Uncoupling the exploitation and climate change effects on the biology of Cape monkfish, *Lophius vomerinus* Valenciennes 1837 in Namibia

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Preface

This thesis consists of seven chapters: a general introduction (Chapter 1), a description of the study area, the Namibian waters, and general materials and methods (Chapter 2), four research chapters (Chapters 3, 4, 5, and 6), and a final general discussion and overall conclusion (Chapter 7). A combined references list that includes all referenced materials for all chapters is provided at the end of the thesis. Research work for this study was conducted under the Rhodes University Animal Ethics and Standards Council approval number: DIFS0118.

Publications during my time as a PhD student:

- **Erasmus, V. N.,** Currie, G., Roux, J-P., Elwen, S. H., Kalola, M. S., Tjizoo, B., Kathena, J. N. & Iitembu, J. A. 2021. Predatory species left stranded following the collapse of the sardine *Sardinops sagax* Pappe 1854 stock off the northern Benguela upwelling system: A review. *Journal of Marine Science.*
- **Erasmus, V. N.**, Kadhila, T., Thyberg, K. L., Kamara, K. & D' Almaida, G. 2021. Public perceptions and factors affecting domestic marine fish
- consumption in Namibia, southwestern Africa. *Regional Studies in Marine Science.* 47
- Iitembu, J. A., **Erasmus V. N.**, Uanivi, U., Nangolo, E., Horaeb, R., Iita, T., Nashima, P., Nakwaya, D. & Mwandemele, O. (2021). The hits and misses of Namibia's attempt to implement the Ecosystem Approach to Fisheries (EAF) Management. *Ecosystem and Sustainability Journal.*
- **Erasmus, V. N**, Kadhila, T., Gabriel, N. N., Thyberg, K. L., Ilungu, S. & Machado, T. 2021. Assessment and quantification of Namibian seafood waste production. *Ocean and Coastal Management*. 199, 105402.
- **Erasmus, V. N.** & Iitembu, J. A. 2019. Characterising the trophic relationships between cuttlefishes, myctophids and round herring in the northern Benguela. *Welwitschia International Journal of Agricultural Sciences.* 1, 59–67.
- **Erasmus, V. N.,** Iitembu, J. A., Hamutenya, S. & Gamatham, J. C. 2019. Evidence of possible influences of methylmercury concentration on condition factor and maturation of Cape monkfish (*Lophius vomerinus*). *Marine Pollution Bulletin.* 146, 33–38.
- **Erasmus, V. N.**, Hamutenya, S., Iitembu, J. A. & Gamatham, J. C. 2018. Mercury concentrations in muscles and liver tissues of Cape monkfish (*Lophius vomerinus*) from the Northern Benguela, Namibia. *Marine Pollution Bulletin.* 135, 1101–1106.

Conference presentations:

- 4th Annual Research Conference of the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC), 3–4 October 2019
- The 7th Annual Science and Governance Forum of the Benguela Current Convention (BCC), Nampower Convention, Windhoek, Namibia, 25–27 October 2017
- 2nd Annual Research Conference of the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC), 28–29 September 2017

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- Bergen Summer Research School, 11–21 June 2018, on Global Development Challenges, Bergen, Norway.
- ECOFISH - Stock Assessment Interpretation Course, 18–21 April 2017, DAFF, Cape Town, South Africa.
- Summer School Ecology of Eastern Boundary Upwelling Systems, 25 April–01 May 2016, Saint-Louis, Senegal.

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Dedications

This work is dedicated to the Mutumbulwas who are no longer physically with us. I also dedicate it to the memory of my late papa, Augustus Erasmus Nuule. I know that you will continue to guide me in all my endeavours. May your souls continue to rest in peace.

Declaration

I, Victoria Ndinelago Erasmus, hereby declare that the work described in this thesis was carried out in the Department of Ichthyology and Fisheries Science, Rhodes University, under the supervision of Prof. Warwick H. H. Sauer, Dr Amber-Robyn Childs, Prof. Warren M. Potts, and Prof. Ian Meiklejohn. The components of this thesis comprise original work by the author and have not been submitted to any other university. This work is my own, but some maps were generated by my supervisor using his GIS software during learning sessions.

Signed:

Date: 26/03/2021

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List of Abbreviations

ABF	Angola-Benguela frontal
ANOVA	Analysis of variance
ASPM	Age Structure Production Model
BCC	Benguela Current Convention
BCLME	Benguela Current Large Marine Ecosystem
BF	Batch Fecundity
CPUE	Catch per unit effort
CTD	Conductivity, temperature and depth
CV	Coefficient of variation
EAF	Ecosystem Approach to Fisheries
EBSA	Ecologically and Biologically Significant Areas
EEZ	Economic Exclusive Zone
ERSST	Extended Reconstructed Sea Surface Temperature
FAO	Food and Agricultural Organisation
FIMS	Fisheries Information Management System
FMC	Fisheries Monitoring Centre
FOA	Fisheries Observer Agency
FRA	Fisheries Restricted Areas
GDP	Gross Domestic Product
GIS	Geographic Information System
GLM	Generalised Linear Model
GRT	Gross Register Tonnage
GSI	Gonadosomatic index
HSI	Hepatosomatic index
ICCAT	International Commission for the Conservation of Atlantic Tunas
ICSEAF	International Commission for the Southeast Atlantic Fisheries
IRI	Index of Relative Importance
IUCN	International Union for the Conservation of Nature
IUU	Illegal, Unreported and Unregulated
LRT	Likelihood ratio test
LWR	Length-weight relationship
MFMR	Ministry of Fisheries and Marine Resources

MSY	Maximum Sustainable Yield
MWG	Monkfish Working Group
NatMIRC	National Marine Information and Research Centre
nBE	northern Benguela Ecosystem
nMDS	Non-metric multidimensional scaling
NOAA	National Oceanic and Atmospheric Administration
PCA	Principal component analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
POF	Post-ovulatory follicles
PPE	Policy, Planning and Economics
RESDAT	Research database data
RSS	Residual sum of square
SADC	South African Developing countries
sBE	southern Benguela Ecosystem
SCA	Stomach content analysis
SIA	Stable isotope analysis
SST	Sea Surface Temperature
TAC	Total allowable catch
TL	Total length
UNEP	United Nations Environment Programme
VBGF	Von Bertalanffy growth function
VMS	Vessel Monitoring System
WSSD	World Summit on Sustainable Development

General abstract

Cape monkfish, *Lophius vomerinus* Valenciennes 1837, has supported the Namibian fishing industry for decades, historically as by-catch and recently as a target species. This species is also an important predator in this region. With increasing levels of exploitation and unprecedented climate change, an understanding of the changes in the long-term biological parameters of this species is critical. To date, there has been a scarcity of spatio-temporal studies that have examined and compared the biological aspects of Cape monkfish in relation to climate change and exploitation pressure. Investigations into changes in feeding habits, reproduction strategy, age and growth can provide valuable information for the sustainable management and conservation of this species. This thesis aimed to improve our understanding of the impacts of exploitation and climate variability on the biological parameters of Cape monkfish in the Namibian marine waters, thereby contributing to efforts directed at sustainable harvest and management of this resource. This was achieved through temporal and spatial comparisons of feeding, reproductive scope, age and growth, and catch statistics. The study used data collected during the monkfish swept-area biomass surveys of 2001–2005 and for 2007–2018, hake (deep-water hake *Merluccius paradoxus* Franca 1960 and shallow-water hake *M. capensis* Castelnau 1861) swept-area biomass surveys of 2017 and 2019, port sampling programme data collected from April 2014 to December 2019, and monkfish commercial fishing activities collected between April 2001 and December 2019.

Based on historical feeding data (1986 – 1987) and contemporary feeding data (2015-2018), Cape monkfish feeds on a variety of prey species from seven groups: Teleost, Cephalopoda, Crustacea, Echinoidea, Elasmobranchii, Gastropod and Porifera. The diet was characterised by a high prevalence of empty stomachs (43.9%), showing low feeding intensity, but most prevalent in juveniles (52.9%). Although the diet composition varied at different life stages, Teleosts (especially deep-water hake *Merluccius paradoxus* Franca 1960) were the main constituents of the diet for all size classes as per the Index of Relative Importance (%IRI). The results highlight the particular importance of the deep-water hake *M. paradoxus* (by %IRI) in the diet of Cape monkfish across all size classes. There is a clear dominance of hake in both studies, which means that any overexploitation or climate-driven population decline in hake will most likely have an impact on Cape monkfish. Feeding composition was dependent on the season ($p < 0.05$), with the type and quantity of prey ingested changing seasonally, showing the ability of Cape monkfish to adjust its diet, depending on possible environmental parameters which consequently influence prey availability. In general, the spatial and temporal variability of the main prey items suggests that the species is highly opportunistic with a broad trophic adaptability. Comparison of historical and contemporary stomach content data indicates that Cape monkfish appear to have changed their diet, probably reflecting the availability of forage species over time and space, possibly due to climate change, fishing pressure, or both. The broad trophic adaptability for Cape monkfish highlights their adaptive potential to increasing anthropogenic stressors such as climate change. However, the dominance of the commercially important deep-water hake, *M. paradoxus,* in the diet during contemporary times highlights that complex trophic interactions may play a role in altering the northern Benguela fisheries.

The general male to female sex ratio was measured at 1:1.67, with significant variation across depth, size class, and year ($p < 0.05$). Comparison of length at 50% maturity (L_{50}) for Cape monkfish between historical (2004–2006) and contemporary time (2015–2019) showed no significant differences in both sexes, with no significant changes in the L_{50} for females ($\chi^2 = 1.53$, df = 1, $p = 0.2154$), and males ($\chi^2 = 0.41$, df = 1, $p = 0.5204$) between the two periods. The monthly gonadosomatic index (GSI) showed that Cape monkfish spawn throughout the year with peaks between July and September for females and August for males, similar to those observed 20 years ago. Spawning hotspot areas were identified and were consistently located between 22° and 25°S in deeper water (> 250 m) for the 2001–2018 time series. Comparison of the contemporary (2015–2019) proportions of developing, ripe and spent gonads to the historical study data (1996 – 2000) show minimal differences. Ripe ovaries capable of spawning (Stage IV) were dominant in July (23.8%) and August (26.2%), while ripe testes were prevalent in April (52.5%) and November (28.5%). The discovery of the veil (a gelatinous, flat ribbon structure containing individual eggs) off Namibia for the first time (during this study) is a significant because this result provides important reproduction activities information of this species, which were never recorded off Namibia. The location where the veil was discovered, off Swakopmund (22°30'S, 13°25'E), provides further evidence of the identified spawning hotspot areas, this location is also identified as a monkfish consecutive hotspot fishing area.

The ages, growth rates, and length-weight relationships were compared between fish collected during monkfish commercial fishing activities between 1996 and 1998 (Period 1) and during monkfish routine monitoring surveys from 2014 to 2016 (Period 2). A total of 607 (size range: 9–96 cm total length (TL)) and 852 (size range: 9–96 cm TL) Cape monkfish were aged by reading sectioned illicia, during Periods 1 and 2, respectively. The length-weight relationships were $W = 0.012L^{3.035}$ ($r^2 = 0.98$) and $W = 0.014L^{2.989}$ ($r^2 = 0.98$) for females and males,

respectively, during Period 1, and $W = 0.01L^{2.97}$ ($r^2 = 0.98$) and $W = 0.01L^{3.03}$ ($r^2 = 0.98$) for females and males, respectively, in Period 2. The growth of Cape monkfish (in cm) for combined sexes was described by $Lt = 94(1 - e(-0.10(t-(-0.31)))$ in Period 1 and $Lt = 98(1 - e(-0.10(t-(-0.33)))$ in Period 2. Females grew significantly faster during Period 1 (LRT results from Maartens et al., 1999), while male and female growth was not significantly different during Period 2 ($F = 0.65$, $p = 0.58$). There were no significant differences between the male and female growth curve in Period 2 ($F = 0.65$, $p = 0.58$). Although the growth curves are similar between Period 1 and Period 2, the larger fish are in Period 2 are lighter than those in Period 1. This finding is important to the monkfish fishing industry because fish is sold by weight. This finding may suggest that although the fish grow similarly by length, changes in the environmental conditions may have resulted in a reduced condition of the fish. In terms of mean age, the historical Period 1 had a slightly lower mean age of 4.40 compared with a mean age of 5.49 during Period 2. Slight differences were also observed in the age structure between the two periods, with 2-year-olds (20.3%) the most abundant age class in the historical period while 5-year-old fish (18.3%) were most abundant in Period 2. Although the spatial distribution of the catch was not available for Period 1, 0-year-old fish were distributed from 22° to 24°S, and 25° to 26°S in shallower waters of 166–290 m during Period 2. Only fish between 5 and 16 years old were found off the documented historical nursery area off 28° S. The similar growth curves and spatial overlap of nursery habitats between Period 1 and Period 2 suggest that Cape monkfish may be fairly resilient to the rapid environmental change reported in this region and to the extensive levels of exploitation for the species. However, the recent spatial shifts in the nursery areas are sensitive to disturbance and may indicate that these changes could be having an impact on the early life stages of the species. Continued monitoring may be necessary to understand the consequences of these spatial shifts for the age and growth and resilience of the species.

Analysis of the overall spatial and temporal catches of monkfish (both Cape monkfish and shortspine African monkfish) off Namibia between 1998 and 2018 identified noticeable spatio-temporal trends. The pattern of fishing activities for Cape monkfish is heterogeneous, with identified 'hotspots' in specific areas. Of particular importance is the consecutive hotspot, between 1998 to 2018 for monkfish fishing activities between 25° and 26° S. The kernel density analysis indicated that the area around 24°S, and between 26° and 27 °S, between Walvis Bay and Lüderitz, had the highest total catch densities (~300 kg/km^2), suggesting that this is the core of the stock abundance. Annual monkfish catches have fluctuated since the inception of the

fishery in 1994, with a drastic decline in the catch recorded after 2003 through to 2018. Generally, there has been an underutilisation of the total allowable catch (TAC) for most of the years. The decrease in catches and the underutilisation of the TAC might be indicative of the reduction in the stock abundance. However, external factors such as lack of capacity of the fishing industry and the administration can contribute to underutilisation of TAC. Basic regression analysis between total monthly catches and monthly sea surface temperature (SST) yielded low r-squared values indicate that in all three grids, only ~ 1% of the variation is explained between SST and total monkfish catches in these areas.

The most prominent points to consider from this study are the results of the comparative feeding study (Chapter 3), reproductive indicators (Chapter 4) and age and growth (Chapter 5). Certainly, there have been changes in feeding, demography, and distribution of the species in the last two decades – climate-driven changes were recorded in the feeding habits of Cape monkfish, spatially and temporally – but despite the changes in prey species composition, distribution and abundance in various habits and periods, Cape monkfish was able to switch prey species, reflecting wide trophic adaptability. The dominance of *M. paradoxus* at all size classes in all analysed habitats is a significant result because. The peak spawning period has remained the same between July and September, as previously reported in Period 1. The consecutive spawning hotspots were identified in the areas between 22° and 25°S. From a fisheries management perspective, the spawning ground and spawning season should be protected (by means of closure). The evidence of changes in length at 50% maturity presented in this study hints at both climate change and extensive exploitation pressure. The discovery of the veil for the first time in this study is very important; however, it might be sampling related and not driven by climate or exploitation pressure. Finally, the change in the Cape monkfish distribution discussed in Chapter 6 may be attributed to a shift in the distribution or fishing effort as a consequence of shallow water depletion.

Keywords: Age and growth, Cape monkfish, catch statistics, climate change, feeding, fishing pressure, maturity, Namibian waters, spatial management, spawning.

Chapter 1: General introduction

Multiple studies have provided evidence that marine resources worldwide are under serious threat (Morishita, 2008; Wheeler et al., 2009; Kirkman et al., 2013; Boyd et al., 2018; Mazumder et al., 2015). Fluctuations in the fish growth patterns (Mazumder et al., 2015), changes in reproductive patterns (Pankhurst & Munday, 2011) and feeding behaviour (Grémillet et al., 2019) are some of the unprecedented consequences of these threats. Changes in the biology of species are complex and can result from several factors, but many studies have identified climate change and anthropogenic activities, such as fishing, as ubiquitous stressors to marine organisms (e.g., Garrod & Shumacher, 1994; Fu et al., 2019). Other stressor such as habitat modification and marine pollution (Dulvy et al. 2003) also influence the abundance and distribution of marine resources. Of these stressors, climate change and exploitation pressure are the subject of this study. There are various climate change sensitivities among marine organisms due to differences in genetic make-up, growth rate, and body size, among other factors. However, studies that seek to uncouple exploitation pressure and climate change effects on the biological aspects of these fish stocks are under-represented. Obtaining information on the synergistic effects of climate change and exploitation pressure is critical in the management and conservation of these resources.

1.1 Climate change

Globally, a large body of research (Kirkman et al., 2013; Simpson et al., 2013; Jarre et al., 2015a; Potts et al., 2016; Gíslason et al., 2020; Mendenhall et al., 2020) has documented the mounting concern over the impacts of climate change. It is noted that marine heat waves are becoming more frequent and intense, on a global scale (Simpson et al., 2013; Frölicher et al., 2018). There is vast evidence that climate-driven changes in marine waters have led to low primary production, the collapse of some fisheries and poor recruitment of some fish stocks (Hamukuaya et al., 1998; Daskalov et al., 2003; Cisneros-Mata et al., 2019; du Pontavice et al., 2021). Climate change coupled with excessive fishing pressures has been identified as an important threat to marine resources at a population level (Hamukuaya et al., 1998; Morishita, 2008; Perry et al., 2005; Kirkman et al., 2013). The synergistic effects of climate change and overexploitation play a key role in shifts in the abundance and distribution of marine fish and invertebrates (Jennings & Kaiser, 1998; Hutchings et al., 2009), and the impact on the marine environment can cause unprecedented challenges for marine fisheries management, and threats to the global seafood production and supply (Weatherdon et al., 2016; Cisneros-Mata et al., 2019).

Monitoring of environmental parameters of the ocean is critical to assess interdecadal variability (Junker et al., 2017). The environmental parameters of the Benguela upwelling system have been extensively observed since the 20th century (Taunton-Clark & Shannon, 1988; Boyer et al., 2001; Monteiro et al., 2008; Junker et al., 2017), and in Namibia, many studies have indicated variation in dissolved oxygen levels (Hamukuaya et al., 1998; Bartholomae & van der Plas, 2007; Monteiro et al., 2008), frequency and intensity of *Benguela Niño* events (Boyer et al., 2001; Monteiro et al., 2008; Hampton & Willemse, 2012), sea surface temperature changes (Junker et al., 2017), intrusions of warm, nutrient- and oxygen-poor water from southern Angola (Boyd et al., 1987; Bartholomae & van der Plas, 2007; Hampton & Willemse, 2012) and wind stress, particularly in the Lüderitz area (Monteiro et al., 2008). Changes in environmental parameters have resulted in several negative impacts, including the vertical distribution of hake over the Namibian shelf as a result of low oxygen levels near the seabed (Mas-Riera et al., 1990, Hamukuaya et al., 1998; Hampton & Willemse, 2012). Changes in these environmental parameters have implications for the Namibian fishing industry. For instance, when hake species change their vertical distribution (e.g., due to environmental variables) they become less available to the trawl and longline fleets (Hampton & Willemse, 2012). These long-term decline of present ecosystem functions with climate change has been predicted in the BCLME (Monteiro et al., 2008).

Therefore, monitoring climate change parameters, the impact on marine resources and the oceanographic environment is a vital part of integrated and adaptive ecosystem management systems (Morishita, 2008; du Pontavice et al., 2021) and enables the prediction of future climate change effects that are yet not fully understood (van der Lingen et al., 2006). Studying the impact of climate change on the biological aspects of fish and consequently on their populations, is complex, because climate change influences a multitude of environmental variables, such as temperature and wind strength, that may also have subsequent impacts at different levels of biological organisation (Tasker, 2008; Rijnsdorp et al., 2009).

1.2 Global fishing

Fishing is by far the greatest human exploitative activity and has been conducted for centuries in the marine environment (Jennings & Kaiser, 1998; Watson et al., 2013). Based on world fishery data (Figure 1.1), the fishing harvest worldwide has increased to its highest total in 2011

(69 951 064.49 tonnes). However, recently fish catches have been declining globally following extensive fishing pressure, and this decline has led to an increasing concern among fisheries managers (Trippel, 1995; Worm et al., 2006; Paterson, 2015; De Mitcheson 2016; Heymans & Tomczak, 2016). The collapse of many fisheries globally, including sardine *Sardinops sagax* Pappe 1854 in Namibia, is one of the direct impacts of uncontrolled fishing (Oelofsen, 1999; Boyer et al., 2001b; Daskalov et al., 2003; Jarre et al., 2013, 2015b).

Figure 1.1: World capture fish quantities (data sourced from 'Our World in Data', https://ourworldindata.org/).

Even with the decrease in the world fish catches, the worldwide demand for seafood continues to increase (Valdimarsson & James, 2001). According to an FAO report for 2016, seafood is a significant food source that supplies about 20% of the animal protein consumed globally in 2013 (FAO, 2016). This demand will continue to increase as the world population increases. It is well documented that fisheries resources are finite and perspectives on exploitation and management need to be changed if these resources are to benefit future generations (Oelofsen, 1999; Watson et al., 2013). Each fish species has unique environmental preferences, for example, specific locations and depths of the sea. As a result, fishing activities may be directed on the surface, midwater, or bottom (Jennings & Kaiser, 1998), and may employ a large variety of fishing techniques such as drive netting, spearing, pots or traps, baited hooks and gill nets (Jennings & Kaiser, 1998; Yamashita et al., 2009). Fishing techniques and equipment are continuously being modified to exploit the behaviour and habitat preferences of target species and to achieve maximum catch per unit effort (CPUE) (Jennings & Kaiser, 1998; Gabriel et al., 2005). Fishers are also constantly upgrading their fishing techniques, gears, and vessels to ensure a maximum harvest (Gabriel et al., 2005). For instance, some monkfish-targeting vessels fishing off Namibia have been reported to employ the use of double-belly nets that maximise their harvest (MFMR, 2018). These nets also have tickle chains that "dig" monkfish out of the sea bottom. The increasing horsepower of fishing vessels has also enabled the use of larger and heavier trawls and dredges, so increasing the catch (Jennings & Kaiser, 1998; Gabriel et al., 2005). It is thus important to monitor and investigate the impacts of fishing pressure and fishing technology on fish populations globally. Despite the increasing developments to improve fishing gear and hence catch rates, studies dedicated to understanding the impacts of this technology creep on fishing exploitation are limited.

1.2.1 Impacts of fishing

There is an increasing concern over the impacts of fishing globally (Tasker et al., 2000; Worm et al., 2006). Since the beginning of industrial exploitation, overfishing, habitat disturbance and destruction, imbalanced predator-prey relationships, alteration in population size and structures have been observed (Jennings & Kaiser, 1998; Tasker et al., 2000; Kaiser et al., 2003; Worm et al., 2006). Most fishing activities, especially demersal, scrape the seabed, scouring and resuspending the substratum (Jennings & Kaiser, 1998). Other indirect impacts include spatial changes in the distribution of small pelagic fish, increases in biomass of other species (e.g., pelagic goby *Sufflogobius bibarbatus* von Bonde 1923 and jellyfish *Chrysaora* and *Aequorea* species), and shifts in environmental variability, all of which affect levels of productivity and resource biomass. These changes have considerably interrupted fish assemblages and have also altered the trophic functioning of the system (Jennings & Kaiser, 1998; Graham et al., 2005; Heymans & Tomczak, 2016), resulting in ecological regime shifts and/or an alternate stable state of the ecosystem (Shannon et al., 2003; Heymans & Tomczak, 2016). Several studies have outlined the negative impacts of fishing activities on benthic fauna and habitat, community structure and trophic interactions, both at a short- and long-term level (Jennings & Kaiser, 1998; Tasker et al., 2000; Kaiser et al., 2003; Graham et al., 2005; Jarre et al., 2013, 2015b). Fishing activities impact marine habitats and affect the diversity, composition, biomass, and productivity of the associated biota; however, the magnitude of these impacts varies with the type of fishing gear used and the habitat fished (Tasker et al., 2000; Kaiser et al., 2003; Cisneros-Mata et al., 2019).

Fishing directly influences the marine ecosystem because it causes high mortality of both target and by-catch species/incidental catches (Jennings & Kaiser, 1998; Tasker et al., 2000; Cisneros-Mata et al., 2019). Fishing activities targeting prey species alter the food web and regulate fish stocks, with the resultant poor availability of prey negatively affecting the growth and reproduction of predators (Jennings & Kaiser, 1998; Frid et al., 2005). Equally, heavy fishing on target species may reduce their abundance, thereby reducing species competition for resources, consequently resulting in the proliferation of non-target and forage species (Jennings & Kaiser, 1998; Tasker et al., 2000; Roux et al., 2013). Some fishing gear such as gill nets, when lost or discarded at sea, may continue to fish (known as 'ghost fishing') for a long time, killing marine organisms mostly through entanglement (Sancho et al., 2003; Masompour et al., 2018). Understanding the potential impacts of exploitation on important fishery species, both prey and/or predator, are critical for maintaining population persistence and resilience (Watson et al., 2013; Potts et al., 2014).

1.2.2 Indicators of fishing pressure

A solid comprehension of the effects of fishing requires the integration of population and ecosystem-centred research (Kaiser et al., 2003; Jennings & Kaiser, 1998; Porobic et al., 2019). For example, trophic interactions may change due to the impacts of different fishing activities (Moloney, 2010). Thus, an evaluation of the impacts of fishing pressure on the marine ecosystem is a crucial component that should be considered in any future management plans (Kaiser et al., 2003; Coll et al., 2016). However, the effects of fishing are complex and often interact with other factors, such as climate change and make them difficult to identify and quantify (Tasker et al., 2000).

To understand the impacts of fishing on the marine environment and its resources, researchers monitor changes in the behavioural responses and biological aspects of fish (Worm et al., 2006). Early maturation, for example, has been linked to excessive exploitation pressure in several fish species (Trippel, 1995; Rochet, 1998; Wheeler et al., 2009; Butler et al., 2018). Past and present knowledge on the life-history traits of target and valuable retained by-catch species, including feeding behaviours, reproductive strategies, age- and size-at-maturity, growth patterns, as well as information on the spatial and temporal distribution of vital life-history stages, is critical to identify change. Since these parameters act as crucial indicators of exploitation pressure (Trippel, 1995; Walters, 2003; Wheeler et al., 2009; Butler et al., 2018), they are important inputs in studies investigating the impacts of fishing activities.

1.3 Fishing in Namibian waters

The Namibian waters form part of the Benguela Current Large Marine Ecosystem (BCLME), which is one of four eastern boundary systems (Shannon, 1985). The BCLME has some of the world's most productive fishing grounds (Crawford, 1987), resulting in a large fishing industry off Namibia, ranked the third highest in Africa after Morocco and South Africa (MFMR, 2015; NDP5, 2017). The Namibian fishing industry is the third-highest contributor to Namibia's Gross Domestic Product (GDP), contributing 3.6% in 2017 (NDP5, 2017; MFMR, 2018) and employing more than 16 300 people in 2017 (NDP5, 2017). Namibia exports most of the fish and fisheries products to other countries, with Spain, DRC and South Africa importing the largest portion (Chiripanhura & Teweldemedhin, 2016; MFMR, 2018). The Namibian waters are home to various marine resources, ranging from small fish to large predators, of which 20 species are commercially important. Eight of these species (Cape horse mackerel *Trachurus capensis* Castelnau 1861, deep-water hake *Merluccius paradoxus* Franca 1960 and shallow-water hake *M. capensis* Castelnau 1861, Cape fur seals *Arctocephalus pusillus pusillus* Schreber 1776, monkfish (*Lophius vomerinus* Valenciennes 1837 and *L. vaillanti* Regan 1903), red crab *Chaceon maritae* Manning & Holthuis 1981, rock lobster *Jasus lalandii* Milne-Edwards 1837, sardine *Sardinops sagax* Pappe 1854 and orange roughy *Hoplostethus atlanticus* Collett 1889 are regulated through a Total Allowable Catch (TAC) system which is a tool founded on the concept of Maximum Sustainable Yield (MSY) (Martell & Froese, 2013). The TAC is the total amount of fish allowed or permitted to be caught from a particular stock (e.g., Cape horse mackerel), in a specific fishing season. Sardine and orange roughy are currently under a catch moratorium. Tuna *Thunnus alalunga* Bonnaterre 1788 and *T. obesus* Lowe 1839 resources are also harvested off Namibia, but the TAC is allocated on an international level by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Additionally, there are non-target species that are commercially important, but they have no direct fishery and instead are harvested as by-catch. These include Cape anchovy *Engraulis encrasicolus* Linnaeus 1758, angelfish *Brama brama* Bonnaterre 1788, jacopever *Helicolenus dactylopterus* Delaroche 1809, kingklip *Genypterus capensis* Smith, 1847 and west coast sole *Austroglossus microlepis* Bleeker 1863.

1.3.1 Characteristics of the Namibian fishery

The Namibian fishing industry can be categorised into a pre-independence fishing industry (before March 1990) and a post-independence fishing industry (after March 1990).

1.3.1.1 Namibian Fisheries before Independence

Industrial fishing off the coast of Namibia was first recorded in the 1950s when Namibia, and its water bodies, was still under the South African Administration. In the 1950s and 1960s fishing activities off Namibia were spearheaded mainly by European fleets who started with an inshore pelagic fishery for sardine and Cape anchovy (Bianchi et al., 1999; Boyer et al., 2001; Kirchner et al., 2010). In the beginning, fishing off Namibia was open access, with no limit or regulations governing the exploitation of marine resources off the coast (van der Westhuizen, 2001). In 1969 the International Commission for the Southeast Atlantic Fisheries (ICSEAF) was established to control and regulate the harvest of marine resources off the coasts of Namibia and South Africa (Bianchi et al., 1999; van der Westhuizen, 2001; Paterson et al., 2013). Despite the fisheries management measures implemented by ICSEAF, such as the implementation of legal minimum mesh size and member country quotas, the abundance of marine resources continued to decline, mostly because overfishing continued (Roux & Shannon, 2004).

1.3.1.2 Contemporary Fishing off Namibia (post-independence)

Immediately after independence in 1990, the Namibian government declared the 200 nautical miles (nm)Exclusive Economic Zone (EEZ) intending to rebuild the Namibian fish stocks which were overfished (MFMR, 1990; Oelofsen, 1999; van der Westhuizen, 2001). Most fisheries had a reduced catch after independence (Oelofsen, 1999; Boyer et al., 2001; van der Westhuizen, 2001; Roux & Shannon, 2004) (Figure 1.2), which was ascribed to the departure of the foreign fishing vessels and the strict management measures put in place after independence.

Currently, Cape horse mackerel, hake (deep-water hake and shallow-water hake) and monkfish are the three major commercially exploited fish species off the coast of Namibia (MFMR, 2018). Cape horse mackerel have been exploited by purse seine since the early 1960s (Olivar & Shelton, 1993; van der Westhuizen, 2001; Kirchner et al., 2010). The catches of Cape horse mackerel dominated the Namibian fishery for decades, reaching a peak in 1982 (FAO, 1999b Kirchner et al., 2010). After the 1990s, the catches declined until they reached the lowest records of 191 000 t in 2007 (MFMR, 2000). Although of relatively low value, Cape horse mackerel is the largest fishery in terms of landed volumes in Namibia (van der Westhuizen, 2001; Kirchner et al., 2010; MFMR, 2018).

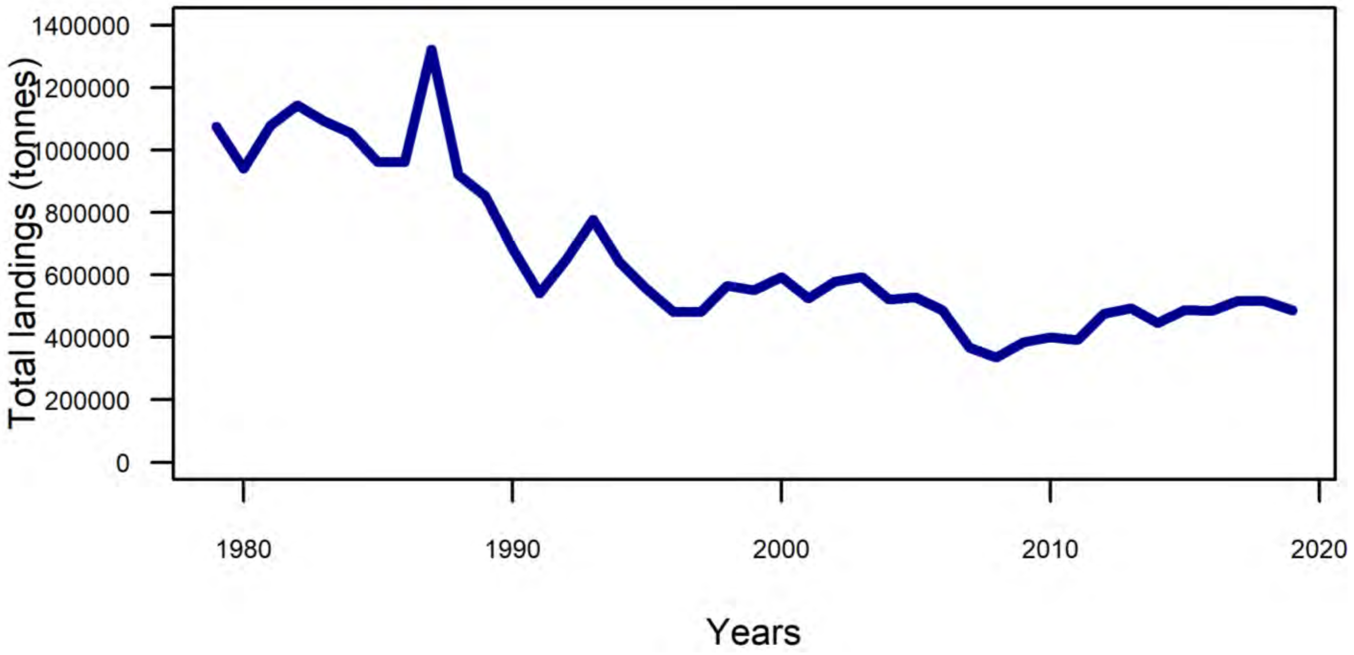


Figure 1.2: Namibia fishing total landings for nine top commercial important species: *Trachurus capensis,* hake (*Merluccius capensis* and *M. paradoxus*)*, Arctocephalus pusillus pusillus,* monkfish (*Lophius vomerinus* and *L. vaillanti*), *Chaceon maritae*, *Jasus lalandii, Sardinops sagax*, *Hoplostethus atlanticus*, and tuna (*Thunnus alalunga* and *T. obesus*) for 1979–2019.

Three hake species (*Merluccius capensis, M. paradoxus* and *M. polli*) occur in Namibian waters, with *M. capensis* and *M. paradoxus* forming the major part of the hake fishery (Boyer & Hampton, 2001; Strømme & Iilende, 2001; van der Westhuizen, 2001). The Namibian hake fishery started in the 1960s, targeted by foreign fishing fleets (Gordoa et al., 1995; van der Westhuizen, 2001) and was unregulated between 1964 and 1976, with the highest catches recorded in 1972. After 1972, hake catches decreased annually, attributed mainly to unsustainable exploitation (Butterworth & Geromont, 2001; van der Westhuizen, 2001), and they continued to decline until they reached their lowest level in 1990, a year that is currently considered a reference point in Namibian hake stock assessment. After 1990 the catches increased, up to the present. The hake fishery remains the highest contributor to GDP and employment in Namibia (Oelofsen, 1999; van der Westhuizen, 2001; MFMR, 2018).

Monkfish catches were first recorded in 1974 as by-catch in the hake (*Merluccius spp.*) targeting trawls (Maartens, 1999; Boyer & Hampton, 2001). However, as the demand for monkfish increased, a monkfish-directed fishery was developed in 1994 (Maartens & Booth, 2001a). Monkfish landings decreased to approximately 10 000 tonnes between 1995 and 1997, followed by the highest catches ever of almost 17 000 tonnes in 1998 (MFMR, 2019). Since 2000, monkfish resources have been regulated through TAC determination. Currently, most of the monkfish landed in Namibia is caught using demersal bottom trawling (Maartens, 2001; Kathena et al., 2018).

The population sizes of some species, which were of great commercial importance, have declined due to various factors, including high exploitation pressure, unfavourable environmental conditions, or both. Records of how these species have been heavily fished are profoundly disturbing (Boyer et al., 2001; van der Westhuizen, 2001; Paterson, 2015). For instance, orange roughy, and sardine fish stocks were once of significant commercial importance (Oelofsen 1999; Boyer et al., 2001b; van der Westhuizen, 2001) but have now collapsed and a moratorium has been enforced on their fisheries (MFMR, 2018). The sardine stock was abundant, estimated at 11 million tonnes in Namibian waters in the late 1960s but it declined to less than 1 million tonnes by mid-1970s due to a combination of high catches, unsustainable harvest, poor recruitment and the *Benguela Niño* events in 1972, 1984, and 1995 (Boyer et al., 2001; Erasmus et al., 2021a). The sardine stock continued to decline, which led to the first fishing moratorium in 2001 (Boyer et al., 2001; Roux & Shannon, 2004). After the moratorium was lifted, fisheries continued with limited sardine catches, but both the catches and biomass estimates continued to drop, resulting in a second moratorium imposed from 2018 to 2020 (Government Gazette of the Republic of Namibia, 2017). When a resource is found to be heavily exploited and needs a “ban” from fishery until it can recover from fishing pressure, a moratorium is imposed (Roux & Shannon, 2004; Purcell & Pomeroy, 2015; MFMR, 2018). A moratorium is a drastic measure, usually the last resort, taken to halt fishing activities (Purcell & Pomeroy, 2015). Locally, orange roughy fishery and the sardine fishery are currently under moratorium (Government Gazette of the Republic of Namibia, 2017; MFMR, 2018; Erasmus et al., 2021a).

Despite remarkable success reported in the Namibian fishing industry, such as the Marine Stewardship Council (MSC) certification of the Namibian hake fishery (https://fisheries.msc.org/en/fisheries/namibia-hake-trawl-and-longline-fishery/@@assessments), the reduction in seabird mortality (Da Rocha et al., 2021) and the recognition of Namibia as having relatively well-managed fisheries worldwide (Sumaila et al., 2004; Paterson et al., 2013), the industry still faces challenges. For instance, a large proportion of the fish captured in the monkfish fishery are undersized and should not be fished until they become part of the fishable biomass

(Maartens & Booth, 2001a); by-catches (incidental catches) (Belhabib et al., 2016) and the industry generate a lot of seafood waste (Erasmus et al., 2021b). Based on the chain analysis study by the United Nations Environment Programme (UNEP) in 2016, lack of access to capital and vessel ownership has resulted in the significant presence of foreign capital in Namibia's fishing industry, which defeats the purpose of the "Namibianisation" of the Namibian fishing industry (Chiripanhura & Teweldemedhin, 2016). Skills shortage and multiple challenges with Namibian boatmen's qualifications were also listed (Chiripanhura & Teweldemedhin, 2016) as barriers to the transformation of the industry.

1.3.2 Fisheries management in Namibia

Namibia, like other countries, is a party to several regional and international legal instruments and agreements. These include the United Nations Convention on the Law of the Sea, 1982; the United Nations Fish Stocks Agreement, 1995; the FAO Compliance Agreement, 1993; the Code of Conduct for Responsible Fisheries and its associated International Plans of Action, and the South African Developing countries (SADC) Regional Protocol on Fisheries; the 2001 Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem, and the Rio (1992) and Johannesburg (2002) declarations on sustainable development. These bodies and the laws continue to be considered in the development of the management plan of various Namibian marine species. Namibia is also a signatory nation to the 2002 World Summit on Sustainable Development (WSSD), and its management plan thus recognises the importance of an Ecosystem Approach to Fisheries (EAF) (Roux & Shannon, 2004; Wilhelm et al., 2015). In Namibia, there are studies (Heymans & Tomczak, 2016; Iitembu & Richoux, 2016) that have looked at feeding ecology at an ecosystem level, the interaction between various marine organisms, and not just focusing on single species. Several aspects, including recording seabird mortality in the hake fishery, have been revised to embrace EAF (Da Rocha et al., 2021). These actions are thus important in implementing the EAF (Layman et al., 2007; Mohanraj & Prabhu, 2012; Iitembu et al., 2021). To date, Namibia is recognised for having one of the best fisheries management policies globally (described as a model in many respects) (Sumaila et al., 2004), and won the Food Security Leadership Award in 2000 and Silver Future Award in 2012 (Paterson et al., 2013).

At a national level, Namibia has management measures in place focused on rebuilding fish stocks to their full potential, especially those that were overfished before independence (Boyer & Hampton, 2001). The steps aimed to rebuild the fish stocks started with the declaration of the EEZ in 1990 (MFMR, 1990; Oelofsen 1999; van der Westhuizen, 2001). This was followed by the draft of the Sea Fisheries Act in 1992 (Act 29 of 1992; MFMR, 1992), which was repealed in 2000 and replaced by the Marine Resources Act (Act No. 27 of 2000; MFMR, 2000). The Marine Resources Act (Act No. 27 of 2000) is regulated by the Marine Resources Regulations of 2001 (MFMR, 2001). A new White Paper, Namibia's Marine Resources Policy, was drafted in 2004 (MFMR, 2004) followed by the Marine Resources Act (No. 27 of 2000) amendment (Act No. 9 of 2015; MFMR, 2015). Fisheries management is a task of the Ministry of Fisheries and Marine Resources (MFMR), which is responsible for setting TACs, formulating policies, research, monitoring catches, vessel licensing and monitoring, surveillance and control (Oelofsen 1999; MFMR, 2000; MFMR, 2001). The National Marine Information and Research Centre (NatMIRC) of MFMR, deals with research and monitors the marine living resources to inform policy development, stock assessment and TAC determinations. NatMIRC is the research office of MFMR based in Swakopmund, Namibia. From this section, NatMIRC is referred to as MFMR. The MFMR has contracted the Fisheries Observer Agency (FOA) to complement its efforts to combat Illegal, Unreported and Unregulated (IUU) fishing, control overfishing, by-catch, undersize fish, and to collect biological data (Oelofsen, 1999; MFMR, 2000). The MFMR also works with the Namibian Maritime and Fisheries Institute (NAMFI), whose aim is to provide training and maritime vocational skills development to the staff of MFMR, FOA, supporting agencies and seafarers.

The MFMR conducts dedicated annual research surveys for the main, commercially exploited species (red crabs, deep-water and shallow-water hake, Cape horse mackerel, monkfish, orange roughy, rock lobster and sardine) using various methods such as swept-area bottom trawl, midwater trawl, acoustics, traps, and pots. The Cape fur seals research surveys (census) take place after every third year using a low-flying helicopter, whereby the researchers take pictures on seal colonies, which are later counted to quantify the number of seals. The research surveys take place at different times of the year; monkfish swept area biomass surveys take place annually in November. The main objectives of these surveys are to: obtain biomass indices of the Namibian commercially exploited fisheries, monitor recruitment, map out the geographical distribution of commercially important species, collect biological information of commercially important species, and collect environmental data to establish linkages between the environment and the species distribution (Schneider & Johnsen, 2000).

As in many other fisheries globally, entry into the Namibian fishery is limited through rights of exploitation. Fishing off the coast of Namibian without a fishing rights/licence is prohibited. Fishing companies are granted fishing rights which expire within different periods, ranging from seven to twenty years, depending on various factors specified in the Marine Resources Act (Act No. 27 of 2000; MFMR, 2000), such as the level of Namibian ownership, investments, and fishing experience. In addition to these, there are several specific management measures in place to manage the Namibian fisheries resources. The measures include TAC, licensing to limit entry into the fishery, quota system, closing season, by-catch fees and other technical measures (MFMR, 2001). There is also by-catch control. When a fishing vessel catches and lands a resource (e.g., fish) that it does not have a fishing or exploratory rights to catch, the right holder is charged with by-catch fees (Oelofsen, 1999; MFMR, 2000; Wilhelm et al., 2015). These fees are therefore important management tools. To avoid by-catch penalty fees, fishing vessels limit their species by-catch harvests, mostly by avoiding fishing grounds where these species are abundant.

Fisheries technical measures are a suite of rules governing how, when and where fishers may fish (van der Westhuizen, 2001; Moore et al., 2011; Purcell & Pomeroy, 2015; de Mitcheson, 2016). As with all fisheries, Namibia has several technical measures in place aimed at managing fishing activities off the coast. There is an annual closed season in October for the hake fishery, which came into effect in 2006 and aims at protecting juveniles and the adult spawning fish from being fished (MFMR, 2014). Fishing by trawlers (all trawlers for instance, the trawling fishing vessels targeting either hake, Cape horse mackerel or monkfish) within the 200 m isobath is restricted since 1993 by MFMR as a management measure to protect fish that aggregate to spawn and their juvenile fish, to protect small pelagic species, and to safeguard Ecologically and Biologically Significant Areas (EBSA) (Oelofsen, 1999; Sundby et al., 2001). Fisheries Restricted Areas (FRAs) play an integral part in fisheries management (Botsford et al., 2009; Purcell & Pomeroy, 2015). There are also gear restrictions in place which are specific to each fishery, for instance, the minimum cod-end mesh size is 110 mm for hake and orange roughy, 60 mm for Cape horse mackerel, 12.7 mm for sardine, and 75 mm or 110 mm for monkfish and west coast sole. The minimum cod-end mesh-sizes were set to allow the juvenile fish to escape from the fishing nets during trawling. To ensure adherence to the technical management measures, fishing vessels are fitted with comprehensive Automatic Location Communicators (ALCs) which report important vessel information to the Vessel Monitoring System (VMS) located at the MFMR`s Fisheries Monitoring Centre (FMC) in Walvis Bay. The

VMS records information on vessel position and movement (Paterson, 2015), and it is enforced through regulations.

Commercial fishing vessels fishing in the Namibian waters are mandated to carry a fisheries observer (hereafter referred to as "the Observer") aboard and to record daily fishing activities in logbooks (MFMR, 2000; Boyer & Hampton, 2001; MFMR, 2001). Recording fishery-dependent data is critical as it forms an input into stock assessment (Paterson, 2015; Kathena et al., 2018). The daily logbooks are completed by the fish vessel captain and verified daily by the observer (Boyer & Hampton, 2001; Paterson, 2015). The primary role of observers is to monitor and observe the harvesting, handling, and processing of marine resources and ensure that the at-sea provisions of the Marine Resources Act and Regulations are adhered to. The observers report any at-sea discarding that may take place and they also play an important role in collecting biological data such as length and sex, or any other data requested by MFMR.

The management of the Namibian fisheries resources is single species oriented, and species are managed through the determination of annual TACs, based on stock assessment models, to ensure the long-term sustainability of fish stocks. The main aim of the TAC is to set a limit on the quantity of particular marine resources that can be harvested within a specific period (MFMR, 2000; Mohanraj & Prabhu, 2012). The determination of the TAC involves various data, such as survey data and the commercial catch data. Once models are fitted to the data, a TAC is then recommended, based on the status of the stock. As in other countries, the recommended TAC is subject to discussions and decisions by various stakeholders with conflicting interests and takes into consideration various factors such as socio-economic factors (del Valle & Astorkiza, 2007). To promote economic efficiency, the MFMR Minister allocates the TAC as individual quotas to rights holders who have been granted rights to fish off the coast of Namibia (Oelofsen, 1999). During each fishing season, rights holders pay quota fees based on the quotas issued. Quotas are allocated based on the criteria stipulated in the Marine Resources Act (Act No. 27 of 2000; MFMR, 2000). All these target species are managed through TAC allocation: Cape horse mackerel (*Trachurus capensis*), hake (*Merluccius capensis* and *M. paradoxus*), Cape fur seals (*Arctocephalus pusillus pusillus*), monkfish (*Lophius vomerinus* and *L. vaillanti*), red crab (*Chaceon maritae*), rock lobster (*Jasus lalandii*), and sardine (pilchard) (*Sardinops sagax*). Cape monkfish, *Lophius vomerinus* Valenciennes 1837 (ex *L. upsicephalus*, Smith 1841), the subject of this study, is an important commercial and ecological fish species that thrives in the Namibian waters. Despite the economic and ecological role of Cape monkfish*,* there are knowledge gaps regarding their biology, life history and rate of exploitation.

1.4 General description of the genus *Lophius*

The genus *Lophius* of the lophiidae family has seven species worldwide: *Lophius americanus* Valenciennes 1837 off the coast of the north-eastern United States and North Carolina (Steimle et al., 1999; Able et al., 2007)*; Lophius budegassa* Spinola 1807 in the eastern Atlantic Ocean (Preciado et al., 2006); *Lophius litulon* (Jordan 1902) in the north-west and east Pacific Ocean (Yoneda et al., 2001); *Lophius gastrophysus* Miranda-Ribeiro 1915 in the south-west Atlantic Ocean; *Lophius piscatorius* Linnaeus 1758 in the north-east Atlantic Ocean (Afonso-Dias & Hislop, 1996); *Lophius vomerinus* Valenciennes 1837, previously known as *L. upsicephalus* (Smith, 1841), off the South African and Namibian coasts (Leslie & Grant, 1991; Maartens & Booth, 2001a, b; Walmsley et al., 2005), and *Lophius vaillanti* Regan 1903 off Namibia (Leslie & Grant, 1991).

Lophius species are commonly called goosefish, monkfish, or anglerfish. They are characterised by the dorso-ventrally compressed morphology of the head and body, a wide and cavernous mouth with strong jaws. Their skin is thin, with no scales and is covered in a mucous layer. These species also have a modified first dorsal fin ray, known as illicia, above their heads. Studies focusing on *Lophius* species describe them as typically sit-and-wait predators (Macpherson, 1985; Gordoa & Macpherson, 1990). They are a demersal species with no swim bladders (Griffiths & Hecht, 1986; Fariña et al., 2008). Although most of the *Lophius* species have been caught as by-catch worldwide, they now have well-developed directed fisheries targeting them (Afonso-Dias & Hislop, 1996; Steimle et al., 1999; Maartens & Booth, 2001a, b).

1.5 Cape monkfish

The Cape monkfish, *Lophius vomerinus* Valenciennes 1837 (Figure 1.3) is one of two monkfish species which occur off the Namibian coast. The other is the shortspine African Angler, *L. vaillanti*. The syntopic species are morphologically similar but differentiated by the colouration of their dorsal and ventral sides. The dorsal body of Cape monkfish is brown, and the ventral side is white, whereas the dorsal and ventral sides of the shortspine African Angler are a dark purple colour. Another distinct difference between Cape monkfish and shortspine African

Angler is the fleshy appendix on the tip of the illicium, which is present in Cape monkfish but absent in the shortspine African Angler. The Cape monkfish is the most abundant monkfish species in Namibia (Maartens & Booth, 2001a, b; Fariña et al., 2008), and is the focus species for this study.

Figure 1.3: An adult (44 cm total length) Cape monkfish, *Lophius vomerinus* held by the author during port sampling in October 2019 (Photo credit: Esther Shoopala).

Habitat

The distribution of the Cape monkfish extends from northern Namibia (21° S) to Durban, South Africa (30°S, 31°E) (Leslie & Grant, 1990; MFMR, 2020). Cape monkfish is a bottom-dwelling species, inhabiting sandy and muddy sediment waters between 150 and 500 m (Leslie & Grant, 1991; FAO, 1999b), with the highest densities occurring at 300–400 m off the coast of Namibia (Maartens, 1999). Boyer and Hampton (2001) suggested the possibility of an interaction between the Cape monkfish populations found in the southernmost part of Namibian waters and on the South African west coast. The egg and larval stage of Cape monkfish, as with other *Lophius* species, are found in the water column, but later move to a benthic existence as juveniles and adults (Fariña et al., 2008). This species is one of the most important predators in the Benguela region (Gordoa & Macpherson, 1990).

Stock structure

Cape monkfish has been reported in Namibia and South Africa (Leslie & Grant, 1990; Fariña et al., 2008). The taxonomic status of Cape monkfish, *L. vomerinus,* has not always been clear. Some studies (Griffiths & Hecht, 1986; Gordoa & Macpherson, 1990), refer to *L. vomerinus* as *L. upsicephalus*, however, Leslie and Grant (1991) revised this species and concluded that *L. upsicephalus* was a junior synonym of *L. vomerinus.*

In Namibia, this species is distributed throughout the region; however, the stock structure of Cape monkfish is uncertain. The only available genetic information is based on a historical genetic study (Leslie & Grant 1990) which found significant genetic variation between *L. vomerinus* and *L. budegassa,* and between *L. vomerinus* and *L. piscatorius*; documented that Namibian Cape monkfish individuals appear darker in colour when compared to the others (Leslie & Grant, 1990). However, there is no evidence to suggest whether the Cape monkfish off Namibia comprises a single stock or several stocks.

Fishery

Cape monkfish is a valuable component of the commercial fisheries off both Namibia and South Africa (Maartens & Booth, 2001a, b; Walmsley et al., 2005; Fariña et al., 2008). The monkfish fishery off Namibia is relatively new in comparison with other Namibian fisheries, such as the hake fishery, and as a result, research on the stock dynamics of monkfish before the mid-1990s (Boyer & Hampton, 2001) is limited. Off the coast of Namibia, Cape monkfish has been exploited since 1974 as by-catch, mainly in the hake fishery (Boyer & Hampton, 2001; Maartens & Booth, 2001a, b). However, owing to the increasing catches and demand, a monkfish fishery (targeting both Cape monkfish and the African Shortspine monkfish) was established in 1994. Monkfish is managed through TAC since the inception of its fishery in 1994. Due to the close depth distribution of monkfish and with shallow-water hakes, about 5-7 % of the monkfish TACs, is allocated to the hake directed fishery as unavoidable by-catch (Kathena, 2019). Monkfish is harvested by two fisheries: as a target species in the monkfish fishery, and as by-catch in the hake-directed fishery. Cape monkfish is harvested by both freezer (vessels that catch and process at sea) and wet fish vessels (fishing vessels that catch and process the catches onshore).

The Cape monkfish fishery has grown steadily since its inception in 1994, and the value of Cape monkfish in Namibia is especially high in terms of price per unit weight, which made it the third-highest contributor to the country’s fishing industry in 2017 (MFMR, 2018). About 94% of the total monkfish landed is Cape monkfish (Maartens & Booth, 2001a, b; Fariña et al., 2008). Studies have indicated an increase in Cape monkfish catches from less than 2000 tonnes to 12 000 tonnes since 1994 (Booth & Quinn, 2006) (as also seen in Figure 1.4).

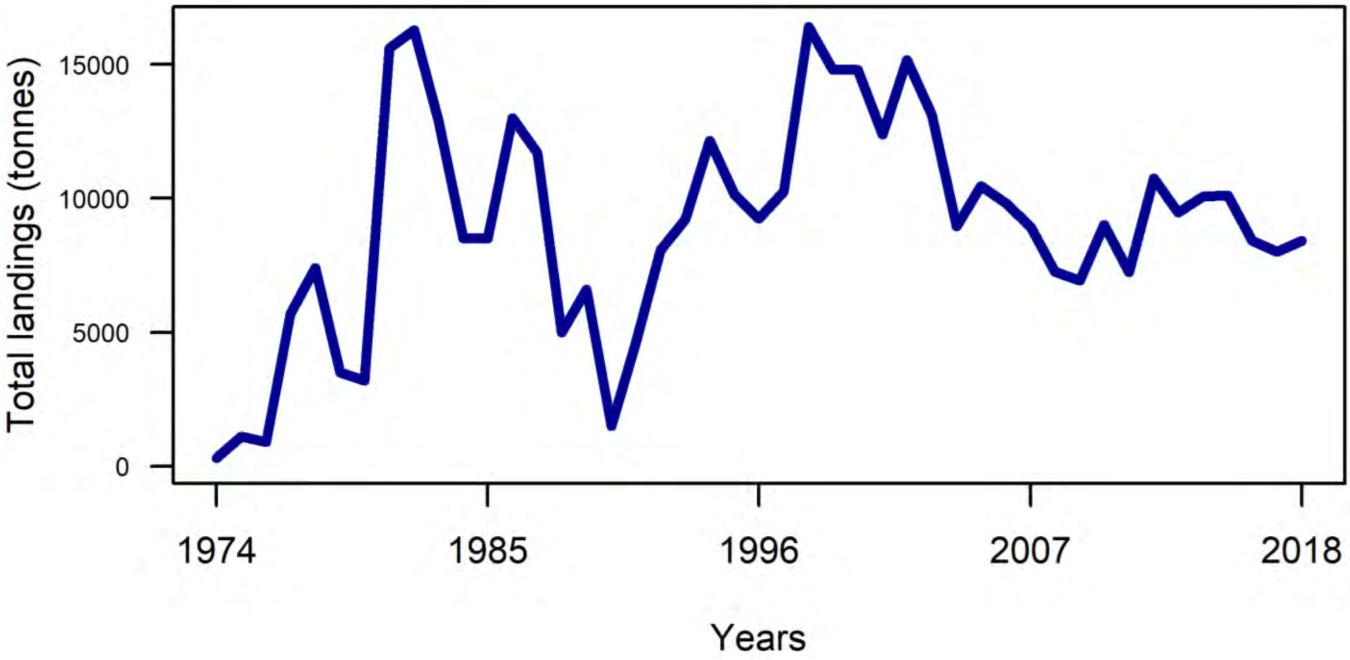


Figure 1.4: Monkfish (*Lophius vomerinus* and *Lophius vaillanti*) total catch between 1974 and 2018 and the Total Allowable Catches (TAC) set each year between 2001 and 2018, off the coast of Namibia. Cape monkfish represents 94% of the catches.

Based on a harvest rate above MSY, Cape monkfish is reported to be under extensive fishing pressure and was classified by the International Union for the Conservation of Nature (IUCN) as Near Threatened on their Red List in 2010 (Dooley et al., 2010). The IUCN assigns the following classifications: Critically endangered/Endangered = 3, Vulnerable = 2, Near Threatened = 1, and Least Concern = 0. In 2005, the monkfish abundance was already said to have been declining, based on the monkfish-directed biomass survey (Booth & Quinn, 2006). Similarly, the commercial data analysed in 2005 showed exploitable biomass during that time to be over 30% higher than MSY levels (Booth & Quinn, 2006). The species is also reported to be threatened by mercury contamination which suggests an increase in poor body condition of fish with high mercury concentrations (Erasmus et al., 2018; 2019). The latest published data (Kathena et al., 2018) estimated the MSY to be 9 000–11 000 tonnes, approximately 36–44% of its pristine state.

Life history

The Cape monkfish is a slow-growing, long-lived species, living more than 10 years (Maartens et al., 1999; Walmsley et al., 2005; Fariña et al., 2008). Female Cape monkfish grow larger than males (Maartens & Booth, 2005), a common trait in other *Lophius* species (Richards et al., 2008). Although previous studies have provided crucial information on the life-history traits of this species, it is not known how growth parameters of Cape monkfish compare between historical and contemporary times, especially in the face of climate change and extensive exploitation pressure.

The spawning behaviours and locations of Cape monkfish have not yet been described, although *Lophius* species are generally known to spawn in deep water, releasing eggs in long, gelatinous ribbons called egg veils (Afonso-Dias & Hislop, 1996; Yoneda et al., 2001; Colmenero et al., 2017). There is limited information on the spawning of the Cape monkfish, however, Walmsley et al. (2005) suggested it takes place in deeper water off South Africa. The nursery grounds of Cape monkfish are reported to be off Walvis Bay (23º–25º S) at depths between 150 and 300 m and near the Orange River 28º 35'S at depths between 100 and 300 m (ICSEAF, 1984). Male Cape monkfish mature at a smaller size (39.9 cm total length (TL)) than females (58.2 cm TL; Maartens & Booth, 2005). Reproduction aspects of the Namibian Cape monkfish are not fully understood. For instance, there are no known studies on fecundity estimation of Cape monkfish and no spawning grounds have been identified off Namibia.

Diet and feeding

An early account of Cape monkfish feeding was provided by Macpherson (1985) who described them as daytime predators. Cape monkfish are typically sit-and-wait predators; they are opportunistic, non-selective feeders, their diet influenced by the behaviour of the prey and the size of their mouths (Gordoa & Macpherson, 1990). Off Namibia, their diet primarily comprises the shallow-water hake *Merluccius capensis,* cuttlefish *Sepia australis* Quoy & Gaimard 1832, pelagic goby (*Nematogobius bibarbatus* now revised to *Sufflogobius bibarbatus* von Bonde 1923) and Angolan flying squid *Todarodes sagittatus* Adam 1962 (Macpherson, 1985; Gordoa & Macpherson, 1990).

1.6 Knowledge gaps and purpose of the study

The MFMR is tasked with the responsibility of managing fisheries resources in Namibia. This task involves implementing a knowledge-based EAF (Heymans & Tomczak, 2016; Iitembu &

Richoux, 2016; Iitembu et al., 2021), which is improved when adequate information on the fishery is attained. Although Namibia is currently using a single species approach, it is committed to the implementation of EAF. There is, however, a lack of knowledge on some of the basis of EAF.

Understanding feeding linkages provides some basis for understanding the ecosystem linkage as evident in various feeding studies (Crozier, 1985; Young & Blaber, 1986; Herman et al., 2005; Michener & Lajtha, 2007; Emmanuel & Ajibola, 2010; Iitembu & Richoux, 2015; Potts et al., 2016). These studies are good examples of how organisms relate to each other (predator-prey relationship), which is an important aspect in understanding the role that a particular organism plays in its habitat and related ecosystems (Carrasco et al., 2012; Mohanraj & Prabhu, 2012; Iitembu & Richoux, 2016). Some of these feeding linkages may be influenced by climate change because it forms an important part of EAF. Climate change, therefore, has the potential to affect the bases of EAF implementation.

Cape monkfish is an important species ecologically, chiefly because it is a top predator that feeds on a variety of prey species (Macpherson, 1985; Gordoa & Macpherson, 1990), but the strength of its feeding linkages is not known. The role that Cape monkfish plays in relation to other organisms needs to be revised, especially in relation to climate change and exploitation pressure. However, uncertainties exist surrounding the Cape monkfish resource. The species has been a commercially important fish species in Namibia for decades, historically as by-catch and since 1994 as a target species. This study attempts to fill the knowledge gaps on multiple questions concerning the feeding habits and spawning behaviours of Cape monkfish, questions that arise at annual monkfish Working Group (MWG) meetings of the MFMR. The MWG is a group of experts that includes scientists, monkfish rights holders, economists, observers, fisheries inspectors, and other stakeholders in the fishery industry who convene meetings annually to discuss matters of common interest. The main objective of these meetings is to discuss the data used in the Stock Assessment Model to determine the status of the monkfish resource and to enable scientists to provide the best possible scientific advice on management measures (as stated in various MFMR reports e.g., MFMR, 2014, 2015). These questions can only be addressed through dedicated studies on the spatial and temporal aspects of the biology and life history of the species. To date, no recent life-history studies have been conducted nor has any spatial analysis research of Cape monkfish in this region been carried out. Previous studies focusing on the biology of Cape monkfish (Maartens et al., 1999; Maartens & Booth

2001a, b; Maartens & Booth 2005; Erasmus et al., 2018, 2019) serve as baseline studies but they have not linked the biology of Cape monkfish to climate change or exploitation pressure. In this study, it was hypothesised that climate change and exploitation pressure may have altered the life-history traits, biomass distribution and the abundance of Cape monkfish, spatially and temporally. Both temporal and spatial components of research are important because they provide room for a comparison of various biological aspects. An investigation of possible long-term changes in the biology of Cape monkfish, with a focus on feeding patterns, maturation dynamics, age and growth, and exploitation patterns in Namibian waters has not yet been carried out, though exploitation patterns have been described until 2018. Such information, when linked to historical data, is critical to improve our understanding of the impacts of climate change and overexploitation of this commercially important species. Such an investigation has the potential to improve management plans of this species.

1.7 Aims and objectives of this thesis

The broad aim of this study is to contribute to our understanding of both the life history and the exploitation rate of Cape monkfish in the Namibian marine ecosystem through new research and a comparison with historical data. The objectives of this study were to:

i. identify the dominant prey species of Cape monkfish in the Namibian waters, using stomach content analysis data (from 2015 to 2018) and compare this to a historical study (from 1986 to 1987);
ii. investigate the seasonal and spatial variation of Cape monkfish diet, to identify any ontogenetic shifts in diet, and assess the trophic adaptability;
iii. examine the life history of Cape monkfish and identify any spatial and temporal changes in reproduction, including spawning area and season;
iv. investigate the differences in annual growth rates of Cape monkfish between historical (1996 to 1998) and contemporary (2014 to 2016);
v. explore changes in catch and effort temporally (from 1998 to 2018) and spatially (the Namibian waters) with a view to better understand possible changes over time, and
vi. to link any observed changes in the above to exploitation patterns and the climatic environment in the Namibian waters.

The findings from this study are expected to contribute to our understanding of biological aspects of Cape monkfish in relation to climate change and exploitation pressure; findings which will aid the successful implementation of EAF (Cochrane et al., 2009) to sustainably manage this resource. The results may also contribute to the maintenance of essential ecological processes in the environment.

1.8 Thesis overview

To achieve the aims and objectives, this thesis is divided into seven chapters. The first chapter (Chapter 1) provides a general introduction to global fishing and available knowledge on climate change. This chapter highlights how fishery species (globally) are threatened by anthropogenic impacts such as overexploitation and climate change. It gives details on the Namibian fishery, and in particular, how the demersal fishery species in Namibia are managed. It concludes with a background on the environmental conditions off the coast of Namibia and information of Cape monkfish, the subject of this study.

Chapter 2 provides a description of the study area; it gives a general description of the BCLME in which the Namibian marine ecosystem is found. This chapter also provides background information on how the data were collected (research survey, port sampling and commercial catches) and describes various historical and contemporary data sources, general methods, and maps of predetermined survey stations.

Chapter 3 presents a spatial and temporal analysis of feeding patterns of Cape monkfish in Namibia, based on stomach content analysis. A comparison between historical (Gordoa & Macpherson, 1990) and contemporary feeding habits of Cape monkfish is presented.

Chapter 4 explores the spatio-temporal analysis of the reproductive biology of Cape monkfish throughout its Namibian distribution and compares this information to historical data, extending the work of Maartens and Booth (2005).

Chapter 5 provides a comparison of historical (Maartens et al., 1999) and contemporary age and growth of Cape monkfish in Namibia.

Chapter 6 is an attempt to answer the question “Where do monkfish-targeting vessels fish?” As such it explores main monkfish fishing grounds, and possible changes in the temporal and spatial patterns of the general monkfish resource distribution and catches statistics in Namibian waters, including the trend in catch statistics of monkfish.

Chapter 7 is the final chapter and gives a general discussion linking possible changes in the temporal and spatial biological aspects of Cape monkfish to climate change and exploitation pressure. The chapter closes with conclusions and proposes recommendations in the management context.

Chapter 2: Study area and general materials and methods

Map of the Namibian coast showing the dust storm during the east wind period (photo credit: LandWaterSA)

2.1 Benguela Current Large Marine Ecosystem and the marine waters off Namibia

The Namibian waters form part of the Benguela Current Large Marine Ecosystem (BCLME), which is one of the world's four major eastern boundary currents (Hill et al., 1998; Shannon & O'Toole, 1998; Bode et al., 2014) (Figure 2.1). The BCLME is one of the most productive marine ecosystems of the world, mainly due to the strong upwelling features that provide highly productive ecosystems (Cochrane et al., 2009; Hutchings et al., 2009; Huenerlage & Buchholz, 2013; Jarre et al., 2013). It is a unique eastern boundary current because it is bounded by two warm-water regimes: the Angola Current system that separates the warm water of the Angola Current from the cold Benguela waters in the north, and by the Agulhas Current System that separates it from the Indian Ocean in the south (Shannon, 1985; Hutchings et al., 2009; Santos et al., 2012) (Figure 2.1). The BCLME has a permanent upwelling cell off Lüderitz (25º–27º S) that effectively divides it into two regions; the northern Benguela Ecosystem (nBE) north of the Lüderitz upwelling cell, and the southern Benguela Ecosystem (sBE) south of the Lüderitz upwelling cell (Figure 2.1; Shannon, 1985). The Lüderitz upwelling cell acts as an environmental barrier for some key species (van der Lingen et al., 2006; Lett et al., 2007; Hutchings et al., 2009; Santos et al., 2012). Upwelling cells of lesser intensity also occur further north, the most notable being off Cape Frio.

The BCLME is characterised by cold, nutrient-rich waters, hypoxic conditions and a high primary production that reaches an average of 400–900 g C m-2 yr-1 annually (Boyd et al., 1987; Brown et al., 1991; Heymans et al., 2004; Heileman & O'Toole, 2008). Although high primary productivity (measured by the abundance of phytoplankton) is an important feature of the BCLME, most of it ends up not utilised; it then dies, sinks and settles at the sea bottom where it creates anoxic conditions (Bailey, 1991). From time to time, the warm tropical surface waters enter the Angola Current warm (Figure 2.1). Here, the warm tropical waters mix with the cold upwelled water in the Angola-Benguela frontal (ABF) system (located at 15–17° S) (Figure 2.1) (Bartholomae & van der Plas, 2007).

The Namibian waters form part of the BCLME, covering a coastline of 1572 km, from 17°12'S, along the border with Angola (covering part of the nBE) to 29°30'S, to the border with South Africa (covering part of the sBE) (Figure 2.1). The mid-shelf Namibian waters (180–350 m bottom depth) are defined by a wind-driven upwelling cycle (Gibbons & Buecher, 2001; Hutchings et al., 2009; Jarre et al., 2013).

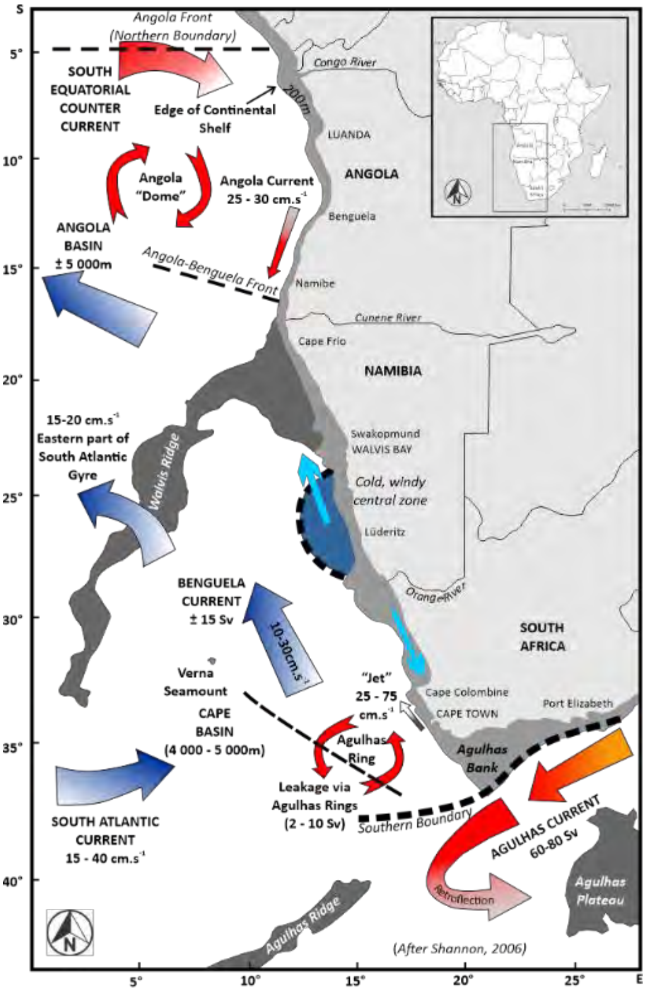


Figure 2.1: A general map of the Benguela Current Large Marine Ecosystem (BCLME) showing the major physical features within this region (adapted from Shannon, 2006, p. 4).

2.2 Environmental conditions in the Namibian Marine Ecosystem

Various environmental factors such as wind strength and direction, upwelling intensity, dissolved oxygen, and sea surface temperature give the BCLME its unique features. The BCLME is primarily a wind-driven system with an equatorward wind (Hutchings et al., 2009), thus, wind strength is an important feature of this system. Specifically, in the Namibian waters, the upwelling intensity has been fluctuating (Hutchings et al., 2009; Chen et al., 2012), driven primarily by wind strength (Jackson et al., 2013). The high abundance of phytoplankton biomass is also associated with strong winds (Hutchings et al., 2009, Louw et al., 2016). The combination of wind, rotation of the earth (Coriolis force) and Ekman transport brings cold nutrient-rich waters to the surface during upwelling (Hutchings et al., 2009). The major upwelling cell off the Lüderitz is critical for sustaining biological productivity in the Namibian waters and the BCLME and can be a limiting factor for primary production (Taylor et al., 2013).

The Lüderitz upwelling cell is the strongest wind-driven upwelling zone in the BCLME (Chen et al., 2012) and is characterised by persistent, perennial, high equatorward wind speeds that generate powerful offshore transport and mixing in the water column (Bakun, 1996; Hutchings et al., 2009; Chen et al., 2012). As such, primary production, measured by the growth of phytoplankton, is influenced by upwelling activities. The Benguela current system has a high mean annual primary production, which was reported at 1.25 kilograms of carbon per square metre in 2003, about six times higher than the North Sea ecosystem (Shannon & O'Toole, 2003). This high level of primary productivity of the BCLME supports an important global reservoir of biodiversity and biomass of zooplankton, fish, sea birds and marine mammals. Hutchings et al. (2006) reported a substantial long-term increase in zooplankton over five decades, followed by a decrease since 1995.

The distribution and abundance of marine organisms in the Namibian waters is influenced by limiting factors such as dissolved oxygen and water temperature. The dissolved oxygen level is important as it is a determining factor of habitable locations in aquatic systems (Wu, 2002). Generally, oxygen concentration increases from north to south (Bartholomae & van der Plas, 2007; Jarre et al., 2015a). However, there is variation in oxygen concentration, both at a seasonal and interannual scale and lately, frequent low oxygen events in the Namibian marine waters have been reported (Boyd et al., 1987; van der Lingen et al., 2006; Bartholomae & van der Plas, 2007; Hutchings et al., 2009). Low oxygen water in the Namibian marine waters mainly comes from the Angolan Basin (Hamukuaya et al., 1998). The effects of oxygen depletion in the water include hypoxic-anoxic conditions which further result in sulphur outbreaks (Boyd et al., 1987; Monteiro et al., 2008; Ohde & Mohrholz, 2011). Underutilisation of phytoplankton build-up at the seabed contributes to the build-up of poorly oxygenated water, possibly leading to the production of toxic hydrogen sulphide. The sulphur eruptions reduce species abundance and distribution, especially off Walvis Bay, where the most severe anoxic conditions develop regularly.

Marine organisms are reported to adjust their behaviour (e.g., feeding) in response to ocean temperature warming or cooling (Johansen et al., 2014). The BCLME experiences recurring large-scale extreme warming of the ocean waters termed *Benguela Niño* events, which have been occurring with almost decadal regularity (Shillington et al., 2006). These events occurred in 1934, 1963 (Stander & De decker, 1969), 1972, 1984 (Taunton-Clark & Shannon 1988; Florenchie et al., 2003) and 1995 (Gammelsrød et al., 1998; Florenchie et al., 2003). In 2001, the Namibian waters had another extreme warming since the last *Benguela Niño* in 1995 (Rouault et al, 2007). The 2001 warming event is not termed a *Benguela Niño* event because of its short duration, and because the intrusion of warm water did not go as far south as the other warm waters during *Benguela Niño* events (Bartholomae & van der Plas, 2007; Rouault et al., 2007). During intense *Benguela Niño* events, the intrusion of warm waters has been reported to reach as far south as Walvis Bay (22° S) (Florenchie et al., 2003). Recent environmental data collected in the Namibian marine ecosystem indicate general warming of the sea surface temperature, especially in 2007 and 2011 (Junker et al., 2017).

These events are thought to have a significant influence on the abundance of fishes (Boyer et al., 2001). Important findings on the effects of *Benguela Niño* events are detailed in Stander and De decker (1969), Shannon et al. (1986), Taunton-Clark and Shannon (1988), Gammelsrød et al. (1998), Hamukuaya et al. (1998) and Rouault et al. (2007). Some of the main consequences of *Benguela Niño* in the Namibian marine waters are fish mortalities of, for example, sardine, Cape horse mackerel and kob (*Argyrodomus inordorus*) in 1995 (Gammelsrød et al., 1998), and the displacement of fish from the northern part of Namibia toward the southern part (making fish more susceptible to fishing) (Gammelsrød et al., 1998, Boyer & Hampton, 2001; Monteiro et al., 2008).

2.3 The study area

This study was conducted off the entire coast of Namibia (Figures 2.1 and 2.2). As pointed out previously, Namibian waters form part of the Benguela Current Ecosystem, one of the four major eastern boundary current systems of the world. The area is about 1572 km long and extends from the Cunene River at 17°12'S (along the border with Angola) to the Orange River at 29°30'S (to the border with South Africa). The shelf area from the shore to a depth of 200 m is approximately 110 00 km^2, it is widest off the Orange River and off Walvis Bay, and narrowest off the Cunene River to Cape Frio (FAO, 1999b). The Lüderitz upwelling cell situated between 25° and 27°S (Figure 2.1), is a key feature of Namibia. Upwelling cells of lesser intensity also occur further north, the most notable being off Cape Frio. Additionally, the presence of a 500 km long mud belt (muddy bottom) in the mid-shelf of the Namibian marine ecosystem is a significant feature in the Namibian marine waters (Bianchi et al., 1999), and it is associated with poor oxygen concentration (FAO, 1999b). Off Namibia, strong upwelling is particularly experienced during the cooler months, which reinforces the seasonal effect and causes a definite temperature cycle (Gordoa et al., 2000).

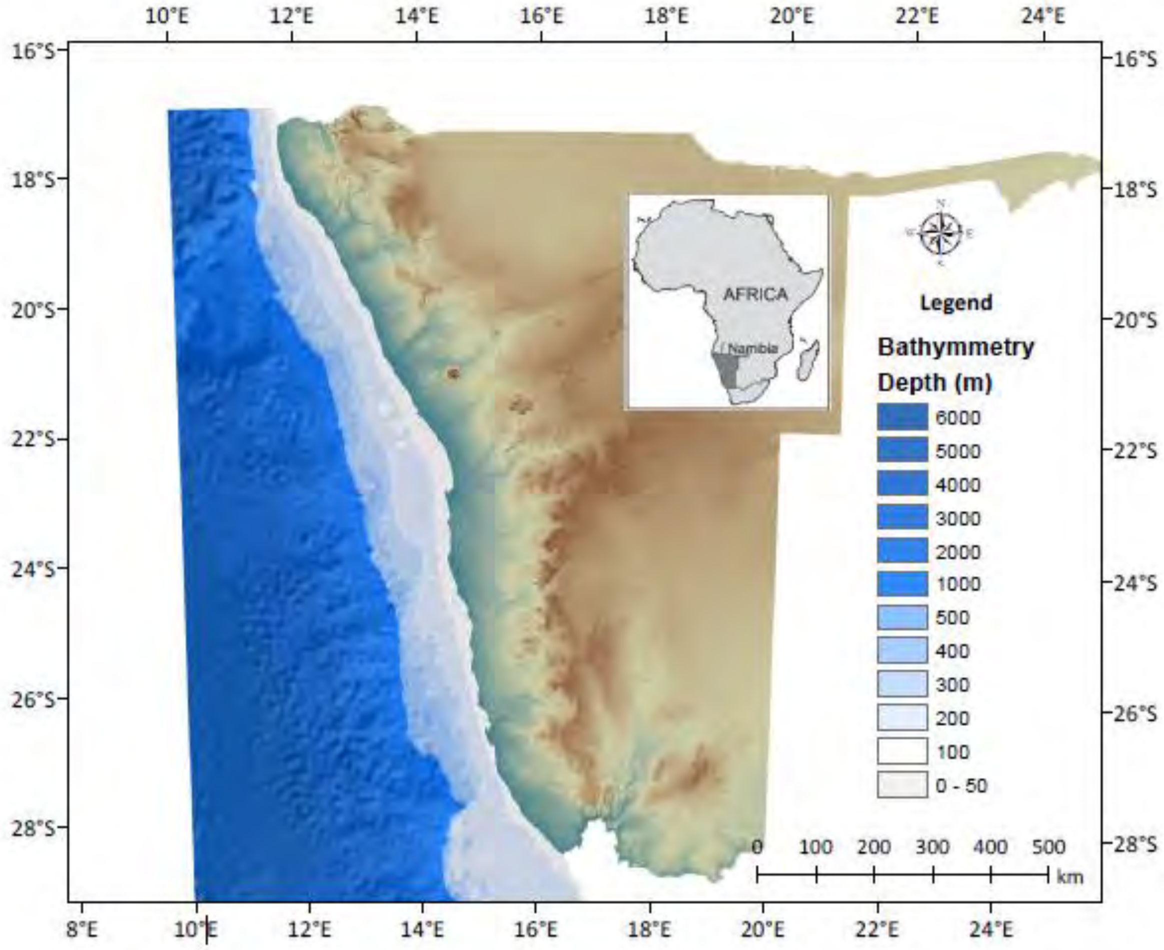


Figure 2.2: Map of the study area between 17°12'Sand 29°30'S (Namibian coast) showing the 200, 500 and 1000 m depth contour. Map constructed using ArcGIS 10.8 Software.

Fishing off Namibia takes place within the 200 nm EEZ which contains various commercially important species, including small-sized pelagic species, such as Cape anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), and medium-sized pelagic species including adult Cape horse mackerel (*Trachurus capensis*). The demersal species include hake (mostly *Merluccius capensis* and *M. paradoxus*), Cape monkfish (*Lophius vomerinus*), west coast sole (*Austroglossus microlepis*), red crab (*Chaceon maritae*) and other bottom-dwelling species. Sampling was confined between latitudes 17°12'S and 29°30'S (Figure 2.1), covering the spatial distribution of Cape monkfish. The study area ranges from depths of 90 to 837 m, which is the area fished commercially and that which is covered through research biomass surveys.

2.4 Data acquisition

Data used in this thesis were sourced from various databases and institutions summarised in Table 2.1. The spatial and temporal data collected included stomach content data (Chapter 3), reproduction and maturity data (Chapter 4), age and growth data (Chapter 5) and catch data (Chapter 6). Collection methods included survey cruises, observer sampling and port sampling. This study used historical data (1974 to 1989, collected before independence) and contemporary data (collected between 1990 and 2019). The data available for assessment of the Cape monkfish resource can be divided into fisheries-independent (research survey data) and fisheries-dependent (commercial fishing) data (Table 2.1).

Table 2.1: Details of data used in this study; data type, sampling year, data source and the thesis chapter in which the data is used.

Data type	Sampling year	Data source	Chapter in which the data is used
Biological data			
Stomach content data	2015-2018	port sampling and research survey	Chapter 3
Sexual maturity data	2004-2019	port sampling and research survey	Chapter 4
Age and growth data	2000-2005, 2007-2019	port sampling and research survey	Chapter 5
Length frequency data	2001-2018	MFMR-Fisheries Observer data	Chapter 6
			Catch data
Historical catch data	1974-1990	MFMR-ICSEAF datasheets	Chapter 6
Contemporary data	1991-2018	MFMR – fishery data	Chapter 6
Mean length	1998-2018	MFMR-fishery data	Chapter 6
Environmental data			
Bottom temperature	1998-2018	MFMR logbook data	Chapter 6
Sea Surface Temperature	1998-2018	NOAA (https://doi.org/10.7289/V5T72FNM)	Chapter 6
Other available data			
Monkfish survey data	2001-2005, 2007-2018	MFMR – survey data	Chapter 2, 3,4 & 5
Past feeding study data	1986 - 1987	Gordoa and Macpherson (1990) study	Chapter 3
Past reproduction data	1996 - 2000	Maartens and Booth (2005) study	Chapter 4
Age and growth data	1996 - 1998	Maartens et al. (1999) study	Chapter 5

2.4.1 Catch data

The daily catch data were obtained from the daily fishing logbooks of monkfish-targeting vessels between 1998 and 2018. The daily catches consisted of vessel ID, fishing position (for the first trawl of the day, fishing year, month, and day, catch in kg (a sum of the total catch for the day from all the trawls made in one day), duration of the trawl in hours (a sum of the trawling time for all trawls in a given day), vessel Gross Register Tonnage (GRT) and depth in metres (depth of the first trawl of the day).

The annual TAC data were obtained from the Economics Division under the Directorate of Policy, Planning and Economics (PPE) at the MFMR. From these data, annual total catch, and annual CPUE were calculated from 1998 to 2018. Catch data were used to determine catch and effort, and distribution and abundance patterns, both spatially and temporally. The abundance data were derived from three sources: the commercial catch data of the monkfish-directed fishery (obtained through MFMR, in Swakopmund), Fisheries Observer data (research database data (RESDAT)) obtained through MFMR, and historical monkfish catch data collected by the International Commission for South-East Atlantic Fisheries (ICSEAF) and obtained through MFMR.

2.4.2 Survey biomass data

The first dedicated monkfish swept-area biomass survey was carried out in November 2000 (Schneider & Johnsen, 2000) with the objective of testing the differences between length frequency and biomass estimates of monkfish from a hake-dedicated survey compared to a monkfish dedicated survey (Schneider & Johnsen, 2000). This investigation became an annual biomass survey and time-series data are available for 2001–2005 and for 2007–2018. The monkfish swept-area biomass surveys were carried out on *RV Welwitschia* from 2001 to 2005 but, due to delays in the tendering process, the *RV Welwitschia* was unable to carry out the annual monkfish survey in 2006. However, surveys continued uninterrupted on this vessel until 2011. In 2012, MFMR purchased a new research vessel, *RV Mirabilis,* and this research vessel has been used to conduct the annual monkfish biomass surveys since 2014.

2.4.3 Fisheries Observer data

Sampling on commercial fishing vessels was done by observers who are tasked to collect biological data on board fishing vessels. They also recorded environmental data, mostly sea surface temperature (SST), bottom temperature, sky cover and wind direction. The Observer programme (where Observers sample all commercially important species) was established in 1996 (Boyer & Hampton, 2001; Maartens & Booth, 2001b). The biological data collected, comprising species identification (species name), length (measure to the nearest cm below), sex and maturity stages, are recorded on Research Database forms (RESDAT) and brought to MFMR for data capture and analysis. Because there are variations in the education levels and ranks of observers, not all Observers collect all the data. For instance, observers with Grade 1 training level record only species identity and take length measurements, while Observers with Grade 3 training level collect and record species identity, length, sex and maturity stages. Additionally, it is almost impossible to attain 100% observer coverage, thus some fishing trips took place without observers onboard. Observer data used in this study were collected on commercial fishing vessels, which used a bottom trawl net with a head length of 55 m, a footrope of 70 m, and an average 5 m vertical net opening. Commercial vessels trawl at an average speed of 3.8 knots and an average trawling time of five hours, using either 75 or 110 mm mesh size. Data for 338 407 fish were collected from fishing trips that were undertaken from April 2001 to December 2019 at depths of between 214 and 611 m.

2.4.4 Environmental data

The only environmental data used were bottom temperature and sea surface temperature (SST). The bottom sea temperature data were collected and recorded in logbooks by fishing vessel captains during monkfish commercial fishing activities between 1998 and 2018. Even so, these data are recorded for only some trawl stations. The SST data were satellite derived from the National Oceanic and Atmospheric Administration (NOAA) (NOAA, 2020 - https://doi.org/10.7289/V5T72FNM). The SST was extracted only for the areas where monkfish catches were taken.

2.5 Study population

Cape monkfish of between 4 and 130 cm TL were considered in this study. However, for the comparison between contemporary and historical samples in Chapters 3, 4, and 5, the specific size range is described in each comparative chapter. For the comparative study in Chapter 3, fish between 20 and 75 cm TL were used, similar to the size range in Period 1 (Gordoa & Macpherson, 1990). For the comparative study in Chapter 4, fish between 6 and 99 cm TL were investigated, as was the case in Period 1 (Maartens & Booth, 2005). For the comparative study in Chapter 5, fish between 9 and 96 cm TL were considered, as this was the case in Period 1(Maartens et al., 1999). For Chapter 6, the total catch (fish of all sizes) between 1974 and 2018 was considered.

2.6 Field sampling and sample preparations

The sampling area for the contemporary data collection is shown in Figure 2.2, with specimens collected between 2016 and 2019 by the author with assistance from MFMR staff and the research vessel crew. Sampling took place at various times using different sampling techniques, depending on the type and use of the data in question. Samples were collected during annual biomass surveys of both hake and monkfish of MFMR on board the *RV Mirabilis* and following predetermined stations off the Namibian hake and monkfish survey stations. These surveys are mainly done to estimate the biomass, size composition and geographical distribution of the hake and monkfish stock off Namibia; they have been carried out since November 2000 for monkfish and 1990 for hake.

2.6.1 Hake annual biomass survey

Sampling was done on board the *RV Mirabilis* during the annual hake (*Merluccius capensis* and *M. paradoxus*) biomass surveys conducted by the MFMR. Samples for this study were collected between 11 January and 24 February 2016, and between January and February 2018, between 06:00 and 19:00. The survey used a systematic transect design. Transects ran perpendicular to the Namibian coastline, about 20–25 nm apart, with transect lengths ranging from 20 to 80 nm (Figure 2.3a). The surveys had 218 predetermined stations distributed semi-randomly along transects (Figure 2.3a). Sampling was done using a Gisund Super two-panel bottom trawl with head length 31 m, footrope 47 m with the vertical net opening of 4.2–4.5 m as described in Strømme et al. (1999). The distance between the wings during towing was 18–21 m. The depth of sampling tows was 90–600 m at an average trawling speed of three knots and average trawling time of 30 minutes. All trawl hauls were monitored by SCANMAR trawl sensors and trawl depth, bottom water temperature, catch sensors, headline height, and the distance between the doors were used to determine the vertical opening of the net, clearance from the bottom, and the distance between the doors during trawling.

2.6.2 Monkfish biomass survey

The monkfish (both *L. vomerinus* and *L. vaillanti*) swept-area biomass surveys take place annually during November. Biological samples were collected during the period of 2–17 November 2015 on board the *RV Welwitschia* and 8–24 November 2016, 11–27 November 2017 and 5–23 November 2018 on board the *RV Mirabilis*. These surveys were carried out within the boundary of the Namibian EEZ between 17 and 29° S, following 94 predetermined trawl stations (Figure 2.3b).

The monkfish research vessels operate 24 hours, making between one and eight trawls per day, depending on various factors such as weather condition, size of the catch and the distance from one sampling station to another. Trawling was mostly between 98 and 909 m. The survey design followed the optimised geo-statistical stratified random design described in Schneider and Johnsen (2000) and all other monkfish Biomass Survey Cruise Reports of the MFMR. The distance between 17°12' and 29°30'S off the coast was divided into 40 equal intervals, while the east-west direction was divided into 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 targeted an average of 30 minutes at a trawling speed of 3.5 knots; the speed was not allowed to drop below 2.5 or exceed 3.5 knots. A commercial type '*Albatross*' monkfish bottom trawl rigged with tickler chains along the footrope was used. The sweep lines consisted of 25 m double bridles and 20 m long single sweeps. 'Thyboron' trawl doors (7.93 m^2), weighing 1936 kg each were used. The cod-end mesh size was 133 mm but a smaller 50 mm blinder was installed inside the cod-end to catch smaller fish also. The SCANMAR trawl sensors were used to monitor ground-bottom contact and opening height of the trawl. The research vessel trawled in a northerly direction.

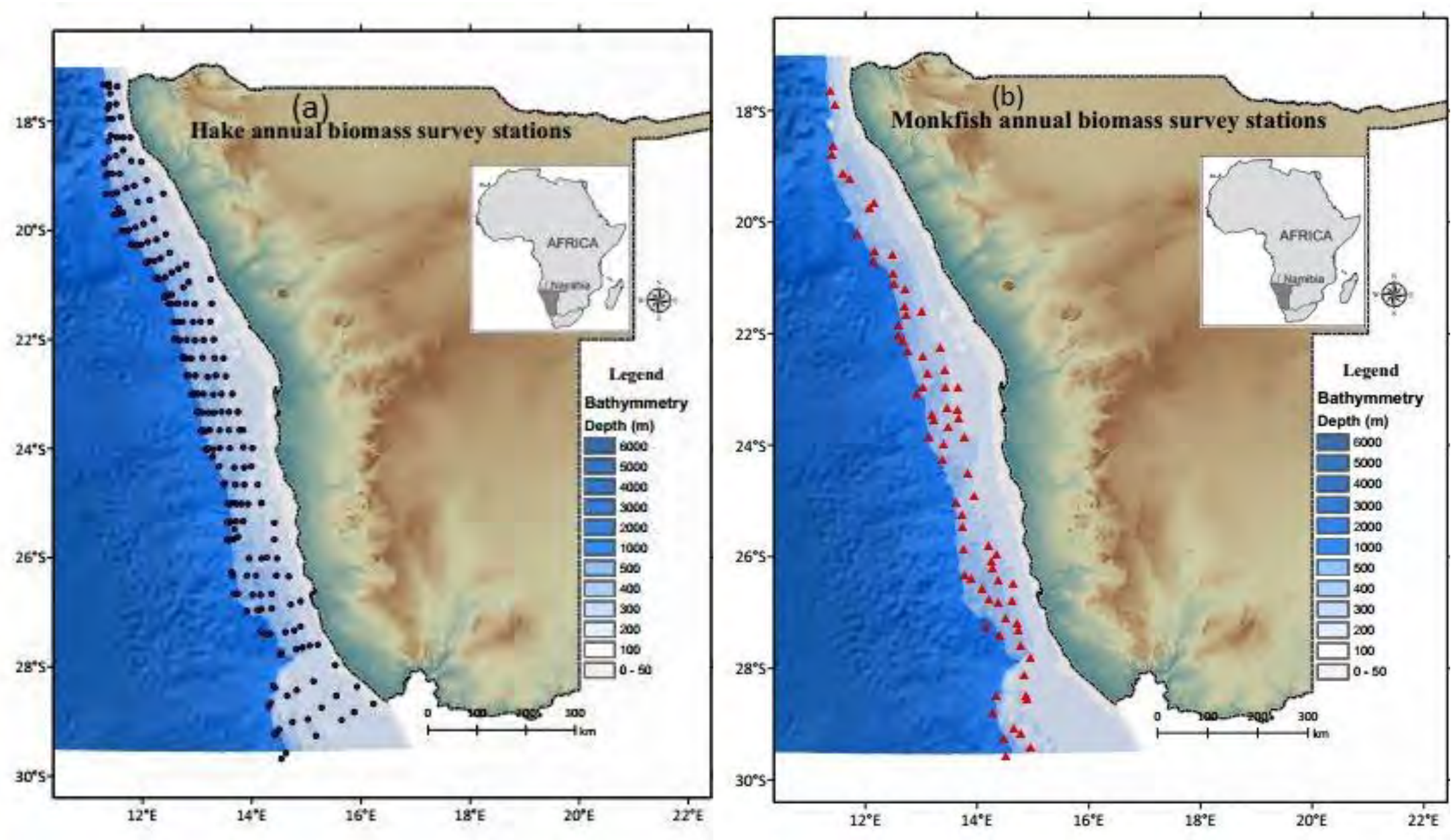


Figure 2.3: Map showing the layout of the general hake (a) and monkfish (b) annual biomass survey predetermined trawl stations off the coast of Namibia. Depth contour lines represent 100, 200, 500 and 1000 m. Map constructed by the author using ArcGIS 10.8 Software.

2.6.3 Port sampling

Additional monthly samples were collected by monkfish commercial fishing vessels from April 2014 to December 2019 (Figure 2.3) at Walvis Bay port, through a port sampling project run by MFMR. The commercial fishing vessels mostly use a bottom trawl net with a head length of 55 m, a footrope of 70 m, and an average vertical net opening of 5 m. Monkfish-targeting vessels fish at an average trawling speed of 3.8 knots and an average trawling time of five hours. These fishing vessels fished between 217 and 558 m using either 75 or 110 mm mesh size. Monkfish port sampling is an ongoing project that started in April 2014, to supplement data collected by Observers because some data (such as gonad and liver weight, otoliths, and stomach contents) are currently not provided by Observers owing to lack of experience and the unavailability of specific equipment at sea. The commercial fishing vessels pack two to three bins of whole round Cape monkfish (with head and gut) from the last trawls of their fishing trips. The samples were preserved on ice until they reached the laboratory at to MFMR within a day or two following the docking of the fishing vessels. Samples were accompanied by catch information which included the vessel name, fishing position, depth, and date of catch.

2.7 Comparison with historical studies (Gordoa & Macpherson, 1990; Maartens & Booth, 2005; and Maartens et al., 1999)

Chapters 3, 4 and 5 have comparative sections where data from the present study (referred to as ‘Period 2’) in each chapter were compared to data in three historical studies (each referred to as ‘Period 1’). For Chapter 3, ‘Period 1’ was based on a feeding study conducted by Gordoa and Macpherson (1990). These data were collected between 1986 and 1987, from 23 to 30º S, between 100 and 400 m (see Chapter 3). This was compared to data in the present study (‘Period 2’) collected between 2015 and 2018. For the comparative study in Chapter 4, ‘Period 1’ was based on the reproductive biology study by Maartens and Booth (2005). The data were collected between 1996 and 2000 off Namibia, from a depth ranging between 97 m and 686 m. For ‘Period 2’ (this study), samples were collected between 2001 and 2018 off Namibia. For Chapter 5, ‘Period 1’ was based on age and growth data collected between 1996 and 1998 by Maartens et al. (1999). These samples were collected between 1996 and 1998, from a depth of 200–450 m (see Chapter 5). These samples were compared with data from the present study (‘Period 2’) collected between 2014 and 2016.

Chapter 3: Spatial analysis of feeding patterns of Cape monkfish, *Lophius vomerinus* in Namibia

A picture of the researcher with a stomach of Cape monkfish, *Lophius vomerinus* (photo credit: Manga Simasiku).

3.1 Introduction

Information on the feeding ecology is crucial for determining the role that a particular organism plays in its habitat and ecosystem (Carrasco et al., 2012; Mohanraj & Prabhu, 2012; Iitembu & Richoux, 2016) and is thus important for implementing the Ecosystem Approach to Fisheries Management (EAF) (Layman et al., 2007; Mohanraj & Prabhu, 2012). Globally, various feeding studies have been carried out (Arrhenius, 1996; Casini et al., 2004; Madurell & Cartes, 2005; Bacha & Amara, 2009; Mihalitsis & Bellwood, 2017). Feeding studies yield information on daily rations (Madurell & Cartes, 2005), dietary relationships among organisms (Iitembu & Richoux, 2016), feeding preferences of organisms (Casini et al., 2004), dietary composition and food selectivity of various predators (Arrhenius, 1996), which in turn, contribute to our understanding of trophic ecology and energy transfer through the food web (Madurell & Cartes, 2005; Mihalitsis & Bellwood, 2017).

The spatial feeding analysis of organisms is crucial to understanding the ecology and management of a particular species, especially when considering spatial management (Gell & Roberts, 2003; Bacha & Amara, 2009; Falkenhaug & Dalpadado, 2014). Spatial dietary analysis data are essential in efforts aimed at locating the potential feeding grounds which may, in turn, be insightful for exploiting and managing these resources (Dutta et al., 2013). Fisheries management measures such as closed areas, protection of spawning grounds, and nursery areas all have a spatial component (Frid et al., 2005). By excluding spatial feeding, studies may limit efforts to manage commercially important fishery species (Khan & Fatima 1994; Bacha & Amara, 2009).

For a comprehensive understanding and prediction of the impacts of climate change on organisms, and their response to climate change, studies on feeding ecology should be explored (Davis et al., 1998; Potts et al., 2016; van der Grient & Rogersa, 2021). Knowledge about the diet of fish in relation to climate change could bring us a step closer to a solid understanding of the climate influence on fish populations dynamics (Bacha & Amara, 2009; van der Grient & Rogersa, 2021). Diet studies in the context of climate change will also provide information on the likely impact of changes in prey abundance on the species, and an understanding of the trophic adaptability of a species will improve our understanding of the impact of fluctuations in the abundance of the primary prey of a species. It is predicted that the distribution and abundance of fish populations will shift and fluctuate with climate change (Potts et al., 2016).

Species are likely to change their metabolism and therefore feeding rates, which may have food web impacts.

Globally, populations of marine resources are thought to be declining t owing to climate change (Morishita, 2008; Kirkman et al., 2013). The Namibian waters have undergone major changes especially sea surface temperature, dissolved oxygen and upwelling intensity (Monteiro et al., 2008; Jackson et al., 2013; Jarre et al., 2013). For instance, Junk et al. (2017) described warming of the Namibian waters, especially north of the Lüderitz upwelling cell, in recent years. These changes in environmental parameters are thought to have resulted in spatial changes in the distribution of some pelagic fishes (Shannon et al., 2003; Cury & Shannon, 2004) which are food for predators. Climate change in this region has resulted in increased biomass of some species, such as jellyfish and pelagic goby (Crawford, 1987; Utne-palm et al., 2010; Roux et al., 2013), while a drastic reduction in the abundance of some species, such as sardine and Cape anchovy, has been noted (Hutchings et al., 2009). While several studies (Crozier, 1985; Young & Blaber, 1986; Herman et al., 2005; Michener & Lajtha, 2007; Emmanuel & Ajibola, 2010; Iitembu & Richoux, 2015; Potts et al., 2016) have assessed the feeding habits of organisms and have expanded our understanding of the ecology of predatory fishes both the nBE and sBE, only limited studies exist that examine trophic adaptability and the complex effect of climate change on species interactions (Wisz et al., 2013). Few studies (except Potts et al., 2016) have examined changes in the diet of predatory fishes over time.

The Cape monkfish, *Lophius vomerinus*, which supports an important commercial fishery off the coast of Namibia, historically as by-catch and recently as a target species (see Chapter 1), is an important predator in the Namibian waters. Despite its economic and ecological importance (Maartens & Booth, 2001a,b; 2005), there is a paucity of information on its biology and ecology, and only limited information is available on diet composition and prey selectivity for Cape monkfish (Macpherson, 1985; Gordoa & Macpherson, 1990). Monkfish are typically non-selective predators, relying on ambush behaviour to attract potential prey using the modified first ray of the dorsal fin that acts as a lure (Crozier, 1985; Laurenson & Priede, 2005; Johnson et al., 2007; Fariña et al., 2008; Maguire et al., 2008). Detailed information on food habits and diet composition is only known for *Lophius americanus* (Johnson et al., 2007; Fariña et al., 2008; Johnson et al., 2008), *Lophius piscatorius* (Crozier, 1985; Laurenson & Priede, 2005), *Lophius budegassa* (Preciado et al., 2006), and *Lophius litulon* (Jordan 1902) (Yoneda et al., 2001; Fariña et al., 2008). The Cape monkfish off the coast of Namibia and South Africa has been reported to feed on hake (*Merluccius spp*), cuttlefish (*Sepia australis*), pelagic goby (*Sufflogobius bibarbatus*) and ladder dragonets (*Paracallionymus costatus* Boulenger 1898) (Macpherson, 1985; Gordoa & Macpherson, 1990; Walmsley et al., 2005). While the Gordoa and Macpherson (1990) and Macpherson (1985) studies provided some baseline biological information of this species, from which comparisons can be made, there are still knowledge gaps on dietary composition and cannibalism, including an understanding of the food web relationships in the Namibian waters.

Feeding behaviours of marine organisms have been extensively studied, using various techniques such as fatty acid profiles (Iitembu & Richoux, 2016), stable isotope analysis (SIA) (Iitembu et al., 2012; Erasmus & Iitembu, 2019) and stomach content analysis (SCA) (Casini et al., 2004; Dutta et al., 2013). The SCA techniques have been used to understand the feeding ecology of organisms for decades (Pennington, 1985; Varela et al., 2013). However, this method has drawbacks, one of which is the difficulty of identifying partially digested prey items (Mqoqi et al., 2007; Mohanraj & Prabhu, 2012; Iitembu & Richoux, 2015; Saikia, 2015), the differential digestion rates of prey items which introduce bias (Tollit et al., 1997), and the instantaneous "snapshot" of the most recent meals, which provides limited evidence of long-term feeding patterns of the individual (van der Lingen & Miller, 2011; Carrasco et al., 2012). Despite these limitations, SCA provides a direct method for measuring food web deformation (Michener & Lajtha, 2007) and identifies the common foods ingested by a predator population (Saikia, 2015). Additionally, the SCA results can be obtained right away without delay, it is easy to record presence and absence of prey items and SCA requires fewer and less sophisticated tools (scissors, measuring tape, scale, sieve, and microscope). Although demersal fish are in some cases known to regurgitate their stomach when brought to the surface (Carrasco et al., 2012), this technique is still considered appropriate for species like the Cape monkfish as they do not have a swim bladder (Griffiths & Hecht, 1986; Thangstad et al., 2002; Fariña et al., 2008) and therefore do not regurgitate stomach contents.

This chapter aims to contribute to our spatial and temporal understanding of the diet and feeding habits of Cape monkfish, including prey composition, cannibalism aspects, trophic adaptability, and ontogenetic shifts in their diet. This research was carried out by comparing the historical stomach content data (Period 1, Gordoa & Macpherson, 1990) with that collected during this study in order to explore possible changes in feeding over time.

3.2 Materials and methods

3.2.1 Field sampling

Sampling was conducted during (i) annual monkfish (*Lophius* spp) swept-area biomass surveys, (ii) hake (*Merluccius* spp) annual swept-area biomass surveys and (iii) the commercial monkfish-directed fishery via the port sampling initiative (Table 2.1). In total, 896 (4–115 cm TL) Cape monkfish were collected between 17°12'S (along the border with Angola) and 29°30'S (to the border with South Africa) at depths from 150 m to 619 m (Figures 2.2 and 3.1) between February 2015 and November 2018 (Table 3.1). The specimens were classified as juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50} – L_{100}, 37 – 47cm TL) and adults (> L_{100}, 47cm TL) Cape monkfish.

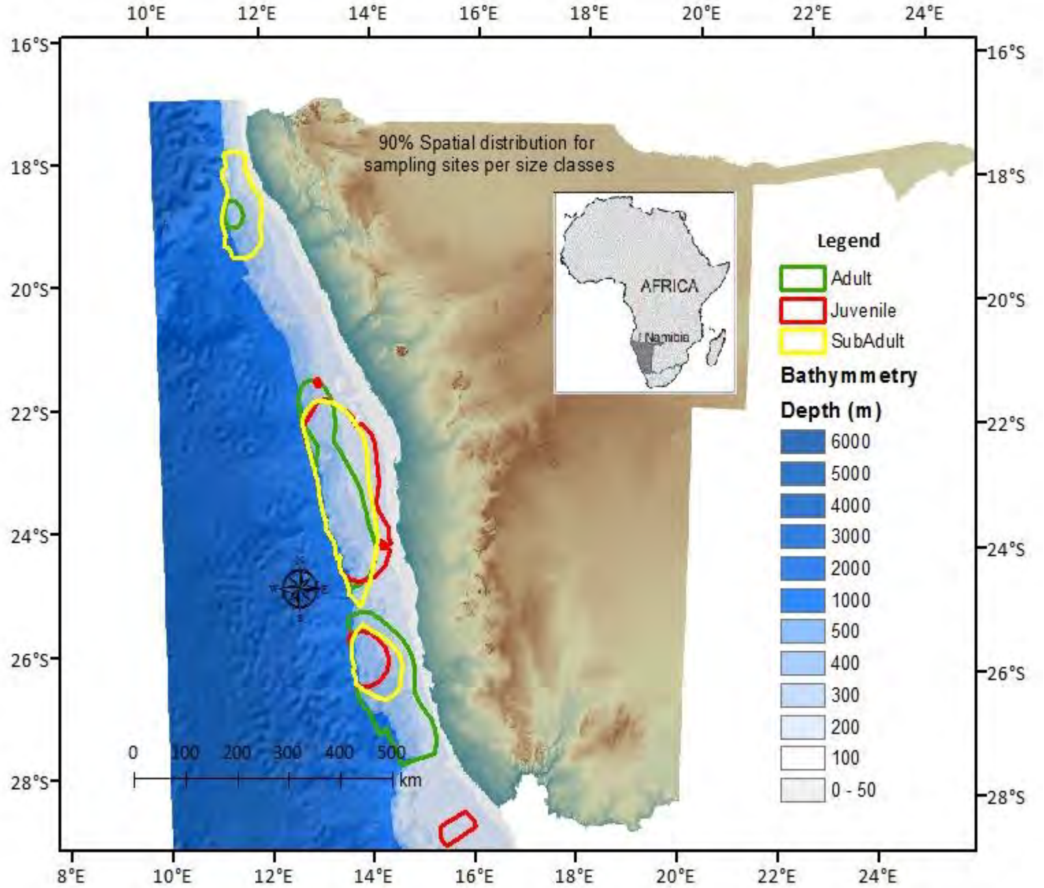


Figure 3.1: Map indicating areas where juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50} – L_{100}, 37 – 47cm TL) and adults (> L_{100}, 47cm TL) Cape monkfish, *Lophius vomerinus* were sampled off the coast of Namibia between 2015 and 2018. Areas are shown as polygons of 90th percentile of the kernel density. Map constructed using ArcGIS 10 Software.

The samples used for the feeding study were collected during the monkfish annual biomass surveys (described in Chapter 2, Section 2.6.2) during the period of 2–17 November 2015, 8–24 November 2016, 11–27 November 2017 and 5–23 November 2018. During the survey, stomachs were collected from between four and six specimens from each trawl when Cape monkfish was present. Additional samples were collected during the commercial monkfish-directed fishery via the port sampling programme (described in Chapter 2, Section 2.6.3). Sampling was conducted monthly between February 2015 and November 2018, on board commercial fishing vessels as shown in Table 3.1. On average about 40 fish are sampled twice a month are received for port sampling, however only about 15 stomachs are collected per month. No sampling occurred in October because the fishing season for hake is closed and most fishing vessels, including some monkfish-targeting vessels, do not trawl in October.

On board the research vessel and/or in the laboratory, sampled fish were measured (total length) to the nearest cm below, gutted and weighed wet to the nearest gram (g), sexed and the maturity stages were categorised and recorded. Stomachs of individual fish were cut out, weighted and placed in plastic bags that were sealed and frozen at -20 ºC to limit post-capture digestion (Andersen, 2012). Information of the samples used in SCA is described in Table 3.1.

Table 3.1: Sampling information for stomach contents of Cape monkfish, *Lophius vomerinus*, collected between February 2015 and November 2018 off Namibia; sampling month, number (n), total length (cm), wet weight (g), and sampled depth (m).

Sampling month	N	Size range (cm TL)	Wet weight range (g)	Depth range (m)
January	61	24–115	194–22750	177–356
February	51	13–84	52–11691	172–381
March	59	26–73	233–5032	313–483
April	62	28–84	314–13531	262–403
May	78	9–93	5–10825	262–421
June	87	22–82	140–7417	291–439
July	80	27–69	224–4880	267–375
August	115	25–85	200–7080	267–388
September	124	6–72	2–5821	296–395
November	94	4–96	2–17200	150–619
December	85	36–67	630–5315	339–406
Total	896			

3.2.2 Analysis of stomach contents

Stomachs were defrosted and laid out on towelling to remove excess water. Items in the buccal cavity were purposely excluded from the analysis. The stomach was then weighed, cut open with scissors, after which, the content was emptied into a sieve. Prey items found were sorted and identified to the lowest taxon possible, depending on the state of digestion. The names of the species recovered in the analysed stomachs were verified using the electronic Eschmeyer's Catalog of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). The otolith (as hard remains) found in the examined stomachs were retained and matched to the otoliths of known fish. The prey items were also enumerated, weighed to the nearest 0.01 g and measured to 0.01 cm where possible. The digestive state for each recovered prey item was estimated using a digestive stage table (see Appendix A) and recorded. All recovered prey items in digestive Stage 1 (fresh) were excluded from the analysis, because they are mostly fed on in the net, termed “net feeding”, and they have the potential to bias the analysis if not excluded (Zacharia & Abdurahiman, 2004). In total, 896 stomachs were examined, of which specimens of Cape monkfish were grouped into three size categories; juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50} – L_{100}, 37–47 cm TL) and adults (> L_{100}, 47 cm TL) (Table 3.2). For juvenile fish, 210 stomachs were examined, and 110 stomachs were empty. For sub-adults, 299 stomachs were examined of which 116 were empty. For adult fish, 387 stomachs were examined and 165 of these were empty. Unfortunately, it was not possible to analyse comparable numbers of samples from each geographic location due to the sporadic nature of the trawls and therefore such a bias must be considered when analysing and interpreting the data.

3.2.3 Comparison with historical feeding study (Gordoa & Macpherson, 1990)

For the comparative study, stomach content data collected during Period 1 were compared to data collected in Period 2 (this study). For this chapter, Period 1 refers to the study by Gordoa and Macpherson (1990) (see Chapter 2). The samples in Period 1 were collected between 1986 and 1987, from 23 to 30° S, between 100 and 400 m. For Period 2 (this study), samples were collected between 2015 and 2018 from the same area. The area was sectioned into three areas; (i) ‘Area 1’: 23°00’S to 27°59’S at 100–300 m, (ii) ‘Area 2’: 23°00’S to 27°59’S at 300–400 m, and (iii) ‘Area 3’: 28°00’S to 30°00’S at 100–300 m. Fish size ranges were the same as in the historical classes, ranging between 20 and 75 cm, and divided into three size classes; (i) 20–

39 cm, (ii) 40–59 cm and (iii) 60–75 cm TL. For historical studies (Gordoa and Macpherson, 1990), no original field data were available, thus only the study description, methods used (limited) and the results were compared to the contemporary study.

3.2.4 Data analysis

Diet composition and relative importance of prey items

Specimens of Cape monkfish were grouped into three size categories; juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50} – L_{100}, 37–47 cm TL) and adults (> L_{100}, 47 cm TL), based on the length at maturity ogives estimated by Walmsley et al. (2005). The Index of Relative Importance *(IRI)*, for each prey species, was calculated based on the formulae described in Pinkas et al. (1971):

(i) $IRI = (\%N + \%W)\ \%F$ (Equation 3.1)

where $\%N$ is the percentage of a certain food organism, $\%W$ is the percentage of food weight and, $\%F$ is the percentage of frequency of occurrence.

The percent *IRI* was then calculated for each of the prey items at each life stage as:

(ii) $\%IRI = (IRI/\sum IRI) \times 100$ (Equation 3.2)

For this study, the %*IRI* was grouped into four categories; where items contributing (i) > 30% *IRI* were regarded as dominant prey, (ii) between 10.1 and 29.9% *IRI* were regarded as secondary, (iii) between 1 and 10% regarded as less important, and (iv) < 1% *IRI* were regarded as incidental prey.

Variation in feeding intensity

The feeding intensity was investigated by means of number and percentage of empty stomachs per: (i) size class, (ii) season, and (iii) depth strata. A chi-squire test was used to examine the correlations between the proportion of empty stomachs and size class, season and depth strata. The size classes are described above. The seasons considered were summer (December–February), autumn (March–May), winter (June–August) and spring (September–November), from February 2015 to November 2018. The depth where samples were collected were grouped into four depth strata: (i) < 200 m, (ii) 200–299 m, (iii) 300–400 m and (iv) > 400 m.

Seasonal dietary trends

A chi-squire test was used to examine the compare dietary composition and seasons between February 2015 and November 2018, by comparing the *%IRI* contributions of prey items to the diet of the three size classes by season. The seasons are described above. February 2015 to November 2018.

Spatial dietary trends and diet composition in the contemporary study

A regression analysis was used to compare the relationship between dietary composition and four depth categories. Specimens were grouped into four depth strata: (i) < 200 m, (ii) 200–299 m, (iii) 300–400 m and (iv) > 400 m. The prey diversity was calculated using the Shannon-Wiener diversity index for the four areas: (i) Cape Frio upwelling cell, (ii) Central region, (iii) Lüderitz upwelling cell and (iv) Southern region, for Study 1.

Spatial variation in diet composition was analysed as a single dataset portioned into a 10 x 10 nm grid. To examine the results in terms of historical information, three geographical areas based on features of the Namibian coast (Monteiro et al., 2008; Chen et al., 2012; Bode et al., 2014) were also included in the mapping: (i) 17°12'S–19º59'S (Cape Frio upwelling cell), (ii) 20°00'S–25º59'S (Central region), (iii) 26°00'S–27º59'S (Lüderitz upwelling cell) and (iv) 28°00'S–29º59'S (south of the Lüderitz upwelling cell). Data were confined between 100 and 700 m owing to the distribution of the study species. Additionally, the area between 28º59' and 29º24'S was excluded since there is limited commercial fishing in that area, mainly because of the rocky bottom (Schneider & Johnsen, 2000). Spatial variation in dietary composition was explored using non-metric multidimensional scaling (nMDS) and hierarchical cluster analysis, followed by a Permutational Multivariate Analysis of Variance (PERMANOVA; 1000 permutations). Principal component analysis (PCA) was carried out to examine the spatial pattern of relationships among all prey species in the diet. The dependence of similarity on the selected metric (Bray-Curtis metric) was plotted using the Shepard diagram. All spatial data were visualised using ArcGIS software version 10.8 on a Geographic Information System (GIS) (URL https://www.arcgis. org/).

Predator-prey size relationships

The relationship between predator size and prey size was investigated using Pearson's product-moment correlation (Zar, 1999). A linear model (lm.01) was used to fit a trendline. Calculations were done using R version 3.3.1 (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018).

Comparison with the historical feeding study (Gordoa & Macpherson, 1990)

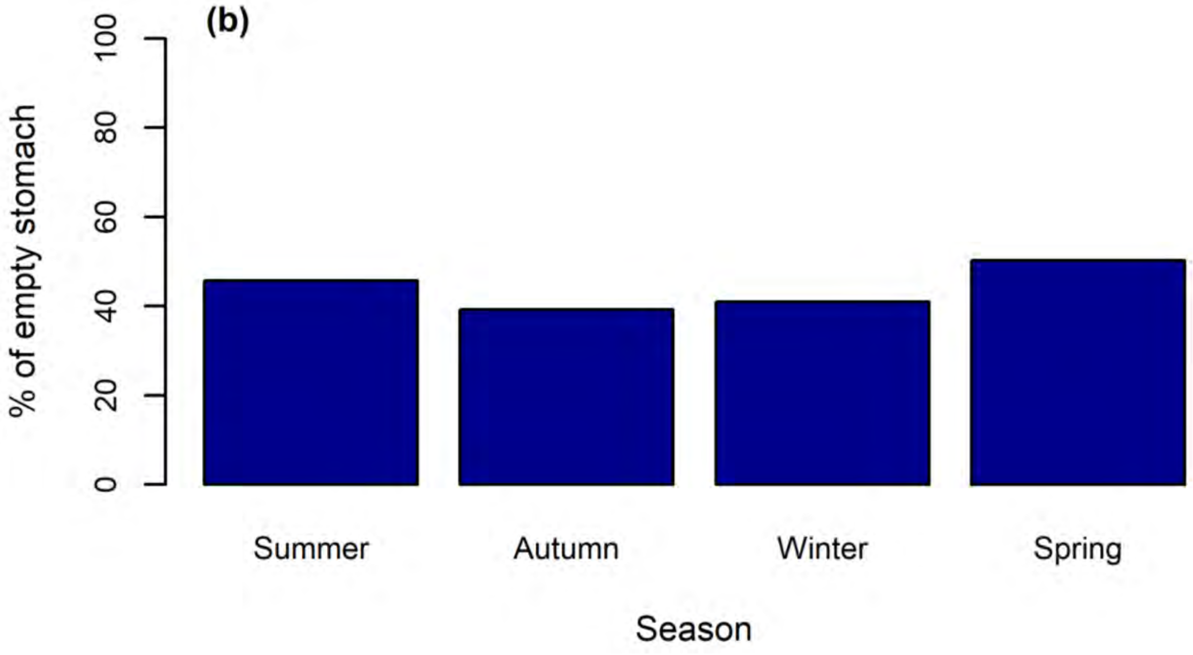
A comparison between the findings of this study (Period 2) and those from a previous historical feeding study (Period 1, Gordoa & Macpherson, 1990) was conducted. The dietary composition of Cape monkfish was compared for the same locations and depth; (i) 23º00'S to 27º59'S at 100–300 m ('Area 1'); (ii) 23º00'S to 27º59'S at 300–400 m ('Area 2') and (iii) 28º00'S to 30º00'S at 100–300 m ('Area 3'), and same size classes; (i) (20–39 cm, 40–59 cm and (ii) 60–75 cm TL. A non-metric multidimensional scaling (nMDS) was applied to the data to compare dietary species composition in the same areas for the two periods ('Period 1' and 'Period 2'). A PCA was carried out to examine the relationship pattern among all prey species in the diet of the Cape monkfish sampled from six areas used in the comparative study. Data analysis was performed using R version 3.3.1 (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018).

3.3 Results

3.3.1 Variation in feeding intensity

A high number of empty stomachs were recorded overall (43.9%), with a greater frequency of empty stomachs found in juveniles (52.9%) than in adults (42.8%) and sub-adults (38.8%). However, the difference between empty stomachs across size classes was not significant ($X^2 = 2.3473$, df = 2, $p = 0.3092$) (Figure 3.2a). There was a significant negative correlation ($r = -0.63$) between the proportion of empty stomachs and predator size. For the empty stomachs per season, a Chi-square test showed a significant difference ($X^2 = 26.08$, df = 3, $p < 0.05$) in the proportion of empty stomachs across seasons, with the highest proportion of empty stomachs recorded in spring (50.2%) and the lowest in autumn (39.2%) (Figure 3.2b). A significant difference was observed in the proportion of empty stomachs among depth strata ($X^2 = 2861.4$, df = 3, $p < 0.05$) and there was a weak correlation between the proportion of empty stomachs and depth ($r = -0.14$, $p > 0.05$) (Figure 3.2c).


(a)
% of empty stomach
0
20
40
60
80
100
Juvenile
Sub-adult
Adult
Size classes


(b)
% of empty stomach
0
20
40
60
80
100
Summer
Autumn
Winter
Spring
Season

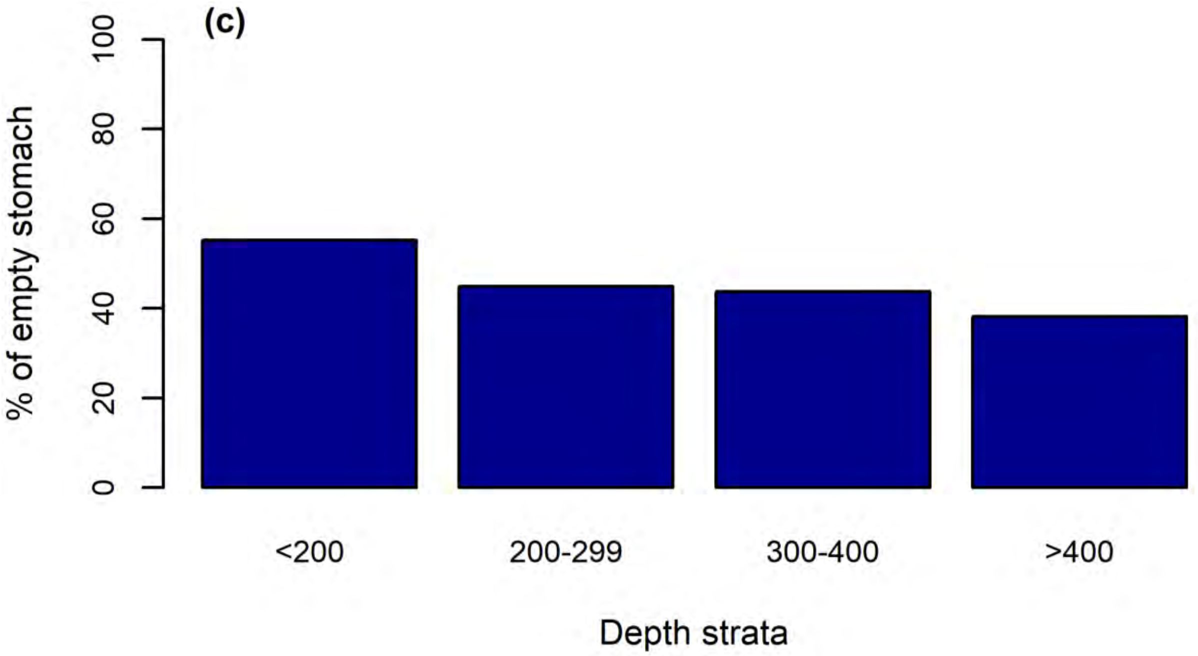


Figure 3.2: Proportions of empty stomachs for Cape monkfish, *Lophius vomerinus*, collected off Namibia between 2015 and 2018, according to size classes; juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50} – L_{100}, 37 – 47cm TL) and adults (> L_{100}, 47cm TL) (a), season; summer (December–February), autumn (March–May), winter (June–August), spring (September–November) (b) and depth strata; (i) < 200 m, (ii) 200–299 m, (iii) 300–400 m and (iv) > 400 m (c).

3.3.2 Diet composition and relative importance of prey items

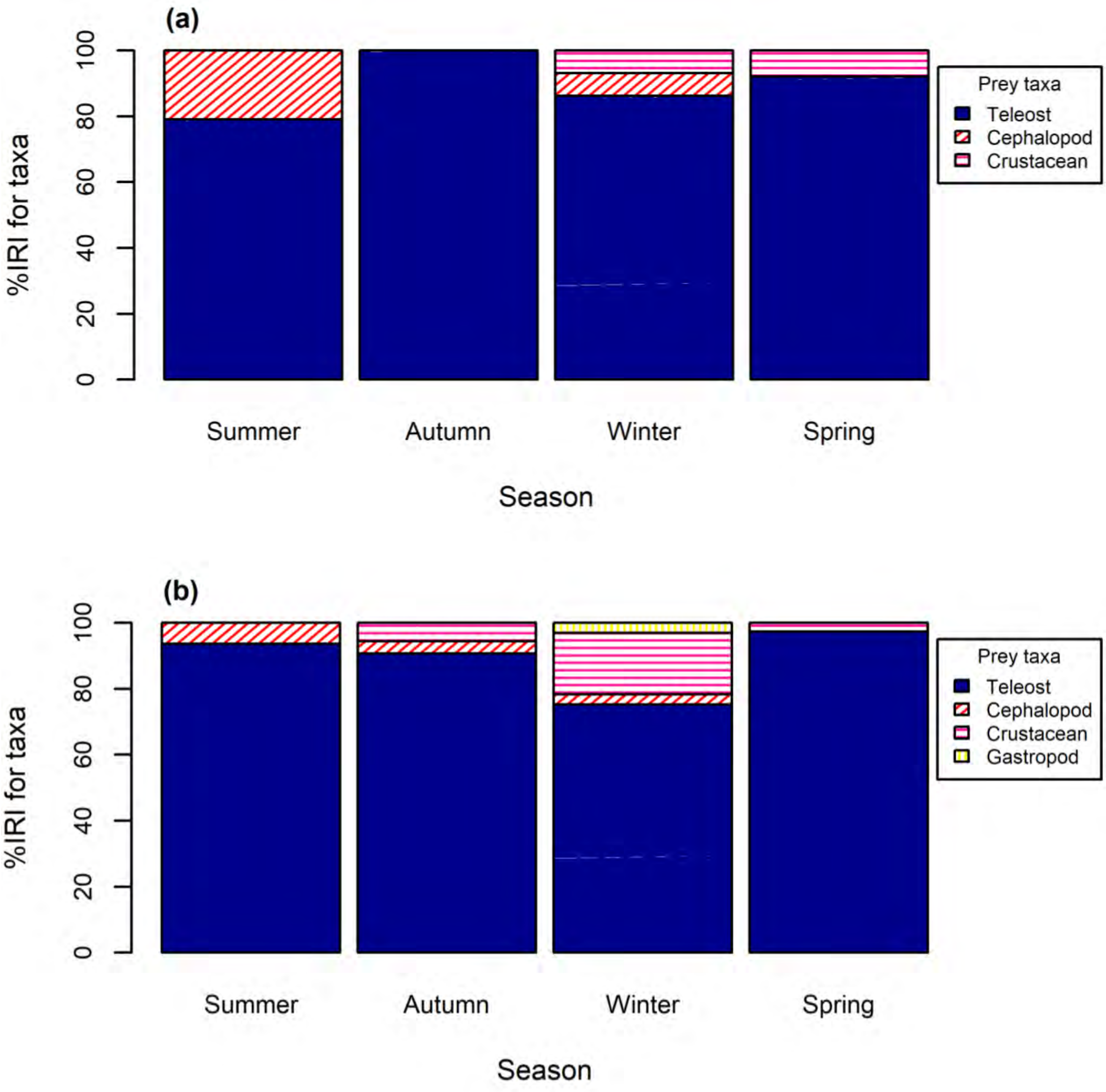
The stomach contents of the 896 fish examined contained a variety of pelagic and benthic prey items belonging to seven taxa (teleosts, cephalopods, crustaceans, echinoderms, elasmobranchs, gastropods, and porifera). Of the stomachs containing food, 60% contained a single prey type. The main prey taxa observed in Cape monkfish were crustaceans, cephalopods and teleosts. From the values of %*IRI*, teleosts dominated the diet of all size classes (%*IRI* > 90%). *Merluccius paradoxus* was the most dominant prey species for all size classes, but more so in adult fish (%*IRI* = 89.7%), followed by sub-adults (%*IRI* = 47.2%) and juveniles (%*IRI* = 30.2%). Although crustaceans, elasmobranchs, echinoderms, gastropods, and porifera were observed in the diet, they contributed little (< 1% *IRI*, Appendix B). Juvenile Cape monkfish (< L_{50}, 37 cm TL) (n = 210) fed predominantly on teleosts (%*IRI* = 97.2%), cephalopods (%*IRI* = 2.2%) and crustaceans (%*IRI* = 0.7%) (Appendix B). Their diet was dominated by *Sufflogobius bibarbatus* (18.1%) and unidentified fish (17.2%) in terms of percentage of number, and by *M. paradoxus* (16.3%) and *Caelorinchus simorhynchus* (9.7%) in terms of percentage of wet weight. *Sufflogobius bibarbatus* were most frequently observed (*%Fc* = 18.7%) in the juvenile stomachs (Appendix B). The stomach contents of sub-adults (L_{50}–L_{100}, 37–47 cm TL) (n = 299) were dominated by teleosts (%*IRI* = 99.2%), crustaceans (%*IRI* = 0.07%), cephalopods (%*IRI* = 0.76%), and gastropods (%*IRI* <0.01). Unidentified fish (18.1%), *M. paradoxus* (15.9%) and *Merluccius* spp (9.3%) were numerically dominant, while *Helicolenus dactylopterus* (15.7%) and *M. paradoxus* (29.8%) dominated in terms of wet weight. *Merluccius paradoxus* (*%Fc* = 15.9%) and unidentified fish (*%Fc* = 19.3%) were the items most frequently observed in the stomachs (Appendix B).

All seven taxa (teleosts, cephalopods, crustaceans, echinoderms, elasmobranchs, gastropods, and porifera) of prey were observed in the stomachs of adults (> L_{100}, 47 cm TL) (n = 387). *Merluccius paradoxus* dominated the diet of adults in terms of percentage in number (33.7%), wet weight (58.4%) and frequency of occurrence (*%Fc* 28.5%). Cannibalism was only observed in 0.7%, of the stomachs examined.

3.3.3 Seasonal dietary trends

Juvenile Cape monkfish fed exclusively on teleosts in autumn (%*IRI* = 100) and on teleosts (%*IRI* = 79.1%) and cephalopods (%*IRI* = 20.9%) in summer. Teleosts were the dominant prey item in winter (%*IRI* = 86.2) and spring (%*IRI* = 92.1), with crustaceans the most important secondary prey items in winter (%*IRI* = 6.9) and spring (%*IRI* = 7.9) (Figure 3.3a and Appendix C). Similarly, teleosts were the dominant (%*IRI* > 74) prey item of sub-adults in all seasons, while cephalopods were secondary items in summer (%*IRI* = 6.3). Crustaceans were secondary items (%*IRI* = 6.3%, 5.6%, 8.6% and 2.7%) in autumn, winter, and spring, respectively. Gastropods (%*IRI* = 3.1%) were only consumed by sub-adults in winter (Figure 3.3b and Appendix C).

Like the other life stages, teleosts dominated the diet of adult Cape monkfish in all seasons. However, secondary prey items were more varied in adults and included cephalopods (%*IRI* = 8.5%, 13.7%, 9.8% and 16.1%) in all four seasons. Echinoidea were only consumed in summer (%*IRI* = 8.4%). Gastropod and Porifera were consumed only in winter, where they were the least important items (%*IRI* = 1.2%), while elasmobranchii were consumed only in autumn, where they were the least important items (%*IRI* = 1.7%) (Figure 3.3c and Appendix C). A Chi-squared test on the %*IRI* contribution of prey items consumed indicated that stomach contents were significantly different between the seasons for juveniles ($X^2 = 114.2$, df = 6, $p < 0.05$), sub-adults ($X^2 = 49.024$, df = 9, $p < 0.05$) and adults ($X^2 = 203.36$, df = 18, $p < 0.05$).


(a)
%IRI for taxa
0
20
40
60
80
100
Summer
Autumn
Winter
Spring
Season
Prey taxa
Teleost
Cephalopod
Crustacean
(b)
%IRI for taxa
0
20
40
60
80
100
Summer
Autumn
Winter
Spring
Season
Prey taxa
Teleost
Cephalopod
Crustacean
Gastropod

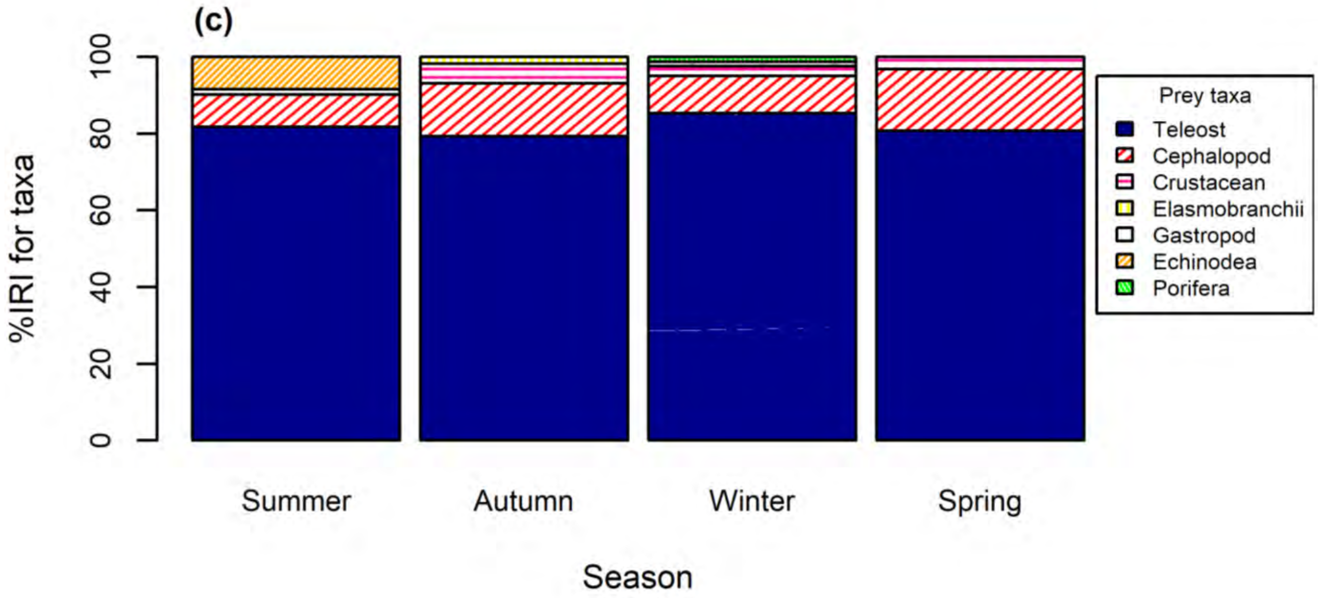


Figure 3.3: Seasonal stomach content analysis composition, illustrated by the percentage Index of Relative Importance (%*IRI*) of Cape monkfish, *Lophius vomerinus*, collected off Namibia between 2015 and 2018, according to size classes, (a) juveniles (< L_{50}, 37 cm TL), (b), sub-adults (L_{50} – L_{100}, 37 – 47cm TL) and (c) adults (> L_{100}, 47cm TL).

3.3.4 Spatial dietary trends and diet composition in the contemporary study

The measure of prey species richness in the Cape monkfish stomachs in four areas showed more richness (n = 28) in the Central region and poor (n = 6) in the Southern region (south of the Lüderitz upwelling cell), while prey diversity was 13 and 17 at Cape Frio upwelling cell and Lüderitz upwelling cell, respectively. Cluster analysis and ordination by nMDS indicated spatial variation in the diet, with four main assemblages identified: the Southern region (south of the Lüderitz upwelling cell), the Cape Frio upwelling cell, the Central region, and the Lüderitz upwelling cell (Figure 3.4). The hierarchic cluster analysis showed similarities in the diet of Cape monkfish in the Central region and Lüderitz upwelling cell region, using a distance of < 0.45 as a cut-off (i.e., similarity level of 45%) (Figure 3.4).

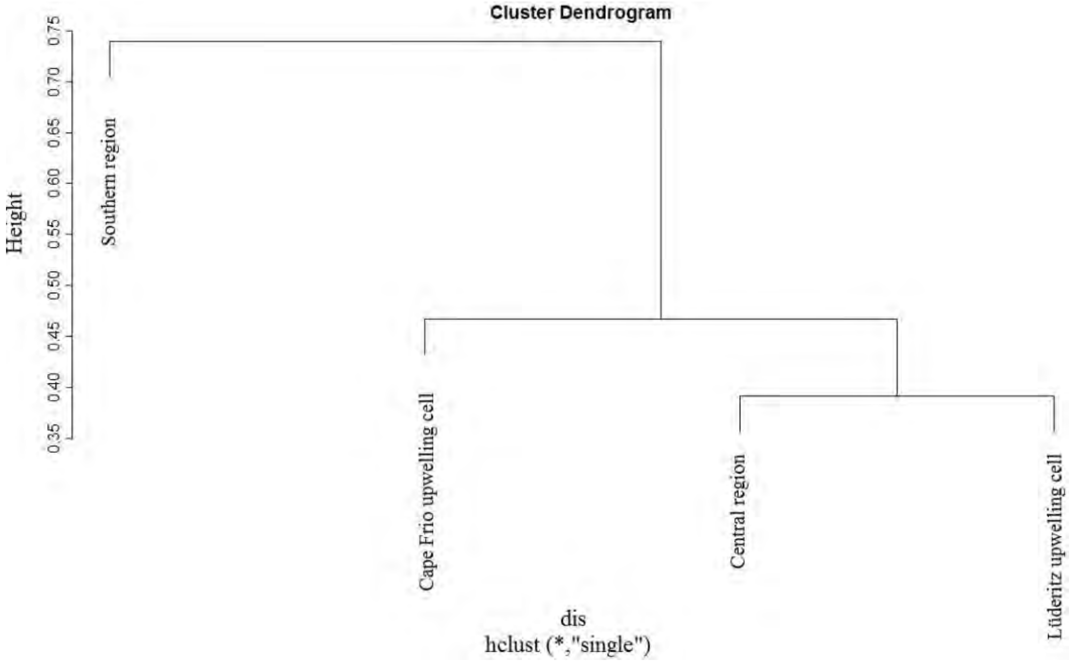
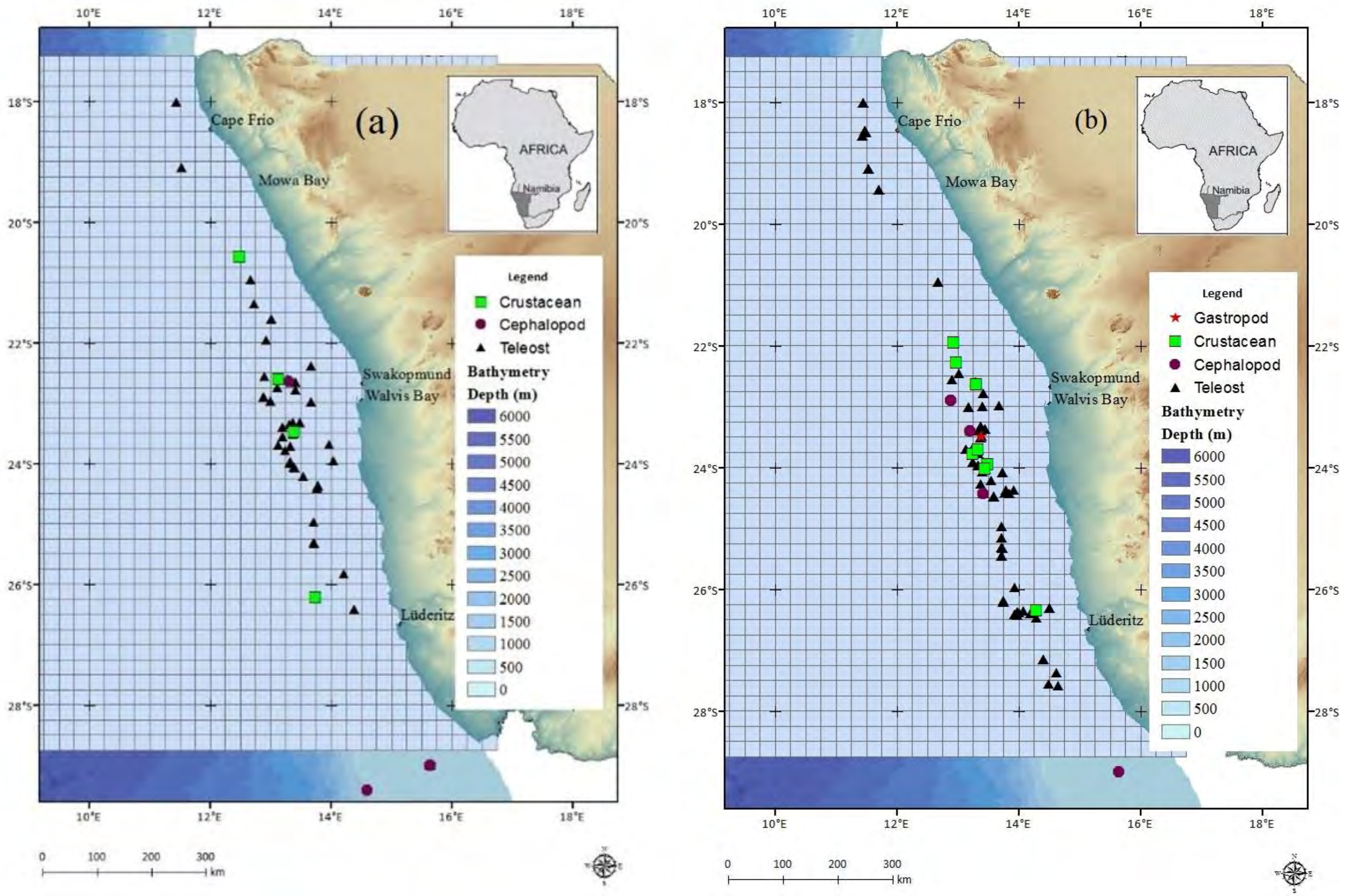


Figure 3.4: Cluster analyses based on normalised Euclidean distances of prey species in the diet of Cape monkfish, *Lophius vomerinus*, at Cape Frio upwelling cell, Central region, Lüderitz upwelling cell and Southern region, based on the data collected between 2015 and 2018 off Namibia.

Juveniles fed on teleosts along the entire coast, but only fed on crustaceans in the Central region and cephalopods in the Central and Southern region. For sub-adults and adult fish, cephalopods were primarily important in the Central region (between 22^o and 25^{o}S) and in the far south at 28^o and 29^{o}S, while crustaceans were consumed between 20^o and 25^{o}S and around 27^{o}S (Figure 3.5).


(a)
(b)
10°E
12°E
14°E
16°E
18°E
18°S
20°S
22°S
24°S
26°S
28°S
Cape Frio
Mowa Bay
Swakopmund
Walvis Bay
Lüderitz
AFRICA
Namibia
Legend
Gastropod
Crustacean
Cephalopod
Teleost
Bathymetry
Depth (m)
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
0
100
200
300
km

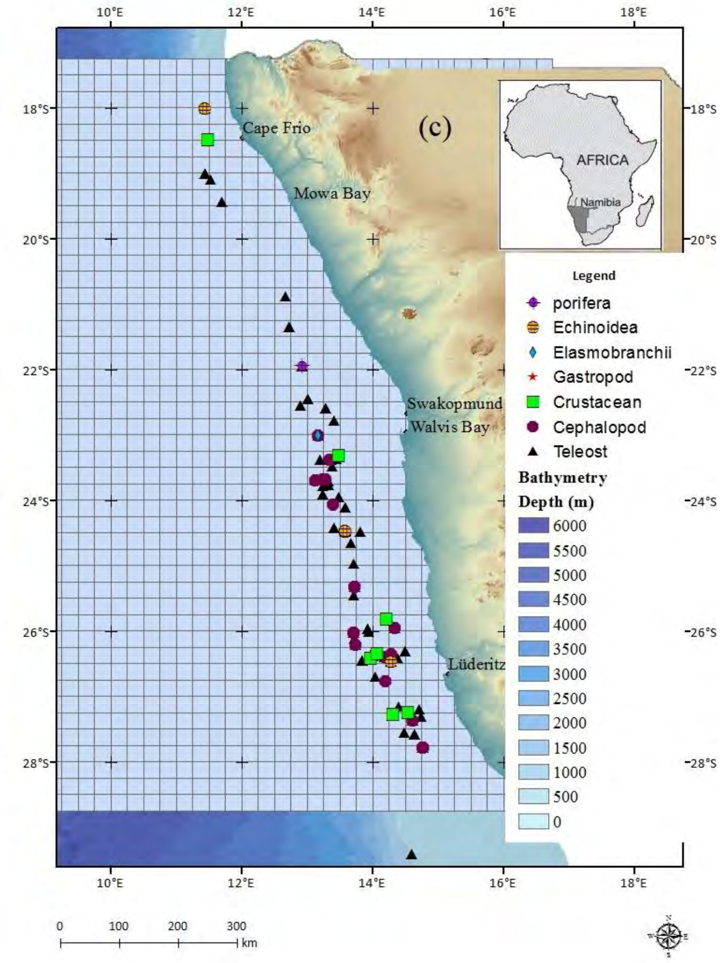


Figure 3.5: The spatial dietary composition (per *IRI*%) of Cape monkfish, *Lophius vomerinus* according to size classes, (a) juveniles (< L_{50}, 37 cm TL), (b), sub-adults (L_{50} – L_{100}, 37 – 47cm TL) and (c) adults (> L_{100}, 47cm TL) of the coast of Namibia between 2015 and 2018. Map constructed using ArcGIS 10 Software.

Teleosts dominated the stomach contents of fish caught along the entire coast. Areas where hake predominated (*M. capensis* and *M. paradoxus*), the main teleost consumed in all regions, are presented in Figure 3.6. The kernel density analysis of the combined diet of Cape monkfish showed that 90% of the hake consumed were south of 22ºS (Figure 3.6).

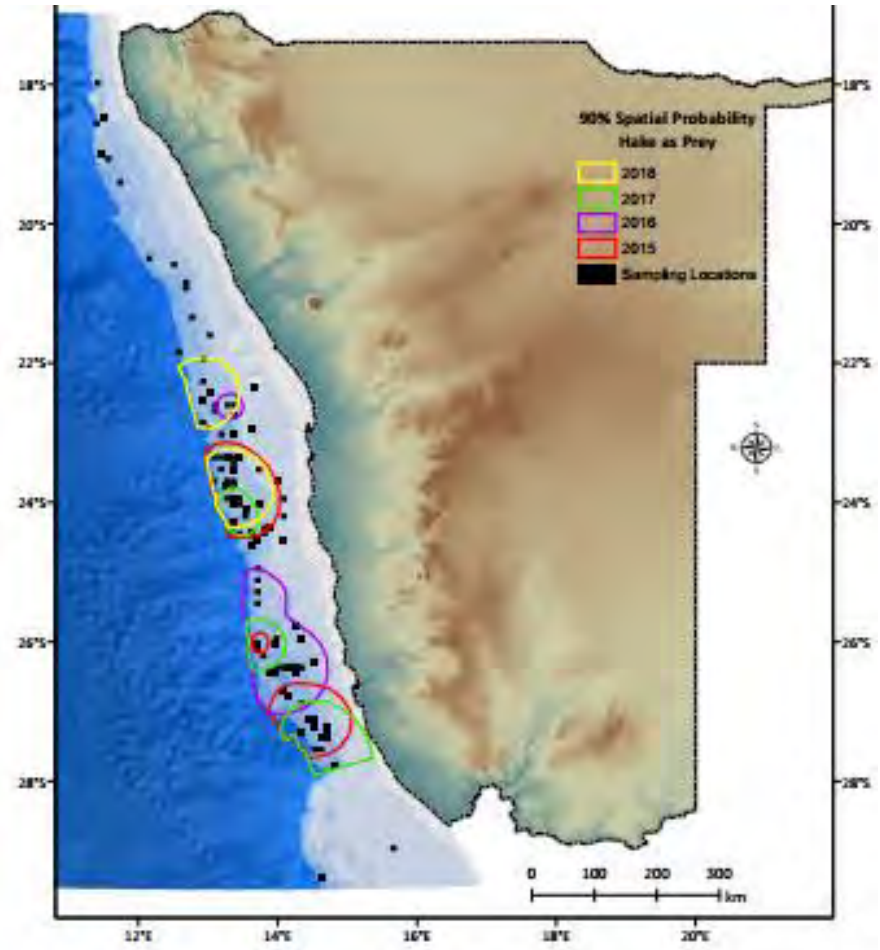


Figure 3.6: Spatial and temporal representations of 90% probability of hake (*Merluccius capensis* and *Merluccius paradoxus*) as prey in the diet of Cape monkfish, *Lophius vomerinus*, off the coast of Namibia between 2015 and 2018. Map constructed using ArcGIS 10 Software.

The PCA of the spatial diet composition for Cape monkfish (Figure 3.7) showed a different stomach composition in the four regions; Cape Frio upwelling cell, Central region, Lüderitz upwelling cell and Southern region, consistent with the spatial dietary composition (per %*IRI*) in Figure 3.5.

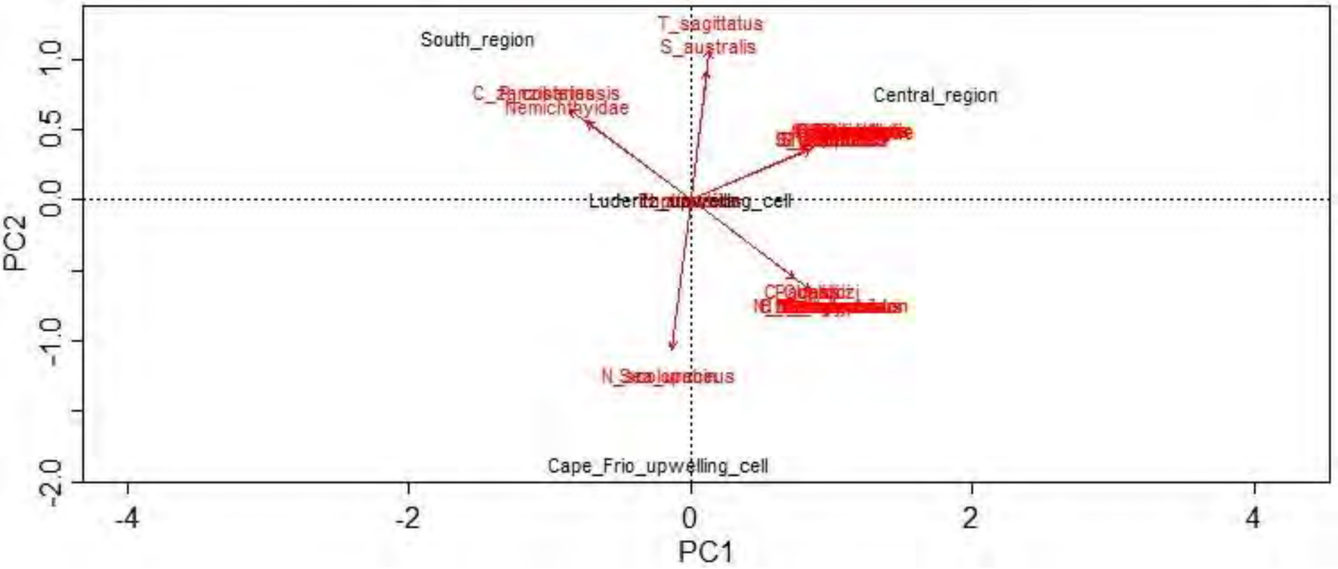


Figure 3.7: Principal component analysis (PCA) for spatial diet composition of Cape monkfish, *Lophius vomerinus*, collected in four regions; Cape Frio upwelling cell, Central region, Lüderitz upwelling cell and Southern region of Namibia between 2015 and 2018.

The diversity of the Cape monkfish diet composition increased with depth. In shallow waters (< 200 m), Cape monkfish fed only on teleosts and cephalopods, with *Paracallionymus costatus* fed on exclusively at < 200 m depth (Figure 3.8). At the 200–299 m depth stratum, the diet comprised teleosts, cephalopod, crustaceans, and echinoderms. *Sufflogobius bibarbatus* was preyed upon in the 200–299 m and 300–400 m strata, but not in deeper waters (> 400 m) (Figure 3.8). All seven taxa of prey items were consumed at the 300–400 m depth stratum. The deeper waters (> 400 m) were less diverse, with only teleosts and cephalopods consumed. Only Cape monkfish in deeper waters preyed on black slimehead *Hoplostethus cadenati* Quéro 1974 (Figure 3.8). Despite the increased diversity with depth, teleosts were still the most dominant prey groups at all depth strata (Figure 3.8). The % *IRI* contribution of prey items indicated that feeding composition depends on depth ($X^2 = 234.51$, df = 18, $p < 0.05$) (Figure 3.8).

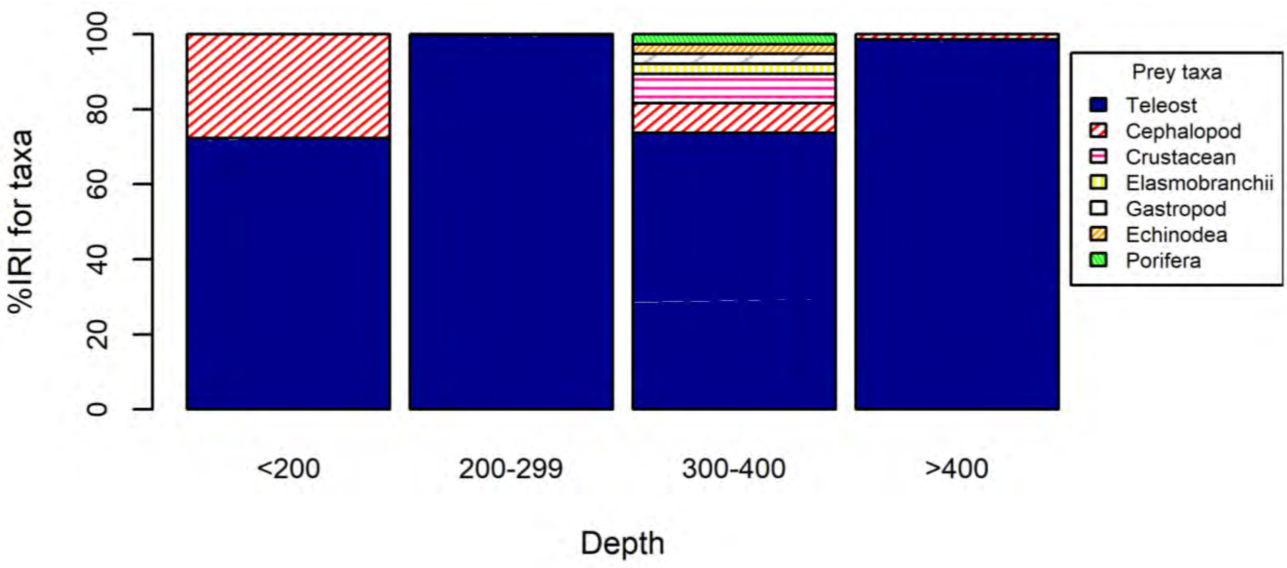


Figure 3.8: Dietary composition according to depth strata of Cape monkfish, *Lophius vomerinus*, off the coast of Namibia between 2015 and 2018.

3.3.5 Predator-prey size relationships

Cape monkfish appeared to consume prey (n = 214) relative to their size. There was a significant positive correlation (r^2 = 0.56) between prey length (Standard length (SL)) and predator Cape monkfish, length (TL) ($p < 0.05$, $r^2 = 0.56$) (Figure 3.9).

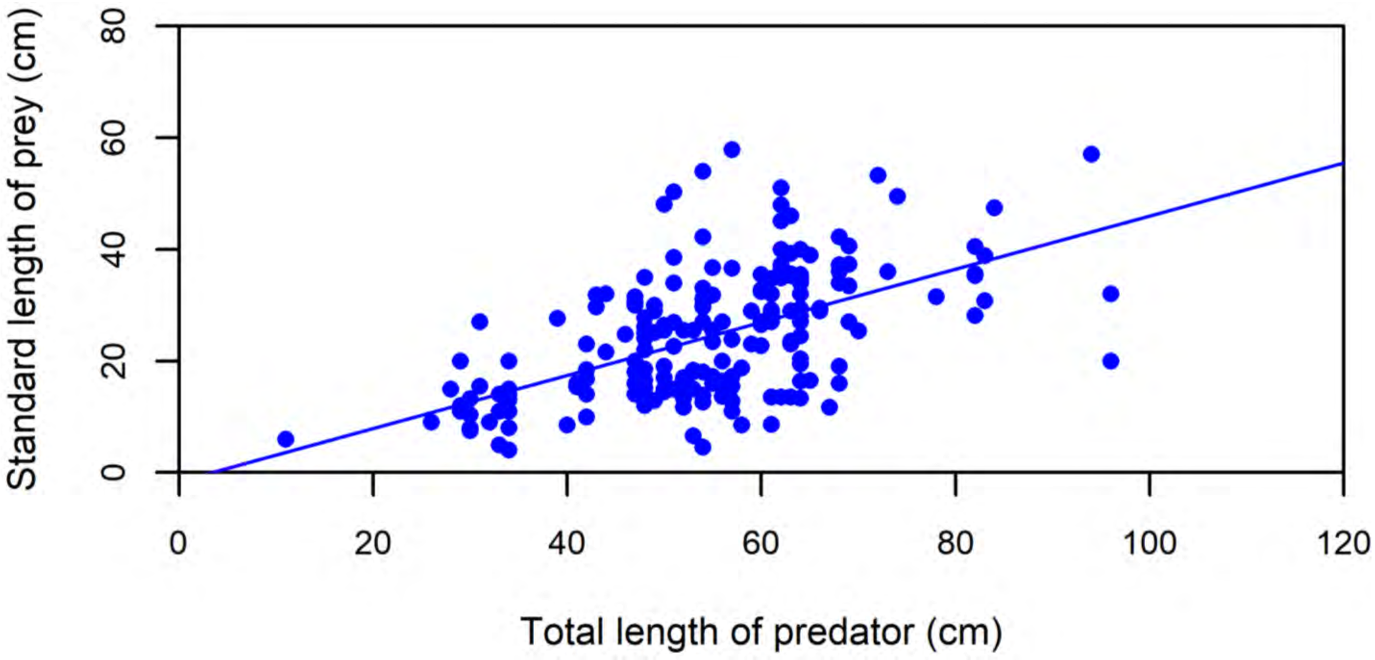


Figure 3.9: The relationship between prey length (cm) (n = 214) and the length of Cape monkfish, *Lophius vomerinus,* (cm TL) collected off the coast of Namibia between 2015 and 2018.

3.3.6 Comparison with the historical feeding study (Gordoa & Macpherson, 1990)

The diet of Cape monkfish captured in Namibia between 1986 and 1987 (Gordoa & Macpherson, 1990) ('Period 1') comprised far fewer species (11) compared with this study (30 species) ('Period 2') (as described in Section 3.2.3). The dependence of similarity on the selected metric plotted using a Shepard diagram showed a perfect match (Figure 3.10).

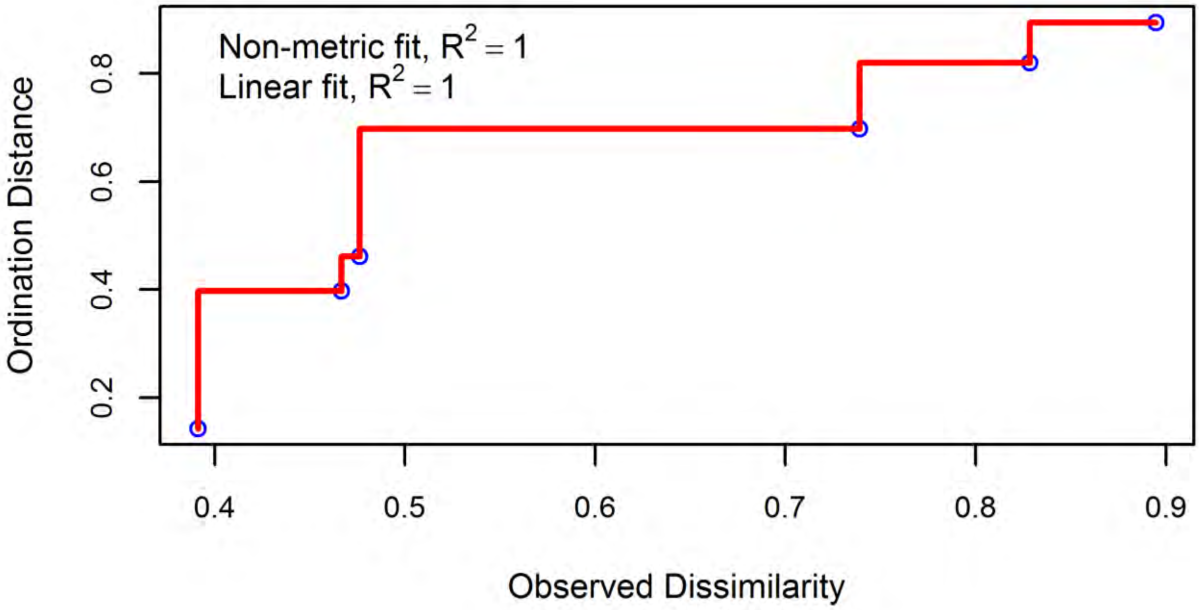


Figure 3.10: Shepard plot of prey species in the diet of Cape monkfish, *Lophius vomerinus*, at three areas (Areas 1, 2 and 3) for Period 1 (Gordoa & Macpherson, 1990) and Period 2 (this study).

Dominant prey species (*M. capensis*, *Todarodes sagittatus*, *Sepia australis*, *C. simorhynchus*, *P. costatus* and *Sufflogobius bibarbatus*) found in Period 1 were compared with dominant species found in Period 2 (Table 3.2). There are changes in the areas historically dominated by pelagic goby, *C. fasciatus*, and *Sepia australis* that are now dominated by *M. paradoxus*, *M. paradoxus* and *P. costatus* (Table 3.2).

Table 3.2: The dominant prey items found in the stomachs of Cape monkfish, *Lophius vomerinus* in (i) 'Area 1' (23°00'S to 27°59'S at 100–300 m), (ii) 'Area 2' (23°00'S to 27°59'S at 300–400 m), and (iii) 'Area 3' (28°00'S to 30°00'S at 100–300 m) of Namibia, used in Period 1 (1986–1987, Gordoa & Macpherson, 1990) and Period 2 (2015–2018).

Area	1986–1987, Gordoa & Macpherson, 1990, 'Period 1'	2015–2018, contemporary study 'Period 2'
'Area 1' (23°00'S to 27°59'S at 100–300 m)	*Nematogobius bibarbatus* (revised to *Sufflogobius bibarbatus*), *Merluccius capensis*	*Merluccius paradoxus*, *Trachurus capensis,* *Nematogobius bibarbatus* (revised to *Sufflogobius bibarbatus*),
'Area 2' (23°00'S to 27°59'S at 300–400 m)	*Coelorhynchus fasciatus* (revised to *C. simorhynchus*), *Merluccius capensis,* *Todarodes sagittatus*	*Merluccius paradoxus* *Helicolenus dactylopterus* *Trachurus capensis*
'Area 3' (28°00'S to 30°00'S at 100–300 m)	*Sepia australis*, *Merluccous capensis,* *Paracallionymus costatus*	*Sepia australis,* *Merluccius paradoxus* *Paracallionymus costatus*

In terms of spatio-temporal distribution, there was greater diversity in the stomach contents of fish in all areas in the contemporary study. In terms of the spatial distribution, the stomach contents of fish in Area 3 had few species and thus poor species richness in both studies (Figure 3.11).

The dendrogram of the cluster analysis revealed three distinct clusters (Figure 3.12). Area 1 and Area 2 in Period 2 were most similar, as were Area 1 and 2 in Period 1. However, Area 3 clustered out with similarities observed in both periods (Figure 3.12). There were differences in the dominant species in the different areas between the historical and contemporary studies. *Sufflogobius bibarbatus* dominated the stomach contents of fish in Area 1, but this changed to *M. paradoxus* (18.3%) in Period 2. Area 1 (*C. fasciatus*-dominated area) is now dominated by deep-water hake (*M. paradoxus*, 31.2%). 'Period 1' Area 3 (*S. australis*-dominated area) is now dominated by *P. costatus* (37.5%). The stomach contents of Cape monkfish were most diverse (26 species) in Area 2 during the Period 2.

Richness was marginally higher in the Central area between 23°00'S and 27°59'S, at 300–400 m depth, in Period 2 (28 species). Cannibalism for this species was only reported in 'Period 2'. The hierarchic cluster analysis showed that the same areas, 'Period 1' Area 1 and

‘Period 2’ Area 1, ‘Period 1’ Area 2 and ‘Period 2’ Area 2, ‘Period 1’ Area 3 and ‘Period 2’ Area 3 are clustered separately in the multivariate analysis (Figure 3.12).

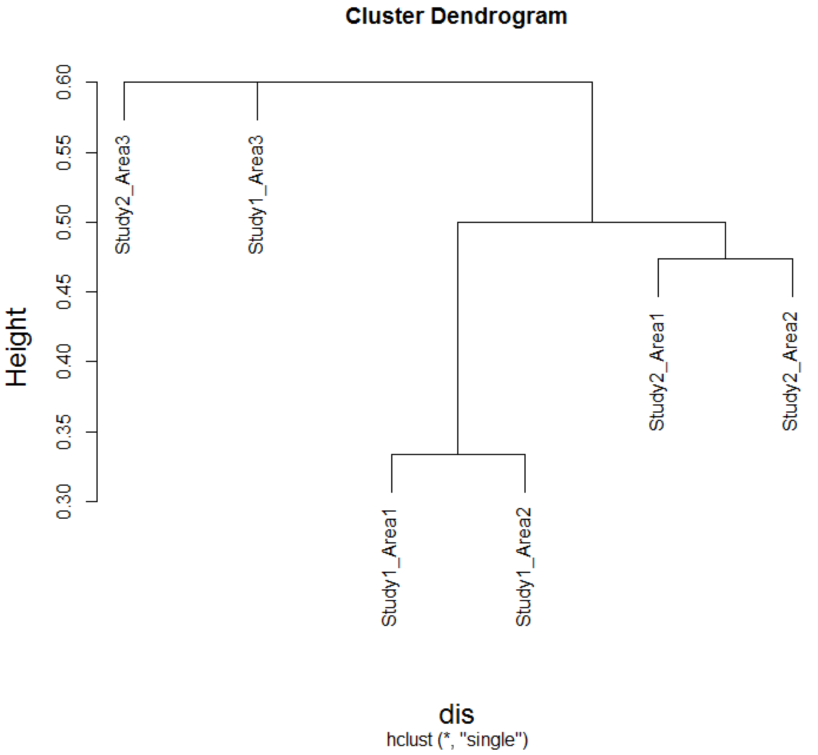


Figure 3.11: Cluster analysis based on Normalised Euclidean distances of prey species in the diet of Cape monkfish, *Lophius vomerinus*, in (i) 23º00’S to 27º59’S at 100–300 m (‘Area 1’); (ii) 23º00’S to 27º59’S at 300–400 m (‘Area 2’) and (iii) 28º00’S to 30–00’S at 100–300 (‘Area 3’), of Period 1 (1986–1987, Gordoa & Macpherson, 1990) and Area 1, 2 and 3 of Period 2 (2015–2018).

Richness was marginally higher in the Central area between 23º00’S and 27º59’S, at 300–400 m depth, in both Period 1 and Period 2. Cannibalism for this species was only reported in ‘Period 2’. The hierarchic cluster analysis showed that the same areas, ‘Period 1’ Area 1 and ‘Period 2’ Area 1, ‘Period 1’ Area 2 and ‘Period 2’ Area 2, ‘Period 1’ Area 3 and ‘Period 2’ Area 3 are clustered separately in the multivariate analysis (Figure 3.11). ‘Period 1’ Area 1 (*S. bibarbatus*-dominated area) is now dominated by *M. paradoxus* (18.3%). ‘Period 2’ Area 1 (*C. fasciatus*-dominated area) is now dominated by *M. paradoxus* (31.2%). ‘Period 1’ Area 3 (*S. australis*-dominated area) is now dominated by *P. costatus* (37.5%).

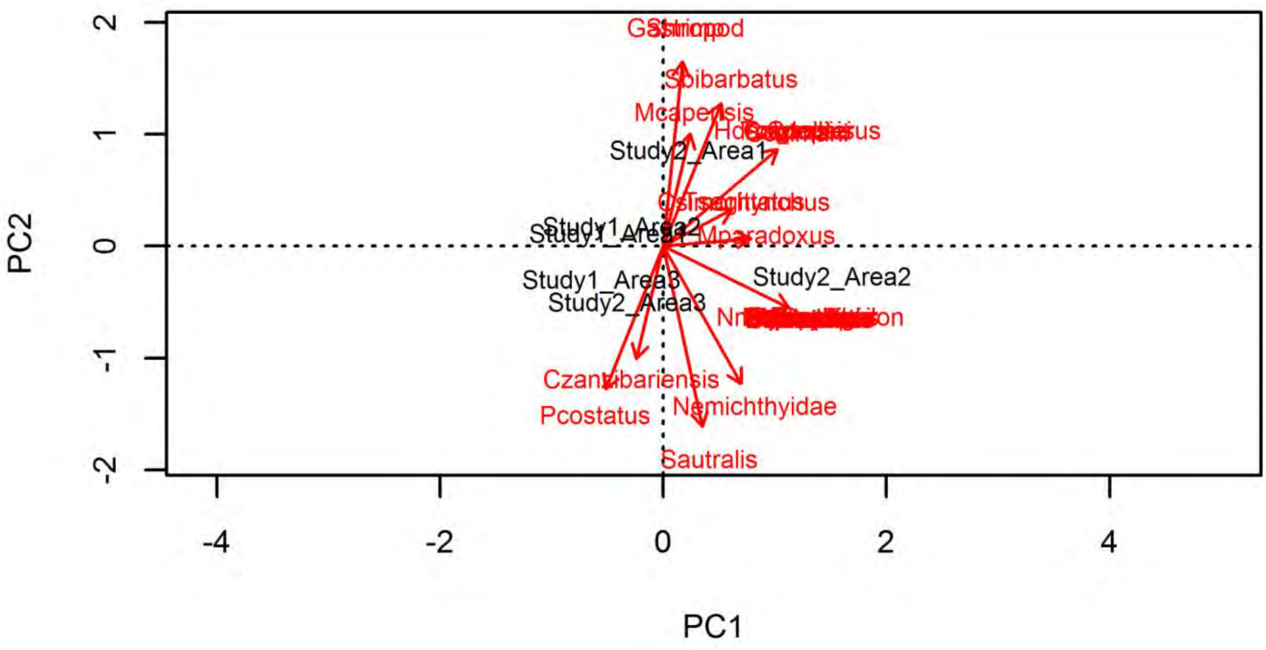


Figure 3.12: Non-metric multidimensional scaling (nMDS) for temporal diet composition for Cape monkfish, *Lophius vomerinus* in three areas ((i) 23º00’S to 27º59’S at 100–300 m (‘Area 1’); (ii) 23º00’S to 27º59’S at 300–400 m (‘Area 2’) and (iii) 28º00’S to 30º00’S at 100–300 m (‘Area 3’), for Period 1 study (1986–1987, Gordoa & Macpherson, 1990) and Period 2 study (2015–2018).

3.4 Discussion

The results of this chapter showed that Cape monkfish, *Lophius vomerinus*, has a broad dietary composition that is not constant spatially nor temporally, feeding opportunistically on a diverse array of prey (teleosts, cephalopods, crustaceans, gastropods, and echinoderms, elasmobranchs, and porifera). The spatial and temporal comparative analysis of the dietary composition of Cape monkfish between the historical (Period 1) and the present (Period 2) study indicated a high trophic adaptability, with the stomach contents more similar between habitats (at the same time) than the same habitats at different times. The increased diversity of prey in Period 2 may also reflect the adaptability of Cape monkfish to changing availability of prey species with time. While both studies highlighted the importance of hake in the diet of Cape monkfish, the results showed that Cape monkfish was previously dependant on shallow-water hake, *M. capensis*, while in Period 2, the main prey was observed to be deep-water hake, *M. paradoxus*. Despite the observed broad trophic adaptability of Cape monkfish, the diet dominance of hake in both studies suggests that any form of overexploitation or climate-driven population declines of hake will most likely impact monkfish.

Various organisms feed at different times of the day and time intervals (Macpherson, 1985; Lall & Tibbetts, 2009; Nikolioudakis et al., 2011). The high prevalence of empty stomachs in Cape monkfish (43.9%) presented here indicates a low feeding intensity. This result supports existing evidence (Macpherson, 1985) that Cape monkfish is not an active predator, but instead feeds infrequently. While the frequent occurrence of empty stomachs and low feeding intensity is common among *Lophius* species (Laurenson & Priede, 2005; Preciado et al., 2006; Johnson et al., 2007), it is uncertain whether the infrequent feeding pattern is behavioural, or a reflection of food availability (Lall & Tibbetts, 2009). In this study, feeding frequency increased with predator size, which was also observed in *L. americanus* (Armstrong et al., 1996) and *L. piscatorius* (Laurenson & Priede, 2005). The higher proportion of empty stomachs (52.9%) among the juveniles might suggest that they do not feed as frequently as adults and sub-adults. However, it is also possible that, because juveniles feed on smaller prey species such as *S. bibarbatus* and myctophids and have a faster digestive rate than large-bodied prey ingested by adults and sub-adults, that their stomachs may empty faster. Overall, the high number of empty stomachs could be influenced by differences in the distribution of samples over area, depth, and season for each size class (for instance more samples were collected from adults than juvenile and sub-adult), thus, it is advisable in future to use as much balanced sampling as possible.

Prey size and shape influence prey ingestion, especially in younger fish (Gordon & Macpherson, 1990; Mihalitsis & Bellwood, 2017). The prey species consumed by juvenile fish belonged mostly to the teleost and a few to cephalopods and crustacean groups. Crustaceans were most likely uncommon in juveniles' diet probably highlighting the role of the mouth gape in relation to the size and shape of prey that can be consumed by a predator ((Ortiz & Arim, 2016). Additionally, this suggests a low abundance of crustaceans in the shallow waters (Macpherson, 1985), where juvenile fish were found in our study.

The results indicated that Cape monkfish has a broad dietary composition, with a range of prey items from seven groups (Appendix B); however, teleosts contributed largely (> 70%) to the diet of all life-history stages, affirming the piscivorous behaviour of this species (Macpherson, 1985). Gastropods and echinoderms were infrequent in the diet (%*IRI* < 2% each) and were categorised as incidental prey items. Cape monkfish are sedentary predators employing an ambush method by attracting prey species using a lure (esca) on the tip of the illicium (Fariña et al., 2008), thus they are most likely to feed on active swimming prey species that are attracted to the esca. This mode of foraging might explain the low frequency of gastropods, echinoderms and porifera, in its diet because these are sessile species. Similarly, some prey species such as *Bathyuruconger vicinus* and west coast sole, *A. microlepis,* were less important in the stomach contents (< 0.6 *IRI*%) although they are usually caught as by-catch in Cape monkfish-directed fishery (pers. obs.). The rare encounter of these species in the Cape monkfish diet may suggest that they are not active prey. Elasmobranchs are often top predators (Filiz, 2009), and might be challenging to prey upon.

At different sizes, predators fed on various prey species. For example, the pelagic goby, *S. bibarbatus,* dominated the diet of juveniles, by percentage in number and occurrence. They are a smaller, soft-bodied species that might be required in large amounts compared to large-bodied prey species such as *M. paradoxus* (which had the highest %*IRI* of 32.6%) for juveniles. Pelagic goby are widely distributed off Namibia, especially in waters of 50 to 300 m depth (Olivar et al., 1992), in the same areas inhabited by juveniles, thereby making them readily available to juvenile Cape monkfish.

The feeding composition diversified with predator size. In addition to cephalopod, crustaceans and teleosts, sub-adults also fed on gastropods, hence a broader diet than juveniles. The decrease in the importance of pelagic species, such as Euphausiids, in the stomach contents with an increase in size, is probably due to the observed occurrence of larger Cape monkfish in deeper waters, reducing their encounters with pelagic prey species. Surprisingly, some small species such as *Sepia australis* and *Sufflogobius bibarbatus*, although in low quantities, still appeared in the adult diet.

Many teleosts exhibit ontogenetic shifts in prey diversity (Preciado et al., 2006; Bacha & Amara, 2009; Falkenhaug & Dalpadado, 2014; Mihalitsis & Bellwood, 2017), with larger/adult fish exhibiting a broad diversity in prey composition (Morato et al., 2000; Preciado et al., 2006). This shift has been attributed to energy demand as the fish grows (Lall & Tibbetts, 2009) and was also observed in this study, where adult Cape monkfish fed on more prey taxa (n = 7) than juveniles (n = 3) and sub-adults (n = 4) did. The diverse adult diet composition was also wider than for juvenile and sub-adults, which is energetically beneficial for adult fish. The adult diet demonstrated a notable shift from soft-bodied prey to include large and hard-shelled prey, for example, crustaceans. The presence of sessile species such as gastropod in the diet of Cape monkfish was surprising, however, these partially digested gastropods and porifera found in the stomachs were included in the analysis, although they are not active swimmers and therefore not usual prey targeted by an ambush predator, they were also not likely to have been freshly digested as a result of the trawl process and therefore could not be discounted. The high diversity of prey species in the adult diet can be attributed to the larger mouth gape, which enables the fish to feed on a variety of prey species of various sizes and shapes (Ortiz & Arim, 2016). Additionally, the inclusion of more prey groups and large-bodied prey items in the adult diet suggests higher metabolic requirements/return among adult fish (Ortiz & Arim, 2016). Similarly, Ortiz and Arim (2016) observed progressive incorporation of prey items with an increase in predator size of the South American killifishes (*Austrolebias spp.*). Moreover, the shift in prey size observed in Cape monkfish is also likely to be due to the habitat, as large and hard-shelled prey species occur at overlapping depth distribution with adult Cape monkfish.

It has been well documented that food limitation is a driver of cannibalism in predators, especially those that aggregate (Neuenfeldt & Köster, 2000; Ibanez & Keyl, 2010). When examining the findings of Period 2 and Period 1 (Gordoa & Macpherson, 1990) and a feeding study on monkfish conducted in South Africa (Walmsley et al., 2005), it appears that cannibalism is not common in monkfish. Similarly, no evidence of cannibalism was observed in *L. piscatorius* and *L. budegassa* (Thangstad et al., 2002). Since Cape monkfish feeds on a wide range of prey species, as demonstrated in this study, the low rate of cannibalism may be related to the availability of a range of other prey types, thus rendering cannibalism unnecessary.

The dominance of *T. capensis*, *H. dactylopterus* and *M. paradoxus* by weight in the sub-adult and adult diets is possible because these prey species, unlike elasmobranchs, are abundant, especially in the benthic zone (Kirchner et al., 2010). The results of this study highlight the spatial and temporal dominance, by number, weight, and frequency of occurrence (Figures 3.5b, 3.5c and 3.6), of *M. paradoxus* in the diet of both sub-adults and adults, highlighting some degree of selectivity. *Merluccius paradoxus* is a demersal species (Iitembu et al., 2012; Wilhelm et al., 2015), inhabiting deeper waters (between 250 and 600 m, Burmeister, 2001) than Cape monkfish (347 m on average, see Chapter 6) and is also the most abundant of the three hake species off Namibia. Off South Africa, *M. paradoxus* also made up a large proportion of the Cape monkfish diet (Walmsley et al., 2005). However, in Period 1, *M. paradoxus* was not listed as a prey species (only *M. capensis* was listed), but in Period 1, it was consumed at all size classes, in all areas, and it was dominant in terms of %*IRI*. This may suggest an increase in the abundance and distribution of *M. paradoxus* and hence increased availability to monkfish when compared to *M. capensis*. Nonetheless, the clear dominance of hake in both studies implies that any overexploitation or climate-driven population declines of hake will probably impact monkfish. Cape horse mackerel were also numerically dominant in the diet. These fish exhibit diel vertical migrations (Pillar & Barange, 1997, 1998), which would make them accessible prey items for Cape monkfish. The Angolan flying squid, *T. sagittatus,* also formed an important dietary component in terms of mass, both in Period 1 (Gordoa & Macpherson, 1990) and Period 2 (present study). Cape monkfish and *T. sagittatus* have an overlapping depth distribution (FAO, 1993; Kathena et al., 2018) which makes them readily available as prey to Cape monkfish. Squids are common food for *Lophius* species (Preciado et al., 2006).

The type and quantity of food ingested can vary seasonally (Madurell &. Cartes, 2005; Bacha & Amara, 2009; Falkenhaug & Dalpadado, 2014). Across all size classes, the diet appeared to be less diverse in summer than in winter (see Figure 3.3). Indeed, species are most abundant and reach reproduction peaks in the winter months in the northern Benguela Ecosystem (nBE) (Olivar & Shelton, 1993). The seasonal variation observed in the diet of Cape monkfish may be attributed to seasonal changes in physical parameters, such as water temperature (Hutchings et al., 2009; Kainge et al., 2017) (see Chapter 2), which in turn, influences prey distribution and abundance. A study on the larvae of yellow goosefish *Lophius litulon* demonstrated the influence of temperature on their feeding activities, with an increase in temperature leading to a shortened period of initiation of first feeding and starvation tolerance (Nakaya et al., 2017). For this study, the sea bottom temperature data (associated with catches) presented in Chapter 6 did not show significant trends. Van der Lingen et al. (2006) documented extensive seasonal variability in the distribution and abundance of several species, including sardine and Cape horse mackerel, which are forage species of Cape monkfish, in this region and concluded that interannual and decadal-scale variability in abundance, distribution and biological characteristics of various species in both the northern Benguela Ecosystem and southern Benguela Ecosystem has major effects on the food web and ecosystem in these regions. Although the broad trophic adaptability observed in this chapter suggests that monkfish may be resilient to such variability, anthropogenic impacts such as overexploitation may render Cape monkfish less resilient to such changes.

The stomach contents of Cape monkfish may serve as an effective indicator of changing benthic assemblages in this region (Crawford, 1987; Crawford et al., 1992). Several authors have reported how organisms demonstrate dietary change with geographical locations (Falkenhaug & Dalpadado, 2014), and the dietary composition of Cape monkfish exhibited spatial variation that coincided with changes in species abundance in different areas at different seasons of the year. The observed pattern of trophic adaptability of Cape monkfish to available prey species in presented in this study corresponds to diet studies on *L. budegassa* (Preciado et al., 2006) and yellow goosefish, *L. litulon* (Kosaka, 1966), which also found significant seasonal variation in the diet composition for all size classes. Thus, Cape monkfish's generalist opportunistic feeding behaviour allows it to adjust its diet in response to seasonal and spatial changes in food availability. This broad trophic adaptability allows it to utilise a wide variety of the most readily available prey species in the environment at any time. Several predators in this region are described as opportunistic non-selective feeders, for example, shallow-water hake (Payne et al., 1987), Cape horse mackerel (Hecht, 1976, Konchina 1986), and snoek, *Thyrsites atun* (Crawford, 1987). The opportunistic non-selective feeding characteristics of predatory species provide them with resilience to large changes in their prey species' abundance, which appears to be common in Namibian waters (Crawford, 1987).

The spatial variations observed in the diet of Cape monkfish may be attributed to the physical characteristics of Namibian waters. Species richness was highest in the stomach contents (n = 28 species) of fish captured in the Central region in Period 2. The Cape Frio upwelling cell which recorded a species richness of 13 species, has a phytoplankton signal masked by the intrusion of chlorophyll-a-poor waters from Angola each austral summer, resulting in low species abundance, despite the perennial upwelling off Cape Frio (at 17° S) (Monteiro et al., 2008; Hutchings et al., 2009). The similarity in species composition between the Central and Lüderitz upwelling region as per the hierarchical cluster analysis (Bray-Curtis) was expected because they are geographically close to each other. Species richness was poorest (n = 6) in the region south of Lüderitz (n = 6). This may suggest that the area is species-poor in comparison to the rest of the Namibian coast. The absence of some commonly observed species such as *B. albescens*, *C. simorhynchus*, *H. dactylopterus*, *M. capensis*, *N. micronychodon*, and *T. capensis* in the south, although observed in the northern part, may explain the dissimilarity between regions. This finding indicated that habitat attributes such as the proximity to the Lüderitz upwelling cell, a biological boundary that effectively divides the BCLME (Junker et al., 2017; Hutchings et al., 2009; Bode et al., 2014; Martin et al., 2014) influence species distribution. Although the barrier mostly influences phytoplankton and pelagic fish (Lett et al., 2007), it may have an indirect effect on deep-water species with regards to predator-prey interaction.

Based on the comparison between the historical (Period 1) and contemporary (Period 2) studies, a notable temporal shift was evident in the dietary composition of Cape monkfish. Areas where the diet was previously dominated by *Coelorhynchus fasciatus* (revised to *C. simorhynchus*), *Nematogobius bibarbatus* (revised to *Sufflogobius bibarbatus*), and *Sepia australis*, are now dominated by *M. paradoxus* and *P. costatus*. These changes may be attributed to the well-documented regime shift in the Namibian waters (Monteiro et al., 2008; Jackson et al., 2013; Jarre et al., 2013) and the consequent changes in the species abundance and distribution in this region (van der Lingen et al., 2006). Our results indicate that the two studies' time frame (historical and contemporary) was more important than the area. In the past, the Southern African sardine (*S. sagax*) was listed as one of the prey species of Cape monkfish (Bianchi et al., 1999), but this was not found in Period 2 diet nor Period 1. This absence is most likely a result of sardine's collapsed population in the nBE (Crawford, 1987; Roux et al., 2013; Erasmus et al., 2021a). Changes in the abundance of prey species have been mentioned as indirect impacts of fishing activities (Crawford, 1987; Tasker et al., 2000). It is well documented that fishing forage species influence the diet composition of their predators (Hilborn et al., 2017). The abundance of pelagic goby has increased in the Namibian waters, replacing sardine and Cape anchovy, which were key forage species in this region (Crawford, 1987; Cury & Shannon, 2004; Roux et al., 2013).

The switch from shallow-water hake (*M. capensis*) to deep-water hake (*M. paradoxus*) as a dominant prey in the diet of the Cape monkfish, which was the staple diet item in the past (Macpherson, 1985; Gordoa & Macpherson, 1990), is interesting. Deep-water hake was not listed even as a less important prey in Period 1 but now in Period 2, it is fed on in all areas, at all size classes. The reason for this is most likely twofold: firstly, the change could be influenced by the change in biomass of the two hake species. It is difficult to conclude with certainty on the biomass size of the two hake species in Namibia because they are assessed jointly as a single stock (Kathena et al., 2016). However, the species-specific abundance index available from the scientific biomass surveys (MFMR, unpublished) indicates an increase in the biomass estimation of *M. paradoxus* compared to the earlier 1990s. There is evidence from van der Westhuizen (2001) that since 1991, the fishable *M. capensis* biomass has been declining. In contrast, *M. paradoxus* has not only increased its biomass, but has also expanded its geographic distribution. Secondly, the monkfish population has shifted vertically, towards deeper waters which are more inhabited by *M. paradoxus* than *M. capensis* (as evidenced in Chapter 6). This information shows that Cape monkfish can switch their diet composition depending on their prey species' availability and abundance. There are thus signals of both climate change and exploitation impacts on the diet of Cape monkfish manifested in the abundance and distribution of prey species. However, when the predators switch prey species, they might replace high-energy food with poor-energy food, such as the pelagic goby (Ludynia et al., 2010; Roux et al., 2013). The switch from one main prey to another is common in this region (Cooper, 1985; Ludynia et al., 2010; Grémillet et al., 2019), but may have important implications for the species' productivity, due to changes in the energy budgets of individuals. Although the diet shifted with an increase in Cape monkfish size and depth distribution, some prey species, such as the pelagic goby, *N. bibarbatus* (revised to *S. bibarbatus*), remained an important component of the diet. Pelagic goby were the second most important prey items (17.3% *IRI*) in the Cape monkfish juvenile diet and continue to constitute the sub-adult and adult Cape monkfish diet. Additionally, they persisted in the diet of Cape monkfish during the two study periods in this region, which could be owing to their extensive ability to adapt to diverse environmental conditions (e.g., low oxygen zones) (Utne-Palm et al., 2010; Salvanes et al., 2015; Currie et al., 2018; Salvanes et al., 2018). Moreover, pelagic gobies have expanded their geographical distribution in Namibia (Salvanes et al., 2018). They are reported to be tolerant of low oxygen, limiting other species by causing poor recruitment and mortality (Woodhead et al., 1997) and a reduction in fish habitat (Monteiro et al., 2008; Stramma et al., 2010). Previous work on feeding ecology in this region (Jarre et al., 2015b; Heymans & Tomczak, 2016) also highlighted the increasing importance of the pelagic goby as a forage fish in the diet of several species. Indeed, following the collapse of sardine, some predators substituted sardine with pelagic goby (Moloney, 2010).

While this study has provided much-needed insights into the spatial and temporal diet of Cape monkfish, it is not without limitations. For example, the use of stomach content analysis (SCA) only provides a snapshot of information, which can make interpretation challenging. A simple approach (spatial and temporal diet composition) was used to assess trophic adaptability of Cape monkfish, and although it presented evidence of trophic adaptability, the use of stomach contents for inferring diet is limited, and future work should thus consider using stable isotope analysis techniques to look at long-term trends in the diet of Cape monkfish. Additionally, although it is common for demersal fish to regurgitate their stomach when brought to the surface, rendering the SCA technique biased (Carrasco et al., 2012), this regurgitating effect does not affect Cape monkfish, as they do not have a swim bladder (Griffiths & Hecht, 1986). Lastly, since most SCA samples were collected from the central and southern part of Namibia (Figure 3.1), the conclusion based on data from the northern part of Namibia is not concreate. However, the sample collection is reflective of the nature of the fishery, which indicates more fishing activities in the area where more samples were collected, an area coinciding with the main monkfish fishing grounds (especially between 25º and 26ºS) as shown in Chapter 6.

In summary, the results of this study suggest that Cape monkfish are piscivorous generalist predators, feeding opportunistically on whatever prey is abundant. This generalist feeding appears to be beneficial in that it provides Cape monkfish with a wide trophic adaptability as a response to changes in its prey species abundance and distribution. The results highlight the particular importance of the deep-water hake, *M. paradoxus,* in the Cape monkfish diet across all size classes and imply that any change in the population size of *M. paradoxus* may have a domino effect on the Cape monkfish. Importantly, the results suggest that Cape monkfish have shifted their diet over the last 29 years, probably reflecting the availability and abundance of forage fishes in the Namibian waters, possibly due to exploitation pressure (in the case of *M. capensis*), climate change (in the case of *S. bibarbatus*), or a combination of both. Our results suggest that their broad trophic adaptability, despite their dependence on a dominant teleost, would render them resilient to the synergistic effects of climate change and overfishing. The increasing presence of pelagic goby in the diet of Cape monkfish is a concern because pelagic goby is a poor quality prey and hence are less energetically valuable, which may lead to a decline in population productivity of Cape monkfish in the future.

Chapter 4: Spati0-temporal analysis of reproductive indicators for the Cape monkfish (*Lophius vomerinus*) in Namibia

The Cape monkfish egg veil when it was discovered off Namibia in November 2018 (photo credit: Ndamona Mathew)

4.1 Introduction

As mentioned in the introduction, the impacts of climate change and exploitation pressure on world fish populations are becoming a mounting concern (Law, 2007; Potts et al., 2014). These global threats induce stress in fish and lead to changes in life-history events, such as reproduction strategies (Buxton, 1993; Wheeler et al., 2009; Hunter et al., 2015). Reproduction aspects, including age at first maturity, fecundity, spawning period, spawning grounds, and spawning frequency are influenced by exploitation pressure (Buxton, 1993; Trippel, 1995; Rochet 1998; Wheeler et al., 2009; Butler et al., 2018) and environmental variability (Boyer et al., 2001; Pankhurst & Munday, 2011; Kujawa et al., 2015). Climate change causes stress in fish which then manifests in changes in life-history traits, for example, early maturation (Trippel, 1995; Pankhurst & Munday, 2011). It is important to understand the reproductive dynamics of fish in the context of fisheries management in relation to climate change and extensive fishing pressure.

Studies on reproduction and maturation dynamics are critical for fisheries management as they provide information on the state of the stock (Trippel, 1995; Blamey et al., 2015). Information derived from reproductive strategies and maturation dynamics of any organism is significant in comprehensively understanding population dynamics (Kjesbu et al., 1998; Colmenero et al., 2013; Jansen et al., 2015), and it is critical for assessing the exploitation pressure at a population level when attempting to develop appropriate management measures (Afonso-Dias & Hislop, 1996; Duarte et al., 2001; Potts et al., 2014; Grabowska & Przybylski, 2015). Many studies have reported fishery-induced changes in reproductive strategies (e.g., Trippel, 1995; Law, 2007). Monitoring biological aspects, such as reproduction and maturation characteristics, can therefore serve as good indicators for both climate change and exploitation pressure (Buxton, 1993; Trippel, 1995; Pankhurst & Munday, 2011).

Globally, multiple studies have investigated the influence of climate change (Buxton, 1993; Rijnsdorp et al., 2009; Pankhurst & Munday, 2011) and exploitation pressure (Hunter et al., 2015) on reproduction strategies of marine fisheries, including maturation, spawning timing, and spawning grounds. However, to date, no such study has been done on Cape monkfish off Namibia. This species plays a key ecological role, mainly as a top predator in the BCLME (Macpherson, 1985; Gordoa & Macpherson, 1990; Walmsley et al., 2005) as also shown in Chapter 3. Although some aspects of the reproductive biology of this species have been studied previously (Maartens & Booth, 2005), no attempts have been made to date to link the biological aspects of this species with environmental variables and exploitation pressure. This chapter aims to conduct a spatio-temporal analysis of the reproductive biology of Cape monkfish throughout its Namibian distribution and to compare this information to historical data to examine any potential changes. Specifically, the objectives were to investigate whether the reproductive strategies of Cape monkfish have changed in response to the extensive fishing pressure targeting this species, and to the climate change in this region; to validate the macroscopic sexual stages, compare the current spawning season to the historical spawning season (both spatially and temporally), and to compare the fecundity, sex ratio and current spawning grounds to those identified in previous studies (both spatially and temporally).

4.2 Materials and methods

4.2.1 Field sampling

A total of 360 530 Cape monkfish specimens ranging in size from 10 to 130 cm TL (measured to the nearest cm below) were collected for reproductive analysis off the coast of Namibia (Figure 4.1). Data used in this chapter were collected between April 2001 and December 2019. For sex ratio, data for 2001–2019 were used, GIS data used were for 2001–2019, length at 50% maturity (L_{50}) data for 2004–2006 and 2015–2019. For fecundity and histology analysis, the data used was collected in 2017. Spawning ground data (677 records of co-ordinates) were collected between 2001 and 2018 (Table 4.1). Maturity data were compared spatially (10 by 10 nm blocks) and temporally from 2001 to 2019, covering the entire shelf area of Namibia between 138 and 837 m depth range.

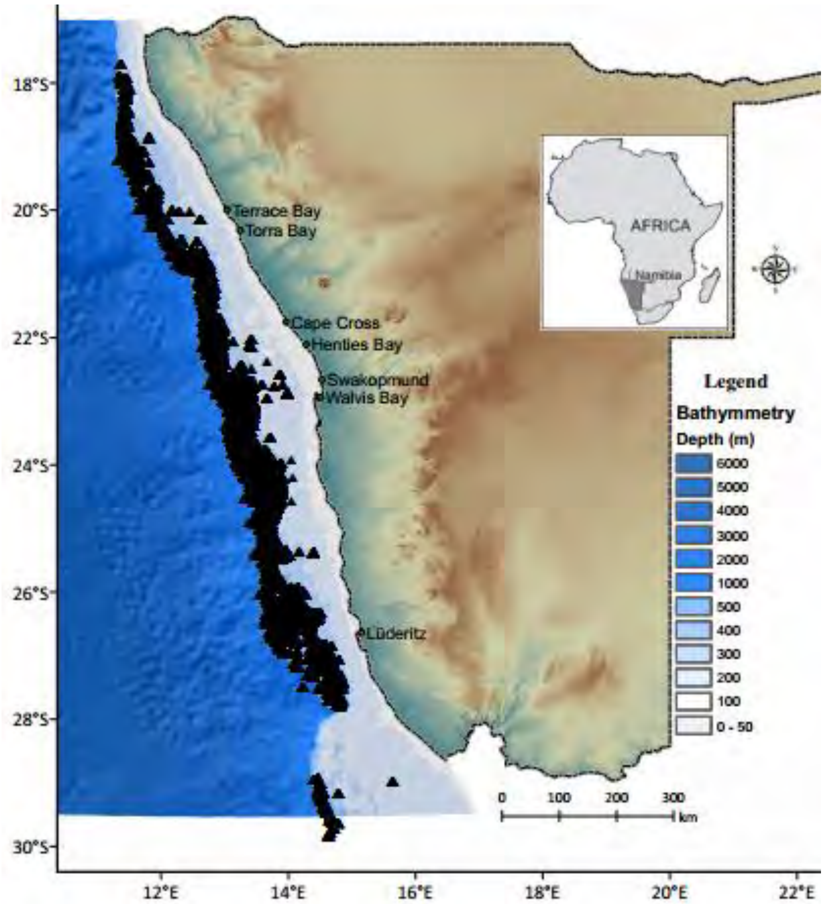


Figure 4.1: Spatial distribution of sampling stations for Cape monkfish, *Lophius vomerinus*, off the coast of Namibia between April 2001 and December 2019. Map constructed using ArcGIS 10 Software.

Samples were obtained from three sources: (i) observer sampling on board the commercial fishing vessels off Namibia (collected by Observers on board the commercial fishing vessels- see Chapter 1, Section 1.3.3), (ii) survey sampling on board the research vessels (by researchers), and (iii) port sampling (samples collected by the Namibian Ministry of Fisheries and Marine Resources researchers by the sampling of commercial landings in Walvis Bay) as indicated in Table 4.1. Details of the survey are given in Chapter 2 and further details are found in Strømme and Iilende (2001).

Table 4.1: Sampling information for Cape monkfish, *Lophius vomerinus*, specimens including the type of data collected, source of data, sampling period, sample number (n), sampling month, total length (cm) range, and depth range (m). Samples were collected between 2001 and 2019 off Namibia.

Data type	**Sampling period**	**Data source**	**Sample No**	**Total Size range (cm TL)**	**Sampling depth range (m)**
Sex ratio	2001-2019	Fisheries Observer data, port sampling & research survey	360530	10-130	138-837
Histology	July 2017	port sampling	23	26-77	290-370
L_{50}	2015-2019	Fisheries Observer data and port sampling	8853	21-93	230-480
GIS and HIS	2015-2019	port sampling & research survey	2257	26-103	150-558
Monthly gonad proportions	2015-2019	Fisheries Observer data, port sampling & research survey	10827	23-130	150-670
Spawning ground	2001-2018	port sampling & research survey	677	28-108	142-719
Fecundity	Aug - Sep 2017	Port sampling	18	46-75	267-475

Length at sexual maturity

The length at 50% maturity (L_{50}) was estimated from a combination of Observer and port sampling data collected in 2004–2006 (n = 378), and 2015–2019 (n = 4475) (Table 4.4), during the spawning period (February, July, August and September). Samples collected during other months were excluded from the L_{50} estimation to avoid some adults that are resting. No biological data were collected during the spawning months of the missing years. The following maturity descriptions were used to determine the maturity stages of Cape monkfish: Stage I: Immature, Stage II: Developing, Stage III: Mature, Stage IV: Ripe, and Stage V: Spent. Fish were classed as immature or mature, based on the maturity stage of the gonad (Table 4.2). Only fish classified as Stage III to V were considered mature because they had advanced yolked (vitellogenic) oocytes. Total length was used to estimate L_{50} for Cape monkfish, for samples ranging in size from 21 cm to 93 cm TL.

4.2.2 Comparison with the historical reproduction study (Maartens and Booth, 2005)

For the comparative study in this chapter, reproduction and maturity data collected during Period 1 and data collected in Period 2 (this study) were used. For this chapter, Period 1 refers to the study by Maartens and Booth (2005) (see Chapter 2). The samples in Period 1 were collected during both monkfish commercial fishing activities and during hake biomass survey, between 1996 and 2000 off Namibia, from a depth of 97 m–686 m. For Period 2 (this study), samples were collected during biomass monkfish survey, commercial fishing activities and port sampling between 2001 and 2018. For historical studies (Maartens and Booth, 2005), no original field data were available from the historical study, thus only the study description, methods used (limited), and the results were compared to the contemporary study.

4.2.3 Laboratory analysis of samples

Sex determination and macroscopic examination of gonads

Specimens collected during the commercial survey and port sampling programme between 2001 and 2019 were measured (TL, ± 0.1 cm, to the nearest cm below). The sex of the specimens was determined as male, female, or unknown. Cape monkfish are not sexually dimorphic, thus sex was determined through a macroscopic examination of the gonads, after dissection. Gonads were removed, weighed individually to the nearest gram (g), and macroscopically assigned to a gonadal stage based on a five-stage maturity scale for both females and males (Table 4.2). Male gonads consist of a pair of white tubes (sausage-like), while female gonads are confluent in shape in a single, compressed orange tube. In both sexes, gonads in Stage I are transparent. Fish too small to determine their sex were categorised as unknown (juvenile). Table 4.2 gives a physical description of male and female gonads in various maturity stages.

Histological examination of gonads

A total of 23 Cape monkfish specimens were measured for total length (TL, ± 0.1 cm), total weight (TW, ± 0.0 g), gutted weight (GW, ± 0.1 g) m, gonad weight (GNW, ± 0.01 g) and liver weight (LW ± 0.01 g). In total, 14 females and nine males of 26–77 cm (TL) were collected in July 2017 and classified into the five macroscopic maturity stages for female fish and male fish as described in Table 4.2. Upon dissection, the gonads were immediately preserved in 10% formalin to avoid post-mortem degeneration of cells that can be confused with atresia. Histological examination of gonads was done to validate the macroscopically assigned maturity stages (Table 4.2). Sections of 3 mm thickness were cut transversely through the anterior, median, and posterior regions of each gonad using a razor blade. Gonad sections were embedded in paraffin wax, sectioned (about 5 microns thick) and thereafter, histological analysis was performed following Austin and Austin (1989), by means of staining with haematoxylin and eosin (HE). From these sections, oocyte development stages in ovary sections were microscopically classified, based on the developmental stage of the most advanced oocytes. An Axio camera mounted on a Zeiss compound microscope (x10 magnification) was used to digitise the pictures used for microscopic maturity staging. Oocyte size, colour, and the presence or absence of specific spawning features such as oil droplets, yolk vesicles, and postovulatory follicles (POFs) were used to microscopically classify the gonads. Histological analysis was done at the Department of Paraclinical Sciences, University of Pretoria, South Africa.

Table 4.2: Description of the five-stage scale macroscopic maturity stages for female and male Cape monkfish, *Lophius vomerinus,* (sourced from Period 1 study, Maartens and Booth (2005) and modified to include a veil, which was recorded for the first time in this study).

Maturation	Female	Male
I. Immature	Ovaries are greyish-pink in colour, relatively small, ribbon-like and appear empty with no vascularisation.	Testes are white to tan in colour and very small.
II. Developing	Ovaries are orange-pink, larger than the immature stage and with little vascularisation. No ova are visible.	Testes are white to tan in colour, much larger than the immature stage, and a small amount of milt is sometimes present when dissected.
III. Mature	Ovaries are orange, highly vascular and ova are evident by eye.	Testes are blotchy cream- to tan-coloured and very firm in texture. Moderate to large amounts of milt are present when dissected.
IV. Ripe	Ovaries are straw-coloured to almost clear and highly vascular. Distinct ova are present. *Presence of a cream/pale yellow delicate gelatinous flat ribbon structure containing individual eggs floating in separate chambers, within the gonad or being excreted from the gonad.	Testes are blotchy cream- to tan-coloured with areas of pink, extremely firm in texture and abundant amounts of milt are present when dissected.
V. Spent	Ovaries are grey, extremely flaccid, moderately vascular and appear almost empty. Atretic ova appear as black or white dots.	Testes are greyish-tan, extremely flaccid, edges appear translucent and a small amount of milt is sometimes present when dissected.

*Observed when a veil was found

Fecundity determination

Batch fecundity was estimated from ovaries of 18 Cape monkfish (Stage IV) of 46–75 cm (TL) (Table 4.1). After biometric data including total length (to the nearest cm below), gutted weight (g), whole weight (g) and sex determination. For each individual, the whole gonad was weighed and three subsamples, ranging between 7.0 and 9.9 g, were cut from three different sections of the ovary; anterior, middle, and posterior. Only ovaries containing oocytes in the secondary yolk stage were used, no veil were used to estimate batch fecundity. The total number of oocytes was estimated by direct counts in the ovary subsamples using a stereo microscope on the assumption that all oocytes were evenly packed in the gonads.

4.2.4 Data analysis

Sex ratio

The sex ratio of 360 530 fish was determined by counting the number of male and female specimens per depth stratum and size class for specimens collected during the commercial, research survey and port sampling between 2001 and 2019. The depth strata (i) < 200 m, (ii) 200–299 m, (iii) 300–399 m, (iv) 400–500 m, (v) 500–599 m, and (vi) > 600 m were considered. Length class: juveniles (< L_{50}, 37 cm TL), sub-adults (L_{50}–L_{100}, 37–47 cm TL) and adults (> L_{100}, 47 cm TL), were determined based on the length at maturity ogives estimated in Walmsley et al. (2005). Spatio-temporal sex ratio was determined for three-year intervals between 2001 and 2019. Spatial analysis was done for the entire Namibian coast (between 17°2'S and 29°30'S, Figure 4.4 a (1-6), b (1-6)).

There is uncertainty over the accuracy of data collected by Observers for some of the maturity stages, therefore only mature fish were used as a comparison for the years from 2001 to 2019. Where serious doubt was experienced, the data in question were excluded from the analysis. The Chi-square (X^2) test of homogeneity was used to test for the goodness-of-fit for the years between 2001 and 2019, based on the formula:

$$X^2 = \frac{\Sigma(O-E)^2}{i-E} \qquad \text{(Equation 4.1)}$$

Where O = Observed, and E = Expected.

Length at sexual maturity

The length class in which 50% of fish were mature was estimated by fitting a logistic function to the estimated proportion of matured males and females per length class (cm) per year for the contemporary samples (Period 2: set 1; 2015–2019 and set 2; 2004–2006). Maturity was modelled as a function of total length (cm), with length used as opposed to age as length data were available for all fish sampled while many fish did not have age data. L_{50} and δ parameters were obtained using solver. The logistic ogive was expressed as:

$$P(li) = (1)/(1+e^{-li-l_{50}/\delta}) \qquad \text{(Equation 4.2)}$$

where $p(li)$ is the probability that fish in length class i are matured, li the midpoint of length class i, l_{50} is the length at which 50% of the sex is matured, and δ is the steepness of the ogive. The differences in L_{50} among the years for both male and female fish were statistically determined using a chi-square analysis (Zar, 1999). Maturity ogives were used to examine temporal changes in maturation.

Reproductive seasonality

Reproductive seasonality was assessed by examining the proportion of fish with macroscopically-staged ripe gonads and determining the peak monthly gonadosomatic index (GSI) and hepatosomatic index (HSI) in both sexes. Only mature specimens (Stage III–V) were used to determine the mean monthly changes in GSI and HSI for both male and female fish. The GSI was used to investigate spatio-temporal patterns in the distribution of spawning individuals. A threshold, established from a reproduction baseline study of Cape monkfish (Maartens & Booth, 2005) was used as a reference point for peak spawning. These indices were then used to determine the spawning season and duration. A combination of samples collected during the survey (n = 6) and port sampling (n = 2 251) from 2015 to 2019 were used to calculate GSI and HSI. Data collected by Observers during monkfish fishing activities were not used in GSI calculations because observers do not record fish weight and gonad weight on board the fishing vessels due to unavailability of equipment on board. Calculations of monthly GSI and HSI done according to Yoneda et al. (2001) as per the following formula:

$$GSI = \left(\frac{GNW}{GW}\right) 100 \qquad \text{(Equation 4.3)}$$

$$HSI = \left(\frac{LW}{GW}\right) 100 \qquad \text{(Equation 4.4)}$$

where GNW is gonad weight (g), LW is the liver weight (g), GW is the gutted weight (g). The GSI thresholds (1.5% for females and 0.6% for males) were defined as the average GSI value, derived from Maartens and Booth (2005).

Comparison of the GSI between sexes was tested using Student's paired t-test (Zar, 1999), while the temporal trend of GSI for each month and the differences in GSI among the months were tested using a non-parametric Kruskal-Wallis test for each sex. Statistical significance was defined at $p < 0.05$ and 0.95 confidence intervals. Monthly GSI was represented as boxplots using R (version 3.3.1) (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018) software application.

To determine the spawning grounds, spatial data for ripe and running gonads were recorded and analysed. The Period 1 study (1996–2000) did not investigate the spawning ground, hence the comparison of the spawning ground was done only for data collected during Period 2 (2001–2018). An overlap was done using Boolean map algebra to show where ripe and running gonads of both sexes were found. The kernel densities were determined using a grid size of 500 x 500 m and a search radius of 50 km.

The monthly distribution of maturity Stage III, IV and V of Cape monkfish for 2015–2019 was subsequently compared to Period 1 maturity stages distribution as presented in Maartens and Booth (2005) from samples collected between 1996–2000. Data on maturity stages between 2000 and 2014 were not included in this analysis because it is very few with most of the months missing.

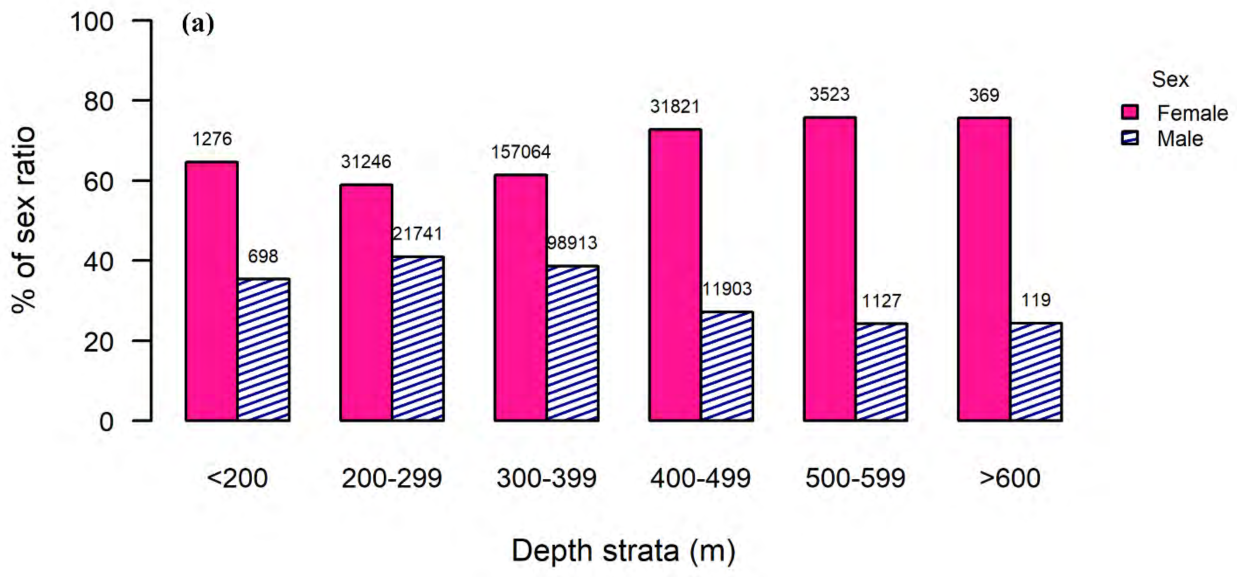
Assessment of fecundity

Batch fecundity was estimated from ovaries of 18 Cape monkfish (Stage IV) of 46–75 cm (TL) (Table 4.1). The total number of oocytes was estimated by direct counts in the ovaries using a stereo microscope on the assumption that all oocytes were evenly packed in the gonads. The number of oocytes in the three subsamples was counted, and then recounted if the coefficient of variation (CV) for two or three subsamples was larger than 5%. Batch fecundity for each female was calculated as the product of the number of oocytes per unit of weight multiplied by the total gonad weight. Linear regression analysis was used to examine the relationship between batch fecundity and fish size (total length).

4.3 Results

4.3.1 Sex ratio

Sex ratio was calculated from 360 530 (female n = 225 667 and male n = 134 863) Cape monkfish across depth strata, size class, and year, with the result of a male to female sex ratio of 1:1.67 (37.4%:62.6%). The sex ratio was skewed in favour of females at all depth strata. The test for the goodness-of-fit, determined statistically by a Chi-square (X^2) test of homogeneity, showed that the sex ratio is significantly dependant on depth ($X^2 = 2784.5$, df = 5, $p < 0.05$). The highest proportion of females was found in the deepest depth stratum of > 600 m (Figure 4.2a). A significant variation in the sex proportions by size class was also found ($X^2 = 18802$, df = 2, $p < 0.05$). The largest size class (> 47 cm TL) contained the highest proportion of females (77.9%), while the lowest proportion of females (53.8%) was recorded in the juvenile class (< 37 cm TL) (Figure 4.2b).



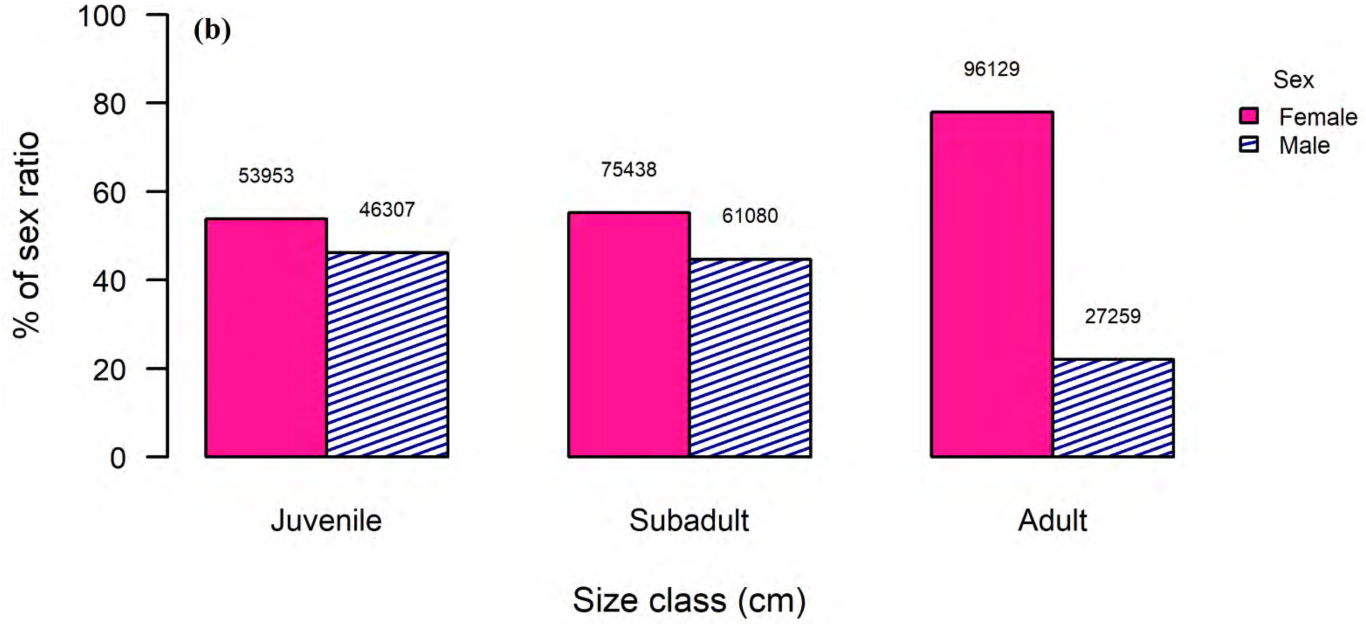


Figure 4.2: Male (n = 134 646) to female (n = 225 520) sex ratio of Cape monkfish, *Lophius vomerinus*, off the coast of Namibia, by depth (a) and size class (b) for 2001 and 2019.

There was a significant temporal difference in sex ratio ($X^2 = 2310.6$, df = 17, $p < 0.05$), with females significantly more numerous in all years, with the greatest proportions (68.5%) of females recorded in 2017 (Figure 4.3).

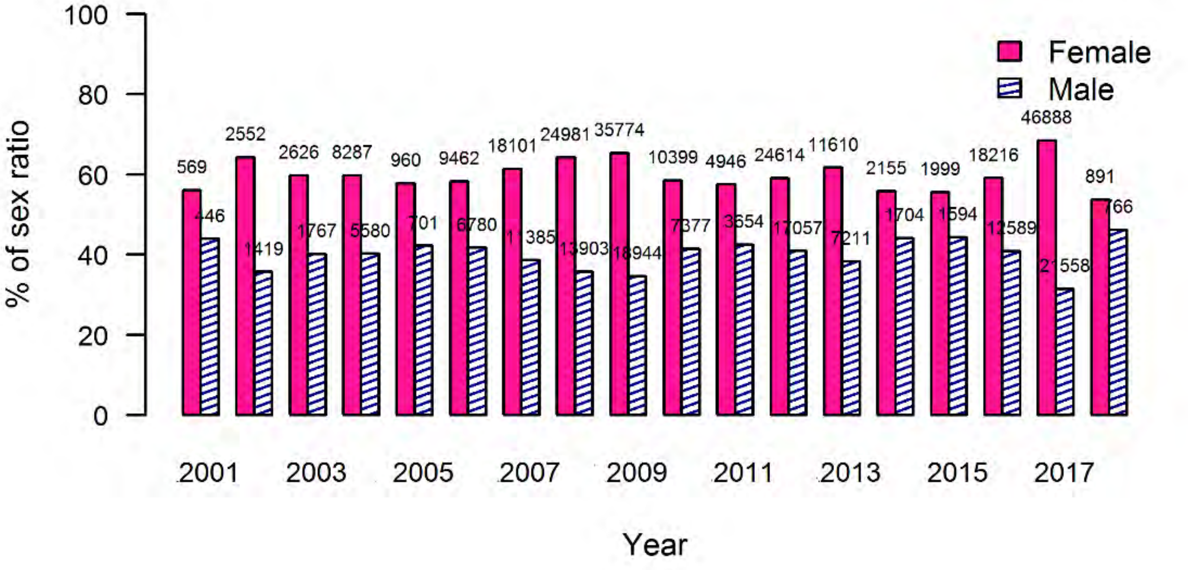
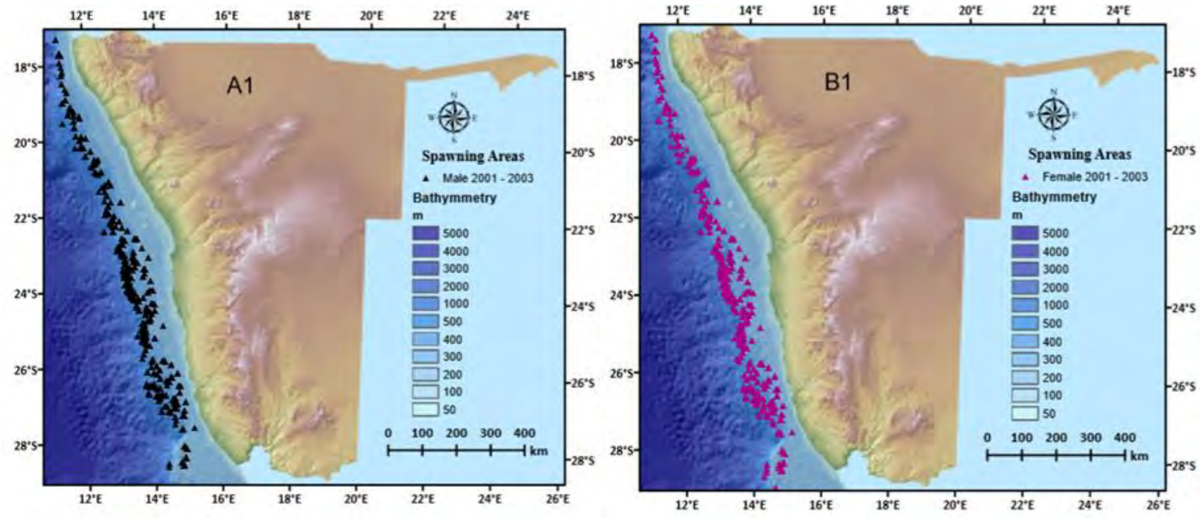
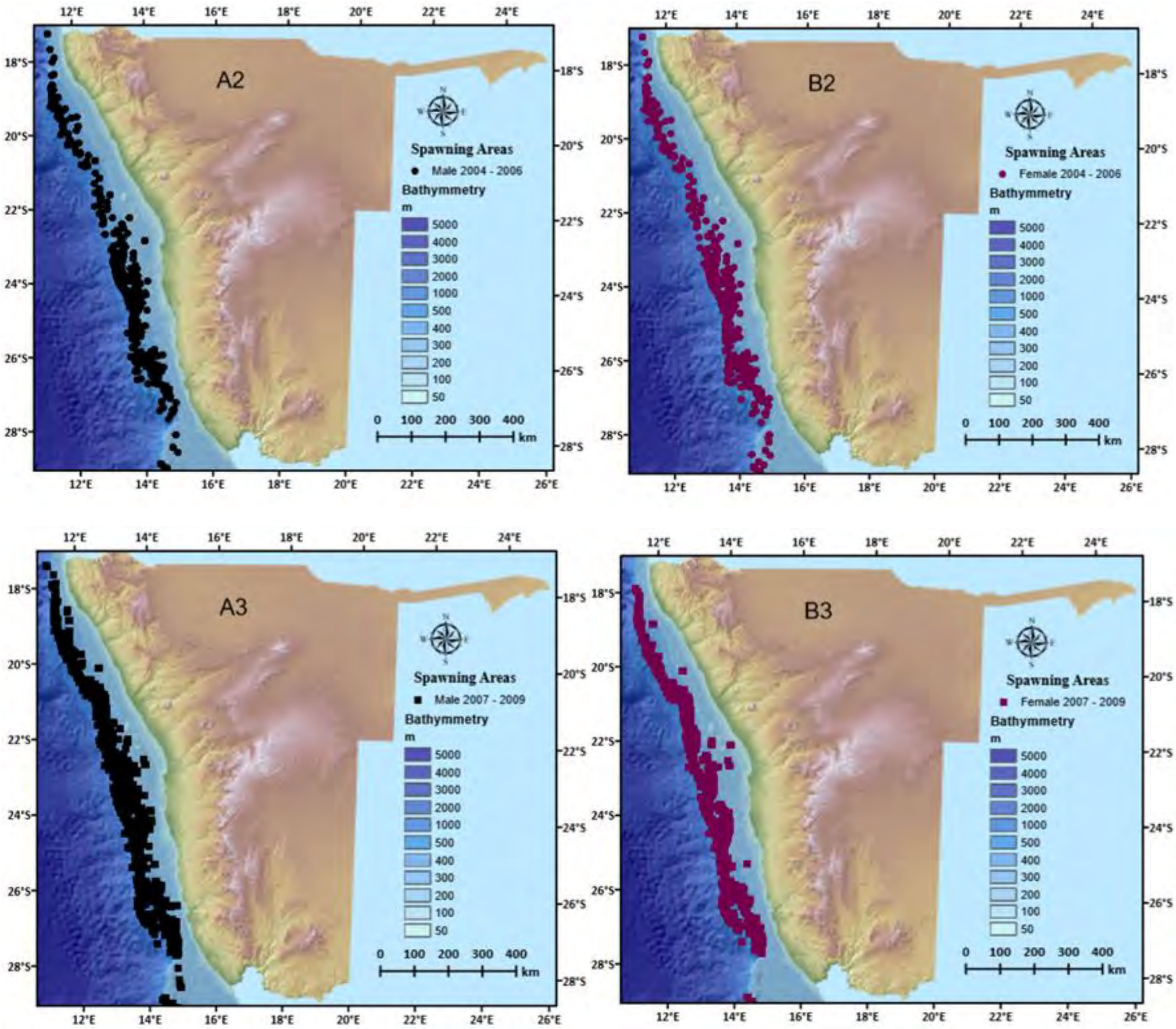


Figure 4.2: Temporal distribution of female (n = 225 520) to male (n = 134 646) Cape monkfish, *Lophius vomerinus*, off the coast of Namibia between 2001 and 2019.

The spatial distribution of male and female fish in 2001–2003 was similar, with females extending further south than males. Between 2007 and 2009, females were mostly further offshore than the males, except between 22º and 23ºS, where females were predominated inshore. Generally, between 2001 and 2019, along the entire Namibian coast (between 17°12'S and 29°30'S), there was a consistent pattern with females mostly offshore with an inshore distribution at 22º and 23ºS for all years except from 2001–2003 (Figures 4.4a (1-6) and 4.4b (1-6).




A2
Spawning Areas
● Male 2004 - 2006
B2
Spawning Areas
● Female 2004 - 2006
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Spawning Areas
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Spawning Areas
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26°S
28°S

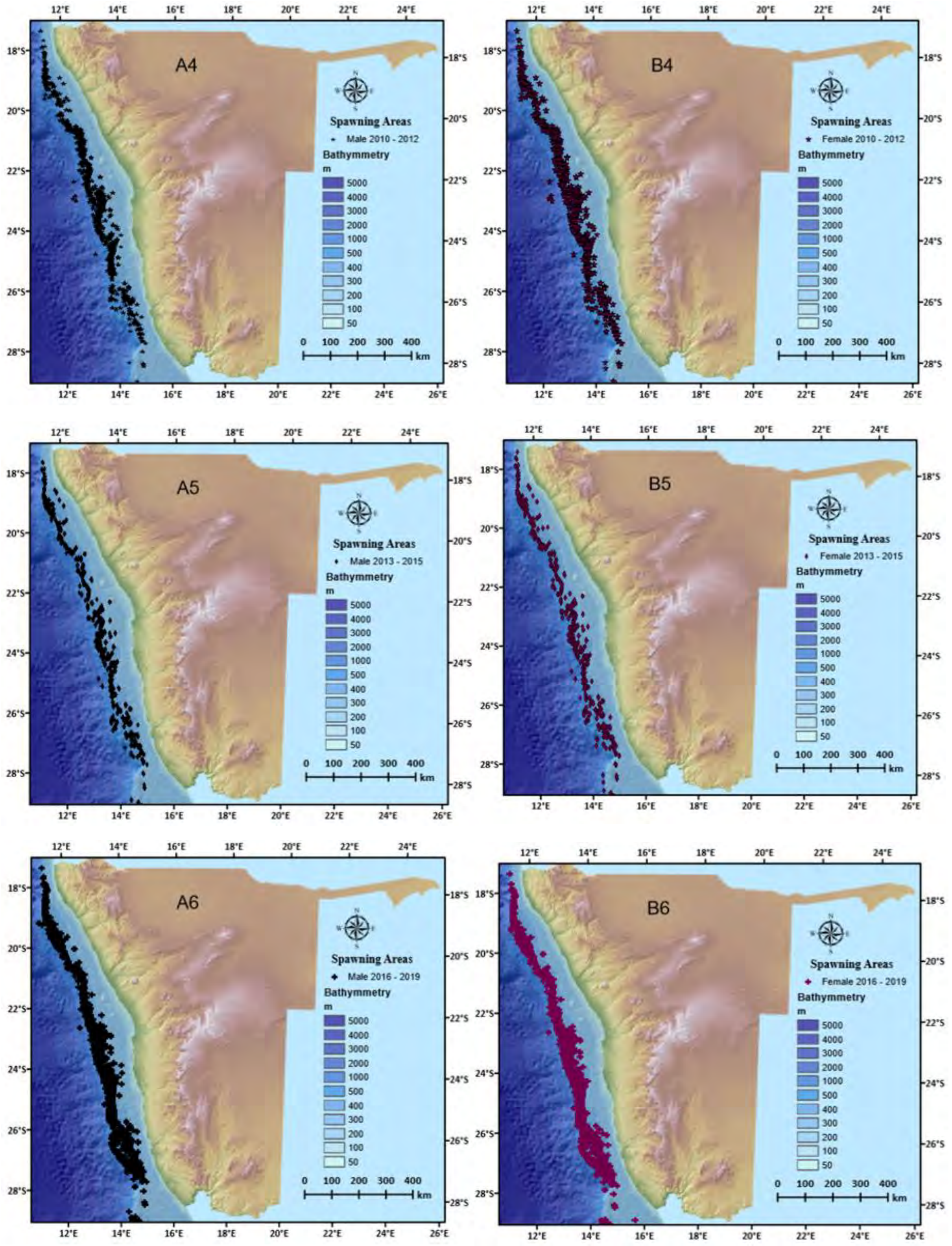


Figure 4.3: Spatio-temporal distribution of male (A1-6) and female (B1-6) Cape monkfish, *Lophius vomerinus*, off the coast of Namibia between 2001 and 2019. Map constructed using ArcGIS 10.8 Software.

4.3.2 Histological observation of gonads

The histological study validated the five macroscopic stages (described in Period 1, Maartens & Booth, 2005) for females and males with no adjustments required.

Females:

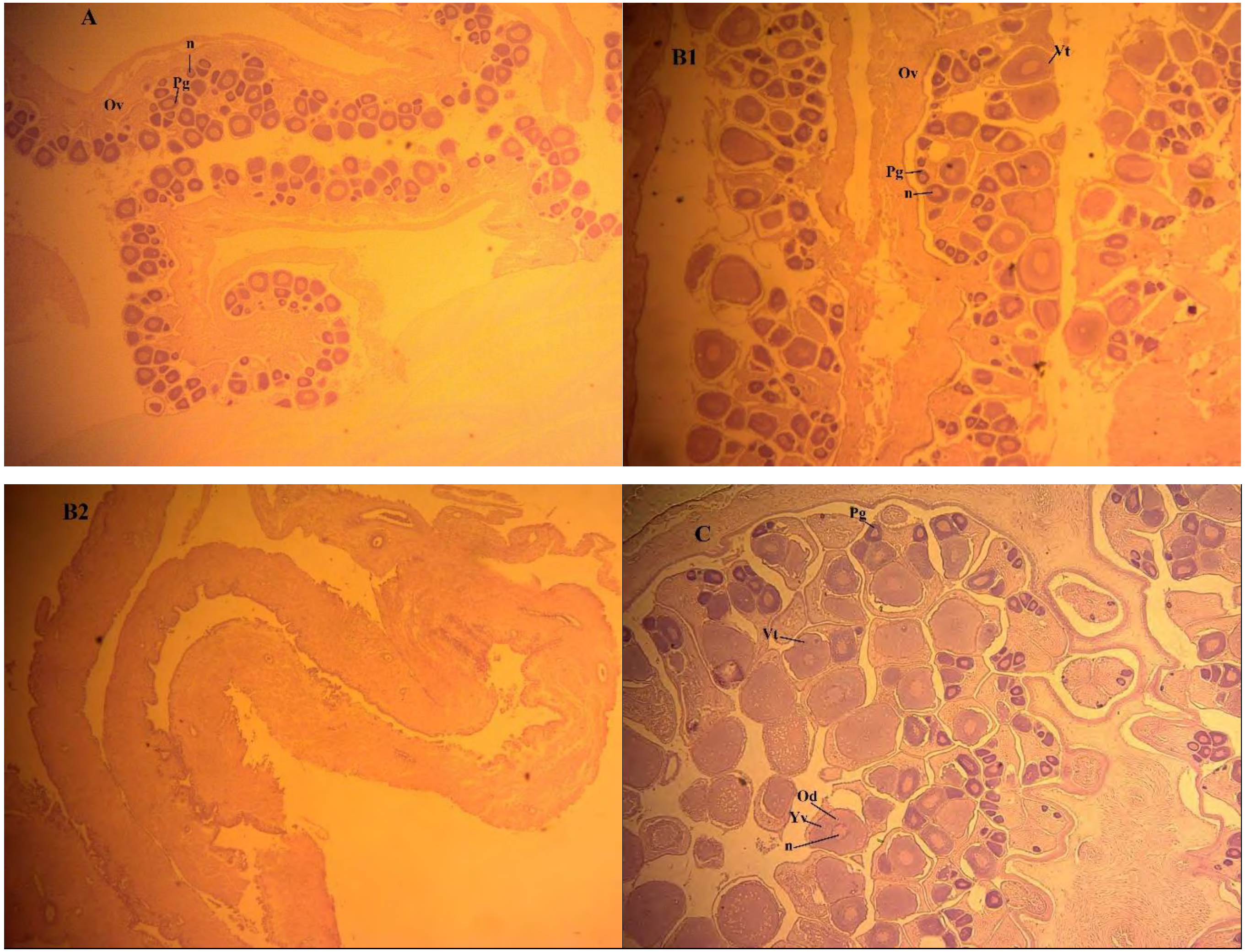
Female immature ovaries (Stage I) were characterised by non-clustered primary growth oocytes (Pg) or oogonia attached to the ovigerous membrane (Ov) (Figure 5A). The primary growth oocytes were of different sizes (based on the oocyte diameter) and shapes and they had large nuclei (n) occupying about a third of the oocytes.

Female developing ovaries (Stage II) were characterised by empty sections and sections with developing oocytes (B1 and B2) (Figure 5B). The gonads had oocytes in the primary development phase in addition to oocytes in a vitellogenesis stage (Vt). Some oocytes formed clusters in bag-like structures, which were detached from the Ov. The bigger the oocyte, the smaller the nuclei become (Figure 5B).

Stage II contains virgin fish with gonads developing for the first time, and some resting adult fish that had spawned before. Four female gonads were macroscopically staged as Stage II, but after microscopic examination, two gonads were classified as Stage VI (spent).

Mature ovaries (Stage III) are in the primary yolk vesicle oocyte stage (Figure 5C). There are relatively few primary growth oocytes. The secondary vitellogenic oocytes seem to be more spherical, with the presence of small, undefined yolk vesicles (Yv) and oil droplets (Od).

Ripe ovaries (Stage IV) have oocytes that are more spherical and detached from each other (Figure 5D). Most oocytes are fully developed although there are still some oocytes from Stage III but no primary growth oocytes. The oocytes are mature and characterised by large, well-defined reddish yolk vesicles. There are cortical alveoli (Ca) that have aggregated in the nuclei region and the nuclei have shifted from the centre to the periphery of the cytoplasm. Spent gonads (Stage V) are characterised mostly by empty regions, atretic oocytes and few postovulatory follicles (POFs) (Figure 5E). The presence of POFs was indicative of recent spawning activities.


A
n
Pg
Ov
B1
Ov
Vt
Pg
n
B2
C
Pg
Vt
Od
Yv
n

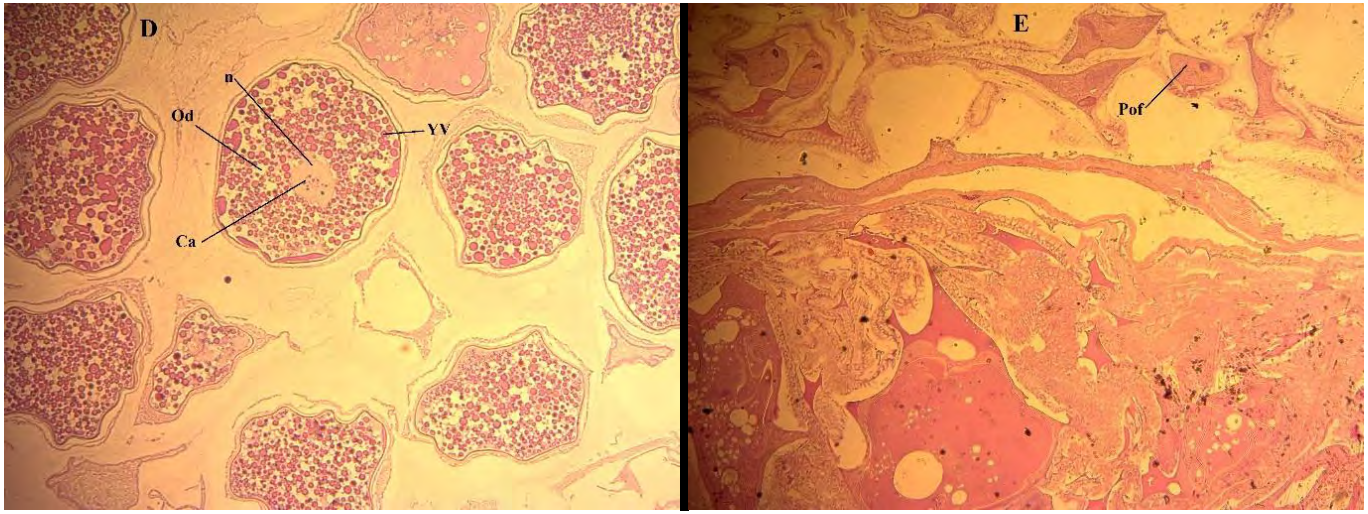


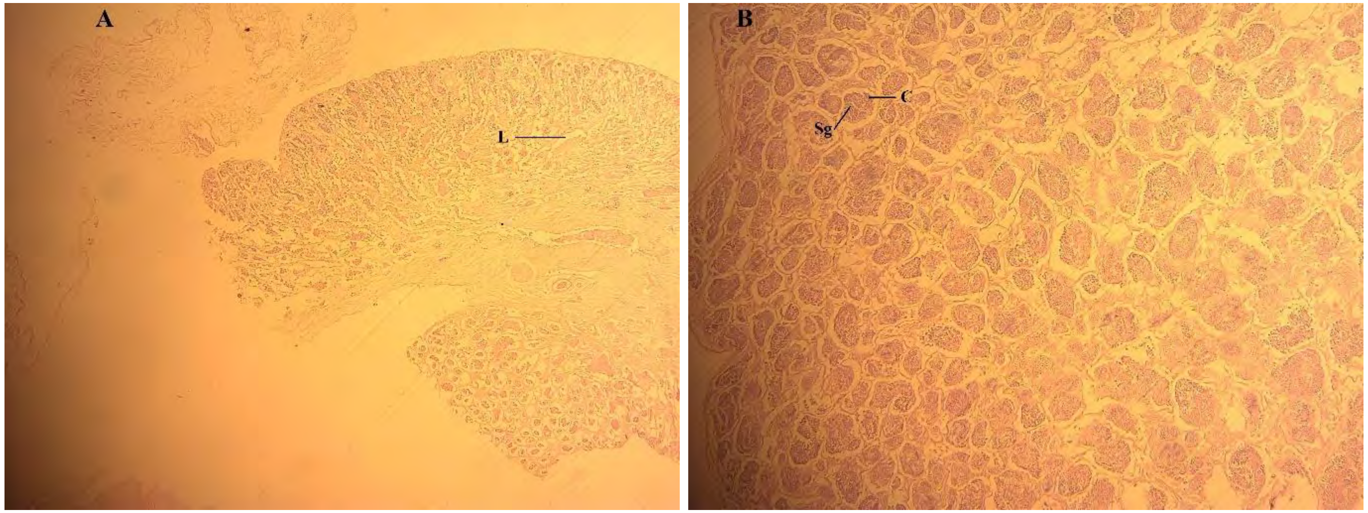
Figure 4.4: Images of histological sections through ovaries of Stage I (A), Stage II (B1 and B2), Stage III (C), Stage IV (D) and Stage V (E) Cape monkfish, *Lophius vomerinus*. Ov = ovigerous membrane, Od = oil droplet, n = nucleus, Pg = primary growth, POF = postovulatory follicle, Vt = vitellogenesis stage, Yv = yolk vesicle. (Bb) empty lobules. Scale bars = 100 µm. Pictures were taken from samples collected in July 2017 off the coast of Namibia.

Males:

The gonads of immature testes were in a spermatogonial proliferation stage (Stage I) which starts in the cysts, and the seminal lobule is organised and appears empty (Figure 4.6A). The gonads of developing testes (Stage II) are in an early spermatogenesis stage (Figure 4.6B). The seminal lobules contain spermatogonia (Sg) packed in cysts, which are bag-like structures. No visible spermatids (St) contained in cysts. Developing testes (Stage III) are in late spermatogenesis (Figure 4.6C), with single spermatozoa (Sz), together with the spermatid.

In mature testes (Stage IV), the lumen of the sperm duct is populated with fully mature spermatozoa with elongated head structures, now mixed with plenty of seminal fluid (Figure 4.6D).

Spent testes (Stage V) are characterised by few residual spermatozoa and some spermatogonia contained in seminal fluid, with some regions empty (Figure 4.6E).



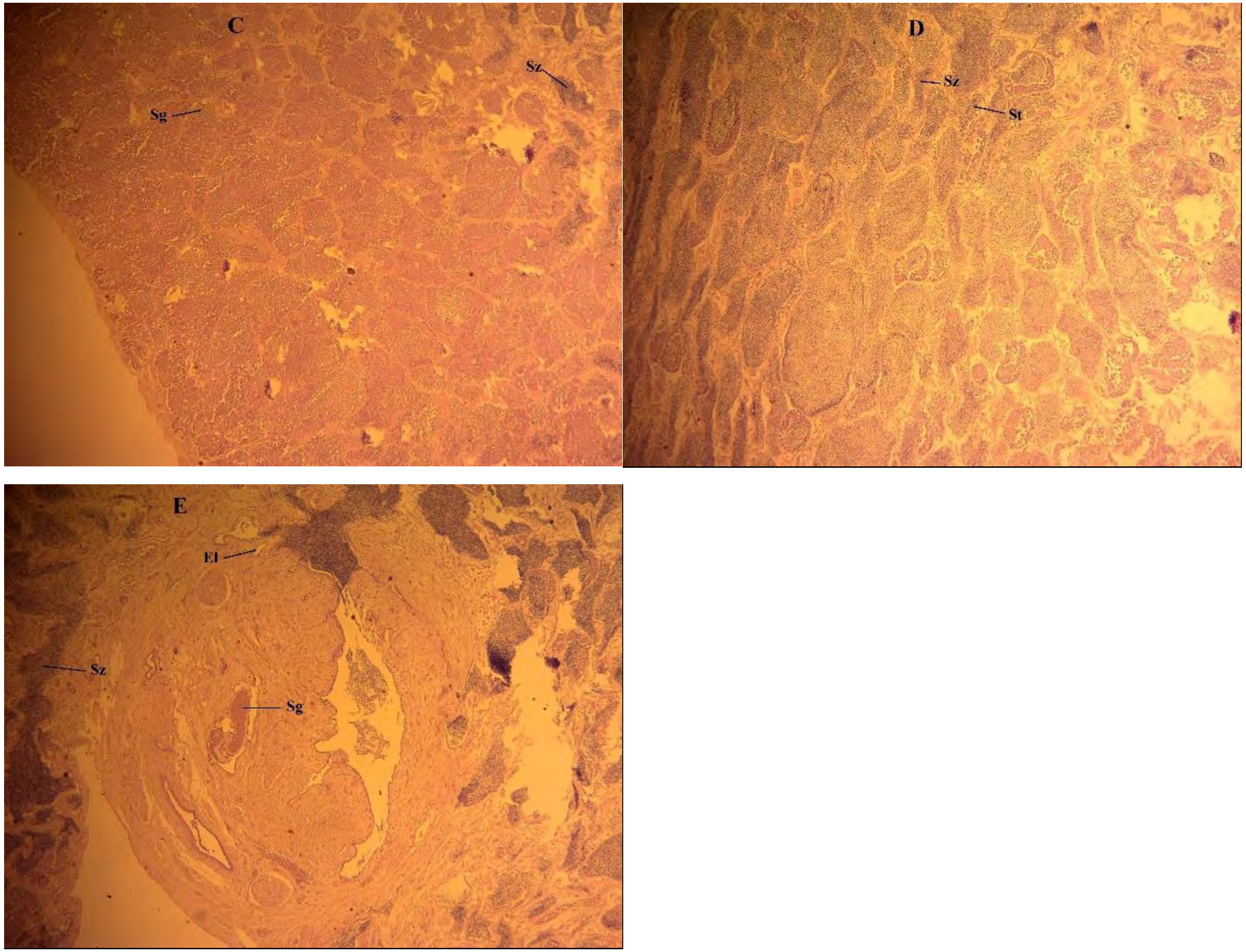


Figure 4.5: Images of histological sections through testes of Stage I (A), Stage II (B), Stage III (C), Stage IV (D) and Stage V (E) Cape monkfish, *Lophius vomerinus*. Ta = tunica albuginea, L = seminal lobule, C = cyst, El = empty lobule, Bv = blood vessel, Sz = spermatozoa, Sg = spermatogonia, Sc = spermatocyte, St = spermatid, Scale bars = 25 µm. Pictures were taken from samples collected in July 2017 off the coast of Namibia.

4.3.3 Temporal trends in length at sexual maturity

The length at 50% maturity (L_{50}) for the contemporary samples (set 2; 2015–2019) was estimated at 53.01 cm, $\alpha = 7.03$ for females and 35.08 cm, $\alpha = 5.35$ for males. These estimates were larger than the L_{50} estimations for the historical samples (set 1; 2004–2006), which were estimated at 40.99 cm TL, $\alpha = 6.86$ for females and at 29.89 cm TL, $\alpha = 4.72$ in males. In both the historical and contemporary samples, males matured at a smaller size (length) than females. Based on a Chi-square (X^2) test of homogeneity, the estimated length at 50% maturity for female ($X^2 = 1.53$, df = 1, $p = 0.2154$) and male fish ($X^2 = 0.41$, df = 1, $p = 0.5204$) did not vary significantly between the two periods (Figure 4.7).

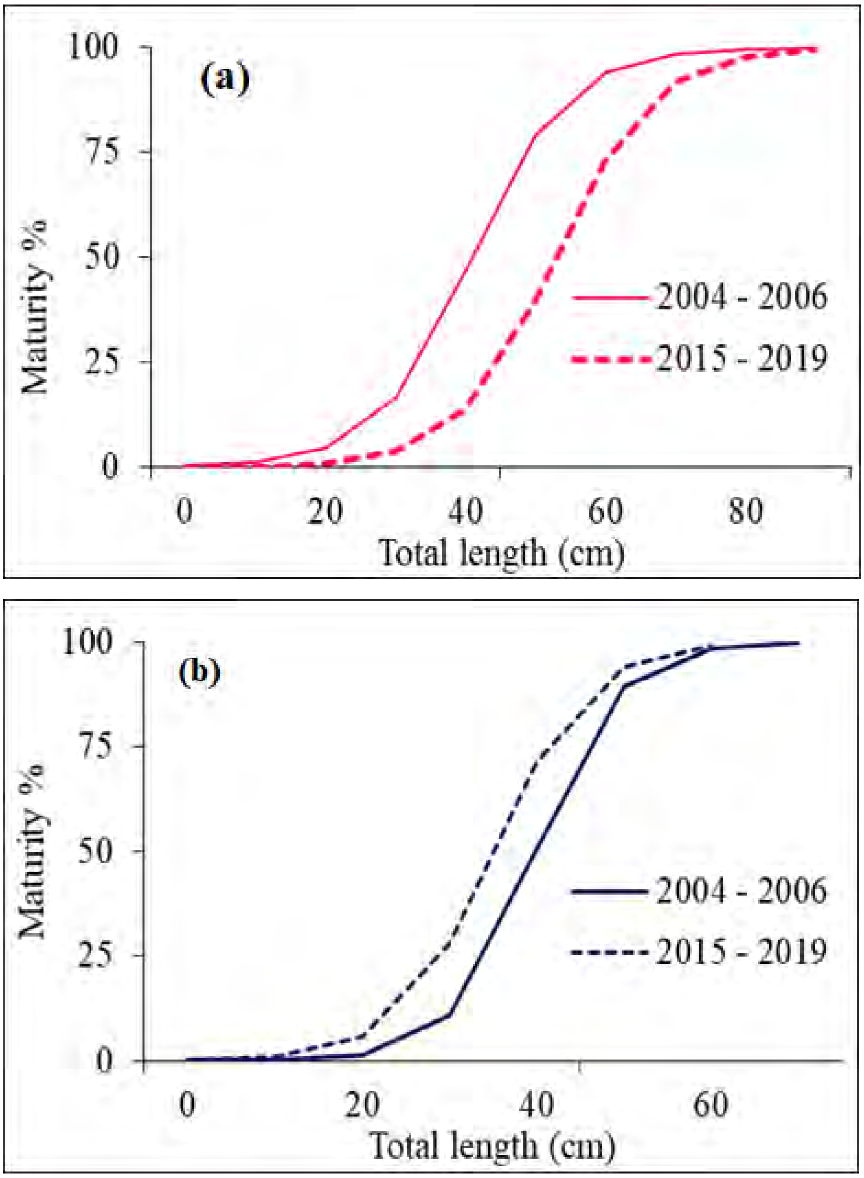
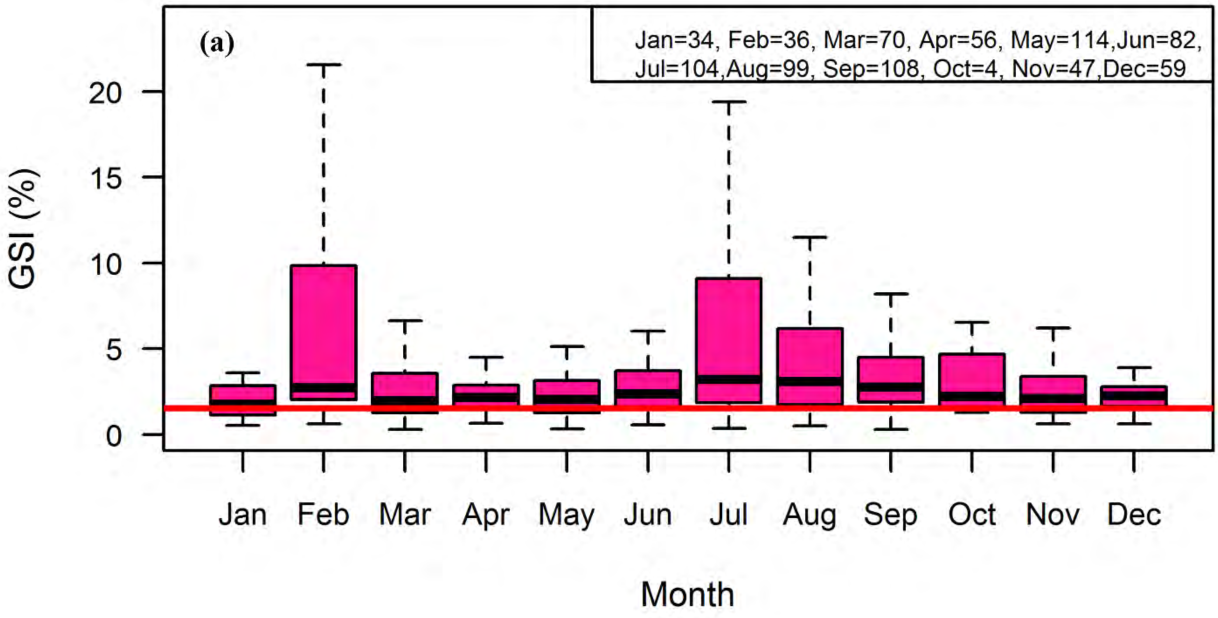


Figure 4.6: Temporal length at maturity for (a) female and (b) male Cape monkfish, *Lophius vomerinus,* off the coast off Namibia sampled during 2004–2006 (n = 378) and 2015–2019 (n = 4475).

4.3.4 Spawning season

Gonadosomatic Index

There was a significant difference between the female GSI (M = 3.82 (±5.48) and male GSI (M = 1.14 (± 2.18), Student's paired t-test, (DF = 579), $p < 0.05$). The mean GSI for both sexes remained fairly constant but peaked between July and September for females, and August (2.0% ± 2.6) for males. The GSI varied significantly among months for females (Kruskal-Wallis chi-squared = 34.107, df = 11, $p < 0.05$). A Kruskal-Wallis test for differences among GSI for male was not significant (df = 11, $p = 0.08$). The lowest mean GSI values were recorded in January for females (2.6% ± 2.53) and October for males (0.7% ± 0.27) (Figure 4.8).



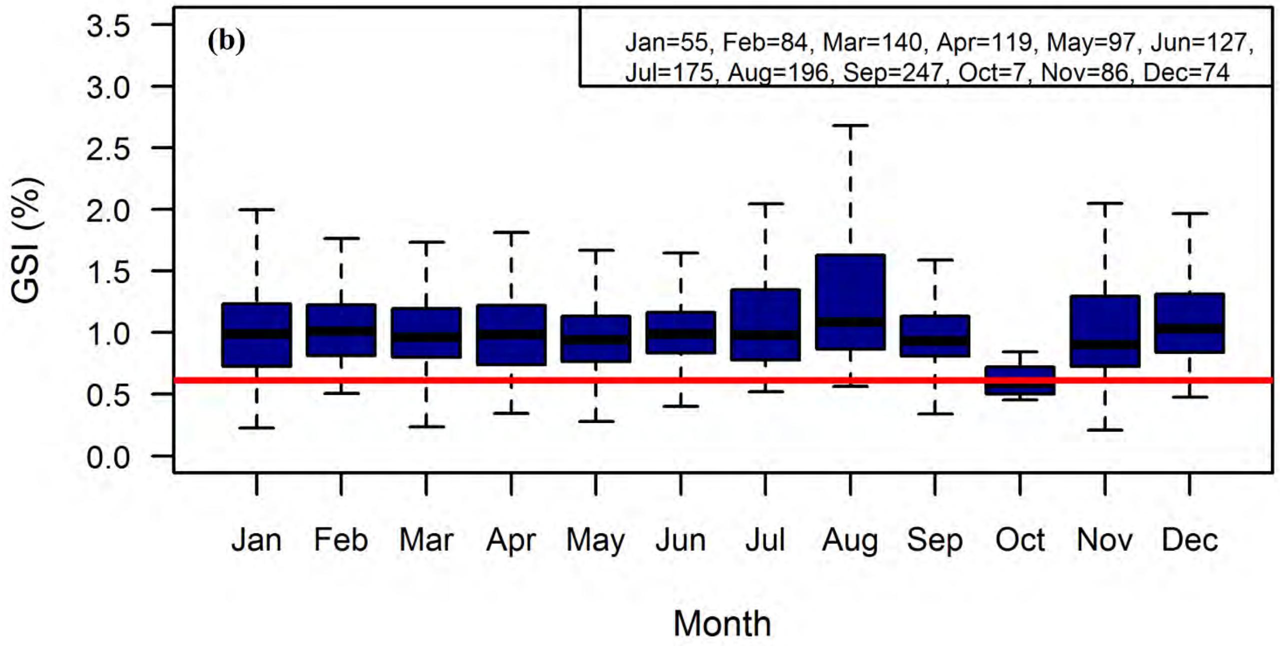


Figure 4.7: Mean monthly gonadosomatic index (GSI) values with standard error for (a) female (n = 836) and (b) male (n = 1 421) (b) Cape monkfish, *Lophius vomerinus*, collected off the coast of Namibia between January 2015–December 2018. The horizontal solid lines indicate the threshold value (1.5% for females and 0.6% for males).

Hepatosomatic index

Based on a paired t-test, there was a significant difference, t = 6.9098, df = 10, $p < 0.05$), in the mean HSI values between males (2.54 ± 0.24) and females (3.14 ± 0.26). Kruskal-Wallis chi-squared analysis showed a monthly significant difference in the HSI for both females (Kruskal-Wallis chi-squared = 21.757, df = 11, $p < 0.05$), and males (Kruskal-Wallis chi-squared = 29.483, df = 11, $p < 0.05$). Mean monthly HSI peaked in November (3.63 ± 4.97) for females, and in January (2.84 ± 0.99) for males (Figure 4.9).

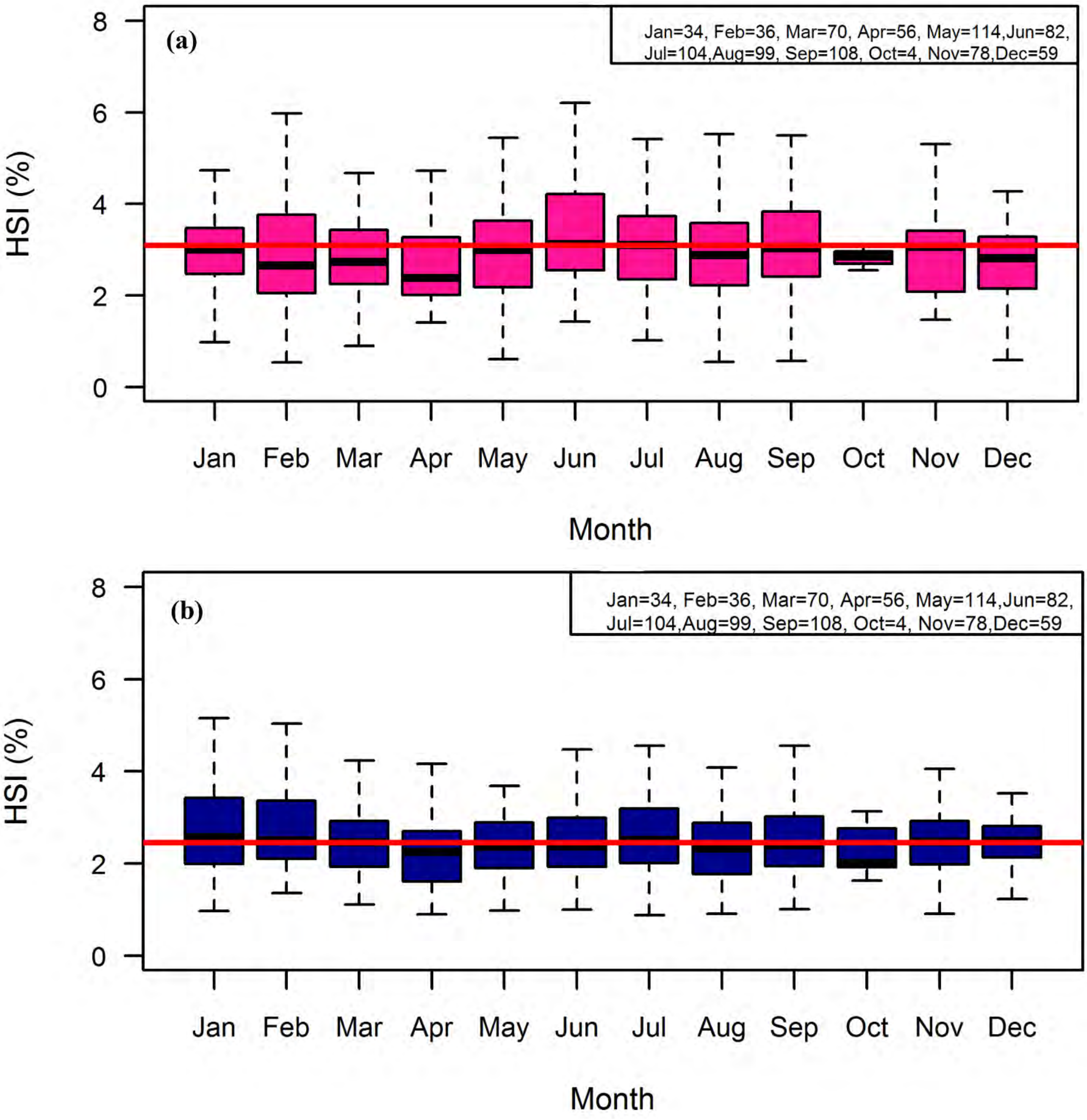


Figure 4.8: Mean monthly hepatosomatic index (HSI) values with standard errors for (a) female (n = 517) and (b) male (n = 925) Cape monkfish, *Lophius vomerinus*, collected off the coast of Namibia between January 2015–December 2018. The horizontal dotted lines indicate the average value (3.1% for females and 2.5% for males).

4.3.5 Temporal distribution of spawning Cape monkfish

The proportions of mature individuals capable of spawning (Stage IV) were dominant in July

(23.8%), August (26.2%) and September (22.9%) for females, and in April (52.5%) and November (28.5%) for males. Female spent gonads (V) were prevalent in January (45.6%) and October (43.4%), while spent males were prevalent in October (30%) (Figure 4.10a and 4.10b)

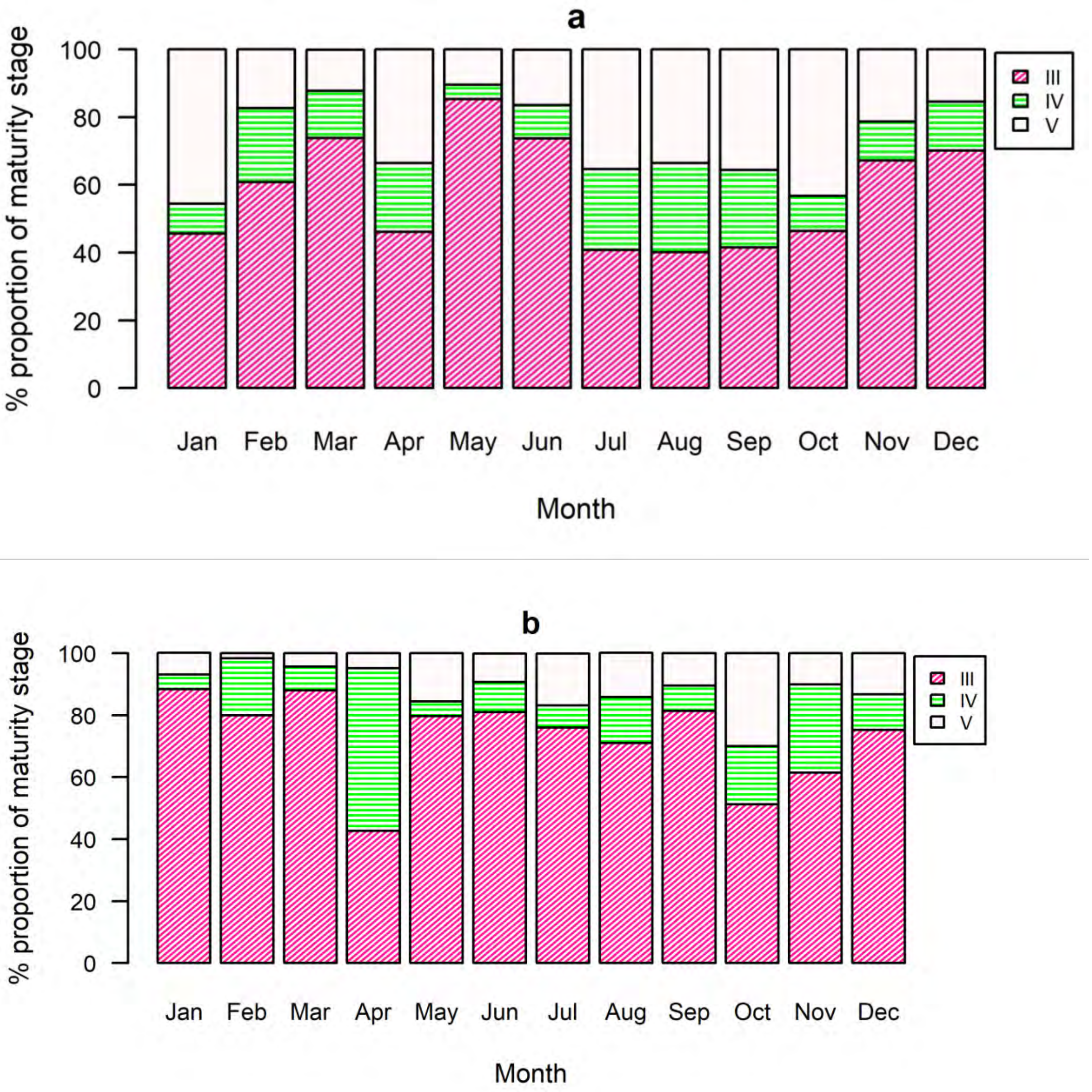


Figure 4.9: Monthly proportions of maturity stages of gonads for a) females (III = 3879, IV = 932, V = 1631) and b) males (III = 3112, IV = 940, V = 433) Cape monkfish, *Lophius vomerinus*, collected off the coast of Namibia between January 2015 and December 2019.

4.3.6 Spatial and temporal distribution of spawning Cape monkfish

Latitudinal distribution of maturity Stage IV was used to serve as an indication of spawning grounds. The boundaries of the 90th percentile of the kernel density determinations for females and males with ripe and running gonads are shown in Figure 4.11. Cape monkfish appear to spawn throughout Namibian waters, with evidence of hotspot spawning aggregation between 21^o and 25^o S. Based on the temporal analysis of distribution of fish in maturity Stage IV, there was a great overlap in the area between 22^o and 26^o S.

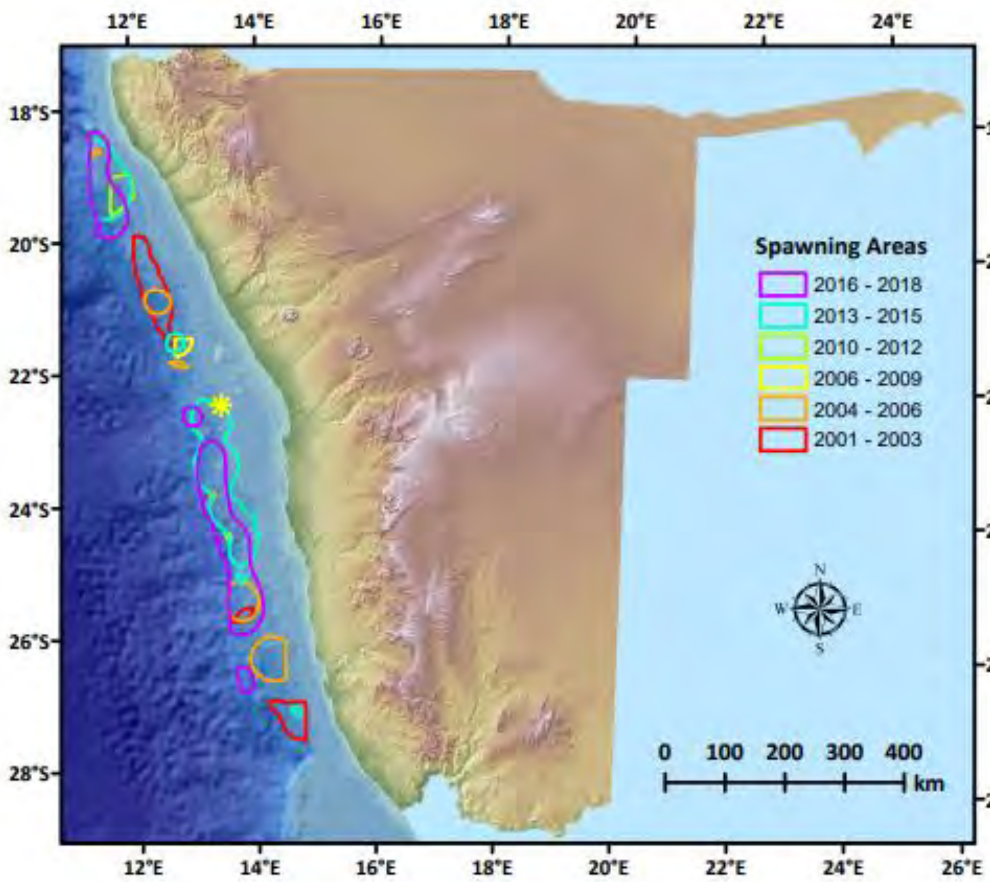


Figure 4.10: Spatial and temporal distribution of ripe and running female (Stage IV) (n = 277) and male gonads (n = 400) of Cape monkfish, *Lophius vomerinus*, for 2001–2018 off the coast of Namibia. The yellow asterisk indicates the location where the veil was found. Map constructed using ArcGIS 10.8 Software.

In this study, one veil, which houses the spawned eggs, was recorded for the first-time off Namibia as indicated by the yellow asterisk in Figure 4.11. The veil is an off-white, delicate, gelatinous, flat ribbon structure containing individual mature oocytes. The veil was found during the monkfish annual swept-area biomass survey in November 2018, at a depth of 248 m in the area off Swakopmund (22º30'S, 13º25'E). The veil was 3.3 m long, 1.48 m wide and 1 568 g (wet weight) (Figure 4.12).

Figure 4.11*:* A 3.3 m veil collected from a 54 cm (TL), female Cape monkfish, *Lophius vomerinus*, caught in November 2018, off the coast of Namibia (Picture credit: Ndamona Mathew, 2018).

4.3.7 Fecundity

Batch Fecundity (BF) ranged from 76 695 to 182 440 oocytes and a mean of 136 732 oocytes (± 29228.54) for females between 46–75 cm TL (n = 18) (Figure 4.13). Batch fecundity tended to increase linearly with total length (cor 0.8453) based on Pearson's product-moment correlation; $t = 6.3292$, $df = 16$, $p < 0.05$.

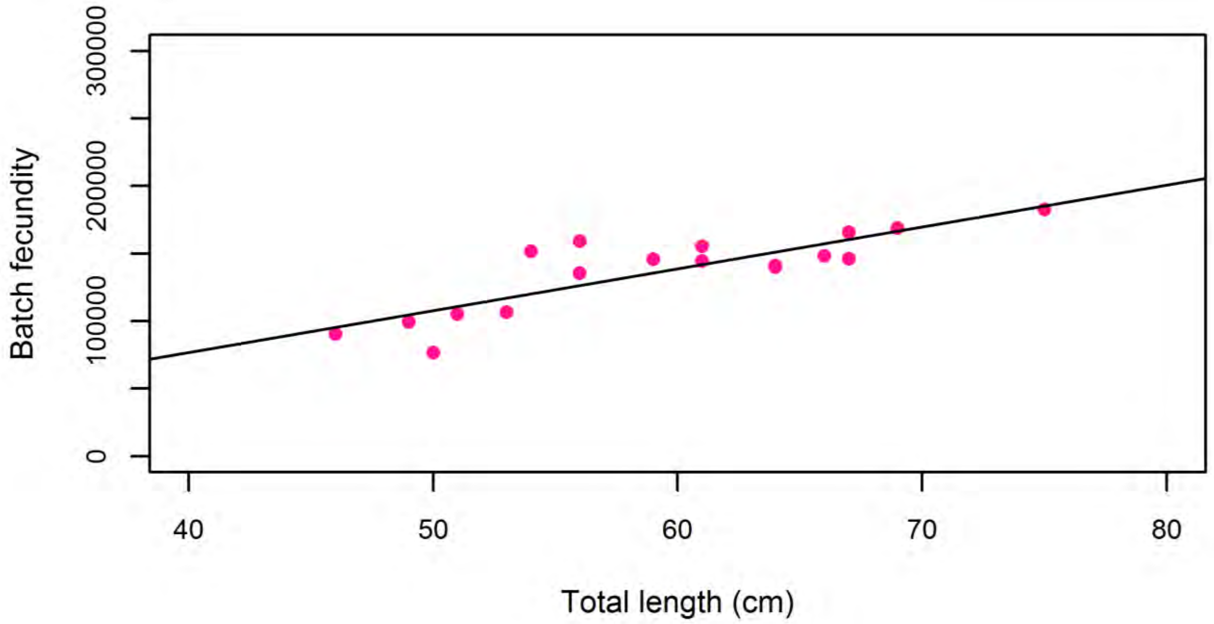


Figure 4.12: Relationship between batch fecundity and total length (TL) for Cape monkfish, *Lophius vomerinus*, (n = 18) collected off the coast of Namibia, between August and September 2017.

4.4 Discussion

To investigate whether the reproductive strategies of Cape monkfish have changed in the Namibian marine waters, results of Period 2 (2001–2019) were compared to the results of Period 1 (1996–2000). Results of the sex ratio between Period 1 (1996–2000) and Period 1 (2001–2019), show that the sex ratio is still skewed in favour of female in Period 2 as was the case in Period 1. However, the proportion of males to females had changed, from 1:1.21 (in Period 1) to 1:1.67 (in Period 2). The sexual maturity stages from Period 1 were microscopically validated with no adjustments. The length at 50% maturity (L_{50}) was compared between Period 1 (1996–2000) and Period 2 (2004–2006, 2015–2019). In all sets of data (1996–2000, 2004–2006 and 2015–2019), females matured at a smaller size (length) than males. However, the L_{50} values were larger during Period 1 (1996–2000) than the L_{50} estimations for both 2004–2006 and 2015–2019 samples, suggesting that fish are maturing at a smaller size in recent years than in the past.

Comparisons of the spawning season for Period 1 to Period 2 show that female Cape monkfish spawn throughout the year with a peak between July and September in both periods. However, what stands out is an additional elevated spawning activity in February during Period 2, which was not reported in Period 1. For both periods, the GSI for males did not differ significantly throughout the year. The proportions of ripe and running eggs were high in the months of high GSI. Analysis of spawning grounds, using spatial data for ripe and running gonads, shows spawning activities throughout the coast but the great intensity was recorded between 22^{0} and 26^{0} S. The most interesting result of this study was the first-time discovery of the veil off Namibia, around Swakopmund.

The sex ratio in Period 2 was skewed in favour of females as was also reported in Period 1 (Maartens & Booth, 2005). However, the proportion of the males to females had increased from 1:1.21 (in Period 1) to 1:1.67 (in Period 2). The significantly skewed temporal sex ratio in favour of female fish found in Period 2 (this study) is similar to the monthly sex ratio variation reported in *L. budegassa* (Duarte et al., 2001). Although in the 18 years between 2000 and 2018, females were temporally significantly more numerous than the males, the proportions are seen to fluctuate, possibly due to the level of exploitation, or in response to environmental variables (e.g., water temperature), or a combination of both. Water temperature has been reported as among the most important environmental factors able to affect sex determination in fish (Geffroy & Wedekind, 2020). Other *Lophius* species, including *Lophius americanus* (Richards et al., 2008), *Lophius budegassa* and *Lophius piscatorius* (Afonso-Dias & Hislop, 1996; Duarte et al., 2001) display a similar trend. The skewed sex ratios may have resulted from unequal fishing mortality between the sexes because females tend to attain a larger size than male fish (Maartens & Booth, 2005), and the current fishing net mesh size is selective for larger fish (although small fish are also caught to a certain extent). The fact that males grow more slowly and attain a smaller maximum size than females implies that males will be smaller than females of the same age, thus, even a sex ration of 1:1 per cohort, it will nonetheless be skewed towards females in the larger size classes. Fish growth rate is the largest factor influencing sex ratio in fish (Vicentini & Araújo, 2003), with the fast-growing sex tending to outgrow the most vulnerable smaller size phase quickly, leading to a skewed sex ratio. Additionally, when there is a difference in the growth rate of different sexes of the same species, the fast-growing sex diminishes the predation proportion (Vicentini & Araújo, 2003). Maartens and Booth, (2005) and Richards et al. (2008) previously observed that male *Lophius* species grow slowly, causing the male numbers to accumulate near the maximum size, thereby skewing the sex ratio. The skewed sex ratio in favour of females with depth, suggests a movement of large females into deeper waters, an observation comparable to those of Richards et al. (2008). It was hypothesised that the differences in sex ratio among size classes and depth strata are possibly due to behavioural differences, including single-sex movement patterns, because large catches of entirely single-sex during sampling activities were observed in this study. Large males were few in both Period 1 (Maartens & Booth, 2005) and Period 2 (this study), suggesting that as these species get older, the proportion of female fish outnumber male fish. A similar trend was observed in *L. americanus* (Johnson et al., 2008), *L. piscatorius* (Afonso-Dias & Hislop, 1996), and *L. litulon* (Yoneda et al., 2001, Sun et al., 2020). Interestingly the significantly female-dominant sex ratio may have an implication in stock assessment because the use of the age-length keys and other inputs into the Age Structure Production Model (ASPM) currently used to assess the Namibian monkfish stock does not consider this sex ratio imbalance.

The sexual maturity stages from Period 1 were microscopically validated with no adjustments. This study is the first to microscopically examine gonads of Cape monkfish. Histological examination of gonads, which is more reliable (Yoneda et al., 2001), validated the five macroscopic maturity stages proposed in Period 1 (Maartens & Booth, 2005). Interestingly, Stage II had empty regions (with no oocytes), an indication of post-spawning activity, while at the same time, other regions had small oocytes, showing the growth of new oocytes. The presence of both regions with no oocytes and regions filled with oocytes can be attributed to the gradual development of oocytes. It remains difficult to distinguish the virgin female fish in Stage II from resting females in Stage II that are restarting the spawning cycle. At each given maturity stage, the oocytes of the same gonads were not in the same developmental stages. For instance, Stage III contains oocytes in both Stage II and Stage III, an observation also made for *L. budegassa* (Colmenero et al., 2013). Equally, it was noted that oocytes in the same stage, for example, Stage III, were of various shapes and sizes (based on the oocyte diameter), similar to what was observed in *L. budegassa* (Colmenero et al., 2013). The spent gonads (Stage V) of other *Lophius* species such as *L. litulon* (Yoneda et al., 2001) had oocytes in the primary or secondary yolk oocyte stages; however, this was not observed in Period 2. This was not found to be surprising since the veil containing mature oocytes and developing oocytes had been released, thus developing oocytes were not expected to be left in the gonad. Observers tend to classify fish in Stage V as Stage II possibly because both gonads in these stages are similar and, after completing Stage V, the mature fish return to Stage II (resting stage). It is necessary to train samplers involved in the macroscopic staging of Cape monkfish. Additionally, there is an assumption that oocytes are evenly distributed, but this does not seem to be true in Cape monkfish. Large portions of gonads were empty, especially in Stages II and III of female gonads.

The results of the comparison of length at 50% maturity (L_{50}) between Period 1 (1996–2000) and Period 2 (2004–2006, 2015–2019), show that L_{50} of Cape monkfish varied in all datasets (1996–2000, 2004–2006 and 2015–2019). Although the variation is not significant ($p > 0.05$), it is interesting that females matured at a smaller size than males. The L_{50} values were larger during Period 1 (1996–2000) than the L_{50} estimations for both 2004–2006 and 2015–2019 samples, suggesting that fish have been maturing at a smaller size recently than in the past. Specifically, results show that males mature at a smaller size than females in all datasets, an observation that seems to be a genus trait because it has been observed in *L. budegassa* (Colmenero et al., 2013) and *L. americanus* (Richards et al., 2008) of the same genus. However, an interesting result is that each maturation is now at a smaller size than in Period 1. Additionally, the dataset for 2015–2019 shows that both male and female fish are maturing at a larger size than in the dataset of 2004–2006, but still smaller than in 1996–2000, which could be a sign of stock recovery. However, this observation requires further investigation.

Changes in maturation timing have been linked to exploitation pressure (Rochet 1998; Wheeler et al., 2009; Butler et al., 2018) and climate change (Pankhurst & Munday, 2011; Kujawa et al., 2015). Both these factors have been reported in this region. Length at maturity has been used as an indicator of fishing pressure (Buxton, 1993; Trippel, 1995; Lappalaine et al., 2016) while early maturation is said to be a manifestation of stress in fish as a result of climate change (Trippel, 1995; Pankhurst & Munday, 2011). For instance, in North Atlantic, early maturation was detected in some of the American plaice (*Hippoglossoides platessoides*) fish cohorts that experienced higher temperatures (Morgan & Colbourne, 1999). Male Cape monkfish mature at a smaller size than female fish as evident in Period 1; however, this change in the length at maturity (L_{50}) for female or male fish is not significant, despite the climate change reported in this region and the extensive fishing pressure directed at this species. It could be that the maturity rate of Cape monkfish is resilient to external factors such as fishing pressure and/or climate change. Woodhead et al. (1996) found that monkfish is generally tolerant of relatively low oxygen conditions. It is also possible that the time series studied (2004–2019) is too short for Cape monkfish, which is a slow-growing and long-lived species (see Chapter 5), to exhibit changes as a response to the external factors (Hunter et al., 2015). Law (2007) suggested that sometimes changes in maturation may only be detected on decadal time-scales. Additionally, although changes have been recorded in many environmental variables, for example, sea surface temperature (SST) and oxygen concentration in this region, Cape monkfish inhabit deeper waters (e.g., 400 m) where physiological conditions (e.g., temperature) are mostly more stable than in shallow waters. It is important to note that not all fish populations that have declined exhibit changes such as early maturation (Berlinsky et al., 1995), and to consider the inherent caveats associated when comparing two different studies; there is always the element of bias associated with the differences in sampling techniques and sampling location. For example, in this study, resting adults were classified as immature fish in the L_{50} estimation methodology, which could have biased our results. Despite these caveats, the compared contemporary and historical estimates of L_{50} provide much-needed insight into understanding how reproductive biology has changed over the past decade. Understanding the reproductive dynamics of fish in relation to climate change and extensive fishing pressure is important in the context of fisheries management.

Female Cape monkfish spawned throughout the year with a peak between July and September in both periods. However, what is salient is an additional, elevated spawning activity in February during Period 2, which was not reported in Period 1. For both periods, the GSI for males did not significantly differ throughout the year. The proportions of ripe and running eggs were high in the months of high GSI. Gonadosomatic index (GSI) is useful in determining the spawning seasons (Yoneda et al., 2001; Ghaffari et al., 2011; Jansen et al., 2015), and in Period 2, the mean monthly GSI was above the estimated mean GSI in both sexes for this species in Period 1 (Maartens & Booth, 2005). The female GSI estimates in Period 2 peaked between July and September, as was also observed in Period 1 (Maartens & Booth, 2005). Period 2 is distinctive in that the results show an additional GSI peak in February that was not recorded previously. Although there is evidence that fishing pressure leads to changes in life-history traits (Buxton, 1993; Franco et al, 2012), solid conclusions could not be made with certainty that the additional peak in February in Period 2 denotes changes in the biology of this species. There is evidence of climate change in this region (Hamukuaya et al., 1998; Kirkman et al., 2013; Jarre et al., 2015a) and these changes might have contributed to the new observations in this study. Results of Period 1 showed no significant differences in the male GSI; similarly, no distinctive differences were found.

Monthly HSI calculated for this species showed no pattern for both sexes; however, this contradicts results obtained by Walmsley et al. (2005) for the same species off South Africa. a decline in HSI was expected to be closely associated with an increase in GSI, as demonstrated in various studies (Yoneda et al., 2001; Mahboob & Sheri, 2002; Ghaffari et al., 2011), but this pattern is not distinctively demonstrated in this study. No plausible explanation for this observation could be found. For instance, when female GSI reached a maximum in July, female HSI was expected to reach the minimum, but this is not evident in this study. Discrepancies (especially of the February peak) between Period 1 and Period 2 may be attributed to the differences in sampling periods and not necessarily due to fishing pressure and climate change.

The proportions of ripe and running eggs were high in the months of high GSI; however, there was a relatively low number of mature gonads recorded throughout Period 2, as was also evident in Period 1. The scarcity of ripe and running gonads suggests a low catchability of spawning individuals. The scarcity of mature individuals was also noted in *L. piscatorius* of the same genus (Hislop et al., 2001). The seasonal distribution of mature ovaries and testes (Stages III, IV and V) between Period 1 (Maartens & Booth, 2005) and Period 2 (this study) is similar, except that no spent ovaries were recorded in November in Period 1, while the present study recorded spent ovaries in all months. In addition, this study recorded ripe and running ovaries in all months, while in Period 1 there was no evidence of ripe ovaries in December and January. There might be some changes leading to an extended spawning peak. Cape monkfish spawn throughout the year, with spawning peaks observed between July and August for females but no significant peak for males (inferred from GSI in Figure 4.8 and based on the proportions of ripe and running gonads in Figure 4.10.) Based on these observations, the main spawning season was from July through September with a second season in February.

Latitudinal distribution of ripe and running gonads (maturity Stage IV) was used to identify spawning grounds. Evidence (distribution of ripe and running gonads) from this study shows that Cape monkfish spawn throughout Namibian waters with a great spawning intensity between 22º and 26ºS which might be important spawning hotspots for Cape monkfish. The spawning-capable gonads were found mainly in deep waters. Both *L. americanus* and *L. piscatorius* migrate into deeper waters for spawning (Hislop et al., 2001; Richard et al., 2008). The location where the veil was found (Figure 4.11) is a monkfish fishing ground hotspot (see Chapter 6), and this finding has management implications because this area is extensively fished, making spawning individuals more available to fishing fleets. Spawning grounds are frequently targeted by fishers (de Mitcheson, 2016), leading to serious declines in fish populations due to overfishing. Overfishing and fishing in spawning aggregation areas lead to size-selective fishing (de Mitcheson, 2016) which is significantly detrimental to a population. Our results indicate that the spawners, although very few were found, maybe specifically vulnerable to overexploitation pressure. As a precaution, fishing should be limited or restricted in spawning grounds because, when fishing takes place during spawning aggregation in these hotspot spawning grounds, these species are exposed to both increased catchability and biological factors as described in de Mitcheson (2016). Based on catch statistic results presented in Chapter 6, the area with high spawning activity (spawning ground) coincides with the monkfish fishing hotspots. Identification of spawning grounds and season is a prerequisite in management decisions to guide and manage harvest and sustainable utilisation of resources. It is critical to protect identified spawning grounds from fishing and other anthropogenic activities, including mining, to avoid disrupting spawning activities (de Mitcheson, 2016).

Since 2010, Namibia has been debating at a national level whether to allow or not to allow phosphate mining (Chiripanhura & Teweldemedhin, 2016; Erasmus et al., 2019); the area mapped for phosphate mining overlaps with the main areas where fish with ripe and running gonads were found (this study). Recruitment depends on the successful spawning and survival of larvae, and the disturbance of these grounds would defeat the purpose of sustainable management of these species (Moore et al., 2011). Any changes in spawning area could not be determined because no spawning grounds have previously been identified off Namibia. However, nursery habitats were recorded off Walvis (23°–25° S) and the Orange River (28°35’S) based on the presence of the 0-year-olds (ICSEAF, 1984).

The most interesting result of this study was the discovery of the veil (n = 1), which is excreted from the gonad and denotes an active spawning event from a ripe and running gonad. This was the first time a Cape monkfish veil has been found off Namibia, (pers. obs.). The veil was found in November although the peak spawning period is between July and September and confirms the idea that spawning takes place throughout the year. The discovery of the veil in this study contradicts previous studies that have reported that no veils have ever been observed off Namibia (Maartens & Booth, 2005; Fariña et al., 2008), although veils have been reported in other *Lophius* species such as *L. americanus* (McBride et al., 2017) and *L. piscatorius* (Colmenero et al., 2013). The veil is described as a replica of the gonad (Rasquin, 1958); however, the veil found in Period 2 was 3.3 m, about twice the size of the gonad (1.01 m). This raises the question of whether the veil is folded inside the gonad to ensure that it fits in the gonad. Although numerous studies have described the veil (Fariña et al., 2008; Colmenero et al., 2013; Colmenero et al., 2017; McBride et al., 2017), there is no record of the stage at which this veil is produced, whether it is produced immediately before it is excreted or produced through the ripe and running stage (IV). It has been proposed that the release of eggs in these veils is beneficial in facilitating their dispersal because the egg veil floats near the surface and is subject to the actions of wind, currents, and waves (Colmenero et al., 2017). The veil seems to rebut the idea of broadcasting a large number of eggs over great geographical distances because the eggs are likely to end up in one place since they are lumped together in this structure. Further investigation would provide evidence whether the veil has repellent substances that would protect it from predators. The discovery of this veil, which represents evidence of the early life of Cape monkfish off Namibia, needs further investigation. This study recommends a Cape monkfish "veil hunt" for future studies.

Ichthyoplankton surveys are crucial because they provide information on specific spawning grounds and spawning seasons and might shed light on the physical features influencing larval survival (Brander, 1994). Overall, the relatively low number of veils (< 0.1%) and fish with ripe gonads (5.6%) recorded in this study has left certain questions unanswered. Several studies (Maartens & Booth, 2005; Walmsley et al., 2005; McBrideon et al., 2017) on the reproduction of *Lophius* species did not observe veils and this general scarcity of veils in other *Lophius* species studies warrants further investigation. Spawning fish might have gone into inaccessible spawning grounds, for example, shallow grounds (within the 200 m isobath) inaccessible to trawlers (MFMR, 2001). To obtain veils and/or larvae, the correct gear, for example, drift nets cuff must be used, and sampling must take place during the spawning season in the spawning ground (Roseman et al., 2011). The above conditions were not necessarily satisfied, and this might be a contributing factor to the scarcity of veils and larvae in this study.

Batch fecundity in Cape monkfish was estimated at 136 732 oocytes (± 29 228.54), which is lower than fecundity in *L. budegassa* mean 218 020 (Colmenero et al., 2013) and *L. americanus* 838 900 (McBride et al., 2017) of the same genus. However, no large fish (> 75 cm TL) were used in this study, which might have contributed to the lower batch fecundity in Cape monkfish, compared to other *Lophius* species. The fish size and the number of oocytes linearly correlated in this study, as noted in other *Lophius* species (Yoneda et al., 2001; Colmenero et al., 2013; McBride et al., 2017). Our study is the first to estimate fecundity in Cape monkfish, an aspect important for stock assessments (Trippel et al., 1997). Large spawning females are more fecund than smaller fish, which has implications for the management of this commercially exploited species because, with high levels of exploitation targeting mostly large individuals, the populations lose the buffering capacity provided by the exceedingly fecund large fish (Trippel et al., 1997). Fishing mortality of large fish leads to a contracted spawning period for the whole population (Trippel, 1995). This study does not provide evidence of whether this fecundity is annual or seasonal because the number of veils released by this species annually is unknown since only one veil was recorded in Period 2. The presence of developing oocytes together with fully matured oocytes in the female ripe ovaries (Stage IV) observed during Period 2, might suggest that the Cape monkfish releases multiple batches within the spawning season, as suggested in McBride et al. (2017) for *L. americanus* and in Yoneda et al. (2001) for *L. litulon*. However, this seems unpredictable because the release of a whole veil implies that all oocytes (both mature and immature) are released, leaving no oocytes behind to mature into spawnable oocytes at a later stage. The fate of the developing oocytes that are released in the veil is therefore unknown and needs further investigation.

Several questions arose during this study, and some remain unanswered. For instance, although variations were observed in the monthly proportions of various maturity stages, the bulk of fish was in Stage II. It is not known how long a fish spends in a particular stage, but very few ripe and running ovaries gonads were recorded throughout the year, suggesting that fish probably spend a very short time in Stage IV, for example, 24 hours. Because only one veil was found, possibly excretion takes only a few minutes, making it more difficult to encounter them. Samplers may be influenced by the size of the individual and not by the characteristics of the gonad, leading to possible bias. A caveat may exist in Stage II classification because this stage contains both the virgin fish and mature resting adult fish. It is macroscopically impossible to differentiate the two groups, apart from their length, which is not precise. Fish in Stages II and V look similar macroscopically and can easily be mixed up.

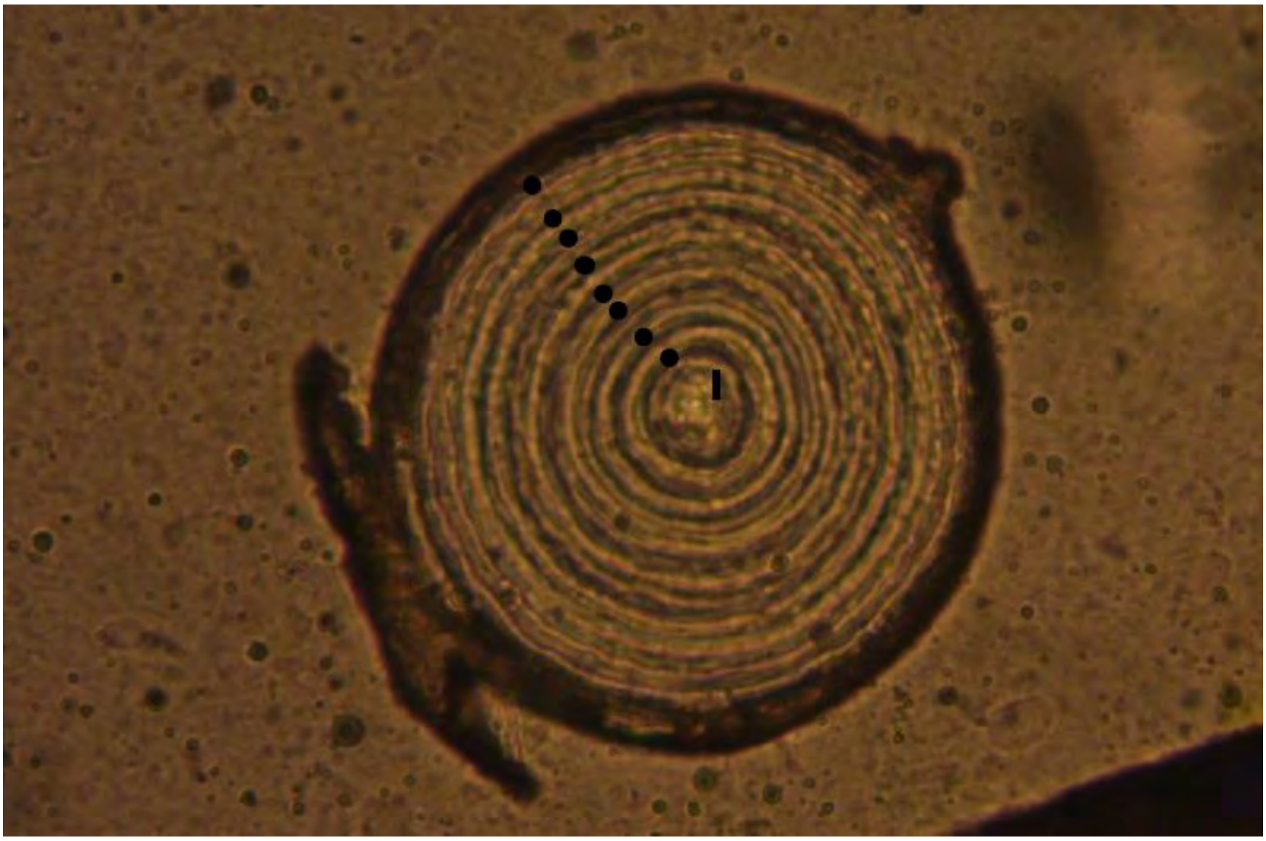
The scarcity of information on the spawning frequency in Cape monkfish has been noted previously (Maartens & Booth, 2005; Walmsley et al., 2005). However, based on a reproduction study on *L. americanus*, there is a possibility that large female monkfish may spawn more than once a year (Johnson et al., 2008), although *L. americanus* spawn once a year (Afonso-Dias & Hislop, 1996). The work by Duarte et al. (2001) identified protracted spawning in *L. budegassa*. Information on spawning frequency for any species is crucial for estimating its reproductive potential (Yoneda et al., 2001).

Gear restrictions, (e.g., the mesh size in commercial fishing activities) limited the number of juvenile fish sampled. Additionally, the restriction of the commercial trawling within the 200 m depth zone, led to under-sampling in the < 200 m depth stratum because it was only sampled during the monkfish annual swept-area biomass survey which has no spatial trawling restrictions. The technique of counting eggs using a stereo microscope is very lengthy and tedious. Future studies should employ other methods, such as automated particle counting. The October closed season for the hake fishery also affects the monkfish fishery (especially wet vessels that provide samples for the port sampling programme), consequently, fewer samples were collected during October than in the other months.

In conclusion, this study makes important contributions to the reproductive strategy and maturation dynamics of Cape monkfish in the Namibian marine waters. Our most important results include the evidence of the veil which was not observed in previous studies and the estimation of batch fecundity of 136 732 oocytes (± 29 228.54). Empirical evidence from this study suggests female fish tend to outnumber males spatially and temporally and at any size class. Male Cape monkfish mature at a smaller size than female fish as also demonstrated in Period 1; however, there is no significant change in the length at maturity (L_{50}) for female and male fish. Cape monkfish appear to spawn throughout the Namibian coast with consecutive spawning hotspots in areas between 22° and 26° S, mainly in the deeper waters.

The months of July to September were identified as the peak spawning season. The primary drivers of reproductive traits, reported here, such as sex ratio, length at maturity, spawning season, and spawning ground are relevant for sustainable management because they influence population parameters. For the Namibian Ministry of Fisheries and Marine Resources to sustainably manage this resource by protecting the spawning stock, the identified spawning areas between 22° and 26°S should be protected by means of closure or limited fishing activities, and a month between July and September should be chosen as a closed season for monkfish fishery. This study provides significant reproductive trait information such as sex ratio, spawning season, and gonadal maturation process which are critical in understanding the life cycle, and they are thus relevant in defining management measures (Sauer & Lipinski, 1990; Pankhurst & Munday, 2011; Colmenero et al., 2013).

Chapter 5: Comparison of the historical and contemporary age and growth of Cape monkfish in Namibia



Cape monkfish illicia section as seen under a microscope (photo credit: Collette Mwanangombe)

5.1 Introduction

Information on the age and growth rates of fish is crucial for estimating population productivity and resilience to external factors such as fishing pressure and climate change (Buxton, 1993; Landa et al., 2002; Fariña et al., 2008). Several fish growth models, including the widely used somatic growth equation, the von Bertalanffy growth function (VBGF), require an accurate portrayal of growth because age and growth are important inputs in these models (Johnson et al., 2007; Landa et al., 2008; Snover, 2008; Ogle & Isermann, 2017). A comprehensive understanding of key fish species traits, such as life span, age at recruitment and age at sexual maturity, is derived from data on age and growth (Preciado et al., 2006; Landa et al., 2018). Information derived from growth and age studies is significant in decision making and management plans of fish populations (Griffiths & Hecht, 1986; Farthing et al., 2016).

Accurate information on the age and growth of fish is significant for fisheries management although, at times, age information is both expensive to attain and susceptible to errors (Kathena et al., 2018). Life-history traits such as length and age-at-maturity are dynamic, mostly due to external factors such as fishing pressure (Buxton, 1993; Hewett & Kraft, 1993; Lappalainen et al., 2016). There have been difficulties in determining accurate age and growth in various fish species globally (Griffiths & Hecht, 1986; Maartens et al., 1999; Salvanes et al., 2018), difficulties which are frequently attributed to the structure used for age determination, such as otolith, illicia, scales, and vertebrae (Griffiths & Hecht, 1986; Maartens et al., 1999; Salvanes et al., 2018).

Spatial variations in the age distribution and growth rates have been observed in several species. For example, Adams (2017) documented variation in depth distribution in Atlantic butterfish, *Peprilus triacanthus,* in the north-west Atlantic Ocean. They found that ages 2 and 3 were found farther north-east and deeper than age 1, while in the fall, age 3 butterfish were found farther north-east and deeper than ages 0. Evidence of significant seasonal and spatial variations in growth rates of the same species has also been documented by Buxton (1993), Beckman and Wilson (1995) and Fablet et al. (2011). Various environmental or physiological changes within habitats are often key drivers of fish growth (Griffiths & Hecht, 1986). As such, growth curves and other life-history traits of the same species may vary depending on the environmental variables, genetics, fishing pressure and food availability (Hewett & Kraft, 1993; Sandstrom et al., 1995). Studies (e.g., Thresher et al., 2007) focusing on the comparison of growth parameters between different periods can provide much-needed insight into the effects of climate change and exploitation pressure (Rochet, 1998) on various marine resources. Additionally, some studies have found climate-induced distributional changes over time (Perry et al., 2005; du Pontavice et al., 2021). Spatial information is critical for improved management of commercial fishery species, especially of those fisheries inhabiting climate change hotspots.

Cape monkfish are a valuable resource to the Namibian fishing industry, where it is managed through TAC (Maartens et al., 1999; Maartens & Booth, 2001a; Kathena et al., 2018), and where information on age and growth serves as input in the Stock Assessment Model of this species (Maartens et al., 1999; Maartens & Booth, 2001a). Illicia are mostly used in monkfish age and growth studies because they are easy to collect, read and they provide accurate age results (Maartens et al., 1999; Walmsley et al., 2005; Fariña et al., 2008; Şenbahar & Özaydin, 2020). Since changes in growth rates influence the productivity of stocks, such changes must be incorporated into stock assessment models. Cape monkfish is a slow-growing species (Griffiths & Hecht, 1986; Maartens et al., 1999; Walmsley et al., 2005) that lives for more than 10 years (Fariña et al., 2008). Historical spatial data (ICSEAF, 1984) point to areas off Walvis Bay (23º–25ºS) and near the Orange River (28º35'S) as nursery areas based, on the presence of 0-year-old fish. Although the age and growth characteristics of Cape monkfish have been described previously (Griffiths & Hecht, 1986; Maartens et al., 1999), providing crucial information on the life-history traits of this species, to date no study has compared growth parameters of Cape monkfish between historical and contemporary times. As a result, there is no information on whether there has been any spatial or temporal variation in the age and growth structure of this species over time.

This chapter aimed to provide comparisons of the age and key growth parameters; $L\infty$, K and t_0 between the historical (1994–1996, Period 1) and contemporary (2014–2016, Period 2) times and to explore any spatial change in the distribution of different life stages of Cape monkfish. To do this, the age and growth of Cape monkfish and the spatial distribution of the different age classes between the two periods were compared. This information was related to recent changes in the environment and levels of exploitation in the region.

5.2 Materials and methods

5.2.1 Study area

This study was conducted in the Namibian marine waters, as described in Chapter 2. For Period 1 (Maartens et al., 1999) fish were captured using commercial fishing vessels, for which there is no geographic information provided. For this chapter, Period 1 refers to the study by Maartens et al. (1999). For Period 2, the samples were collected during monkfish surveys which follow predetermined stations described in Chapter 2 (Figure 2.3).

5.2.2 Field sampling

For Period 1 (Maartens et al., 1999) sagittal otoliths and illicia were collected from 607 Cape monkfish specimens ranging in size between 9 and 96 cm TL. The samples were collected between 7 September and 14 October 1996 on board the Norwegian research vessel, *Dr Fridtjof Nansen*. An additional 570 samples of Cape monkfish were obtained from the monkfish fishing vessels between March 1997 and March 1998. Most samples used for the Period 1 study were taken at depths ranging between 200 and 450 m using either 75 or 110 mm mesh cod-ends. For historical studies (Maartens et al., 1999), no original field data were available, thus only the study description, methods used (limited) and the results were compared to the contemporary study. Similarly, no actual samples from Period 1 were available for reading.

For Period 2 (this study), a total of 852 Cape monkfish samples ranging in size from 9 to 96 cm TL were used. The samples were collected during monkfish annual biomass surveys of November 2014, November 2015, and November 2016 at a depth of 98–909 m using a cod-end mesh size of 133 mm with a 50 mm blinder installed inside the cod-end. The fish were generally collected at random but ensuring that the very large and smaller fish were collected. This was important because these individuals are hard to come by and not selecting them might lead to a gap in the sample collection. Otolith collected during the monkfish annual biomass surveys of November 2014, November 2015 and November 2016 were read and the subsequent age data were compared to Cape monkfish age data collected from 1996 to 1998 in Period 1.

Standard data collection methods were used during both periods. Fish were worked up immediately after capture. Biometric data such as total length (TL, ± 0.1 cm, recorded to the nearest cm below), sex, whole weight, and gutted weight (± 0.1 g) were recorded. Illicia were collected and stored dry in labelled manila envelopes. Fish were aggregated into males, females, or juveniles. Cape monkfish have several dorsal fin rays, but the first one close to the mouth is called an illicium. For each individual, it was cut off at the base with a pair of scissors.

A comparison between the historical age and growth patterns (Period 1) and the present study (Period 2) was conducted. The aspects of age and growth were compared for the Namibian Cape monkfish, using the same fishing depth range (between 200 and 450 m) and the same fish size range (between 9 and 96 cm TL), using identical equations as described below. However, no consideration was given to the geographical position because the Period 1 study did not provide information on the geographical position where the samples were taken. The Period 1 study used age and growth data collected during monkfish fishing activities and the hake annual biomass survey, while the contemporary study used data collected during the monkfish annual biomass survey; as such, the sampling gear used differed.

Pilot study

Prior to any analysis, a pilot study involving 43 otoliths and 14 illicia from Cape monkfish was conducted to determine the most suitable hard structure to carry out the objectives of this chapter. The otoliths and illicia were collected from the same specimens caught off Namibia in 2017. Otoliths were collected, cleaned with saline water, and laid out individually onto the solidified resin in the silicon tubs, together with their labels. Another layer of resin was poured into the silicon tubs to embed the otoliths overnight. Once solidified, a double-bladed, diamond-edged saw was used to slice the otoliths transversely at a 0.2–0.9 mm thickness. Similar to what was reported in Period 1 (Maartens et al., 1999), the pilot study showed that Cape monkfish otoliths are irregular in shape and thickness. The growth zones in otoliths were unclear and difficult to read compared to the illicia, so they are therefore not the best structure to be used in age determination of Cape monkfish, as was also suggested in Maartens et al. (1999). Hence, only data derived from sectioned illicia were used for age determination in this study.

5.2.3 Laboratory analysis

Illicia preparation

Period 1 used illicia sectioned to 0.2–0.5 mm at 0.5 cm from the base using a double-bladed diamond saw. The illicia sections were mounted on microscope slides with DPX mountant, illuminated using transmitted light and read under a binocular stereo microscope at 20x magnification. For Period 2, Luxor resin mixed with a catalyst (hardener) was poured onto silicon tubs and allowed to solidify for 24 hours. The illicia base sections were carefully laid out individually onto the solidified resin in the silicon tubs, together with their labels, and another layer of resin was poured into the silicon tubs to embed the illicia (Figure 5.2). A double-bladed, diamond-edged saw was used to slice the illicia transversely (between 0.2 and 0.5 mm) approximately 0.5 cm above the base (as per the methods of Maartens et al., 1999). The illicia slices were mounted onto microscope slides which were prepared as per the methods described in Landa et al. (2002).

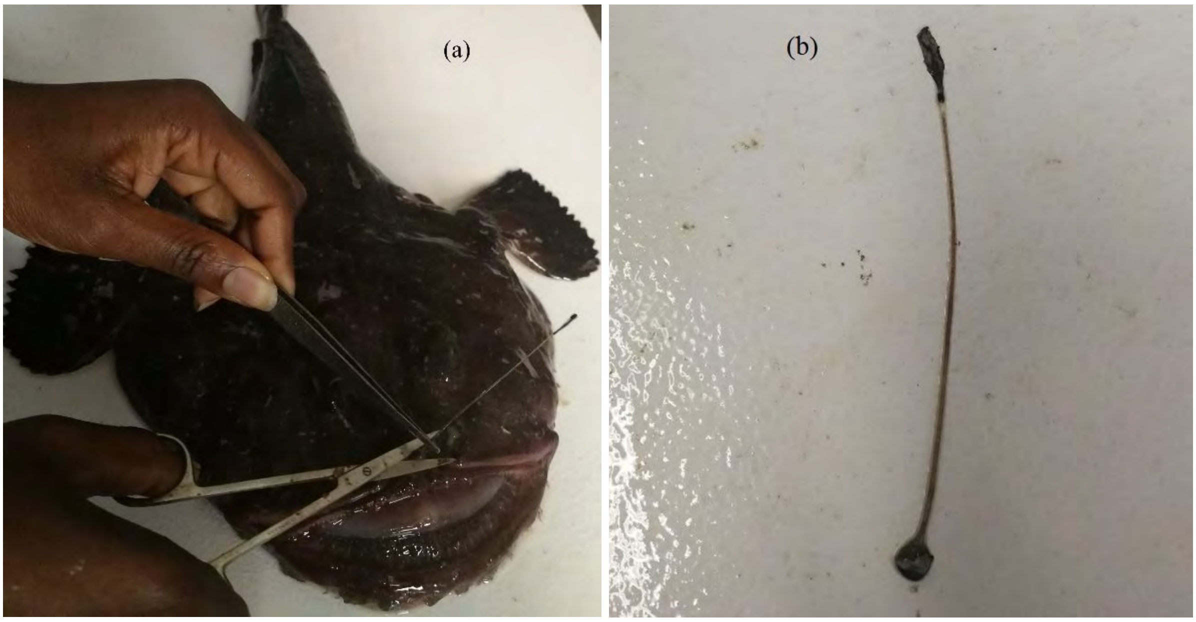


Figure 5.1: Photographs of (a) the first dorsal spine (illicium) being cut off of Cape monkfish, *Lophius vomerinus* caught off Namibia and (b) the resultant illicium (Picture credit: Manga Simasiku, 2019).

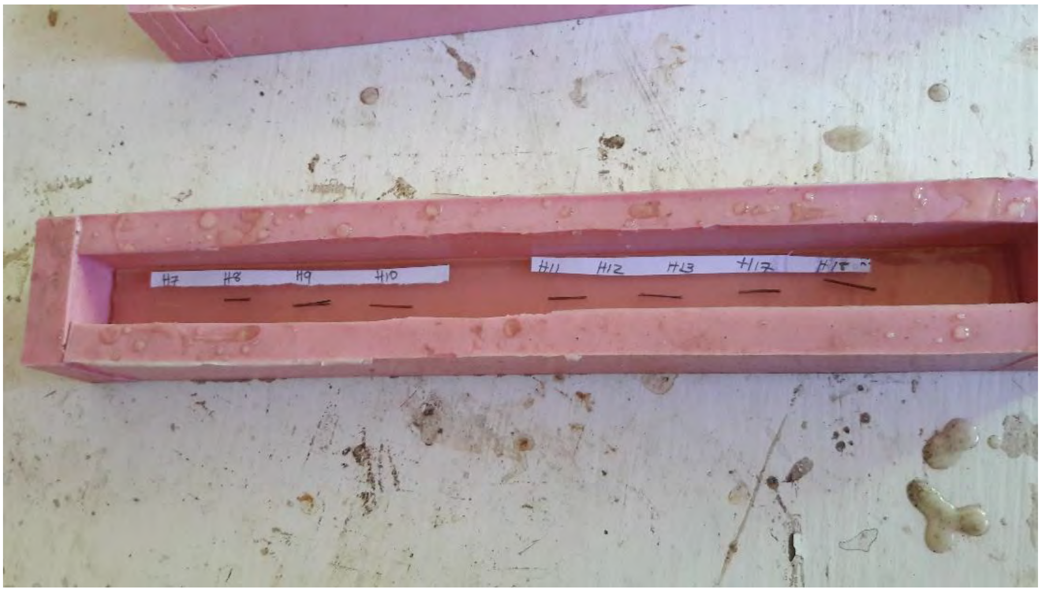


Figure 5.2: The silicon tub mould with a base layer of solidified Luxor resin, labelled paper and the 0.5 mm sectioned illicia sample of Cape monkfish, *Lophius vomerinus*, caught off Namibia.

Illicia reading and age determination

Illicia reading was done by three readers, two experienced readers and me. The numbers of translucent zones were counted from the nucleus towards the post-rostrum edge of the illicium section using a Zeiss compound microscope at 40× magnification, under reflected light. The clarity of the increment patterns was categorised as high or low, and those that were considered low were excluded from the analyses.

Age validation

It was assumed that a singular annulus is deposited annually, based on the findings of Griffiths & Hecht (1986) and Maartens et al. (1999). Thus, it was assumed that an opaque and a translucent zone, which appears as a wide light and narrow dark ring, respectively, under reflected light, is deposited each year (see Figure 5.3).

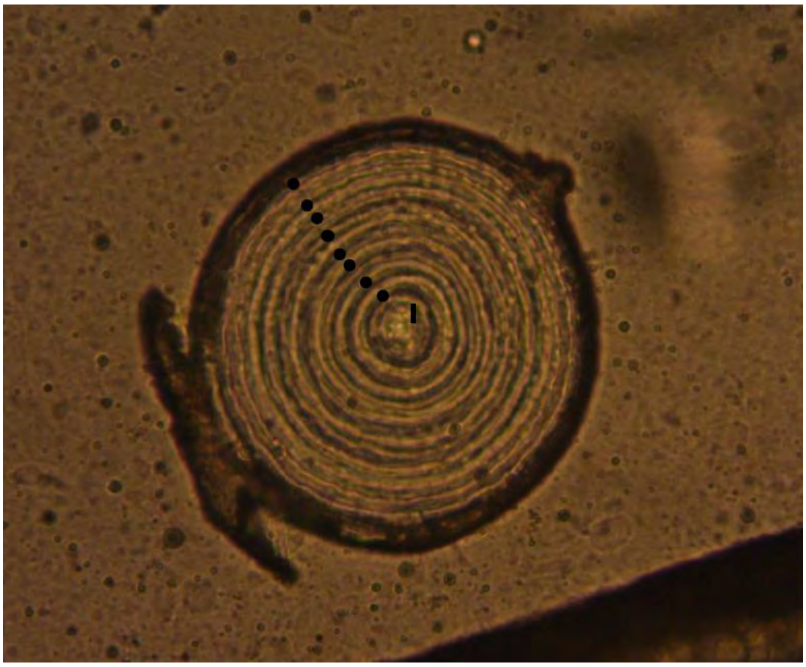


Figure 5.3: A transverse cross-section of a 55 cm (TL), 8-year-old female Cape monkfish, *Lophius vomerinus*, illicium collected in April 2016, off the coast of Namibia. Yearly growth increments are dotted (Picture credit: Collette Mwanangombe, 2016).

5.2.4 Data analysis

Growth model

For comparative purposes, the age and growth modelling used by Maartens et al. (1999) was also followed during Period 2. A general, three-parameter VBGF (Ricker, 1975) was fitted to the observed length at age data for each sex and the pooled data (males, females and fish of unknown sex). The VBGF was also used in Period 1 to determine the length at age, calculated based on the Beverton and Holt (1957) equation below:

$$L_t = L_\infty(1 - e(-K(t - t_0))) \qquad \text{(Equation 5.1)}$$

where L_t is the length at age t, L_∞ is the maximum observed length, K is the growth coefficient, and t_0 is the theoretical age at zero length.

The VBGF parameters, L_∞, K and t_0 were obtained based on the lowest residual sum of square (RSS) determined using the Microsoft Excel Solver. Using Microsoft Excel, a likelihood ratio test (LRT) (Cerrato, 1990) was used to test the difference between the growth curves of males and females. The growth curves between females and males were also compared in Period 1 (Maartens et al., 1999).

Length-weight relationship

A power curve model was fitted to the observed length-weight data for each sex separately, and then to the pooled samples to estimate the *a* and *b* parameters, using the least-square method as described in (Ricker 1973) (also see Maartens et al., 1999). The length-weight relationship (LWR) equation is described as follows:

$$W = aL^\wedge b \qquad \text{(Equation 5.2)}$$

where a is the condition factor, and b is the regression coefficient of the length-weight curve (providing information about the fish growth), the allometric factor, L is the total length (cm TL), and W is the body wet weight (g) (Ricker, 1975; Basusta et al., 2013). When $b = 3$, the increase in weight is isometric, $b < 3$, the fish attains more length than weight and this is negatively allometric; $b > 3$, is the opposite and the growth is positively allometric (Tesch, 1971; Hamid et al., 2015).

Spatial and temporal age distribution

A spatial analysis of the age distribution was conducted for the Period 2 data. Fish were grouped into the age classes: (i) 0 years, (ii) 1–4 years, (iii) 5–8 years (iv) 9–12 years and (v) 13–16 years. These data were then compared to previously/historically identified known life-history stage hotspots, for example, nursery habitats (based on ICSEAF data of 1984). Data analysis was performed using R version 3.3.1 (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018). All spatial data were visualised on a Geographic Information System (GIS) ArcGIS 10.8 Software) (URL https://www.arcgis. org/).

5.3 Results

5.3.1 Longevity

Period 1 analysed 554 illicia with a total of 67 (12.1%) sectioned illicia rejected as unreadable, in the end, only 487 illicia were considered. Period 2 used 894 sectioned illicia and 42 (4.7%) were rejected; in the end, only 852 illicia were readable and used to determine the age and growth patterns of Cape monkfish. During age interpretation, it was observed that the opaque zones tended to split in two, while one side of the sectioned illicia remained intact, further hindering the interpretation of age readings. The split of the opaque zone was also observed in the historical Period 1.

The mean age in Period 1 was 4.40, while in Period 2 it was 5.49. Fish of age 2 were numerous (20.3%) in Period 1, while fish of age 5 (18.3%) were numerous in Period 2. The maximum age of fish was 11 years during Period 1 and 16 years during Period 2. Considering only the age results derived from illicia, the age demographic appeared truncated/shortened (without the older individuals) in Period 1 with 7.5% of fish over eight years. In contrast, 16.2% of the fish aged in Period 2 were older than eight years (Figure 5.4).

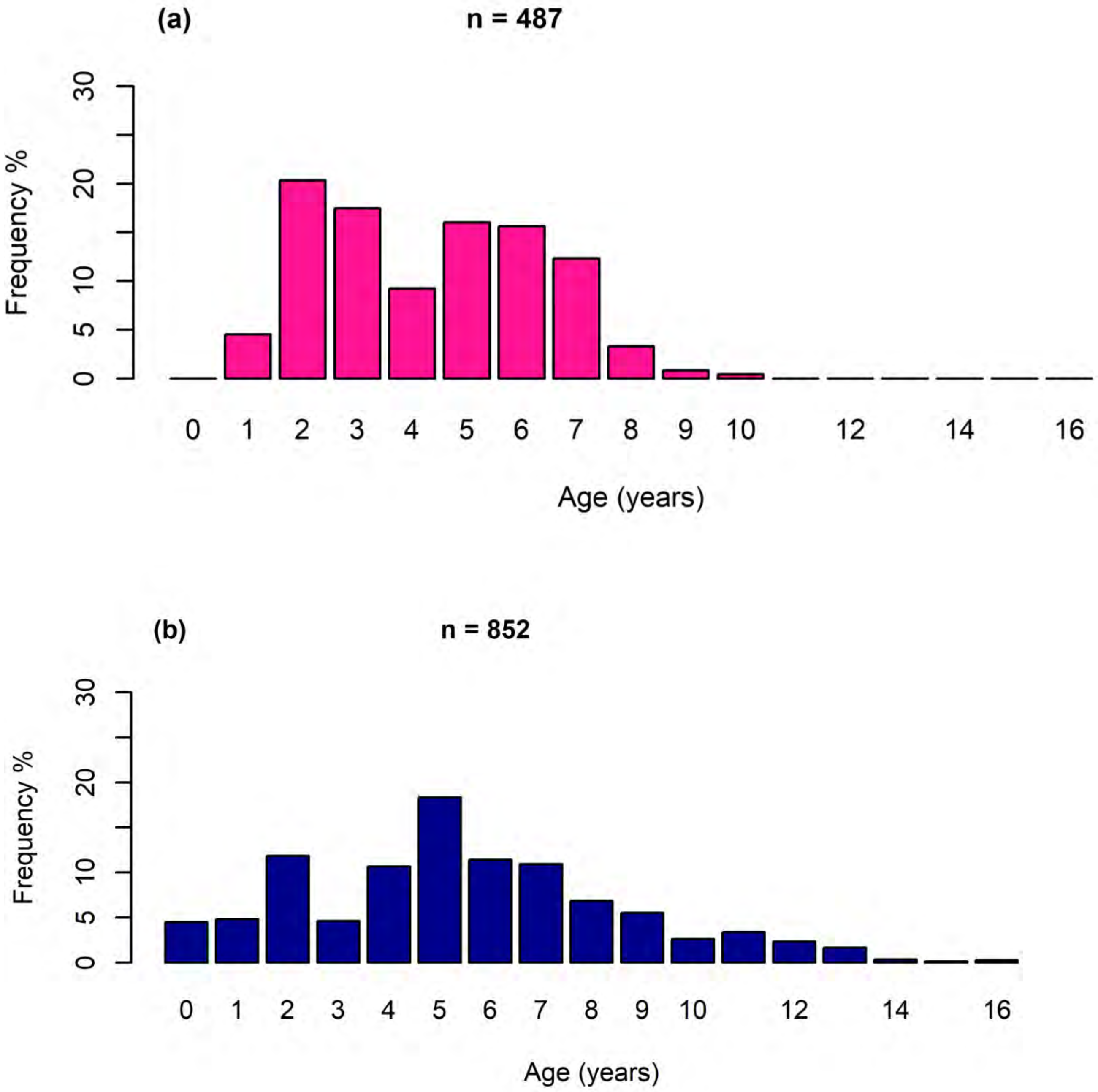


Figure 5.4: Age distribution frequency (%) of Cape monkfish, *Lophius vomerinus*, caught off the coast of Namibia (a) for 1996 - 1998 (Maartens et al., 1999), and (b) for 2014 - 2016.

5.3.2 Growth comparison

The oldest Cape monkfish found in Period 1 was 11 years old, while that found in Period 2 (the contemporary study) was 16 years old. In terms of sex, the oldest female was 16 years old in Period 2 (Table 5.1). Period 1 showed a maximum age of 11 years but it was not clear whether the oldest individual was male or female. Females tended to be smaller during Period 1 (max.

length = 96 cm TL) than during Period 2 (max length = 119 cm TL), whereas males in Period 1 were larger (max. length = 72 cm TL) than the males in Period 2 (max. length = 63 cm TL).

Table 5.1: Age, sample size, total size range, mean observed length (standard deviation) and expected lengths-at-age determined from female (n = 473), male (n = 339) and pooled samples (n = 852) of Cape monkfish, *Lophius vomerinus,* sampled during November 2014, 2015 and 2016 off the coast of Namibia.

Female					Male					Male + Female + Unknown				
Age	n	Total Size range (cm)	Mean observed length (cm)	Expected length (cm)	Age	N	Total Size range (cm)	Mean observed length (cm)	Expected length (cm)	Age	n	Total Size range (cm)	Mean observed length (cm)	Expected length (cm)
0	3	15 -20	17±1.73	2.65	0	4	16-18	17.25±17.55	3.70	0	38	9-20	13.63±3.24	3.30
1	17	17 -26	21.71±15.39	11.08	1	15	18-25	20.80±15.46	13.67	1	41	14-26	20.27±15.50	12.69
2	49	19-31	24.78±15.07	18.89	2	52	20-30	24.98±15.12	22.14	2	101	12-31	24.75±15.08	21.15
3	17	27-34	30.47±14.94	26.15	3	22	25-34	30.05±14.83	29.33	3	39	25-34	30.23±14.83	28.77
4	41	30-42	34.39±14.98	32.87	4	50	29-44	34.54±13.78	35.44	4	91	29-44	34.47±13.78	35.63
5	79	33-52	39.63±13.60	39.11	5	77	32-48	39.23±13.70	40.63	5	156	32-52	39.43±13.54	41.81
6	52	38-52	45.35±14.14	44.90	6	45	37-53	45.22±14.25	45.04	6	97	37-53	45.29±14.11	47.38
7	49	44-57	50.53±14.81	50.27	7	44	44-55	49.52±14.84	48.79	7	93	44-57	50.05±14.81	52.40
8	40	49-63	54.53±15.67	55.25	8	18	48-62	52.50±15.46	51.97	8	58	48-63	53.90±15.50	56.92
9	37	50-79	58.73±15.13	59.87	9	10	51-61	57.00±15.75	54.68	9	47	50-79	58.38±15.13	60.99
10	21	58-70	62.62±16.40	64.16	10	1	62	-	56.97	10	22	58-70	62.69±16.4	64.66
11	28	61-73	66.96±17.59	68.14	11	1	63	-	58.93	11	29	61-73	66.83±17.59	67.97
12	20	65-77	71.55±17.61	71.83	12	0	-	-		12	20	65-77	71.55±17.61	70.95
13	14	73-84	78.50±17.55	75.25	13	0	-	-		13	14	73-84	78.50±17.55	73.63
14	3	86-89	87.33±17.55	78.42	14	0	-	-		14	3	86-89	87.33±16.49	76.04
15	1	94	-	81.37	15	0	-	-		15	1	94	-	78.22
16	2	89-96	-	84.10	16	0	-	-		16	2	89-96	92.5±3.61	80.18

The results of the von Bertalanffy growth function for the two periods are presented in Table 5.2 and in Figure 5.5. There were no significant differences between the growth curves of males and females in Period 2 (F = 0.65, $p = 0.58$). However, significant differences between males and females for both the survey ($F_{(6.604)} = 19.82$, $p < 0.001$) and commercial data (F(1.559) = 17.85, $p < 0.001$) were observed in Period 1. The growth curve in Period 1 was $L_t = 94(1 - e(-0.10(t-(-0.31)))$ and for Period 2 was $L_t = 98(1 - e(-0.10(t-(-0.33)))$ for pooled data. The rate at which females reached Lif (K) in both periods was similar (K = 0.08). Additionally, K was also similar (K = 0.10) for pooled data in both periods.

In Period 2 Cape monkfish attained a greater asymptotic length ($L\infty$) of 119 cm, 69 cm and 98 cm for female, male and pooled fish, respectively, as compared to 112 cm, 72 cm and 94 cm for female, male and pooled fish, respectively. The K value (the rate at which the fish reach Lif) was similar (K = 0.08) for females in both periods. The males in Period 2 had the highest K value (K = 0.16) compared to the males (K = 0.14) in Period 1 (Figure 5.5 and Table 5.2).

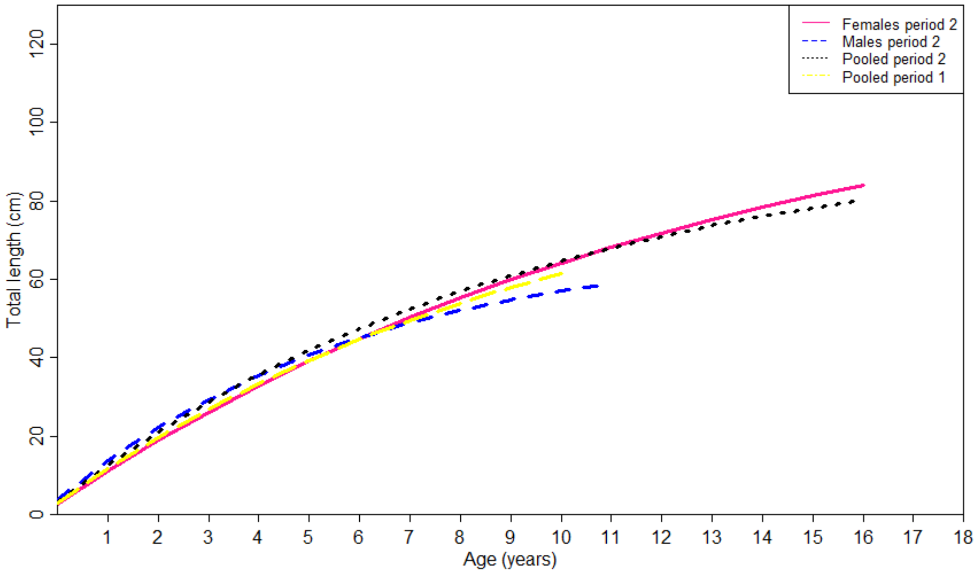


Figure 5.5: Relationship between age and total length for female, male, and pooled Cape monkfish, *Lophius vomerinus*, off the coast of Namibia for the Period 1 (1996–1998, Maartens et al., 1999, n = 487) and the Period 2 dataset (2014–2016, n = 852).

Table 5.2: A comparison of the von Bertalanffy growth function parameter estimates for length at age data of female, male, and pooled Cape monkfish, *Lophius vomerinus,* in Period 1 (1996–1998, Maartens et al., 1999) and Period 2 (2004–2006, this study), off the coast of Namibia. Sample sizes (n) are given, along with K, $L\infty$, and t_0.

Period 1					Period 2			
Sex	N	$L\infty$	K	t_0 (years)	N	$L\infty$	K	t_0 (years)
Female	193	112	0.08	-0.36	473	119	0.08	-0.30
Male	249	72	0.14	-0.30	339	69	0.16	-0.34
Pooled	487	94	0.10	-0.33	852	98	0.10	-0.33

K = growth coefficient, $L\infty$ = maximum total length, t_0 = theoretical age at zero length.

5.3.3 Length-weight relationship

Period 1 yielded $W = 0.01L^{2.97}$, ($r^2 = 0.98$) for females and $W = 0.01L^{3.03}$ ($r^2 = 0.98$) for males while Period 2 yielded the length-weight relationship (LWR) for females as $W = 0.07L^{2.63}$ ($r^2 = 0.95$), and males: $W = 0.16L^{2.38}$, ($r^2 = 0.88$) (Figure 5.6a). Both female and male fish in both periods showed rapid, almost linear, growth up until about 50 cm. At total length of less than 65 cm for males and 78 cm for females, Cape monkfish in Period 2 were heavier (Figure 5.6a) than in Period 1 at the same length (Figure 5.6 b). Larger females and males in Period 2 were lighter than fish of the same length in Period 1 (Figure 5.65a and b). The LWR regression coefficient *b* values of female and male fish in Period 1 were approximately 3.0, thereby representing isometric growth, an indication of an ideal shape of fish. The LWR regression coefficient *b* values for both male and female fish in Period 2 were less than 3.0, indicating a negative allometric growth (Table 5.3).

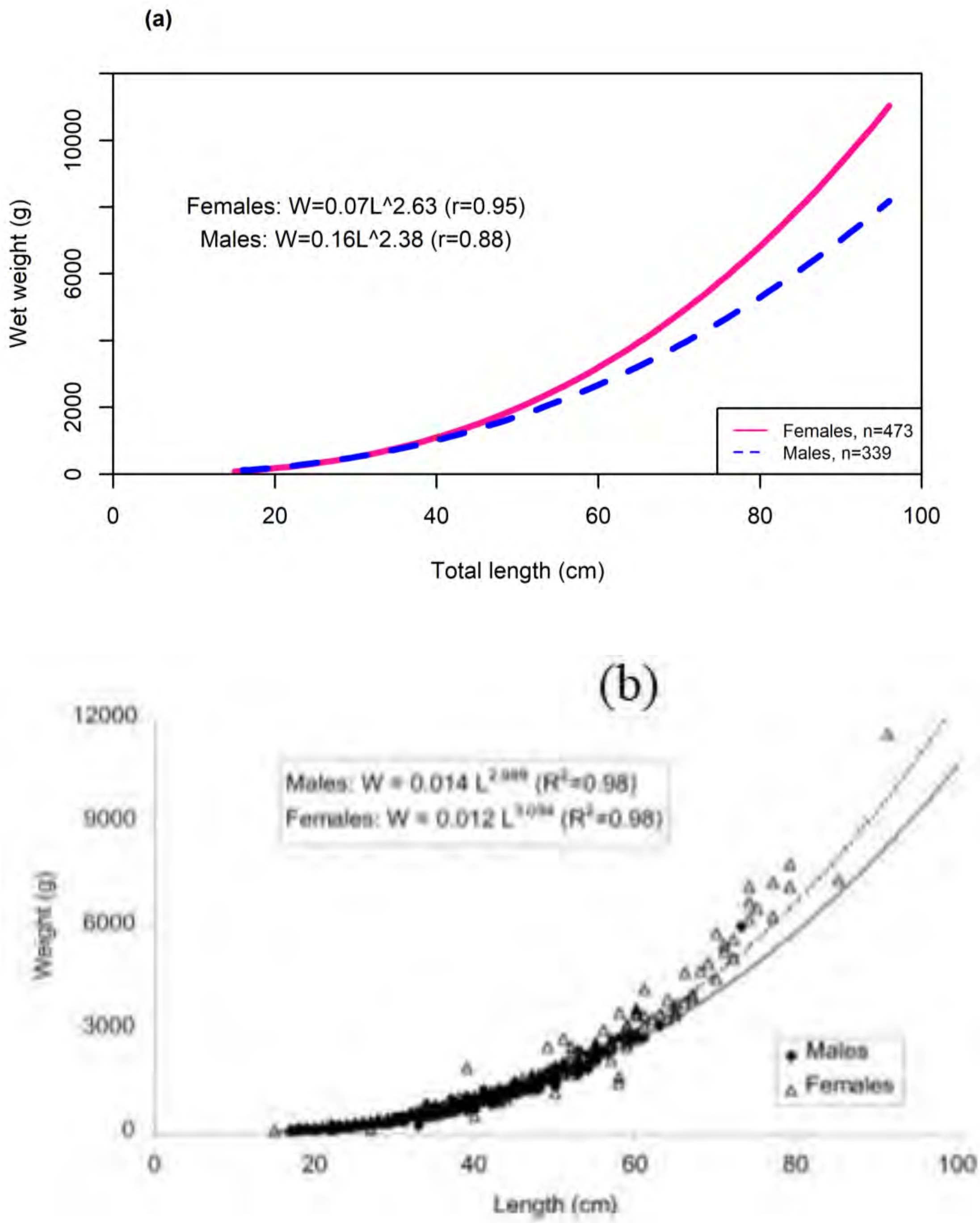


Figure 5.6: Length-weight relationship of female, male and pooled data Cape monkfish, *Lophius vomerinus*, off the coast of Namibia according to (a) the Period 2 dataset (2014–2016, n = 852) (b) Period 1 dataset (1996–1998, Maartens et al., 1999, n = 607). [Note: Figure 5.6 (b) was adapted from Maartens et al. (1999) because no data were available to generate the length-weight relationship for Period 1 samples.]

Table 5.3: Length-weight relationships between total length (cm) and wet weight (g) for female, male fish, and pooled data in Period 1 and Period 2 for fish sampled off the coast of Namibia. Samples were collected during 1996–1998 and 2014–2016 in Periods 1 and 2, respectively.

Period 1					Period 2			
Sex	N	A	B	r^2	n	a	B	r^2
Female	306	0.01	2.97	0.98	473	0.07	2.63	0.95
Male	301	0.01	3.03	0.98	339	0.16	2.38	0.88

a = is the condition factor, and *b* is the regression coefficient of the length-weight curve.

5.3.4 Spatial-age distribution

The 0-year-old fish were distributed between 22º and 26ºS in shallower waters of < 250 m during Period 2. Fish between 1 and 4 years old were found along the entire coast at depths of less than 300 m. The oldest fish (between 13 and 16 years old) were found from the Central region southwards and generally deeper than the other age classes (Figure 5.7).

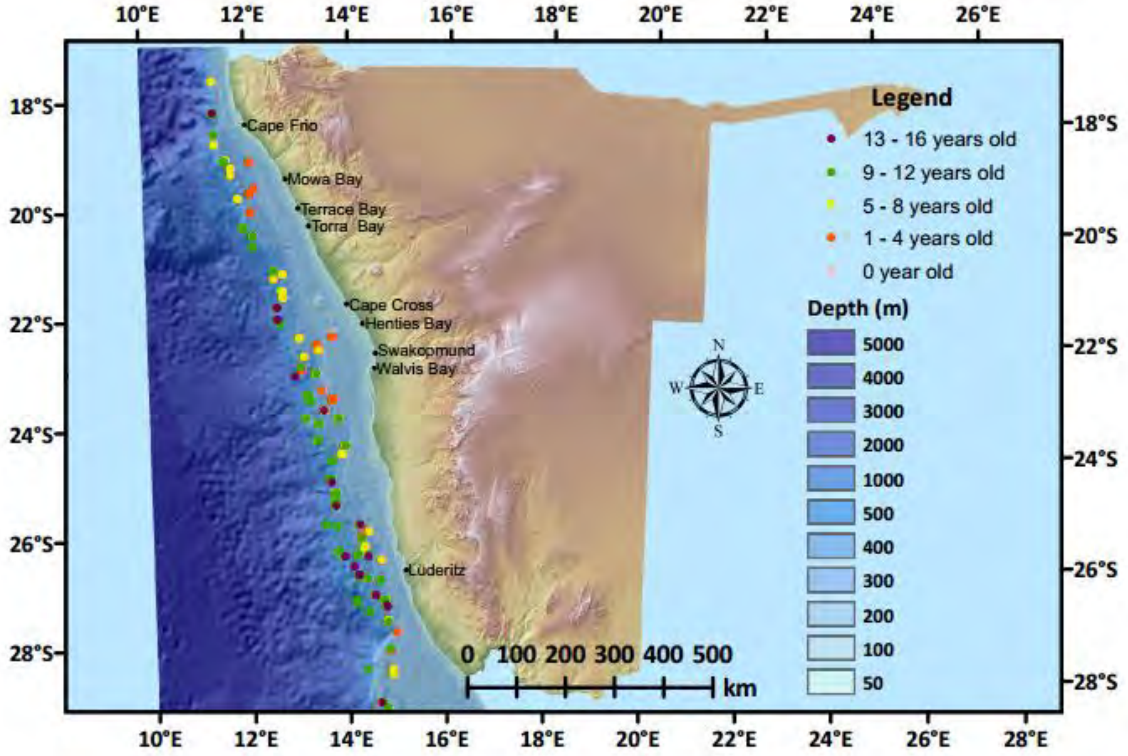


Figure 5.7: Spatial-age distribution of Cape monkfish, *Lophius vomerinus*, sampled off the coast of Namibia during Period 2 (between 2014 and2016, n = 848). Map constructed in ArcGIS 10.8 Software.

5.4 Discussion

While basic age and growth information of Cape monkfish has been reported previously (Griffiths & Hecht, 1986; Maartens et al., 1999), this study provides the first spatio-temporal analysis on the age and growth of this species. Results from Period 2 are comparable to Period 1 results in several ways, but they include some important differences. There were no differences in the growth curves between Periods 1 and 2. There were also no significant differences in the growth rate between males and females. These results are unexpected and suggest that both male and female fish have similar growth curves, contrary to what was previously reported (Maartens et al., 1999). However, some differences were observed between Periods 1 and 2, including a reduction in population age truncation and a potential shift in the nursery habitat of the species. These differences suggest that other changes may occur, and that these may, in turn, influence growth over time, and they suggest that monitoring growth will be important during the Anthropocene. Results indicate that the population was more truncated in Period 2, evidenced by the fact that the female Cape monkfish attained an asymptotic TL of 119 cm in Period 2, while in Period 1, it was 112 cm. Male Cape monkfish attained an asymptotic TL of 69 cm, while in Period 1 it was 72 cm.

There were no differences in the growth rates between period 1 and 2. The species appears to be relatively resilient to the impacts of overexploitation and climate change. Similar growth curves were reported between Period 1 and Period 2 samples. It is evident (from Figure 5.6) that the female curve from Period 2 is close to the Period 1 female curve. Similarly, the male curve from Period 2 is similar to the male curve from Period 2. However, it is important to note here that in Period 2 older specimens were collected than in Period 1. Consequently, differences in maximum age were observed between the two periods. The presence of older individuals in Period 2 is probably not a climate signal, but rather a consequence of extensive sampling in Period 2. an ontogenetic offshore habitat shifts with age was also noted.

When comparing Period 2 results on life-history traits of Cape monkfish, with those published in Period 1 (Maartens et al., 1999), the various parameters reflect differences, for example, in the life span. Results from Period 2 suggest a longer life span because of the 16-year-old individual found in Period 2 as opposed to the oldest individual of 11 years in Period 1 (Table 5.3). At the time of Period 1, the monkfish fishery was relatively new (see Chapter 6) as compared to the current study (Period 2); as such, greater depths and some geographical areas were possibly not exploited in the past as they were in Period 2, possibly leading the older individuals being missed in Period 1. Given the tendency for larger fish to be females, the increased proportion of females (55%) in Period 2 compared to Period 1 (40%) may have also contributed to the larger maximum age observed in Period 2.

A similarity between Periods 1 and 2 is that female fish in both periods attained a larger asymptotic size and reached an older age than males. This is a common trait in other *Lophius* species such as *L. americanus* (Richards et al., 2008) and this result accords with earlier reproduction work (Chapter 4) where mature female fish house large egg veils, which necessitate the females growing larger than males. A longevity gender gap is common in fishes (e.g., *Antimora rostrata*; Fossen & Bergstad, 2006, *L. americanus*; Richards et al., 2008, *Oryzias latipes*; Gopalakrishnan et al., 2013) and has been attributed to the sex difference in telomere length and oestrogen levels (Gopalakrishnan et al., 2013; Noreikiene et al., 2017). This difference can contribute significantly to population persistence as large females are critical for maintaining population reproductive potential. The comparatively shorter male life span, reported in both Periods 1 and 2, has been already reported for other *Lophius* species (Richards et al., 2008; Şenbahar & Özaydin, 2020), but it warrants further investigation.

Sectioned illicia of Cape monkfish showed noticeable growth rings, which consisted of both an opaque zone and a translucent zone, interpreted altogether as one year. Younger fish up to the age of six years old were easier to read than older fish. This result contrasts with that of some other species, for example, Farthing et al. (2016) found it easier to determine the age of older *Rhabdosargus holubi* fish than for younger fish. While most sectioned illicia demonstrated a clear increment pattern, some were difficult to read, resulting in a 4.7% rejection. The 4.7% rejected samples in Period 2 is an improvement on 12.1% rejected sectioned illicia in Period 1 (Maartens et al., 1999). These disparities can be attributed to the differences in the level of the age determination experience. The readers in Period 1 might have been less experienced than those in Period 2. Maartens and Booth (authors for the Period 1 study were not experienced otolith readers – Potts. pers. Comm.) The researcher (Erasmus) for Period 2 is a relatively new reader, but the other two readers from Period 2 have more than five years of reading experience. The potential differences between experienced and inexperienced readers can affect accuracy verification and precision of fish age determination (Campana, 2001).

When comparing fish age in Period 1 to fish age in Period 2, it was noted that most fish in Period 1 were from age group 2 (20.3%); fish in age group 5 (18.3%) were numerous in Period 2 (Figure 5.4). This difference can be explained by the recruitment size. The numerous fish in age group 2 in Period 1 suggests that the population had relatively good recruitment two years prior, consequently, this cohort dominated Period 1 samples. The numerous fish in age group 5 in Period 2 also shows relatively good recruitment five years earlier. Recruitment of fish species is said to be influenced by various factors, including levels of exploitation (Boyer et al., 2001), predation mortality on age 0-group, parental stock size (Neuenfeldt & Köster, 2000) and environmental variables (Cury & Roy, 1989; Kujawa et al., 2015). It is well known that several factors, such as environmental parameters (Kujawa et al., 2015), food availability (Berrigan & Charnov, 1994; Massutõ et al., 2000), reproductive strategy (Massutõ et al., 2000) and exploitation influence the growth of fishes (Griffiths & Hecht, 1986). For instance, there was a pronounced *Benguela Niño* event in 1995 (Bartholomae & van der Plas, 2007; Hutchings et al., 2009). Based on the Bertalanffy growth curve for Period 2, the rate at which pooled samples of Cape monkfish reached Lif was identical (K = 0.10) to Period 1, with a rapid growth curve in the first five years of life resulting in fish attaining an average size of 40 cm (TL), followed by considerably slower growth in the remaining years (Figure 5.6 and Table 5.2). The similar growth curves of Cape monkfish observed in both Periods 1 and 2, however, suggests that anthropogenic stressors such as climate change and exploitation were not significant enough to bring about changes in the growth curves between the two time periods. It is also possible that this species is resilient to changes in these factors. For instance, although there is an increasing concern over the decrease in oxygen in this region (Bartholomae & van der Plas, 2007; Hutchings et al., 2009), monkfish can tolerate relatively low levels of oxygen (Woodhead et al., 1996). A comparative study on the diet composition of Cape monkfish between the historical and contemporary times (Chapter 3 of this study), showed that Cape monkfish has wide trophic adaptability, hence food availability is not likely to influence its growth pattern.

Changes in the growth curves of fishes are concerning, particularly with commercially important species, as these changes can be used as indicators for both exploitation pressure and climate change (Rochet 1998). Generally, species characterised by large size, late maturity, slow growth, low mortality rate and a long lifespan are particularly susceptible to overfishing (Freitas et al., 2019). While trends obtained in Period 2 showed that Cape monkfish is a slow-growing and long-lived fish species (as was also previously noted in Maartens et al. (1999)), no major changes in most of the biological parameters in this species were found. It appears that fluctuations in the biological parameters, such as a change in growth rate, are more common in fast-growing species such as Cape horse mackerel (Kirchner et al., 2010).

Both female and male Cape monkfish fish during Period 1 exhibited isometric growth ($b = 3$) (i.e., they followed an ideal shape of fish, Tesch, 1971). On the other hand, the length-weight relationship (LWR) regression coefficient b values for both male and female fish in Period 2 indicated a negative allometric growth ($b < 3$). This means that, historically, both female and male fish were growing more in length than in weight when compared to females in Period 2. It is not uncommon for fish of the same species to exhibit variation in growth patterns. Able et al. (2007) also observed allometric shift (body proportions changing) in *L. americanus* of the same genus, during the transition from the juvenile to the adult phase. Growth (in length) is the same between the two periods, but the larger fish are lighter in Period 2, than fish of the same length in Period 1. The differences in weight at length has implications for the monkfish fishing industry because fish is sold by weight. The rightholders would now have to sell more fish (in number) for the same weight. A reduction in fish weight (poor body condition) may be linked to influences from external factors such as environmental variables (e.g., water temperature and salinity), food availability and geographical distribution (Kjesbu et al., 1998; Hossain et al., 2006). Boveng et al. (2020) linked the poor body condition of phocid seals (*Histriophoca fasciata*, *Phoca largha* and *Phoca vitulina richardii*) to the rapid increase in water temperatures in the Bering Sea and Aleutian Islands. The general warming of the marine waters globally has led to a decrease in the average sizes of individuals within populations of many commercially exploited species (Simpson et al., 2013). Differences in the length-weight relationship between the two periods can be attributed to different oceanographic conditions between the two time periods, which could affect the distribution, population structure, and growth patterns. The current environmental condition of the Namibian waters is characterised by a reduction in dissolved oxygen concentration (Shannon & O'Toole, 2003), warming events (Hutchings et al., 2009; Santos et al., 2012) and weakening of the upwelling intensity (Kirkman et al., 2013). These may influence food availability and the physiological processes of this species and may explain the observed differences. These changes have led to changes in species composition and abundance, some of which are food for Cape monkfish (see Chapter 3). The changes have been described as "regime shifts" in the Namibian marine waters, as documented by various authors (Boyer et al., 2001; Moloney, 2010; Heymans & Tomczak, 2016). The "Regime shift" resulted in a decrease in some prey species which are of high quality (e.g., sardine) and an increase in some prey species of poor quality (e.g., the pelagic goby) (Boyer et al., 2001; Erasmus et al., 2021a). Prey species with high energy density increase production in other trophic levels when consumed (Dunlop et al., 2020). A recent paper (du Pontavice et al., 2021) has highlighted the climate-induced decrease in biomass flow in marine food webs which has domino effects on predators and ecosystem production.

Spatial analysis of the age distribution of Cape monkfish in the contemporary study identified key habitats for the various life-history stages. The 0-year-old fish were mostly distributed in shallow waters ranging from 166 to 290 m, between 22º and 26ºS. While no spatial data were available from Period 1, the results of Period 2 support historical evidence (ICSEAF, 1984) of identified nursery habitats, where 0-year-old fish were also found between 23ºS and 25ºS and at depths between 150 and 300 m. However, historical evidence showed 0-year-olds were found off 28ºS and around 23°S - 25°S (ICSEAF, 1984), which was not evident in Period 2, with only older fish between 5 to 16-years-old found in this habitat. The absence of 0-year-old fish off 28º35'S might be an indication that this habitat is no longer a Cape monkfish nursery area. These areas were defined as nursery areas over three decades ago (ICSEAF, 1984), and it is possible that, with time, these areas have changed. The reason for this is less understood, but what is known, is that many factors, including climate change and food availability, influence the distribution and abundance of juvenile fish in nursery habitats (Perry et al., 2005). Nursery areas might be more sensitive to disturbance than other areas. Changes in the nursery habitats, including the change in the size and availability of such areas have been linked to climate change, as a direct effect of changes in physiochemical characteristics of such nursery habitats (Perry et al., 2005; Rijnsdorp et al., 2009). No environmental data are available from 1984, however recent observations from the 2011 environmental survey indicate that the area around 28º had an average of 9.79 ºC bottom water temperature and 2.94 ml/l dissolved oxygen in 2011. Additionally, there is an extensive anthropogenic activity associated with diamond mining around this area (Kampf, 2007; Schneider, 2020) that might have caused disturbances and altered these habitats. Diamonds were discovered in 1908 off Namibia and mining has been ongoing since (Kampf, 2007).

Fish at various stages of their life history tend to shift vertically or horizontally in response to factors such as environmental variables (Mendenhall et al., 2020). Ontogenetic distribution of fish in terms of size has been reported in many benthic fishes (Booth, 2000; Perry et al., 2005; Adams, 2017). In Period 2, fish between one and four years old were found along the entire coast in water less than 300 m depth, while the oldest fish (13 to 16 years old) were found from the Central region to farther south and deeper than 300 m. This suggests an ontogenetic spatial habitat shift, with older fish moving offshore to deeper waters with age. The offshore movement to deeper waters with age is most likely in response to food availability (as shown in Chapter 3 of this study), and other conducive environmental conditions necessary for this demersal species to complete their life stages. Alterations in the depth distribution of benthic fishes in response to ocean warming have been reported in the North Sea (Perry et al., 2005). There is evidence, then, that the depth distribution of Cape monkfish may have changed over time, and this may have considerable consequences for the fisheries, mainly because of the new distribution of this resource. This study provides a good baseline from which distributional shifts can be monitored, and this spatial distribution analysis is important as it can be input into verifying the Cape monkfish spatial equilibrium assumption for the calculation of biological reference points (Adams, 2017), and hence should be a research priority in future studies. The study also provides the first comparison of the LWR of Cape monkfish, between the historical and the present times. These comparisons are important when evaluating and determining changes in the physiological status of the species, which can inform resource management decisions. A comprehensive understanding of these changes in a species' life-history, coupled with historical environmental and fisheries data is critical for effective sustainable management.

Some of the plausible causes of differences can be attributed to the consequences of several factors including, (1) the different periods of sampling (1996–1998 (throughout the year) and 2014–2016 only in November), (2) the experience of age determining experts (3) sampling sites, (4) environmental conditions, and (5) different fishing pressures on the population during the two time periods. Dendrochronology studies (see Black et al., 2005; Black et al., 2012) in illicia of this species are recommended, as an attempt to understand the variation in environmental variables as a possible factor influencing the growth rate in this species.

While this study provides a much-needed spatial perspective and temporal comparison, it is not without limitations. This study was limited in that fewer young fish (n = 41) and male fish (n = 339) were sampled in comparison to female fish (n = 473). Few males were caught during the biomass surveys, as is evident from the sex ratio presented in Chapter 4 of this study. This was not surprising as the proportion of male fish tends to reduce with age, which is not unusual for species in this genus (Colmenero et al., 2016; Afonso-Diaz, 1996). The average size at age in the earlier size classes (0 – 1 year old) may be overestimated due to the inherent selectivity of the sampling gear used. Additionally, samples collected and used for Period 1 had no geographical position data (co-ordinates) hence spatial analysis on age distribution was done for the contemporary study only, but no comparison was possible.

Another potential caveat was the different sampling methods between the two periods. Period 1 used age and growth data collected during monkfish commercial fishing activities and hake annual biomass survey, while Period 2 used data collected during the monkfish annual biomass survey (in November each year between 2014 and 2016). Bias may well have been introduced into the comparison because of the difference in the sampling season and the sampling gear used; thus, there was no consistency in the sampling season and gear. The survey tends to explore a wide depth range while the commercial fish does not, mostly because of spatial fishing restrictions. Additionally, surveys use a much smaller mesh size as opposed to fishing nets used during commercial fishing activities. These differences might also influence the size composition of the samples. Sampling in one month (November) could influence the sample compositions because of factors such as migration when compared to sampling throughout the year.

In conclusion, despite the limitations, this study has provided much-needed information on the comparison of the age and growth curve for Cape monkfish, both spatially and temporally. The results presented in this study show similarities and dissimilarities with the historical study. In general, the growth rate of Cape monkfish was similar, especially for pooled data and for female fish between the historical and contemporary times. In Period 1, significant differences were found between the growth curves of females and males, but no significant differences were detected between the growth curves of males and females in Period 2. This might suggest significant variations in the growth parameters between the two studies (rather than between sexes). No possible explanation could be attributed to this observation, hence further investigation is recommended. However, there have been notable changes in environmental condition and levels of exploitation pressure directed to Cape monkfish population in this region, between Periods 1 and 2. Single-sex movement, reported in Chapter 4, coupled with the diminishing number of males > 70 cm could be the underlying cause of variation in growth curves between sexes, but this change warrants further research, for instance, by investigating the telomere length. The main changes observed between Periods 1 and 2 are in longevity; fish in Period 2 were as old as 16 years, while fish in Period 1 only reached 11 years. The similarity lies in the rate (K) at which the fish attained the maximum length, but larger fish in Period 2 were lighter than larger fish in Period 1, a factor that has implications for the fishing industry, especially for the bigger fish which are sought after in the market (Erasmus et al., 2021b). There are no obvious differences in the growth pattern between Period 1 and 2, except that larger individuals were collected in Period 2 than in Period 1. Although these findings may suggest that, unlike Thresher et al. (2007), this species is not responding to changes in the thermal environment, this may simply be because of the short time differences (20 years) between the studies.

Chapter 6: Exploring possible spatial and temporal changes in the catch statistics of monkfish, *Lophius vomerinus* and *Lophius vaillanti* in Namibia

A monkfish fishing net being dragged by MFV Kaume in Namibian waters; November 2020 (photo credit: Eduardo Coastas Torres)

6.1 Introduction

Globally, the fishing rate has been increasing due primarily to the demand for more food and because of improvements in fishing technologies (World Bank and FAO 2009). An increase in fishing activities has resulted in a growing concern over their impact on world fish populations and the marine ecosystem (Albaret & Laë, 2003; Watson et al., 2013; Potts et al., 2014). Extensive fishing pressure has resulted in changes in population structures of various marine species (Albaret & Laë, 2003; Worm et al., 2006; Hunter et al., 2015; Ben-Hasan et al., 2018), including changes in the mean length of fish (Ben-Hasan et al., 2018) and the abundance and distribution patterns of various fish species (Hilborn et al., 2017). The effect of overexploitation is exacerbated by the impacts of climate change, which adversely affect fish populations and marine ecosystems (Blamey et al., 2015; Tasker et al., 2000; Potts et al., 2014; Cisneros-Mata et al., 2019).

The catch weight for any given species continues to be the most used measure to quantify fisheries production (Maunder & Punt, 2004), which is used as an indicator for overfishing (Moloney et al., 2005). However, various factors such as climate change cause shifts in the distribution of fish populations (Mendenhall et al., 2020), which can influence catches and can make management of these resources challenging. For example, the vertical and horizontal movement of fish is influenced by water temperature (Monteiro et al., 2008; Morley et al., 2018). Vertical migration was reported in *Lophius americanus* western north Atlantic (Rountree et al., 2006). Similarly, *L. americanus*, *L. budegassa*, and *L. litulon,* of the same genus have been reported to display seasonal onshore-offshore movements in response to thermal conditions (Steimle et al., 1999). No known study in Namibia has investigated the possibility of vertical migration in monkfish off Namibia, however, Chapter 4 might suggest this possibility of both vertical migrations, and offshore-onshore migration. In Namibian waters, the intense *Benguela Niño* event in 1994/1995 was linked to a southerly shift (28ºS) in the biomass density of the deep-water hake, *M. paradoxus*, a commercially-important fishery species (Monteiro et al., 2008). This highlights the importance of spatial data in fisheries management.

The inclusion of spatial data contributes to better decision-making (Booth, 2000; Geronimo et al., 2018; Everett et al., 2021) such as when determining which areas to close/protect. Therefore, an important strategy to formulate effective management plans is to collect and include information on the spatial and temporal changes in various fish stocks' catch statistics

(Walters, 2003; McCluskey & Lewison, 2008; Moutopoulos et al., 2020). Spatial data on catches and catch-per-unit-effort (CPUE) can be challenging to analyse, mostly because of differences in fishing gears and activities, and regulations, at any given time or area (McCluskey & Lewison, 2008; Geronimo et al., 2018). When spatial representation of catch and effort are omitted from stock assessment analyses, an assumption is made that catches are even over a fishing ground (including unfished and rarely fished grounds). This, however, creates uncertainty over the abundance indices for fisheries that have developed progressively over fishing grounds (Booth, 2000; Walters, 2003; Geronimo et al., 2018). Historically, there has been little attempt to include the spatial variability inherent in the age and length structure and growth patterns of populations into a stock assessment framework (Booth, 2000).

Given the significance of spatial data in identifying important feeding grounds (see Chapter 3), the spawning season and spawning grounds (see Chapter 4) and distribution of age (see Chapter 5) of commercially important species such as the monkfish, few studies have incorporated spatial analyses into stock assessment models (Goethel et al., 2011; Kritzer & Liu, 2014). While previous stock assessment studies focusing on monkfish off Namibia have provided insight into their stock status (Maartens & Booth, 2001a, b; Kathena et al., 2018), there is a need for a spatio-temporal understanding of the catch statistics of this species for their effective management.

Setting of TAC is a good management practice employed in many fisheries around the world. Although the TAC setting process is complex, and sometimes not accurate, TACs still represent one of the critical components of fisheries management globally (del Valle & Astorkiza, 2007). The stakeholders in the monkfish fishery meet yearly during Monkfish Working Group (MWG) meetings (as described in Chapter 1, section 1.6) to discuss data that would later form part of the stock assessment analyses that would inform decisions on annual TAC. The data used in the stock assessment models determine the status of the monkfish resource and enables researchers to provide the best possible scientific advice on management measures (MFMR, 2013, 2014 and 2015), including catch statistics, observer data and annual monkfish biomass survey data. During the MWG meetings, results on monkfish annual biomass survey, observer coverage and fleet dynamics, standardisation of catch rates of Namibian monkfish stock using generalised linear modelling (GLM) and the overall status of the monkfish stock using the Age Structure Production Model (ASPM) model are discussed. This chapter provides a first exploration of available spatial information on monkfish catch and effort data to provide a first impression of the spatial nature of the monkfish fishing grounds. This chapter aimed to (i) identify hotspot fishing areas over time, (ii) examine spatial changes in exploitation patterns of monkfish since the inception of the fishery in 1994, and (iii) explore the relationship between monkfish catch and bottom sea temperature.

6.2 Materials and Methods

6.2.1 Study area

General methods concerning the study area (where fishing took place) were discussed in Chapter 2. Fishery-dependent data were collected from the fishing grounds, between 17.11° and 29.96°S and at a depth between 200 and 748 m. Catch data were recorded by fishing vessel captains in daily logbooks. and compiled by the Namibian Ministry of Fisheries and Marine Resources (MFMR). The data were combined for both monkfish species (Cape monkfish and shortspine African monkfish) because the monkfish landings harvested off Namibia are not separated by species, however as mentioned previously, Cape monkfish represent 94% of the total catch.

6.2.2 Data collection

Commercial catch data

For this chapter, the primary data are (i) the commercial catch data, (ii) the length-frequency and sex data based on commercial catches (Table 6.1). The commercial catch data were recorded daily in logbooks by fishing vessel captains during fishing activities off Namibia. Fishing vessel captains recorded vessel details (such as vessel licence, net mesh size and gear type), environmental data (such as SST, wind speed and direction), operations information (such as haul position and time, number of trawls and duration of trawl), catch information describing the type and quantity (kg) of species caught per trawl and the catch information describing the type and quantity of products processed from each species caught. Fisheries observers onboard the fishing vessels verify the data recorded in daily logbooks. The logbooks are collected from the fishing vessels by fishing inspectors who verify the recorded catches with the landed products. The catch data recorded in logbooks are checked for accuracy and captured into the Fisheries Information Management System (FIMS) database for commercial logbook data owned by MFMR. Historical data on the monkfish catch were from the International Commission for the Southeast Atlantic Fisheries (ICSEAF) between 1974 and 1989 recorded only for the areas around 20°S to 25°S and 25°S to 30°S as by-catch in the hake directed fishery (ICSEAF, 1982). The monkfish directed fishery only started in 1994 (Maartens & Booth, 2001a). The ICSEAF data were obtained from MFMR (see Chapter 2, section 2.4.1). Yearly average monkfish catches were obtained for 1974-2018, as described in Table 6.1. These data were obtained through MFMR (see Chapter 2, section 2.4.1). The monkfish fishery was established in 1994, thus, for this study 1994 will be taken as a reference point to refer to the stock status when it was not targeted as a fishery.

Fishing vessels fishing in the Namibian waters are mandated to carry observers onboard (for the full description of the functions of fisheries observers, see Chapter 2, section 2.4.3). The length-frequency and sex data were collected and recorded by observers onboard the commercial fishing vessels. Observers sampled at least three stations a day, depending on the number of trawls made per day. During sampling, at least three bins (weight 30 kg on average) were sampled, whereby observers scope the fish from the vessel deck or from the conveyer belt in the processing factory. Observers only sample unprocessed (whole round) fish. They record vessel information, environmental data, species composition in the sample, length measurements of target species recorded to the nearest cm below, sex and maturity stages. If time allowed, observers also sampled the main bycatch species on each fishing vessel. The data collected by observers is scrutinised and captured into the database by researchers. These data were obtained through MFMR (Table 6.1). It is important to note that both the observers and the researchers who collected length frequency data, recorded the total length (TL) in cm to the nearest cm below. These sets of data are discussed at the monkfish working group (MWG) (described in Chapter 1, section 1.6). The MWG met annually and collated the monkfish catches, observer data and annual monkfish biomass survey data.

Monkfish annual biomass survey data

The monkfish biomass data were recorded by researchers during annual monkfish research surveys. The biomass survey data include station depth and position, species composition, and biometric data (sex, maturity, length and weight measurements). The numbers of fish per station and length from monkfish surveys were recorded during the monkfish survey in November each year from 2000 to 2005 and 2004 to 2018). These data were obtained from the Nan-SIS database (Strømme, 1992), which is a collation of demersal biomass surveys conducted by MFMR (Table 6.1). The survey data were obtained through MFMR (see Chapter 2, section 2.4.2 for the full description of the survey).

Table 6.1: Sources of data relating to the stock status and harvesting of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) in Namibia between 1974 and 2018.

Type of data	Source of data	Database	Sampling period
Catch-at-length	Logbooks of MFMR	FIMS	1998–2018
Daily catch data	Logbooks of MFMR	FIMS	1998–2018
Catch-Per-Unit-Effort (CPUE)	Logbooks of MFMR	FIMS	1998–2018
Bottom sea temperature data	Logbooks of MFMR	FIMS	1998–2018
Sea Surface Temperature	NOAA satellite		1998–2018
Total Allowable Catches (TAC)	PPE	PPE	2001–2018
Total annual catches	Nan-sin data of MFMR	Nan-sis, FIMS	1974–2018

Note: MFMR = Ministry of Fisheries and Marine Resources; FIMS = Fisheries Information Management System; PPE = Policy, Planning and Economics; NOAA = National Oceanic and Atmospheric Administration.

Environmental data

Monthly average satellite-derived sea surface temperature (SST) data from the National Oceanic and Atmospheric Administration (NOAA) from 1998 to 2018 ((NOAA, 2020 - https://doi.org/10.7289/V5T72FNM) were used to evaluate any possible dependency of catches on ocean surface temperature. The Extended Reconstructed Sea Surface Temperature (ERSST) data set in a CSV format was utilised. These data were provided in 2° x 2° grids, which formed the spatial template for categorising the catch weights.

Sea bottom temperatures, coinciding with monkfish catches between 1998 and 2002, were recorded on logbooks by fishing vessel captains during commercial fishing activities. Bottom temperatures outside of the 1998 to 2002 period were not available. Other in *situ* climatology data such as salinity and dissolved oxygen are not recorded during monkfish commercial fishing activities and were thus not available for analysis.

6.2.3 Data Analysis

The MFMR has mandated all fishing vessel captains to complete and submit logbook data for every fishing trawl made in Namibian waters. The data collected in logbooks are utilised routinely in the assessment models. The annual average catch data were analysed between 1974 and 2018, as well as the annual mean length (ML) of fish caught between 1998 and 2018. Catch data were arranged to reflect vessel Id, fishing positions, fishing year, month and day, catch in kg (a sum of the total catch for the day from all the trawls made in one day), duration of the trawl in hours (a sum of the trawling time for all trawls in a given day), vessel Gross Register Tonnage (GRT) and gear depth in m. Catches made before Independence (pre-1990) were recorded by the ICSEAF (but these data are now kept by MFMR), while MFMR recorded the catches after 1990.

The length of all individual fish sampled by observers for each year (e.g., 75600 records in 2017) was raised to the vessel total catch. An annual mean length and standard deviation were then calculated. Annual mean length (TL) values were compared between 1998 and 2018. A one-way analysis of variance (ANOVA) test in R (version 3.3.1) (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018) was used to test for significant differences among the annual mean length (total length, cm) from 1998 to 2018. For spatial analysis, a geostatistical aggregation curve was constructed for the catch positions for 1998 – 2018 using ArcGIS Pro (http://desktop.arcgis.com/en/arcmap/10.5/tools/space--time-pattern-mining-toolbox/learnmoreemerging.htm). Areas were identified as coldspots and hotspots, and defined as 'oscillating hotspot', 'consecutive hotspot', 'oscillating coldspot' and ‘sporadic hotspot’, and also included areas with ‘no pattern detected’ (Table 6.2), based on the conceptualisation of spatial relationships.

Table 6.2: The definitions of 'sporadic hotspot', 'oscillating hotspot', 'consecutive hotspot', 'oscillating coldspot' and 'no pattern detected' as per ESRI. 2021.

Term	Definition
'consecutive hotspot'	An area with a single uninterrupted run of statistically significant hotspot bins in the final time-step intervals. The area has never been a statistically significant hotspot before the final hotspot run and less than ninety percent of all bins are statistically significant hotspots.
'oscillating hotspot'	A statistically significant hotspot for the final time-step interval that has a history of also being a statistically significant cold spot during a prior time step. Less than ninety percent of the time-step intervals have been statistically significant hotspots.
'sporadic hotspot'	An area that is an on-again then off-again hotspot. Less than ninety percent of the time-step intervals have been statistically significant hotspots and none of the time-step intervals have been statistically significant cold spots.
'oscillating coldspot'	A statistically significant cold spot for the final time-step interval that has a history of also being a statistically significant hotspot during a prior time step. Less than ninety percent of the time-step intervals have been statistically significant cold spot.
'no pattern detected'	Does not fall into any of the hot or cold spot patterns defined above.

Firstly, a composite map for 1998–2018 data was produced. Subsequently, hotspot maps for 1998–2000, 2001–2003, 2004–2006, 2007–2009, 2010–2012, 2013–2015 and 2016–2018 were plotted. The hot and coldspots were evaluated using the Mann-Kendall trend test as described (ESRI, 2021).

The areas of catches were analysed for the period 1998 to 2018 and traditional estimates of space were calculated employing a Gaussian kernel density to show the clustering of total catches over the years. Calculations were based on a 5km x 5km, using a search radius of 100 km from each sampling location, the total catch densities were categorised into 50, 100, 150, 200, 250 and 300 kg/km^2 classes.

Annual mean length (TL) values were compared between 1998 and 2018. A one-way analysis of variance (ANOVA) test in R (version 3.3.1) (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018) was used to test for significant differences among the annual mean length (total length, cm) from 1998 to 2018. For the analysis of long-term trends in fishing depth, the annual mean depth fished between 1998 and 2018 was calculated. No trawling is permitted within the 200 m isobath in Namibia since 1993 (Boyer & Hampton, 2001), so no catch data exist for these depths. Depths recorded with no units (fathom or meter) and depths shallower than 200 m (47 depth records (0.07%)) were excluded from this analysis. Changes in fished depth per year were tested using a one-way analysis of variance (ANOVA) test in R. Statistical significance was defined at $p < 0.05$ and 0.95 confidence intervals.

For the water temperature data versus catch, the following analyses were performed. As stated above, the data were provided in 2° x 2° grids, which formed the spatial template for categorising the catches. For each 2° x 2° square, the total monthly catch was graphed against the monthly average SST for the three cells; their central coordinates were 21°S; 13°E, 23°S; 13°E and 25°S; 13°E, that had catch data across the entire study area. No data (zero) values were excluded from the analyses.

An exploratory analysis of the influence of bottom sea temperature on monkfish catches between 1998 and 2002 was conducted using the same 2° x 2° grids as above. The bottom temperatures for each month were averaged for each cell. Zero data cells and obvious outliers were excluded from the analyses. The same three cells utilised for the SST analyses were selected for comparing temperature with catch weights. Detailed spatial mapping was conducted on the bottom and sea surface temperature data for 1998 and 1999. In addition, diffuse spatial interpolation was undertaken on data for 1998–2002. Regression analyses were conducted on SST and BT data and the total monthly catches in the three areas. Statistical analysis was undertaken in R (version 3.3.1) (R Core Team 2018, http://www.r-project.org/) and accompanying open-source interface Rstudio v0.99.902 (RStudio 2018).

6.3 Results

6.3.1 Total monkfish catches and TAC

The highest annual catch recorded was 16 600 tonnes in 1998 (Figure 6.1). Between 1998 and 2003, the total annual catch exceeded the reference point (12 158 tonnes, in 1994). The catches in 1994 were used as a reference point in this study because that is when the monkfish directed fishery was introduced. The lowest total catches since the inception of the fishery in 1994 were recorded in 2011 (7 200 tonnes) (Figure 6.1). The setting of a TAC commenced in 2001, with the TAC not caught in most years (61.1%), although in some years this was exceeded. For example, the 2002 catch far exceeded the set TAC, by 3 200 tonnes. Most recently, however, in 2018, catches were 7.3% less than the set TAC for that year (Figure 6.1).

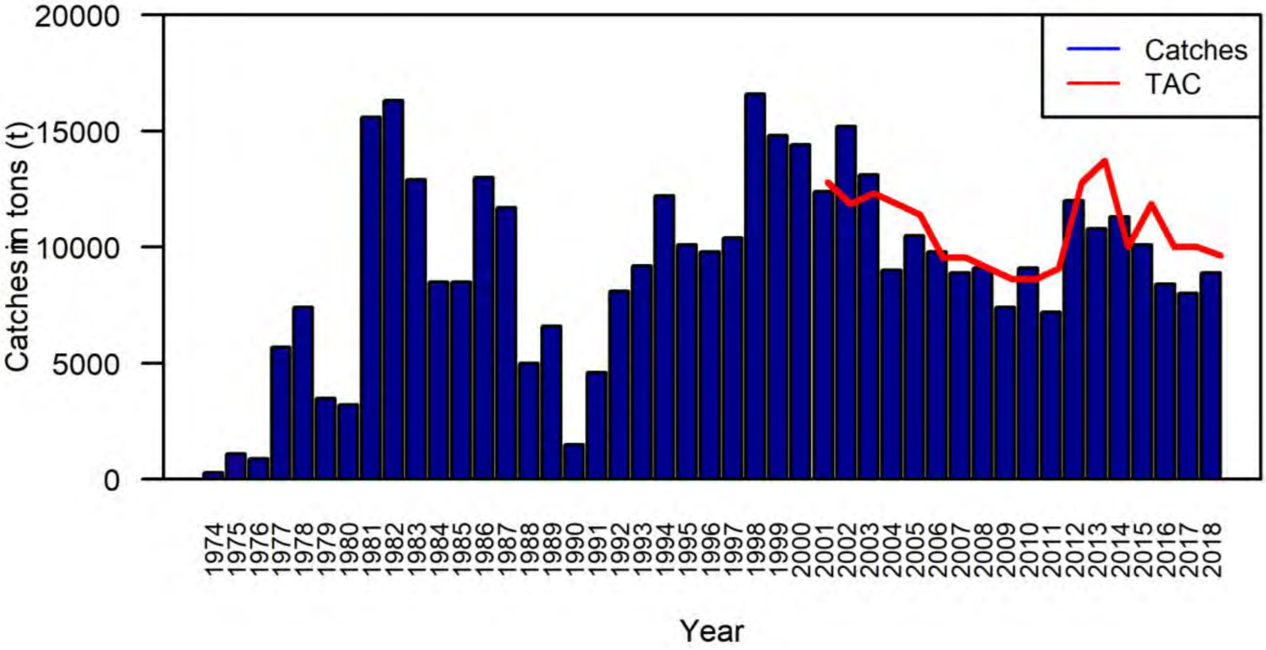


Figure 6.1: Monkfish (*Lophius vomerinus* and *Lophius vaillanti*) total catch between 1974 and 2018 and the Total Allowable Catches (TAC) set each year between 2001 and 2018, off the coast of Namibia. Cape monkfish represents 94% of the catches.

6.3.2 Annual mean length (TL) between 1998 and 2018

The annual mean length (TL) for monkfish between 1998 and 2018, fluctuated between 39 and 50 cm (TL) (Figure 6.2). The shortest mean length (39 cm, TL) was recorded in 1998, 2007 and 2009, while the highest annual mean length (50 cm, TL) was recorded in 2017. However, the was no significant difference among the annual mean length between 1998 and 2018 (F = 2.873, df = 1, p = 0.106).

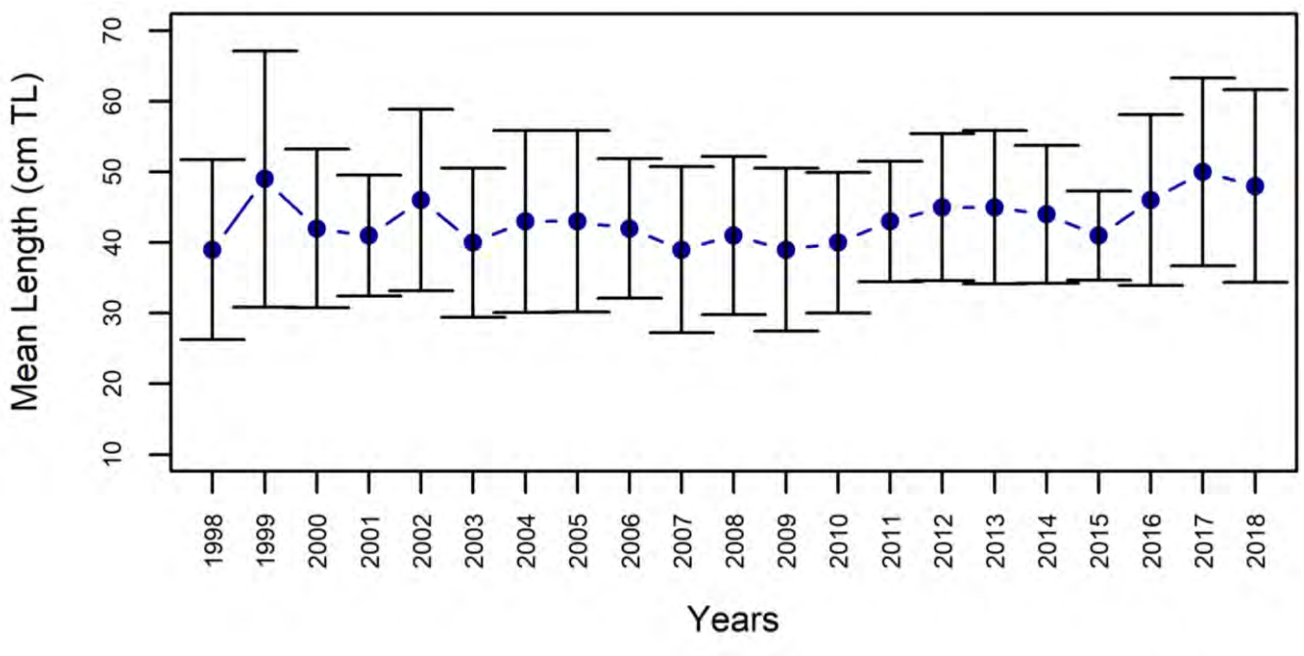


Figure 6.2: Annual mean total length (TL) (cm) of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) for commercial catches between 2001 and 2018, off the coast of Namibia. Cape monkfish represents 94% of the catches. The bars represent the standard deviations for each mean.

6.3.3 Spatial analysis of fishing patterns to identify monkfish "hotspots"

A total of 65 044 catch records (geographical positions) were recorded between 1998 and 2018. Catches were documented along the entire coast, between 17° and 28°S, with little fishing effort between 27° and 28°S (Figure 6.3). Similarly, the area between 17° and 18°S was seldom trawled. Spatial analyses of 1998 – 2018 dataset showed that consistently high catch volumes (Consecutive Hotspots) were observed south of Walvis Bay, between latitude 25°S and 26°S, with the sporadic fishing hotspots located just north of the consecutive hotspots, at 25°S (Figure 6.3). The oscillating hotspots were observed in two areas between Walvis Bay and Lüderitz, adjacent to the consecutive and oscillating hotspots, between 25°S and 26°S. The oscillating coldspots were more fragmented along the coast, between 19°S and 20°S, 21°S and 23° and at 27°S (Figure 6.3).

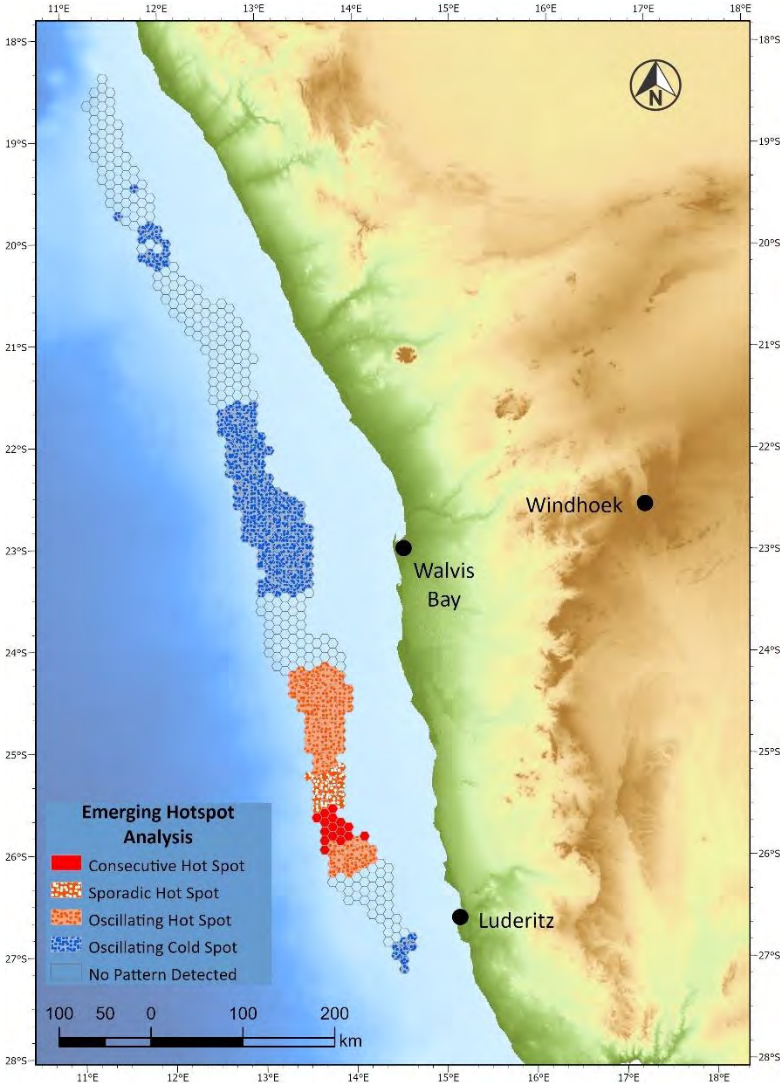


Figure 6.3: Identified hotspots based on monkfish (*Lophius vomerinus* and *Lophius vaillanti*) catch off the coast of Namibia between 1998 and 2018. Cape monkfish represents 94% of the catches. Map constructed in ArcGIS 10.8 Software.

6.3.4 Spatial analysis of monkfish catch to identify high-density areas

The kernel density analysis indicated that the latitudes around 24ºS, and between 26º and 27ºS, between Walvis Bay and Lüderitz, had the highest total catch densities (~ 300 kg/km2) (Figure 6.4). The area north of 23ºS produces lower catch densities that never exceeded 150 kg/m2 (Figure 6.4).

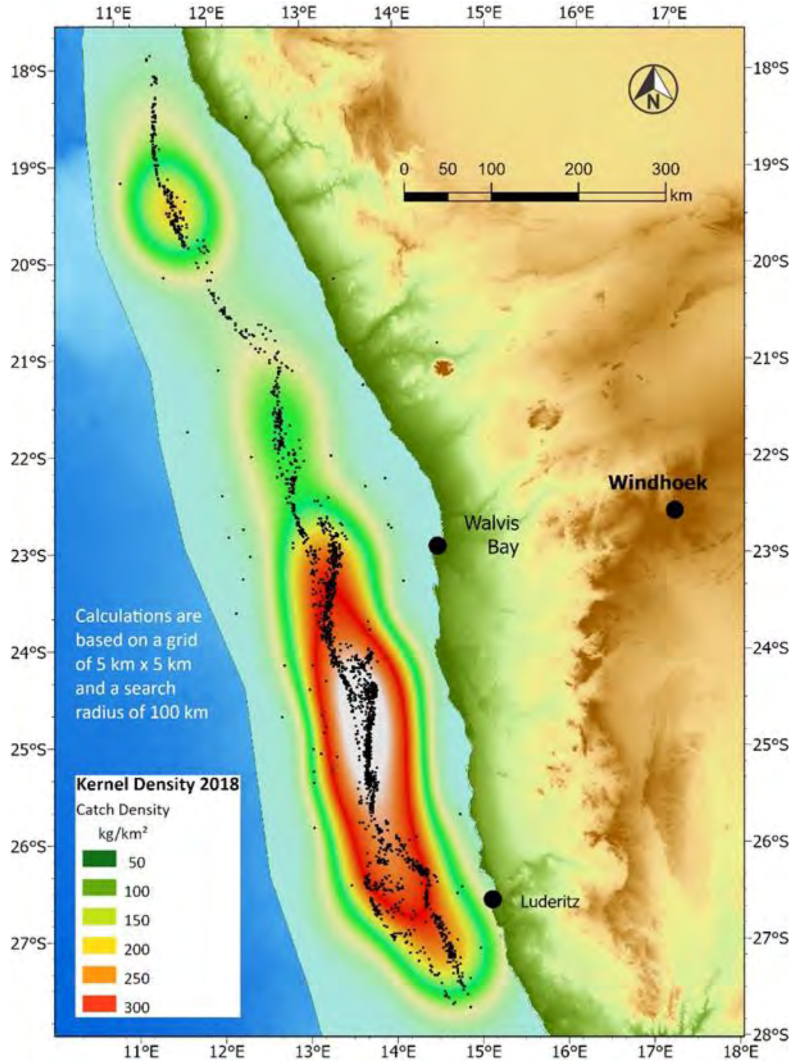


Figure 6.4: Spatial distribution of total monkfish (*Lophius vomerinus* and *Lophius vaillanti*) catches based on kernel density of data collected between 1998 and 2018 off the coast of Namibia. The catches are shown as densities of 50, 100, 150, 200, 250 and 300 kg/km2. Black dots indicate monkfish fished positions between 1998 and 2018. Cape monkfish represents 94% of the catches. Map constructed using ArcGIS 10.8 Software.

6.3.5 Temporal changes in fishing depth

The depth fished did not vary significantly between 1998 and 2018 (($F = 0.168$, df = 1, $p = 0.686$). On average, the deepest depth was in 2001 (369 m ± 62.34 m) and the shallowest depth was in 1998 (324 m ± 47.89) (Figure 6.5). Interestingly, although not significant, the average fishing depth has been steadily increasing, from about 324 m in 1998 to 367 m in 2018.

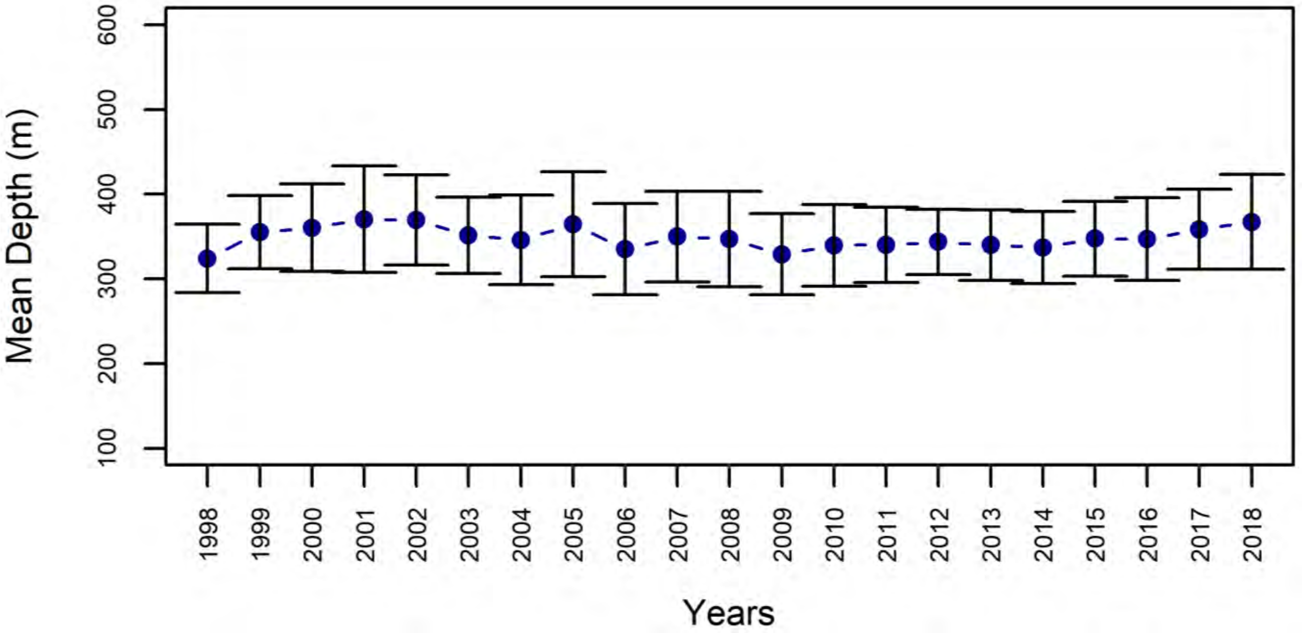


Figure 6.5: The mean annual depth (n = 64 995) of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) catches off the coast of Namibia between 1998 and 2018. The bars represent the standard deviations for each mean.

6.3.6 Sea surface temperature and total monkfish catches between 1998 and 2018

The regression analysis between sea surface temperature (SST) and the monthly spatial catches of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) in three 2° x 2° Cells; 21°S 13°E, 23°S 13°E and 25°S 13°E, between 1998 and 2018 revealed no significant relationship (p = 0.230, r^2=0.0059, p = 0.797, r^2=0.0114 and p = 0.041, r^2=0.0158, respectively) (Figure 6.6). These low r^2 values indicate that in all three grid cells, only ~ 1% of the variation is explained between SST and total monkfish catches in these areas.

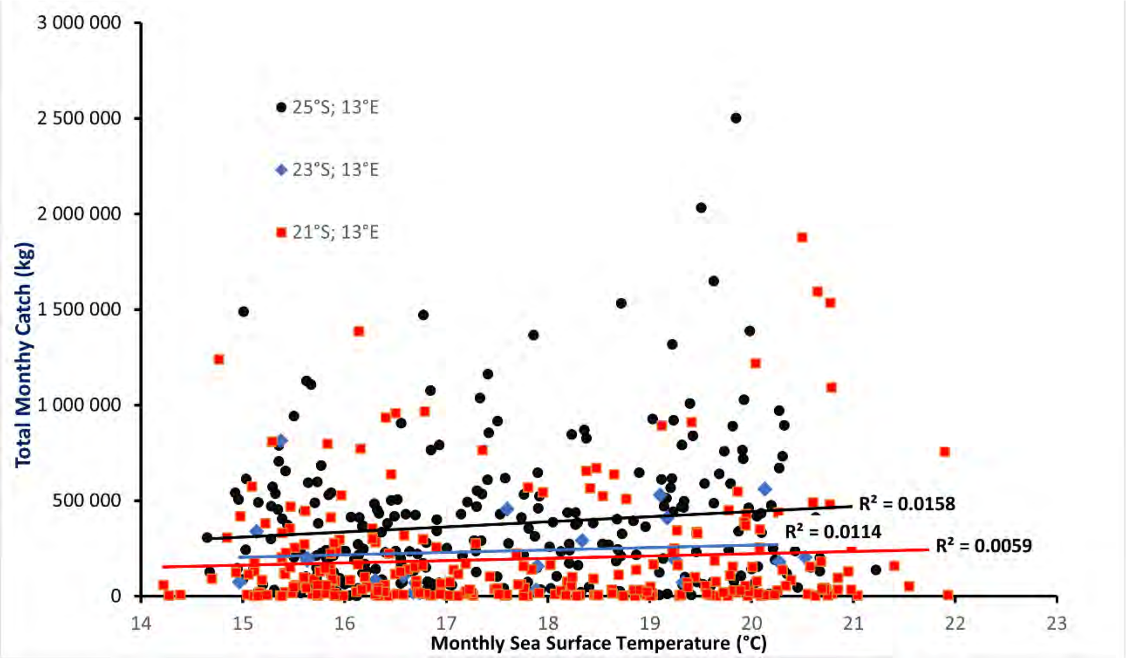


Figure 6.6: Sea surface temperature profile and the total monthly catches of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) at three 2° x 2° Cells; 21°S 13°E, 23°S 13°E and 25°S 13°E, off the coast of Namibia between 1998 and 2018.

6.3.7 An association between temporal changes in bottom sea temperature and monkfish catches

The bottom sea temperature data represent a dynamic environment that changes on an inter and intra-annual basis. Similarly, catches vary considerably. This is illustrated in Figure 6.7, which is an example of spatially analysed annual catch and bottom sea temperature data. The maps show annual data for two years (1998 and 1999) and are based on diffuse interpolation and Geographically Weighted Regression, and kernel density interpolation of bottom sea temperature and monkfish catches. The regression analysis between sea bottom temperature (BT) and the monthly spatial catches of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) in three 2° x 2° Cells; 21°S 13°E, 23°S 13°E and 25°S 13°E, between 1998 and 2002 revealed no significant relationship (p = 0.601, r^2=0.0126, p = 0.947, r^2=0.0055 and p = 0.205, r^2=0.0717, respectively) (Figure 6.7). These low r^2 values indicate that in all three grids, only ~ 1% of the variation is explained between BT and total monkfish catches in these areas.

However, although not significant, the areas with high catches in 1998 coincided with areas of higher bottom temperature (Figure 6.8).

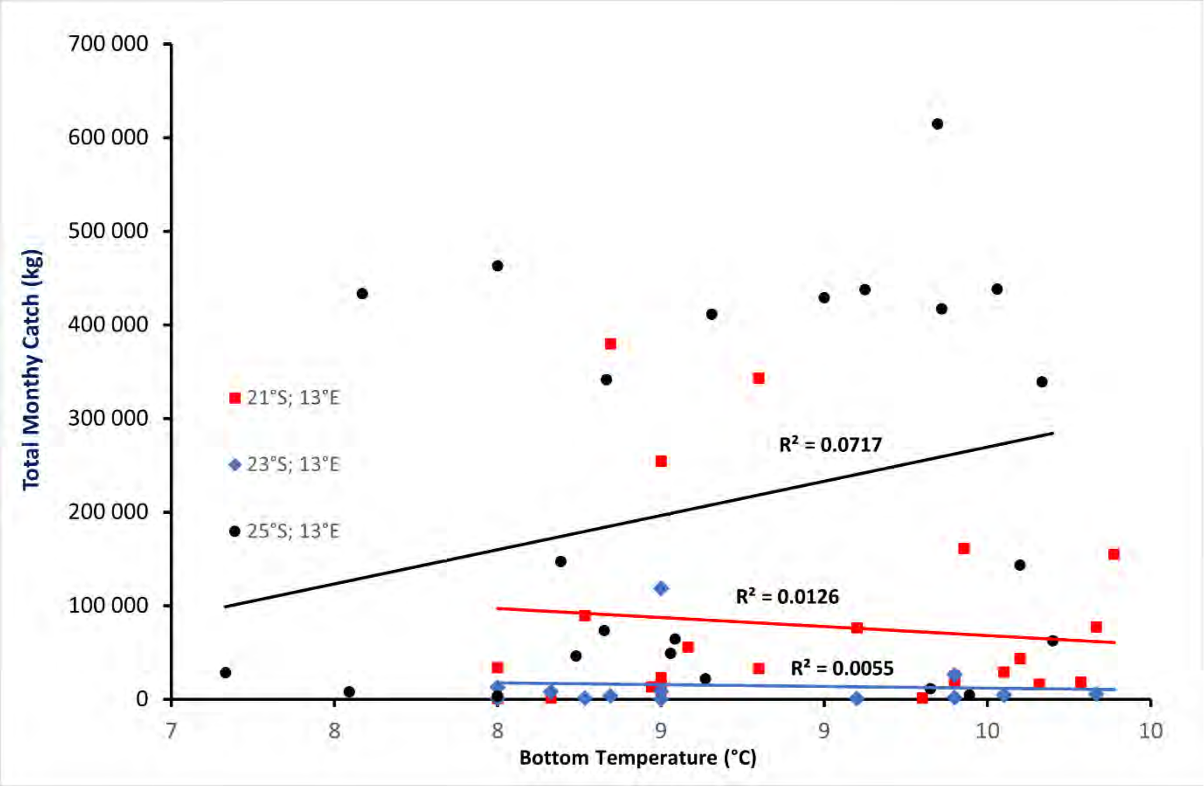


Figure 6.7: Sea bottom temperature and the total monthly catches of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) at three 2° x 2° Cells; 21°S 13°E, 23°S 13°E and 25°S 13°E, off the coast of Namibia between 1998 and 2002.

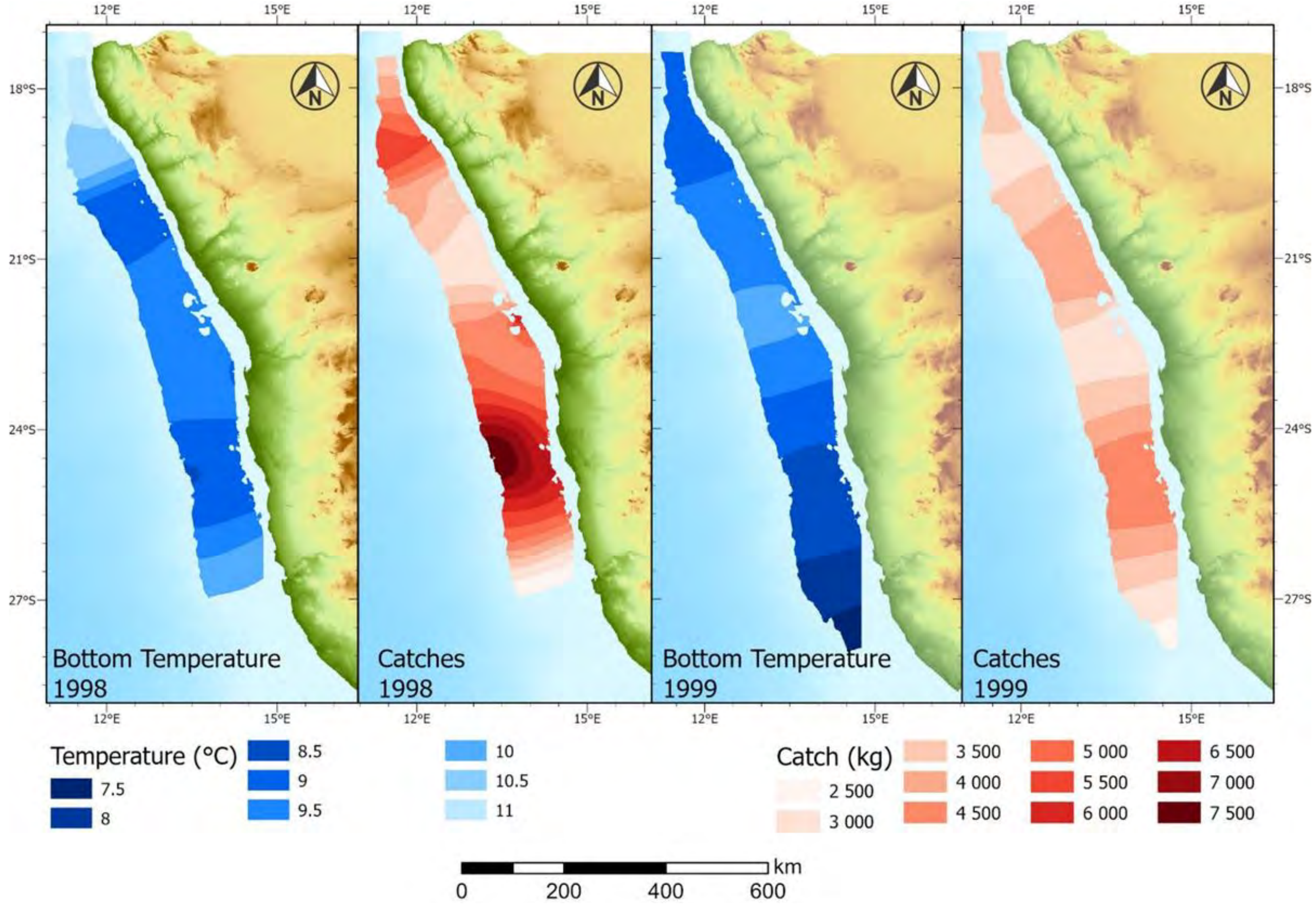


Figure 6.8: A qualitative appraisal of bottom seawater temperature profile and the spatial catches of monkfish (*Lophius vomerinus* and *Lophius vaillanti*) off the coast of Namibia for 1998 and 1999. Map constructed using ArcGIS 10.8 Software.

6.4 Discussion

Although there are yearly MWG and monkfish TAC reports (e.g., MFMR, 2018; MFMR, 2019; MFMR, 2020) and stock assessment studies focusing on monkfish (Maartens & Booth, 2001a, b; Kathena et al., 2016; Kathena et al., 2018), in-depth research on monkfish spatial catch statistics is limited (MFMR, 2019). The previous work on monkfish catches is centred around the temporal trends of monkfish since the inception of the monkfish fishery in 1994. Particularly, the importance of spatial data is acknowledged but spatial data are not included in stock assessment models (e.g., a generalised metapopulation model; Goethel et al., 2011). The results from this study provide a first examination of the spatial catch and effort statistics of the monkfish fishery since its inception in 1994, and therefore, presents important information e.g., the main fishing grounds identified between 25° and 26°S in this study. However, the spatial catches analysis showed the highest catch densities (300 kg/km2) in the 1998–2018 catch time series around 24°S, and between 26° and 27°S, between Walvis Bay and Lüderitz (Figure 6.3). Additionally, a basis is provided to investigate changes in the stock status that may result from climate change and the extensive fishing pressure directed at monkfish since the inception of its fishery. Findings from this study can be used as input in management decisions for the Namibian monkfish stock. The annual catch statistics for monkfish between 1974 and 2018 are presented, which show variability, with the lowest total catch recorded in 2011 (7 200 tonnes) since the inception of the fishery in 1994. No significant variations were observed in the annual mean length between 1998 and 2018. Similarly, no significant variation was observed in fishing depth for the same period.

To comprehensively understand the catch trends for monkfish, it is important to consider all catch data; however, data before the inception of the monkfish fishery (before 1994) are limited. Maartens and Booth (2001b) ascribed the increase in catches between 1991 and 1994 to an improvement in the efficiency of the monkfish fleet. The increase in fishing vessel numbers catching monkfish, with direct targeting, may be reflected in the declining trend in the catch in recent years. Alternatively, environmental change to the ecosystem may be impacting the resource in ways not yet understood. A decline in catches of other monkfish species such as *L. piscatorius* (Afonso-Dias & Hislop, 1996), *L. americanus* (Steimle et al., 1999) and *L. litulon* (Sun at al., 2020), has also been noted, and ascribed to an increase in the harvest. Locally, overfishing has been attributed to the cause of the collapse of species such as the pilchard *Sardinops sagax* and orange roughy *Hoplostethus atlanticus*, both of significant commercial importance (Oelofsen, 1999; Boyer et al., 2001b; van der Westhuizen, 2001; Jarre et al., 2015a). These species are currently under moratorium to rebuild their stocks. The declining trend of monkfish catches is worrisome. In addition to the extensive fishing of the monkfish resource, it has been indicated in MWG that more catches of monkfish have been reported by the hake fishing industry. For this reason, stringent measures must be taken to deter hake fleets from landing excessive monkfish (more than allowed (5%) in the Marine Resource Act, Act No 27 of 2000).

TAC limits have not been fully utilised by the fishery (Figure 6.1). For instance, in 2013, the TAC was the highest (14 000 tonnes) in the catch time series, while the actual catches were substantially lower. The underutilisation of the TAC suggests that the set TAC did not reflect the abundance of the stock. In 2011 when the yields were the lowest, catches were 20% less than the TAC. The underutilisation of the TAC in some years can be attributed to several fishery-depended and fisheries-independent factors, namely, (i) a reduction in biomass; (ii) overexploitation of the resource, such that in 2005, the Cape monkfish stock was already said to be overexploited (Booth & Quinn, 2006); (iii) a lack of capacity to land the set TAC; (iv) some of the monkfish rights expired in 2017 and were not renewed; (v) there is mostly always a late allocation of monkfish quotas, such that the fishing season can lapse without the right holder landing their quotas.

Spatial analysis allows a more comprehensive investigation on changes in stock abundance (Booth, 2000; Geronimo et al., 2018; Everett et al., 2021), and overfishing is often associated with a reduction in fish size at capture (Wheeler et al., 2009). Yet for the monkfish resource, although there was a fluctuation in the annual mean size, the variation in mean length was not significant. Variation in annual mean length may be due to the nature of the fishery. Fishing vessel movement is spatially dynamic, if fishers fish in areas with a high abundance of large fish, then the mean length would be high, the opposite is also true. This is often called the basin effect – a decline in size is rarely observed because effort changes according to hotspots. Although this is rarely observed, Ben-Hasan et al. (2018) showed a significant decline in the mean length of yellow-fin seabream *Acanthopagrus latus* with an increase in catches.

The areas that were oscillating "coldspots" (Figure 6.3) suggest fewer fishing activities targeting the monkfish resource, especially between 19ºS and 20ºS, between 21ºS and 23º and at 27ºS. These areas might not be suitable fishing grounds or that monkfish is not abundant in these areas. Climate change may have resulted in the movement of the species, with the fleets following a change in distribution and density (Mendenhall et al., 2020). However, despite the expansion of the fishing grounds, there is an area south of 28ºS which showed marginal catches, likely due to a rocky bottom that is not able to be trawled as shown in Schneider & Johnsen (2000) and Johnsen & Kathena (2012). Results indicate that the pattern of monkfish fishing activities is heterogeneous, leading to 'hotspots' in specific areas. Importantly, this study has identified the area around 25ºS and 26ºS as consecutive fishing hotspots for the 1998–2018 fishing time series. The consecutive hotspot areas are constantly exposed to fishing pressure. Studies of these areas show that the area around 25ºS has a high concentration of food and is a preferred habitat for sardine spawning (Bakun, 1993). Additionally, these areas form part of the area with the maximum upwelling alongshore wind (at about 25º–27ºS) (Santos et al., 2012). These features likely make these areas attractive to fishers. Part of the 25ºS area is seen as sporadic. This might indicate localised enriched areas in terms of monkfish abundance, which is further confirmed by the biomass survey density (weight) in these areas is also high Clustering of important fishing areas has also been observed in similar studies (Saul et al., 2013; Moutopoulos et al., 2020). Frequently fished areas coincide with areas of high relative abundance for the target species. The consecutive hotspots fishing ground around 25ºS suggest an area prone to extensive fishing pressure and may lead to local depletion. Although the fishing area may change annually, the spatial analysis of fishing grounds helps in the identification of frequently fished areas (core fishing areas), which are important in delineating fisheries management areas, which is key in the implementation of the Ecosystem Approach to Fisheries (EAF) (Geronimo et al., 2018; Everett et al., 2021) and Marine Spatial Planning (MSP). Because the ocean is utilised by many parties such as fishers and miners, spatial data are also important in resolving conflicts between ocean users (Moutopoulos et al., 2020). For instance, the recently demarcated phosphate mining areas (discussed also in Chapter 4) fall within monkfish spawning grounds (Chapter 4) and the areas with the highest monkfish density (this chapter, Figure 6.4). Results from this study can be used to inform management decisions to restrict phosphate mining in this important area.

Spatial analysis and mapped geographical positions of catches for 1998 to 2018 show how monkfish fishing grounds have evolved spatially. In recent years (from 2011) monkfish fishing grounds have expanded southward and northward compared to before 2000 when fishing was mostly confined between 21° and 27°S (Figure 6.2). Similarly, historical studies have indicated that monkfish was only distributed from 21°S southward (Leslie & Grant, 1990; Maartens & Booth, 2001a, b). In recent years, monkfish have also been harvested north of 21°S. The increase in the demand for more monkfish products is one possible driver towards both increasing fishing intensity and expansion horizontally (Figure 6.4) and vertically (Figure 6.5).

Although most monkfish fishing effort (indicated by hotspots) is around 25°S and 26°S, the abundance of monkfish appears to be primarily concentrated around 24°S latitude, and between 26° and 27°S, between Walvis Bay and Lüderitz, with the highest total catch densities (~ 300 kg/km2) (Figure 6.4). It appears that the environmental conditions in these areas are conducive for monkfish, hence their aggregation. The spatial variation in the distribution might be following oxygen concentration at the sea bottom, which plays a vital role in the dynamics of species e.g., shallow-water hake (*M. capensis*) (Bartholomae & van der Plas, 2007). Oxygen concentration at the bottom varies both temporally and spatially and this influences species distribution (Bartholomae & van der Plas, 2007; Hamukuaya et al., 1998; Monteiro et al., 2008). Furthermore, the topography of the seabed in these areas might also be suitable as a monkfish habitat. Smith et al. (2008) showed that habitat type was a key determinant in monkfish *L. litulon* abundance and distribution. Monkfish are generally abundant in sandy and muddy bottoms (Leslie & Grant, 1991). Several studies have shown that fish are not evenly distributed in each area, but aggregate into patches (Downing, 1986). The kernel density distribution of monkfish catches reflects both the species distribution and the fishing effort. Identification of areas of high density is important for species management, EAF and MSP (Kavadas et al., 2015; Moutopoulos et al., 2020). The low density of monkfish north of 23°S might be due to extreme environmental variables in the northern part of Namibia, mainly due to intrusion of warmer water from Angola, the highest frequency of warm events occurred between 1995 and 2003 (Bartholomae & van der Plas, 2007; Hutchings et al., 2009). Interestingly, the catch data analysed in this study show no clear trends with bottom sea temperature. Monkfish catches show an area between 19° and 20°S with an increased catch density. The observed distribution might originate from a different stock, but this needs to be investigated. There is a need to investigate whether the commercial catches in the north (between 19º and 20ºS) are those of Cape monkfish or the shortspine African monkfish. Currently, the shortspine African monkfish stock size off Namibia is difficult to investigate because the records of monkfish catches do not separate species. It should be noted that fishing activities also do not necessarily cover the full portion of a species' distribution, or species may be inaccessible by the fishery in parts of the grounds due to gear incompatibilities (Everett et al., 2021); thus, caution should be exercised when interpreting these spatial distribution results of monkfish. Additionally, the numbers of the shortspine African monkfish encountered on monkfish surveys are very minimum, usually representing between 1 and 2% of the monkfish surveyed. For instance, only 26 individuals were recorded in 2014, none individuals in 2015 and 44 in 2016 (based on the MFMR survey dataset).

There was no significant variation in average fishing depth (Figure 6.2), hence no direct evidence of monkfish moving into deeper waters. Globally, there is a trend of deeper fishing occurring for bottom-dwelling marine species (Morato et al., 2006), which was not observed. For example, Simpson et al. (2013) found a downward movement of cold-water demersal fish species such as cod and monkfish in response to the warming of the European seas. On average, the fishing depth changed from 324 m in 1998 to 367 m in 2018 (a difference of 43 m). The collection of accurate data is a crucial aspect for fisheries managers and stock assessment however, this study found several limitations in the data. For example, on several occasions, depth data did not align with associated coordinates and simple measures of units (fathoms or metres) were omitted from the data. While all such discrepancies were omitted from the analyses in the present study, such errors raise concerns and highlight the importance of researchers at MFMR to constantly engage and remind fishing vessel captains to ensure that they use correct units when they record the catches and to take care in data collection. Fishing vessel captains need to use one measurement unit (meters) for consistency to allow for accurate analysis and solid conclusions on depth data. Moreover, the researchers can identify a few fishing vessels that can be fitted with temperature reading instruments on the fishing nets so that bottom temperature associated with catches can be recorded. Additionally, all fishing vessel captains should be compelled to fill out all environmental data such as SST and observers tasked to ascertain that all information is indeed captured.

Water temperature is a key determinant in the spatial distribution and preferred habitats of marine species (Morley et al., 2018; Wang et al., 2021). There is often a relationship between catch size (magnitude of catches) and temperature (Sumaila et al., 2011). No known studies in the Namibian waters have investigated the change in bottom temperature versus catches. These studies are important because they provide information about the conducive bottom temperature of species. This information also indicates shift/movement of fish which can be used to improve their management. The bottom sea temperature data in this study suggest a dynamism of the ocean currents in the Benguela System and episodic upwellings, indeed a dynamic environment that changes on an inter and intra-annual basis, which has also been extensively highlighted in various studies in this region (Gibbons & Buecher, 2001; Hutchings et al., 2009; Jarre et al., 2013). Similarly, spatial catches varied considerably (Figure 6.6). In the 1998 – 2002 catch time series, only data from 1998 showed discernible trends, where high catches aligned with high bottom sea temperatures.

Sea surface temperature affects the distribution of fish (Wang et al., 2021), spawning activities (Wang et al., 2021) and feeding (Sun et al., 2020). For example, SST is considered a major environmental factor that affects the wintering and spawning of chub mackerel (Wang et al., 2021). However, in this study, only ~1% of the variation could be explained between the SST and the monthly total catches of monkfish at three 2° x 2° Cells; 21°S; 13°E, 23°S; 13°E and 25°S; 13°E, between 1998 and 2018. Similar findings were obtained in the analysis of bottom temperature and monthly total catches. However, the period of analysis was limited to five years between 1998 and 2002, and more detail is required here in future studies.

Although the literature shows warming of the Namibian waters, especially north of the Lüderitz upwelling cell, in recent years (Junker et al., 2017), the bottom limited water temperature data collected concurrently with fishing data of monkfish does not show clear warming patterns of the bottom water temperature but instead demonstrates significant variability which was expected because the nBE is highly variably largely due to the upwelling intensity. In general, recent environmental studies in Namibia show general warming of the SST, especially in 2006 (Chen et al., 2012 and 2011 (Junker et al., 2017), the years considered as *Benguela Niño* years, with the SST off Namibia much warmer than average. Chen et al. (2012) described the intrusion of sea surface waters in the northern part of Namibia as the main cause of warming events.

O'Toole and Bartholomae (1998) discussed the water warming event in 1995, which coincides with the low catches in other fisheries in 1995 although the catches were high in the previous year (1994). The decline in catches was also observed in other fisheries, and it is said to have lasted until 1997 (O'Toole & Bartholomae, 1998). Temperature differences in the waters are known to influence the distribution patterns of organisms (Mqoqi et al., 2007). Some *Lophius* species (*L. americanus*, *L. budegassa*, and *L. litulon*) have been reported to display seasonal onshore-offshore movements in response to thermal conditions (Steimle et al., 1999). The nBE is currently experiencing variability in sea surface temperature (Hutchings et al., 2009; Rouault et al., 2007; Santos et al., 2012), wind (Monteiro et al., 2008; Peard, unpublished data), with an increase in the warming events since the 1990s (Jarre et al., 2015a). Warming waters induce vertical and horizontal shifts in fish populations, making the same fish populations accessible in new areas (Jennings & Kaiser, 1998; Perry et al., 2005; Hampton & Willemse, 2012; Mendenhall et al., 2020). The bottom water temperature data analysed in the present study showed great variability with mostly warming in 1998. There have been records of North-south temporal shifts in the catchability of the Namibian hake in summer, which happen to coincide with the southward movement of the warm Angolan tropical water (Gordoa et al., 2000). This might be true for monkfish as well because Figure 6.4 illustrates high catches in central and south of Namibia when compared to the catches in the north where temperatures are warmer. Similarly, in the nBE, the intrusions of warm, nutrient and oxygen-poor water from southern Angola have been linked to changes in the vertical distribution of both hake species making them less available to the trawl and long-line fleets (Hampton & Willemse, 2012). Globally, marine waters are generally warming in recent years (Frölicher et al., 2018). Analysing monkfish tracks and trawls using monkfish fishery captains' (as previously carried out by Peterson (2014) for the hake fishery) might shed more light on the spatial distribution of fishing activities of monkfish off Namibia. The annual catch statistic (Figure 6.1) was also found to indicate high total catches in 1998 when the bottom temperatures were high. It is possible that catchability for monkfish increase with an increase in temperature. However, for this study, no trend and no statistical relationship could be established between bottom temperature and catch size and between sea surface temperature and catch size. The system's dynamism made the correlation between bottom temperature and catches difficult, for two reasons. Firstly, the temperature is ever-changing in different areas where the catches were recorded, and second, the bottom temperature data were limited and were not recorded for the entire Namibian coast. As such, no trend and no statistical relationship could be established between temperature and catch size.

To conclude, there is a need for more data on temperature associated with catches along the entire Namibian coast. There is also a need for intra-annual analyses, the role of upwelling, among other elements in relation to monkfish. Although MFMR already records temperature profiles (i.e., CTD data), regional ocean current and SST, there is a potential avenue for future research to utilise CTD data for these analyses. Although CTD data are collected during monkfish annual surveys, the data were not available for analysis in this study. Additionally, detailed environmental data were not available to explain the density of monkfish in different areas. In future, these areas with high catch densities need to be profiled in terms of oceanography. This can be done by for instance installing a CTD instrument.

Finally, management measures may be assessed using spatial information, such as in marine spatial planning (MSP). The identified consecutive fishing grounds and areas with high and low fish density in this study are important results to the monkfish fishery and should be considered when making fisheries area management decisions e.g., MSP. The results of this study also highlight the importance of analysing spatial catch trends, and the need for fisheries managers to consider variations in spatial data when formulating and implementing management measures. Interesting to note here is the fact that specific monkfish fishing grounds are currently heavily fished (consecutive fishing hotspots) than other areas (no pattern detected), yet these areas remain the most productive areas yielding the highest catches. There are numerous management measures already in place, however, the stock continues to decline, and for this reason, the Namibia monkfish management team could consider such measures as closed areas and seasons making use of the data from this study and investigating the monitoring measures that would be required such as the VMS currently in place.

Chapter 7: General discussion and conclusion

7.1 Ecology of Cape monkfish

Improved management measures of the Namibian Cape monkfish, *Lophius vomerinus* fishery resource rely on accurate data contributing to the understanding of its status. The Cape monkfish is one of two monkfish species that occur off the Namibian coast: the other being the shortspine African Angler, *L. vaillanti* (Chapter 1). The Cape monkfish is the most abundant monkfish species in Namibia (Maartens & Booth, 2001a, b; Fariña et al., 2008), and is the focus species for this study (Chapter 1). Leslie and Grant (1990) indicated that this species is distributed from northern Namibia (21°S) to Durban, South Africa (30°S, 31°E). Cape monkfish is slow-growing and lives more than 10 years (Maartens et al., 1999; Walmsley et al., 2005; Fariña et al., 2008). A historical study found the oldest individuals to be 11 years old, with females growing larger than males, but males mature at a smaller size than females (Maartens & Booth, 2005). No veil (that host spawned eggs) had been observed off Namibia before the present study. Spawning takes place throughout the year but peaks between July and September (Maartens & Booth, 2005). Similarly, no spawning grounds had been identified previously but the nursery areas were documented off Walvis Bay (23º – 25ºS) and near the Orange River (28º 35'S) (ICSEAF, 1984).

7.2 Changes recorded between historical studies and contemporary studies

As mentioned previously, the life-history parameters of fish may vary, spatially and temporally (Pankhurst & Munday, 2011; Falkenhaug & Dalpadado, 2014) as a result of stress on their populations (Pankhurst & Munday, 2011). Monitoring changes in the life history of species can provide indications of the responses of populations to external factors such as fishing pressure and climate change which can inform management decisions (Trippel, 1995; Pankhurst & Munday, 2011). Climate change coupled with extensive fishing pressure has been linked to a "regime shift' in the BCLME, especially in the nBE (Moloney, 2010; Heymans & Tomczak, 2016). Uncoupling the effects of climate change from overfishing is challenging because, in most circumstances, the impacts of extensive exploitation pressure are exacerbated by the complexities of climate change. Multiple authors (Gammelsrød et al., 1998; Bartholomae & van der Plas, 2007; Monteiro et al., 2008) have documented environmental changes in the Benguela system, and in Namibia in particular. Variations in environmental parameters have been significantly noted including oxygen concentration (Bartholomae & van der Plas, 2007), sea surface temperature (Junker et al., 2017) and wind strength (Monteiro et al., 2008). Frequent low oxygen events in the Namibian marine waters limit fish distribution (Boyd et al., 1987; van der Lingen et al., 2006; Bartholomae & van der Plas, 2007; Hutchings et al., 2009). The Namibian waters, especially in the north, have experienced recurring large-scale extreme warming of the ocean waters (*Benguela Niño* events) (Shillington et al., 2006), which result in catastrophic effects such as the change in the abundance of fishes (Boyer et al., 2001) and fish mortality (Gammelsrød et al., 1998). These changes in environmental variables are not uniform either spatially or temporally. For this reason, changes must be monitored in this region on both spatial and temporal scales.

For the present study, biological aspects of Cape monkfish between historical and contemporary data were compared to look for changes and relate these to possible climate change impacts and exploitation pressure directed at this resource. Data were sourced from various databases including port sampling and observer data (Chapter 2). When the biological results of this study were compared to the historical information, some significant changes between the current study (Period 2) and the past studies (Period 1) in Chapter 3, 4 and 5 were found. Results from Chapter 3 showed that the feeding habits differed significantly between Period 2 (current study) and Period 1 (Gordoa & Macpherson, 1990), using the same study site and same data analysis methods. The changes, especially in the temporal diet composition, appear to be largely due to the types of prey species available. During the monkfish trawl swept area research biomass surveys, there was variation in the species composition over time suggesting that the benthic fauna is diverse in places and this matches with the stomach content diversity from this study. Previous studies (Roux 1998; Boyer et al., 2001) have documented a decline in small pelagic fish especially the Southern African sardine (pilchard), which is food for top predators such as Cape monkfish. At the same time, the nBE (from the Angola front to the Lüderitz upwelling cell) is reported to be experiencing a regime shift with an increase in the abundance of jellyfish and pelagic goby (Roux et al., 2013). Chapter 3 highlighted the particular importance of the deep-water hake *M. paradoxus* in the diet, across all size classes. The study provided evidence that although the composition, abundance, and distribution of some prey species in this region have changed, Cape monkfish was able to switch prey species and exhibit wide trophic adaptability (Chapter 3). This adaptation, however, might not be enough as total catches continue to decline (Chapter 6), and the possibility exists that negative impacts of overfishing on their dominant prey (hake spp) may be contributing to this reduction. This study suggests that the diet of Cape monkfish may be used as an indicator of available forage fish both spatially and temporally, and the changes in the types, abundance, and distribution of these prey species are suggested to be partly ascribed to fishing pressure, along with possible climate change effects.

Cape monkfish have previously been documented to spawn throughout the year and along the entire coast (Maartens & Booth, 2005). Key consecutive spawning hotspots identified from this study were between 22° and 25°S, spawning mainly in deep waters (Chapter 4). Interestingly fishing hotspots were found around 25°S and 26°S (Chapter 6, Figure 6.3) and the highest catches were taken from around 24° S, and between 26° and 27°S (Chapter 6, Figure 6.4). This overlap has some management implications as besides overfishing, fishing spawning aggregations can lead to size-selective fishing (de Mitcheson, 2016), removing fecund adults. Although this species spawns throughout the coast, the consecutive hotspots between 22° and 26°S (Chapter 4) suggest that the resource might benefit from some spatial management, for example closing some areas (e.g., between 22° and 26°S) between July and September, the peak spawning season.

Nursery areas identified previously were off Walvis Bay (23°–25°S) at depths between 150 and 300 m and near the Orange River 28°35’S at depths between 100 and 300 m (ICSEAF, 1984). Interestingly, this study noted the absence of 0-year-old fish in the area around 28° S, in contrast to the ICSEAF data of 1984. The area around 28°S is close to extensive mining activities (Kampf, 2007; Schneider, 2020) as discussed in Chapter 5, which may be detrimental. Because of a dearth of historical data on fecundity, no historical comparison could be made to the contemporary findings. A continuous monitoring study on maturation dynamics and reproduction strategies of this species should be maintained to make temporal comparisons in the future.

Although monkfish catches are declining (Chapter 6), the results of the age and growth analysis between the historic and present study did not show major differences, with similar growth curves (Chapter 5), suggesting some resilience to both overfishing and climate change. Interestingly, 2-year-old fish (20.33%) were dominant in the historic study, while 5-year-olds (18.3%) were prominent here. Additionally, the current study aged the oldest individual as 16 years old, while the historical study did not find fish older than 11 years. This counterintuitive result is difficult to explain but may be due to the more extensive sampling in this study, possibly coupled with better age reading experience.

It is noteworthy that there is an underutilisation of the monkfish TAC in most years. The question of whether the TAC might be set too high, in part perhaps due to pressure from stakeholders, needs to be discussed and investigated further. Although this study found fishing to occur in larger area than historically, there was no evidence that the fishery is moving deeper. Also increasing numbers of monkfish have been reported in the hake directed fishery, perhaps indicating some illegal targeting of monkfish, and flouting the current bycatch regulations. This would add pressure to the resource.

Bottom water temperatures analysed in Chapter 6 were variable between 1998 and 2018, possibly influencing the distribution and abundance of monkfish. The trend shows warmer years (2003, 2006 to 2009) and colder years (e.g., 2004). These are average bottom water temperature, but it should be noted that environmental variables, such as temperature and oxygen content, vary both with depth and in particular with latitude. Although this study did not establish the optimum temperature for monkfish, it is evident from environmental data collected during the monkfish survey, that monkfish were abundant in bottom water temperature of 8.73 ºC (MFMR. 2019). However, for this study, no trend and no statistical relationship could be established between bottom temperature and catch size and between sea surface temperature and catch size. The system's dynamism made the correlation between bottom temperature and catches difficult, for two reasons. Firstly, the temperature is ever-changing in different areas where the catches were recorded, and second, the bottom temperature data were limited and were not recorded for the entire Namibian coast.

7.3 Current management measures for the Namibia monkfish

In Namibia, stock assessments are the basis for advice to the fisheries managers. Mathematical models and data from surveys and commercial fisheries are used to conduct the assessment. Hence, there is a high reliance on statistical analysis, when providing management advice. Currently, *L. vomerinus* stock is assessed annually using an Age-Structured Production Model (ASPM, Rademeyer and Nishida, 2011). Input data to the model are stock and catch weight-at-age, maturity-at-age, natural mortality, survey biomass index, commercial catch rates, survey catch-at-age and commercial-catch-at-age (see Chapter 2). The CPUE (as an index of relative abundance) is calculated and standardised using a GLM. The MWG (described in Chapter 1, section 1.6), considers various data including catch and effort, data on length at age, mean length and length at maturity. When the data are scrutinised and the MWG members are satisfied, the ASPM is executed annually, and the model produces TAC for that assessment year and a number of management quantities. The management quantities are often used as reference points. Thereafter, The MFMR scientists then present the TAC recommendations to the Marine Resource Advisory Council (MRAC). MRAC consists of members from the fishing industry, banking sector, labour union, legal fraternity, and fishery experts. MRAC considers the scientific advice and draft recommendations to the Minister of Fisheries and Marine Resources. The minister then presents these recommendations to the cabinet, and the cabinet decides on the TAC. The cabinet decision is passed on to the Attorney-General.

Namibia has comprehensive management measures in place, including regular MWG meetings, setting of TACs, recording of fishery-depended data in logbooks and the use of VMS. Additionally, other management measures guiding the harvesting of monkfish include a minimum cod-end mesh-size of 75 or 110 mm, to allow juveniles to escape although this study showed that commercial fishing vessels (through port sampling data) were able to retain some unquantified immature monkfish, indicating that the 75 mm net mesh-size for Cape monkfish might need to be re-evaluated. Fishing vessels in Namibia are fitted with a compulsory VMS, to provide information on vessel position and movement to the fisheries management agency (Paterson, 2015), however, the extent to which this is monitored and the use of information for management requires attention.

Several barriers to management were identified which appear to be hindering the successful management of this fishery. Compulsory logbooks, which must be completed daily at the end of every fishing day, were found to be sometimes incomplete e.g., the bottom water temperature was only recorded at some fishing stations between 1998 and 2018 (see Chapter 6). Apart from annual survey data collected by MFMR, the other data are collected by the fisheries observers operating under the Fisheries Observer Agency (FOA). The FOA, established in May 2002 under Section 8 of the Marine Resource Act, Act No. 27 of 2000 (as described in Chapter 1) plays a key role in the collection of biological data, but verification of information recorded on an ongoing basis is essential.

There is no annual closed season for monkfish, thus, the introduction of a closed season during the peak spawning period, identified here as July to September, maybe beneficial and should be further discussed. The inclusion of spatial closures to fishing into conservation and fisheries management strategies to protect marine organisms from human exploitation is on a rise globally (Botsford et al., 2009). Historical data show 0-year-old fish between 23ºS and 25ºS and off 28ºS, while the current study found 0-year-old fish only between 23ºS and 25ºS and not off 28ºS. Protection of key nursery areas should be contemplated as an additional management measure, given the decline in the commercial catches.

7.4 Caveats associated with the data used in this study

There were inconsistencies in the type of data collected during observer sampling and monkfish swept area biomass surveys. Some records had full biological data on length, sex, weight, and maturity stage, while some records were missing some of the biological data (see Chapter 4). For instance, for L_{50} estimation, the full biological data for all fish collected during the spawning months is required. However, the spawning months (February, July, August, and September) were only fully sampled in 2004, 2006, 2011, and 2015 – 2018. As a result, conclusions could not be made on size at maturity for some years e.g., before 2004 and the years between 2011 and 2015. The port sampling programme MFMR, through the sampling of commercial landings in Walvis Bay, provided the most reliable data, and it is important that this should be continued to build a long-term time series. Studies on monkfish (Erasmus et al., 2018; Erasmus et al., 2019) have been carried out using this port sampling data. As mentioned, the logbooks completed by the fishing vessel captains do not always contain required fishery-dependent data, and intervention is required to ensure that these mandatory data are recorded.

7.5 Future work

This study provides a first cursory examination of spatial information but highlights areas for future work. Investigation of the impacts of climate change on fish populations is complex because climate change affects a multitude of environmental factors that may affect various processes at different levels of biological organisation (Rijnsdorp et al., 2009). In this study, no evidence of the direct impacts of climate change on the biological aspects of Cape monkfish was found, and possibly the habitat is more stable and less vulnerable to climate change as opposed to shallow and mid-waters. The fact that Cape monkfish were able to shift their diet and exhibit wide trophic adaptability might indicate an adaptation to change. Interestingly the bottom temperature at considerable depth was found to vary, and a dedicated study looking at the changes in bottom temperature over time may provide some information on possible change, and future implications for benthic fauna. Experiments on the physiology of key benthic species would be of interest. Sundby et al. (2001) carried out an experiment on the buoyancy of eggs and larvae and larval behaviour of *M. capensis*. Additionally, because in Chapter 5 there is evidence of offshore movement with an increase in the fish size, studies on the effects of environmental variables on growth should be carried out at different life-history stages of marine fishes that undergo ontogenetic habitat shifts.

Although the focus of this study was on juvenile, sub-adult, and adults Cape monkfish, not much is known about the eggs and larvae stage of this species in the Namibian waters. Moreover, physio-chemical characteristics of the nursery area and if/how these have changed over time would be interesting.

Further capacity building of the observers currently deployed is encouraged. Personal communication with observers revealed that some observers (with limited qualifications, often less than grade 12 certificate) have no scientific interest in the data they collect, so they might not endeavour to collect error-free data. To redress the imbalances caused by the apartheid regime, the authorities recruited from within the ranks of previously disadvantaged communities whether or not they had the required qualifications (Stanley Ndara – CEO at FOA; pers. comm.). Other observers e.g., at the Falkland Islands have advanced qualifications; they are qualified biologists/zoologists or related fields (Honours and masters degrees). They process data, analyses and write reports (CPUEs, length frequencies, maturities, birds and sea mammals interactions with the fishing and vessels compliance) after each deployment, thus they know the importance of quality data. They are part of the research team and they are involved in other scientific projects for publications (which mostly comes from observers' data). They also collect other data when required, such as feeding and histology data (Vasana Tutjavi – observer at the Falkland Islands; pers. comm.). Together with the landing data; the scientific observers collect biological data (otoliths fused in age determination, sex and maturity and lengths) from all the commercial species, which are used in the assessment models. The scientific observers in the Falklands are part of the Research team, thus they take part in research cruises, data analyses and report writing. They also take part in scientific meetings (if they are on land), which discusses research findings and management measures. Locally (in Namibia) there is generally a poor involvement of the observers in discussions on data and TAC recommendations (pers. obs.). If observers get more involved, they are likely to become more interested and simultaneously improve the quality of data that they collect. These issues are not unique to Namibia; Wang and DiCosimo, (2019) reported concerns regarding data quality, training costs, shortage of available observers, and safety and harassment of observers in the National Oceanic and Atmospheric Administration (NOAA) Fisheries which may potentially compromise the quality of data. To address this issue, as an area of high priority, the current observers need to be refreshed and trained. Hiring criteria for observers also need to be revised so that well qualified observers can be hired to collect accurate and reliable data. The observer training aspect has been previously highlighted more than a decade ago (Oelofsen, 1999).

7.6 Conclusion and management recommendations

The following is recommended:

- This study indicates that most female fish landed are below L_{50}. The small fish are part of the non-fishable biomass, which end up in the catch as evidenced from the observer data. They are mostly reported, except when they are not sampled. They are quantified by raising the sampled data to the total catch, which indicate the quantities of under-size being landed. Landing of under-size is a concern to stock assessment because that amount to recruitment overfishing something that should be avoided. This calls for a change in regulation e.g., increase in minimum mesh size, close area, close seasons. Changes to those regulations could address the concern of landing under-size fish. A revision of the mesh size from 75 or 110 mm to at least 140 mm to allow fish smaller than 48 cm (TL) to escape is therefore recommended. This would limit catches of fish at the L_{50} or slightly above (48 cm TL) so that the fish have a chance to mature and spawn before capture.

- The current monkfish stock assessment does not fully incorporate spatial data. It is therefore recommended to incorporate more spatial catch data in stock assessment. Spawning and nursery areas should be considered in management discussions, with considerations for possible closed areas and/or seasons.
- The current education level for observers limits the quality of data collected. Requirements for observers to be recruited should be revised to discourage candidates without first degrees in science from applying. Additionally, current observers should be mentored, and additional training incorporated.

We live in a changing environment, and the management of fisheries becomes ever more complex. The first look at the spatial complexity of the monkfish resource underlines the challenges faced but highlights some of the research and management directions to follow in the future.

References

Able, K., W., Clarke, P. J. P. J., Chambers, R. C. & Witting, D. A. 2007. Transitions in the morphological features, habitat use, and diet of young-of-the-year goosefish (*Lophius americanus*). *Fish Bulletin*. 105, 457–469.

Adams, C. F. 2017. Age-specific differences in the seasonal spatial distribution of butterfish (*Peprilus triacanthus*). *ICES Journal of Marine Science.* 74, 170–179.

Afonso-Dias, I. P. & Hislop, J. R. G. 1996. The reproduction of anglerfish *Lophius piscatorius* Linnaeus from the north-west coast of Scotland. *Journal of Fish Biology*. 49, 18–39.

Albaret, J. J. & Laë, R. 2003. Impact of fishing on fish assemblages in tropical lagoons: the example of the Ebrie lagoon, West Africa. *Aquatic Living Resources.* 16, 1–9.

Andersen, N. G. 2012. Influences of potential predictor variables on gastric evacuation in Atlantic cod *Gadus morhua* feeding on fish prey: Parameterization of a generic model. *Journal of Fish Biology.* 80, 595–612.

Armstrong, M. P., Musick, J. A. & Colvocoresses, J. A. 1996. Food and ontogenetic shifts in feeding of the goosefish, *Lophius americanus*. J*ournal of Northwest Atlantic Fishery Science*. 18, 99–103.

Arrhenius, F. 1996. Diet composition and food selectivity of 0-group herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus (L.)*) in the northern Baltic Sea. *ICES Journal of Marine Science*. 53, 701–712.

Austin, B. & Austin, D. A. 1989 Methods for the microbiological examination of fish and shellfish. Chichester: Ellis Horwood.

Bacha, M. & Amara, R. 2009. Spatial, temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). *Estuarine, Coastal and Shelf Science*. 85, 257–264.

Bartholomae, C. H. & van der Plas, A. K. 2007. Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. *African Journal of Marine Science*. 29, 25–35.

Başusta, A., Başusta, N. & Ozer, E. I. 2013. Length-weight relationship of two puffer fishes, *Lagocephalus sceleratus* and *Lagocephalus spadiceus*, from Iskenderun Bay, northeastern Mediterranean, Turkey. *Pakistan Journal Zoology*. 45, 1047–1051.

Beckman, D. & Wilson, C. A. 1995. Seasonal timing of opaque zone formation in fish otoliths. In: Secor DH, Dean JM, Campana SE (eds) Recent developments in fish otolith research. University of South Carolina Press, Columbia, SC, p 27−43.

Belhabib, D., Mendy, A., Subah, Y., Broh, N. T., Jueseah, A. S., Nipey, N., Boeh, W. W., Willemse, N., Zeller, D. & Pauly, D. 2016. Fisheries catch under-reporting in The Gambia, Liberia and Namibia and the three large marine ecosystems which they represent. *Environmental Development*. 17, 157-174.

Ben-Hasan, A., Walters, C., Christensen, V., van Poorten, B., Rajab, S., Al-Husaini, M. & Al-Foudari, H. 2018. Predicting changes in mean length with an age-structured stock assessment model. *Natural Resource Modeling*. 32, e12218.

Berlinsky, D. L., Fabrizio, M. C., O'Brien, J. F. & Specker, J. L. 1995. Age at maturity estimates for Atlantic coast female striped bass. *Transactions of the American Fisheries Society.* 124, 207–215.

Beverton, R. J. H. & Holt. S. J. 1957. On the dynamics of exploited fish populations. Fisheries Investigations Series II, volume 19. Ministry of Agriculture, Fisheries, and Food, Her Majesty's Stationery Office, London.

Bianchi, G., Carpenter, K. E., Roux, J.-P., Molloy, F. J., Boyer, D. & Boyer, H. J. (Eds) 1999. Food and Agricultural Organisation (FAO). FAO species identification guide for fishery purposes. A field guide to the living marine resources of Namibia. The living marine resources of the Western Central Pacific. Food and Agricultural Organisation of the United Nations. Rome, Italy.

Black, B. A., Boehlert, G. W. & Yoklavich, M. M. 2005. Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. *Canadian Journal of Fisheries and Aquatic Sciences.* 2284, 2277–2284.

Black, B. A., von Biela, V. R., Zimmerman, C. E. & Brown, R. J. 2012. Lake trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. *Polar Biology.* 36, 147–153.

Blamey, L. K., Shannon, L. J., Bolton, J. J, Crawford, R. J. M., Dufois, F., Evers-King, H., Griffiths, C. L., Hutchings, L., Jarre, A., Rouault, M., Watermeyer, K. E. & Winker, H. 2015. Ecosystem change in the southern Benguela and the underlying processes. *Journal of Marine Systems*. 144, 9–29.

Bode, M., Kreiner, A., van der Plas, A. K., Louw, D. C., Horaeb, R., Auel, H. & Hagen, W. 2014. Spatio-temporal variability of copepod abundance along the 20°S monitoring transect in the northern Benguela upwelling system from 2005 to 2011. *PLoS One.* 9, e97738.

Booth, A. J. 2000. Incorporating the spatial component of fisheries data into stock assessment models. *ICES Journal of Marine Science*. 57, 858–865.

Booth, A. J. & Quinn, T. J. 2006. Maximum likelihood and Bayesian approaches to stock assessment when data are questionable. *Fisheries Research*. 80, 169–181.

Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B., Largier, J., O'Farrell, M. R., Ralston, S., Soulanille, E. & Wespestad, V. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*. 19, 69–95.

Boveng, P. L., Ziel, H. L., McClintock, B. T. & Cameron, M. F. 2020. Body condition of phocid seals during a period of rapid environmental change in the Bering Sea and Aleutian Islands, Alaska. *Deep-Sea Research II.* 181–182.

Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J-P, Havenhand, J., Hutchins, D. A., Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., et al. 2018. Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change - a review. *Global Change Biology*. 24, 2239–2261.

Boyd, A., Salat, J. & Masó, M. 1987. The seasonal intrusion of relatively saline water on the shelf off northern and central Namibia. *South African Journal of Marine Science*. 5, 107–120.

Boyer, D. C., Boyer, H. J., Fossen, I. & Kreiner, A. 2001. Changes in Abundance of the Northern Benguela Sardine Stock During the Decade 1990–2000, with Comments on the Relative Importance of Fishing and the Environment. *South African Journal of Marine Science*. 23, 67–84.

Boyer, D. C. & Hampton, I. 2001. An overview of the living marine resources of Namibia. In: Payne, A. I. L., Pillar, S., C. & Crawford, R. J. M. (eds), A decade of Namibian fisheries science. *South African Journal of Marine Science.* 23, 5–35.

Brander, K. M. 1994. The location and timing of cod spawning around the British Isles. *ICES Journal of Marine Science.* 51, 71–89.

Burmeister, L. M. 2001. Depth-stratified density estimates and distribution of the Cape hake *Merluccius capensis* and *M. paradoxus* off Namibia deduced from survey data, 1990–1999. *South African Journal of Marine Science*. 23, 347–356.

Butler, E. C., Childs, A., Winkler, A. C., Milner, M. V. & Potts, W. M. 2018. Evidence for protandry in *Polydactylus quadrifilis* in the Kwanza Estuary, Angola, and its implications for local fisheries. *Environmental Biology of Fishes.* 101, 301–313.

Butterworth, D. S. & Geromont, H. F. 2001. Evaluation of a range of possible simple interim management procedures for the Namibian hake fishery. *South African Journal of Marine Science*. 23, 357–374.

Buxton, C. D. 1993. Life history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes.* 36, 47–63.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. 59, 197–242.

Carrasco, N. K., Perissinotto, R. & Nel, H. A. 2012. Diet of selected fish species in the freshwater-deprived St Lucia Estuary, South Africa, assessed using stable isotopes. *Marine Biology Research.* 8, 701–714.

Casini, M., Cardinale, M. & Arrhenius, F. 2004. Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES Journal of Marine Science.* 61, 1267–1277.

Chen, Z., Yan, X-H., Jo, Y-H., Jiang, L. & Jiang, Y. 2012. A study of Benguela upwelling system using different upwelling indices derived from remotely sensed data. *Continental Shelf Research.* 45, 27–33.

Chiripanhura, B. & Teweldemedhin, M. 2016. AGRODEP Working Paper 0021. *An Analysis of the Fishing Industry in Namibia : The Structure, Performance, Challenges, and Prospects for Growth and Diversification.*

Cisneros-Mata, M. A., Mangin, T., Bone, J., Rodriguez, L., Smith, S. L. & Gaines, S. D. 2019. Fisheries governance in the face of climate change: Assessment of policy reform implications for Mexican fisheries. *PLoS ONE*. 14, e0222317.

Colmenero, A. I., Tuset, V. M., Recasens, L. & Sánchez, P. 2013. Reproductive biology of Black Anglerfish (*Lophius budegassa*) in the northwestern Mediterranean Sea. *Fishery Bulletin*. 111, 390–401.

Colmenero, A. I., Tuset, V. & Sánchez, P. 2017. Reproductive strategy of white anglerfish (*Lophius piscatorius*) in Mediterranean waters: implications for management. *Fishery Bulletin.* 60–73.

Crawford, R. J. M. 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. *South African Journal of Marine Science.* 5, 735–757.

Crawford, R. J. M., Underhill, L. J., Raubenheimer, C. M., Dyer, B. M. & Martin, J. 1992. Top predators in the Benguela ecosystem – implications of their trophic position. *South African Journal of Marine Science*. 12, 675–687.

Crozier, W. W. 1985. Observations on the Food and Feeding of the Angler-Fish, *Lophius piscatorius L*, in the Northern Irish Sea. *Journal of Fish Biology*. 27, 655–665.

Cruickshank, R. A., Cooper, J. & Hampton, I. 1980. Extension to the geographical distribution of pelagic goby *Sufflogobius bibabartus* off South West Africa and some mensural and energetic information. *Fisheries Bulletin*. 13, 77–82.

Cury, P. M. & Shannon, L. J. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Progr. Oceanogr. 60, 223–243.

Da Rocha, N., Oppel, S., Prince, S., Matjila, S., Shaanika, T. M., Naomab, C., Yates, O, Paterson, J. R., B., Shimooshili, K., Frans, E., Kashava, S. & Crawford, R. 2021. Reduction in seabird mortality in Namibian fisheries following the introduction of bycatch regulation. *Biological Conservation*. 253, 108915.

Daskalov, G. M., Boyer, D. C. & Roux, J-P. 2003. Relating sardine *Sardinops sagax* abundance to environmental indices in northern Benguela. *Progress in Oceanography*. 59, 257–274.

del Valle, I. & Astorkiza, K. 2007. Institutional designs to face the dark side of total allowable catches. *ICES Journal of Marine Science.* 64, 851–857.

De Mitcheson, Y. S. 2016. Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach. *Bioscience*. 66, 295–306.

Dooley, J., Matsuura, K., Collette, B., Nelson, J., Fritzsche, R. & Carpenter, K. 2010. *Lophius vomerinus* (errata version published in 2017). *The IUCN Red List of Threatened Species 2010*: e.T154748A115229991. https://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T154748A4624479.en. Downloaded on 28 September 2020.

Downing, J. A. 1986. Spatial heterogeneity: evolved behaviour or mathematical artefact? *Nature.* 323, 255–257.

Duarte, R., Azevedo, M., Landa, J. & Pereda, P. 2001. Reproduction of angler sh (*Lophius budegassa* Spinola, 1807 and *L. piscatorius* Linnaeus, 1758) from the Atlantic Iberian coast. *Fisheries Research*. 51, 349–361.

Dunlop, K., Eloranta, A. P., Schoen, E., Wipfli, M., Jensen, J. L. A., Muladal, R. & Christensen, G. N. 2020. Evidence of energy and nutrient transfer from invasive pink salmon (*Oncorhynchus gorbuscha*) spawners to juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in northern Norway. *Ecology of Freshwater Fish*. 30, 270–283.

du Pontavice, H., Gascuel, D., Reygondeau, G., Stock, C. & Cheung, W. W. L. 2021. Climate-induced decrease in biomass flow in marine food webs may severely affect predators and ecosystem production. *Global Change Biology.* 27, 2608-2622.

Dulvy, N. K., Sadovy, Y. & Reynolds, J. D. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries*. 4, 25–64

Dutta, S., Maity, S., Bhattacharyya, S. B., Sundaray, J. K. & Hazra, S. 2013. Diet Composition and Intensity of Feeding of *Tenualosa ilisha* (Hamilton, 1822) Occurring in the Northern

Bay of Bengal, India. *Proceedings of the Zoological Society*.

Emmanuel, O. L. & Ajibola, E. T. 2010. Food and feeding habits and reproduction in Frillfin goby, *Bathygobius soporator* (Cuvier and Valenciennes, 1837) in the Badagry Creek, Lagos, Nigeria. *International Journal of Biodiversity and Conservation*. 2, 414–421.

Erasmus, V. N., Hamutenya, S., Iitembu, J. A. & Gamatham, J. C. 2018. Mercury concentrations in muscles and liver tissues of Cape monkfish (*Lophius vomerinus*) from the Northern Benguela, Namibia. *Marine Pollution Bulletin*. 135, 1101–1106.

Erasmus, V. N. & Iitembu, J. A. 2019. Characterising the trophic relationships between cuttlefishes, myctophids and round herring in the northern Benguela. *Welwitschia International Journal of Agricultural Sciences.* 1, 59–67.

Erasmus, V. N, Iitembu, J. A, Hamutenya, S. & Gamatham, J. C. 2019. Evidence of possible influences of methylmercury concentration on condition factor and maturation of Cape monkfish (*Lophius vomerinus*). *Marine Pollution Bulletin*. 146, 33–38.

Erasmus, V. N., Currie, G., Roux, J-P., Elwen, S. H., Kalola, M. S., Tjizoo, B., Kathena, J. N., Iitembu, J. A. 2021a. Predatory species left stranded following the collapse of the sardine *Sardinops sagax* (Pappe, 1854) stock off the northern Benguela upwelling system: A review. *Journal of Marine System*. 224, 103623.

Erasmus, V. N., Kadhila, T., Gabriel, N. N., Thyberg, K. L., Ilungu, S. & Machado, T. 2021b. Assessment and quantification of Namibian seafood waste production. *Ocean and Coastal Management*. 199. 105402.

Eschmeyer's Catalog of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp) for the current names of fishesband to WoRMs for other marine organisms

ESRI, 2021. How emerging hotspot analysis works. http://desktop.arcgis.com/en/arcmap/10.5/tools/space--time-pattern-mining-toolbox/learnmoreemerging.htm. (Accessed 22 March 2021).

Everett, I., Fennessy, S. T. & van den Heever, N. 2021. Using hotspot analysis to track changes in the crustacean fishery off KwaZulu-Natal, South Africa. *Regional Studies in Marine Science*. 41, 01553.

Fablet, R., Pewcquerie, L., de Pontual, H., Høie, H., Millner, R., Mosegaard, H. & Kooijman, S.A.L.M. 2011. Shedding light on fish otolith biomineralization using a bioenergetic approach. PLOS ONE 6: e27055

Falkenhaug, T. & Dalpadado, P. 2014. Diet composition and food selectivity of sprat(*Sprattus sprattus)* in Hardangerfjord, Norway. *Marine Biology Research*. 10, 203–215.

Fariña, A. C., Azevedo, M., Landa, J., Duarte, R., Sampedro, P., Costas, G., Torres, M. A. & Cañás, L. 2008. *Lophius* in the world: A synthesis on the common features and life strategies. *ICES Journal of Marine Science.* 65, 1272–1280.

Filiz, H. 2009. Diet composition of smooth-hound, *Mustelus mustelus* (Linnaeus, 1758), in Aegean Sea, Turkey. *Belgian Journal of Zoology*. 139, 81–84.

Florenchie, P., Lutjeharms, J. R. E., Reason, C. J. C., Masson, S. & Rouault, M. 2003. The source of *Benguela Niños* in the South Atlantic Ocean. *Geophysical Research Letters.* 30, 1505.

Food and Agricultural Organisation (FAO). 1999. The Dr Fridtjof Nansen Programme 1975–1993. *Investigations of fishery resources in developing countries. History of the programme and review of results. Fao Fish. Tech. Pap. 391 434*. Rome, Italy: FAO.

Food and Agricultural Organisation (FAO). 2016. The State of World Fisheries and Aquaculture 2016. Contributing to Food Security and Nutrition for All. Food and Agricultural Organisation of the United Nations. Rome, Italy: FAO.

Fossen, I. & Bergstad, O. A. 2006. Distribution and biology of blue hake *Antimora rostrata* (Pisces: Moridae), along the mid-Atlantic Ridge and off Greenland. *Fisheries Research*. 82, 19–29.

Franco, A., Malavasi, S., Pranovi F., Franzoi, P. & Torricell, P. 2012. Age and reproductive investment in grass goby females in the Venice lagoon. *Environmental Biology of Fishes*. 93, 419–425.

Freitas, M. O., Previero, M., Leite, J. R., Francini-Filho, R. B., Minte-Vera, C. V. & Moura, R. L. 2019. Age, growth, reproduction and management of Southwestern Atlantic's largest and endangered herbivorous reef fish, *Scarus trispinosus* Valenciennes, 1840. *PeerJ.* 7, e7459.

Frid, C., Paramor, O. & Scott, C. 2005. Ecosystem-based fisheries management: Progress in the NE Atlantic. *Marine Policy.* 29, 461–469.

Fr¨olicher, T. L., Fischer, E. M. & Gruber, N. 2018. Marine heatwaves under global warming. *Nature*. 560, 360–364.

Fu, C., Xu, Y., Gru¨ss, A., Bundy, A., Shannon, L., Heymans, J. J., Halouani, G., Akoglu, E., Lynam, C. P., Coll, M., Fulton, E. A., Velez, L. & Shin, Y.-J. 2019. Responses of ecological indicators to fishing pressure under environmental change: exploring non-linearity and thresholds. *ICES Journal of Marine Science*. 77, 1516–1531.

Gabriel, O., Lange, K., Dahm, E. & Wendt, T. 2005. Von Brandt's Fish Catching Methods of the World. (4th ed). (Eds.) Gabriel, O., Lange, K., Dahm, E., Wendt, T. Wiley-

Blackwell, Oxford.

Gammelsrød, T., Bartholomae, C. H., Boyer, D. C., Filipe, V. L. L. & O'Toole, M. J. 1998. Intrusion of warm surface water along the Angolan-Namibian coast in February–March 1995: the 1995 Benguela Niño. In: Pillar S. C., Moloney, C. L., Payne, A. I. L, Shillington F. A. (eds) Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources. *South African Journal of Marine Science*. 19, 41–56.

Garrod, D. J. & Shumacher, A. 1994. North Atlantic cod: a broad canvas. *ICES Marine Science Symposia*. 198, 59–76.

Geffroy, B. & Wedekind, C. 2020. Effects of global warming on sex ratios in fishes. *Journal of Fish Biology*. 1–11.

Gell, F. R. & Roberts, C. M. 2003. Benefits beyond boundaries: The fishery effects of marine reserves. *Trends in Ecology and Evolution*. 18, 448–455.

Geronimo, R. C., Franklin, E. C., Brainard, R. E., Elvidge, C. D., Santos, M. D., Venegas, R. & Mora, C. 2018. Mapping Fishing Activities and Suitable Fishing Grounds Using Nighttime Satellite Images and Maximum Entropy Modelling. *Remote Sensing*. 10, 1604.

Ghaffari, H., Ardalan, A. A., Sahafi, H. H., Babaei, M. M. & Abdollahi, R. 2011. Annual Changes in Gonadosomatic Index (GSI), Hepatosomatic Index (HSI) and Condition Factor (K) of Largescale Tonguesole *Cynoglossus arel* (Bloch & Schneider, 1801) In The Coastal Waters of Bandar Abbas, Persian Gulf. *Journal of Applied Sciences Research*. 5, 1640–1646.

Gibbons, M. J. & Buecher, E. 2001. Short-term variability in the assemblage of medusae and ctenophores following upwelling events in the southern Benguela ecosystem. *Marine Ecology Progress Series*. 220, 169–177.

Gíslason, D., Helyar, S. J., Óskarsson, G. J., Ólafsdóttir, G., Slotte, A., Jansen, T., Jacobsen, J. A., Ólafsson, K., Skirnisdottir, S., Dahle, G., Siegstad, H., Joensen, H., Curti, K. L., Grégoire, F., Masse, J., Sveinsson, S., Daníelsdóttir, A. K. & Pampoulie, C. 2020. The genetic composition of feeding aggregations of the Atlantic mackerel (*Scomber scombrus*) in the central North Atlantic: A microsatellite loci approach. *ICES Jurnal Marine Science*. 77, 604–612.

Goethel, D. L., Quinn II, T. J. & Cadrin, S. X. 2011. Incorporating Spatial Structure in Stock Assessment: Movement Modeling in Marine Fish Population Dynamics. *Reviews in Fisheries Science*. 19, 119–136.

Gopalakrishnan, S., Cheung, N. K., Yip, B. W. & Au, D. W. T. 2013. Medaka fish exhibits longevity gender gap, a natural drop in estrogen and telomere shortening during aging: a unique model for studying sex-dependent longevity. *Frontiers in Zoology*. 10, 78.

Gordoa, A. & Macpherson, E. 1990. Food selection by a sit-and-wait predator, the monkfish, *Lophius upsicephalus*, off Namibia (South West Africa). *Environmental Biology of Fishes*. 27, 71–76.

Gordoa, A., Macpherson, E. & Olivar, M. P. 1995. Biology and fisheries of Namibian hakes (*M. paradoxus* and *M. capensis*). In: Alheit J. & T. J. Pitcher (Eds.) *Hake: Biology, Fisheries and Markets*. London; Chapman & Hall. 49–88.

Grabowska, J. & Przybylski, M. 2015. Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. *Reviews in Fish Biology and Fisheries*. 25, 165–178.

Griffiths, M. H. & Hecht, T. 1986. A preliminary study of age and growth of monkfish Lophius upsicephalus (Pisces: Lophiidae) on the Agulhas Bank, South Africa. *South African Journal of Marine Science*. 4, 51–60.

Grémillet, D., Collet, J., Weimerskirch, H., Courbin, N., Ryan, P. G. & Pichegru, L. 2019. Radar detectors carried by Cape gannets reveal surprisingly few fishing vessel encounters. *PLoS ONE*. 14, e0210328.

Hamid, M. A., Mansor, M. & Siti-Azizah, M. N. 2015. Length-weight rela-tionship and condition factor of fish populations in Temengor reservoir: indication of environmental health. *Sains Malaysiana*. 44, 61–66.

Hampton, I. & Willemse, N. E. 2012. Potential effects of climate change and environmental variability on the resources of the Benguela Current Large Marine Ecosystem. In: Sherman, K., McCovern, G. (Eds.), *Frontline Observations on Climate Change and Sustainability of Large Marine Ecosystems*. Global Environment Facility, New York. 16–50.

Hamukuaya, H., O'Toole, M. J. & Woodhead, P. M. J. 1998. Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. In: Pillar SC, Moloney, C. L, Payne, A. I. L. & Shillington, F. A. (Eds.) Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources. *South African Journal of Marine Science*. 19, 57–61.

Herman, D. P., Burrows, D. G., Wade, P. R., Durban, J. W., Matkin, C. O., Leduc, R. G. & Krahn, M. M. 2005. Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies.

Marine Ecology Progress Series. 302, 275–291.

Heymans, J. J. & Tomczak, M. T. 2016. Regime shifts in the Northern Benguela ecosystem: Challenges for management. *Ecological Modelling*. 331, 151–159.

Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C. & Walters, C. J. 2017. When does fishing forage species affect their predators? *Fisheries Research*. 191, 211–221.

Hislop, J. R. G., Gallego, A., Heath, M. R., Kennedy, F. M., Reeves, S. A. & Wright, P. J. 2001. A synthesis of the early life history of the anglerfish, *Lophius piscatorius* (Linnaeus 1758) in northern British waters. *ICES Journal of Marine Science.* 58, 70–86.

Huenerlage, K. & Buchholz, F. 2013. Krill of the northern Benguela Current and the Angola-Benguela frontal zone compared : physiological performance and short-term starvation in Euphausia hanseni. *Journal of Plankton Research*. 35, 337–351.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M. S., Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R. G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J. C. & Monteiro, P. M. S. 2009. The Benguela Current: An ecosystem of four components. *Progress in Oceanography.* 83, 15–32.

Hutchings, L., Verheye H. M., Huggett J. A., Demarcq H., Cloete R. R., Barlow R.G., Louw D., da Silva A. J. 2006. Variability of plankton with reference to fish variability in the Benguela current large marine ecosystem – An overview. *Large Marine Ecosystems*. 14, 91–124.

International Commission for the Southeast Atlantic Fisheries (ICSEAF), 1982. Proc. Rep. Meet. int. Commn SE. Atl. Fish. (ICSEAF) 1982 (I), 1983, Madrid.

International Commission for the Southeast Atlantic Fisheries (ICSEAF), 1984. Proc. Rep. Meet. int. Commn SE. Atl. Fish. (ICSEAF) 1984 (II), 1985, Madrid.

Iitembu, J. A., Erasmus, V. N., Uanivi, U., Nangolo, E., Horaeb, R., Iita, T., Nashima, P, Nakwaya, D. & Mwandemele, O. 2021. The hits and misses of Namibia's attempt to implement the Ecosystem Approach to Fisheries (EAF) Management. *Ecosystem and Sustainability Journal*. 7, 1920340.

Iitembu, J. & Richoux, N. 2016. Characterisation of the dietary relationships of two sympatric hake species, *Merluccius capensis* and *M. paradoxus*, in the northern Benguela region using fatty acid profiles. *African Journal of Marine Science.* 38, 39–48.

Iitembu, J. A. & Richoux, N. B. 2015. Trophic relationships of hake (*Merluccius capensis* and

M. paradoxus) and sharks (*Centrophorus squamosus*, *Deania calcea* and *D. profundorum*) in the Northern (Namibia) Benguela Current region. *African Zoology.* 50, 273–279.

Iitembu, J. A., Todd, W., Ohmori, K. & Wells, S. 2012. Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. *Fisheries Oceanography.* 21, 215–225.

Jackson, A. T., Adite, A., Roach, K. A. & Winemiller, K. O. 2013. Primary production, food web structure, and fish yields in constructed and natural wetlands in the floodplain of an African river. *Canadian Journal of Fisheries and Aquatic Sciences*. 553, 543–553.

Jansen, T., Kainge, P., Singh, L., Wilhelm, M., Durholtz, D., Strømme, T., Kathena, J. & Erasmus, V. 2015. Spawning patterns of shallow-water hake (*Merluccius capensis*) and deep-water hake (*M. paradoxus*) in the Benguela Current Large Marine Ecosystem inferred from gonadosomatic indices. *Fisheries Research*. 172, 168–180.

Jarre, A., Hutchings, L., Crichton, M., Wieland, K., Lamont, T., Blamey, L. K., Illert, C., Hill, E. & van den Berg, M. 2015a. Oxygen-depleted bottom waters along the west coast of South Africa. *Fisheries Oceanography.* 24, 56–73.

Jarre, A., Hutchings, L., Kirkman, S. P., Kreiner, A., Tchipalanga, P. C. M., Kainge, P., Uanivi, U., van der Plas, A. K., Blamey, L. K., Coetzee, J. C., Lamont, T., Samaai, T., Verheye, H. M., Yemane, D. G., Axelsen, B. E., Ostrowski, M., Stenevik, E. K. & Loeng, H. 2015b. Synthesis: Climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fisheries Oceanography*. 24, 122–149.

Jarre, A., Ragaller, S. M. & Hutchings, L. 2013. Long-term, ecosystem-scale changes in the Southern Benguela marine pelagic social-ecological system: Interaction of natural and human drivers. *Ecology and Society*. 18, 917–180455.

Jennings, S. & Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology*. 34, 201–212.

Johnson, A., Richards, A., Cullen, D., Nguluwe, B. & Lang, K. 2007. Biology of large Monkfish, *Lophius americanus*. *ICES Journal of Marine Science*. 65, 1291–1305.

Johnson, A. K., Richards, R. A., Cullen, D. W. & Sutherland, S. J. 2008. Growth, reproduction, and feeding of large monkfish, *Lophius americanus*. *ICES Journal of Marine Science.* 65, 1306–1315.

Junker, T., Mohrholz, V., Siegfried, L. & van der Plas, A. 2017. Seasonal to interannual variability of water mass characteristics and currents on the Namibian shelf. *Journal of*

Marine Systems. 165, 36–46.

Kainge, P., van der Plas, A. K., Bartholomae, C. H. & Wieland, K. 2017. Effects of environmental variables on survey catch rates and distribution by size of shallow- and deep-water Cape hakes, *Merluccius capensis* and *Merluccius paradoxus* off Namibia. *Fisheries Oceanography*. 26, 680–692.

Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S. & Poiner, I. R. 2003. Impacts of Fishing Gear on Marine Benthic Habitat. In: *Responsible fisheries in the marine ecosystem*. FAO, Rome (Italy). pp. 197–217.

Kampf, A. R. 2007. Gem News International: Namibian diamond mining by Namdeb. *Gems & Gemology*. 43, 367–70.

Kathena, J. N. 2019. Contributions to the assessment of demersal fish stocks off Namibia. PhD thesis. Kgl. Lyngby: Technical University of Denmark (DTU).

Kathena, J. N., Nielsen, A., Thygesen, U. H. & Berg, C. W. 2016. Hake species (*Merluccius capensis* and *M. paradoxus*) assessment in the Benguela Current Large Marine Ecosystem. *Environmental Development*. 17, 193–201.

Kathena, J., Kokkalis, A., Pedersen, M., Beyer, J. & Thygesen, U. 2018. Data-moderate assessments of Cape monkfish *Lophius vomerinus* and west coast sole *Austroglossus microlepis* in Namibian waters. *African Journal of Marine Science.* 40, 293–302.

Kavadas, I., Maina, D., Damalas, I., Dokos, M. & Pantazi, V. 2015. Vassilopoulou Multi-criteria decision analysis as a tool to extract fishing footprints: Application to small-scale fisheries and implications for management in the context of the maritime spatial planning directive. *Mediterranean Marine Science*. 16, 294–304.

Khan, A. A. & Fatima, M. 1994. Feeding ecology of the Grey Mullet, *Rhinomugil corsula* (Hamilton) from the River Yamuna, North India. *Asian Fisheries Science.* 7, 256–266.

Kimura, D. K. 1980. Likelihood Methods for the von Bertalanffy Growth Curve. *Fisheries Bulletin*. 77, 765–776.

Kirchner, C., Bauleth-D'Almeida, G. & Wilhelm, M. R. 2010. Assessment and management of Cape horse mackerel *Trachurus capensis* off Namibia based on a fleet-disaggregated age-structured production model. *African Journal of Marine Science*. 32, 525–541.

Kirkman, S. P., Stephen, P., Yemane, D., Kathena, J., Mafwila, S. K., Nsiangango, S. E., Samaai, T., Axelsen, B. & Singh, L. 2013. Identifying and characterizing demersal fish biodiversity hotspots in the Benguela current large marine ecosystem: Relevance in the light of global changes. *ICES Journal of Marine Science.* 70, 943–954.

Kjesbu, O. S., Witthames, P. R., Solemdal, P. & Greer, W. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (Gadus morhua) in response to natural changes in food and temperature. *Journal of Sea Research*. 40, 303–321.

Konchina, Y. V. 1986 — Distribution and feeding of the South African horse mackerel and hake in the Namibian shelf waters. Colln scient. Pap. int. Commn SE. Atl. Fish. 13, 7–18

Kosaka, M. 1966. Feeding habits of angler fish, *Lophius litulon*. J. Fac. Oceanogr. Tokai Univ. 1:51–70. [In Japanese.]

Kritzer, J. P. & Liu, O. W. 2014. Fishery management strategies for addressing complex spatialstructure in marine fish stocks. In Stock identification methods: an overview. Edited by Cadrin, S. X., Kerr, L. A. & Mariani, S. Elsevier Science and Technology, Burlington, MA. pp. 29–57.

Kujawa, R., Mamcarz, A., Lach, M. & Kucharczyk, D. 2015. Influence of temperature on the growth and survivability of sichel larvae, *Pelecus cultratus,* reared under controlled conditions. *Ichthyological Research*. 62, 163–170.

Lall, S, P. & Tibbetts, S. M. 2009. Nutrition, Feeding, and Behavior of Fish. *Veterinary Clinics of North America: Exotic Animal Practice*. 12, 361–372.

Landa, J., Duarte, R. & Quincoces, I. 2008. Growth of white anglerfish (*Lophius piscatorius*) tagged in the Northeast Atlantic, and a review of age studies on anglerfish. *ICES Journal of Marine Science*. 65, 72–80.

Landa, J., Duarte, R., Quincoces, I., Dupouy, H., Bilbao, E., Dimeet, J., Lucio, P., Marçal, A., McCormick, H. & Ni Chonchuir, G. 2002. *Report of the 4th International Ageing Workshop on European Anglerfish.* 14–18

Lappalainen, A., Saks, L., Šuštar, M., Heikinheimo, O., Jürgens, K., Kokkonen, E., Kurkilahti, M., Verliin, A. & Vetemaa, M. 2016. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (Sander lucioperca) stocks in the northern Baltic Sea, *Fisheries Research*. 174, 47-57.

Laurenson, C. H. H. & Priede, I. G. G. 2005. The diet and trophic ecology of anglerfish *Lophius piscatorius* at the Shetland Islands, UK. *Journal of the Marine Biological Association of the United Kingdom.* 85, 419–424.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series.* 335, 271– 277.

Layman, C. A., Arrington, A., Montan, C. G. & Post, D. M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*. 88, 42–48.

Leslie, R. W. & Grant, W. S. 1991. Redescription of the southern African anglerfish *Lophius* *vomerinus* Valenciennes, 1837 (Lophiiformes: Lophiidae). *Copeia.* 1991, 787–800.

Leslie, R. W. & Grant, W. S. 1990. Lack of congruence between genetic and morphological stock structure of the southern African anglerfish *Lophius vomerinus. South African Journal of Marine Science*. 9, 379–398.

Lett, C., Veitch, J., Lingen, C. D. & Hutchings, L. 2007. Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. *Marine Ecology Progress Series*. 347, 247–259.

Ludynia, K., Roux, J.-P., Jones, R., Kemper, J. & Underhill, L. G. 2010. Surviving off junk: Low-energy prey dominates the diet of African penguins *Spheniscus demersusat* Mercury Island, Namibia, between 1996 and 2009. *African Journal of Marine Science*. 32, 563–572.

Maartens, L. 1999. *An assessment of the monkfish resource of Namibia*. PhD thesis. Rhodes University.

Maartens, L. & Booth, A. J. 2001a. Assessment of the monkfish *Lophius vomerinus* resource off Namibia. *South African Journal of Marine Science.* 23, 275–290.

Maartens, L. & Booth, A. 2001b. Quantifying Commercial Catch and Effort of Monkfish. *South African Journal of Marine Science.* 23, 291–306.

Maartens, L. & Booth, A. J. 2005. Aspects of the reproductive biology of monkfish Lophius vomerinus off Namibia. *African Journal of Marine Science*. 27, 325–329.

Maartens, L., Booth, A. J. & Hecht, T. 1999. The growth of monkfish *Lophius vomerinus* in Namibian waters, with a comparison of otolith and illicia methods of ageing. *Fisheries Research*. 44, 139–148.

Maartens, L., Gamst, K. & Schneider, P. M. 2002. Size selection and release of juvenile monkfish *Lophius vomerinus* using rigid sorting grids. *Fisheries Research*. 57, 75–88.

Macpherson, E. 1985. Daily ration and feeding periodicity of some fishes off the coast of Namibia. *Marine Ecology*. 26, 253-260.

Madurell, T., Cartes, J. E. 2005. Temporal changes in feeding habits and daily rations of *Hoplostethus mediterraneus* in the bathyal Ionian Sea (eastern Mediterranean). *Marine Biology*. 146, 951–962.

Maguire, J. J., Pereda, P., Duarte, R., Dobby, H. & Azevedo, M. 2008. Monkfish/anglerfish across the world; common problems and common solutions: An introduction to papers presented at the ICES Theme Session in September 2007. *ICES Journal of Marine Science.* 65, 1270–1271.

Mahboob, S. & Sheri, A. N. 2002. Relationships among gonad weight, liver weight and body weight of major, common and some Chinese carps under composite culture system with special reference to pond fertilization. *Asian-Australasian Journal of Animal Sciences.* 15, 740–744.

Marine Stewardship Council (MSC). 2020. Namibian hake trawl and longline fishery. https://fisheries.msc.org/en/fisheries/namibia-hake-trawl-and-longline-fishery/@@assessments.

Martell, S. & Froese, R. 2013. A simple method for estimating MSY from catch and resilience. *Fish and Fisheries*. 14, 504–514.

Martin, B., Eggert, A., Koppelmann, R., Diekmann, R., Mohrholz, V. & Schmidt, M. 2014. Spatio-temporal variability of zooplankton biomass and environmental control in the Northern Benguela Upwelling System: Field investigations and model simulation. *Marine Ecology*. 36, 637–658.

Masompour, Y., Gorgin, S., Pighambari, S., Y., Karimzadeh, Gh., Babanejad, M. & Eighani, M. 2018. The impact of ghost fishing on catch rate and composition in the southern Caspian Sea. *Marine Pollution Bulletin.* 135, 534–539535.

Massutõ, E., Morales-Ninc, B. & Morantac, J. 2000. Age and growth of blue-mouth, *Helicolenus dactylopterus* (Osteichthyes: Scorpaenidae), in the western Mediterranean. *Fisheries Research*. 46, 165–176.

Mas-Riera, J., Lombarte, A., Gordoa, A. & Macpherson, E. 1990. Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. *Marine Biology*. 104, 175–182.

Maunder, M. N. & Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*. 70, 141–159.

Mazumder, S. K., De, M., Mazlan, A. G., Zaidi, C. C., Rahim, S. M. & Simon, K. D. 2015. Impact of global climate change on fish growth, digestion and physiological status: Developing a hypothesis for cause and effect relationships. *Journal of Water and Climate Change*. 6, 200–226.

McBride, R. S., Johnson, A. K., Lindsay, E. K., Walsh, H. J. & Richards, R. A. 2017. Goosefish *Lophius americanus* fecundity and spawning frequency, with implications for population reproductive potential. *Journal of Fish Biology*. 90, 1861–1882.

McCluskey, S. M. & Lewison, R. L. 2008. Quantifying fishing effort: a synthesis of current methods and their applications. *Fish and Fisheries.* 9, 188–200.

Mendenhall, E., Hendrix, C., Nyman, E., Roberts, P. M., Hoopes, J. R., Watson, J. R., Lam, V. W. Y. & Sumaila, U. R. 2020. Climate change increases the risk of fisheries conflict.

Marine Policy. 117, 103954.

Michener, R., Lajtha, K. (Eds.). 2007. *Stable Isotopes in Ecology and Environmental Science* (2nd ed.). Malden: Blackwell Publishing Ltd.

Mihalitsis, M. & Bellwood, D. R. 2017. A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS ONE* 12, e0184679.

Ministry of Fisheries and Marine Resources (MFMR). 1990. *Territorial sea and Exclusive Economic Zone of Namibia. (Act No. 3 of 1990)*. Government Gazette, Republic of Namibia. Windhoek, Namibia.

Ministry of Fisheries and Marine Resources (MFMR)/ 1991. *Towards responsible development of the Fisheries Sector.* White paper of the Ministry of Fisheries and Marine Resources, Republic of Namibia: 65 pp.

Ministry of Fisheries and Marine Resources (MFMR). 1992. *Sea Fisheries Act (Act No. 29 of 1992).* Government Gazette of the Republic of Namibia, 493: 57 pp.

Ministry of Fisheries and Marine Resources (MFMR). 2000. *Marine Resource Act, 2000. Act No. 27 of 2000.* Government Gazette Republic of Namibia 6–11. http://209.88.21.36/opencms/opencms/grnnet/MFMR/Laws_and_Policies/marineAct.html.

Ministry of Fisheries and Marine Resources (MFMR). 2001. *Regulations relating to the exploitation of Marine Resources. The Marine Fisheries Regulations (Government notice No. 241*). Government Gazette of the Republic of Namibia, 2657: 50 pp. http://209.88.21.36/opencms/opencms/grnnet/MFMR/Laws_and_Policies/marineregulation.html.

Ministry of Fisheries and Marine Resources (MFMR), 2004. *Namibia's Marine Resources Policy. Towards Responsible Development and Management of the Marine Resources Sector*. Ministry of Fisheries and Marine Resources, Republic of Namibia: 23 pp. http://209.88.21.36/opencms/opencms/grnnet/MFMR/Laws_and_Policies/whitepaper.html.

Ministry of Fisheries and Marine Resources (MFMR). 2014. *Namibian Management Plan for the Hake Fishery*. Ministry Of Fisheries And Marine Resources. Windhoek, Namibia.

Ministry of Fisheries and Marine Resources (MFMR). 2015. *Final Draft Fisheries Policy*. Ministry of Fisheries and Marine Resources, Windhoek, Namibia.

Ministry of Fisheries and Marine Resources (MFMR). 2018. Ministry of Fisheries And Marine Resources Annual Report 2017/2018. (unpublished report). Ministry of Fisheries and Marine Resources, The Republic of Namibia, Windhoek.

Ministry of Fisheries and Marine Resources (MFMR), 2020. Ministry of Fisheries And Marine Resources Annual Report 2019/2020. (unpublished report). Ministry of Fisheries and Marine Resources, The Republic of Namibia, Windhoek.

Mohanraj, T. & Prabhu, K. 2012. Food Habits and Diet Composition of Demersal Marine Fishes from Gulf of Mannar, Southeast Coast of India. *Advances in Biological Research.* 6, 159–164.

Moloney, C. L. 2010. The humble bearded goby is a keystone species in Namibia's marine ecosystem. *South Africa Journal of Science*. 106, 9–10.

Moloney, C. L., Jarre, A., Arancibia, H., Bozec, Y-M., Neira, S., Roux, J-P. & Shannon, L. J. 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science.* 62, 493–502.

Monteiro, P. M. S., van der Plas, A. K., Mélice, J. L. & Florenchie, P. 2008. Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange, climate and ecosystem-state implications. *Deep-Sea Research Part I: Oceanographic Research Papers,* 55, 435–450.

Moore, B. R., Welch, D. J. & Simpfendorfer, C. A. 2011. Spatial Patterns in the Demography of a Large Estuarine Teleost: King Threadfin. *Marine and Freshwater Research*. 62, 937–951.

Morato, T., Santos, R. S. & Andrade, J. P. 2000. Feeding habits, seasonal and ontogenetic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic. *Fisheries Research*. 49, 51–59.

Morato, T., Watson, R., Pitcher, T. J. & Pauly, D. 2006. Fishing down the deep. *Fish and Fisheries.* 7, 23–33.

Morgan, M. J. & Colbourne, E. B. 1999. Variation in maturity-at-age and size in three populations of American plaice. *ICES Journal of Marine Science*. 56, 673–688.

Morishita, J. 2008. What is the ecosystem approach for fisheries management? *Marine Policy*. 32, 19–26.

Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J. & Pinsky, M. L. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLoS ONE* 13, e0196127.

Mqoqi, M., Lipiński, M. R. & Salvanes, A. G. V. 2007. The ecology of Sepia australis (Cephalopoda: Sepiidae) along the south coast of South Africa. *ICES Journal Marie Science.* 64, 945–955.

Nakaya, M., Takeya, Y., Suzuki, R., Noro, K., Gao, W. & Takatsu, T 2017. The effect of temperature on the early development and starvation tolerance of yellow goosefish *Lophius litulon*. *Aquaculture Science*. 65, 251-254.

National Development Plan 5 (NDP5), 2017. Namibia's Fifth National Development Plan (NDP5) - 2017/18–2021/22. National Planning Commission, Windhoek.

National Oceanic and Atmospheric Administration (NOAA). 2021. NOAA Extended Reconstructed Sea Surface Temperature (ERSST). https://doi.org/10.7289/V5T72FNM

Neuenfeldt, S. & Köster, F. W. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES Journal of Marine Science.* 57, 300–309.

Nikolioudakis, N., Palomera, I., Machias, A. & Somarakis, S. 2011. Diel feeding intensity and daily ratio of the sardine *Sardina pilchardus*. *Marine Ecology Progress Series*. 437, 215–228.

Noreikiene, K., Kuparinen, A. & Merilä, J. 2017. Age at maturation has sex- and temperature-specific effects on telomere length in a fish. *Oecologia.* 184, 767–777.

Oelofsen, B. W. 1999. Fisheries management: The Namibian approach. *ICES Journal of Marine Science.* 56, 999–1004.

Ohde, T. & Mohrholz, V. 2011. Interannual variability of sulphur plumes off the Namibian coast. *Journal of Remote Sensing*. 32, 9327–9342.

Olivar, M. P., Rubiés, P. & Salat, J. 1992. Horizontal and vertical distribution patterns of ichthyoplankton under intense upwelling regimes off Namibia. *South African Journal of Marine Science*. 12, 71–82.

Olivar, M. P. & Shelton, P. A. 1993. Larval Fish Assemblages of the Benguela Current. *Bulletin of Marine Science.* 53, 450–474.

Ortiz, E. & Arim, M. 2016. Hypotheses and trends on how body size affects trophic interactions in a guild of South American killifishes. *Austral Ecology*. 41

Our World in Data. Available from: https://ourworldindata.org/. (Accessed 17 February 2021).

Pankhurst, N. W. & Munday, P. L. 2011. Effects of climate change on fish reproduction and early life-history stages. *Marine and Freshwater Research.* 62, 1015–102.

Paterson, B. 2015. Tracks, trawls and lines–Knowledge practices of skippers in the Namibian hake fisheries. *Marine Policy.* 60, 309–317.

Paterson, B., Kirchner, C. & Ommer, R. E. 2013. A short history of the Namibian hake fishery, a social-ecological analysis. *Ecology and Society.* 18, 66.

Payne, A. I. L., Rose, B. & Leslie, R. W. 1987 — Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. In The Benguela and Comparable Ecosystems. Payne, A. I. L., Gulland, J. A. & K. H. Brink (Eds). *South African Journal of Marine Science*. 5, 471–501

Pennington, M. 1985. Estimating the average food consumption by fish in the field from stomach contents data. *Dana*. 5, 81–86.

Perry, A. L., Low, P. J., Ellis, J. M. & Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. *Science.* 308, 1912–1915.

Pillar, S. C. & Barange, M. 1997. Diel variability in bottom trawl catches and feeding activity of the Cape hakes off the west coast of South Africa. *ICES Journal of Marine Science.* 54, 485–499.

Pillar, S. C. & Barange, M. 1998. Feeding habits, daily ratio and vertical migration of the Cape horse mackerel off South Africa. *South African Journal of Marine Science*. 19, 263–274.

Pinkas, L., Olipham, M. S. & Iverson, I. L, K. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. *Fish Bull. Calif.* 152, 105.

Porobic, J., Fulton, E. A., Parada, C., Frusher, S., Ernst, B. & Manríquez, P. 2019. The impact of fishing on a highly vulnerable ecosystem, the case of Juan Fernández Ridge ecosystem. *PLOS ONE*. 14, e0212485.

Potts, W. M., Bealey, R. S. J. & Childs, A. R. 2016. Assessing trophic adaptability is critical for understanding the response of predatory fishes to climate change: a case study of *Pomatomus saltatrix* in a global hotspot. *African Journal of Marine Science*. 38, 539–547.

Potts, W. M., Henriques, R., Santos, C. V., Munnik, K., Ansorge, I., Dufois, F., Booth, A. J., Kirchner, C., Sauer, W. H. H. & Shaw, P. W. 2014. Ocean warming contributes to a rapid distributional shift and hybridization of a coastal fish species. *Global Change Biology.* 20, 2765–2777.

Preciado, I., Velasco, F., Olaso, I. & Landa, J. 2006. Feeding ecology of black anglerfish *Lophius budegassa*: Seasonal, bathymetric and ontogenetic shifts. *Journal of the Marine Biological Association of the United Kingdom.* 86, 877–884.

Rasquin, P. 1958. Ovarian morphology and early embryology of the pediculate fishes *Antennarius* and *Histrio*. *Bulletin of the Am. Mus. Nat. Hist*. 114, 327–372.

Richards, R. A., Nitschke, P. C. & Sosebee, K. A. 2008. Population biology of monkfish *Lophius americanus*. *ICES Journal of Marine Science*. 65, 1291–1305.

Ricker, W. E. 1973. Linear regressions in fishery research. *Fisheries Research Board of*

Canada Bulletin. 30, 309-434.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. (Whole issue.) *Journal of the Fisheries Research Board of Canada.* 191, 1–382.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*. 66, 1570–1583.

Rochet, M.-J. 1998. Short-term effects of fishing on life-history traits of fishes. *ICES Journal of Marine Science*. 55, 371–391.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL https://www.Rproject. org/.

Roseman, E. F., Boase, J., Kennedy, G., Craig, J. & Soper, K. 2011. Adaption of egg and larvae sampling techniques for lake sturgeon and broadcast spawning fishes in a deep river. *Journal of Applied Ichthyology.* 27, 89–92.

Rouault, M., Illig, S., Bartholomae, C., Reason, C. J. C. & Bentamy, A. 2007. Propagation and origin of warm anomalies in the Angola Benguela upwelling system in 2001. *Journal of Marine Systems*. 68, 473–488.

Rountree, R. A., Gro¨ger, J.P., Martins, D. 2006. Extraction of daily activity pattern and vertical migration behavior from the benthic fish, Lophius americanus, based on depth analysis from data storage tags .ICES CM Document CM2006/Q:01;2006.

Roux, J-P. & Shannon, L. J. 2004. Ecosystem approach to fisheries management in the northern Benguela: the Namibian experience. *African Journal of Marine Science*. 26, 79–93.

Roux, J.-P., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D. M. & Cury, P. M. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: Lessons from the Benguela. *Bulletin of Marine Science.* 89, 249–284.

Saikia, S. K. 2015. Food and Feeding of Fishes. What Do We Need to Know? *Transylvanian Review of Systematical and Ecological Research*. 17, 71–84.

Salvanes, A. G. V., Christiansen, H., Taha, Y., Henseler, C., Seivåg, M. L., Kjesbu, O. S., Folkvord, A., Utne-Palm, A. C., Currie, B., Ekau, W., van der Plas, A. K. & Gibbons, M. J. 2018. Variation in growth, morphology and reproduction of the bearded goby (*Sufflogobius bibarbatus*) in varying oxygen environments of northern Benguela. *Journal of Marine Systems.* 188, 81–97.

Sancho, G., Puente, E., Bilbao, A., Gomez, E. & Arregi, L. 2003. Catch rates of monkfish (*Lophius* spp.) by lost tangle nets in the Cantabrian Sea (northern Spain). *Fisheries*

Research. 64, 129–139.

Santos, F., Gomez-Gesteira, M., de Castro, M. & Alvarez, I. 2012. Differences in coastal and oceanic SST trends due to the strengthening of coastal upwelling along the Benguela current system. *Continental Shelf Research*. 34, 79–86.

Saul, S. E., Walter, J. F., Die, D. J., Naar, D. F. & Donahue, B. T. 2013. Modelling the spatial distribution of commercially important reef fishes on the West Florida Shelf. *Fisheries Research*. 143, 12–20.

Schneider, G. I. C. 2020. Marine diamond mining in the Benguela Current Large Marine Ecosystem: The case of Namibia. *Environmental Development*. 36, 100579.

Schneider, P. & Johnsen, E. 2000. *Monkfish Biomass Survey. Cruise Report.* Swakopmund, Namibia. Ministry of Fisheries and Marine Resource. pp.2.

Shannon, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology Annual Review.* 23, 105–182.

Shannon, V. 2006. 1. A plan comes together. In Shannon, V. Hempel, G. Malanotte-Rizzoli, P. Moloney C. & Woods J. (Eds.), *Large Marine Ecosystems*. 14, 3–10.

Shannon, L. J., Moloney, C. L., Jarre, A. & Field, J. G. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. 39, 83–116.

Shillington, F. A., Reason, C. J. C., Duncombe Rae, C. M., Florenchie, P. & Penven, P. 2006. Large Scale Physical Variability of the Benguela Current Large Marine Ecosystem (BCLME). Large Marine Ecosystems. 14

Simpson, S., Blanchard, J. & Genner, M. 2013. Impacts of climate change on fish. *MCCIP Science Review.* 113–124.

Smith, M. D., Grabowski, J. H. & Yund P. O. 2008. The role of closed areas in rebuilding monkfish populations in the Gulf of Maine. *ICES Journal of Marine Science*. 65, 1326–1333.

Snover, M. L. 2008. Ontogenetic habitat shifts in marine organisms: Influencing factors and the impact of climate variability. *Bulletin of Marine Science.* 83, 53–67.

Stander, G. H. & De decker, A. H. B. 1969. *Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963*. Investigational Report Division of Sea Fisheries, South Africa. 81, 46.

Steimle, F., Morse, W. & Johnson, D. 1999. Goosefish, *Lophius americanus*, *Life History and Habitat Characteristics.* NOAA Technical Memorandum NMFS-NE-127:1–40.

Strømme, T. & Iilende, T. 2001. Precision in systematic trawl surveys as assessed from replicate sampling by parallel trawling off Namibia. *South African Journal of Marine Science.* 23, 385–396.

Strømme, T., Huse, I. & Staalesen, B. 1999. Surveys of the hake stocks, 11 January–21 February 1999. Cruise report 1/99. NORAD-FAO UNDP PROJECT 92/013. Ministry of Fisheries and Marine Resources, Namibia: 52 pp. (mimeo).

Sumaila, U. R., Boyer, D., Skogen, M. D. & Steinshamn, S. I. 2004. Namibia's fisheries: introduction and overview. In: Sumaila, U. R., Steinshamn, S. I., Skog, M., Boyer, D. C. (Eds.), *Ecological, Economic and Social Aspects of Namibian Fisheries.* Eburon, Netherlands, pp. 1–9.

Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D. & Herrick, S. 2011. Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change.*1, 449–456.

Sun, Y., Zhang, C., Tian, Y. & Watanabe, Y. 2020. Age, growth, and mortality rate of the yellow goosefish *Lophius litulon* (Jordan, 1902) in the Yellow Sea. *Journal of Oceanology and Limnology*.

Sundby, S., Boyd, A. J., Hutchings, L., O'Toole, M. J., Thorisson, K. & Thorsen, A. 2001. Interaction between Cape hake spawning and the circulation in the northern Benguela upwelling ecosystem. *South African Journal of Marine Science.* 23, 317–336.

Tasker, M. (Ed.) 2008. The effects of climate change on the distribution and abundance of marine species in the OSPAR maritime area. *ICES Cooperative Research Report*, 293. 45 pp.

Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A. & Blaber, S. J. M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science.* 57, 531–547.

Taunton-Clark, J. & Shannon, L. V. 1988. Annual and interannual variability in the southeast Atlantic during the 20th century. *South African Journal of Marine Science.* 6, 97–106.

Tesch, F. W. 1971. Age and growth. In: W. E. Ricker (Ed.) *Methods for assessment of fish production in freshwaters*. Blackwell Scientific Publications, Oxford, 99–130.

Thangstad, T., Dyb, J., Jónsson, E., Laurenson, C., Ofstad, L. H. & Reeves, S. 2002. *Anglerfish (Lophius spp.) in Nordic and European waters: Status of current knowledge and ongoing research*. Unpublished Report.

Thresher, R. E, Koslow, J. A., Morison, A. K. & Smith, D. C. 2007. Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences*. 104, 7461–7465.

Tollit, D. J, Steward, M. J., Thompson, P. M., Pierce, G. J., Santos, M. B. & Hughes, S. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Canadian Journal of Fishries and Aquatic Science.* 54, 105–119.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries: Biological processes related to reproduction in northwest Atlantic groundfish populations that have undergone declines. *Bioscience*. 45, 759–771.

Trippel, E. A., Kjesbu, O. S. & Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA eds. Early life history and recruitment in fish populations. New York, Chapman & Hall. Pp. 31–62.

Utne-Palm, A. C., Salvanes, A. G. V., Currie, B., Kaartvedt, S., Nilsson, G. E., Braithwaite, V. A., Stecyk, J. A. W., Hundt, M., van der Bank, M., Flynn, B., et al. 2010. Trophic structure and community stability in an overfished ecosystem. *Science*. 329, 333–336.

Valdimarsson, G. & James, D. 2001. World fisheries – utilisation of catches. *Ocean & Coastal Management.* 44, 619–633.

van der Grient, J. M. & Rogers, A. D. 2021. Environmental influence on the distribution of polychaete families and feeding guilds in benthic communities of the Grand Banks and Flemish Cap (NW Atlantic). *Deep Sea Research Part I: Oceanographic Research Papers.* 171, 103498, ISSN 0967–0637.

van der Lingen, C. D. & Miller, T. W. 2011. Trophic Dynamics of Pelagic Nekton in the Southern Benguela Current Ecosystem: Calibrating Trophic Models with Stable Isotope Analysis. I*nterdisciplinary Studies on Environmental Chemistry—Marine Environmental Modeling & Analysis*. Omori, K., Guo, X., Yoshie, N., Fujii, N., Handoh, I. C., Isobe, A. & Tanabe, S. (Eds). Terrapub, South Africa. 85–94.

van der Lingen, C. D., Shannon, L. J., Cury, P., Kreiner, A., Moloney, C. L., Roux, J. P. & Vaz-Velho, F. 2006. 8Resource and ecosystem variability, including regime shifts, in the Benguela Current System. *Large Marine Ecosystems.* 14, 147–184.

van der Westhuizen, A. 2001. A decade of exploitation and management of the Namibian hake stocks. *South African Journal of Marine Science.* 7615, 307–315.

Varela, J. L., Rodríguez-Marín, E. & Medina, A. 2013. Estimating diets of pre-spawning Atlantic bluefin tuna from stomach content and stable isotope analyses. *Journal of Sea Research*. 76, 187-192.

Vicentini, R. N. & Araújo, F. G. 2003. Sex Ratio and Size Structure of *Micropogonias furnieri* (Desmarest, 1823) (Percifomers, Sciaenidae) In Sepetiba Bay, Rion De Janeiro, Brazil.

Brazilian Journal of Biology. 63, 559–566.

Walmsley, S., Leslie, R. & Sauer W. 2005. The biology and distribution of the monkfish *Lophius vomerinus* off South Africa. *African Journal of Marine Science*. 27, 157–168.

Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. *Canadian Journal of Fisheries and Aquatic Science.* 60, 1433–1436.

Wang, L., Ma, M., Liu, Y., Li, J., Liu, S., Lin, L. & Tian, Y. 2021. Fluctuations in the abundance of chub mackerel in relation to climatic/oceanic regime shifts in the northwest Pacific Ocean since the 1970s. *Journal of Marine System*. 218, 103541.

Wang, Y. & Di Cosimo, J. 2019. National Observer Program 2016 Fishery Observer Attitudes and Experiences Survey. NOAA. Memo. NMFS-F/SPO-186, 50.

Watson, R., Cheung, W. W. L., Anticamara, J., Sumaila, U. R., Zeller, D. & Pauly, D. 2013. Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries*. 14, 493–503.

Weatherdon, L. V., Magnan, A. K., Rogers, A. D., Sumaila, U. R. & Cheung, W. W. 2016. Observed and projected impacts of climate change on marine fisheries, aquaculture, coastal tourism, and human health: an update. *Frontiers Marine Science.* 3, 48.

Wheeler, J. P., Purchase, C. F., Macdonald, P. D. M., Fill, R., Jacks, L., Wang, H. & Ye, C. 2009. Temporal changes in maturation, mean length-at-age, and condition of spring-spawning Atlantic herring (*Clupea harengus*) in Newfoundland waters. *ICES Journal of Marine Science.* 66, 1800–1807.

Wilhelm, M. R., Kirchner, C. H., Roux, J. P., Jarre, A., Iitembu, J. A., Kathena, J. N. & Kainge, P. 2015. Biology and fisheries of the shallow-water hake (*Merluccius capensis*) and the deep-water hake (*Merluccius paradoxus*) in Namibia. *Hakes: Biology and Exploitation.* pp.70-100. Ed. by H. Arancibia. John Wiley & Sons, Ltd: Chichester, UK.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann, C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K., Høye, T. T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N. M., … Svenning, J.-C. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews.* 88, 15–30.

Woodhead, P. M. J. Hamukuaya, H. & O'Toole, M. J. 1996. Co-operative studies on the ecology of Cape hake in Namibian waters with particular reference to the effects of low oxygen conditions. In: *Proceedings of a Seminar and Workshop, The Benguela Current and Comparable Eastern Boundary Upwelling Systems*, Swakopmund, Namibia, May

1995, 112 –116.

Woodhead, P. M., Hamukuaya, H., O'Toole, M. J., Stroemme, T., Saetersdal, G. & Reiss, M. 1997. Catastrophic loss of two billion Cape hake recruits during widespread anoxia in the Benguela Current off Namibia. In Proceedings of *ICES International Symposium on Recruitment Dynamics of Exploited Marine Populations: Physical-Biological Interactions.* 22–24.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. U. B. C., Lotze, H. K., Micheli, G. T., Palumbi, S. R., Sala, E., Selkoe, K., Stachowicz, J. J. & Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science.* 314, 787–790.

Wu, R. S. S. 2002. Hypoxia: from molecular responses to ecosystem responses. *Marine Pollution Bulletin*. 45, 35–45.

Yamashita, H., D. Shiode, T. & Tokai, T. 2009. Longline hook selectivity for red tilefish *Branchiostegus japonicus* in the East China Sea. *Fisheries Science*. 75, 863–874.

Yoneda, M., Tokimura, M., Fujita, H., Takeshita, N., Takeshita, K., Matsuyama, M. & Matsuura, S. 2001. Reproductive cycle, fecundity, and seasonal distribution of the anglerfish *Lophius litulon* in the East China and Yellow seas. *Fishery Bulletin.* 99, 356–370.

Young, J. W. & Blaber, S. J. M. 1986. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology.* 93, 147–156.

Zacharia, P. U. & Abdurahiman, K. P. 2004. Methods of stomach content analysis of fishes. CMFRI, 148–158

Zar, J. H. 1999. Biostatistical Analysis. 4nd ed. New Jersey: Prentice-Hall Inc. 663p.

Şenbahar, A. M. & Özaydin, O. 2020. Age and growth of black-bellied anglerfish *Lophius budegas*sa (Spinola, 1807) from the Central Aegean sea, Turkey. *Croatian Journal of Fisheries*. 78, 45-51.

Appendix A

Table of digestion stages of fish prey items (adapted from Filiz, 2009)

Digestive state	Description
Stage 1	Shiny body surface – probably with scales. Clear eyes, fresh; prey without signs of digestion.
Stage 2	Digestion just started; prey intact except for the more delicate parts, body parts may be discoloured (brownish, especially in the margins).
Stage 3	Moderately digested; prey clearly affected by digestion.
Stage 4	(a) Severely digested; prey highly fragmented; (b) Digestion almost complete, unidentifiable remains with little muscle; (c) only backbone or hard parts such as otoliths left.

Appendix B

Overall diet composition expressed as percentages by number (*%N*), weight (*%W*), frequency of occurrence (*%Fc*), Index of Relative Importance (*IRI*) and percentage of Index of Relative Importance (*%IRI*), for juveniles (< L_{50}, 37 cm TL) (n = 210), sub-adults (L_{50} – L_{100}, 37–47 cm TL) (n = 299) and adults (> L_{100}, 47 cm TL) (n = 387) Cape monkfish *Lophius vomerinus* collected off Namibia between 2015 and 2018.

		Juveniles (<L_{50}, 36cm TL)					Sub-adults (L_{50}–L_{100}, 36–47cm TL)					Adults (>L_{100}, 47cm TL)				
Taxon	Prey item	%N	%W	%*Fc*	IRI*i*	%IRI	%N	%W	%Fc	IRIi	%IRI	%N	%W	%Fc	IRIi	%IRI
Teleost	*Austroglossus microlepis*	0.86	7.62	0.93	1.41	1.14	-	-	-	-	-	-	-	-	-	-
	Bassanago albescens	-	-	-	-	-	0.44	0.27	0.48	0.19	0.01	0.82	0.13	1.07	0.91	0.01
	Bathyuroconger vicinus	-	-	-	-	-	-	-	-	-	-	0.27	0.08	0.36	0.19	0.00
	Beryx splendens	1.72	8.08	1.87	3.00	2.43	-	-	-	-	-	-	-	-	-	-
	Celorhinchus caelorhinchu	1.72	0.97	1.87	0.40	0.32	3.10	1.98	2.90	8.28	0.58	0.82	0.36	1.07	2.54	0.02
	Caelorhincus acanthiger	0.86	5.90	0.93	1.09	0.88	-	-	-	-	-	-	-	-	-	-
	Caelorinchus simorhynchu	8.62	9.66	9.35	18.70	15.16	3.54	1.35	3.38	6.73	0.47	2.74	1.25	3.20	26.41	0.22
	Unidentified Caelorinchus	1.72	1.41	1.87	0.56	0.45	-	-	-	-	-	-	-	-	-	-
	Chlorophthalmus agassizi	1.72	1.48	1.87	0.58	0.47	3.54	1.94	1.45	4.08	0.29	6.03	1.49	2.85	28.25	0.23
	Unidentified Congridae	-	-	-	-	-	1.33	0.40	1.45	0.87	0.06	1.92	0.38	2.14	5.43	0.04
	Cynoglossus zanzibariensis	0.86	1.21	0.93	0.23	0.19	-	-	-	-	-	-	-	-	-	-
	Epigonus telescopus	0.86	1.43	0.93	0.27	0.22	-	-	-	-	-	0.82	0.20	0.71	0.95	0.01
	Helicolenus dactylopterus	4.31	8.70	4.67	8.22	6.67	9.29	15.65	10.14	224.87	15.81	6.58	5.36	7.83	274.22	2.27
	Hoplostethus cadenati	0.86	1.22	0.93	0.23	0.19	-	-	-	-	-	-	-	-	-	-
	Lophius vomerinus	-	-	-	-	-	-	-	-	-	-	0.55	1.92	0.71	8.88	0.07
	Unidentified macrouridae	5.17	4.93	5.61	5.78	4.69	8.41	4.05	8.70	51.26	3.60	3.84	1.13	4.63	34.59	0.29
	Merluccius capensis	0.86	0.99	0.93	0.19	0.16	3.54	9.24	3.86	50.39	3.54	3.84	6.63	4.27	184.22	1.53
	Merluccius paradoxus	10.34	16.30	11.21	37.28	30.24	15.93	29.76	15.94	671.30	47.20	33.70	58.43	28.47	10823.16	89.69
	Merluccius spp	2.59	6.33	2.80	3.57	2.89	9.29	9.81	9.18	128.32	9.02	4.11	3.19	4.98	103.87	0.86
	Myctophids	4.31	1.25	3.74	1.12	0.91	1.33	0.31	1.45	0.69	0.05	-	-	-	-	-
	Nemichthyidae	-	-	-	-	-	0.88	0.14	0.97	0.21	0.01	0.82	0.05	0.71	0.24	<0.01
	Nemichthys scolopaceus	-	-	-	-	-	0.44	0.04	0.48	0.03	<0.01	-	-	-	-	-
	Nezumia micronychodon	-	-	-	-	-	3.10	1.64	3.38	8.04	0.57	3.01	1.42	3.91	36.65	0.30
	Notacanthidae	-	-	-	-	-	-	-	-	-	-	0.55	0.04	0.36	0.10	<0.01
	Paracallionymus costatus	5.17	4.08	1.87	1.62	1.31	-	-	-	-	-	-	-	-	-	-
	Pterothrissus belloci	-	-	-	-	-	0.44	1.08	0.48	0.74	0.05	0.27	0.28	0.36	0.66	0.01
	Selacophidium quentheri	-	-	-	-	-	0.88	1.11	0.97	1.53	0.11	1.10	0.46	1.42	4.36	0.04
	Sufflogobius bibarbatus	18.10	4.66	18.69	21.31	17.28	0.44	0.31	0.48	0.22	0.02	0.82	0.02	0.71	0.14	<0.01
	Trachurus capensis	0.86	3.29	0.93	0.61	0.50	8.41	15.18	7.25	155.69	10.95	3.29	3.31	2.85	61.47	0.51
	unidentified fish	17.24	3.03	16.82	13.64	11.06	18.14	3.25	19.32	97.02	6.82	9.59	1.89	11.39	144.58	1.20
	Trachyrinchus scabrus	-	-	-	-	-	-	-	-	-	-	0.82	0.67	1.07	4.70	0.04
Cephalopoda	Unidentified Cephalopod	1.72	0.65	1.87	0.28	0.23	1.77	0.27	1.93	0.81	0.06	4.66	5.94	5.34	206.74	1.71
	Sepia australis	3.45	2.38	3.74	1.91	1.55	0.44	0.18	0.48	0.13	0.01	0.27	0.01	0.36	0.04	<0.01
	Todarodes sagittatus	0.86	2.65	0.93	0.49	0.40	-	-	-	-	-	3.01	4.63	3.56	107.18	0.89
Crustacea	unidentified Crustacean	-	-	-	-	-	0.44	0.02	0.48	0.02	<0.01	0.82	0.02	1.07	0.15	<0.01
	Euphausiids	3.45	0.04	2.80	0.15	0.12	-	-	-	-	-	-	-	-	-	-
	Nephropsis atlantica	-	-	-	-	-	-	-	-	-	-	0.27	0.01	0.36	0.04	<0.01
	Shrimps	-	-	-	-	-	0.44	0.03	0.48	0.02	<0.01	-	-	-	-	-
	Squilla aculeata calmani	1.72	1.72	1.87	0.67	0.54	3.98	1.93	3.86	10.85	0.76	0.82	0.03	1.07	0.24	<0.01
Elasmobranchi	*Galeus polli*	-	-	-	-	-	-	-	-	-	-	0.27	0.11	0.36	0.26	<0.01
Gastropoda	Gastropod	-	-	-	-	-	0.44	0.06	0.48	0.04	<0.01	0.55	0.04	0.36	0.11	<0.01
Echinoidea	Sea urchin	-	-	-	-	-	-	-	-	-	-	2.19	0.46	2.14	6.57	0.05
Porifera	Sponge	-	-	-	-	-	-	-	-	-	-	0.82	0.05	0.36	0.14	<0.01
– Absent.																

Appendix C

Overall diet composition expressed as percentages of Index of Relative Importance (%*IRI*), for juveniles (< L_{50}, 37 cm TL) (n = 210 stomachs), sub-adults (L_{50} – L_{100}, 37–47 cm TL) (n = 299) and adults (> L_{100}, 47 cm TL) (n = 387) Cape monkfish, *Lophius vomerinus,* in summer, autumn, winter and spring, collected off Namibia between 2015 and 2018.

	Juveniles (<L_{50}, 36cm TL)				Sub-adults (L_{50}–L_{100}, 36–47cm TL)				Adults (> L_{100}, 47cm TL)			
Taxon	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Teleost	79.1	100.0	86.2	92.1	93.7	90.8	75.2	97.3	81.8	79.4	85.3	80.7
Cephalopoda	20.9	0.0	6.9	0.0	6.3	3.7	3.1	0.0	8.4	13.7	9.8	16.1
Crustacea	0.0	0.0	6.9	7.9	0.0	5.6	18.6	2.7	1.4	5.2	2.5	3.2
Elasmobranchii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0
Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	1.2	0.0
Echinoidea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.4	0.0	0.0	0.0
Porifera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0