Estimates of Length-at-50% maturity of two South African demersal species: Monkfish, *Lophius vomerinus*, and Kingklip, *Genypterus capensis*

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Abstract

Long-lived and slow-growing fish species are especially vulnerable to overfishing. Deep-sea species are elusive and difficult to study, making their management challenging. South African monkfish, *Lophius vomerinus*, and kingklip, *Genypterus capensis*, are two demersal species living off the west and south coast of South Africa. These species are exploited as bycatch in the Hake fisheries, and represent an important resource for the fishery. However, reproductive information is scarce, and key life-history parameters have not been updated in recent years. Length-at-50% maturity (L_{50}) is a fundamental biological parameter to monitor stock-health, spawning potential and improve fishery management. This research was focused on computing L_{50} estimates for both species, separated by sex and coast. As the stock structure for both species is still under debate, reproductive information and L_{50} estimates were compared between west and south coast. In addition, L_{50} was compared with previous studies to detect significant differences or changes over time. Demersal survey samples were used. Individuals were classed a 5 stage maturity scale and consequently referred to as mature or immature. For *L. vomerinus,* a significant difference in L_{50} between sexes was found, in contrast with previous findings in literature. However, no significant difference between the two areas was reported, corroborating the one-stock hypothesis. Furthermore, I speculate that *L. vomerinus* aggregate for spawning activities. The analysis of *G. capensis* revealed differences between coasts, reinforcing the theory of multiple South African stocks. Most importantly, the results showed a critical reduction in females L_{50} from previous studies. This reduction is believed to be a consequence of excessive fishing pressure exerted particularly during the latter half of the 20th century, which over-exploited immature females on the west coast and main female spawners on the south coast. Further research needs to be done to verify these findings and the stock structure of the populations.

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This work is dedicated to my parents, who made this dream come true with their unconditional love and support. Last but not least, to my beloved better half, *mi amado pesecito,* who has been there for me every second of this crazy adventure.

TABLE OF CONTENTS

1. INTRODUCTION

1.1An overview of South African fisheries

In South Africa, coastal resources are divided into inshore and offshore resources that are directly exploited by commercial, recreational and subsistence fishing (Griffiths et al., 2010). Commercial fisheries include 22 sectors, which employ directly around 27 700 people with an overall contribution to GDP of 322 million USD in 2008 (FAO, 2010). Most commercial fisheries are concentrated in the west coast and partially on the south coast, due to the influence of coastal upwelling in this region. Most of these revenues come from the Western Cape Province, up to 90% of the total in 1999, as most of the fish are caught and processed in the area (Karaan and Rossouw, 2004).

Primary commercial fisheries in South Africa are: small pelagic fisheries, with species of interest including anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and redeye round herring (*Etrumeus whiteheadi*); Cape Hakes fishery, with two species targeted (*Merluccius capensis* and *M. paradoxus*) and west coast rock lobster (*Jasus lalandii*). Although the most important fishery for landings is the small pelagic fishery, the Cape Hakes fishery is the most valuable nationwide in terms of generated revenue (Durholtz et al., 2015). The Cape Hakes fishery is one of the oldest fisheries in South Africa and it is concentrated on the west and south coast, where both species are exploited (Durholtz et al., 2015). This sector provides around 30 000 jobs and R5.2 billion of annual landed value (DAFF, 2016).

There are four fishery sectors that target the Cape hakes, namely deep-sea and inshore demersal trawl, longline and handline. The deep-sea trawl sector is the most prevalent, landing 84% of all hake quota and it is the only national fishery certified as sustainable by the Marine Stewardship Council (MSC) international standards, making exports vital for the market.

The Cape hake fishery OMP sets an annual TAC depending on research surveys and includes Precautionary Upper Catch Limit (PUCLs), which are limits for by-catch species (DAFF, 2016). Non-targeted species caught during harvesting are defined as by-catch and it is a common event in global fisheries and their management is important (Davies et al, 2009). Normally, species that have market value are retained, while the ones with the least profit potential are discarded (Saila, 1983). In the Cape hake fishery, the main by-catch species are South African monkfish, *Lophius vomerinus,* and South African kingklip, *Genypterus capensis*. These species have a similar spatial distribution to the Cape hakes, but they are not directly exploited: they do, however, form a considerable portion of the by-catch associated with the Cape hakes fishery and their considerable commercial value makes them a precious resource for the industry (DAFF, 2016).

PUCLs for *L. vomerinus* and *G. capensis* are based on a Replacement Yield (RY) model, which is a biomass dynamics model (BDM) based on the annual surplus biomass production of the population at harvest (de Moor, 2015). It is indeed defined as "the amount of yield in weight that can be removed from a population of fish without leading to biomass increase or decline" (Froese and Pauly, 2018). Biomass dynamics models (BDMs) are the simplest stock assessment models applied in fishery management. Data fed to the model only consider biomass harvested and biomass estimates, while population structure data, such as age or length, are not included (Colvin et al., 2012). BDMs are a convenient method to assess fish stocks and they form the basis of more complex models (Cooper, 2006). However, as de Moor et al. (2015) pointed out, the RY assessments for *L. vomerinus* and *G. capensis* cannot provide the needed information regarding the stocks current status in relation to reference points, which are target levels for biomass or mortality rates that the managers plan to attain (Cooper, 2006).

1.2 *Lophius vomerinus*

South African Monkfish belongs to the genus *Lophius*, which includes seven species worldwide. This genus is the most important commercial resource of the family Lophiidae, which is found in temperate, tropical and subtropical waters: six of the seven species inhabit both coasts of the Atlantic Ocean, one inhabits the west Indian Ocean and the other the western Pacific, with no records for eastern Pacific (Fariña et al., 2008).

Morphologically, the genus *Lophius* is defined by a dorso-vertical compression of head and body, no scales and swim bladder, large mouth and an illicium, which is a modified first dorsal fin that attracts prey (Fariña et al, 2008; Fig. 1).

The illicia has been used as an alternative way to age monkfish since otoliths were considered lacking in precision (Dupouy et al., 1986; Griffiths and Hecht, 1986; Maartens et al., 1999). However, estimates of age based on the illicia also demonstrate imprecision (Laurenson et al., 2005; Landa et al., 2008). Research conducted by Duarte et al. (2005) comparing the readings of experts on both illicia and otoliths, found the former method generated more accurate estimates of age.

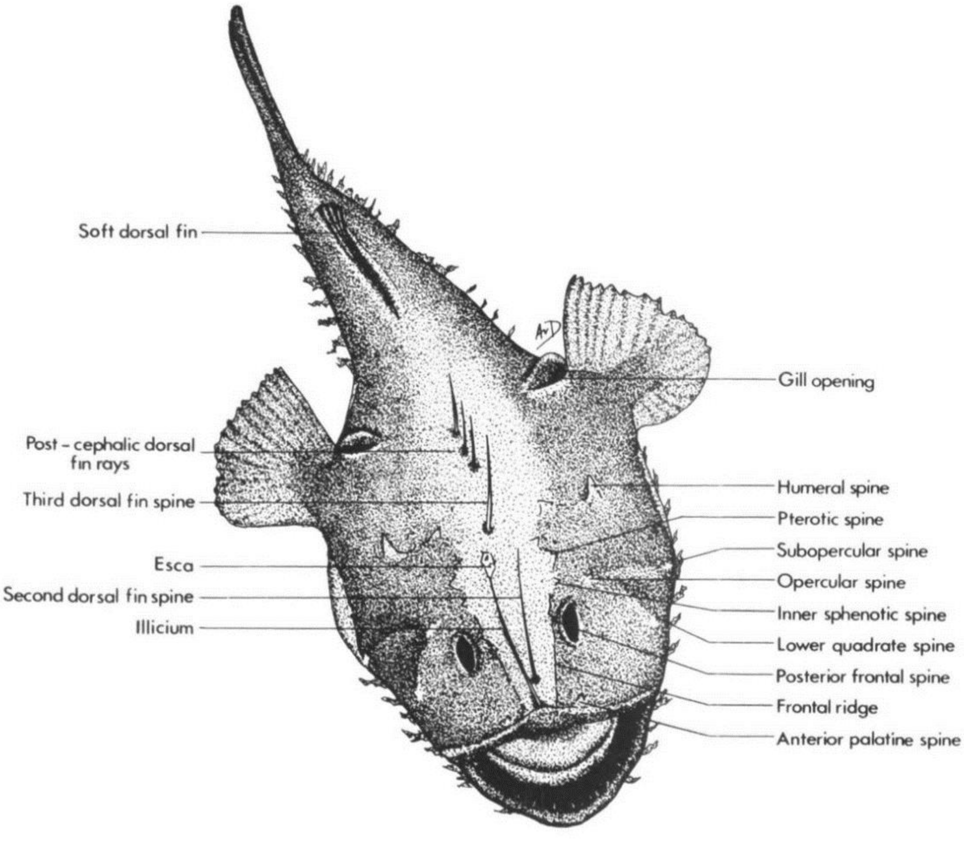

Fig. 1 Diagram showing the general morphology of *Lophius vomerinus* (from Leslie and Grant, 1990).

Global distribution

Monkfish are demersal and occur over different types of substrata, from soft to hard sandy and gravel bottoms located on the upper slope of the continental shelf and over the continental shelf itself, moving deeper with increasing age (Fariña et al., 2008). Distribution data studied by Walmsley et al. (2005) regarding the South African monkfish *L. vomerinus* (Valenciennes, 1837), shows that juvenile and adult distributions overlap, meaning fish of all ages are vulnerable to fishing activities.

The South African monkfish, *L. vomerinus,* occurs in waters from the southeast Atlantic, off Namibia, down to the southwest Indian Ocean, off KZN, South Africa (Leslie and Grant, 1990), at depths ranging from 50 to 1000 meters (DAFF, 2016) and is characterised by the presence of vomerine teeth.

Little is known about the migration patterns of *L. vomerinus*. In the case of *L. pescatorius,* occuring in the northeast Atlantic, long migrations covering up to 800 km as juveniles have been recorded in addition to residency (Pereda and Landa, 1997; Laurenson et al. 2005). Adult specimens of *L. piscatorius, L. americanus* and *L. litulon* also migrate, and these migrations are driven primarily by environmental factors such as temperature changes, food availability and reproduction: normally these movements are from onshore to offshore areas (Steimle et al., 1999; Landa et al., 2001; Yoneda et al., 2002).

Biology

Subsequent to the pelagic egg and larval stages, *L. vomerinus* become benthic as juvenile specimens, while adults live semi-sedentary lives on the seabed, waiting for prey (Pereda and Landa, 1997). *Lophius* spp. in general employ a common predation tactic, which includes mainly camouflage and ambush. Adults lure prey by moving the illicium enticingly as bait. They are opportunistic feeders and their diets starts with invertebrate species whilst they are juveniles, with fish forming a more considerable percentage of the diet as the fish ages. Stomach contents analysed by Walmsley et al. (2005) indicate that the main food for *L. vomerinus* is benthic fish such as the Cape hakes and dragonets (*Paracallionymus costatus*); however, the presence of a smaller proportion of other pelagic species shows the ability of this fish to feed in the water column as well (Hislop et al., 2000). For *Lophius* spp. in general, growth parameters have proved challenging to calculate with precision, with the primary point of contention being the otoliths/illicia debate mentioned previously. For *L. vomerinus* lifespan is considered approximately 17 years with the largest specimens attaining lengths of up to 1 m (Leslie and Grant, 1990).

Management and history of *Lophius vomerinus* fishery

Lophius vomerinus are a high-value product for their lobster-like flesh and in South Africa it is an important and coveted commodity. They are caught almost exclusively as incidental by-catch by the hake trawl fishery (*Merluccius capensis* and *M. paradoxus*) and Agulhas sole fishery (*Austroglossus pectoralis*), both deep-sea and inshore sectors (DAFF, 2016). The WWF Southern Africa Sustainable Seafood Initiative (SASSI) list, whose goal is educating consumers and encouraging sustainable seafood purchase, classified Cape monkfish as orange on a three colors scale (green=sustainable, orange=think twice, red=not sustainable; WWF SASSI, 2019).

As illustrated in Fig. 2, the first available data came from the Cape hake trawl fishery in 1974 and until 1994 the total catches fluctuated around 4700 t per annum (DAFF, 2016). From 1990 it was recorded that most of the catches were from the west coast, and it is sensibly assumed to be the same for previous years before accurate record keeping began. Currently, a Precautionary Upper Catch Limit (PUCL) is set at 8300 t and it has remained at this level since the 2013 fishing season. This limit was based on a 2011 assessment and confirmed after 2013 and 2015 assessments (DAFF, 2016). After an alarming increase in catches in 2001, which peaked at 10 000 t, scientists started assessing the resource and used a coast-disaggregated Replacement Yield (RY) approach to calculate sustainable catches, which indicated that total catches should not be over 7300 t. Hence, the first PUCL was implemented in 2006 with a maximum annual total catch of 7000 t (DAFF, 2016).

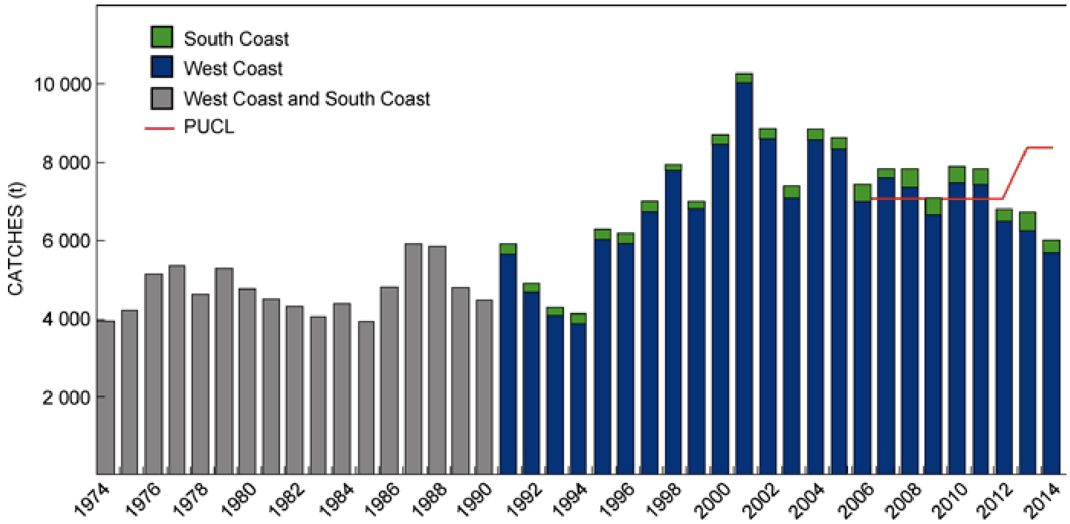

Fig. 2 Annual catches of *Lophius vomerinus* (tons) landed by the hake trawl fishery for the period 1974–2014, and the Precautionary Upper Catch Limit (PUCL) that was introduced in 2006. Catches after 1990 are divided by coast (DAFF, 2016).

Population structure of *Lophius vomerinus*

In South Africa *L. vomerinus* have a large distribution but no significant genetic differentiation to separate the species into two different stocks, south and west coast stock. This was determined by Leslie and Grant (1990), who found morphological differences that could indicate multiple stocks, but genetic differentiation was too weak to confirm the hypothesis. They explained this based on the assumption that eggs and larvae have an enormous dispersal potential. In fact, as is common among the genus, eggs and larvae remain on the surface for four to eight weeks where they are passively transported by surface currents for 400 to 800 km (Mean speed of the north-flowing Benguela system is 17 cm·s-I, Shannon 1985) before stopping and settling on the sea floor (Leslie and Grant, 1990).

Currently, the structure of the stock is still uncertain, with the two stock measurement hypotheses both still under consideration and subject to debate. The 2015 DAFF assessment, using a Replacement Yield model, shows that the stock on the west coast is slightly improving while the one on the South Coast remains moderately stable (DAFF, 2016).

Reproduction

Reproductive dynamics information on *L. vomerinus* in particular are scarce, whereas for *Lophius* spp. in general more is known (Griffiths and Hecht, 1986, Maartens and Booth, 2005, Fariña, 2008). The morphology of the ovaries is significantly different from other teleosts (Alfonso-Dias and Hislop, 1996). A very long gelatinous ribbon-like matrix characterized the ovaries interior, in which mature eggs float individually in separate chambers (Alfonso-Dias and Hislop, 1996). Even if spawning behavior for *Lophius* spp. is not well documented, it is generally believed that a long trailing egg mass is released when spawning, which can contain more than a million eggs in fecund females, and the ribbon will float on surface waters (Armstrong et al., 1992; Yoneda et al., 2001). Moreover, it has been estimated that gonad mass of a mature female in spawning condition could be 35 to 50% of total body mass (Armstrong et al., 1992; Yoneda et al., 2001; Walmsley et al., 2005), this large proportion of body mass demands a commensurately large proportion of the fish energy.

Most of *Lophius* spp. reach their peak in boreal spring or early summer to take advantage of the seasonal plankton bloom (Fariña et al, 2008). For *L. vomerinus*, Griffiths and Hecht (1986) assumed a well-defined summer breeding for the south coast area. However, Walmsley et al. (2005) evaluated annual trends in the gonadosomatic index (GSI) and no significant difference was found between spawning and non-spawning male testes, while female monthly GSI values peaked in September, which coincide with the austral spring in South Africa.

Work conducted by Fariña et al. (2008), which studied the genus *Lophius*, stated that generally females attain sexual maturity at a larger size than males, however, there have been contradictory results relating to this topic for Cape monkfish. In fact, the length-at-50% maturity of *L. vomerinus* is almost identical for both sexes, estimated to be approximately 37 cm that in terms of age is around 6 years (Walmsley et al., 2005). Interestingly, when Marteens and Booth (2005) investigated reproduction of the same species in Namibian waters, they found a different pattern. There was a significant difference between sexes in length and age-at-50% maturity, with females being 58.2 cm and males 39.9 cm, and respectively 8 years and 5 years (Maartens and Booth, 2005).

1.3 *Genypterus capensis*

Genypterus capensis (Smith 1847), commonly known as South African kingklip, is a Southern African endemic, whose genus *Genypterus* is found only in the temperate waters of the southern hemisphere (Hecht, 1976; Japp, 1990). It belongs to the family Ophidiidae and, in keeping with the general characteristics of this family, its body shape is similar to that of eels, with a pink to orange coloration of the head and body, and dark spots and blotches mainly occurring in the dorsal area (Nielsen et al, 1999; Fig. 3). It is closely related to *Genypterus blacodes*, but studies demonstrated enough genetic difference to refuse the hypothesis of a unique species for the Southern Hemisphere in spite of morphological and biological similarities (Japp, 1990).

Fig. 3 Line drawing of kingklip, *Genypterus capensis* (from WWF SASSI, 2019).

Distribution

Genypterus capensis is a deep-water demersal fish, dwelling in benthic habitats, occurring mostly in rocky areas of the shelf and upper continental slope (Macpherson, 1983; DAFF 2016). It is believed that during the day this fish lives in burrows on the sea floor, or alternatively in small holes in the mud or in caves when a rocky substratum is present (Macpherson, 1983). Its distribution range covers a wide swathe of Southern Africa, from north Namibian waters to eastern South Africa borders (Payne, 1985). It lives mostly at depths ranging from 50 to 500 m, however, it has been found as deep as 800 m (DAFF, 2016).

Biology

Genypterus capensis is a carnivorous and nocturnal predator, using ambush or stalking as tactics (Macpherson 1983). Juveniles, which are mostly found in waters shallower than 200 m, feed on crustaceans, benthic fish and squid, whereas adults move offshore in to deeper waters and feed almost exclusively on demersal fish species, in particular, the ones with a marked day-night migration

(Macpherson, 1983; DAFF, 2016). Slow growth and long life are characteristic of this species, a 25-year-old specimen was found in the waters off South Africa, with a maximum length of 150 cm (Japp, 1990).

Management and history of *G. capensis*

Genypterus capensis is well known for its white flavory meat and low-in-fat flesh, which made it a popular delicacy in South African restaurants. It is commonly found in retail outlets, where it is prone to be mislabeled as *G. blacodes* (Cawthorn et al., 2012). This mislabeling could potentially have a dangerous impact on the species, whose abundance could be misread by the public and undermine the conservation effort of the fish (Cawthorn et al., 2012). Currently, it is mainly fished as incidental by-catch in the hake trawl and Cape hake longline fisheries (DAFF, 2016). The SASSI list makes a distinction in sustainability between the kingklip from the two fisheries, considering the product from longlining more environmental-friendly than trawl (WWF SASSI, 2019).

Genypterus capensis as by-catch in hake trawling activities was first recorded in 1932 (Fig. 4). A slow but gradual increase in catches was present in the next few decades, until a kingklip-directed longline fishery was opened in 1983. In 1986, catches spiked to 11 000 t and after this peak a dramatic decline took place in the next four years, recording a total catch as low as 2500 t. At this stage, studies demonstrated that the spawning biomass estimate was between 23 to 40% of pre-exploitation and further research confirmed the assumption of overexploitation (Punt and Japp, 1994). Hence, the longline direct fishery was closed in 1990.

Clear seasonal pattern in catches were noticed during 1980s and an aggregating behavior theory for the South Coast was reported (Japp, 1989). Indeed, aggregating behavior is characteristic of the Ophidiidae and it has been reported in the New Zealand ling (name for kingklip in NZ) fishery by Roberts (1987) and this is purported to be the reason why fishermen had sensible seasonal increases in catches. However, besides these profitable catches, fishing was removing mainly spawner individuals, leading inevitably to a collapse (Punt and Japp 1994).

After closure, trawl sectors experienced constant growth up to 2002, after which another decline affected the catches. This decline eventually showed the need of better management tools, so in 2006 a PUCL was introduced. This system is a total by-catch limit for all hake fishery sectors combined and it was set at 3000 t. Currently, a 5264 t PUCL is active from 2014 fishing season as a total bycatch for trawl and longline fisheries. This amount was modified after the RY assessment of 2013.

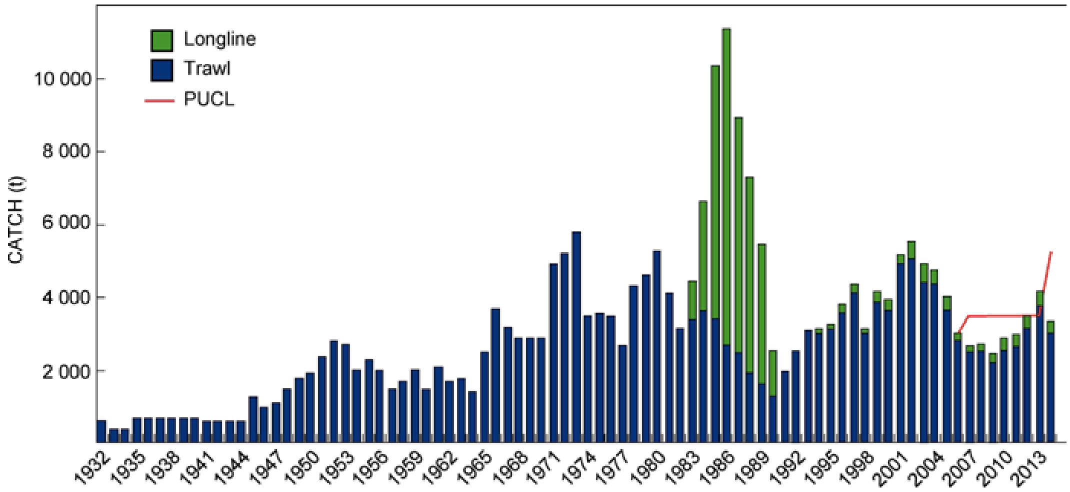

Fig. 4 Annual catches of *Genypterus capensis* (tons) landed by the hake trawl and longline fishery for the period 1932–2014, and the Precautionary Upper Catch Limit (PUCL) that was introduced in 2006 (DAFF, 2016).

Stock structure

The number of *G. capensis* stocks present in South African waters is still under dispute. Morphometric, otolith shape and differences in growth rates suggest the presence of two separate stocks: west coast and south coast (Japp, 1990, Punt and Japp, 1994). However, Grant and Leslie (2005) analysis of allozyme markers resulted in one stock structure hypothesis. Nevertheless, a recent breakthrough was achieved by Henrique et al. (2017), whose research identified genetic sub-structuring in the *G. capensis* population, detecting two distinct sub-populations in South African waters. In the same study, the hypothesis of a decrease in population size and genetic diversity due to past fishing depletion has been reinforced.

Two stocks approach shows a depleted but relatively healthy stock on the west coast and a fully exploited stock on the South Coast (Punt and Japp, 1994; Brandão and Butterworth, 2008). Abundance estimates from DAFF (2016) indicate a slight increase in abundance during the last years, and if the analysis is made with the single population theory, the stock appears in better condition. This is the reason why, without further revisions and updates, the management of kingklip has been based on the one population principle (de Moor et al., 2015).

Reproduction

Much of the knowledge gained regarding *G. capensis* spawning patterns can be attributed to Japp (1989) who described different lengths and ages-at-50% maturity for both sexes depending on the spatial distribution. On the west coast, male fish are approximately 65.5 cm and 4.8 years at 50%

maturity. Females, instead, are 81 cm and 6.5 years. On the South Coast, length-at-50% maturity is 62 cm and age 4.4 years for males, while for females is 72.5 cm and 5.6 years. Peak spawning is believed to be between June and September, but covering a longer period starting in autumn and finishing in spring (Japp, 1989).

Larval stages are subjected to considerable variability in surface water temperature, depending on spatial distribution: on the Agulhas Bank, larvae have been recorded from April-May (temperature decrease) to November–December (temperature increase), with the highest concentration when water temperature is lowest (Olivar and Sabates, 1989). On the west coast however, they are influenced by upwelling. Hence, they start appearing in May when upwelling normally decreases and diminishing when upwelling intensity increases in October and disappearing in December (Olivar and Sabates, 1989).

Even if a mating ground was recognized on the south coast, the possibility of one on the west coast is strong. Given the widely demonstrated aggregation mating behavior characteristic of *Genypterus* spp., it makes the population vulnerable to fishing, as shown by the long-lining seasonal success. As a consequence, to protect the spawning stock and to enhance recovery, an area on the shelf edge near Port Elizabeth has been seasonally closed since 2008 (DAFF, 2016).

The deep-sea is a challenging environment, and fish may experience difficulties in finding a mate (Mead et al., 1964). *Genypterus capensis* is a benthic species and noticing that males maintain a higher average GSI than females, it is believed that a state of "readiness" is characteristic of males in order to maximize the success of mating (Japp, 1989). Moreover, Japp (1989) showed that males have bigger and more used inner drumming muscles than females. These muscles are attached to the swim bladder and they have a sound producing function. It is believed by the same author that drumming muscles are needed to locate mates in low light habitats. As a matter of fact, not only this feature is common to other Ophidiids, but it is also a characteristic of the genus (Marshall, 1960; Courtenay, 1971).

1.4 The importance of length-at-50% maturity

Fish stock assessments are used by scientists to provide decision makers valuable and usable information on fish population health, to facilitate informed decision making regarding the management of the resources (Cooper, 2006). Stock assessments are based on availability of data and they can range from basic to very complex depending on the type and amount of information put into the model (Cooper, 2006).

Where comprehensive assessments of fish populations are not feasible due to constraints on resources/time etc. then analysis of fish length, sex and maturity stage provide valuable insight for fisheries management. These characteristics can give a fair overview of the fishery without large use of resources and time, due to the relatively easy collection process (Reynolds et al., 2005).

Length-at-50% maturity (L_{50}), which is defined as the total length at which 50% of the adult individuals in a population reach sexual maturity, is broadly considered an indicator for changes in fish populations yielded by fishing pressure (Chen and Paloheimo, 1994).

It is shown that fishing pressure can affect size distribution, causing a reduction in large individuals, which are the most fecund fish and also the most effective spawners (Hutchings and Reynolds, 2004; Olsen et al., 2004, 2005). Moreover, this pressure could, over significant time scales, begin to play a role in evolutionary changes towards a smaller L_{50}, yielding long-term negative effects on fish harvests (Law and Grey, 1989).

More in-depth, knowledge of reproductive patterns of fish species (i.e. fecundity and L_{50}) would make it possible to estimate the reproductive potential and the resource renewal rate in the species studied; these features are considered essential to understand the dynamics of fish populations (Japp, 1989).

In particular, for species that have slow growth rates and moderately late maturity, this information is essential. In fact, the proportion of the catch accounted for by juvenile and sexually immature fish, must be considered in terms of recruitment-overfishing and the future collapse of the fishery (Walmsley et al., 2005).

In South Africa, the main fisheries resources have been examined with a mixture of assessments, most of which relate directly to the data available (de Moor, 2015). *Lophius vomerinus* has little or no length/age data available, so this species has been assessed with simple replacement yield (RY) models. On the other hand, RY model for *Genypterus capensis* has been used only for the most recent assessment, being proportion-at-length data not updated yet (de Moor et al., 2015).

Although these assessments provide valuable indications for fisheries management, they lack sufficient complexity to provide information for better management standards (de Moor et al., 2015). It stands to reason, that increasing volumes of sound scientific and biological information available to the model, yield outputs of higher accuracy, precision and complexity. A basic level of survey, which may possess sufficient complexity for use in management decisions, may include examination of length distribution data and other biological information such as length at 50% maturity (de Moor et al., 2015).

Length at sexual maturity is vital information for management and it is influenced by exploitation patterns and fishing pressure, causing genetic modification to assure the survival of the species (Kvamme and Bogstad, 2007; Lowerre-Barbieri et al., 2011a). Hence, length-at-maturity would indicate if any changes in reproductive dynamics have taken place, showing possibly better or worse condition of the stock studied. Moreover, length-at-maturity helps to better understand species recruitment and, in terms of management, ensure that juvenile fish reach sexual maturity and are able to undergo at least one reproductive cycle (Karna and Panda, 2012).

1.5 Study objective

This study aims to investigate the reproductive dynamics of South African monkfish, *Lophius vomerinus*, and kingklip, *Genypterus capensis*, through biological information, by specifically calculating length-at-50% maturity (L_{50}) using historical data collected by DAFF during the annual demersal survey of the west and south coast of South Africa.

L_{50} will be estimated for west and south coast samples for both sexes and species. Afterwards, a comparison between coasts estimates will be performed to detect any significant difference among areas. This will be the first study of this type for *L. vomerinus*. Moreover, the results will be compared with previous studies of the same species found in literature. The ultimate goal of this study is to provide updated information for stock assessment models to support sustainable management of these two important by-catch species of South Africa.

2. METHODS

2.1 Study area

The study area was the west coast and south coast of South Africa: the former is the area between the Orange Mouth river and Cape Agulhas (20°E), while the latter is from Cape Agulhas to Port Alfred (27°E).

The west coast abuts the Atlantic Ocean where the nutrient-rich Southern Benguela Region assures high productivity due to the southeasterly (summer) and northwesterly (winter) wind driven upwelling (Andrews and Hutchings, 1980; Fig. 5). Upwelling systems are associated with high biological productivity and important fisheries resources. The Benguela system supports most of South Africa's commercial fisheries (Shannon, 1985).

The east coast, instead, borders by the Indian Ocean and the warm, fast flowing Agulhas Current coming from the equatorial Indian Ocean, whose tropical water favors biodiversity, but not productivity (Lutjeharms, 2007). The east coast is characterized by the proximity of the continental shelf, which widens close to East London and forces the current offshore. At this point, the current retroflects and creates a transition zone between the two ocean currents (Lutjeharms, 2007). This transition zone, which is located on the south coast is characterised by the underlying Agulhas Bank, a large shallow bank that has a high natural importance. Not only is this region one of the most important mating aggregation sites for pelagic species in South African waters, but occasional upwellings encourage productive fishing areas (Gründlingh, 1983; Lutijeharms et al., 2000; Hutchings et al., 2009; Fig. 5).

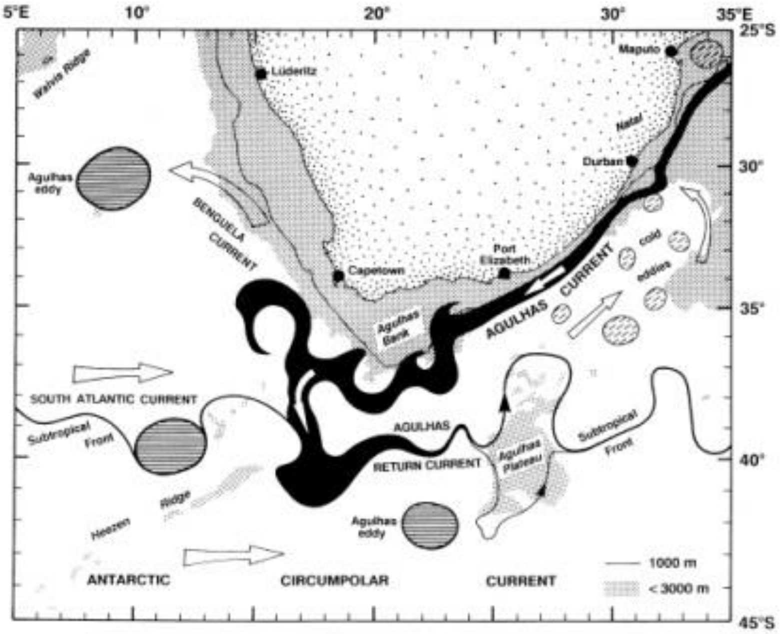

Fig. 5 Overview of South Africa major currents. Benguela Current northward direction characterizes the west coast, while Agulhas Current southward flow and consequent retroflection characterize the east and south coast. Arrows indicate the direction of the current (from Peterson and Stramma, 1991).

2.2 Sampling

Samples of *L. vomerinus* and *G. capensis* were collected by DAFF research cruises annually during demersal surveys designed to estimate Cape Hakes abundance, from 1984 to 2017, using the swept area method (Sparre, 1998). Cruises were performed during the months of January, February, June, July and August every year on the west Coast, and between March and October every year on the South Coast. The most consistent data for the west coast were recorded during the summer surveys, which cover the months of January and February, annually. The winter cruises (June, July and August) took place less regularly and were eventually lost due to budget constraints (DAFF, pers. Comm. 2018). The same is valid for the south coast, where irregularity and scarcity in winter surveys could not provide the same amount of data as summer surveys (Fig. 6).

Samples were collected by means of stratified bottom trawling covering different substrata for depths from 0 to 1000 m, based on the selection of random stations provided for each depth stratum. The method involves a pseudo-random stratified selection of trawling positions at intervals along the coast, with the number of stations per depth and longitude being directly proportional to the area of each stratum.

Once collected samples were bagged, labeled and frozen on board each vessel and transported to the Department of Agriculture, Forestry and Fisheries freezers in Cape Town for later dissection. Prior to dissection samples were allowed to defrost, and subsequently sexed, measured to the closest cm (TL) and weighted to the closest g. Gonads were extracted, staged and weighted to the closest 0.1 g.

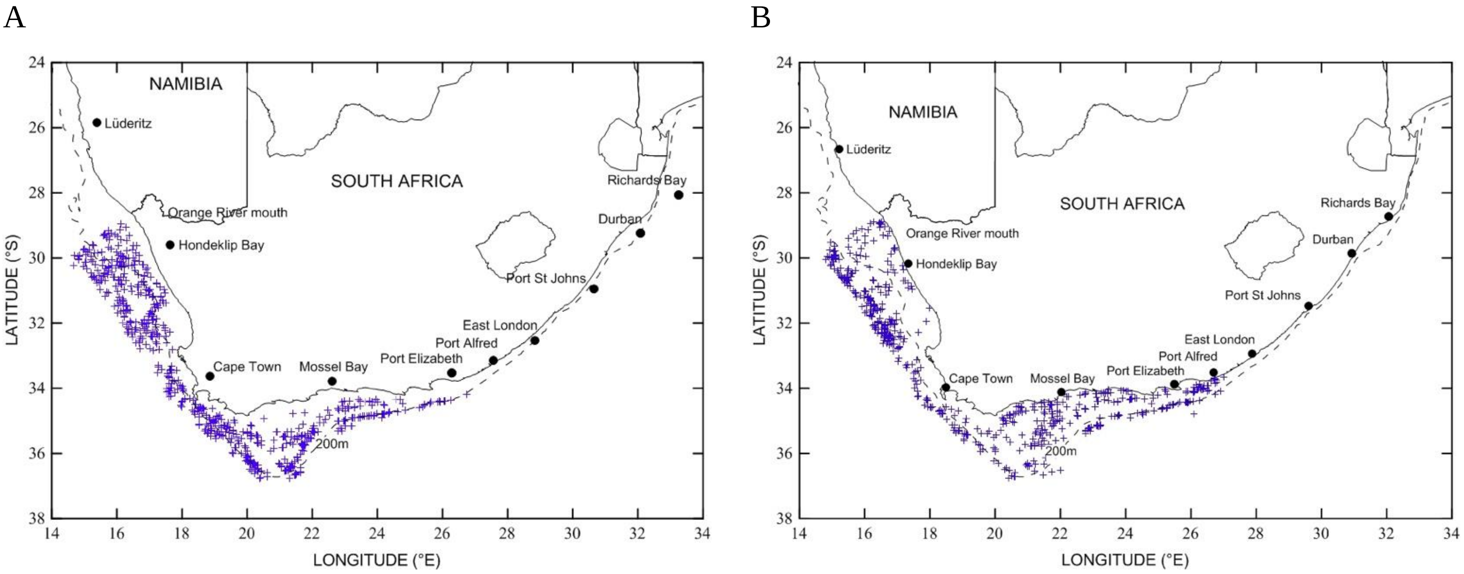

Fig. 6 Maps of Southern Africa showing the location of transects performed during annual DAFF Demersal surveys, where *L. vomerinus* (A) and *G. capensis* (B) were sampled from 1984 to 2017.

2.3 Data Analysis

Lophius vomerinus and *G. capensis* datasets included respectively 6437 and 6397 individuals at first analysis. However, some exclusions needed to be made to improve data quality. Data from the 1980s did not seem consistent and were therefore excluded from this analysis. The final dataset included 5141 individuals of *L. vomerinus* and 4097 *G. capensis*.

Length frequency distributions per 4 cm interval class were calculated for both species (Neumann et al., 2012). Sex ratios were computed per interval class and tested by means of a contingency table to verify the null hypothesis of no difference from 1:1 sex ratio. Mean lengths (TL, cm) for each species, coast and sex were tested for significant differences using a sample t-test.

The Length-Weight relationship (LWR) was calculated for both species, disaggregated by sex and coast. This was achieved by plotting the untransformed total length (TL, cm) versus wet body mass (g). A least-squares regression was fitted using the equation:

$$\ln W = a + \ln TL\ b \tag{1}$$

Where W is the wet body mass of the fish and TL is the total length, while a and b are the estimated parameters of the LWR (Marquardt, 1963). Influence of sex and coast on Length-Weight relationships were tested with Anova F-statistic. For *G. capensis* no outliers were found, whereas for *L. vomerinus* outliers were found and excluded from the dataset.

LWR parameter b was used to analyze allometric growth and differences between sexes and areas. Both parameters were used to calculate condition factor, from the formula:

$$CF = W/aTL^{\wedge}b \tag{2}$$

Where CF is condition factor.

2.4 Length-at-50% maturity

For sexual maturity, a macroscopic gonad assessment was performed, and the individuals were staged by the criteria reported in Table 1, after visual inspection of the gonads. Although the maturity scales were based on 5 levels, the dataset included recordings of stages 6 for kingklip and 6 and 7 for monkfish. Hence, to standardize the maturity stages, some modifications were made. For the former, 81 females and 9 males individuals staged as 6 were re-staged as 5. It was assumed that stage 6 were spent ovaries, as the last stage of a 6 stages scale. For those assessed on a 7-stage maturity scale, stage 6 was assumed to be stage 4 on a 5 stages scale, while stage 7 corresponded to stage 5. So, 333 females and 2 males were reclassified as stage 4.

The gonadosomatic index (GSI) was calculated for each individual from both species to allow collection of information on spawning condition and season. The following formula was used:

$$GSI=(G/W\text{-}G) *100 \tag{3}$$

Where G is the mass of the gonad (g) and W is the total wet weight (g).

Length-at-50% maturity (L_{50}) was calculated for each species disaggregated by sex and area, using a logistic curve fitted to the data, based on the binomial nature of the logistic regression. All fishes in stage 1 were considered immature and fishes in stages 2 to 5 were regarded as mature (Table 1). Maturity ogives were plotted under these assumptions and by calculating the predicted proportion of fish mature (p^i) at each 4 cm length-class (Li) from the logistic:

$$P(L_j)= \frac{1}{1+e^{\beta 0+\beta 1 Lj}} \tag{4}$$

Where $P(L_j)$ is the proportion of mature individuals in the size interval j, β_0 and β_1 the intercept and slope parameters of the logistic function. To find the best parameters of the model, iteratively weighted least squares method (IRLS) was used (Green, 1984).

Confidence intervals were found using the likelihood profile method. These were calculated by finding minimum and maximum values of all coefficient sets that satisfied the following:

$$-2\log\left(\frac{L(\beta 0,\beta 1|y1,\ldots,yn)}{L(\beta 0,\beta 1|y1,\ldots,yn)}\right) < \chi^2{}_{1,1-\alpha} \qquad (5)$$

Where the denominator is the likelihood of the model and the numerator is the likelihood of the same model with different coefficients. The result of this calculation is the likelihood ratio test (LRT) statistic, which is based on the asymptotic chi-square distribution.

To get the estimate for L_{50}, equation 4 was solved for x and then p=0.5 was put in the equation:

$$X = \frac{\ln\left(\frac{p}{1-p}\right) - \beta 1}{\beta 2} \qquad (6)$$

Leaving the following equation:

$$L_{50} = -\frac{\beta 1}{\beta 2} \qquad (7)$$

For $L_{50\%}$, confidence intervals were formed by computing L_{50} function for each bootstrap sample and then extracting the values for the upper and lower 2.5% of L_{50}. To test the influence of the sex and coasts on the models, a likelihood ratio test (LRT) was computed. Data analysis was performed in Microsoft Excel (2013) and statistics were done using R 3.5.1 (R Core Team, 2018), the FSA (Ogle et al., 2018) and car package (Fox and Weisberg, 2011).

Table 1 Maturity scales for gonads visual assessment for *L. vomerinus* (A) and *G. capensis* (B) (DAFF, unpublished).

A

Stage	**Maturation**	**Ovaries description**	**Testis description**
1	Juvenile	Ovaries very narrow (<2cm), thin and ribbonlike. Translucent, no vascularization or oocyte clusters can be seen.	Testes long and narrow tube-like (<1cm), translucent, medial seminiferous duct is distinct and with no visible vascularization.
2	Developing virgin/ Resting spent	Ovaries wider (2-4cm) and less translucent, visible vascularization, no visible oocyte clusters. Ovaries occupy roughly the same space as the intestine	Testes flattened tubular and wider than stage 1, creamy, opaque. Blood vessels visible around the medial seminiferous duct. Testes occupy roughly ½ the space occupied by the intestine.
3	Ripening	Ribbonlike, highly vascularized, individual oocyte clusters visible embedded in gelatinous matrix. Ovaries occupy most of the abdominal cavity	Testes very firm texture, milt is produced when dissected, but testes do not run under pressure. Seminiferous duct highly vascularized. Testes still occupy less space than the intestine
4	Ripe/running	Ovaries extremely long (>6m) and wide (>30cm) Ovaries highly vascularized, oocytes hyaline, round and gelatinous with yellow-brown center, look like frog spawn.	Milt runs on slight pressure. Large amounts of milt are produced when dissected.
5	Spent	Ovaries flaccid and opaque, with longitudinal striations, still very wide (10-15cm) and highly vascularized. Some oocytes might still be present	Testes very flaccid, can have bruised appearance. Some milt often presents in seminiferous duct. Testes still highly vascularized near seminiferous duct.

B

Stage	**Maturation**	**Ovaries description**	**Testis description**
1	Immature inactive	Ovary is small, globular and light pink, the tunica is transparent, no eggs can be distinguished	Almost transparent thin and threadlike
2	Mature inactive	Ovary is larger and speckled with minute eggs hardly visible with the naked eye, the tunica is now opaque (whitish), and in some cases dark red or violet	Elongated, cylindrical, creamy white and opaque
3	Mature active	Ovary is distended and filled with eggs, eggs are small but can be easily seen through the tunica, the tunica is opaque and has a speckled appearance, it is often translucent and may have an orange or deep pink color, it is often bloodshot	Larger than previous stage, still creamy white and opaque, testes bulky and lumpy, often bloodshot
4	Mature Ripe and running	Eggs are large and translucent, with slight pressure eggs run out of ovisac which is bloodshot	Similar to stage 3 except sperm flows under slight pressure, testes bloodshot
5	Mature spent	Deflated and bloodshot	Testes deflated and darker in color

3. RESULTS

3.1 *Lophius vomerinus*

Sample size

Lophius vomerinus individuals were counted for year, month, and sex, based on their area of sampling. A total of 3367 *L. vomerinus* samples were analysed from the west coast, of which 1807 (size range: 14-101 cm) were female and 1560 (size range: 18-83cm) were male (Table 2). A total of 1774 *L. vomerinus* samples were analysed from the south coast, of which 928 (size range: 18-96 cm) were female and 846 (size range: 16-69 cm) were male (Table 3).

Samples of the west coast were collected from 1990 to 2012, skipping 1998, 2001 and 2002. After 2012, the only year sampled was 2017. Of the months sampled, the majority of specimens were recorded in January and February, whereas June, July and August had a significant lower number of individuals (Table 2). On the South Coast, specimens were collected from 1991 to 2011, skipping 1998 and 2002. After 2011, only 2016 was sampled. The months of collection were from March to October, with the highest number of individuals in April, followed by September and May (Table 3).

Table 2 Number of *L. vomerinus* individuals collected off the west coast of South Africa from 1990 to 2017 disaggregated by year of collection, month and sex. F = female; M = male; - = no samples

Month	**January**		**February**		**June**		**July**		**August**	
Year	F	M	F	M	F	M	F	M	F	M
1990	20	22	-	1	-	3	6	3	12	3
1991	59	45	-	11	-	2	-	2	-	-
1992	-	29	41	13	-	1	-	3	-	3
1993	28	45	29	14	-	-	-	6	-	-
1994	68	52	-	9	-	-	-	4	-	1
1995	81	60	-	14	-	1	-	1	-	2
1996	14	39	52	16	-	-	-	1	-	3
1997	63	38	-	3	-	2	-	2	-	-
1999	67	44	2	7	-	-	-	-	-	-
2000	17	41	33	8	-	-	-	-	-	1
2003	38	37	30	12	-	1	-	3	-	3
2004	68	68	16	20	-	2	-	5	-	6
2005	37	25	-	6	-	-	-	-	-	-
2006	106	99	30	20	-	1	-	1	-	-
2007	63	26	-	8	-	1	-	2	-	-
2008	94	63	-	11	-	1	-	3	-	3
2009	67	63	23	22	-	-	-	1	-	2
2010	69	67	26	16	-	-	-	1	-	-
2011	81	82	57	17	-	2	-	3	-	2
2012	218	135	45	39	-	2	-	12	-	6
2017	98	87	49	14	-	-	-	3	-	2
Total	**1356**	**1167**	**433**	**281**	**-**	**19**	**6**	**56**	**12**	**37**

Table 3 Number of *Lophius vomerinus* individuals collected off the south coast of South Africa from 1991 to 2016 disaggregated by year of collection, month and sex. F = female; M = male; - = no samples

Month	**March**		**April**		**May**		**June**		**July**		**August**		**September**		**October**	
Year	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
1991	-	-	-	4	-	1	12	1	-	-	-	-	-	2	-	-
1992	-	-	22	4	-	7	-	1	-	1	-	-	7	3	-	3
1993	-	-	36	31	5	3	-	-	-	-	-	-	19	-	-	3
1994	-	2	-	18	-	2	22	1	1	-	-	1	1	7	8	2
1995	-	-	24	17	10	7	-	2	-	-	-	-	-	7	21	3
1996	-	-	29	19	-	1	-	1	-	-	-	-	-	3	-	1
1997	-	-	10	4	1	5	-	-	-	-	-	-	-	7	-	1
1999	-	1	43	8	5	8	-	-	-	-	-	1	-	5	-	4
2000	-	-	-	-	4	1	-	-	-	-	-	1	-	1	-	2
2001	-	-	-	3	-	3	-	2	-	-	8	2	9	2	-	3
2003	-	-	22	21	-	6	-	2	-	-	14	1	11	5	-	-
2004	13	-	1	5	-	1	-	2	-	-	-	-	5	8	2	5
2005	-	-	49	21	-	3	-		-	-	-	-	-	9	-	11
2006	-	3	17	44	25	11	-	2	-	1	-	2	46	19	-	7
2007	-	-	92	66	1	17	-	2	-	1	-	2	-	13	35	3
2008	-	-	49	102	20	16	-		-	-	-	1	38	10	-	5
2009	-	-	75	28	8	11	-	2	-	1	-	2	-	12	-	5
2010	-	-	15	8	23	8	-	3	-	-	-	1	-	7	-	6
2011	-	-	37	29	11	11	-	3	-	-	-	-	-	14	-	4
2016	-	-	-	11	-	6	-	2	-	-	-	3	16	13	6	7
Total	**13**	**6**	**521**	**443**	**113**	**128**	**34**	**26**	**1**	**4**	**22**	**17**	**152**	**147**	**72**	**75**

Frequency distributions for length class (4 cm) of *L. vomerinus* showed that the largest specimens collected were females for both the west and south coasts. Male size distribution was normal on both coasts, whereas female distribution was slightly skewed to the left, particularly on the west coast where females dominated the length classes greater than 58 cm (Fig. 7-A). On the south coast, females dominate size classes greater than 62 cm (Fig. 7-B).

Mean lengths were greater on the South Coast for both sexes: 43.8 ±13.2 cm and 50.3 ±13.6 cm for females, 40.2 ±9.4 cm and 46.2 ±8.9 cm for males.

The results from the two-sample t-test showed a significant difference between the mean lengths of female and male samples from the west coast and that of the south coast (Females: t= -11.93867371; df=2733; p<0.05; Male= t= -15.2039; df= 2404; p<0.05)

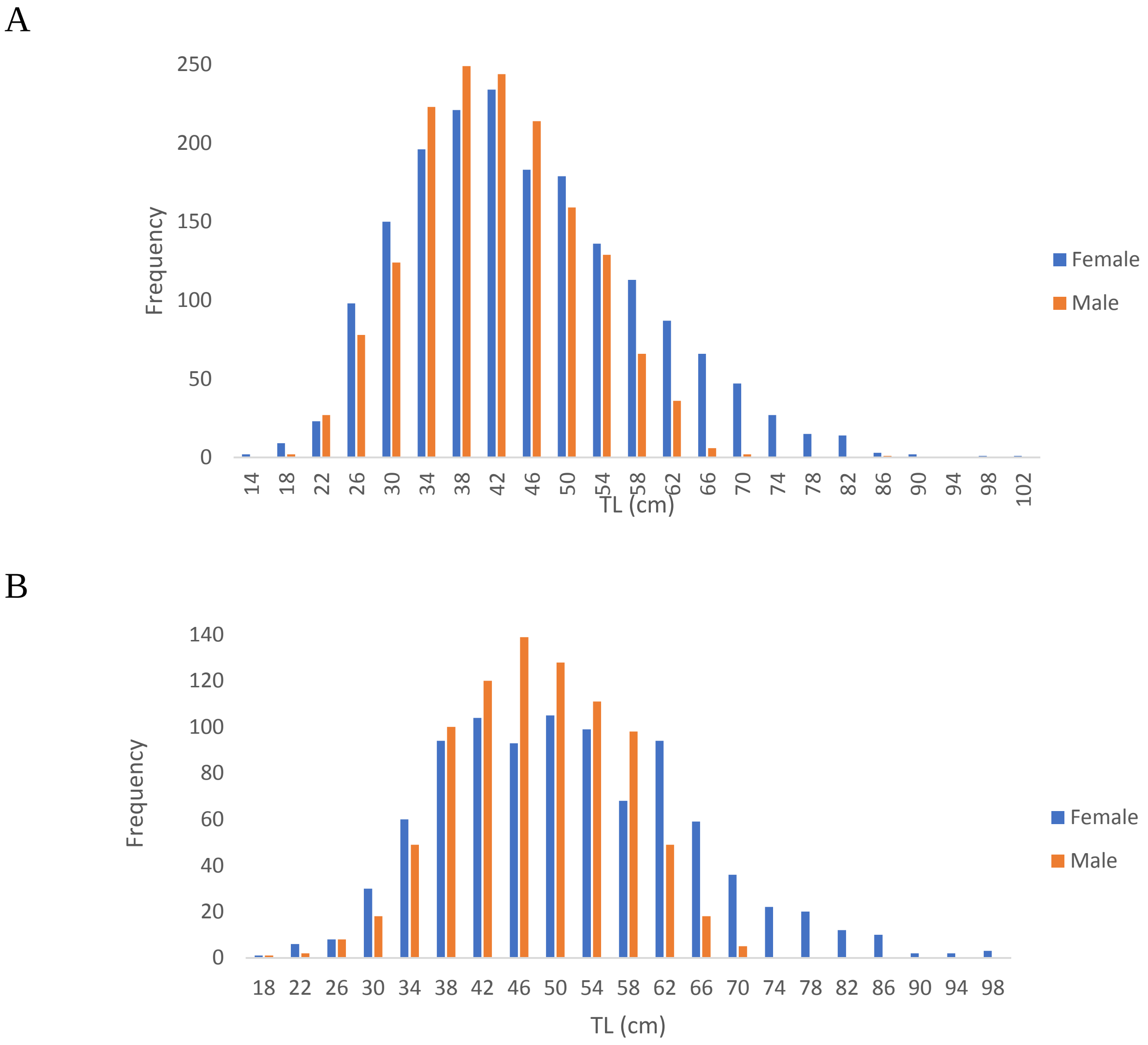

Fig. 7 Length distribution for *L. vomerinus* for female and male specimens on the west (A) and south coast (B) collected off the coast of South Africa from 1990 to 2017.

Sex ratio and Length-Weight relationship

According to overall sex ratio analysis, chi-square contingency tables showed a significant difference from the expected 1:1 (F/M) ratio (χ^2= 21.054, df = 1, p<0.05). This female inclined ratio was confirmed on the west coast, where it was 1.16 female for 1 male (χ^2= 18.12, df=1, p<0.05). On the south coast, however, sex ratio was 1.1:1 (χ^2=3.7903, df=1, p=0.515), and therefore with no significant difference from 1:1 ratio. When sex ratio for length classes was visually inspected, a dominance of females in the higher classes was reported (Fig. 8).

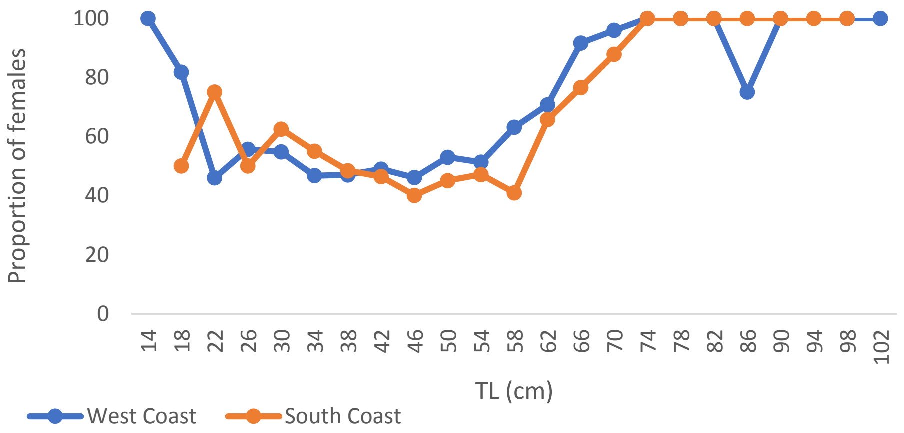

Fig. 8 Percentages of females per length class for *L. vomerinus* collected off the coast of South Africa from 1990 to 2017.

Length-Weight relationships were plotted (Fig. 9). When all samples were included, ANOVA showed that sex contributed significantly to the differences in Length-Weight relationship (F=150.88, df_1=1, df_2=5137, p<0.05). Successively, the influence of the coast was tested for each sex with ANOVA. Coast factor also contributed significantly for females (F=25.158, df_1=1, df_2=2731, p<0.05), but not for males (F=2.556, df_1=1, df_2=2402, p=0.11).

The values of exponent b were checked to verify allometric and isometric growth. When the 95% confidence interval of b included 3, isometric growth was assumed, if not, positive or negative allometric growth were reported. Only females on the south coast showed isometric growth whilst all others showed negative allometric growth (b<3, Table 4).

Table 4 Length-weight relationships (LWR) equation parameters a and b and R^2 for each sex and coast of origin for *L. vomerinus* collected off the west and south coasts of South Africa from 1990 to 2017. WC = west coast; SC = south coast.

	a	**b**	**R^2**
Female WC	0.022	2.9061	0.976
Female SC	0.015	3.0141	0.971
Male WC	0.0233	2.8789	0.957
Male SC	0.0199	2.9237	0.952

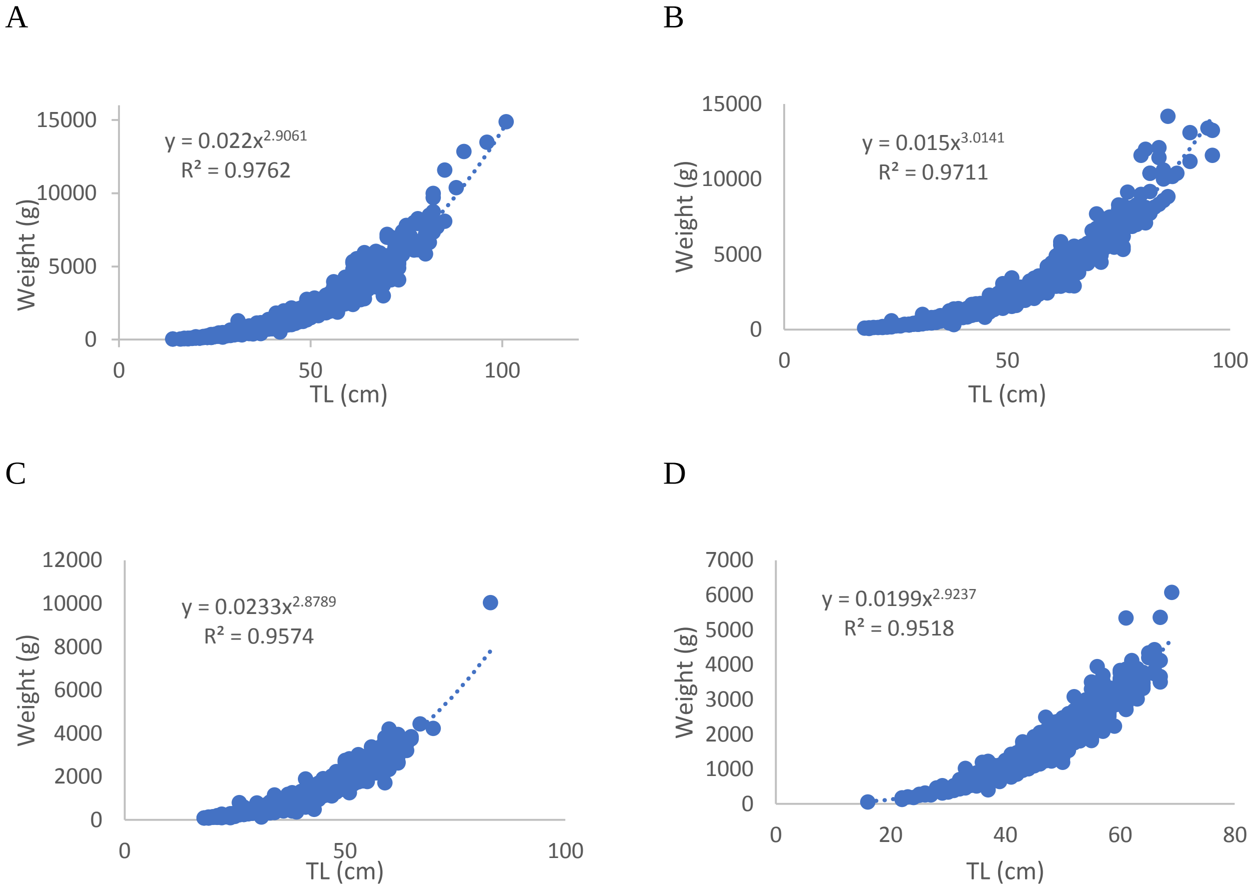

Fig. 9 Length-weight relationships for *Lophius vomerinus* females on the west coast (A) and south coast (B) and males on the west (C) and south coast (D) collected off South Africa from 1990 to 2017.

Spawning season

The percentage of individuals per each maturity stage was calculated per month over all years collected. On the west coast, the largest percentage of male *L. vomerinus* were classed as stage 1 (20.5%) and stage 2 (68.5%). The highest percentage of female *L. vomerinus* sampled in January and February was classed as stage 1, respectively 46.3 and 31.6% of the month total. February had high proportion of females staged 4 (25.6%) and 5 (17.1) (Table 5).

On the south coast, the largest percentage of male *L. vomerinus* were classed as stage 2 (66.3%), followed by stage 3 and 1, respectively 14.4 and 12.2%. *L. vomerinus* females were mostly classed as stage 1 (27.9%) and 2 (34.3%). April, September and October were the months with the highest proportion of females in maturity stages greater than 2. More than half of the fishes found in March were in stage 5, however the small sample size (n=13) did not make it significant (Table 6).

Table 5 Percentage of individuals per maturity stage: proportions are divided by sex, month and area of collection for *Lophius vomerinus* collected off the west coast of South Africa from 1990 to 2017.

	January		**February**		**June**		**July**		**August**		**Total**	
Maturity stage	F	M	F	M	F	M	F	M	F	M	F	M
1	46.3	21.7	31.6	17.8	-	15.8	100	16.1	91.7	10.8	43.2	20.5
2	27.7	66.7	21.3	69.0	-	84.2	0.0	83.9	8.3	89.2	26.0	68.5
3	3.8	6.5	4.4	6.4	-	0.0	0.0	0.0	0.0	0.0	3.9	6.0
4	10.8	2.0	25.6	5.4	-	0.0	0.0	0.0	0.0	0.0	14.2	2.4
5	11.4	3.1	17.1	1.4	-	0.0	0.0	0.0	0.0	0.0	12.7	2.6

Table 6 Percentage of individuals per maturity stage: proportions are divided by sex, month and area of collection for *Lophius vomerinus* collected off the south coasts of South Africa from 1991 to 2016.

	March		**April**		**May**		**June**		**July**		**August**		**September**		**October**		**Total**	
Maturity stage	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
1	7.7	0.0	20.5	9.9	29.2	13.3	70.6	11.5	100	0.0	54.5	41.2	30.2	13.6	48.6	16.0	27.9	12.2
2	38.5	50.0	36.5	64.6	42.5	71.1	29.4	84.6	0.0	50.0	9.1	58.8	34.2	61.9	15.3	74.7	34.3	66.3
3	0.0	0.0	6.5	15.1	11.5	14.1	0.0	3.9	0.0	50.0	13.6	0.0	3.3	18.4	8.3	9.3	6.6	14.4
4	0.0	0.0	17.9	0.2	12.4	0.0	0.0	0.0	0.0	0.0	22.7	0.0	14.5	4.1	19.5	0.0	15.9	0.8
5	53.8	50.0	18.6	10.2	4.4	1.6	0.0	0.0	0.0	0.0	0.0	0.0	17.8	2.0	8.3	0.0	15.3	6.3

Mean GSI was calculated per maturity stage for all samples combined, disaggregated by coast (Fig. 10). Results showed that females at maturity stage 3 had the highest GSI values for both the west and south coast samples. Males on the west coast also experienced the highest GSI in stage 3, whereas on the south coast the highest GSI was in stage 4. Females at stage 3 maturity, in each case, showed a higher GSI value when compared to males (Fig. 10 A and B).

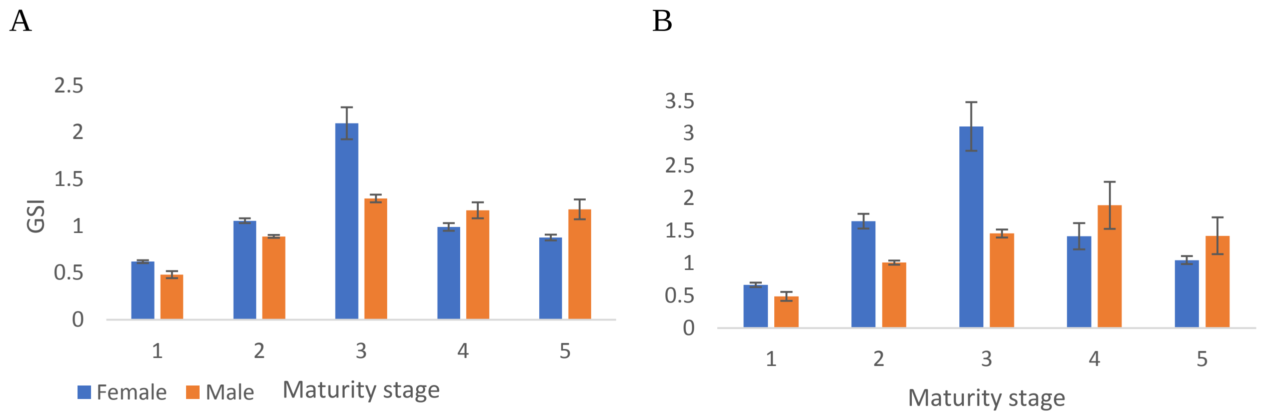

Fig. 10 Mean GSI, with standard errors, for maturity stage for female and male specimens of L. *vomerinus*, from the west coast (A) and south coast (B) collected off the coast of South Africa from 1990 to 2017.

Monthly mean GSI was plotted for all sampled years and for both sexes to identify spawning season (Fig. 11). Female *L. vomerinus* GSI from the west coast ranged between 0.66 and 0.88%. No apparent peak in GSI was seen, likely due to the lack of samples collected during the months February to July. Male *L. vomerinus* GSI on the west coast ranged between 0.73 and 1.08%. A peak was noticed in June. However, the small sample size of this month reduced the significance of the peak (n=19) (Fig. 11-A).

On the south coast, GSI in *L. vomerinus* females show a slight peak for the months of August and September, with GSI values around 2%. A dip in GSI values for females on the west coast can generally be seen every year in July. South coast males, showed two apparent peaks in GSI annually around March and again in July. The sample sizes for these months were, however, small (n_{March}=6, n_{July}=4). Then, a stable pattern around 1% characterized the remaining months (Fig. 11-B).

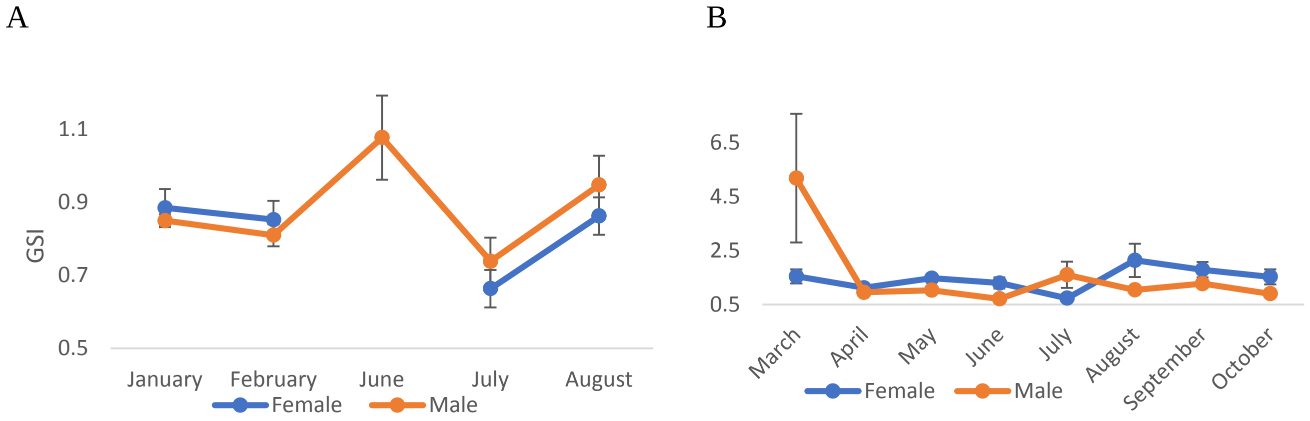

Fig. 11 Mean Gonadosomatic Index (GSI) (with standard errors) by month for for *L. vomerinus* collected off the coast of South Africa from 1990 to 2017. A) West coast; B) South coast.

Condition factor (CF) was lower in July/August than January/February for females on the west coast. Males of the same coast had a steady CF, between 1 and 1.05 (Fig. 12-A). CF on the south coast showed females experiencing two peaks: first one in May and second one in August. Males experienced a low condition in March and a progressive increase until July/August when a peak in condition was reached. Afterwards, CF decreased gradually in September and October (Fig. 12-B).

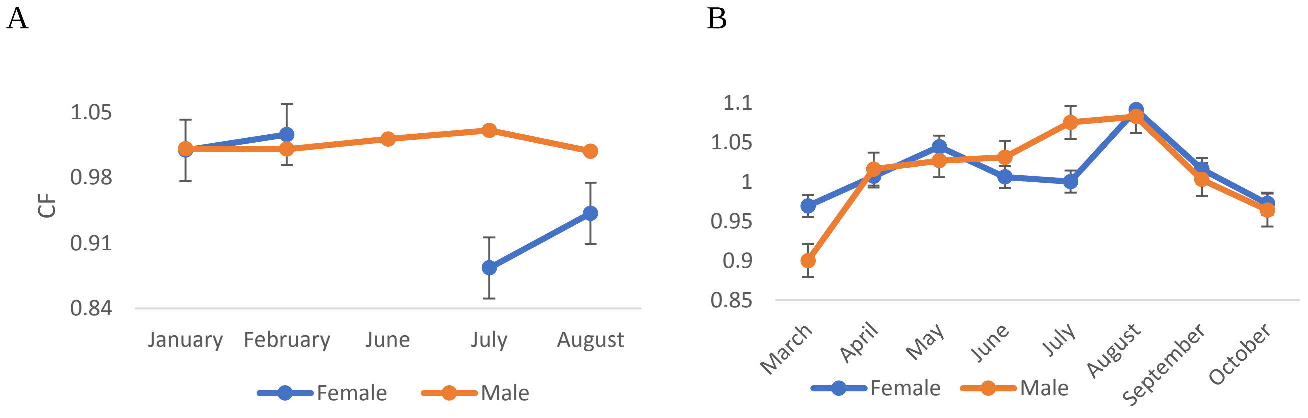

Fig. 12 Mean condition factor (CF) (with standard errors) by month for *L. vomerinus* collected off the coast of South Africa from 1990 to 2017. A) West coast; B) South coast.

Length-at-50% maturity

Maturity ogives were constructed for each sex and coast independently, fitting a logistic curve to the data (Fig. 13). The length-at-50% maturity for females from the west coast was estimated to be 40 cm (95% Confidence interval: 39.22-40.67 cm), whereas on the south coast length-at-50% maturity for females was 38.9 cm (37.45-40.21 cm). For males, 50% of the west coast sample reached maturity at an estimated length of 30.8 cm (30.20-31.38 cm), while on the South Coast 50% of the male's sample reached maturity at 33.4 cm (32.15-34.49 cm).

A likelihood ratio test between ogives of females from different coasts showed no significant differences between the areas ($\chi^2(1)=0.54$, $p=0.46$), whereas for males did ($\chi^2(1)=21.71$, $p<0.05$). A significant difference was found between all males and females, irrespective of coast ($\chi^2(1)= 548.40$, $p<0.05$).

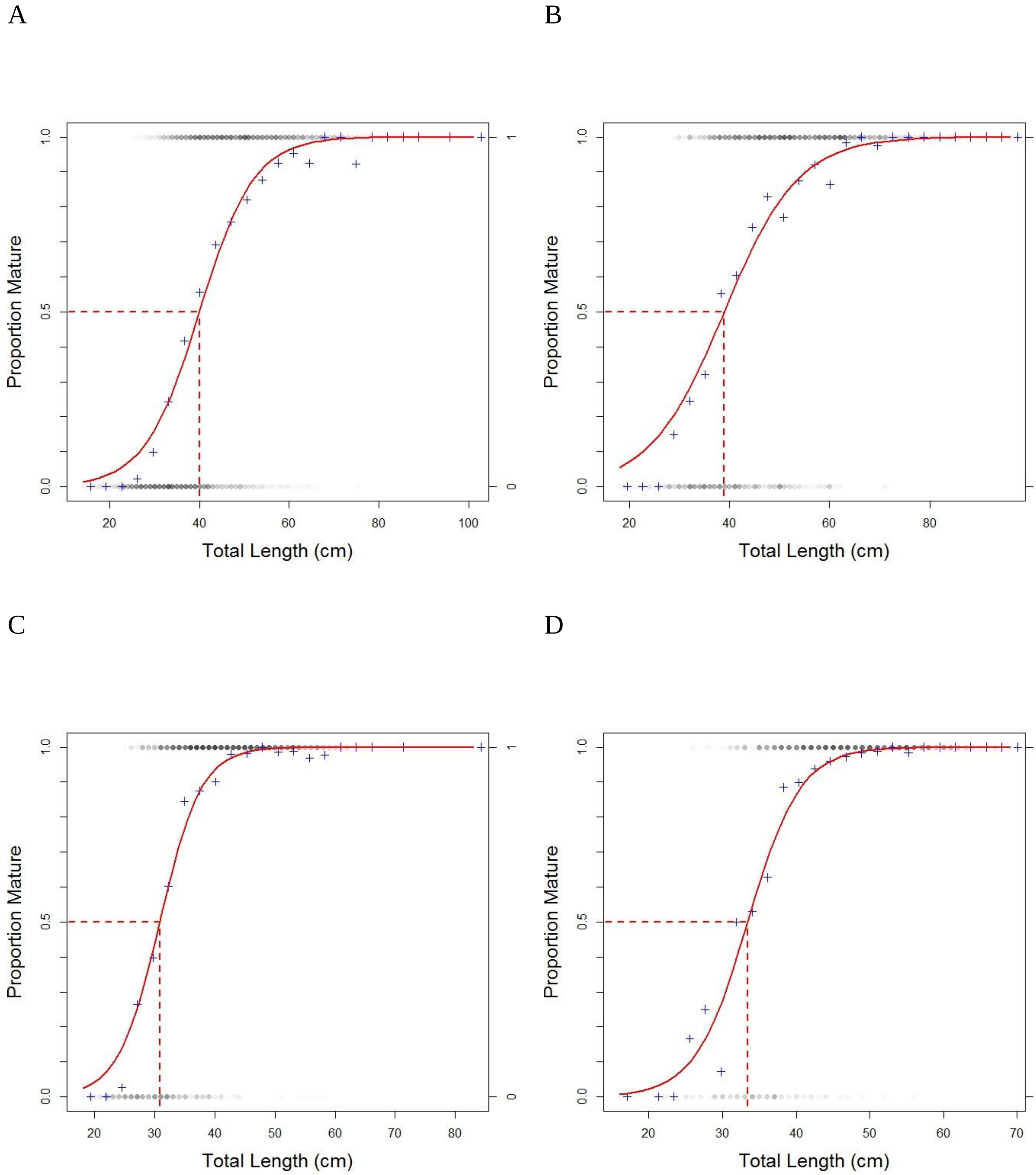

Fig. 13 Maturity ogives for females *L. vomerinus* on the west (A) and south coast (B) and males on the west (C) and south coast (D) collected off the coast of South Africa from 1990 to 2017. L_{50} is where dotted lines intercept the logistic curve.

3.2 *Genypterus capensis*

Sample size

Genypterus capensis individuals were counted for year, month, and sex, based on their area of sampling. A total of 2265 *G. capensis* samples were analysed from the west coast, of which 1418 (size range: 20-123 cm) were female and 847 (size range: 20-130cm) were male (Table 7). A total of 1832 *G. capensis* samples were analysed from the south coast, of which 958 (size range: 19-140 cm) were female and 874 (size range: 18-133 cm) were male (Table 8).

Samples of the west coast were collected for the first year in 1990, after which all year but one (1998) were sampled up to 2012. Afterwards, only 2017 survey was performed. Most of the same years were sampled on the south coast. However, data from 2002, 2012 and 2017 are missing, whereas those from 2016 are present.

The most visible difference is the months of surveys: on the west coast, January and February had the most data. South coast sampling provided a longer period, covering months from March to July plus September and October, skipping August.

Table 7 Number of G. *capensis* individuals collected off the west coast of South Africa from 1990 to 2017 disaggregated by year of collection, month and sex. F = female; M = male; - = no samples

Month	**January**		**February**		**July**	
Year	F	M	F	M	F	M
1990	61	40	-	-	5	-
1991	30	20	-	-	-	-
1992	-	-	59	52	-	-
1993	40	19	33	18	-	-
1994	34	26	-	-	-	-
1995	50	15	-	-	-	-
1996	5	5	48	17	-	-
1997	40	19	-	-	-	-
1999	40	24	-	-	-	-
2000	14	20	41	31	-	-
2001	-	-	19	7	-	-
2002	73	30	-	-	-	-
2003	47	19	19	17	-	-
2004	48	37	12	15	-	-
2005	10	15	-	-	-	-
2006	85	81	26	10	-	-
2007	52	32	-	-	-	-
2008	92	43	-	-	-	-
2009	82	25	8	2	-	-
2010	56	29	47	23	-	-
2011	74	41	28	22	-	-
2012	84	54	17	18	-	-
2017	30	16	10	6	-	-
Total	**1047**	**610**	**367**	**238**	**5**	**-**

Table 8 Number of *G.s capensis* individuals collected off the south coast of South Africa from 1990 to 2016 disaggregated by year of collection, month and sex. F = female; M = male; - = no samples

Month	**March**		**April**		**May**		**June**		**July**		**September**		**October**	
Year	F	M	F	M	F	M	F	M	F	M	F	M	F	M
1990	-	-	-	-	44	45	19	25	-	-	-	-	-	-
1991	-	-	-	18	-	-	60	62	-	-	24	24	-	-
1992	-	-	12	10	-	-	-	-	-	-	24	26	-	-
1993	-	-	30	-	26	20	-	-	-	-	6	6	-	-
1994	-	-	-	2	-	-	23	27	7	3	2	8	2	3
1995	-	-	8	10	12	18	-	-	-	-	-	-	3	5
1996	-	-	15	21	-	-	-	-	-	-	-	-	-	-
1997	-	-	40	42	6	15	-	-	-	-	-	-	-	-
1999	-	-	19	-	-	-	-	-	-	-	-	-	-	-
2000	-	-	-	-	15	30	15	7	-	-	-	-	-	-
2001	-	-	-	21	-	-	-	-	-	-	12	18	-	-
2003	-	-	10	12	-	-	-	-	-	-	7	2	-	-
2004	9	1	6	35	-	-	-	-	-	-	-	-	14	7
2005	-	-	34	14	-	-	-	-	-	-	-	-	-	-
2006	-	-	25	47	10	10	-	-	-	-	61	41	-	-
2007	-	-	52	42	7	1	-	-	-	-	-	-	2	8
2008	-	-	52	52	5	5	-	-	-	-	73	34	-	-
2009	-	-	43	27	3	2	-	-	-	-	-	-	-	-
2010	-	-	24	32	25	15	-	-	-	-	-	-	-	-
2011	-	-	47	-	10	11	-	-	-	-	-	-	-	-
2016	-	-	-	-	-	-	-	-	-	-	5	-	10	10
Total	**9**	**1**	**417**	**385**	**163**	**172**	**117**	**121**	**7**	**3**	**214**	**159**	**31**	**23**

Frequency distribution for class length (4 cm) of *Genypterus capensis* revealed that that the largest specimens collected were females for both coasts, particularly on the west coast (Fig. 14). Females from the west coast outnumbered males above 66 cm. On the south coast, middle length classes were slightly dominated by males, but after 100 cm, females prevailed. When visually assessed, both frequency distributions for the west coast were slightly skewed to the right, whereas on the south coasts were relatively normal.

Females mean lengths were 69.79 ±25.8 cm for the South Coast and 72.81 ±18.2 cm for the West Coast. Males were 65.78 ±22.3 cm and 62.82 ±16.8 cm, respectively. When means of the same sex were compared, t-test p-values were both less than 0.05, therefore a significant different between the coasts was found (Female: $t = -3.350539436$; $df = 2374$, $p< 0.05$; Male: $t = 3.099436$; $df = 1719$, $p< 0.05$).

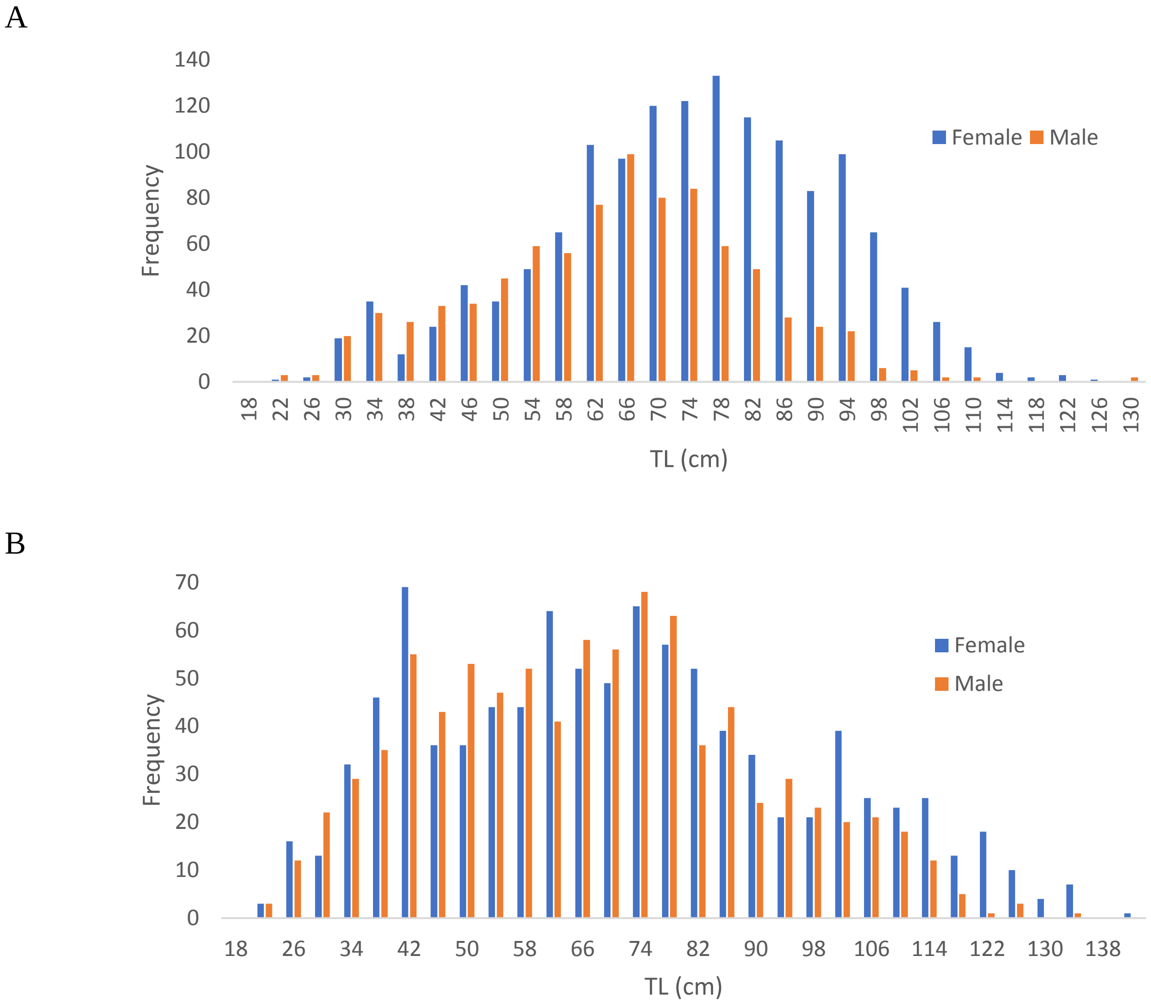

Fig. 14 Length distribution for *L. vomerinus* for female and male specimens on the west (A) and south coast (B) of South Africa, collected from 1990 to 2017.

Sex ratio and Length-Weight relationship

The overall sex ratio female:male was 1.37 : 1, which was not equal to 1 : 1 expected (χ^2= 104.72, df= 1, p< 0.05). On the west coast, the sex ratio was 1.67 : 1, whereas for the south coast it was 1.1 : 1. Both coasts were significantly different from 1:1 ratio (west coast: χ^2= 143.95, df = 1, p<0.05; south coast: χ^2= 3.8515, df = 1, p= 0.0497). The sex ratios were significantly different between coasts (χ^2= 44.212, df = 1, p< 0.05). When sex ratio for length classes was visually inspected, a dominance of females in the higher classes was reported for the west coast, whereas on the south coast, even though females still predominating at greater lengths, until 110 cm the sexes tend to 1 : 1 (Fig. 15).

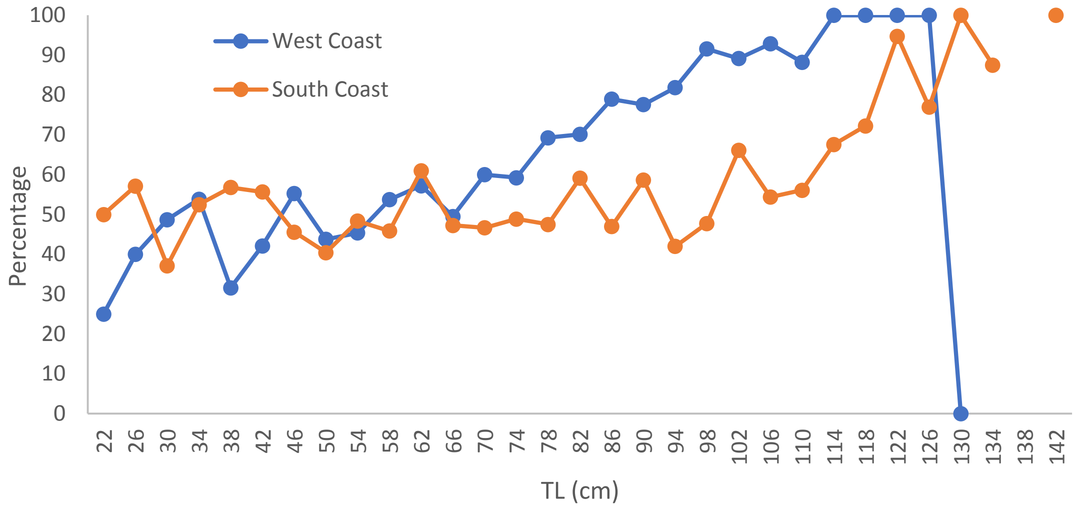

Fig. 15 Percentage of females *G. capensis* per length class for west and south coast collected off the coast of South Africa from 1990 to 2017.

Length-Weight relationships were plotted (Fig. 16). When all samples were included, the ANOVA used to test for difference between Length-Weight relationship of males and females showed that sex effect was significant (F=6.9, df_1=1, df_2=4093, $p<0.05$). Successively, the influence of the coast was tested for each sex with ANOVA. Coast factor also contributed significantly on both sexes (Females: F=7, df_1=1, df_2=2372, $p<0.05$; Males: F=99.6, df_1=1, df_2=1717, $p<0.05$)

The values of exponent b were checked to verify allometric and isometric growth. When the 95% confidence interval of b included 3, isometric growth was assumed, if not, positive or negative allometric growth were reported. Positive allometric growth was reported for all samples (b>3, Table 9).

Table 9 Length-weight relationships (LWR) equation parameters a and b and R^2 for each sex and coast of origin for *G. capensis* collected off the west and south coasts of South Africa from 1990 to 2017. WC = west coast; SC = south coast.

	a	**b**	**R^2**
Female WC	0.001	3.373	0.986
Female SC	0.0012	3.3351	0.989
Male WC	0.0009	3.3825	0.98
Male SC	0.0013	3.3183	0.989

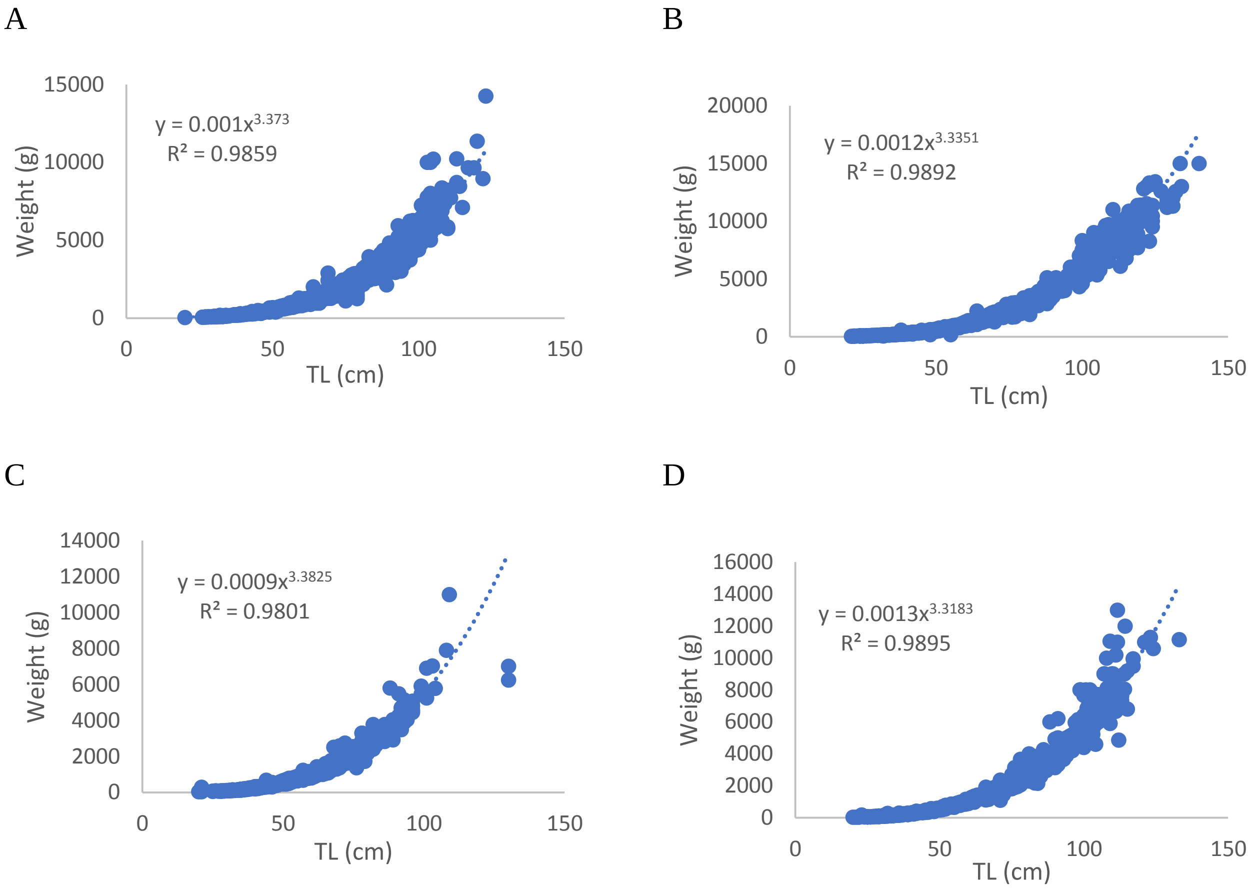

Fig. 16 Length-weight relationships for *G. capensis* females on the west (A) and south coast (B) and males on the west (C) and south Coast (D) collected off South Africa from 1990 to 2017.

Spawning season

The percentage of individuals per each maturity stage was calculated per month over all years collected. On the West Coast, the largest percentage of male *G. capensis* were classed as stage 1 (55%) and stage 2 (36.8%). The highest percentage of female sampled in January and February was classed as stage 2 (42.5%). The proportion of specimens in maturity stages greater than 2 was 26% for females and 8.2% for males (Table 10).

On the south coast, the largest percentage of male *G. capensis* were classed as stage 1 (42.2%) and 2 (37.6%). Females were mostly classed as stage 1 (34.6%) and 2 (37.1%). June, September and October had at least 30% of the female fish recorded in the maturity stages higher than 2. September was the highest (50%) (Table 11). In March most fish were matured, but the number of specimens was not big enough to constitute it a valuable information (n=9).

Table 10 Percentage of individuals per maturity stage: proportions are divided by sex, month and area of collection for *G. capensis* collected off the west coast of South Africa from 1990 to 2017.

	January		**February**		**July**		**Total**	
Maturity stage	F	M	F	M	F	M	F	M
1	35.3	60.7	21.3	40.3	20.0	-	31.6	55.0
2	40.8	32.5	46.9	47.9	80.0	-	42.5	36.8
3	7.1	1.1	14.4	5.0	0.0	-	8.9	2.2
4	2.3	0.8	4.9	0.8	0.0	-	3.0	0.8
5	14.5	4.9	12.5	5.9	0.0	-	14	5.2

Table 11 Percentage of individuals per maturity stage: proportions are divided by sex, month and area of collection for *G. capensis* collected off the south coasts of South Africa from 1990 to 2016.

	March		**April**		**May**		**June**		**July**		**September**		**October**		**Total**	
Maturity stage	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
1	0.0	100	47.5	57.1	35.0	31.4	19.7	24.8	0.0	0.0	22.0	29.6	19.4	57.6	34.6	42.2
2	0.0	0	36.2	31.7	44.2	35.5	42.7	44.6	100	100	28.0	48.4	48.4	36.4	37.1	37.6
3	0.0	0	7.0	4.2	17.8	25.6	26.5	30.6	0.0	0.0	44.9	20.1	22.6	6.1	20.0	15.0
4	0.0	0	0.7	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.9	0.0	3.2	0.0	0.7	0.0
5	100	0	8.6	7.0	3.1	7.6	10.3	0	0	0	4.2	1.9	6.5	0	7.6	5.0

Mean GSI was calculated per maturity stage for all samples combined, disaggregated by coast (Fig. 17). Results showed that, on the west coast, female mean GSI ranged between 0.5 and 1% for all maturity stages: the lowest GSI was in stage 1, while the peak was in stage 3. For males, all the stages were under 0.2% (Fig. 17-A). A different scenario was observed for the south coast sample: female maturity stages 3 and 4 spiked to the value of approximately 4%. Males had a low mean GSI for all maturity levels, as noticed for the west coast (Fig. 17-B).

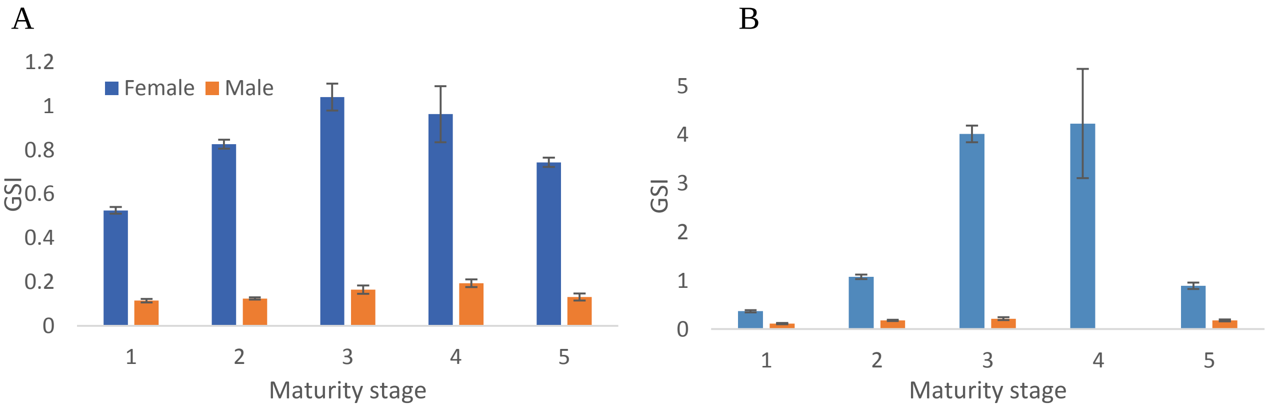

Fig. 17 Mean Gonadosomatic Index (GSI) (with standard errors) by maturity stage for *G. capensis* collected off the coast of South Africa from 1990 to 2017. A) West coast; B) South coast.

Monthly mean GSI was plotted for all sample years and for both sexes to identify spawning season (Fig. 18). Female *G. capensis* GSI from the west coast ranged between 0.7 and 3.05%. Actually, the monthly mean GSI remained similar for January and February, while in July it increases 3 times. However, just 5 individuals were recorded in July. Therefore, no significant peak in females GSI was seen on the west coast. Male GSI on the west coast were similar, 0.12 and 0.10% for January and February respectively (Fig. 18-A).

On the south coast, males monthly GSI had a peak in September, followed by a decrease in October. Females monthly GSI experienced a gradual increase until June, when a first mild peak was noticed (2.03%). A stronger peak was registered in September (2.85%). However, July and October GSI dropped down to 1% (Fig. 18-B).

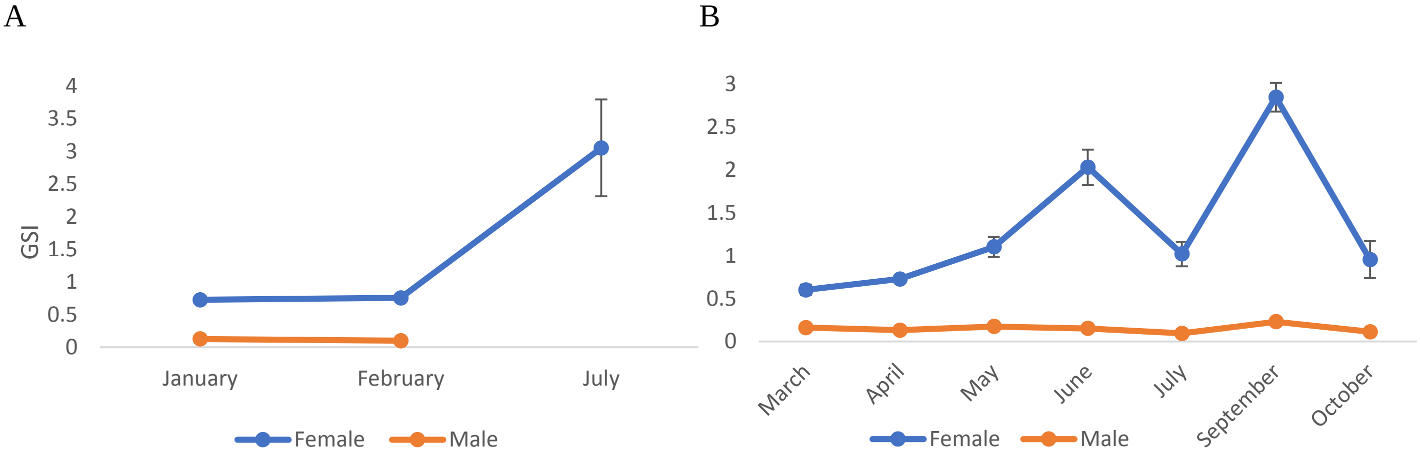

Fig. 18 Mean GSI and mean condition factor (CF, with standard errors) for *G capensis* by month for west (A) and south coast (B) of South Africa, collected from 1990 to 2017. They should indicate any pattern for spawning season.

Condition factor (CF) on the west coast showed higher values for males. Male CF started at 1.07 and decreased to 1.04. Females starting CF was 0.97, experiencing a decrease to 0.96 and, in July, 0.94. On the south coast, both sexes started with a high CF in March. Then, it decreased in April and started gradually to increase until a peak was reached in July. Afterwards, another drop occurred in September and October (Fig. 19).

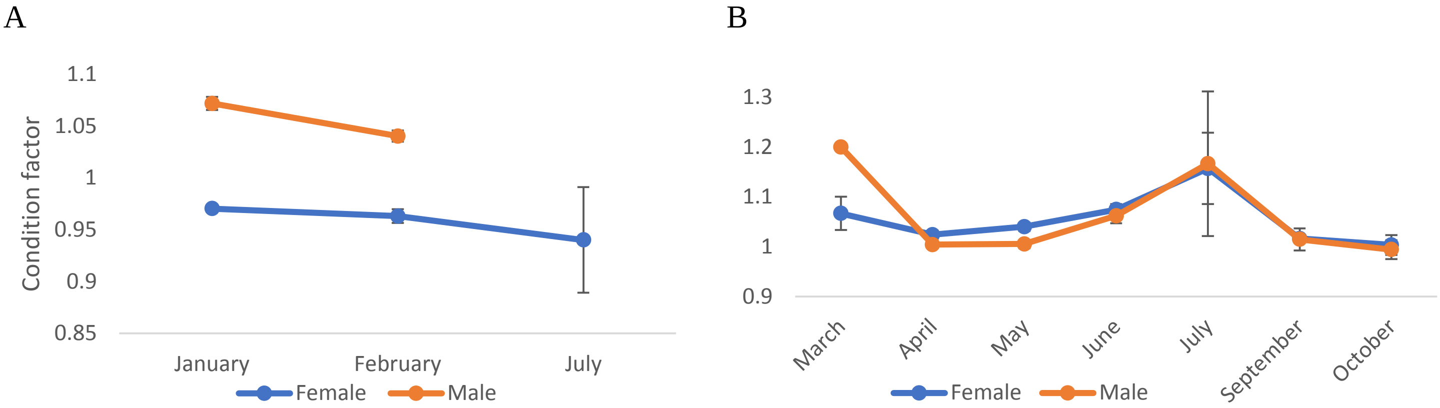

Fig. 19 Mean condition factor (CF) (with standard errors) by month for *G. capensis* collected off the coasts of South Africa from 1990 to 2017. A) West coast; B) South coast.

Length-at-50% maturity

Maturity ogives were constructed per sex and coast independently, fitting a logistic curve to the data (Fig. 20). The total length-at-50% maturity for female of the west coast was 62.8 cm (95% Confidence interval: 61.41-63.97 cm), whereas on the south coast was 56.3 cm (54.76-57.74 cm). For males, 50% of the west coast sample reached maturity at 66.0 cm (64.44-67.49 cm) and on the south coast at 59.7 cm (58.06-61.29 cm).

Likelihood ratio test detected significant differences between sexes ($\chi^2(1)= 2286.8$, $p<0.05$) and, when each sex was pooled, between coasts (Females: $\chi^2(1)= 1438.08$, $p<0.05$; Males: $\chi^2(1)= 896.61$, $p<0.05$).

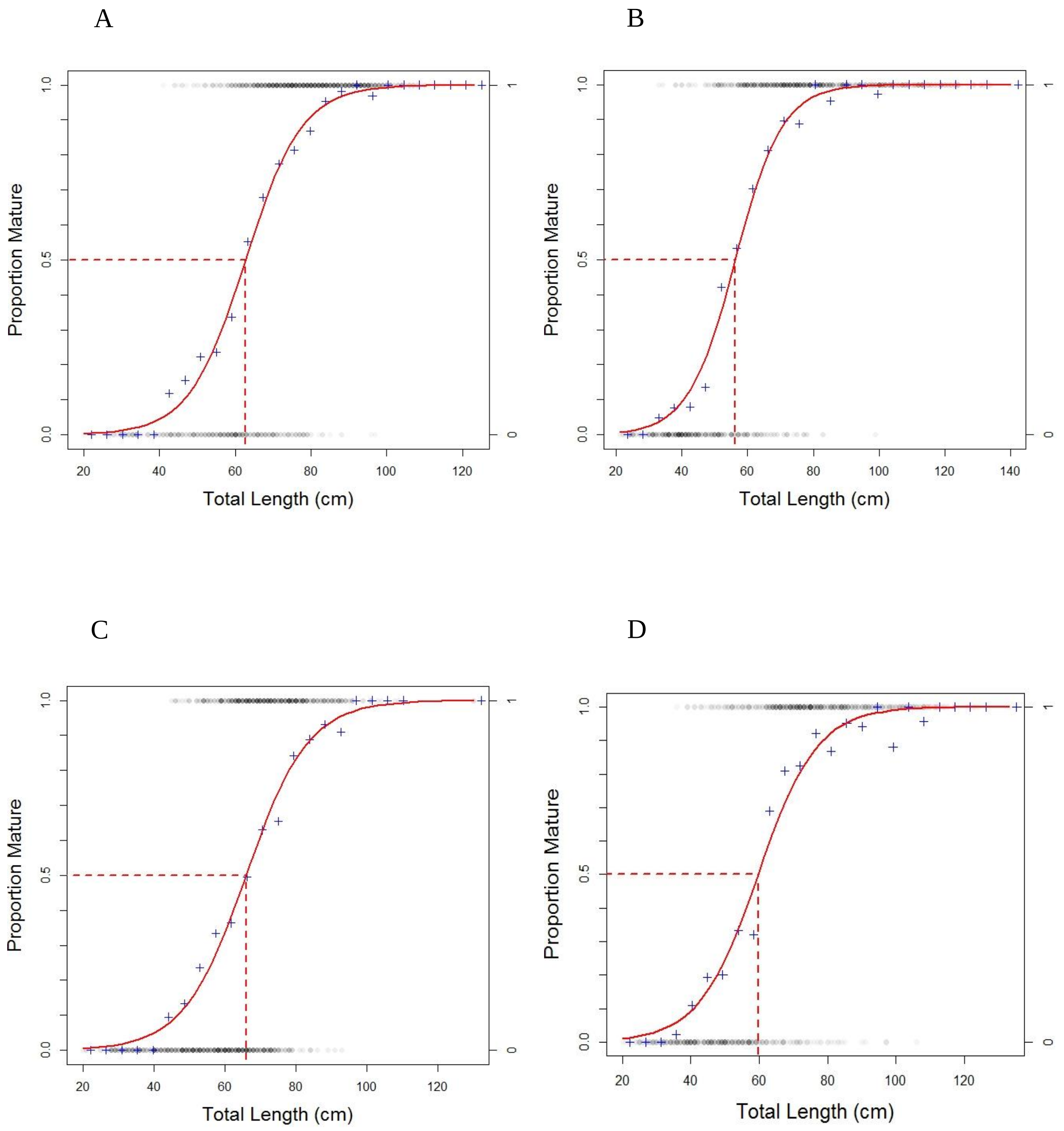

Fig. 20 Maturity ogives for female *G. capensis* on the west (A) and south coast (B) and males on the west (C) and south coast (D) of South Africa, collected from 1990 to 2017. L_{50} is where dotted lines intercept the logistic curve.

4. DISCUSSION

4.1 *Lophius vomerinus*

Sample size

This analysis was based on 5141 fish obtained from fishery-independent trawl surveys, from 1990 to 2017, in comparison to the 3263 fish analysed by Walmsley et al. (2005) and the 4325 by Maartens and Booth (2005). The Walmsley et al. (2005) samples were obtained from commercial catches over 12 consecutive months in the years 1997-1998, but were unequally distributed, as after data cleaning 81 came from the south coast and 1259 from the west coast. This study had bigger samples for the south and west coast than Walmsley et al. (2005). This could provide more accurate estimates of reproduction parameters of *L. vomerinus*. However, the comparison with Walmsley et al. (2005) estimates is confused by the fact that all my south coast samples were obtained in the months from March to October and the west coast samples in January and February. Very few specimens were collected in June, July or August. Maartens and Booth's (2005) samples came from commercial catches and surveys in Namibia from March 1997 to June 2000.

Length-Weight relationship and sex ratio

In *Lophius* spp., females outgrow males (Fariña et al, 2008). This study shows that, based on mean lengths, females *L. vomerinus* are larger than males. When analysed by coast, mean lengths showed larger fishes on the south coast for both sexes. It is believed that females grow bigger than males because of reproductive needs: egg ribbons can be >10 m long and can contain more than a million eggs (Amstrong et al., 1992; Yoneda et al, 2001; Walmsley et al, 2005). Moreover, Length-Weight relationships showed differences between sexes, and this dissimilarity could be linked to the influence of the ovary on body shape. The weight of females' gonads of *L. vomerinus* can represent up to 35% of the total weight (Maartens et al., 1999; Walmsley et al., 2005). For *L. americanus*, the result of the proportion was 50% (Armstrong et al., 1992). In the current study, GSI was calculated on body weight without gonads, so to compare it to the other studies, a conversion was needed. The result of the conversion showed that the biggest gonads recorded in this study represented 21.5% of the total weight, confirming the high investment of *L. vomerinus* in gonads development.

Parameter b of the Length-Weight relationship gives information on the type of growth of the fish: when it is equal to 3, the growth is isometric, whereas for a value of b greater or smaller than 3, positive or negative allometric growth occurs (Froese, 2006). When negative allometry occurs, individuals grow faster in length than they do in weight, whereas with positive allometry weight increases faster than length (Froese, 2006). Only for females of the south coast did b approximate 3, whilst for the rest of the sample it was smaller than 3. Negative allometric growth is common for other *Lophius* spp. (Landa and Antolinez, 2018). On the other hand, isometric growth of the south coast females could be a consequence of a variety of circumstances. Food availability, habitat, season, sex and gonad development can all affect the length-weight relationship (Froese, 2006). Also, the failure to reject isometric growth is likely a result of south coast's small sample size.

The overall sex ratio was 1.13 : 1, marginally different from a 1 : 1 ratio, in favour of females. No significant difference was found between the sex ratios of each coast, even though the west coast female:male ratio differed from expected 1 : 1 and the south coast did not. Trawling, and heavy fishing in general, could impact the sex ratio by reducing the larger sex. West coast *L. vomerinus* have been more depleted than on the south coast (DAFF, 2016), but they have the same sex ratio as the south coast, which therefore suggests that the ratio is not affected by fishing.

Female skewed sex ratio is typical for polygynous species. Polygyny is a mating strategy which involves a high number of females for individual male. Here the polygyny hypothesis is rejected as sex ratio for these species is heavily female-biased, whereas my results are very close to balanced (1 : 1).

Fisher's principle showed that when the reproductive investment by each sex is equal, the population will tend toward a 1 : 1 sex ratio. Polygamy provides no exception (Hamilton, 1967), so the mechanism of the skewed sex ratio is difficult to explain.

Lophius spp. are known to migrate, as juveniles and adults (Fariña et al., 2008). Although little is known about *L. vomerinus* migrations, vertical and spatial movements of this species are likely to occur, possibly causing a slight change in sex ratio at the time of sampling.

Spawning season

The spawning season for *Lophius vomerinus* is believed to occur during the southern hemisphere's spring (Fariña et al., 2008). Walmsley et al. (2005) and Maartens and Booth (2005) analysed year-round samples and noticed a peak in female GSI in September and between June and October respectively. Only females showed an increase in monthly GSI, whereas males showed low GSI throughout the whole year. In this study, female GSI of the south coast was different between autumn/winter (March to July) and winter/spring (August, September and October). However, the same comparison for the west coast was not applicable, having a significant disparity between seasonal sample sizes. Furthermore, GSI in Maartens and Booth (2005) and this study were similarly calculated, and, when compared, the monthly GSI values were alike. January and February were lower than 1% for both sexes in both analysis. Namibian *L. vomerinus* GSI increases in winter (July) and drops in spring (October). For South Africa south coast, the highest GSI values are in August, September and October. Seasonality varies with latitude, and Namibia, being closer to the equator, experiences different seasonality to South Africa. This may explain the one-month delay.

A peak in condition factor may indicate that a spawning event is likely to occur in the short term. Fish accumulate fat to store energy. After the necessary energy has been accumulated, fish use the stored energy to reach their peak condition. Hereafter, they allocate most of their energy available to gonad development, resulting in a peak in GSI. Condition factor for males peaked on both coasts in July and August, and for females in August. Thus, it corroborates the fact that *L. vomerinus* spawns in September.

Hilsop et al. (2001) and Laurenson et al. (2008) found evidence that *Lophius piscatorius* spawning activities take place in deep waters, possibly inaccessible to trawling. The size of females increases with depth and males move deeper in the spawning season, increasing the proportion of males at these depths (Laurenson, 2008). Indeed, juveniles *Lophius* tend to be in shallower waters and adults in deeper waters (Fariña et al., 2008). However, an overlap in depth distribution has been reported for *L. vomerinus* in South Africa (Walmsley et al., 2005). Migration patterns for *L. vomerinus* are unknown, but it is plausible that monkfish aggregate to spawn in deep waters. *Lophius* is believed to be a solitary fish and not to form shoals, therefore they need to actively look for sexual partners. Considering the previous assumptions, and that testis can ripen faster than ovaries, the paucity of males sampled in stage 3 to 5 is explained. Additionally, it may partially explain why it is challenging to find ripe and running fish in surveys (Walmsley et al., 2005).

The highest GSI value for males and females was 14 and 27% respectively. Notwithstanding this difference, this is a massive energy investment in both sexes. Testes development indicates spawn competition within males (Helfman et al., 2009). This behaviour is characteristic of group spawning, and supports the hypothesis that *L. vomerinus* aggregate to spawn.

The deep-sea is a challenging environment for locating sexual partners for non-shoaling fish as they have to overcome light deficiency, vast search areas and low food availability (Mead et al., 1964).

Other families of Lophiiformes employ a range of peculiar adaptations for reproduction, including (1) sexual parasitism, in which females host much smaller males through shared blood vessels, using the sperm at necessity in exchange of food, and (2) highly developed eyesight or olfactory organs to detect pheromones released by the females (Pietsch, 2005). A few of these strategies may not apply to *L. vomerinus* (i.e. sexual parasitism). However, possible adjustments/variations cannot be discarded and should be further researched.

My study cannot provide new information on spawning season, as a year-round sample was not available. However, these results reinforce previous findings, confirming the late winter-early spring spawning activities. Furthermore, it appears that males invest a large amount of energy to compete for eggs, and that vertical migrations for spawning are likely. This may suggest that *L. vomerinus* aggregate in deep water for reproduction, probably far from trawling grounds, and spawning events are relatively short.

Length-at-50% maturity

During peak spawning periods, gonads are easy to stage macroscopically, thus mistakes by observers are reduced. Immature and developing gonads can be visually confused out of season. Sampling in the peak spawning period minimizes this problem and improves the accuracy of L_{50} estimates (ICES, 2007, Lowerre-Barbieri et al. 2011b). However, L_{50} estimates from Walmsley et al. (2005), Marteens and Booth (2005) and this research are not from the spawning season.

Length-at-50% maturity was significantly influenced by sex, however not by coasts, reinforcing the hypothesis of one South African genetic stock (Leslie and Grant, 1990). For females, the lengths at maturity for each coast were not significantly different, resulting in L_{50} estimate of 39.42 cm for the pooled female sample. On the other hand, there were significant difference in L_{50} for males from the two coasts. South coast males reached 50% maturity at greater length. When the data were pooled, male L_{50} was 31.2 cm. When estimated growth rates by Walmsley et al. (2005) are applied, females mature later than males, at approximately 7 and 5 years old.

A difference in female and male L_{50} is common in *Lophius* spp. However, South African monkfish was considered the only member in the taxon to have similar L_{50} between sexes (Walsmley et al., 2005; Fariña et al., 2008). The results of this study disagree with the former hypothesis, as they show that *L. vomerinus* may follow the general trend in the genus. Even though Walmsley et al. (2005) considered conceivable flaws in methodology to explain the results, the difference in size and maturity between sexes is more likely, as this feature is shared within deep sea fish species. Also, the difference in age and size at maturity between females and males is reasonable to assume, as the peculiar egg veils of females demand individuals to be large with enough space and energy to invest. This strategy could be a basic parental care as it gives higher opportunity to the offspring to survive (Armstrong et al., 1992; Colmanero et al., 2017).

Female L_{50} confirmed previous measurements made by Walmsley et al (2005). However, the Namibian L_{50} between female lengths at maturity is greater than South African estimates (Table 12). Walmsley et al. (2005) explained this on the basis of faster growth of Namibian population. Nevertheless, asymptotic lengths of each sex are not different between the two regions. Hence, faster growth is partly the explanation, yet the difference between methodologies in L_{50} estimates should be considered and explored. Only a standardized study between populations can provide realistic terms of comparison.

L. vomerinus' large body size, longevity and late maturation make it extremely vulnerable to fishing. In addition, trawl fishery indiscriminately catches juveniles and adults, increasing the risk of growth overfishing (Walmsley et al., 2005; Colmenero et al., 2017). Furthermore, South African deep sea ecosystems are under threat from the trawling activities (Sink et al., 2012). Habitat loss and food availability play an important role in the well-being of *L. vomerinus* and, even though the management of the Hake fishery improved substantially in the last 20 years, the past and present impacts of harvesting cannot to be underestimated (Durholtz et al., 2015).

Solmundsson et al. (2009) found that in Icelandic water, *Lophius piscatorius* reproduction benefitted from an increase in temperature and salinity. In South Africa, the extent of climate change and its effect on monkfish are unknown. Changes in temperature and salinity in the Southern Benguela region are expected to impact several species and the ecosystem in general, with profound consequences for the environment and the fishing industry (Lutjeharms et al., 2001).

All things considered, it appears that females attain maturity at a greater size and age than males. Females require a large amount of space and energy for the eggs veil, and thus more time to grow to the desired size. This would decrease the possibility that all females reach maturity. Sperm has less production and storage costs, thus males do not need to reach a large size. To succeed, they just need to produce sperm, making early maturation an advantage as they can participate in more spawning events. This may eventually increase the presence of males on the spawning grounds, and to correct this trend, *L. vomerinus* might favour female offspring.

Table 12 Length-at-50% maturity for *L. vomerinus* for the compared studies. The first column specifies Authors (date of publication), place of the study. L_{50} estimates of this study for west (WC) and south (SC) coast have been reported below main estimate.

	L_{50} Female (cm)	**L_{50} Male (cm)**
Maartens and Booth (2005), Namibia	58.2	39.9
Walmsley at al. (2005), South Africa	36.9	37.6
This study, South Africa	39.4	31.2
	(WC=40; SC=38.9)	(WC=30.8; SC=33.4)

4.2 *Genypterus capensis*

Sample size

This analysis was based on 4097 fish from fishery-independent trawl surveys from 1990 to 2017, in comparison to the 1090 fish analysed by Payne (1985) and the 1732 by Japp (1989). Payne's (1985) samples were collected during routine trawl surveys of the south coast between April 1975 and October 1978. Japp's (1989) samples included 815 specimens from the west coast and 917 from the south coast, collected mostly from longline commercial catches between February 1987 and May 1988, but also from fishery-independent trawl surveys in the same period. The sample used for this study was divided by coast in the same way as Japp's (1989), but had approximately twice the number of individuals. Another similarity was that the data were not collected year-round, but only for some months. In Japp (1989), the west coast was sampled from February to July, whereas the South Coast from May to October. In this study, January, February and July were the months sampled on the west coast, whereas March to July and September/October were the months sampled for the south coast.

Length-weight relationship and sex ratio

Females *Genypterus capensis* attain larger size than males, a common life-history strategy of deep sea fish species (Payne, 1985; Japp, 1990). This study is not focused on growth, but confirms the trend, as female individuals had larger mean lengths than males. However, the effect of sex on Length-Weight relationships was not particularly significant, confirming that body shape is similar between sexes (Japp, 1989). The influence of the area of collection was significant on Length-Weight relationships, with individuals on the south coast reaching a greater weight for a given length. Furthermore, asymptotic lengths of fish on the south coast confirmed the larger size that individuals from this area might reach (Japp, 1990). Length distribution on the west coast showed a dominance of females over 66 cm total length, whereas the same happened at 98 cm on the south coast.

Japp (1989) suggested that the seasonal difference of sampling caused different body conditions. The south coast was sampled during spring, which is expected to be the peak or the end of the spawning activity, when the body condition in *G. capensis* is likely to be low due to reproductive costs (Hecht, 1976). The west coast was sampled in summer, when body condition is believed to be at its highest as reproduction activity is at its lowest. Thus, explaining the differences in Length-Weight relationship between the coasts. The sampling of this study was similarly biased, but, even though Japp's (1989) hypothesis is valid, this study showed that females had worst condition in summer. However, Length-Weight relationship and growth of fish in different areas may be influenced by a variety of environmental factors, and neither the Length-Weight relationship nor growth differences alone indicate two different stocks. Positive allometric growth is typical of the genus *Genypterus*, as was reflected in this study's findings.

The overall sex ratio was female-biased, resulting in a ratio of 1 male to every 1.37 females. However, the sex ratio on the west coast (1 : 1.67) is more female-skewed than the south coast (1 : 1.1), and they are significantly different from each other. Male and females *G. capensis* are believed to frequent different areas, only aggregating when the spawning season approaches (Roberts, 1987; Japp, 1989). Also, it is assumed that the normal sex ratio for *G. capensis* tends to be 1 : 1. Therefore, considering the different seasonal activity between the coasts during the sampling, the dissimilarity between sex ratios can be explained. Furthermore, it may explain the different length frequency distribution between coasts, supporting the former hypothesis.

The difference in sex ratios, Length-Weight relationships and length distributions between the coasts have been observed and may support the hypothesis by Henrique et al. (2017) that two genetically distinct stocks are present in South Africa. Although the hypothesis of more than one stock is not unanimously shared, multiple stock management has been constantly advised (Japp, 1990; Grant and Leslie, 2005). The current analysis *per se* is not specific enough to conclude that the two coasts represent different stocks. However, for an explanatory comparison of Length-Weight relationships and sex ratio, the sampling should be done during the same season/period.

Spawning season

Genypterus spp. are believed to aggregate for spawning events, and pre-spawning aggregations of *Genypterus* spp. are well known among fishermen and scientists (Roberts, 1987; Japp, 1989). The spawning season for *G. capensis* is believed to be long on the south coast, from August to November (Japp, 1989), whereas information on the west coast spawning season is scarce. In Japp's (1989) study, male and female GSI values of the south coast increased in July and August, reaching a peak in September. Even though the current analysis did not include August, and July has a low number of samples, it corroborates Japp's (1989) results, as the peak for male and female GSI was found in September. Also, condition factor for both sexes increased slowly until July and dropped in September, confirming the assumed high condition anticipating spawning season efforts. Japp's (1989) GSI analysis of the west coast showed peaks in male GSI from April to June, suggesting a spawning season during this time. However, females low GSI in the same months did not confirm the trend. Thus, he inferred that the spawning season on the west coast might occur during the half of the year that was not sampled. The second assumption was that *G. capensis* only spawn on the south coast. However, a small proportion of the females sampled on the west coast showed high GSI values and reproductive activity. Furthermore, even though males GSI were calculated differently between this study and Japp's (1989), ripe testes were found on both coasts, suggesting reproductive activity is likely occurring on the west coast as well.

According to the current analysis, September can be confirmed as the peak month in spawning activity for the south coast. For the west coast speculations are more complicated. Nevertheless, the west coast sample provides valuable information as mature females have been found. In fact, a few of ripe and running *G. capensis* had been collected. This may indicate the existence of a spawning ground/aggregation on the west coast. However, flaws were assumed in the maturity scales used for visual assessment during the years, but the occurrence of ripe and running females on the west coast have been recorded previously (Durholtz, pers. comm.). Furthermore, Olivares and Sabates (1989) deduced from larvae distribution that different spawning grounds and seasons are plausible.

G. capensis is not believed to undertake long migrations. It is a benthic/demersal species with a particular reproductive adaptation, a drumming muscle which produces sound allowing fish to locate one another in the darkness of the oceans depths (Macpherson, 1983). Japp (1989) analysed inshore trawl catches from the west coast, and 80% of the catches were immature females. When fishing moved to the deeper water of the outer shelf of the south coast during winter-spring longlining season, the females' catches dropped to 40%. However, most of the total female catches were mature specimens. These findings support the movement toward deeper water with size and, in particular, the spawning aggregation that occurs on rocky grounds in deep water, far from the reach of trawling.

On the south coast, spawning aggregation has been recognized and the spawning area protected from fisheries (DAFF, 2016). Even though genetic exchange between the west and south coast has been found, the occurrence of mating grounds on the west coast is very likely, however, they have not been located yet.

Length-at-50% maturity

As mentioned in the discussion of *Lophius vomerinus*, to improve the accuracy of L_{50} estimates, only specimens from the spawning peak should be analysed. Japp (1989) and this study took into consideration the full sample available, as incomplete year-round sampling could not provide exhaustive information on spawning seasons.

The comparison between studies estimates highlighted the difference between females L_{50} and the similarity between male L_{50}, on both coasts (Table 13). Also, this study confirmed that *G. capensis* living in the south coast area reached 50% maturity at a smaller size than the west coast individuals. For the discrepancy between coasts, an explanation based on growth difference is plausible (Japp, 1990). However, the disparity between Japp's (1989) and this study females L_{50} estimates is significant. Fishing effects from past exploitation can be speculated, in particular on the spawning stock of the south coast (Punt and Japp, 1994). Yet, Payne (1985) estimated L_{50} only for the South-East Coast of South Africa, and his result for females is close to my estimate, whereas his estimate for male L_{50} is smaller. Nevertheless, Payne (1985) did not provide information on methods and maturity sample, making any comparison challenging.

In addition, when the growth parameter calculated by Japp (1990) is applied to the findings of this research, females' age-at-50% maturity would be approximately 4 and 4.5 years on both coasts. These ages are one and two years less than previous research and indicate that both sexes reach L_{50} at the same age. Furthermore, males' L_{50} is greater than females. Under the assumption that *G. capensis* females attain bigger size than males, this result raises questions about the health of the stocks. Also, *G. capensis* is a slow growing and long-living fish, thus it is speculated that the differences in female L_{50} estimates between studies are the long term consequence of fishing (Punt and Japp, 1994; Law, 2007; Henriques et al., 2017). Indeed, most of the main female spawners were caught by longline fishermen on the south coast during the 1980s, whereas trawling had tremendous impacts on the west coast long before longlining was initiated (Punt and Japp, 1994).

This study found significant differences between coasts, corroborating Japp's (1989) findings, and most importantly, a potentially alarming reduction in female L_{50}. Even if this study does not prove that multiple stocks exist for *G. capensis*, it reinforces the suggestion that management should be addressed differently for the west and south coast of South Africa.

Table 13 Length-at-50% maturity for *G. capensis* for the compared studies. On the left, Author (date) of the study. L_{50} is reported for west (WC) and south (SC) coast of South Africa.

	L_{50} Female (cm)		**L_{50} Male (cm)**	
	WC	SC	WC	SC
Payne (1986)	-	62	-	49
Japp (1989)	81	72.5	65.5	62
This study	62.8	56.3	66	59.7

4.3 Conclusion

The aim of this study was to analyse the reproductive dynamics of *Lophius vomerinus* and *Genypterus capensis* in order to estimate length-at-50% maturity (L_{50}), disaggregated by sex and area of collection. Hereafter, the study focused on (1) comparing L_{50} estimates between west and south coast of South Africa and (2) assessing if any dissimilarity occurred from previous studies. The ultimate goal was to provide updated life-history parameters that are valuable for stock assessments.

Lophius vomerinus showed evidence of a tendency to form spawning aggregations. This is an important feature that management needs to take into consideration for preserving the reproductive success. No significant differences between coasts were found throughout the analysis, supporting previous evidence of one South African stock (Leslie and Grant, 1990). L_{50} did not show any clear effect from past fishing. However, my results showed that there is a significant difference between male and females L_{50} estimates, in contrast to the previous literature for South African monkfish.

Genypterus capensis appeared to have reduced significantly female L_{50}. It is assumed that this change was caused by fishing exploitation. On the west coast, constant trawling activities from the 1940s mostly removed immature females, whereas on the south coast, main spawners were hugely depleted during the 1980s longline fishery (DAFF, 2016). In terms of stock numbers, the differences between the coasts corroborate the presence of two stocks (Henriques et al., 2017). My findings reinforced the hypothesis of a spawning ground on the west coast, which has important implications for the effective management of the species.

Information on spawning season and L_{50} is fundamental to manage fisheries sustainably. They provide insights on the biology and life-history of the fish. The former suggests when, and possibly where, aggregating species spawn, whilst the latter could be used to set a minimum size for catches or as a tool to model the reproductive potential of a population or stock (Lappalainen et al., 2016). Protecting spawning grounds is essential to avoid over-exploitation and preserve the integrity of the stock. Furthermore, when L_{50} estimates from different timelines are compared, they may offer more understanding of the condition of the stock over time. Finding differences may indicate that broader changes have occurred within the system and further research could elucidate the possible causes, informing management strategies.

Even though the spawning season could not be determined with precision, the findings of this study provide valuable information on *L. vomerinus* and *G. capensis* reproductive dynamics and their L_{50} parameters. Such species, which are demersal, mature slowly and are long lived, are extremely vulnerable to fishing and overexploitation. Furthermore, information on reproductive dynamics is scarce, increasing the potential for ineffective management practices.

5. REFERENCES

Alfonso-Dias, I., and 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.

Andrews, W.R.H., Hutchings, L., 1980. Upwelling in the southern Benguela Current. *Progress in Oceanography* 9: 1–81.

Armstrong, M.P., Musick, J.A., and Colvocoresses, J.A., 1992. Age, growth, and of the goosefish *Lophius americanus* (Pisces: Lophiiformes). *Fishery Bulletin US* 90: 217–230.

Brandão, A. and Butterworth, D.S., 2008. An updated assessment of the South African kingklip resource including some sensitivity tests. In: Marine Resource Assessment and Management Group (ed). University of Cape Town.

Cawthorn, D.M., Steinman, H.A. and Witthuhn, R.C., 2012. DNA barcoding reveals a high incidence of fish species misrepresentation and substitution on the South African market. *Food Research International* 46: 30-40.

Chen, Y. and Paloheimo, J.E., 1994. Estimating fish length and age at 50% maturity using a logistic type model. *Aquatic Sciences* 56: 206-219.

Colmenero, A.I., Tuset, V.M. and Sánchez, P., 2017. Reproductive strategy of white anglerfish (*Lophius piscatorius*) in Mediterranean waters: implications for management. *Fishery Bulletin* 115: 60-73.

Colvin, M. E., Pierce, C. L. and Stewart, T. W., 2012. Semi-discrete biomass dynamic modeling: an improved approach for assessing fish stock responses to pulsed harvest events. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1710–1721.

Cooper, A.B., 2006. A guide to fisheries stock assessment: from data to recommendations. University of New Hampshire, Sea Grant College Program. 44 pp.

Courtenay Jr, W.R., 1971. Sexual dimorphism of the sound producing mechanism of the striped cusk-eel, *Rissola marginata* (Pisces: Ophidiidae). *Copeia*: 259-268.

DAFF (Department of Agriculture, Forestry and Fisheries), 2016. Status of the South African marine fishery resources 2016. Cape Town: DAFF

Davies, R. W. D., Cripps, S. J., Nickson, A., & Porter, G., 2009. Defining and estimating global marine fisheries bycatch. *Marine Policy* 33: 661-672.

de Moor, C.L., Johnston, S.J., Brandão A., Rademeyer, R.A., Glazer, J.P., Furman, L.B. and Butterworth, D.S., 2015. A review of the assessments of the major fisheries resources in South Africa, *African Journal of Marine Science* 37: 285-311.

Duarte, R., Landa, J., Morgado, C., Marçal, A., Warne, S., Barcala, E., Bilbao, E., Dimeet, J., Djurhuus, H., Jónsson, E., McCormick, H., Ofstad, L., Quincoces, I., Rasmussen, H., Thaarup, A., Vidarsson, T. and Walmsley, S., 2005. Report of the Anglerfish Illicia/Otoliths Ageing Workshop. IPIMAR, Lisbon (Portugal). 47 pp.

Durholtz, M.D., Singh, L., Fairweather, T.P., Leslie, R.W., van der Lingen, C.D., Bross, C.A.R., Hutchings, L., Rademeyer, R.A., Butterworth, D.S. and Payne, A.I.L., 2015. Fisheries, ecology and markets of South African hake. In: Aranciabia H. (ed), *Hakes: Biology and Exploitation.* John Wiley and Sons. pp 38-69.

Dupouy, H., Pajot, R., Kergoat, B., 1986. Study on age and growth of the anglerfishes, *Lophius piscatorius* and *L. budegassa*, from northeast Atlantic using illicium. *Revue des travaux de l'Institut des Pêches Maritimes* 48: 107-131.

FAO, 2010. Fishery and Aquaculture Country Profiles. South Africa. Country Profile Fact Sheets. In: *FAO Fisheries and Aquaculture Department* [online]. Rome. Updated 1 May 2010. [Cited 6 September 2018]. http://www.fao.org/fishery/

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

Fox, J. and Weisberg, S., 2011. An {R} Companion to Applied Regression, Second Edition.

Thousand Oaks CA: Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Froese, R., 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of applied ichthyology* 22: 241-253.

Froese, R. and D. Pauly. Editors. 2018. FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2018)

Grant, W.S. and Leslie, R.W., 2005. Bayesian analysis of allozyme markers indicates a single genetic population of kingklip *Genypterus capensis* off South Africa. *African Journal of Marine Science* 27: 479-485.

Green, P.J., 1984. Iteratively reweighted least squares for maximum likelihood estimation, and some robust and resistant alternatives. *Journal of the Royal Statistical Society. Series B (Methodological)*: 149-192.

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

Griffiths, C.L, Robinson, T.B., Lange, L., Mead, A., 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. *PLoS ONE* 5: e12008.

Gründlingh, M.L., 1983. On the course of the Agulhas Current. *South African Geographical Journal* 65: 49-57.

Hamilton, W.D., 1967. Extraordinary sex ratios. *Science* 156: 477-488.

Hecht, T., 1976. The general biology of six major trawl fish species of the Eastern Cape coast of South Africa, with notes on the demersal fishery, 1967-1975. Ph.D. thesis, University of Port Elizabeth, 353 pp.

Helfman, G.S., Collette, B.B., Facey, D.E. and Bowen, B.W., 2009. Fishes as social animals: reproduction. In: Helfman, G.S., Collette, B.B., Facey, D.E. and Bowen, B.W. (eds), *The* *diversity of fishes: biology, evolution, and ecology*. John Wiley and Sons. pp 455-477.

Henriques, R., Nielsen, E.S., Durholtz, D., Japp, D. and von der Heyden, S., 2017. Genetic population sub-structuring of kingklip (*Genypterus capensis*–Ophidiidiae), a commercially exploited demersal fish off South Africa. *Fisheries Research* 187: 86-95.

Hislop, J.R.G., Holst, J.C. and Skagen, D., 2000. Near-surface captures of post-juvenile anglerfish in the North-east Atlantic—an unsolved mystery. *Journal of Fish Biology* 57: 1083-1087.

Hislop, J.R., Gallego, A., Heath, M.R., Kennedy, F.M., Reeves, S.A. and 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.

Hutchings, J.A. and Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. *AIBS Bulletin* 54: 297-309.

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. and Fidel, Q., 2009. The Benguela Current: An ecosystem of four components. *Progress in Oceanography* 83: 15-32.

ICES, 2007. Report of the Workshop on Sexual Maturity Staging of Hake and Monk (WKMSHM). 21-24 November 2007, Lisbon, Portugal. ICES CM 2007/ACFM: 34. 82 pp.

Japp, D. W., 1989. An assessment of the South African longline fishery with emphasis on stock integrity of kingklip, *Genypterus capensis* (Pisces: Ophidiidae). M.Sc. thesis, Rhodes University, 138 pp.

Japp, D. W., 1990. A new study on age and growth of kingklip *Genypterus capensis* off the south and west coasts of South Africa, with comments on its use for stock identification. *South African Journal of Marine Science* 9: 223-237.

Karaan, M. and Rossouw, S., 2004. The Microeconomic Strategy Project: A baseline assessment of the fishing and aquaculture industry in the Western Cape. Study commissioned by the Western Cape Provincial Government. 50 pp.

Karna, S. K., and Panda, S., 2012. Length-weight relationship (LWR) of 20 fish species in Chilika Lagoon, Odisha (India). *Asian Journal of Experimental Biological Sciences* 3: 243-246.

Kvamme, C., and Bogstad, B., 2007. The effect of including length structure in yield-per-recruit estimates for northeast Arctic cod. *ICES Journal of Marine Science* 64: 357–368.

Landa, J., Pereda, P., Duarte, R. and Azevedo, M., 2001. Growth of anglerfish (Lophius piscatorius and L. budegassa) in Atlantic Iberian waters. *Fisheries Research* 51: 363-376.

Landa, J., Duarte, R., and 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. and Antolínez, A., 2018. Weight–length relationships, weight conversion factors and somatic indices from two stocks of black anglerfish (*Lophius budegassa*) and white anglerfish (*L. piscatorius*) in north-eastern Atlantic waters. *Regional studies in marine science* 23: 87-96.

Lappalainen, A., Saks, L., Šuštar, M., Heikinheimo, O., Jürgens, K., Kokkonen, E., Kurkilahti, M., Verliin, A. and 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., Johnson, A., and Priede, I. G., 2005. Movements and growth of monkfish *Lophius piscatorius* tagged at the Shetland Islands, northeastern Atlantic. *Fisheries Research* 71: 185–195.

Laurenson, C.H., Dobby, H., McLay, H.A. and Leslie, B., 2008. Biological features of the *Lophius piscatorius* catch in Scottish waters. *ICES Journal of Marine Science* 65: 1281-1290.

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

Law, R. and Grey, D.R., 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* 3: 343-359.

Leslie R. W. and 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.

Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., Murua, H., Hunter, J.R., 2011a. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries* 3: 71-91.

Lowerre-Barbieri, S. K., Brown-Peterson, N. J., Murua, H., Tomkiewicz, J., Wyanski, D. M., and Saborido-Rey, F., 2011b. Emerging issues and methodological advances in fisheries reproductive biology. *Marine and Coastal Fisheries 3*: 32-51.

Lutjeharms, J.R.E., Cooper, J. and Roberts, M., 2000. Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737-761.

Lutjeharms, J.R.E., Monteiro, P.M.S., Tyson, P.D. and Obura, D., 2001. The oceans around southern Africa and regional effects of global change: START Regional Syntheses. *South African Journal of Science* 97: 119-130.

Lutjeharms, J.R.E., 2007. Three decades of research on the greater Agulhas Current. *Ocean Science* 3: 129-147.

Marquardt, D.W., 1963. An algorithm for least-squares estimation of nonlinear parameters. *Journal of the society for Industrial and Applied Mathematics* 11: 431-441.

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

Macpherson, E., 1983. Feeding pattern of the kingklip (*Genypterus capensis*) and its effect on the hake (*Merluccius capensis*) resource off the coast of Namibia. *Marine biology* 78: 105-112.

Marshall, N.B., 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery Reports* 27: 1-121.

Mead, G. W., Bertelsen, E. and Cohen, D. M., 1964. Reproduction among deep-sea fishes. *Deep Sea Research* 11: 569-596.

Neumann, R. M., Guy, C. S., and Willis, D. W. (2012). Length, weight, and associated indices. In Zale, A. V., Parrish, D. L., and Sutton, T. M. (eds), *Fisheries Techniques*, American Fisheries Society. pp 637-676.

Nielsen, J.G., Cohen, D.M., Markle D.F. and Robins, C.R., 1999. Ophidiiform fishes of the world (Order Ophidiiformes). An annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other ophidiiform fishes known to date. *FAO Fisheries Synopsis* 125: 178 pp.

Ogle, D.H., P. Wheeler, and A. Dinno. 2018. FSA: Fisheries Stock Analysis. R package version 0.8.22, https://github.com/droglenc/FSA.

Olivar, M-P., Sabatés, A., 1989: Early life history and spawning of *Genypterus capensis* (Smith, 1849) in the southern Benguela system. *South African Journal of Marine Science* 8: 173-181.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. and Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932.

Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J. and Dieckmann, U., 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 62: 811-823.

Payne, A. I. L., 1985. Growth and stock differentiation of kingklip (*Genypterus capensis*) on the south-east coast of South Africa. *African Zoology* 20: 49-56.

Pereda, P., and Landa, J. 1997. Recuperaciòn de dos ejemplares de rape *Lophius piscatorius* Linnaeus, 1758 en el stock norte (divisiones VIIIa y b del CIEM) tras ser marcados en el stock sur (division VIIIc). *Boletın del Instituto Espanol de Oceanografıa*, 13: 91–94.

Peterson, R.G. and Stramma, L., 1991. Upper-level circulation in the South Atlantic Ocean. *Progress in oceanography* 26(1): 1-73.

Pietsch, T.W., 2005. Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). *Ichthyological Research* 52: 207-236.

Punt, A.E. and Japp, D.W., 1994. Stock assessment of the kingklip Genypterus capensis off South Africa. *South African Journal of Marine Science*, *14*(1), pp.133-149.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B. and Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B: Biological Sciences* 272: 2337-2344.

Roberts, C.D., 1987. First records of demersal fishes from the North Cape - Three Kings area of New Zealand, with a record of a prespawning aggregation of ling, *Genypterus blacodes*. *New Zealand Journal of Marine and Freshwater Research* 21: 157-161.

Saila, S.B., 1983. Importance and assessment of discards in commercial fisheries. *FAO Fisheries Circular* 765. 62 pp.

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.

Sink, J.S., Wilkinson, S., Atkinson, L.J., Sims, P.F., Leslie, R.W. and Attwood, C.G., 2012. The potential impacts of South Africa's demersal hake trawl fishery on benthic habitats: Historical perspectives, spatial analyses, current review, and potential management actions. Unpublished report, South African National Biodiversity Institute. 74 pp.

Solmundsson, J., Jonsson, E. and Bjornsson, H., 2010. Phase transition in recruitment and distribution of monkfish (*Lophius piscatorius*) in Icelandic waters. *Marine biology* 157: 295-305.

Sparre, P., 1998. Introduction to tropical fish stock assessment. Part 1. Manual. *FAO Fisheries and Aquaculture Technical Paper* 306: 1-407.

Steimle, F.W., Morse, W.W. and Johnson, D.L., 1999. Essential fish habitat source document. Goosefish, *Lophius americanus*, life history and habitat characteristics. NOAA Technical Memorandum NMFS NE 127. 31 pp.

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

WWF SASSI. (2019). *Fish detail*. [online] Available at: http://wwfsassi.co.za/fish-detail/54/ [Accessed 5 Feb. 2019].

WWF SASSI. (2019). *Fish detail*. [online] Available at: http://wwfsassi.co.za/fish-detail/65/ [Accessed 5 Feb. 2019].

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

Yoneda, M., Tokimura, M., Horikawa, H., Yamamoto, K., Matsuyama, M., and Matsuura, S., 2002. Spawning migration of the anglerfish *Lophius litulon* in the East China and Yellow Seas. *Fisheries Science* 68: 310–313.

6. APPENDIX

Table 14 Estimates of logistic model parameters, β_0 and β_1, for *Lophius vomerinus* of South Africa disaggregated by sex and coast: females of the west coast (A) and south coast (B), and males of the west (C) and south coast (D). Upper and lower limits of the 95% Confidence intervals are reported in bracket after estimates, followed by standard error.

A

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-6.583(-7.235/-5.963)	0.324	-20.29	<0.05
β_1	0.164 (0.149/0.180)	0.008	20.82	<0.05

B

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-5.272 (-6.180/-4.418)	0.449	-11.74	<0.05
β_1	0.135 (0.116/0.156)	0.010	13.29	<0.05

C

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-8.957 (-10.117/-7.875)	0.571	-15.68	<0.05
β_1	0.291 (0.259/0.325)	0.017	17.08	<0.05

D

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-9.408 (-11.453/-7.569)	0.988	-9.518	<0.05
β_1	0.281 (0.233/0.336)	0.026	10.745	<0.05

Table 15 Estimates of each logistic model parameters, β_0 and β_1, for *Genypterus capensis* of South Africa disaggregated by sex and coast: females of the west coast (A) and south coast (B), and males of the west (C) and south coast (D). Upper and lower limits of the 95% Confidence intervals of the parameter estimates are reported in bracket, followed by standard error.

A

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-8.443 (-9.468/-7.487)	0.505	-16.73	<0.05
β_1	0.134 (0.120/0.150)	0.007	18.00	<0.05

B

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-7.888 (-9.003/-6.879)	0.544	-14.49	<0.05
β_1	0.140 (0.123/0.159)	0.009	15.14	<0.05

C

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-7.519 (-8.629/-6.494)	0.544	-13.82	<0.05
β_1	0.114 (0.098/0.131)	0.008	13.85	<0.05

D

Parameter	Estimate (CI)	Std. error	Z value	P value
β_0	-6.935 (-7.903/-6.045)	0.473	-14.65	<0.05
β_1	0.116 (0.102/0.132)	0.008	15.23	<0.05