The biology, ecology and population trends of jacopever *Helicolenus dactylopterus* in South Africa

Laura Frances Weston

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Supervised by Associate Professor Colin G. Attwood[1] and Professor Kerry J. Sink[2]

[1] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[2] South African National Biodiversity Institute, Cape Town, South Africa

University of Cape Town

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Helicolenus dactylopterus *caught in a research trawl on the west coast of South Africa (photograph supplied by Dr L. Atkinson).*

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ABSTRACT

Helicolenus dactylopterus is a deep-water benthic fish in the subfamily Sebastinae. Sebastinae species are slow-growing, long-lived and potentially vulnerable to overexploitation. *Helicolenus dactylopterus* is exploited throughout its Atlantic distribution. In South Africa, it is the eighth-most landed species in the demersal trawl fishery. Because little research has been conducted on *H. dactylopterus* locally, it is difficult to understand its response to fishing pressure. The life history, habitat preference and population trends of the species in South Africa were thus investigated. The age, growth, reproductive characteristics and diet were examined from 719 specimens collected from west and south coast trawls. The maximum age estimated was 32 years and the growth rate was low ($k=0.13$ year^{-1}). Gamete release in both sexes was asynchronous, suggesting an unusual delay between insemination and fertilisation. Sperm storage was found in histologically analysed ovaries. The diet investigation indicated a selective benthic predator with an ontogenetic shift in diet from crustaceans to teleosts. To assess habitat preference, generalised linear models were fitted to broad and fine resolution abundance data from research trawls and video footage respectively. Trawl data indicated that *H. dactylopterus* primarily occurs in the Atlantic, decreasing in abundance in the Indian Ocean. Depths from 100 to 600 m were preferred, corresponding with the offshore demersal trawl footprint. Video data highlighted that *H. dactylopterus,* especially individuals >200 mm TL, preferred complex benthic habitat, typical of deep-water reef systems on the South African outer shelf and shelf edge. Standardised catch-per-unit-effort from trawl data indicated an increase in the abundance of *H. dactylopterus* from 1987 to 2001 in response to management reforms. Subsequently, a reduction in abundance occurred, but sustained population growth of 1.42% per year since 2005 suggests a national classification of the species as Least Concern against the IUCN Red List criteria. This study provides a thorough region-specific account of a previously data-limited species. *Helicolenus dactylopterus* shows life history traits typical of the Sebastinae, yet, in South Africa, the species has not succumbed to fishing pressure to the expected extent.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

With the continued increase in the global demand for fish to meet the needs of a growing human population, the sustainable management of fish stocks is of fundamental importance. In recent decades, there has been a global shift in fisheries management from being primarily concerned with the target stock to considering the entire ecosystem in which the target stock exists (Bellido et al., 2011). This is termed the Ecosystems Approach to Fisheries (EAF) Management and is an essential requirement for long term environmental sustainability (Garcia et al., 2003). The intention of including EAF into traditional fisheries management was formalised in 2001 when 57 countries, including South Africa, adopted the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem (FAO, 2002). Through the application of EAF, the capture of non-target species, termed bycatch, is of prime concern (Hall et al., 2000; Garcia et al., 2003; Roux et al., 2015). Scientific assessment and management of these species is required.

In South Africa, there has been advancement in the implementation of EAF, but broader ecosystem concerns such as bycatch still require greater attention (Cochrane et al., 2009, 2015). The South African demersal trawl fishery, which nominally targets deep and shallow-water hake *Merluccius paradoxus* and *Merluccius capensis*, is currently suitably managed with hake stocks remaining mostly stable (Department of Agriculture Forestry and Fisheries, 2016; Williamson and Japp, 2018). However, the capture of many species as bycatch due to the poorly selective fishing method used and the limited assessment and management of these species is one of the main threats to the sustainability of the fishery.

Helicolenus dactylopterus is one such bycatch species that is caught in large quantities in the South African demersal trawl fishery. The species is widely distributed throughout the Atlantic and Mediterranean where it is fished extensively. Research on *H. dactylopterus* in the northern hemisphere has been conducted over the last two decades, but little is known about the biology, ecology and abundance trends of the species in South Africa.

1.2 The South African demersal trawl fishery

The demersal trawl fishery in South Africa started in the late 1800s with vessels mainly operating on the shallower grounds on the Agulhas Bank, targeting Agulhas and west coast sole *Austroglossus pectoralis* and *A. microlepis* (Currie et al., 2020). The targeting of hake, *Merluccius paradoxus* and *M. capensis*, began between 1910 and 1920. The fishery started to grow in the 1930s with rapid expansion into deeper fishing grounds further offshore occurring in the mid-1940s (Durholtz et al., 2015). In the early 1960s, foreign trawlers began targeting hake on South African trawl grounds. By the 1970s, the annual hake catch in South Africa had peaked at approximately 300 000 t and then declined rapidly because of overexploitation (Durholtz et al., 2015). As a result, management of the demersal trawl fishery was implemented from the late 1970s to assist in the rebuilding of the hake stock (Nel et al., 2007).

Currently, the demersal trawl fishery operates on the west and south coasts of South Africa. It is the country's most commercially valuable marine fishery accounting for approximately half of the overall value of landed catch in all South African fisheries (Butterworth and Rademeyer, 2005; Cooper, 2015; Fiandeiro et al., 2019). The fishery is split into two sectors that mainly operate in different areas. The offshore sector operates in depths between 110 and 1 000 m, from the Orange River mouth on the west coast to Port Elizabeth on the south coast (Fairweather et al., 2006; Sink et al., 2012a). *Merluccius paradoxus* is the main target species (Department of Agriculture Forestry and Fisheries, 2016), although *Lophius vomerinus* is also targeted (Stuttaford, 2000; Walmsley et al., 2007). The offshore sector contributes R4.5 billion in sales to the South African economy annually and directly employs approximately 7 300 people (Fiandeiro et al., 2019). The inshore trawl fishery is smaller than its offshore counterpart in terms of volumes caught and nominally targets *M. capensis* and *Austroglossus pectoralis* (Attwood et al., 2011). The inshore fishery operates mainly in depths of 80 to 110 m on the south coast, from Cape Agulhas to the Great Kei River (Attwood et al., 2011).

The demersal trawl fishery (both inshore and offshore sectors) is currently the only fishery in South Africa to obtain Marine Stewardship Council (MSC) certification. It was certified in 2004 (Durholtz et al., 2015) and has since retained its certification, being recertified in 2010, 2015 and 2021. Certification suggests that there is sustainable management of the targeted stocks, fishing operations do not significantly negatively impact the surrounding ecosystem, and the fishing is managed effectively and responsibly within national and international jurisdictions (Marine Stewardship Council, 2018). Whether MSC certification reflects actual sustainability of a fishery is a debate in itself (Ponte, 2012; Christian et al., 2013) which is not discussed here. In the latest certification report, areas where the demersal trawl fishery's performance could be improved were mainly related to managing of the impacts of fishing on the surrounding ecosystem (Lloyd's Register, 2021). In recent years, particular focus areas for the maintenance of the fishery's MSC certification have included the improved data collection and management of non-target bycatch species, and the improved management of the interaction of the fishery with Vulnerable Marine Ecosystems (VMEs).

Demersal trawling involves the use of poorly selective gear designed to remain in close contact with the seafloor to maximise catch. In South Africa, in both the inshore and offshore demersal trawl sectors, otter trawl gear is used, with door and net size depending on vessel size and power (Sink et al., 2012a). Typically, the two doors weigh the net down and keep it open horizontally, while a headline floats to keep it open vertically. A groundline, which may be modified for protection using wire, rubber discs, rollers or bobbins, also assists in keeping the net open vertically and drags along or just above the seafloor (Sink et al., 2012a). A minimum net mesh size of 110 mm is prescribed (FAO, 2010).

Disturbance to benthic ecosystems occurs due to direct interaction with trawl gear (Atkinson et al., 2011; Clark et al., 2016; Collie et al., 2000; Kaiser et al., 2006). The scraping of the seabed by trawl gear leads to the disturbance, damage or complete removal of benthic habitat and associated fauna (Kaiser et al., 2006; Clark et al., 2016). This can alter community structure and function and result in reductions in productivity (Kaiser et al., 2006). Many of these affected habitats host unique, fragile and structurally complex species that play an important functional role and have slow recovery rates, and thus may be indicative of VMEs (FAO, 2009).

Trawl gear catches not only the target species but many non-target species as well. These non-target species are referred to as bycatch. The unregulated, large-scale capture of bycatch can result in changes in community structure and the alteration of trophic flows. This can lead to changes in ecosystem functioning (Alverson et al., 1994; Hall et al., 2000; Garcia et al., 2003). The unregulated capture and mortality of large numbers of slow-growing and long-lived species can result in population declines and conservation concerns (Hall et al. 2000).

1.2.1 Bycatch in the demersal trawl fishery

The occurrence of bycatch and discards is an inherent and long-standing problem associated with fisheries management (Alverson et al., 1994). The scope of the bycatch issue is large and complex (Kennelly, 1995; Hall et al., 2000) and differs with each fishery, the gear used and the habitat in which the fishing occurs (Hall, 1996). The problem is compounded by the difficulties in reporting bycatch and discard rates. The data are often non-existent or of poor quality, which can lead to inaccurate estimations of mortality (Alverson et al., 1994; Hall, 1996; FAO, 1999; Walmsley et al., 2007). Contributing to the complexity of the issue is the definition and the use of the terminology “bycatch” and “discards”. In this study, bycatch is used as a generic term and, as defined by McCaughran (1992), is all non-targeted catch, whether retained or discarded, but does not include target species of non-desirable size.

Walmsley et al. (2007) conducted the first quantitative assessment of bycatch and discards in the South African demersal trawl fishery using fisheries observer data. The composition of catches made by vessels operating on the west and south coasts of South Africa were analysed. Catches were separated by area, depth and species targeted. It was found that catches reflected the community assemblages previously identified to occur in the trawl grounds, demonstrating the unselective nature of the gear (Walmsley et al., 2007). Teleosts dominated all catches, and species diversity was high, particularly on the Agulhas Bank. In the inshore hake-directed fishery, the bycatch rate was 46.89%, and in the inshore sole-directed fishery, it was 21.30%. In the offshore hake-directed fishery on the south coast, bycatch comprised 43.78% and 30.21% of the total catch in western (off Mossel Bay) and eastern (off Port Elizabeth) areas, respectively. In the offshore fishery on the west coast, bycatch rates were estimated per depth class and ranged from 7.61% to 34.64%. Bycatch rates were reduced in trawls deeper than 300 m. Though bycatch rates were highest on the south coast, the authors state much of the catch is retained, landed and processed, whereas, on the west coast, much of the catch is not utilised. This leads to a similar proportion of discarded bycatch on both the south and west coasts of approximately 10% of the total catch.

Attwood et al. (2011) used updated fisheries observer records to estimate catch volumes and catch composition in the South African inshore demersal trawl fishery. The random sampling of unsorted catches as well as of discarded catch was undertaken. Overall, 137 species were caught in the trawl fishery between 2003 and 2006 (Attwood et al., 2011). The target species *Merluccius capensis* and *Austroglossus pectoralis* comprised the majority of the annual catch, contributing 58.3% to the total unsorted catch. The estimated bycatch rate of 41.7% was comparable to the bycatch rate recorded in the inshore hake-directed fishery by Walmsley et al. (2007). The inshore demersal trawl fishery has the second-highest bycatch rate of any South African fishery (Attwood et al., 2011), surpassed only by the east coast prawn trawl fishery.

The prawn trawl fishery had a bycatch rate of approximately 70% but now operates at a low capacity since the declaration of the uThukela Marine Protected Area (MPA), which prevents fishing on the former inshore grounds (Everett, 2014). Unlike the prawn fishery, much of the bycatch in the inshore trawl fishery is retained and sold, which leads to lower levels of discards (Attwood et al., 2011). Nevertheless, the findings of Attwood et al. (2011) highlight the need to appropriately manage the harvesting of bycatch species in the demersal trawl fishery.

In unpublished research conducted by Daneel and Attwood (2013), a bycatch rate of 26.79% in the offshore hake-directed demersal trawl fishery was estimated. Again, fisheries observer records were used to estimate catch volumes and catch composition across the fishery. In contrast to Walmsley et al. (2007), catches were not separated by area or depth. Catches from the west and south coasts were analysed together. The bycatch rate estimated was within the range of that recorded by Walmsley et al. (2007) on the offshore south and west coast trawl grounds, respectively (Daneel and Attwood, 2013).

Presently in the demersal trawl fishery, target species (*Merluccius* spp.) catch is controlled through the application of a total allowable catch (TAC) limit. Bycatch is principally managed through effort limitation (SADSTIA, 2019). A restriction in the number of allowable sea days per year limits the excessive catch of bycatch species as it prevents trawlers from targeting bycatch once hake quotas are filled. Species-specific precautionary upper catch limits have been set for two bycatch species, namely kingklip *Genypterus capensis* and monkfish *Lophius vomerinus* (Department of Agriculture Forestry and Fisheries, 2016). However, regulations or management plans do not exist for any other bycatch species caught in the fishery.

Key bycatch species in the South African offshore demersal trawl fishery, in terms of biomass landed, were identified by industry representatives (Smith et al., 2013). These species included monkfish and kingklip, as well as horse mackerel *Trachurus capensis*, ribbonfish *Lepidopus caudatus*, snoek *Thyrsites atun*, Cape dory *Zeus capensis*, jacopever *Helicolenus dactylopterus*, angelfish *Brama brama*, gurnard *Chelidonichthys* spp. and panga *Pterogymnus laniarius* (Smith et al., 2013). Greenstone (2015) highlighted the importance of increased monitoring of these bycatch species to improve the sustainability of the fishery. Consequently, the Demersal Scientific Working Group developed planned work activities to address the ecological impacts of the fishery, with research and management initiatives focussing on these species (Fairweather and Durholtz, 2017; Fairweather et al., 2017). To support the activities, the South African Deep-Sea Trawling Association (SADSTIA) and WWF South Africa established a

Fisheries Conservation Project (FCP) in 2016 (SADSTIA, 2019). The FCP aimed to improve data collection for the main bycatch species caught in the fishery, with the intention that the data collected will support the assessment and management of the species and will contribute to their improved assessment under the WWF Southern African Sustainable Seafood Initiative (SASSI) (Greenstone, 2015). The FCP was completed in 2019, but the continued research on and monitoring of these key bycatch species remains a priority.

1.3 *Helicolenus dactylopterus*

Helicolenus dactylopterus (Delaroche, 1809) (Figure 1.1) is closely related to the rockfish of the genus *Sebastes*, as both genera are in the sub-family Sebastinae. *Sebastes* is an extremely diverse and species-rich genus, with 108 species recognised (Froese and Pauly, 2019). Along with *Sebastes capensis, H. dactylopterus* is the only other Sebastinid species found in southern African waters.

In South Africa and Namibia, *H. dactylopterus* is commonly referred to as jacopever and was reportedly named after a Dutch sailor named Jacob Evertson, who was notorious for his red face and large eyes (Barnard, 1947). Elsewhere, the species is commonly referred to as the blackbelly rosefish or the bluemouth rockfish.

Figure 1.1: A Helicolenus dactylopterus *specimen caught on the east coast of South Africa during a bottom trawl research survey conducted in January/February 2018 (photograph supplied by K. Sink).*

1.3.1 Taxonomy

The genus *Helicolenus* is of the order Scorpaeniformes and the suborder Scorpaenoidei (Ishida, 1994; Love et al., 2002; Bailly, 2015), but there is disagreement over its classification at the family level. Following the comprehensive systematic work done by Matsubara (1943), there was consensus that the genus *Helicolenus* was part of the family Scorpaenidae. However, Ishida (1994) conducted a study to examine the phylogeny of 55 genera of the Scorpaenoidei and proposed that the family be split into twelve with *Helicolenus*, *Sebastes, Sebastiscus, Hozukius, Adelosebastes* and *Sebastolobus*, forming their own family – the Sebastidae. Subsequent literature is divided on the acceptance of this classification. However, more recent studies, as well as WoRMS, FishBase and the Catalog of Fishes accept the classification of Sebastidae (Bailly, 2015; Eschmeyer et al., 2017; Froese and Pauly, 2019).

Regardless of the classification at the family level, it is agreed that there are two sub-families in the Sebastidae. *Helicolenus*, along with *Sebastes*, *Hozukius* and *Sebastiscus*, are included in the sub-family Sebastinae. Johansen et al. (1993) reported strong intergeneric variation between *Helicolenus* and *Sebastes*, confirming the validity of the genera.

Species of *Helicolenus* have a complete suborbital stay and are classified based on the lack of a swim bladder and the presence of 25 vertebrae (Abe and Eschmeyer, 1972). The genus comprises nine species (Table 1.1) (Froese and Pauly, 2019). WoRMS (Bailly, 2015) and the Fish Tree of Life (Rabosky et al., 2018) recognise a tenth species, *Helicolenus alporti*. However, no genetic data are available for *H. alporti* (Rabosky et al., 2018), and FishBase considers *H. alporti* to be a synonym of *H. percoides.*

Table 1.1: The nine species within the genus Helicolenus *according to Froese and Pauly (2019).*

Genus	**Species**
Helicolenus	*avius* (Abe and Eschmeyer, 1972)
Helicolenus	*barathri* (Hector, 1875)
Helicolenus	*dactylopterus* (Delaroche, 1809)
Helicolenus	*fedorovi* (Barsukov, 1973)
Helicolenus	*hilgendorfii* (Doderlein, 1884)
Helicolenus	*lahillei* (Norman, 1937)
Helicolenus	*lengerichi* (Norman, 1937)
Helicolenus	*mouchezi* (Sauvage 1875)
Helicolenus	*percoides* (Richardson and Solander, 1842)

Based on morphological differences, Eschmeyer (1969) postulated the existence of two subspecies of *H. dactylopterus*: *Helicolenus dactylopterus lahillei* (now classified as *H. lahillei*) occurring in the South West Atlantic and *H. dactylopterus dactylopterus* occurring in the East Atlantic, with a population of the latter occurring in South African waters. Barsukov (1980) proposed a further four subspecies, differentiated by their geographic ranges and by morphological characteristics. These included *H. dactylopterus maderensis, H. dactylopterus maculatus, H. dactylopterus gouphensis* and *H. dactylopterus angolensis.* These subspecies are, however, not accepted by WoRMS and by FishBase (Bailly, 2015; Eschmeyer et al., 2017; Froese and Pauly, 2019), and therefore are not referred to further.

1.3.2 Morphology

Helicolenus dactylopterus is a robust, muscular fish with a moderately compressed body form. They have overlapping scales, and their head and body range in colour from light yellowish orange to bright red, with vertical darker coloured bars that run dorso-ventrally. The belly and chest are distinctively more pale in colour- usually white or light pink (van der Elst, 1993; Heemstra and Heemstra, 2004; Rodríguez-Mendoza, 2013). The species has large eyes and a mouth that opens wide and is grey-black in colour (Figure 1.2). Villiform teeth occur along both jaws and on the roof of the mouth (van der Elst, 1993; Heemstra and Heemstra, 2004; Rodríguez-Mendoza, 2013).

In comparison to other Scorpaenid and Sebastid species, *H. dactylopterus* generally has smaller head spines, with sharp projections occurring on top of the head, under the eye, and on the gill covers. The species has a single dorsal fin consisting of 12 spines, with 12 or 13 soft rays, and an anal fin with three spines and five soft rays (van der Elst, 1993; Heemstra and Heemstra, 2004). The presence of 12 dorsal spines is distinctive and separates the species from *S. capensis* (van der Elst, 1993). Pectoral fins are large and consist of 18 to 20 rays, the top of which are truncated, while the bottom few rays are free at the tips (Figure 1.2). *Helicolenus dactylopterus* has 25 vertebrae and does not have a swim bladder, which forms the basis of its classification within the genus (Abe and Eschmeyer, 1972).

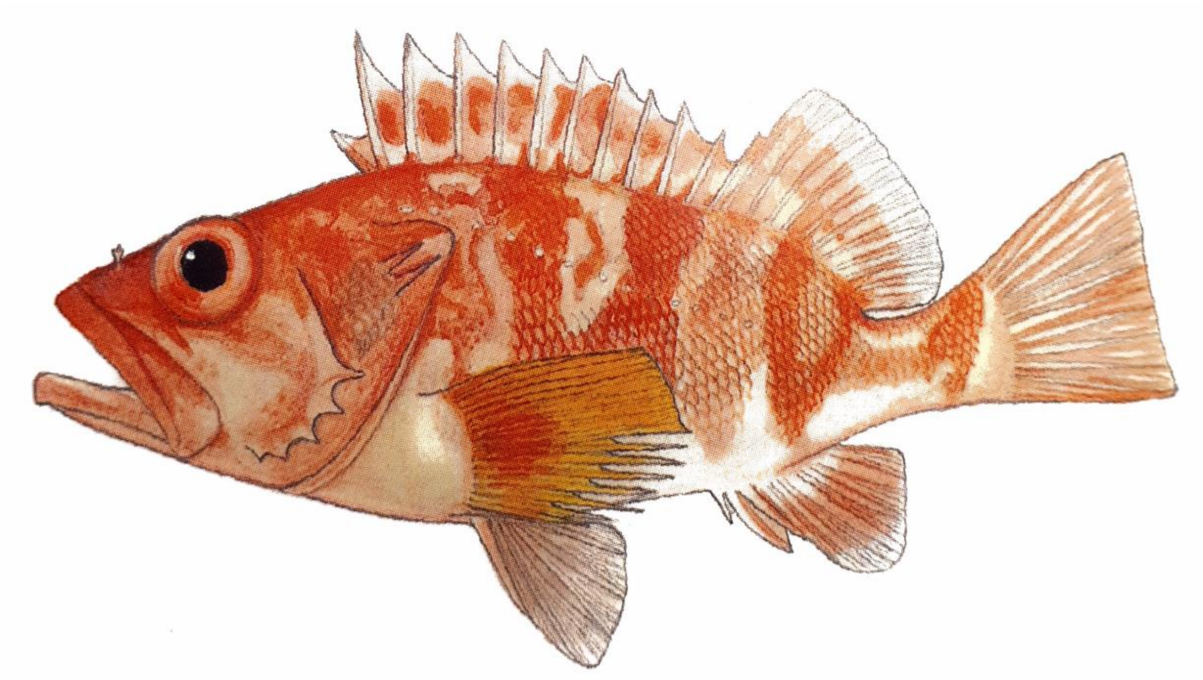


Figure 1.2: Helicolenus dactylopterus *(Delaroche, 1809), as depicted by Heemstra and Heemstra (2004).*

1.3.3 Distribution

Sebastinids are distributed throughout the world’s oceans, occurring in subtropical and temperate waters of the North and South Pacific, the North and South Atlantic, the Mediterranean and in the South West Indian Ocean (Smith et al., 2009). Most *Sebastes* species occur off the west coast of the United States and Canada. There is a hotspot of *Sebastes* diversity in southern California, where at least 60 species of the genus have been recorded (Love et al., 2002; Froese and Pauly, 2019). Many of these are the target of important commercial and recreational fisheries. None of the other Sebastinid genera occur in the North East Pacific, with most occurring in the North West Pacific (three *Helicolenus* spp., two *Hozukius* spp. and three *Sebastiscus* spp.). The remainder of the *Helicolenus* species are distributed throughout the North and South Atlantic, the Mediterranean, the West Indian and the South East Pacific Ocean (Froese and Pauly, 2019).

Helicolenus dactylopterus is widely distributed throughout the eastern Atlantic from Norway to South Africa (Heemstra and Heemstra, 2004) (Figure 1.3). It has been recorded within the North Sea (Heessen et al., 1996; Mamie et al., 2007) and at Rockall Trough in the northeast Atlantic (Kelly et al., 1999). It occurs off the Azores and the Canary Islands (Heessen et al., 1996; Esteves et al., 1997), off Portugal (Sequeira et al., 2003) to offshore of the uThukela mouth, on the east coast of South Africa (van der Elst, 1993; Heemstra and Heemstra, 2004; Eschmeyer et al., 2017). It also commonly occurs throughout the western and central basins of the Mediterranean (Pirrera et al., 2009) but has not been recorded in the Black Sea (Bilecenoğlu et al., 2014). In the West Atlantic, it occurs from Georges Bank down to Florida (Heessen et al., 1996), although some authors have reported it to occur from Nova Scotia to Venezuela (Eschmeyer, 1969; Eschmeyer et al., 2017). There is some doubt about the conspecificity of the species throughout its distribution (Aboim et al., 2005), but several records on the Barcode of Life Data (BOLD) System (Ratnasingham and Hebert, 2007) indicate that sequences from the cytochrome c oxidase subunit I (COI) gene of specimens collected in South Africa are representative of the species.

Helicolenus dactylopterus has an extensive bathymetric distribution. In Portugal, it occurs at depths between 200 and 1000 m, in outer shelf and slope habitats, with highest biomass and abundance occurring between 200 and 500 m (Neves et al., 2011). This has been attributed to the distribution of important crustacean prey items at these depths (Massutí et al., 2001; Pirrera et al., 2009; Romeo et al., 2009; Neves et al., 2011).

In South Africa, the species forms a significant component of demersal fish communities in outer shelf and shelf edge habitats along the west, south and east coasts, from the Namibian border to the uThukela mouth (Roel, 1987; Smale et al., 1993; van der Elst, 1993; Heemstra and Heemstra, 2004).

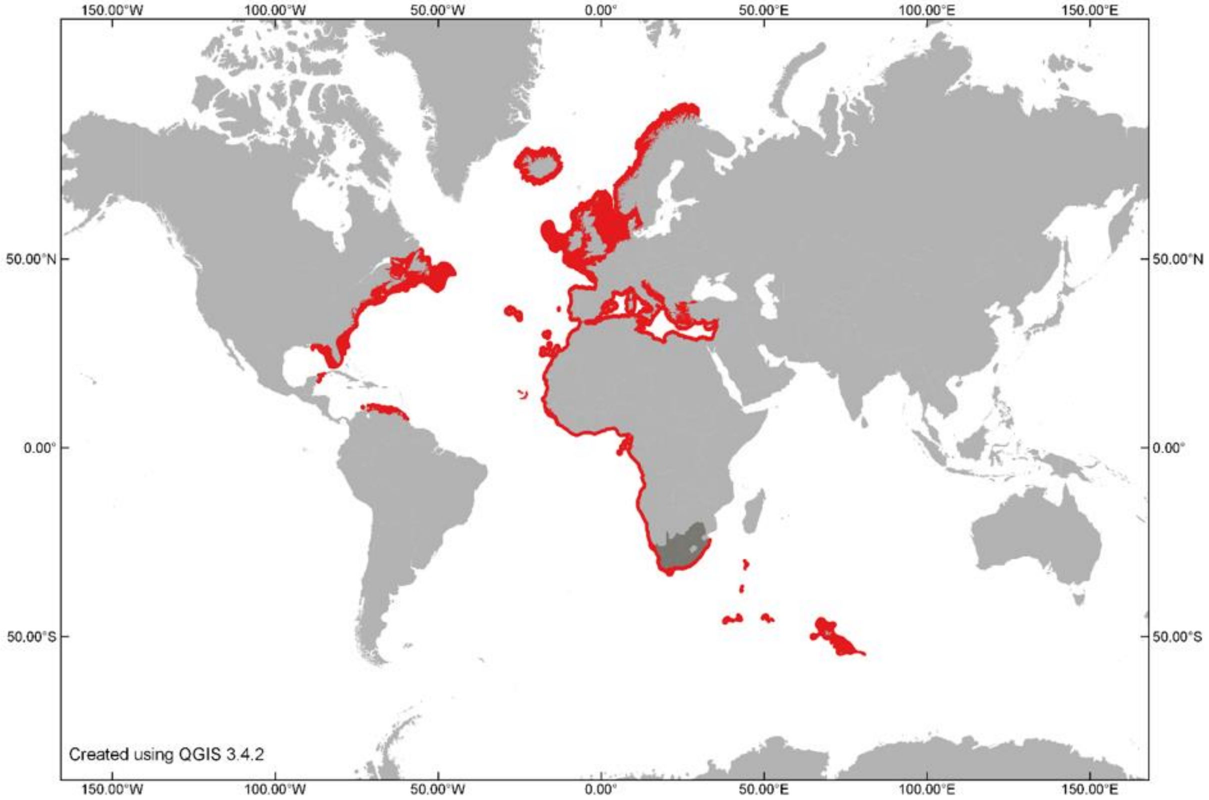


Figure 1.3: Global distribution of Helicolenus dactylopterus. *Data were obtained from Nunoo et al. (2015). The population off South Africa, shaded in dark grey, is the focus of this study.*

1.3.4 Biology

Most species in the Sebastinae exhibit life history characteristics typical of periodic strategists (Winemiller and Rose, 1992). Species are generally slow-growing, long-lived, show delayed maturation but have high fecundity (Adams, 1980; Haldorson and Love, 1991). Species within the subfamily show similar but unusual reproductive traits in which individuals have internal fertilisation and are either viviparous or display intermediate forms of reproduction between oviparity and viviparity (Muñoz, 2010). Egg production occurs until an advanced age (de Bruin et al., 2004), suggesting that many species in the Sebastinae have long reproductive life spans (Muñoz, 2010). The conservative life history traits of the Sebastinae generally result in low population resilience and high vulnerability to overexploitation (Parker et al., 2000; Berkeley et al., 2004; Magnuson-Ford et al., 2009). In the northeast Pacific, several rockfish stocks have suffered precipitous declines or collapsed over the last 40 years (Ralston, 1998; White et al., 1998; Parker et al., 2000; Berntson et al., 2007).

Helicolenus dactylopterus is thought to share many of the conservative life history traits of its close relatives, with some studies reporting the maximum age of the species to be greater than 40 years (Kelly et al., 1999) and the growth rate to be as low as 0.03 year^{-1} (Morales-Nin, 1989). There is, however, considerable variation in these estimates in the literature.

1.3.5 Fishing pressure

Across their ranges, Sebastinid species form an important part of commercial and recreational fisheries (Espiñeira and Vieites, 2012). In California, approximately 85% of the *Sebastes* species that occur there are fished commercially and recreationally, with some of these being fished for over a century (Yoklavich et al., 2000). More than 30 *Sebastes* species occur in British Columbia, with many of these being caught in commercial and recreational hook and line and demersal trawl fisheries, often as bycatch (Parker et al., 2000). The British Columbia groundfish trawl and longline fisheries have successfully implemented bycatch quotas for several *Sebastes* species, within an individual transferable quota (ITQ) framework, which has led to the avoidance of high bycatch areas and a reduction in the catch of these species (Branch and Hilborn, 2008; Forrest et al., 2020). Some *Sebastes* species, such as *S. schlegelii*, are fished commercially in the North West Pacific (Froese and Pauly, 2019). In East Asia, *S. schlegelii* is an important mariculture species (Kusakari, 1991; Lee et al., 2011).

Helicolenus dactylopterus is the most exploited species within the *Helicolenus* genus (Espiñeira and Vieites, 2012). The species is mostly caught as bycatch in demersal trawl, longline and gillnet fisheries throughout the Atlantic and Mediterranean (for example, White et al., 1998; Kelly et al., 1999; Sequeira et al., 2009; Rodriguez-Mendoza et al., 2011; Deval et al., 2018; González-García et al., 2020), although it is targeted by some fisheries in the Tyrrhenian Sea (Consoli et al., 2010; Sami et al., 2016). The species is marketed in areas throughout its distribution and has high commercial value in Portugal, the Azores, Spain, Italy, Turkey and Tunisia (Esteves et al., 1997; Abecasis et al., 2006; Ribas et al., 2006; Sequeira et al., 2009; Consoli et al., 2010; Sami et al., 2016; Bayhan et al., 2018; Deval et al., 2018). In Portugal and the Azores, an average of 2 500 t of *H. dactylopterus* was landed annually between 2001 and 2011 (Neves et al., 2011; Sequeira et al., 2012). In Turkey, *H. dactylopterus* is the most abundant bycatch species in the demersal trawl fishery (Bayhan et al., 2018; Deval et al., 2018).

In South Africa, *H. dactylopterus* is the sixth most caught bycatch species, in terms of weight, in the offshore demersal trawl fishery (Daneel and Attwood, 2013). The species is also caught as bycatch in lesser quantities in the inshore trawl fishery (Attwood et al., 2011) and in the demersal longline fishery (Greenstone et al., 2016). Using independent fisheries observer data averaged over 2002 to 2006, it was estimated that approximately 1 711 t of *H. dactylopterus* per annum was caught in the offshore demersal trawl fishery, and 17 t per annum was caught in the inshore demersal trawl fishery (Attwood et al., 2011; Daneel and Attwood, 2013). In the demersal longline fishery, 2.5 t of *H. dactylopterus* was caught by vessels on which fisheries observers were deployed between November 2013 and October 2014, comprising 1.07% of the overall catch (Weston and Attwood, 2017). Smith et al. (2013) used landed catch data from 2000 to 2010 and estimated that an average of 789 t of *H. dactylopterus* was caught annually in the offshore demersal trawl fishery. Baust et al. (2015) also utilised landed catch data reported by South African authorities to the United Nations Food and Agriculture Organisation (FAO). It was estimated that an average of 870 t of *H. dactylopterus* was landed annually between 1950 and 2014 by commercial fisheries (Baust et al., 2015). The landings data excluded discards and thus are lower than estimates derived from fisheries observer data.

Data from the *Sea Around Us Project* (Pauly and Zeller, 2015), to which Baust et al. (2015) contributed, show that catch of *H. dactylopterus* in the South African exclusive economic zone (EEZ) has contributed substantially to the overall global catch of the species. From 1950 to 2014, catch in South Africa constituted between 13 and 76% of the global catch of *H. dactylopterus* per year (Figure 1.4). The majority of the landed catch of *H. dactylopterus* in South Africa over the last seven decades was used for direct human consumption, but a small portion was used for fish meal and fish oil processing (Baust et al., 2015).

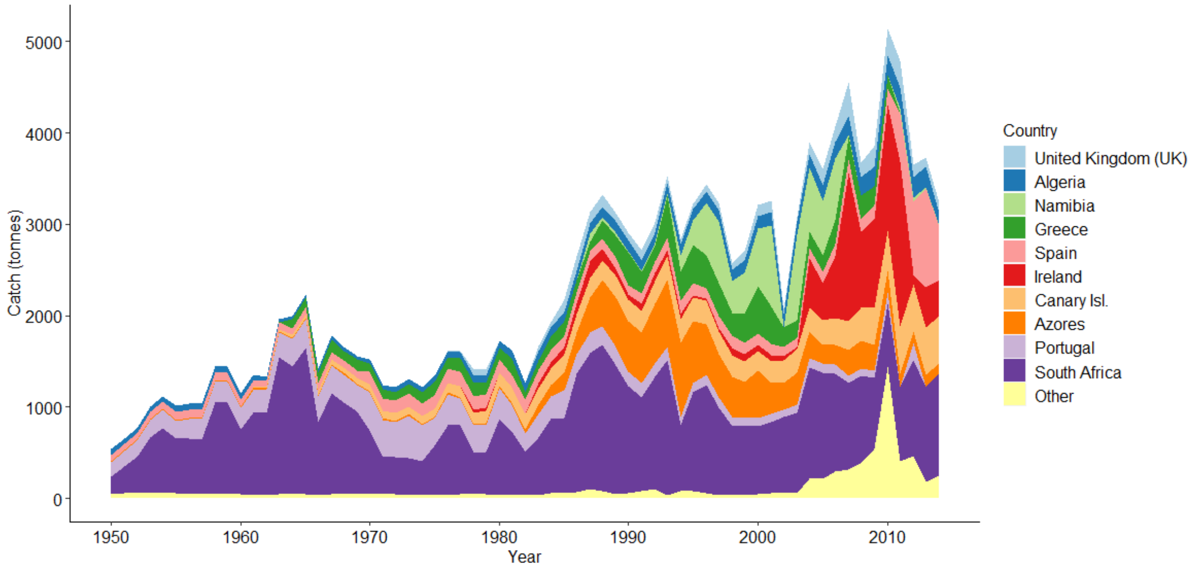


Figure 1.4: Global catch (tonnes) of Helicolenus dactylopterus *per country (within the respective exclusive economic zones) from 1950 to 2014. Data were obtained from Pauly and Zeller (2015). Catch data included official reported catch only.*

Apart from effort limitation, there are currently no regulations or management plans in place for *H. dactylopterus* in South Africa. As a part of the Fisheries Conservation Project, *H. dactylopterus* has been identified as an important bycatch species in the South African demersal trawl fishery, on which future research and management initiatives should be focussed (Fairweather and Durholtz, 2017; Winker et al., 2017).

1.4 Research required on *Helicolenus dactylopterus*

Little research has been conducted on the biology, ecology and abundance trends of *H. dactylopterus* in South Africa. Given this, it is difficult to describe the population status of *H. dactylopterus* in local waters and its vulnerability to fishing pressure. This is problematic because the species is a prominent bycatch in the demersal trawl fishery.

Investigation of the life history characteristics, including the age, size, growth, maturity and reproductive rates of *H. dactylopterus* in South Africa, is needed to assess the population resilience, productivity, and the maximum amount of fishing effort the population can endure. Information on the diet and trophic ecology of the species is required to obtain insight into its role in the ecosystem and can be used in ecosystem models. A description of the habitat preference of *H. dactylopterus* is important to understand the distribution patterns of the species and may provide insights into any essential habitat requirements and guide habitat management. Knowledge of the abundance trends of *H. dactylopterus* is required to estimate the population status of the species in South Africa.

1.5 Aim, objectives and structure of the study

Overall, this study aimed to generate biological and ecological information for this data-limited species in South Africa. The provision of baseline data describing the biology and ecology of *H. dactylopterus* will contribute to the improved ecosystem-level management of the demersal trawl fishery and have application to the conservation assessment of the species in South African waters.

This study comprises three data chapters. Chapter 2 investigates the life history traits of *H. dactylopterus* in South Africa and compares these traits to those of conspecifics in other regions of the Atlantic and Mediterranean. The age, growth, reproductive characteristics and diet of the species are detailed. Chapter 3 investigates the habitat preference of *H. dactylopterus* in South Africa by identifying key factors that influence the abundance and distribution of the species. Chapter 4 assesses the trends in the relative abundance of *H. dactylopterus* in South Africa to classify the local conservation status of the species. Chapter 5 provides a summary of the study and details the main conclusions and contributions of the work.

CHAPTER 2

LIFE HISTORY AND DIET OF *HELICOLENUS DACTYLOPTERUS* IN SOUTH AFRICA

2.1 Abstract

The age, growth, reproductive characteristics and diet of *Helicolenus dactylopterus* was investigated in South Africa to complete the global picture of this broadly distributed species. A total of 719 specimens, primarily collected from commercial trawls on the west and south coasts, were examined. *Helicolenus dactylopterus* was shown to be slow-growing and long-lived. The analysis of sectioned otoliths indicated that opaque ring formation occurred annually from September to January. The estimated age ranged from 0+ to 32 years corresponding to fish from 20 to 494 mm in total length. No difference in the total length or growth was found between sexes and the combined von Bertalanffy growth model was $TL\ (mm) = 365.66(1 - e^{-0.13(t+1.14)})$. Gamete release in females and males was asynchronous. Females spawned from June to November and males released sperm from September to June. The asynchronicity in gamete release between sexes suggested a delay between insemination and fertilisation which was confirmed by sperm storage in most ovaries that were histologically analysed. Length and age at maturity were lower than estimates from other areas. Diet investigation yielded 66 prey taxa and aligned with previous research indicating that this species is a selective benthic predator with an ontogenetic shift in diet from crustaceans to larger prey such as teleosts. This ontogenetic shift was also reflected in a change in trophic level as fish grew larger. The new knowledge presented here will allow for the assessment of the vulnerability of the species to local fishing pressure, which will contribute to the improved management of the South African demersal trawl fishery, in which *H. dactylopterus* is primarily caught.

2.2 Introduction

The life history traits of a species determine how that species responds to environmental perturbations (King and McFarlane, 2003). Knowledge of these traits is important for the general understanding of a species' biology, ecology and behaviour and central to the interpretation of responses to disturbances such as fishing and climate change. Biological data on fish size, age, growth rates and reproductive cycles provide an understanding of productivity and can contribute to stock assessment. The collection of these data is imperative for improving fisheries management (Mendonça et al., 2006; Sequeira et al., 2009). Fish diet analysis provides insight into resource requirements and the trophic niche that the species occupies.

Helicolenus dactylopterus is a deep-water benthic fish that has an extensive distribution on continental shelves on both sides of the Atlantic and as far east as the uThukela Banks on the east coast of South Africa. The species is closely related to the rockfish group, which is comprised of *Sebastes* species. Both genera occur in the sub-family Sebastinae.

Sebastinae species are generally slow-growing and long-lived with delayed maturity (Adams, 1980; Haldorson and Love, 1991). At least 35 *Sebastes* species attain maximum ages greater than 30 years (Cailliet et al., 2001). Among these, the longest lived species are *Sebastes ruberrimus,* which is reported to reach 118 years, *S. borealis* which attains an age of 157 years and *S. aleutianus* which is one of the longest living fish species, living up to 205 years (Cailliet et al., 2001). Growth rates of species in the subfamily are generally slow, relative to other fish species, with k ranging from 0.1 to 0.3 year^{-1} in most *Sebastes* (Love et al., 2002). Based on their occurrence in the Sebastinae, *Helicolenus* species are thought to exhibit similar life history traits.

Some studies conducted on *H. dactylopterus* in the North Atlantic and the Mediterranean suggest longevity and slow growth, but there is considerable variation in these estimates. Maximum age reported for the species north-west of Ireland at Rockall Trough in the North Atlantic is 43 years in males and 37 years in females (Kelly et al., 1999) and in Madeira, it is 34 years across both sexes (Sequeira et al., 2012). In the Mediterranean, the maximum age is estimated at 30 years in males and 26 years in females (Massutí et al., 2000). Growth rates are low, ranging from 0.05 to 0.09 year^{-1} (Abecasis et al., 2006; Deval et al., 2018). Other studies, however, found substantially lower maximum ages but higher growth rates of *H. dactylopterus*. In the Azores, the maximum age was reported to range from 12 to 16 years and growth rates ranged from 0.10 to 0.18 year^{-1} (Isidro, 1987; Esteves et al., 1997). In the Mediterranean, lower maximum age estimates were found by Ragonese and Reale (1995), Demirhan and Akbulut (2015) and Sami et al. (2016) who estimated the maximum age of individuals at ten, eight, and nine respectively. In these studies, growth rates ranged from 0.06 year^{-1} (Demirhan and Akbulut, 2015) to 0.14 year^{-1} (Sami et al., 2016). One study has been conducted on the age and growth of the species in the southern hemisphere, in Namibia, where the maximum age was estimated to be 14 years (Morales-Nin, 1989).

Age and length at maturity in *H. dactylopterus* at Rockall Trough was 13 years at 23 cm total length in females and 16 years at 26 cm total length in males (Kelly et al., 1999). Similar age and length at maturity estimates were found for individuals occurring in the North West Atlantic (White et al., 1998). Sequeira et al. (2012), however, reported length at maturity in *H. dactylopterus* in the Azores and Portugal to be lower, ranging from 16.40 to 18.60 cm and Deval et al. (2018) reported it to range from 17.30 to 21.80 cm in the Mediterranean. In most studies, mature *H. dactylopterus* were defined as those with gonads in the developing phase and onwards.

The reproductive characteristics of *H. dactylopterus* have mainly been studied in Portugal and the Mediterranean. Like many Sebastinids, *H. dactylopterus* is a periodic strategist in that it is slow-growing and long-lived but has high fecundity (Winemiller and Rose, 1992; King and McFarlane, 2003). The species has internal fertilisation and releases embryos in the early stages of development. Cleavage and blastula stage embryos are the most frequently observed in spawning females (Sequeira et al., 2003, 2011). Female and male gamete release occurs at different times of the year. Females generally spawn over boreal winter and spring and males release sperm from boreal summer to early winter. The length of the estimated spawning period differs among studies. Nouar (2003) reported female spawning in Algeria to occur from October to April and Muñoz and Casadevall (2002) reported spawning to only occur in January and February in the Catalan Sea. The separation between the female and male reproductive cycles suggests that females store sperm. Intraovarian sperm storage has been reported in the North Atlantic and the Mediterranean (Mendonça et al., 2006; Muñoz et al., 1999; White et al., 1998).

Helicolenus dactylopterus is a carnivorous, opportunistic feeder, showing characteristics typical of a sit-and-wait predator (van der Elst, 1993; Uiblein et al., 2003). All diet studies from the Mediterranean report specialist feeding (Nouar and Maurin, 2000; Consoli et al., 2010;

Gastoni et al., 2011; Capezzuto et al., 2020). This is despite Consoli et al. (2010) recording organisms from 67 taxa in the stomachs of 455 fish. Merrett and Marshall (1981) also described the diet of *H. dactylopterus* off the coast of North Africa, in the North Atlantic, to be selective. The same does not apply to the diet of *H. dactylopterus* in Portuguese waters though, where Neves et al. (2012) identified 81 prey items in the stomachs of 619 individuals and described the diet of the species as being diverse, with specialisation only in larger fish. The diet is generally dominated by benthic crustaceans but other crustaceans, benthic and pelagic fish, pelagic tunicates, cephalopods and polychaetes are also preyed upon (for example Collignon and Aloncle, 1960; Macpherson, 1985; Consoli et al., 2010; Capezzuto et al., 2020). Only two studies have been conducted on the diet of *H. dactylopterus* in the southern hemisphere. Macpherson (1985) analysed stomach contents from 647 Namibian fish and Meyer and Smale (1991) examined the diet in 437 South African specimens. In both studies, the diet was found to mainly comprise decapods, stomatopods, euphausiids and mysids.

Helicolenus dactylopterus has interesting and, in the case of reproduction, unique life history traits. Although well studied in the North Atlantic and Mediterranean, there is little agreement on many aspects of the age and growth, reproduction and diet of the species. Previous literature has presented conflicting results in the maximum age, the growth rate, the age and length at maturity, the length of the spawning season and the diversity of the diet of *H. dactylopterus*. Whether observed differences in life history parameters are an artefact of sampling or due to real differences in the age and growth of fish from different regions is unclear. Little research has been conducted on the species in the southern hemisphere and even less in South Africa, despite it being caught in large quantities as bycatch in the South African demersal trawl fishery (Daneel and Attwood, 2013).

This study, therefore, aimed to assess the life history traits of *H. dactylopterus* in South Africa and to compare these with individuals in other regions to clarify some of these confounding patterns. The biological information generated can be used to improve the management of this prominent bycatch species.

The objectives of this chapter were fourfold. The first objective was to characterise the age and growth of *H. dactylopterus* in South Africa and establish whether differences in the age and growth patterns exist between sexes. Secondly, this study sought to understand the reproductive characteristics of the species in South Africa in terms of the population sex ratio, maturity and reproductive cycle. The third objective was to describe the diet of the species in South Africa and determine whether it is affected by fish size and depth. Finally, it was aimed to conduct a meta-analysis to place the characteristics estimated in this study in the context of those estimated for *H. dactylopterus* in other regions.

2.3 Materials and Methods

2.3.1 Sampling

Helicolenus dactylopterus specimens were sampled through the South African Deep-Sea Trawling Industry Association (SADSTIA) Observer Programme from landed bycatch on offshore commercial hake trawlers from November 2017 to October 2019. Observers are deployed randomly on vessels in the inshore and offshore demersal trawl sectors based on vessel availability. Target observer coverage is 90 days per month (i.e. at least three vessels observed per day during a 30-day month), with the aim of covering as many different vessels as possible. Sample collection was randomly assigned to observers who were provided with printed instructions before their departure, detailing the sampling procedures. Samples were collected every month from one or multiple randomly selected trawls from the west and south coasts of South Africa. An effort was made to collect at least 30 fish each month from both coasts, but this was not always feasible. Samples were thus primarily collected from the west coast, and south coast samples were collected when possible. Fish were selected to cover a variety of size classes.

Eight *ad hoc* supplementary samples, comprising 53 fish, were obtained from bottom trawl research surveys conducted by the Oceanographic Research Institute on the east coast of South Africa in January/February 2018, and by the Department of Forestry, Fisheries and the Environment (DFFE, previously the Department of Agriculture, Forestry and Fisheries) on the west coast in January and February 2019. Additionally, two samples comprising 45 recruits were obtained from a pelagic spawner biomass survey conducted by DFFE in shallower water (< 200 m) on the west coast in October 2018. These fish yielded length and weight data only. All specimens were frozen, and the date, location and depth (trawl start depth) were recorded. Fresh samples could not be obtained due to commercial and research vessels going out to sea for several days/weeks at a time.

Samples were grouped into six areas based on catch locality and proximity (Figure 2.1). On the west coast of South Africa (west of 20°E), area one occurred north of 34°S, area two spanned from 34 to 35°S and area three from 35 to 36°S. On the south coast (east of 20°E), area four was south of 36°S and area five spanned from 34 to 35°S offshore between Mossel Bay and Port Elizabeth. Area six occurred further north on the east coast of South Africa from 29 to 30°S (Figure 2.1).

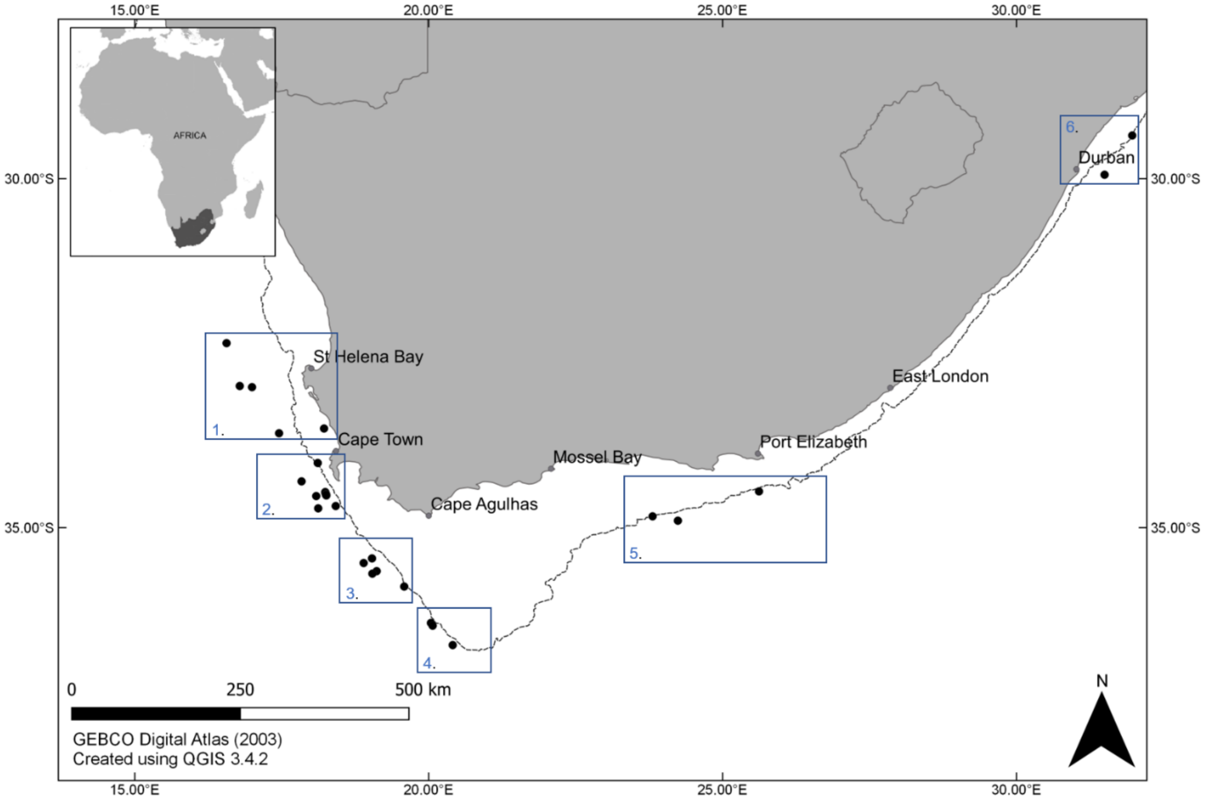


Figure 2.1: Map of South Africa showing the localities of study samples of Helicolenus dactylopterus *collected from commercial and research trawls. The numbered blue boxes indicate the six areas in which samples were grouped. The dashed line shows the 200 m bathymetric contour derived from the GEBCO Digital Atlas* (IOC et al., 2003).

2.3.2 Morphometrics and meristics

In the laboratory, fish were defrosted and photographed. Total length and standard length were measured to the nearest millimetre (Figure 2.2). Total weight and eviscerated weight were measured to the nearest 0.1 g.

Meristics data were recorded for *H. dactylopterus* specimens randomly selected from each monthly sample. The number of spines and rays on the dorsal and anal fins were counted

(Figure 2.2). The most exterior left gill arch was removed using scissors and forceps. The number of gill rakers were counted separately for the upper and lower segments of the gill arch and recorded.

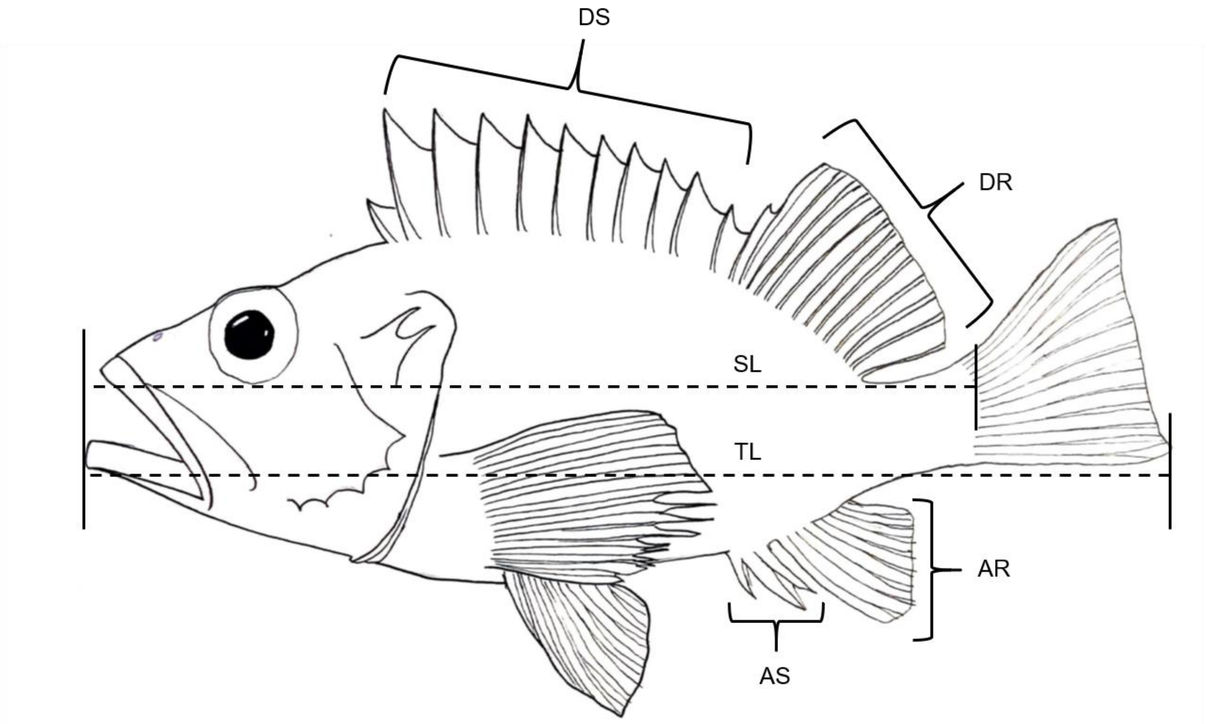


Figure 2.2: Schematic illustrating morphometric and meristics measurements obtained from Helicolenus dactylopterus *from South Africa. SL = standard length, TL = total length, DS = dorsal spines, DR = dorsal rays, AS = anal spines, AR = anal rays.*

Statistical analyses of morphometric measurements

Normality was assessed using frequency distributions, and homogeneity of variances were tested using the Levene method (Zar, 1996), before conducting parametric tests.

The differences in mean total length between the sexes of *H. dactylopterus* were tested using a two-sample t-test unless assumptions of normality and homogeneity of variances were not met, in which case data were log-transformed or a Wilcoxon rank-sum test was used (Zar, 1996).

Both standard length and weight of *H. dactylopterus* specimens were regressed against total length (in mm), for all data combined and separately for females and males. A linear equation was fitted to the standard length versus total length data using a least-squares regression procedure (Zar, 1996):

$$SL = m\,TL + c \tag{2.1}$$

SL is the standard length (mm), TL is the total length (mm), m denotes the slope of the line and c is the intercept.

A power function was fitted to the length versus weight data using a least-squares regression procedure on ln-transformed data (Zar, 1996):

$$W = aTL^b \tag{2.2}$$

W is the total mass (g), a is the intercept of the regression line and is the coefficient related to body shape, and b is the regression coefficient which indicates allometric ($b \neq 3.00$) or isometric ($b = 3.00$) growth (Froese, 2006). To test for allometric or isometric growth in *H. dactylopterus* specimens, unpaired Student's t-tests were conducted on the linear regression parameters to test whether the slope (b) was significantly different from three (Zar, 1996):

$$t = \frac{b_1 - 3}{s_{b1}}, \tag{2.3}$$

where s_b is the standard error of the slope.

Differences in the length-weight relationships between males and females were tested by fitting a linear regression model to the log-transformed length and weight data. Sex was included as an interaction variable with two levels, as all fish of indeterminate sex were excluded from the analysis. An analysis of variance (ANOVA) was used to compare the slopes and intercepts of the two regression lines (Ogle, 2013).

The effect of depth and location (as area, Figure 2.1) on total length was tested using a one-way ANOVA unless assumptions of normality and/or homogeneity of variances were not met. If the assumptions of normality and homogeneity of variances were not met, data were log-transformed and an ANOVA was used (provided that the transformed data fulfilled the assumptions), otherwise, a Kruskal Wallis test by ranks was used. However, if the data were approximately normal but the variances were not homogenous, data were not transformed, and a Welch's ANOVA was used. Pairwise comparisons were done using Tukey's HSD or the Games-Howell post-hoc test (Ruxton and Beauchamp, 2008). Depths were represented as 100-m classes (from 201 to >601 m). It was assumed that the depth of each trawl did not vary by more than 100 m.

Specimens from the eight research samples collected were excluded from the total length comparisons among depths and areas to limit the potential bias that may have been present because of the use of a smaller net mesh size during research trawls. This resulted in the exclusion of area six from the comparison.

Statistical analyses of meristic variables

The number of spines and rays on the dorsal and anal fins and the number of vertical and horizontal gill rakers were compared among fish from the six areas. Normality was assessed visually using frequency distributions and homogeneity of variances were tested using the Levene method (Zar, 1996). In cases where distributions were non-normal or there were unequal variances, data were log-transformed. If transformed data fulfilled the assumptions of normality and homogeneity of variance, an ANOVA was used for the comparisons among areas. When the assumptions were not met, a Kruskal Wallis test by ranks was used.

All analyses were conducted using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020) or Microsoft Excel 2016. The R packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2020), ggpubr (Kassambara, 2018), FSA (Ogle et al., 2020), MASS (Venables and Ripley, 2002) and coin (Hothorn et al., 2008) were all utilised.

2.3.3 Age and growth

Age estimation

Sagittal otoliths were used to estimate the age of *H. dactylopterus*. Some authors have found evidence of age underestimation when using whole otoliths to age *H. dactylopterus* specimens older than seven years, and thus instead advocate for the use of sectioned otoliths (Kelly et al., 1999; Abecasis et al., 2006). Sequeira et al. (2013), however, found no significant difference in age estimation between the two aging methods, regardless of fish size. In this study, a conservative approach was taken and the otoliths were sectioned following the method outlined by Bedford (1983). The left or the right otolith was randomly selected from each fish and set in clear polyester resin before slicing transversally, through the nucleus, using a precision saw fitted with twin diamond wafering blades set 0.35 mm apart. Each section was then mounted and fixed to a glass slide using DPX Mountant. To increase the clarity of the section, DPX Mountant was placed on top of each section.

The reading of sectioned otoliths was undertaken using a Leica DM750 compound microscope fitted with a Leica ICC50 digital camera attachment with transmitted light at 40X magnification. Images were processed using the Leica LAS EZ software. Readings were independently conducted by three observers without prior knowledge of fish length. Opaque rings were counted along the proximal axis when possible or readings were undertaken along the dorsal and ventral axes. Counts were accepted when there was agreement between two or more readers. Accepted annuli counts were converted to ages for each fish, assuming 1 January as the birth date.

Ageing bias and precision

Age estimates are susceptible to reader bias and so systematic differences and the consistency of ageing among readers should be quantified. To detect systematic differences, an age bias plot was used (Campana et al., 1995). The age readings of each observer were plotted against one another. The readings of the observer plotted on the y-axis were presented as the mean age (± 95% CI) of each age category of the readings reported by the observer plotted on the x-axis. Differences were compared to the line of equivalence, where observer x = observer y. Once patterns in bias were identified, the consistency and reproducibility of age estimations among readers were analysed by calculating the coefficient of variation (CV, Campana et al., 1995; Chang, 1982). The average percentage error (APE, Beamish and Fournier, 1981) can also be used as a precision measurement, but Campana (2001) found it to be functionally equivalent to the CV and thus it is not presented here. The equation for CV is as follows:

$$CV = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(x_{ij} - x_j)^2}{R-1}}}{x_j}, \qquad (2.4)$$

where x_{ij} is the ith age determination of the jth fish, x_j is the mean age of the jth fish and R is the number of times the fish was aged. The CV was averaged across fish and was calculated for all three observers and each pair of observers respectively.

Analyses were done using the FSA package (Ogle et al., 2020) in the R statistical platform, version 3.6.3 (R Core Team, 2020).

Age validation

Otolith margins were analysed and categorised as either opaque or hyaline to confirm that *H. dactylopterus* otolith rings are laid down annually and to validate the age estimation method used. Margin categorisation was accepted when there was an agreement between two readers.

Modelling growth

To estimate the growth parameters of *H. dactylopterus*, the von Bertalanffy growth (VBG) model was fitted to length at age data by means of non-linear least squares regression using the FSA package (Ogle et al., 2020) in the R statistical platform, version 3.6.3 (R Core Team, 2020). The simplified von Bertalanffy growth model is:

$$TL_t = L_\infty(1 - e^{-k(t-t_0)}), \tag{2.5}$$

where TL_t is the total length at t years, L_∞ is the predicted asymptotic length, k is the annual growth rate coefficient and t_0 is the theoretical age at length zero.

The growth performance index (Munro and Pauly, 1983) was calculated to facilitate the comparison of the results with those published for other regions. This index describes the relationship between the parameters L_∞ (cm) and k ($year^{-1}$). While these parameters may differ among similar populations and species, the growth performance indices of these groups are often similar. The growth performance index was calculated as:

$$\phi = 2\log L_\infty + \log k \tag{2.6}$$

Growth was modelled for females and males separately and for the pooled data. Small fish of indeterminate sex, including recruits from the October 2018 samples, were included in the female and male data, apportioned according to the estimated sex ratio (Section 2.3.4). Statistical comparisons of the growth parameters between sexes were made using likelihood ratio tests (Kimura, 1980) using the *fishmethods* package (Nelson, 2019) in the R statistical platform, version 3.6.3 (R Core Team, 2020).

2.3.4 Reproduction

The gonads were weighed to the nearest 0.01 g and classified into their various macroscopic phases. The classification of all gonads was confirmed by a second observer. In cases when the classification of a gonad differed between observers, the differences were discussed until consensus was reached.

Selected gonads were photographed for the construction of an image catalogue, and all were preserved in 10% buffered formalin for at least six weeks before further histological processing.

Four gonads were selected from each macroscopic phase for each sex for histological examination. Either the left or the right gonad lobe was randomly selected from each sample and small sections (~1 cm) were cut from the proximal, middle and distal ends. Sections were processed and dehydrated in alcohol followed by xylol and then embedded in paraffin wax. Embedded gonads were cross-sectioned into 4 µm slices using a microtome and placed on glass slides. Slices were stained with Mayer's haematoxylin and eosin (H and E) following the methods detailed in Culling (1974) and mounted on the slide with a coverslip using Entellan mounting medium. Gonad cross-sections were observed and photographed at 40X to 1000X magnification using either a Leica DM750 compound microscope fitted with a Leica ICC50 camera or a Nikon Ti-E inverted microscope.

Microscopic developmental phases were identified and compared to the macroscopic phases. Phase descriptions and terminology were based on those proposed by Brown-Peterson et al. (2011), and were augmented with species-specific information from Mendonça et al. (2006) (Table 2.1). Phases identified included immature, developing, spawning capable (and the subphase actively spawning), regressing and regenerating.

Table 2.1: The scale used to determine macroscopic and microscopic gonad phases in female and male Helicolenus dactylopterus *in South Africa. The phase descriptions were based on those proposed by Brown-Peterson et al. (2011), augmented with information from Mendonça et al. (2006).*

Phase	**Macroscopic description**	**Microscopic description**
	Females	
Immature (I)	The gonads are small, translucent and round in cross-section as opposed to being ribbon-like.	Only primary or previtellogenic oocytes present. The ovary wall is thin and there is little space between oocytes.
Developing (D)	The gonads are larger than those in the regenerating phase and have a firm consistency with some vascularisation. They are reddish to pink in colour and some oocytes are just visible.	Oocytes are yolked, undergoing primary and secondary vitellogenesis, with yolk granules in the cytoplasm. No evidence of tertiary vitellogenesis.
Spawning capable (SC)	The gonads are large with a firm consistency and prominent vascularisation. They are pink to orange in colour with some white streaks. Oocytes are visible, and the gelatinous matrix is still intact resulting in less fluid in the ovaries.	Oocytes are in the final maturation stages and are undergoing tertiary vitellogenesis. Nuclei are in the process of migrating to the periphery of the cell and there is an amalgamation of yolk material.

Phase	**Macroscopic description**	**Microscopic description**
Actively spawning (AS, spawning capable subphase)	The gonads are large with a firm consistency and prominent vascularisation. They are pink to orange in colour. Oocytes are very visible, and are in a gelatinous matrix which, in some cases, is separated from the ovary.	Oocytes are hydrated or undergoing hydration and there is at least evidence of their presence.
Regressing (RGS)	The gonads are more flaccid than those in previous phases. They have a reddish colour and in some cases, residual oocytes are still present.	Atretic oocytes and post-ovulatory follicles present, accompanied by unyolked oocytes.
Regenerating (RGN)	The gonads are small with a firm consistency. They are reddish to pink in colour with some blood vessels present, but the oocytes are not visible.	Only primary and unyolked oocytes present, usually at the start of yolk vesicle formation at the periphery of the cell. The ovarian wall is thicker than that of an immature ovary.
	Males	
Immature (I)	The gonads are small, translucent and ribbon-like in shape.	In comparison to a regenerating male, the cross-section section of the testes is small. Spermatogonia are present with very little spermatocyte development. Sperm ducts and the main spermatic duct are not as evident as in the regenerating phase.
Developing (D)	The gonads are large and white with a firm consistency. Very little vascularisation is present.	There is a development of cysts containing spermatogonia in mitosis, and primary and secondary spermatocytes and spermatids.
Spawning capable (SC)	The testes are larger and more developed than those in the developing phase and are white with a firm consistency. Some vascularisation is present, and sperm may be visible.	Cells in all stages of development are present, and there is some accumulation of spermatozoa in sperm ducts and in the main spermatic duct.
Actively spawning (AS, spawning capable subphase)	The testes are large, white and well vascularised. Sperm may be visible and may run when the abdomen is pressed.	There is a predominance of spermatozoa in the sperm ducts and in the main spermatic duct with little spermatogenesis occurring.
Regressing (RGS)	The gonads are more flaccid than those in previous phases and are whitish-grey, with some red colouration.	Some residual spermatozoa are present in the sperm ducts and in the main spermatic duct, and some spermatogonia may be present, but otherwise, there is no occurrence of spermatogenesis.
Regenerating (RGN)	The gonads are small, ribbon-like and white or grey.	In comparison to an immature male, the cross-section of the testes is large. Spermatogonia are present with some or no spermatocyte development. Sperm ducts are visible but are mostly empty.

Sex ratio

The ratio of males to females was compared to a hypothetical 1:1 ratio using a chi-squared goodness-of-fit test as defined by Zar (1996):

$$\chi^2 = \sum_{i=1}^{k} \frac{(f_i - \hat{f}_i)^2}{\hat{f}_i}, \tag{2.7}$$

where k is the number of classes, f_i is the observed frequency of class i and $\widehat{f_i}$ is the expected frequency of class i. The monthly variation in sex ratios was compared. A significant difference in sex ratio was considered to occur if $p<0.05$.

Gonadosomatic index

The seasonal variability in the reproductive status of *H. dactylopterus* was assessed using the gonadosomatic index (GSI). The gonadosomatic index was calculated as:

$$GSI = \frac{gonad\ weight}{(total\ weight - gonad\ weight)} \times 100 \tag{2.8}$$

GSI was compared among maturity phases for females and males. Normality was assessed visually using frequency distributions, and homogeneity of variances were tested using the Levene method (Zar, 1996). If the assumptions of normality and homogeneity of variances were met, an ANOVA was used, otherwise, a Kruskal Wallis test by ranks was used.

Condition index

Fulton's condition index could not be used as *H. dactylopterus* did not show isometric growth. Therefore, as recommended by Froese (2006), the relative condition factor (K_{rel}) proposed by Le Cren (1951) was calculated for all fish. The relative condition factor compensates for changes in condition with a change in length and is suitable for the comparison of the condition in a population. It is calculated as follows:

$$K_{rel} = \frac{W}{aTL^b}, \tag{2.9}$$

where W is the total observed weight of the fish in grams and aTL^b is the calculated weight (g) according to the length-weight relationship defined in Section 2.3.2.

As with GSI, relative condition factor was compared among maturity phases for females and males. Normality was assessed visually using frequency distributions, and homogeneity of variances were tested using the Levene method (Zar, 1996). If the assumptions of normality and homogeneity of variances were met an ANOVA was used, otherwise, a Kruskal Wallis test by ranks was used.

Sperm storage in females

To assess sperm storage in *H. dactylopterus,* three ovaries (from the developing phase onwards and additional to those used in the analyses above) were selected per month for histological analysis. Ovary cross-sections were examined for the presence of sperm cells.

Length and age at 50% maturity

Mature individuals included those from the developing phase onwards, including the regenerating phase.

To determine the length and age at 50% maturity, a logistic regression was fitted to the length and age data for females and males separately. All fish of identifiable sex were used to estimate length at 50% maturity and only fish with accepted age readings were used to estimate age at 50% maturity. Maturity was treated as a binary response variable, where 1 = mature and 0 = immature, and modelled using a binomial distribution with logit transformation where:

$$\log\left(\frac{p}{1-p}\right) = \alpha + \beta X \tag{2.10}$$

p is the proportion of mature fish per 10-mm length class or 1-year age group, X is the total length or age and α and β are the model parameters.

Length and age at 50% maturity (L_{50} or A_{50}), where p = 0.5, was thus calculated as:

$$X = -\frac{\alpha}{\beta}, \tag{2.11}$$

where X is L_{50} or A_{50} and α and β are the model parameters in equation 2.10.

All analyses on reproductive parameters were conducted using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020) or Microsoft Excel 2016. The R packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2020), ggpubr (Kassambara, 2018), FSA (Ogle et al., 2020) and MASS (Venables and Ripley, 2002) were all utilised.

2.3.5 Diet

Stomachs were removed from the oesophagus to the pylorus, weighed to the nearest 0.1 g and preserved in 70% ethanol for later analyses. Analyses of stomach contents were conducted under a Leica MZ9.5 stereomicroscope. Stomachs were cut longitudinally, and fullness was estimated and scored using a scale from zero to four, where zero indicated an empty stomach, one indicated a stomach that was less than half full, two indicated a half-full stomach, three indicated a stomach that was more than half full and four indicated a full stomach (Gerringer et al., 2017). As mentioned, *H. dactylopterus* does not have a swim bladder, and so regurgitation as a result of swim bladder expansion during surfacing did not contribute to the proportion of empty stomachs observed. Stomach contents were removed, and prey items were identified down to the lowest possible taxonomic level according to Smith et al. (1986) for fishes and Kensley (1972), Griffiths (1976), Manning (1969), and Atkinson and Sink (2018) for invertebrates. The digestion state of each prey item was noted as being very digested, partially digested or not digested, following which they were counted. When prey items were not whole, the minimum count represented by the number of body parts present was used (Loury et al., 2015). Prey were dried using blotting paper, and the different taxonomic groups were weighed to the nearest 0.01 g. All non-prey items were noted and were excluded from the analyses. Prey that were not digested, that may have been eaten whilst in the net, were not included in the analyses.

Sample size sufficiency

To measure whether the sample size was adequate, a prey species accumulation curve was plotted using the Vegan Community Ecology Package (Oksanen et al., 2019) in the R statistical platform, version 3.6.3 (R Core Team, 2020). Cumulative prey items were plotted against the number of stomachs analysed, in random order, and averaged over 1000 random permutations. The sample size was considered sufficient when the resultant curve reached an asymptote, indicating that diet breadth had been adequately defined (i.e. there was a low probability of new prey species being identified with the examination of additional stomachs).

Visual examination of the prey curve for an asymptote is unreliable. The method used by Bizzarro et al. (2009) and advocated by Brown et al. (2012) was used to quantitatively measure sample size sufficiency. Linear regression was fitted to the final five points of the cumulative prey curve and the slope (b) of the corresponding line of best fit was determined. The sampling for diet characterisation was deemed acceptable when the slope was less than 0.05, indicating that the curve was levelling off and reaching an asymptote.

Diet composition

The contribution of each identified prey item to the diet of *H. dactylopterus* was estimated through the calculation of several dietary measures and indices. Dietary measures calculated included the percent frequency of occurrence of each prey group among stomach samples (%F) (Hyslop, 1980), and the average percent numerical abundance of prey (%N) and the average percent wet weight of prey (%W), as described in Brown et al. (2012). In an attempt to reduce the effect of discrete absences in prey data on the above dietary measures, zero values when prey items were not present in *H. dactylopterus* stomachs were excluded and the prey specific abundance for numerical abundance (%PN) and weight (%PW) were calculated based on Amundsen et al. (1996) as described in Brown et al. (2012). Dietary measures were thus defined as follows:

Frequency of occurrence (%F):

$$\%F_i = \frac{n_i}{n} \times 100 \tag{2.12}$$

Average percent numerical abundance and weight (%N, %W):

$$\%A_i = \frac{\sum_{j=1}^{n} A_{ij}}{n} \times 100 \tag{2.13}$$

Prey specific abundance (%PN, %PW):

$$\%PA_i = \frac{\sum_{j=1}^{n} A_{ij}}{n_i} \times 100, \tag{2.14}$$

where n_i is the number of stomachs containing prey item i, n is the total number of non-empty stomachs and A_{ij} is the abundance by number or weight (standardised to proportion by total individual stomach content) of prey item i in stomach j.

Prey specific abundances (%PN and %PW) were combined with the frequency of occurrence (%F) to calculate the prey-specific index of relative importance which was standardised as a percentage (%PSIRI) for each prey group, based on Brown et al. (2012). The %PSIRI is an alteration of the index of relative importance (%IRI) initially proposed by Pinkas et al. (1971). The %PSIRI uses the prey specific numeric abundances and weight rather than the non-prey specific counterparts (%N and %W). The inclusion of the prey specific measures corrects for inherent bias in the traditional %IRI when previously the inclusion of zero values resulted in an overestimation of the contribution of %F. The %PSIRI is also additive across taxonomic levels. The %PSIRI now replaces the %IRI (Simenstad and Cailliet, 2017). The %PSIRI was defined as follows:

$$\%PSIRI_i = \frac{\%F_i \times (\%PN_i + \%PW_i)}{2} \tag{2.15}$$

The rate of feeding activity of *H. dactylopterus* was measured using the vacuity coefficient, estimated as the percentage of empty stomachs of the total number of stomachs analysed (Ellis et al., 1996):

$$\%V = \frac{number\ of\ empty\ stomachs}{total\ number\ of\ stomachs} \times 100 \tag{2.16}$$

Levin's standardised index (Krebs, 1999) was used to calculate the breadth of the diet of *H. dactylopterus*:

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_{j=1}^{n} p_{ij}^2} - 1\right), \tag{2.17}$$

where B_i is the diet breadth of predator i, p_{ij} is the proportion of prey group j in the diet of predator i and n is the total number of prey categories. %PSIRI values converted to proportions were used in the index calculation. Index values range from 0 to 1 with lower values indicating a more specialised diet, dominated by only a few prey items, while larger values indicate a more generalist diet (Krebs, 1999).

To investigate the feeding strategy of *H. dactylopterus,* prey importance was depicted graphically using the method proposed by Amundsen et al. (1996), which is a modification of that proposed by Costello (1990). The analysis comprised a two-dimensional graphical representation of the frequency of occurrence relative to the prey specific numerical abundance (%PN) of each prey taxon. This provides a graphical depiction of how frequently prey items occurred in the diet of *H. dactylopterus* and their average percentage contribution.

The feeding strategy is represented by the vertical axis of the graph in which a predator will either be a specialist feeder on certain prey items (i.e. high prey-specific abundance) or a generalist feeder on others. Prey importance, as rare or dominant species in the diet, is represented by the diagonal running from the bottom left to the top right. Dietary niche breadth is represented by the diagonal running from the top left to the bottom right of the graph and is comprised of two elements: the between phenotype component (BPC) and the within phenotype component (WPC). A predator population with a narrow dietary niche breadth is comprised of individuals that show a specialist feeding strategy with only a few prey items, a high prey-specific abundance and prey that occur frequently in the diet. This results in a population with high variation in diet between phenotypes, in which many prey items are fed on in high numbers by a few individuals. Conversely, a population with a broad dietary niche is either comprised of specialised individuals feeding on a variety of different prey with little overlap in resource use with conspecifics or individuals that are generalist predators feeding on a wide range of overlapping resources. This results in a population that displays variation in the diet within the phenotype, in which prey items are fed on more occasionally by most individuals (Amundsen et al., 1996).

The trophic level of *H. dactylopterus* ($TROPH_i$) was calculated following Cortés (1999):

$$TROPH_i = 1 + (\sum_{j=1}^{n} P_j \times TROPH_j), \tag{2.18}$$

where P_j is the proportion of prey group j in the diet of predator i, $TROPH_j$ is the trophic level of prey group j and n is the number of prey groups in the diet of species k. Trophic level was calculated based on the average percent weight of prey (equation 2.13) converted to proportions as in Córdova-Zavaleta et al. (2018) and Loury et al. (2015). Trophic levels of prey categories were assigned based on Ebert and Bizzarro (2007). Unknown stomach contents were not included in the analyses.

Diet comparison

Diet was compared among fish of different lengths, fish caught at different depths and fish caught from different localities. A description of each of these factors and the factor levels is provided in Table 2.2. For the subsequent analyses, outliers were removed. The prey taxa were merged into major taxonomic groups at the order level when possible. In the case when a prey item was not identified to order, it was grouped to the next lowest possible taxonomic level. Only fish with at least one prey item in the stomach were included.

Multivariate analyses were done solely on prey abundance, which was square-root transformed to down-weight the dominance of abundant species. A Bray-Curtis similarity resemblance matrix was created. Nonmetric multidimensional scaling (MDS) ordination was conducted based on the prey abundance data and plots were generated to visualise dietary patterns among fish of different lengths, from different areas and caught at different depths. To statistically assess whether diet varied among and within the levels of these factors, a permutational multivariate analysis of variance (PERMANOVA) was used (Anderson et al., 2008). Owing to the unbalanced and asymmetrical nature of the data a nested model was used and type III sums of squares partitioning was employed with the permutation of residuals under a reduced model. The factors used and the design of the model is detailed in Table 2.2.

Following the PERMANOVA, a similarity percentage analysis (SIMPER) was done on each significant factor to determine which prey items were important in driving dissimilarity among levels.

Table 2.2: Factors used and design of the PERMANOVA for the analysis of dietary variation in Helicolenus dactylopterus *in South Africa.*

Factor	**Type**	**No. of levels**	**Nested in**	**Description**
Area	Categorical, random	6		Catch locality where fish were caught, as start location of each trawl, grouped into those areas previously defined by longitude and latitude in Section 2.3.1: 1, 2, 3, 4, 5 and 6.
Depth class	Categorical, random	5	Area	Depth in which fish were caught, as start depth of each trawl, binned into 100-m depth classes: 201-300, 301-400, 401-500, 501-600 and >600 m.
Length class	Categorical, random	9	Depth class	Total length of each fish, grouped into 50-mm length classes: <100, 100-149, 150-199, 200-249, 250-299, 300-349, 350-399, 400-449, >449 mm.

As the multivariate analyses were only conducted on prey abundance, consideration was given to prey weight by calculating the percent prey specific index of relative importance (%PSIRI, equation 2.15) and comparing among levels of each significant factor.

The trophic level of each length class was also calculated using equation 2.18 as described above.

Where not defined, all analyses on diet were conducted using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020) or Microsoft Excel 2016. The R packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2020), RColorBrewer (Neuwirth, 2014) and vegan community ecology (Oksanen et al., 2019) were all utilised. Multivariate analyses were conducted using PRIMER, version 6.1.11 (Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER, version 1.0.1 (Anderson et al., 2008).

2.3.6 Meta-analysis

The life history traits of South African *H. dactylopterus* were compared with those from other regions of the Atlantic using a meta-analysis. Data on selected traits were collated based on a comprehensive review of the published and unpublished scientific literature. Literature sources were initially found using the Google Scholar search engine and then these were reviewed to find additional relevant work.

Traits used in the analysis were maximum total length (mm), the slope (b) of the length-weight relationship, maximum age, asymptotic length (L_∞ or $L_{inf,}$, mm), annual growth rate (k, year^{-1}), growth performance index (ϕ), sex ratio and length at 50% maturity (mm). Only studies that reported sample sizes and relevant trait information could be included. In total, 21 studies were used in the analysis. Of these, nine studies were conducted in the Mediterranean, 11 were conducted in the North Atlantic, and one was conducted in Namibia (Table 2.3). Where reported, data were presented for sexes separately, otherwise, a combined value was used.

Table 2.3: Studies used in the meta-analysis of selected life history traits of Helicolenus dactylopterus.

Trait	**Region**	**Studies used**
Maximum total length (mm)	Mediterranean	Anastasopoulou et al. (2017); Consoli et al. (2010); Demirhan and Akbulut (2015); Deval et al. (2018); Massutí et al. (2000); Pirrera et al. (2009); Ragonese and Reale (1995); Sami et al. (2016)
	North Atlantic	Abecasis et al. (2006); Allain and Lorance (2000); Borges et al. (2003); Esteves et al. (1997); Isidro (1987); Kelly et al. (1999); Pereira et al. (2012); Sequeira et al. (2009); Sequeira et al. (2012); White et al. (1998)
	Namibia	Morales-Nin (1989)*
Length-weight relationship slope (b)	Mediterranean	Anastasopoulou et al. (2017); Consoli et al. (2010); Demirhan and Akbulut (2015); Deval et al. (2018); Massutí et al. (2000); Sami et al. (2016)
	North Atlantic	Borges et al. (2003); Kelly et al. (1999); Pereira et al. (2012)
Maximum age (years)	Mediterranean	Anastasopoulou et al. (2017); Consoli et al. (2010); Demirhan and Akbulut (2015); Deval et al. (2018); Massutí et al. (2000); Ragonese and Reale (1995); Sami et al. (2016)
	North Atlantic	Abecasis et al. (2006); Allain and Lorance (2000); Esteves et al. (1997); Isidro (1987); Kelly et al. (1999); Sequeira et al. (2009); Sequeira et al. (2012); White et al. (1998)
	Namibia	Morales-Nin (1989)*
VBG parameters: asymptotic length ($L_{\infty,}$ mm), annual growth rate (k, year^{-1})	Mediterranean	Anastasopoulou et al. (2017); Consoli et al. (2010); Demirhan and Akbulut (2015); Deval et al. (2018); Massutí et al. (2000); Pirrera et al. (2009); Ragonese and Reale (1995); Sami et al. (2016)
	North Atlantic	Abecasis et al. (2006); Allain and Lorance (2000); Esteves et al. (1997); Isidro (1987); Sequeira et al. (2009)
	Namibia	Morales-Nin (1989)*

Trait	Region	Studies used
growth performance index (ϕ)	Mediterranean	Consoli et al. (2010); Deval et al. (2018); Massutí et al. (2000); Pirrera et al. (2009); Ragonese and Reale (1995); Sami et al. (2016)
	North Atlantic	Abecasis et al. (2006); Allain and Lorance (2000); Esteves et al. (1997); Isidro (1987); Sequeira et al. (2009)
	Namibia	Morales-Nin (1989)
Sex ratio (male:female)	Mediterranean	Demirhan and Akbulut (2015); Deval et al. (2018); Massutí et al. (2000); Muñoz and Casadevall (2002)
	North Atlantic	Mendonça et al. (2006); Sequeira et al. (2009); White et al. (1998)
Length at 50% maturity (mm)	Mediterranean	Deval et al. (2018)
	North Atlantic	Kelly et al. (1999); White et al. (1998)

*Study was not seen, but estimates were obtained from other studies in which it was referenced

Estimates for each trait were plotted against the respective sample size reported. Records were categorised based on the region of study as either occurring in the Mediterranean or the North Atlantic. The mean of a given estimate per region was calculated using the sample size as a weighting factor. For the few studies outside of these areas, data were differentiated and categorised under the country in which they were collected. Estimates from the present study were included as a separate regional category for comparison. The overall mean for all regions was also calculated.

Life history traits for which age estimation was required (maximum age, L_∞, k, ϕ), the ageing method used (sliced otoliths or whole otoliths) in each respective study was differentiated in each plot. This was done to assess whether the differences observed in estimated traits are an artefact of the ageing method used or whether they are due to actual differences among fish from different regions. Sex was not differentiated in the plots.

2.4 Results

A total of 719 *H. dactylopterus* specimens were dissected and examined. These were obtained from 26 samples that were collected from November 2017 to October 2019 from different localities on the west, south and east coasts of South Africa, in depths ranging from 73 to 697 m (Table 2.4). Samples were mainly acquired during 2018, but in March, July and October of that year, commercial samples could not be collected and therefore samples for those months were collected in 2019.

Table 2.4: Details of Helicolenus dactylopterus *samples used for this study that were collected from commercial and research trawls in South Africa.*

Month	Year	Latitude	Longitude	Area	Depth	Commercial/research trawl	n
November	2017	-35.6028	19.1162	3	406 m	Commercial	35
January	2018	-34.3522	17.8377	2	347 m	Commercial	32
January	2018	-29.9400	31.5000	6	495 m	Research	15
February	2018	-29.3600	31.9700	6	397 m	Research	2
February	2018	-33.0192	16.9950	1	440 m	Commercial	40
February	2018	-35.6375	19.0428	3	697 m	Commercial	37
April	2018	-36.3162	20.0385	4	285 m	Commercial	30
April	2018	-36.3538	20.0687	4	293 m	Commercial	34
May	2018	-34.9022	24.2405	5	461 m	Commercial	31
May	2018	-36.6183	20.4095	4	277 m	Commercial	32
June	2018	-34.5083	18.2423	2	385 m	Commercial	49
August	2018	-35.4903	18.8945	3	560 m	Commercial	29
August	2018	-33.6740	17.4552	1	443 m	Commercial	30
September	2018	-34.5140	18.2428	2	385 m	Commercial	72
October	2019	-33.6070	18.2205	1	73 m	Research	25
October	2019	-34.0938	18.1130	2	168 m	Research	20
November	2018	-34.5418	18.2540	2	402 m	Commercial	20
December	2018	-33.0028	16.7863	1	640 m	Commercial	31
January	2019	-34.5582	18.0872	2	315 m	Research	3
January	2019	-34.6977	18.4193	2	249 m	Research	2
January	2019	-34.7302	18.1206	2	443 m	Research	1
February	2019	-34.4928	25.6207	5	521 m	Commercial	29
February	2019	-35.8158	19.5845	3	248 m	Research	30
March	2019	-34.8417	23.8102	5	208 m	Commercial	30
July	2019	-32.3896	16.5618	1	410 m	Commercial	30
October	2019	-35.4268	19.0367	3	259 m	Commercial	30

2.4.1 Morphometrics and meristics

Morphometric relationships

Length and weight data were recorded from all 719 specimens (Figure 2.3). Of these, 318 were females, 345 were males and 56 were of indeterminate sex. Total length ranged from 22 to 494 mm (Figure 2.4), and was similar in both sexes (t = -0.63, df = 661, p = 0.53), averaging 277.83 (±61.47 SD) mm in females and 280.63 (±52.92 SD) mm in males (Figure 2.5). Total weight ranged from 0.2 to 2 077.6 g. The mean weight of females and males was 383.97 (±303.04 SD) g and 378.87 (±246.27 SD) g respectively.

Figure 2.3: A Helicolenus dactylopterus *specimen measured, weighed and dissected for this study. This individual was male and had a total length of 295 mm.*

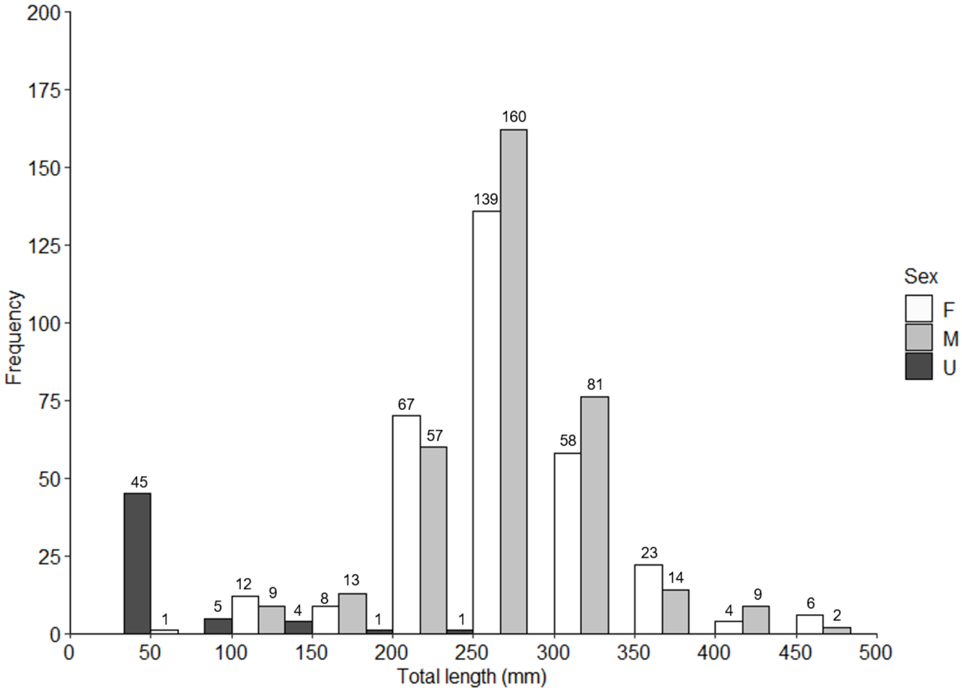


Figure 2.4: Length-frequency distribution of Helicolenus dactylopterus *sampled from November 2017 to October 2019 (n=719) in South Africa. Length distributions are presented separately for females (F), males (M) and specimens of indeterminate sex (U). The sample size for each is indicated above the bar.*

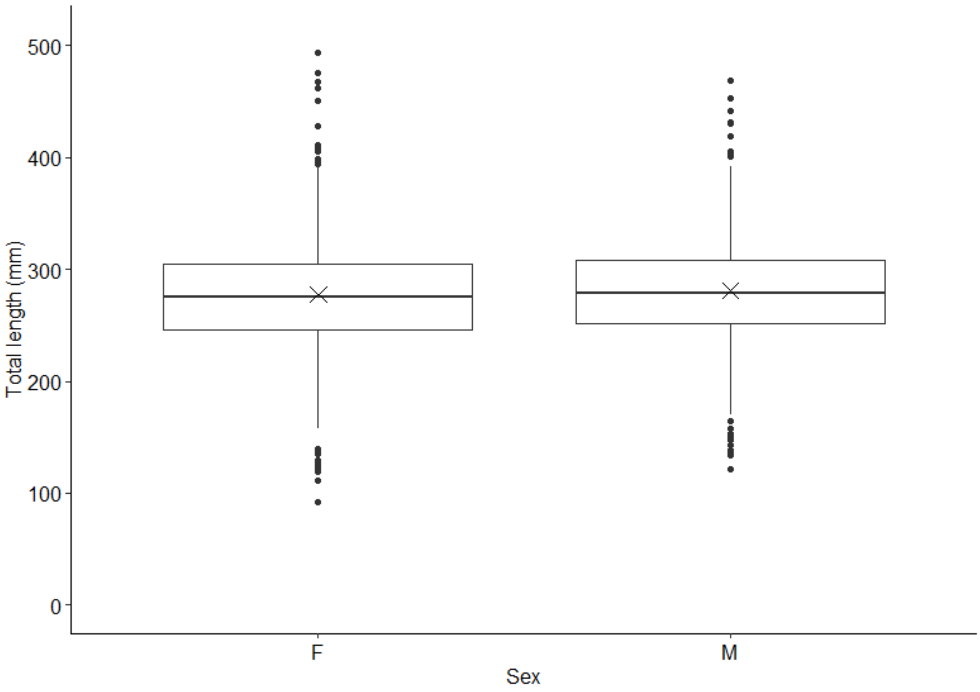


Figure 2.5: Boxplot showing the distribution of the total length (mm) of female (n=318) and male (n=345) Helicolenus dactylopterus *sampled from November 2017 to October 2019 in South Africa. Minimum, median and maximum values are shown by horizontal lines, whereas the mean is indicated by the cross.*

Linear regression estimates for the relationships between standard length (SL) and total length (TL) are shown in Table 2.5. The equations of the best-fit relationship between TL and weight (W) of *H. dactylopterus* are detailed in Table 2.6 and Figure 2.6 and Figure 2.7. Equations are shown for all data combined and for females and males separately.

Table 2.5: Linear regression equations showing the relationship between the standard length (SL) (mm) and total length (TL) (mm) of South African Helicolenus dactylopterus. *Relationships are shown for all data combined (females, males and specimens of indeterminate sex) and for females and males separately.*

Group	**n**	**Equation**	**r^2**
All fish	719	$SL = 0.81\,TL - 1.77$	0.998
Females	318	$SL = 0.81\,TL - 3.31$	0.996
Males	345	$SL = 0.81\,TL - 3.79$	0.994

Table 2.6: Equations expressing the relationship between the total length and weight of South African Helicolenus dactylopterus. *Equations are shown for all data combined (females, males and specimens of indeterminate sex) and for females and males separately.*

Group	**n**	**Equation**	**r^2**	**Figure**
All fish	719	$W = 9.86 \times 10^{-6}\,TL^{3.08}$	0.997	Figure 2.6
Females	318	$W = 4.21 \times 10^{-6}\,TL^{3.23}$	0.989	Figure 2.7
Males	345	$W = 3.93 \times 10^{-6}\,TL^{3.24}$	0.984	Figure 2.7

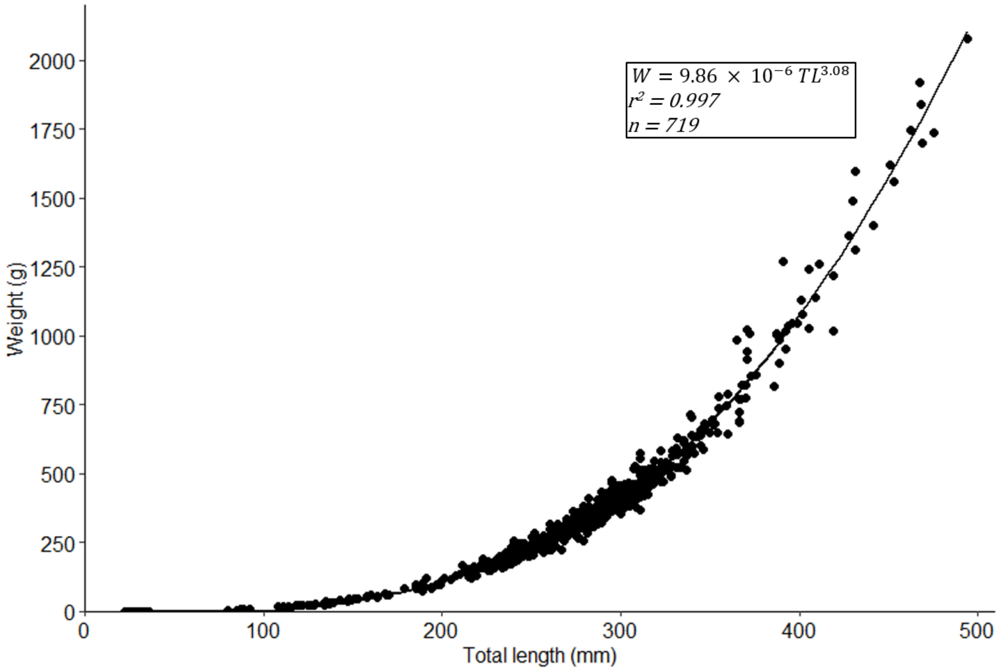


Figure 2.6: The best-fit length-weight relationship of South African Helicolenus dactylopterus. *The relationship is fitted to all fish regardless of sex.*

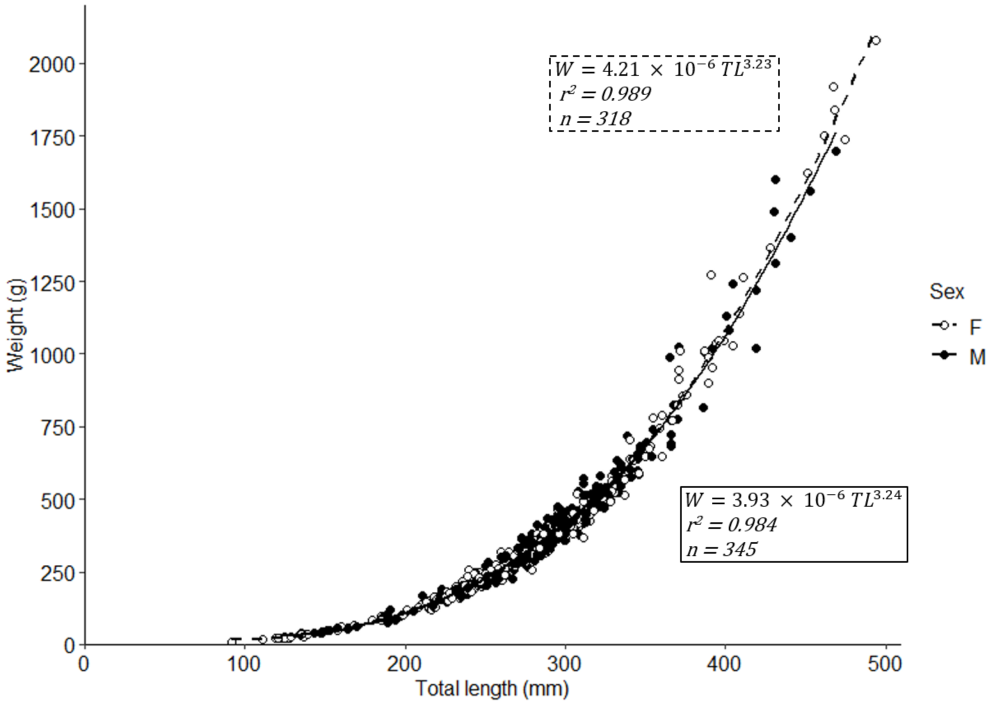


Figure 2.7: The best-fit length-weight relationship of South African Helicolenus dactylopterus. *Relationships are shown for females (dashed line) and males (solid line) separately.*

All length-weight models indicated hyper-allometric growth, as the slopes of the models were all significantly greater than 3 (t = 11.86, df = 717, $p < 0.001$; t = 12.03, df = 316, $p < 0.001$; and t = 10.79, df = 343, $p < 0.001$ for all data combined and for females and males respectively). Length-weight relationships of females and males were not different in slope (F = 0.17, df = 1, p = 0.68) or intercept (F = 0.01, df = 1, p = 0.91).

Total length was approximately normally distributed, but variances differed among depths (F = 25.57, df = 4, $p < 0.001$) and among areas (F = 22.80, df = 4, $p < 0.001$). A Welch's ANOVA and a Games-Howell post-hoc test was therefore used for the analysis of the effect of depth and location on total length (Zar, 1996; Ruxton and Beauchamp, 2008).

Total length varied among depth classes (Figure 2.8, F = 11.04, df = 4, $p < 0.001$). It was significantly lower in the shallowest depth class (201-300 m), averaging 271 (±31.2 SD) mm, compared to others (Table 2.7).

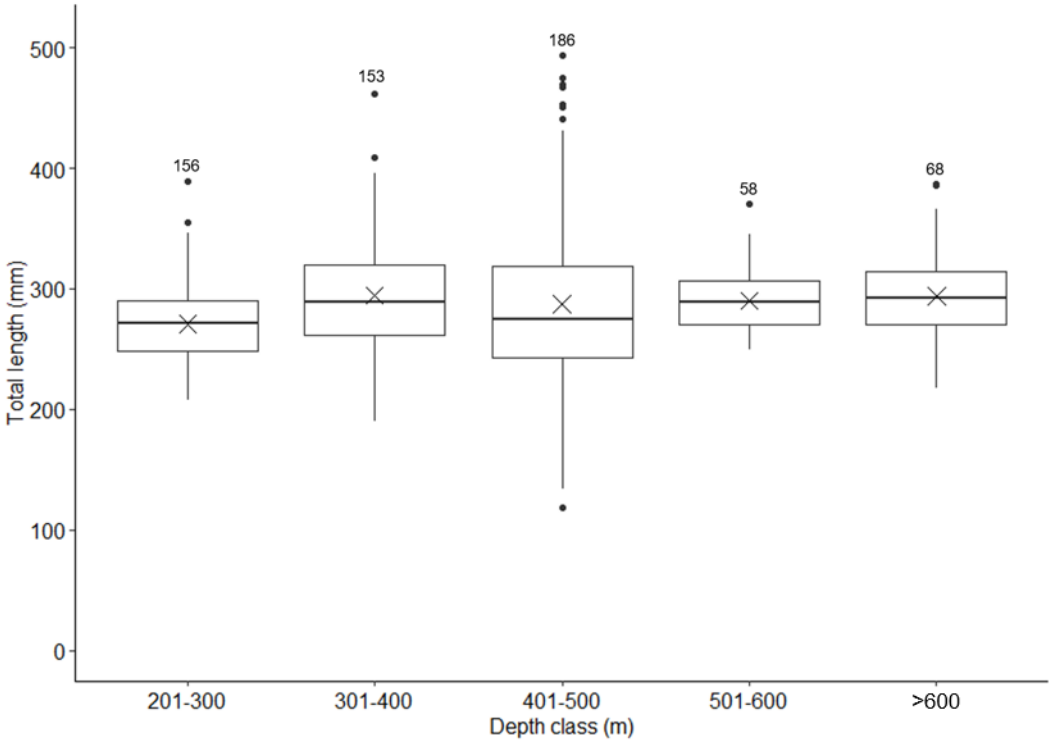


Figure 2.8: Boxplot showing the distribution of the total length (mm) of South African Helicolenus dactylopterus *in different depth classes. Minimum, median and maximum values are shown as horizontal lines and the means as crosses. The sample size in each depth class is shown above the bar. All research samples were excluded from the depth analyses resulting in a sample size of 621 fish.*

Table 2.7: Games-Howell post-hoc test results showing the pairwise comparison of the total length of South African Helicolenus dactylopterus *in different 100 m depth classes. Significant p values (<0.05) are highlighted in bold.*

Depth class	**201-300 m**	**301-400 m**	**401-500 m**	**501-600 m**
301-400 m	**<0.001**			
401-500 m	**0.04**	0.81		
501-600 m	**<0.001**	0.93	0.99	
>601 m	**<0.001**	1.00	0.87	0.97

Total length also varied among areas (Figure 2.9, F = 19.30, df = 4, p < 0.001). *Helicolenus dactylopterus* specimens caught in areas one, on the west coast, three, on the south-west coast, and four, on the south coast of South Africa, were significantly smaller than fish in areas two and five. The average length of fish in areas one, three and four was 274 (±34.3 SD), 265 (±50.4 SD) and 278 (±33.0 SD) mm respectively. The largest fish were caught in area five on the south coast, averaging 328 (±68.8 SD) mm (Table 2.8).

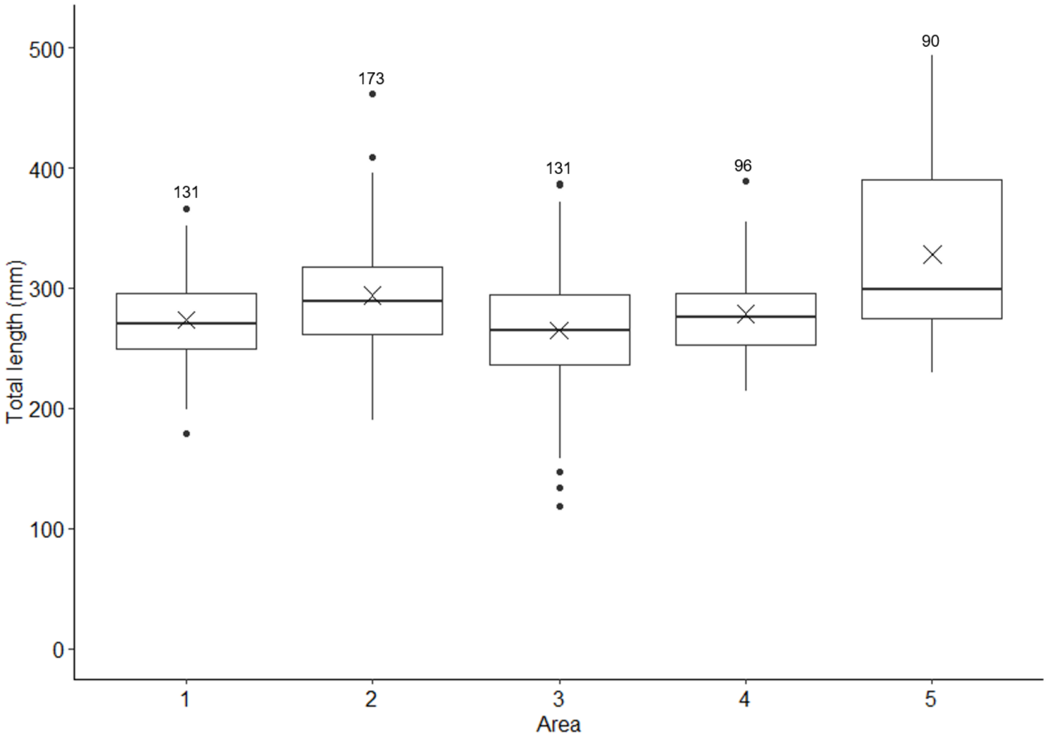


Figure 2.9: Boxplot showing the distribution of the total length (mm) of South African Helicolenus dactylopterus *in different areas. Minimum, median and maximum values are shown as horizontal lines and the means as crosses. The sample size in each area is shown. All research samples were excluded from the depth analyses resulting in a sample size of 621 fish.*

Table 2.8: Games-Howell post-hoc test results showing the pairwise comparison of the total length of South African Helicolenus dactylopterus *in different areas. Significant p values (<0.05) are highlighted in bold.*

Area	**1**	**2**	**3**	**4**
2	**<0.001**			
3	0.45	**<0.001**		
4	0.81	**0.01**	0.10	
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Meristic comparisons

For the area comparisons of meristic variables, fish caught in area six were removed from the analyses due to a lack of samples. Analyses were done on 197 fish for dorsal and anal fin spine and ray counts and on 194 fish for gill raker counts. The distributions of all meristic variables, untransformed and log-transformed, were non-normal. Variances of dorsal spine and upper gill raker counts differed among areas (F = 3.84, df = 4, p < 0.01; F = 6.07, df = 4, p < 0.001). Non-parametric Kruskal Wallis tests by rank were therefore used.

Meristic counts were stable among *H. dactylopterus* specimens with no significant differences found in any of the meristic variables among fish caught in different areas on the South African coast (p > 0.05, Table 2.9). Specimens had 11 to 13 dorsal spines (usually 12), 12 to 14 dorsal rays (usually 13), three anal spines, five anal rays and 27 to 34 gill rakers (usually 30). Eight to 11 gill rakers occurred in the horizontal segment (usually 9) and 18 to 23 occurred in the vertical segment (usually 21).

Table 2.9: Statistical summary of meristic variable counts of Helicolenus dactylopterus *from five different areas in South Africa. Kruskal Wallis test results are shown indicating the comparison of counts among areas.*

Area	**n**	**Median**	**Mode**	**Min**	**Max**	**$\chi 2$**	**df**	**p**
				Dorsal spines				
1	41	12	12	11	12	6.54	4	0.16
2	53	12	12	12	12			
3	41	12	12	12	13			
4	32	12	12	12	13			
5	30	12	12	12	12			
				Dorsal rays				
1	41	13	13	13	14	3.72	4	0.44
2	53	13	13	13	14			
3	41	13	13	12	14			
4	32	13	13	13	14			
5	30	13	13	12	14			

Area	n	Median	Mode	Min	Max	χ2	df	p
Anal spines								
1	41	3	3	3	3	NA	4	NA
2	53	3	3	3	3			
3	41	3	3	3	3			
4	32	3	3	3	3			
5	30	3	3	3	3			
Anal rays								
1	41	5	5	5	5	NA	4	NA
2	53	5	5	5	5			
3	41	5	5	5	5			
4	32	5	5	5	5			
5	30	5	5	5	5			
Total gill rakers								
1	40	30	30	29	31	5.37	4	0.25
2	53	30	30	27	32			
3	39	30	30	27	32			
4	32	30	30	29	34			
5	30	30	30	28	32			
Upper gill rakers								
1	40	9	9	8	10	8.66	4	0.07
2	53	9	9	8	10			
3	39	9	9	8	10			
4	32	9	9	9	11			
5	30	9	9	9	10			
Lower gill rakers								
1	40	21	21	20	22	4.12	4	0.39
2	53	21	21	18	23			
3	39	21	21	18	22			
4	32	21	21	20	23			
5	30	21	21	19	22			

2.4.2 Age and growth

Age estimation

Otoliths from 672 fish were extracted and sectioned for age estimation. Of these, 618 were readable, of which there was agreement between two or more readers in 349 otoliths. All three readers agreed on 25 fish whereas two readers agreed on the remaining 324 fish. Readings from readers 1 and 2 and readers 1 and 3 did not differ significantly from each other over the age range, however, readings of readers 2 and 3 differed significantly in fish with otolith increment counts of 0, 6, 7 and 8 (Figure 2.10). Reader bias became increasingly apparent in fish older than 25 years. Overall, the CV value was 16.94%, while between reader 1 and reader 2 it was 9.45%, between reader 1 and reader 3 it was 11.12%, and between reader 2 and reader 3 it was

17.41%, indicating that the readings of readers 1 and 2 were the most consistent and reproducible.

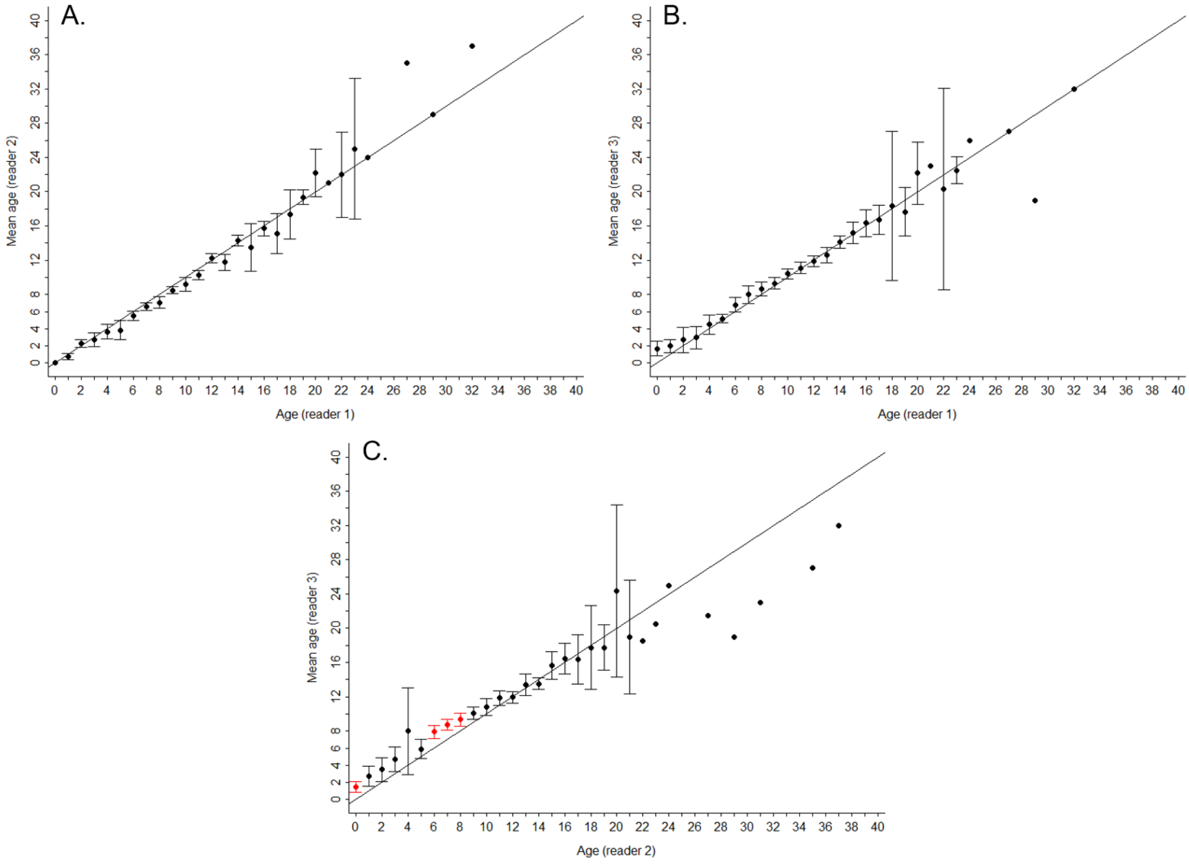


Figure 2.10: Age bias plots comparing South African Helicolenus dactylopterus *otolith increment counts (age) between A. reader 1 and reader 2; B. reader 1 and reader 3; and C. reader 2 and reader 3. The mean (± 95 % CI) of the readings of the reader plotted on the y-axis relative to the readings of the reader on the x-axis are shown. Red points indicate where the mean plotted on the y-axis was significantly different from the reading on the x-axis, as determined by a one-sample t-test.*

Under transmitted light, the sliced otoliths showed alternating dark (opaque) and light (hyaline) concentric rings surrounding a dark (opaque) nucleus (Figure 2.11). The opaque rings were larger than the hyaline rings and the first three to six increment pairs were larger than subsequent pairs. In older fish, the outer increments were narrow and closely spaced, making the reading of these difficult (Figure 2.11 D).

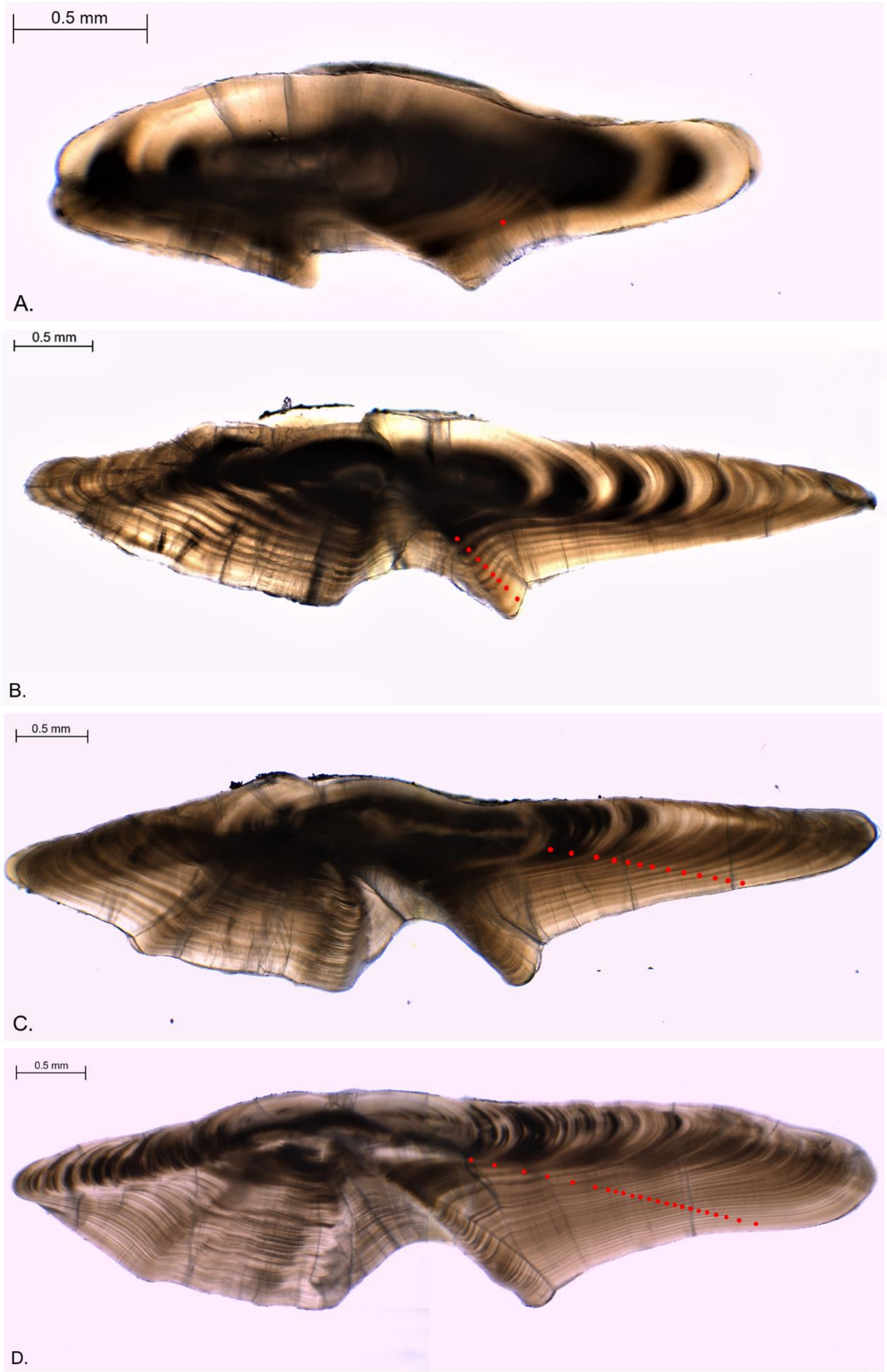


Figure 2.11: Images of the sectioned otoliths of A. a 1-year-old, B. an 8-year-old; C. a 13-year-old; and D. a 23-year-old South African Helicolenus dactylopterus *specimen. Counted increments are denoted by red dots.*

Age validation

Margins were difficult to categorise because of the refraction of light on the otolith edges and because the outer rings were closely spaced in old fish. Nevertheless, there was agreement between two readers in the categorisation of the margins of 318 otoliths. Most of those categorised showed that a large proportion of fish laid down opaque rings in spring and summer, from September to January, and hyaline rings were laid down from late summer to winter, from February to August (Figure 2.12). This indicates that one opaque increment was formed during spring/summer each year and that the greatest growth occurred over this period.

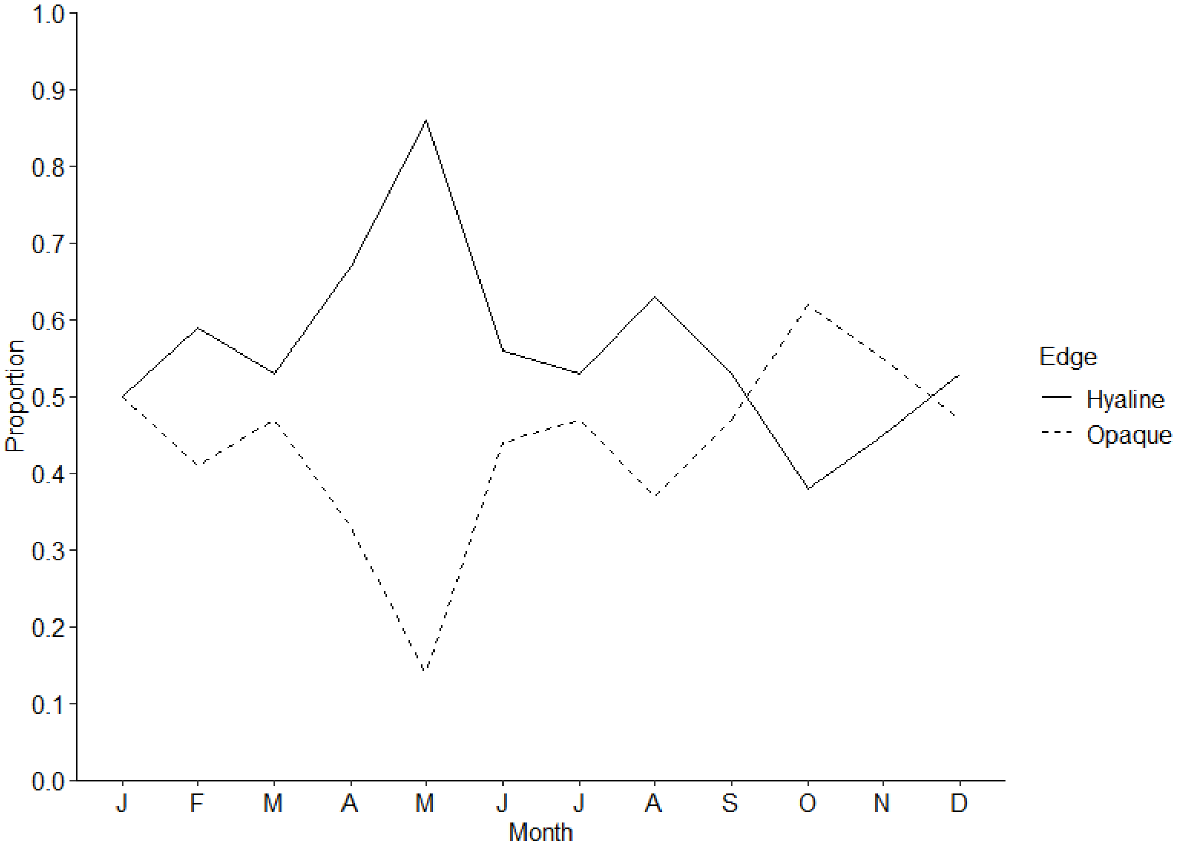


Figure 2.12: Proportions of opaque and hyaline otolith margins in South African Helicolenus dactylopterus *per month.*

Modelling growth

The estimated ages of South African *H. dactylopterus* ranged from 0 to 32 years in females (Table 2.10) and 0 to 24 years in males (Table 2.11).

Table 2.10: Age-length key for female Helicolenus dactylopterus *in South African waters. The number of individuals for which otoliths were examined is shown.*

TL (mm)	**Estimated age (years)**																												
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**22**	**23**	**24**	**27**	**29**	**30**	**31**	**32**
90-99		1																											
100-109																													
110-119		1	1																										
120-129		2		1																									
130-139	1	1																											
150-159				1																									
160-169						1																							
170-179					1																								
180-189			1			1																							
190-199							1																						
200-209							1																						
210-219					1	1		1	1		1	1																	
220-229						2	1		1			1																	
230-239							1	1	2	1		1																	
240-249				1			1		2	2	2	1	1		1														
250-259					1	1				7	3	3																	
260-269							2	1	3	1	6	4	2		1														
270-279						2		1	2		1	4	3	3	1		1												
280-289								1		2	1		3	1	2	1	1												
290-299								1			2	2	3	2	3		2	1		1									
300-309												1	1	1	1	1				1						1			
310-319													1	1	2	1													
320-329														1		1		1											
330-339															1	1	1					1							
340-349															1		1		2		1								
350-359																	1						1						
360-369													1		1					1									
370-379																							2	1					
380-389																1					1								
390-399																					2		1						
400-409																				1									
410-419																													
420-429																													
430-439																													
440-449																													
45--459																													
460-469																									1				1
n	1	5	2	3	3	8	7	6	11	13	16	18	15	9	14	6	7	2	2	4	4	1	4	1	1	1			1

Table 2.11: Age-length key for male Helicolenus dactylopterus *in South African waters. The number of individuals for which otoliths were examined is shown.*

TL (mm)	**Estimated age (years)**																								
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
80-89	3	1																							
90-99																									
100-109		1																							
110-119	1																								
120-129	1																								
130-139			1		1			1																	
140-149		1	1			1																			
150-159			1	1																					
160-169			1	1		1																			
170-179						1																			
180-189								1																	
190-199			1				1																		
200-209						1																			
210-219						1				1															
220-229						1	2	2	1																
230-239							3	1	5	3	3		1												
240-249								1	1	6	6	1	1												
250-259									5	2		1	1		1			1					1		
260-269							1			2	4	2	2												
270-279						1		2	4		4	2	3												
280-289								1	3	2	3	2	3	1		1				1					
290-299								2		1	3	5	1	3		1						1			
300-309										2	2	1	1	2	1										
310-319										1	1	2	5	1	2	1		1							
320-329								1	1						1			1			1				
330-339														1	1		1	1	1				1		
340-349														3	1		1								
350-359																		1	1						
360-369																1	1					1			
370-379																	1								
390-399																		1							
400-409																									
410-419																									1
420-429																									
430-439																				1					
440-449																									
450-459																									
460-469																							1		
n	5	3	5	2	1	7	7	12	20	20	26	16	18	11	7	4	4	6	2	2	1	2	3		1

The VBG parameters estimated for length at age data are shown in Table 2.12. Models fitted to female and male data were not significantly different ($\chi^2 = 4.51$, df = 3, p = 0.21) and so the final model included data with both sexes combined (Figure 2.13).

Table 2.12: von Bertalanffy growth parameters for South African Helicolenus dactylopterus. *Data are shown for females and males, but the final model includes all data combined.*

Group	**n**	**L_∞ (mm)**	**k (year^{-1})**	**t_0**	**ϕ**
Females	191	374.39 (±12.43)	0.11 (±0.01)	-1.46 (±0.22)	2.19
Males	204	360.57 (±11.35)	0.14 (±0.01)	-0.88 (±0.17)	2.26
Combined	395	365.66 (±8.15)	0.13 (±0.01)	-1.14 (±0.13)	2.24

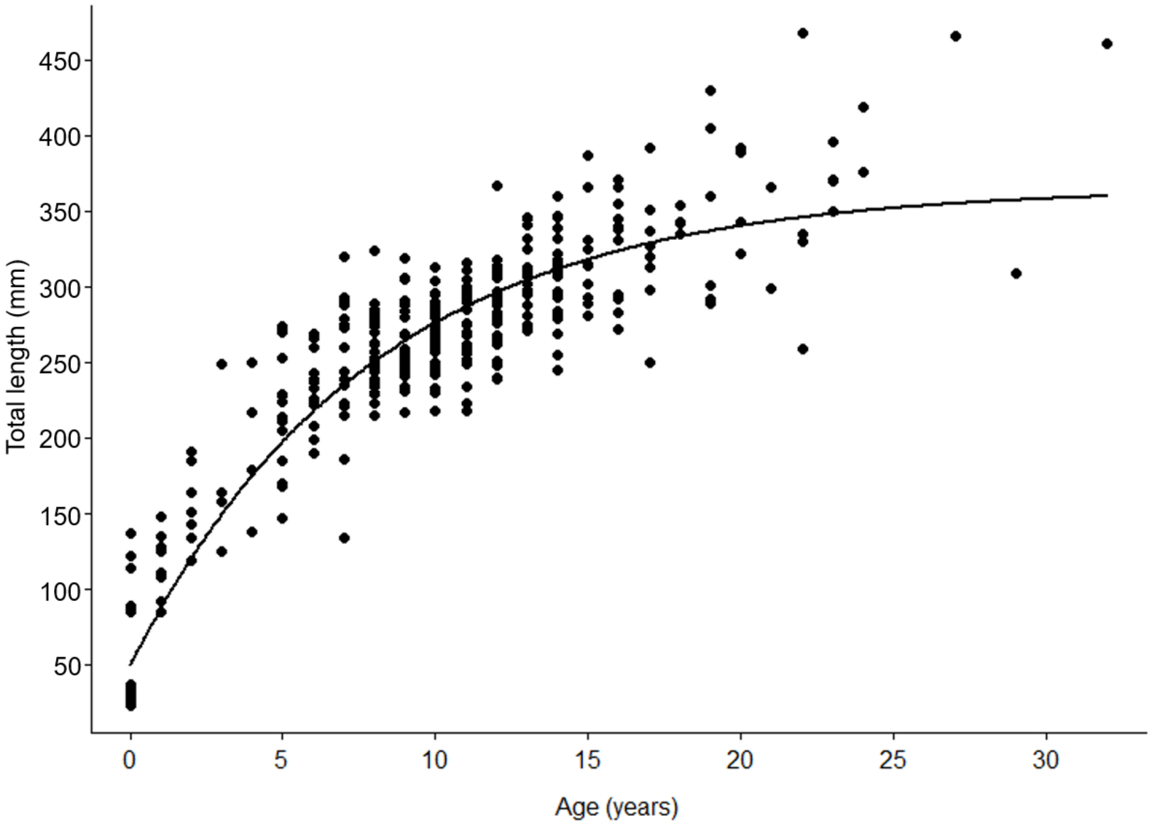


Figure 2.13: Total length at age data for South African Helicolenus dactylopterus *(males and females combined) with the estimated von Bertalanffy growth curve.*

2.4.3 Reproduction

A total of 674 specimens were sexed and classified macroscopically. Of these, 318 were females, 345 were males and 11 were of indeterminate sex. This resulted in an overall ratio of males to females of 1.08, which did not differ significantly from 1 ($\chi^2 = 1.10$, df =1, p = 0.294).

Sex ratios per month are shown in Table 2.13 and indicate that no significant differences in the presence of males or females occurred in any of the months either.

Table 2.13: Monthly sex ratios of South African Helicolenus dactylopterus *with Chi-Squared goodness-of-fit test results showing the statistical comparison to a hypothetical 1:1 ratio.*

Month	**n males**	**n females**	**χ^2**	**df**	**p**
January	32	20	2.77	1	0.10
February	71	59	1.11	1	0.29
March	13	17	0.53	1	0.47
April	39	25	3.06	1	0.08
May	29	34	0.40	1	0.53
June	23	26	0.18	1	0.67
July	17	13	0.53	1	0.47
August	32	27	0.42	1	0.52
September	30	42	2.00	1	0.16
October	15	15	0.00	1	1.00
November	29	24	0.47	1	0.49
December	15	16	0.03	1	0.86

Macroscopic and microscopic staging of gonads

A total of 48 gonads, 24 ovaries and 24 testes, were processed for histology. The total lengths of these fish ranged from 125 to 372 mm for females and 164 to 431 mm for males.

Agreement between the microscopic and macroscopic phases was higher in females than it was in males. Out of the 24 ovaries analysed histologically, there was agreement on 20. Two gonads were underestimated and two were overestimated by the macroscopic classification (Table 2.14). In the males, there was agreement in 17 of the testes analysed, whereas four were underestimated and three were overestimated by the macroscopic classification (Table 2.15).

Table 2.14: Comparison of the macroscopic and microscopic classification of ovaries in South African Helicolenus dactylopterus. *Agreement is highlighted in bold. Values above the diagonal line indicate underestimation by macroscopic classification, whereas values below indicate overestimation.*

Macroscopic classification	**Microscopic classification**					
	I	**D**	**SC**	**AS**	**RGS**	**RGN**
I	**4**					
D		**3**				1
SC			**3**	1		
AS				**4**		
RGS		1			**3**	
RGN		1				**3**

Table 2.15: Comparison of the macroscopic and microscopic classification of testes in South African Helicolenus dactylopterus. *Agreement is highlighted in bold. Values above the diagonal line indicate underestimation by macroscopic classification, whereas values below indicate overestimation.*

Macroscopic classification	**Microscopic classification**					
	I	**D**	**SC**	**AS**	**RGS**	**RGN**
I	**2**					2
D		**3**	1			
SC			**3**	1		
AS			1	**3**		
RGS			1		**3**	
RGN		1				**3**

Images of whole gonads and the histological sections were captured for females and males from selected specimens and compiled into an image catalogue (Table 2.16 and Table 2.17). When possible, the images of whole gonads that were included were from specimens in which gonad phases were microscopically confirmed. When this was not possible, images of whole gonads that most closely matched the macroscopic descriptions as defined by Mendonça et al. (2006) were used. Microscopic features, as defined in Table 2.1, are labelled in each image.

Table 2.16: Macroscopic and microscopic characteristics of the gonad phases in South African female Helicolenus dactylopterus. *OW = ovarian wall, Y = yolked oocyte, MN = migratory nucleus, HY = hydrated oocyte, AT = atresia.*

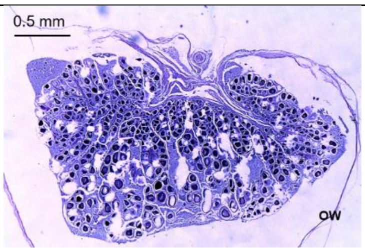
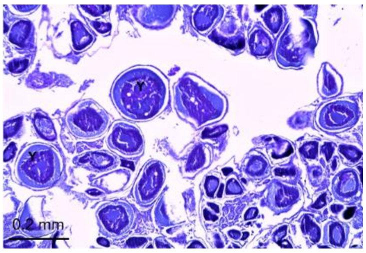
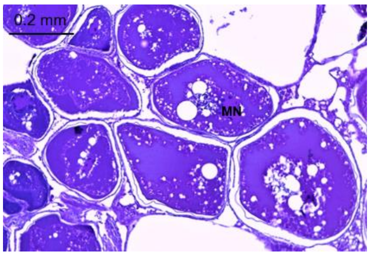
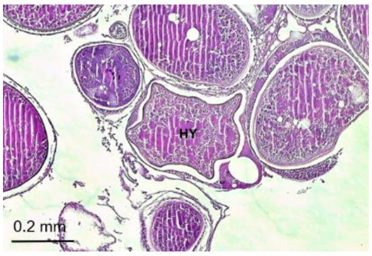
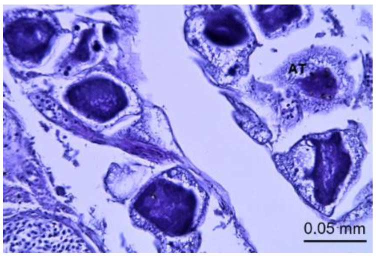
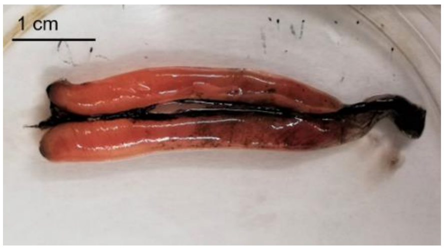
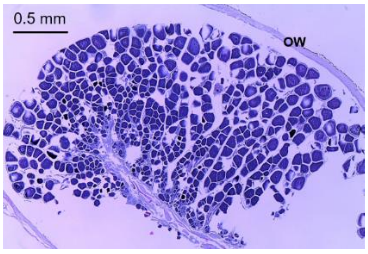
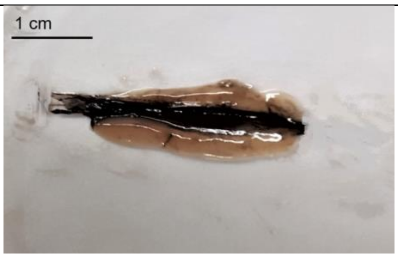
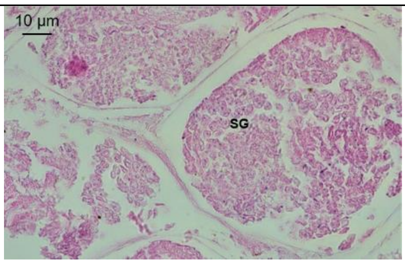
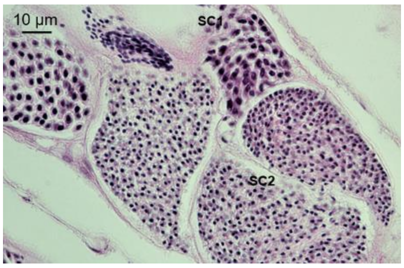
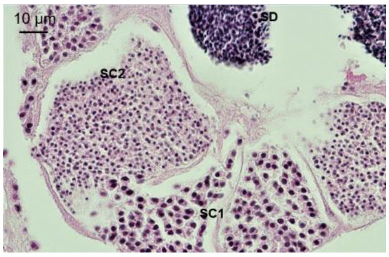
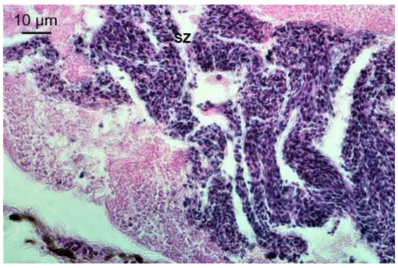
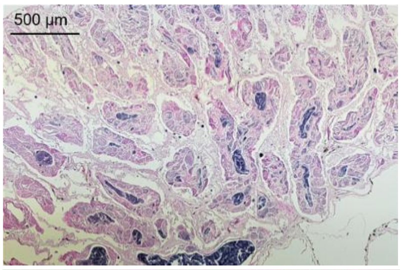
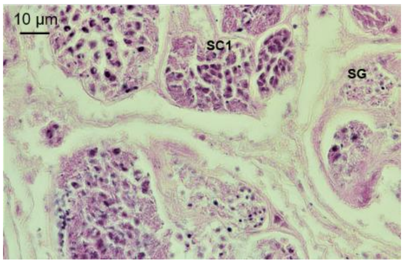
Phase	**Macroscopic characteristics**	**Microscopic characteristics**
I	 	
D	 	
SC	 	
AS	 	
RGS	 	
RGN	 	

Table 2.17: Macroscopic and microscopic characteristics of the gonad phases in South African male Helicolenus dactylopterus. *SG = spermatogonia, SC1 = primary spermatocytes, SC2 = secondary spermatocytes, SD = spermatids, SZ = spermatozoa.*

Phase	Macroscopic characteristics	Microscopic characteristics
I		
D		
SC		
AS		
RGS		
RGN		

Spawning season

All maturity phases in both sexes were recorded. Actively spawning ovaries, identifiable from the unlinked gelatinous matrix, were recorded in four months only, primarily from September to November, peaking in September when 54.76% of females were spawning (Figure 2.14). A smaller percentage (3.85%) of actively spawning females were recorded in June. The testicular development cycle was less distinguishable. Actively spawning males were recorded in eight months: in January and February, April to June, and September to November (Figure 2.15). Sperm production and release in males peaked in January (31.25%), September (30.00%) and November (24.14%).

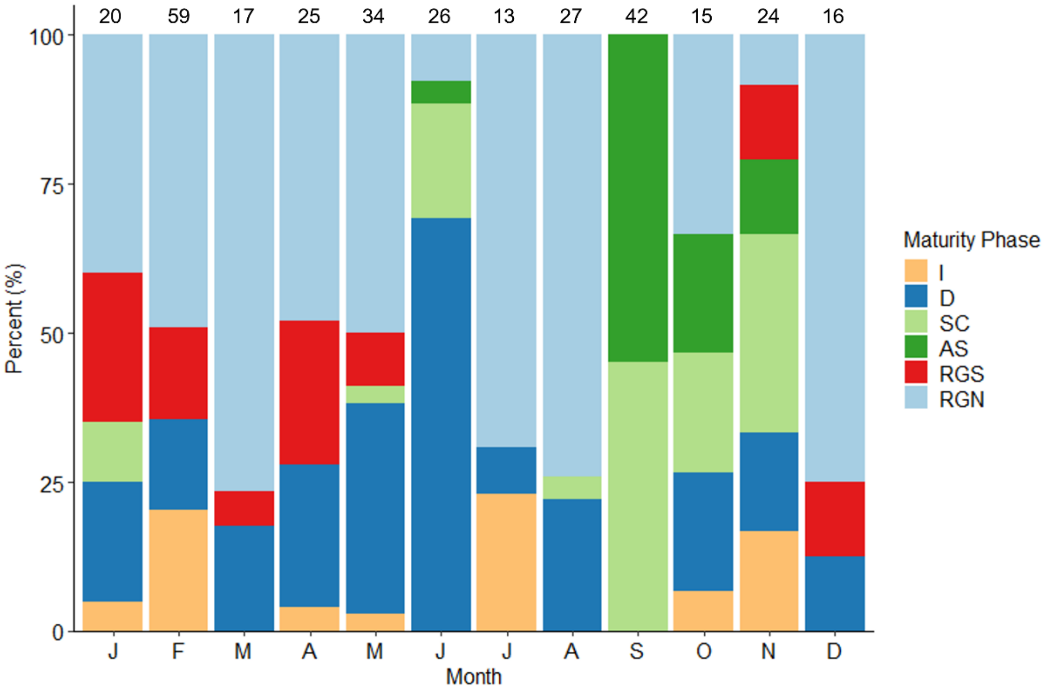


Figure 2.14: Monthly percent frequencies of ovarian phases of South African Helicolenus dactylopterus, *based on macroscopic criteria. Sample sizes per month are indicated above each bar.*

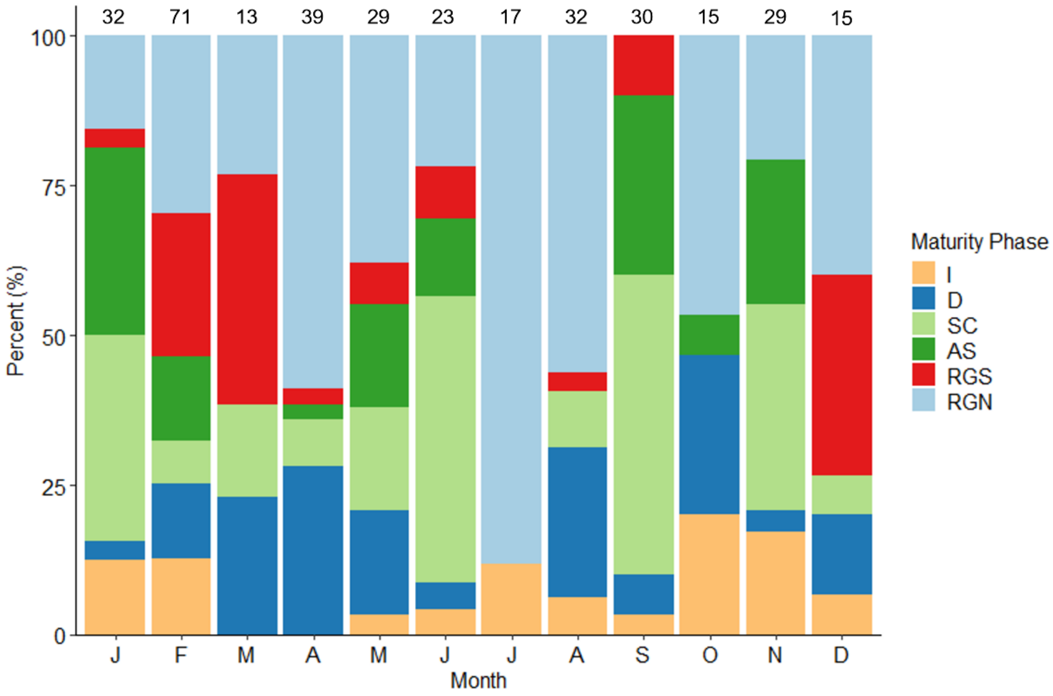


Figure 2.15: Monthly percent frequencies of testes phases in South African Helicolenus dactylopterus, *based on macroscopic criteria. Sample sizes per month are indicated above each bar.*

Gonad phase distributions were reflected in the average monthly gonadosomatic indices (GSIs) (Figure 2.16). Female GSI increased in June and peaked from September to November with the highest GSI value in September (4.11 ± 0.21 SE). Male GSI was highest in January (0.60 ± 0.07 SE), September (0.50 ± 0.03 SE) and November (0.43 ± 0.05 SE). In all months, the male GSIs were lower than those of the females.

In both sexes GSI differed significantly among all maturity phases ($\chi^2 = 248.12$, df = 5, $p < 0.001$ and $\chi^2 = 235.83$, df = 5, $p < 0.001$ for females and males respectively) (Figure 2.17).

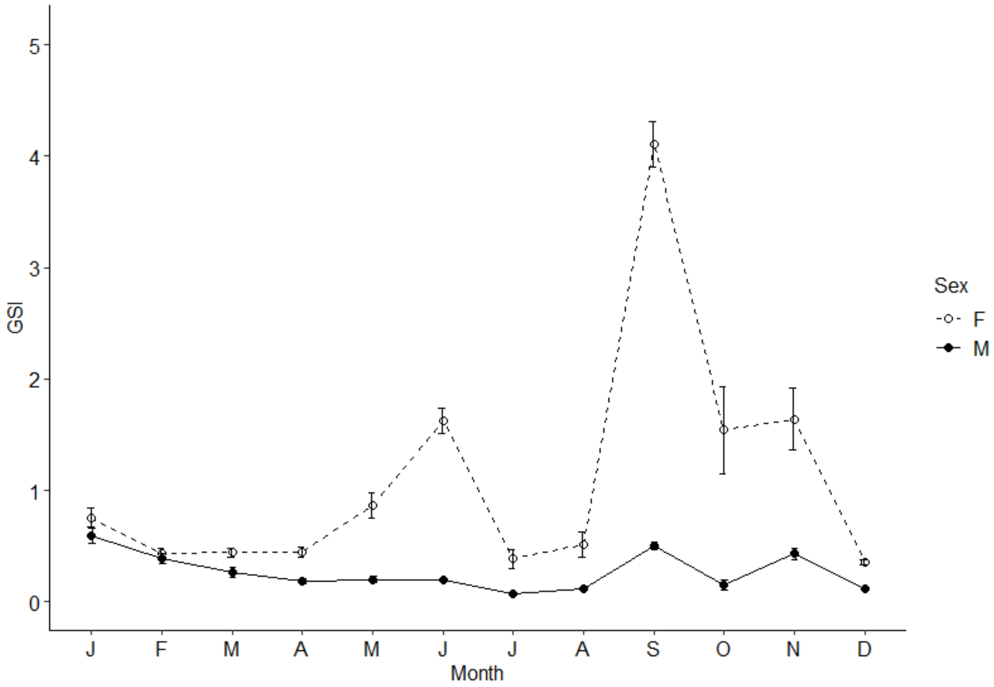


Figure 2.16: Average (± SE) monthly gonadosomatic indices (GSIs) of female (n=318) and male (n=345) South African Helicolenus dactylopterus.

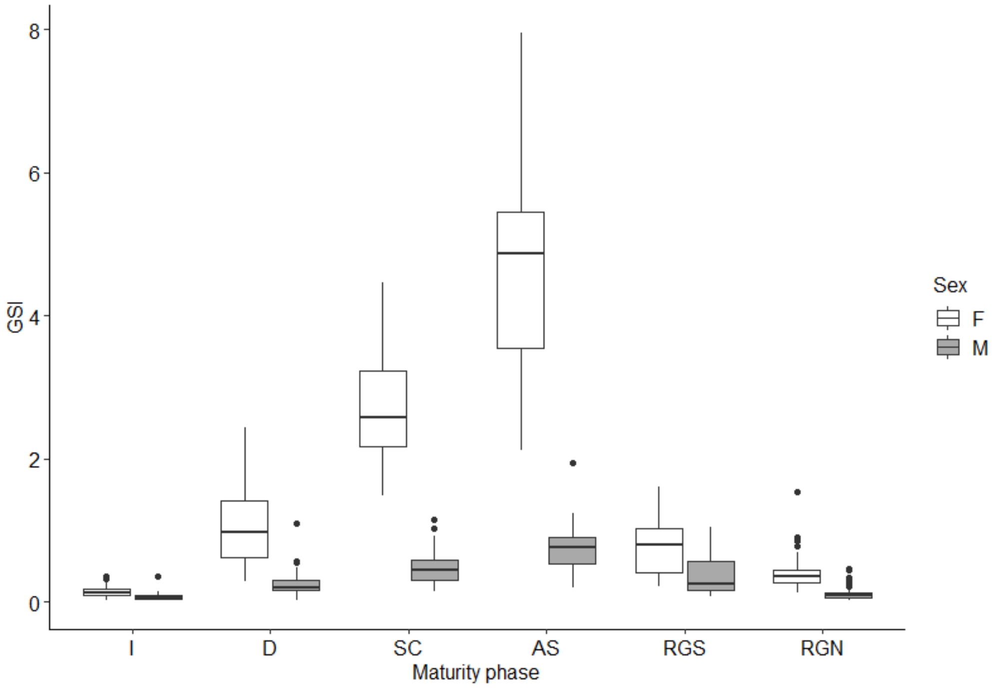


Figure 2.17: Boxplot showing the distribution of gonadosomatic index (GSI) per maturity phase in female (n=318) and male (n=345) South African Helicolenus dactylopterus.

The relative condition indices followed similar trends over the year for both sexes and the amplitudes of the female and male cycles were low (Figure 2.18). Condition index remained between 0.9 and 1.1 for both sexes. Female condition peaked in April (1.02 ± 0.02 SE) and

May (1.05 ± 0.01 SE) before the June spawning peak and remained between 0.95 and 0.99 during the other months of the year. No increase in condition was seen before the main spawning peak from September to November, however, the lowest relative condition of females was seen following this in January (0.95 ± 0.02 SE). Male condition peaked in April (1.03 ± 0.02 SE) and May (1.03 ± 0.02 SE) but also increased in November (1.03 ± 0.01 SE) and December (1.02 ± 0.02 SE). Condition ranged from 0.96 to 0.99 in other months and was poorest in October (0.96 ± 0.02 SE).

In both sexes, relative condition factor was approximately normally distributed, and variances were similar among maturity phases (F = 1.01, df = 5, p = 0.41; F = 0.74, df = 5, p = 0.59 for females and males respectively). In females and males, relative condition did not differ among maturity phases (F = 0.32, df = 5, p = 0.90 and F = 1.88, df = 5, p = 0.10 for females and males respectively).

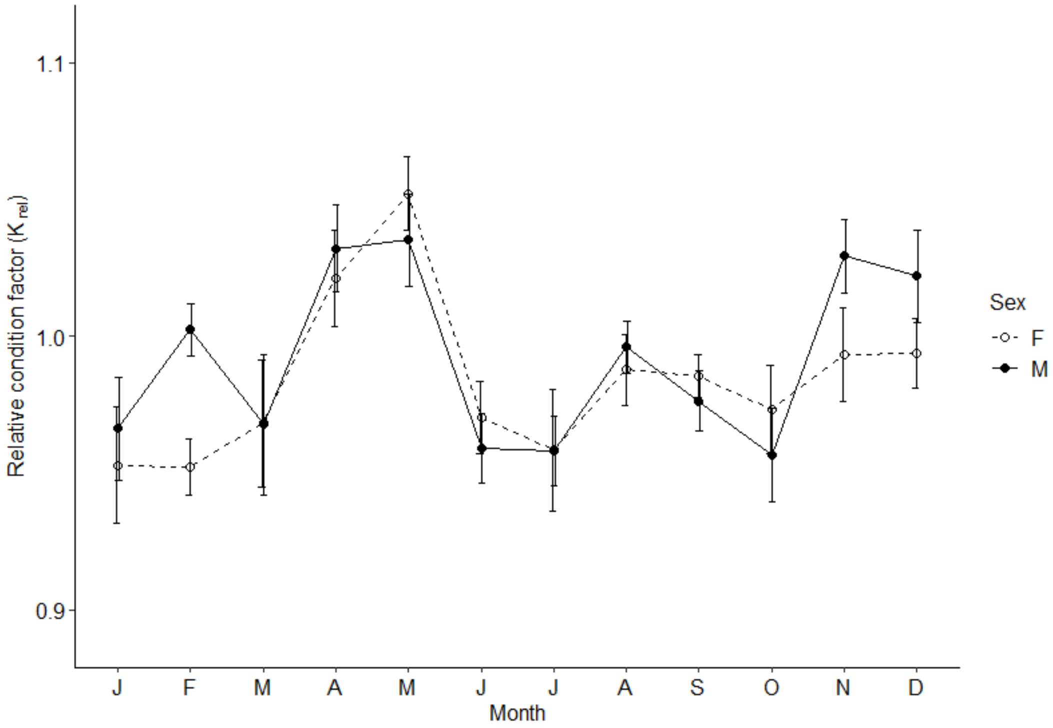


Figure 2.18: Average (±SE) monthly relative condition index of female (n=318) and male (n=345) South African Helicolenus dactylopterus.

Sperm storage in females

Of the 36 ovaries selected for sperm storage examination, 34 contained sperm cells. The two ovaries without sperm cells were collected in March and November. Sperm cells that were observed were mainly present in the central ovarian rachis and at the base of the lamellae

(Figure 2.19 A), with some floating in the ovarian cavity (Figure 2.19 B). Many were located in rounded or cylindrical storage structures (Figure 2.19 A). Large numbers of sperm cells were observed in ovaries collected in February, March, April and October (Figure 2.19 C).

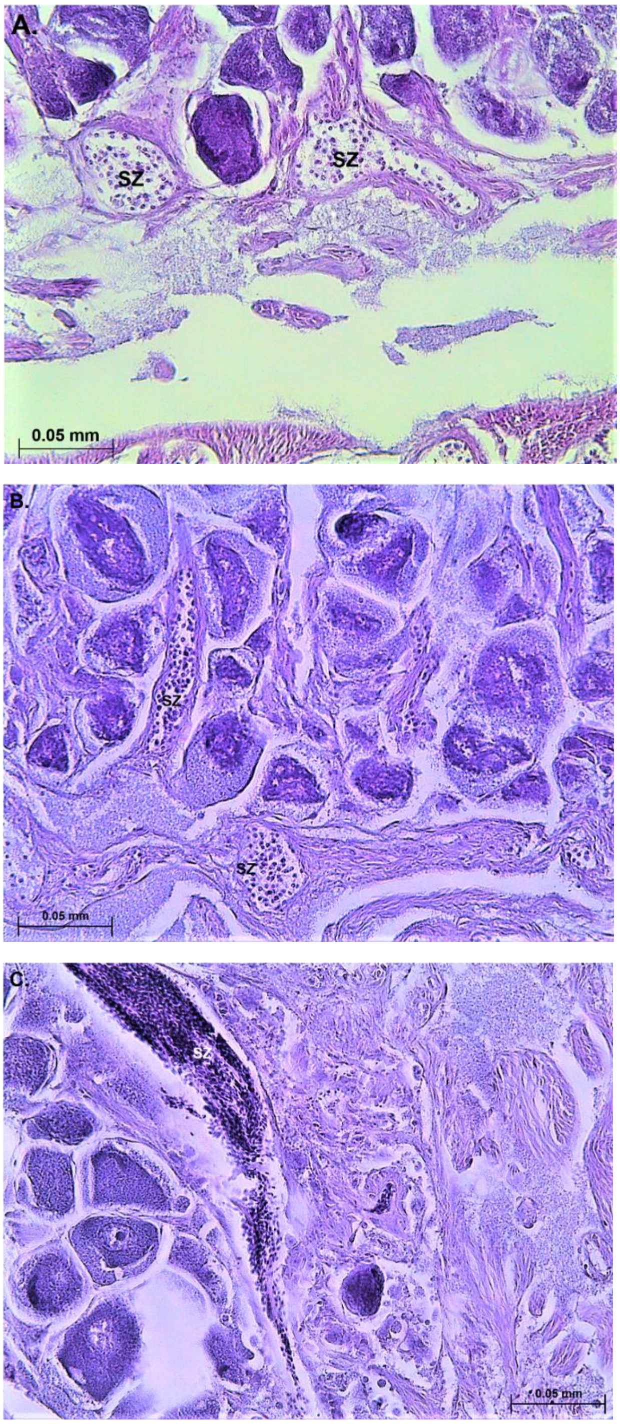


Figure 2.19: Histological cross-sections of the ovaries of South African Helicolenus dactylopterus *showing A. sperm storage in circular structures at the base of the ovarian lamellae; B. sperm cells in the ovarian cavity and the central rachis; and C. abundant spermatozoa in the ovaries of an individual caught in April 2018. SZ indicates the presence of spermatozoa/sperm cells.*

Length and age at 50% maturity

Length at 50% maturity was estimated at 185.07 mm [95% C.I.: 170.91 – 199.86 mm] for females (Figure 2.20) and 188.41 mm [95% C.I.: 167.35 – 207.65 mm] for males (Figure 2.21). The smallest mature female was 158 mm and the smallest male was 148 mm.

Age at 50% maturity in females was estimated at 3.61 years, [95% C.I.: 2.39 – 4.64 years] (Figure 2.20), and in males at 4.32 years, [95% C.I.: 2.49 – 5.59 years] (Figure 2.21).

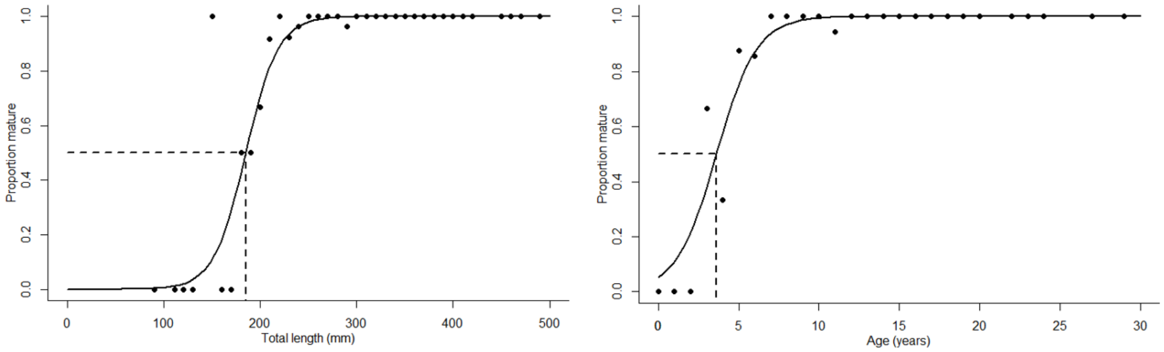


Figure 2.20: Maturity ogives illustrating length (n=318) and age (n=165) at 50% maturity estimated for South African female Helicolenus dactylopterus.

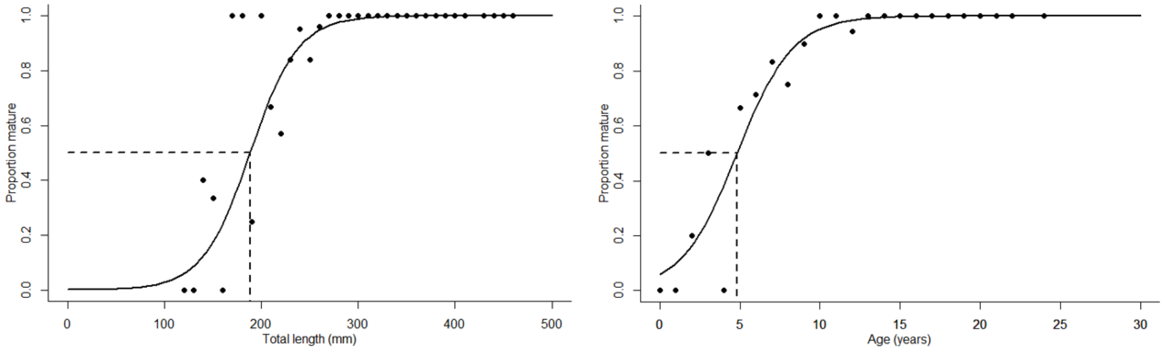


Figure 2.21: Maturity ogives illustrating length (n=345) and age (n=176) at 50% maturity estimated for South African male Helicolenus dactylopterus.

2.4.4 Diet

Of 674 stomachs, 439 contained food remains. The feeding activity rate (vacuity index, %V) was 34.87%. Of the stomachs with food remains, 251 stomachs contained only one prey taxon, 123 contained two, and the remaining 65 contained three to six types of prey.

The slope of the linear regression through the last five points of the prey accumulation curve (Figure 2.22) was 0.04.

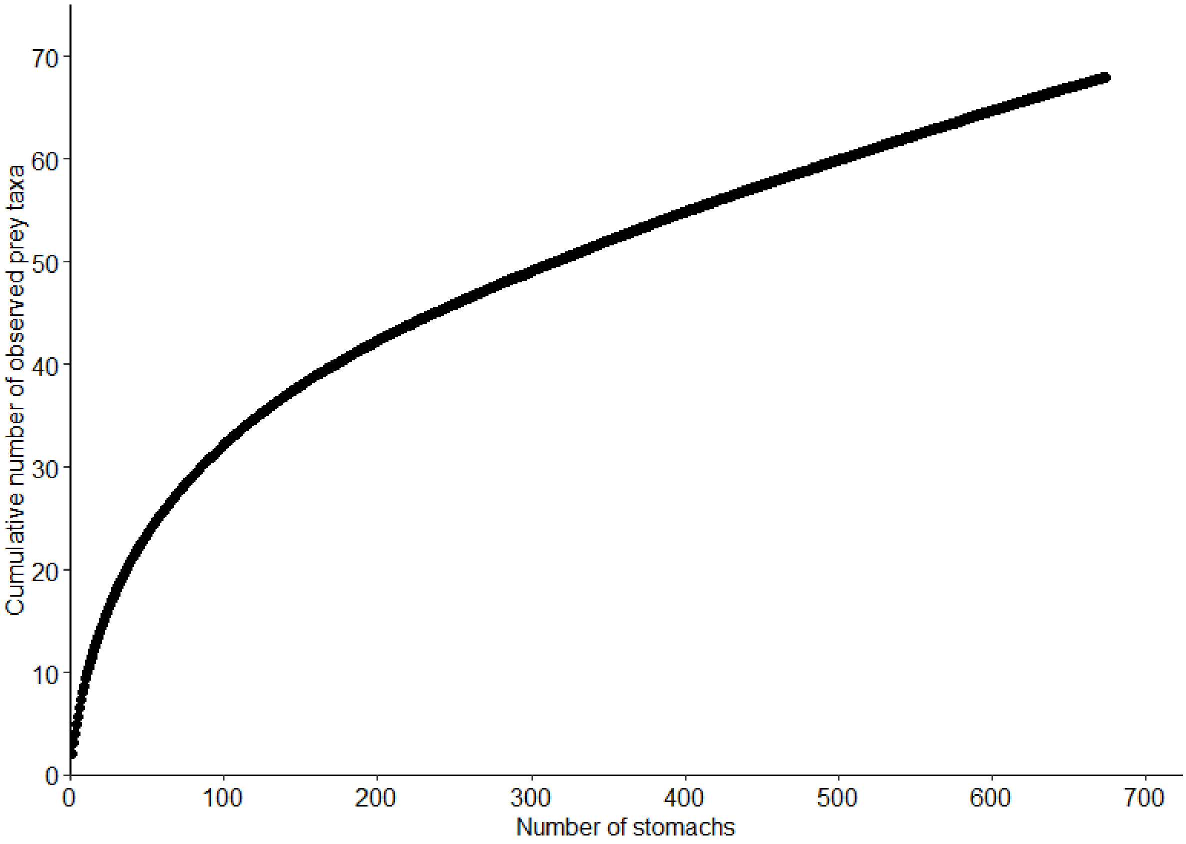


Figure 2.22: Prey accumulation curve, plotted in random order, for South African Helicolenus dactylopterus.

Diet composition

A total of 6 819 prey items were found, comprising 66 taxonomic levels, of which 30 of these were malacostracans and 17 were teleosts (Table 2.18). Malacostraca comprised the most important prey group and occurred most frequently in the diet (%PSIRI = 39.55%, %F = 69.93%). The main malacostracan groups were decapods (%PSIRI = 10.11%, %F = 22.55%), mainly Caridea shrimp (%PSIRI = 4.92%, %F = 11.39%), and euphausiids (%PSIRI = 14.92%, %F = 18.00%). Teleosts were the second most important group of prey (%PSIRI = 19.83%,

%F = 31.89%), with unidentified fish species forming a large proportion of this group (%PSIRI = 16.39%, %F = 26.20%). Many of the teleost prey items found in stomachs were well digested and were identified on the presence of bony vertebrae. Of the identified teleost species, macrourids were the most important prey group (%PSIRI = 1.47%, %F = 1.82%). Other prey that contributed substantially and occurred commonly in the diet of *H. dactylopterus* were the Ophiuroidea (% PSIRI = 11.51%, %F = 16.40%), in which *Ophiura trimeni* were dominant (%PSIRI = 10.02, %F = 12.98%) and the Thaliacea, which consisted exclusively of species from the genus *Pyrosoma* (%PSIRI = 11.44%, %F = 14.58%). Diet breadth, according to Levin's standardised index and calculated based on the %PSIRI of each prey group, was 0.17.

The trophic level of *H. dactylopterus,* for all size classes pooled, was 3.64.

Table 2.18: Diet composition of South African Helicolenus dactylopterus *based on the analysis of stomach contents. The percent frequency of occurrence (%F), average percent numerical abundance (%N), prey specific numerical abundance (%PN), average percent weight (%W), prey specific weight (%PW) and the prey specific index of relative importance (%PSIRI) is shown for each prey item. Bold values represent summed values for each prey group. The trophic level of each prey group is based on the Ebert and Bizzarro (2007) classification.*

Group	**Family**	**Prey Species**	**Trophic level**	**%F**	**%N**	**%PN**	**% W**	**%PW**	**%PSIRI**
POLYCHAETA				**7.06**	**4.41**		**4.87**		**4.64**
Polychaeta		Polychaeta	2.60	2.28	1.30	57.00	1.34	58.84	1.32
Amphinomida	Amphinomidae	*Chloeia inermis*	2.60	4.78	3.11	65.10	3.53	73.74	3.32
MALACOSTRACA				**69.93**	**41.89**		**37.21**		**39.55**
Malacostraca		Malacostraca	2.4	10.25	4.94	48.17	2.46	24.01	3.70
Amphipoda		Amphipoda	3.18	4.33	1.98	45.72	1.47	33.87	1.72
		Gammaridea	3.18	2.05	1.07	51.99	0.67	32.88	0.87
		Hyperiidea	3.18	0.68	0.19	27.74	0.21	30.28	0.20
		Caprilloidea	3.18	0.23	0.03	14.29	0.01	4.76	0.02
	Cyphocarididae	*Cyphocaris faurei*	3.18	2.05	1.48	72.20	0.89	43.24	1.18
Decapoda		Decapoda	2.52	5.24	3.27	62.40	3.26	62.26	3.27
	Sergestidae	Sergestidae	2.52	0.23	0.02	10.00	0.09	40.00	0.06
	Palinuridae	Palinuridae	2.52	0.68	0.16	23.98	0.18	25.73	0.17
		Anomura	2.52	0.23	0.05	20.00	0.00	0.40	0.02
	Paguridae	*Goreopagurus poorei*	2.52	1.14	0.23	20.10	0.33	29.00	0.28
	Axiidae	*Calocaris barnardi*	2.52	0.23	0.04	16.67	0.17	76.74	0.11
		Brachyura	2.52	0.91	0.15	16.47	0.08	8.62	0.11
	Inachidae	Inachidae	2.52	0.23	0.02	10.92	0.02	6.67	0.02
	Mathildellidae	*Neopilumnoplax heterochir*	2.52	0.23	0.01	5.88	0.03	14.63	0.02
	Calappidae	*Mursia cristiata*	2.52	2.05	0.78	37.83	1.49	72.51	1.13
		Caridea	2.52	4.78	2.74	57.34	2.64	55.24	2.69
	Acanthephyridae	*Acanthephyra pelagica*	2.52	3.42	1.00	29.18	1.15	33.52	1.07
	Crangonidae	Crangonidae	2.52	0.46	0.09	18.84	0.14	31.47	0.11
	Crangonidae	*Parapontophilus* spp.	2.52	0.46	0.26	56.25	0.23	50.56	0.24

Group	**Family**	**Prey Species**	**Trophic level**	**%F**	**%N**	**%PN**	**% W**	**%PW**	**%PSIRI**
	Hippolytidae	*Merhippolyte* spp.	2.52	0.23	0.23	100.00	0.23	100.00	0.23
	Pandalidae	*Plesionika martia*	2.52	0.23	0.11	50.00	0.18	80.00	0.15
	Pasiphaeidae	*Pasiphaea* spp.	2.52	1.59	0.50	31.49	0.30	19.10	0.40
	Oplophoridae	Oplophoridae	2.52	0.23	0.01	6.25	0.02	9.90	0.02
Euphausiacea		Euphausiacea	2.25	18.00	15.86	88.13	13.98	77.71	14.92
Isopoda		Isopoda	3.18	2.51	1.17	46.52	0.92	36.58	1.04
Stomatopoda		Stomatopoda	2.40	0.68	0.51	75.00	0.63	91.82	0.57
	Squillidae	Squillidae	2.40	2.96	2.57	86.92	2.90	97.98	2.74
	Squillidae	*Pterygosquilla capensis*	2.40	1.14	0.80	70.67	1.03	90.19	0.92
Tanaidacea		Tanaidacea	2.40	2.51	1.61	64.39	1.50	59.75	1.56
OSTRACODA				**0.23**	**0.08**		**0.05**		**0.06**
Ostracoda		Ostracoda	2.40	0.23	0.08	33.33	0.05	20.00	0.06
ASCIDIACEA				**0.23**	**0.11**		**0.01**		**0.06**
Ascidiacea		Ascidiacea	2.50	0.23	0.11	50.00	0.01	5.52	0.06
THALIACEA				**14.58**	**10.87**		**12.01**		**11.44**
Pyrosomatida	Pyrosomatidae	*Pyrosoma* spp.	2.50	14.58	10.87	74.59	12.01	82.37	11.44
TELEOSTEI				**31.89**	**17.80**		**21.86**		**19.83**
Unidentified Teleostei		Teleosts	3.24	26.20	14.70	56.11	18.08	69.03	16.39
Aulopiformes	Paralepididae	Paralepididae	3.24	0.23	0.11	50.00	0.08	34.57	0.10
Clupeiformes	Clupeidae	Clupeidae	3.24	0.23	0.23	100.00	0.23	100.00	0.23
	Engraulidae	*Engraulis japonicus*	3.24	0.23	0.11	50.00	0.08	35.00	0.10
Gadiformes	Macrouridae	Macrouridae	3.24	1.59	1.27	79.76	1.45	90.99	1.36
	Macrouridae	*Coelorinchus* spp.	3.24	0.23	0.08	33.33	0.14	63.16	0.11
	Moridae	*Physiculus capensis*	3.24	0.23	0.23	100.00	0.23	100.00	0.23
Lampriformes	Trachipteridae	Trachipteridae	3.24	0.23	0.02	10.00	0.20	87.36	0.11
Myctophiformes	Myctophidae	Myctophidae	3.24	0.23	0.02	8.33	0.01	2.30	0.01
	Myctophidae	*Lampanyctus* spp. (likely *L. australis*)	3.24	0.91	0.32	35.66	0.53	58.25	0.43
Ophidiiformes	Carapidae	Carapidae	3.24	0.23	0.06	25.00	0.09	38.46	0.07

Group	**Family**	**Prey Species**	**Trophic level**	**%F**	**%N**	**%PN**	**% W**	**%PW**	**%PSIRI**
Scorpaeniformes	Scorpaenidae	Scorpaenidae	3.24	0.23	0.11	50.00	0.01	6.45	0.06
	Sebastidae	*Helicolenus dactylopterus*	3.24	0.23	0.15	66.67	0.20	86.96	0.17
Stomiiformes		Stomiiformes	3.24	0.23	0.01	5.88	0.01	2.94	0.01
	Sternoptychidae	Sternoptychidae	3.24	0.23	0.11	50.00	0.15	65.00	0.13
	Stomiidae	Idiacanthinae	3.24	0.23	0.23	100.00	0.23	100.00	0.23
	Stomiidae	*Malacosteus niger*	3.24	0.23	0.03	11.11	0.16	68.42	0.09
CHONDRICHTHYES			3.65	**0.23**	**0.23**		**0.23**		**0.23**
Rajiformes		Rajiformes	3.65	0.23	0.23	100.00	0.23	100.00	0.23
ASTEROIDEA				**0.23**	**0.11**		**0.08**		**0.09**
Valvatida	Solasteridae	*Crossaster penicillatus*	2.50	0.23	0.11	50.00	0.08	33.33	0.09
OPHIUROIDEA				**16.40**	**11.83**		**11.20**		**11.51**
Unidentified Ophiuroidea		Ophiuroidea	2.50	2.51	1.21	48.27	0.90	35.81	1.05
Amphilepidida	Ophiotrichidae	*Ophiothrix aristulata*	2.50	0.23	0.03	11.11	0.03	12.82	0.03
Ophioscolecida	Ophioscolecidae	*Ophiolycus dentatus*	2.50	0.46	0.13	29.17	0.23	51.19	0.18
Ophiurida	Ophiuridae	*Ophiura costata costata*	2.50	0.23	0.23	100.00	0.23	100.00	0.23
	Ophiuridae	*Ophiura trimeni*	2.50	12.98	10.23	78.80	9.81	75.55	10.02
FORAMINIFERA				**4.78**	**1.30**		**0.76**		**1.03**
Foraminifera		Foraminifera	2.50	4.78	1.30	27.24	0.76	15.94	1.03
BIVALVIA				**0.23**	**0.23**		**0.23**		**0.23**
Nuculida	Nuculidae	*Nucula nucleus*	2.10	0.23	0.23	100.00	0.23	100.00	0.23
CEPHALOPODA				**10.71**	**6.78**		**8.22**		**7.50**
Unidentified Cephalopoda		Cephalopoda	3.20	8.43	5.29	62.80	6.18	73.31	5.74
Oegopsida	Ommastrephidae	Ommastrephidae	3.20	1.59	0.81	50.60	1.36	85.39	1.08
	Ommastrephidae	*Todaropsis eblanae*	3.20	0.68	0.68	100.00	0.68	100.00	0.68
PORIFERA				0.46	0.30	66.67	0.44	96.67	0.37
Porifera		Porifera	2.50	0.46	0.30	66.67	0.44	96.67	0.37
UNKNOWN				**7.29**	**4.05**		**2.84**		**3.44**
Unknown		Bone and tissue		7.29	4.05	55.55	2.84	38.96	3.44

A graphical representation of the diet of South African *H. dactylopterus* based on the Amundsen et al. (1996) method is shown in Figure 2.23. All prey items were distributed on the left of the diagram with many occurring in the upper left quadrant, indicating that a large number of prey species were consumed by only a few individuals. Prey items distributed in the lower left quadrant of the diagram were rare in the diet of *H. dactylopterus*. The most dominant prey species in South African individuals' diet included teleosts, euphausiids, *Pyrosoma* spp., *Ophiura trimeni*, cephalopods and malacostracans. The importance of teleosts and cephalopods is affected by the taxonomic resolution to which organisms were identified.

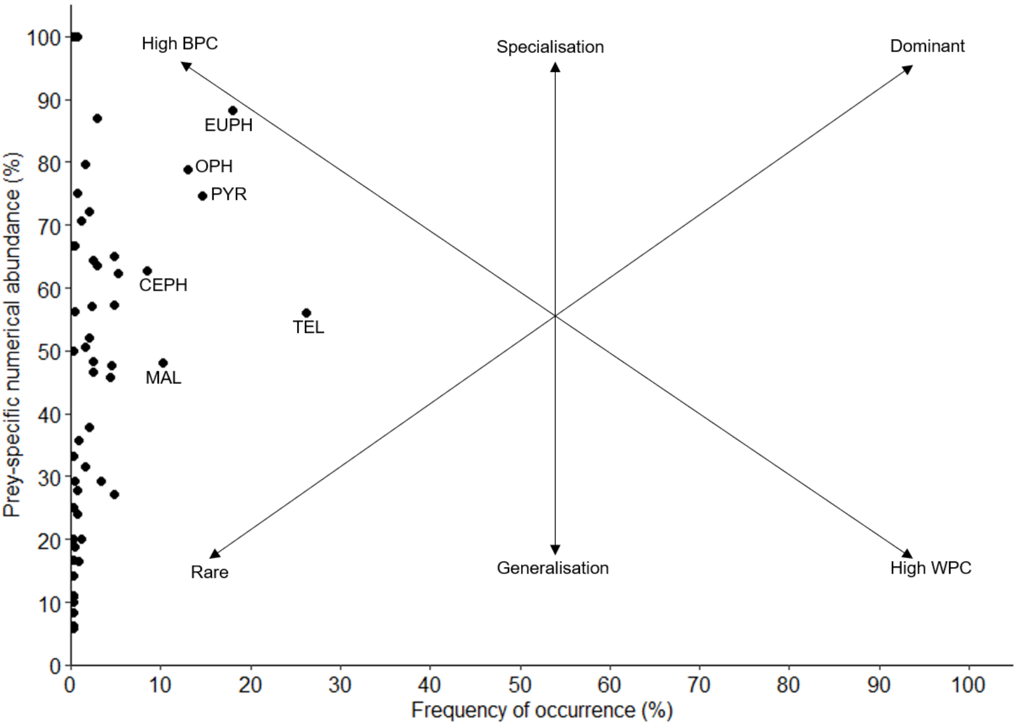


Figure 2.23: Representation of the diet of South African Helicolenus dactylopterus, *based on the graphical method proposed by Amundsen et al. (1996). The prey-specific numerical abundance and frequency of occurrence of each prey taxon are shown, with the most important taxa labelled: teleosts (TEL), euphausiids (EUPH), Pyrosoma spp. (PYR), Ophiura trimeni (OPH), malacostracans (MAL) and cephalopods (CEPH). The explanatory axes are also shown.*

Diet comparison

Stomach contents from 438 fish were used for dietary comparisons. Area six was excluded from the analyses due to a lack of replication. Prey taxa were grouped into major taxonomic groups at the order level when possible, resulting in a total of 33 prey groups (Table 2.18).

For the nonmetric MDS ordination, 13 outliers were removed to aid in the graphical representation of the data (Figure 2.24). The 13 outliers mainly consisted of teleost and chondrichthyan species (Rajiformes, Clupeiformes, Myctophiformes, Stomiiformes and Gadiformes). One outlier contained a species from the order Nuculida, and another contained a Poriferan. The stress of the nonmetric MDS ordination (excluding outliers) was 0.08, indicating a good representation of the diet (<0.2) (Clarke, 1993).

The diets of *H. dactylopterus* individuals from different areas overlapped substantially, but there was more separation in the diets of fish from different depth classes and those of different lengths (Figure 2.24). There was a separation in the diet of fish from depths of 301 to 400 m, and those from depths of 201 to 300 m, 401 to 500 m and >600 m. The diet of fish from 301 to 400 m appeared to overlap more with those from 501 to 600 m (Figure 2.24 B). The diet of larger fish (>199 mm) overlapped with smaller fish (<199 mm), however, the diet of smaller fish did not overlap with that of the larger specimens (Figure 2.24 C).

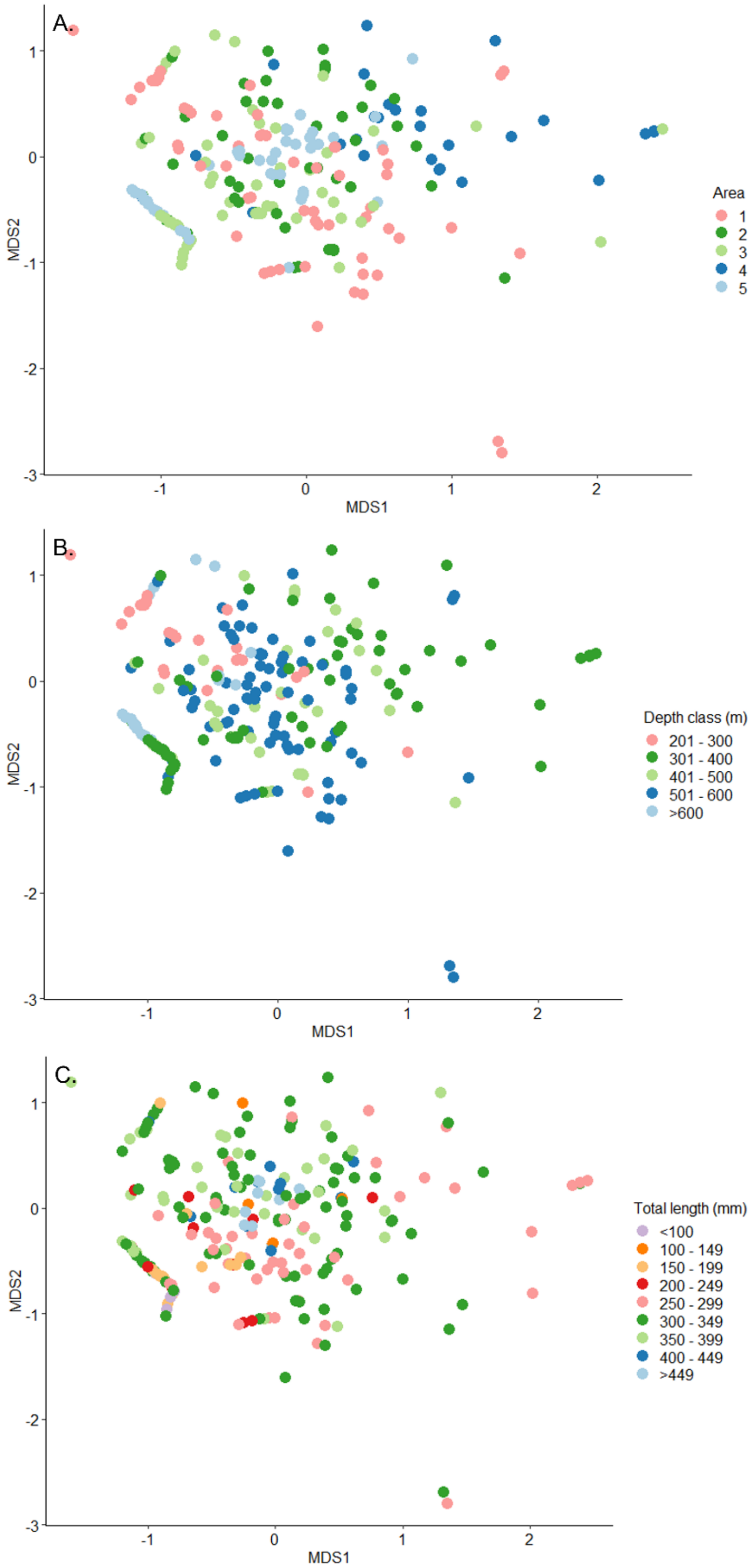


Figure 2.24: Nonmetric MDS plot representing Bray-Curtis similarity for prey abundance in the diet of South African Helicolenus dactylopterus *comparing the distribution of prey items among (A) fish from different areas, (B) fish from different 100-m depth classes, and (C) fish in different 50-mm length classes. Stress=0.08.*

PERMANOVA results suggested a significant variation in the diet of *H. dactylopterus* individuals among depth classes and length classes but no variation in the diet among different areas (Table 2.19).

Table 2.19: Results of the PERMANOVA comparing the diet of South African Helicolenus dactylopterus *among fish from different areas, from different depths classes and of different lengths. Significant values are highlighted in bold.*

	df	SS	MS	Pseudo-F	P (perm)
Area	4	51554	12888	0.84	0.67
Depth class(Area)	**8**	**$1.31E^{05}$**	**16342**	**4.10**	**0.001**
Length(Depth class(Area))	**38**	**$1.87E^{05}$**	**4916.3**	**1.51**	**0.001**
Residuals	387	$1.26E^{06}$	3255.1		
Total	437	$1.85E^{06}$			

The SIMPER analysis based on prey abundance indicated which prey contributed most to the diet of fish from each depth class: euphausiids and teleosts contributed 33.94 and 23.66% to the diet of fish between 201 and 300 m; teleosts and ophiurids contributed 41.04 and 33.31% to the diet of fish between 301 and 400 m; decapods and teleosts contributed 28.68 and 26.05% to the diet of fish between 401 and 500 m, euphausiids contributed 79.98% to the diet of fish between 501 and 600 m; and pyrosomes contributed 75.82% to the diet of fish deeper than 600 m. Decapods were important in the diet of *H. dactylopterus* from most depths, as were pyrosomes. Pyrosomes were not present in the stomachs of fish occurring from 201 to 300 m but their importance in the diet of *H. dactylopterus* increased with depth. Teleosts were important in the diet of fish at all depths apart from 501 to 600 m.

The %PSIRI results showed that when prey weight was incorporated and considered, teleosts were an important component of the diet of *H. dactylopterus* individuals occurring in all depth classes. Other than this, the %PSIRI (Table 2.20) and SIMPER results were largely similar.

Other prey items including malacostracans, amphipods, cephalopods and unknown tissue occurred in the diet of fish from all or most depths classes but had a minor contribution to the diet.

Table 2.20: Prey-specific index of relative importance (%PSIRI) of the most consumed prey groups by South African Helicolenus dactylopterus *by depth class.*

Depth class (m)	**n**	**Prey and %PSIRI**
201 - 300	125	Euphausiacea (22.50%), Teleostei (15.32%), Stomatopoda (14.83%), Cephalopoda (10.97%), Decapoda (10.18%), Amphinomida (4.37%), unknown (3.95%), Pyrosomatida (2.40%), Amphipoda (2.07%), Malacostraca (1.80%), Ophiurida (1.60%), other (10.02%).
301 - 400	96	Ophiurida (23.26%), Teleostei (22.55%), Euphausiacea (8.12%), Pyrosomatida (8.01%), Decapoda (6.32%), unknown (5.93%), Malacostraca (5.35%), Cephalopoda (4.79%), Amphinomida (4.29%), Amphipoda (1.32%), other (10.09%).
401 - 500	132	Teleostei (15.69%), Decapoda (14.41%), Ophiurida (14.33%), Amphipoda (9.94%), Pyrosomatida (6.74%), Malacostraca (5.63%), Euphausiacea (5.06%), Cephalopoda (3.98%), Amphinomida (3.79%), unknown (1.70%), other (18.73%).
501 - 600	41	Euphausiacea (53.66%), Pyrosomatida (20.48%), Teleostei (10.58%), Cephalopoda (3.96%), unknown (2.44%), Decapoda (0.98%), Malacostraca (0.83%), other (7.07%).
>600	44	Pyrosomatida (50.57%), Teleostei (13.89%), Decapoda (11.76%), Ophiurida (3.96%), unknown (2.84%), Malacostraca (2.46%), Euphausiacea (2.08%), Amphipoda (1.30%), other (11.14%).

The SIMPER analysis based on prey abundance showed that euphausiids contributed most to the diets of fish less than 200 mm total length, contributing 100, 84.58 and 65.24% to the diets of fish less than 100 mm, from 100 to 149 mm and from 150 to 199 mm respectively. Ophiurids (28.67%), stomatopods (18.48%), euphausiids (15.22%) and teleosts (11.82%) were the main contributors to the diet of fish from 200 to 249 mm. Unidentified teleosts contributed most to the diet of fish from 250 to 399 mm, contributing 39.32, 45.31 and 51.38% to the diet of fish in each 50 mm length class respectively. In fish from 250 to 349 mm, pyrosomes were also important components of the diet contributing 14.68% to the diets of fish from 250 to 299 mm and 26.44% to the diets of fish from 300 to 349 mm. Amphipods and decapods were important in the diets of fish larger than 350 mm. Second to teleosts, amphipods contributed 20.64% to the diet of fish from 350 to 399 mm, and they were the most important component of the diet in fish from 400 to 449 mm, contributing 44.57%. Decapods were the second most important contributor to the diet of fish from 400 to 449 mm (31.36%) and contributed the most (72.27%) to the diet of fish greater than 449 mm.

The %PSIRI results (Table 2.21) were largely similar to those from the SIMPER analysis. Crustaceans, including amphipods, decapods and euphausiids, were important contributors to the diet of South African *H. dactylopterus* individuals across all length classes. Euphausiids showed a clear pattern of decreasing in the importance of diet with increasing fish length, while decapods showed the opposite with an increase in their contribution to the diet in larger fish. Unidentified teleosts and cephalopods also showed a pattern of increasing dietary importance in larger fish. Cephalopods occurred in the diet of fish greater than 150 mm in length, whereas teleosts only occurred in the diet of fish greater than 200 mm in length. Cephalopods appeared to be less important in the diet of fish greater than 400 mm.

The change in the diet of *H. dactylopterus* with length was reflected in the trophic level in which trophic level was calculated as 3.25, 3.33, 3.56, 3.56, 3.64, 3.64, 4.00, 4.05 and 4.02 for fish from each size class (<100 to >449) respectively.

Table 2.21: Prey-specific index of relative importance (%PSIRI) of the most consumed prey groups by South African Helicolenus dactylopterus *by 50-mm length class.*

Length class (mm)	n	Prey and %PSIRI
<100	5	Euphausiacea (100%)
100 – 149	22	Euphausiacea (53.77%), Decapoda (14.11%), Pyrosomatida (13.64%), Malacostraca (9.09%), Amphipoda (6.43%), other (2.95%).
150 – 199	14	Euphausiacea (36.71%), Malacostraca (17.52%), Ophiurida (14.29%), Amphipoda (13.99%), Cephalopoda (5.16%), Decapoda (3.21%), other (9.12%).
200 – 249	75	Ophiurida (20.07%), Stomatopoda (15.68%), Euphausiacea (14.36%), Teleostei (10.77%), Decapoda (9.99%), Malacostraca (3.86%), Amphinomida (3.06%), Cephalopoda (2.53%), Amphipoda (2.24%), Oegopsida (1.33%), other (16.11%).
250 – 299	193	Teleostei (18.60%), Pyrosomatida (13.53%), Euphausiacea (11.76%), Ophiurida (11.64%), Decapoda (9.42%), Cephalopoda (5.84%), Stomatopoda (3.52%), Amphinomida (3.33%), Malacostraca (2.95%), Amphipoda (1.86%), Oegopsida (0.87%), other (16.68%).
300 – 349	87	Teleostei (23.25%), Pyrosomatida (21.63%), Euphausiacea (11.49%), Decapoda (8.17%), Cephalopoda (7.60%), Ophiurida (6.29%), Amphinomida (4.00%), Malacostraca (3.09%), Oegopsida (1.73%), Amphipoda (0.21%), other (12.54%).
350 – 399	24	Teleostei (25.43%), Amphipoda (16.39%), Decapoda (12.42%), Amphinomida (9.88%), Pyrosomatida (8.09%), Cephalopoda (7.96%), Oegopsida (5.67%), Malacostraca (0.54%), other (13.62%).
400 – 449	10	Amphipoda (36.14%), Decapoda (19.88%), Cephalopoda (15.56%), Teleostei (11.89%), Oegopsida (5.06%), Malacostraca (3.73%), Euphausiacea (0.65%), other (7.09%).
>449	8	Decapoda (25.90%), Oegopsida (21.47%), Cephalopoda (15.30%), Amphipoda (14.61%), Teleostei (5.69%), Pyrosomatida (4.53%), other (12.50%).

2.4.5 Meta-analysis

The meta-analysis of morphometric results shows that the maximum total length (494 mm) of South African *H. dactylopterus* is similar to some records in the North Atlantic and is higher than the maximum length recorded in a Namibian sample, which had a similar sample size. Generally, North Atlantic fish obtain greater lengths than those in the Mediterranean, regardless of sample size (Figure 2.25). Overall, the mean maximum total length of *H. dactylopterus* was 352 mm.

Helicolenus dactylopterus in the North Atlantic showed hypo-allometric growth, although this was based on only three estimates. In most Mediterranean studies, *H. dactylopterus* showed hyper-allometric growth, aligning with the findings of this study (Figure 2.26). The mean for all regions was 3.01 indicating overall hyper-allometric growth in the species.

Predicted weights of South African *H. dactylopterus* individuals were lower than North Atlantic individuals but higher than those in the Mediterranean (Figure 2.27). Predicted weights for a fish of 300 mm in South African, North Atlantic and Mediterranean waters was 420.14 g, 451.60 g and 416.97 g respectively.

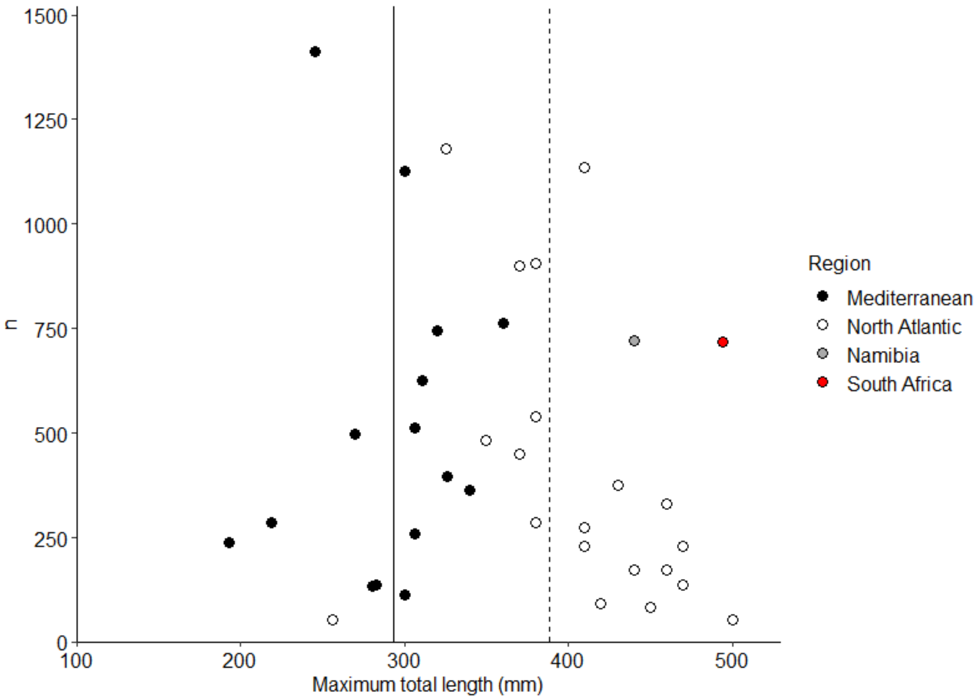


Figure 2.25: Maximum total length (mm) values of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean, North Atlantic and Namibia, plotted against the respective sample sizes. The vertical lines indicate the weighted mean calculated for the Mediterranean (solid line) and the North Atlantic (dashed line).*

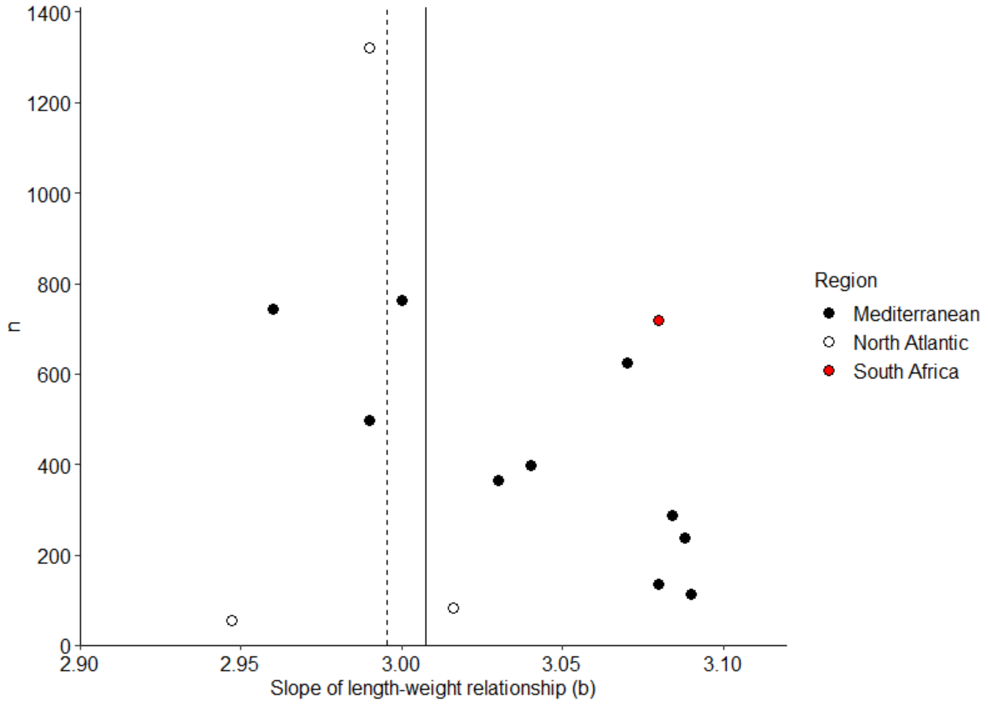


Figure 2.26: The slope (b) of the estimated length-weight relationships of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean and North Atlantic, plotted against the respective sample sizes. The vertical lines indicate the weighted mean calculated for the Mediterranean (solid line) and the North Atlantic (dashed line).*

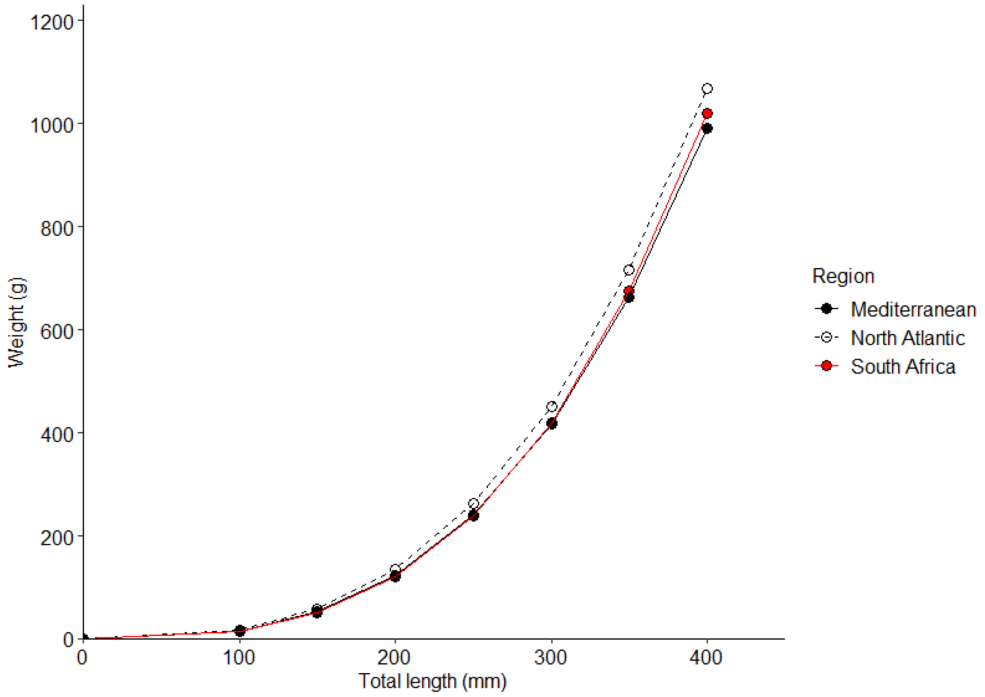


Figure 2.27: The length-weight relationship of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean and the North Atlantic. The relationships presented for the Mediterranean and North Atlantic were calculated using the weighted mean of parameters a (not presented) and b.*

The maximum age of South African *H. dactylopterus,* estimated to be 32 years, aligns with the weighted mean maximum age of fish from the North Atlantic (29 years) and is greater than the maximum age of most fish in the Mediterranean. It is, however, lower than the highest maximum age estimate for the species (43 years, Figure 2.28). The mean maximum age of *H. dactylopterus* for all regions was 25 years.

In the majority of the studies included in this analysis, the age of *H. dactylopterus* was estimated by reading whole otoliths. This method provided lower maximum age estimates compared with sectioned otoliths, regardless of the region in which the fish were from (Figure 2.28). The mean maximum age, weighted by sample size, of *H. dactylopterus* in the Mediterranean using whole and sectioned otoliths was 17 and 25 years respectively and in the North Atlantic, it was 37 and 27 years respectively. Other ageing methods used, including back calculation and length-frequency analysis, resulted in lower maximum age estimates of *H. dactylopterus* compared to whole and sectioned otoliths.

Of the von Bertalanffy growth parameters, the asymptotic length of individuals is greater in the North Atlantic than in the Mediterranean, but the growth rate is greater in the Mediterranean (Figure 2.29). In South Africa, the asymptotic length is lower than all estimates from North Atlantic studies but greater than the average calculated for Mediterranean waters. Asymptotic length is substantially lower in South African fish compared to Namibian fish (L_∞ of 366 mm compared to 763 mm respectively). Mean asymptotic length for all regions was 389 mm. The growth rate of South African individuals is greater than the North Atlantic and Mediterranean averages but aligns with the estimates from several Mediterranean studies. Global mean growth rate was 0.10 year^{-1}.

The variance in asymptotic length and growth rate resulted in differences in the von Bertalanffy growth curves among *H. dactylopterus* individuals from different regions (Figure 2.30).

A comparison of growth performance indices show that average indices were lower for the Mediterranean than the North Atlantic (2.09 and 2.17 respectively), and both estimates were lower than the growth performance index of South African *H. dactylopterus* (2.24; Figure 2.31). The global mean growth performance index for the species was 2.14. In asymptotic length, growth rate and growth performance index, the ageing method employed does not appear to have a clear effect on estimates.

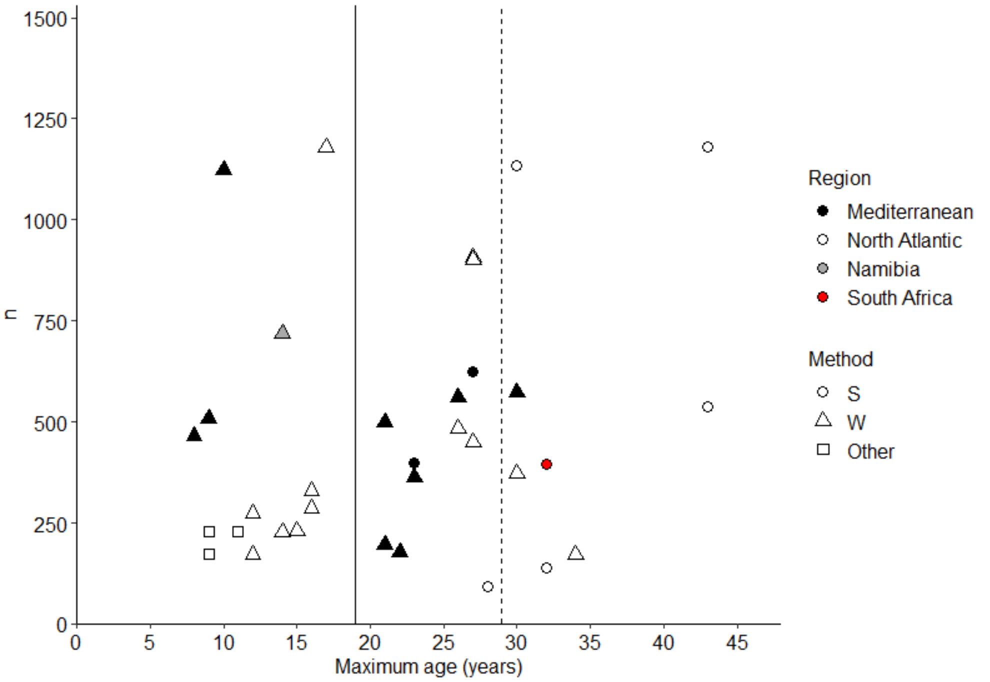


Figure 2.28: Estimates of maximum age (years) of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean, North Atlantic and Namibia, plotted against the respective sample sizes. The vertical lines indicate the weighted mean calculated for the Mediterranean (solid line) and the North Atlantic (dashed line).*

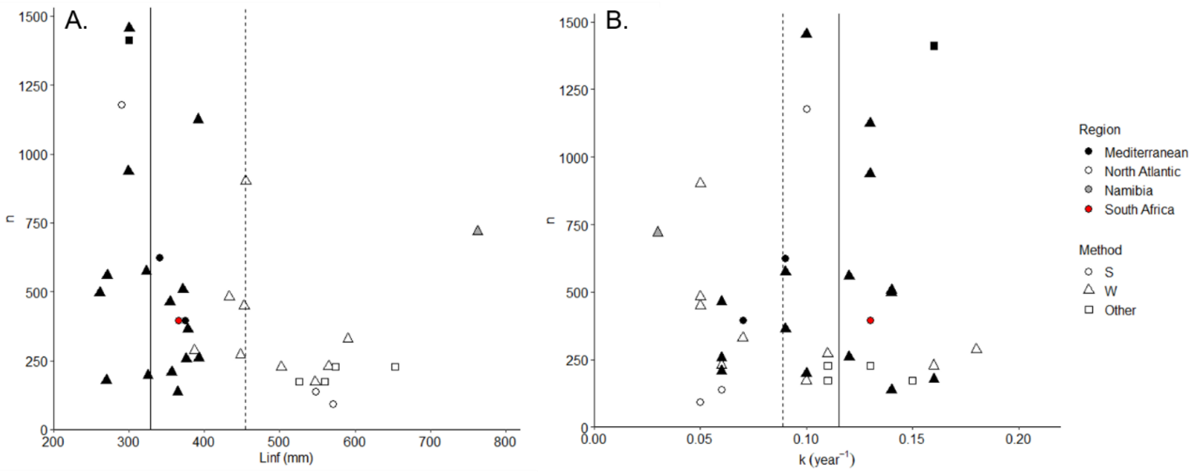


Figure 2.29: The von Bertalanffy growth parameters A). asymptotic length (mm) and B). annual growth rate (year^{-1}) of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean, North Atlantic and Namibia, plotted against the respective sample sizes. The vertical lines indicate the weighted mean calculated for the Mediterranean (solid line) and the North Atlantic (dashed line).*

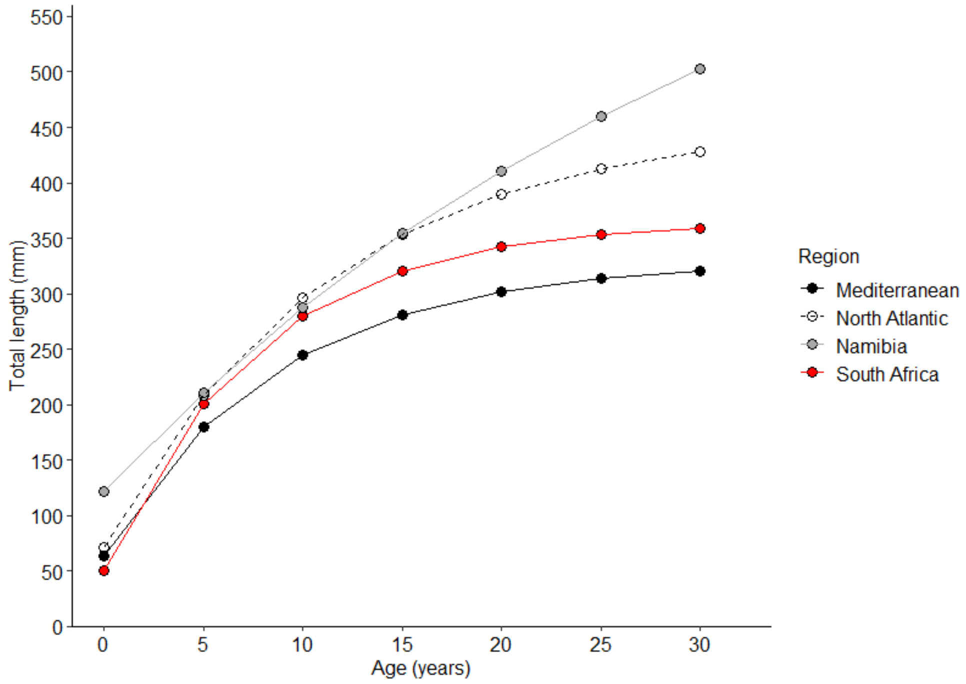


Figure 2.30: The von Bertalanffy growth curve of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean, the North Atlantic and Namibia. The curves presented for the Mediterranean and North Atlantic were calculated using the weighted mean of parameters L_∞, k and t_0 (not presented).*

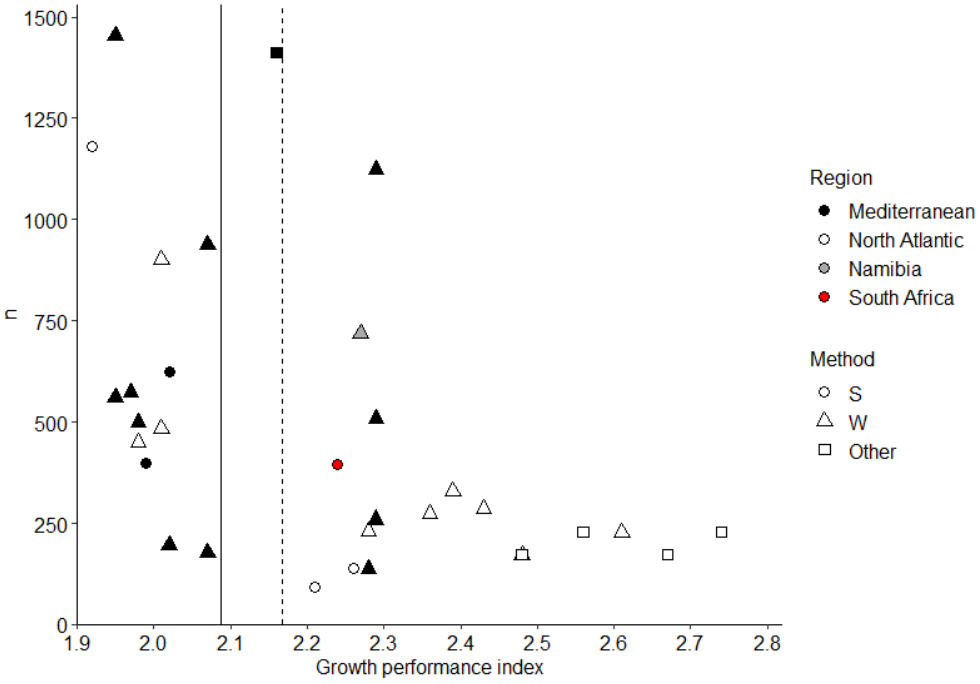


Figure 2.31: Estimates of the growth performance index of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean, North Atlantic and Namibia, plotted against the respective sample sizes. The horizontal lines indicate the weighted mean calculated for the Mediterranean (solid line) and the North Atlantic (dashed line).*

In most studies included in the meta-analysis, there was an equal representation of female and male *H. dactylopterus*, with the sex ratios being close to 1:1 (Figure 2.32). A similar representation of the sexes was found in South African waters. The weighted average for all regions was 1.11 and thus was also close to a 1:1 ratio.

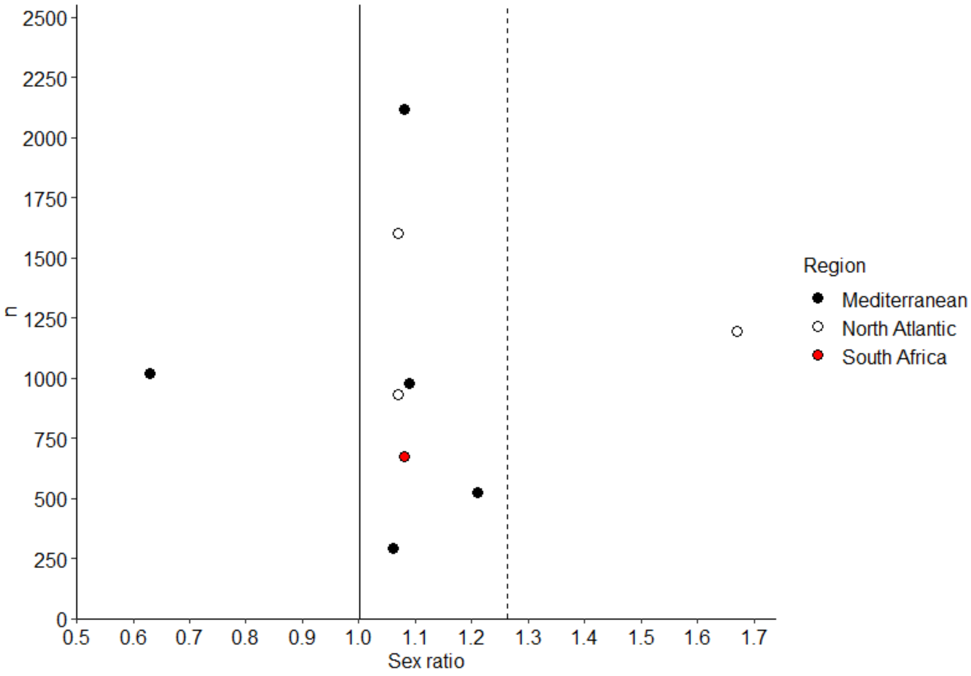


Figure 2.32: Sex ratio (males:females) of Helicolenus dactylopterus *from South Africa (this study) the Mediterranean and North Atlantic, plotted against the respective sample sizes.*

Few studies provided length at 50% maturity estimates for *H. dactylopterus*, and thus regional means were not calculated. Estimates were higher in North Atlantic fish compared to Mediterranean fish, and in all studies, males matured at a larger size than females. The length at 50% maturity in South African *H. dactylopterus* (185 and 188 mm in females and males respectively) was substantially lower than that of individuals in the North Atlantic and was more similar to individuals in the Mediterranean (Figure 2.33). The global mean length at maturity for females was 201 mm and for males was 240 mm.

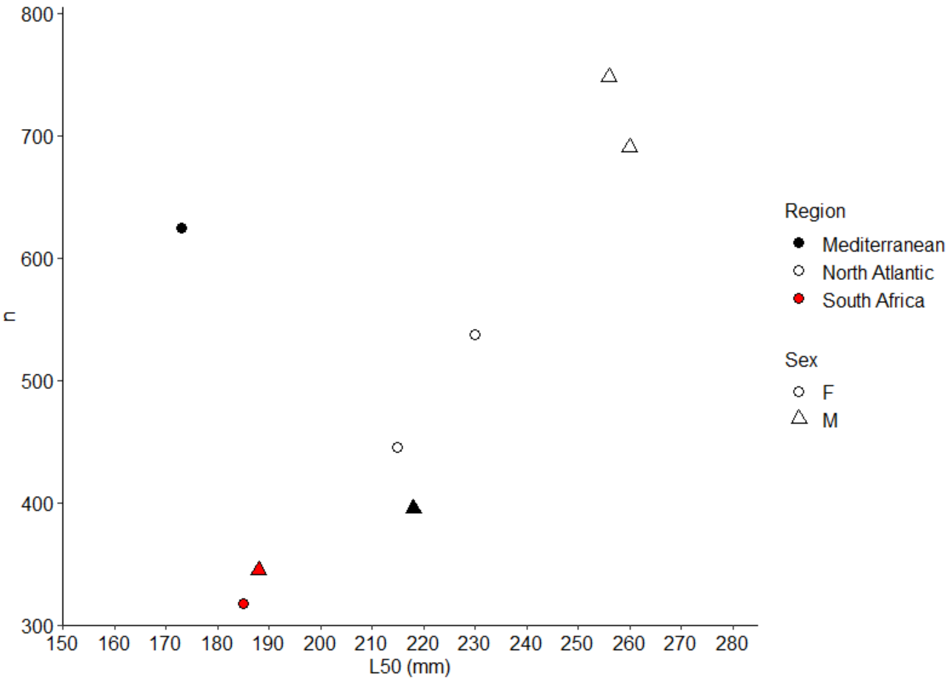


Figure 2.33: Estimates of length at 50% maturity (mm) of Helicolenus dactylopterus *from South Africa (this study), the Mediterranean and North Atlantic, plotted against the respective sample sizes.*

2.5 Discussion

The number of specimens examined in this study, and the spatial and temporal coverage of samples, provided ample information to meet the study objectives for the general description of the biology of *H. dactylopterus* in South Africa. Sample numbers for most analyses were in the mid- to upper range of the sample sizes in other studies done on the species (Table 2.3 and Section 2.4.5). Samples were mainly from within the commercial trawl footprint in the 200 to 700 m depth range. In other areas of the Atlantic, *H. dactylopterus* has been shown to have a wide bathymetric range, occurring up to 1000 m (Neves et al., 2011), with the highest biomass occurring from 200 to 500 m (Massutí et al., 2001; Pirrera et al., 2009; Romeo et al., 2009). Commercial trawl samples covered most of this depth range, but the inclusion of *ad hoc* research samples allowed for the coverage of shallower depths and geographic areas outside of where commercial trawling takes place, such as on the east coast of South Africa.

A concern with sampling only by commercial trawl is a limitation to the size of specimens that can be caught. The use of research samples helped mitigate this, with recruits (22-137 mm) sampled by the smaller net mesh size. On the other end of the size spectrum, the largest fish sampled was close to the maximum length recorded for the species. It, therefore, can be assumed that the full size range of *H. dactylopterus* was sampled. It has been proposed that larger, older *H. dactylopterus* specimens show preference to rocky grounds, generally considered inaccessible to trawlers, and this preference has been postulated as a reason for the smaller fish sampled in some studies (Pirrera et al., 2009; Consoli et al., 2010; Demirhan and Akbulut, 2015). The preclusion of large individuals due to the use of trawl gear and the habitat preference of *H. dactylopterus* did not apply in this study.

Samples were obtained for all months, allowing for sufficient temporal coverage of the reproductive cycle of the species. However, during the months when spawning females were recorded, samples were only available from areas two and three on the western Agulhas Bank. Inferences about the spawning patterns of female *H. dactylopterus* from the south coast of South Africa, therefore, cannot be made. The spatial coverage of samples during the months when ripe males were recorded was better with samples from the west, south and east coasts. There were few instances in which samples were available from multiple areas in the same month, mainly due to limited observer deployments.

2.5.1 Meristics, morphometrics, age and growth

The meristic counts of *H. dactylopterus* did not differ among individuals from different areas and were typical of the morphological description of the species (for example in Smith, 1986; van der Elst, 1993; Heemstra and Heemstra, 2004). This points to a homogenous stock structure of *H. dactylopterus* in South Africa. Dorsal and anal fin spine and ray counts were the same as those recorded in fish in the North Atlantic and the Mediterranean by Rodríguez-Mendoza (2013), suggesting little variation in these external meristic traits throughout the distribution of the species. South African fish, however, generally had a greater number of gill rakers, particularly in the lower segment, than North Atlantic or Mediterranean fish. The number of gill rakers influences feeding efficiency which affects the fitness of an individual (Swain et al., 2005). Differences in the number of gill rakers are thus usually driven largely by genetic factors (Swain et al., 2005). The differences observed in the number of gill rakers among fish from South Africa compared to those in the North Atlantic and the Mediterranean suggests some extent of population differentiation.

South African *H. dactylopterus* individuals attain a large size, relative to individuals from elsewhere, particularly the Mediterranean (Figure 2.25). The maximum length recorded in this study (494 mm) was close to the maximum (500 mm) recorded for the species (Pereira et al.,

2012) and was higher than those reported by van der Elst (1993) and Heemstra and Heemstra (2004).

Larger fish occurred in deep water. The trend of increasing length with depth is common in demersal species and applies to *H. dactylopterus* at Rockall Trough west of Ireland and Scotland (Kelly et al., 1999), in the Mediterranean (Massutí et al., 2001; Pirrera et al., 2009) and Namibia (Gordoa and Duarte, 1992). This depth pattern is attributed to individuals migrating down the continental slope as they get older (Heincke, 1913). Several physiological and ecological mechanisms have been proposed to explain body size patterns with depth including density-dependent food availability, predator avoidance and different temperature requirements for the optimal growth of individuals (Audzijonyte and Pecl, 2018). Fishing may also have an effect (Frank et al., 2018), although this is not the case for all stocks (Baudron et al., 2019). In *H. dactylopterus,* as in many other fish species, temperature is likely to play a major role in the patterns of size with depth (Macpherson and Duarte, 1991). Temperature affects metabolism and growth rates. The warmer temperatures of shallow water are conducive to the faster growth required by young individuals.

The majority of South African *H. dactylopterus* individuals (68%) were larger than 250 mm, which is contrary to the findings in the Mediterranean, where trawl samples were dominated by recruits and juveniles less than 200 mm (Massutí et al., 2000; Pirrera et al., 2009; Consoli et al., 2010). The difference in depths among studies may have an influence on this finding, but it also suggests, along with differences in the maximum size attained by individuals, that there are differences in the overall size structure of *H. dactylopterus* among regions. Reasons for these regional differences are explored in Section 2.5.4.

Growth was hyper-allometric, aligning with most other studies on the species and corresponding to morphological descriptions in which *H. dactylopterus* is described as being robust (Heemstra and Heemstra, 2004) and moderately compressed (van der Elst, 1993). *Helicolenus dactylopterus* is a sedentary, ambush predator (Uiblein et al., 2003) and its hyper-allometric growth likely reflects this behaviour in which a deep, muscular body is beneficial for propulsive movements to attack prey over short distances (Webb, 1984; Rodriguez-Mendoza et al., 2011).

No dimorphism in size or growth between female and male *H. dactylopterus* was found. There is currently no clarity on whether sexual dimorphism in the species is shown elsewhere. Some studies have found males to grow larger and faster than females (for example Kelly et al., 1999;

Massutí et al., 2000; Abecasis et al., 2006; Sami et al., 2016) but other studies have found no difference in size and growth between the sexes (Esteves et al., 1997; Pereira et al., 2012; Sequeira et al., 2009). Sequeira et al. (2009) suggested that the inconsistencies in the occurrence of sexual dimorphism among studies were because of the different length ranges and distributions sampled. This is supported by White et al. (1998) who found a significant difference in the mean length of *H. dactylopterus* between sexes for selected age classes only. The large length range sampled in this study along with the large number of fish greater than 250 mm may explain the lack of sexual dimorphism seen here, compared to previous studies. Sample size does not appear to play a role in the inconsistencies in sexual dimorphism reported, with most studies having sample sizes greater than 700 fish. The implications of the lack of sexual dimorphism in *H. dactylopterus* are discussed further in Section 2.5.2.

Otolith margins varied seasonally with a high proportion of fish showing opaque ring formation in spring and summer. This was a preliminary method of validation, but it signals the annual formation of one opaque and one hyaline ring and thus validates the use of otoliths as an ageing method for *H. dactylopterus.* Similar corroboration and patterns in otolith margins have been found elsewhere in the species (Abecasis et al., 2006; Consoli et al., 2010; Isidro, 1987). The pattern of otolith increment formation was similar to that described by other studies on this species and genus (Massutí et al., 2000; Paul and Horn, 2009; Sequeira et al., 2009). The change in otolith formation, when rings became smaller and were more closely spaced after approximately six years, is attributed to the slowing of growth after the age at first maturation (Massutí et al., 2000; Sequeira et al., 2009).

Overall, the agreement among readers was low and the CV value of 16.94% was relatively high, exceeding the precision estimate of 7.6% established by Campana (2001). There were also a wide range of ages estimated for individuals of each length class, especially for larger fish (Table 2.10 and Table 2.11). Some caution when interpreting the age estimates of *H. dactylopterus* in South Africa should thus be applied. Nevertheless, the maximum observed age in South African fish was 32 years which was attained by a female. This estimate aligns with findings in the North Atlantic and is higher than the maximum age estimated in most studies on the species in the Mediterranean, irrespective of sample size (Figure 2.28). A maximum age greater than 30 years is not unique for the genus, where *H. percoides* individuals of 35 and 59 years, determined using sectioned otoliths, were reported in New Zealand (Paul and Horn, 2009). Like *Sebastes,* species of the genus *Helicolenus* are long-lived.

The asymptotic length calculated here was less than the observed maximum length, reflecting individual variation in growth. The growth rate of *H. dactylopterus* in South Africa (0.13 year^{-1}) was higher than the weighted averages calculated for the North Atlantic (0.09 year^{-1}) and Mediterranean (0.12 year^{-1}). In other Sebastinids, the growth rates of most *Sebastes* species range from <0.1 to 0.3 year^{-1} (Haldorson and Love, 1991). In longer-lived species, such as *S. ruberrimus* and *S. borealis,* the growth rate is as low as 0.05 year^{-1} (Anderson et al. 2019). The growth rate of *H. dactylopterus* is thus towards the middle of the spectrum for the subfamily.

The age and length at maturity estimates for *H. dactylopterus* in South Africa were lower than that reported for the species by White et al. (1998) and Kelly et al. (1999) and were lower relative to other species in the Sebastinae. White et al. (1998) found that females mature between 215 and 289 mm (10 to 15 years) and males between 256 and 275 mm (14 to 15 years). Kelly et al. (1999) reported females to mature at 230 mm (13 years) and males to mature at 260 mm (15 to 16 years). Love et al. (2002) reported on the relationship between maximum length and length at maturity of 47 *Sebastes* species and found most to mature at approximately 50% of their maximum length. Early maturation, when compared to the maximum size and age attained, may, therefore, be unusual for the species and the subfamily. However, while unusual, it is not unique as recent length at maturity estimates in *H. dactylopterus* from Portuguese and Azorean waters align more closely with what was found in South African individuals. Length at maturity in fish from Portugal was estimated to range from 163.7 to 164.1 mm in females and 172.8 to173.1 mm in males and in fish from the Azores it was estimated to range from 130.6 to191.7 mm in females and from 146.1 to 181.5 mm in males (Sequeira et al., 2012). Estimates from that study were not included in the meta-analysis due to the sample size of each sex not being defined.

2.5.2 Reproduction

Overall and monthly, the ratio of female to male *H. dactylopterus* did not differ from equity. A balanced sex ratio was found in most other studies on the species in the North Atlantic and Mediterranean. An unbalanced sex ratio in a population can be related to sex differences in size, growth or mortality and/or differences in the energetic cost of reproduction (Charnov, 1993; Marshall et al., 1998). The balanced sex ratio found here, therefore, aligns with the lack of sexual dimorphism observed.

In fish such as *H. dactylopterus* that have internal fertilisation, dimorphism between the sexes is expected due to the energetic cost of parental care imposed on females and competition between males during courtship and mating (Muñoz et al., 1999). The lack of sexual dimorphism in *H. dactylopterus* suggests that parental care does not impose an undue energetic cost on females. This is likely because females are zygoparous and release embryos in the early stages of development (White et al., 1998; Muñoz et al., 2002; Sequeira et al., 2003) and so parental care in the species is limited. The GSI values of females and males were similar during months when gametes were not released. However, during spawning, the GSI values of females were more than double those of males, indicating that females may expend more energy on egg production than males spend on sperm production. This was reflected in the condition of females during spawning which was mostly lower than that of males. Relative condition, however, did not differ significantly among maturity phases in either females or males, suggesting that muscle reserves do not play a substantial role in gamete development (Sequeira et al., 2012).

The temporal variation in the frequency of macroscopic gonad phases was reflected in the average monthly GSIs. GSI also differed significantly among all maturity phases in both sexes and was highest during active spawning when gametes were released and gonads were heaviest. This suggests agreement between the macroscopic assessment of gonads and the use of GSI to measure gonadal development of *H. dactylopterus*. Histology is the most accurate way to determine gonad phases in fish (Lowerre-Barbieri et al., 2011a), but histological analysis of all gonads could not be completed in this study due to cost constraints. Although this is a limitation that can be improved on in future studies, the agreement between macroscopic and microscopic gonad phases achieved in this study was satisfactory. Agreement was better in ovaries than in testes, likely because of the morphological similarities of the testes across different phases.

Results from the gonad classification and the GSI suggest that the reproductive cycle of female *H. dactylopterus* in South Africa, on the western Agulhas Bank, involves an extended spawning season from June to November, when actively spawning females were found. This was corroborated by the presence of spawning capable females from May to November. These results align with the findings on the species in the northern hemisphere where female spawning occurs over winter and spring. South African females, however, may spawn for one month longer than fish in the North Atlantic (Kelly et al., 1999; Sequeira et al., 2012; White et al., 1998) and three months longer than fish in the Mediterranean (Muñoz and Casadevall, 2002; Deval et al., 2018). The development of ovaries in South African fish was also less synchronised than the development reported in studies in the northern hemisphere. Developing and regenerating females were present throughout the year in South African waters except for during active spawning. This points to a longer and less intense spawning season in South Africa. Reasons for these regional differences in spawning are explored in Section 2.5.4.

It must be noted that no actively spawning females were sampled in July or August. The samples from these months were from different areas to those sampled in June and September and sample sizes were smaller, which may explain the lack of spawning females. The possibility of slight differences in the reproductive timing of female *H. dactylopterus* on the south coast of South Africa compared to those on the west coast, thus, cannot be disregarded. Further research on the annual reproductive cycle of the species in South Africa should focus on obtaining sufficient data to consider geographic areas separately.

South African *H. dactylopterus* males release sperm for a much longer period than females spawn. Actively spawning males were from the west, south and east coasts and were sampled in January, February, April, May, June, September, and November. Spawning capable males were found throughout the year except for July. Insemination by males is thus considered to occur from September to June. Likewise, elsewhere the insemination period of males is longer than the spawning period of females (Mendonça et al., 2006; Muñoz and Casadevall, 2002; Sequeira et al., 2012).

In most previous studies on the species, there has been little to no overlap recorded in the release of gametes by males and females, suggesting a delay between insemination and spawning. In this study, an overlap in the gamete release by both sexes was seen and male sperm production peaked towards the end and after the female spawning season. Nevertheless, here, actively spawning males were sampled outside of the female spawning season and so some delay between insemination and spawning can be assumed.

The mismatch of female and male gamete release suggests that sperm is stored by females. Sperm storage was confirmed by the presence of spermatozoa in all, but two, ovaries analysed, and in some cases, spermatozoa were highly abundant. Spermatozoa occurred either floating in the ovarian cavity or in rounded storage structures at the base of the lamellae. Muñoz et al. (2002) hypothesised that these storage structures were specialised to allow for the nourishment of the sperm cells, enabling storage in the ovaries for up to ten months. The storage of sperm by females implies the guaranteed fertilisation of oocytes once mature.

The occurrence of sperm cells floating in the ovarian cavity along with those in storage suggests that females may copulate repeatedly and may do so with multiple males. Genetic studies have confirmed the occurrence of multiple paternity in *Sebastes atrovirens* (Sogard et al., 2008) and *S. melanops* (Karageorge and Wilson, 2017), and unpublished accounts exist for several other *Sebastes* species. Multiple paternity and female promiscuity coupled with the storage of sperm by females suggests the possibility of post-copulatory sperm competition (Sogard et al., 2008). It points to a polygamous mating system with polyandrous mating in which sexual selection before copulation may be reduced (Karageorge and Wilson, 2017). This may contribute to the lack of sexual dimorphism observed in *H. dactylopterus*.

2.5.3 Diet

The dietary results generally conform with patterns observed in the North Atlantic and the Mediterranean and suggest *H. dactylopterus* in South Africa is a selective, opportunistic ambush predator, primarily feeding on prey of benthic and benthopelagic origin. This type of predation is reflected in the mouth morphology of *H. dactylopterus* in which individuals have large terminal mouths with villiform teeth and thus are adapted to grasp and engulf prey whole (Mihalitsis and Bellwood, 2019).

Pelagic and mesopelagic organisms were also present in the diet of South African specimens suggesting some predation in the water column (Capezzuto et al., 2020). Foraging by *H. dactylopterus* is, however, likely limited to lower depths of the water column because the species does not have a swim bladder which makes swimming in the pelagic zone energetically expensive. Furthermore, there is no evidence of *H. dactylopterus* occurring at mid-water depths from mid-water trawl data (Reed et al., 2017). Other explanations for the presence of typical pelagic species in the diet of *H. dactylopterus* include individuals feeding on dead organisms that have sunk to the bottom (Neves et al., 2012) or individuals feeding on pelagic organisms that undertake diel migration (Mauchline and Gordon, 1991). The presence of a rajiform in one of the stomachs, in which only a portion of a fin was present, suggests that *H. dactylopterus* may scavenge dead organisms. In a study on the feeding periodicity of *H. dactylopterus* in Namibia, Macpherson (1985) found that individuals fed mainly during the day. Considering that a large proportion of organisms undertake diel migrations to depth during the daytime, for example, some *Pyrosoma* species (Henschke et al., 2019), the predation by *H. dactylopterus* on these organisms during this time could be expected. The occurrence of pelagic and mesopelagic organisms in the diet indicates that *H. dactylopterus* plays a role in linking energy transfer between pelagic and benthic ecosystems (Meyer and Smale, 1991).

The large number of prey taxa recorded in South African *H. dactylopterus* stomachs was similar to the number of taxa found individuals in Portugal and the Mediterranean (Consoli et al., 2010; Neves et al., 2012; Capezzuto et al., 2020). The slope of the linear regression through the last five points of the prey accumulation curve was less than 0.05 indicating that sampling was acceptable for the diet description of the species (Bizzarro et al., 2009; Brown et al., 2012).

Crustaceans comprised 31 out of the 66 identified taxa and, as in all other studies on the species, were the dominant prey of *H. dactylopterus*. Decapods, especially Caridea shrimp (mainly *Acanthephyra pelagica*), and euphausiids were the most represented crustacean species. Euphausiids were far more prominent in the diet of South African *H. dactylopterus* than what has been seen elsewhere, a conclusion supported by Meyer and Smale (1991). Euphausiids comprise a large component of the zooplankton community in South Africa, especially on the west coast where their biomass is driven by the upwelling-related high primary productivity (Gibbons, 1995). Dominant species in South Africa include *Euphausia lucens* and *Nyctiphanes capensis* which occur in shelf waters on the west and south coasts respectively and *E. recurva* and *Nematoscelis megalops* which occur in deeper waters on the shelf edge and slope (Pillar et al., 1992; Gibbons, 1995). All four of these species are known to undertake extensive vertical migration. *Euphausia recurva* migrate into waters deeper than 600 m (Werner and Buchholz, 2013). All four species are thus potential prey to *H. dactylopterus.*

In general, the dominant prey of *H. dactylopterus* were of moderate to high nutritional value. The mean energy content of Caridea shrimp, euphausiids, teleosts, pyrosomes and cephalopods ranges from 17.9 to 25.2 kJ.g^{-1} dry weight (Blaber and Bulman, 1987). Prey of lower energy content were also important though. Ophiuroids have previously been found to be preyed upon by *H. dactylopterus* in low quantities, however, in this study, the brittle star *Ophiura trimeni* was consumed in large amounts. Ophiuroids are largely calcareous with a mean energy content of 4.17 kJ.g-1 dry weight (Wacasey and Atkinson, 1987), but are extremely abundant in South African shelf and shelf edge habitats (Atkinson and Sink, 2018).

Regardless of the large number of different prey taxa found in the stomachs of South African *H. dactylopterus,* the diet breadth of the species, according to Levin's index, was low, indicating a specialist predator in which the diet is dominated by only a few taxa. Values of Levin's index are considered to be high when above 0.6, moderate when from 0.6 to 0.4 and low when below 0.4 (Sá-Oliveira et al., 2014). The graphical representation of the diet based on the Amundsen et al. (1996) method provides insight into the diet breadth of the species.

Individual fish consume large numbers of specific prey items, but there is little overlap in the consumption of these prey among individuals. The diet of South African *H. dactylopterus* at the individual level is therefore specialised, but at the population level, the species has a broader dietary niche width. The patterns seen in dietary niche width reflects the sedentary nature of the species and its opportunistic feeding behaviour in which individuals feed extensively on organisms within their proximity and active hunting for specific prey items is limited.

The trophic level of South African *H. dactylopterus,* for all size classes pooled, was 3.64. A trophic level of below 3.7 indicates that individuals are carnivores that feed on a wide variety of prey but show a preference for animals such as brachyurans, amphipods, euphausiids, gastropods, ophiurids and polychaetes (Stergiou and Karpouzi, 2002). The trophic level of South African fish reflects the dominance of smaller herbivorous crustaceans in the diet, particularly euphausiids. A similar trophic level was reported for *H. dactylopterus* in muddy habitats in the Mediterranean, but in that study a higher trophic level, greater than 3.7, was reported for individuals occurring in cold-water coral habitats (Capezzuto et al., 2020).

An ontogenetic dietary shift was found in South African *H. dactylopterus.* Clear differences in diet were seen among individuals that were less than 200 mm, those that were greater than 250 mm and those that were greater than 400 mm, with fish ranging from 200 to 250 mm in total length feeding on a more transitionary diet. This shift was reflected in the different trophic levels calculated for each size class, with fish below 350 mm being secondary consumers and those 350 mm and above being tertiary consumers with a preference for large decapods, fish and cephalopods. Larger *H. dactylopterus* individuals were also found to feed on a greater variety of prey items in comparison to smaller conspecifics. Similar ontogenetic patterns in the diet have been recorded in most other studies on the species and genus (Blaber and Bulman, 1987; Consoli et al., 2010; Neves et al., 2012; Capezzuto et al., 2020).

Ontogenetic changes in the diet likely reflect the increased energy requirements of larger individuals. Neves et al. (2012) reported a dietary shift in *H. dactylopterus* at 200 mm total length and postulated that it was related to the sexual maturation of fish. This explanation may apply to the first dietary shift observed in this study, given the length at first maturity for both sexes found here (185 and 188 mm in females and males respectively). Additionally, ontogenetic changes have been found to occur in the size and the shape of the mouth of *H. dactylopterus,* with the upper and lower jaw becoming more oblique relative to the central axis of the body with an increase in body size (Rodriguez-Mendoza et al., 2011), which likely influences the change in the diet of the species with growth. The change in the size and the position of the mouth allows for the capture of larger and an increased variety of prey.

2.5.4 Regional differences in life history traits

The varying patterns in size, age, growth and reproductive cycles among *H. dactylopterus* specimens from different regions can be attributed to several factors, and most likely are a result of a combination of these. Factors include environmental differences among regions, differences in latitude and differences in fishing pressure. Differences in sample size, composition, sampling and analysis methods and sampling errors in each study also play a role.

A greater sample size increases the precision and reliability of the findings of a study (Møller and Myles, 2016). The weighted means calculated in the meta-analysis highlighted differences in the life history parameters among *H. dactylopterus* individuals from different regions while accounting for the effect of sample size. South African fish were of a similar size and age but grew faster than North Atlantic fish, and were larger, older and grew marginally faster than Mediterranean conspecifics. The meta-analysis, however, did not account for heterogeneity in study design, which may contribute to the regional differences observed.

The size composition of a sample can reflect actual differences among individuals from different regions, but the differences can also be an artefact of the sampling method used. For example, the exclusion of small fish from a sample due to the use of trawl gear can influence the estimation of growth parameters, resulting in imprecision. In all studies in which the asymptotic length of *H. dactylopterus* was large, above 500 mm, fish below 120 mm were not sampled (for example Morales-Nin, 1989; Esteves et al., 1997; Abecasis et al., 2006). The size composition of samples may thus contribute to the differences observed in the von Bertalanffy growth parameters among fish from different regions. In the case of the differences observed in the von Bertalanffy growth parameters between South African and Namibian fish, the sample size composition is considered to play a large role. In the Namibian study by Morales-Nin (1989), fish below 130 mm total length were not sampled.

The use of whole as opposed to sliced otoliths has commonly been cited as a reason for the differences in age and growth patterns seen in *H. dactylopterus* (Abecasis et al., 2006; Sequeira et al., 2009; Consoli et al., 2010). Whole otoliths can result in the underestimation of age in older individuals above seven years (Beamish and McFarlane, 1983; Abecasis et al., 2006). However, Sequeira et al. (2013) found no difference between whole and sliced otolith age estimates. The meta-analysis showed that studies in which whole otoliths were used had lower maximum age estimates compared with those in which sectioned otoliths were used, regardless of the region the study was conducted. The ageing method, however, had less of an effect on the von Bertalanffy growth parameters. These results point to the importance of standardising the ageing method used, in which sectioned otoliths are advocated as a more conservative approach, but suggest that the different ageing methods are not solely responsible for the differences seen in age and growth of *H. dactylopterus* individuals among regions. Aside from differences in study design, extrinsic factors likely also play a large role in influencing the regional patterns in life history traits.

Environmental conditions can result in direct physiological changes at the individual level (Boehlert and Kappenman, 1980). For a species that occurs at great depth, temperature and dissolved oxygen play an important role in an individual's allocation of energy to growth and reproduction, and thus can affect key life history characteristics such as size and growth rate. It has been hypothesised that temperature is a primary factor that influences the growth patterns of *Sebastes maliger* in the Salish Sea, with much smaller individuals occurring in inland areas where water temperature is highest (West et al., 2014). Temperature changes with depth but also typically changes with latitude and can cause latitudinal variation in the life history traits of a species that shows a wide distribution (Bergmann, 1847). In South Africa (Chapters 3 and 4) and the Mediterranean (Massutí et al., 2001; Pirrera et al., 2009; Romeo et al., 2009), *H. dactylopterus* biomass peaks at depths of 200 to 500 m. The temperature in this depth range in South Africa averages approximately 7°C (Dingle and Nelson, 1993), whereas in the Mediterranean it averages approximately 13°C (Massutí et al., 2004). A lower temperature has previously been recognised as a reason for the increased size and slower growth of *H. dactylopterus* in the North Atlantic relative to individuals in the Mediterranean (Massutí et al., 2004; Rodríguez-Mendoza et al., 2019). Similarly, the lower temperature in South Africa may influence the greater size attained by South African fish compared to those in the Mediterranean. The lower temperatures do not, however, appear to influence the growth rate of South African fish, where the growth rate of fish in local waters is faster than those in the North Atlantic and Mediterranean.

Food availability is another factor that can have a direct effect on life history characteristics (Boehlert and Kappenman, 1980). South Africa's west and south coasts form part of the Benguela Current Large Marine Ecosystem (BCLME), one of the four major eastern boundary upwelling systems in the world (Shannon and O'Toole, 2003). As a result of this upwelling, the BCLME is highly productive, supporting a large and diverse marine trophic web (van der Lingen et al., 2006). The prominence of euphausiids in the diet of South African *H. dactylopterus* compared to those in the North Atlantic and the Mediterranean is driven by this upwelling-driven high productivity. The increased availability of food in South African waters, in contrast to the mesotrophic and oligotrophic waters in the North Atlantic and Mediterranean (Azov, 1991; Morel et al., 2010), likely influences the growth rate of *H. dactylopterus* and is at least partly responsible for the increased growth rate of fish in local waters.

The availability of food can interact with density-dependent mechanisms and have an indirect effect on some of the life history characteristics of a species. Fishing pressure reduces the density of individuals which can increase food availability and individual growth rates in some cases (Boehlert and Kappenman, 1980; Zimmermann et al., 2018). Fishing pressure in the Mediterranean is high (Smith and Garcia, 2014; Vasilakopoulos et al., 2014). Despite the oligotrophic conditions, the increased availability of food due to fishing pressure may, along with temperature, contribute to the growth rate of *H. dactylopterus* in the Mediterranean which was only marginally lower than the growth rate of fish in South Africa.

Fishing pressure has the added effect of truncating the size and age structure of a population, in which larger, older individuals are selectively removed (Bianchi et al., 2000). In the case of *H. dactylopterus,* fishing pressure may be at least partly responsible for the smaller maximum total length attained by individuals in the Mediterranean compared to those in the North (Sequeira et al., 2009) and South Atlantic. The harvesting of large, old individuals and their subsequent removal from the spawning stock may eventually result in a more permanent evolutionary shift towards lower sizes and earlier maturation in the exploited population (Kuparinen and Merilä, 2007).

Spawning periodicity is related to food availability and the surrounding environmental variables that may influence the condition of females and larval survival (Moser and Boehlert, 1991; Winemiller and Rose, 1992). As a result, the spawning period of a species can vary spatially with latitude and with predominant oceanographic conditions which drive productivity (Lowerre-Barbieri et al., 2011b). South Africa occurs at a lower latitude than many of the North Atlantic and Mediterranean locations included in the meta-analysis. The period during which conditions are optimal for growth is thus longer and the winter (non-growth season) is shorter, so spawning can extend over a longer time (Conover, 1992). Related to this, the higher productivity of South African waters relative to those in the Mediterranean and

North Atlantic (Morel et al., 2010) extends the spawning period of fish as the survival of larvae are less dependent on the period when zooplankton abundance is at its greatest.

Extrinsic factors can result in changes in the life history traits of a species at the individual level or in the short-term at the population level, but they can also result in more permanent population differences. These permanent differences were alluded to above when discussing fishery-induced size truncation. Permanent population differences require an extent of reproductive isolation and can involve genetic differentiation (Swain et al., 2005). Given the broad distribution of *H. dactylopterus* in the Atlantic and the sedentary nature of the species (Uiblein et al., 2003), fish in the Mediterranean, North Atlantic, South Atlantic and South Africa may comprise different populations. This is supported by the differences in the number of gill rakers in fish from South Africa compared to those from the North Atlantic and the Mediterranean studied by Rodríguez-Mendoza (2013). In Portuguese and Azorean waters, the existence of localised populations of *H. dactylopterus* is probable (for example Aboim et al., 2005; Neves et al., 2011; Sequeira et al., 2012; Rodríguez-Mendoza et al., 2019; Santos et al., 2020). The presence of localised populations of *H. dactylopterus* provides some reasoning for the variation seen in some life history estimates among different regions and among different studies in the same region. Based on the localised population differentiation that has been postulated in the species elsewhere, the occurrence of *H. dactylopterus* subpopulations in South Africa cannot be disregarded. The analysis of the genetic variability among fish from different areas in South Africa is required to assess the occurrence of subpopulations, however, it is considered unlikely as no differences in meristics were found among fish in this study.

2.5.5 Implications of life history traits on vulnerability to exploitation

Globally, many Sebastinid species have suffered depletion by fishing. Since 1999, seven *Sebastes* species occurring on the west coast of the United States have been declared as being overfished by NOAA (Ralston, 1998; Enticknap and Sheard, 2005; Yoklavich et al., 2007). The life history traits which generally characterise species in the Sebastinae have been recognised as major contributing factors to these declines. In the case of *H. dactylopterus,* the longevity and slow growth shown make the species vulnerable to exploitation in South Africa. The management of the capture of *H. dactylopterus* as bycatch in the demersal trawl fishery is therefore important. However, in contrast to many overfished *Sebastes* species, *H. dactylopterus* matures young. Early maturation results in a larger proportion of the fished population being reproductively active and thus contributes to increased spawning output. This, coupled with the ability of females to store sperm, which increases the probability of fertilisation and fecundity, may provide resilience to fishing pressure.

2.6 Conclusion

The data generated here provide important information on the life history and diet of *H. dactylopterus* in South Africa, completing the global picture for this broadly distributed species. Drawing from more than 700 specimens, this study provided a first comprehensive description of the biology of a prominent bycatch species caught in South Africa's most valuable fishery (Department of Agriculture Forestry and Fisheries, 2016). Like other species in the subfamily and as for *H. dactylopterus* from other regions, individuals in South Africa are slow-growing and long-lived. These traits may make *H. dactylopterus* vulnerable to local fishing pressure. However, contrary to findings at Rockall Trough and in the North-West Atlantic, the early maturation of South African *H. dactylopterus*, relative to the maximum size and age attained, may counteract this vulnerability to some extent. Like many other Sebastinids, internal fertilisation is practised, and females store sperm. This trait may further contribute to resilience against exploitation. Females have an extended spawning season from June to September that may be one month longer than North Atlantic conspecifics and three months longer than Mediterranean conspecifics. Males release sperm for a longer period than females spawn, from September to June. Dietary results aligned with previous research and suggested that *H. dactylopterus* is a selective benthic predator, feeding mainly on crustaceans, although larger prey such as teleosts and pyrosomes become more important as individuals get larger.

These results provide biological insights that contribute to the understanding of the role that *H. dactylopterus* plays in the ecosystem and will support improved assessment of its vulnerability to fishing pressure in South African waters. The life history parameters estimated here can be used in the future stock assessment of *H. dactylopterus* and in the implementation of management initiatives for this species. This will ultimately improve the management and sustainability of the South African demersal trawl fishery.

CHAPTER 3

THE HABITAT PREFERENCE OF *HELICOLENUS DACTYLOPTERUS* IN SOUTH AFRICA

3.1 Abstract

The factors influencing the distribution and abundance of *Helicolenus dactylopterus* were investigated using data obtained using two sampling methodologies at two spatial resolutions to describe the habitat preferences of this species in South Africa. Data from 915 research trawls and 34 video transects conducted on the west and south coasts were used to examine the effect of longitude, depth and benthic habitat on *H. dactylopterus* abundance at broad (trawls one to two kilometres in length) and fine (video segments 25 m in length) resolutions. The lengths and behaviour of fish recorded in the video footage were measured and categorised to analyse ontogenetic differences in habitat preference and to make inferences about habitat utilisation. In broad resolution trawl surveys, longitude and depth explained patterns of *H. dactylopterus* abundance. *Helicolenus dactylopterus* is primarily an Atlantic species decreasing in abundance with extension into the Indian Ocean from an average of 146 fish.km^{-2} at 15°E to 73 fish.km^{-2} at 27°E. Depths from 100 to 600 m were preferred, and abundance peaked between 200 and 300 m at 125 fish.km^{-2}. In fine resolution video surveys, depth was an important correlate of abundance, but the data highlighted that benthic habitat also had a significant influence. An ontogenetic difference in benthic habitat preference was shown. Individuals larger than 200 mm were abundant in complex benthic habitats characterised by rocky and mixed substrata most inhabited by bryozoans, octocorals, hydroids and hydrocorals. These habitats are typical of the deep-water rocky ecosystems on the South African outer shelf and shelf edge. The occurrence of mainly adult specimens in these rocky reef habitats suggests two alternatives that are not mutually exclusive. Rocky habitats may be actively selected by individuals for spawning and shelter, and/or the apparent habitat selection may be due to higher fishing pressure in less complex, trawlable areas. The role of rocky reef communities as refuge from fishing pressure and their use as a potential spawning area highlights the importance of these habitats in the renewal of the South African *H. dactylopterus* population in neighbouring trawl grounds. The findings from this study provide insight into the habitat requirements of *H. dactylopterus*, which can contribute to the ecosystem-level management of the South African demersal trawl fishery, in which the species is an important component of the bycatch.

3.2 Introduction

The distribution of fish is driven by a combination of biological, ecological and environmental factors that act over multiple spatial scales (Quattrini et al., 2012). Understanding the habitat requirements of a species can allow for the prediction of their distribution. Fish-habitat associations can also highlight the importance of some habitat components in maintaining a functioning ecosystem. Some areas form essential fish habitat providing refuge and space for feeding and breeding (Costello et al., 2005; Ross and Quattrini, 2007; D'Onghia et al., 2010; Pham et al., 2015; Kritzer et al., 2016). Improved knowledge of fish-habitat associations is central to an Ecosystems Approach to Fisheries management and is required to establish effective management strategies for sustainable resource use and conservation (Rice, 2005; Pham et al., 2015; Milligan et al., 2016).

Depth and benthic habitat type influence the distribution and abundance of deep-sea fish, including those in the subfamily Sebastinae (Costello et al., 2005; Quattrini et al., 2012). *Helicolenus dactylopterus,* a sit-and-wait benthic predator, occurs in highest abundances between 200 and 500 m depth on continental shelf and shelf edge areas (Massutí et al., 2001; Uiblein et al., 2003; Atkinson et al., 2011). Benthic habitat type characterised mainly by substrata and topographic complexity also influences the distribution of *H. dactylopterus* in the North Atlantic and the Mediterranean. However, *H. dactylopterus* individuals have been found to utilise a wide range of benthic habitats and their degree of habitat selectivity is uncertain.

Helicolenus dactylopterus is trawled in high numbers over unconsolidated sediments (Ross and Quattrini, 2007) but several studies have not detected any difference in the abundance of the species among different substratum types (Ross and Quattrini, 2007; D'Onghia et al., 2011; Biber et al., 2014; Ross et al., 2015). Quattrini et al. (2012) and Milligan et al. (2016) consider *H. dactylopterus* to be a transient reef species occurring in habitats of high topographic complexity but also in low profile habitat characterised by coral rubble and unconsolidated sediment. Other studies, however, have reported the species to occur exclusively in areas of high topographic complexity. Literature from the North Atlantic (from the Azores and Explorer Canyon) and from the Mediterranean (from the Santa Maria di Leuca coral banks and the Cabliers Coral Mounds) suggests that, like many other rockfish species, *H. dactylopterus* shows a strong preference for cold-water coral reef habitat (D'Onghia et al., 2010; Pham et al., 2015; Capezzuto et al., 2019; Corbera et al., 2019; Price et al., 2019). These studies suggest that individuals used the surrounding complex reef habitat for feeding, refuge from predators and for spawning and nursery areas, indicating that cold-water coral reefs may be essential for *H. dactylopterus* survival. These confounding results suggest that the factors that drive the distribution and abundance of *H. dactylopterus* are not fully known and may be location-specific.

Our knowledge on the use of space by a species may be biased by the sampling technique and the spatial resolution of sampling (Anderson and Yoklavich, 2007; Quattrini et al., 2012; Vad et al., 2019). Traditionally, the distribution and use of space by demersal fish communities in waters below depths accessible by scuba were only investigated using trawl or longline surveys (Gibbons et al., 2000; Yoklavich et al., 2000; Ross and Quattrini, 2007). These surveys were seldom coupled with the collection of high-resolution environmental data, an opportunity now provided by more modern visual survey techniques. The study of fish-habitat associations was previously limited to broad-scale interactions with mainly abiotic variables such as water column characteristics and bathymetry (Gibbons et al., 2000). Associations with benthic habitat could not be properly investigated due to gear limitations in structurally complex areas such as deep reef ecosystems. With the improvement of camera technology over the last three decades, there has been an increased capability to quantitatively analyse the associations of fish in deep water environments using *in situ* observations (Anderson and Yoklavich, 2007). The use of cameras, although more spatially constrained, enables sampling in a range of habitats and allows for the simultaneous sampling of a broad spectrum of abiotic and biotic variables (Gibbons et al., 2000; Anderson and Yoklavich, 2007; D’Onghia et al., 2018; Capezzuto et al., 2019). Analysis of video footage, obtained over finer spatial resolutions, can provide a greater understanding of the potential drivers of fish distribution over finer spatial scales, in more structurally complex benthic habitat (Quattrini et al., 2012; D’Onghia et al., 2018; Capezzuto et al., 2019).

Benthic ecosystems, deeper than 100 m, are generally understudied in South Africa (Sink, 2016). Over the last decade, however, a number of habitat types have been recognised on the outer continental shelf, shelf edge and slope. These include canyons and seamounts as well as hard and soft bottom areas characterised by the presence of deep-water sponge aggregations, cold-water coral communities, octocorals, sea pens and bryozoans (Samaai et al., 2020). Many of these habitats host species that may be indicative of Vulnerable Marine Ecosystems (VME), as defined by FAO (2009), and some occur within the South African demersal trawl fishery footprint. In a bid to protect these sensitive areas, some were included in the 20 new marine protected areas (MPA) declared by the South African government in 2019 (Sink et al., 2019).

However, the role that many of these habitat types play in broader ecosystem functioning is still relatively unknown. There is a paucity of studies examining the interactions and associations of species that form some of these biogenic habitats with other organisms including fish. Formal monitoring of benthic habitats in South Africa was instituted in 2011 (Atkinson and Sink, 2018), and since then various offshore video surveys have been conducted. In much of this footage, *H. dactylopterus* has been observed to commonly occur in several different habitat types. It is, however, unclear whether the species is any more abundant in topographically complex rocky and biogenic habitats compared to less complex unconsolidated sediment habitats.

An investigation into the habitat association of *H. dactylopterus* in South Africa, using different sampling methodologies at different spatial resolutions, may provide insight into the essential habitat required for this species. Further investigation may also clarify the variability in the habitat selectivity of the species reported across its range. Given that *H. dactylopterus* is caught in large quantities as bycatch in the South African demersal trawl fishery, an understanding of the habitat preferred by the species can further inform the ecosystem-level management of the fishery. This is important for the maintenance of the Marine Stewardship Council (MSC) certification of the fishery, and, more broadly, for spatial management and marine spatial planning initiatives.

The aim of this chapter was to determine and describe the habitat preference and use of *H. dactylopterus* in South Africa by identifying and comparing key factors that influence the abundance and distribution of this species from data collected using different sampling methodologies at different spatial resolutions. The objectives were threefold. The first objective was to investigate the factors that influence the abundance of *H. dactylopterus* in South Africa using broad resolution trawl survey data (trawls one to two kilometres in length) with a wide spatial coverage. Secondly, fine resolution video survey data (video segments 25 m in length) covering a greater diversity of habitat types were used to examine factors influencing abundance. Finally, the total length and behaviour of individuals were examined using the video survey data to determine ontogenetic differences in habitat preference and to make inferences about the habitat utilisation of the species.

3.3 Materials and Methods

3.3.1 Trawl surveys

The habitat use of *H. dactylopterus* at a broad spatial resolution was analysed using abundance data from demersal research trawl surveys conducted by the Fisheries Branch of DFFE from 2015 to 2019. This period was selected to align with the video data collected in 2016 and used for analyses. Eight research surveys were conducted over this period, during which a total of 933 successful trawls were undertaken (Figure 3.1 and Table 3.1). An additional 21 trawls were abandoned due to gear failure.

Research trawl surveys were conducted annually to estimate the abundance of hake, *Merluccius paradoxus* and *M. capensis*, and other demersal fish on the South African continental shelf and slope. Surveys were conducted from the Namibian border to approximately 27°E and were split into west and south coast components at 20°E. During each survey, trawl sites were selected using a random stratified approach with depth as the stratifying variable. Samples were collected using a four-panel German 55 m trawl net. The net had a 75 mm mesh codend with a 35 mm mesh liner which enabled the capture of smaller fish than the commercial fishery. Trawl duration at each site was typically 30 minutes and towing speed was approximately 3.5 knots.

For each trawl sample, catch composition as abundance and weight of each species was recorded. The start and end position of each trawl was recorded and the distance between these points was calculated. The wingspread of the net was measured throughout the trawl and the average was calculated. The area swept was estimated as the product of the trawl distance and wingspread (Ryan et al., 2020). The start and end depth of each trawl were also recorded.

Table 3.1: Research trawl surveys conducted by DFFE on the west and south coasts of South Africa from 2015 to 2019 included in this study. No surveys were conducted in 2018.

Year	**Month/s**	**Coast**	**Depth range**	**Number of trawl sites sampled**
2015	February/March	West	63 – 883 m	120
2015	April/May	South	33 – 997 m	116
2016	February/March	West	49 – 861 m	125
2016	April/May	South	35 – 945 m	114
2016	September/October	South	18 – 796 m	98
2017	January/February	West	34 – 718 m	124
2019	January/February/March	West	40 – 853 m	121
2019	March/April/May	South	34 – 881 m	115

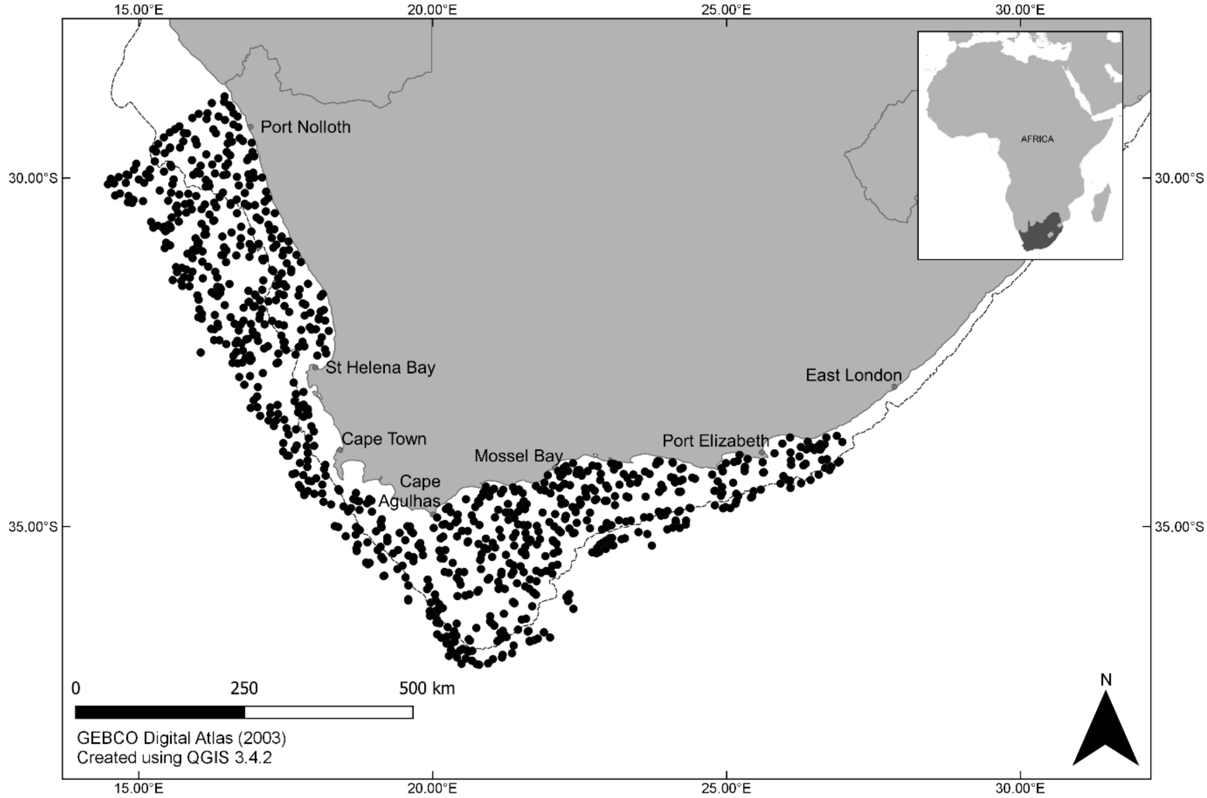


Figure 3.1: The localities of trawl samples used in this study from DFFE research trawl surveys on the west and south coasts of South Africa (2015 to 2019). The dashed line shows the 200 m bathymetric contour derived from the GEBCO Digital Atlas (IOC et al., 2003).

Data analyses

Generalised Linear Modelling (GLM) was used to assess the potential factors that determine the variation in *H. dactylopterus* abundance among trawl samples. The predictor variables that were considered were start longitude, start depth and benthic habitat type of each trawl site along with the year in which each trawl was conducted (Table 3.2). To account for the difference in sampling effort per site the area trawled was included as an offset term (Zuur et al., 2009).

Longitude was used in the modelling to test eastward penetration into Indian Ocean waters, as *H. dactylopterus* is primarily an Atlantic species with South Africa being at the end of its geographic range. Depth was binned into 100-m depth classes. It was assumed that the depth of each trawl did not vary by more than 100 m.

Benthic habitat types were based on the broad ecosystem groups identified in the National Biodiversity Assessment 2018 (NBA 2018, Sink et al., 2019). In the NBA 2018, ecosystem types were primarily classified using a nested hierarchical approach in which four levels of classification were used. In addition to these four levels, 15 broad ecosystem groups were identified. These ecosystem groups were not nested in the classification hierarchy but were included as an update to the broad ecosystem types identified in the National Biodiversity Assessment 2011 (Sink et al., 2012b). Classification into the broad ecosystem groups considered terrestrial and benthic-pelagic connectivity, substratum type, grain size, depth, and the presence of features such as kelp forests, bays and canyons. Classification was thus based on functional similarities in ecosystems but did not account for biogeographic patterns in species composition and ecology (Sink et al., 2012b). Based on this functional grouping, and that the inclusion of longitude in the modelling will account for geographic differences in *H. dactylopterus* abundance, the use of broad ecosystem groups to define benthic habitat type at a broad spatial resolution was considered appropriate. The benthic habitat type at each trawl site was extracted from the NBA 2018 broad ecosystem type GIS spatial layer in QGIS version 3.4 Madeira (QGIS Development Team, 2018). Trawls occurred across seven broad ecosystem groups including bay, shallow soft shelf, shallow rocky shelf, deep soft shelf, deep rocky shelf, canyon, and slope.

Data exploration followed the protocols detailed by Zuur et al. (2010). Predictor and response variable outliers were assessed by plotting Cleveland dotplots, boxplots and frequency distributions. Outliers were removed when they were thought to have been caused by measurement error or a lack of sample size.

A total of nine, one and eight trawl samples were obtained from sites in bay, shallow rocky shelf and canyon ecosystems respectively. These were removed from further analysis due to the low sample size. All other samples were included in the analysis, resulting in a total sample size of 915.

Table 3.2: Factors used in the Generalised Linear Modelling of Helicolenus dactylopterus *abundance in trawl surveys conducted in South Africa.*

Factor	Type	No. of levels	Description
Longitude	Continuous		The longitude of each site, as the start longitude of the trawl
Depth class	Categorical	8	The depth of each site, at the start depth of each trawl, binned into 100-m depth classes: <101, 101-200, 201-300, 301-400, 401-500, 501-600, 601-700, >700.
Benthic habitat type	Categorical	4	The benthic habitat type of each site: shallow soft shelf (SSS), deep soft shelf (DSS), deep rocky shelf (DRS), slope (S).
Year	Categorical	4	The year in which each trawl was conducted: 2015, 2016, 2017, 2019.

Collinearity between predictor variables was assessed by calculating the generalised variance inflation factors (GVIF) (Fox and Monette, 1992). The GVIF is a generalised form of the variance inflation factor (VIF). The VIF is a measure of how much the variance of an estimated regression coefficient is inflated because of collinearity with another continuous predictor variable (Zuur et al., 2010), where

$$VIF = \frac{1}{(1-R^2)} \tag{3.1}$$

The GVIF is used to evaluate categorical variables that have more than one degree of freedom and thus require more than one regression coefficient. Fox and Monette (1992) suggest the use of GVIF$^{(1/(2 \text{ x } Df)}$, where Df is the number of coefficients associated with the variable, to make GVIFs comparable. This value is equivalent to the square root of the VIF when the Df = 1. As a rule of thumb, Zuur et al. (2010) suggested that the VIF should not exceed three. Given the relationship between the GVIF$^{(1/(2 \text{ x } Df)}$ and the VIF when Df = 1, the square-root of three (1.73) was used as the threshold value. When collinearity between variables was found, a backwards selection procedure was used in which the variable with the highest GVIF$^{(1/(2 \text{ x } Df)}$ was dropped and the GVIF was calculated for the remaining variables. This was repeated until the GVIF$^{(1/(2 \text{ x } Df)}$ for all variables was below the threshold.

Depth and benthic habitat type were collinear due to how the ecosystem groups were classified in the NBA 2018 (habitat GVIF$^{(1/(2 \text{ x } Df)}$ = 1.84). These two variables were therefore included in separate models. To assess the relative effects of depth and benthic habitat type on *H. dactylopterus* abundance a third model was fitted to a subset of the data. The data subset comprised samples that occurred in habitats in a similar depth range including those from shallow soft shelf, deep soft shelf and deep rocky shelf habitats up to depths of 500 m. No further collinearity was found between variables included in the three models.

The three models run were therefore of the form:

$$M1_{depth}: y = long + depth\ class + year + offset(area\ trawled) + error, \quad (3.2)$$

$$M2_{habitat}: y = long + habitat + year + offset(area\ trawled) + error, \quad (3.3)$$

$$M3_{ss}: y_{ss} = long + depth\ class + habitat + year + offset(area\ trawled) + error, \quad (3.4)$$

where y is the abundance of *H. dactylopterus* in trawl samples from the full dataset and y_{ss} is the abundance of *H. dactylopterus* in trawl samples from the data subset.

The Poisson and negative binomial distributions were considered as alternative error models that are suitable for modelling count data (Zuur et al., 2009). *Helicolenus dactylopterus* count data included numerous zeros and so the possibility of the data being zero-inflated was considered. Four different model distributions (Poisson (P), negative binomial (NB), zero-altered Poisson (ZAP) and zero-altered negative binomial (ZANB) were compared for each saturated model. The dispersion parameter for each model was estimated and the model suitability assessed using Akaike's Information Criterion (AIC) (Zuur et al., 2009). For the zero-inflated and zero-altered models, the AIC was calculated for both model components combined.

Poisson and negative binomial GLMs were fitted using the log-link function to ensure positive fitted values. In the zero-altered Poisson and negative binomial models (also known as hurdle models), the zero and non-zero (count) data were modelled in two parts. First, a binomial model with a logit link function was used to model the zero and non-zero data as absence and presence. The non-zero observations (count data) were then modelled using a zero-truncated Poisson or negative binomial model with a log-link function (Zuur et al., 2009). In the saturated model, the same factors were assumed to influence the presence and the abundance of *H. dactylopterus.*

Once a suitable model distribution was identified, the inclusion of the optimal combination of covariates in the final model and the significance of each covariate was assessed using stepwise likelihood-ratio testing. Non-significant covariates were removed. Using likelihood-ratio tests to compare nested models with the saturated model is approximate (Bolker et al., 2009; Zuur et al., 2009). Model covariates were thus considered to have a significant effect on *H. dactylopterus* presence and abundance if $p < 0.01$ (Milligan et al., 2016). The AICs of each model were also computed and compared. Model validation was done by plotting Pearson's residuals against the fitted values and each explanatory variable included in the final model.

To plot the effects of predictor variables on the variation in *H. dactylopterus* abundance in research trawls, predicted values from each of the fitted models were standardised. All predictor variables, apart from the variable of interest, were fixed to standardised values, which were the levels in which mean *H. dactylopterus* abundance was greatest.

When zero-altered models were used, predicted values were calculated from each model component separately. Expected mean abundance was calculated as the product of the probability of a positive observation of *H. dactylopterus* and the positive catch of *H. dactylopterus* for a given factor level (Lo et al., 1992).

All analyses on the patterns in the habitat preference of *H. dactylopterus* from broad resolution trawl data were done using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020). The R packages ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2018), MASS (Venables and Ripley, 2002), lattice (Sarkar, 2008), car (Fox and Weisberg, 2019), AER (Kleiber and Zeileis, 2008) and pscl (Zeileis et al., 2008) were utilised.

3.3.2 Video surveys

The habitat preference of *H. dactylopterus* at a fine spatial resolution was analysed using video footage collected during the African Coelacanth Ecosystem Programme (ACEP) Deep Secrets research cruise on the *RV Algoa* in September and October 2016. The Deep Secrets Project is a multi-disciplinary project that aims to generate knowledge of previously understudied deep-water ecosystems on the outer shelf and shelf edge on the South African south coast to improve understanding and support management initiatives in these areas. Benthic habitats at 58 stations, in waters from 100 to 700 m deep, were surveyed via tow camera. Footage was obtained from Table Bay off Cape Town to the Kei River mouth northeast of East London.

Video and photographs were collected using the SkiMonkey towed benthic camera system which is mounted on weighted skis and is equipped with a wide-angle lens and LED lights positioned on the front of the sled along with triangular laser pointers. The camera system can record high-definition imagery at depths up to 1000 m, while sending real-time feedback to the surface, via the tow cable. All camera functions are controlled from the surface.

The camera system was deployed at a speed of 1.2 m.s^{-1} to 7 m above the seabed, before being lowered onto the seabed at the lowest speed possible to avoid disturbance. Once landed and the focus and lighting on the camera were set, the vessel towed the system at between 0.5 and 1.5 knots. When it was not possible to tow the camera in more rugged and complex terrain, a drop and lift approach was used in which the camera was lifted to avoid rocky features. At each station, a ten-minute video transect was recorded. Location, time and depth, obtained from the vessel's echosounder, were recorded at the beginning and end of each transect. The camera system was equipped with a Seabird Micro-CAT CTD measuring salinity, temperature and depth over the entire transect.

Video footage was available from 44 transects. From these, transects were selected for analysis based on three factors. Firstly, at least ten minutes of visible footage had to have been obtained over the entire transect. Secondly, video footage had to have been collected from along a transect (i.e. the tow camera did not remain in one place). Finally, all other supplementary data including location, time and depth had to have been recorded for the transect. The requirements for analysis were not met at ten transects and so footage from 34 transects was analysed (Figure 3.2 and Table 3.3). At site DSC011, two transects were conducted and were analysed separately (as one and two respectively).

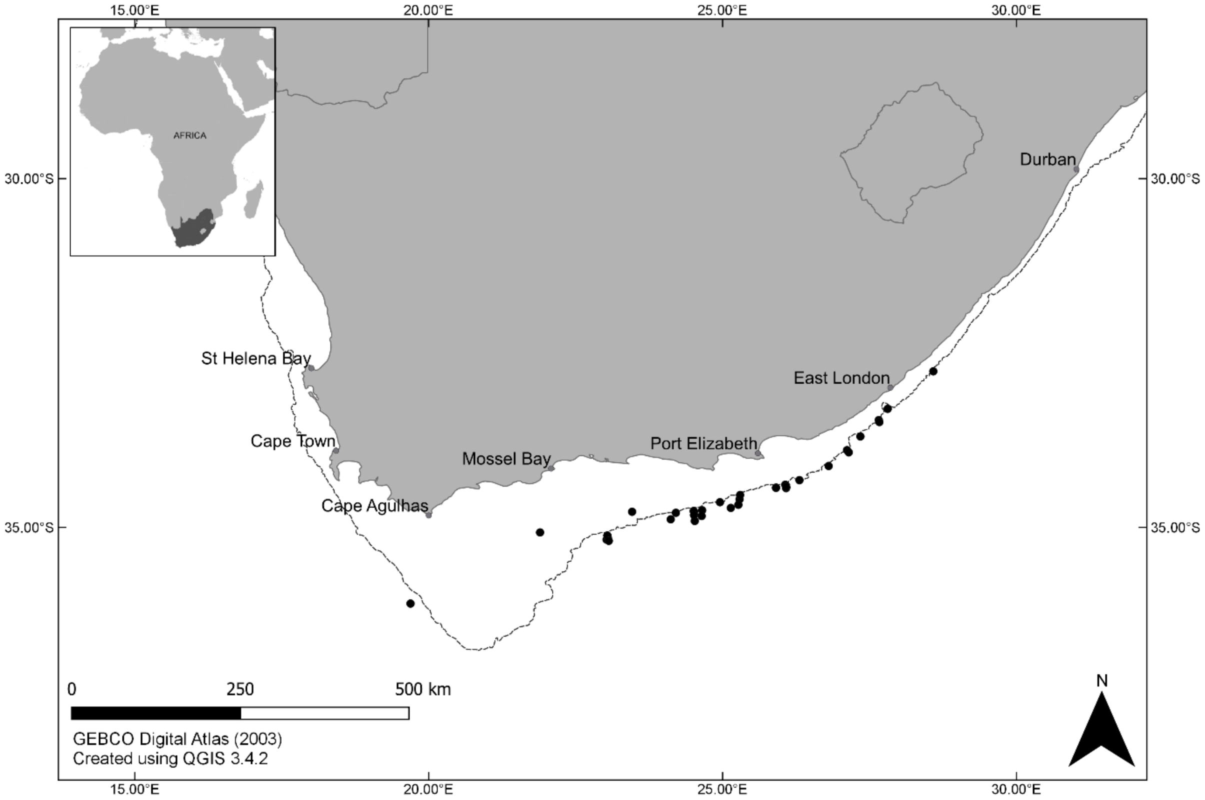


Figure 3.2: The location of analysed video transects conducted on the outer shelf and shelf edge of South Africa in September and October 2019. The dashed line shows the 200 m bathymetric contour derived from the GEBCO Digital Atlas (IOC et al., 2003).

Table 3.3: Details of analysed video transects that were conducted along the outer shelf and shelf edge of the South African south coast during September and October 2016.

Transect	**Date**	**Latitude**	**Longitude**	**Transect length (m)**	**Start depth**
DSC003	30/09/2016	-36.0550	19.6909	685	482
DSC010	5/10/2016	-34.7825	23.4611	404	138
DSC011_1	5/10/2016	-35.1709	23.0274	297	476
DSC011_2	5/10 /2016	-35.1490	23.0495	390	435
DSC012	6/10/2016	-35.1131	23.0404	390	336
DSC014	6/10/2016	-35.1876	23.0645	359	531
DSC016	7/10/2016	-34.8878	24.1186	341	352
DSC018	7/10/2016	-34.7967	24.2063	271	277
DSC020	7/10/2016	-34.9109	24.5269	356	532
DSC021	8/10/2016	-34.7706	24.5097	385	401
DSC022	8/10/2016	-34.7797	24.5130	239	422
DSC023	8/10/2016	-34.8284	24.5141	292	492
DSC024	8/10/2016	-34.7613	24.6526	424	547
DSC027_1	15/10/2016	-34.7283	25.1403	290	612
DSC029	21/10/2016	-34.6082	25.2890	359	485
DSC030	15/10/2016	-34.6849	25.2692	581	558
DSC031	16/10/2016	-34.3394	26.3084	366	260
DSC035	17/10/2016	-33.7235	27.3457	211	186
DSC036	17/10/2016	-33.3316	27.8092	278	125
DSC038	18/10/2016	-32.7968	28.5857	295	358
DSC040	18/10/2016	-33.4910	27.6665	345	307
DSC041	18/10/2016	-33.5193	27.6684	335	552
DSC042	19/10/2016	-33.9171	27.1179	408	308
DSC043	19/10/2016	-33.9480	27.1473	425	520
DSC044	19/10/2016	-34.1406	26.8050	190	356
DSC047	20/10/2016	-34.4034	26.0676	355	235
DSC048	20/10/2016	-34.4511	26.0813	483	623
DSC049	20/10/2016	-34.4319	26.0805	854	412
DSC050	20/10/2016	-34.4433	25.9107	453	435
DSC051	20/10/2016	-34.4481	25.9095	441	507
DSC053	21/10/2016	-34.5482	25.2982	594	322
DSC054	21/10/2016	-34.6483	24.9561	506	333
DSC056	22/10/2016	-34.8417	24.6444	413	555
DSC059	23/10/2016	-35.0706	21.8953	714	117

Transects were subsampled and analysed in segments to standardise surveyed area. Transect segments of 25 m were analysed, which is broadly similar to previous studies (for example Frid et al., 2018). The measurement of the 25 m segments was based on time, in which the average speed of the camera was calculated from the video time and transect length. This was the only feasible way to estimate distance, given that the tow camera was not fitted with an underwater positioning system. Five segments were randomly selected and analysed per transect. This was done in an attempt to avoid spatial autocorrelation.

Environmental variable and benthic habitat sampling

The vessel’s onboard positioning system and echosounder recorded location, course over ground and depth along each transect. The start location of each segment was extrapolated from the vessel tracks and the offset position of the tow camera relative to the vessel. The offset position was calculated based on the depth of the vessel and the length of the tow camera cable released.

Depth data were obtained from the micro-CAT CTD by aligning the timestamps of the CTD data with those of the video footage. Depth was recorded as the start depth of each segment.

Benthic habitat along each segment was analysed from the tow camera footage, using the software TransectMeasure (SeaGIS Pty Ltd, http://www.seagis.com.au). Five frames per segment were randomly selected for analysis.

Benthic habitat was characterised in terms of the following categories: substrata, relief and visible biota. Categorisation was done following the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al., 2014; Edwards, 2014). The CATAMI classification scheme is a hierarchical system designed to standardise the classification of images and video obtained from a wide variety of marine environments by scoring and categorising the abiotic and biotic components of a given habitat (Althaus et al., 2014; Edwards, 2014). Classification of biota is primarily based on taxonomy, however, in taxa where classification is reliant on fine-scale details not easily identified in imagery, morphological characteristics are used (Edwards, 2014). The hierarchical scheme avoids duplication and accounts for the fact that it is not always possible to identify habitat characteristics to the lowest classification level (Edwards, 2014).

The dominant substrata and relief per frame and the dominant biota per 2 x 2 grid cell overlaid on each frame were recorded. Characteristics that were not clear or visible because of footage quality were classified as not scorable and were excluded from analyses. The area of each frame was not calculated, and so the benthic habitat data recorded provided an estimate of dominance of habitat characteristics.

Classification of benthic habitat type

Substrata, relief, and visible biota data were square-root transformed to reduce the weighting of dominant characteristics and a resemblance matrix was created using the Bray-Curtis measure of similarity. Data were hierarchically clustered, using average linkage, to establish whether there was any grouping of segments based on similarity in habitat characteristics. A cluster dendrogram was generated. The final number of clusters was selected to ensure representativity of observed habitat types and that there was an adequate number of segments in each and to avoid model overfitting. A similarity percentage analysis (SIMPER) was done to identify the habitat components that most distinguished each benthic habitat type. Analyses were done using Plymouth Routines in Multivariate Ecological Research (PRIMER) version 6.1.11 (Clarke and Gorley, 2006).

Fish sampling

The absolute abundance of *H. dactylopterus* along each segment was recorded from the tow camera footage. Where possible, the length of each fish was estimated using the camera's onboard lasers. The position and activity of each individual was also recorded to gain qualitative insight into habitat use. Fish position and activity categories were adapted from Uiblein et al. (2003) and D'Onghia et al. (2011). Position was recorded as being one of three categories: in the water column, near the seabed (within 0.5 m) or on the seabed. Activity was recorded as being one of seven categories: actively swimming, drifting (movement laterally or backwards), hovering (fish stationary but with active swimming), moving on the seabed, resting on the seabed, sheltering (within one body distance of a benthic feature) or feeding. Video footage was viewed frame-by-frame. When possible, the position and behaviour of individuals was noted prior to any disturbance response being shown. A disturbance response was classified as that in which an individual showed high or increasing swimming speed, indicative of burst swimming, in reaction to the tow camera. Individuals that could not be observed prior to their disturbance response were excluded from the analyses.

Data analyses

The analysis of multiple segments along a single transect imposed the need for mixed-effects modelling. Generalised linear mixed modelling (GLMM) was therefore used to assess the factors that determine the variation in *H. dactylopterus* abundance among video segments. Transect was included as a random effect and the predictor variables that were considered included the start longitude, the start depth, and the benthic habitat type of each segment (Table 3.4). Longitude was binned into 1°E longitude classes and depth was binned into 100-m depth classes. It was assumed that the depth of each trawl did not vary by more than 100 m. Temperature and salinity recorded along the transects were not included to avoid model overfitting.

As in the broad resolution trawl analyses, data exploration followed the protocols detailed by Zuur et al. (2010). Predictor and response variable outliers were assessed by plotting Cleveland dotplots, boxplots and frequency distributions. Outliers were removed when they were thought to have been caused by measurement error or a lack of sample size.

Segments occurred in depths from 117 to 653 m across six 100-m depth classes and the majority were located between 21 and 29°E. Five segments occurred west of 20°E, but these were from a single transect (DSC003) and were thus removed from further analysis due to a lack of sample size. This resulted in 165 segments being included in the modelling.

Table 3.4: Fixed effect factors used in the Generalised Linear Mixed Modelling of Helicolenus dactylopterus *abundance in video surveys conducted in South Africa.*

Factor	**Type**	**No. of levels**	**Description**
Longitude	Categorical	5	The start longitude of each site binned into 1°E longitude classes: <24 (<24.00), 24 (24.00 – 24.99), 25 (25.00 – 25.99), 26, (26.00 – 26.99), >27 (>26.99).
Depth class	Categorical	6	The depth of each site, as the start depth of each trawl, binned into 100-m depth classes: <201, 201-300, 301-400, 401-500, 501-600, >600.
Benthic habitat type	Categorical	3	The benthic habitat type of each segment, as defined by the hierarchical clustering.

Collinearity between predictor variables was assessed by calculating the generalised variance inflation factors (GVIF) (Fox and Monette, 1992). No collinearity was found ($GVIF^{(1/(2 \times Df)} < 1.73$).

The full model used to analyse *H. dactylopterus* abundance in fine resolution video footage was therefore of the form:

$$M4\colon y = long + depth\ class + habitat + (1|transect) + error, \tag{3.5}$$

where y is the abundance of *H. dactylopterus* in video segments.

The Poisson and negative binomial distributions were considered as two alternative error models that are suitable for modelling count data (Zuur et al., 2009). Initially, a Poisson model was fitted to the data and potential overdispersion was identified by calculating the sum of the squared Pearson residuals and dividing by the residual degrees of freedom (Bolker et al., 2009). When there was no evidence of overdispersion (overdispersion < 1), the response was assumed to follow a Poisson distribution, otherwise, a negative binomial model was fitted. Poisson and negative binomial GLMMs were fitted using the log-link function to ensure positive fitted values (Zuur et al., 2009).

Backwards selection of covariates was used to fit the final, most parsimonious model. The significance of each covariate was assessed using likelihood-ratio testing, and non-significant covariates were removed. Model covariates were considered to have a significant effect on *H. dactylopterus* abundance if $p < 0.01$ (Bolker et al., 2009; Zuur et al., 2009; Milligan et al., 2016). Model validation was done by plotting Pearson's residuals against the fitted values and against each explanatory variable included in the final model as well as those that were not included.

To plot the effects of predictor variables on the variation in *H. dactylopterus* abundance at a fine spatial resolution in video segments, predicted values from the fitted GLMM were standardised. All predictor variables, apart from the variable of interest, were fixed to standardised values, which were selected as the levels in which mean *H. dactylopterus* abundance was greatest. The standard errors and lower and upper 95% confidence intervals of predicted values were estimated using a semiparametric bootstrapping approach (Efron, 1982; Carpenter and Bithell, 2000; Bates et al., 2015). A total of 200 simulations were run, each time generating a new dataset by resampling the residuals from the fitted model with replacement (Hilborn and Walters, 1992; Carpenter and Bithell, 2000). The GLMM was fitted to each new dataset to obtain the bootstrap estimates and confidence intervals were estimated from the bootstrap distribution (Carpenter and Bithell, 2000).

Ontogenetic differences in the habitat preference of *H. dactylopterus* were tested by comparing the total length of observed fish among longitude classes, depth classes and habitats. Differences were tested using a one-way ANOVA unless assumptions of normality and homogeneity of variances were not met, in which case a Kruskal Wallis test by ranks was used. If the data were approximately normal but the variances were not homogeneous, a Welch's ANOVA was used. Pairwise comparisons were done using Tukey's HSD or the Games-Howell post-hoc test (Ruxton and Beauchamp, 2008).

Finally, the behaviour and habitat use of *H. dactylopterus* was presented graphically. Differences in fish position and activity among benthic habitat types were compared using chi-squared tests of independence as defined by Zar (1996):

$$\chi^2 = \sum_{i=1}^{k} \frac{(f_i - \hat{f}_i)^2}{\hat{f}_i} \tag{3.6}$$

where k is the number of benthic habitat types, f_i is the observed frequency of benthic habitat type i and $\widehat{f_i}$ is the expected frequency of benthic habitat type i.

All analyses on the habitat preference and use of *H. dactylopterus* from fine resolution video data were done using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020). The R packages ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2018), MASS (Venables and Ripley, 2002), lattice (Sarkar, 2008), car (Fox and Weisberg, 2019) and lme4 (Bates et al., 2015) were utilised.

3.4 Results

3.4.1 Trawl surveys

On average, trawls were 2.70 (±0.10 SD) km long and covered an area of 0.08 (±0.01 SD) km^2. The 915 trawls included in this study covered a total area of 75.10 km^2 in depths ranging from 18 to 997 m.

Potential drivers of Helicolenus dactylopterus *abundance*

Helicolenus dactylopterus individuals were present in 71% of the 915 trawls. Abundance ranged from 0 to 614 specimens per trawl (Figure 3.3), averaging 66 (±91 SD) individuals per sample.

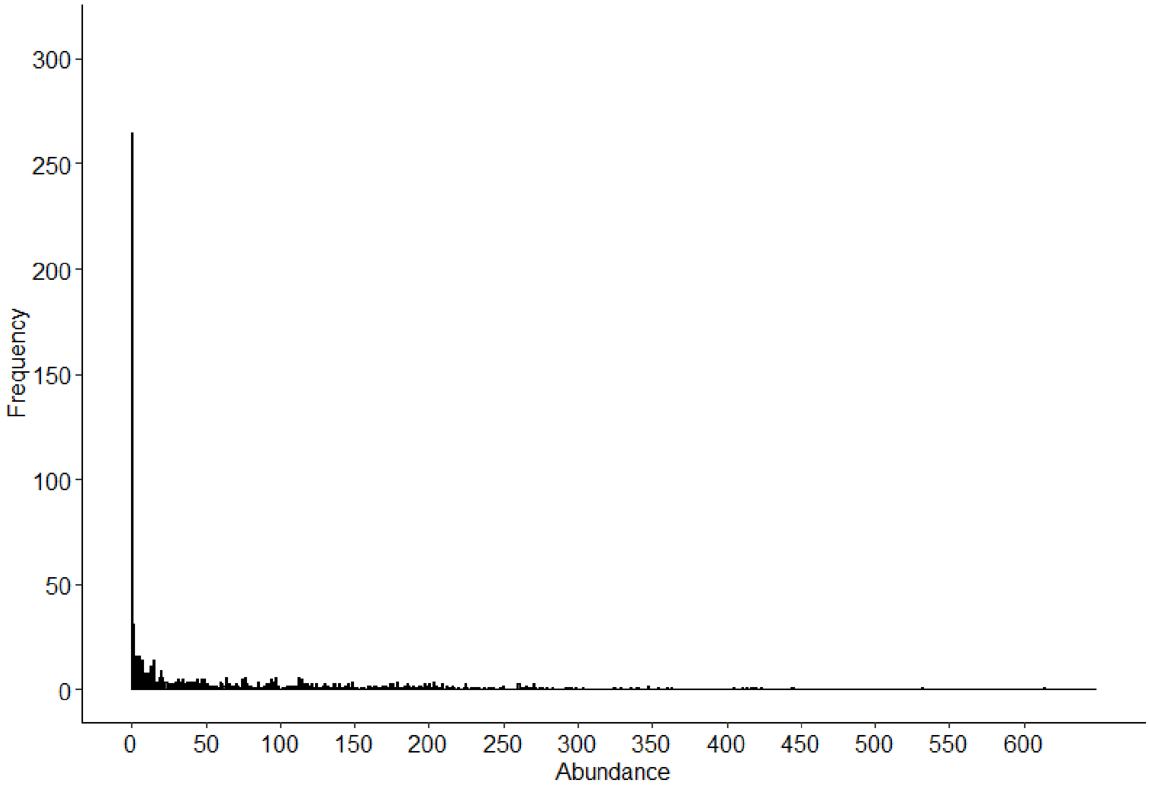


Figure 3.3: Frequency distribution of Helicolenus dactylopterus *abundance in 915 research trawl samples collected on the west and south coasts of South Africa from 2015 to 2019.*

At a broad spatial resolution, the abundance of *H. dactylopterus* in South Africa decreased with an increase in longitude (Figure 3.4). A unimodal pattern with depth was shown in which abundance peaked in the 201 to 300 m depth class where the median equalled 130 (interquartile range (IQR) 61 – 212.50) fish per trawl sample. There was a less distinct pattern with habitat type in which *H. dactylopterus* individuals were equally abundant in deep soft shelf (median 26, IQR 0 – 120 fish) and deep rocky shelf (median 20, IQR 0 – 112.75 fish) habitats, although fish were relatively more abundant in shallow soft shelf areas (median 55, IQR 14 – 100.75 fish) and less abundant in slope habitat (median 3, IQR 0 – 30.25 fish). The abundance of *H. dactylopterus* was greater in 2017 (median 58, IQR 13 – 200 fish) compared to other years. The patterns of *H. dactylopterus* abundance with longitude, depth class, habitat type and year did not change substantially when the data were disaggregated to only include samples from deep rocky shelf, deep soft shelf and shallow soft shelf habitats.

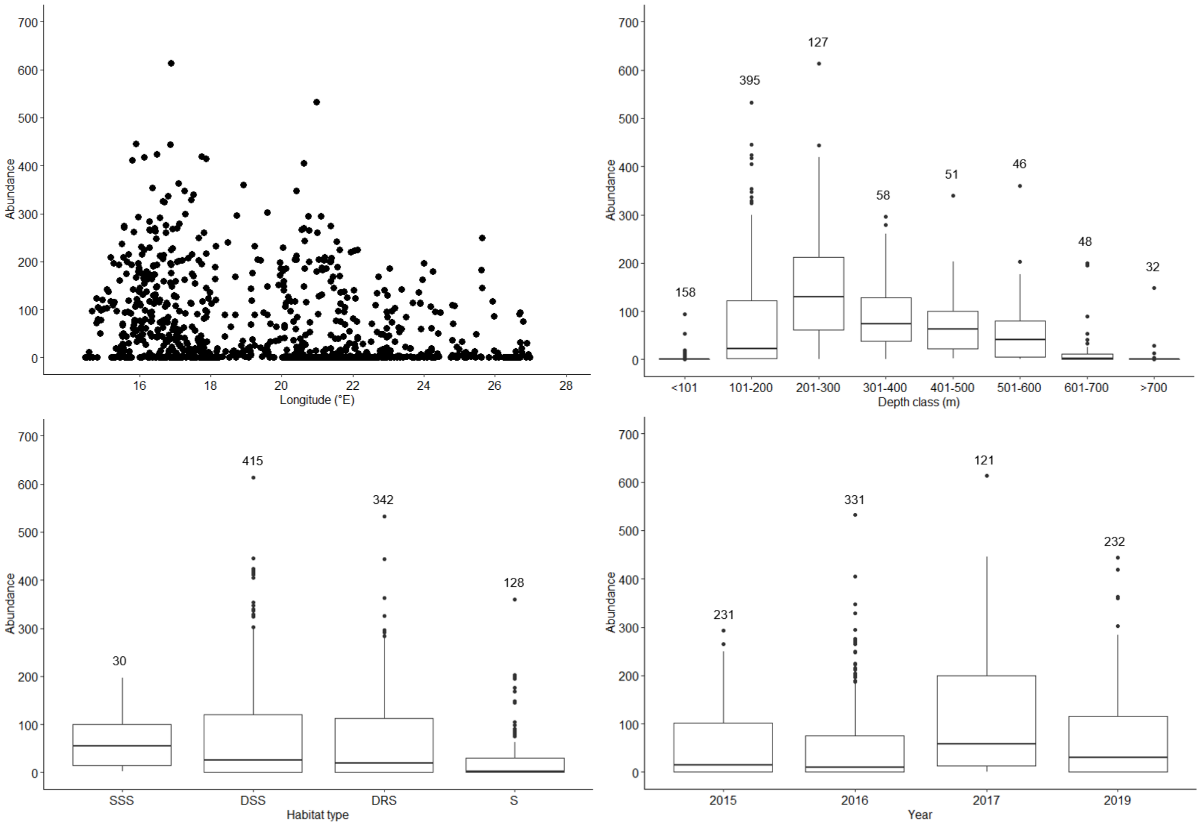


Figure 3.4: Patterns of Helicolenus dactylopterus *abundance in broad resolution trawl surveys with longitude, depth class, habitat type (SSS=shallow soft shelf, DSS=deep soft shelf, DRS=deep rocky shelf, S=slope), and year. Trawl samples were collected during research surveys in South Africa from 2015 to 2019. The sample size in each group is shown above the bar.*

Helicolenus dactylopterus individuals were absent in a large proportion (30%) of trawl samples included in this study and abundance data were zero-inflated (Figure 3.3).

For all three proposed models ($M1_{depth}$, $M2_{habitat}$ and $M3_{ss}$), the comparison showed that the hurdle model with a negative binomial distribution was most suitable, as indicated by the lack of over-dispersion and the lowest AIC scores (Table 3.5).

Table 3.5: Comparison of model distributions for the three proposed models, $M1_{depth}$, $M2_{habitat}$ and $M3_{ss}$, of Helicolenus dactylopterus *abundance in research trawl samples collected in South Africa from 2015 to 2019. The most suitable distribution for each model is highlighted in bold.*

Model	Distribution	Df	Dispersion	AIC
$M1_{depth}$	Poisson	12	90.22	68933.43
	Negative binomial	13	2.14	7976.96
	Poisson hurdle	24	13.17	53741.84
	Negative binomial hurdle	**25**	**0.98**	**7676.08**
$M2_{habitat}$	Poisson	8	112.92	90015.29
	Negative binomial	9	0.61	8253.19
	Poisson hurdle	16	6.03	57845.43
	Negative binomial hurdle	**17**	**0.85**	**8092.18**
$M3_{ss}$	Poisson	11	89.08	61277.54
	Negative binomial	12	2.13	7065.00
	Poisson hurdle	22	15.12	48433.15
	Negative binomial hurdle	**23**	**1.00**	**6786.07**

In $M1_{depth}$, year was not significant in the count (χ^2 = 8.74; df = 3; p = 0.03) and zero (χ^2 = 3.43; df = 3; p = 0.33) model components and longitude was not significant in the zero model component (χ^2 = 5.01; df = 1; p = 0.03). The AICs of the models with and without these factors were similar and so they were removed from the final model. All other variables were significant and were included (Table 3.6).

In $M2_{habitat}$, year was not significant in the count (χ^2 = 7.32; df = 3; p = 0.06) and zero (χ^2 = 7.21; df = 3; p = 0.07) model components, and the AICs of the models with and without year were similar. Year was therefore removed from the final model. Longitude and habitat type were significant in the count and zero model components (Table 3.6).

Table 3.6: Results of the model selection for $M1_{depth}$ and $M2_{habitat}$ showing significant covariates included in the final negative binomial hurdle model of Helicolenus dactylopterus *abundance (n=915).*

Model	Variable dropped	Negative binomial (count)		Binomial (zero)	
		AIC	Likelihood ratio test	AIC	Likelihood ratio test
$M1_{depth}$	None	7060.20		653.49	
	Longitude	7079.60	χ^2=21.38; df=1; p<0.001	-	-
	Depth class	7118.10	χ^2=71.91; df=7; p<0.001	1101.89	χ^2=462.40; df=7; p<0.001
$M2_{habitat}$	None	7096.30		1036.30	
	Longitude	7126.20	χ^2=31.82; df=1; p<0.001	1081.70	χ^2=47.43; df=1; p<0.001
	Habitat type	7115.60	χ^2=25.21; df=3; p<0.001	1074.40	χ^2=44.13; df=3; p<0.001

Both M1$_{depth}$ and M2$_{habitat}$ showed a significant decrease in *H. dactylopterus* abundance with an increase in longitude (Figure 3.5 and Figure 3.6). In M1$_{depth}$, *H. dactylopterus* abundance peaked from 201 to 300 m (Figure 3.5). In M2$_{habitat}$, *H. dactylopterus* abundance was highest in shallow soft shelf habitat and lowest in slope habitat (Figure 3.6). The abundance in shallow soft shelf habitat was not significantly higher than that in deep soft shelf and deep rocky shelf habitat (p = 0.64 and 0.71 respectively).

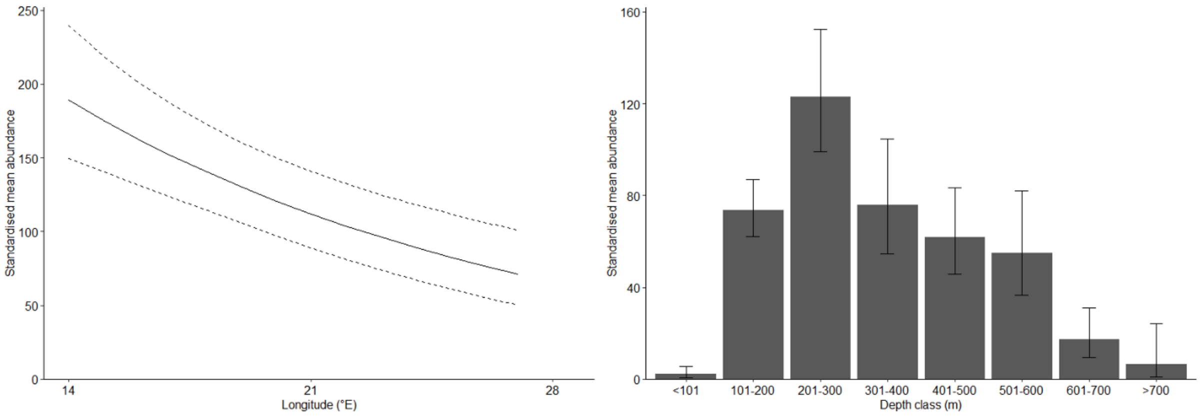


Figure 3.5: Standardised mean abundance (±95% CI) of Helicolenus dactylopterus *in research trawl samples collected in South Africa from 2015 to 2019 (n = 915) by longitude and depth class, as predicted by M1$_{depth}$.*

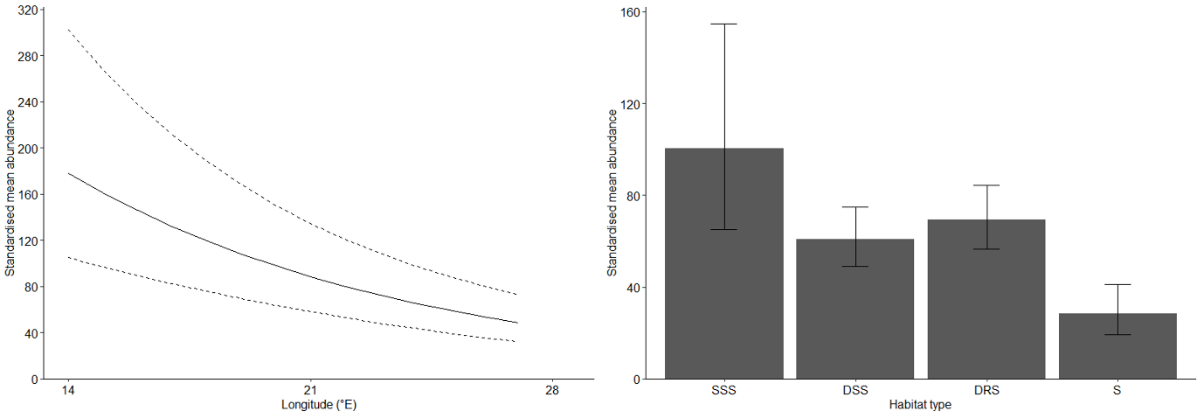


Figure 3.6: Standardised mean abundance (±95% CI) of Helicolenus dactylopterus *in research trawl samples collected in South Africa from 2015 to 2019 (n = 915) by longitude and habitat type (SSS=shallow soft shelf, DSS=deep soft shelf, DRS=deep rocky shelf, S=slope), as predicted by M2$_{habitat}$.*

When depth class and benthic habitat type were incorporated in M3$_{SS}$ and fitted to the disaggregated dataset, year was not significant in the count (χ^2 = 7.92; df = 3; p = 0.05) and zero (χ^2 = 2.79; df = 3; p = 0.42) model components, habitat type was not significant in the count model (χ^2 = 0.69; df = 2; p = 0.71) and longitude was not significant in the zero model (χ^2 = 1.68; df = 1; p = 0.19). As confirmed by the AIC values, these terms were removed sequentially from the final model. The remaining terms were all significant (Table 3.7).

Table 3.7: Results of the model selection for M3$_{ss}$ showing significant covariates included in the final negative binomial hurdle model of Helicolenus dactylopterus *abundance (n=786).*

Variable dropped	**Negative binomial (count)**		**Binomial (zero)**	
	AIC	**Likelihood ratio test**	**AIC**	**Likelihood ratio test**
None	6288.60		514.60	
Longitude	6303.00	χ^2=16.35; df=1; p<0.001		
Depth class	6319.50	χ^2=38.87; df=4; p<0.001	909.82	χ^2=403.22; df=4; p<0.001
Habitat type			528.65	χ^2=18.06; df=2; p<0.001

As in M1$_{depth}$ and M2$_{habitat}$, M3$_{ss}$ showed a significant decrease in *H. dactylopterus* abundance with an increase in longitude (Figure 3.7). Abundance was also greatest in depths from 201 to 300 m (Figure 3.7). Unlike M2$_{habitat}$, abundance was not significantly different among habitat types, but it was included in the final model because it significantly influenced the probability of encountering *H. dactylopterus.*

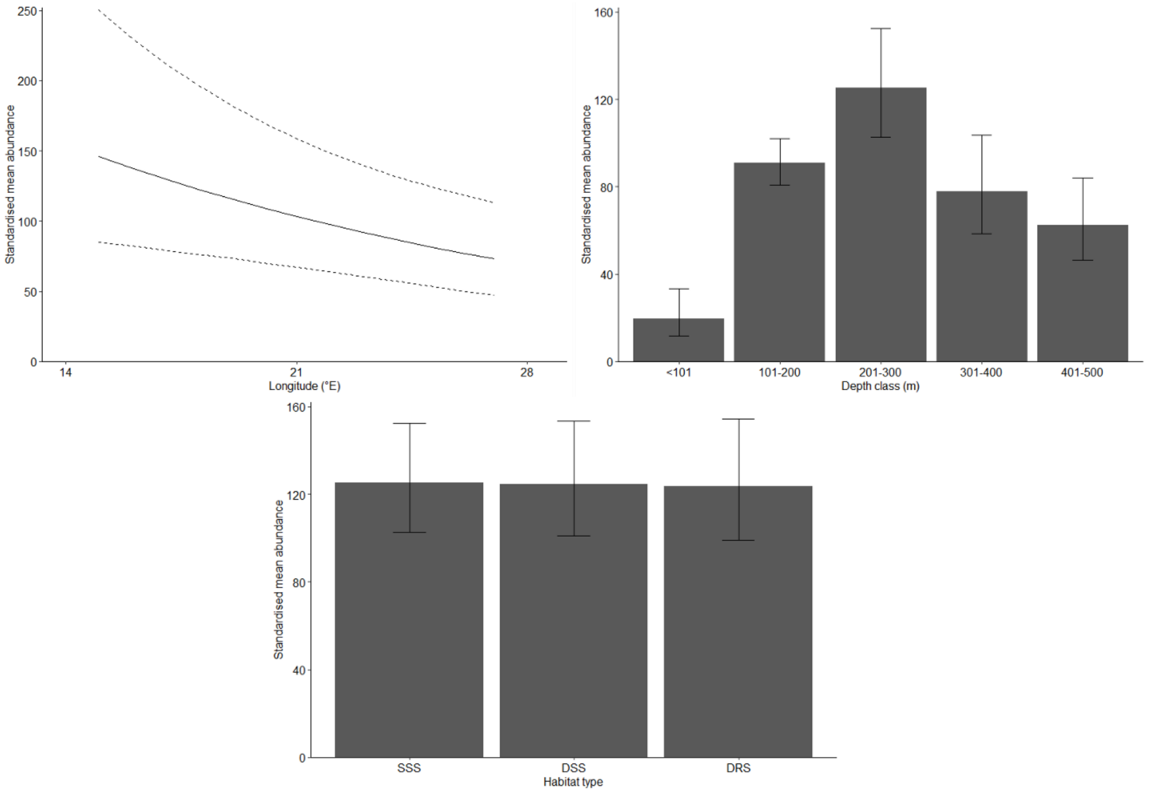


Figure 3.7: Standardised mean abundance (±95% CI) of Helicolenus dactylopterus *in research trawl samples collected in South Africa from 2015 to 2019 (n = 915) by longitude, depth class and habitat type (SSS=shallow soft shelf, DSS=deep soft shelf, DRS=deep rocky shelf), as predicted by M3$_{SS}$.*

Model validation of $M1_{depth}$, $M2_{habitat}$ and $M3_{ss}$ showed no obvious patterning in the residuals and no violation of independence among independent variables (Figure 3.19, Figure 3.20 and Figure 3.21 in Section 3.7 Appendix). All three models were thus accepted.

3.4.2 Video surveys

Benthic habitat type

The habitats surveyed along segments were mainly characterised by unconsolidated sand and mud (57.29%) and pebbles and gravel (30.24%), with rocky substrata occurring less frequently (12.47%). Unconsolidated sand and mud comprised coarse sand (45.76%) and fine sand (11.53%). Unconsolidated pebbles and gravel consisted of shellhash (8.82%), coral rubble (2.35%), gravel (8.82%) and pebbles (10.24%). Consolidated substrata were dominated by boulders (7.29%) and rock (4.47%).

The benthic habitats were largely flat (84.47%), but habitats of low (< 1 m) (8.59%) and moderate (1 – 3 m) (6.94%) relief were also sampled.

Epifauna were observed in 69.18% of video segments. Habitats in which biota were observed were dominated by polychaetes (mainly tube worms), anemones, echinoderms (mainly crinoids and brittle stars), octocorals (mainly simple bottle-brush forms, of which many were *Thouarella* spp.), foraminiferans, crustaceans (mainly hermit crabs and prawns) and scleractinians (mainly solitary tusk corals of the family Caryophylliidae) (Table 3.8).

Table 3.8: Dominance and composition of visible benthic epifauna sampled along video segments from the outer shelf and shelf edge of the south coast of South Africa in September and October 2016. Biota were grouped based on the CATAMI classification scheme (Althaus et al., 2014; Edwards, 2014).

Group	**Dominance (%)**	**Biota**
Bryozoa	3.23	Hard branching (2.69%), hard fenestrate (0.39%), soft dendroid (0.15%)
Octocorals	7.86	Fleshy arborescent (0.03%), fleshy mushroom (1.94%), non-fleshy (0.18%), non-fleshy arborescent (0.03%), simple bottle-brush (3.53%), 2D fan (0.03%), rigid 2D fan (0.30%), seapen (0.96%), whip (0.87%)
Scleractinia	6.25	Branching (0.69%), solitary tusk coral (5.56%)
Hydrocorals	2.81	Branching (2.81%)
Anemones	9.60	Classic (5.20%), tube (4.39%)
Crustacea	6.58	True crabs (0.60%), hermit crabs (2.63%), squat lobsters (0.36%), prawns/shrimps (2.18%)
Echinodermata	9.06	Stalked feather stars (2.96%), unstalked feather stars (0.39%), basket stars (0.18%), brittle stars (2.93%), sea stars (0.42%), sea urchins (2.18%)
Foraminifera	6.70	
Polychaeta	13.60	Tube worms (13.60%)
No biota	30.82	
Other	3.50	Ascidians (1.07%), hydroids (0.90%), sponges (1.29%), molluscs (0.24%)

Substrata, relief and epifauna clustered into three benthic habitat types at 28% similarity (Figure 3.8). Habitat A occurred most abundantly (86% of segments) and was characterised as being flat with coarse sand and little biota. When biota were present, they were dominated by polychaetes and anemones (Figure 3.9). Habitat B and C occurred much less frequently than habitat A, in 6% and 7% of the segments respectively, reflecting habitat availability across the outer shelf and shelf edge of the South African south coast. Both these habitats were more heterogenous than habitat A. Habitat B had low (<1 m) relief with boulders interspersed with coarse sediment, and was characterised by the presence of hydroids, branching stylasterine hydrocorals, octocorals (including simple bottle-brush and fleshy mushroom forms such as *Thouarella*, *Eleutherobia* and *Anthomastus* spp.), and solitary tusk corals (family Caryophylliidae) (Figure 3.10). Habitat C had medium (1-3 m) relief and comprised rocks and boulders with hard, branching bryozoans (mainly *Adeonella* spp.), prawns, some ascidians and fleshy, mushroom octocorals (Figure 3.11).

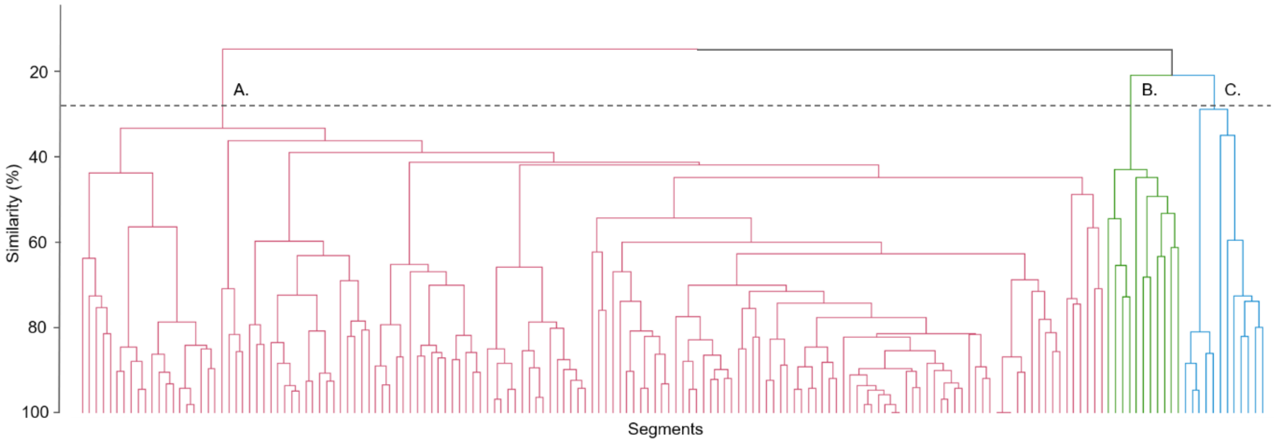


Figure 3.8: Dendrogram of benthic habitat types produced by cluster analysis of substrata, relief and visible benthic biota sampled in the analysed video segments from the outer shelf and shelf edge of the South African south coast in September and October 2016.

Figure 3.9: Examples of benthic habitat type A that occurred in 86% of the analysed video segments from the outer shelf and shelf edge of the South African south coast. Photographs were from A. transect DSC018, B. transect DSC023, C. transect DSC031 and D. DSC051.

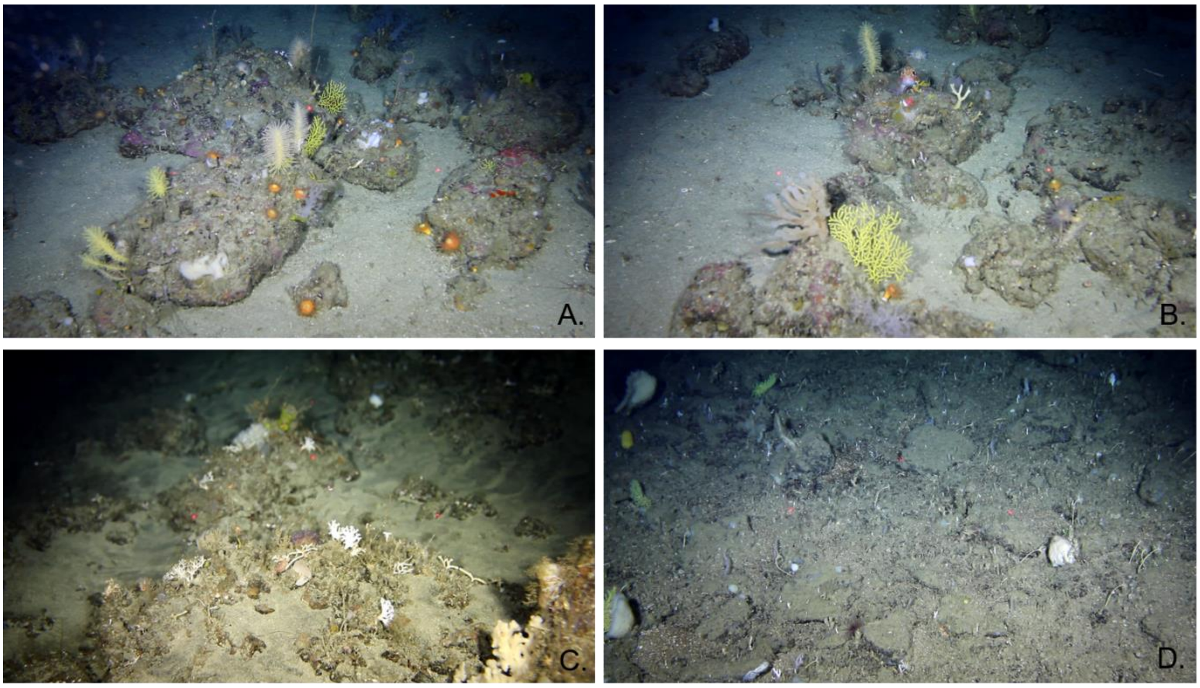


Figure 3.10: Examples of benthic habitat type B that occurred in 6% of the analysed video segments from the outer shelf and shelf edge of the South African south coast. Photographs were from A and B. transect DSC010, C. transect DSC016, and D. DSC043.

Figure 3.11: Examples of benthic habitat type C that occurred in 7% of the analysed video segments from the outer shelf and shelf edge of the South African south coast. Photographs were from A. transect DSC012, B. and C. transect DSC020, and D. DSC027.

Potential drivers of Helicolenus dactylopterus *abundance*

A total of 61 *H. dactylopterus* individuals were identified, occurring in 45% of the transects and 22% of the segments. Abundance in each segment mostly ranged from zero to three individuals, although eight fish were present in one video segment in transect DSC047 off Port Elizabeth (Figure 3.12).

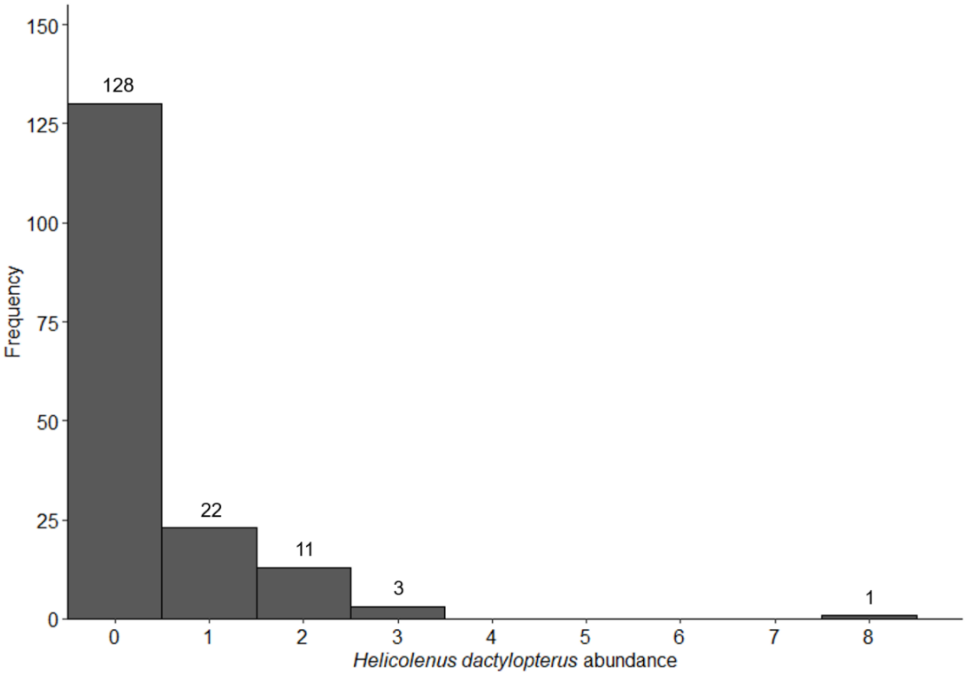


Figure 3.12: Frequency distribution of Helicolenus dactylopterus *abundance along video segments from the outer shelf and shelf edge of the South African south coast in September and October 2016. The frequency is indicated above each bar.*

At a fine spatial resolution, *H. dactylopterus* individuals were present across all longitudes surveyed, in all depth classes (from 117 to 653 m) and across all three habitat types (Figure 3.13). Contrary to the findings from the trawl surveys, abundance did not show a clear pattern with longitude but was greater in longitudes greater than 26°E. As in the trawl surveys, abundance in the video surveys showed a clear pattern with depth, peaking from 201 to 300 m where the median equalled 1 (IQR 0 – 2) fish per segment. The absolute abundance of *H. dactylopterus* was greatest in habitat type A, in which 42 fish were identified. However, when this was normalised by the number of segments occurring in each habitat type, a clear pattern was shown in which *H. dactylopterus* specimens were more abundant in habitats B (median 1, IQR 0.5 – 1) and C (median 1.5, IQR 0 – 2) compared to habitat A in which abundance per segment was typically zero, although outliers were present.

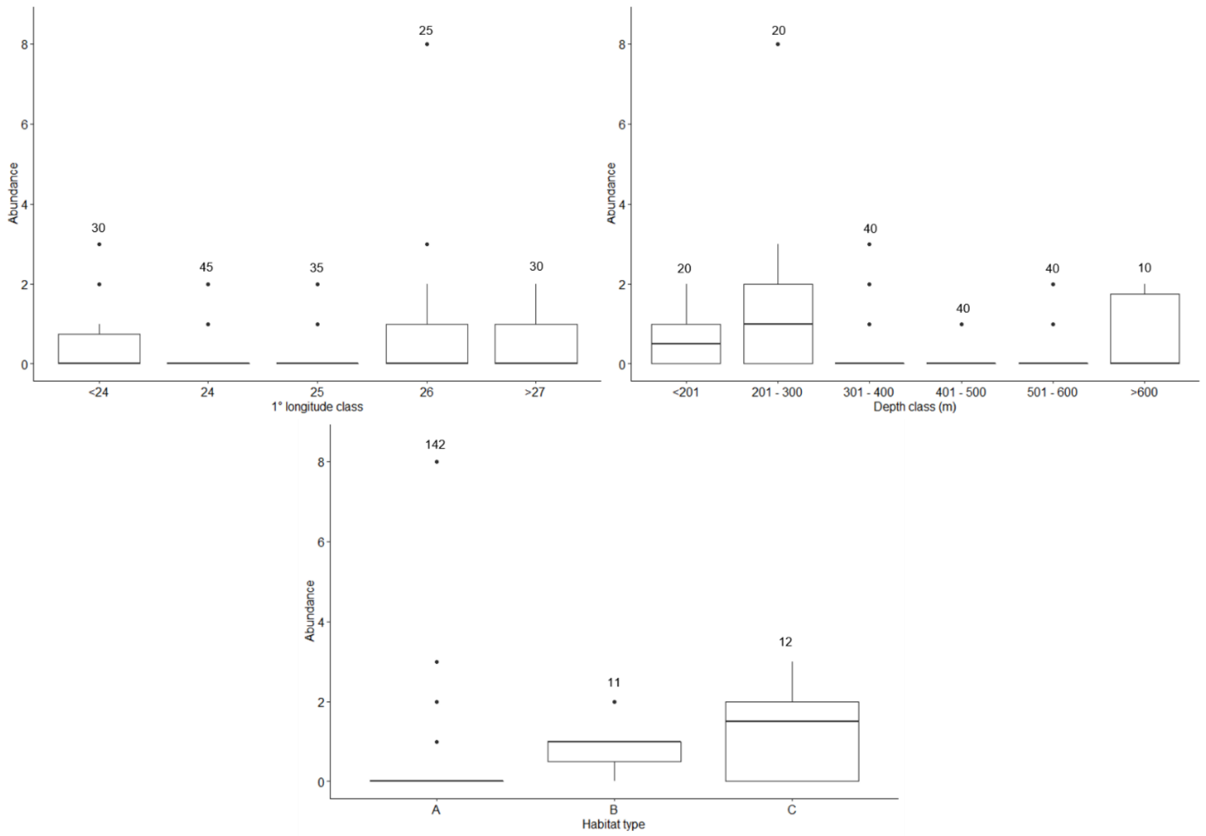


Figure 3.13: The overall patterns of Helicolenus dactylopterus *abundance along video segments with longitude class, depth class and habitat type. The sample size in each group is shown above the bar.*

The effect of longitude class, depth class and habitat on *H. dactylopterus* abundance in fine resolution video surveys was modelled assuming a Poisson distribution. The ratio of dispersion equalled 0.74. Longitude was non-significant (χ^2 = 6.44, df = 4, p = 0.17) and so the final model only included depth class and habitat type (Table 3.9).

Abundance was greatest in depths less than 400 m and peaked from 201 to 300 m. Unlike $M3_{ss}$, *H. dactylopterus* abundance in video surveys was significantly different among habitat types. Abundance was estimated to be highest in habitat type C and was significantly greater in this habitat type compared to habitat type A (p < 0.001) (Figure 3.14).

Table 3.9: Results of the model selection for M4 showing the significant covariates included in the final Poisson GLMM of Helicolenus dactylopterus *abundance (n=165).*

Variable dropped	**AIC**	**Df**	**Likelihood ratio test**
None	209.85		
Depth class	216.18	6	χ^2=16.32; p=0.006
Habitat type	226.01	2	χ^2=20.16; p<0.001

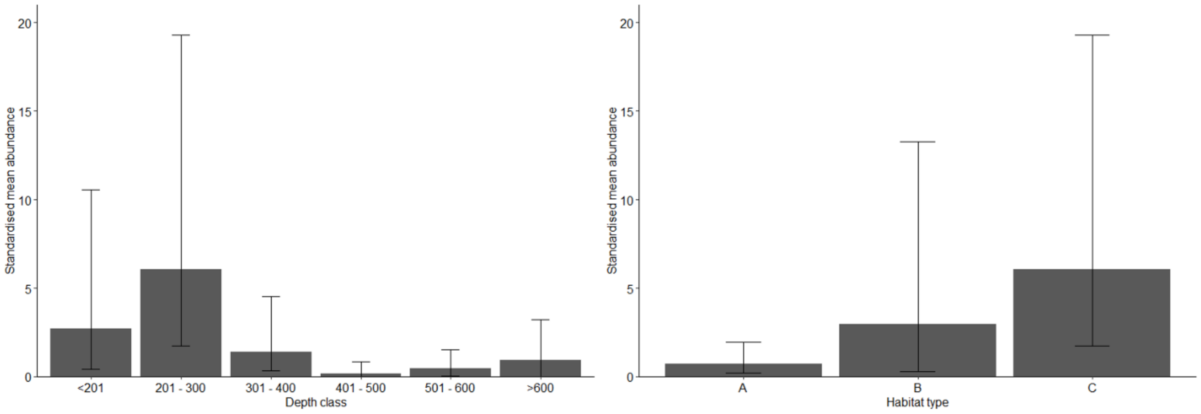


Figure 3.14: Standardised mean abundance (±95% CI) of Helicolenus dactylopterus *in video footage from the South African south coast in September and October 2016 (n = 165) by depth class and habitat type, as predicted by the Poisson GLMM (M4).*

Validation of M4 indicated no obvious violation of the model assumptions (Figure 3.22 in Section 3.7 Appendix), and the model was thus accepted.

Ontogenetic differences in habitat preference, fish behaviour and habitat use

Length measurements were obtained from 52 *H. dactylopterus* individuals recorded in the video segments analysed. Total length ranged from 69 to 461 mm (Figure 3.15).

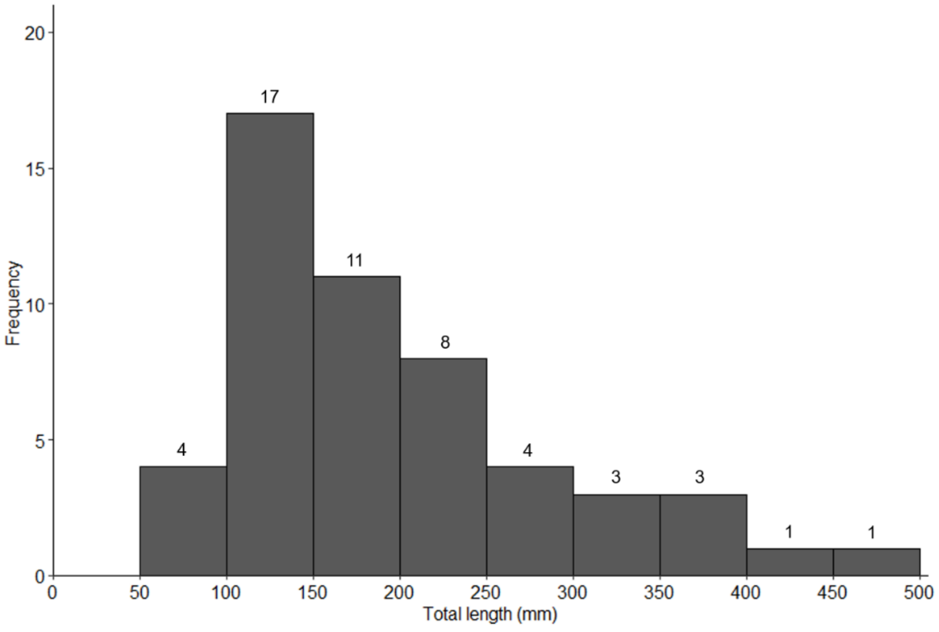


Figure 3.15: Length frequency distribution of Helicolenus dactylopterus *recorded in video segments from the outer shelf and shelf edge of the South African south coast in September and October 2016. The frequency is shown above each bar.*

Total length was approximately normally distributed. Variances were homogenous among longitude (F = 0.80, df = 4, p = 0.53) and depth classes (F = 0.59, df = 4, p = 0.67) but differed among habitat types (F = 5.57, df = 1, p = 0.02). One-way ANOVAs and Tukey's post-hoc tests were therefore used for the analysis of the effect of longitude and depth on total length and a Welch's ANOVA was used to analyse the effect of habitat type.

Total length differed among longitude classes, depth classes and habitat types (Figure 3.16). Only one fish that was measured occurred in the 401 – 500 m depth class and two fish occurred in habitat type B and so these observations were removed from further statistical analysis. While results should be interpreted carefully due to the low number of individuals observed, the largest fish occurred from 24 to 25°E and fish in this class were significantly larger (F = 6.94, df = 4, p < 0.001, Table 3.10) compared to fish in the other longitude classes. Smaller fish occurred in depths <201 m and from 301 to 400 m, but the effect of depth was not significant (F = 1.03, df = 4, p = 0.40). Total length was significantly greater in habitat type C (F = 21.87, df = 1, p = 0.04) compared to habitat types A and B.

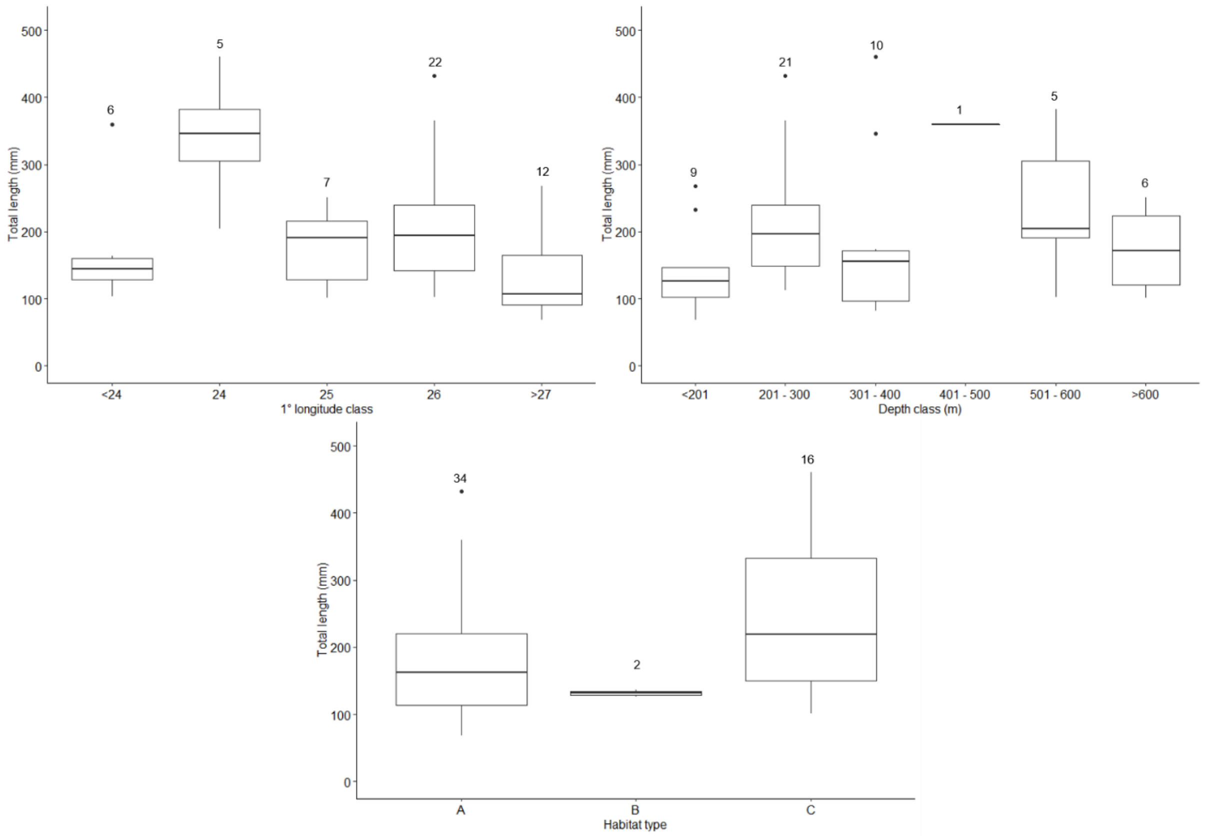


Figure 3.16: Boxplots showing the distribution of the total length (mm) of Helicolenus dactylopterus *in different longitude classes, depth classes and habitat types along video segments from the outer shelf and shelf edge of the South African south coast in September and October 2016. The sample size in each group is shown above the bar.*

Table 3.10: Tukey's post-hoc test results showing the pairwise comparison of the total length (mm) of Helicolenus dactylopterus *in different 1° longitude classes recorded in video segments. Significant p values (<0.05) are highlighted in bold.*

Longitude class	**<24°**	**24°**	**25°**	**26°**
24°	**0.007**			
25°	0.96	**0.006**		
26°	0.60	**0.01**	0.87	
>27°	0.10	**<0.001**	0.80	0.08

The positions and activities of 61 individuals were recorded. Most fish (88.52%) were observed on the seabed with the remaining individuals occurring near the seabed. Fish were observed swimming, hovering or moving on the seabed but most (54.10%) were resting on the seabed or sheltering near benthic features (34.43%) such as boulders, corals and anemones (Figure 3.17).

Fish position did not differ with benthic habitat type ($p < 0.05$) but activity was significantly different among habitats A, B and C ($\chi^2 = 22.33$, df = 8, $p = 0.004$, Figure 3.18). Most individuals in habitat A (72.22%) were observed resting on the seabed, while in habitat B an equal number of individuals (42.86%) were observed resting on the seabed and sheltering and in habitat C most individuals were observed sheltering near benthic structures (55.56%).

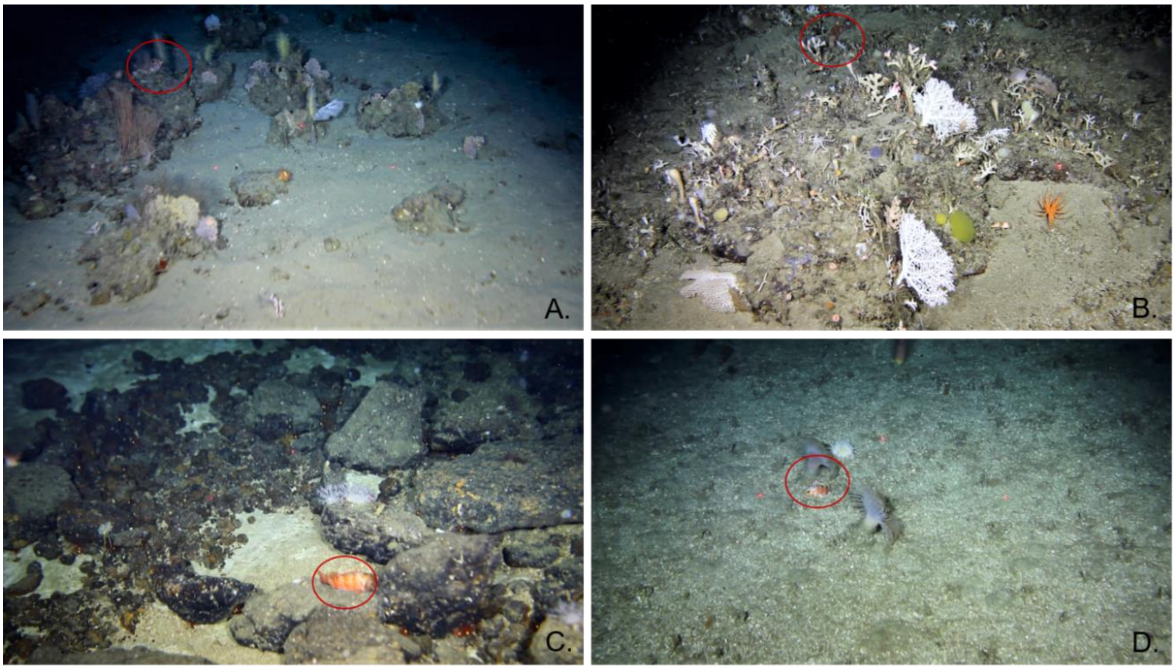


Figure 3.17: Examples of Helicolenus dactylopterus *(circled in red) sheltering in different habitat types observed in video footage collected along the outer shelf and shelf edge of the South African south coast in September and October 2016. Photographs were from A. transect DSC010, B. transect DSC012, C. transect DSC027 and D. transect DSC047.*

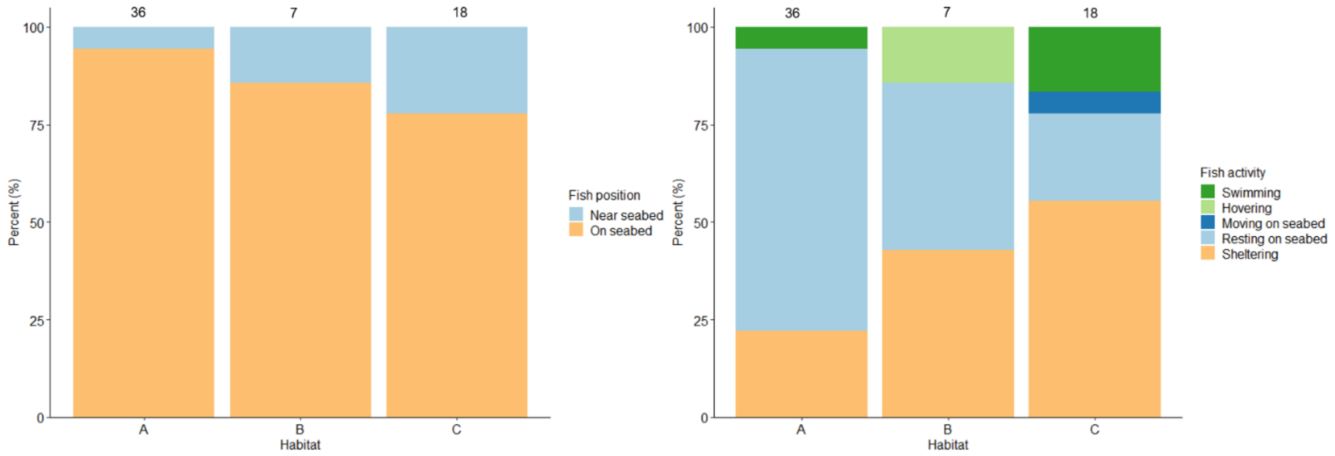


Figure 3.18: The frequencies (%) of Helicolenus dactylopterus *position and activity in the three habitat types observed in video footage collected along the outer shelf and shelf edge of the South African south coast in September and October 2016.*

3.5 Discussion

The analysis of the habitat preference of *H. dactylopterus* in South Africa using two different sampling methodologies at different resolutions allowed for the consideration of multiple spatial scales over which factors affecting habitat association may function. Although the video data were collected opportunistically, had a smaller sample size than the trawl data, and were spatially constrained, their inclusion in this study allowed for the sampling of a range of habitat types, including more complex rocky terrain. The inclusion of video data also allowed for the sampling of smaller fish, which were excluded in trawl surveys. Conversely, the trawl data did not adequately sample structurally complex habitat but provided a large sample size with thorough spatial coverage of the South African continental shelf and shelf edge. Given the general lack of data on structurally complex habitat types in shelf and shelf edge ecosystems in South Africa, the proportion of these habitats excluded by trawl surveys is presently unknown, but this is a potential area of further research.

The analysis of the trawl data highlighted the broad scale abiotic drivers of *H. dactylopterus* abundance, with longitude and depth being important correlates. Although the smaller sample size is a limitation that should be improved on in future studies, results from the video analysis reinforced the findings from the trawl data. Additionally, results from the video analysis demonstrated the influence of benthic habitat type on the abundance and distribution of *H. dactylopterus*, an interaction that was not discernible in the trawl data.

The analysis of *H. dactylopterus* abundance in trawl surveys confirmed that the species primarily occurs in the Atlantic. In all three models fitted to the broad resolution data, abundance decreased with an increase in longitude and extension into the Indian Ocean. Currie et al. (2019) suggested that there has been a minor south-westward shift in the average location of *H. dactylopterus* in South Africa but overall, the spatial distribution of the species has remained largely stable over the last 30 years. The findings from this study, coupled with those of Currie et al. (2019) are in agreement with the supposition that the distribution centre of *H. dactylopterus* occurs off central West Africa (Massutí et al., 2001) where abundance estimates were highest.

Previous studies have described *H. dactylopterus* as sedentary (Uiblein et al., 2003; D'Onghia et al., 2011; Santos et al., 2020). Findings from tagging studies done in the Azores suggest that adult migration does not occur (Aboim et al., 2005; Santos et al., 2020). Aboim et al. (2005) found that many tagged individuals were recaptured in the same location as they were originally caught, more than a year after tagging. Santos et al. (2020) found 80% of tagged and recaptured individuals were recaptured within 5 km of the original release site. Thus, as suggested by Aboim et al. (2005), the geographic expansion of *H. dactylopterus* is likely mainly reliant on pelagic larval dispersal. In this respect, the presence of the warm, poleward-flowing Agulhas Current on the east and south coasts of South Africa likely limits the geographic extension of the species during the larval phase northwards into the Western Indian Ocean. The Agulhas Current is one of the strongest western boundary currents in the world. It originates in the Mozambique Channel and travels down the east coast of South Africa, retroflecting at 21°E where water flows eastwards as the Agulhas Return Current at approximately 40°S (Gordon et al., 1987; Lutjeharms, 2006). The distribution of *H. dactylopterus* in the South West Indian Ocean (SWIO) reflects this water movement. The species has not been found further north than offshore of the uThukela Banks on the east coast of South Africa but does occur on seamounts in the SWIO, south of Madagascar (Nunoo et al., 2015).

The analysis of *H. dactylopterus* abundance in fine resolution video data revealed less of an effect of longitude. Several outliers were, however, observed in which increased abundances were present at some longitudes. The most notable outliers occurred at approximately 26°E, along transect DSC047. Large abundances of other fish and invertebrate species, including south coast rock lobster *Palinurus gilchristi*, were also observed along this transect. During the research cruise, it was noted that transect DSC047 occurred in a region where several large canyons were observed (K. Sink pers. comm.). The transect also occurred near the steep shelf edge where the depth increased from 230 m to 650 m within five kilometres. The proximity to and steepness of the shelf edge in this area may facilitate the transport of cold, nutrient-dense water from the slope to the adjacent, shallower continental shelf waters resulting in increased productivity in the area. These productivity increases may drive changes in abundance over relatively fine scales which are not discernible at a broad sampling resolution.

The effect of depth in structuring demersal fish communities is well documented globally (for example Costello et al., 2005; Quattrini et al., 2012; Milligan et al., 2016) and has been established on the west and south coasts of South Africa (Roel, 1987; Smale et al., 1993; Yemane et al., 2010; Atkinson et al., 2011; Kirkman et al., 2013; Yemane et al., 2014, 2015). *Helicolenus dactylopterus* was most abundant in depths from 100 to 600 m and abundance peaked in the 200 to 300 m depth range. These findings align with international literature in which the species is consistently reported to form an important component of demersal fish assemblages between 200 and 500 m (Massutí et al., 2001; Pirrera et al., 2009; Romeo et al., 2009).

In the South African context, previous studies have reported *H. dactylopterus* to occur in depths between 100 and 500 m (Smale and Badenhorst, 1991; Atkinson et al., 2011), supporting the findings in this study. On the south coast, Smale and Badenhorst (1991) found *H. dactylopterus* to be more abundant in waters deeper than 150 m and Smale et al. (1993) found the species to be prominent in shelf (90 – 190 m) and shelf edge/slope (>190 m) communities. On the west coast, Roel (1987) found *H. dactylopterus* to contribute substantially to the demersal community biomass on the continental shelf in waters less than 380 m. The occurrence of *H. dactylopterus* between 100 and 600 m coincides with the footprint of the offshore demersal trawl fishery which operates in depths between 110 and 1000 m (Fairweather et al., 2006; Sink et al., 2012a) and in which *H. dactylopterus* is caught in large quantities. On the west coast, trawling is concentrated between 300 and 500 m (Fairweather et al., 2006) and on the south coast, it is concentrated between 200 and 500 m (Wilkinson and Japp, 2005). A large portion of the South African *H. dactylopterus* population is thus susceptible to capture by the fishery. On the south coast, the peak in *H. dactylopterus* abundance overlaps with concentrated trawl effort.

The video analyses indicated no effect of depth on the total length of *H. dactylopterus.* These results are contrary to those reported in Chapter 2 in which data from commercial landings and some research trawls showed that larger fish occurred in waters deeper than 200 m. This was attributed to ontogenetic migration and has been widely reported in the species in the North Atlantic and Mediterranean (Kelly et al., 1999; Massutí et al., 2001; Pirrera et al., 2009). The differences observed here are most likely due to the lower number of fish measured in video analyses compared to those measured from commercial landings. Nevertheless, three age 0 fish (< 88 mm TL based on the von Bertalanffy growth model estimated in Chapter 2) were observed in video footage obtained from depths greater than 300 m. While the sample size is small, this finding may suggest that recruits have a wider bathymetric distribution than was previously recognised (Chapter 2), aligning with findings from the Mediterranean (Massutí et al., 2001; Pirrera et al., 2009).

As their name suggests, rockfish (*Sebastes* spp.) tend to be associated with complex, rocky reef habitat. Similar habitat usage is exhibited by many of the species within the sub-family, however, literature on *H. dactylopterus* has presented confounding results (for example D’Onghia et al., 2010, 2011). In this study, *H. dactylopterus* occurred across a range of different benthic habitat types, including reef habitat and that characterised by unconsolidated sediment. Broad resolution trawl data obscured the habitat findings to an extent. A significant relationship between *H. dactylopterus* abundance and habitat type was found at a broad resolution when depth was excluded from the model, however, when depth and habitat were included in the same model, habitat type was no longer important. This suggests that the habitat effect that was seen at a broad resolution was most likely confounded with depth. On the contrary, data from video footage at a fine spatial resolution highlighted the importance of rocky reef habitats to which a degree of habitat selectivity was shown by the species. Unconsolidated sediment was by far the most surveyed habitat type, but still, *H. dactylopterus* was more abundant on reef. Furthermore, observations of the total length of *H. dactylopterus* in video footage demonstrated that while smaller individuals (<150 mm) were observed, it was mainly larger individuals (>200 mm) that occurred in reef habitats. Similar patterns of increasing body size with increased topographic structural complexity have been reported for low-mobility, demersal *Sebastes* species (McGreer et al., 2020).

The benthic habitat preference shown by *H. dactylopterus* at the broad and fine spatial resolutions suggests that it is a transient reef species and indicates two alternatives. The first is that *H. dactylopterus* prefers and actively selects rocky reef habitat, at least during certain parts of its life or reproductive cycle, a signal that is only observable over a fine spatial scale using fine resolution data. The second and perhaps more plausible alternative is that *H. dactylopterus* occurs in multiple habitat types but is fished heavily on unconsolidated sediment, and thus the apparent habitat selection of the species is because of selection by the fishery. These two alternatives are not mutually exclusive and may both contribute to the pattern in habitat preference observed.

Aligning with the first alternative, the presence of larger fish in rocky habitats suggests that there may be an ontogenetic element to the habitat preference of *H. dactylopterus* as has been reported in the North Atlantic (Kelly et al., 1999) and the Mediterranean (Romeo et al., 2009; D’Onghia et al., 2010). D’Onghia et al. (2010) concluded that the greater abundance of adult specimens caught by longline in the coral habitat at the Santa Maria di Leuca (SML) coral province, relative to that outside of this habitat, was linked to spawning. Capezzuto et al. (2018) found large numbers of pre-spawning, spawning and spent individuals in cold-water coral habitats in the central Mediterranean, and concluded that these areas act as a spawning area for the species. Likewise, in Norway, larger *Sebastes* spp. were found in coral habitat than in non-coral habitat and dense aggregations of gravid individuals were observed in coral habitat in spring (Fosså et al., 2002; Husebo et al., 2002). In this study, fine resolution video sampling was undertaken during September and October when a peak in female spawning was observed in fish on the western Agulhas Bank (Chapter 2). *Helicolenus dactylopterus* individuals on the south coast may spawn over this period as well, although further research into this is required. Thus, the occurrence of spawning fish in the reef habitat observed in the video footage and the active selection of this habitat by adults for spawning is possible.

The presence of larger *H. dactylopterus* individuals in rocky habitat is, however, more likely related to fishing pressure. Unsurprisingly, dominant habitats in the South African demersal trawl footprint comprise sandy substrata on the outer shelf and shelf edge (Sink et al., 2012a). On the South African south coast average trawling intensity calculated from 2005 to 2018 was lower in areas characterised by more complex, rockier benthic habitat (Currie et al., 2021). Given the bathymetric distribution of the species, *H. dactylopterus* individuals occurring in low relief habitat characterised by unconsolidated sediment are thus subjected to greater fishing pressure than conspecifics that occur in complex rocky habitat, much of which is inaccessible to trawlers. Complex rocky habitat thus provides refuge from commercial trawling activities and individuals occupying this habitat type can attain large sizes.

Behavioural observations of *H. dactylopterus* demonstrated that the species primarily uses the complex rocky reef habitat for sheltering and refuge. Most individuals were observed seeking refuge under or next to benthic features. Even when in less structurally complex habitat with unconsolidated sediment, some individuals were observed trying to seek refuge under available structures such as anemones or octocorals. Almost all individuals were inactive and were closely associated with the seabed, regardless of the habitat in which they occurred. These observations align with previous accounts of the species in which it is described as a benthic sit-and-wait predator (Uiblein et al., 2003; D’Onghia et al., 2011). The cryptic colouration of the species coupled with the observed behaviour facilitates its ability to ambush prey while allowing it to seek refuge from predators (D’Onghia et al., 2011).

The rocky reef habitats with which *H. dactylopterus* was found to associate were characterised by the presence of bryozoans including those of the genus *Adeonella,* octocorals of the genera *Thouarella, Eleutherobia* and *Anthomastus* and lace hydrocorals of the family Stylasteridae. Recent work by Atkinson and Sink (2018) identified 22 potential VME indicator species occurring in South African benthic ecosystems, including *Adeonella* spp., *Thouarella* spp. and five stylasterine species. Both complex habitat types identified in this study (habitats B and C) were characterised by the presence of potential VME indicator species. The role of these deep-water reef communities in providing refuge for *H. dactylopterus* from fishing pressure, and their potential use as a spawning area by the species, highlights the roles and the importance of these habitats in the renewal of the South African *H. dactylopterus* population in neighbouring trawl grounds (D’Onghia et al., 2016; Capezzuto et al., 2018). Furthermore, although much of the more complex reef habitat is inaccessible to trawlers, some hard ground habitats do occur within the demersal trawl footprint (Sink et al., 2012a). The association of *H. dactylopterus* with habitat that is characterised by the presence of VME indicator species suggests that there may be some level of interaction between these ecosystems and the South African demersal trawl fishery, in which *H. dactylopterus* is caught. Interactions may include physical damage to VME species due to contact with trawl gear. This has implications for the management of the fishery in terms of the spatial protection of these ecosystems and the implementation of move-on rules for vessels.

3.6 Conclusion

The data analysed in this chapter provided comprehensive insight into the association of *H. dactylopterus* with certain habitat features on the outer continental shelf and shelf edge of South

Africa. The results demonstrated the importance of including data obtained using different sampling techniques at different resolutions to account for factors that influence habitat associations that operate over a range of spatial scales.

Helicolenus dactylopterus is primarily an Atlantic species. The distribution of the species is likely driven by predominant ocean currents, with the Agulhas Current probably limiting the further geographic expansion into the Western Indian Ocean region. As has been found in other parts of its range, in South Africa, *H. dactylopterus* mainly occurs in depths from 100 to 600 m, with abundance peaking between 200 and 300 m. The depth pattern of the species overlaps substantially with the depth distribution of the South African demersal trawl fishery, particularly on the south coast, indicating that a large portion of the population is susceptible to capture by the fishery. Findings from broad and fine spatial resolution data indicated that *H. dactylopterus* occurred over a range of different benthic habitat types, confirming that the species is a transient reef species and is not exclusively associated with rocky reef habitat. Nevertheless, some selection of more complex rocky habitat was highlighted in the video analysis. Individuals, mainly adults larger than 200 mm, were abundant in complex benthic habitats typical of the deep-water rocky ecosystems on the South African outer shelf and shelf edge. It was postulated that the selection of rocky habitat was due to active habitat selection by the species for spawning and sheltering, the selection of large fish on more accessible, unconsolidated substrata by the fishery, or was as a result of a combination of these two alternatives. The role of reef communities as a refuge for *H. dactylopterus* from fishing pressure and their potential use as a spawning area highlights the importance of these habitats in the renewal of the South African *H. dactylopterus* population in neighbouring trawl grounds.

3.7 Appendix

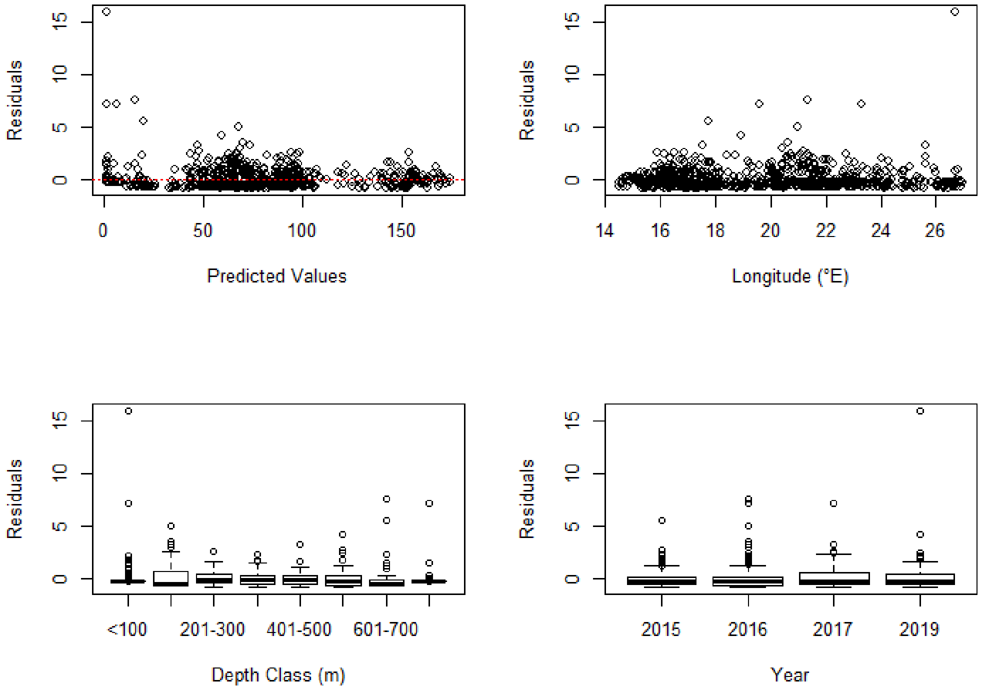


Figure 3.19: The validation for model $M1_{depth}$ of Helicolenus dactylopterus *abundance and presence in research trawl samples collected from the west and south coasts of South Africa from 2015 to 2019.*

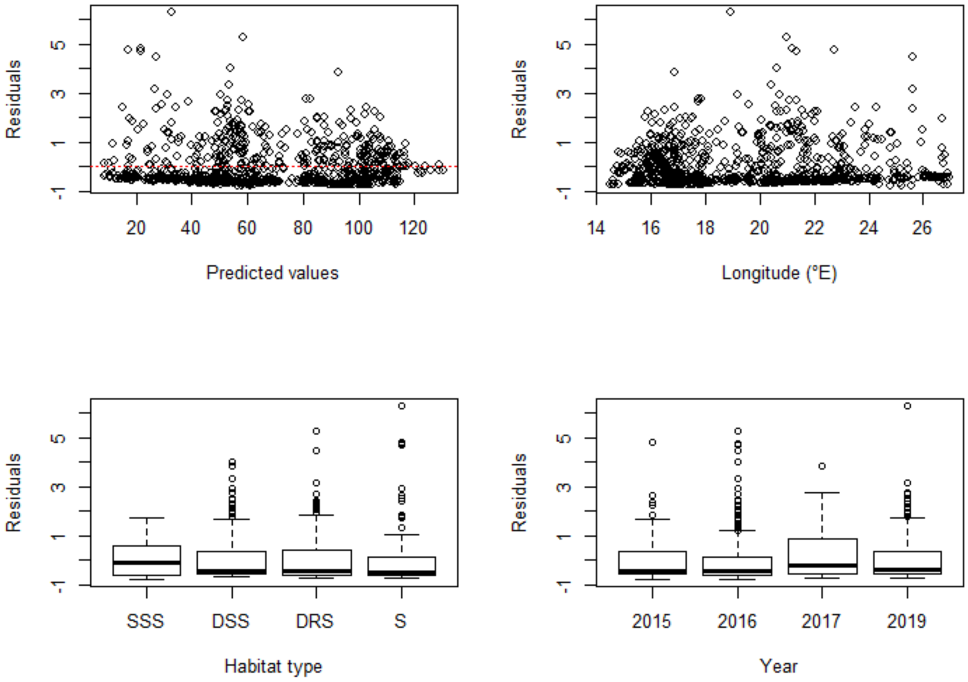


Figure 3.20: The validation for model $M2_{habitat}$ of Helicolenus dactylopterus *abundance and presence in research trawl samples collected from the west and south coasts of South Africa from 2015 to 2019.*

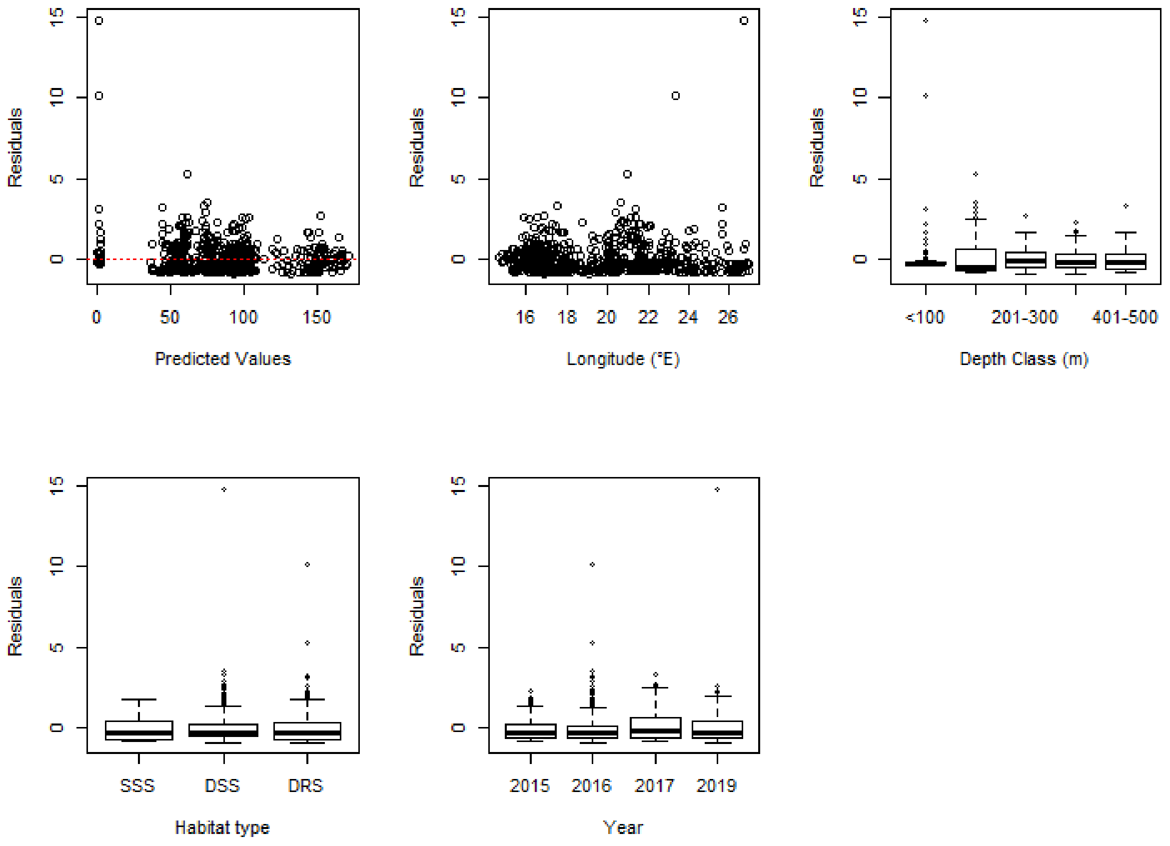


Figure 3.21: The validation for model $M3_{SS}$ *of* Helicolenus dactylopterus *abundance and presence in research trawl samples collected from the west and south coasts of South Africa from 2015 to 2019.*

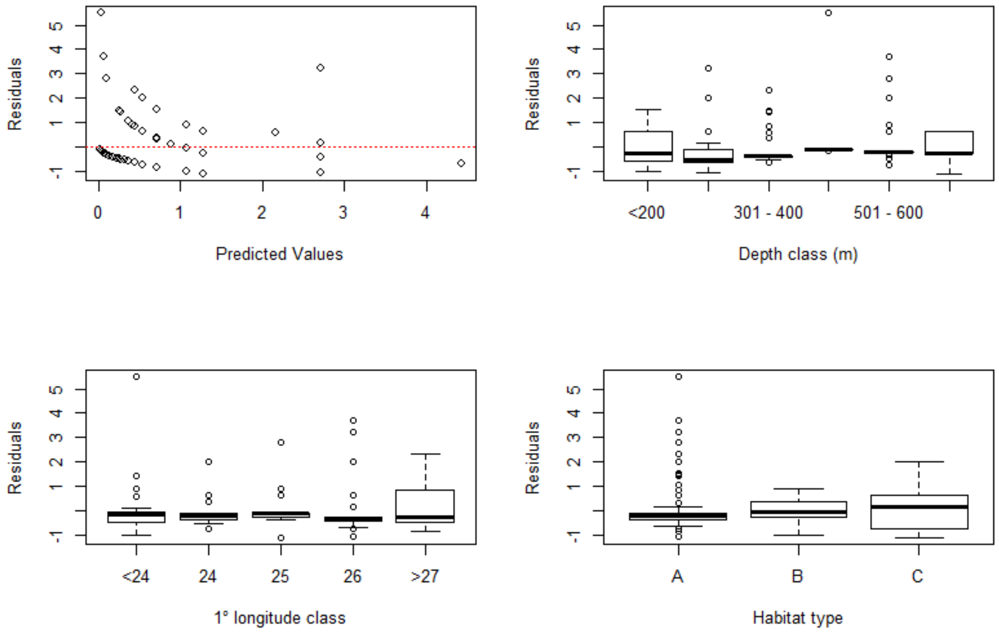


Figure 3.22: The validation for model M4 of Helicolenus dactylopterus *abundance in video segments analysed from transects conducted along the outer shelf and shelf edge of the South African south coast in September and October 2016.*

CHAPTER 4

ABUNDANCE TRENDS OF *HELICOLENUS DACTYLOPTERUS* IN SOUTH AFRICA

4.1 Abstract

Two independent long-term time-series were examined to describe the population trends and conservation status of *Helicolenus dactylopterus* in South Africa. Catch-per-unit-effort (CPUE) in research trawls (from 1987 to 2019) and commercial trawls (from 2004 to 2018) were standardised using delta lognormal Generalised Linear Models (GLMs). Standardised CPUE estimates from both datasets were used in a population risk assessment in which the Bayesian state-space framework, Just Another Red List Assessment (JARA), was applied. The significant ($p<0.001$) predictor variables included in the final GLM fitted to the research data were year, location, depth class and fishing cluster, and those included in the final model fitted to the commercial data were vessel, year, season, location, depth class and fishing cluster. Fishing cluster was derived by clustering the catch composition data of each trawl. The inclusion of fishing cluster in the models provided insight into the species associations of *H. dactylopterus* and accounted for fishing strategies applied by commercial skippers. *Helicolenus dactylopterus* CPUE was greatest in trawls in which *Genypterus capensis*, *Lophius vomerinus*, *Lepidopus caudatus* and *Zeus capensis* were caught. In research and commercial trawls, *H. dactylopterus* CPUE was greatest in depths between 301 and 400 m. No seasonal trends in commercial catch data were detected. Standardised CPUE time-series from research and commercial trawls were comparable. *Helicolenus dactylopterus* showed sustained population growth from the early 1990s to 2001 when the population more than doubled, after which there was an approximate 50% decline until 2005 and then subsequent growth until 2010. Since 2011, abundance trends have remained largely stable. Although the life history characteristics of *H. dactylopterus* suggests that the species has low productivity and resilience, the population risk assessment conducted provided an optimistic outlook for *H. dactylopterus* in South Africa. Relative abundance increased by 0.83% per year over the study period. Population growth accelerated over time increasing by 1.08% per year from 1990 to 2019, and by 1.42% per year since 2005. The JARA model predicted a 45.9% growth in the South African population of *H. dactylopterus* over three generation lengths, classifying the species to be of low conservation concern.

4.2 Introduction

The quantification and understanding of variation in population abundance over time and space is a central topic in ecological research (Gunderson, 1993). In the case of a harvested resource, knowledge of population trends is fundamental in developing effective management strategies. The detection of temporal trends in abundance is an important component of conservation biology and abundance indices are required to assess the status of fish stocks. Moreover, information on the abundance of a species over time can provide insight into community structure and function (Verberk, 2011).

Many Sebastinid species are vulnerable to exploitation due to their conservative life history characteristics (Love et al., 1990; Love et al., 2002). In the North East Pacific, on the west coast of the United States, several Sebastinids, mainly in the genus *Sebastes,* have experienced substantial declines in abundance over the last 40 years (Love et al., 1998; Parker et al., 2000; Yoklavich et al., 2007). These declines, in part are attributed to oceanographic variability but are also largely a result of extensive fishing pressure (Love et al., 1998). In the 1990s, seven *Sebastes* species were declared by the National Oceanic and Atmospheric Administration (NOAA) as being overfished and extensive management actions had to be implemented to support the recovery of these populations (Ralston, 1998; Enticknap and Sheard, 2005; Yoklavich et al., 2007).

Helicolenus dactylopterus shares many of the conservative life history traits of its close relatives. The species is a periodic strategist in that it is slow-growing and long-lived but has high fecundity (Muñoz and Casadevall, 2002; Sequeira et al., 2015). In South Africa, the length-based growth rate of the species was estimated to be 0.13 year^{-1} and the maximum age was 32 years (Chapter 2). *Helicolenus dactylopterus* is considered to have very low population resilience based on the productivity index parameters suggested by Musick (1999).

On the global scale and regionally in Europe and the Mediterranean, the International Union for the Conservation of Nature (IUCN) categorises *H. dactylopterus* as being of Least Concern (Papaconstantinou et al., 2011; Lorance et al., 2015; Nunoo et al., 2015). The population trends of *H. dactylopterus* have not been quantified. Categorisation was based on the widespread distribution of the species and the assumption that population decline has not occurred at the rate required for a species to be listed as threatened under Criterion A of the IUCN Categories and Criteria (Malak et al., 2011; Papaconstantinou et al., 2011; Lorance et al., 2015; Nieto et al., 2015; Nunoo et al., 2015). Criterion A is the most widely used criterion to assess the conservation status of a species in the context of the IUCN Red List (Winker et al., 2020). The criterion is based on population decline that has occurred over the last ten years or three generation lengths, whichever is longer (IUCN, 2012).

Concerns about the impacts of fishing pressure on *H. dactylopterus* populations in the North Atlantic and the Mediterranean have, however, been raised. Throughout the Mediterranean declining mean lengths of *H. dactylopterus* in trawl catches have been reported with catch being dominated by recruits and juveniles (Massutí et al., 2000; Pirrera et al., 2009; Consoli et al., 2010). Larger *H. dactylopterus* specimens are more fecund than smaller conspecifics (Muñoz and Casadevall, 2002; Sequeira et al., 2015). Size truncation of fished *H. dactylopterus* populations may thus be indicative of longevity overfishing (Beamish et al., 2006). In Ireland, a recent assessment of *H. dactylopterus* indicated that since 2004 abundance was below the 75th percentile calculated from historical data and concluded that the species was not compatible with Good Environmental Status (Palma-Pedraza et al., 2020). Improved collection of abundance data and analysis of abundance trends of this species in these areas is being prioritised (Santos et al., 2020).

In South Africa, there are several data sources from which abundance information for *H. dactylopterus* can be obtained. Chief among these is the research trawl survey dataset. The use of research survey data in estimating abundance indices is beneficial in that surveys have a random stratified design to reduce the effect of unknown and potentially confounding factors (Hilborn and Walters, 1992; Gunderson, 1993; Rago, 2005). Site selection and gear use are controlled and all catch is recorded appropriately (Hilborn and Walters, 1992). The collection of these data are however limited due to costs and generally have limited temporal and spatial coverage (Hilborn and Walters, 1992).

Commercial catch and effort data are also available. In contrast to the research trawl data, commercial data are less temporally or spatially limited and provide higher sample numbers (Hilborn and Walters, 1992). Such catch and effort data, typically summarised as catch-per-unit-effort (CPUE), can be obtained in several ways including from observer records, from landings data and from logbooks (Hilborn and Walters, 1992). Logbooks can provide valuable and detailed information on the catch at a fine spatial resolution (i.e., per trawl), but rely on accurate reporting by skippers (Hilborn and Walters, 1992; Gunderson, 1993). For a bycatch species such as *H. dactylopterus,* catch volumes may be underestimated due to insufficient reporting of discards. In addition, logbook data is constrained by standardisation issues which may confound the interpretation of abundance indices (Gunderson, 1993). Catch rates may be affected by several factors including differences in vessels, fishing gear and the fishing strategy applied. Standardisation of these effects is therefore required and is most often achieved using generalised linear modelling (GLM) which allows for the estimation of CPUE while considering the effects of a linear combination of some predictor variables (Maunder and Punt, 2004).

In a multispecies fishery such as the demersal trawl fishery, accounting for fishing strategy in the standardisation of CPUE data is an important consideration. The spatial distribution of fish is not random, and most species, including *H. dactylopterus* (as shown in Chapter 3), are associated with specific habitats. Fishing strategy is likely influenced by skippers choices in fishing techniques, fishing grounds or habitat types to allocate more effort towards a particular target species (Winker et al., 2013), and away from other species. The catch composition will vary accordingly (Winker et al., 2014). Fishing strategy can thus influence the observed abundance trends and information on catch composition can reflect the fishing strategy employed (Pelletier and Ferraris, 2000; Deporte et al., 2012; Winker et al., 2013).

Winker et al. (2017) conducted a preliminary investigation in which geostatistical delta-generalised linear mixed models (geostatistical GLMMs) were fitted to demersal research trawl survey data to estimate abundance indices for prioritised bycatch species in the demersal trawl fishery, including *H. dactylopterus*. No further work on quantifying the abundance of *H. dactylopterus*, either in research trawl surveys or in commercial catch in South Africa, has, however, been conducted. Consequently, there is little information to support the quantitative assessment of the species and as a result, the capture of *H. dactylopterus* (and others) as bycatch in the demersal trawl fishery is currently managed through effort limitation (SADSTIA, 2019). There remains a need to further investigate the catch rate trends and to estimate abundance indices of *H. dactylopterus* in South Africa. This information will improve understanding of the population status in South African waters, with application to conservation assessment and the management of the demersal trawl fishery. It will also provide ecological insight into the species associations and interactions in demersal fish communities.

This chapter aimed to estimate and assess the trends in relative abundance of *H. dactylopterus* in South Africa using two data sources to classify the national conservation status of the species. There were three objectives. The first objective was to standardise and investigate the

CPUE trends of *H. dactylopterus* in research trawl surveys conducted in South Africa from 1987 to 2019. The second objective was to standardise and investigate the CPUE trends of *H. dactylopterus* caught in the South African demersal commercial trawl fishery. Finally, research and commercial trawl derived CPUE trends were compared and were used to estimate the population changes of *H. dactylopterus* in South Africa over the last 30 years and to infer its conservation status at a national scale in the context of the IUCN Species Red List.

4.3 Materials and methods

4.3.1 Research trawl data

Fisheries independent data were obtained from demersal research trawl surveys conducted by the Fisheries Branch of DFFE. Research trawl surveys were undertaken in South Africa since 1984 (Department of Agriculture Forestry and Fisheries, 2016). The main objective of these surveys is to estimate the abundance of hake, *Merluccius paradoxus* and *M. capensis*, and other demersal fish on the South African continental shelf and slope. Surveys are conducted annually during summer on the west coast, from the Namibian border to approximately 20°E, and during autumn on the south coast, from 20°E to approximately 27°E off Port Elizabeth. On occasion, additional surveys were conducted during winter on the west coast and during spring on the south coast. During each survey, trawl sites are selected using a random depth-stratified approach. Trawl duration at each site is typically 30 minutes and towing speed is approximately 3.5 knots.

Samples are collected using a 55 m German trawl net with a 75 mm mesh codend and a 35 mm mesh liner. Since 2003 there has been a change to the configuration of the trawl gear to prevent horizontal over-spreading of the net opening. Before 2003, a two-panel 55 m German trawl net was used with a 2 m vertical and 26 m horizontal mouth opening and door spread was 120 m (Yemane et al., 2008; Atkinson et al., 2011). Subsequently, a four-panel net has been used with a 3 to 4 m vertical and 20 to 29 m horizontal mouth opening and a door spread of 60 to 75 m (Atkinson et al., 2011). The increased vertical mouth opening of the new gear has resulted in greater sampling of the water column and the narrower door spread has a reduced herding effect (Atkinson et al., 2011).

For each trawl sample, the catch composition as abundance and weight of each species is recorded. Other auxiliary data recorded include the start and end time and data of each trawl, the start and end position of each trawl and the start and end depth of each trawl.

Trawl survey data collected from 1987 to 2019, comprising 62 surveys, were used. No surveys were conducted in 1989, 1998, 2000, 2018 and 2020. Based on the findings in Chapter 3, in which *H. dactylopterus* primarily occurred in waters deeper than 100 m, trawls between 100 and 700 m were included. All failed trawls, trawls shorter than 20 minutes and those in which no species were caught were excluded from the analysis. Consequently, 4 455 trawls were included in this analysis (Figure 4.1).

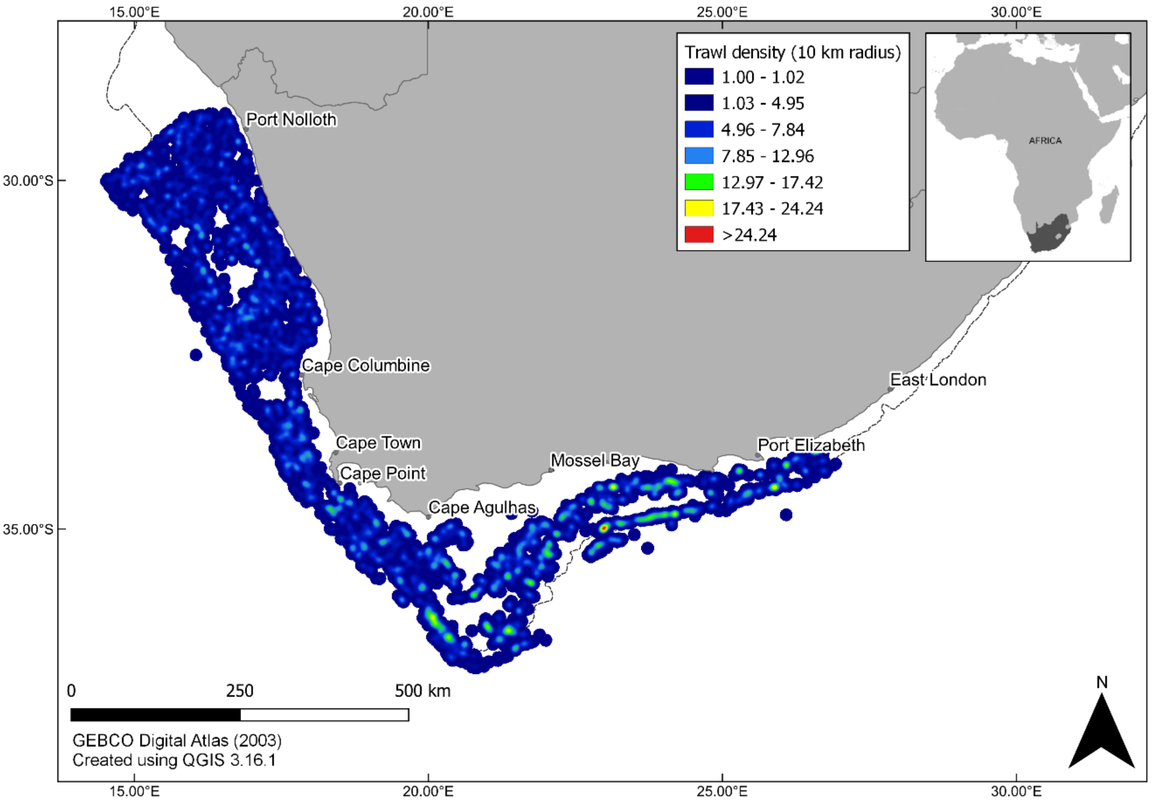


Figure 4.1: Heatmap showing the spatial distribution of research trawls, conducted from 1987 to 2019, included in this study, represented as the number of trawls in a 10 km radius. The dashed line shows the 200 m bathymetric contour derived from the GEBCO Digital Atlas (IOC et al., 2003).

4.3.2 Commercial trawl catch and effort data

Fisheries dependent data were obtained from commercial logbook records from the South African demersal trawl sector. Commercial logbook records are required of all fishing operations by rights holders in the sector and the data are recorded on a database that is curated by DFFE. Records comprise catch composition and weight per species per trawl estimated by the skipper, the vessel number, the company number, trawl start and end date and time, start and end locations, depth, duration of trawling and concurrent metocean conditions.

Records are available since 1983 but it was only in 2001 that commercial skippers were requested to start recording the start and end positions of trawls. Spatial reporting of commercial trawls improved from 2004 onwards (T. Fairweather 2020 pers. comm.). Catch data from 2004 to 2018 were thus used in this study. Data from 2019 onwards were not available at the time of data acquisition. As for the research data, only trawls from 100 to 700 m were included. All trawls in which there were conceivable errors in the values recorded, such as negative values for the start date and time, location, depth or trawl duration were excluded from the analyses as were all trawls for which there were no effort, location or depth data. Unsuccessful trawls in which no species were caught and trawls shorter than one hour or longer than six hours were also excluded.

The South African demersal commercial trawl dataset comprised 188 commercial vessels from 74 companies. These included demersal trawl vessels and those which have dual rights to use demersal trawl gear and mid-water trawl gear. To reduce the variability in vessels in operation over the 15 years, only trawls that were conducted by vessels that were in operation for at least eight years (between 2004 to 2018) and that conducted more than 0.1% of trawls were included. This ensured that annual vessel turnover remained below 10%. Overall, a total of 61 vessels that conducted 309 075 successful trawls in the South African EEZ in depths from 100 to 700 m were included in the analysis (Figure 4.2).

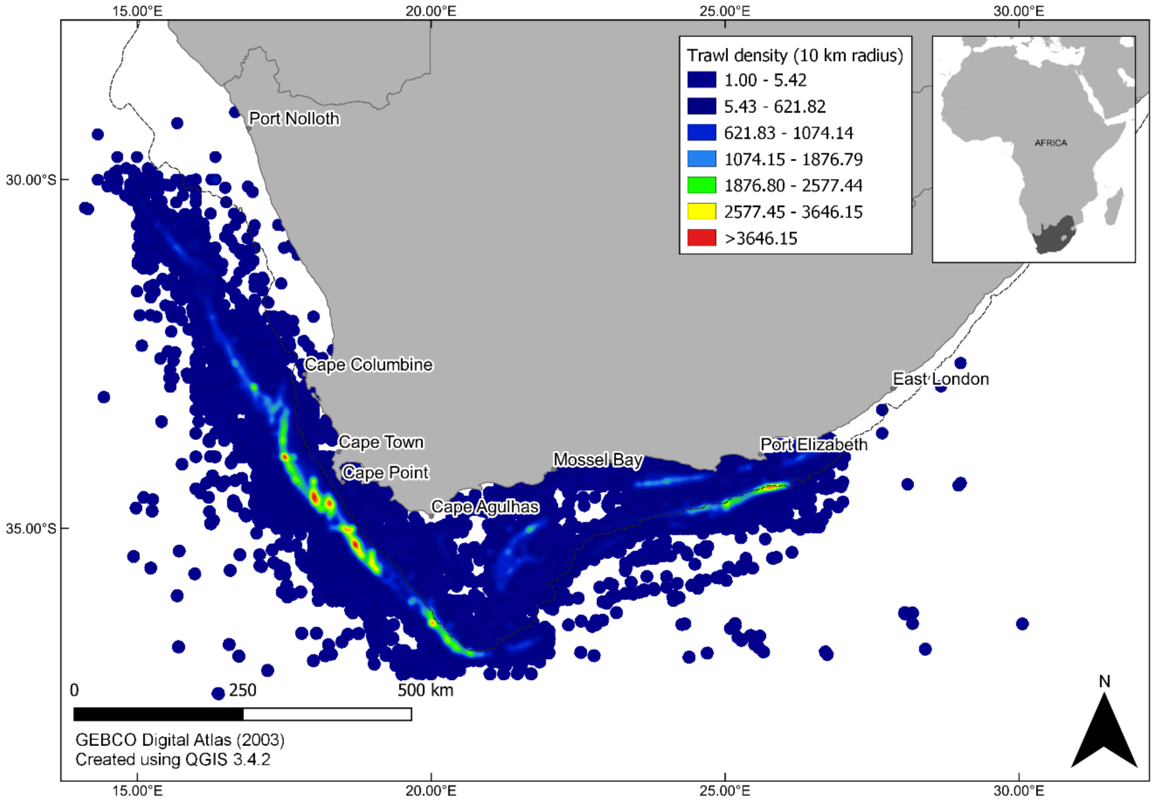


Figure 4.2: Heatmap showing the spatial distribution of the commercial trawls, conducted from 2004 to 2018, included in this study, represented as the number of trawls in a 10 km radius. The dashed line shows the 200 m bathymetric contour derived from the GEBCO Digital Atlas (IOC et al., 2003).

4.3.3 CPUE standardisation and estimation of relative abundance indices

Generalised Linear Modelling (GLM) was used to standardise the CPUE of *H. dactylopterus* caught in research and commercial trawls. Trawl distance and wingspread were not recorded in commercial logbook data and so could not be used to account for the difference in effort per trawl. For both research and commercial trawl datasets, *H. dactylopterus* CPUE was expressed as biomass (kg) normalised by trawl duration (hours).

For the research data, the predictor variables that were considered were all categorical and included year, location, depth class and gear type (Table 4.1). Likewise, for the commercial data, the predictor variables were categorical and included vessel number, year, season, location and depth class (Table 4.1). Season was not incorporated in the model fitted to research trawl data as surveys were conducted on the west and south coasts during specific seasons only. For both datasets, trawls were grouped into five locations and depth was binned into 100-m depth classes (Table 4.1). It was assumed that the depth of each trawl did not vary by more than 100 m.

Fishing cluster was included as an additional predictor variable in models fitted to both research and commercial data. The development of fishing clusters involved ordination and clustering of the catch composition data to provide insight into the association among species caught in trawls and, in the case of commercial data, to provide information on the fishing strategies employed. In the research and commercial trawl datasets, the catch composition was limited to include those species that contributed more than 0.5% and 0.1% to the total catch weight, respectively. For each dataset, a catch composition matrix, comprising species CPUE ($kg.hr^{-1}$) records, was created. The CPUE of each species was standardised into relative proportions per trawl (Winker et al., 2013) and then was square-root transformed to downweight the contribution of highly dominant species (Clarke and Warwick, 2001).

Initially, a Principal Component Analysis (PCA) was applied to the standardised and transformed multidimensional catch composition matrices to reduce each dataset to a smaller number of informative Principal Components (PCs) (Deporte et al., 2012; Winker et al., 2013). The number of PC axes to be retained was selected using a combination of the Kaiser-Guttman rule (Guttman, 1954), in which only PCs with an eigenvalue greater than one were retained, and a non-graphical solution to Cattel's scree-test termed the Optimal Coordinate test (Raîche et al., 2013; Winker et al., 2014).

The derived PC axes were taken forward into the cluster analyses in which the non-hierarchical clustering method Clustering Large Applications (CLARA) (Struyf et al., 1996; Kaufman and Rousseeuw, 2005) was used (Winker et al., 2013). For the research and commercial trawl datasets, the CLARA algorithm applied the Partitioning Around Medoids (PAM) method to 200 samples of the larger datasets, each comprising 250 records. The optimal number of clusters were considered to be the number of retained PCs plus one (Winker et al., 2014; Parker et al., 2017). For the research data, six PCs were retained and seven clusters were selected for the CLARA analysis. For the commercial data, three PCs were retained and so four clusters were selected for the CLARA analysis. The identified clusters were aligned with each trawl record in the original datasets and the covariate, fishing cluster, was treated as a categorical factor (Table 4.1).

Table 4.1: Factors used in the Generalised Linear Models to standardise the CPUE of Helicolenus dactylopterus *caught in the South African commercial demersal trawl fishery from 2004 to 2018 and in research trawls conducted in South Africa from 1987 to 2019.*

Data	**Categorical factor**	**No. of levels**	**Description**
Research trawl	Gear type	2	The trawl gear configuration that was used, either old (before 2003) or new (from 2003 onwards).
	Year	29	The year in which each trawl was conducted: from 1987 to 2019.
	Location	5	The location in which each trawl was conducted: 1 (north of Cape Columbine), 2 (Cape Columbine to Cape Point), 3 (Cape Point to Cape Agulhas), 4 (Cape Agulhas to Mossel May), 5 (north-east of Mossel Bay).
	Depth class	5	The start depth of each trawl binned into 100-m depth classes: <201, 201-300, 301-400, 401-500, 501-600, >600.
	Fishing cluster	7	The fishing cluster in which each trawl occurred, based on the respective catch composition, as determined by the CLARA analysis.
Commercial catch and effort	Year	15	The year in which each trawl was conducted: from 2004 to 2018.
	Season	4	The season in which each trawl was conducted: summer (December to February), autumn (March to May), winter (June to August), spring (September to November).
	Location	5	The location in which each trawl was conducted: 1 (north of Cape Columbine), 2 (Cape Columbine to Cape Point), 3 (Cape Point to Cape Agulhas), 4 (Cape Agulhas to Mossel May), 5 (north-east of Mossel Bay).
	Depth class	5	The start depth of each trawl binned into 100-m depth classes: <201, 201-300, 301-400, 401-500, 501-600, >600.
	Fishing cluster	4	The fishing cluster in which each trawl occurred, based on the respective catch composition, as determined by the CLARA analysis.

Data exploration followed the protocols detailed by Zuur et al. (2010). The distributions of the predictor and response variables were assessed by plotting boxplots and frequency distributions, and outliers were identified. Collinearity between predictor variables was assessed by calculating the generalised variance inflation factors (GVIF) (Fox and Monette, 1992).

In the research dataset, gear type and year were related. The two different gear types were used consecutively. Old and new gear configurations were only used in the same year in 2003. Gear type and year could, therefore, not be included in the same model. Before fitting the models described in equations 4.1 to 4.4 below, an initial, simplified model was fitted to research trawl data in 2003 only, to establish the effect of gear type on *H. dactylopterus* CPUE. A delta model with a lognormal distribution, as described below, was used and the other predictor variables included in the simplified model were location and depth class. Gear type did not have a significant effect on *H. dactylopterus* CPUE and thus was not included in further modelling. No collinearity was found between the other predictor variables in the research trawl dataset ($GVIF^{(1/(2 \times Df)} < 1.73$). In the commercial dataset, no collinearity was found ($GVIF^{(1/(2 \times Df)} < 1.73$).

To account for the high proportion of zeros in the catch data, which is typical of a bycatch species, two delta models with a lognormal distribution (Lo et al., 1992) were used to standardise the CPUE of *H. dactylopterus* caught in research and commercial trawls. There are several alternatives to deal with zero-inflated catch data (Maunder and Punt, 2004). The use of delta models was recommended by Shono (2008) and ICES (2018) and was used in the standardisation of *H. dactylopterus* CPUE in the Azorean longline fishery (Santos et al., 2020).

The delta lognormal model had two components. First, the probability of obtaining a zero or positive observation of *H. dactylopterus* was modelled using a binomial distribution and a logit link function. The positive catch rate, where the catch of *H. dactylopterus* was non-zero, was then modelled separately using a lognormal distribution and an identity link function. The lognormal distribution was used as positive catch rates were right-skewed (Winker et al., 2013). The positive CPUE was thus transformed to its natural logarithm, ln(CPUE).

The binomial model component for the probability of obtaining zero catch in research trawls was, therefore, of the form:

$$logit(y) = year + location + depth\ class + fishing\ cluster + error, \qquad (4.1)$$

the lognormal model component for the positive catch rate in research trawls was of the form:

$$\ln(y) = year + location + depth\ class + fishing\ cluster + error, \qquad (4.2)$$

the binomial model component for the probability of obtaining zero catch in commercial trawls was of the form:

$$logit(y) = vessel + year + season + location + depth\ class + fishing\ cluster + error, \tag{4.3}$$

and the lognormal model component for the positive catch rate in commercial trawls was of the form:

$$\ln(y) = vessel + year + season + location + depth\ class + fishing\ cluster + error, \tag{4.4}$$

where y is the presence/absence or CPUE of *H. dactylopterus* respectively.

The optimum combination of predictor variables for the binomial and lognormal model components in each model was selected using the Akaike's Information Criterion (Zuur et al., 2009) and sequential χ^2 tests to minimise model deviance (Ortiz and Arocha, 2004; Pons et al., 2010). Based on the degrees of freedom added to each model with the addition of every predictor variable, the change in model deviance was approximately χ^2 distributed. The effect of adding each predictor to the models was therefore assessed using the χ^2 statistic (Ortiz and Arocha, 2004; Winker et al., 2013) and significant predictors ($p < 0.05$) were retained. The total deviance explained by each component of the final models fitted to the research and commercial trawl datasets was calculated using the pseudo coefficient of variation where:

$$R^2 = 1 - \frac{residual\ deviance}{null\ deviance} \tag{4.5}$$

The models were validated by plotting Pearson's residuals against the fitted values and each predictor variable.

Using the final models fitted to the research and commercial data, standardised *H. dactylopterus* CPUE trends were estimated by fixing all predictor variables, apart from the variable of interest. Predictor variables were fixed to the levels in which mean nominal *H. dactylopterus* CPUE was greatest in each dataset.

Predicted values were calculated from each model component separately. Expected mean CPUE was calculated as the probability of a positive observation of *H. dactylopterus* multiplied by the positive catch rate of *H. dactylopterus* for a given factor level in each model (Lo et al., 1992; Maunder and Punt, 2004).

For research and commercial datasets, the annual trends in standardised CPUE were compared to respective nominal CPUE values. Values were normalised by dividing by their means.

4.3.4 Assessment of national population trends and conservation status

Size composition, mortality and generation length

To make inferences about the population trends of *H. dactylopterus* in South Africa, the size composition of catch in research trawls was investigated which allowed for the estimation of the mortality and generation length of the species. As a part of the trawl surveys conducted by DFFE, total length data (measured to the nearest centimetre) have been obtained from a random subsample of individuals of each species caught in each trawl since 1991. The mean total length of *H. dactylopterus* in research trawls per year was estimated. To account for the trend of increasing length with depth, a GLM with a gaussian distribution was fitted to the length data and year and 100-m depth class were included as predictor variables. Mean total length per year was estimated by fixing the depth class to 301 to 400 m.

The length data were also used to estimate the natural mortality (M) of *H. dactylopterus* through the application of a catch curve (Ricker, 1975; Simpfendorfer, 1999). The total length of each fish was converted to age using the von Bertalanffy growth model estimated in Chapter 2 (TL (mm) = $365.66(1\text{-}e^{-0.13(t+1.14)})$). The frequency of individuals in each age class was determined. Frequencies were transformed to their natural logarithm and plotted against age. A linear regression was fitted to the descending limb of the resultant curve. Total mortality was estimated as the slope of the regression. The estimate of total mortality was halved to approximate natural mortality.

The generation length of *H. dactylopterus* was estimated using a life history table based on the Euler-Lotka equation:

$$\sum_{x=\alpha}^{W} I_x m_x e^{-rx} = 1, \tag{4.6}$$

where I_x is the survival at age x, m_x is the fecundity at age x, r is the intrinsic rate of population growth and W is the maximum reproductive age (Krebs, 2009).

The survival of the population at the beginning of each age class was calculated as:

$$I_x = I_{x-1} e^{-M}, \tag{4.7}$$

where M is the natural mortality rate of *H. dactylopterus.*

The fecundity of *H. dactylopterus* was estimated by multiplying the mean weight of mature fish at age x by the mean GSI of actively spawning females as estimated in Chapter 2 (4.63).

The weight of each fish was calculated by applying the length-weight relationship calculated in Chapter 2 (Weight = $9.86 \times 10^{-6} TL^{3.08}$).

The reproductive rate of the species was calculated as the product of the proportion surviving at age x and the fecundity at age x. This rate was summed over all ages (W) to calculate the lifetime fecundity. The generation length of *H. dactylopterus* was calculated as the product of the reproductive rate at age x and age x, divided by the lifetime fecundity.

Population trends and conservation status

The annual trends in the normalised standardised CPUE values derived from the research trawl data were compared to those derived from the commercial trawl data. The annual variability of each dataset was calculated and analysed.

Standardised CPUE estimates from research and commercial trawls were included in a Bayesian state-space modelling framework, Just Another Red-List Assessment (JARA) (Winker et al., 2020), to assess the population trends and conservation status of *H. dactylopterus*. JARA is a decision support tool that uses derived abundance indices to calculate the Bayesian posterior probability of the variation in population size. The model compares the probability distribution of the estimated population trend to each of the IUCN Red List Categories and estimates the probability of meeting each of the category thresholds, as stipulated by Criterion A (Winker et al., 2020) to assign IUCN Red List status to a population. The model was run with three Monte Carlo Markov chains, with 9000 iterations each, a burn-in of 2000 and a thinning rate of two.

The state-space model construction of JARA is detailed in Sherley et al. (2020) and Winker et al. (2020). JARA assumes that each CPUE time series is a Markov process such that CPUE (I_t) in year t is conditioned on CPUE in the previous year (I_{t-1}) and that the underlying trends in CPUE follow an exponential growth model. State-space models separate an observed time-series into two components: the system process which accounts for the underlying population trend and the observation error which accounts for the uncertainty in the system process due to measurement error (King, 2012; Winker et al., 2018; Winker et al. 2020). The system process equation is the exponential growth model in logarithmic form:

$$\mu_{ti+1} = \mu_{ti} + r_{ti} \tag{4.8}$$

where μ_{ti} is the log expected CPUE in year t for index i and r_{ti} is the normally distributed log annual population growth rate in year t for index i.

Based on the notation and approach used by Winker et al. (2018), the associated observation equation assumes that the underlying mean population trend is a latent state variable. The observation equation is thus:

$$\log(y_{ti}) = \mu_{ti} + \log(q_i) + E_{ti} \tag{4.9}$$

where y_{ti} is the observed relative CPUE in year t for index i, μ_{ti} is the log expected CPUE in year t for index i, q_i is a scaling parameter for index i in which the oldest record is used as the reference index and fixed to a value of 1, and E_{ti} is the lognormal observation error in year t for index i. Each index is assumed to be independent of one another.

The estimated posterior probability of the population trend for year t and index i is then calculated as:

$$I_{pti} = \exp(\mu_{ti}) \tag{4.10}$$

The individual posterior probabilities for each index are summed to estimate the overall posterior probability of the population trend, accounting for all indices. In cases when the observed time-series is less than three generation lengths, JARA provides projections so that the time-series is greater than three times the generation length plus two. Projections in years without observations are based on the posterior realizations of r_{ti} across all years.

All analyses on the research and commercial trawl datasets were conducted using RStudio version 1.1.453 (RStudio Team, 2016) with the R statistical platform, version 3.6.3 (R Core Team, 2020) or Microsoft Excel 2016. The R packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2020), ggpubr (Kassambara, 2018), MASS (Venables and Ripley, 2002), car (Fox and Weisberg, 2019), lattice (Sarkar, 2008), vegan community ecology (Oksanen et al., 2019), nFactors (Raiche and Magis, 2020), cluster (Maechler et al., 2019) and JARA (Winker et al., 2020) were all utilised.

4.4 Results

4.4.1 Indices of abundance from research trawl data

Data description and exploration

On average, research trawls were 28 minutes and 48 seconds long (±02 min 24 sec SD). The number of trawls conducted per year was dependent on the number of surveys done and ranged from 50 to 241 trawls. Trawl frequency increased from 2003 onwards except for during 2010, 2012, 2013, 2017 and 2018. Most research trawls were conducted on the west coast, north of Cape Columbine (location one) but a large number were also conducted on the south coast (locations four and five). Trawls were mainly conducted in depths less than 201 m (Figure 4.3).

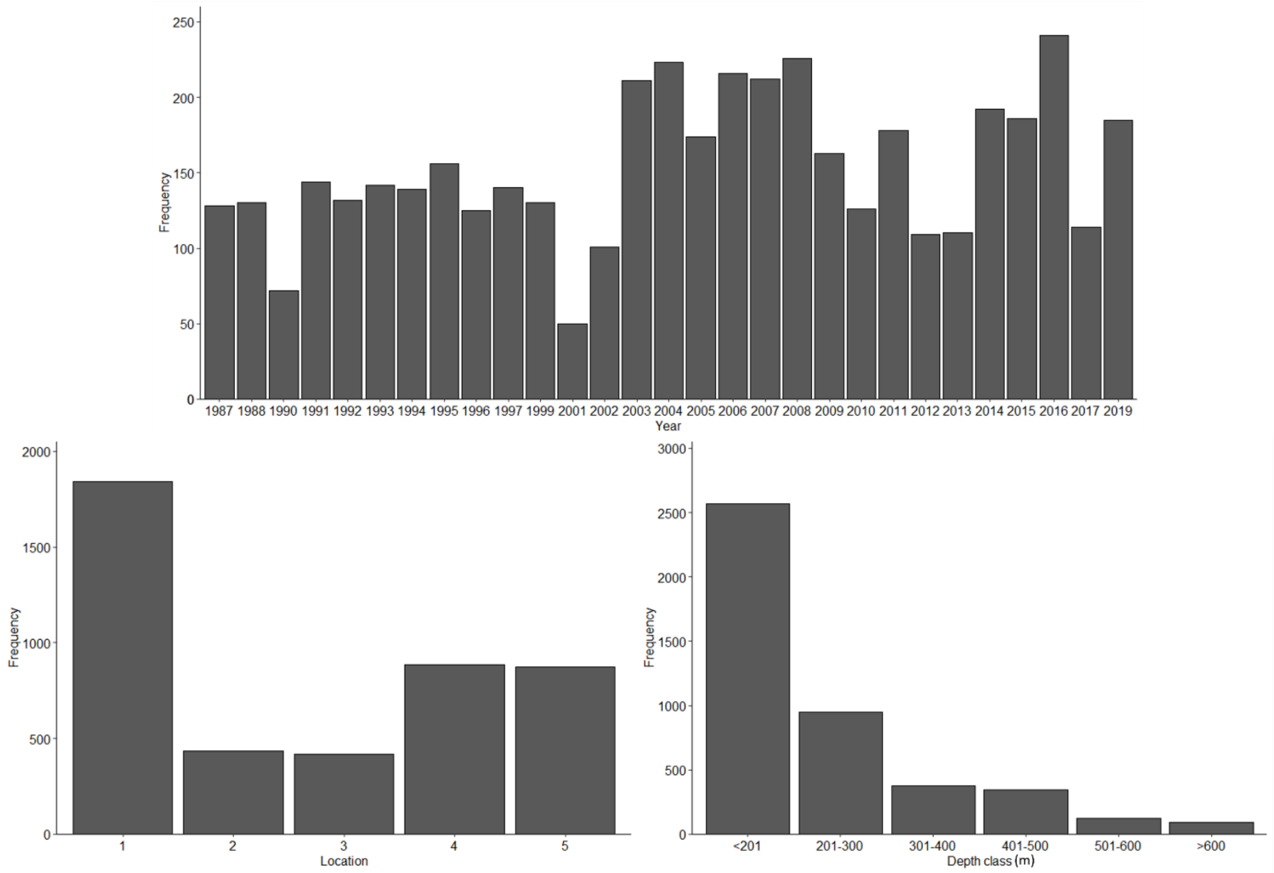


Figure 4.3: The frequency of demersal research trawls in South Africa from 1987 to 2019 that were included in this analysis, by year, location and depth class.

Research trawls contained 967 species or species groups including 381 teleosts, 100 chondrichthyans, 66 cephalopods, 416 other invertebrates and four algal species. Of these, 23 species accounted for 91.85% of the total catch and each contributed more than 0.5% to the overall biomass. Catch data for these 23 species were used in the principal components and clustering analysis. The species included *Merluccius paradoxus* (Mp), *Trachurus capensis* (Tc), *M. capensis* (Mc), *Squalus megalops* (Sm), *Etrumeus whiteheadi* (Ew), *Pterogymnus laniarius* (Pl), Suberites (SS), *Zeus capensis* (Zc), *Lophius vomerinus* (Lv), *Lepidopus caudatus* (Lc), *Chelidonichthys capensis* (Chec), *Coelorinchus simorhynchus* (Cs), *H. dactylopterus* (Hd), *Callorhinchus capensis* (Calc), *Genypterus capensis* (Gc), *Chelidonichthys queketti* (Cq), *Raja straeleni* (Rs), *Loligo reynaudii* (Lr), *Thyrsites atun* (Ta), *Todaropsis eblanae* (Te), *Sepia australis* (Sa), *Sympagurus dimorphus* (Sd) and *Emmelichthys nitidus* (En).

Seven PC axes were retained and used in the cluster analysis, resulting in seven fishing clusters. *Helicolenus dactylopterus* featured in all of these and was most dominant in fishing clusters four and five, in which it was associated with *Z. capensis*, *L. caudatus*, *G. capensis*, *L. vomerinus*, *C. simorhynchus* and *M. paradoxus* (Table 4.2 and Figure 4.4).

Table 4.2: Species composition of the seven different fishing clusters indicative of associations between species caught in South African demersal research trawls. The clusters in which Helicolenus dactylopterus *were prominent are highlighted in bold.*

Fishing cluster	**Species composition**
1	*M. paradoxus* (71.40%), *C. simorhynchus* (5.40%), *G. capensis* (5.30%), *L. vomerinus* (5.10%), *H. dactylopterus* (4.00%), *M. capensis* (2.70%), *T. capensis* (1.60%), *Z. capensis* (1.40%), *L. caudatus* (1.30%), *T. eblanae* (0.50%), *S. megalops* (0.20%), Suberites (0.20%), *Callorhinchus capensis* (0.20%), *R. straeleni* (0.20%), *S. dimorphus* (0.20%), *E. whiteheadi* (0.10%), *Chelidonichthys capensis* (0.10%), *T. atun* (0.10%), *S. australis* (0.10%)
2	*M. capensis* (32.90%), *Chelidonichthys capensis* (15.80%), *M. paradoxus* (15.00%), *Callorhinchus capensis* (8.30%), *E. whiteheadi* (5.50%), *L. vomerinus* (4.50%), *T. capensis* (3.70%), *S. australis* (2.70%), *T. atun* (2.40%), *R. straeleni* (2.20%), *S. megalops* (1.70%), *H. dactylopterus* (0.80%), *G. capensis* (0.80%), *T. eblanae* (0.70%), *C. simorhynchus* (0.50%), *L. reynaudii* (0.50%), Suberites (0.40%), *L. caudatus* (0.40%), *E. nitidus* (0.40%), *C. queketti* (0.30%), *S. dimorphus* (0.30%), *Z. capensis* (0.20%), *P. laniarius* (0.10%)
3	*T. capensis* (28.40%), *M. capensis* (21.80%), *S. megalops* (18.60%), *P. laniarius* (7.20%), *Chelidonichthys capensis* (4.40%), *Callorhinchus capensis* (3.30%), *R. straeleni* (2.80%), *C. queketti* (2.60%), *L. reynaudii* (2.60%), *E. whiteheadi* (2.40%), *L. vomerinus* (1.80%), *H. dactylopterus* (0.90%), *L. caudatus* (0.70%), *M. paradoxus* (0.50%), *Z. capensis* (0.50%), *G. capensis* (0.50%), *T. atun* (0.30%), *S. australis* (0.20%), *T. eblanae* (0.10%), *S. dimorphus* (0.10%), *E. nitidus* (0.10%)
4	*P. laniarius* (22.20%), *S. megalops* (19.30%), *M. capensis* (13.00%), *E. whiteheadi* (12.10%), *T. capensis* (7.60%), ***H. dactylopterus* (5.70%)**, *L. reynaudii* (5.00%), *C. queketti* (3.80%), *L. vomerinus* (2.60%), *Chelidonichthys capensis* (2.00%), *R. straeleni* (1.50%), *Callorhinchus capensis* (1.40%), *Z. capensis* (1.30%), *M. paradoxus* (1.10%), *L. caudatus* (0.50%), *G. capensis* (0.40%), *T. atun* (0.10%), *T. eblanae* (0.10%), *S. australis* (0.10%)
5	*M. paradoxus* (16.30%), *Z. capensis* (14.00%), *M. capensis* (11.80%), *L. caudatus* (9.50%), *T. capensis* (8.40%), ***H. dactylopterus* (7.90%)**, *L. vomerinus* (6.80%), *S. megalops* (4.30%), *C. simorhynchus* (4.20%), *E. nitidus* (3.70%), *T. eblanae* (2.30%), *E. whiteheadi* (2.00%), *C. queketti* (2.00%), *Callorhinchus capensis* (1.40%), *T. atun* (1.20%), *Chelidonichthys capensis* (0.90%), *G. capensis* (0.90%), *L. reynaudii* (0.80%), *R. straeleni* (0.70%), *P. laniarius* (0.40%), *S. australis* (0.30%), *S. dimorphus* (0.30%)
6	Suberites (31.70%), *M. paradoxus* (15.40%), *S. australis* (12.90%), *M. capensis* (11.90%), *E. whiteheadi* (10.90%), *Chelidonichthys capensis* (3.80%), *T. atun* (3.40%), *L. vomerinus* (3.00%), *Callorhinchus capensis* (1.80%), *T. eblanae* (1.70%), *T. capensis* (0.90%), *H. dactylopterus* (0.90%), *R. straeleni* (0.50%), *G. capensis* (0.40%), *L. caudatus* (0.20%), *C. simorhynchus* (0.20%)
7	*M. paradoxus* (40.20%), *M. capensis* (11.20%), *S. dimorphus* (9.20%), *L. vomerinus* (5.60%), *C. simorhynchus* (5.20%), *Chelidonichthys capensis* (5.00%), *T. capensis* (3.90%), *E. whiteheadi* (3.70%), *T. atun* (2.40%), *T. eblanae* (2.40%), *Callorhinchus capensis* (2.30%), *R. straeleni* (2.00%), *S. megalops* (1.80%), *H. dactylopterus* (1.60%), *Z. capensis* (0.80%), *L. caudatus* (0.60%), *L. reynaudii* (0.60%), *S. australis* (0.60%), *G. capensis* (0.50%), *C. queketti* (0.40%), Suberites (0.10%)

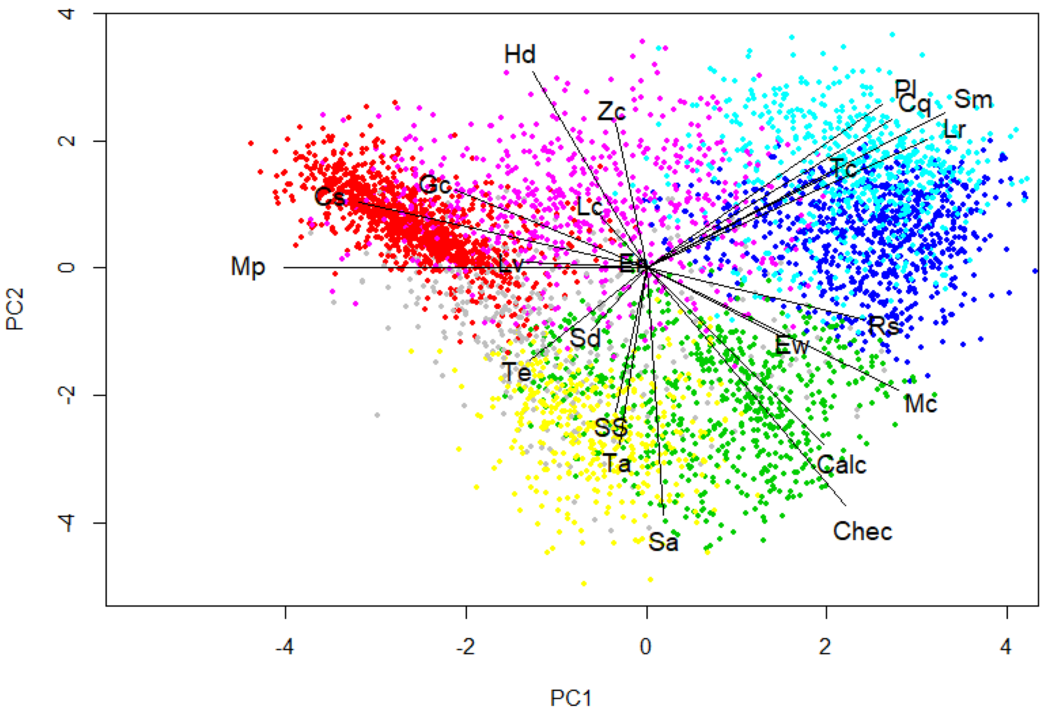


Figure 4.4: Representation of the seven fishing clusters indicative of associations between species caught in South African demersal research trawls, projected over the first two Principal Components (PCs). The colours denote each cluster (dark blue = 1, green = 2, light blue = 3, purple = 4, red = 5, yellow = 6, grey = 7) and the letters denote each species with vectors showing their influence on the principal components.

Most trawls were characterised by fishing cluster three (Figure 4.5) which comprised large proportions of *T. capensis* and *M. capensis* but was also characterised by *S. megalops*, *P. laniarius*, *C. queketti* and *L. reynaudii*.

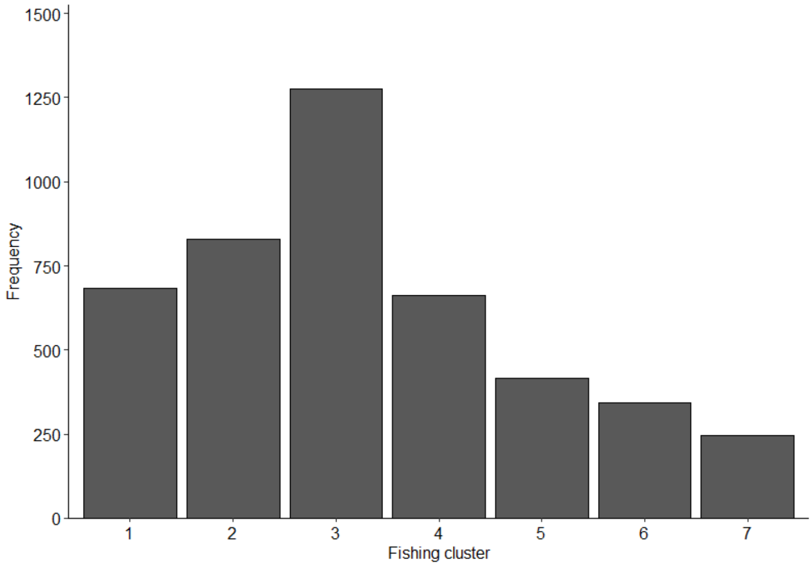


Figure 4.5: The frequency of demersal research trawls in South Africa from 1987 to 2019 that were included in this analysis, by fishing cluster.

Helicolenus dactylopterus occurred in 85.30% of the research trawls. Nominal CPUE of *H. dactylopterus* per trawl varied widely and ranged from 0 to 1.12 t.hr^{-1}. CPUE data were right-skewed and zero-inflated. When ln-transformed, data were left-skewed (Figure 4.6).

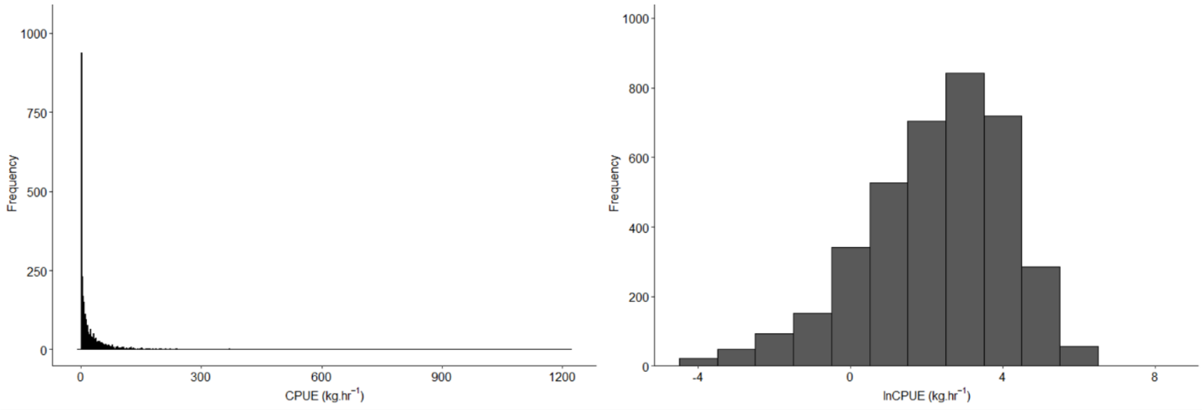


Figure 4.6: Frequency distribution of Helicolenus dactylopterus *CPUE and ln-transformed CPUE in 4455 demersal research trawls conducted in South Africa from 1987 to 2019.*

The mean nominal CPUE of *H. dactylopterus* in research trawls per annum ranged from 11.99 (±2.20 SE) to 67.87 (±14.56 SE) kg.hr^{-1} (Figure 4.7). Mean nominal CPUE peaked in 2001 and remained more stable thereafter.

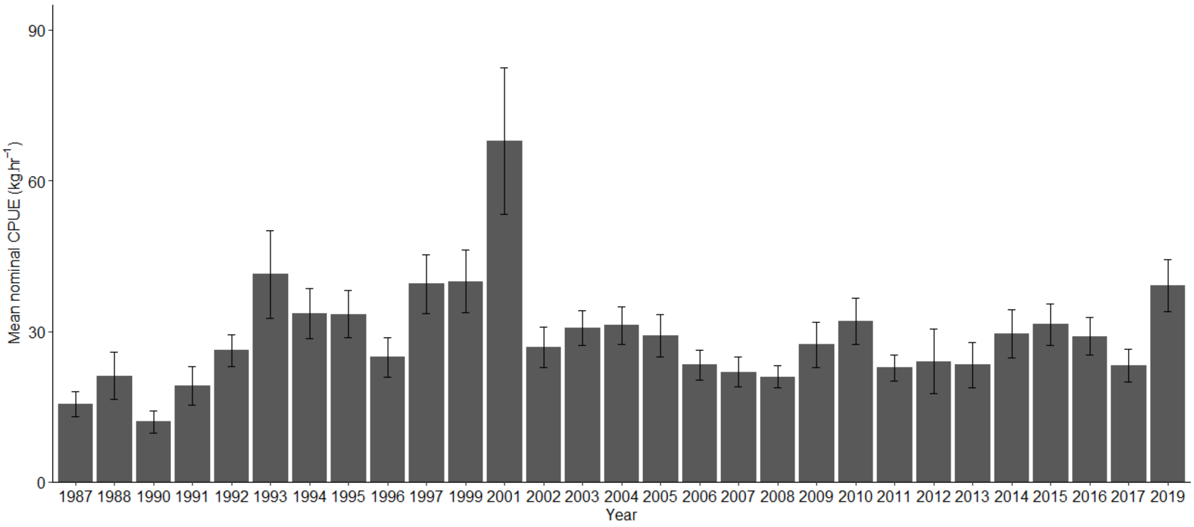


Figure 4.7: Mean (±SE) nominal CPUE of Helicolenus dactylopterus *caught in demersal research trawls conducted in South Africa from 1987 to 2019.*

The effect of gear type

In 2003, 211 research trawls were conducted across all five locations and in depths ranging from 101 to 500 m. Overall, 150 trawls were conducted using the old demersal trawl gear, of which 80% of these contained *H. dactylopterus*, and 61 trawls were conducted using the new gear, of which 77% contained *H. dactylopterus*.

In the initial, simplified delta-lognormal model run, the type of fishing gear used was a not a significant predictor of either the probability of encountering *H. dactylopterus* ($\chi^2 = 0.08$; df = 1; $p = 0.78$) or of *H. dactylopterus* CPUE ($\chi^2 = 0.15$; df = 1; $p = 0.70$). The effect of gear type was therefore excluded from further analyses.

Model selection

Although slightly left-skewed, the distribution of *H. dactylopterus* CPUE transformed by its natural logarithm approximated a lognormal distribution and thus a delta lognormal GLM was used.

In the final model fitted to all research trawl data, all predictor variables were retained in the binomial and lognormal model components, as supported by the AIC and analysis of deviance (Table 4.3). All factors were highly significant ($p < 0.001$) (Table 4.3). The pseudo-R^2 for the binomial model component was 0.25 and for the lognormal model component was 0.29. The models explained 24.66% of the variation in the probability of encountering *H. dactylopterus* in a trawl and 29.28% of the variation in *H. dactylopterus* CPUE.

In both model components, depth class explained most of the variation in the probability of encounter and CPUE (56.37% and 51.63% in the binomial and lognormal models respectively). The inclusion of the effect of fishing cluster was also important and was the next highest contributor in both components, explaining 31.48 and 37.41% of the variation in each model component, respectively. Year was the next highest contributor in both components and location was less influential, only contributing marginally to the model deviance.

Table 4.3: Statistics for the predictor variables included in the final binomial and lognormal GLM models of Helicolenus dactylopterus *presence and CPUE in demersal research trawls conducted in South Africa from 1987 to 2019. The degrees of freedom (df), AIC value, residual deviance, change in the residual deviance (Δ deviance), percentage of reduction in deviance explained (% explained) and corresponding p-values of a χ^2 test of significance are shown for each predictor variable.*

Model structure	**df**	**AIC**	**Residual deviance**	**Δ deviance**	**% explained**	**p(χ^2)**
Binomial						
NULL		3 711.50	3 709.50			
+ year	28	3 707.73	3 649.70	-59.76	6.53%	<0.001
+location	4	3 664.35	3 598.30	-51.39	5.62%	<0.001
+depth class	5	3 158.80	3 082.80	-515.55	56.37%	<0.001
+fishing cluster	6	2 882.86	2 794.90	-287.94	31.48%	<0.001
Total variation explained: 24.66%						
Lognormal						
NULL		15 647.90	13 652.70			
+ year	28	15 614.03	13 333.70	-319.07	7.98%	<0.001
+location	4	15 587.98	13 214.70	-118.97	2.98%	<0.001
+depth class	5	14 952.49	11 150.30	-2 064.40	51.63%	<0.001
+fishing cluster	6	14 417.26	9 654.80	-1 495.48	37.41%	<0.001
Total variation explained: 29.28%						

Validation of the lognormal model component showed no obvious patterning in the residuals and no violation of independence among independent variables (Figure 4.23 in Section 4.7 Appendix). The binomial and lognormal models were thus accepted.

Trends in CPUE

For the generation of the predictor datasets, variables (apart from the one of interest) were fixed to year 2001, location four, depth class 301 to 400 m and fishing cluster four.

Standardised CPUE of *H. dactylopterus* caught in research trawls showed a clear pattern with depth (Figure 4.8). Standardised CPUE was significantly greater from 201 to 500 m than in depths less than 201 m or greater than 600 m. Standardised CPUE was highest between 301 and 400 m. *Helicolenus dactylopterus* showed clear species associations with the highest CPUE values in research trawls characterised by fishing clusters four and five (Figure 4.8). Although significant (Table 4.3), location had less of an influence on *H. dactylopterus* CPUE. Nevertheless, standardised CPUE of *H. dactylopterus* was greatest in locations three and four, between Cape Point and Mossel Bay (Figure 4.8).

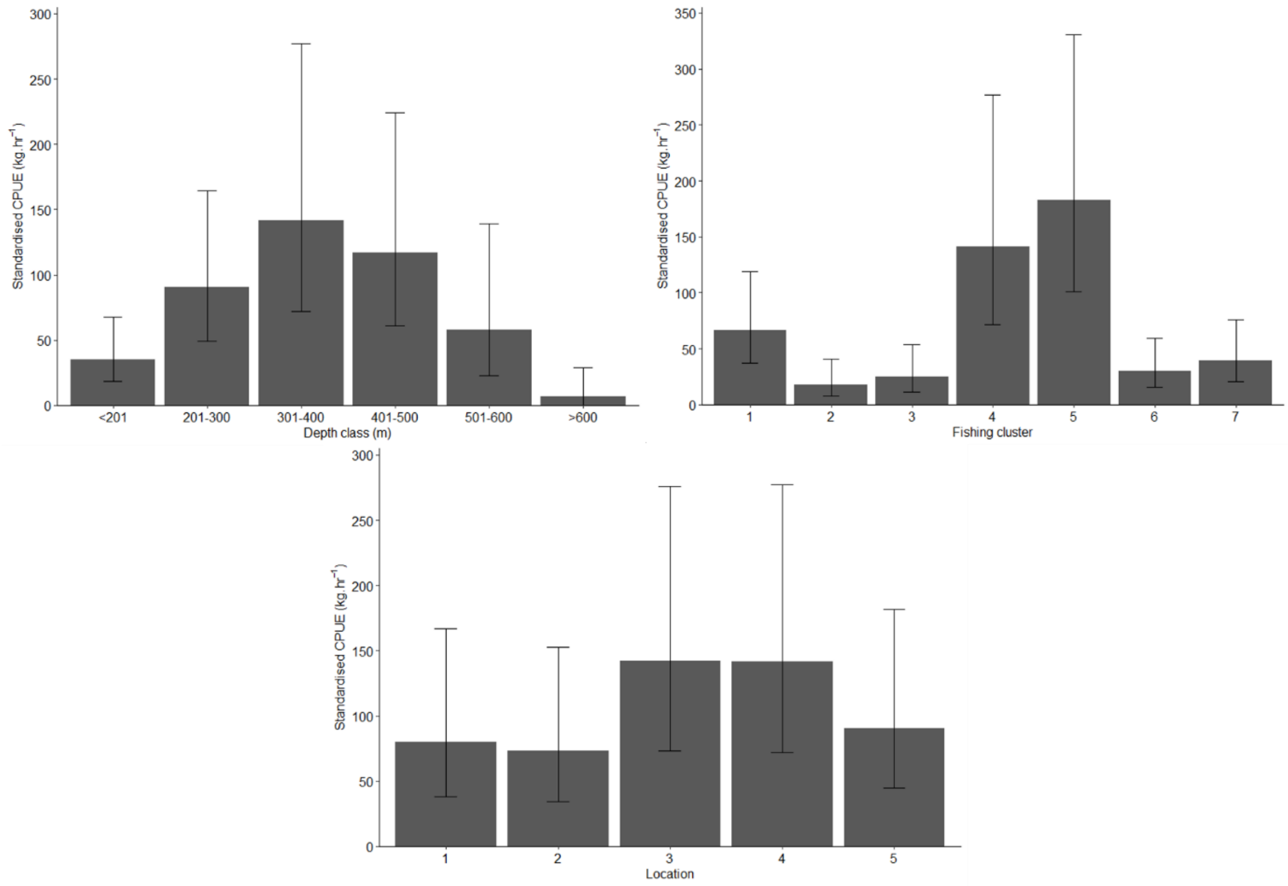


Figure 4.8: The influence of depth class, fishing cluster and location on the standardised CPUE of Helicolenus dactylopterus *when modelled using a delta lognormal GLM applied to the South African research trawl data from 1987 to 2019.*

The nominal and standardised *H. dactylopterus* CPUE annual trends were mostly similar (Figure 4.9). The magnitude of estimates, however, differed substantially (Table 4.4). The CPUE of *H. dactylopterus* caught in research trawls was lowest in 1991 (45.82 kg.hr^{-1}) and peaked in 2001 (141.38 kg.hr^{-1}), before decreasing again from 2002 to 2007. Another peak in CPUE occurred in 2010 at 99.21 kg.hr^{-1}. Since 2011, standardised CPUE estimates remained relatively stable ranging between 58.53 and 93.10 kg.hr^{-1} (Table 4.4).

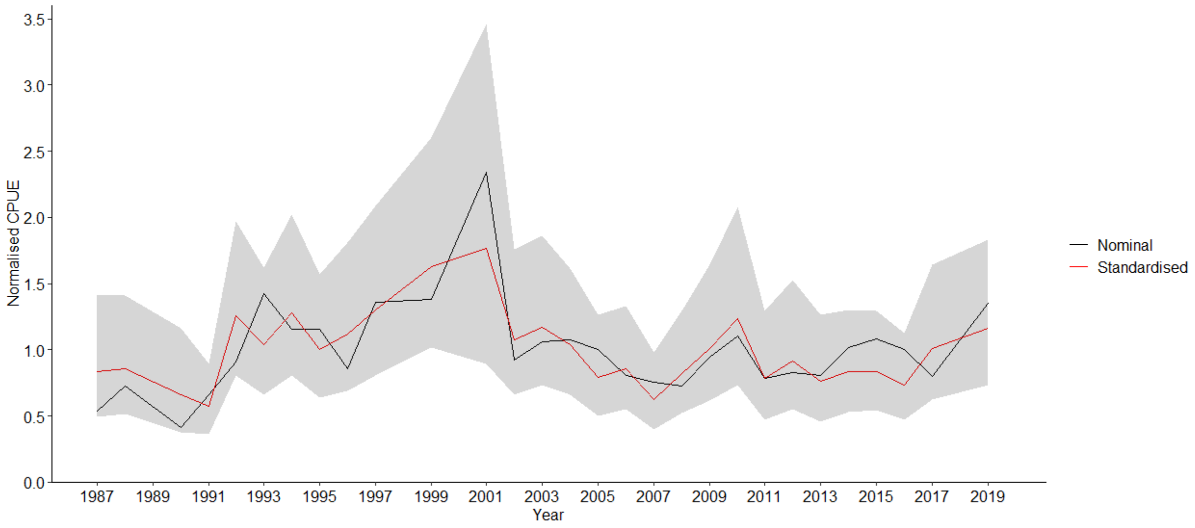


Figure 4.9: A comparison of the nominal and standardised CPUE of Helicolenus dactylopterus *caught in research trawls conducted in South Africa from 1987 to 2019. Values were normalised by dividing by their means. The 95% confidence intervals for the standardised CPUE are shaded grey.*

Table 4.4: The nominal and standardised CPUE of Helicolenus dactylopterus *in research trawls conducted in South Africa from 1987 to 2019. The standard errors and 95% confidence intervals for the standardised CPUE estimated by the final delta lognormal GLM are included.*

Year	Nominal mean CPUE (kg.hr^{-1})	Standardised CPUE (kg.hr^{-1})	SE	Lower CI	Upper CI
1987	15.58	66.99	0.04	39.56	113.00
1988	21.16	68.58	0.03	41.56	112.91
1990	11.99	52.97	0.03	30.04	93.22
1991	19.24	45.82	0.01	29.29	71.66
1992	26.23	100.95	0.01	64.60	157.69
1993	41.36	83.11	0.02	53.12	129.93
1994	33.54	102.49	0.02	64.88	161.80
1995	33.44	80.23	0.02	51.23	125.56
1996	24.84	89.64	0.02	55.35	145.03
1997	39.43	103.98	0.02	64.72	166.80
1999	39.98	130.56	0.02	81.67	208.48
2001	67.87	141.38	0.04	71.87	276.91
2002	26.84	86.14	0.02	52.67	140.81
2003	30.69	93.82	0.04	58.84	148.93
2004	31.17	83.04	0.03	53.23	129.26
2005	29.15	63.61	0.03	39.86	101.26
2006	23.32	68.88	0.03	44.37	106.73
2007	21.94	50.08	0.03	31.75	78.74
2008	20.99	65.98	0.03	41.85	103.69
2009	27.38	80.87	0.04	49.55	131.39
2010	31.99	99.21	0.04	58.89	166.28
2011	22.76	62.71	0.05	37.67	103.52
2012	24.04	73.53	0.03	44.04	122.51
2013	23.33	60.93	0.03	36.57	101.26
2014	29.54	66.75	0.03	42.58	104.43
2015	31.39	67.03	0.02	43.44	103.33
2016	29.00	58.53	0.03	37.83	90.32
2017	23.22	81.09	0.02	49.87	131.70
2019	39.14	93.10	0.03	58.92	146.69

4.4.2 Indices of abundance from commercial trawl data

Commercial effort

Since 1987 total effort in the demersal trawl fishery has gradually declined and stabilised to between 37 000 and 47 000 trawls per year over the last ten years (2009 to 2018) (Figure 4.10).

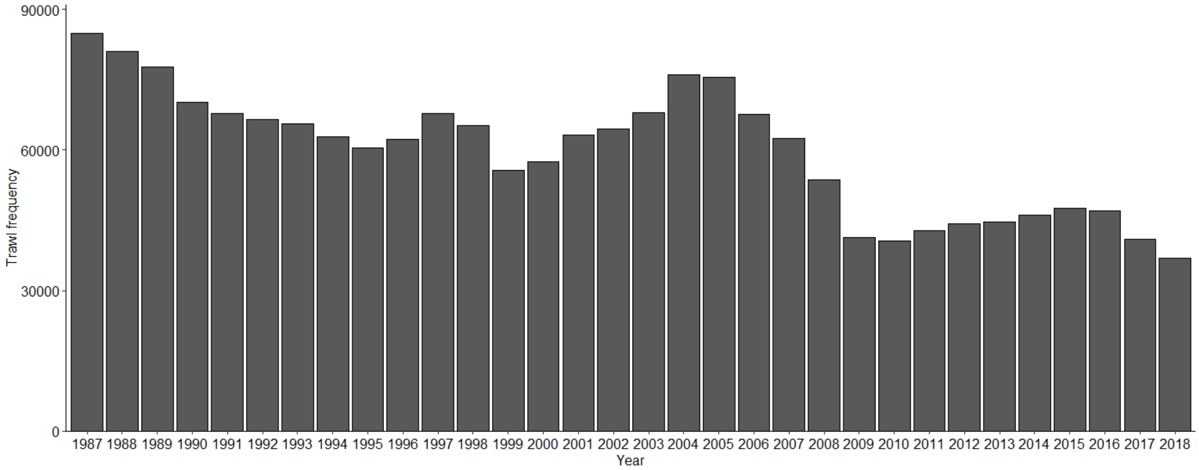


Figure 4.10: Total effort as the number of trawls conducted per year from 1987 to 2018 in the South African demersal trawl fishery. All trawls conducted by all demersal and dual-rights holder vessels were included.

Description and exploration of included trawl data (2004 – 2018)

On average, the commercial trawls included in the analyses for this study were two hours and 58 minutes long (±1 h 05 min SD). The number of trawls per year ranged from 14 118 to 24 658 (Figure 4.11). No seasonal pattern in trawling was observed. Trawling mainly occurred between Cape Columbine and Cape Point (location two) but was also widespread on the Agulhas Bank (locations three, four and five). Trawls were mainly conducted in depths from 100 to 500 m. Start trawl depth averaged 347.72 m (±145 m SD) (Figure 4.11).

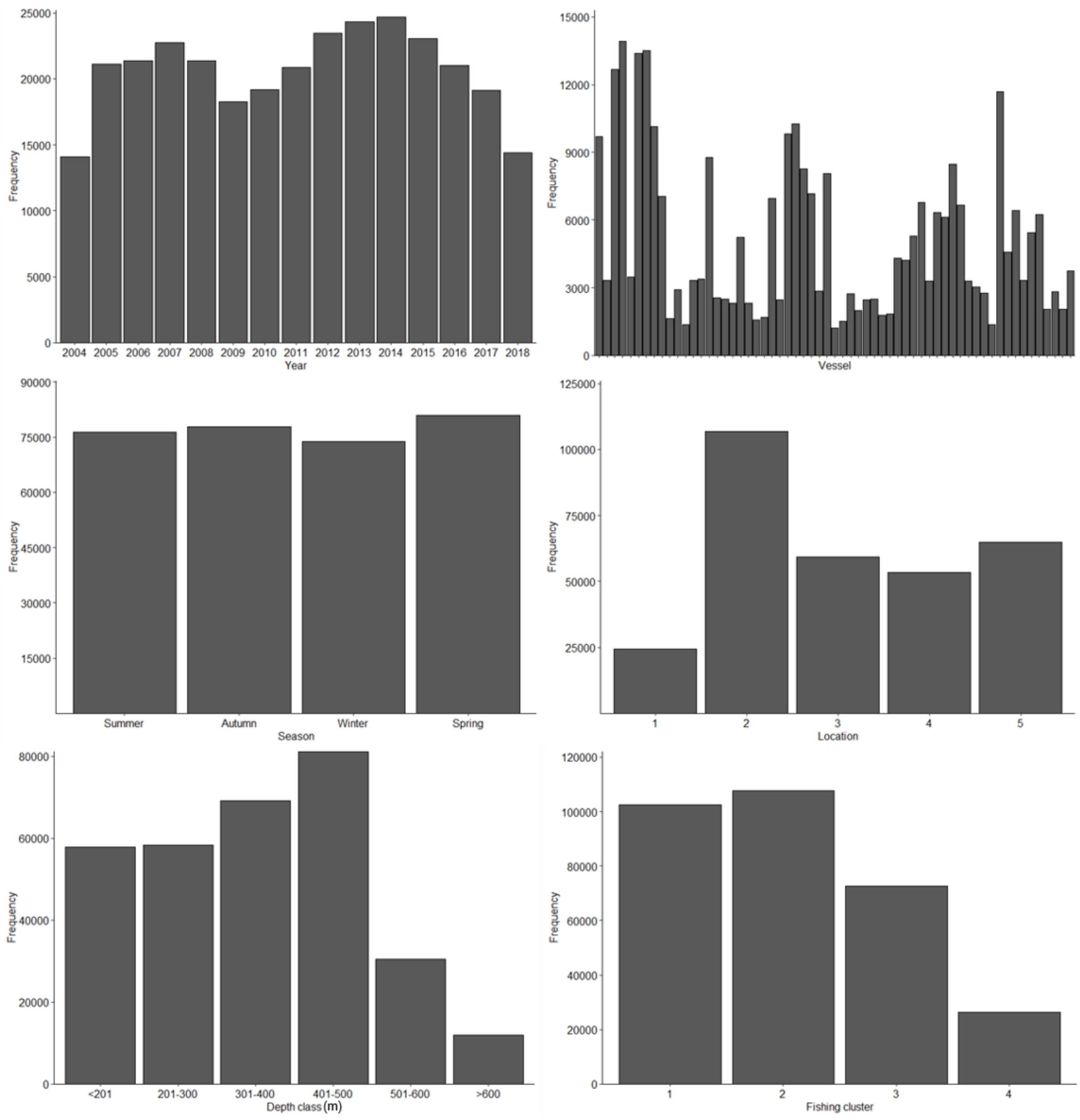


Figure 4.11: The frequency of trawls in the South African commercial demersal trawl fishery that were included in this analysis, by year, vessel, season, location, depth class and fishing cluster.

Commercial trawls contained 55 different species or species groups including 45 teleosts, six chondrichthyans and four cephalopods. Of the 55 species, 17 accounted for 99.62% of the total catch and each contributed more than 0.1%. Unidentified teleosts accounted for 2.27% of the catch but were removed from further analysis. For the principal components and clustering analysis catch composition was thus limited to 16 species that accounted for 97.35% of the total catch. These included *Brama brama* (Bb), *Lepidopus caudatus* (Lc), *Loligo reynaudii* (Lr), *Chelidonichthys* spp. (CH), *Merluccius* spp. (ME), *Trachurus capensis* (Tc), *Helicolenus* *dactylopterus* (Hd), *Zeus capensis* (Zc), *Genypterus capensis* (Gc), *Scomber japonicus* (Sj), *Emmelichthys nitidus* (En), *Lophius vomerinus* (Lv), *Pterogymnus laniarius* (Pl), Rajiformes spp. (RA), *Etrumeus whiteheadi* (Ew) and *Thyrsites atun* (Ta).

Three PC axes were non-trivial and thus four were retained and used in the cluster analysis. This resulted in four fishing clusters. *Helicolenus dactylopterus* featured in three of these and was most dominant in fishing cluster three, in which it was associated with *L. vomerinus*, *L. caudatus* and *Z. capensis*. It was also prominent in cluster one in which it was associated with *G. capensis* (Table 4.5 and Figure 4.12).

Table 4.5: Species composition of the four different fishing clusters that reflect the fishing strategies employed in the South African commercial demersal trawl fishery. The clusters in which Helicolenus dactylopterus *were prominent are highlighted in bold.*

Fishing cluster	**Species composition**
1	*Merluccius* spp. (83.30%), *L. vomerinus* (5.70%), *G. capensis* (4.10%), *B. brama* (2.50%), *L. caudatus* (1.50%), ***H. dactylopterus* (1.30%)**, *Z. capensis* (0.80%), *T. capensis* (0.30%), *T. atun* (0.30%), *L. reynaudii* (0.1%)
2	*Merluccius spp.* (97.30%), *T. capensis* (0.70%), *B. brama* (0.40%), *G. capensis* (0.40%), *L. vomerinus* (0.40%), *L. reynaudii* (0.30%), *T. atun* (0.20%), *L. caudatus* (0.10%), *Chelidonichthys* spp. (0.10%), *P. laniarius* (0.10%)
3	*Merluccius spp.* (38.70%), *L. vomerinus* (21.50%), *T. capensis* (13.10%), *L. caudatus* (7.70%), *T. atun* (6.10%), *G. capensis* (3.70%), *Z. capensis* (3.50%), ***H. dactylopterus* (2.30%),** *B. brama* (1.30%), Rajiformes (0.60%), *E. nitidus* (0.50%), *S. japonicus* (0.40%), *L. reynaudii* (0.30%), *Chelidonichthys* spp. (0.20%), *E. whiteheadi* (0.10%)
4	*Merluccius spp.* (61.30%), *P. laniarius* (12.40%), *Chelidonichthys* spp. (8.00%), *L. reynaudii* (6.40%), Rajiformes (5.00%), *T. capensis* (3.60%), *L. vomerinus* (2.30%), *T. atun* (0.30%), *G. capensis* (0.20%), *L. caudatus* (0.10%), *H. dactylopterus* (0.10%)

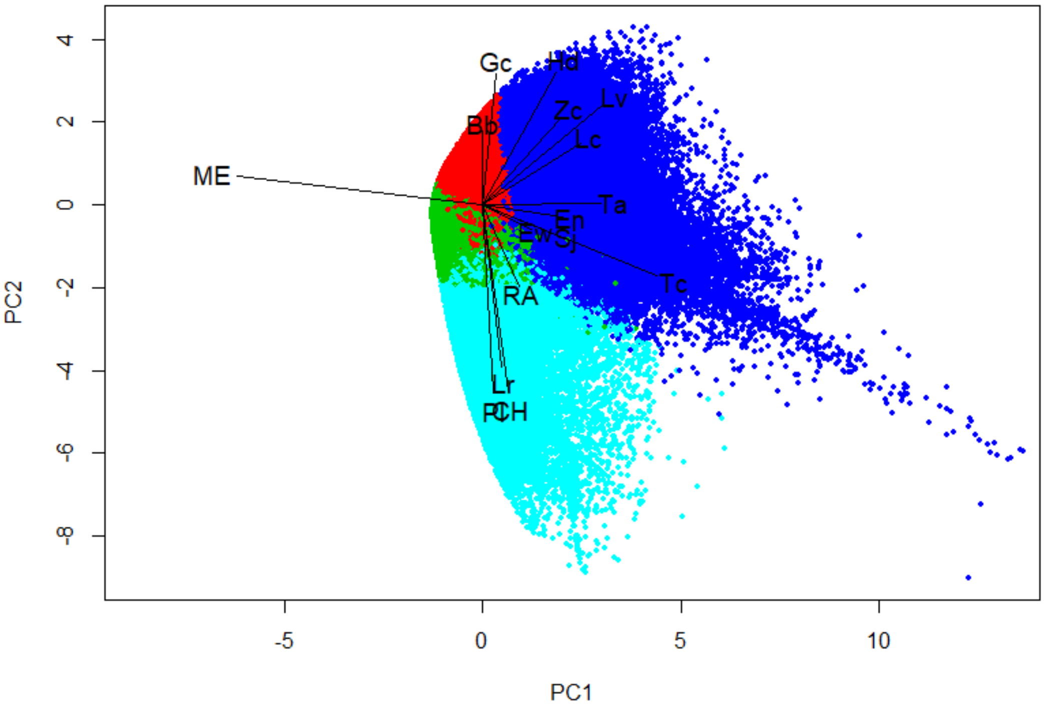


Figure 4.12: Representation of the four fishing clusters that characterise the different fishing strategies employed in the South African commercial demersal trawl fishery, projected over the first two Principal Components (PCs). The colours denote each cluster (red = 1, green = 2, dark blue = 3, light blue = 4) and the letters denote each species with vectors showing their influence on the principal components.

Most trawls were characterised by fishing clusters one or two (Figure 4.11) in which *Merluccius* species were primarily targeted. A large proportion of trawls were also characterised by fishing cluster three in which, along with *Merluccius* species, *L. vomerinus*, *Z. capensis* and *L. caudatus* were also caught.

Helicolenus dactylopterus individuals were caught in 31.47% of the commercial trawls. Nominal CPUE per trawl varied widely and ranged from 0 to 5.34 $t.hr^{-1}$. CPUE data were right-skewed and zero-inflated but were approximately normally distributed when ln-transformed (Figure 4.13).

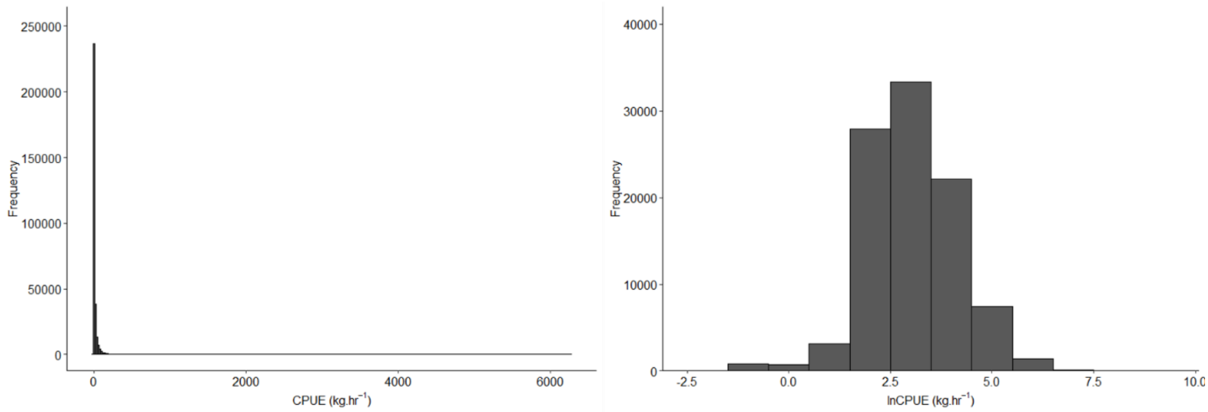


Figure 4.13: Frequency distribution of Helicolenus dactylopterus *CPUE and ln-transformed CPUE in 309 075 trawls conducted by the South African commercial demersal trawl fishery from 2004 to 2018.*

On average, from 2004 to 2018, 704.92 (±199.83 SD) t of *H. dactylopterus* was caught per annum in the South African demersal trawl fishery. Nominal mass increased from 2008 onwards and peaked from 2012 to 2015 (Figure 4.14). A similar pattern was observed with mean nominal CPUE increasing from 2008 onwards (Figure 4.15).

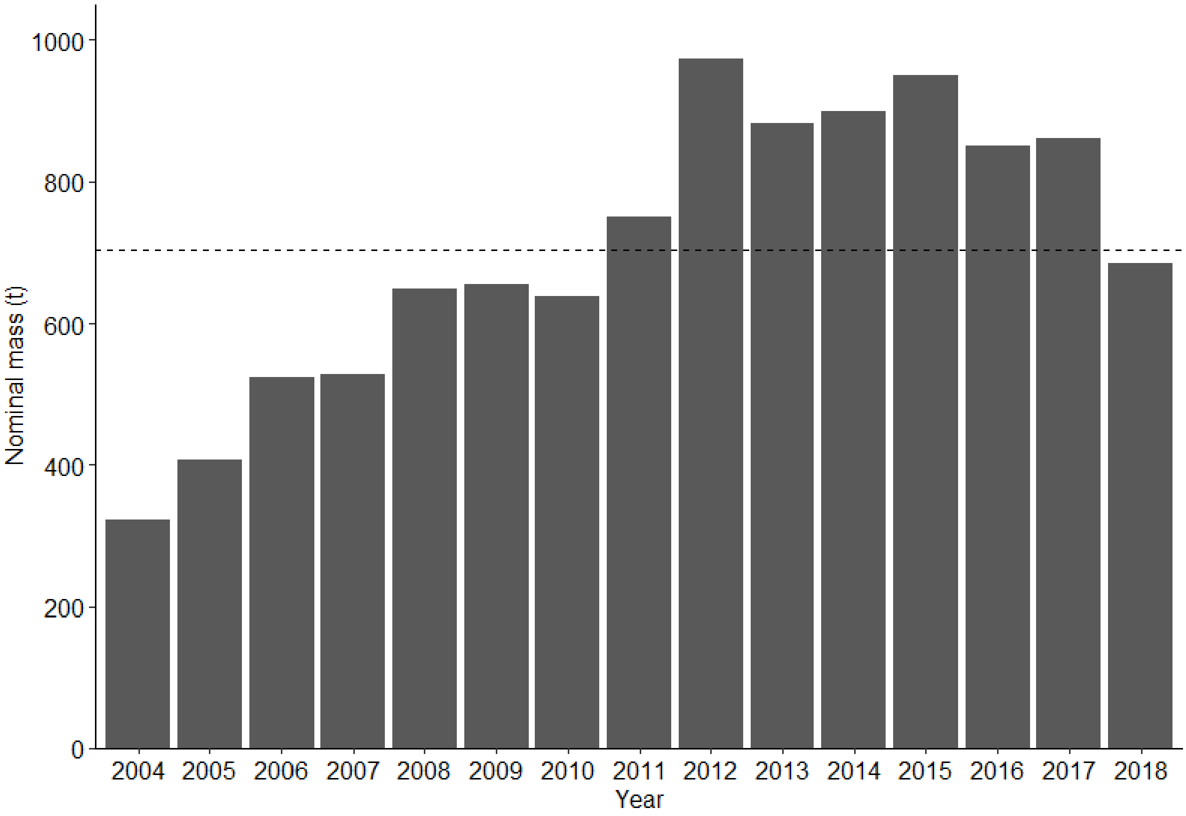


Figure 4.14: Total annual nominal catch (t) of Helicolenus dactylopterus *by 61 commercial vessels operating in the South African EEZ from 2004 to 2018. The dashed line shows the annual mean.*

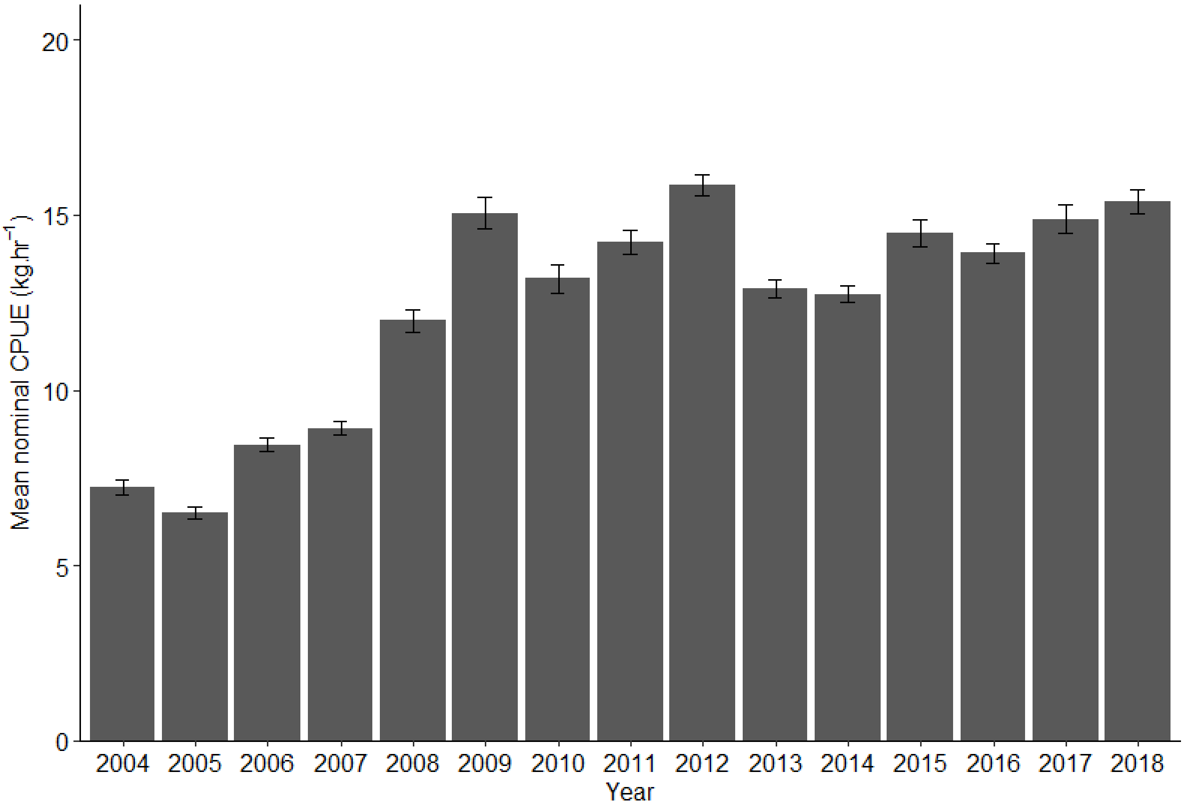


Figure 4.15: Mean (±SE) nominal CPUE of Helicolenus dactylopterus *caught in the South African demersal trawl fishery from 2004 to 2018.*

Model selection

All predictor variables were retained in the final binomial and lognormal model components, as supported by the AIC and analysis of deviance (Table 4.6). All factors were highly significant ($p < 0.001$) (Table 4.6). The pseudo-R^2 for the binomial model component was 0.37 and for the lognormal model component was 0.25. The models thus explained 37.28% of the variation in the probability of encountering *H. dactylopterus* in a trawl and 25.24% of the variation in *H. dactylopterus* CPUE.

In both model components, vessel explained most of the variation in the probability of encounter and CPUE (66.57% and 72.92% in the binomial and lognormal models respectively). As in the model fitted to the research trawl data, the inclusion of the effect of fishing cluster was, however, also important and was the next highest contributor in both components, explaining 25.03 and 11.46% of the variation in each model component, respectively. Year and depth were the next highest contributors, contributing similarly to the variation in the probability of encountering *H. dactylopterus* but with depth explaining more of the variation in CPUE. Location and season were less influential and only contributed marginally to the model deviances.

Validation of the lognormal model component showed no obvious patterning in the residuals and no violation of independence among independent variables (Figure 4.24 in Section 4.7 Appendix). The binomial and lognormal models were thus accepted.

Table 4.6: Statistics for the predictor variables included in the final binomial and lognormal GLM models of Helicolenus dactylopterus *presence and CPUE in demersal commercial trawls in the South African EEZ from 2004 to 2018. The degrees of freedom (df), AIC value, residual deviance, change in the residual deviance (Δ deviance), percentage of reduction in deviance explained (% explained) and corresponding p-values of a χ^2 test of significance are shown for each predictor variable.*

Model structure	**df**	**AIC**	**Residual deviance**	**Δ deviance**	**% explained**	**p(χ^2)**
Binomial						
NULL		380 197	380 195			
+ vessel	60	285 964	285 842	-94 353	66.57%	<0.001
+ year	14	281 124	280 974	-4 868	3.43%	<0.001
+season	3	280 938	280 782	-192	0.14%	<0.001
+location	4	278 939	278 775	-2 007	1.42%	<0.001
+depth class	5	274 110	273 936	-4 839	3.41%	<0.001
+fishing cluster	3	238 649	238 469	-35 467	25.03%	<0.001
Total variation explained: 37.28%						
Lognormal						
NULL		296 479	120 018			
+ vessel	58	276 812	97 930	-22 088	72.92%	<0.001
+ year	14	275 496	96 586	-1 344	4.44%	<0.001
+season	3	275 397	96 481	-105	0.34%	<0.001
+location	4	274 775	95 859	-623	2.06%	<0.001
+depth class	5	272 050	93 201	-2 658	8.78%	<0.001
+fishing cluster	3	268 363	89 728	-3 472	11.46%	<0.001
Total variation explained: 25.24%						

Trends in CPUE

For the generation of the predictor datasets, variables (apart from the one of interest) were fixed to vessel RSA,193,346, year 2012, season winter, location two, depth class 301 to 400 m and fishing cluster three.

Standardised CPUE for *H. dactylopterus* caught by commercial trawl showed a clear pattern with fishing strategy, in which CPUE was highest when the fishing strategies with catch representative of clusters one and three were used (Figure 4.16). Both clusters were characterised by large proportions of *Merluccius* spp. and *L. vomerinus* (Table 4.5).

Standardised CPUE was also influenced by depth, in which the *H. dactylopterus* CPUE was highest in depths from 301 to 400 m, and location, in which CPUE was highest in locations two (between Cape Columbine and Cape Point) and four (between Cape Agulhas and Mossel Bay) (Figure 4.16). While significant, as indicated in the binomial and lognormal model selection, the influence of season on *H. dactylopterus* CPUE was less apparent with similar CPUE values estimated in all seasons (Figure 4.16).

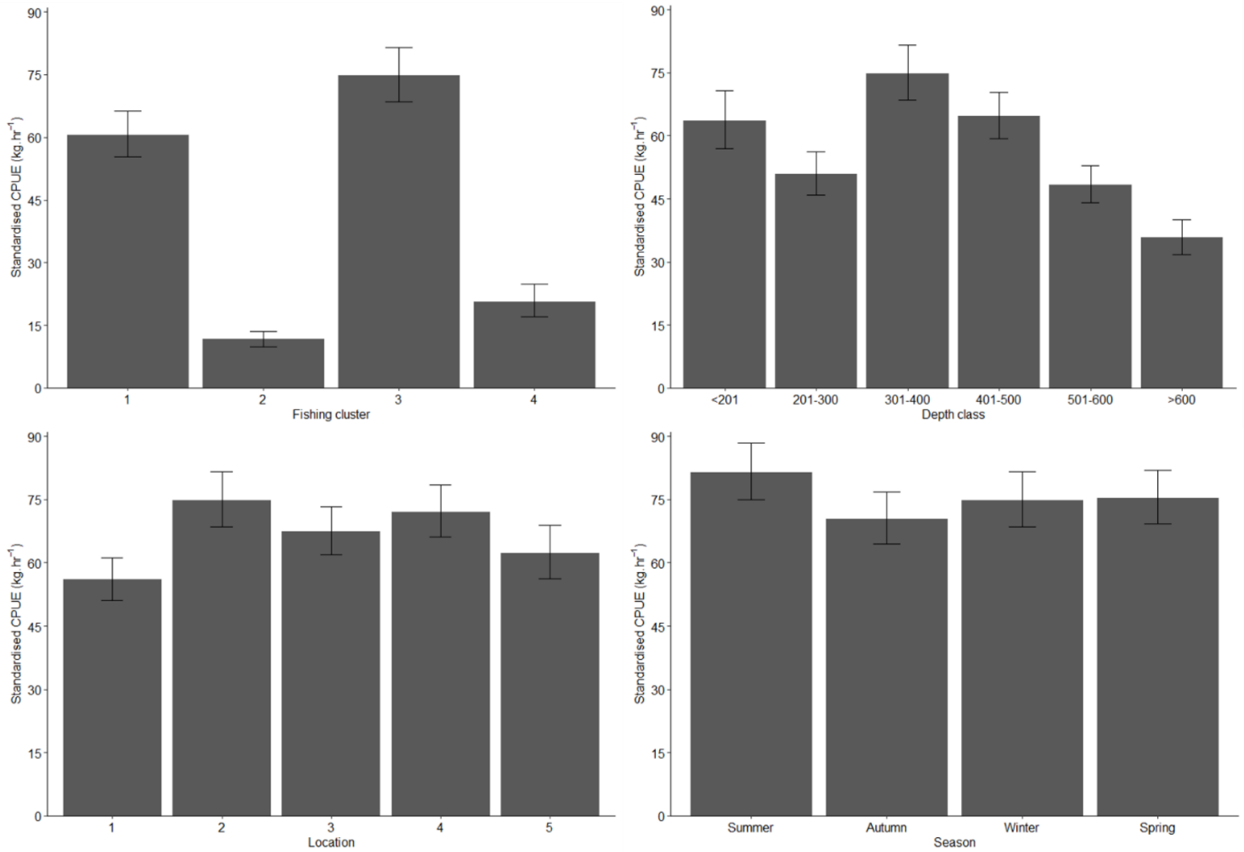


Figure 4.16: The influence of fishing cluster, depth class, location and season on the standardised CPUE of Helicolenus dactylopterus *when modelled using a delta lognormal GLM applied to the South African demersal commercial trawl dataset.*

The nominal and standardised *H. dactylopterus* CPUE annual trends were mostly similar (Figure 4.17), with the standardised estimates generally being more conservative. The magnitude of estimates, however, differed substantially (Table 4.7). The CPUE of *H. dactylopterus* in the commercial demersal trawl fishery was lowest in 2005 (43.42 kg.hr^{-1}) and peaked in 2009 (75.83 kg.hr^{-1}) and 2012 (74.76 kg.hr^{-1}) before decreasing again from 2013 to 2018. Standardised CPUE estimates from 2013 to 2018 ranged from 65.93 to 71.21kg.hr^{-1} (Table 4.7).

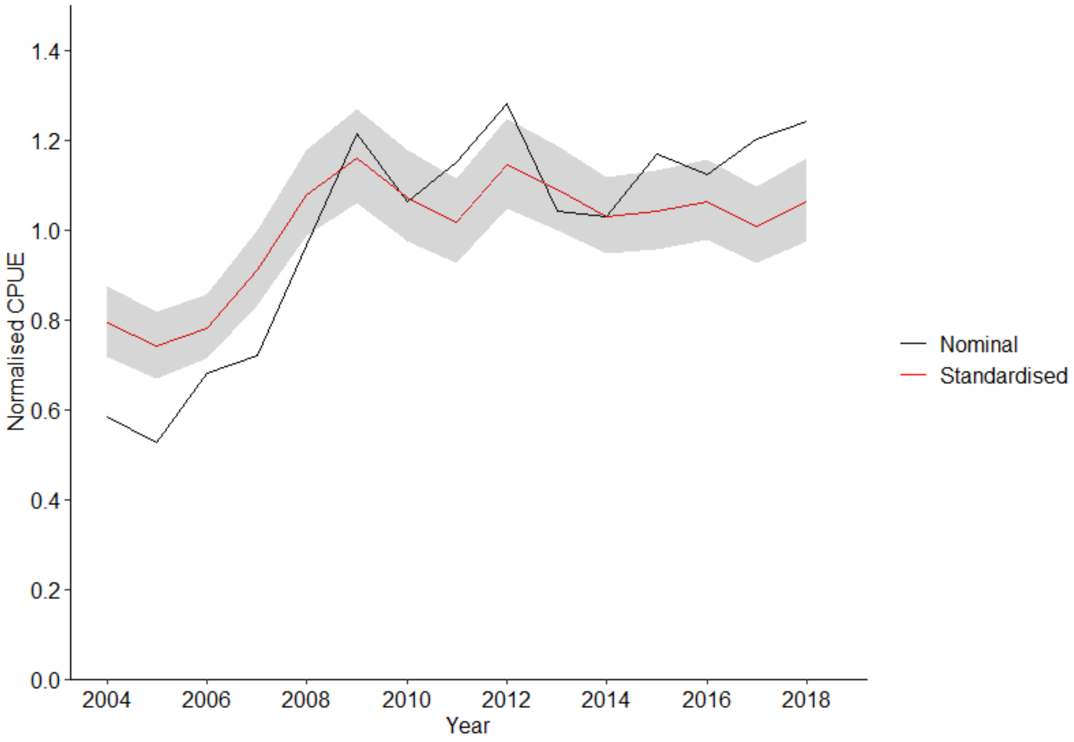


Figure 4.17: Comparison of the nominal and standardised CPUE of Helicolenus dactylopterus *in the South African commercial demersal trawl fishery from 2004 to 2018. Values were normalised by dividing by their means. The 95% confidence intervals for the standardised CPUE are shaded grey.*

Table 4.7: The nominal and standardised CPUE of Helicolenus dactylopterus *in demersal commercial trawls conducted in the South African EEZ from 2004 to 2018. The standard errors and 95% confidence intervals for the standardised CPUE estimated by the final GLM are included.*

Year	**Nominal mean CPUE (kg.hr^{-1})**	**Standardised CPUE (kg.hr^{-1})**	**SE**	**Lower CI**	**Upper CI**
2004	7.23	51.82	0.012	46.87	57.24
2005	6.52	48.42	0.012	43.83	53.45
2006	8.45	51.09	0.011	46.62	55.96
2007	8.93	59.60	0.011	54.37	65.28
2008	11.98	70.49	0.010	64.44	77.06
2009	15.05	75.83	0.009	69.36	82.86
2010	13.18	70.03	0.011	63.67	76.97
2011	14.23	66.50	0.011	60.65	72.87
2012	15.85	74.76	0.009	68.50	81.57
2013	12.90	71.21	0.009	65.32	77.59
2014	12.74	67.30	0.007	61.96	73.07
2015	14.46	68.08	0.008	62.62	74.00
2016	13.90	69.57	0.007	64.03	75.57
2017	14.88	65.94	0.008	60.63	71.69
2018	15.38	69.56	0.008	63.81	75.80

4.4.3 Assessment of national population trends and conservation status

Size composition, mortality and generation length

The mean total length of *H. dactylopterus* in research trawls has shown variability over time (Figure 4.18). From 1991 the annual mean length increased from 186 (±0.72 SE) mm to a peak of 244 (±0.90 SE) mm in 2001. Mean total length remained relatively high between 2001 and 2003, thereafter decreasing to 187 (±0.50 SE) mm in 2009. From 2009 to 2019, the mean total length fluctuated between 181 (±0.55 SE) and 215 (±0.56 SE) mm.

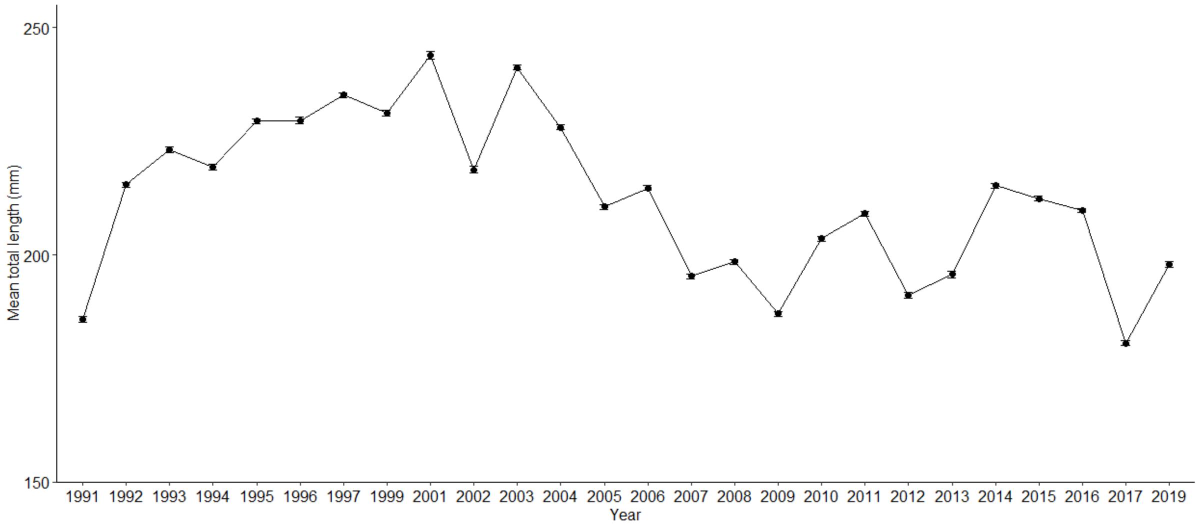


Figure 4.18: Trends in mean total length (mm) of Helicolenus dactylopterus *caught in research trawls conducted in South Africa from 1991 to 2019.*

The slope of the linear regression fitted to the catch curve (Figure 4.19) was 0.23 [95% C.I.: 0.19 to 0.27] and thus the natural mortality of *H. dactylopterus* was estimated to be 0.12 year^{-1}. The generation length was 14.41 years.

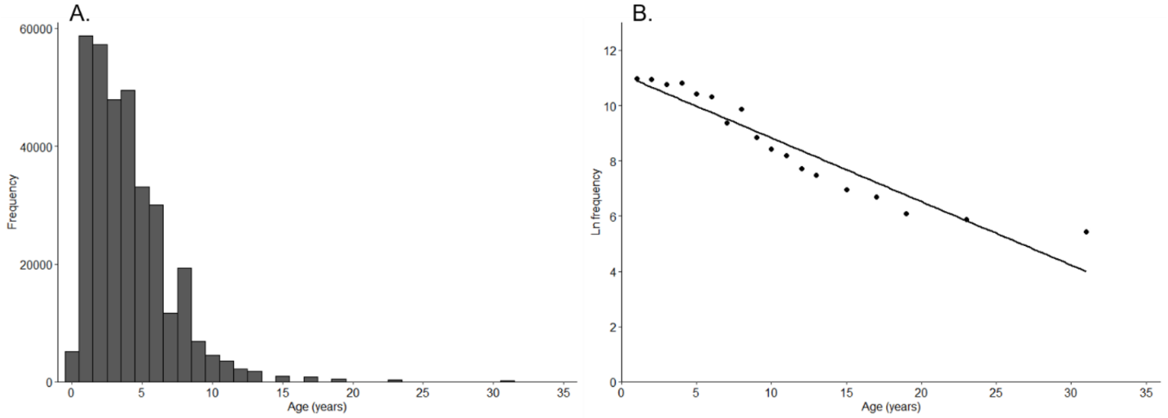


Figure 4.19: A. Age frequency distribution of Helicolenus dactylopterus *caught in research trawls from 1991 to 2019. B. Catch curve for* Helicolenus dactylopterus *caught in research trawls from 1991 to 2019.*

Population trends and conservation status

Standardised abundance indices from research data were generally more conservative than those derived from commercial data (Figure 4.20). The magnitude of change in estimated abundance indices between years differed between the two datasets (Table 4.8), but annual trends were largely similar. *Helicolenus dactylopterus* CPUE increased from 2007 to 2009/2010, thereafter decreasing slightly, but remaining relatively stable until 2017. From 2016 to 2017, standardised CPUE estimates from research trawl data increased substantially (38.54%,), however, this trend was not present in commercial data where standardised CPUE decreased by 5.22% over the same period (Table 4.8).

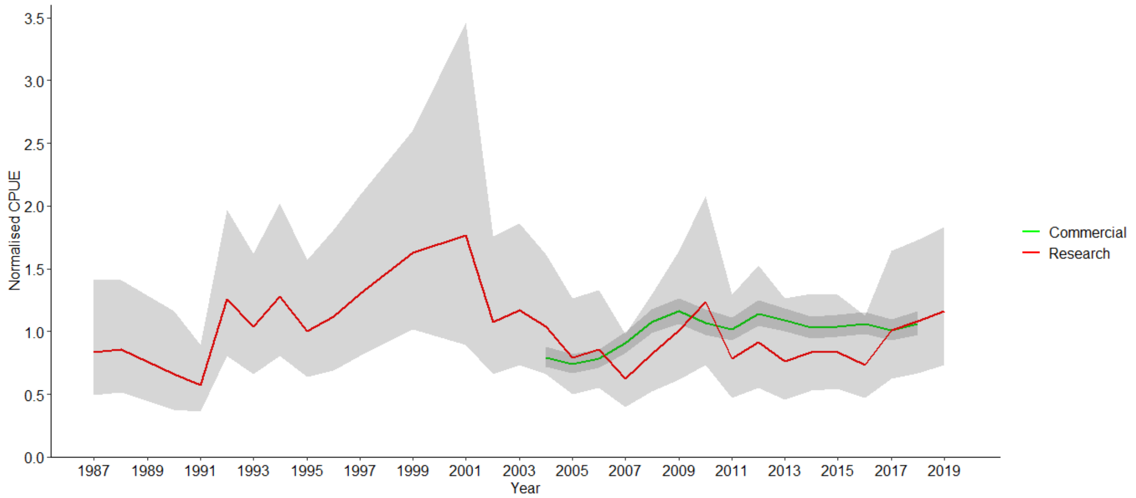


Figure 4.20: A comparison of the standardised CPUE estimates of Helicolenus dactylopterus *derived from research and commercial trawl data. Values were normalised by dividing by their means. The 95% confidence intervals for the standardised CPUE estimates are shaded grey.*

Table 4.8:The standardised CPUE estimates of Helicolenus dactylopterus *derived from research and commercial trawl data and the percent interannual change.*

Year	**Research trawl estimates**		**Commercial trawl estimates**	
	Standardised CPUE ($kg.hr^{-1}$)	**Interannual change (%)**	**Standardised CPUE ($kg.hr^{-1}$)**	**Interannual change (%)**
1987	66.99	2.37		
1988	68.58	-22.76		
1990	52.97	-13.49		
1991	45.82	120.30		
1992	100.95	-17.67		
1993	83.11	23.32		
1994	102.49	-21.72		
1995	80.23	11.72		
1996	89.64	16.01		
1997	103.98	25.55		
1999	130.56	8.29		
2001	141.38	-39.07		
2002	86.14	8.91		
2003	93.82	-11.49		
2004	83.04	-23.39	51.82	-6.55
2005	63.61	8.28	48.42	5.51
2006	68.88	-27.29	51.09	16.65
2007	50.08	31.75	59.60	18.27
2008	65.98	22.56	70.49	7.58
2009	80.87	22.68	75.83	-7.65
2010	99.21	-36.79	70.03	-5.03
2011	62.71	17.25	66.50	12.42
2012	73.53	-17.14	74.76	-4.76
2013	60.93	9.55	71.21	-5.49
2014	66.75	0.41	67.30	1.17
2015	67.03	-12.68	68.08	2.18
2016	58.53	38.54	69.57	-5.22
2017	81.09	14.81	65.94	5.49
2018			69.56	
2019	93.10			

Despite fluctuations in abundance, the JARA model fitted to the standardised *H. dactylopterus* CPUE estimates from research and trawl data estimated that the population has increased annually by 0.83% over the study period, since 1987 (Figure 4.21). The population increased by 1.08% over the last two generation lengths, from 1990 to 2019, and more recently, since 2005 it has increased by 1.42% per year (Figure 4.21).

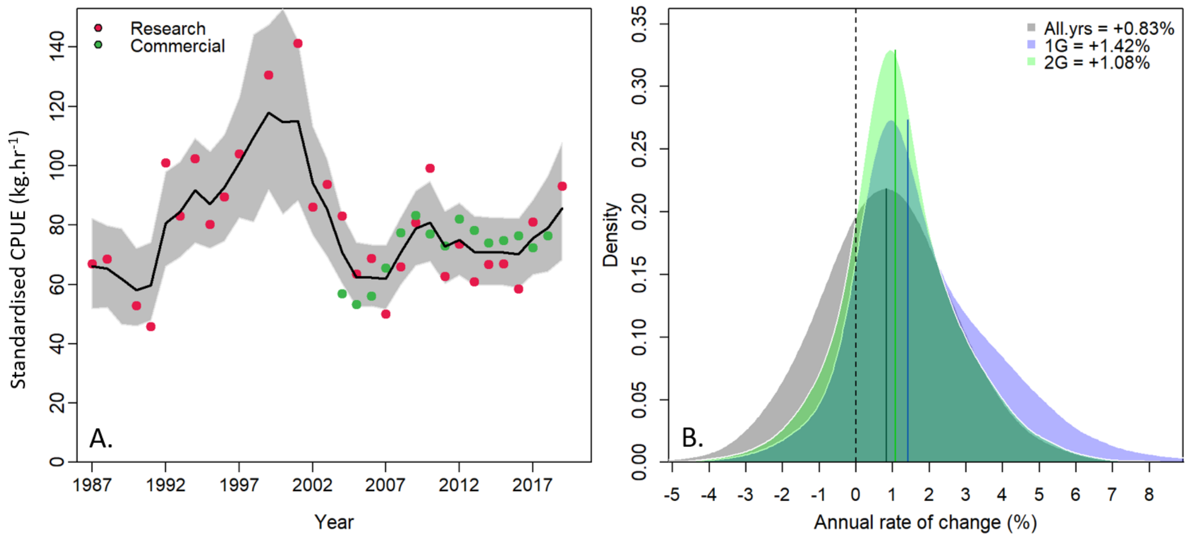


Figure 4.21: A. the fit of the JARA model (black line) to the standardised CPUE estimates of Helicolenus dactylopterus *derived from research and commercial trawls, with 95% credible intervals (grey polygon). B. the posterior probability distributions for the yearly rate of* Helicolenus dactylopterus *population change (%) estimated over all observed years (grey), and over the last one – (1G, blue) and two-generation (2G, green) lengths shown relative to a stable population when percentage change is 0 (black dashed line). Medians are shown as solid lines.*

The combined research and commercial trawl time-series extended over 30 years, however, was insufficient to cover three generation lengths, as required by the IUCN Red List criteria (IUCN, 2012). The JARA model thus projected population change of *H. dactylopterus* over three generation lengths (Figure 4.22 A) and estimated an overall increase in the population of 45.2%. Based on the projected population increase and according to the IUCN Red List categories and criteria, the assessment suggests the South African population of *H. dactylopterus* is classified as Least Concern (Figure 4.22 B).

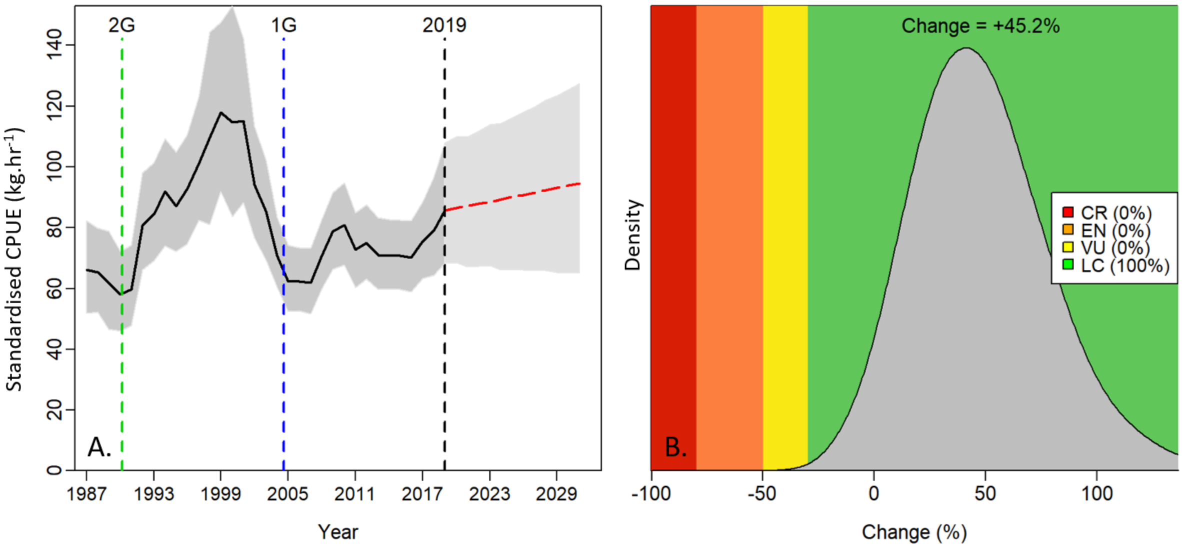


Figure 4.22: A. the estimated population trajectory (with 95% credible intervals) of South African Helicolenus dactylopterus *over one-and two-generation lengths, denoted by the vertical dashed lines and projected over three-generation lengths where the red line indicates model projection. B. The median change in the relative abundance of* Helicolenus dactylopterus *over three-generation lengths as projected by the JARA model. The corresponding Bayesian posterior probability for that change is denoted by the grey polygon which is overlaid on the IUCN Red List category thresholds for criteria A2. The percentage of the posterior probability distribution falling in each of the Red List categories (LC – Least Concern, Vu – Vulnerable, EN – Endangered, CR – Critically Endangered) is shown in the legend.*

4.5 Discussion

The fishery-independent and fishery-dependent datasets used in this chapter both had their benefits and limitations for estimating the abundance indices of *H. dactylopterus*. The fishery-independent research trawl data provided temporally extensive and reliable coverage and the commercial trawl data complemented the research trawl data in that it provided broader seasonal and spatial coverage. The most important step in estimating abundance indices from commercial data is standardisation, particularly to account for different fishing strategies used by skippers (Winker et al., 2013). In this chapter, the inclusion of fishing cluster in the model accounted for the fishing strategy employed by commercial skippers and improved the standardisation of *H. dactylopterus* CPUE significantly. The abundance indices derived from research and trawl data were largely comparable when the time-series overlapped. The use of both datasets provided a comprehensive description of the population trend of *H. dactylopterus* in South Africa over the last 30 years.

Since 1987, the long-term abundance trends of South African *H. dactylopterus* have oscillated, showing sustained periods of population growth and decline (Figure 4.21), typical of a long-lived species (Shelton and Mangel, 2011). The population assessment provided an optimistic outlook for *H. dactylopterus* in South Africa with a net increase in the population shown since 1987. Population growth has accelerated over time from 0.83% per year over the whole study period to 1.42% per year since 2005. These results generally align with those of Winker et al. (2017), who, from 2007 to 2017, found an annual rate of increase in the abundance of *H. dactylopterus* on the west coast and south coasts of 1.2% and 3% per year respectively.

Although the data used in this chapter provided insight into the population growth of *H. dactylopterus* over the last thirty years, the abundance of the species prior to 1987 is unknown. It is thus important to consider that while a net increase in abundance occurred, it was relative to the abundance estimated in 1987. Preceding abundances of *H. dactylopterus* may have been much greater, particularly before the expansion of the commercial trawl fishery into deeper fishing grounds in the 1940s.

Temporal fish population abundance trends are affected by a combination of fishing mortality and factors acting in a density-dependent or density-independent manner that affect recruitment, growth and natural mortality (Sissenwine, 1984). The overall population increase of South African *H. dactylopterus* is likely largely in response to improved management of the demersal trawl fishery over the last 50 years. The short-term oscillations in CPUE, however, probably reflect a combination of fishing effects and changes in reproduction, growth and survival which are related to the biology and the life history characteristics of the species (Hutchings, 2000; Kindsvater et al., 2016).

In the mid-1970s, in response to unprecedented fishing effort and declining hake catch rates, management measures including a larger minimum mesh size and quota allocations were implemented in the demersal trawl fishery (Durholtz et al., 2015). In 1977, South Africa established a 200 nm exclusive fishing zone (EFZ) (Durholtz et al., 2015). Consequently, foreign vessels were excluded from fishing in South African waters, unless under bilateral agreement. A total allowable catch (TAC) limit was introduced to further constrain fishing effort and TACs were specified for each company in 1979 (Durholtz et al., 2015). By the early 1990s, foreign vessels no longer operated in the South African demersal trawl fishery. As intended, the management reforms resulted in a decrease in effort in the fishery, at least during the 1990s, as evidenced in Figure 4.10. The reforms were primarily aimed at rebuilding the depleted hake resource (Augustyn et al., 2018), however, the substantial increase in the abundance of *H. dactylopterus* from the early 1990s to 2001 indicates that, due to the multispecies nature of the demersal trawl fishery, the management reforms also likely benefitted *H. dactylopterus*.

In 2006, permit conditions were amended to include several clauses aimed at addressing the ecosystem impacts of the fishery (Department of Agriculture Forestry and Fisheries, 2016). MSC certification was also obtained in 2004 which required stringent management of target stocks and a reduction of impacts of the fishery on the surrounding ecosystem (Marine Stewardship Council, 2018). Restrictions to trawl gear were implemented and fishing operations were limited to previously trawled grounds to reduce seabed impacts. A simultaneous decrease in fishing effort was observed (Figure 4.10). To reduce bycatch, annual and per trip catch limits for *Genypterus capensis* and *Lophius vomerinus* were imposed as were catch thresholds for *G. capensis* and *Thyrsites atun* (Department of Agriculture Forestry and Fisheries, 2016).

Catch composition data provided insight into the associations of *H. dactylopterus* with other species. Observed associations were similar in research and commercial trawls. The higher number of species in research trawls compared to commercial trawls was attributed to the higher precision in species identification in the former. *Helicolenus dactylopterus* was most dominant in trawls in which *G. capensis, L. vomerinus, Lepidopus caudatus* and *Zeus capensis* were caught. All five species are predominant components of demersal shelf and shelf edge communities in South Africa, mainly occurring in waters deeper than 200 m (Roel, 1987; Badenhorst and Smale, 1991; Smale and Badenhorst, 1991; Atkinson et al., 2011). Similarly to *H. dactylopterus,* adult *G. capensis* occur over rocky substrata and smaller individuals occur in shallower (< 200 m), sandy habitat (Badenhorst and Smale, 1991). *Lophius vomerinus* is generally found over sandy substrata (Walmsley, 2004). The implementation of catch limits for *G. capensis* and *L. vomerinus* therefore likely indirectly reduced the exploitation of *H. dactylopterus.* The increase in abundance of *H. dactylopterus* from 2007 onwards supports this inference.

The low natural mortality and long generation time of *H. dactylopterus* estimated in this study align with estimates of other Sebastinids (Palsson et al., 2009) and are typical of slow-growing, long-lived periodic strategists (Winemiller and Rose, 1992). The longevity of periodic strategists results in a long reproductive lifespan during which individuals survive to breed repeatedly (Goodwin et al., 2006). Annual recruitment is variable and is generally influenced by density-independent factors, but periodic strategists also show strong density-dependent regulation of recruitment at large population sizes (Fowler, 1981; Winemiller, 2005; Goodwin et al., 2006). The density-dependence is likely due to increased competition among adults at high densities resulting in a decline in ovary mass and subsequent reduction in fecundity, increased competition at the larval stage or due to increased competition among recruits and adults (Goodwin et al., 2006). Thus, while recruitment can be low, periodic strategists can exploit optimum environmental conditions, increasing recruit production. Due to low natural mortality, these strong annual cohorts can persist in the population for many years which can eventually lead to density-dependent responses (Winemiller, 2005).

The increase and subsequent decrease in *H. dactylopterus* CPUE between 1990 and 2005 can be explained by the dynamics described above. The reduction in fishing pressure during the 1990s would have increased spawner biomass. For recruit production to increase, density-independent factors need to promote recruit survival. Thus, with favourable environmental conditions, there was likely an increase in recruit production, contributing to the subsequent population increase. This is reflected in the relatively low mean total length of the population observed, particularly in the early 1990s (Figure 4.18), indicating high recruitment.

The increase in CPUE was sustained until 2001, driven largely by the continued increase in spawner biomass due to the strong annual cohorts in the early 1990s. A simultaneous gradual increase in the mean total length of the population was observed over this time. From 2001, density-dependent regulation potentially occurred due to space and resource limitations and intra-specific competition among larvae, recruits or adults. At that point, the population had likely expanded beyond what the environment could sustain and there may have been a subsequent density-dependent reduction in recruitment, a so-called carrying capacity overshoot (Whittaker, 1975; Wisniewski, 1980), resulting in the population decline from 2001 to 2005. The population decline coincided with a peak in mean total length, indicating low recruitment (Figure 4.18). Effort in the commercial fishery also increased between 2001 and 2005 (Figure 4.10) which may have contributed to the decline. The *H. dactylopterus* population showed signs of recovery from this overshoot from 2005 onwards. Mean total length decreased from 2004 onwards suggesting an increase in recruitment, and as mentioned, fishing pressure decreased from 2005 onwards.

The importance of the interaction between a reduction in fishing pressure and strong recruitment years, and the impact that these two factors have on fish population growth, has been demonstrated in several oviparous *Sebastes* species that were previously declared as overfished. The population dynamics of *Sebastes diploproa* in the North East Pacific were modelled and indicated an increase in the population since the early 2000s primarily in response to a reduction in exploitation rates coupled with above-average recruitment (Gertseva and Cope, 2011). As with *H. dactylopterus*, *S. diploproa* is a bycatch species. The reduction in exploitation was, at least partly, due to management reforms aimed at rebuilding *S. crameri* and *S. alutus* populations, with which *S. diploproa* co-occurs (Gertseva and Cope, 2011). With a reduction in exploitation, the spawning output of *S. diploproa* was substantially increased, corresponding with an increase in survey abundance indices (Gertseva and Cope, 2011). Similarly, a recent assessment indicated the population recovery of *S. paucispinis* on the west coast of the United States (He and Field, 2017). After several decades of high fishing pressure, severe management restrictions to limit the catch of the species were implemented in the late 1990s. Several strong recruitment years occurred over the same period, starting in 1999. Subsequently, the spawning output and biomass of the *S. paucispinis* population has been increasing steadily since the early 2000s (He and Field, 2017).

In addition to recruitment, variation in the mean total length of the *H. dactylopterus* population may also be in response to fishing pressure. Higher exploitation rates pre-1990 may have contributed to the relatively low mean total length of adult specimens observed in the early 1990s. The subsequent reduction in fishing pressure may have allowed for the increase in mean total length seen between 1991 and 2001. The fecundity of *H. dactylopterus* increases with size (Muñoz and Casadevall, 2002; Sequeira et al., 2015) and so the increased occurrence of larger, older individuals in the spawning stock in South Africa in the 1990s may have also indirectly influenced the increased recruitment that led to the population growth over this period.

Since 2011, the abundance trends of *H. dactylopterus* remained relatively stable with net population growth. Fishing effort was lower than that prior to 2008 and was constant between 2011 and 2018, ranging between approximately 37 000 and 47 000 trawls per annum. There was, however, an increase in the nominal catch of *H. dactylopterus* from 2011 to 2017 (Figure 4.14) which was not reflected in the standardised CPUE estimates. There was also fluctuation in the mean total length of the population between 2011 and 2019, indicating more variable recruitment. Recruitment was thus sufficient to allow for population growth, but the short-term fluctuation in recruitment coupled with an increase in fishing mortality may have limited the occurrence of density-dependent regulation, thus preventing an overshoot of the carrying capacity.

Although a net increase in *H. dactylopterus* abundance occurred from 1987 to 2019 (Figure 4.21), the projected overall population increase of 45.2% over three generation lengths must be interpreted with caution (Figure 4.22). Due to the long generation length of South African *H. dactylopterus,* even with 30 years of research trawl data, the time-series was insufficient to cover three generation lengths, as required by the IUCN Red List Criterion A (IUCN, 2012). The JARA predicted the population trajectory from 2019 to 2030 based on observed trends, but this does not make allowance for changes in fishing pressure or the effects of environmental variability. The current population growth trends certainly suggest the species in South Africa is not of conservation concern. The Bayesian posterior probability for the projected population trajectory indicates no uncertainty in the classification of the species as Least Concern (Figure 4.22 B). Continued classification of *H. dactylopterus* in South Africa as Least Concern according to the IUCN Red List criteria, is, however, dependent on exploitation levels remaining sustainable and the absence of any large-scale, sustained environmental changes that could detrimentally affect recruitment success.

Seasonally, *H. dactylopterus* abundance did not vary significantly in the commercial trawls. These results are supported by those of Smale and Badenhorst (1991) who did not find a seasonal difference in the abundance of *H. dactylopterus* on the south coast of South Africa over a four-year period (1986-1990). The lack of seasonality in *H. dactylopterus* abundance shown in this study may highlight an absence of transient spawning aggregations. Male and female spawning is asynchronous, and females can store sperm (Chapter 2) for up to several months at a time. Sperm storage may therefore negate the need to increase mate-encounter rate during a spawning aggregation. In the Azores, tagging studies have indicated that *H. dactylopterus* is a sedentary species showing high residency and no evidence of transient spawning aggregations (Santos et al., 2020). The same may apply to the species in South Africa.

Spatially, in research and commercial trawls, *H. dactylopterus* CPUE was significantly greater in waters 301 to 400 m deep. These findings vary slightly to those in Chapter 3 where *H. dactylopterus* abundance was greatest in depths from 201 to 300 m. In the previous chapter, abundance was measured as the number of fish per trawl or video segment, however, here, abundance indices, estimated from CPUE, were based on biomass. *Helicolenus dactylopterus* in South Africa exhibits ontogenetic migration, with larger fish occurring in deeper waters (Chapter 2). Thus, while abundance may be greater in waters from 201 to 300 m deep, the larger fish occurring in waters 301 to 400 m contribute to greater biomass than those in shallower waters.

4.6 Conclusion

The findings from this study, generated from two complementary datasets, provide a comprehensive understanding of the population trend and dynamics of *H. dactylopterus* in South Africa over the last 30 years. The data produced have application to resource and conservation assessment and the management of the demersal trawl fishery.

Although the life history characteristics of *H. dactylopterus* are suggestive of low resilience and high vulnerability to exploitation, the population in South Africa has increased over the last 30 years. This trend is largely attributed to a reduction in fishing effort in the South African demersal trawl fishery because of management reforms, but several years of strong recruitment, as evidenced by average length data, have also played a key role.

While net population growth was recorded, several fluctuations in abundance occurred over the 30-year period. These patterns were related to the life history characteristics of *H. dactylopterus* and were typical of a periodic strategist. Due to the longevity of *H. dactylopterus,* the strong year classes persisted in the population for an extended period and contributed to increased spawning output. This eventually resulted in density-dependent population regulation and a subsequent short-term decline in abundance.

The findings are in general agreement with a preliminary study conducted by Winker et al. (2017). The population growth recorded suggests the species is currently of low conservation concern in South Africa. Looking ahead, the overall trend in the abundance of *H. dactylopterus* in South Africa indicates an optimistic view if exploitation levels remain sustainable and there are no large-scale environmental changes that affect recruitment success.

4.7 Appendix

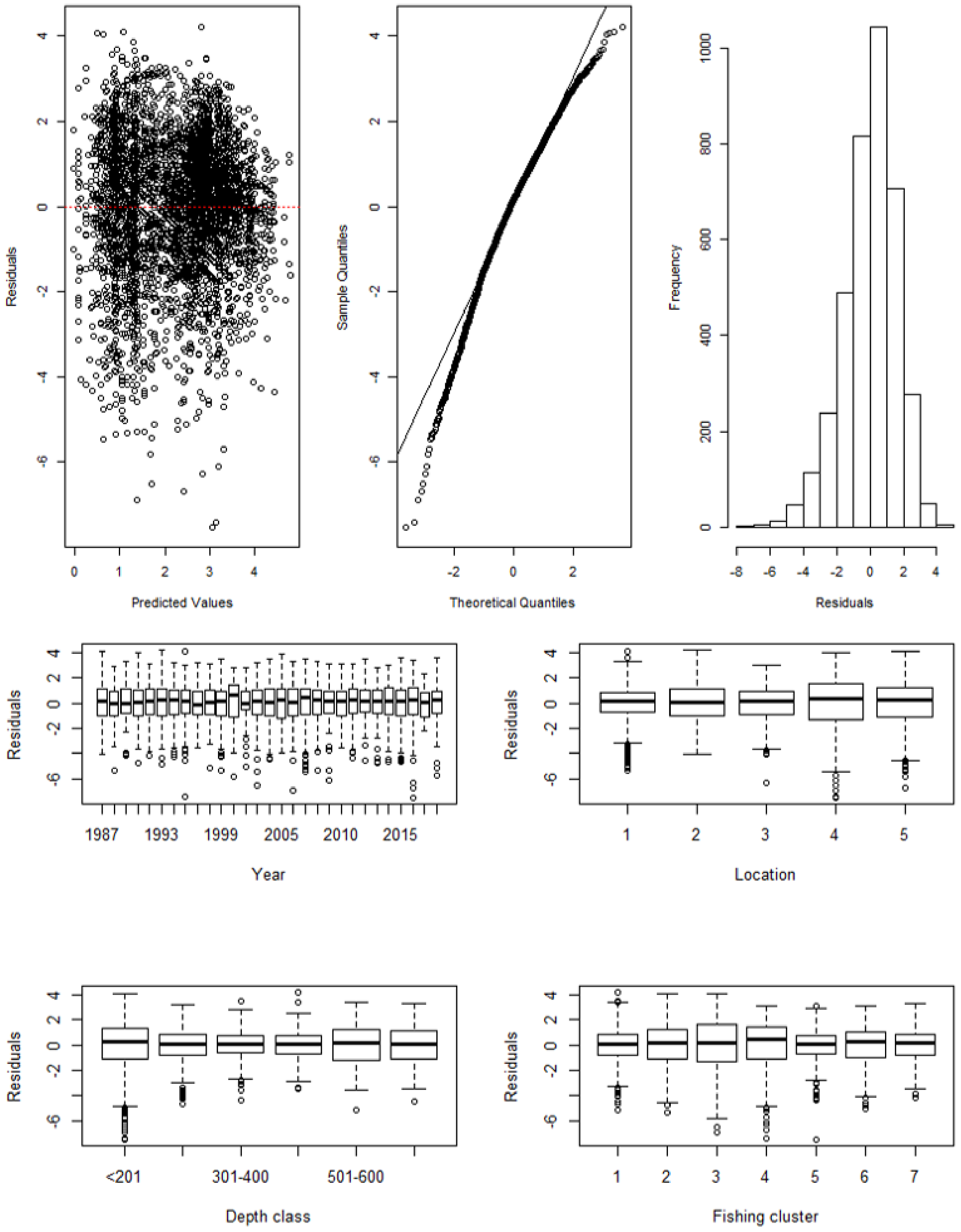


Figure 4.23: Model validation of the lognormal GLM of Helicolenus dactylopterus *CPUE in demersal research trawls conducted in South Africa from 1987 to 2019.*

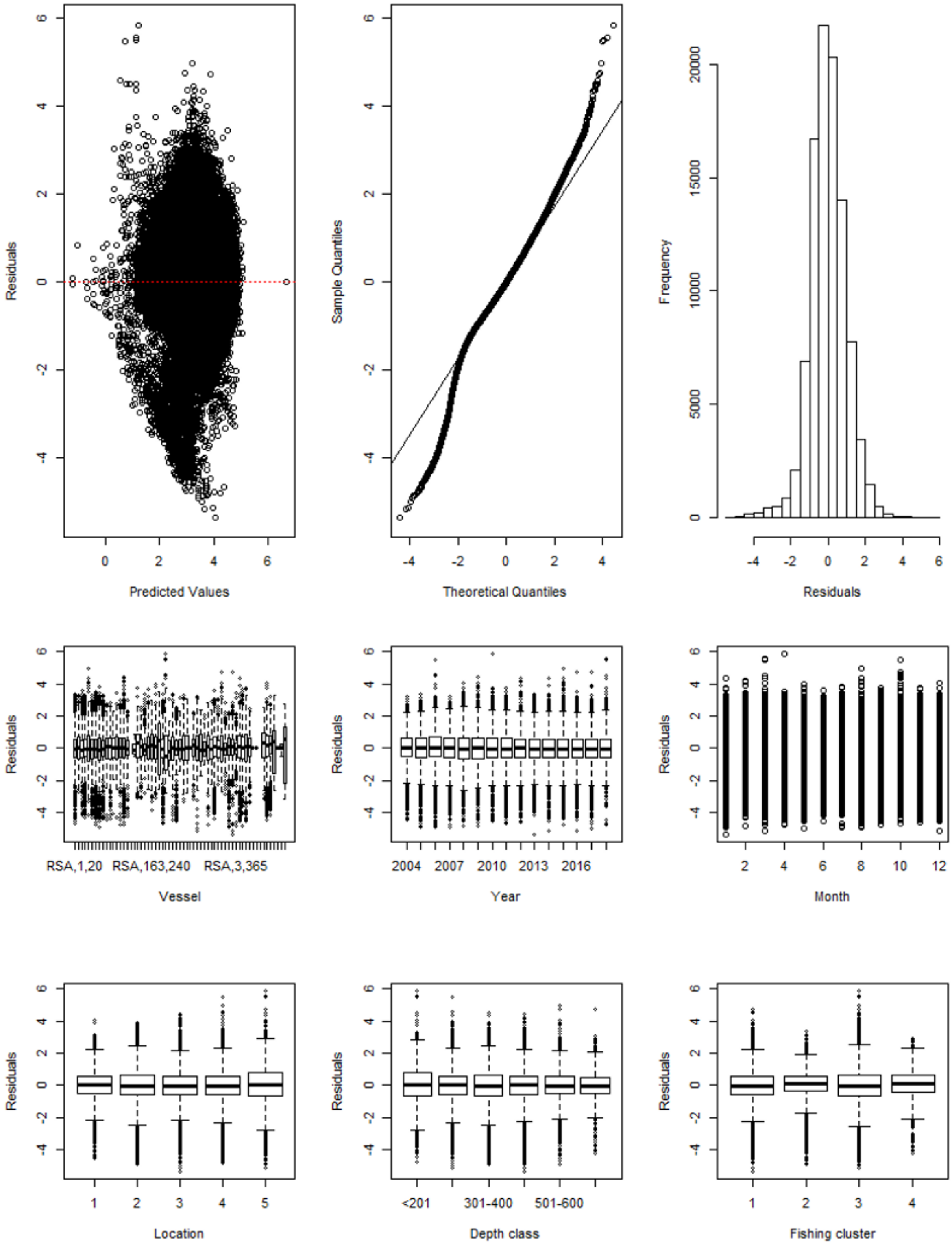


Figure 4.24: Model validation of the lognormal GLM of Helicolenus dactylopterus *CPUE in demersal commercial trawls in the South African EEZ from 2004 to 2018.*

CHAPTER 5

SYNTHESIS AND CONCLUSION

The scientific assessment and management of a fish stock requires extensive information on the life history, ecology, population structure and abundance trends of the harvested species. These data can be used to derive indicators and biological reference points which give insight into the status of and the impact of fishing on the stock (Hilborn and Walters, 1992). Traditionally, the collection of these biological and ecological data for the target species of a given fishery were prioritised. However, for the effective implementation of an Ecosystems Approach to Fisheries management, data on the non-target bycatch species are also required. The consideration of bycatch species is especially important in a multispecies fishery that uses poorly selective gear, such as the South African demersal trawl fishery. Key bycatch species in the demersal trawl fishery have been identified and progress is being made on improving the collection of data for and the understanding of these species' populations. *Helicolenus dactylopterus* is one such bycatch species, being the sixth most caught by weight in the offshore trawl sector (Daneel and Attwood, 2013).

Helicolenus dactylopterus is well studied in the North Atlantic and Mediterranean. However, apart from two studies done in the early 1990s on the diet and abundance trends (Badenhorst and Smale, 1991; Meyer and Smale, 1991), little research had been conducted on the species in South Africa. The data and findings presented in this thesis provided a comprehensive, current biological and ecological assessment of *H. dactylopterus* in South Africa.

Chapter 2 provided the first thorough description of the life history traits of *H. dactylopterus* in South Africa and an update of the diet description of the species. Like other Sebastinids, *H. dactylopterus* is a periodic strategist. Drawing from more than 700 samples, obtained mainly from the commercial trawl fishery, the species in South Africa was found to be slow-growing and long-lived. The growth rate was 0.13 year^{-1} and it attained a maximum age of 32 years. The maximum total length was 494 mm, close to the maximum length (500 mm) for the species. The maximum age and length of fish in South Africa generally aligned with those in the North Atlantic. Fish in South Africa were older and larger than fish in the Mediterranean. These differences were attributed to the warmer water occurring in the Mediterranean compared to the North Atlantic and South Africa, and the greater fishing pressure in the

Mediterranean. The growth rate of South African fish was faster than fish in the North Atlantic, and aligned more with the growth rates of individuals from the Mediterranean. It was postulated that the high productivity in local waters, compared to the mesotrophic and oligotrophic waters of the North Atlantic and Mediterranean, influenced the growth rate of South African fish. There was no difference in the size attained or growth between sexes.

Like other species in the subfamily, the reproductive characteristics of *H. dactylopterus* in South Africa were found to be unusual. *Helicolenus dactylopterus* has internal fertilisation and there is a delay between insemination and spawning. Females spawned in austral winter and spring, from June to November and males spawned in austral spring, summer, and autumn, from September to June. Females stored sperm in the intraovarian cavity or in rounded storage structures at the base of the lamellae. It was hypothesised that females copulate with and store sperm from multiple males, a strategy that may increase fertilisation success. Length and age at maturity of South African *H. dactylopterus* relative to the maximum length and age attained was lower than other Sebastinids but was comparable to conspecifics in Portuguese waters.

Although a greater number of stomachs were analysed, diet investigation yielded similar results to the study conducted 30 years previously by Meyer and Smale (1991). Like in other parts of its range, *H. dactylopterus* in South Africa was found to be a selective benthic predator with benthic crustaceans dominating the diet. Some pelagic organisms were preyed upon, suggesting that, in South African continental shelf and slope habitats, *H. dactylopterus* plays a role in energy transfer from pelagic to benthic ecosystems. A change in diet as fish grew larger was observed. The ontogenetic shift is thought to reflect a change in energy requirements when fish reach sexual maturity and may be related to changes in mouth morphology as fish grow larger.

The findings of Chapter 3 described the habitat preference of *H. dactylopterus* in South Africa. Broad resolution data from more than 900 research trawls revealed that the species primarily occurs in the Atlantic in depths between 100 and 600 m. Abundance decreased with extension into the Indian Ocean, a pattern that likely reflects the oceanography off South Africa. It was hypothesised that the geographic expansion of *H. dactylopterus*, which is primarily reliant on larval dispersal (Aboim et al., 2005), is limited in the Indian Ocean due to the strong, southward-flowing Agulhas Current. The depth distribution of the species overlapped substantially with the footprint of the offshore demersal trawl fishery, in which effort is concentrated between 300 and 500 m on the west coast and between 200 and 500 m on the south coast (Wilkinson and Japp, 2005; Fairweather et al., 2006). A large portion of the South African *H. dactylopterus* population is thus susceptible to capture by the fishery.

Fine resolution video data were useful in identifying factors that influenced *H. dactylopterus* distribution patterns over finer spatial scales. Video data highlighted the importance of topographically complex rocky reef habitat in influencing the abundance of especially larger (>200 mm) individuals. Two alternatives were proposed for the observed patterns. The selection of reef habitat was due to the active habitat selection by individuals for spawning and sheltering, and/or was an apparent signal because of the selection of large fish on more accessible, unconsolidated substrata by the fishery. These two alternatives are not mutually exclusive and may both contribute to the pattern in habitat preference observed.

The abundance trends of *H. dactylopterus* in South Africa were examined and described in Chapter 4. Standardised CPUE estimates from two independent, complementary time-series provided a comprehensive description of the population trend and dynamics over the last 30 years. Overall, a net increase in the relative abundance of *H. dactylopterus* of 0.83% per year was recorded over the study period but several fluctuations occurred over that time. These patterns were attributed to a reduction in fishing pressure, due to management reforms, acting together with density-dependent factors. It was postulated that several years of strong recruitment, as evidenced by the low population mean total length in the early 1990s, contributed to the population growth of *H. dactylopterus*. However, the longevity of the species resulted in the strong year classes persisting in the population for an extended period, eventually causing density-dependent regulation and a short-term decline in abundance. Fishing pressure may have also influenced the low mean total length observed in the early 1990s. Since 2005, the population growth of the species accelerated to 1.42% per year. The population risk assessment suggested the species is currently of low conservation concern, suggesting a classification as Least Concern according to the IUCN Species Red List. The findings thus indicate an optimistic outlook for the South African *H. dactylopterus* population.

The findings of this thesis confirm that the life history characteristics of *H. dactylopterus* make the species vulnerable to fishing pressure. Based on the criteria defined by Musick (1999), *H. dactylopterus* in South Africa has very low productivity and resilience to perturbation. This classification is based primarily on the longevity of the species. When considering the vulnerability of the species to fishing, the effect that exploitation has had on other species of the Sebastinae and the impact of fisheries on conspecifics in the Mediterranean, poor stock status could be anticipated. However, the data from this thesis show that *H. dactylopterus* has not succumbed to fishing pressure to the extent expected in South Africa.

Several reasons for the resilience of South African *H. dactylopterus* to fishing pressure are postulated and are alluded to in Chapters 2, 3 and 4. The estimated early maturation of the species compared to other species in the sub-family likely influences their ability to resist exploitation. Species with early maturity have higher intrinsic rates of population growth (Musick, 1999). A larger proportion of the fished population is reproductively active and thus contributes to increased spawning output. The reproductive strategy of *H. dactylopterus* may also increase productivity and population resilience. The ability of females to store sperm from multiple males may increase fertilisation success and fecundity. During periods of optimal environmental conditions, increased fecundity may contribute to strong recruitment.

The potential use of rocky habitat on the South African continental shelf and shelf edge for spawning may also contribute to the resilience of *H. dactylopterus* to fishing pressure. Trawling may occur over some rocky habitat, but many areas are untrawlable and provide refuge from fishing. Large individuals that occupy and spawn in these untrawlable areas thus play a role in renewing the *H. dactylopterus* population on neighbouring trawl grounds. This renewal may occur to the extent that it mitigates against the fishing pressure exerted on the species in local waters. The importance of maintaining the integrity of these reef habitats for the spawning and refuge by fish species is thus highlighted.

Finally, and perhaps most importantly, as shown in Chapter 4, the management reforms implemented in the demersal trawl fishery over the last 40 years have resulted in a reduction in fishing pressure on *H. dactylopterus.* The exploitation of the species is thus at a level at which population recovery and growth is enabled.

Overall, the findings of this thesis have contributed to completing the global picture of a widely distributed species. A thorough, population-specific account of *H. dactylopterus* in South Africa was given so that the vulnerability to and the effect of fishing on the species could be assessed. The information can be applied to local stock assessment to improve the ecosystem-level management of the South African demersal trawl fishery and has application to the further conservation assessment of *H. dactylopterus*. The findings also provide important information that can be used to improve the scientific assessment of *H. dactylopterus* under initiatives to support sustainable seafood. These initiatives include eco-certification and awareness programmes such as certification by the Marine Stewardship Council (MSC) and assessment under the South African Sustainable Seafood Initiative (SASSI). This thesis therefore provides data and knowledge relevant to scientists, fisheries managers, conservation practitioners and consumers.

REFERENCES

Abe, T. and Eschmeyer, W.N. 1972. A new species of the scorpionfish genus *Helicolenus* from the North Pacific Ocean. *Proceedings of the California Academy of Sciences*. 39(4):47–53.

Abecasis, D., Costa, A.R., Pereira, J.G. and Pinho, M.R. 2006. Age and growth of bluemouth, *Helicolenus dactylopterus* (Delaroche, 1809) from the Azores. *Fisheries Research*. 79:148–154.

Aboim, M.A., Menezes, G.M., Schlitt, T. and Rogers, A.D. 2005. Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. *Molecular Ecology*. 14:1343–1354.

Adams, P. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery Bulletin*. 78(1):1–12.

Allain, V. and Lorance, P. 2000. Age estimation and growth of some deep-sea fish from the northeast Atlantic Ocean. *Cybium*. 24(3):7–16.

Althaus, F., Hill, N., Edwards, L. and Ferrari, R. 2014. *CATAMI Classification Scheme for Scoring Marine Biota and Substrata in Underwater Imagery- a Pictorial Guide to the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) Classification Scheme*. Version 1. Available: http://catami.org/classification [accessed 03 September 2018].

Alverson, D.L., Freeberg, M.H., Murawski, S.A. and Pope, J.G. 1994. *A global assessment of fisheries bycatch and discards*. FAO Fisheries Technical Paper 339. Rome: FAO. 233 pp.

Amundsen, P.A., Gabler, H.M. and Staldvik, F.J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data - modification of the Costello (1990) method. *Journal of Fish Biology*. 48:607–614.

Anastasopoulou, A., Mytilineou, C., Dimitriadis, G. and Smith, C.J. 2017. Aspects on age and growth of *Helicolenus dactylopterus* from the deep waters of the eastern Ionian Sea. In Pauly, D., Hood, L. and Stergiou, K.I. (Eds.) *Belated Contributions on the Biology of Fish, Fisheries and Features of their Ecosystems.* Fisheries Centre Research Reports 25(1). Vancouver: Institute for the Oceans and Fisheries, The University of British Columbia. 61–66.

Anderson, T.J. and Yoklavich, M.M. 2007. Multiscale habitat associations of deepwater demersal fishes off central California. *Fishery Bulletin*. 105:168–179.

Anderson, M.J., Gorely, R.N. and Clarke, K.R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E Ltd. 214 pp.

Anderson, S.C., Keppel, E.A. and Edwards, A.M. 2019. *A reproducible data synopsis for over 100 species of British Columbia groundfish*. Canadian Science Advisory Secretariat Research Document 2019/041. 330 pp.

Atkinson, L.J., Field, J.G. and Hutchings, L. 2011. Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. *Marine Ecology Progress Series*. 430:241–256.

Atkinson, L.J., Leslie, R.W., Field, J.G. and Jarre, A. 2011. Changes in demersal fish assemblages on the west coast of South Africa, 1986–2009. *African Journal of Marine Science*. 33(1):157–170.

Atkinson, L.J. and Sink, K.J. 2018. *Field Guide to the Offshore Marine Invertebrates of South Africa*. Pretoria: Malachite Marketing and Media. 498 pp.

Attwood, C.G., Petersen, S.L. and Kerwath, S.E. 2011. Bycatch in South Africa's inshore trawl fishery as determined from observer records. *ICES Journal of Marine Science*. 68(10):2163–2174.

Audzijonyte, A. and Pecl, G.T. 2018. Deep impact of fisheries. *Nature Ecology and Evolution*. 2(9):1348–1349.

Augustyn, C.J., Cockcroft, A., Coetzee, J., Durholtz, D. and van der Lingen, C.D. 2018. Rebuilding South African fisheries: three case studies. In Garcia, S.M. and Ye, Y. (Eds.) *Rebuilding of Marine Fisheries. Part 2*. FAO Fisheries and Aquaculture Technical Paper 630/2. Rome: FAO. 107–143.

Azov, Y. 1991. Eastern Mediterranean-a marine desert? *Marine Pollution Bulletin*. 23:225–232.

Badenhorst, A. and Smale, M.J. 1991. The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. *South African Journal of Marine Science*. 11(1):377–393.

Bailly, N. 2015. *Sebastidae Kaup, 1873*. Available through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetailsandid=125596 [accessed 13 September 2017].

Barnard, K. 1947. *A Pictorial Guide to South African Fishes: Marine and Freshwater*. Cape Town: Maskew Miller Limited. 226 pp.

Barsukov, V. V. 1980. Subspecies of the Atlantic blackbelly rosefish, *Helicolenus dactylopterus* (De La Roche, 1809). *Journal of Ichthyology*. 19:1–17.

Bates, D., Machler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67(1):1–48.

Baudron, A.R., Pecl, G., Gardner, C., Fernandes, P.G. and Audzijonyte, A. 2019. Ontogenetic deepening of Northeast Atlantic fish stocks is not driven by fishing exploitation. *Proceedings of the National Academy of Sciences of the United States of America*. 116(7):2390–2392.

Baust, S., Teh, L., Harper, S. and Zeller, D. 2015. South Africa's marine fisheries catches (1950-2010). In Le Manach, F. and Pauly, D. (Eds.) *Fisheries Catch Reconstructions in the Western Indian Ocean, 1950-2010.* Fisheries Centre Research Reports 23(2). Vancouver: Fisheries Centre, University of British Columbia. 129–150.

Bayhan, Y.K., Ergüden, D. and Cartes, J.E. 2018. Deep sea fisheries in Mersin Bay, Turkey, Eastern Mediterranean: diversity and abundance of shrimps and benthic fish fauna. *Acta Zoologica Bulgarica*. 70(2):259–268.

Beamish, R.J. and Fournier, D.A. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*. 38(8):982–983.

Beamish, R.J. and McFarlane, G.A. 1983. The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society*. 112(6):735–743.

Beamish, R.J., McFarlane, G.A. and Benson, A. 2006. Longevity overfishing. *Progress in Oceanography*. 68:289–302.

Bedford, B.C. 1983. A method for preparing sections of large number of otoliths embedded in black polyester resin. *Journal du Conseil*. 41:4–12.

Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X. and Pierce, G.J. 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management? *Hydrobiologia*. 670:317–333.

Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der thiere zu ihrer grösse. *Gottinger Studien*. 3:595–708.

Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*. 29:23–32.

Berntson, E.A., Levin, P.S. and Moran, P.C. (Eds.). 2007. *Conservation of North Pacific Rockfishes: Ecological Genetics and Stock Structure. Proceedings of the Workshop, March 2-3, 2004*. Seattle: NOAA. 80 pp.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Payá, I., Sainsbury, K., Sanchez, F. and Zwanenburg, K. 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*. 57(3):558–571.

Biber, M.F., Duineveld, G.C.A., Lavaleye, M.S.S., Davies, A.J., Bergman, M.J.N. and van den Beld, I.M.J. 2014. Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. *Deep-Sea Research Part II: Topical Studies in Oceanography*. 99:134–145.

Bilecenoğlu, M., Kaya, M., Cihangir, B. and Çiçek, E. 2014. An updated checklist of the marine fishes of Turkey. *Turkish Journal of Zoology*. 38:901–929.

Bizzarro, J.J., Smith, W.D., Márquez-farías, J.F., Tyminski, J. and Hueter, R.E. 2009. Temporal variation in the artisanal elasmobranch fishery of Sonora, Mexico. *Fisheries Research*. 97:103–117.

Blaber, S.J.M. and Bulman, C.M. 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology*. 95(3):345–356.

Boehlert, G. and Kappenman, R. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the Northeast Pacific Ocean. *Marine Ecology Progress Series*. 3:1–10.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. and White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*. 24(3):127–135.

Borges, T.C., Olim, S. and Erzini, K. 2003. Weight-length relationships for fish species discarded in commercial fisheries of the Algarve (southern Portugal). *Journal of Applied Ichthyology*. 19: 394–396.

Branch, T.A. and Hilborn, R. 2008. Matching catches to quotas in a multispecies trawl fishery: targeting and avoidance behavior under individual transferable quotas. *Canadian Journal of Fisheries and Aquatic Sciences*. 65:1435–1446.

Brown, S.C., Bizzarro, J.J., Cailliet, G.M. and Ebert, D.A. 2012. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fishes*. 95:3–20.

Butterworth, D.S. and Rademeyer, R.A. 2005. Sustainable management initiatives for the southern African hake fisheries over recent years. *Bulletin of Marine Science*. 76(2):287–319.

Cailliet, G.M., Andrews, A.H., Burton, E.J., Watters, D.L., Kline, D.E. and Ferry-Graham, L.A. 2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? *Experimental Gerontology*. 36:739–764.

Campana, S.E., Annand, M.C. and McMillan, J.I. 1995. Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society*. 124(1):131–138.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. 59(2):197–242.

Capezzuto, F., Sion, L., Ancona, F., Carlucci, R., Carluccio, A., Cornacchia, L., Maiorano, P., Ricci, P., Angelo, T. and D'Onghia, G. 2018. Cold-water coral habitats and canyons as Essential Fish Habitats in the southern Adriatic and northern Ionian Sea (central Mediterranean). *Ecological Questions*. 29:9–23.

Capezzuto, F., Calculli, C., Carlucci, R., Carluccio, A., Maiorano, P., Pollice, A., Sion, L., Tursi, A. and D'Onghia, G. 2019. Revealing the coral habitat effect on benthopelagic fauna diversity in the Santa Maria di Leuca cold-water coral province using different devices and Bayesian hierarchical modelling. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 1–15.

Capezzuto, F., Ancona, F., Calculli, C., Sion, L., Maiorano, P. and D’Onghia, G. 2020. Feeding of the deep-water fish *Helicolenus dactylopterus* (Delaroche , 1809) in different habitats: from muddy bottoms to cold-water coral habitats. *Deep-Sea Research Part I: Oceanographic Research Papers*. 159:103252.

Carpenter, J. and Bithell, J. 2000. Bootstrap confidence intervals: when, which, what? A practical guide for medical statisticians. *Statistics in Medicine*. 19:1141–1164.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*. 39:1208–1210.

Charnov, E.L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. New York: Oxford University Press. 167 pp.

Christian, C., Ainley, D., Bailey, M., Dayton, P., Hocevar, J., LeVine, M., Nikoloyuk, J., Nouvian, C., Velarde, E., Werner, R. and Jacquet, J. 2013. A review of formal objections to Marine Stewardship Council fisheries certifications. *Biological Conservation*. 161:10–17.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*. 18(1):117–143.

Clarke, K.R. and Gorley, R.N. 2006. *PRIMER: User Manual/Tutorial*. Plymouth: PRIMER-E Ltd. 190 pp.

Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A. and Rowden, A.A. 2016. The impacts of deep-sea fisheries on benthic communities: a review. *ICES Journal of Marine Science*. 73(1):i51–i69.

Clarke, K.R. and Warwick, R.M. 2001. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Second Edition. Plymouth: PRIMER-E Ltd. 176 pp.

Cochrane, K.L., Augustyn, C.J., Fairweather, T., Japp, D., Kilongo, K., Iitembu, J., Moroff, N., Roux, J.P., Shannon, L., Van Zyl, B. and Velho, V. 2009. Benguela Current Large Marine Ecosystem- governance and management for an ecosystem approach to fisheries in the region. *Coastal Management*. 37(3–4):235–254.

Cochrane, K.L., Joyner, J., Sauer, W.H.H. and Swan, J. 2015. An evaluation of the Marine Living Resources Act and supporting legal instruments as a framework for implementation of an ecosystem approach to fisheries in South Africa. *African Journal of Marine Science*. 37(4):437–456.

Collie, J.S., Hall, S.J., Kaiser, M.J. and Poiner, I.R. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*. 69:785–798.

Collignon, J. and Aloncle, H. 1960. Le regime alimentaire de quelques poissons benthiques des cotes Marocaines. *Bulletin de l’Institut des Peches Maritimes du Maroc.* 5:17–29.

Conover, D.O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*. 41:161–178.

Consoli, P., Battaglia, P., Castriota, L., Esposito, V., Romeo, T. and Andaloro, F. 2010. Age, growth and feeding habits of the bluemouth rockfish, *Helicolenus dactylopterus dactylopterus* (Delaroche 1809) in the central Mediterranean (southern Tyrrhenian Sea). *Journal of Applied Ichthyology*. 26(4):583–591.

Cooper, R. 2015. Systems modelling of the South African offshore demersal hake trawl fishery: an economic perspective. PhD thesis: University of Cape Town.

Corbera, G., Iacono, C.L., Gràcia, E., Grinyó, J., Pierdomenico, M., Huvenne, V.A.I., Aguilar, R. and Gili, J.M. 2019. Ecological characterisation of a Mediterranean cold-water coral reef: Cabliers Coral Mound province (Alboran Sea, western Mediterranean). *Progress in Oceanography*. 175:245–262.

Córdova-Zavaleta, F., Mendo, J., Briones-Hernández, S.A., Acuña-Perales, N., Gonzalez-Pestana, A., Alfaro-Shigueto, J. and Mangel, J.C. 2018. Food habits of the blue shark, *Prionace glauca* (Linnaeus, 1758), in waters off northern Peru. *Fishery Bulletin*. 116:310–322.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*. 56(5):707–717.

Costello, M.J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology*. 36(2):261–263.

Costello, M.J., McCrea, M., Freiwald, A., Lundälv, T., Jonsson, L., Bett, B.J., van Weering, T.C.E., de Haas, H., Roberts, J.M. and Allen, D. 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In Freiwald, A. and Roberts, J.M. (Eds.) *Cold-Water Corals and Ecosystems*. Berlin: Springer-Verlag. 771–805.

Culling, C.F.. 1974. *Handbook of Histopathological and Histochemical Techniques*. Third Edition. London: Butterworths. 729 pp.

Currie, J.C., Thorson, J.T., Sink, K.J., Atkinson, L.J., Fairweather, T.P. and Winker, H. 2019. A novel approach to assess distribution trends from fisheries survey data. *Fisheries Research*. 214:98–109.

Currie, J.C., Atkinson, L.J., Sink, K.J. and Attwood, C.G. 2020. Long-term change of demersal fish assemblages on the inshore Agulhas Bank between 1904 and 2015. *Frontiers in Marine Science*. 7:355.

Currie, J.C., Atkinson, L.J., Fairweather, T. and Amoroso, R.O. 2021. *Mapping the Distribution of South African Demersal Trawl Activity, 2005-2018*. Technical Report. 18 pp.

D'Onghia, G., Maiorano, P., Sion, L., Giove, A., Capezzuto, F., Carlucci, R. and Tursi, A. 2010. Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*. 57(5–6):397–411.

D'Onghia, G., Indennidate, A., Giove, A., Savini, A., Capezzuto, F., Sion, L., Vertino, A. and Maiorano, P. 2011. Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. *Marine Ecology Progress Series*. 443:95–110.

D'Onghia, G., Calculli, C., Capezzuto, F., Carlucci, R., Carluccio, A., Maiorano, P., Pollice, A., Ricci, P., Sion, L. and Tursi, A.. 2016. New records of cold-water coral sites and fish fauna characterization of a potential network existing in the Mediterranean Sea. *Marine Ecology*. 37(6):1398–1422.

D'Onghia, G., Capezzuto, F., Carlucci, R., Carluccio, A., Maiorano, P., Panza, M., Ricci, P., Sion, L. and Tursi, A.. 2018. Using a benthic lander to explore and monitor vulnerable ecosystems in the Mediterranean Sea. *Acta IMEKO*. 7(2):45–49.

Daneel, C. and Attwood, C.G. 2013. Bycatch in South Africa’s offshore trawl fishery as determined from observer records. University of Cape Town.

de Bruin, J.-P., Gosden, R.G., Finch, C.E. and Leaman, B.M. 2004. Ovarian aging in two species of long-lived rockfish, *Sebastes aleutianus* and *S. alutus*. *Biology of Reproduction*. 71:1036–1042.

Demirhan, S.A. and Akbulut, F. 2015. Age and growth of the bluemouth rockfish, *Helicolenus dactylopterus* (Delaroche 1809) from the north-eastern Mediterranean Sea, Turkey. *Pakistan Journal of Zoology*. 47(2):523–527.

Department of Agriculture Forestry and Fisheries. 2016. *Status of the South African Marine Fishery Resources 2016*. Cape Town: DAFF. 102 pp.

Deporte, N., Ulrich, C., Mahevas, S., Demaneche, S. and Bastardie, F. 2012. Regional metier definition: a comparative investigation of statistical methods using a workflow applied to international otter trawl fisheries in the North Sea. *ICES Journal of Marine Science*. 69:331–342.

Deval, M.C., Kebapçıoğlu, T., Güven, O. and Olguner, M.T. 2018. Population pattern and dynamics of the Bluemouth *Helicolenus dactylopterus* (Delaroche, 1809) in the eastern Mediterranean Sea. *Journal of Applied Ichthyology*. 34(3):568–580.

Dingle, R. V. and Nelson, G. 1993. Sea-bottom temperature, salinity and dissolved oxygen on the continental margin off south-western Africa. *South African Journal of Marine Science*. 13(1):33–49.

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 Arancibia, H. (Ed.) *Hakes: Biology and Exploitation*. Chichester: John Wiley and Sons. 38–69.

Ebert, D.A. and Bizzarro, J.J. 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes*. 80:115–131.

Edwards, L. 2014. *CATAMI Classification Scheme for Scoring Marine Biota and Substrata in Underwater Imagery*. Version 1.4. Available: http://catami.org/classification [accessed 03 September 2018].

Efron, B. 1982. *The Jackknife, the Bootstrap, and Other Resampling Plans*. Philadelphia: Society for Industrial and Applied Mathematics. 85 pp.

Ellis, J.R., Pawson, M.G. and Shackley, S.E. 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the North-East Atlantic. *Journal of the Marine Biological Association of the United Kingdom*. 76(1):89–106.

Enticknap, B. and Sheard, W. 2005. *Conservation and Management of North Pacific Rockfishes*. Alaska Marine Conservation Council Technical Report. Anchorage: Alaska Marine Conservation Council. 37 pp.

Eschmeyer, W.N. 1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). *Occasional Papers of the California Academy of Sciences*. 79:130 pp.

Eschmeyer, W.N., Fricke, R. and van der Laan, R. 2017. *Catalog of fishes: Genera, Species, References*. Available: https://www.calacademy.org/scientists/projects/catalog-of-fishes [accessed 07 August 2017].

Espiñeira, M. and Vieites, J.M. 2012. Authentication of the most important species of rockfish by means of fins. *European Food Research and Technology*. 235(5):929–937.

Esteves, E., Anibal, J., Krug, H. and Da Silva, H.M. 1997. Aspects of age and growth of bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche,1809) from the Azores. *Arquipelago. Life and Marine Sciences*. 15A:83–95.

Everett, B.I. 2014. *Marine and Estuarine Fisheries along the KwaZulu-Natal Coast: an Inventory and Brief Description*. Oceanographic Research Institute Special Publication 11. Durban: South African Association of Marine Biological Research. 106 pp.

Fairweather, T.P., Booth, A.J., Sauer, W.H.H. and Leslie, R.W. 2006. Spatial description of hake-directed fishing activity off the west coast of South Africa. *African Journal of Marine Science*. 28(1):13–24.

Fairweather, T.P. and Durholtz, D. 2017. *Data for simple assessments of key hake trawl by-catch species – part II*. Technical Report Fisheries/2017/OCT/SWG-DEM/46. 16 pp.

Fairweather, T.P., Durholtz, D., Winker, H., Cooper, R., Kerwath, S. and Reed, J. 2017. *Data for simple assessments of key hake trawl by-catch species - part I*. Technical Report Fisheries/2017/FEB/SWG-DEM/04. 16 pp.

FAO. 1999. *Guidelines for the Routine Collection of Capture Fishery Data*. FAO Fisheries Technical Paper 382. Rome: FAO. 113 pp.

FAO. 2002. *Report of the Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem*. FAO Fisheries Report 658. Rome: FAO. 128 pp.

FAO. 2009. *International Guidelines for the Management of Deep-Sea Fisheries in the High Seas*. Rome: FAO. 73 pp.

FAO. 2010. *Fishery and Aquaculture Country Profiles: the Republic of South Africa*. Rome: FAO. 14 pp.

Fiandeiro, F., Ntanzi, A., van der Hoven, Z., Moses, P.-J. and Msimango, N. 2019. *Economic Study of the Hake Deep-Sea Trawl Fishery and the Implications for Future Fishing Rights Allocation Policy*. Technical Report. 122 pp.

Forrest, R.E., Stewart, I.J., Monnahan, C.C., Bannar-Martin, K.H. and Lacko, L.C. 2020. Evidence for rapid avoidance of rockfish habitat under reduced quota and comprehensive at-sea monitoring in the British Columbia Pacific halibut fishery. *Canadian Journal of Fisheries and Aquatic Sciences*. 77:1409–1420.

Fosså, J.H., Mortensen, P.B. and Furevik, D.M. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*. 471:1–12.

Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology*. 62(3):602–610.

Fox, J. and Monette, G. 1992. Generalized collinearity diagnostics. *Journal of the American Statistical Association*. 87(417):178–183.

Fox, J. and Weisberg, S. 2019. *An R Companion to Applied Regression.* Third Edition. Los Angeles: Sage Publications. 608 pp..

Frank, K.T., Petrie, B., Leggett, W.C. and Boyce, D.G. 2018. Exploitation drives an ontogenetic-like deepening in marine fish. *Proceedings of the National Academy of Sciences of the United States of America*. 115(25):6422–6427.

Frid, A., McGreer, M., Gale, K.S.P., Rubidge, E., Blaine, T., Reid, M., Olson, A., Hankewich, S., Mason, E., Rolston, D. and Tallio, E. 2018. The area–heterogeneity tradeoff applied to spatial protection of rockfish (*Sebastes* spp.) species richness. *Conservation Letters*. 11(6):e12589.

Froese, R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*. 22(4):241–253.

Froese, R. and Pauly, D. 2019. *FishBase*. Available: www.fishbase.org [accessed 10 October 2019].

Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T. and Lasserre, G. 2003. *The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook*. FAO Fisheries Technical Paper 443. Rome: FAO. 76 pp.

Gastoni, A., Mulas, A., Porcu, C. and Cabiddu, S. 2011. Trophic habits of the blackbelly rockfish, *Helicolenus dactylopterus* (Osteichthyes, Scorpaeniformes) in the Sardinian Channel. *Biologia Marina Mediterranea*. 18(1):346–347.

Gerringer, M.E., Popp, B.N., Linley, T.D., Jamieson, A.J. and Drazen, J.C. 2017. Comparative feeding ecology of abyssal and hadal fishes through stomach content and amino acid isotope analysis. *Deep-Sea Research Part I: Oceanographic Research Papers*. 121:110–120.

Gertseva, V. V. and Cope, J.M. 2011. Population dynamics of splitnose rockfish (*Sebastes diploproa*) in the Northeast Pacific Ocean. *Ecological Modelling*. 222(4):973–981.

Gibbons, M.J. 1995. Observations on euphausiid assemblages of the south coast of South Africa. *South African Journal of Marine Science*. (16):141–148.

Gibbons, M.J., Sulaiman, A., Hissman, K., Schauer, J., McMillan, I. and Wickens, P.A. 2000. Video observations on the habitat association of demersal nekton in the midshelf benthic environment off the Orange River, Namibia. *South African Journal of Marine Science*. 22(1):1–7.

González-García, E., Mateo-Ramírez, Á., Urra, J., Farias, C., García, T., Gil, J., Raso, J.E.G, López-González, N., Rueda, J.L. 2020. Bottom trawling activity, main fishery resources and associated benthic and demersal fauna in a mud volcano field of the Gulf of Cádiz (southwestern Iberian Peninsula). *Regional Studies in Marine Science*. 33: 100985.

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K. and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences*. 63(3):494–509.

Gordoa, A. and Duarte, C.M. 1992. Size-dependent density of the demersal fish off Namibia: patterns within and among species. *Canadian Journal of Fisheries and Aquatics Sciences*. 49:1990–1993.

Gordon, A.L., Lutjeharms, J.R.E. and Gründlingh, M.L. 1987. Stratification and circulation at the Agulhas Retroflection. *Deep Sea Research*. 34(4):565–599.

Greenstone, J. 2015. *Improving the WWF-SASSI Sustainability Rating of Key Non-Target Species from the Hake Offshore Trawl Sector*. Technical Report. 11 pp.

Greenstone, J., Ngcongo, V. and Bodenham, C. 2016. *The South African Hake Longline Fishery Conservation Project*. Technical Report. 25 pp.

Griffiths, C. 1976. *Guide to the Benthic Amphipods of Southern Africa*. Cape Town: Trustees of the South African Museum. 106 pp.

Gunderson, D.R. 1993. *Surveys of Fisheries Resources*. New York: John Wiley and Sons. 256 pp.

Guttman, L. 1954. Some necessary conditions for common-factor analysis. *Psychometrika*. 19(2):149–161.

Haldorson, L. and Love, M. 1991. Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. *Marine Fisheries Review*. 53(2):25–31.

Hall, M.A. 1996. On bycatches. *Reviews in Fish Biology and Fisheries*. 6:319–352.

Hall, M.A., Alverson, D.L. and Metuzals, K.I. 2000. By-catch: problems and solutions. *Marine Pollution Bulletin*. 41:204–219.

He, X. and Field, J.C. 2017. *Stock Assessment Update: Status of Bocaccio,* Sebastes paucispinis, *in the Conception, Monterey and Eureka INPFC areas for 2017*. Pacific Fishery Management Council Technical Report. 224 pp.

Heemstra, P. and Heemstra, E. 2004. *Coastal Fishes of Southern Africa*. Grahamstown: NISC and SAIAB. 488 pp.

Heessen, H.J.L., Hislop, J.R.G. and Boon, T.W. 1996. An invasion of the North Sea by blue-mouth, *Helicolenus dactylopterus* (Pisces, Scorpaenidae). *ICES Journal of Marine Science*. 53:874–877.

Heincke, F. 1913. *Investigation on the plaice. General report 1.* Rapports et Procès-Verbaux des Réunions (International Council for the Exploration of the Sea, Copenhagen),Vol 17.

Henschke, N., Pakhomov, E.A., Kwong, L.E., Everett, J.D., Laiolo, L., Coghlan, A.R. and Suthers, I.M. 2019. Large vertical migrations of *Pyrosoma atlanticum* play an important role in active carbon transport. *Journal of Geophysical Research: Biogeosciences*. 124(5):1056–1070.

Hilborn, R. and Walters, C.J. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Dordrecht: Springer Science and Business Media. 575 pp.

Hothorn, T., Hornik, K., van de Wiel, M.A. and Zeileis, A. 2008. Implementing a class of permutation tests: the coin package. *Journal of Statistical Software*. 28(8):1–23.

Husebo, A., Nottestad, L., Fossa, J.H., Furevik, D.M. and Jorgensen, S.B. 2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia*. 471:91–99.

Hutchings, J.A. 2000. Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences? *Marine Ecology Progress Series*. 208:299–303.

Hyslop, E.J. 1980. Stomach contents analysis- a review of methods and their application. *Journal of Fish Biology*. 17(4):411–429.

ICES. 2018. *Report of the Working Group on the Biology and Assessment of Deep-sea Fisheries Resources (WGDEEP), 11-18 April 2018, Copenhagen, Denmark*. Technical Report ICES CM 2018/ACOM:14. 771 pp.

IOC, IHO and BODC. 2003. *Centenary Edition of the GEBCO Digital Atlas*. Liverpool: British Oceanographic Data Centre.

Ishida, M. 1994. Phylogeny of the suborder Scorpaenoidei (Pisces: Scorpaeniformes). *Bulletin of the Nansei National Fisheries Research Institute*. 27:1–112.

Isidro, E.J. 1987. *Age and growth of the bluemouth, Helicolenus dactylopterus dactylopterus (Delaroche, 1809) off the Azores*. Technical Report ICES CM 1987/G: 63. 6 pp.

IUCN. 2012. *IUCN Red List Categories and Criteria: Version 3.1*. Second Edition. Gland: IUCN. 38 pp.

Johansen, T., Nedreaas, K. and Nævdal, G. 1993. Electrophoretic discrimination of blue mouth, *Helicolenus dactylopterus* (de La Roche, 1809), from *Sebastes* spp. in the Northeast Atlantic. *Sarsia*. 78(1):25–29.

Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C. V., Somerfield, P.J. and Karakassis, I. 2006. Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*. 311:1–14.

Karageorge, K.W. and Wilson, R.R. 2017. An integrative mating system assessment of a nonmodel, economically important Pacific rockfish (*Sebastes melanops*) reveals nonterritorial polygamy and conservation implications for a large species flock. *Ecology and Evolution*. 7:11277–11291.

Kassambara, A. 2018. *'ggplot2' Based Publication Ready Plots*. R package version 0.1.8.

Kaufman, L. and Rousseeuw, P.J. 2005. *Finding Groups in Data: an Introduction to Cluster Analysis*. Hoboken: John Wiley and Sons. 355 pp.

Kelly, C.J., Connolly, P.L. and Bracken, J.J. 1999. Age estimation, growth, maturity, and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche 1809) from the Rockall Trough. *ICES Journal of Marine Science*. 56(1):61–74.

Kennelly, S.J. 1995. The issue of bycatch in Australia's demersal trawl fisheries. *Reviews in Fish Biology and Fisheries*. 5:213–234.

Kensley, B. 1972. *Shrimps and Prawns of Southern Africa*. Cape Town: Trustees of the South African Museum. 65 pp.

Kimura, D. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*. 77(4):765–776.

Kindsvater, H.K., Mangel, M., Reynolds, J.D. and Dulvy, N.K. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution*. 6(7):2125–2138.

King, J.R. and McFarlane, G.A. 2003. Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*. 10(4):249–264.

King, R. 2012. A review of Bayesian state-space modelling of capture-recapture-recovery data. *Interface Focus*. 2:190–204.

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

Kleiber, C. and Zeileis, A. 2008. *Applied Econometrics with R*. New York: Springer-Verlag. 222 pp.

Krebs, C.J. 1999. *Ecological Methodology*. Second Edition. Menlo Park: Addison Wesley Longman. 620 pp.

Krebs, C.J. 2009. *Ecology: the Experimental Analysis of Distribution and Abundance*. Sixth Edition. San Francisco: Pearson Benjamin Cummings. 655 pp.

Kritzer, J.P., DeLucia, M.B., Greene, E., Shumway, C., Topolski, M.F., Thomas-Blate, J., Chiarella, L.A., Davy, K.B. and Smith, K. 2016. The importance of benthic habitats for coastal fisheries. *BioScience*. 66(4):274–284.

Kuparinen, A. and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution*. 22(12):652–659.

Kusakari, M. 1991. Mariculture of kurosoi, *Sebastes schlegeli*. *Environmental Biology of Fishes*. 30:245–251.

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *The Journal of Animal Ecology*. 20:201–219.

Lee, S.B., Cho, M.-J., Kim, J.H., Kim, Y.S. and Jin, H.-J. 2011. Production of bioactive rockfish (*Sebastes schlegeli*) myostatin-1 prodomain in an Escherichia coli system. *Protein Journal*. 30:52–58.

Lloyd's Register. 2021. *Marine Stewardship Council Fisheries Assessments: South Africa Hake Trawl: Public Certification Report*. Technical Report. 552 pp.

Lo, N.C.-H., Jacobson, L.D. and Squire, J.L. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. *Canadian Journal of Fisheries and Aquatic Sciences*. 49:2515–2526.

Lorance, P., Cook, R., Herrera, J., de Sola, L., Papaconstantinou, C. and Florin, A. 2015. *Helicolenus dactylopterus*. *The IUCN Red List of Threatened Species*. Available: https://www.iucnredlist.org/species/195093/45859093 [accessed 01 March 2021].

Loury, E.K., Bros, S.M., Starr, R.M., Ebert, D.A. and Cailliet, G.M. 2015. Trophic ecology of the gopher rockfish *Sebastes carnatus* inside and outside of central California marine protected areas. *Marine Ecology Progress Series*. 536:229–241.

Love, M.S., Morris, P., McCrae, M. and Collins, R. 1990. *Life history aspects of 19 rockfish species (Scorpaenidae: Sebastes) from the southern California Bight*. NOAA Technical Report NMFS 87. 44 pp.

Love, M.S., Caselle, J.E. and Van Buskirk, W. 1998. A severe decline in the commercial passenger fishing vessel rockfish (*Sebastes* Spp.) catch in the Southern California Bight, 1980-1996. *California Cooperative Oceanic Fisheries Investigations Reports*. 39:180–195.

Love, M.S., Yoklavich, M.M. and Thorsteinson, L. 2002. *Rockfishes of the Northeast Pacific*. Berkley: University of California Press. 404 pp.

Lowerre-Barbieri, S.K., Brown-Peterson, N.J., Murua, H., Tomkiewicz, J., Wyanski, D.M. and Saborido-Rey, F. 2011a. Emerging issues and methodological advances in fisheries reproductive biology. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*. 3(1):32–51.

Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., Murua, H. and Hunter, J.R. 2011b. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*. 3(1):71–91.

Lutjeharms, J.R.E. 2006. *The Agulhas Current*. Berlin: Springer-Verlag. 329 pp.

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

Macpherson, E. and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship? *Marine Ecology Progress Series*. 71(2):103–112.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. and Hornik, K. 2019. *cluster: cluster analysis basics and extensions.* R package version 2.1.0.

Magnuson-Ford, K., Ingram, T., Redding, D.W. and Mooers, A. 2009. Rockfish (*Sebastes*) that are evolutionarily isolated are also large, morphologically distinctive and vulnerable to overfishing. *Biological Conservation*. 142(8):1787–1796.

Malak, D.A., Livingstone, S.R., Pollard, D., Polidoro, B., Cuttelod, A., Bariche, M., Bilecenoğlu, M., Carpenter, K.E., Collette, B.B., Francour, P., Goren, M., Kara, M.H., Massutí, E., Papaconstantinou, C. and Tunesi, L. 2011. *Overview of the Conservation Status of the Marine Fishes of the Mediterranean Sea*. Gland: IUCN. 61 pp.

Mamie, J.C.J., Beare, D.J., Jones, E.G., Kienzle, M., Dobby, H., Heath, M.R. and Reid, D.G. 2007. Aspects of the distribution and growth of bluemouth (*Helicolenus dactylopterus*, Delaroche 1809) since its invasion of the northern North Sea in 1991. *Fisheries Oceanography*. 16(1):85–94.

Manning, R.B. 1969. *Notes on Some Stomatopod Crustacea from Southern Africa*. Washington: Smithsonian Institution Press. 17 pp.

Marine Stewardship Council. 2018. *MSC Fisheries Standard Version 2.01*. London: Marine Stewardship Council. 289 pp.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P. and Ulltang, O. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*. 55(7):1766–1783.

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

Massutí, E., Moranta, J., Gil de Sola, L., Morales-Nin, B. and Prats, L. 2001. Distribution and population structure of the rockfish *Helicolenus dactylopterus* (Pisces: Scorpaenidae) in the western Mediterranean. *Journal of the Marine Biological Association UK*. 81:129–141.

Massutí, E., Gordon, J.D.M., Moranta, J., Swan, S.C., Stefanescu, C. and Merrett, N.R. 2004. Mediterranean and Atlantic deep-sea fish assemblages: differences in biomass composition and size-related structure. *Scientia Marina*. 68:101–115.

Matsubara, K. 1943. Studies on the Scorpaenoid fishes of Japan (II). *Trans Sigenkagaku Kenkyusho*. 2:147–486.

Mauchline, J. and Gordon, J.D.M. 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series*. 74:109–115.

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

McCaughran, D.A. 1992. Standardized nomenclature and methods of defining bycatch levels and implications. In Schoning, R., Jacobson, R.W., Alverson, D.L., Gentle, T.H. and Auyong, J. (Eds.) *Proceedings of the National Industry Bycatch Workshop, 4-6 February, Newport, OR*. Seattle: Natural Resource Consultants Inc. 200–201.

Mendonça, A., Isidro, E., Menezes, G., Pinho, M.R., Melo, O. and Estácio, S. 2006. New contribution to the reproductive features of bluemouth *Helicolenus dactylopterus dactylopterus* from the Northeast Atlantic (Azores Archipelago). *Scientia Marina*. 70(4):679–688.

Merrett, N.R. and Marshall, N.B. 1981. Observations on the ecology of deep-sea bottom-living fishes collected off Northwest Africa (08°-27°N). *Progress in Oceanography*. 9(4):185–244.

Meyer, M. and Smale, M.J. 1991. Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 2. Benthic and epibenthic predators. *South African Journal of Marine Science*. 11(1):409–442.

Mihalitsis, M. and Bellwood, D. 2019. Functional implications of dentition-based morphotypes in piscivorous fishes. *Royal Society Open Science*. 6:190040.

Milligan, R.J., Spence, G., Roberts, J.M. and Bailey, D.M. 2016. Fish communities associated with cold-water corals vary with depth and substratum type. *Deep-Sea Research Part I: Oceanographic Research Papers*. 114:43–54.

Møller, A.M. and Myles, P.S. 2016. What makes a good systematic review and meta-analysis? *British Journal of Anaesthesia*. 117(4):428–430.

Morales-Nin, B. 1989. Edad, crecimento y mortalidad de Helicolenus dactylopterus (Cuvier) en aguas de Namibia. *Colln. Scient. Pap. Int. Commun. Se. Atl. Fish.* 243–248.

Morel, A., Claustre, H. and Gentili, B. 2010. The most oligotrophic subtropical zones of the global ocean: similarities and differences in terms of chlorophyll and yellow substance. *Biogeosciences*. 7(10):3139–3151.

Moser, H.G. and Boehlert, G.W. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Environmental Biology of Fishes*. 30(1–2):203–224.

Muñoz, M., Casadevall, M. and Bonet, S. 1999. Annual reproductive cycle of *Helicolenus dactylopterus dactylopteru*s (Teleostei: Scorpaeniformes) with special reference to the ovaries sperm storage. *Journal of the Marine Biological Association of the United Kingdom*. 79(3):521–529.

Muñoz, M. and Casadevall, M. 2002. Reproductive indices and fecundity of *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaenidae) in the Catalan Sea (western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*. 82(6):995–1000.

Muñoz, M., Koya, Y. and Casadevall, M. 2002. Histochemical analysis of sperm storage in *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaenidae). *Journal of Experimental Zoology*. 292:156–164.

Muñoz, M. 2010. Reproduction in Scorpaeniformes. In Cole, K.S. (Ed.) *Reproduction and Sexuality in Marine Fishes: Patterns and Processes*. Berkley: University of California Press. 432 pp.

Munro, J.L. and Pauly, D. 1983. A simple method for comparing the growth of fishes and invertebrates. *Fishbyte*. 1(1):5–6.

Musick, J.A. 1999. Criteria to define extinction risk in marine fishes. *Fisheries*. 24(12):6–14.

Nel, D.C., Cochrane, K.L., Petersen, S.L., Shannon, L.J., van Zyl, B. and Honig, M.B. 2007. *Ecological Risk Assessments: a Tool for Implementing an Ecosystem Approach for Southern African Fisheries*. WWF South Africa Report Series 2007/Marine/002. 225 pp.

Nelson, G.A. 2019. *fishmethods: Fishery Science Methods and Models.* R package version 1.1.11.

Neuwirth, E. 2014. *RColorBrewer: ColorBrewer Palettes.* R package version 1.1.2.

Neves, A., Sequeira, V., Farias, I., Vieira, A.R., Paiva, R. and Gordo, L.S. 2011. Discriminating bluemouth, *Helicolenus dactylopterus* (Pisces: Sebastidae), stocks in Portuguese waters by means of otolith shape analysis. *Journal of the Marine Biological Association UK*. 91(6):1237–1242.

Neves, A., Sequeira, V., Barros Paiva, R., Vieira, A.R. and Gordo, L.S. 2012. Feeding habits of the bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) (Pisces: Sebastidae) in the Portuguese coast. *Helgoland Marine Research*. 66:189–197.

Nieto, A., Ralph, G.M., Comeros-Raynal, M.T., Kemp, J., Garcia Criado, M., Allen, D.J., Dulvy, N.K., Walls, R.H.L., Russell, B., Pollard, D., Garcia, S., Craig, M., Collette, B.B., Pollom, R., Biscoito, M., Labbish Chao, N., Abella, A., Afonso, P., Alvarez, H., Carpenter, K.E., Clo, S., Cook, R., Costa, M.J., Delgado, J., Dureuil, M., Ellis, J.R., Farrell, E.D., Fernandes, P., Florin, A-B., Fordham, S., Fowler, S., Gil de Sola, L., Gil Herrera, J., Goodpaster, A., Harvey, M., Heessen, H., Herler, J., Jung, A., Karmovskaya, E., Keskin, C., Knudsen, S.W., Kobyliansky, S., Kovacic, M., Lawson, J.M., Lorance, P., McCully Phillips, S., Monroe, T., Nedreaas, K., Nielsen, J., Papaconstantinou, C., Polidoro, B., Pollock, C.M., Rijnsdorp, A.D., Sayer, C., Scott, J., Serena, F., Smith-Vaniz, W.F., Soldo, A., Stump, E. and Williams, J.T. 2015. *European Red List of Marine Fishes*. Luxembourg: Publications Office of the European Union. 88 pp.

Nouar, A. and Maurin, C. 2000. Regime alimentaire de *Helicolenus dactylopterus dactylopterus* (Pisces: Scorpaenidae) des fonds chalutables des cotes algeriennes. *Cahiers de Biologie Marine*. 41(3):313–320.

Nouar, A. 2003. Ecologie, biologie et exploitation d'une espèce de la famille des Scorpaenidae *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) des côtes algériennes. University of Science and Technology Houari Boumediene.

Nunoo, F., Bannermann, P., Russell, B. and Poss, S. 2015. *Helicolenus dactylopterus*. *The IUCN Red List of Threatened Species 2015*. Available: https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T195093A15592445.en [accessed 17 January 2021].

Ogle, D. 2013. *FishR Vignette- Length-Weight Relationships*. Available: derekogle.com/fishR/examples/oldFishRVignettes/LengthWeight.pdf [accessed 13 April 2020].

Ogle, D.H., Wheeler, P. and Dinno, A. 2020. *FSA: Fisheries Stock Analysis.* R package version 0.8.30.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H. 2019. *vegan: Community Ecology Package.* R package version 2.5.6.

Ortiz, M. and Arocha, F. 2004. Alternative error distribution models for standardization of catch rates of non-target species from a pelagic longline fishery: billfish species in the Venezuelan tuna longline fishery. *Fisheries Research*. 70:275–297.

Palma-Pedraza, S., Sarrazin, V., Clarke, M. and Stokes, D. 2020. *Status of Non-Assessed Fish Species in Irish waters*. Irish Fisheries Bulletin 51. 34 pp.

Palsson, W.A., Tsou, T.-S., Bargmann, G.G., Buckley, R.M., West, J.E., Mills, M. Lou, Cheng, Y.W. and Pacunski, R.E. 2009. *The Biology and Assessment of Rockfishes in Puget Sound*. Technical Report. 208 pp.

Papaconstantinou, C., Golani, D., Palmeri, A. and Keskin, C. 2011. *Helicolenus dactylopterus. The IUCN Red List of Threatened Species 2011*. Available: https://www.iucnredlist.org/species/195093/8942482#assessment-information [accessed 01 March 2021].

Parker, S.J., Berkeley, S.A., Golden, J.T., Gunderson, D.R., Heifetz, J., Hixon, M.A., Larson, R., Leaman, B.M., Love, M.S., Musick, J.A., O'Connell, V.M., Ralston, S., Weeks, H.J. and Yoklavich, M.M. 2000. Management of Pacific rockfish. *Fisheries*. 25(3):22–30.

Parker, D., Winker, H., West, W. and Kerwath, S.E. 2017. Standardization of the catch per unit effort for swordfish (*Xiphius gladius*) for the South African longline fishery. *Collective Volume of Scientific Papers, ICCAT*. 74(3):1295–1305.

Paul, L.J. and Horn, P.L. 2009. Age and growth of sea perch (*Helicolenus percoides*) from two adjacent areas off the east coast of South Island, New Zealand. *Fisheries Research*. 95:169–180.

Pauly, D. and Zeller, D. 2015. *Sea Around Us: Concepts, Design and Data*. Available: www.seaaroundus.org [accessed 11 October 2019].

Pelletier, D. and Ferraris, J. 2000. A multivariate approach for defining fishing tactics from commercial catch and effort data. *Canadian Journal of Fisheries and Aquatic Sciences*. 57:51–65.

Pereira, J.N., Simas, A., Rosa, A., Aranha, A., Lino, S., Constantino, E., Monteiro, V., Tariche, O. and Menezes, G. 2012. Weight-length relationships for 27 demersal fish species caught off the Cape Verde archipelago (eastern North Atlantic). *Journal of Applied Ichthyology*. 28:156–159.

Pham, C.K., Vandeperre, F., Menezes, G., Porteiro, F., Isidro, E. and Morato, T. 2015. The importance of deep-sea vulnerable marine ecosystems for demersal fish in the Azores. *Deep-Sea Research Part I: Oceanographic Research Papers*. 96:80–88.

Pillar, S.C., Stuart, V., Barange, M. and Gibbons, M.J. 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. *South African Journal of Marine Science*. 12(1):393–409.

Pinkas, L., Oliphant, M.S. and Iverson, I.L.K. 1971. *Food habits of Albacore, Bluefin Tuna, and Bonito in California Waters*. The State of California Department of Fish and Game Fish Bulletin 152. 105 pp.

Pirrera, L., Bottari, T., Busalacchi, B., Giordano, D., Modica, L., Perdichizzi, A., Perdichizzi, F., Profeta, A. and Rinelli, P. 2009. Distribution and population structure of the fish *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) in the central Mediterranean (southern Tyrrhenian Sea). *Marine Ecology*. 30(1):161–174.

Pons, M., Domingo, A., Sales, G., Niemeyer Fiedler, F., Miller, P., Giffoni, B. and Ortiz, M. 2010. Standardization of CPUE of loggerhead sea turtle (*Caretta caretta*) caught by pelagic longliners in the Southwestern Atlantic Ocean. *Aquatic Living Resources*. 23(1):65–75.

Ponte, S. 2012. The Marine Stewardship Council (MSC) and the making of a market for ‘sustainable fish’. *Journal of Agrarian Change*. 12:300–315.

Price, D.M., Robert, K., Callaway, A., Lo lacono, C., Hall, R.A. and Huvenne, V.A.I. 2019. Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs*. 38:1007–1021.

QGIS Development Team. 2018. *QGIS Geographic Informtion System. Open Source Geospatial Foundation Project*. Available: http://qgis.osgeo.org.

Quattrini, A.M., Ross, S.W., Carlson, M.C.T. and Nizinski, M.S. 2012. Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. *Marine Biology*. 159(5):1079–1094.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available: https://www.r-project.org/.

Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T.J., Cole, M. and Alfaro, M.E. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*. 559:392–395.

Rago, P.J. 2005. Fishery independent sampling: survey techniques and data analyses. In Musick, J.A. and Bonfil, R. (Eds.) *Elasmobranch Fisheries Management Techniques*. J. Rome: FAO. 201–215.

Ragonese, S. and Reale, B. 1995. Distribuzione e crescita dello scorfano di fondale, *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) nello Stretto di Sicilia (Mar Mediterraneo). *Biologia Marina Mediterranea*. 2(2):269–273.

Raîche, G., Walls, T.A., Magis, D., Riopel, M. and Blais, J.-G. 2013. Non-graphical solutions for Cattell’s Scree Test. *Methodology*. 9(1):23–29.

Raiche, G. and Magis, D. 2020. *nFactors: Parallel Analysis and Other Non Graphical Solutions to the Cattell Scree Test.* R package version 2.4.1.

Ralston, S. 1998. The status of federally managed rockfish on the U.S. west coast. In Yoklavich, M. (Ed.) *Marine Harvest Refugia for West Coast Rockfish: A Workshop.* Pacific Grove: NOAA. 6–16.

Ratnasingham, S. and Hebert, P.D.N. 2007. BOLD: The Barcode of Life Data System. *Molecular Ecology Notes*. 7(3):355–364.

Reed, J.R., Kerwath, S.E. and Attwood, C.G. 2017. Analysis of bycatch in the South African midwater trawl fishery for horse mackerel *Trachurus capensis* based on observer data. *African Journal of Marine Science*. 39(3):279–291.

Ribas, D., Munoz, M., Casadevall, M. and Gil de Sola, L. 2006. How does the northern

Mediterranean population of *Helicolenus dactylopterus dactylopterus* resist fishing pressure? *Fisheries Research*. 79:285–293.

Rice, J.C. 2005. Understanding fish habitat ecology to achieve conservation. *Journal of Fish Biology*. 67:1–22.

Ricker, W.E. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*. Bulletin of the Fisheries Research Board of Canada: Bulletin 191. 401 pp.

Rodriguez-Mendoza, R., Munoz, M. and Saborido-Rey, F. 2011. Ontogenetic allometry of the bluemouth, *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaenidae), in the Northeast Atlantic and Mediterranean based on geometric morphometrics. *Hydrobiologia*. 670:5–22.

Rodríguez-Mendoza, R.P. 2013. Population structure of the bluemouth, *Helicolenus dactylopterus* (Teleostei: Sebastidae), in the Northeast Atlantic and Mediterranean using geometric morphometric techniques. Phd thesis: University of Vigo.

Rodríguez-Mendoza, R., Muñoz, M. and Saborido-Rey, F. 2019. Structure and connectivity of bluemouth, *Helicolenus dactylopterus*, populations in the NE Atlantic and Mediterranean. *Fisheries Research*. 213:56–66.

Roel, B.A. 1987. Demersal communities off the west coast of South Africa. *South African Journal of Marine Science*. 5(1):575–584.

Romeo, T., Castriota, L., Consoli, P., Falautano, M., Florio, G., Perdichizzi, F., Finoia, M.G., Andaloro, F. and Rinelli, P. 2009. Bathymetric and longitudinal distribution analysis of the rockfish *Helicolenus dactylopterus* (Delaroche, 1809) in the southern Tyrrhenian Sea (central Mediterranean). *Mediterranean Marine Science*. 10(1):73–82.

Ross, S.W. and Quattrini, A.M. 2007. The fish fauna associated with deep coral banks off the southeastern United States. *Deep-Sea Research Part I: Oceanographic Research Papers*. 54(6):975–1007.

Ross, S.W., Rhode, M. and Quattrini, A.M. 2015. Demersal fish distribution and habitat use within and near Baltimore and Norfolk Canyons, U.S. middle Atlantic slope. *Deep-Sea Research Part I: Oceanographic Research Papers*. 103:137–154.

Roux, M., Edwards, C., Dunn, A., Clark, M. and Doonan, I. 2015. A sustainability assessment framework for fish by-catch in New Zealand deepwater fisheries. *ICES Annual Science Conference*. Copenhagen, September 2015. A:19.

RStudio Team. 2016. *RStudio: Integrated Development for R.* Boston: RStudio. Available: http://www.rstudio.com/.

Ruxton, G.D. and Beauchamp, G. 2008. Time for some a priori thinking about post hoc testing. *Behavioral Ecology*. 19(3):690–693.

Ryan, P.G., Weideman, E.A., Perold, V., Durholtz, D. and Fairweather, T.P. 2020. A trawl survey of seafloor macrolitter on the South African continental shelf. *Marine Pollution Bulletin*. 150:110741.

Sá-Oliveira, J.C., Angelini, R. and Isaac-Nahum, V.J. 2014. Diet and niche breadth and overlap in fish communities within the area affected by an Amazonian reservoir (Amapá, Brazil). *Anais da Academia Brasileira de Ciencias*. 86(1):383–405.

SADSTIA. 2019. *Bycatch management*. Available: https://www.sadstia.co.za/sustainability/bycatch-management/ [accessed 19 October 2019].

Samaai, T., Sink, K., Kirkman, S., Atkinson, L., Florence, W., Kerwath, S., Parker, D. and Yemane, D. 2020. The marine animal forests of South Africa: importance for bioregionalization and marine spatial planning. In Rossi, S and Bramanti, L. (Eds.) *Perspectives on the Marine Animal Forests of the World*. Switzerland: Springer Nature. 17–61.

Sami, M., Rym, E., Fatma, A., Bachra, C. and Hechmi, M. 2016. Age and growth of bluemouth *Helicolenus dactylopterus* (Delaroche, 1809) in the northern waters of Tunisia. *Greener Journal of Life Sciences*. 3(1):1–12.

Santos, R., Pabon, A., Silva, W., Silva, H. and Pinho, M. 2020. Population structure and movement patterns of blackbelly rosefish in the NE Atlantic Ocean (Azores archipelago). *Fisheries Oceanography*. 29(3):227–237.

Sarkar, D. 2008. *Lattice: Multivariate Data Visualisation with R.* New York: Springer Science and Business Media. 268 pp.

Sequeira, V., Figueiredo, I., Muñoz, M. and Gordo, L.S. 2003. New approach to the reproductive biology of *Helicolenus dactylopterus*. *Journal of Fish Biology*. 62:1206–1210.

Sequeira, V., Neves, A., Vieira, A.R., Figueiredo, I. and Gordo, L.S. 2009. Age and growth of bluemouth, *Helicolenus dactylopterus*, from the Portuguese continental slope. *ICES Journal of Marine Science*. 66(3):524–531.

Sequeira, V., Vila, S., Neves, A., Rifes, P., Nunes, M.L., Vieira, A.R., Barros Paiva, R., Muñoz, M. and Gordo L.S. 2011. The gelatinous matrix of the teleost *Helicolenus dactylopterus dactylopterus* (delaroche, 1809) in the context of its reproductive strategy. *Marine Biology Research*. 7(5):478–487.

Sequeira, V., Neves, A., Barros Paiva, R., Pereira de Lima, J., Vieira, A.R. and Gordo, L.S. 2012. Life history parameters as possible discriminators of bluemouth *Helicolenus dactylopterus* (Delaroche, 1809) populations in Portuguese waters. *Fisheries Research*. 125–126:69–76.

Sequeira, V., Vieira, A.R., Neves, A., Barros Paiva, R., Canário, A. and Gordo, L.S. 2013. Whole or sectioned otoliths? Choosing the best method for aging bluemouth, *Helicolenus dactylopterus* (Delaroche, 1809). *Fisheries Research*. 147:235–239.

Sequeira, V., Neves, A., Vieira, A.R., Barros Paiva, R., Canário, A. and Gordo, L.S. 2015. Estimating fecundity in the zygoparous species *Helicolenus dactylopterus* (Actinopterygii, Scorpaeniformes): adaptation of the gravimetric method. *Hydrobiologia*. 758(1):211–222.

Shannon, L.V. and O’Toole, M.J. 2003. Sustainability of the Benguela: ex Africa semper aliquid novi. In Hempel, G. and Sherman, K. (Eds.) *Large Marine Ecosystems of the*

World: Trends in Exploitation, Protection and Research. Amsterdam: Elsevier. 227–253.

Shelton, A.O. and Mangel, M. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America*. 108(17):7075–7080.

Sherley, R.B., Winker, H., Rigby, C.L., Kyne, P.M., Pollom, R., Pacoureau, N., Herman, K., Carlson, J.K., Yin, J.S., Kindsvater, H.K. and Dulvy, N.K. 2020. Estimating IUCN Red List population reduction: JARA—A decision-support tool applied to pelagic sharks. *Conservation Letters*. 13(2): e12688.

Shono, H. 2008. Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fisheries Research*. 93:154–162.

Simenstad, C.A. and Cailliet, G.M. 2017. Retrospective on the origin, intent, and impact of the Gutshops and some directions for the future. *Environmental Biology of Fishes*. 100(4):299–308.

Simpfendorfer, C.A. 1999. Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia. *Fishery Bulletin*. 97(4):978–986.

Sink, K.J., Wilkinson, S., Atkinson, L.J., Sims, P.F., Leslie, R.W. and Attwood, C.G. 2012a. *The Potential Impacts of South Africa's Demersal Hake Trawl Fishery on Benthic Habitats: Historical Perspectives, Spatial Analyses, Current Review and Potential Management Actions*. Cape Town: South African National Biodiversity Institute. 84 pp.

Sink, K., Holness, S., Harris, L., Majiedt, P., Atkinson, L., Robinson, T., Kirkman, S., Hutchings, L., Leslie, R., Lamberth, S., Kerwath, S., vonder Heyden, S., Lombard, A., Attwood, C., Branch, G., Fairweather, T., Taljaard, S., Weerts, S., Cowley, P., Awad, A., Halpern, B., Grantham, H. and Wolf, T. 2012b. *National Biodiversity Assessment 2011: Technical Report. Volume 4 : Marine and Coastal Component*. Pretoria: South African National Biodiversity Institute. 325 pp.

Sink, K. 2016. The marine protected areas debate: implications for the proposed Phakisa Marine Protected Areas network. *South African Journal of Science*. 112:1–4.

Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. and Karenyi, N. 2019. *National Biodiversity Assessment 2018: Technical Report. Volume 4: Marine Realm*. Pretoria, South African National Biodiversity Institute. 599 pp.

Sissenwine, M.P. 1984. Why do fish populations vary? In May, R.M. (Ed.) *Exploitation of Marine Communities*. Berlin: Springer-Verlag. 59–94.

Smale, M.J. and Badenhorst, A. 1991. The distribution and abundance of linefish and secondary trawlfish on the Cape south coast of South Africa, 1986–1990. *South African Journal of Marine Science*. 11(1):395–407.

Smale, M.J., Roel, B.A., Badenhorst, A. and Field, J.G. 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. *Journal of Fish Biology*. 43:169–191.

Smith, M.M., Heemstra, P.C. and Smith, J.L.B. 1986. *Smiths' Sea Fishes*. First Edition. Johannesburg: Macmillan. 1047 pp.

Smith, P.J., Struthers, C.D., Paulin, C.D., McVeagh, S.M. and Daley, R.K. 2009. Shallow genetic and morphological divergence among seaperches in the South Pacific (family Scorpaenidae; genus *Helicolenus*). *Journal of Fish Biology*. 74:1104–1128.

Smith, M., Cochrane, K.L. and Japp, D. 2013. *Review of significant bycatch and joint product species in the South African hake-directed trawl fishery*. Technical Report. 69 pp.

Smith, A.D.M. and Garcia, S.M. 2014. Fishery management: contrasts in the Mediterranean and the Atlantic. *Current Biology*. 24(17):R810–R812.

Sogard, S.M., Gilbert-Horvath, E., Anderson, E.C., Fisher, R., Berkeley, S.A. and Garza, J.C. 2008. Multiple paternity in viviparous kelp rockfish, *Sebastes atrovirens*. *Environmental Biology of Fishes*. 81(1):7–13.

Stergiou, K.I. and Karpouzi, V.S. 2002. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*. 11:217–254.

Struyf, A., Hubert, M. and Rousseeuw, P.J. 1996. Clustering in an object-oriented environment. *Journal of Statistical Software*. 1:1–30.

Stuttaford, M. 2000. *Fishing Industry Handbook: South Africa, Namibia and Mozambique*. Cape Town: Exbury Publications. 433 pp.

Swain, D.P., Hutchings, J.A. and Foote, C.J. 2005. Environmental and genetic influences on stock identification characters. In Cadrin, S., Kerr, L.A., Friedland, K., Mariani, S. and Waldman, J. (Eds.) *Stock Identification Methods: Applications in Fishery Science*. First Edition. Cambridge: Academic Press. 45–85.

Uiblein, F., Lorance, P. and Latrouite, D. 2003. Behaviour and habitat utilisation of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. *Marine Ecology Progress Series*. 257:223–232.

Vad, J., Kazanidis, G., Henry, L., Jones, D.O.B., Gates, A.R. and Roberts, J.M. 2019. Environmental controls and anthropogenic impacts on deep-sea sponge grounds in the Faroe-Shetland Channel, NE Atlantic: the importance of considering spatial scale to distinguish drivers of change. *ICES Journal of Marine Science*. 77(1): 451-461.

van der Elst, R. 1993. *A Guide to Common Sea Fishes of Southern Africa*. Cape Town: Struik Nature. 398 pp.

van der Lingen, C.D., Shannon, L.J., Cury, P., Kreiner, A., Moloney, C.L., Roux, J.-P. and Vaz-Velho, F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current System. In Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C. and Woods, J. (Eds.) *Benguela: Predicting a Large Marine Ecosystem*. Amsterdam: Elsevier. 147–184.

Vasilakopoulos, P., Maravelias, C.D. and Tserpes, G. 2014. The alarming decline of Mediterranean fish stocks. *Current Biology*. 24:1643–1648.

Venables, W.N. and Ripley, B.D. 2002. *Modern Applied Statistics with S-PLUS.* New York:

Springer Science and Business Media. 501 pp.

Verberk, W.C.E.P. 2011. Explaining general patterns in species abundance and distribution. *Nature Education Knowledge*. 3(10):38.

Vila, S., Muñoz, M., Sabat, M. and Casadevall, M. 2007. Annual cycle of stored spermatozoa within the ovaries of *Helicolenus dactylopterus dactylopterus* (Teleostei, Scorpaenidae). *Journal of Fish Biology*. 71:596–609.

Vila, S., Sàbat, M., Hernandez, M.R. and Muñoz, M. 2007. Intraovarian sperm storage in *Helicolenus dactylopterus dactylopterus*: fertilization, crypt formation and maintenance of stored sperm. *Raffles Bulletin of Zoology*. 14:21–27.

Wacasey, J. and Atkinson, E. 1987. Energy values of marine benthic invertebrates from the Canadian Arctic. *Marine Ecology Progress Series*. 39:243–250.

Walmsley, S.A. 2004. The assessment and management of bycatch and discards in the South African demersal trawl fishery. Phd thesis: Rhodes University.

Walmsley, S.A., Leslie, R.W. and Sauer, W.H.H. 2007. Bycatch and discarding in the South African demersal trawl fishery. *Fisheries Research*. 86:15–30.

Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*. 120:107–120.

Werner, T. and Buchholz, F. 2013. Diel vertical migration behaviour in euphausiids of the northern Benguela Current: seasonal adaptations to food availability and strong gradients of temperature and oxygen. *Journal of Plankton Research*. 35(4):792–812.

West, J.E., Helser, T.E. and O'Neill, S.M. 2014. Variation in quillback rockfish (*Sebastes maliger*) growth patterns from oceanic to inland waters of the Salish Sea. *Bulletin of Marine Science*. 90(3):747–761.

Weston, L. and Attwood, C. 2017. *Monitoring of Endangered , Threatened and Protected (ETP) Species Caught as Bycatch in Five Major South African Fisheries*. Technical Report. 65 pp.

White, D.B., Wyanski, D.M. and Sedberry, G.R. 1998. Age, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, U.S.A. *Journal of Fish Biology*. 53:1274–1291.

Whittaker, R.H. 1975. *Communities and Ecosystems*. Second Edition. New York: Macmillan. 385 pp.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis.* New York: Springer-Verlag. 213 pp.

Wickham, H., Francois, R., Henry, L. and Muller, K. 2020. *dplyr: A Grammar of Data Manipulation.* R package version 0.8.5.

Wilkinson, S. and Japp, D. 2005. *Description and Evaluation of Hake-Directed Trawling Intensity on Benthic Habitat in South Africa*. Technical Report. 69 pp.

Williamson, M. and Japp, D. 2018. *Status and Management of the South African Hake Trawl*

Fishery – 2018. Technical Report. 6 pp.

Winemiller, K.O. and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*. 49(10):2196–2218.

Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*. 62:872–885.

Winker, H., Kerwath, S.E. and Attwood, C.G. 2013. Comparison of two approaches to standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line fishery. *Fisheries Research*. 139:118–131.

Winker, H., Kerwath, S.E. and Attwood, C.G. 2014. Proof of concept for a novel procedure to standardize multispecies catch and effort data. *Fisheries Research*. 155:149–159.

Winker, H., Thorson, J., Fairweather, T., Leslie, R. and Durholtz, D. 2017. *Towards Improving Precision in South African Demersal Trawl Survey Indices Using Geostatistical GLMMs*. Technical Report MARAM/IWS/2017/Hake/BG8. 18 pp.

Winker, H., Carvalho, F. and Kapur, M. 2018. JABBA: Just Another Bayesian Biomass Assessment. *Fisheries Research*. 204:275–288.

Winker, H., Pacoureau, N. and Sherley, R.B. 2020. JARA: Just another red-list assessment. *bioRxiv*. 42 pp.

Wisniewski, R.L. 1980. Carrying capacity: understanding our biological limitations. *Humboldt Journal of Social Relations*. 7(2):55–70.

Yemane, D., Field, J.G. and Leslie, R.W. 2008. Indicators of change in the size structure of fish communities: a case study from the south coast of South Africa. *Fisheries Research*. 93(1–2):163–172.

Yemane, D., Field, J.G. and Leslie, R.W. 2010. Spatio-temporal patterns in the diversity of demersal fish communities off the south coast of South Africa. *Marine Biology*. 157:269–281.

Yemane, D., Kirkman, S.P., Kathena, J., N'siangango, S.E., Axelsen, B.E. and Samaai, T. 2014. Assessing changes in the distribution and range size of demersal fish populations in the Benguela Current Large Marine Ecosystem. *Reviews in Fish Biology and Fisheries*. 24(2):463–483.

Yemane, D., Mafwila, S.K., Kathena, J., Nsiangango, S.E. and Kirkman, S.P. 2015. Spatio-temporal trends in diversity of demersal fish species in the Benguela Current Large Marine Ecosystem region. *Fisheries Oceanography*. 24:102–121.

Yoklavich, M.M., Greene, H.G., Cailliet, G.M., Sullivan, D.E., Lea, R.N. and Love, M.S. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fishery Bulletin*. 98(3):625–641.

Yoklavich, M.M., Love, M.S. and Forney, K.A. 2007. A fishery-independent assessment of an overfished rockfish stock, cowcod (*Sebastes levis*), using direct observations from an occupied submersible. *Canadian Journal of Fisheries and Aquatic Sciences*. 64:1795–1804.

Zar, J.H. 1996. *Biostatistical Analysis*. Third Edition. Upper Saddle River, New Jersey: Prentice-Hall. 662 pp.

Zeileis, A., Kleiber, C. and Jackman, S. 2008. Regression models for count data in R. *Journal of Statistical Software*. 27(8):1–25.

Zimmermann, F., Ricard, D. and Heino, M. 2018. Density regulation in Northeast Atlantic fish populations: Density dependence is stronger in recruitment than in somatic growth. *Journal of Animal Ecology*. 87(3):672–681.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. London: Springer Science and Business Media. 595 pp.

Zuur, A.F., Ieno, E.N. and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1(1):3–14.