

**The effects of an unidentified pathogen, 'Frill on Gill', on body condition of Cape hake *Merluccius capensis*, on the south coast of South Africa**

**Kim-Kelly Hunt**

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Supervisors: Dr. Cecile. C. Reed <sup>1</sup>, A Prof. Colin Attwood<sup>1</sup>, Ms. Larvika Singh <sup>2</sup>

<sup>1</sup> Marine Research Institute, Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, 7700, South Africa

<sup>2</sup> Branch: Fisheries Management, Department of Agriculture, Forestry and Fisheries, Private Bag X2 Rogge Bay 8012, South Africa

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## Abstract

The unidentified pathogen, known as 'Frill on Gill' (FOG), infects the shallow-water Cape hake *Merluccius capensis* off the south and west coast of South Africa. This pathogen, a parasitic castrator, occurs on the gill filaments of infected fish. This study investigates the effects of this pathogen on the body condition of *M. capensis* on the south coast of South Africa, through the use of two body condition measures, condition factor and hepatosomatic index (HSI). A total of 24275 *M. capensis* were sampled, of which 825 (3.4%) were infected with the FOG pathogen. The smallest *M. capensis* infected with FOG was 10 cm, and the largest was 84 cm. The smallest uninfected *M. capensis* sampled was 6 cm and the largest was 106 cm. The presence of FOG had a significant impact on the condition factor and HSI of *M. capensis* (three-way analysis of variance (ANOVA): p-value = 0.002, and p-value =  $5.13e^{-09}$  respectively), with the effect of the pathogen varying with length. For fish with a total length smaller than 26 cm, infected *M. capensis* were in poorer condition than uninfected fish at the same length, with lower condition factors and HSI values. However, for *M. capensis* with lengths between 30 and 34 cm, 42 and 46 cm, 54 and 62 cm, and 78 and 82 cm, the condition factors of FOG infected fish were higher than uninfected fish. The HSI values of *M. capensis* infected with FOG also steadily increase above those of uninfected fish, for lengths greater than 42 cm. The lower body condition measures of uninfected *M. capensis* could be linked to the large amounts of energy that these fish expend during reproduction and gonad maturation. In contrast, *M. capensis* infected with FOG do not partake in the energy intensive task of reproduction. *Merluccius capensis* infected with FOG don't contribute to reproduction, but still compete with uninfected *M. capensis* for resources. The effect of FOG as a type of parasitic castrator on the regulation of *M. capensis* populations could become a concern for fishery managers, as they reduce reproductive output and impact fish body condition.

# 1. Introduction

## 1.1. The genus *Merluccius*- a global perspective

The species of the genus *Merluccius* (commonly known as hake) are widely distributed in the cool waters (4 to 14 °C) of the Atlantic and Pacific oceans (Quinteiro et al., 2000; Torres et al., 2000). This taxonomically complex genus, is believed to be made up of 13 species, with highly conservative external morphology (Perez et al., 2005; Quinteiro et al., 2000). These species include *M. albidus*, *M. angustimanus*, *M. australis*, *M. bilinearis*, *M. capensis*, *M. gayi gayi*, *M. hubbsi*, *M. merluccius*, *M. paradoxus*, *M. patagonicus*, *M. polli*, *M. productus*, and *M. senegalensis* (Lloris et al., 2005). They represent a taxonomically complex group lacking conspicuous identification keys for each species, and as a result the extent of their commercial importance and the impact of fisheries on their sustainability is not yet fully understood (Perez et al., 2005).

Hakes are capable of long migrations, and in most areas two hake species overlap considerably in their geographical ranges (Quinteiro et al., 2000). These fish are also able to migrate between depth zones effectively, as a result of physiological adaptations to their swim bladders and blood systems that facilitate vertical mobility (Quinteiro et al., 2000). Effective vertical mobility is needed to switch between the near bottom depths where they spend their days, to the mid-water or near-surface depths where they migrate to feed at night (Quinteiro et al., 2000). Hake are demersal fishes but they prey on fast-moving pelagics, which they ambush higher up in the water column (Pitcher & Alheit, 1995). Generally, hakes have a spawning season that peaks in spring and summer, but many have prolonged spawning periods, with some species even being reported to spawn all year round (Pitcher & Alheit, 1995). *Merluccius* species have pelagic eggs, with larvae that remain in the water column for approximately two months before descending to the bottom (Quinteiro et al., 2000).

The species in the genus *Merluccius* are generally high value commercial species, exploited in fisheries around the world (Lloris et al., 2005). In the last century, these fish have been heavily fished as their fisheries are important in many regions (Perez et al., 2005; Campo et al., 2007). At the end of the twentieth century, the FAO reported a total catch of *Merluccius* species of around 1 200 000 tonnes (Lloris et al., 2005). They are mostly caught using bottom trawls, but also with gillnets and longlines (Lloris et al., 2005). Traditionally, much of the hake caught outside of Europe would be used as pet food or in fish meal production. However, in more recent times hake is processed into a great variety of products for human consumption (Pitcher & Alheit, 1995).

## 1.2. South African Cape Hakes

South Africa's hake resource, collectively known as the 'Cape hakes', comprises two species, namely the shallow-water hake *Merluccius capensis*, and the deep-water hake *M. paradoxus* (DAFF, 2016). Both species occur on the continental shelf and upper slope along the coast of Southern Africa (DAFF, 2016). The shallow-water hake *M. capensis* has a distribution that runs mainly from Southern Angola to northern KwaZulu-Natal (DAFF, 2016). *Merluccius capensis* occurs at a depth range of 30-500m, with most of the population found between 100 and 300m (DAFF, 2016). In contrast, *M. paradoxus* has a distribution spanning from northern Namibia to southern Mozambique, occurring at depths between 110m to around 1000m, but most of the population occurs between 100 and 300m (DAFF, 2016). As they age and grow, individuals of both species move further offshore (Garcia & Ye, 2018). Movement offshore results in larger *M. capensis* coexisting, and feeding extensively, on smaller *M. paradoxus* (DAFF, 2016). Both *M. capensis* and *M. paradoxus* exhibit diel vertical migration behaviour, moving up into the water column to feed at night, and then returning to the seabed during the day (Garcia & Ye, 2018).

The relative abundances of the two hake species differs between the coasts of Southern Africa. On the west coast *M. paradoxus* makes up the majority of biomass, but on the south coast it only makes up 35% of the biomass (Durholtz et al., 2015). Although the reason for these coastal differences in relative abundances is not well known, the width and shape of the continental shelf has been suggested as a possible reason behind these changes in abundance (Durholtz et al., 2015). A wider shelf would mean a more extensive habitat for the shallow-water *M. capensis*, and a more gently sloping shelf would provide habitat better suited to *M. paradoxus* (Durholtz et al., 2015). On the south coast over the Agulhas bank, and off the mouth of the Orange River, where the continental shelf area is wider, *M. capensis* dominates catches and biomass (Pillar & Wilkinson, 1995; Durholtz et al., 2015). In contrast, off the south-western Cape of South Africa, where the shelf is narrow and the slope is gentler, *M. paradoxus* makes up the bulk of the catches (Durholtz et al., 2015).

These two species are morphologically similar and are generally marketed and processed together as a single commodity (DAFF, 2016; Garcia & Ye, 2018). In terms of morphological dissimilarities, *M. capensis* and *M. paradoxus* have slightly different colouring (Figures 1 and 2)(Lloris et al., 2005). *Merluccius capensis* is lead-grey, with a darker dorsum, whitish belly and grey fins (Figure 1)(Lloris et al., 2005). In contrast, *M. paradoxus* is dark grey with a light grey belly and sides (Figure 2) (Lloris et al., 2005). *Merluccius paradoxus* also has a distinctive submandibular black mark, and a greyish mouth cavity and tongue (Lloris et al., 2005). Another major visible difference between the two Cape hake species is the scales that are present on the preopercular, interopercular and lacrimal of *M. paradoxus*

specimens and not *M. capensis* (Lloris et al., 2005). Females of both the Cape hake species have been suggested to grow faster than their male counterparts (Durholtz et al., 2015). Both *M. capensis* and *M. paradoxus* typically grow between 10 – 12 cm a year, for the first few years of life, and usually reach lengths of 50 – 60 cm by their fifth year of life (Durholtz et al., 2015). Growth rates are faster earlier in life, and the growth rates of both species decreases with age (Durholtz et al., 2015).

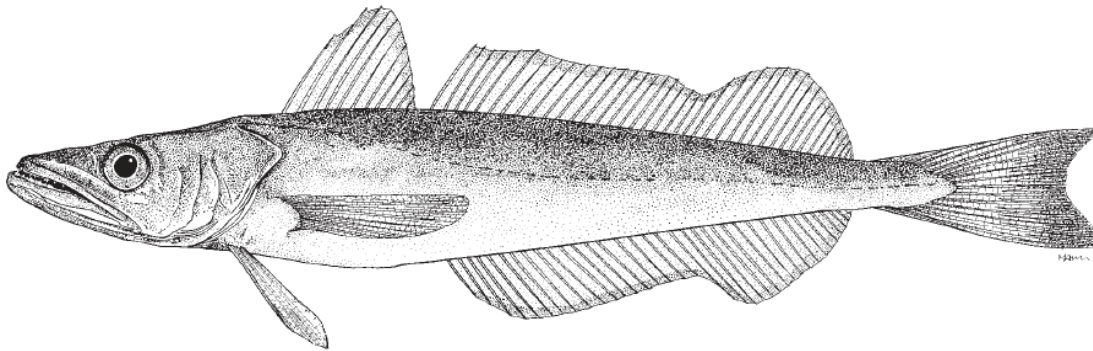


Figure 1: Shallow-water Cape hake *Meluccius capensis* (from Lloris et al., 2005)

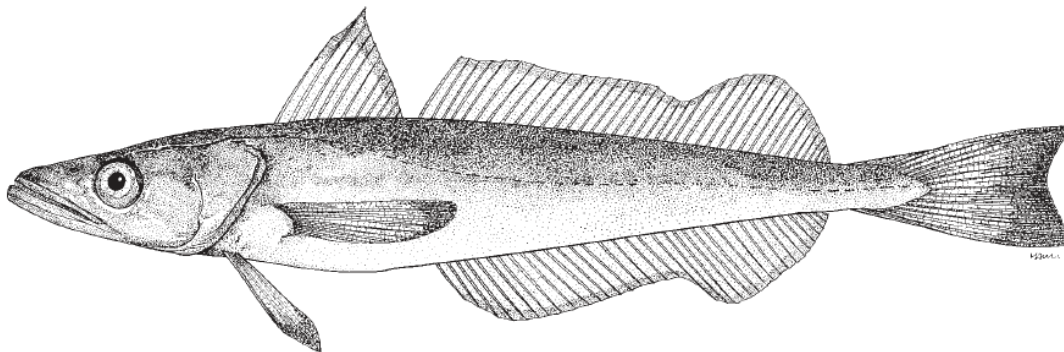


Figure 2: Deep-water Cape hake *Merluccius paradoxus* (from Lloris et al., 2005)

The spawning activities in the Cape hakes are not well understood (von der Heyden et al., 2007). Females, of both *M. capensis* and *M. paradoxus*, generally mature at greater lengths than males (Botha, 1986b). Botha (1986b) described a length at 50% maturity of 360 mm for *M. capensis* males and 380 mm for *M. paradoxus* males, sampled in the Cape of Good Hope area. Alternatively, females in this area were described with a length at 50% maturity of around 480 mm for *M. capensis* and 470 mm for *M. paradoxus* (Botha, 1986b). In contrast, a length at 50% maturity for both sexes, for individuals sampled on the west and south coasts of South Africa, was reported as 53.8 cm for *M. capensis*, and 41.5 cm for *M. paradoxus* (Singh et al., 2011).

Serial spawning has been shown for *M. capensis* and *M. paradoxus*, and oocytes mature continuously from the immature (or resting) stage, while at the same time adults continue to release batches of eggs (Osborne et al., 1999; Kainge et al., 2007). This continuous reproductive cycle makes it difficult to clearly classify degrees of maturity into developmental stages (Kainge et al., 2007). *M. capensis* in South African waters, appear to spawn predominantly off the south coast (von der Heyden et al., 2007). The presence of hake larvae all year round suggests that spawning may be taking place throughout the year (von der Heyden et al., 2007). However, spawning peaks have been reported for both species later in the year, and also during February and March (von der Heyden et al., 2007). For *M. paradoxus*, spawning takes place between the western Agulhas Bank and Elands Bay, with the major nursery ground between Hondeklip Bay and the northern tip of Orange Banks, on South Africa's west coast (Strømme et al., 2016).

### **1.3. South African Hake Fishery**

The Cape hake species have made up one of the most valuable fishery resources in the Benguela region of Africa since the 1950s (Strømme et al., 2016). In the early 1970s annual catches of the Cape hake resource in the Benguela region reached peaks of around 80 000 tonnes (Strømme et al., 2016). Within the entire Benguela system, South African and Namibian stocks of both species are managed separately, although it could be argued that *M. paradoxus* in Namibia and South Africa is a single stock, and *M. capensis* are largely separate stocks (Durholtz et al., 2015). The populations of *M. paradoxus* in South African and Namibian waters don't have any obvious morphological differences, whereas Namibian *M. capensis* differ in anal fin and iris colour when compared with populations in South African waters (Durholtz et al., 2015). Genetic research conducted in the 1980s supported the idea that *M. paradoxus* in Namibian and South African waters are a single stock, as allozyme and restriction fragment mapping methods found no difference between the two populations (Durholtz et al., 2015).

Directed fishing of the Cape hakes began towards the end of the First World War, with hake being caught as an incidental bycatch species from around 1899 until this time (DAFF, 2016). Initially, catches were averaging about 1000 t per annum, but after the Second World War the fishery started escalating, with catches reaching around 170 000 t by the early 1960s (DAFF, 2016). Annual catches reached a peak in 1972 at over 295 000 t (DAFF, 2016). After the declaration of a 200 nautical mile Exclusive Fishing Zone (EFZ) by South Africa in November 1977, and the direct management of South Africa's hake resource by the South African government, catch rates started to substantially decrease (DAFF, 2016). The morphologically similar Cape hake species were originally assessed and managed as a single resource in South Africa. Today, they are managed as separate resources, and through the implementation of an Operational Management Procedure (OMP) approach (DAFF, 2016). The hake

OMP is a set of guidelines that determine how the Total Allowable Catch (TAC) is calculated (DAFF, 2016). The OMP uses commercial and fishery-independent indices of abundance that are derived from commercial catch and effort data, which are collected from demersal research surveys (DAFF, 2016).

Cape hakes are targeted by four fishery sectors; deep-sea demersal trawl, inshore demersal trawl, hake longline and the hake handline sectors, and contribute to 70% of the demersal catches from South African waters (Pillar & Wilkinson, 1995; DAFF, 2016). *Merluccius capensis* and *M. paradoxus* are also caught as incidental by-catch in the mid-water directed trawl fishery for horse mackerel, and also in very low numbers in the demersal shark longline and linefish sectors (Durholtz et al., 2015). The hake fishery is the most valuable of South Africa's fisheries, providing some 30 000 jobs and an annual landed value in excess of R5.2 billion (DAFF, 2016). The bulk of South Africa's total hake biomass, approximately 70%, occurs off the west coast (Durholtz et al., 2015). Exports play a pivotal role in South Africa's hake fishery, with around 64% of the country's hake catch being exported and consumed elsewhere (Durholtz et al., 2015).

#### **1.4. The Marine Environment around South Africa**

The South African coastline is influenced by broad interactions between three ocean systems, the Atlantic, Indian and Southern Oceans (Durholtz et al., 2015). The east coast is affected by the warm Agulhas Current, and the west coast is affected by the cold Benguela Current (Figure 3). The Benguela current upwelling ecosystem is one of the world's four eastern boundary current systems (Ekau & Verheye, 2005). It is characterized by wind-driven coastal upwelling and as a result, high productivity (Roux et al., 2013). However, it is unusual as there are two stratified subtropical or warm temperate boundary regions on either side of it, the warm temperate Agulhas current in the south, and the warm subtropical Angola current in the north (Figure 3)(Hutchings et al., 2009; Roux et al., 2013). The Benguela Current system is divided into the northern and southern subsystems by the world's strongest upwelling cell, located at Luderitz (27°S), off the coast of Namibia (Figure 3) (Roux et al., 2013). The Southern Benguela subsystem, off the coast of South Africa, can be further divided into a coastal upwelling system off the west coast and the Agulhas Bank system off the south coast (Roux et al., 2013). The west coast system is characterized by seasonal, pulsed, wind-driven upwelling, that results in nutrient enriched shelf waters with high productivity (Roux et al., 2013; Shannon & Cury, 2003). The Agulhas bank has characteristics of an upwelling and a temperate shallow shelf system. It experiences seasonal stratification and mixing, dynamic upwelling, moderate productivity and a well oxygenated shelf (Hutchings et al., 2009).

On the east coast of southern Africa, the Agulhas current transports warm, sub-tropical water from the equator southwards (Reed, 2015). This sub-tropical water is transported along the eastern shores

of South Africa before it eventually retroflects near Cape Agulhas and rejoins the Indian Ocean Gyre (Figure 3)(Reed, 2015). As a result of this current, South Africa’s east coast is characterized by warmer waters, lower nutrient levels and high species diversity (Reed, 2015). The west coast acts as an important nursery ground for several fish species which spawn on the Agulhas bank, and then are transported by alongshore jet currents to the west coast (Hutchings et al., 2009).

Due to the high productivity of the Benguela ecosystem it supports large commercial fisheries for anchovy, sardine, the Cape hakes and horse mackerel (Bowker, 2013). In the Southern Benguela, fisheries for small pelagics, hakes, and Cape horse mackerel have established since before 1950 (Roux et al., 2013). Within the waters of the Northern Benguela, purse-seining for small pelagics started over 60 years ago, but demersal and mid-water trawling for other species started in the mid- to late 1960s (Roux et al., 2013).

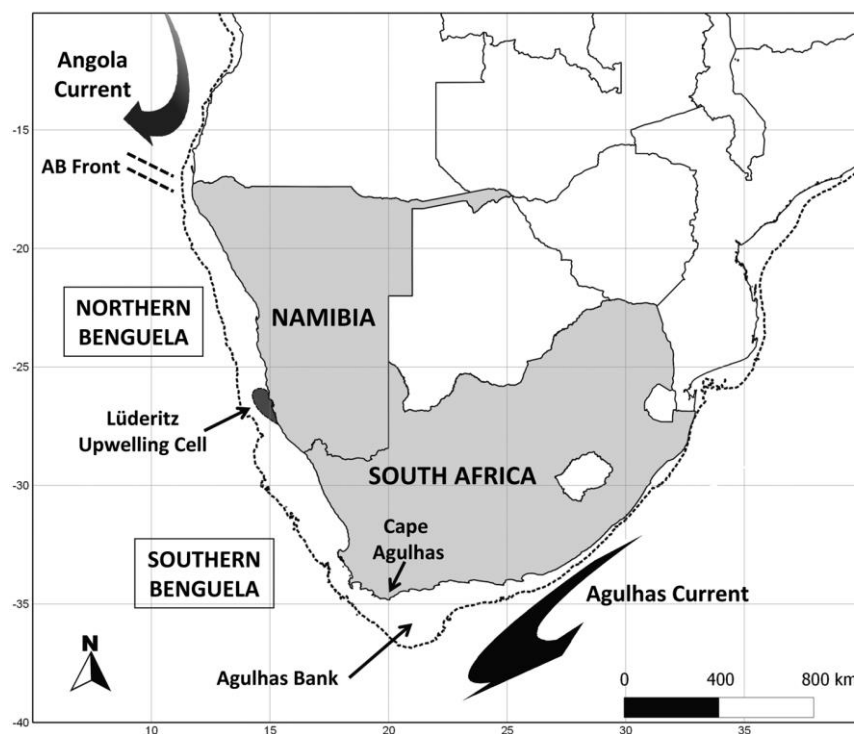


Figure 3: Map of the Benguela current region, bordering the west coast of southern Africa. The dashed line represents the 500-m depth contour. The approximate positions of the Angola Current, the Angola/Benguela (AB) Front, the Luderitz upwelling cell separating the northern and southern Benguela subsystems, and the Agulhas Current are also represented (from Roux et al., 2013).

### 1.5. Parasites of Commercial Fishes

Fish are hosts to a wide range of endo- and ectoparasites, and the diversity and abundance of these parasites vary greatly among populations of the same host species (Khan & Thulin, 1991; Bagge et al., 2004). In order to be classified as a parasite, an organism must fulfil the criteria that its presence

inflicts harm to its host (Barber et al., 2000). They affect their hosts in various ways, all the while optimising their own fitness (Ravichandran & Rameshkumar, 2012). Thus parasites often have important consequences for host biology, despite generally being much smaller than their hosts (Barber et al., 2000). As parasites invade, move around and grow within or on their hosts, they can have an impact on fish behaviour, metabolism, body condition, fecundity and survival (Lagrue & Poulin, 2015). These consequences of infection could come about through associated pathology, physiological imbalance or general malaise (Barber et al., 2000).

The taxonomically diverse range of parasites that infect fish exhibit a wide variety of life cycle strategies (Barber et al., 2000). While many parasites move between ultimate hosts, some have to pass between intermediate hosts before reaching an ultimate host where they reach sexual maturity (Barber et al., 2000). Some parasites require their hosts to be eaten by certain predators in order to ensure transmission, which contradicts the notion that parasites need to minimise the negative consequences they inflict on their host in order to be successful (Barber et al., 2000). Understanding host-parasite relationships can be important in helping to predict changes in environmental conditions, as they can act as sensitive indicators of pollution and heavy metal accumulation (Reed, 2015). Parasites can also serve as important tools in stock discrimination studies as they can serve as biological tags for fish (Reed, 2015). This “biotagging” is the main application of parasitology in fisheries science (MacKenzie and Abaunza, 1998; Mosquera et al., 2003).

Parasites can have a range of negative impacts on fish populations, including the potential to devastate stocks through impairing spawning, influencing product quality through myoliquefaction, and effecting human health through inducing allergies (Reed, 2015). Thus the study of fish parasites is an important area of research and could contribute to successful and sustainable management of fisheries and aquaculture systems throughout the world (Reed, 2015). To understand how characteristics constrain the productivity of the fish resource, it is important to better understand and disentangle the roles of natural and man-made factors in generating the changes in the exploited fish populations (Dobson & May, 1987). Parasites may have a considerable impact on a fishery and it is important to consider how this impact may affect a fishery, especially when developing management strategies.

### **1.6. Gill Pathologies and Gill Parasites**

Fish gills are a particularly sensitive, multifunctional organ (Strzyzewska et al., 2016). They are responsible for respiration, while also regulating optimal osmotic pressure and acid-base balance of a fish's bodily fluids (Strzyzewska et al., 2016). The complex structural and vascular anatomy, and

elaborate vascular control systems, all reflect the multitude of tasks the gills undertake (Sollid & Nilsson, 2006). In general, gills are composed of a main axis bearing filaments which may or may not have their surfaces further subdivided (Hughes & Morgan, 1973). Fish gills are supplied with copious amounts of blood. At sites of gaseous exchange, this blood flows through thin epithelial plates that are separated by pillar-like trabeculae (Hughes & Morgan, 1973). The short diffusion distances and vast surface area enables rapid gaseous exchange (Sollid & Nilsson, 2006). The large surface area, however, is not desirable for osmoregulatory processes as it results in increased ion and water fluxes over the gill surface (Sollid & Nilsson, 2006). These increased fluxes not only mean increased osmoregulatory costs, but also means the fish is more exposed to toxic substances and pathogens (Sollid & Nilsson, 2006).

Different mechanisms and processes apply different demands on the gills, and as a result the gill structure will need to find an optimal compromise between these demands (Sollid & Nilsson, 2006). With changing environmental conditions, the demands placed on the gills are likely to change (Sollid & Nilsson, 2006). The large gill surface area in contact with the external environment also means the gills are often the first area of contact for many contaminants carried in water (Strzyzewska et al., 2016). Thus, studying the gill morphology of fish can provide important insight into the health status of the fish, as well as provide important information on the health hazards coming from the environment (Strzyzewska et al., 2016).

Environmental change brought about by anthropogenic impacts and pollutants may not necessarily cause harm, but in combination with other factors it could induce stress (Khan & Thulin, 1991). Several fish diseases and abnormalities have been shown to increase in prevalence with high levels of pollution (Khan & Thulin, 1991). Pollutants and environmental change may directly or indirectly influence the prevalence, intensity and pathogenicity of gill parasites (Khan & Thulin, 1991). Parasitism may increase if the environmental change affects the ability of a host to defend itself, or if the change results in an increase in the number of intermediate or definitive hosts (Lafferty, 1997). Pollutants and contaminants enter the fish from the external environment via three routes, through the mouth, integument or gills (Khan & Thulin, 1991). Contaminants that enter the fish through the gills and integument are carried via the blood to the tissues and organs (Khan & Thulin, 1991).

There are a limited number of ways in which gills respond to infection and damage, and there are virtually no responses that can be solely linked to a single causative agent (Ferguson et al., 1994). Therefore, diagnosing the root cause of the damage becomes tricky and integrating the results of multiple testing techniques, such as histopathology and blood chemistry, would be recommended in order to reach a true diagnosis (Ferguson et al., 1994).

### **1.7. Parasitic infection and its Effect on Fish as a Food Source for Humans**

Parasitisation of commercially exploited fish can have important consequences both socially and economically (Botha, 1986a). Most fish, both those in natural populations and those found in aquacultural systems, carry a parasite burden that is detrimental to their health (Barber, 2007). In addition to affecting fish health and survival, parasites can also have a major impact on conventional seafood quality and price (Ravichandran & Rameshkumar, 2012). In aquaculture systems any pathogenic infection that influences product quality, or has the potential to cause large-scale mortalities, is a major concern and a constant threat (Reed, 2015). For wild-caught marine fisheries, knowledge of parasites is just as important. Any industry that offers a fresh meat product is concerned with flesh quality, and the factors that affect it (Ravichandran & Rameshkumar, 2012).

Parasitic infection can impact fishery operations, and even influence season closures. The South African snoek (*Thyrsites atun*) fishery is an example of this, where their season is limited and closed due to an aesthetically unacceptable helminth parasite that infects snoek at a certain time of the year (Botha, 1986a). Occurrences of parasites that infect fish and carry human disease are relatively rare, but they do occur. For example, the fish parasite *Anisakis* which has been known to induce allergic reactions in some humans when they come into contact with infected fish (Kirstein et al., 2010). *Anisakis* can induce acute gastroallergic or anaphyletic reactions, after parasitizing humans and causing anisakiasis, a zoonotic disease (Kirstein et al., 2010).

Depending on their target organ, parasites are able to impact the reproductive processes of their fish hosts both directly and indirectly (Sitjá-Bobadilla, 2009). Through impacting reproductive processes, parasites have the potential to devastate fish stocks and, in turn, hinder their availability as a food source. The exact processes behind the alteration of fish reproduction by non-gonadal parasites are not yet well known, but several possibilities have been proposed (Sitjá-Bobadilla, 2009). These possibilities include: (i) the parasite extracts energy and nutrients from the host, and as a result these extractions can no longer be used for reproduction; (ii) the parasite can inflict physiological, immunological, or ethological changes in their host, resulting in impaired mating, gonad maturation, or larval survival (Sitjá-Bobadilla, 2009). The multivalvulid, non-gonadal parasite *Kudoa paniformis* has been shown to negatively affect the reproductive effort of Pacific hake, *Merluccius productus* (Sitjá-Bobadilla, 2009). The decrease in hake fecundity was shown to be proportional to the intensity of infection, with a female with a muscle parasite load of 340 pseudocysts per gram having only 10 percent of the fecundity of a non-infected fish (Sitjá-Bobadilla, 2009).

### **1.8. Parasitic Castration**

Parasitic castrators commonly infect crustacean, mollusc and echinoderm hosts, with relatively few studies focussing on possible fish hosts (Lafferty, 1993). According to Baudoin (1975), parasitic castration is : “a destruction or alteration of gonad tissue, reproductive behavior, hormonal balance, or other modification that results in reduction in host reproduction above and beyond that which results from non-selective use of host energy reserves by the parasite” (p. 348). This definition emphasizes the reallocation of resources away from host reproduction, through hormonal control or through attacking the endocrine glands of the infected host (Hall et al., 2007). Parasitic castrators essentially steal the reproductive resources from their hosts and convert them into new propagules that infect new hosts (Hall et al., 2007). The reproductive activities of hosts can be negatively impacted by their parasites due to metabolic disturbances in somatic investments, sex determination, sexual behaviour and population recruitments (Lima et al., 2007). The intra- and interspecific competition between parasitic castrators may be intense as a result of the consumption of the limited host reproductive energy resource (Lafferty & Kuris, 2009).

Parasitic castrators are relatively host-specific, when compared with other infectious agents, synchronizing their growth with their infected host and reaching a large size relative to their host (>1%) (Fogelman et al., 2008). The host population dynamics may also be altered via competition, with castrated individuals still utilising resources yet they are not able to reproduce (Fogelman et al., 2008). Castrators can also have an influence on the morphology, behaviour and the evolution of life history traits of their infected hosts (Fogelman et al., 2008). For example, host populations subject to high rates of parasitisation may respond by selecting for more rapid maturation and earlier reproduction (Fogelman et al., 2008; Lafferty & Kuris, 2009). Infected hosts may produce a brood before the castration has taken full effect, or the host in some cases can outlive the castrator and regain some reproductive potential (Fogelman et al., 2008). However, when the prevalence of a parasitic castrator is high, the reproductive output of the host population can significantly diminish (Fogelman et al., 2008).

Castration of the gonads by a parasite serves to override the energy allocation strategy, with the parasite taking up all the reproductive energy of their host (Lafferty & Kuris, 2009). This reallocation of reproductive energy allows the parasite to divert this energy to its own growth and reproductive output, and even benefit as a result of the increased longevity of its host (Fogelman et al., 2008). Parasitic castration serves as a response by parasites to the trade-off that exists between consumption and longevity (Lafferty & Kuris, 2009). Parasites must carry out a balancing act between reaping the benefits of their own reproduction and suffering the costs of harming their hosts (Hall et al., 2007).

### 1.9.X-Cell Disease and Other Gill Diseases

Gill diseases have had a particularly significant impact on marine aquaculture industries around the world. These infectious gill syndromes or disease conditions include amoebic gill disease (AGD), proliferative gill inflammation (PGI), X-cell disease and tenacibaculosis (Mitchell & Rodger, 2011). Increased risk of infection has been closely associated with the uncontrolled transfer and introduction of live aquatic organisms from one location to another (Bower et al., 1994). Layered epithelia comprising of living cells cover the skin and gills of fish, and form the first barrier between the external and internal environment (Nolan et al., 1999). A chemically and functionally complex mucus layer, excreted by specialized mucus cells in the epidermis, forms a protective coat over the body surface (Nolan et al., 1999). Ectoparasite infection has been found to adversely affect the functioning of these epithelia, and in turn negatively affect osmoregulatory processes (Nolan et al., 1999). Fish are vulnerable to a range of pathogens or toxins that can induce a hyperplastic response, especially when reared under culture conditions (Adams et al., 2004).

X-cell disease is found in wild-caught marine teleost fish and has been described for a number of fish species in both the northern and southern hemispheres (Davison, 1998; Davison & Franklin, 2003). Some notable cases of infection include cod (*Gadus morhua*) and dab (*Limanda limanda* L.) species from the North Sea and Icelandic waters, as well as a number of notothenoid fishes in Antarctic waters (McVicar et al., 1987; Dethlefsen et al., 1996; Davison & Franklin, 2003). This disease presents itself as tumour-like swellings in the pseudobranchial region that can be easily seen on the upper edge of the operculum (Dethlefsen et al., 1996). These tumour-like swellings are as a result of hyperplasia of a cell type known as X-cell, denominated such as a result of its unknown origin and nature (Davison et al., 1990). It is primarily associated with epidermal tissues, such as those found in the pseudobranchial region, but it has also been shown to affect the kidney, spleen and ovary (Davison, 1998). These swellings are as a result of an intra-epidermal accumulation of X-cells (Mc Vicar et al., 1987). Within Antarctic waters this disease seems to impact the bald rock cod (*Pagothenia borchgrevinki*) most severely, where up to 15% of the population within the waters of the Ross Sea show signs of the disease (Davison & Franklin, 2003). The white tumour-like swellings characteristic of the disease have given rise to the local name 'fluffy gill disease', in and around Antarctica (Davison & Franklin, 2003).

Little is known about the effect of X-cell disease on the physiology of infected fishes. However, a low condition factor was reported for diseased bald rock cod (*Pagothenia borchgrevinki*) (Davison, 1998). X-cell affected fish have also been reported to have significantly reduced liver and gonad masses, especially female fish infected with the disease (Davison & Franklin, 2003). The swelling of the gill tissue as a result of the X-cell disease, reduces the surface area for gaseous exchange, as the X-cells

invade the spaces between secondary lamellae (Davison & Franklin, 2003). This reduced gaseous exchange surface area has a rather negligible effect on the resting oxygen uptake, but rather affects the fish's ability to swim as it reduces aerobic potential (Davison et al., 1990). Thus the ability of infected fish to avoid predators and catch prey could decrease significantly (Davison et al., 1990).

Amoebic gill disease (AGD) is an ectoparasitic condition caused by an amoeboid parasite from the genus *Neoparamoeba* (Morrison et al., 2006). The disease presents itself as raised, multifocal white mucoid patches upon the gills, as a result of a pronounced inflammatory response (Adams & Nowak, 2003; Morrison et al., 2006). It is thought that these characteristic mucoid patches are caused by hyperplasia of undifferentiated epithelial cells that can fuse secondary lamellae, and as a result the surface area of the respiratory epithelium can be significantly reduced (Morrison et al., 2006). Amoebae are often found on or around the gill lesions and are sometimes found entrapped within the interlamellar vesicles or 'cysts' (Adams & Nowak, 2003). Gill trauma from harmful algal or jellyfish blooms have been suggested to increase the risk of AGD development (Adams & Nowak, 2003). Amoebic gill disease (AGD) has proved to be a significant health problem affecting the commercial culture of Atlantic salmon, *Salmo salar* L., in Tasmania (Adams et al., 2004). Reduced appetite, lethargy, respiratory distress, loss of equilibrium, and even mortality, are all possible side effects of AGD (Morrison et al., 2006). Salinity and water temperature have a major influence on the outbreak severity of AGD within Tasmanian salmon farms (Adams et al., 2004). Freshwater bathing of infected pens has been shown to be a successful mitigation technique for AGD. However, this technique is limited by the requirement of an extensive nearby freshwater source, and the pathogen does not get completely eradicated from the gills (Bridle et al., 2003; Adams et al., 2004).

#### **1.10. 'Frill on Gill' in *Merluccius capensis***

An unknown pathogen, known to fisheries scientists in South Africa as 'Frill on Gill' (FOG) has been documented to infect *M. capensis* off the coast of South Africa (Verlaque-Napper & Singh, 2017). As the name suggests, this pathogen occurs on the gill filaments of infected fish, and hake documented with FOG were found to lack gonads (Verlaque-Napper & Singh, 2017). Relatively little is known about the causes and effects of FOG. It is unknown whether FOG is caused by a micro or macro pathogen, but comparisons have been made with "X-cell disease" in cod from the North Sea and "amoebic gill disease" caused by a pathogenic amoeba in marine fish (Dethlefsen et al., 1996; Dykova et al., 2007; Verlaque-Napper & Singh, 2017). Both possibilities cause considerable strain on the gill filaments of the infected host, which may affect respiration and the uptake of oxygen, as well as the release of carbon dioxide, ammonia and other metabolites (Verlaque-Napper & Singh, 2017).

“Frill on Gill” (FOG) affects the two species of hake in South Africa unequally, with FOG having a rather negligible effect on populations of *M. paradoxus*, as opposed to the more significant effect observed for *M. capensis* (Verlaque-Napper & Singh, 2017). FOG has also been observed more frequently on *M. capensis* populations in the colder south and west coast South African fishing grounds, with no incidences recorded in the warmer waters of the east coast (Verlaque-Napper & Singh, 2017). This coincides with differences identified between the bacterial skin parasites of *M. capensis* and *M. paradoxus* found on the west coast and those found on the east coast of South Africa (Botha, 1986a). Georgala (1958) attributed this difference between coasts to a difference in the spoilage rates of fish found at the different fishing grounds. As with other parasitic castrators, high rates of infection of FOG are expected to reduce host density, and hinder host growth and sexual maturation, which in turn could be detrimental to host population growth dynamics (Fogelman et al., 2009).

#### **1.11. The Economic Importance of Understanding ‘Frill on Gill’**

The parasites that infect hake have received relatively little attention, especially when considering the commercial importance of the *Merluccius* genus worldwide (Botha, 1986a). Within the coastal region of sub-Saharan Africa very little research has been focussed on the effects of parasitic species associated with commercially important hosts on the fishery resources of the region (Reed, 2015). However, out of the entire sub-Saharan African region, marine parasitic species are best documented in southern Africa (Reed, 2015). Considering the substantial aquaculture and wild-caught fisheries that exist throughout sub-Saharan Africa, and the benefit that understanding host-parasite relationships brings when implementing fishery management strategies, the attention given to parasites and their associated fish hosts falls short within this region.

The hake fishery is extremely important for South Africa’s people and economy, understanding the relationship between the two Cape hake species and the parasites that infect them is important. Within southern Africa, the parasites of Cape hakes have been somewhat documented (Reed, 2015). However, as with most species in the region, taxonomic studies far outnumber applied research. Davies & Beyers (1947), recorded a high incidence of the myxozoan *K.thyrsites* in *M. capensis* and *M. paradoxus* (Reed, 2015). More recently, studies have focused on looking into the use of parasitic data as biological tags to contribute to understanding the number of Cape hake sub-populations in southern Africa (Reed, 2015). However, the unknown pathogen FOG and its effects in this region remain a mystery.

#### **1.12. Measures of Fish Health**

Body condition indices are a simple and common method to estimate the effects of parasites on their fish hosts (Lagrué & Poulin, 2015). Body condition indices usually make use of length and mass

relationships, as they require just fish body length and total mass measurements to calculate and they are easy and cheap to obtain (Lagrue & Poulin, 2015). The analysis of length-weight assumes that heavier fish of a given length are in better condition (Bolger & Connolly, 1989). Measurements of fat or protein content, lipid composition and RNA: DNA ratios are also useful alternatives to assessing fish condition (Lagrue & Poulin, 2015). The hepatosomatic index (HSI) is another useful alternative index for fish body condition. HSI is the relative measure of liver weight to body weight and serves as an indication of the status of the energy reserve of an animal (Chellappa et al., 1995). Parasitization is expected to have a negative effect on fish body condition, with infected fish having a lower body condition index than their uninfected conspecifics (Lagrue & Poulin, 2015).

### **1.13. Objectives**

This project aimed to understand the effects of FOG on the body condition of the shallow-water hake *M. capensis* on the south coast of South Africa. Annual research surveys have been conducted by the Department of Agriculture, Forestry and Fisheries (DAFF) demersal sector for approximately 25 years since 1985. This study made use of condition factor, a measurement of fish condition based on length-weight data, and the hepatosomatic index as body condition indices to analyse the effects of FOG on *M. capensis*. The results of this study have contributed towards documenting the effects of this pathogen on *M. capensis* in South Africa.

## **2. Methods**

Samples of *M. capensis* were collected from several annual demersal survey cruises conducted by South Africa's Department of Agriculture Forestry and Fisheries (DAFF), spanning a 31 year period from June 1985 to January 2017. These surveys were conducted on the west and south coasts of South Africa, extending from the Orange River mouth (16°E) to Cape Agulhas (20°E) representing the west coast, and from Cape Agulhas to Port Alfred (27°E) representing the south coast. This study focuses on data collected over this period, and in particular, from the south coast survey (Figure 4). The south coast surveys are conducted in autumn (mid-February to April) each year, with some years affording an extra spring (September to October) south coast survey. However, budgetary and operational constraints have prevented the extra spring sampling excursions from taking place every year.

Sampling took place using demersal trawling equipment between the 50 and 1000 m depth contours, with the selection of trawling positions following a random, stratified design. For the random stratified design, the sampling area was divided into a grid, with each grid block representing a stratum. For the

grid, the survey area from the coast to the 1000 m depth contour was subdivided by latitude or longitude, and depth was subdivided into a number of strata. The sampling stations within the grid were then randomly selected. The number of trawling stations per depth and longitude stratum was directly proportional to the area of each stratum. Areas with rough ground could not be sampled using demersal trawls, and as a result they were excluded from the station selection process. These rough areas were assumed to have the same fish densities as the areas adjacent to them. All trawl sampling took place during the day to avoid possible bias created by the movement of *M. capensis* off the seabed at night to feed.

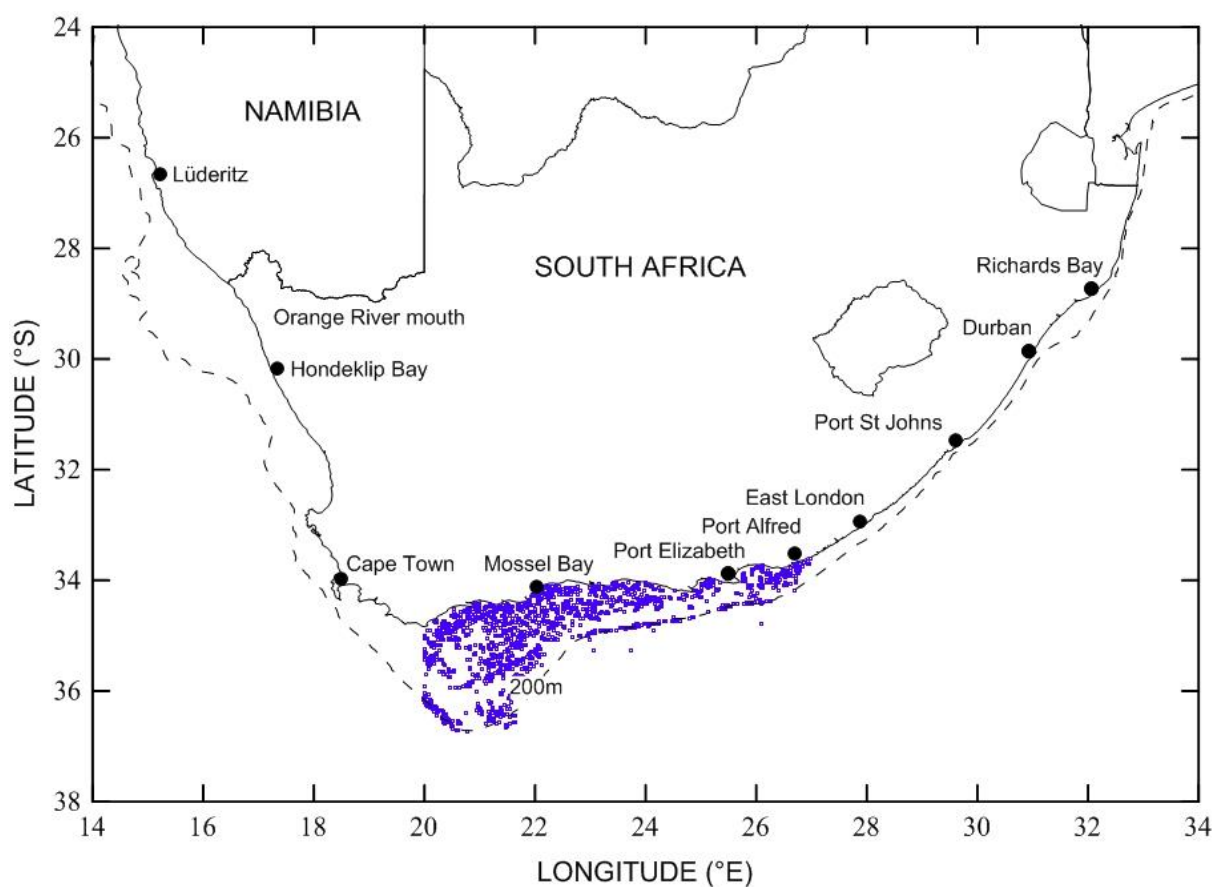


Figure 4: Demersal trawl sampling locations for *Merluccius capensis* samples collected by the Department of Agriculture, Forestry and Fisheries during the annual south coast survey from June 1985 to January 2017. Data points combine 'Frill on Gill' and Non-'Frill on Gill' individuals.

Whole *M. capensis* samples were labelled, bagged and frozen on board at  $-20^{\circ}\text{C}$ , and transported to the DAFF laboratory for storage and later dissection. Data on the sex ratios, gonad stages and the frequency of 'Frill on Gill' (FOG) were collected annually for samples of *M. capensis*. The total length

(cm), wet weight (g), gonad weight (g), stomach weight (g), otolith number, liver weight (g), and a description of the stomach contents were also recorded for each *M. capensis* specimen.

This study utilized two measures of body condition, namely condition factor (CF) and hepatosomatic Index (HSI), to identify and compare differences in body condition between *M. capensis* with FOG and those without, for different size classes, over the 31 year period. Three different size classes based on length were created; 0 – 26 cm, 27 – 52 cm, and >52 cm. These size classes were created to cover the full range of lengths of the *M. capensis* specimens collected.

### 2.1. Length-Weight Relationship

Length-weight regressions were used to calculate the body condition of all fish. The length-weight relationship was calculated using Eq.(1) and the least-squares regression procedure,

$$W=aL^b \quad (1)$$

where  $a$  and  $b$  are the length-weight parameters,  $L$  is total length (cm), and  $W$  is weight in wet weight (g) (Marquardt, 1963).

Length-weight relationships are used to estimate fish weight corresponding to a given length, and condition factors are used to compare the 'condition' of a fish based on the assumption that heavier fish of a given length are in better condition (Froese, 2006).

### 2.2. Condition Factor

The length-weight parameters,  $a$  and  $b$ , were used to calculate the CF. CF was calculated using Eq.(2) (van der Lingen et al., 2006). The expected wet weight was estimated from the length-weight relationships, and was calculated using Eq.(1).

$$CF=\frac{\text{Observed wet weight}(g)}{\text{Expected wet weight}(g)} \quad (2)$$

CF values <0.5 or >2 were considered invalid and discarded.

### 2.3. Hepatosomatic Index

HSI was used as an alternative measure of body condition. The HSI is a relative measure of liver weight to body weight, calculated using Eq.(3),

$$HSI = 100 \times \frac{LW}{W} \quad (3)$$

where LW is the wet weight of the liver(g), and W is wet weight of the fish (g) (Wootton et al., 1978).

#### 2.4. Gonadosomatic Index

The reproductive cycle in fishes involves large fluctuations in the weight of gonads and the fat reserves used to build them, and this change has a large impact on the condition factor and liver weight of fish (Htun-Han, 1978). The gonadosomatic index (GSI) is a relative measure of gonad weight to body weight, calculated using Eq.(4),

$$GSI = 100 \times \frac{GW}{W} \quad (4)$$

where GW is the wet weight of the gonads (g), and W is the wet weight of the fish (g)(Htun-Han, 1978). Seven different GSI categories were created; 0 - 4, 4.1 – 8, 8.1 – 12, 12.1 – 16, 16.1 – 20, 20.1 – 24, and 24.1 – 28.

#### 2.5. Statistical Method

In order to test the significance of gonad maturity on the condition factor of *M. capensis* without the FOG parasite present, two, two-way crossed analysis of variance (ANOVA) tests were conducted. These ANOVAs, with an interaction effect, were conducted on the effects of the two factors, length category and GSI category on the CF, and the HSI of uninfected *M. capensis*.

Two three-way crossed ANOVA tests were conducted, with two interaction effects, for the effects of three factors, length category, GSI category and the presence of FOG, on the CF, and the HSI of *M. capensis* on the south coast of South Africa.

FOG fish lack gonads, thus FOG fish were compared with Non-FOG fish with low GSI values. Two, two-way crossed ANOVA tests were conducted, with an interaction effect, for the effects of two factors, length category, and the presence of FOG, on the CF, and the HSI of *M. capensis* with GSI values lower than 2 on the south coast of South Africa.

For all the two-way crossed ANOVA tests conducted the assumptions of normality, equal variance, and independent errors were tested. All statistical analyses were conducted in R (R Core Team, 2015) and Microsoft office Excel 2016.

### 3. Results

All samples were collected on the south coast of South Africa (Figure 4). In total, 24275 *M. capensis* samples were analysed, of which 825 (3.4 %) were infected with 'Frill on Gill' (FOG). Samples considered were collected over a 30 year period from 1986 to 2016. However, samples are missing for the years 1998, 2002, 2012, and 2013 (Table 1).

Table 1: Sample sizes (N), Length Ranges (cm) and Weight Ranges (g) are presented per year for Non-'Frill on Gill' (Non-FOG) and 'Frill on Gill' (FOG) *Merluccius capensis* collected on the south coast of South Africa from 1986 to 2016. The months during the year that sampling took place are also represented (Sampling Months). The prevalence (%) of FOG is represented in ( ) next to each FOG sample size.

Year	Sampling Months	FOG/ Non-FOG	N(%prevalence)	Length Range (cm)	Weight Range (g)
1986	Sep, Oct	Non-FOG	678	10 - 98	7 - 8200
1987	Sep, Oct	Non-FOG	652	10 - 96	4 - 8400
1988	May, June	Non-FOG	720	10 - 106	7 - 10300
		FOG	37(4.89%)	29 - 80	200 - 4620
1989	May, June	Non-FOG	565	13 - 100	15 - 8338
		FOG	33(5.52%)	16 - 71	23 - 2890
1990	May, June	Non-FOG	420	10 - 94	6 - 7580
		FOG	1(0.24%)		
1991	June, Sep, Oct	Non-FOG	821	10 - 103	5 - 10015
		FOG	33(3.86%)	10 - 80	5 - 5050
1992	April, Sep	Non-FOG	782	11 - 96	11 - 7892
		FOG	10(1.26%)	21 - 73	75 - 3190
1993	April, May, Sep	Non-FOG	849	10 - 102	6 - 11500
		FOG	56(6.19%)	16 - 81	30 - 5025
1994	June, Sep, Oct	Non-FOG	878	10 - 99	7 - 11900
		FOG	40(4.36%)	22 - 76	93 - 4562
1995	April, May, Sep, Oct	Non-FOG	861	9 - 101	5 - 9500
		FOG	30(3.37%)	12 - 77	14 - 3500
1996	April	Non-FOG	390	11 - 100	10 - 9300
		FOG	8(2.01%)	20 - 53	63 - 1270
1997	April, May	Non-FOG	426	10 - 94	7 - 8330
		FOG	4(0.93%)	20 - 77	55 - 3375
1999	April, May	Non-FOG	448	10 - 102	7 - 11000
		FOG	21(4.48%)	24 - 56	100 - 1550
2000	May, June	Non-FOG	417	10 - 102	7 - 9600
		FOG	20(4.58%)	23 - 74	100 - 3810
2001	Aug, Sep	Non-FOG	419	10 - 95	4 - 8229
		FOG	4(0.95%)	26 - 67	143 - 2377
2003	April, May, Aug, Sep	Non-FOG	811	10 - 103	5 - 10400

		FOG	20(2.41%)	16 - 84	25 - 4568
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Table 2: continued.

Year	Sampling Months	FOG/Non-FOG	N(%prevalence)	Length Range (cm)	Weight Range (g)
2004	March, April, Sep, Oct	Non-FOG	1098	6 - 98	2 - 9200
		FOG	21(1.88%)	11 - 70	10 - 3084
2005	April, May	Non-FOG	533	8 - 104	2 - 9650
		FOG	1(0.19%)		
2006	April, May, Sep	Non-FOG	1327	11 - 100	9 - 7250
		FOG	23(1.70%)	30 - 62	198 - 1830
2007	April, May, Oct	Non-FOG	1100	6 - 103	2 - 11200
		FOG	1(0.09%)		
2008	April, May Sep	Non-FOG	1388	10 - 104	9 - 10000
		FOG	48(3.34%)	28 - 81	128 - 4832
2009	April, May	Non-FOG	924	10 - 99	6 - 7800
		FOG	59(6.00%)	27 - 84	134 - 4750
2010	April, May	Non-FOG	1548	20 - 91	49 - 11260
		FOG	176(10.21%)	22 - 70	66 - 3008
2011	April, May	Non-FOG	1178	15 - 104	42 - 9300
		FOG	100(7.82%)	19 - 74	54 - 3050
2014	April, May	Non-FOG	840	12 - 95	12 - 7370
		FOG	2(0.24%)		45 - 51
2015	April, May	Non-FOG	997	17 - 91	46 - 7962
		FOG	9(0.89%)	43 - 59	686 - 1752
2016	April, May, Sep, Oct	Non-FOG	2380	10 - 93	6 - 7885
		FOG	68(2.78%)	19 - 71	54 - 2551

The majority of Non-FOG fish caught off the south coast during the trawl surveys were between 30 and 60 cm, with a peak number of fish occurring between the lengths 43 and 46 cm (Figure 5). After the peak, the length frequencies tail off as they approach 100 cm (Figure 5). The smallest Non-FOG fish caught during the surveys was 6 cm, and the largest fish measured in at 106 cm. For the FOG individuals, the upper quartile of the length frequency data is 54 cm and the lower quartile is 32 cm (Figure 6). The smallest fish infected with FOG caught on the south coast was 10 cm, and the largest was 84 cm. The length frequencies of Non-FOG *M. capensis* and the length frequencies of *M. capensis* infected with FOG were significantly different from each other, with the Non-FOG *M. capensis* having a significantly larger mean length ( $t=5.7707$ ,  $df = 24481$ ,  $p\text{-value} = 7.99e^{-09}$ ).

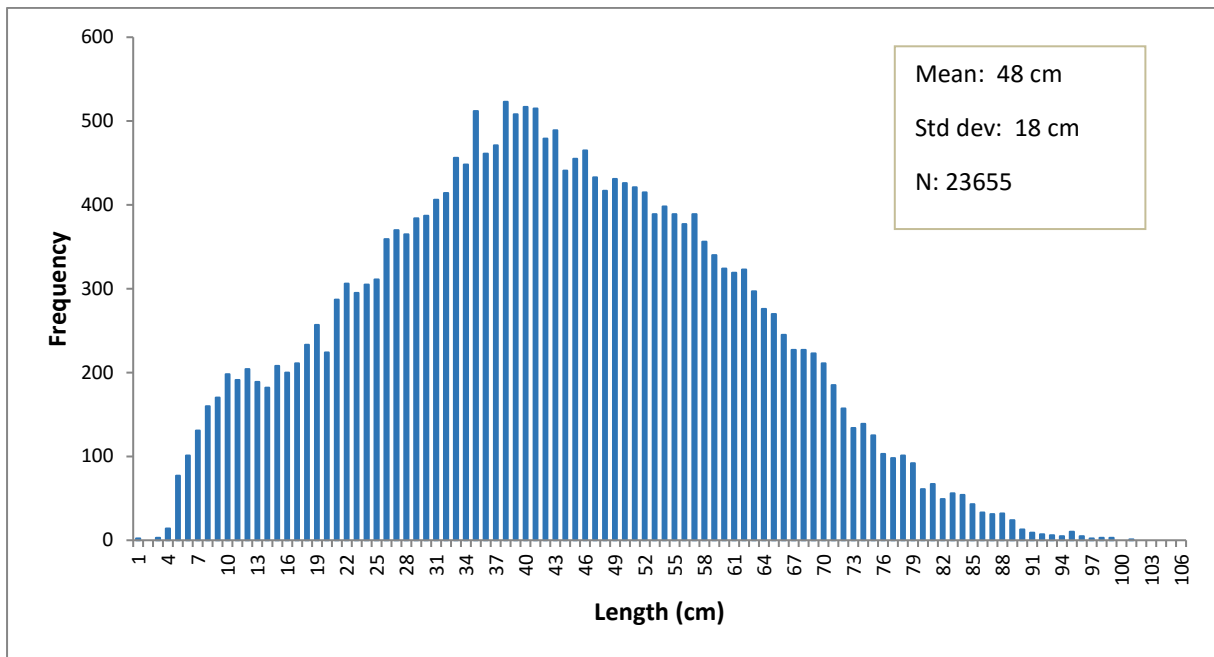


Figure 5: Length Frequency distribution for male and female *Merluccius capensis* combined, for Non-‘Frill on Gill’ (FOG) individuals from the south coast of South Africa, collected from 1986 to 2016 .

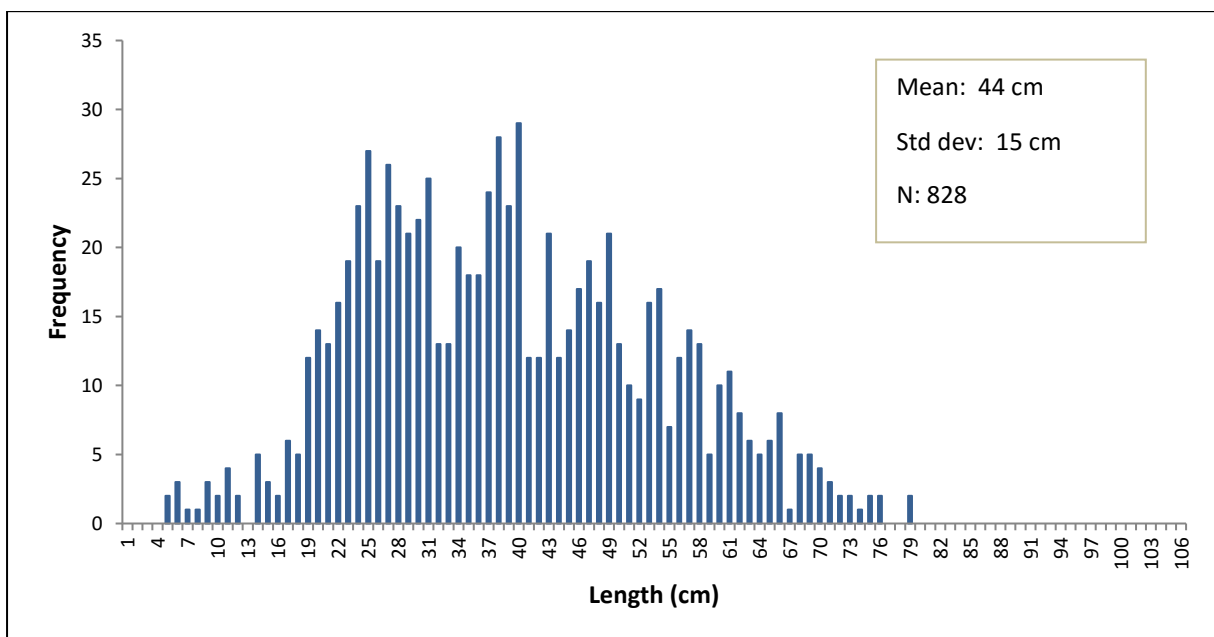


Figure 6: Length Frequency distribution for ‘Frill on Gill’ (FOG) *Merluccius capensis* from the south coast of South Africa, collected from 1988 to 2016.

There were no FOG individuals over 84 cm, as opposed to the 514 Non-FOG fish that measured between 85 cm and 106 cm (Figures 5 & 6). The length-weight measurements for FOG and Non-FOG *M. capensis* lie on either side of the fitted trend line (Figure 7). Both b-values were checked to verify allometric or isometric growth. The 95% confidence intervals of b for both Non-FOG and FOG did not include 3, and therefore positive allometric growth applies to both groups (Non-FOG south coast b-value : 3.0672 > 3, FOG south coast b-value: 3.0231)(Figure 7).

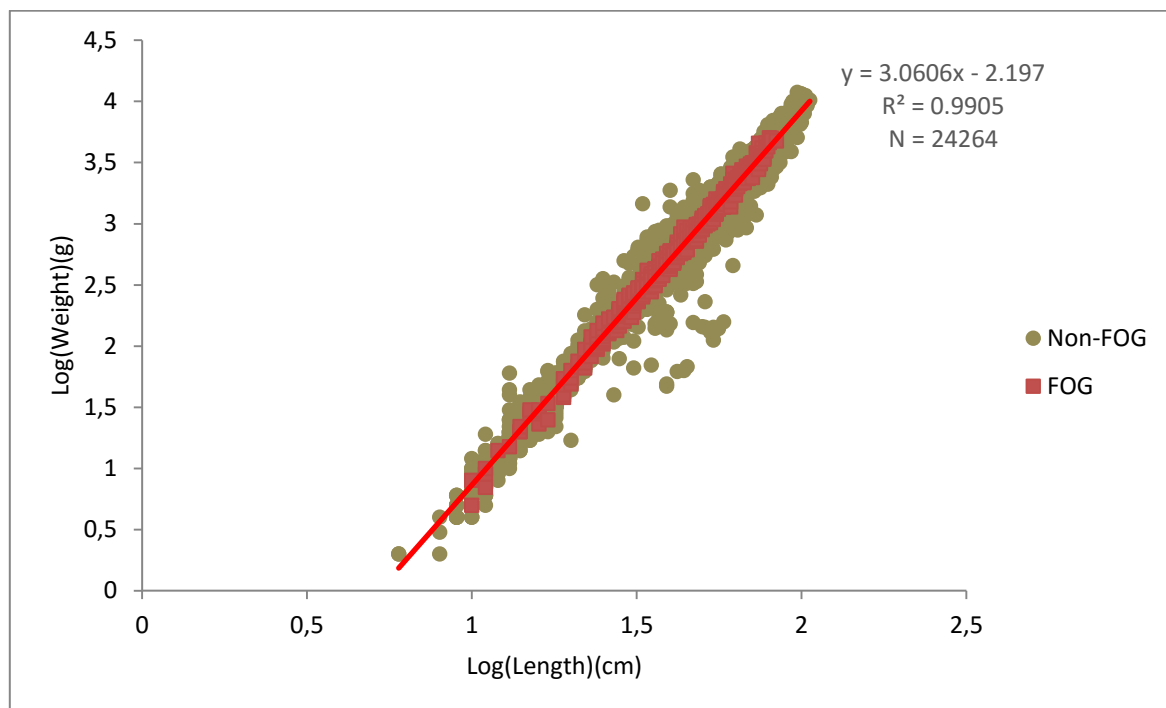


Figure 7: Length-weight regression plot *Merluccius capensis*, sampled on the south coast of South Africa from 1986 to 2016. Red points are *M. capensis* infected with 'Frill on Gill' (FOG), and grey points are uninfected *M. capensis*.

### 3.1. Condition Factor (CF)

The CF of Non-FOG *M. capensis* increase with increasing length until 22 – 26 cm, where it levels out before decreasing with increasing length from the 26 – 30 cm length interval (Figure 9). The CF of *M. capensis* infected with FOG follow this same pattern, but was below the condition factors of uninfected fish, apart from three spikes in FOG CF at 30 – 34 cm, 42 – 46 cm, and 78 – 82 cm (Figure 9). The CF of FOG *M. capensis* is also higher than the CF of Non-FOG *M. capensis* at 54 – 58 cm and 58 – 62 cm (Figure 9). At 54 – 58 cm the condition factors of Non-FOG *M. capensis* start to increase again with increasing length (Figure 9). This increasing trend continues for Non-FOG *M. capensis* apart from two dips at 86 – 90cm and 94 – 98 cm (Figure 9). The CFs of FOG *M. capensis* start to increase before

the Non-FOG fish, at 50 – 54 cm, and are higher than the uninfected *M. capensis* between 50 – 54 cm and 58 – 62 cm (Figure 9). The CFs of FOG *M. capensis* drop slightly below the condition factors of uninfected *M. capensis* from 62 - 66 cm to 74 – 78 cm. Following this slight drop, there is a sharp increase in condition factor from 74 – 78 cm to 78 – 82 cm of infected FOG *M. capensis* (Figure 9).

Length category and GSI category are both significant factors influencing the condition factor of uninfected *M. capensis* (Table 2). The interaction between length category and GSI category also has a significant effect on the CF of uninfected *M. capensis* (Table 2). The length category, GSI category and the presence of FOG all have a significant effects on the condition factor of *M. capensis* (Table 3). The interaction between length category and GSI category, and the interaction between length category and the presence of FOG both have a significant effect on the CF of *M. capensis* (Table 3). For *M. capensis* with GSI values less than 2, the length category and the presence of FOG both have a significant effects on CF (Table 4). The interaction between length category and the presence of FOG also has a significant effect on the condition factors of *M. capensis* with GSI values lower than 2 (Table 4).

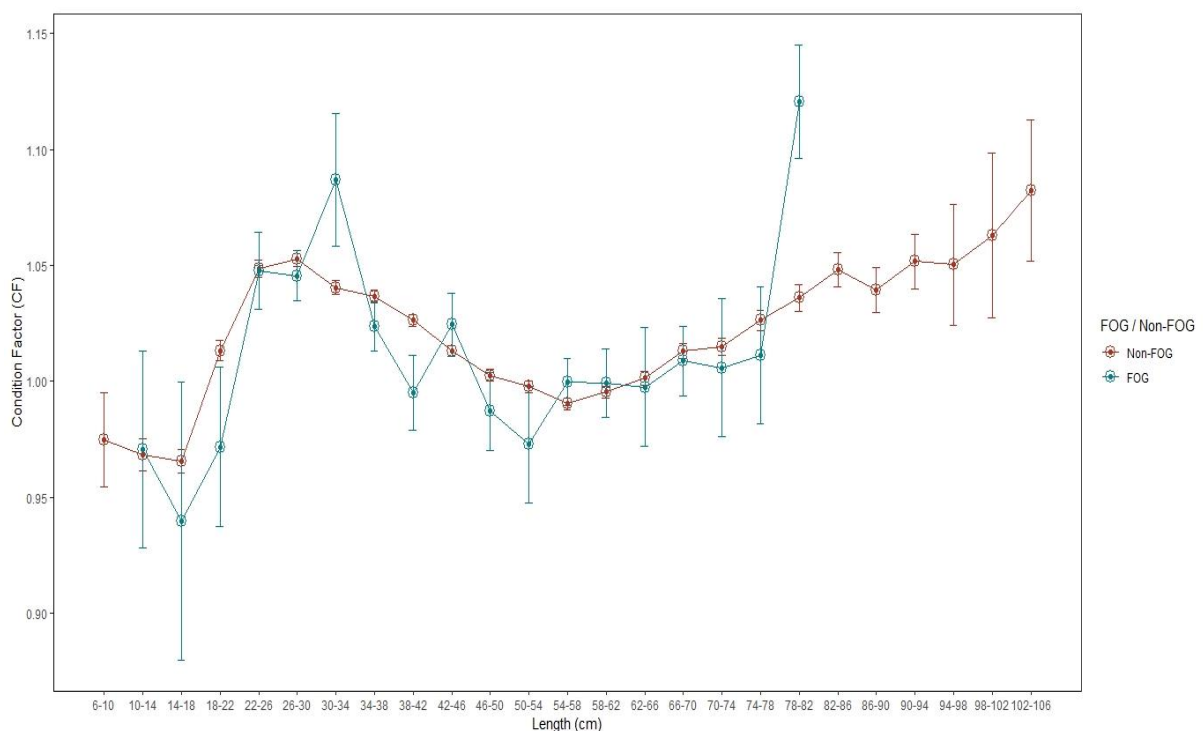


Figure 9: The mean condition factor (CF) for 4 cm length categories, for Non-‘Frill on Gill’ (Non-FOG) and ‘Frill on Gill’ (FOG) *Merluccius capensis* sampled on the south coast of South Africa from 1986 to 2016. The standard error is represented by the error bars.

Table 2: Two-way ANOVA results for the effects of Length category and GSI category on the Condition Factor (CF) of uninfected *Merluccius capensis* (Non-FOG) on the south coast of South Africa sampled from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	P-value
Length category	1.31	2	51.61	<2.2e-16
GSI category	7.80	6	102.57	<2.2e-16
Length category x GSI category	0.36	10	2.82	0.0017
Residuals	290.92	22945		

Table 3: Three-way ANOVA results for the effects of Length category, the presence of 'Frill on Gill' (FOG/Non-FOG) and GSI category on the Condition Factor (CF) of *Merluccius capensis* on the south coast of South Africa sampled from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	p-value
Length category	1.31	2	50.03	<2.2e-16
FOG/Non-FOG	0.13	1	9.55	0.0020
GSI category	7.80	6	99.42	<2.2e-16
Length category x FOG/Non-FOG	0.08	2	3.17	0.0420
Length category x GSI category	0.36	10	2.73	0.0023
Residuals	310.91	23769		

Table 4: Two-way ANOVA results for the effects of Length category and the presence of 'Frill on Gill' (FOG/Non-FOG) on the Condition Factor (CF) of *Merluccius capensis* with GSI values lower than 2, on the south coast of South Africa sampled from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	p-value
Intercept	5165.60	1	3.70e+05	<2.2e-16
Length category	1.60	2	5.57e+01	<2.2e-16
FOG/Non-FOG	0.20	1	1.25e+01	0.0004
Length category x FOG/Non-FOG	0.10	2	3.24e+00	0.0394
Residuals	254.51	18254		

### 3.2. Hepatosomatic Index (HSI)

The HSI of Non-FOG *M. capensis* decreases initially from 10 - 14 cm to 14 - 18 cm, before rising quite sharply with increasing length (Figure 10). This increasing trend stops for Non-FOG *M. capensis* at 22 - 26 cm, where HSI gradually starts to decrease with increasing length (Figure 10). This decreasing trend stops at 54 - 58 cm for Non-FOG *M. capensis*, and HSI increases with increasing length until 70 - 74 cm (Figure 10). From 70 - 74 cm to 94 - 98 cm, HSI decreases with increasing length for Non-FOG *M. capensis*. The HSI of *M. capensis* infected with FOG initially increases with increasing length until

34 - 38 cm (Figure 10). The HSI values of FOG *M. capensis* are below the HSI values of uninfected *M. capensis* until 34 - 38 cm where they rise above the Non-FOG HSIs (Figure 10). The HSI values of FOG *M. capensis* are then higher than the HSI values of uninfected fish until 70 - 74 cm, apart from a dip at 38 - 42 cm (Figure 10). The HSI values of FOG *M. capensis* generally increases with increasing length from 45 – 50 cm to 62 - 66 cm, after which HSI decreases until 70 -74 cm (Figure 10).

Length category and GSI category are both significant factors influencing the HSI of uninfected *M. capensis* (Table 5). The interaction between length category and GSI category also has a significant effect on the HSI of uninfected *M. capensis* (Table 5). The length category, GSI category and the presence of FOG all have a significant effects on the HSI of *M. capensis* (Table 6). The interaction between length category and GSI category and the interaction between length category and the presence of FOG both have a significant effect on the HSI of *M. capensis* (Table 6). For *M. capensis* with GSI values less than 2, the length category and the presence of FOG both have a significant effect on the HSI (Table 7). The interaction between length category and the presence of FOG also has a significant effect on the HSI of *M. capensis* with GSI values lower than 2 (Table 7).

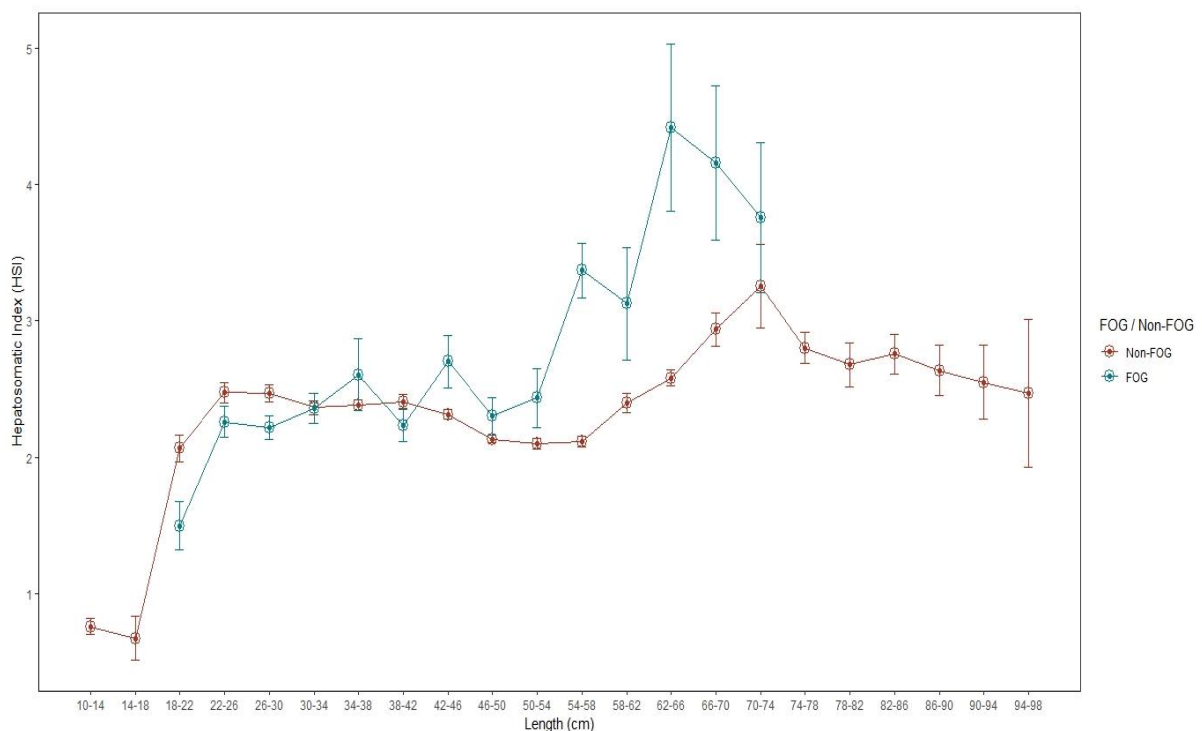


Figure 10 :The mean Hepatosomatic Index (HSI) for 4 cm length categories, for Non-‘Frill on Gill’ (Non-FOG) and ‘Frill on Gill’ (FOG) *Merluccius capensis* sampled on the south coast of South Africa from 1986 to 2016. The standard error is represented by the error bars.

Table 5 :Two-way ANOVA results for the effects of Length category and GSI category, on the Hepatosomatic Index (HSI) of uninfected *Merluccius capensis* (Non-FOG) sampled on the south coast of South Africa from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	p-value
Length category	13.4	2	4.45	0.0118
GSI category	1497.7	6	165.12	<2e-16
Length category x GSI category	499.8	5	66.13	<2e-16
Residuals	9841.1	6510		

Table 6: Three-way ANOVA results for the effects of Length category, the presence of 'Frill on Gill' (FOG/Non-FOG) and GSI category, on the Hepatosomatic Index (HSI) of *Merluccius capensis* sampled on the south coast of South Africa from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	p-value
Length category	13.4	2	4.51	0.012
FOG/Non-FOG	51	1	34.23	5.13e-09
GSI category	1497.7	6	167.68	<2.2e-16
Length category x FOG/Non-FOG	39.7	2	13.34	1.65e-06
Length category x GSI category	499.8	5	67.16	<2.2e-16
Residuals	10204.2	6855		

Table 7: Two-way ANOVA results for the effects of Length category and the presence of 'Frill on Gill' (FOG/Non-FOG), on the Hepatosomatic Index (HSI) of *Merluccius capensis* sampled with GSI values lower than 2, on the south coast of South Africa from 1986 to 2016. The sum of squares (SS), degrees of freedom (df), F-values and p-values are all represented for each source of variation (Source).

Source	SS	df	F-value	p-value
Intercept	6079.4	1	5607.69	<2.2e-16
Length category	19.2	2	8.84	0.00015
FOG/Non-FOG	48.5	1	44.72	2.51e-11
Length category x FOG/Non-FOG	37.4	2	17.24	3.47e-08
Residuals	5456.4	5033		

## 4. Discussion

This study focused on *M. capensis* samples collected from the south coast of South Africa, since the number of 'Frill on Gill' (FOG) samples collected over the 31 years on the south coast is higher than those collected from the other coasts over the same period (south coast: 828 FOG samples; west coast: 464 FOG samples; east coast: No FOG present). This difference in occurrence between coasts could be due to the differing environmental conditions on each coast, affecting the spatial structure of host populations, and influencing the prevalence of a particular parasite or pathogen and thus possible metabolic impacts in the hosts (Lima et al., 2007). There may be more suitable conditions for transmission of this pathogen between individuals on the south coast, but since very little is known about it this would only be an assumption.

Body condition in fish can fluctuate according to the time of the year, such as during breeding seasons or when food is sparse. These events are often associated with a marked decline in body condition (Tierney et al., 1996). By isolating the samples just from the south coast, this study also minimizes the effects of any possible skew in condition factor due to seasonal fluctuations, as all south coast samples were collected annually around a similar time of year.

The length frequency distributions of FOG individuals peaks around a similar weight range to the Non-FOG length frequency distribution. This could suggest that FOG infection is related to abundance, rather than host age or size. Usually, when considering intensity of infection in fish host populations, the intensity of infection by metazoan parasites and pathogens increases with age or size of the fish host (Poulin, 2000). A study by Lo et al. (1998), showed that this relationship between parasite abundance and host age, and size was true for ectoparasites infecting the gills of French Polynesian coral-reef fishes. A possible explanation for this increase in the abundance of gill parasites with fish size is the idea that the gill surface increases with fish size, which in turn means an increase in water flow over the gills (Lo et al., 1998). Being larger, also means there is more external and internal space for parasite establishment (Poulin, 2000). Larger fish within their natural environment have higher physical (ventilation volume) and chemical (mucus) stimuli, making them more attractive to parasites, and also they eat more parasitized prey than smaller fish (Lo et al., 1998; Poulin, 2000). In terms of host age, it is thought that increasing age coincides with increasing time and opportunity to accumulate parasites, resulting in a positive relationship between fish age and parasite load (Poulin, 2000). However, this pattern of host age and size does not appear to be as apparent in this study with the prevalence of the FOG parasite dropping off at either end of the length range.

The positive relationship between parasite infection intensity and the age or size of the fish hosts, sometimes stops beyond a certain host age or size (Poulin, 2000). The largest individual infected with

the FOG pathogen in this study was 84cm, but Non-FOG individuals measured as large as 106cm. In terms of wet weight, there were no FOG individuals over 6 kg, but there were a large number of Non-FOG *M. capensis* weighing over 6 kg. Within fish populations, individuals differ in their ability to acquire limited resources, and this results in varying growth rates, body size and nutritional condition of members of a population (Barber, 2005). Hosts that are in better condition may be more beneficial to parasites, especially parasites that have significant energy requirements, as their hosts are able to provide more energy essential for parasite growth and development (Barber, 2005). Alternatively, better host nutritional condition may mean that the potential host has a better immune system, or it has a better ability to limit the availability of nutrients to growing parasites (Barber, 2005). This increased immunity or ability to restrict parasite resources could be a possible reason behind the lack of FOG individuals above 84cm and 6 kg (Figures 6 and 7). An increased immunity could also possibly explain the drop off in prevalence of FOG in *M. capensis* after 50cm on South Africa's south coast.

Another possible explanation for this lack of infected *M. capensis* over 84 cm could be as a result of hosts outliving their parasites. However, this conclusion would require further investigation into when and how FOG is infecting *M. capensis*, and at what age *M. capensis* is most susceptible to infection. A linear growth rate of around 12.5 cm year<sup>-1</sup> (1.04 cm month<sup>-1</sup>) has been estimated for *M. capensis* (Wilhelm et al., 2017). Correlations between parasite length and host length suggest that infection occurs once, early in life, and then the parasite grows with its host (Parker & Booth, 2013). Decreasing prevalence with increasing size or host age, would then be a more likely consequence of parasite death, rather than the death of infected fish (Parker & Booth, 2013). Parker & Booth (2013), observed similar correlations between the prevalence of the tongue replacement parasite *Cymothoa barbonica*, and the size of its host the Largespotted dartfish, *Trachinotus bolta*. They observed additional evidence for *T. bolta* outliving their tongue replacement parasite *C. barbonica* in the form of basihyal damage on larger fish, where *C. barbonica* was no longer present (Parker & Booth, 2013).

The estimated b-values for both Non-FOG and FOG fish, indicate positive allometric growth. This implies that both infected and non-infected *M. capensis* are becoming relatively stouter or deeper-bodied as they increase in length (Riedel et al., 2007). Organisms that live in ever changing environments must constantly develop the most optimal energy allocation strategies to ensure survival and reproduction. For reproducing individuals in a population, it is important to be able to cope with fluctuations in food supply and the constant risk of predation while foraging, while still being able to accumulate enough stores for reproduction (Post & Parkinson, 2001). For non-reproductive individuals, there are constant trade-offs between energy allocation to growth, predation avoidance, and storage products for when resources are scarce (Post & Parkinson, 2001). These conflicting demands constrain an organism's ability to acquire, expend and store energy (Post & Parkinson, 2001).

In this study, fish infected with FOG do not reproduce and have differing energy allocation demands than Non-FOG fish.

Energy allocation strategies also vary greatly between different age and size cohorts. The growth of fish is well-described by a functional asymptotic relationship, such as the one represented by the von Bertalanffy growth function (Riedel et al., 2007). This growth function implies that fish grow faster earlier in life, before maturity. This strategy of faster growth before maturity could serve as an adaptation against predation (Riedel et al., 2007). In addition, when considering larval development in fish, allometry is a common feature, as at this stage it is crucial to ensure that essential organs for primary functions are developed first, and organs that are of a lower priority for survival are developed thereafter (Gisbert, 1999). Once mature, the gains in length start to level off but weight may still continue to increase (Riedel et al., 2007). Increasing weight after maturity may serve as an adaptation for fecundity, as fecundity and weight are closely related in fish (Riedel et al., 2007). In female fish, fecundity generally increases with female age or body size, as the larger body cavity of older females allows for the development of larger ovaries (Hixon et al., 2014).

The main spawning season for *M. capensis* off South Africa's south coast is suggested to be in summer, around January (Jansen et al., 2015). This peak in spawning has been linked to upwelling conditions in the region, and the consequent peak in phytoplankton production (Jansen et al., 2015). The condition factor of fishes is affected by a variety of factors, including the gonad maturity stage of the fish (Kreiner et al., 2001). Hake condition is suggested to decrease subsequent to the development of gonads (Jansen et al., 2015). The reproductive cycle of a fish induces large changes in the weight of its gonads, and thus its gonadosomatic index (GSI) (Htun-Han, 1978). The GSI and the length of uninfected (Non-FOG) *M. capensis* both had a significant effect on condition factor (CF). The effect of GSI on CF of uninfected *M. capensis* also varies with length, with GSI influencing larger mature individuals differently to smaller immature individuals. The annual spawning cycles of small and large *M. capensis* differ on the south coast of South Africa, which could also be playing a part in the effect of GSI on the CF of *M. capensis* at different lengths (Jansen et al., 2015).

As the gonads of a fish mature, large amounts of proteins and lipids are deposited into developing eggs and spermatozoa (Htun-Han, 1978). These proteins and lipids are, in part, extracted directly from ingested food, but this material largely comes from energy reserves deposited during the active feeding season (Htun-Han, 1978). The liver and muscles of fish serve as important storage vessels for these energy reserves. Therefore, the weight of these organs could provide an indication of the accumulation or utilization of these reserves (Htun-Han, 1978). In addition, fecundity has been linked to liver weight, with females with heavier livers being more fecund than females with lighter livers

(Htun-Han, 1978). The length and GSI both had significant effects on the hepatosomatic index (HSI) of uninfected (Non-FOG) *M. capensis* on the south coast of South Africa. The effect of GSI on the HSI of *M. capensis* also varied with length.

Generally, it is assumed that parasites have deleterious effects on their fish hosts, often resulting in infected fish being in poorer condition than uninfected fish. However, through castrating their hosts parasitic castrators drastically alter the energy allocation strategies of their hosts. Parasitic castrators are able to benefit from the advantage of extra energy that may now be available as a result of their host not participating in reproduction (Hecker & Karbe, 2005). In theory, the host could also stand to benefit from not partaking in the energy intensive act of reproducing. *Merluccius capensis* infected with FOG lack gonads, therefore these fish would not need to deplete liver and muscle energy reserves for gonad maturation. Fish length, GSI and the presence of the FOG parasite all had a significant effect on the condition factor of *M. capensis* on the south coast of South Africa. Again, the interaction between GSI and length also had a significant effect on the condition factor of *M. capensis*, with GSI having varying effects on fish of different lengths. The effect of the FOG pathogen on *M. capensis* on the south coast also varied with length.

*Merluccius capensis*, on the south coast of South Africa, have a length at 50 % maturity of about 53.44 cm (Singh et al., 2015). The energy costs associated with reproduction could provide a possible explanation for the gentle drop in condition factor of uninfected *M. capensis* after 50 cm. Alternatively, *M. capensis* infected with FOG don't reproduce yet the condition factors of FOG *M. capensis* also generally decrease with increasing length from around 26 cm, apart from a spike in condition factor at 30 cm. The CFs of *M. capensis* infected with FOG are higher than condition factors of uninfected *M. capensis* from around 54 cm, before dropping below again at 62 cm. Through inhibiting the reproduction of their hosts, parasitic castrators could in turn benefit due to an increase in host survivorship, growth and energy available to the parasite (Lima et al., 2007). This redirection of energy away from reproduction, could mean that the energy can then be directed toward maintenance and cause an increase in size of host fish (Lima et al., 2007). This increase in energy availability as a result of not partaking in reproductive processes, could provide a possible explanation for the higher condition factor of infected FOG fish when compared with the non-infected fish around 54 cm, and possibly for the late spike in condition factor of FOG *M. capensis* after 78 cm.

The CFs of uninfected *M. capensis* start to increase again with increasing length after 58 cm. Disputes over resources are almost always won by the larger individual (Neat et al., 1998). Thus larger *M. capensis* are able to outcompete smaller *M. capensis* for resources, and with growth in length starting to level off with age, the energy gained from these resources can be allocated towards increasing

weight and fecundity. Gonad size at any particular stage of development increases as fish size increases (West, 1990). Gonad weight, especially when ripe, may constitute a considerable proportion of total body weight (Le Cren, 1951). The increased gonad weight of larger individuals could contribute towards their higher CFs, but also could possibly help explain the lower CF of FOG *M. capensis* around 70 cm as gonad weight does not contribute to elevated CFs in these individuals.

By castrating their host, this extra energy is available to the parasite without draining other hosts resources, which would have otherwise resulted in the decreased health status of their host (Hecker & Karbe, 2005). The survival of parasites directly depends on the health of their hosts, so a drastically deteriorating host condition could result in fatal consequences for parasites (Hecker & Karbe, 2005). This explanation for FOG's effect on the body condition of *M. capensis* does well to answer what is going on in mature infected individuals, but there must be something different happening in pre-reproductive *M. capensis*. When compared with immature Non-FOG individuals (GSI values of 2 or less), the presence of FOG still had a significant effect on the condition factor of *M. capensis*.

The condition factors of FOG *M. capensis* and Non-FOG *M. capensis* follow a similar pattern initially. This rapid increase in condition factor in smaller *M. capensis* (less than 26 cm in length) could be indicative of pre-reproductive fish prioritizing growth. For smaller *M. capensis* (less than 26 cm in length), the condition factors of infected FOG individuals followed a similar pattern to the uninfected *M. capensis*, but always kept below the CFs of uninfected individuals, apart from a spike in FOG condition factors around 30 to 34 cm. In these smaller fish, the energy used for immunity to defend against infection cannot be used for growth, and is drained from the limited energy resources of the host (Hall et al., 2007). In other words, parasitic resistance is costly, and requires the reallocation of internal resources away from other fitness-related traits (Allen & Little, 2011).

HSI of *M. capensis* was significantly affected by the presence of the FOG, GSI and length (Table 6). The effect of GSI on the HSI of *M. capensis* varied significantly with length, but, so too did the effect of the presence of the FOG parasite. When there are high demands for energy, such as during times of rapid growth or reproduction, fish have to mobilize their glycogen reserves for fuel for survival (Chellappa et al., 1995). Initially, the HSI of both infected and uninfected *M. capensis* increases with increasing length. Energy reserves accumulate in the liver when energy intake exceeds the rate of utilization, and the surplus is then stored as reserves (Chellappa et al., 1995). Pre-reproductive fish, apart from growth and predator avoidance, allocate energy towards storage products for when resources are scarce (Post & Parkinson, 2001). For smaller *M. capensis* (smaller than 26 cm), the HSIs of uninfected individuals were higher than those infected with FOG. Smaller infected *M. capensis* could be expending extra energy on fighting infection, and as a result have less energy to allocate towards storage in the liver.

After 26 cm, the HSI of uninfected *M. capensis* gradually decreases with increasing length. After around 53 cm, this decrease in HSI could be indicative of energy reserves used in gonad maturation, the development of secondary sexual characteristics and breeding activities (Chellappa et al., 1995). For non-reproducing *M. capensis* infected with FOG HSI increases with increasing length after 26 cm, and infected HSI values were higher than uninfected *M. capensis* HSI values after this length. Infected FOG *M. capensis* don't need to utilize energy reserves for reproduction, and as a result there is more energy available, which could allow for a higher accumulation of liver glycogen reserves. Parasitic castration may, therefore provide a possible advantage to an individual in the form of growth, by redirecting the host resources away from reproduction and toward maintenance and growth (Lima et al., 2007). However, higher relative liver weights in newly infected fish could also be representative of a pathological or other physiological response to the acquisition of a new infection (Tierney et al., 1996).

*Merluccius capensis* adults and juveniles occupy different depth zones, with juveniles occupying waters more inshore than the adults (Field et al., 2008). The diet of *M. capensis* also varies with age, with juveniles feeding largely on euphausiids and other crustaceans, and as *M. capensis* grows its diet becomes more piscivorous (Field et al., 2008). The right set of environmental variables could promote growth, and improve fish condition (Amara et al., 2007). Shallow coastal habitats are important nursery grounds for many marine fishes and are subjected to a variety of natural and anthropogenic stressors (Amara et al., 2007). These stressors impact juvenile fish growth, survival and in turn subpopulation production and recruitment (Amara et al., 2007). The vulnerability of juvenile fish to predation, and their ability to survive periods when resources are scarce, have been shown to improve with faster fish growth rates and higher levels of energy reserves (Amara et al., 2007). Even small differences in growth and mortality rates within the first year of a fish's life could result in large differences in the number of individuals entering the reproductive stage annually (Vasconcelos et al., 2009). This sensitivity of young, pre-reproductive fish to change could raise concern when considering the apparent negative effects of FOG on young *M. capensis*.

Parasites play an important role in community regulation, and so influence conservation biology and fisheries management (Morand & Poulin, 1998). Castrated individuals continue to utilize resources without contributing to reproduction, which has detrimental effects for the host population (Fogelman et al., 2008). In this way, castrated individuals can alter host population dynamics through competition (Fogelman et al., 2008). The effect of 'Frill on Gill' as a type of parasitic castrator on the regulation of *M. capensis* populations could become a concern for fishery managers, as they reduce reproductive output. Parasitic castrators reduce host density, alter host population dynamics and affect the evolution of life history traits in their fish hosts (Fogelman et al., 2008). The diminishing

effect of parasitic castrators on the reproductive output of host populations becomes increasingly problematic with increasing prevalence of the castrator (Fogelman et al., 2008).

As the prevalence of FOG rises, so too do the numbers of individuals not contributing to reproduction within the population. These individuals make no contribution to reproduction, but they still compete with reproducing individuals for resources. Thus, the rising FOG prevalence could have detrimental effects on the ability of *M. capensis* populations to respond to fishing pressure and environmental change. This is an especially sensitive issue with the hake fishery being South Africa's most valuable marine fishery, responsible for an annual landed value in excess of R5.2 billion (DAFF, 2016). Therefore, understanding the effects of FOG on *M. capensis* populations could have significant repercussions for South Africa's economy.

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