would not be effectively implemented without understanding the trophic relationships of *M. capensis* and *T. capensis*, particularly how these two species are trophically linked. The ecological position of the two species together with their importance to the fishery makes a study of their trophic relationships particularly necessary. Therefore, the findings from this study will aid the consideration of multispecies interactions in the management of these fisheries. Multispecies management will enable the management of these fisheries at ecologically sustainable harvest levels, as it considers feeding interactions or place multi-species trophic interactions into consideration.

1.6 Limitation of the study

The samples size was limited to those that were collected during the monkfish biomass survey of the Ministry of Fisheries and Marine Resources (MFMR). Sampling strategy of collecting samples in the trawls that contain both species also contributed to limited samples size. As well as, the distribution characteristics of the two species also limited to obtaining a wide size distribution of each species examined; mostly *T. capensis* that is mainly distributed from $17°00 – 25°00$ latitudes that lead to sample to be collected from Kunene River (17 °S) to the Conception Bay (24 °S) in the northern Benguela Current ecosystem.

1.7 Delimitation of the study

The study focused only on the population of *M. capensis* and *T. capensis* from the Cunene River (17 °S) to the Conception Bay (24 °S) in the northern Benguela Current ecosystem and the depth ranges covered was from 200 m to 500 m water depth.

1.8 Research ethics

Fish samples were collected from fish caught by the Ministry of Fisheries and Marine Resources research surveys, which is governed and permitted by the Marine Resource Act No.27 of 2000. Apart from that, data collection and processing were done according to the approved methods of marine research protocols and governed by the Research ethic policy of the University of Namibia.

CHAPTER 2

Literature review

2.1 Marine waters off Namibia

The Namibian marine ecosystem form part of the Benguela Current Ecosystem, which extends from southern Angola (17 °S) to the southern tip of Africa near Cape Town (34 °S) (Demarcq et al. 2003). The Benguela Current Ecosystem (BCE) is one of the four major eastern boundary current regions of the world, which are characterized by the presence of cool surface waters and high biological productivity (Shannon 1985; Boyer et al. 2000; Hutchings et al. 2009). The BCE is characterized by very high levels of primary and secondary production from intense coastal upwelling, supporting a high abundance of pelagic and demersal fishes (Shannon et al. 2006; Cochrane et al. 2009). Generally, upwelling systems are unstable environments where physical, chemical and biological characteristics change continuously as a consequence of the upwelling process. These changes have consequences for biological diversity since food, while at times can be abundant, is sporadically distributed and unpredictable (Sakko 1998). Such environments normally support low diversities of species, while at the same time being among the most productive habitats in the world (Barnes and Hughes 1988).

The Benguela Current ecosystem is categorised into two main ecosystems; the southern Benguela off the west coast of South Africa and northern Benguela off the coast of Namibia (Heymans et al. 2004). The Northern Benguela Current (NBC) is separated from the southern Benguela by a strong wind-driven seasonal upwelling cell around 25 – 27 °S (Luderitz upwelling cell). The Luderitz upwelling cell has a Sea Surface Temperature (SST) of 11 °C from June to October, however with high

inter-annual variabilities (Bartholomae and Van der Plas 2007). In the north, there is a convergence of the Angola Current called the Angola-Benguela Frontal Zone (ABFZ) (John et al. 2004; Mohrholz et al. 2008; Hutchings et al. 2009), which is characterized by high salinity and strong horizontal temperature gradients (Shannon et al. 1987; Loick et al. 2005). During late austral summer, the region is characterized with the southernmost reach of the ABFZ seasonal oscillation and minimal upwelling (Hagen et al. 2001). During this season, zooplankton at the NBC are subjected to unfavourable trophic conditions, caused by low nutrient concentrations and may suffer short periods of food deprivation, that will affect secondary consumer negatively. Various dramatic changes for instance physical challenges and overfishing have occurred in the NBCE over the years (Heymans et al. 2004), that include high catches sustained by the system in the 1970s. Despite that, the general energy flow pathway in the NBC remains as: primary production → zooplankton → pelagic fish → demersal fish, with secondary consumers of pelagic and demersal fish (Heymans and Baird 2000).

Namibia's 200 nautical mile Exclusive Economic Zone (EEZ) contains about 20 different species; consisting of pelagic species (sardine, anchovy, round herring, Cape horse mackerel) and demersal species (Cape hake, monkfish, sole, lobster and crab etc.). Out of the 20-fish species commercially exploited in Namibia, eight species (Cape hake, pilchard, Cape horse mackerel, and orange roughy, rock lobster, monk, deep seared crab and seals) are regulated through TACs (Total Allowable Catch) (Food and Agriculture Organization [FAO] 2007). Namibian fisheries are relatively low in diversity (Anon 2004), with *T. capensis* being the dominant species in terms of volume in the Namibian waters (FAO 2007). *Merluccius capensis* is one

of the dominant species in demersal communities in the northern Benguela (Anon 2004).

2.2 Cape horse mackerel (*Trachurus capensis*)

Trachurus capensis, Castelnau, 1861 (Cape horse mackerel) belongs to the family Carangidae (Jacks and pompanos), order Perciformes (perch-likes) and class Actinopterygii (ray-finned fishes). This species is locally known as Maasbanker and is found in high abundance in Namibian waters (Benguela Current Large Marine Ecosystem [BCLME] 2004). The stock of *T. capensis* is distributed from around Tomboa in Southern Angola and throughout Namibia (Krakstad 2001; Boyer and Hampton 2001; Van der lingen et al. 2006). This species usually occurs in waters between 200 – 1000 m depth (Crawford et al. 1985). Uanivi and Van der Plas (2014) documented that *T. capensis* is usually found in the northern Benguela (17 °S – 25 °S) and display a highly migratory and aggregating behaviour with patchy distribution patterns. Geist et al. (2014) reported that *T. capensis* prefer water with a higher temperature of 18 – 21 $^{\circ}$C and can tolerate a wide range of dissolved oxygen concentrations of 0.13 – 6.35 ml/l. *Trachurus capensis* is exploited by mid water trawl fishing method (FAO 2007). This species reaches maximum total length of 60 cm, and 30 cm as the average total length (Bianchi 1986). During the 1970s *T. capensis* fish matured at the length of approximately 26 cm, but from 1999 up to date they have been observed to mature at an earlier length of approximately 19 cm (MFMR 2015). In recent years, fish length maturity has increased to 26 cm from 19 cm (MFMR 2016). *Trachurus capensis* is known to spawn between Cape Frio (18°20′S) and Cape Cross (22 °S), as from October to late February or early March (O'Toole 1977). *Trachurus capensis* is indeterminate, multiple batch spawners (Karlou-Riga and Economides 1997; Abaunza et al. 2003; Gordo et al. 2008, Ndjaula

et al. 2009). Hence, females spawn on several occasions within a single spawning season (Macer 1974) and the ovaries contain many asynchronous oocytes, particularly when their maturity is well advanced towards the start of spawning (Ndjaula et al. 2013). This species is known to exhibit diurnal movement patterns by rising to feed in surface waters at night, but can be found close to the bottom during the day (Bianchi et al. 1999; Krakstad 2001). This species feeds predominantly on zooplankton up to two years of age where they consume it near the sea surface (Venter1976; Smith et al. 2012). Juveniles feed mainly on copepods while adults' prey on fish and a wide range of invertebrates (FAO 1993). Older fish tend to feed in the deeper midwater, and their diet is identical to that of cape hake of a similar size (Krzeptowski 1982).

A study done by Santic et al. (2005) on the feeding habits of the horse mackerel (*Trachurus trachurus*) from the central Adriatic Sea, documented a total of 30 different prey species for *T. trachurus*, belonging to major groups of Crustacea (Euphausiacea, Mysidacea, Decapoda), Cephalopoda, and Teleostei. Euphausiids were the most important ingested prey and the most frequent prey were two species of euphausiids: *Nyctiphanes couchii* and *Euphausia krohni* (Santic et al. 2005). Konchina (1986) studied the food spectrum of *T. capensis* and documented that the diet of this species included pteropods, crustaceans (copepods, euphausiids, hyperiids and decapoda), chetognaths and fish, with euphausiids (euphausia) and shrimps as the main prey items. Results from Andronov (1983) agrees with Konchina (1986), documenting that *T. capensis* feed on copepods, euphausiids, shrimps and fish, with the dominant prey of euphausiids. Krzeptowski (1982) and Andronov (1983) indicated that *T. capensis* is a facultative fish feeder whose diet consists mainly of euphausiids. However, Bayhan and Sever (2009) carried out research on food and

feeding habits of horse mackerel (*T. trachurus)* from the Aegean Sea and; documented a total of 60 different prey species, belonging to five major systematic groups: Polychaeta, Crustacea, Mollusca, Chaetognatha and Osteichthyes. Crustaceans (particularly Copepoda, Euphausiacea and Mysidacea) were the most important food category by percentage of index relative importance (% IRI) and Teleosts were the second most important food category, while Polychaeta and Chaetognatha were occasionally food (Bayhan and Sever 2009). In a study done by Cabral and Murta (2002) Portuguese horse mackerel was observed feeding on copepods, decapod larvae, euphausiids (especially *Meganyctiphanes norvegica* and *Nyctiphanes couchi*) and fish. Horse mackerel is identified as a zooplanktophagous that becomes ichthyphagous when adult (Dahl and Kirkegaard 1987; Murta et al. 1993; Olaso et al. 1999).

Some authors (Cabral and Murta 2000; Santic et al. 2005) observed seasonal changes in the diet of horse mackerel. Cabral and Murta (2000) reported that in summer and winter, euphausiids (*N. couchi*) were the most important prey, while in autumn it was copepods in number and weight of Portuguese horse mackerel. In the other studies (Cabral and Murta 2000; Santic et al. 2005) seasonal changes in the diet corresponded to a higher diversity of prey in autumn compared to other seasons, but euphausiids were the main prey in all seasons. Moreover, Bayhan and Sever (2009) indicated that copepods, euphausiids and mysids were the most significant prey to be consumed by this species in all seasons. They also reported that the percentage of empty stomachs in Portuguese horse mackerel was greatest in winter, due to spawning season of this species on the Portuguese coast (Borges and Gordo 1991).

The diet differences in size (they change their diet as they grow) of this species was highlighted by several researchers (Andronov 1983; Konchina 1986; Cabral and

Murta 2002; Jardas et al.2004; Santic et al. 2005; Bayhan and Sever 2009). In the diet of Atlantic Horse Mackerel of the size that ranged between 10.0 – 12.9 cm copepods were the main prey, while fish of 16.9 cm fed on euphausiids and mysids, but fish larger than 16.9 cm were feeding on teleost larvae (Bayhan and Sever 2009). Santic et al. (2005) observed that, small and medium-size classes fish (< 28 cm TL) were feeding on euphausiids, while fish > 30 cm TL on teleosts. Andronov (1983) and Konchina (1986) noted that, the diet of *T. capensis* up to 20 cm length consisted mainly of copepods (predominantly *Calanoides carinatus*), while larger fish measuring up to 40 cm length preferred euphausiids; as secondary food items. Food habits change considerably as fish grow, small-size class being mostly zooplanktophagous, while large specimens are mainly ichthyophagous (Cabral and Murta 2002; Jardas et al. 2004). Geist et al. (2014) observed an early ontogenic trophic shift in *T. capensis* larvae and early juveniles as their dietary shift with increasing body size by increasing size of calanoid copepods in their gut content. This suggested that major factors are responsible for the changes, including enhanced swimming capacity that enlarges foraging range which increases the access to food source and the developed gut that comes along with a higher digestive effectiveness (Westhaus-Ekau 1988). Geist et al. (2014) further tested the ontogenetic shift (the change with development of a species) in the δ^{15}N-signatures of larvae that were collected at the same station to prevent baseline effect and they found a significant linear correlation between body size and δ^{15}N-signatures. The stepwise increase in δ^{15}N-ratios was from phytoplankton via copepods to fish larvae that resulted in the occupation of the trophic level 3 by *T. capensis* larvae. These results are further supported by a study done by Schukat et al. (2014) who reported that many calanoid copepod species in the Namibian Benguela Current Ecosystem are omnivorous that

consequently feeding on higher trophic level prey items that likely led to the positive correlation of δ^{15}N-ratios with body size of *T. capensis* larvae and juveniles. The trophic level of *T. capensis* has been indicated as 3.7, to be around 3.6 for juveniles and 3.7 for adults based on mass-balanced models (Shannon et al. 2003), while isotope-based calculations indicated that it is around 2.52 (Erasmus 2015).

Figure 1: Illustration of *Trachurus capensis* (Cape horse mackerel)

2.3 Shallow water Cape hake (*Merluccius capensis*)

Merluccius capensis, Castelnau, 1851 is a Cape hake species that belongs to the family Merlucciidae (Merluccid hakes), class Actinopterygii (ray-finned fishes) and order Gadiformes(Cods) (Cohen et al. 1990). *Merluccius capensis* (Shallower water Cape hake) is a demersal species found at depths of 100 – 450 m (Bianchi et al. 1999; Burmeister 2001; Wilhelm et al. 2015). Individuals migrate into deep water as they grow (Jansen et al. 2016). This species is found all along the South-eastern Atlantic, it is known to have a trans-boundary distribution that extends from southern Angola southwards through Namibia and into South African waters (Kirchner 2011). The species is most abundant off the coast of Namibia (more abundant north of 27 ºS by Johnsen and Kathena (2012) and the south coast of South Africa (Macpherson and Gordoa 1994; Von der Heyden et al. 2007). *Merluccius capensis* can tolerate

temperatures ranging from $1 - 10.3$ $^{\circ}$C, with an optimum of 8.8 $^{\circ}$C (Wilhelm et al. 2015). Furthermore, it prefers a dissolved oxygen level of 3.6 ml/l yet, they can endure a range of $1.1 - 6.4$ ml/ l (Wilhelm et al. 2015). This species is harvested by bottom trawling and longlining in Namibian waters (FAO 2007). Cohen et al. (1990) noted that the maximum size for *M. capensis* is 120 cm and the average size is at $40 - 60$ cm with the growth rates of 0.21 mm and length at maturity of 47 cm. *Merluccius capensis* migrate as they grow, at an age of about 1-year-old ($10 - 15$cm total length (TL)) they move from mid- to the inner-shelf, while from $1.5 - 2.0$ years of age ($24 - 29$ cm TL) they move northwards and also from the inner to the mid-shelf (Wilhelm et al. 2015). In addition, when they are $3.5 - 4.5$ years of age, they move from mid to outer shelf at $45 - 63$ cm TL synchronized with their southward migration to spawn and later they return to the mid-shelf again at > 58 cm TL (≥ 4.5 years old) to spawn (Wilhelm et al. 2015). *Merluccius capensis* is known to spawn in Namibian waters (Kainge et al. 2007). Predators of this species are cape fur seal (Mecenero et al. 2006), sea birds and monk fish (Roux and Shannon 2004).

This species is an opportunistic feeder, changing its preferred prey type in relation to their local availability and abundance (Pillar and Wilkinson 1995). Research on a comparison of spatial variability in the diet of *M. capensis* through stomach contents, noted that crustaceans and mesopelagic fishes were important in the diet of smaller (<50 cm TL) fish off the west coast, whereas epipelagic fishes dominated the diet of this species off the south coast analyses (Pillar and Wilkinson 1995). Larger *M. capensis* feed on *T. capensis* and small hake (*via* cannibalism) and other demersal fishes (Pillar and Wilkinson 1995; Kainge et al. 2017). Cape hake feed selectively upon either large crustaceans or fish (Pillar and Barange 1993). According to Roel and Macpherson (1988), the main components of the diet of both hake species were

small crustaceans, fish and cephalopods, but the relative importance of each item varied both geographically and seasonally according to availability of the prey.

The diet of this species, analysed by the use of stomach content; revealed diet change with the increase in size. Euphausiids were found as a major crustacean constituent of the diet of *M. capensis* in the size range of 20 – 39 cm length, but its importance diminishes with size of the predator, while the importance of fish in the diet increases with hake size (Roel and Macpherson 1988). Punt et al. (1992) findings support Roel and Macpherson (1988) results, as young *M. capensis* feed predominantly on planktonic crustaceans (chiefly euphausiids), pelagic gobies, and its diet becoming increasingly piscivorous with age. Assorov and Kalinina (1979) observed that from the 20 – 29 cm length class and ≥ 70 cm, fish of the family Myctophidae and hake were the most abundant in the *M. capensis* diet. However, the proportion of myctophids decreased with *M. capensis* length, while that of hake increased with size (Assorov and Kalinina 1979). In the Bay of Biscay and the Celtic Sea, Mahe et al. (2007) they observed that small European hake (*Merluccius merluccius*) fed almost entirely on crustaceans (mainly euphausiids), with a significant shift towards a fully piscivorous diet in hake > 23 cm. Similarly, Pillar and Wilkinson (1995) and Andronov (1983) observed an ontogenic trophic shift in diet of *M. capensis* from larvae to adult, as their preferences switch from small copepods to larger prey items such as euphausiids, mesopelagic and pelagic fish, and later, when adult, to demersal fish, mostly other hake. Change in feeding behaviour during ontogeny, with fish becoming more prevalent in the diet, is common in non-specialist fish, and is an advantage because fish contain a greater energy content than crustaceans (Juanes et al. 2002). Furthermore, the change in the diet with growth has also been attributed to increasing mouth size and mobility as observed in European hake (Mahe et al. 2007).

Ontogenetic trophic shift in two hake species from the northern Benguela Current ecosystem (Namibia) was also observed by Iitembu et al. (2012) where $\delta^{15}N$ showed a significant positive relationship with size. Van Der Lingen and Miller (2014) researched on the spatial, ontogenetic and interspecific variability in stable isotope ratios of nitrogen and carbon of *Merluccius capensis* and *Merluccius paradoxus* off South Africa, their result agrees with Iitembu et al. (2012). The results corresponded with diet analysis studies of hake species; that have revealed general ontogenetic trends in proportional shifts from zooplanktivory to more piscivory (Bozzano et al. 1997; Carpenteri et al. 2005).

The trophic level of *M. capensis* was documented by different authors (Roux and Shannon 2004; Watermeyer et al. 2008; Schukat et al.2013; Iitembu et al. 2012; Erasmus 2015). Food web models' studies estimated the trophic level of this species at 4.0 for small and 4.5 for large fish (Roux and Shannon 2004; Watermeyer et al. 2008). Their results are closer to Schukat et al. (2013) who reported that this species feeds at a trophic level of 4.7, thus showing that; they feed at a higher trophic level. However, stable isotope results indicated that it feeds at a trophic level (TL) of 3.3 for lengths 20 – 39 cm, while larger fish of 60 – 70 cm had TLs of about 3.5 – 3.6 (Iitembu et al. 2012). Other stable isotopes studies have also indicated that hake feed at the lowest trophic level of 2.15 and 2.9 (Erasmus 2015). The differences in their results were possibly due to different methods used and geographical area covered.

Figure 2: Illustration of *Merluccius capensis* (shallow water Cape hake)

2.4 Trophic relationships

Trophic relationships play significant roles in the structuring of aquatic systems
(Vander Zanden et al. 2000; Heithaus et al. 2008; Laroche et al. 2008). Trophic
relationships are multidimensional, relevant biophysical factors that vary widely in
their spatial and temporal scales of influence and process linkages are complex and
highly non-linear (Wooster and Bailey 1989; Mullin 1993). Understanding the
trophic linkages amongst different marine species is essential for researchers to gain
insights into how they influence food web structure (Pethybridge et al. 2011).
Trophic relationships comprise component of diet, which is a significant component
in understanding the ecology of a species. Organisms within an ecosystem feed on
one another, forming food chains and food webs. Food chains and food webs are two
fundamental conceptual approaches used to signify trophic structure and feeding
relationships at the entire community level. Food webs largely define ecosystems;
describing the relationships between predators and preys, while trophic levels define
the position of organisms within the webs (Zacharia 2007). The trophic level can also
be defined as the position that an organism occupies in a food chain. Organisms in an
ecosystem often interact in complex ways, as some organisms feed on more than one

trophic level, whereas trophic levels of some organisms change as they grow (Mohanraj and Prabhu 2012; Zacharia 2007). Species within an ecosystem are connected through what they eat and in turn what eats them (Vorsatz 2016). Studies of trophic relationships are complicated by various factors such as high levels of spatio-temporal scales of biophysical factors (Paine 1988; Polis and Winemiler 1996; Wainright et al. 1996), intra-population (Gu et al. 1997), inter-population (Vander Zanden and Rasmussen 1996), and ontogenic (Werner and Giliam 1984) variation.

Trophic relationships enhance understanding of the functioning of marine food webs and avail information needed for consideration of trophic interaction in fisheries management decisions (Endjambi et al. 2015). Although, fisheries management in Namibia have mainly used a single-species approach, globally there is a drive towards multi- species fisheries management to managing fisheries resources (Pikitch et al. 2004) that consider interactions amongst species in the ecosystem (Cadima 2003). Understanding trophic relationships can help in this drive, since feeding interactions not only influences community structures but also influences population dynamics (Hobson and Welch 1992; Officer and Parry 1997). Understanding of trophic interactions among different species is necessary for fisheries management that is moving towards a multi- species management (Roux and Shannon 2004; Cochrane et al. 2009). Multi-species management will enable species to be managed at ecological sustainable harvest levels.

A number of methods that include food web models (Roux and Shannon 2004; Watermeyer et al. 2008), faecal analysis, radio tracer, immunological approaches (Kioboe et al. 1990; Bamstedt et al. 2000; Trites 2001), fatty acid biomarkers analysis (Schukat et al. 2013 Iitembu and Richoux 2016), lipid content (Osako et al. 2003; Fernandez-Jover et al. 2007), stomach content (Iitembu 2014) and stable

isotopes (Iitembu et al. 2012; Schukat et al. 2013; Endjambi et al. 2015; Erasmus 2015), have been used to enhance our understanding of trophic relationships. Even though these methods have helped to shed light and resolve food web structure, every analytical method has its own disadvantages and a combination of two or more methods is likely to be the most useful tool to study food webs (Budge et al. 2008). This study used a combination of stomach content and stable isotope to study trophic relationships of *M. capensis* and *T. capensis* to obtain robust results.

2.5 Methods of evaluating trophic relationships

2.5.1 Stomach content analysis (SCA)

Stomach content analysis is a technique that allows identification of the actual prey consumed by a fish (Van Der Lingen and Miller 2011; Carrasco et al. 2012; Iitembu 2014). It entails direct observation of stomach contents, providing an immediate record of what an animal has consumed (Costa et al. 1992; Elliott and Hemingway 2002; Winemiller et al. 2007). Stomach content analysis is considered as one of the main tools for understanding the linkages and dependencies within marine ecosystems (Preciado et al. 2008). This method of analysis has the benefit of giving an initial view of the ichthyological trophic structure of the system by describing the food relations between fish species and their prey (Pasquaud et al. 2008). Food (prey items) is a primary component of the ecology of organisms that is recognized as a key factor in all ecosystems, which is helpful in interpreting some of the higher-level trophic relationships (Mohanraj and Prabhu 2012). Stomach content studies investigated diet habits to determine the most frequently consumed prey and to determine the relative importance of various prey types to fish nutrition, as well as to quantify the consumption rate of individual prey types (Zacharia 2007). Diets of

fishes represent an integration of many important ecological components such as their behaviour, condition, habitat use, energy intake and inter/intra specific interactions (Zacharia 2007). The prey items consumed by predators represents important information which can be used to elucidate trophic aspects, for instance niche breadth, competition for resources and spatial overlap (Hammerschlag-Peyer et al. 2011).

Even though, SCA has helped to shed light and resolve food web structure, several drawbacks have been noted by several authors (Van Der Lingen and Miller 2011; Carrasco et al. 2012; Iitembu 2014). Some biases of the SCA are linked with accurate prey identification, which may be problematic when using this technique (Parkins 1993). Low temporal resolution of this method requires a large number of samples to obtain a representative view of the dietary patterns of a species (Hyslop 1980). Michener and Lajtha (2007) and Schukat et al. (2013) indicated that some organisms digest their prey rapidly thereby deforming the morphology of the ingested prey, making identification problematic. Stomach content analysis requires a knowledgeable taxonomist to identify nearly all the unidentifiable and partially digested organisms found in the stomach (Baker et al. 2013), mostly prey item hard bodies or parts such as fish otoliths bones and scales (Gee 1989). This may lead to over estimation of the significance of upper trophic-level prey such as fish (Hobson 1993). Stomach content examination can also lead to over-estimation of poorly palatable and/or digestible items, as it focuses on ingested food but gives no information about whether this food is actually assimilated and exploited by consumers or not. Stomach content data can, however provide important information on taxonomic and size composition of diets and predator-prey interactions in

complex systems where species consume a diversity of items that may be difficult to identify from stable isotope ratios alone (Layman et al. 2005).

The SCA methods are broadly divided into two analyses, which are qualitative and quantitative (Zacharia 2007). The qualitative analysis entails a complete identification of the organisms in the stomach contents, while the quantitative method includes the numerical (Frequency of occurrence, Dominance, Number and Point); gravimetric and volumetric analysis (Eye estimation, Points and Displacement) (Hynes 1950; Pillay 1952; Hyslop 1980; Chipps et al. 2002). The accuracy of enumerating the importance of prey taxa and understanding the contributions of several prey to predator well-being is essential for the effective management of fisheries resources (Bowen 1996).

Index of Relative Importance (IRI) is a common index used for quantifying prey importance. Therefore, the current study used IRI to compare diet composition of *M. capensis* and *T. capensis*.

The IRI was originally developed by Pinkas et al. (1971) and modified by Hacunda (1981) to overcome the limitations of component indices (% N, % W and % F). IRI is defined as the contribution of prey taxa to nutrition of the predator population as a whole, mediated by the abundance of and likelihood that individual predators will encounter and eat these prey (Liao et al. 2001). IRI = ((% N + % W) x % F), the three parameters were integrated to eliminate any biases created once each method is analysed individually (Goldman and Sedberry 2010). The three-parameter used to calculate IRI are percentage composition by number (% N), percentage composition by volume (% V) or weight (% W), and percentage frequency of occurrence (% F). Each of the three parameter provides a different insight into the feeding habits of fish

(Hyslop 1980). Percentage composition by number provides information about feeding behaviour; percentage composition by weight reflects nutritional value of prey (Cailliet 1977; MacDonald and Green 1983; Cortez 1997) and the percentage frequency of occurrence furnishes some information on population-wide food habits (Cailliet 1977). The frequency of occurrence is a numerical method that determines what organisms are being fed upon (Zacharia 2007), and provides information on the proportion of fish stomachs containing a particular prey item regardless of amount. IRI provides the optimal balancing of frequency of occurrence, numerical abundance, and abundance by weight of taxa in fish diets that represents a more balanced view of dietary importance (Liao et al. 2001).

2.5.2 Stable isotope analysis (SIA)

Stable isotopes are categorised as those that are energetically stable, do not emit radiation and do not decay (Phillips and Gregg 2003; Michener and Lajtha 2007). The fact that they are not radioactive, makes them useful natural tracers (Michener and Lajtha 2007). An isotope is known to be stable when the number of neutrons (N) and the number of protons (Z) are the same (Greenwood and Earnshaw 2012). There are approximately 300 known stable isotopes and more than 1200 radioactive isotopes (Hoefs 1997). However, ecologists have only identified four main elements [carbon, nitrogen, hydrogen and sulphur] that are used in stable isotope analysis (SIA) for ecological research (Jardine et al. 2003; West et al. 2006). The ratios of stable isotopes of carbon, nitrogen, hydrogen and sulphur differ among various substances for instance among animal tissues. These differences allow for dietary assumption to be made, because of the predictability of isotopic relationships between consumers and their food (Jardine et al. 2003; Iitembu 2014). Specifically,

stable carbon and nitrogen isotopes are increasingly used in marine ecosystems, for ecological and environmental studies. The SIA method is known to provide temporally-integrated measures of trophic relationships among species and can detect trophic interactions not observed through stomach content analyses (Herman et al. 2005; Iitembu 2014). The SIA is based on the understanding that there is an isotopic enrichment that occurs at a predictable enrichment factor per trophic level (Minagawa and Wada 1984; Peterson and Fry 1987). For nitrogen, the heavier (δ^{15}N) isotope is retained at a higher rate than the lighter (δ^{14}C) form, with each trophic level accounting for an approximate enrichment of 3.4 ‰ relative to it is diet (Minagawa and Wada 1984; Post 2002). While for δ^{13}C the trophic fractionation is much less predictable, with mean values reported as 0.8 ‰ (Van der Zanden and Rasmussen 2001) to 0.4 ‰ (SD = 1.3; Post 2002) per trophic level from aquatic systems.

Stable isotope analysis yields a longer-term view of feeding relationships by accounting for all sources of energy assimilated during a feeding season (Peterson and Fry 1987). Differences in isotopic composition among organs could also reflect the phenomenon of isotopic routing, which means that dietary nutrient components are allocated differentially to specific tissues and tissue components. Consequently, a tissue often reflects the isotopic composition of the nutrient component of the diet from which it was synthesized, and not the isotopic composition of the whole diet (Gannes et al. 1997). Muscle tissue is preferred for stable isotopes measurement, since it presents the advantage of showing a lower variability in isotopic composition compared to other body parts (Pinnegar and Polunin 1999). Moreover, the use of muscle tissues, whose dependence on oxidative metabolism is limited relatively to

other body parts (e.g. heart, brain, viscera or the hepatobiliary system), allows to reduce any potential effect of rotenone on fish isotopic signatures (Gingerich 1986).

Lately, it has been argued that location on bionomic axes may be quantified using stable isotopic ratios (Bolnick et al. 2003; Bearhop et al. 2004) and have been formalized in the concept of the "isotopic niche" (Newsome et al. 2007). Stable isotope ratios can be used in this respect, since the values measured in consumer tissues are tightly linked to those in their diet. Isotopic data are routinely presented as bi-plots, where the isotopic values of animal tissues may be represented in d-space (Newsome et al. 2007), and this basically delineates an animal's isotopic niche. The isotopic niche is closely related to the trophic niche, and it is therefore used as proxy of the trophic niche. Stable isotope ratios in an organism's tissues drawn from all trophic pathways end up in that individual and may also be used as one means to represent the trophic niche of that organism (Layman et al. 2007). The trophic niche represents the sum of all the trophic interactions that connect it to other species in an ecosystem (Leibold 1995). The trophic niche occupied by an organism can be defined through the food it consumes (Mohanraj and Prabhu 2012). However, the trophic niche of a given organisms may or may not overlap depending on the species' carbon and nitrogen values. Feeding habits are believed to be the largest driving force in niche differentiation (Wang et al. 2012); hence an understanding of species-specific habitat utilization and inter-specific trophic relationships are fundamental to making appropriate conservation and management decisions. Stable isotope analysis of consumer tissues is a proxy for measuring trophic niches in a multidimensional niche space (Newsome et al. 2007) and has been successfully used to identify patterns of intra and interspecific niche partitioning in a variety of systems

(Codron et al. 2015; Fernandez et al. 2011). This study only used two elements [carbon, nitrogen] in stable isotope analysis (SIA).

2.5.2.1 Carbon isotopes (δ^{13}C)

Naturally occurring stable carbon isotopes are both good indicators of the habitat source of carbon and good tracers of food web interactions in marine environments (Fry and Sherr 1984; Pond et al. 1997). In general, the stable carbon isotopic composition of the whole body of an animal is enriched in δ^{13}C relative to its diet by about 0 to 1 ‰ (DeNiro and Epstein 1978). Large differences in δ^{13}C occur from different sources of carbon fixation at the level of primary production (Fry 2006). Ratios of carbon isotopes (δ^{13}C) vary substantially among primary producers with different photosynthetic pathways (e.g. C3 vs. C4 plants), which however change minimally with trophic transfers. Therefore, δ^{13}C can be used to determine ultimate sources of dietary carbon (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002b; Søreide et al. 2006). Furthermore, in aquatic systems there exist differences in δ^{13}C between inshore (more enriched in δ^{13}C) and offshore waters (Miller et al. 2008), as well as with depth (Bosley et al. 2004). Carbon isotopes are necessary in studies of migratory organisms; as differences in isotopic ratios can be used to estimate food ingestion from the different regions that a migratory organism covers (Fry and Sherr 1984; Schell et al. 1989). Apart from that, metabolic fractionation of δ^{13}C signatures within organic tissues of consumers averages 1 ‰ − 1.5 ‰ for marine invertebrates (DeNiro and Epstein 1978; Peterson and Fry 1987; France and Peters 1997). Tissues of consumers are enriched by 1 ‰ per trophic level as one moves further along the food web (Vander Zanden et al. 1998; Post 2002a). Stable carbon isotopes of δ^{13}C are for tracing origins, and sources of primary production

(Schukat et al. 2013), as well as energy flow in aquatic systems and identifying animal movement patterns; since they are known to fractionate little between energy transfers (Peterson and Fry 1987; Carrasco et al. 2012). Moreover, $\delta^{13}C$ do not only act as a strong indicator of an animal's habitat but have been used as main elements in studies that estimate animal's foraging regions (Rubenstein and Hobson 2004). $\delta^{13}C$ can serve as an important environmental indicator of change (Dawson and Siegwolf 2007). It should however be noted that, carbon isotope ratios can be altered by changes in lipids, irrespective of the carbon source (McConnaughey and McRoy 1979).

2.5.2.2 Nitrogen isotopes ($\delta^{15}N$)

The $\delta^{15}N$ values of an animal's tissue are determined by the stable nitrogen isotope ratios of its diet (Schoeninger 1985). The use of stable nitrogen isotopes provides further details of food web structure and the interactions of animals at various trophic levels (Perry et al. 1999). The heavier $\delta^{15}N$ isotope is retained at a higher rate, with each trophic level accounting for an approximate enrichment of +3.4 ‰ relative to its diet (Minagawa and Wada 1984; Post 2002a). The $\delta^{15}N$ exhibits stepwise enrichment with trophic transfers and this allows it to be an effective measure of relative trophic position of an organism (Vanderklift and Ponsard 2003; Layman et al. 2007). Navarro et al. (2011) documented that $\delta^{15}N$ values have been widely used to calculate the trophic level and temporal changes in values ($\delta^{15}N$). $\delta^{15}N$ have been used as indicators of the responses of biological communities to environmental changes (Greenstreet and Rogers 2006). Moreover, $\delta^{15}N$ are frequently used to examine dietary shifts and trophic relationships in food webs (Hussey et al. 2011; Post 2002a). Natural ecosystems and most laboratory experiments have exhibited a

positive correlation between the δ^{15}N and animal position in the food chain (Tiunov 2007). δ^{15}N values are therefore useful as indicators of time-integrated measure of feeding positions of animals (Cabana and Rasmussen 1996; Vander Zanden et al. 1997).

CHAPTER 3

3. Materials and Methods

3.1 Field sampling

The study focused on the population of *M. capensis* and *T. capensis* from the Northern Benguela Ecosystem. Samples covered a wide range of individual fish in terms of sampling sites, and life history stages (length and sex). This study collected quantitative data. Samples were collected during the monkfish (*Lophius vomerinus*) biomass surveys that took place on-board R.V Mirabilis (11th – 27th November 2017. The survey is undertaken mainly to estimate the biomass and size composition of the monkfish stock, following the predetermined stations off the Namibian coast) (**Fig. 3**). Sampling was done using an *Albatross* monkfish bottom trawl rigged with tickler chains along the footrope and the sweep lines consisted of 20 m bridals and 25 m long sweeps (head length 50.3 m, footrope 63.9 m, and the vertical net opening 4.5 – 4.7 m), with depth of sampling tows of between 90 and 600 m at a speed of about three knots. This survey covered a total of 94 stations, covering the bottom depth between 100 to 800 m. The distance between 17°15'S and 30 °S off the coast was divided into 40 equal intervals, while the east-west direction was divided in 19 NM intervals. The survey area was defined by a polygon of the assumed distribution of monkfish, which was then sub-divided into smaller cells. Trawling time averaged 30 minutes at all stations. The survey design followed the optimized geo-statistical stratified random design described in Schneider and Johnsen (2000).
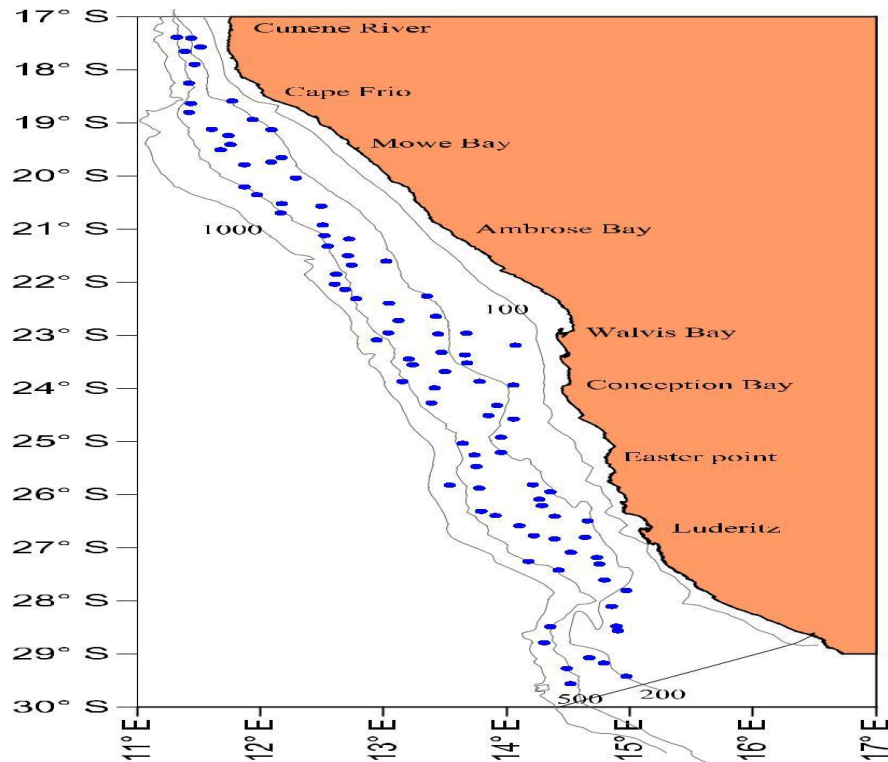
Figure 3: Station layout of the entire region covered during the 2017 monkfish biomass survey (with 200, 500 and 1000 m depth contour lines).

Merluccius capensis and *T. capensis* were collected at 13 stations (the only stations in which the two species were present) from Conception Bay (24 °S) to the Kunene River (17 °S) (**Fig.4**). The exact amount of fish collected at a particular station depended on the total amount of fish for these species in the catch. At all sampling stations the entire catch was dropped on deck. *Merluccius capensis* and *T. capensis* individual fish were collected in equal numbers at stations where they were both present together. The samples were brought to the wet laboratory. Information recorded include: species name, total length and sex. A large portion of muscle of about 0.5 kg, was also cut from the dorsal region of fish and placed in ziploc bags labelled by a fish number (one portion per bag). Stomachs were collected from each fish and stored in different bags and labelled accordingly. All collected samples were

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frozen at -20 °C on the vessel until the end of the survey. Samples were transported to Sam Nujoma Campus (UNAM), Henties Bay for laboratory analyses.
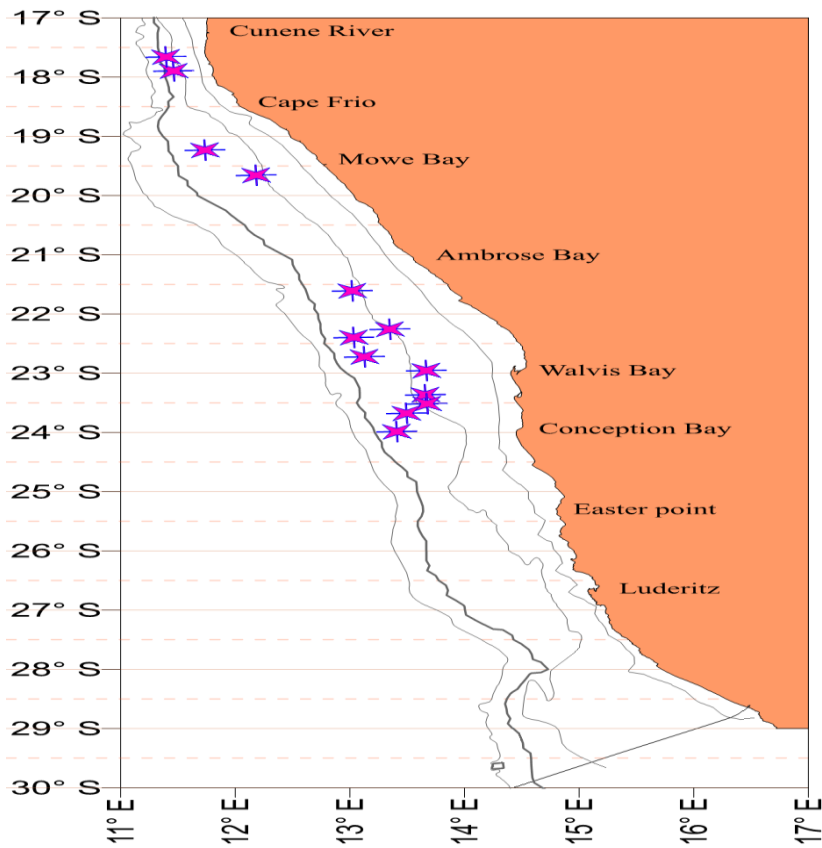
Figure 4: Geographical positions where samples were collected during the monkfish biomass survey. Depth contours represent 100, 200, 500 and 1000 isobaths.

3.2 Laboratory analyses

3.2.1 Stomach content analysis

A total sample of 404 stomachs, 202 for *M. capensis* and 202 for *T. capensis* were examined. The weight of thawed stomachs content was recorded. After weighing each stomach and dissection, their respective content was transferred to a petri dish, wrapped with a paper towel to remove water. Prey were identified to the lowest taxonomic level by visual inspection of stomach contents according to FAO species

identification guide for fishery purposes; field guide to the living marine resources of Namibia (Bianchi et al. 1999). Prey items were counted and weighed (to the nearest gram [g]). The number and weight of the prey were recorded. The contribution of each food item was determined using three parameters: percentage of frequency of occurrence (% F), percentage composition by number (% N) and weight (% W) of each prey (Hyslop 1980). An index of relative importance (IRI) (Hacunda 1981) was calculated by integrating the three parameters to eliminate any biases created once each method is analysed individually (Goldman and Sedberry 2010).

3.2.2 Stable isotopes analysis

A small section of white muscles was oven-dried for 48 hours at 60 °C (Iitembu et al. 2012). The dried muscles were grounded into powder using a mortar and pestle, and placed in small tin capsules of about 9 mm x 5 mm. Isotopic analyses were conducted at iThemba LABS, Johannesburg, South Africa, using a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer through a ConFloIV interface (equipment supplied by ThermoFisher, Bremen, Germany). The stable isotopic values were expressed in delta (δ) notation relative to a reference standard (Pee Dee Belemnite for δ^{13}C and air for δ^{15}N). The δ are defined as δX = {(Rsample ∕ Rstandard) - 1} *1000, where X δ^{13}C or δ^{15}N; R is the ratio of the heavy to light isotope for the sample (Rsample) and standard (Rstandard) in units of parts per thousand (per mille, ‰).Two replicates of known standards were run repeatedly every 24 samples in each sequence to correct stable isotopes values, these being Merck Gel and Urea (IVA Analyse Technik e.K., Meerbusch, Germany).Sample analytical precision was < 0.17 ‰ for both δ^{13}C and δ^{15}N respectively. All samples were not lipid extracted, as it can cause fractionation in

δ^{15}N (Sweeting et al. 2006; Post et al. 2007). However, the δ^{13}C values were mathematically normalised for variations in lipid to correct the values. All C: N values greater than 3.5 (the minimum limit for lipid extraction or correction stipulated in Post et al. (2007) were mathematically corrected for variations in lipid using the normalization equation below from Post et al. (2007): *δ^{13}Cnormalized =* *δ^{13}Cuntreated – 3.32 + 0.99 × C: N;* where δ^{13}C untreated is the δ^{13}C of non-lipid extracted tissue, *C: N* is the mass ratio of carbon and nitrogen.

3.3 Data analysis

3.3.1 Stomach content analysis (Diet calculation)

The contribution of each food item was determined using the following three parameters and index.

Percentage composition by number represents the proportion of the number of a particular prey item expressed as a percentage of the total number of all prey items in the whole stomach contents (Rosecchi et al. 1988). Percentage composition by number was calculated using the formula:

$$\% \ N = \frac{100n_i}{\Sigma n_i},$$

Where n_i is the number of prey item and Σn_i is the total number of all prey items

Percentage composition by weight is the proportion of the biomass of a particular prey item to the total weight expressed as a percentage of all stomach contents (Rosecchi et al. 1988). Percentage composition by weight calculated using the formula:

$$\% \ W = \frac{100W_i}{\Sigma W_i},$$

Where W_i is the weight of prey item and ΣW_i is the total weight of all prey items

Frequency of occurrence calculated using the formula:

$$\% \ F = \frac{100ni}{n},$$

where Fi is frequency of occurrence of the i food item (prey item) in the sample; ni is the number of stomachs in which the prey item is found and n is the total number of stomachs with food in the sample (Hynes 1950; Hyslop 1980; Bowen 1986).

The Index of Relative Importance (IRI) was calculated using the formula:

$$\mathbf{IRI} = \left((\% \ \mathbf{N} + \% \ \mathbf{W}) \times \% \ \mathbf{F}\right),$$

where % $\mathbf{N}$ is percentage composition by number, % $\mathbf{W}$ is percentage composition by weight of each prey and % $\mathbf{F}$ is frequency of prey occurrence (Pinkas et al. 1971; Cortés 1997). The percent IRI was calculated using the formula:

$$\% \ \mathbf{IRI_i} = \frac{IRIi}{\Sigma \ IRIi} \times 100,$$

where $\mathbf{i}$ represents prey species (Cortes 1997).

An index of relative importance (IRI) (Hacunda 1981) was calculated to determine the most important food item and to integrate the three parameters to eliminate any biases created once each method is analysed individually (Goldman and Sedberry 2010). Diets were analysed for ontogenetic differences by categorised fish length into 10 cm – length classes following (Assorov and Kalinina 1979; Roel and Macpherson 1988; Pillar and Wilkinson 1995; Mahe et al. 2007). Diets were also analysed by geographical area for spatial variation; were grouped into two latitude

classes: the northern part (17°00 – 20°59) and the central part (21°00 – 25°00) of the Namibian ocean.

3.3.2 Stable isotopes analysis

The stable isotopes measurements were tested for normality using Kolmogorov Smirnov test. A linear regression (dependent variable: $\delta^{13}C$ or $\delta^{15}N$; independent variable: total length) was performed to investigate the relationships; between size and isotopic measurement ($\delta^{13}C$ and $\delta^{15}N$) of *M. capensis* and *T. capensis.* The data were not normally distributed, as data did not meet the assumptions of normal distributions; therefore, Mann Whitney U Test (non-parametric statistical tests) was used to assess if there is a significant difference in the stable isotope ($\delta^{13}C$ and $\delta^{15}N$) of *M. capensis* and *T. capensis*. The isotope-based metrics calculated included $\delta^{15}N$ range, indicating trophic diversity; $\delta^{13}C$ range representing the niche diversification at the base of a food web, total area (TA) of the convex hull standard ellipse areas and the standard ellipse area, corrected for small sample sizes ($SEA_{C)}$. The differences in between species were estimated via Bayesian interference (SEA_B) (Jackson et al. 2011). Total area of convex hull (TA) and standard ellipse area (SEA_C) were used to determine if there are differences in the trophic niches of the two-species (Jackson et al. 2011). All the statistical analyses were done in R [R Core Team (2018], SPSS and Graph Pad.

4. Results

4.1 Diet compositions of *M. capensis*

A total of 202 stomachs of *M. capensis* were collected and only 56 (27.72 %) were not empty. The total length (TL) of samples ranged from 21 cm to 68 cm. The compositions consisted of 13 different species, with krill being the dominant prey (66.29 % IRI) and white mussels as the least consumed prey (0.05 % IRI) by weight percentages (**Fig.5**). Diet compositions changed with increasing TL, where krill was the utmost important observed prey in ≤ 30 cm (74.23 % IRI) and 31 − 40 cm (82.92 % IRI) length classes. Cape horse mackerel was the most encountered at 41 − 50 cm length class (47.54 % IRI), while, jacopever dominated the ≥ 51 cm length class (64.05 % IRI) (**Table 1**). In terms of latitude, krill was the most important prey item of this species at all latitude classes. (**Table 2**).

66.29% Krill (*Euphausia hanseni*)
16.44% Cape horse mackerel (*Trachurus capensis*)
13.12% Jacopever (*Helicolenus dactylopterus*)
1.33% Shallow water Cape hake (*Merluccius capensis*)
0.82% Goby (*Sufflogobius bibarbatus*)
0.75% Prawns (*Parapenaeus longirostris*)
0.32% Shortnose greeneye (*Chlorophthalmus agassizi*)
0.26% Deep water Cape hake (*Merluccius paradoxus*)
0.24% Squat lobster (*Galathea squamifera*)
0.16% Cephalopods (Class)
0.14% Grenadier (*Nezumia micronychodon*)
0.08% Anchovy (*Engraulis capensis*)
0.05% White mussels

Figure 5: Diet composition of *M. capensis* by index of relative importance (IRI) expressed as a percent of all the prey items consumed based on stomach content analysis.

Table 1: Frequency of occurrence (% F), diet compositions by number (% N), diet compositions by weight (% W) and index of relative importance (IRI) expressed as a percent of prey items found in stomachs of *M. capensis* by length classes.

Prey items	≤ 30 cm (n = 61)				31 – 40 cm (n = 66)				41 – 50 cm (n = 49)				≥ 51 cm (n = 26)			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Krill (*Euphausia hanseni*)	52.94	62.96	16.43	74.23	50.0	81.71	4.06	82.92	19.05	79.67	3.06	39.59	17.65	9.52	0.14	2.65
Prawns (*Parapenaeus longirostris*)	0.00	0.00	0.00	0.00	12.50	3.66	2.36	1.46	9.52	3.25	1.67	1.18	5.88	4.76	0.23	0.46
Grenadier(*Nezumia micronychodon*)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.88	9.52	7.32	1.54
Cape horse mackerel (*Trachurus capensis*)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.57	8.94	57.30	47.54	29.41	23.81	44.64	31.30
Jacopever (*Helicolenus dactylopterus*)	5.88	1.85	2.66	0.47	4.17	1.22	1.18	0.19	14.29	3.25	12.99	5.83	41.18	52.38	47.66	64.05
Goby (*Sufflogobius bibarbatus*)	23.53	11.11	31.40	17.67	8.33	3.66	2.36	0.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Shortnose greeneye(*Chlorophthalmus agassizi*)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.52	1.63	12.33	3.34	0.00	0.00	0.00	0.00
Squat lobster (*Galathea squamifera*)	0.00	0.00	0.00	0.00	4.17	1.22	1.18	0.19	9.52	1.63	3.66	1.26	0.00	0.00	0.00	0.00

Cephalopods (Class)	5.88	20.37	45.89	6.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Deep water cape hake (*Merluccius paradoxus*)	0.00	0.00	0.00	0.00	4.17	1.22	11.43	1.02	4.76	0.81	4.83	0.67	0.00	0.00	0.00	0.00
Shallow water cape hake (*Merluccius capensis*)	0.00	0.00	0.00	0.00	8.33	3.66	76.07	12.84	4.76	0.81	4.16	0.59	0.00	0.00	0.00	0.00
Anchovy (*Engraulis capensis)*	5.88	1.85	1.69	13.47	4.17	2.44	0.79	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
White mussel	5.88	1.85	1.93	0.39	4.17	1.22	0.55	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total		100.00	100.00	100.00		100.00	100.00	100.00		100.00	100.00	100.00		100.00	100.00	100.00

Table 2: Percentages of frequency of occurrence (% F), diet compositions by number (% N), diet compositions by weight (% W) and index of relative importance (IRI) of prey items found in the stomachs of *M. capensis* by latitude classes (°S).

Prey items	17° 00 – 20°59				21°00 – 25°00			
	% F	% N	% W	% IRI	% F	% N	% W	% IRI
Anchovy *(Engraulis capensis)*	2.00	1.11	0.15	0.07	3.45	1.00	0.17	0.07
Krill (*Euphausia hanseni*)	22.00	65.00	1.60	41.64	58.62	84.00	3.69	89.07
White mussel	0.00	0.00	0.00	0.00	6.90	2.00	0.54	0.30
Cephalopods (class)	2.00	6.11	1.41	0.43	0.00	0.00	0.00	0.00
Shortnose greeneye *(Chlorophthalmus agassizi)*	4.00	1.11	5.50	0.76	0.00	0.00	0.00	0.00
Goby *(Sufflogobius bibarbatus)*	12.00	5.00	1.41	2.22	0.00	0.00	0.00	0.00
Deep water cape hake (*Merluccius paradoxus*)	2.00	0.55	2.15	0.16	3.45	1.00	7.09	0.48
Shallow water cape hake (*Merluccius capensis*)	2.00	0.55	5.72	0.36	6.90	3.00	34.47	4.48

Jacopever *(Helicolenus dactylopterus)*	18.00	7.78	32.82	21.08	10.34	3.00	12.25	2.73
Cape horse mackerel (*Trachurus capensis)*	20.00	8.33	46.64	31.72	3.45	1.00	24.44	1.52
Common Atlantic Grenadier (*Nezumia micronychodon*)	0.00	0.00	0.00	0.00	3.45	2.00	15.40	1.04
Prawns (*Parapenaeus longirostris*)	10.00	2.78	0.74	1.02	3.45	1.96	17.11	0.30
Squat lobster (*Galathea squamifera*)	6.00	1.67	1.86	0.54	0.00	0.00	0.00	0.00
Total		100.00	100.00	100.00		100.00	100.00	100.00

4.2 Diet compositions of *T. capensis*

A total of 202 stomachs for *T. capensis* were collected and only 74 (36.63 %) were not empty. The individual fish TL ranged from 19 cm to 40 cm. The diet consisted of three different species, with krill being the major prey (99.96 % IRI) and anchovy being the least prey (0.01 % IRI) (**Fig.6**). In terms of length classes, the diet composition changed with increasing TL; where krill was the most frequently observed prey (99.90 % IRI; 100 % IRI) at both ≤ 30 cm and ≥ 31 cm (**Table 3**). In terms of latitude, krill was the dominant prey item of this species at all latitude classes (**Table 4**).

■ 99.96% Krill *(Euphausia hanseni)*
■ 0.03% Amphipods (order)
■ 0.01% Anchovy *(Engraulis capensis)*
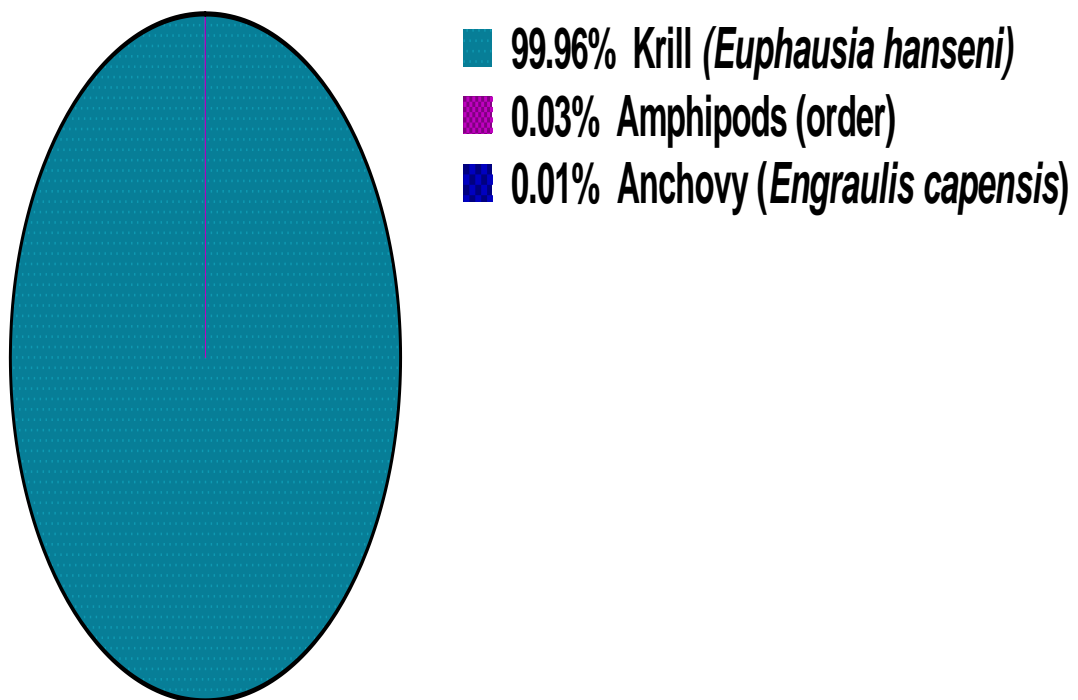
Figure 6: Diet composition of *T. capensis* by index of relative importance (IRI) expressed as a percent of all the prey items consumed based on stomach content analysis.

Table 3: Frequency of occurrence (% F), diet compositions by number (% N), diet compositions by weight (% W) and index of relative importance (IRI) expressed as a percent of prey items found in the stomachs of *T. capensis* by length classes.

	≤ 30 (N = 160)				≥ 31 (N = 42)			
Prey items	% F	% N	% W	% IRI	% F	% N	% W	% IRI
Krill (*Euphausia hanseni*)	94.55	94.41	97.19	99.90	100.00	100.00	100.00	100.00
Amphipods (order)	1.82	5.37	1.96	0.07	0.00	0.00	0.00	0.00
Anchovy *(Engraulis capensis)*	3.64	0.22	1.05	0.03	0.00	0.00	0.00	0.00
Total		100.00	100.00	100.00		100.00	100.00	100.00

Table 4: Percentages of frequency of occurrence (% F), diet compositions by number (% N), diet compositions by weight (% W) and index of relative importance (% IRI) of prey items found in stomachs of *T. capensis* by latitude classes (17 °S – 25 °S).

Prey items	17°00 – 20°59				21°00 – 25°00			
	% F	% N	% W	% IRI	% F	% N	% W	% IRI
Krill (*Euphausia hanseni*)	96.55	99.87	99.56	99.93	95.74	79.50	90.77	99.37
Amphipods (order)	0.00	0.00	0.00	0.00	3.45	20.50	9.23	0.63
Anchovy *(Engraulis capensis)*	4.26	0.13	0.44	0.07	0.00	0.00	0.00	0.00
Total		100.00	100.00	100.00		100.00	100.00	100.00

4.3 Isotopic characteristics

A total of 404 samples that comprised of *M. capensis* (n = 202) and *T. capensis* (n = 202) were analyzed for the stable isotope ratios (δ^{15}N and δ^{13}C). *Trachurus capensis* TL ranged from 19 cm to 40 cm, while *M. capensis* TL ranged from 20 cm to 68 cm. The δ^{15}N values for *M. capensis* had the highest mean δ^{15}N value (11.17 ‰) that ranged from 9.31 ‰ to 13.34 ‰, while that of *T. capensis* ranged 8.75 ‰ to 13.07 ‰. The δ^{13}C values for *M. capensis* ranged from -17.26 ‰ to -14.24 ‰, while that of *T. capensis* ranged from -17.28 to -14.64 ‰. *Merluccius capensis* had a higher (most negative) average δ^{13}C value (-16.10 ‰) than *T. capensis* (-17.10 ‰). The mean mass ratio of carbon-to-nitrogen (C: N) for *T. capensis* ranged from 3.9 to 7.31, while that of *M. capensis* ranged from 3.84 − 7.31. *Trachurus capensis* (4.73) had higher mean C: N ratio; that was higher than *M. capensis* (3.97). There was a significant difference between the δ^{13}C of *M. capensis* and *T. capensis* (Mann Whitney (U) = 13864.00, N = 404, P = 0.000). There was also significant difference observed between the (δ^{15}N) of *M. capensis* and *T. capensis* (Mann Whitney (U) = 15103.00, N = 404, P = 0.000).

In terms of the relationship between the isotopic values and TL, *M. capensis* showed a stronger significant positive relationship between size and δ^{13}C (P = 0.000, R^2 = 0.38) compared to *T. capensis* (P = 0.000, R^2 = 0.02). The length of intersection in terms of δ^{13}C between the two species was between 32 cm and 40 cm (**Fig.7**). There was a slightly significant negative relationship, (P = 0.000, R^2 = 0.01) between δ^{15}N values and TL of *M. capensis*, while for *T. capensis* it was a weak significant positive relationship (P = 0.000, R^2 = 0.08). The length of intersection for δ^{15}N values of the two species was 35 cm (**Fig.8**).
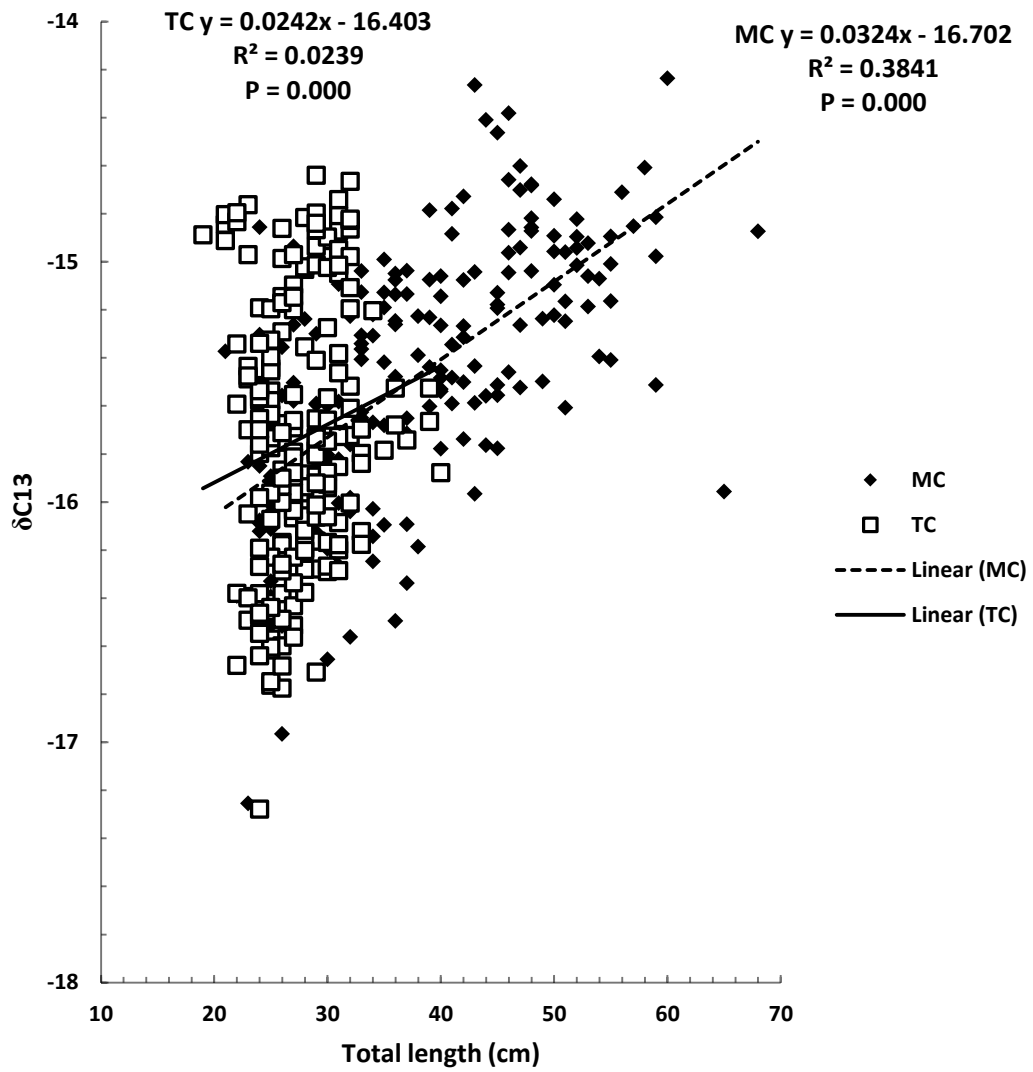
Figure 7: The relationship between $\delta^{13}C$ and total length (cm) of *M. capensis* (MC) and *T. capensis* (TC).
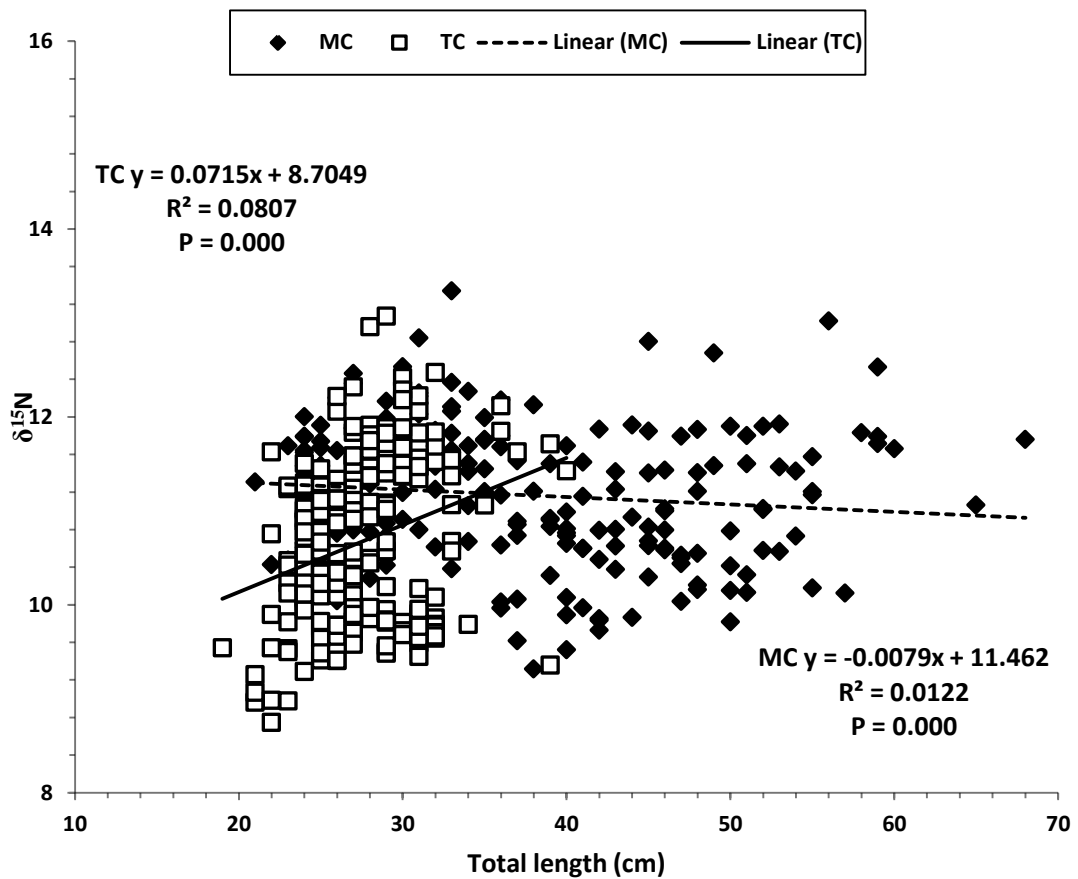
Figure 8*: The relationship between $\delta^{15}N$ and total length (cm) of M. capensis (MC) and *T. capensis* (TC).

4.4 Trophic niche of *M. capensis* and *T. capensis*

A substantial overlap in the isotopic niches of the two species was observed, with *M. capensis* having a wider niche than *T. capensis* (**Fig.9**). The range of $\delta^{13}C$ and $\delta^{15}N$ for *T. capensis* was higher than for *M. capensis* (**Table 5**). *Merluccius capensis* had a larger TA of 7.76 than for *T. capensis*, but the two species had the same SEA$_C$ of 1.24 (**Table 5**). There was no significant difference in terms of SEA$_C$ size of the two species. (**Fig. 10**).
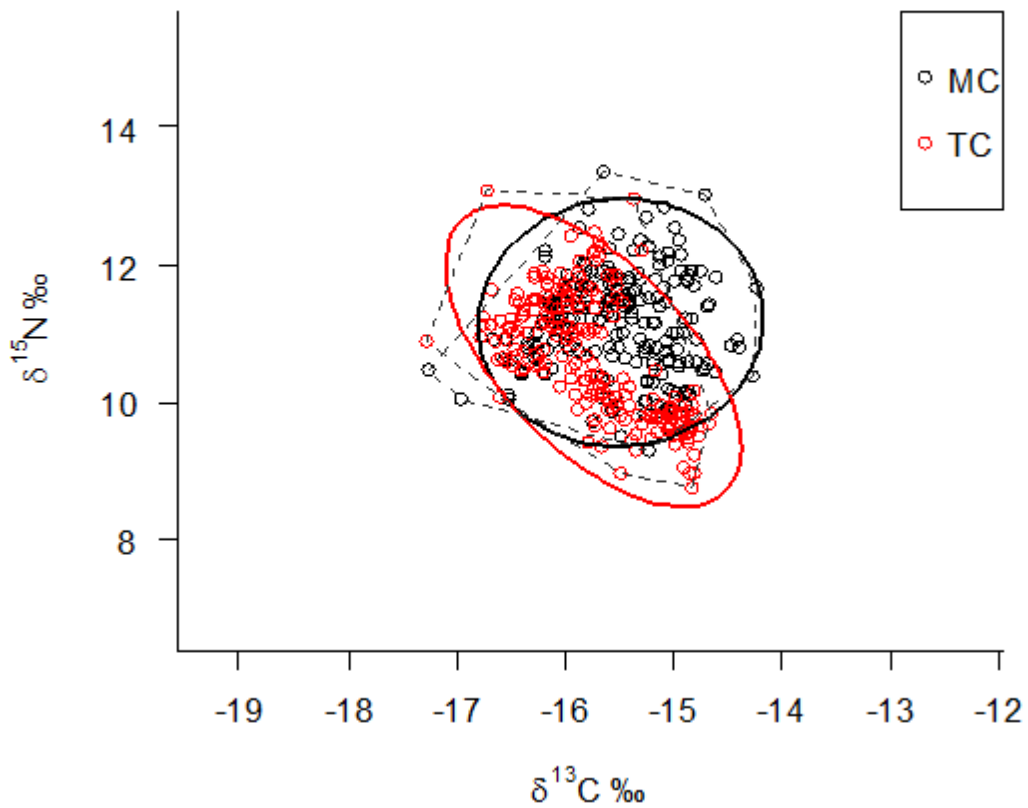
Figure 9: The isotopic niches comparisons of *M. capensis* (MC) and *T. capensis* (TC) as depicted by convex hull (polygons) and SEA$_C$ (ellipses).

Table 5: The carbon – 13 range (δ^{13}CR), nitrogen – 15 range (δ^{15}NR), total area of the convex hull (TA) and standard ellipse area (SEA$_C$) of *M. capensis* and *T. capensis*.

Species	δ^{13}CR	δ^{15}NR	TA	SEA$_C$
Merluccius capensis	-3.00	4.03	7.76	1.24
Trachurus capensis	-2.63	4.33	7.27	1.24
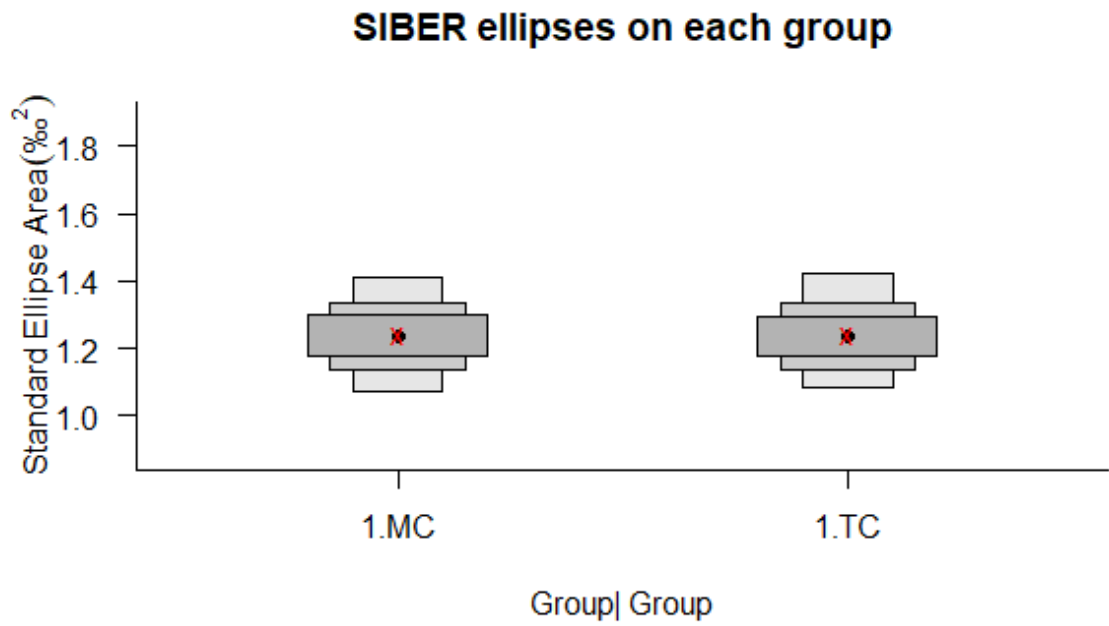
Figure 10: Bayesian estimate of the standard ellipse area (boxplots) and its area SEA$_C$ of *M. capensis* (MC) and *T. capensis* (TC). Dark, median and light grey boxes are respectively the 50 %, 75 % and 95 % credibility intervals of the probability of density function distributions of the model solutions; black dots are the modes of these distributions and red crosses represent the standard ellipse areas computed using a frequents algorithm adapted for small sample sizes (SEA$_C$).

CHAPTER 5

5. Discussion

5.1 General discussion

This study aimed at investigating the trophic relationships of *M. capensis* and *T. capensis* off Namibia, using stomach content and stable isotope analyses. The stomach content analysis showed higher species richness of prey in *M. capensis* than in *T. capensis*. *Merluccius capensis* and *T. capensis* diets were dominated by euphausiids (krill). The diet compositions of the *M. capensis* changed with both length and latitude, an indication of the influence of prey availability (Pillar and Wilkinson 1995). However, the diet of *T. capensis* remained the same with both length and latitude. *Merluccius capensis* had higher mean $\delta^{15}N$ value (11.17 ‰) than *T. capensis* (10.67 ‰), an indication that it fed at relatively higher trophic positions. In terms of $\delta^{13}C$ values *M. capensis* had higher average $\delta^{13}C$ values (-16.10 ‰) than *T. capensis* (-17.10‰), an indication of benthic vs pelagic sources in their respective diets. Significant differences in food sources ($\delta^{13}C$) and feeding positions ($\delta^{15}N$) of both species were also observed. A significant positive relationship was observed between stable isotope measurement [‰] ($\delta^{13}C$) and size (total length (cm)) in both speciesand $\delta^{15}N$, and size for *T. capensis*, but for *M. capensis* was slightly negative; indicating the influence of growth on their feeding strategies. Although, *T. capensis* had a wider trophic niche than for *M. capensis*, there was substantial overlap in their niches. Overall these results indicate that the two species have multiple trophic interactions as *M. capensis* may be dependent on *T. capensis* as one of the second dominant prey, while the two species are possibly competing for smaller prey like krill and anchovy.

5.2 Diet compositions of *M. capensis*

The diet composition of *M. capensis* was different from that of *T. capensis* as most of the important prey consumed by *M. capensis* were bony fishes. The increased prey species richness observed in the diet composition of *M. capensis* could be because it is an opportunistic feeder. In addition, *M. capensis* has a broad feeding range from 100 to 450 m depth. *Merluccius capensis* has been observed as changing its preferred prey type in relation to their local availability and abundance (Pillar and Wilkinson 1995). In this study, krill was observed as a dominant prey (66.29 % IRI) and *T. capensis* was observed as a be a second dominant prey (16.44 % IRI), an indication of the importance of those prey items to the diet of *M. capensis*. This is study agrees with the findings of Punt et al. (1992), Payne et al. (1987) and Roel and Macpherson (1988) found that the hakes feed predominantly on crustaceans (euphausiids [krill]). Worldwide, krill is one of the species that occur in high abundances (Huenerlage and Buchholz 2013), which can be the elucidation of *M. capensis* diet dominance observed in this study. *Merluccius capensis* and *T. capensis* have overlapping depth distributions and the opportunistic nature of *M. capensis* feeding might have contributed to this observation. Additionally, because the stomach contents were only collected at stations where both *M. capensis* and *T. capensis* were present, the availability and abundance of *T. capensis* at these stations might have led to them becoming the second dominant prey. However, Assorov and Kalinina (1979) documented that *M. capensis* fed mainly on the young of their own species and on gobies, which was not observed in this study. Other main *M. capensis* prey observed in this study included Jacopever, shallow water Cape hake, Goby, Shortnose greeneye, deep water Cape hake which corresponds to the findings of Kainge et al.

(2017). White mussels observed in diet of *M. capensis* in this study, was not observed by any of the previous studies (Roel and Macpherson 1988; Pillar and Wilkinson 1995; Mahe et al. 2007; Kainge et al. 2017). The presence of white mussel in the diet of *M. capensis* can be an indication of the opportunistic feeding nature of *M. capensis*, but it can also be that it was consumed by its prey, as shell are normally not fully broken down by the digestion process.

Diet compositions for *M. capensis* changed with TL, an indication of ontogenic trophic shift of this species which was reported in other studies (e.g. Assorov and Kalinina 1979; Roel and Macpherson 1988; Pillar and Wilkinson 1995; Mahe et al. 2007) and confirmed by stable isotopes results (Iitembu et.al 2012). Euphausiids (krill) was found to be one of the crustacean constituents of *M. capensis* especially at small length (20 − 40 cm). Two fish species particularly well represented in *M. capensis* diet were *T. capensis* dominant prey for 41 − 50 cm, and Jacopever for ≥ 51 cm. The above confirm the findings of Roel and Macpherson (1988), who observed that the importance of euphausiids as food diminishes with size of the predator, while the importance of fish in the diet increases with hake size. Similarly, Pillar and Wilkinson (1995) observed ontogenic trophic shift in the diet of this species from larvae to adult, as their preferences switch from smaller copepods to larger prey items such as euphausiids, mesopelagic and pelagic fish (mainly anchovy in the diet of smaller (< 30 cm) and when adult, to demersal fish (mostly other hake). Cannibalism (is the act of one individual of a species consuming an individual of the same species) was also observed in the present study but to lesser extent compared to Punt et al. (1992); Macpherson and Gordoa (1994) and Kainge et al. (2017) findings, where *M. capensis* was feeding on the young *M. capensis*. Suggesting that *M. capensis* tend to prefer the young one of their own. The low abundance of juveniles

(fish that are not matured > 23 cm) and the overlap between distribution patterns of juveniles and adult hake fish seemed to be the influenced of hake cannibalism (Burmeister 2001; Mahe et al. 2007; Kainge et al. 2015). The minor differences in the observations from different diet studies can be related to fluctuations in the prey populations over time (Mehl 1986) or local availability and abundance of these prey as per its distribution range. Mahe et al. (2007) carried out research on ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and in the Celtic Sea, they observed that small hake fed almost entirely on crustaceans (mainly euphausiids), with a significant shift towards a fully piscivorous diet in hake >23 cm. Results from Assorov and Kalinina (1979) support Mahe et al. (2007) findings, as they observed that from the 20 – 29 cm length class and $\geq$ 70 cm, fish of the family Myctophidae and hake were the most abundant in the hake diet; but the proportion of myctophids decreased with hake length while that of hake increased. Myctophids were also observed as prey of *M. capensis* in this study. In general, ontogenic shift in *M. capensis* could be related to ontogenetic development particularly in an increase in mouth size and mobility as they influence shifts in diet (Mahe et al. 2007) and possibly preference for fish that have higher energy content than crustaceans (common in non-specialist fish) (Juanes et al. 2002). The relative importance of each prey item can also vary both geographically and seasonally according to the availability of the prey as per its distributional range (Roel and Macpherson 1988).

In terms of latitude, krill was the dominant prey item encountered by *M. capensis* at all latitude classes, which is an indication of the importance of this species to *M. capensis* diet. Globally, krill is one of the species that occur in high abundances (Huenerlage and Buchholz 2013), which can be the explanation of *M. capensis* diet

dominance observed in this study. There was also a difference in species richness of the prey with latitudes, with high species richness observed at 17 – 21 °S than 21 – 25 °S latitude classes. The higher species richness of prey at lower latitude (17 – 21 °S) can be related to a general pattern of species richness that increases with decreasing latitude (Kaufman 1995). The overall pattern for species richness tends to increase from polar to tropical regions (Willig et al. 2003; Hillebrand 2004), irrespective of the taxonomic affiliation of organisms (e.g. mammals, fishes, insects, and plants) or geographic site in which they occur (e.g. Africa, South America, and the Atlantic Ocean) (Willig et al. 2003).

5.3 Diet compositions of *T. capensis*

The diet of *T. capensis* consisted of three different species, with krill observed as the major prey (99.96 % IRI) and anchovy the least prey (0.01 % IRI). This again could be linked to global distribution and high abundance of krill species (Huenerlage and Buchholz 2013). *Euphausia hanseni* is one of the most abundant krill species of the NBC (Olivar and Barange, 1990; Barange and Stuart, 1991; Barange et al. 1991; Pillar et al. 1992). Krill is also known to exhibit diel vertical migrations (Barange 1990; Barange and Stuart 1991; Barange and Pillar 1992), indicating that it can also be one of the species that influences the diel vertical movement observed in *T. capensis* (Pillar and Barange 1998; Bianchi et al. 1999). Konchina (1986) observed that the diet of horse mackerel included pteropods, crustaceans (copepods, euphausiids, hyperiids and decapodsa), with euphausiids (euphausia) and shrimps being the main food items. Correspondingly, Boyer and Hampton (2001) reported that 95 % of the diet of adult *T. capensis* fish comprised of euphausiid and shrimps. The above results indicate that krill is one of the key prey species of *T. capensis*.

In terms of length classes, the diet compositions for *T. capensis* remained the same with increasing size. This is consistent with the findings of Andronov (1983) agree with Konchina (1986), Cabral and Murta (2000), Santic et al. (2005), Bayhan and Sever (2009) and Smith et al. (2012). Cabral and Murta (2000) also found that horse mackerel of up to 20 cm length feed mainly on copepods (predominantly *Calanoides carinatus*), while larger fish measuring up to 40 cm length preferred euphausiids. Bayhan and Sever (2009) also observed the diets of Atlantic Horse Mackerel fish in 10.0 − 12.9 cm range were mostly copepods, 13.0 − 16.9 cm range were euphausiids and mysids, while fish larger than 16.9 cm were feeding on teleost larvae. Santic et al. (2005) observed that small fish < 28 cm TL were feeding on euphausiids, while fish > 30 cm TL on teleosts. The above is clear influence of fish growth, where small fish are mostly zooplanktophagous, while large specimens are mainly ichthyophagous (Cabral and Murta 2002; Jardas et al.2004). Konchina (1986) observed that 21 − 26 cm (2 years old) horse mackerel were mostly feeding on euphausiids and lanternfishes, this was linked to the fact that in the northern part of the area, horse mackerel fed on mesopelagic migratory animals while moving towards the surface at night. Smith et al. (2012) agree with Konchina (1986) findings, as they reported that this species feed predominantly on zooplankton up to two years of age where they consume it close to the sea surface. All in all, *T. capensis* is considered as a facultative fish feeder (is a fish that feeds mainly on one prey item, but eats other prey items as well) whose diet consists mainly of krill (Andronov 1983; Krzeptowski 1982).

In terms of latitudes, krill was the dominant prey item consumed; which shows the influence of its global distribution and its high abundance in the Northern Benguela Current (NBC) (Olivar and Barange 1990; Barange and Stuart 1991; Barange et al.

1991; Pillar et al. 1992). Anchovy observed to be the least important prey item of *T. capensis*, this is due to depletion of their stock in Namibian waters (Boyer and Hampton 2001; Ekau and Verheye 2005).

5.4 Species isotopic characteristics

Trachurus capensis had a lower average mean $\delta^{15}N$ value than *M. capensis*. The $\delta^{15}N$ values of organisms reflect the trophic level at which they are feeding (Peterson and Fry 1987; Fry 2006). Therefore, the above indicates that *M. capensis* species fed at a higher trophic level than *T. capensis*. These results are also supported by the stomach content results that showed the diet of *M. capensis* have more fish prey than *T. capensis*. Statistically significant differences were also found in terms of $\delta^{15}N$ values, which shows that these species they were not feeding at the same level. The isotope based trophic level (*M. capensis* 2.15 and *T. capensis* 2.52) was also observed to be different by Erasmus (2015), an indication that there were differences in their feeding patterns. The variations in nitrogen values between the species can also be attributed to various factors such as poor food quality and isotopic routing (Gannes et al. 1997; Peterson 1999). *Trachurus capensis* had a significant positive linear relationship between $\delta^{15}N$ and TL (cm), and for *M. capensis* was significant negative relationship, which is an indication of change in feeding habits with growth (Araújo et al. 2011). Generally, that indicated that *M. capensis* feed at lower trophic level as they grow while *T. capensis* feed at higher trophic level as they grow. Positive relationships between total length and trophic positions are common in several marine organisms (Deudero et al. 2004), and have been reported in hake (Iitembu et al. 2012), sharks (Estrada et al. 2006) and shrimps (Endjambi et al. 2015). Although, there was a significant difference in $\delta^{15}N$ values, the two species appear to feed at the

same trophic positions; at the length of < 34 cm and > 36 cm which was the length of $\delta^{15}N$ values intersection. This is an indication that young *M. capensis* interact more with older *T. capensis* as the age range of 34 − 36 cm *T. capensis* is 6 − 7 years (Kirchner et al. 2010), while *M. capensis* of the same length is about 1 − 2.5 years old (Wilhelm et al. 2017). At these length ranges, the two species' diets were dominated by krill, indicating the possibility of interspecific feeding competition between these species. The $\delta^{15}N$ range for *T. capensis* was wider than for *M. capensis*. This indicates that it fed on prey from various trophic levels or greater degree of trophic diversity. In addition, this can be explained by the differences between the trophic position of *T. capensis* prey; which is higher compared to *M. capensis* prey, although *M. capensis* prey are from a relatively higher feeding position.

In terms of $\delta^{13}C$ values *M. capensis* had higher mean (-15.48 ‰) than *T. capensis*. $\delta^{13}C$ can be used to determine ultimate sources of dietary carbon (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). The above results showed that *M. capensis* may be more dependent on pelagic prey, which are generally more enriched in $\delta^{13}C$ than demersal prey (France 1995; Davenport and Bax 2002; Le Loc'h et al. 2008). In most habitats, pelagic phytoplankton yields more negative $\delta^{13}C$ values than alternative carbon sources (Bird et al. 2018). *Trachurus capensis* which had lower average $\delta^{13}C$ value (-15.74 ‰), possibly had few pelagic prey items in its diet. Differences in $\delta^{13}C$ values between the two species may therefore be a result of different benthic - pelagic productions (Takai et al. 2002). The stomach content results also supported the above findings as the diet of *M. capensis* was found to consist of most pelagic prey species such as krill, anchovy and Cape horse mackerel, goby, Shortnose greeneye than *T. capensis* diet. The differences in $\delta^{13}C$ values have

also been attributed to the differences between coastal and offshore waters (Kelly 2000; Miller et al. 2008). Kurle et al. (2011) reported that organisms that feed close to the shore tend to have higher $\delta^{13}C$ values compared to those that feed offshore. Although the two species exhibit overlapping distribution (Burmeister 2001), the inshore- offshore differences might not be significant to influence the $\delta^{13}C$ values differences observed. The observed statistically significant differences between the $\delta^{13}C$ values of these species can also be attributed to the fact that the diet of *M. capensis* has a significant number of prey with pelagic carbon sources compared to *T. capensis*. A positive linear relationship was observed between $\delta^{13}C$ and TL of both species with differences in smaller fish (< 31 cm) and bigger fish (> 40 cm). Both species are considered to have a demersal component of their stocks, with younger ones being pelagic (Cury et al. 2000; Kirchner et al. 2010; Roux et al. 2013; Jansen et al. 2016), which can explain the fact that the main differences is mostly in the larger ones. The length of intersection in terms of carbon sources was 32 – 40 cm, which is possibly the length where these species may have increased interspecific feeding competition. Although *T. capensis* was observed as the prey of *M. capensis*, it is not plausible for hake of the same size to be feeding on the *T. capensis* of the same size. *Merluccius capensis* is an opportunistic predator with more diversity prey of small fishes and crustaceans (Roel and Macpherson 1988), whereas *T. capensis* is mostly zooplanktophagous that become ichthyophagous when matured (Cabral and Murta 2002; Jardas et al.2004). The length of trophic intersection is also the length where their diet is both dominated by krill as observed in their stomach content findings. *Trachurus capensis* had a wider carbon range (CR) ($\delta^{13}CR$) than *M. capensis*, an indication that its prey that might have been dependent on multiple basal resources.

The C: N ratio average value was higher for *T. capensis* than for *M. capensis*. The C: N ratio is considered to be a suitable proxy for organism condition (Schmidt et al. 2003; Sweeting et al. 2006), as well as to closely track changes in organism lipid content, because lipids are composed mainly of carbon, and most lipid classes do not contain nitrogen (Schmidt et al. 2003; Post et al. 2007; Logan et al. 2008). The above therefore shows that *T. capensis* has a higher lipid content and might be in better condition compared to *M. capensis*. Uanivi and Van der Plas (2014) documented that *T. capensis* are highly migratory species which may explain why they had higher lipid content, since they need more energy for that purpose than *M. capensis*. It has been concluded that the long-distance migratory species deposit larger amounts of body lipids (Jonsson and Jonsson 2015), which could be the reason for higher lipid content of *T. capensis* than that of *M. capensis*. This suggests that *T. capensis* are able to fuel a significant amount of their energy demand from these nutritious food sources, known to be rich in lipids (Nishibe and Ikeda 2008). A horse mackerel species, *T. mediterraneus*, is known to use muscle lipids as energy reserves (Tzikas et al. 2007), which possibly apply to *T. capensis* as well. The differences in C: N can also be explained by hake feeding on prey with low lipid content. Lipid storage depots differ among species (Love 1980; Sheridan 1988) and many species may store and utilize lipids throughout the body (Jorgensen et al. 1997; Slater et al. 2007), while others utilize more specific tissues such as muscle, liver, or mesenteric fat (Love 1980; Sheridan 1988). Strong relationships have been found between the C: N ratio and lipid content in aquatic animals, including Atlantic salmon (Bodin et al. 2007; Post et al. 2007; Logan et al. 2008; Mintenbeck et al. 2008). Individuals in better condition (higher lipid content) could be expected to exhibit higher C: N ratios. The use of C: N ratios relies on the assumption that an increase in tissue total

lipid concentrations correlates with increases in C: N ratios, since lipid contains mostly carbon and little-to-no nitrogen (Barnes et al. 2007). Differences among populations may also be related to geographic differences in the stable isotope signatures (Hobson 1999; Layman et al. 2012).

The total area of convex hull (TA) which represents the total amount of niche area occupied by a species (Layman et al. 2007; Quevedo et al. 2009; Newsome et al. 2012) was larger for *M. capensis* than *T. capensis*. A convex hull better emphasises the role of individuals in the general dispersion within isotope niche space (Jackson et al. 2011). A larger trophic niche for *M. capensis* can be an indication of a broader trophic diversity (generalist feeding approach of *M. capensis)*, while narrower trophic niche for *T. capensis* may represent a lower trophic diversity or a more specialized niche. This agrees with stomach content findings, as indicated that the *M. capensis* feed on several prey items, but *T. capensis* feed mainly on krill. In addition, the foraging ranges of *M. capensis* could encompass a wide geographical area (100 – 450 m), which would influence its wider isotopic niche. Feeding habits are believed to be the largest driving force in niche differentiation (Wang et al. 2012); hence an understanding of species-specific habitat utilization and inter-specific trophic relationships is fundamental to making appropriate conservation and management decisions.

The niche overlap observed indicated that they might be competing for the same resources at some life-stages, especially at their length of carbon and nitrogen value intersections. The overlap can also be because of the influence of overlapping depth distribution of these two species (Bianchi et al. 1999). The stomach content results

observed that the two species have common prey (krill and anchovy) and *M. capensis* also predate *T. capensis*. These results support Erasmus (2015) findings, who noted a trophic niche overlap between these two species. Erasmus (2015) revealed that the trophic niche for *M. capensis* and *T. capensis* overlap, indicating similar feeding patterns. The overlap can also be as a result of strong upwelling that can generate substantial deposition of pelagic producers to benthic sediments, ending up into both benthic and pelagic production resulting in homogeneity of food sources for different organisms (Iitembu 2014; Iitembu and Dalu 2018).

In terms of SEA_C, SEA_C is a measure of the mean core population isotopic niche which is robust to variation in sample size (Jackson et al. 2011). SEA_C permits the degree of isotopic niche overlap to be calculated which can be then used as a quantitative measure of dietary similarity among populations (Jackson et al. 2011). These two species had the same SEA_C values, an indication of their overlapping feeding ranges. The same SEA_C could be a result of the same prey species in their diet as observed in their stomach contents and the length of trophic intersection. The above is probably related to their feeding behaviours, as both species have diurnal movements between the pelagic and demersal components of the Benguela ecosystem (Pillar and Barange 1998; Bianchi et al. 1999; Iilende et al. 2001). The overlapping depth distribution of these two species could also have contributed to the similar SEA_C. In addition, the two species have similar prey in their diets, especially with large *T. capensis* that are feeding deeper in midwater and their diet are similar to that of *M. capensis* of similar size (Krzeptowski 1982). SEA_C similarities were also reported by Iitembu and Richoux (2016) in two sharks between the diets of *D. profundorum* and *D. calcea*; suggested that it was due to the morphological

similarities in their body forms and feeding structures (Bianchi et al. 1999; Ferry-Graham et al. 2002).

CHAPTER 6

6. Conclusions and recommendations

Merluccius capensis and *T. capensis* are important predators in the Northern Benguela Ecosystem (NBE). *Trachurus capensis* is a specialised feeder of small crustaceans (euphausiids), amphipods and small fish. While *M. capensis* is a generalised feeder of small crustaceans (euphausiids, prawns), fish, cephalopods and bivalves (white mussels). Diet compositions of the *M. capensis* changed with both length and latitude; an indication of the influence of prey availability, while for *T. capensis* remained the same. The two species have multiple trophic interactions as *M. capensis* may be dependent on *T. capensis* (mostly from 41 − 50 cm) as one of the dominant prey (prey-predators' relationship), while the two species can compete for smaller prey like krill (from 20 − 40 cm and anchovy (20 − 30 cm), as well as krill was the dominant important prey of both species. Significant differences were found in both δ^{13}C values and δ^{15}N values of the two species. The two species showed a high trophic niche overlap, with a wider niche for *M. capensis* and *T. capensis*. However, the possibility of interspecific trophic segregation cannot be ruled out, as isotopic similarity does not necessarily mean true ecological or dietary similarity. Stomach content and stable isotope results confirmed ontogenic shifts in diet and diet overlap that lead to inter-specific competition between the two species. The comparison of this study with previous studies in earlier years, indicates that the diets of these species have not changed much with time. The study highlighted the benefit of combining new approaches (stable isotopes analysis) and traditional approaches (stomach contents analysis) to studying trophic relationships of fish species. The findings from this study also helped in documenting the importance of prey species and inter-specific competition between *M. capensis* and *T. capensis*, as well as to

better understand how these relationships affect economically important species. It is hoped that these findings will enable the management of these two species that considers feeding interactions; that enable species to be managed at ecological sustainable harvest level. *Merluccius capensis* and *T. capensis* are important commercial species and are found in higher abundance in the Namibian marine waters. It is possible that the feeding interaction is one of the factors that could regulate their population dynamics. Because younger *M. capensis* interact more with older *T. capensis*, there is possibility that the *T. capensis* has a direct influence on *M. capensis* recruitment. As older *M. capensis* feed on younger *T. capensis*, there is a possibility that *M. capensis* has a direct influence on *T. capensis* recruitment. Future studies should therefore look at the strength (significant impact of *M. capensis* on *T. capensis*) of the species feeding interaction to ascertain the degree of their influence on their respective population dynamics. Recommending future scientists to collect samples from entire the Namibian coast and to collect samples during hake or horse mackerel surveys.

CHAPTER 7

7. References

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CHAPTER 8

8. Appendices

Appendix 1: Ethical clearance certificate

UNAM
UNIVERSITY OF NAMIBIA

ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SNC /356/2017   Date: 20 November, 2017

This Ethical Clearance Certificate is issued by the University of Namibia Research Ethics Committee (UREC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the Faculty/Centre/Campus Research & Publications Committee sitting with the Postgraduate Studies Committee.

Title of Project: The Relationship Of Lipids And Energy Content To The Trophic Position And Growth Of Cape Hake *(Merluccius Capensis)* And Horse Mackerel *(Trachurus Capensis)*

Researcher: Hendrina Kadila

Student Number: 201303965

Supervisor(s) Johannes Iitembu (Main) Ms Dietlinde Ndakumwa Nakwaya (Co)

Take note of the following:
(a) Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the UREC. An application to make amendments may be necessary.
(b) Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the UREC.
(c) The Principal Researcher must report issues of ethical compliance to the UREC (through the Chairperson of the Faculty/Centre/Campus Research & Publications Committee) at the end of the Project or as may be requested by UREC.
(d) The UREC retains the right to:
(i)   Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,
(ii) Request for an ethical compliance report at any point during the course of the research.

UREC wishes you the best in your research.

Prof. P. Odonkor: UREC Chairperson   Ms. P. Claassen: UREC Secretary

Appendix 2: Research permission letter

CENTRE FOR POSTGRADUATE STUDIES

University of Namibia, Private Bag 13301, Windhoek, Namibia
340 Mandume Ndemufayo Avenue, Pioneers Park
☎ +264 61 206 3275/4662; Fax +264 61 206 3290; URL.: http//www.unam.edu.na

UNAM
UNIVERSITY OF NAMIBIA

RESEARCH PERMISSION LETTER

25 October 2017

Student Name: Ms Hendrina Kadila

Student number: 201303965

Programme: MSc (Fisheries & Aquatic Sciences)

Approved research title: The Relationship of Lipids and Energy Content to the Trophic Position and Growth of Cape Hake *(Merluccius Capensis)* and Horse Mackerel *(Trachurus Capensis)*

TO WHOM IT MAY CONCERN

I hereby confirm that the above mentioned student is registered at the University of Namibia for the programme indicated. The proposed study met all the requirements as stipulated in the University guidelines and has been approved by the relevant committees.

The proposal adheres to ethical principles as per attached Ethical Clearance Certificate. Permission is hereby granted to carry out the research as described in the approved proposal.

Best Regards

25 Oct 17
....
Date

Dr M Hedimbi
Director: Centre for Postgraduate Studies
Tel: +264 61 2063275
E-mail: directorpgs@unam.na

Appendix 3: Total samples number of species collected per station

Stations	*M. capensis*	*T. capensis*
1	20	20
4	30	30
5	10	10
6	30	30
50	2	2
56	4	4
58	6	6
74	33	33
77	18	18
82	25	25
83	10	10
93	2	2
94	12	12

Appendix 4: Images of prey items found in the stomachs of *M. capensis* and *T. capensis*. External morphology of prey items.

Figure 1: Jacopever *(Helicolenus dactylopterus)*

Figure 2:Amphipods (order)

Figure 3:Cephalopods (class)

Figure 4:Shortnose greeneye *(Chlorophthalmus agassizi)*

Figure 5:Anchovy *(Engraulis capensis)*

Figure 6:Squat lobster (*Galathea squamifera*)

Figure 7:Cape horse mackerel (*Trachurus capensis)*

Figure 8:White mussel

Figure 9: Krill (*Euphausia hanseni*)

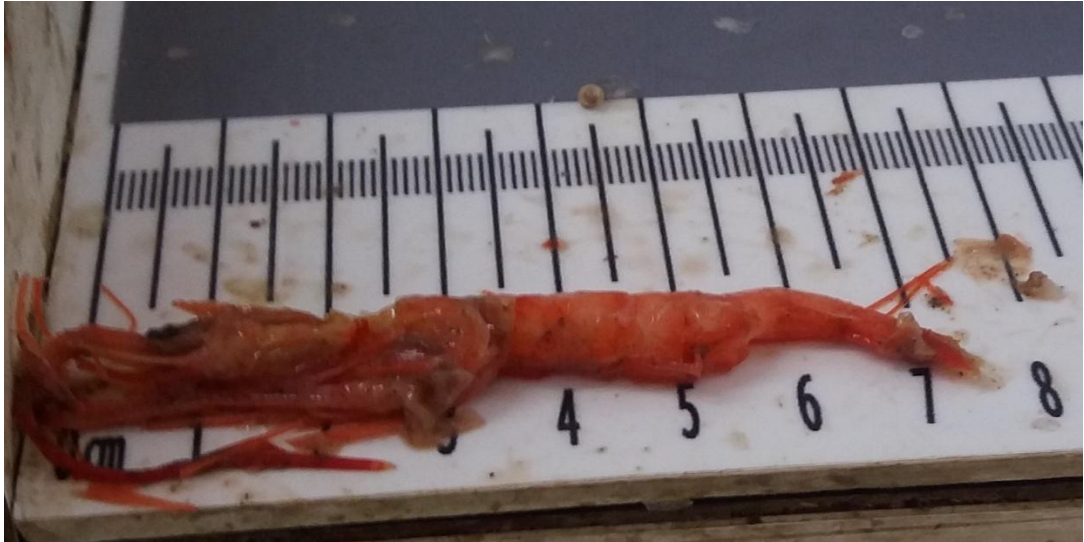Figure 10: Goby (*Sufflogobius bibarbatus*)

Figure 11: Prawns (*Parapenaeus longirostris*)

Figure 12: Cape hake

Figure 13: Common Atlantic Grenadier (*Nezumia micronychodon*)

Appendix 5: Stable isotopes measurement [‰] of *M. capensis* and *T. capensis* with their number of samples, average length (cm), average nitrogen (δ^{15}N) value, average carbon (δ^{13}C) value, standard deviation for δ^{15}N and δ^{13}C, C: N ratio, δ^{13}C range and δ^{15}N range.

Species	Number of samples	Length (cm)	δ^{15}N	δ^{13}C	C: N	δ^{13}C range	δ^{15}N range
M. capensis	202	37.63	11.17 ±0.73	-15.48 ±0.54	3.97	2.96	4.03
T. capensis	202	27.54	10.67 ±0.89	-15.74 ±0.56	4.73	4.01	4.33