

Parasite communities associated with the Cape gurnard
(*Chelidonichthys capensis*) and the lesser gurnard
(*C. queketti*) from South Africa

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Abstract

The Cape gurnard (*Chelidonichthys capensis*) and the lesser gurnard (*Chelidonichthys queketti*) are two members of the Triglidae family found off Southern Africa. *Chelidonichthys capensis* is distributed from depths of 10 m to 390 m in subtropical waters between Namibia and Mozambique, while *C. queketti* is distributed from 0 m to 150 m in subtropical waters from Namibia to southern Mozambique. Little is known about the biology, ecology and life cycles of these two species. Additionally, the parasite community of these two gurnards has not yet been surveyed, although there are records of a number of copepods infecting both species that have been documented for taxonomic purposes. This study aims to examine the macroparasite assemblages of both gurnard species from the west and south coasts of South Africa and determine whether the parasite communities show significant intra-specific, special differences or inter-specific differences. A total of 70 *Chelidonichthys capensis* and 87 *C. queketti* were examined, with a total of 13 parasitic taxa found infecting *C. capensis*, ten of which are new host records, while 15 parasitic taxa were found infecting *C. queketti*, 13 of which are new host records and one of which is a new geographic record. The nematode *Anisakis pegreffii* was the most prevalent parasite infecting *C. capensis* (75.7%), and an unidentified cyst was the most prevalent parasite infecting *C. queketti* (69%). Parasites recorded to infect both gurnard species include the cestode *Tentacularia coryphaenae*, the acanthocephalan *Corynosoma australe*, and the copepods *Lernentoma asellina* and *Medesicaste penetrans*. A *Caligus* species was only recorded to infect *C. capensis* and the unidentified cyst was only recorded infecting *C. queketti*. This study was also able to identify two biological tag species for potential use in population structure studies of both gurnards, namely *A. pegreffii* and *T. coryphaenae*, based on significant regional differences in prevalence and infection intensity levels. In comparison to other *Chelidonichthys* species, *C. capensis* has the second highest and *C. queketti* has the third highest number of recorded parasite taxa, with *C. lucerna* having the highest number (22

species) of parasites recorded. The new host records for *C. capensis* and *C. queketti*, and the new geographic record, contribute to our knowledge of these demersal fish species and of marine biodiversity in South Africa.

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Introduction

1.1 An Overview of Marine Parasitology

Parasitism, the relationship where parasitic organisms are dependent on a host organism, living in or on the host and decreasing the host's fitness to obtain some kind of benefit, most often being food (Rohde, 2005), is found within almost all ecosystems (Marcogliese, 2004). Many organisms adopt this as a way of life (Rohde, 2005) and the parasitic relationship extends across many phyla – often linked to diseases and death in humans and animals (Cox, 2002).

Parasites mostly have a bad reputation, but in truth they form a large and important part of ecosystems where they undertake a variety of complex roles - the importance of which is often undervalued by researchers (Rohde, 2005). Recently, research into marine parasitism and the role of parasites in ecosystems has increased substantially since it was suggested that half of all biodiversity is made up of parasitic species (Hudson et al., 2006), further supporting the idea that parasitism is the most successful mode of life (Poulin & Morand, 2000, Palm & Klimpel, 2007).

1.1.1 The Parasitic Way of Life

Parasitic species can be divided into micro- and macroparasites. Microparasites are small, mostly unicellular organisms, although some such as myxozoans (>50 µm in size) are multicellular (Marcogliese, 2004). These species typically have a high fecundity, and induce immune responses from their hosts (Rohde, 2005). Macroparasites are larger multicellular organisms and differ from microparasites in that they have longer generation times and frequently inhabit multiple hosts throughout their lifetime (Marcogliese, 2004). Parasites can be further divided into endoparasites, which live inside their host in the visceral cavity, organs, muscle tissue and eyes, and ectoparasites, which live on the surface of their host including the body surface, gills, operculum and mouth. Obligate parasites are entirely dependent on their

hosts for their survival while facultative parasites are able to survive as free-living organisms (Rohde, 2005). In terms of life cycle type, parasites with a direct (simple) life cycle infect only one host species and are specialist species, whereas parasites infecting multiple host species have indirect (complex) life cycles and are generalist species (Palm & Klimpel, 2007).

Complex life cycles allow for multiple host types; paratentic hosts house larval stages of parasites which don't develop inside the host, intermediate hosts support immature and developing parasites, while definitive (final) hosts support sexually mature parasites (Rohde, 2005). Often, within complex life cycles, hosts of early development stages of parasites are ingested by the next host in the life cycle which facilitates transmission of the parasite species. Therefore, the diversity of parasites found within a host often indicates the predator-prey relationships of the host and of other hosts which contribute to the life cycles and transmission of the parasites within an ecosystem (Marcogliese, 2004).

1.1.2 Parasite Diversity

Parasitic organisms can be found throughout most phyla, with almost all free-living metazoan species host to one or more parasite species (Rohde, 2005; Poulin & Morand, 2000). Although parasitism has evolved independently more than any other mode of life, it is difficult to estimate parasite diversity as parasite species cannot be definitively identified until their host species (whether one or many) have been identified (Poulin & Morand, 2000). And since many species are still undiscovered (May, 1986), it is impossible to currently determine the diversity of parasites (Poulin & Morand, 2000). Even when a host species has been identified their parasites may go undocumented, due to their small size, low prevalence, and the occurrence of morphologically similar species' (known as cryptic species) which are mistakenly identified as a single species (Poulin & Morand, 2000; Rohde, 2005).

Typically, the probability of a species colonizing, speciating within, and going extinct in a habitat is largely influenced by the characteristics of that habitat (Huston, 1994). Regarding parasite species, the primary habitat is the host and the species richness of parasites within a host is related to the characteristics of that host (Poulin & Morand, 2000). Studies have found that the species richness of parasites is greater in hosts with greater body size, population density, dietary diversity, life span, mobility, and geographical range (Rohde, 2010). Rather than having one trait determine parasite community structure, however, these traits interact with each other across various scales (Poulin & Morand, 2000).

The fundamental characteristics of parasite species also affect their rates of diversification and can create differences in diversity between parasite taxa, although these effects are difficult to isolate (Poulin & Morand, 2000). Evidence generally supports the hypothesis that smaller parasites are more speciose than larger ones (Poulin & Morand, 1997). Furthermore, parasite diversification may be hampered by life cycle complexity, as multiple-host life cycles can limit opportunities for speciation and diversification, although more research is needed to determine the importance of life cycles in influencing parasite diversity (Poulin & Morand, 2000, Rohde, 2010).

1.1.3 Marine Parasite Biogeography

Biogeography seeks to determine and interpret patterns in biodiversity across large spatial and temporal scales (Poulin, 2011). Because parasites have such intimate relationships with their hosts, host specificity is thought to play a key role in the geographic distribution of a parasite (Poulin, 2011) and, therefore, the geographic range of a parasite often reflects the range of its host (Poulin et al., 2011; Thieltges et al., 2011). Host specificity, however, is not the only factor influencing the biogeographical distribution of parasites, as parasitic life cycles and the surrounding environment are thought to interact with host specificity to determine the distribution of parasitic species (Poulin, 2011).

Two main biogeographical patterns for metazoan marine parasites have been shown, the first that the diversity of parasitic helminths is higher in the Indo-Pacific Ocean than in the Atlantic, and the second that monogenean parasite (and a few other ectoparasite species, to a lesser extent) diversity increases with decreasing latitude or increasing temperatures (Poulin & Morand, 2000). These patterns could also be explained by host specificity, as marine species diversity is generally higher at lower latitudes (Rohde, 2010). The increased diversity of marine species in tropical waters is thought to be due to the interactions of multiple biotic and abiotic factors such as the larger size of these areas, the greater age of these oceans (specifically the Pacific Ocean) and the warmer water temperatures (Poulin & Morand, 2000). According to Rohde (2010), warmer areas allow for shorter generation times and increased mutation rates in taxa which, in turn, leads to faster speciation rates than in colder areas.

However, research on the biogeography of marine parasites is scarce, which could mean that the patterns in diversity which have been observed in geographic regions are not due to host specificity or warmer temperatures, but rather due to the inconsistencies and variability in research between regions (Poulin & Morand, 2000). Therefore, further studies, across various spatial and temporal scales, are needed before scientists can fully understand the biogeographical distribution of parasites.

1.2 The Importance of Parasites

Parasites have been found to be of ecological significance throughout the various levels of biological organization, both directly and indirectly (Nunkoo, 2015). Impacts of their ecological significance are most evident at the genetic, individual, community and population levels (Hurd et al., 2001; Barber, 2007).

Research on parasitism has often focused on the relationship between the parasite and the host, and the negative effects associated with this relationship (Timi & MacKenzie, 2014). More

recently, however, the focus of research on marine parasitism has shifted to looking at the role of parasites within communities and ecosystem functioning (Hudson et al., 2006), and their value in terms of fisheries management, biodiversity, human health and the marine environment (Timi & MacKenzie, 2014). From all the recent research into parasitism, it has been suggested that a healthy ecosystem is one that is rich in parasite species (Sures, 2004; Horwitz & Wilcox, 2005; Hudson et al., 2006 and references therein).

1.2.1 Negative Impacts and Health Implications of Parasites

Although a healthy marine environment needs parasites (Hudson et al., 2006), parasites often negatively affect their hosts, human health and fishery and aquaculture industries (Cox, 2002; Henning et al., 2013). Many fish parasites are known to negatively affect the condition of their host and, therefore, the amount of energy it has to dedicate to its life functions (Neff & Cargnelli, 2004; Froese, 2006). Some marine parasites, such as those from the genus *Anisakis* Dujardin, 1845, have been found to negatively impact human health through accidental infection or through inducing allergic reactions (Lopata & Jeebhay, 2007), although all marine parasites are able to complete their life cycles without humans as hosts (Rohde, 2010).

Parasites can cause great economic harm to the fishery and aquaculture industries (Henning et al., 2013). This is more pronounced in the aquaculture industry, as high densities of fish in limited spaces increases parasite transmission between fish and decreases their general health (Barber, 2007). Some parasite species can cause great harm to a population by negatively impacting its reproduction, for example the coccidian *Eimeria sardinae* (Thélohan, 1890) which infects the testes and can cause parasitic castration of small pelagic fish such as Portuguese sardine *Sardina pilchardus* (Walbaum, 1792; Pinto, 1956) and South African sardine *Sardinops sagax* (Jenyns, 1842; Ssempe, 2013). Another parasite *Kudoa thyrsites* (Gilchrist, 1923) causes myoliquefaction - the degradation of fish muscle following death. This parasite is often seen in Pacific hake (*Merluccius productus* (Ayres, 1855)), farm-reared

Atlantic salmon (*Salmo salar* Linnaeus, 1758), South African sardine and Cape snoek (*Thyrsites atun* (Euphrasen, 1791); where infected fish are commonly known as “pap snoek”). Because this parasite decreases the quality of the fish and, therefore its value, infection can result in substantial economic losses (Henning et al., 2013; Nunkoo, 2015).

Common parasites in fish targeted by the fishing industry are nematodes in the genus *Anisakis*, usually *Anisakis simplex* (Rudolphi, 1809) and *Anisakis pegreffii* Campana-Rouget & Biocca, 1955 (Nunkoo, 2015). Species belonging to this genus have a complex life cycle with multiple hosts and infect various fish species as larvae and marine mammals as adults (Nieuwenhuizen et al., 2006; Rohde, 2010). If ingested live by humans through consumption of uncooked fish, members of this genus infiltrate the gastrointestinal tract causing abdominal pain, nausea and diarrhoea as the manifestations of the zoonotic disease called anisakiasis (Nieuwenhuizen et al., 2006; Mattiucci et al., 2013). Anisakiasis causes allergic reactions in the host which, in some cases, can result in fatal anaphylactic shocks (Piccolo et al., 1999; Rohde, 2010). Studies have also found that *Anisakis*-related allergies are a risk for those occupationally exposed to *Anisakis*-infected fish, as these workers become sensitive to the *Anisakis* proteins which provoke allergic reactions (Nieuwenhuizen et al., 2006). Further research is needed in order to prevent and control these parasite infections within the marine fishery and aquaculture industries, as well as prevent and treat marine parasite infections in humans.

1.2.2 Applied Marine Parasitology

Parasites can be used to expand our knowledge of the marine environment and the species that they infect, as seen with using parasites as biological tags. Using naturally occurring parasites as biological tags is a useful method for identifying and monitoring stocks and tracking the migration and movement of a host species (MacKenzie & Hemmingsen, 2014; Oliva et al., 2016). Parasites make for suitable biological tags as many species are specific to a geographical region (where the conditions are optimal for the transmission from host to host), therefore the

host is only infected with the parasite if it has been inside the parasite's endemic area (MacKenzie & Abaunza, 1998). Several criteria need to be met for a parasite to be a suitable biological tag including: significant spatial differences in infection across its geographic range, a relatively long life-span, easy detection and identification, and not affecting host behaviour (Williams et al., 1992; MacKenzie & Abaunza, 1998).

Marine parasites are also used as biological indicators of the quality of the marine environment. Parasite species that have free-living stages (such as helminths) are particularly sensitive to changes in environmental conditions and, therefore, serve as early warning signs of environmental change (MacKenzie, 1999). Heavy metals and pollutants have been shown to accumulate faster in the tissues of certain parasite species than in their hosts, allowing them to be used as early indicators of heavy metal concentrations in the marine environment (Sures et al., 1999; Rohde, 2010; Morris et al., 2016). Since certain metals (such as lead and mercury) can negatively impact human health, parasites are important in monitoring the heavy metal concentrations in the oceans (Sures et al., 1999).

1.2.3 The Significance of Parasites in South Africa

Marine parasites in South Africa have been studied for two centuries, with the first parasite species, the isopod *Anilocra capensis*, described in 1818 by William Elford Leach (Smit & Hadfield, 2015). In southern Africa, taxonomic research of marine parasites far outweighs applied research, due to the efforts of taxonomists from the early 1900s who described large numbers of new species (Reed, 2015). Recently, however, marine parasite research has been aimed towards the parasites of commercially important species in South Africa, with the parasite assemblages of kingklip (*Genypterus capensis*) (Smith, 1847; Payne 1986), sardine (*Sardinops sagax*) (Reed et al., 2012), snoek (*T. atun*) (Nunkoo et al., 2016) and the two hake species (*Merluccius capensis* Castelnau, 1861 and *M. paradoxus* Franca, 1960) (Botha, 1986) having been described. This shift in research has allowed scientists to determine the stock

structure of some of these species, for example the South African *S. sagax* population, which is now thought to comprise three sub-populations (Weston, 2013; van der Lingen et al., 2015; Weston et al., 2015). Although the parasites of some of South Africa's commercially important species have been described, there are still huge gaps in the research regarding other exploited species. The research currently available on the parasite assemblages of South African fish species, however, provides a foundation for determining stock structure and aiding in fisheries management of exploited species (Reed, 2015).

1.3. The Marine Environment off South Africa

The South African coastline is bordered by two contrasting oceanic currents - the cold, northward-flowing Benguela Current along the west coast of South Africa and the warm southward-flowing Agulhas Current along the east coast (Griffiths et al., 2010). These two currents interact periodically, as large eddies (also called Agulhas Rings) break off from the Agulhas Current and travel northwards into the southern Benguela. These eddies introduce warm, salty water into the southern Benguela ecosystem (Hutchings et al., 2009).

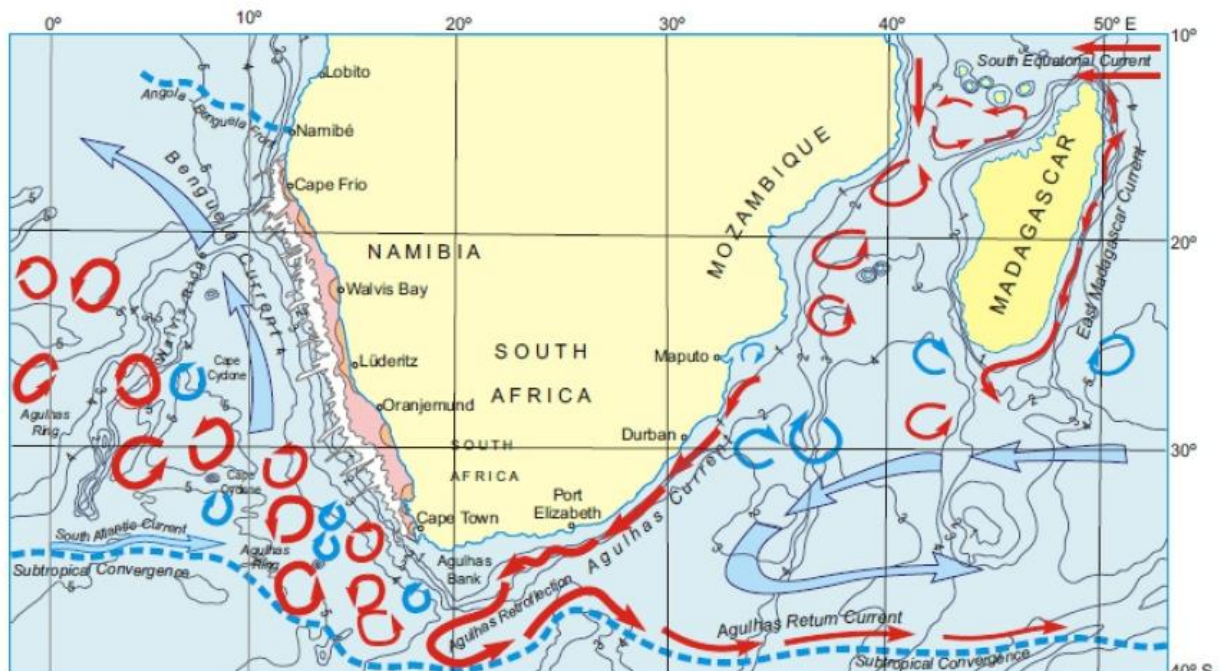


Figure 1: The two currents impacting South Africa's marine environment; the cold Benguela Current on the west coast and the warm Agulhas Current on the east coast. Eddies often spiral into the southern Benguela region from the Agulhas Retroflection, bringing warm and salty water into the southern Benguela ecosystem. Taken from Morris et al., 2017.

1.3.1 The Benguela Ecosystem

The Benguela Current Large Marine Ecosystem (BCLME), one of the world's four major eastern boundary upwelling systems, spans the west coasts of Angola, Namibia and South Africa (Hutchings et al., 2009; Kirkman et al., 2016).

The BCLME can be divided into two sub-regions, a northern sub-region along the west coasts of Angola and Namibia and a southern sub-region along the west and south-west coast of South Africa. They are separated by the Lüderitz upwelling cell and distinguished by distinct properties (Hutchings et al., 2009; Blamey et al., 2014). The Lüderitz upwelling cell separating the two sub-regions is characterised by strong winds, offshore transport and turbulence, and creates a physical barrier to many small epipelagic fish species (Lett et al., 2007; Hutchings et al., 2009; Kirkman et al., 2016).

The southern Benguela is characterised by a shelf-edge north-flowing jet current situated between Cape Point and Cape Columbine, a subsurface poleward counter current and concentrated cells of coastal upwelling driven by wind (Kirkman et al., 2016). The strong, seasonal upwelling along this coast creates highly productive environments as phytoplankton blooms that develop following the upwelling of nutrient-rich water to the surface support high concentrations of zooplankton (Blamey et al., 2014). Some of South Africa's economically important fish species, namely sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) (Linnaeus, 1758), utilise these highly productive areas as nursery grounds (Kirkman et al., 2016). Not only do the rich concentrations of zooplankton benefit the fish species, but the jet currents found adjacent to the upwelling cells limit the movement and loss of larvae and eggs (Kirkman et al., 2016). In large blooms, the phytoplankton will eventually decay, depleting the oxygen levels and creating hypoxic waters, which can lead to mass mortalities of shellfish and rock lobster (Hutchings et al., 2009).

This region supports many of South Africa's commercial fisheries including the small pelagic and demersal fisheries, both of which are of substantial economic importance (Cochrane et al., 2004). The small pelagic fishery is the country's largest in terms of landed mass and uses purse-seine nets to target sardine, anchovy and round herring (*Etrumeus whiteheadii* Wongratana, 1983) (Shannon et al., 2003; Cochrane et al., 2004; Pecquerie et al., 2004; Coetzee et al., 2008). Fisheries for demersal species use bottom trawls, longline and handline, primarily targeting shallow-water hake (*Merluccius capensis*) and deep-water hake (*M. paradoxus*) and Agulhas sole (*Austroglossus pectoralis* Kaup, 1858), with kingklip (*G. capensis*), monkfish (*Lophius vomerinus* Valenciennes, 1837) and snoek (*T. atun*) being some of the commercially important bycatch species (Cochrane et al., 2004, Pecquerie et al., 2004).

1.3.2 The Agulhas Bank

The Agulhas Bank is a temperate shelf system located along the south-west and south-east coast of South Africa between Cape Point and Port Alfred (Smale & Badenhorst, 1991; Kirkman et al., 2016). The western Agulhas Bank, between Cape Point and Cape Agulhas, shares many biological and physical components with the southern Benguela (Kirkman et al., 2016). To the east of Cape Agulhas, the central and eastern Agulhas banks are largely influenced by the warm, turbulent and fast-flowing Agulhas Current, but shelf-edge upwelling and periodic coastal upwelling also occurs there (Kirkman et al., 2016). The Bank itself is made up of a wide shelf with little depth variation, however, there is little distance between the 200 m and 500 m isobaths as the shelf edge declines steeply (Smale & Badenhorst, 1991). Deep seasonal mixing takes place in autumn and winter due to the presence of strong winds blowing from the west to south-east (Kirkman et al., 2016), but there is relatively little temperature fluctuation (Booth & Buxton, 1997).

Many commercially important fish species (such as shallow-water hake, deep-water hake, sardine, anchovy and horse mackerel *Trachurus capensis* Castelnau, 1861) use the Agulhas

Bank as spawning grounds (Kirkman et al., 2016). Here, they are subjected to heavy fishing pressures by the inshore and offshore trawlers who primarily target the two hake species but land many other fish species as bycatch (Booth, 1997). Many inshore areas of the Agulhas Bank are protected from bottom trawls but are instead subjected to fishing pressure from a linefishery that primarily catches carpenter (*Argyrozona argyrozona*) (Valenciennes, 1830) and kob (*Argyrosomus hololepidotus*) (Lacepède, 1801; Smale & Badenhorst, 1991).

1.4 The Genus *Chelidonichthys* (Kaup, 1873)

The family Triglidae (Order Scorpaeniformes) includes fish commonly known as gurnards and comprises eight genera and approximately 125 species, 15 of which are presently undescribed (Richards & Jones, 2002; Quigley, 2005). Typically, members of this family are small to medium in size, red and long-lived, occurring in both tropical and temperate waters worldwide (Leis & Trnski, 1989; Quigley, 2005) where they range from shallow coastal waters to about 500m and live on an assortment of benthic substrate types (Richard & Jones, 2002).

Gurnards have large, armoured heads and modified pectoral fins, with the lowest three rays of each fin thickened and separate, which they use to support themselves on the sea bed whilst searching for food (Papaconstantinou, 1983; McPhail, 1998). Their habit of sometimes using their pectoral fins to “fly” through the water, has earned them the name “sea robins” (Schwartz, 2002).

Triglids are social fish, forming loose shoals during spawning – which typically occurs during an extended period across the summer months (Quigley, 2005). The shoals, also formed during feeding, keep in contact with one another through audible grunts produced by individual gurnards (Quigley, 2005). These grunts are made by the muscular contraction of two muscles situated on the surface of the swim bladder and often also represent aggressive behaviour (Bayoumi, 1970).

The genus *Chelidonichthys* (Kaup, 1873) is widely distributed in the Pacific, Indian and Atlantic Oceans, and comprises ten species; *Chelidonichthys capensis* (Cuvier, 1829), *C. cuculus* (Linnaeus, 1758), *C. gabonensis* (Poll & Roux, 1955), *C. ischyurus* (Jordan & Thompson, 1914), *C. kumu* (Cuvier, 1829), *C. lastoviza* (Bonnaterre, 1788), *C. lucernus* (Linnaeus, 1758), *C. obscurus* (Walbaum, 1792), *C. queketti* (Regan, 1904) and *C. spinosus* (McClelland, 1844).

Chelidonichthys cuculus (red gurnard) and *C. obscurus* (longfin gurnard) are found across the Eastern Atlantic, from the British Isles throughout the Mediterranean Sea to the Eastern Central Atlantic (Labropoulou & Papaconstantinou, 2005; Coll et al., 2006; Boudaya et al., 2007). Both of these species are exploited in Mediterranean countries, where they are sold in local markets, with *C. cuculus* consumed more commonly than *C. obscurus* (Fischer et al. 1987).

Chelidonichthys lucerna (tub gurnard) is distributed across the Eastern Atlantic Ocean, from the British Isles to the Eastern Central Atlantic, but can be found further south in the Atlantic Ocean than *C. cuculus* and *C. obscurus* (Nunoo et al., 2015). This species is also only exploited in the Mediterranean (Nunoo et al., 2015).

Chelidonichthys gabonensis (Gabon gurnard) is distributed along the Eastern Central Atlantic Ocean, where it is caught by local line fisherman and as trawl bycatch (Russell et al., 2015).

The range of *C. lastoviza* (streaked gurnard) extends across the Eastern Atlantic Ocean, including the Mediterranean Sea, down to the Cape Agulhas (South Africa) where it continues into the Southern Indian Ocean, along the coast of Mozambique (Smith & Heemstra, 1986). This species is sometimes caught as bycatch from trawlers. Only the largest of this species is sold in markets of Mediterranean countries while smaller *C. lastoviza* are discarded (Fischer et al. 1987).

Both *C. ischyurus* (known as seppari-hôbô in Japan) and *C. spinosus* (spiny red gurnard) are found in the Northwest Pacific. While *C. ischyurus* has only been recorded from Sagami Bay (Japan) (Masuda et al., 1985), *C. spinosus* has been recorded to extend across Japan to the South China Sea (Richards, 1999).

Chelidonichthys kumu (bluefin gurnard) is found in the Indo-Pacific; including Japan, Australia, New Zealand, Mozambique and South Africa (Morton, 1979; Smith & Heemstra, 1986). This species is targeted in New Zealand and caught and sold as trawl bycatch in South Africa (McPhail, 1998).

Only *C. capensis* and *C. queketti* are endemic to southern Africa and can be found distributed between the Southeast Atlantic Ocean and the Western Indian Ocean (Figure 2; Smith & Heemstra, 1986).

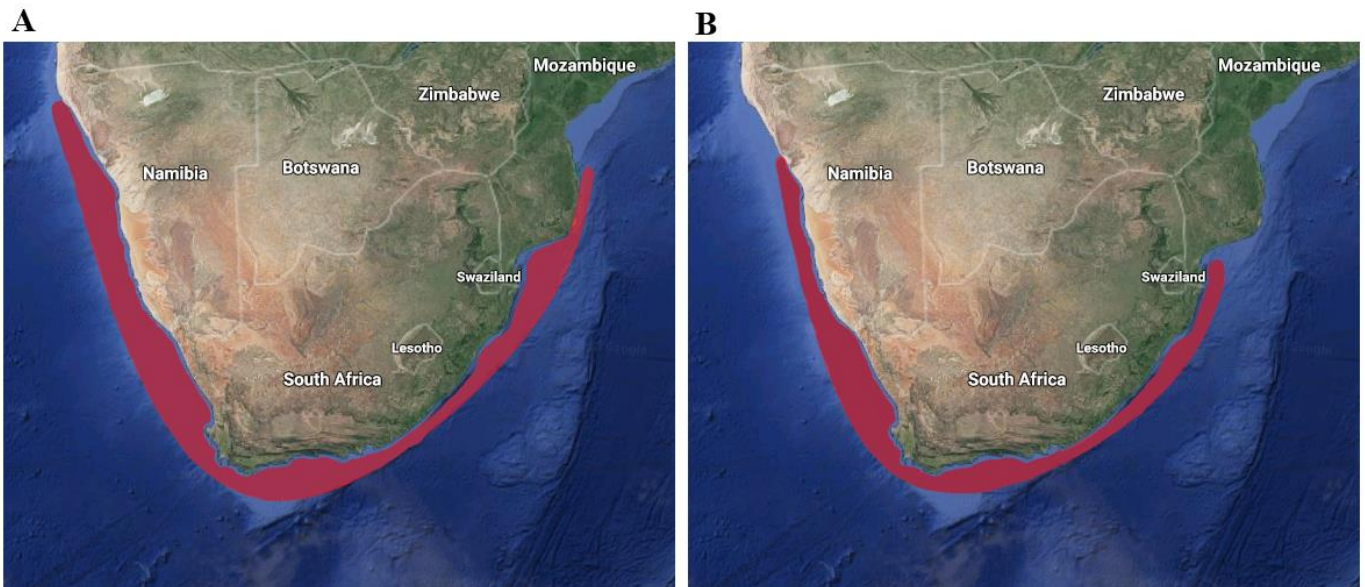


Figure 2: The geographic distributions of *Chelidonichthys capensis* (A) and *C. queketti* (B), both endemic to southern Africa.

1.5 *Chelidonichthys capensis* (Cuvier, 1829)

Chelidonichthys capensis, the Cape gurnard, is one of the larger species in the genus *Chelidonichthys* (McPhail et al., 2001) with a total length (TL) of up to 700 mm (Smith & Heemstra, 1986).

This species was originally thought to have a global distribution (Trunov & Malevany, 1974) but this was disputed by Smith & Heemstra (1986), who determined that it is only found between Namibia and Mozambique. Off South Africa, *C. capensis* has been recorded up to depths of 424 m, although is most common between 50 m and 200 m, over the middle and outer continental shelf (Smale & Badenhorst, 1991).

Chelidonichthys capensis is characterised by features typical to the triglid family, being fast growing, long-lived and r-selected, and small at first breeding (McPhail et al., 2001). It differs from other species in the genus in the number of soft dorsal and anal fin rays (which adds up to between 29 and 33) and having preorbitals with several short subequal spines in front and 13 – 18 gill rakers (Heemstra, 1982). Female *C. capensis* grow at faster rates than males and to larger sizes (Hecht, 1977). Hecht (1977) found that 50% of females reach sexual maturity at 305 mm TL (3 years) and 50% of males at 340 mm TL (4 years) while McPhail et al. (2001) reported 50% sexual maturity at 343 mm TL (3.7 years) for females and 299 mm TL (3.6 years) for males. The differences between McPhail et al. (2001) and Hecht's (1977) findings could be indicative of differences in selective targeting or fishing pressure during the two studies (McPhail et al., 2001).

Chelidonichthys capensis are asynchronous spawners, spawning twice throughout their extended reproductive season, with peaks of reproductive activity observed in late summer and spring (Hecht, 1977; McPhail et al., 2001).

Their diet is dominated by crustaceans, which they crush using their villiform teeth. Off the south coast of South Africa, small *C. capensis* primarily consume the brachyuran *Goneplax angulate* (Pennant, 1777) while larger *C. capensis* mostly prey on tonguefish *Cynoglossus zanzibarensis* Norman, 1939 as well as larger *G. angulate* (Meyer & Smale, 1991). Off the west coast, the diets of both small and large *C. capensis* are dominated by mantis shrimp *Pterygosquilla armata capensis* Manning, 1969, with teleost species such as the ladder dragonet *Paracallionymus costatus* (Boulenger, 1898) and anchovy *Engraulis encrasicolus* also common (Meyer & Smale, 1991).

1.6 *Chelidonichthys queketti* (Regan, 1904)

Chelidonichthys queketti, the lesser gurnard, is much smaller than *C. capensis* (Meyer & Smale, 1991), with the largest recorded sample caught being 354 mm TL (Booth, 1997). This species is distributed between Namibia and southern Mozambique (Smith & Heemstra, 1986), where it inhabits various sediment types between depths of 28 – 288 m, although the majority of the population is found occupying depths of between 50 and 150 m (Booth, 1997).

Like *C. capensis*, *C. queketti* is r-selected, fast growing and long-lived, although females grow at slower rates but to a larger size than males - a characteristic common to the Triglidae (Booth, 1997). This species can be distinguished from other *Chelidonichthys* species by the number of soft dorsal and anal fin rays (which adds up to between 34 and 36) and preorbitals that have one stout spine (Heemstra, 1982). Sexual maturation occurs at the end of the first year of life, at around 60% of maximum size, after which females are able to spawn continuously throughout their lives (Booth, 1977). This species has an extended spawning season, similar to that of *C. capensis*, peaking in late summer and spring (Booth, 1977).

The diet of *C. queketti* consists mainly of mysids, with *Lophogaster challengerii* Fage, 1942 being the most dominant prey species among all size classes of fish off both the south and west

coasts of South Africa (Meyer & Smale, 1991). Other prey species targeted includes brachyurans (*Mursia cristiata* H. Milne Edwards, 1837), gammarid amphipods and small teleosts (*Paracallionymus costatus*) (Booth, 1997). *Chelidonichthys queketti* seem to consume small prey species throughout their lives and size classes, which they crush using their villiform teeth (Meyer & Smale, 1991).

1.7 Economic Importance and Exploitation of *Chelidonichthys* spp. in South Africa

Neither *C. capensis* nor *C. queketti* are targeted by South African fisheries, but both species are caught as incidental by-catch by the offshore and inshore demersal trawl fisheries as well as by the inshore gillnet fishery (Booth & Hecht, 1998; Hutchings & Lamberth, 2002; Walmsley et al., 2007). In the trawl fisheries, gurnard species are of lesser commercial value than the targeted species (such as *Merluccius capensis*) (Smale & Badenhorst, 1991), but are still considered to be two of the more valuable and marketable by-catch species (Atkinson, 2009).

Population size estimates (Fig. 2) derived from research demersal trawl surveys conducted annually by the Department of Agriculture, Forestry and Fisheries over the past three decades show that *C. capensis* is far more abundant than *C. queketti* on the west coast, and whilst the abundance of *C. capensis* has varied over time that of *C. queketti* has remained relatively constant. Off the south coast the abundance of both species generally follows the same declining trend over the time-series, although *C. queketti* is slightly more abundant than *C. capensis* there. Smale & Badenhorst (1991) also observed that *C. queketti* were more abundant off the south coast but because this species is less marketable than *C. capensis*, due to its smaller size, it dominates the fish discarded at sea (Walmsley et al., 2007).

The behaviour and habitat preferences of *C. capensis* make this species particularly vulnerable to trawling gear (Smale & Badenhorst, 1991). It was one of the six species which together made

up 95% of the total annual catch from the inshore demersal trawl fishery off the south coast between 1967 and 1995 but was considered less valuable than the other five species (Cape horse mackerel *Trachurus capensis*, shallow-water Cape hake *M. capensis*, panga *Pterogymnus laniarius* (Valenciennes, 1830), Agulhas sole *A. pectoralis*, and kingklip *G. capensis*) and was not targeted (Booth & Hecht, 1998). Typically, *C. capensis* is caught in the 50 m – 200 m depth range, with the highest trawl landings reported from 101 m – 120 m (Smale & Badenhorst, 1991). Catches are highest in spring and autumn, which could be attributed to the extended spawning periods and high availability of this species when they aggregate during spawning (Booth and Hecht, 1998).



Figure 3: Abundance estimates for *Chelidonichthys capensis* (red) and *Chelidonichthys queketti* (blue) from the west coast (A) and the south coast (B) of South Africa as observed during demersal research surveys conducted by DAFF from 1985 to 2017 (courtesy of Tracey Fairweather, DAFF).

An experimental inshore trawl fishery for Cape gurnard in St. Helena Bay comprising three to five boats was initiated in the early 1990's, but landed catches were low and fishermen appeared to be targeting St. Josephs sharks (*Callorhincus capensis* Duméril, 1865) instead (Hutchings and Lamberth, 2002). No Cape gurnard catches were reported in 1995 and, consequently, permits for catching this species were not renewed for 1997 (McPhail, 1998). As *C. capensis* is a valuable bycatch species, there is a possibility that it may become a target species in the future (Smale & Badenhorst, 1991; McPhail, 1998).

1.8 Parasites of *Chelidonichthys* species

While parasites infecting the common northern hemisphere *Chelidonichthys* species are fairly well-documented (see Discussion), little information is available on the parasite communities infecting *C. capensis* and *C. queketti*. Determining the parasites that infect these two species can provide valuable insight into host-parasite relationships, biodiversity and marine ecology of the South African environment.

1.8.1 Parasites Infecting *Chelidonichthys capensis*

While the parasite assemblage of the Cape gurnard has not been fully documented, seven copepod species, all ectoparasitic, have been recorded to infest *C. capensis* by group specific taxonomists (Table 1).

Table 1: Parasite species known to infect *Chelidonichthys capensis* and their site of infection (B = branchial cavity, BC = buccal cavity, BS = body surface and G = gills).

Parasite Species	Site of Infection	References
Copepoda		
<i>Caligus brevicaudatus</i>	BS	Barnard (1955b), Demirkale et al (2015)
<i>Caligus curtus</i>	BS	Oldewage & Avenant-Oldewage (1993)
<i>Caligus diaphanus</i>	B	Oldewage (1993)
<i>Caligus pelamydis</i>	BC, G, BS	Barnard (1955b), Jones (1988)
<i>Caligus tetrodontis</i>	BS	Oldewage (1992)
<i>Charopinus dubius</i>	G	Oldewage (1993)
<i>Lernentoma asellina</i>	B, G	Kensley & Grindley (1973), Oldewage (1992)
<i>Medesicaste penetrans</i>	BC	Barnard (1955), Oldewage (1992)

Of these species, one of the most notable is *Lernentoma asellina* (Linnaeus, 1758), a parasite specific to triglids (Ho, 1994) and which has been recorded infecting *C. capensis*, *C. cuculus* and *C. lucerna* along the Eastern Atlantic, from European waters (including the Mediterranean Sea) to South Africa (Ho, 1970; Demirkale et al., 2015). Found in the branchial cavity and on the gills, this species has an elongated body, spherical lateral expansions on its head, a swollen

neck and trunk, and a long, cylindrical egg sac filled with multiple rows of eggs (Ho, 1970). Another copepod, *Caligus tetrodontis* Barnard, 1948 has been recorded to infest the buccal cavity of fish off South Africa (Oldewage, 1990), but has also been recorded on the body surface of *C. capensis* (Oldewage, 1992) and also as free-swimming plankton off the coast of south-western Brazil (Luque & Tavares, 2007; Morales-Serna et al., 2016). Although *Caligus curtus* Müller O.F., 1785 has previously been recorded to only parasitise members of the Family Gadidae (Hamre et al., 2011), it was recorded by Oldewage & Avenant-Oldewage (1993) on the body surface of *C. capensis* off the south coast of South Africa.

1.8.2 Parasites Infecting *Chelidonichthys queketti*

Like that of *C. capensis*, the parasite assemblage of *C. queketti* has not been formally documented but some ectoparasitic copepod species have been recorded by taxonomists, although fewer than found on *C. capensis* (Table 2).

Table 2: Parasite species known to infect *Chelidonichthys queketti* and their site of infection (BC = buccal cavity, BS = body surface and G = gills).

Parasite Species	Site of Infection	References
Copepoda		
<i>Caligus curtus</i>	BS	Oldewage & Avenant-Oldewage (1993)
<i>Medesicaste penetrans</i>	BC	Barnard (1995b), Oldewage (1992)
<i>Parabrachiella supplicans</i>	G	Barnard (1955b), Oldewage (1992)

Of these parasite species, both *Caligus curtus* and *Medesicaste penetrans* Heller, 1865 were recorded to also infest the Cape gurnard, but *Parabrachiella supplicans* (Barnard, 1955; formerly *Brachiella supplicans*) has only been recorded infesting the lesser gurnard and was originally described by Barnard (1955b) on kingklip (*Genypterus capensis*) from Table Bay, South Africa. *Caligus curtus* was found on the body surface of *C. queketti*, as it was for *C. capensis* (Oldewage & Avenant-Oldewage, 1993).

1.9 Aims and Objectives

This dissertation aims to contribute to the biological and ecological knowledge of *Chelidonichthys capensis* and *C. queketti* as well as to the knowledge of biodiversity found in the South African marine environment, by documenting the macroparasite assemblages of these two gurnard species. More specifically, this dissertation aims to answer the following questions:

- What parasite taxa are found to infect *C. capensis* and *C. queketti*?
- Do the parasite communities differ between *C. capensis* and *C. queketti*, and relative to parasites known to infect other *Chelidonichthys* species?
- Do indices of parasite infection differ between host size, sex, and location of capture?
- Are there infracommunity interactions between the parasite species infecting *C. capensis* and *C. queketti*?

Methods

2.1 Sample Collection

Gurnards were collected during four separate expeditions (Figure 2), including a demersal research survey and three commercial fishing voyages. The West Coast Demersal Survey (WCDS) was conducted by the Department of Agriculture, Forestry and Fisheries (DAFF) from the 5th of January to the 13th of February 2017 aboard the *RV Africana*. The survey covered the area between 21°E and the international border with Namibia and, from the coast to the 1000 m depth contour, with the main objective being to perform stratified bottom trawls to evaluate the biomass, abundance and distribution of commercially important demersal species including Cape hakes (*Merluccius capensis* and *M. paradoxus*), kingklip (*Genypterus capensis*), monk (*Lophius vomerinus*), horse mackerel (*Trachurus capensis*) and squid (*Loligo reynaudii* d'Orbigny [in Ferussac & d'Orbigny], 1839-1841) on the shelf and upper slope of the west coast (Anon., 2017). Sampling was conducted using a four-panel 180 ft German otter trawl with 9 m sweeps and 1.5 t Morgere multipurpose otter boards, a door spread of 60-75 m and a mouth opening of 3-4 m vertical and 20-29 m horizontal (see Atkinson et al. 2011 for further demersal survey details). Samples of *Chelidonichthys capensis* and *C. queketti* were collected from several of these trawls, with the aim of collecting at least ten individuals of each species per 1° latitude or longitude and covering the shelf along the west coast of South Africa (Anon., 2017).

Samples from commercial fishing vessels were collected by CapFish fisheries observers on-board commercial demersal and midwater trawl fishing vessels fishing off the south coast; details of these and samples collected during the WCDS are given in Table 3.

Table 3: Collection details of *Chelidonichthys capensis* and *C. queketti* samples processed for macroparasites in 2017 and 2018, where SB = southern Benguela, AB = Agulhas Bank.

Source	Region	Sample Identifier	Collection dates	Number (and size range; mm FL) of <i>C. capensis</i>	Number (and size range; mm FL) of <i>C. queketti</i>
West Coast Demersal Survey (<i>RV Africana</i>)	SB & AB	WCDS 2017 Trawl	05/01/17 – 13/02/17	36 (283 – 490)	47 (206 – 344)
Commercial midwater trawler (<i>FV Desert Diamond</i>)	AB	Trawl 24	04 – 05/01/18	7 (450 – 508)	None
Commercial demersal trawler (<i>FV Vuna Elita</i>)	AB	Demersal catch block 555	08/04/18	11 (365 – 545)	30 (237 – 296)
Commercial midwater trawler (<i>FV Desert Diamond</i>)	AB	Trawl 18	18/08/18	16 (29 – 479)	10 (220 – 291)

All samples collected were labelled with the date and catch location, bagged, frozen and retained on-board until the vessels docked after which they were transported to the University of Cape Town for processing.

2.2 Sample Processing

2.2.1 Host Dissection

Prior to dissection, gurnards were thawed to room temperature and were then measured to the nearest millimetre (fork length [FL]) and weighed to the nearest gram (wet body mass [WBM]). A full parasitological survey was then performed. The external surface (including the skin, fins and mouth) was first examined for parasites. Next, the body cavity was cut open and the visceral organs removed for later examination. At that point the eyes, operculae and the gills were removed and examined for parasites using a Nikon SMZ800 dissecting stereomicroscope. Once this was completed, the gonads were separated from the visceral organs and weighed to the nearest gram, and the fish was then sexed. The liver was also separated from the visceral

organs and weighed to the nearest gram. The surfaces of the visceral organs, including the gonads and liver, were then examined for parasites using the dissecting microscope and squash samples of the various organs were further examined for parasites using a Leica ICC50 compound microscope. The gastro-intestinal tract and the stomach were then cut open and examined for parasites using the dissecting microscope. Lastly, the fish were filleted, and squash samples of muscle tissue examined for parasites under the compound microscope.

The taxon, abundance and site of infection were recorded for all parasites found.

2.2.2 Parasite Preservation and Species Identification

Specimens of each macroparasite species found were preserved in 70% ethanol for later identification. Cestodes, copepods, nematodes, digeneans and monogeneans were cleaned using a thin paintbrush and water before preservation, while acanthocephalans were first stored overnight in cold water to induce proboscis extrusion.

Parasites were cleared using glycerine and clove oil, stained using Mexican Red dye and identified to the lowest possible taxonomic level based on their morphological features and relevant literature (Barnard, 1955a; Barnard 1955b; Ho, 1970; Appy & Dadswell, 1981; Amin, 1987; Grobler, 2000; Knoff et al., 2004; Sardella et al., 2005; Palm et al., 2007; Quiazon et al., 2008; Silva et al., 2017; Hernandez-Orts et al., 2017). Parasites were identified with expert help from Irfan Nunkoo (University of Cape Town).

2.3 Statistical Analyses

2.3.1 Exploratory Data Analysis

The first step when analysing data is to conduct exploratory data analyses (EDA), a process which provides an overview of the data and allows one to determine the statistical tests most appropriate for the data set (Zuur et al., 2010; Borcard et al., 2011). Data that do not conform to the assumptions of most statistical tests (e.g. normality, homoscedasticity, collinearity) can

either be transformed in an attempt to fit these assumptions, allowing normal parametric methods to be used, or an alternative method can be used on the untransformed data (e.g. non-parametric tests). The process for EDA, outlined by Zuur et al. (2010) and briefly described below, was followed for this data set.

The first step in data exploration was to determine outliers within the data set, as statistical techniques and methods can vary in their response to outliers. Extreme outliers, if encountered, are to be removed from the data set. Next, the homogeneity of variances and the distribution of the data (i.e. normality) was determined – as this indicates whether a parametric or non-parametric test should be used during statistical analyses. The number of zeros in the data set was then assessed, as an abundance may lead to biases when modelling the data using generalised linear models. Collinearity between variables was tested and the relationships between response and covariate variables was then determined. Lastly, the interactions between any variables were considered and the assumption that all observations of the response variables are independent were met.

The normality and heteroscedasticity of the continuous variables (FL, mass and condition factor – see below) collected from examined hosts were visually assessed from frequency distribution histograms and the Shapiro-Wilks test was then performed to confirm each assessment. In order to detect any collinearity between continuous variables, pair-wise scatterplots for each of these was derived and the correlation coefficients (and their significance) were determined.

2.3.2 Host Biological Data

Understanding the biological characteristics of the sampled host population is imperative in understanding the role parasites play and the effects they may have on the host (Poulin & Morand, 2000).

The condition factor (CF) provides an indication of the ‘well-being’ of an individual fish and is derived using length and weight data (Neff & Cargnelli, 2004) and, assumes that heavier fish of a given length are in a better condition than lighter fish of that length (Froese, 2006). Firstly, the host’s length-weight power relationship was determined and was used to derive an expected wet body mass (WBM) at a given length using Equation 1, below, where FL is the fork length and a and b are coefficients. The condition factor (CF) was then determined for each fish by dividing the observed wet body mass by the expected wet body mass (Equation 2; Kreiner et al., 2001; van der Lingen et al., 2006).

$$WBM = aFL^b \quad \text{Equation 1}$$

$$CF = \frac{\text{Observed wet body mass}}{\text{Expected wet body mass}} \quad \text{Equation 2}$$

The hepato-somatic index (HSI) is the weight of the liver relative to the weight of the fish and indicates the energy reserves stored in the liver and the metabolic activity of the fish (Grant & Brown, 1999; Lenhardt et al., 2009). HSI was calculated using Equation 3, below, where W_L is the weight of the liver of the fish.

$$HSI = \frac{W_L}{W_{BW}} \times 100 \quad \text{Equation 3}$$

The gonado-somatic index (GSI) is the weight of the gonads relative to the weight of the fish and is used to determine the reproductive state of an individual fish and also the spawning seasonality of the species. GSI was calculated using Equation 4, below (Parameswaran et al., 1974) where W_G is the weight of the gonads in grams.

$$GSI = \frac{W_G}{W_{BW}} \times 100 \quad \text{Equation 4}$$

It should be noted that CF, HSI and GSI typically show a seasonal cycle and their values therefore fluctuate over the year (Lenhardt et al., 2009).

Host size distributions were non-normal for both species (see below), so interspecific and intraspecific (e.g. in host size between sexes) differences were assessed using the non-parametric Mann-Whitney U test. A chi-square goodness of fit was used to test whether the sex ratios for each species were significantly different from 1:1. The FL, CF, HSI and GSI of host samples were also compared between regions (i.e. comparing samples from the southern Benguela to those from the Agulhas Bank), using the Mann-Whitney U test for both *Chelidonichthys capensis* and *C. queketti*. Fish characteristics were compared between two regions (the southern Benguela and the Agulhas Bank) as both gurnard species occur in these two biogeographic regions (Teske et al., 2011) and previous studies have shown that some species that occur off the west and south coasts display population structures with different stocks in each region, inferred either from significant phenotypic differences e.g. sardine (van der Lingen et al., 2015; Weston et al., 2015) or significant genotypic differences e.g. kingklip (Henriques et al., 2017).

2.3.3 Parasite Infection Indices

This study aimed at documenting the parasite assemblages of *Chelidonichthys capensis* and *C. queketti* and comparing these assemblages both between the two species and between biogeographic regions within each species. Three indices were used to quantify parasitic infection, namely prevalence, mean infection intensity and mean abundance (Bush et al., 1997). Prevalence is the percentage of the sampled host population infected with one or more individuals of a particular parasite species (Equation 5); mean infection intensity is the average number of parasites of a particular species per infected fish of the sampled hosts (Equation 6); and mean abundance is the average number of parasites of a particular species for the entire sampled host population – whether infected or uninfected (Equation 7).

$$Prevalence = \frac{\text{Number of infected hosts}}{\text{Total number of hosts sampled}} \times 100 \quad \text{Equation 5}$$

$$\text{Mean intensity} = \frac{\text{Total number of a parasite species found}}{\text{Number of hosts infected}} \quad \text{Equation 6}$$

$$\text{Mean abundance} = \frac{\text{Total number of a parasite species found}}{\text{Total number of hosts sampled}} \quad \text{Equation 7}$$

These three indices were calculated for each parasite taxon found on either *C. capensis* or *C. queketti* for all hosts examined, as well as for samples by region (southern Benguela vs western Agulhas Bank).

2.3.4 Parasite-Host Interactions

Since parasite loads can vary between individual hosts, with some hosts having very few (or no) parasites and others having many, parasite data does not often conform to the normal distribution assumed by parametric tests (Wilson & Grenfell, 1997). A popular alternative to parametric tests are non-parametric tests (e.g. Mann-Whitney U test, Shapiro-Wilks test), but they lack the power of parametric tests. Transforming the data (using a log- transformation) can allow for parametric tests to be used, but this has been found to increase the likelihood of type I errors (i.e. incorrectly rejecting the null hypothesis; Wilson & Grenfell, 1997). Generalized Linear Models (GLMs), however, combine otherwise incompatible statistical methods in order to process non-normal, binomial or over-dispersed data. There are three components that make up GLMs; the response (dependant) variable, the explanatory (independent) variables and a link function, which specifies the relationship between the mean of the response variable and each linear explanatory variable used in the model (Nelder & Wedderburn, 1972; Lindsay, 2000). The link function is, therefore, redundant when dealing with non-linear components of the model (Lindsey, 2000).

GLMs for each parasite taxon-host species pairing that met the requirements of the model were employed to determine the relationship between the host response (dependent) variables parasite prevalence and infection intensity, and explanatory (independent) variables and

interactions between explanatory variables that may affect parasite load. The models only incorporated interactions that were found to have a significant effect on the host species and prevalence was only modelled for parasite taxa infecting between 20% and 90% of the sample, while infection intensity was only modelled for parasite taxa that had prevalence levels greater than 45%. This ensured that each model had sufficient data.

The model employed for *C. capensis* GLMs was as follows:

$$G_{(\chi_i)} = \text{FL} + \text{Sex} + \text{Region} + \text{FL} \times \text{Region} + \varepsilon_i \quad \text{Equation 8}$$

While the model employed for *C. queketti* GLMs was:

$$G_{(\chi_i)} = \text{FL} + \text{Sex} + \text{Region} + \varepsilon_i \quad \text{Equation 9}$$

In the above models (equations 8 and 9), G is the appropriate link function and χ represents the response variable (either prevalence or infection intensity). The logit link function was used to assess prevalence as the distribution was binomial (either present or absent), and the logarithmic link function was used to assess infection intensity as the over-dispersion of this response variable assumes a zero-truncated negative binomial error structure (Lindsey, 2000).

Akaike's information criterion (AIC) is used to determine model selection when data are over-dispersed (Anderson et al., 1994) and allows for the comparison of competing models – the model with the lowest AIC value being the most suitable (Lindsey, 2000; Bolker et al., 2008).

A backwards, stepwise AIC was used to determine the most appropriate model for prevalence and infection intensity. This method employed a GLM containing all explanatory variables and significant interactions (Equations 8 and 9) and then, one at a time, non-significant variables and interactions were removed from the model, which was then re-run until the lowest AIC value was reached and only significant variables remained. An analysis of deviance (ANOVA) was then used to test the significance of the selected model and a pseudo-R² value was

calculated (Equation 10) to determine the goodness-of-fit of the selected model. The residuals were then plotted and used to validate the selected model.

$$Pseudo - R^2 = 1 - \frac{Residual\ deviance}{Null\ deviance} \quad \text{Equation 10}$$

Non-metric multidimensional scaling (NMDS) was used to compare the parasite community assemblage between *C. capensis* and *C. queketti*. NMDS is a method of ordination which assigns Euclidean coordinates to objects based off their dissimilarity, allowing them to be scaled to a two, or three, dimensional scale for comparison (Agarwal et al., 2007). The non-parametric analysis of similarities (ANOSIM) was used to test whether parasite assemblages compared using the NMDS were significantly different.

All statistics were completed using R (R Development Core Team, 2015). The R packages used include “exactRankTests” (Hothorn & Hornik, 2007), “ggplots2” (Wickham & Chang, 2013), “gridExtra” (Auguie & Antonov, 2017), “multcomp” (Hothorn et al., 2017), “lmtest” (Hothorn et al., 2018), “vegan” (Oksanen et al., 2013) and “coin” (Hothorn et al., 2008). All distributions were mapped using Surfer® 10 (Golden Software, LLC).

Results

3.1 *Chelidonichthys capensis*

3.1.1 Exploratory Data Analysis

In total 70 *C. capensis* were sampled (Fig. 4A): 36 from the West Coast Demersal Survey, seven from the Pelagic Recruit Survey collection, 16 from the Vuna Elita collection, and 11 from the second Desert Diamond sample collection. The samples consisted of 49 females and 21 males and were caught from two regions, 33 from the southern Benguela ecosystem and 37 from the Agulhas Bank, as well as during two separate seasons, 43 in summer (October – March) and 27 in winter (April – September). The fork length (FL) of *C. capensis* samples ranged from 274 to 522 mm while the wet body mass (WBM) ranged between 204 and 1498 grams.

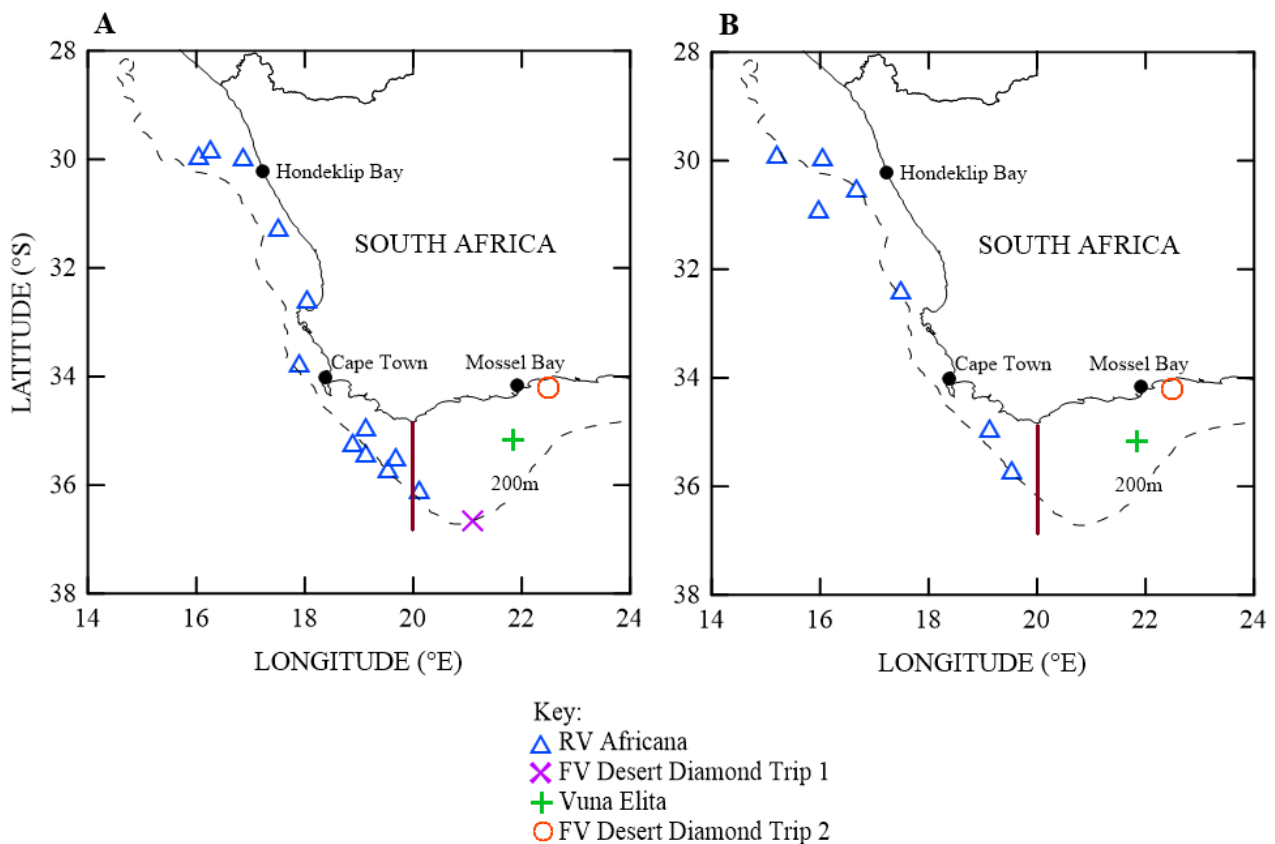


Figure 4: The locations of the samples of *Chelidonichthys capensis* (A) and *C. queketti* (B) processed for parasites. Samples were obtained from four separate sample collections: the RV Africana (WCDS) from January to February 2017, the FV Desert Diamond trip 1 in January 2018, the FV Vuna Elita trip in April 2018, and the FV Desert Diamond trip 2 in August 2018. The red line at Cape Agulhas (20°E) separates the southern Benguela ecosystem from the Agulhas Bank.

A visual assessment of the FL and WBM frequency distributions for *C. capensis* (Figure 5) revealed a non-normal distribution for both. The FL frequency distribution and the mass frequency distribution are both positively skewed, towards larger individuals. The Shapiro-Wilk test confirmed the non-normal distributions for FL ($p = 0.005172$) and WBM ($p < 0.01$) frequencies. The condition appeared to have a normal distribution, which was confirmed by the Shapiro-Wilks test ($p = 0.06498$). The histograms of GSI and HSI displayed distributions that did not appear to conform to normality, with the Shapiro-Wilks test confirming this ($p < 0.01$ and $p = 0.001124$ respectively). An assessment of the collinearity between the variables (FL, WBM, condition, GSI and HSI) revealed that FL and WBM exhibit a significant positive correlation ($R^2 = 984$, $df = 68$, $p < 0.01$). Condition and HSI also exhibit a significant positive, but not as strong correlation ($R^2 = 0.38$, $p < 0.01$).

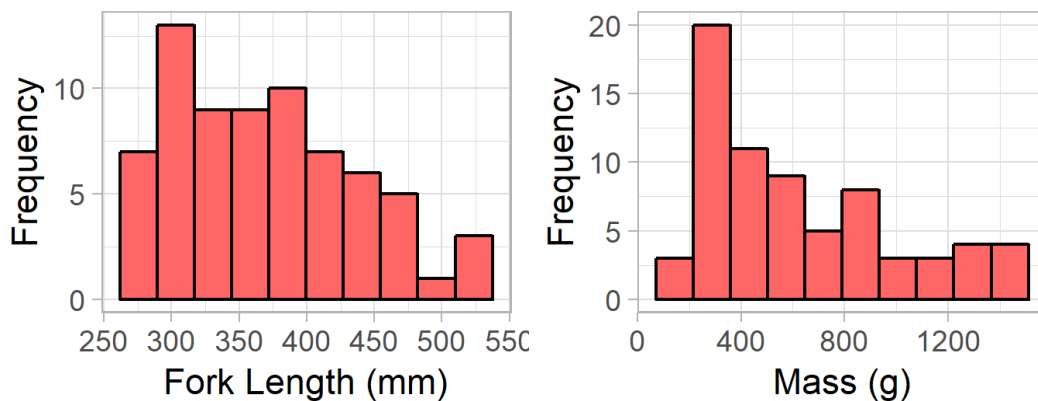


Figure 5: Frequency distributions of the fork length (FL; mm) and wet bodymass (WBM; g) of *Chelidonichthys capensis* caught off South Africa in 2017 and 2018. Both display distributions which are skewed to the right, not conforming to normality.

3.1.2 Host Biological Data

Chelidonichthys capensis samples were found to be biased towards females ($\chi^2 = 11.2$, $df = 1$, $p = 0.000818$). There was no significant difference between female and male mean FL ($U = 612.5$, $p = 0.2121$; 375.73 ± 64.93 mm for females and 355.86 ± 70.62 mm for males) or WBM ($U = 631.5$, $p = 0.1354$; 662 ± 374 g for females and 560 ± 361 g for males). There was also no significant difference between the mean condition factor of female and male samples ($t = 1.1317$, $df = 68$, $p = 0.2618$; 1.38 ± 0.15 for females and 1.34 ± 0.11 for males). The difference

was assessed using an independent t-test, as the Shapiro-Wilk test found that the condition factors of males and females were normally distributed ($p = 0.2403$ and $p = 0.06845$, respectively). The mean GSI of samples was found to differ significantly between female and male samples ($U = 930$, $p < 0.01$), females having a mean GSI of 2.94 ± 2.74 and males of 0.52 ± 0.19 (Figure 6). There was no significant difference between male and female mean HSI values ($U = 297$, $p = 0.372$; 1.76 ± 0.85 for females and 1.51 ± 0.57 for males).

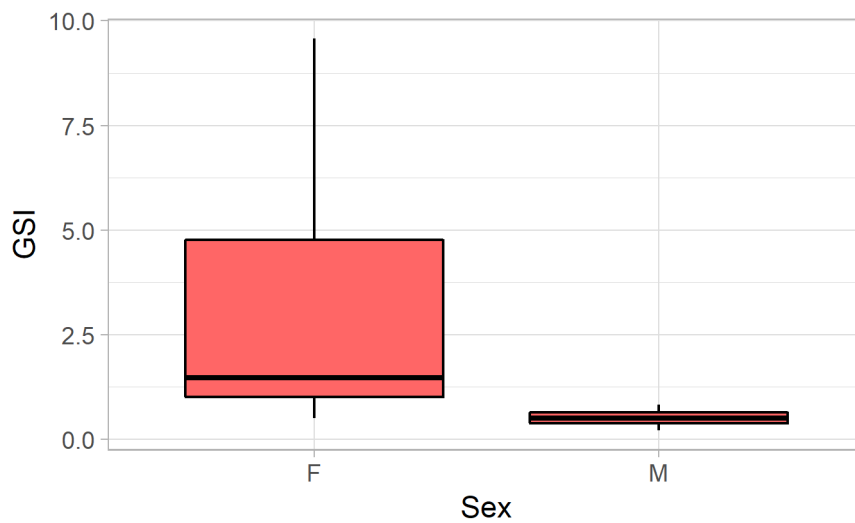


Figure 6: The differences between female and male GSI values for *Chelidonichthys capensis* caught off South Africa in 2017 and 2018.

There was no bias between the ratio of *C. capensis* samples from the Agulhas Bank and from the Benguela ecosystem ($\chi^2 = 0.22857$, $p = 0.6326$). Cape gurnard from the southern Benguela ecosystem were significantly smaller ($U = 954.5$, $p < 0.01$; 334.91 ± 44.75 mm) and weighed significantly less ($U = 936.5$, $p < 0.01$; 446.45 ± 237.00 g) than those from the western Agulhas Bank (400.86 ± 68.30 mm FL and 795.81 ± 393.04 g WBM; Figure 7).

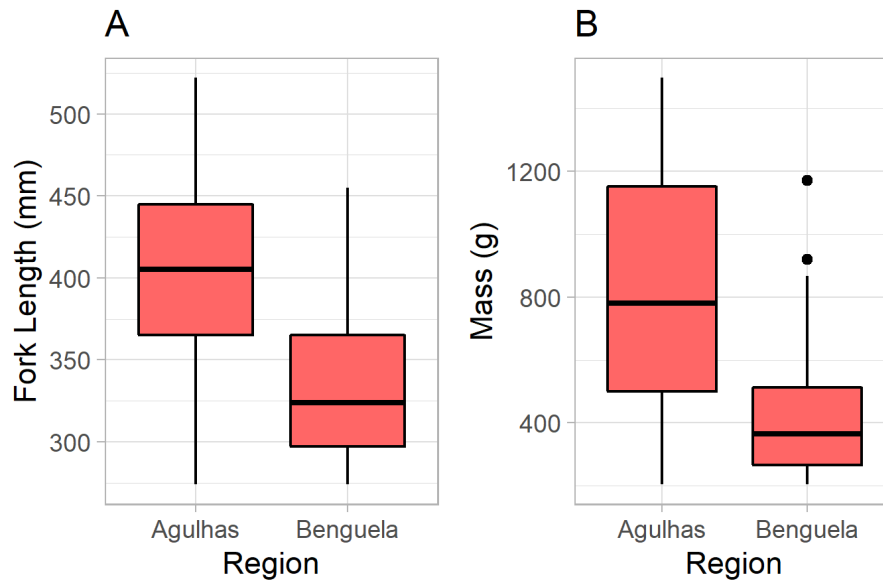


Figure 7: The differences in fork length (A) of *Chelidonichthys capensis* samples from the Agulhas Bank and Benguela ecosystem caught off South Africa in 2017 and 2018, as well as the differences in mass (B) of samples from these two regions.

There was no significant difference between the condition factor of samples from the southern Benguela and samples from the western Agulhas Bank ($U = 486$, $p = 0.1146$; 1.34 ± 0.12 for Agulhas Bank samples and 1.39 ± 0.15 for southern Benguela samples). There was also no difference in the mean GSI of samples from the two regions ($U = 501$, $p = 0.2755$; 1.98 ± 2.43 for Agulhas Bank samples and 2.53 ± 2.69 for southern Benguela samples). A significant difference in mean HSI between regions was observed ($U = 66$, $p < 0.01$; 1.53 ± 0.75 for Agulhas Bank samples and 2.29 ± 0.61 for southern Benguela samples; Figure 8). No relationship was detected between the sex of samples from each region ($\chi^2 = 0.67$, $p = 0.4142$).

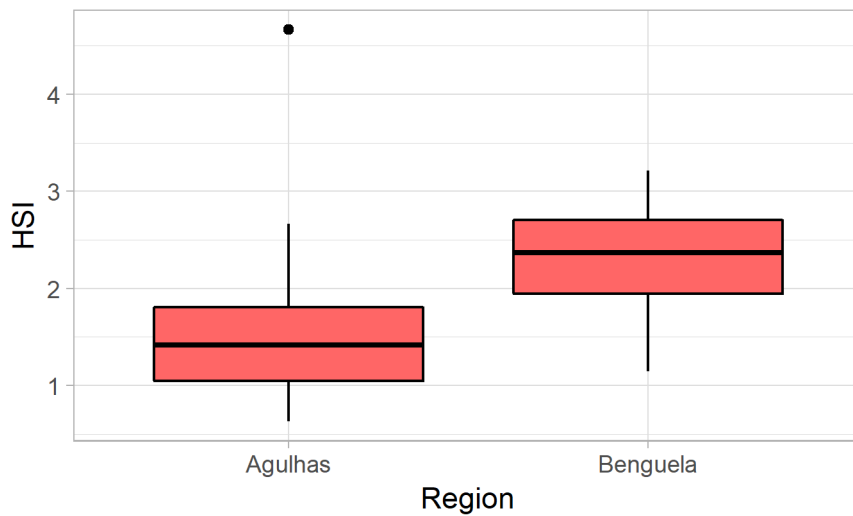


Figure 8: The differences between the HSI values of *Chelidonichthys capensis* samples from the western Agulhas Bank and samples from the southern Benguela ecosystem caught off South Africa in 2017 and 2018.

In terms of seasonality, a difference was observed between the number of samples collected in summer and those collected in winter, but this difference was not significant ($\chi^2 = 3.6571$, $p = 0.05583$). There was also no significant difference found in FL of samples collected in summer and in winter ($U = 451.5$, $p = 0.1208$), as well as the mass of these samples ($U = 464.5$, $p = 0.1636$). Season was found to be independent of sex ($\chi^2 = 2.7591$, $p = 0.0967$), but not independent of region ($\chi^2 = 39.202$, $p < 0.01$).

3.1.3 Parasite Assemblage and Infection Indices

In total, 13 parasite taxa were found to infect *Chelidonichthys capensis* off South Africa, five of which could be identified to species level, one to genus, two to family and five to order, sub-class, class or phylum level. Parasites included (Table 4) an unidentified Monogenean sp. 1, a digenean from the Family Zoogonidae Odhner, 1902, an unidentified digenean sp. 1, a digenean from the Family Opecoelidae Ozaki, 1925, the cestodes *Tentacularia coryphaenae* Bosc, 1802 and unidentified Cestode sp. 1, nematodes *Anisakis pegreffii* (Campana-Rouget & Biocca, 1955; Figure 9A) and unidentified Nematode sp. 1, the acanthocephalan *Corynosoma australe* (Johnston, 1937; Figure 9B), unidentified Isopod sp. 1 and the copepods *Medesicaste*

penetrans (Heller, 1865), *Lernentoma asellina* (Linnaeus, 1758) and *Caligus* sp. (Muller, 1785; Figure 9C). Of the species recorded, ten were new host records for *C. capensis*.

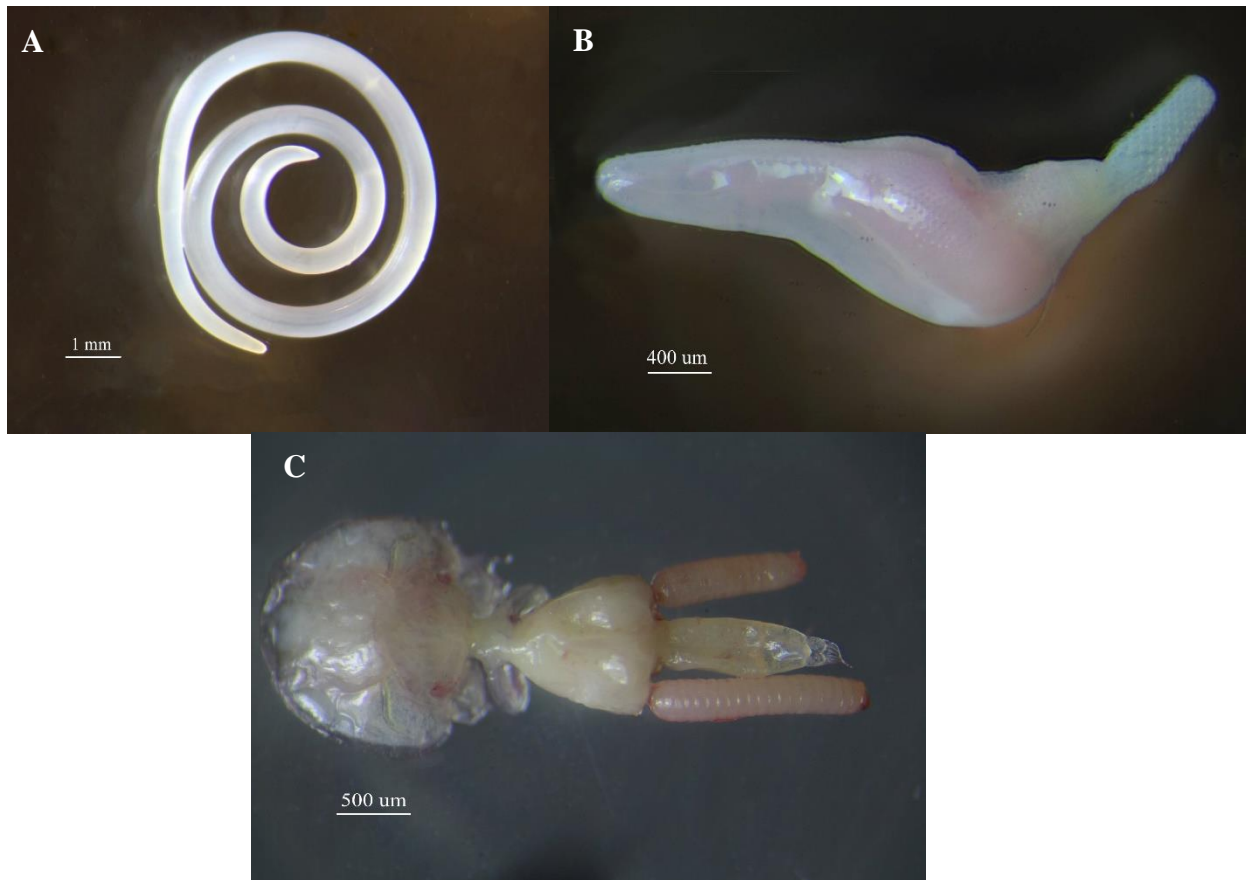


Figure 9: Photographs of *Anisakis pegreffii* (A), *Corynosoma australe* (B) and *Caligus* sp. (C) from *Chelidonichthys capensis*.

The randomised accumulation curve (Figure 10) revealed that species richness increases to its maximum at 70 samples and, whilst the slope of the curve flattens with increasing sample size, it does not reach an asymptote indicating that the parasite community assemblage was not completely documented. *Anisakis pegreffii* was the most prevalent (75.7 %) parasite infecting *C. capensis*, while *Corynosoma australe* had the highest mean infection intensity (30.6 ± 102.67 per infected fish) and the highest mean abundance (13.11 ± 68.29 per fish).

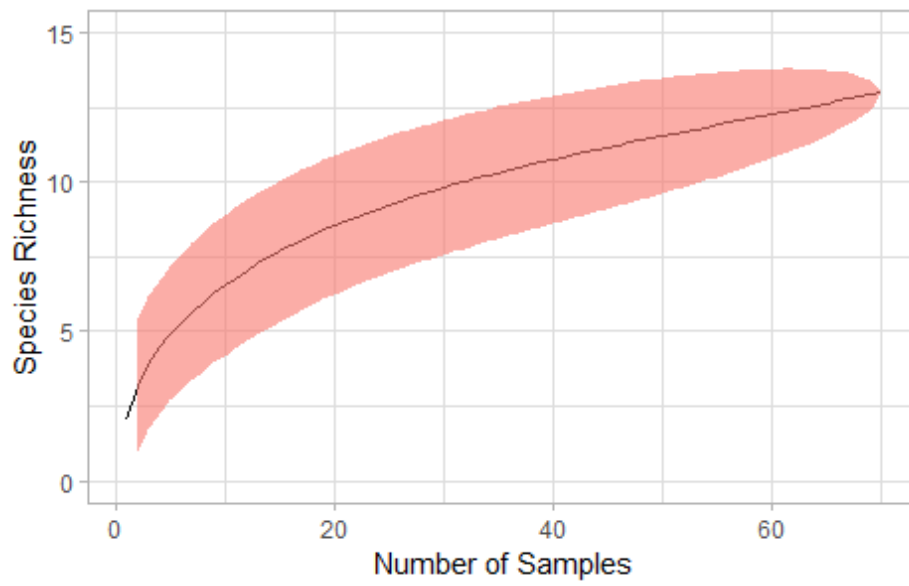


Figure 10: The randomised richness of parasite taxa per number of *Chelidonichthys capensis* hosts sampled off South Africa in 2017 and 2018.

Table 4: The taxonomic composition, site of infection, overall prevalence (%), mean infection intensity \pm sd (per infected fish), mean abundance \pm sd (per fish) and range of the parasite assemblage of *Chelidonichthys capensis* collected off South Africa in 2017 and 2018 (* = new host record, G = gills, BC = buccal cavity, VC = visceral cavity, S = stomach, L = liver, BS = body surface).

Parasite Taxa	Site of Infection	Overall prevalence (%)	Mean Infection Intensity (\pm sd)	Mean Abundance (\pm sd)	Range of Abundance
Monogenea					
Monogenea sp. 1*	G	7.1	2 \pm 1.41	0.14 \pm 0.62	0 – 4
Digenea					
Zoogonidae sp.*	BC, VC	4.3	1	0.04 \pm 0.20	0 – 1
Opecoelidae sp.*	VC	1.4	3	0.014 \pm 0.12	0 – 3
Digenea sp. 1*	VC	1.4	1	0.04 \pm 0.36	0 – 1
Cestoda					
<i>Tentacularia coryphaenae</i> *	VC, S	42.9	6.67 \pm 7.47	2.86 \pm 5.87	0 - 30
Cestode sp. 1*	VC	1.4	1	0.014 \pm 0.12	0 – 1
Nematoda					
<i>Anisakis pegreffii</i> *	VC, S, L	75.7	13.26 \pm 18.0	10.04 \pm 16.66	0 – 90
Nematode sp. 1*	VC	1.4	1	0.014 \pm 0.12	0 – 1
Acanthocephala					
<i>Corynosoma australe</i> *	VC, K	42.9	30.6 \pm 102.67	13.11 \pm 68.29	0 – 501
Isopoda					
Isopod sp. 1*	BS	1.4	1	0.14 \pm 0.12	0 – 1
Copepoda					
<i>Lernentoma asellina</i>	G	7.1	3.29 \pm 4.79	0.33 \pm 1.73	0 – 1
<i>Medesicaste penetrans</i>	BC	10	1	0.07 \pm 0.26	0 – 1
<i>Caligus</i> sp.	G	10	1	0.1 \pm 0.30	0 – 14

3.1.4 Drivers of Parasite Infestation

The model employed for *C. capensis* prevalence and infection intensity consisted of three explanatory variables and one interaction term (Table 5). Three species were modelled in terms of prevalence; *Tentacularia coryphaenae* (42.9%), *Anisakis pegreffii* (75.7%) and *Corynosoma australe* (42.9%), while only *Anisakis pegreffii* was modelled in terms of infection intensity.

Table 5: Description of the variables used in the generalised linear models analysing parasite prevalence and infection intensity for *Chelidonichthys capensis* caught off South Africa in 2017 and 2018.

Variable	Description
FL	Host length (mm FL)
Sex	Sex of host
Region	Capture locality of host samples by region
FL × Region	Interaction between fork length and region

Tentacularia coryphaenae

The AIC analysis and analysis of deviance yielded a model consisting of fork length and region as the explanatory variables influencing the prevalence of *Tentacularia coryphaenae* infecting *C. capensis* (Table 6). This model explained 13.85% of the variance and, although the residual plots reveal some deviations from the model assumptions, they are not extreme.

Table 6: Analysis of deviance for the binomial GLM for the prevalence of *Tentacularia coryphaenae* in *C. capensis* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized for each of the explanatory variables.

Variable	df	Dev.	Res. df	Res. Dev	p
Null			69	95.607	
FL	1	7.9916	68	87.616	**
Region	1	5.2460	67	82.370	*

p < 0.05 *, p < 0.01 **, p < 0.001 ***

The model chosen predicts that whilst prevalence of infection increases as host size increases for *C. capensis* from both the western Agulhas Bank and southern Benguela samples, prevalence-at-length is lower for fish of all sizes from the western Agulhas Bank compared to those from the southern Benguela (Figure 11). This results in the significant difference in mean prevalence of infection between regions (Figure 12), with Cape gurnards from the western Agulhas Bank having an overall lower mean prevalence (40% for a fish of 405 mm FL) than those from the southern Benguela (67% for a fish of 390 mm FL).

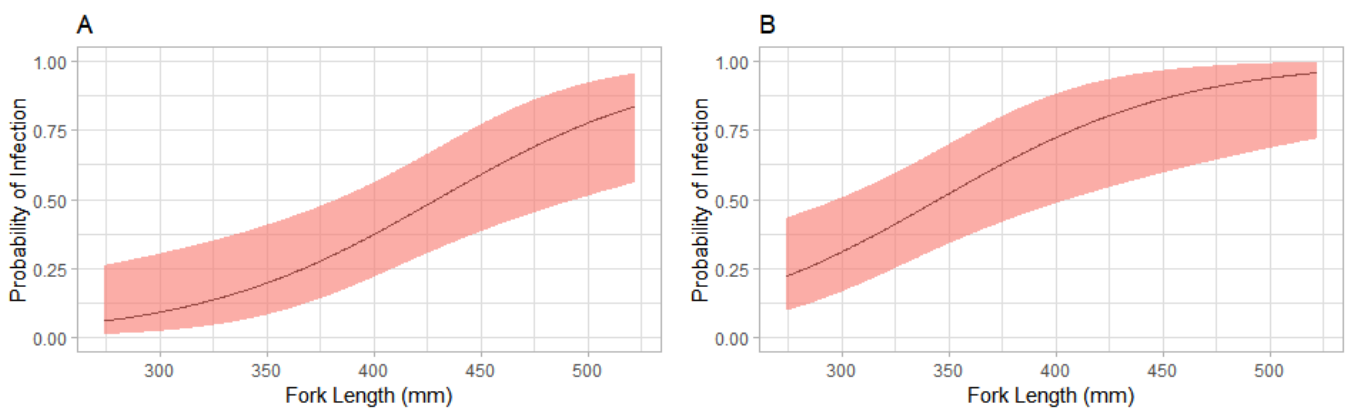


Figure 11: The relationship between host size (mm) and the mean (\pm 95% CI) probability of *Tentacularia coryphaenae* infection, for *C. capensis* samples from the Agulhas Bank (A) and from the Benguela ecosystem (B).

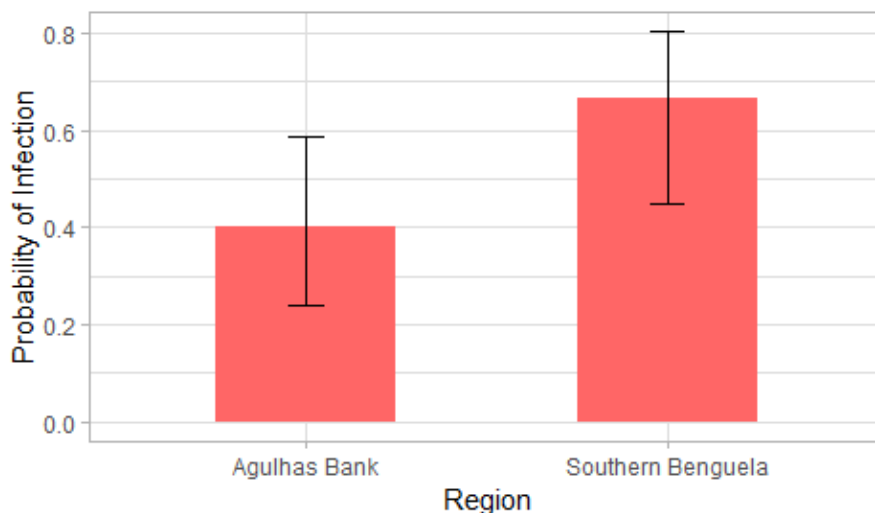


Figure 12: The mean (\pm 95% CI) probability of infection of *Chelidonichthys capensis* from the western Agulhas Bank and southern Benguela by *Tentacularia coryphaenae*.

Anisakis pegreffii

A backwards stepwise AIC analysis and analysis of deviance found that prevalence of *Anisakis pegreffii* was only influenced by the host length (Table 7). Overall the model only explains 5.35% (pseudo-R² value) of the observed variation and analysis of the residual plots do not exhibit any significant deviations from the assumptions of the model.

Table 7: Analysis of deviance for the binomial GLM for the prevalence of *Anisakis pegreffii* in *C. capensis* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev.	p
Null			69	77.609	
FL	1	4.1543	68	73.455	*

p < 0.05 *, p < 0.01 **, p < 0.001 ***

The chosen model predicted a positive relationship between fork length and *A. pegreffii* prevalence (Figure 13). Although the probability of infection is predicted to increase with host size, even small hosts are likely to be infected and show prevalence rates of >50%.

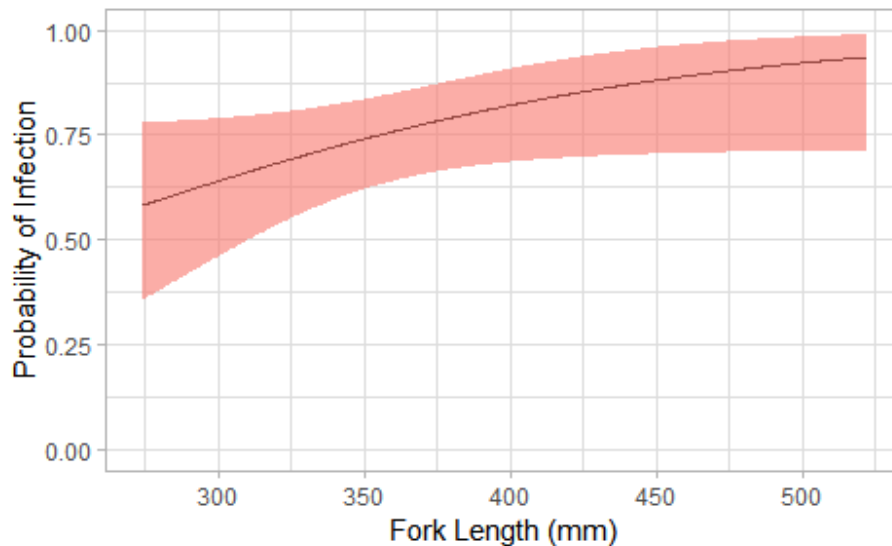


Figure 13: The predicted relationship between *Chelidonichthys capensis* size (mm) and the mean (\pm 95% CI) probability of infection by *Anisakis pegreffii*.

The GLM for the infection intensity of *A. pegreffii* on *C. capensis* found that the most appropriate model had only host size as an explanatory variable (Table 8). This model explains 43.67% of the variation and the plotted residuals of the model conform nicely to the model assumptions.

Table 8: Analysis of deviance for the zero-truncated negative binomial GLM for the infection intensity of *Anisakis pegreffii* in *Chelidonichthys capensis* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev.	p
Null			52	96.773	
FL	1	42.262	51	54.510	***

p < 0.05 *, p < 0.01 **, p < 0.001 ***

The chosen model predicted a positive, non-linear relationship between host size and mean infection intensity of *A. pegreffii* (Figure 14). Whereas smaller (<400 mm FL) fish have low (<15 parasites per infected fish) values, infection intensities of larger fish increase rapidly to >45 parasites per infected fish.

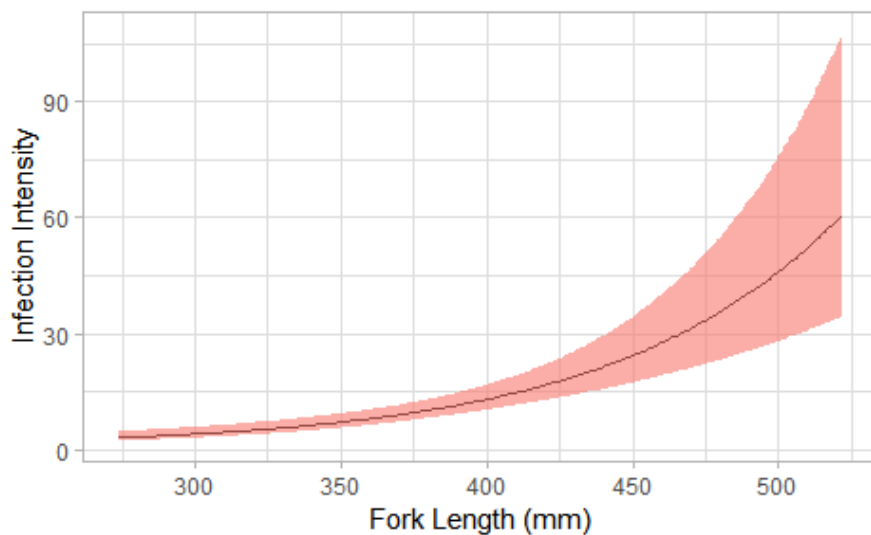


Figure 14: The predicted relationship between *Chelidonichthys capensis* size and mean infection intensity (\pm 95% CI) of *Anisakis pegreffii*.

Corynosoma australe

The AIC values and analysis of deviance revealed that none of the explanatory variables had a significant effect on the prevalence of *Corynosoma australe* in *C. capensis* (Table 9). According to the backwards stepwise AIC, the model most suited to modelling *C. australe* prevalence consisted of only the intercept (Null).

Table 9: Analysis of deviance for the binomial GLM for the prevalence of *Corynosoma australe* in *Chelidonichthys capensis* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev.	p
Null			69	95.607	

p < 0.05 *, p < 0.01 **, p < 0.001 ***

3.2 *Chelidonichthys queketti*

3.2.1 Exploratory Data Analysis

A total of 87 (54 females and 33 males) *C. queketti* were sampled (Figure 4B): 47 collected from the WCDS, 30 from the Vuna Elita sample collection, and ten from the second Desert Diamond sample collection. In total, 40 samples were collected from the Agulhas Bank in winter, while 47 samples were collected from the southern Benguela ecosystem in summer. Samples ranged from 179 to 374 mm FL, between 63 and 309.5 g WBM.

When visually assessing the FL and WBM frequency distributions of *C. queketti* (Figure 15), the FL frequency distribution appeared to be relatively normal while the mass frequency distribution was skewed slightly to the left. However, the Shapiro-Wilks test found both FL and WBM to be non-normally distributed ($p < 0.01$ and $p = 0.04266$, respectively). Condition and GSI were also both found to have non-normal distributions ($p < 0.01$ for both) whereas HSI had a normal distribution ($p = 0.8078$). Assessing the collinearity between continuous variables (FL, WBM, condition, GSI and HSI) revealed that only FL and mass were significantly correlated ($R^2 = 0.86$, $df = 85$, $p < 0.01$).

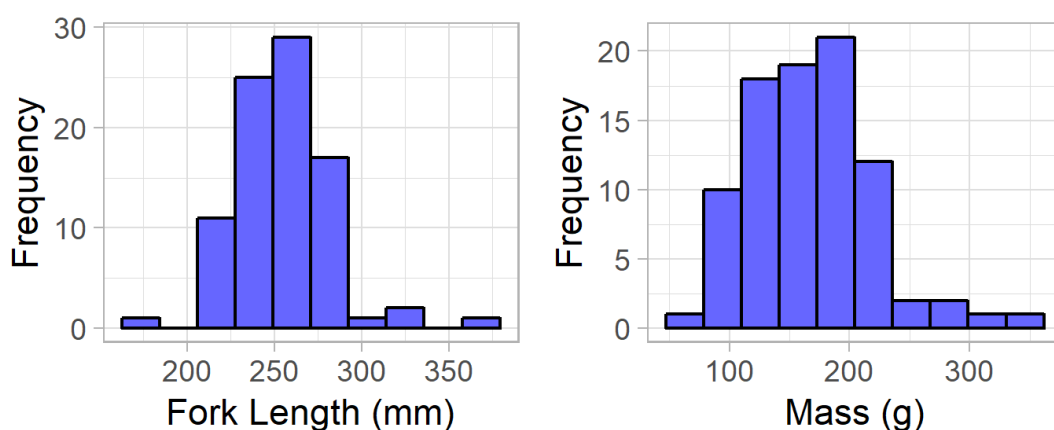


Figure 15: The fork length (mm) and mass (g) frequency distributions for *Chelidonichthys queketti* caught off South Africa in 2017 and 2018.

3.2.2 Host Biological Data

The sex ratio of *C. queketti* was found to be biased towards females ($\chi^2 = 5.069$, $df = 1$, $p = 0.02436$). There was no significant difference between the FL of male and female samples ($U = 1024.5$, $p = 0.2428$; 257.07 ± 24.90 mm for females and 251.12 ± 31.62 mm for males). Since the WBM of both female and male samples were found to have a normal distribution ($p = 0.7317$ and $p = 0.8134$ respectively), an independent t-test was used to show that there was no significant difference between the two ($t = 1.8818$, $df = 85$, $p = 0.06328$; 177.84 ± 55.72 g for females and 156.80 ± 40.73 g for males). No significant difference was observed between the condition factor of female and male samples ($U = 1061$, $p = 0.137$; 1.05 ± 0.12 for females and 1.01 ± 0.17 for males).

A significant difference was observed between female and male mean GSI values ($U = 1556$, $p < 0.01$; 3.22 ± 2.22 for females and 0.45 ± 0.34 for males; Figure 16). The HSI values of female and male samples followed normal distributions ($p = 0.5996$ and $p = 0.7849$ respectively), and an independent t-test determined no significant difference between female and male mean HSI values ($t = 0.61697$, $df = 46$, $p = 0.5403$; 1.74 ± 0.65 for females and 1.63 ± 0.57 for males).

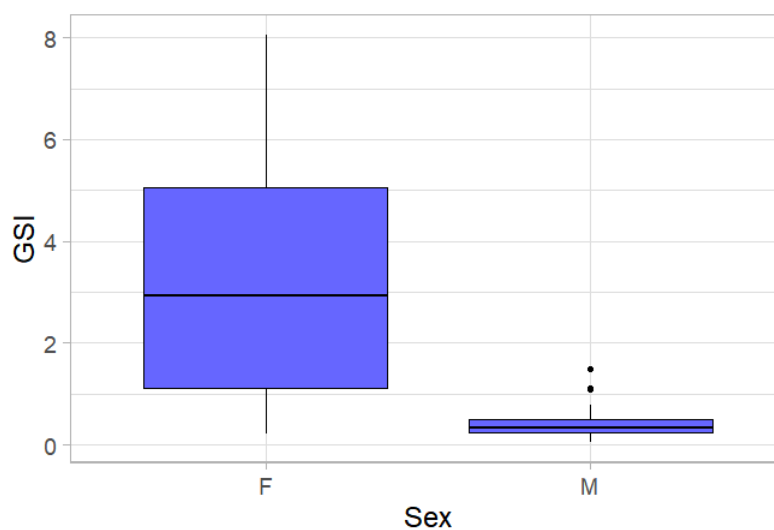


Figure 16: The differences between female and male mean GSI values for *Chelidonichthys queketti* caught off South Africa in 2017 and 2018.

No bias was observed between *C. queketti* samples from the Agulhas Bank and those from the Benguela ecosystem ($\chi^2 = 0.56322$, $df = 1$, $p = 0.453$). No significant difference was observed in between the FL of samples from the two regions ($U = 899$, $p = 0.0.7298$; 252.80 ± 18.19 mm for Agulhas Bank samples and 256.53 ± 33.74 mm for southern Benguela samples). The WBM of samples showed no significant difference between regions ($t = -0.72067$, $df = 85$, $p = 0.4731$; 165.55 ± 35.62 g for Agulhas Bank samples and 173.53 ± 61.83 g for southern Benguela samples).

No significant difference was observed between the condition factor of the *C. queketti* samples from the two regions ($U = 8951$, $p = 0.9291$; 1.04 ± 0.13 for Agulhas Bank samples and 1.03 ± 0.15 for southern Benguela samples). No significant difference in mean GSI was observed between the two regions ($U = 995$, $p = 0.3068$; 2.46 ± 2.27 for Agulhas Bank samples and 1.96 ± 2.20 for southern Benguela samples). There was also no significant difference in mean HSI was found between samples from the two regions ($U = 217$, $p = 0.1195$; 1.76 ± 0.60 for Agulhas Bank samples and 1.36 ± 0.61 for southern Benguela samples).

As samples from the Benguela were collected exclusively in summer and samples from the Agulhas Bank in winter, the outcomes of biological comparisons between regions would be identical for seasonality comparisons.

3.2.3 Parasite Assemblage and Infection Indices

In total, 15 parasite taxa were recorded to infect *Chelidonichthys queketti* off South Africa, six of which were identified to species level, five to order, sub-class or phylum level and four remained unidentified. Parasites included (Table 10) two species of Monogenea (species 1 and 2 respectively), the cestodes *Tentacularia coryphaenae* (Bosc, 1802; Figure 17A) and Cestode species 2, Nematode *Anisakis pegreffii* (Campana-Rouget & Biocca, 1955), two acanthocephalans *Corynosoma australe* (Johnston, 1937) and Acanthocephala species 1,

Isopod species 1, the copepods *Lernentoma asellina* (Linnaeus, 1758; Figure 17B) and *Medesicaste penetrans* (Heller, 1865), the leech (Hirudinae) *Oceanobdella sexoculata* (Malm, 1863) and four unknown species; a Cyst species (Figure 17C) and Unknown species 1, 2 and 3. As only three parasites belonging to Copepoda had been previously recorded to infest *C. queketti* by taxonomists, 14 of the parasite taxa found in this study are new host records.

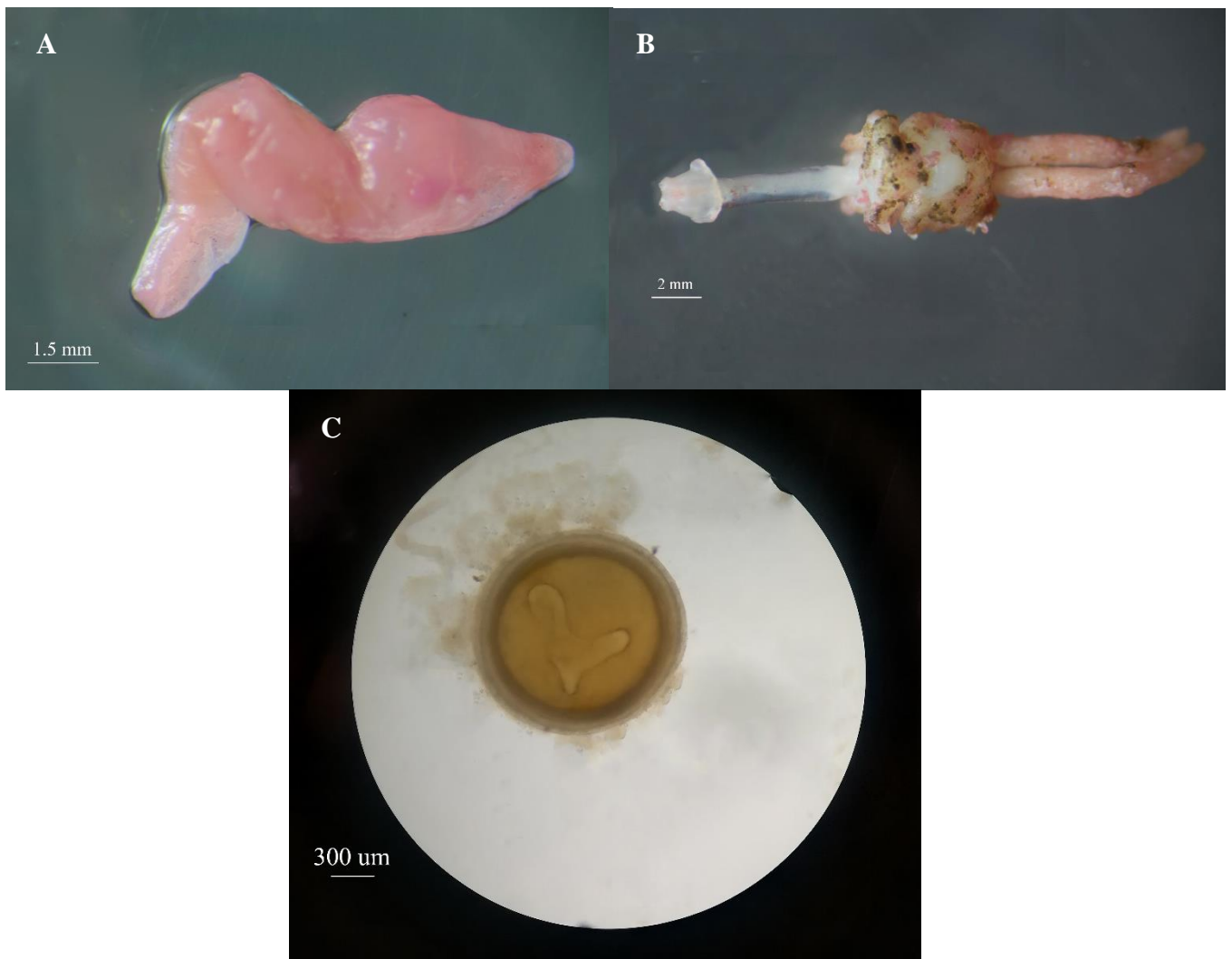


Figure 17: Photographs of *Tentacularia coryphaenae* (A), *Lernentoma asellina* (B) and an unidentified Cyst sp. (C) found infecting *Chelidonichthys queketti*.

The randomised accumulation curve (Figure 18) for parasite taxa found to infect *C. queketti* off South Africa reaches its maximum parasite richness at 87 samples but does not reach an asymptote, indicating that the parasite assemblage of the lesser gurnard has not been fully described.

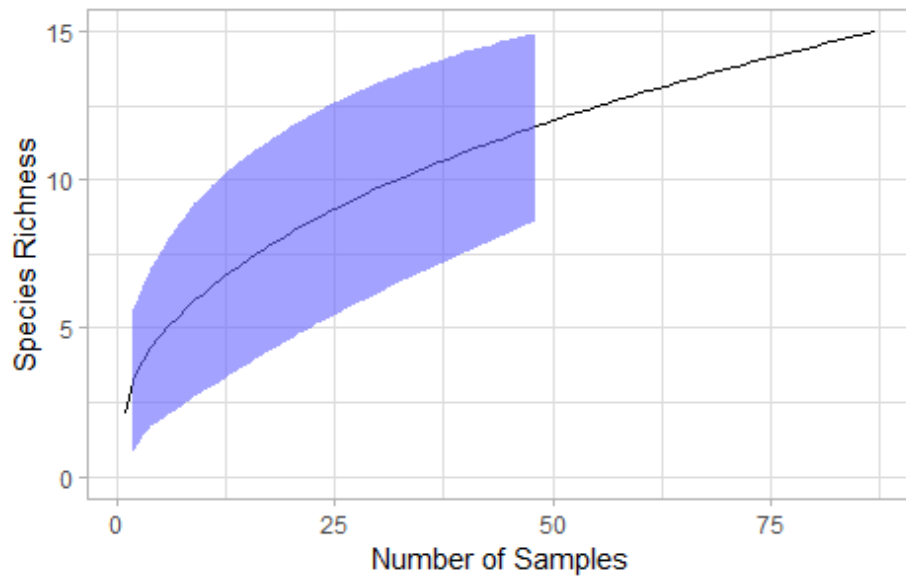


Figure 18: The randomised richness of parasite taxa per number of *Chelidonichthys queketti* hosts sampled off South Africa in 2017 and 2018.

Table 10: The taxonomic composition, site of infection, overall prevalence (%), mean infection intensity \pm sd (per infected fish), mean abundance \pm sd (per fish) and range of the parasite assemblage of *Chelidonichthys queketti* off South Africa in 2017 and 2018 (* = new host record, G = gills, VC = visceral cavity, S = stomach, GI = gastro-intestinal tract, BS = body surface, BC = buccal cavity, L = liver, K = kidneys, Sp = spleen).

Parasite Taxa	Site of Infection	Overall Prevalence (%)	Mean Infection Intensity (\pm sd)	Mean Abundance (\pm sd)	Range
Monogenea					
Monogenea sp. 2*	G	6.9	1.50 \pm 1.22	0.10 \pm 0.48	0 – 1
Monogenea sp. 3*	G	2.3	1.5 \pm 0.71	0.034 \pm 0.24	0 – 1
Cestoda					
<i>Tentacularia coryphaenae</i> *	VC	59.8	6.17 \pm 6.35	3.69 \pm 5.76	0 – 28
Cestode sp. 2*	VC	4.6	5.75 \pm 6.29	0.26 \pm 1.69	0 – 15
Nematoda					
<i>Anisakis pegreffii</i> *	S, VC	44.8	4.41 \pm 4.03	1.98 \pm 3.47	0 – 17
Acanthocephala					
<i>Corynosoma australe</i> *	VC, GI	11.5	1.3 \pm 0.67	0.15 \pm 0.47	0 – 3
Acanthocephala sp. 1*	VC	1.1	1	0.011 \pm 0.11	0 – 1
Isopoda					
Isopod sp. 2*	G, BS	1.1	2	0.023 \pm 0.21	0 – 2
Copepoda					
<i>Lernentoma asellina</i> *	G	3.4	1	0.034 \pm 0.18	0 – 1
<i>Medesicaste penetrans</i>	BC	9.2	1.13 \pm 0.35	0.10 \pm 0.34	0 – 2
Hirudinae					
<i>Oceanobdella sexoculata</i> *	BC	1.1	1	0.011 \pm 0.11	0 – 1

Parasite Taxa	Site of Infection	Overall Prevalence (%)	Mean Infection Intensity (\pm sd)	Mean Abundance (\pm sd)	Range
Unidentified sp.					
Cyst sp. 1*	L, K, Sp	69.0	28.2 \pm 38.33	19.45 \pm 34.35	0 – 180
Unknown sp. 1*	VC	1.1	12	0.14 \pm 1.29	0 – 12
Unknown sp. 2*	VC	1.1	1	0.011 \pm 0.11	0 – 1
Unknown sp. 3*	VC	1.1	5	0.057 \pm 0.54	0 – 5

3.2.4 Drivers of Parasite Infestation

The generalised linear model used for *Chelidonichthys queketti* prevalence and infection intensity consisted of only three explanatory variables (Table 11). Three species were modelled in terms of prevalence; *Tentacularia coryphaenae*, *Anisakis pegreffii* and the unidentified Cyst sp., while only *T. coryphaenae* and the Cyst sp. were modelled in terms of infection intensity.

Table 11: Description of the explanatory variables used in the generalised linear model analysing parasite prevalence and infection intensity for *Chelidonichthys queketti* caught off South Africa in 2017 and 2018.

Variable	Description
FL	Host length (mm FL)
Sex	Sex of host
Region	Capture locality of host samples by region

Tentacularia coryphaenae

The backwards-stepwise AIC and analysis of deviance determined the most appropriate model for the prevalence of *T. coryphaenae* infecting *C. queketti* to consist of host size and region as explanatory variables (Table 12). This model explained 31.3% of the variation and an analysis of the residual plots found them to conform to model assumptions.

Table 12: Analysis of deviance for the binomial GLM for the prevalence of *Tentacularia coryphaenae* in *C. queketti* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev	p
Null			86	117.264	
FL	1	9.594	85	107.670	**
Region	1	27.154	84	80.516	***

p < 0.05 *, p < 0.01 **, p < 0.001 ***

A positive relationship is predicted between the probability of *T. coryphaenae* infection and size of *C. queketti* (Figure 19). In the Agulhas Bank region hosts less than 250 mm FL have a low (<25%) probability of infection, but this increases with host size and is predicted to reach its maximum in hosts larger than 350 mm. In the southern Benguela ecosystem, the probability of infection for host samples >250 mm FL is higher (82%) than in fish from the Agulhas Bank and also has a sharper increase, levelling out at a host size of 300 mm FL.

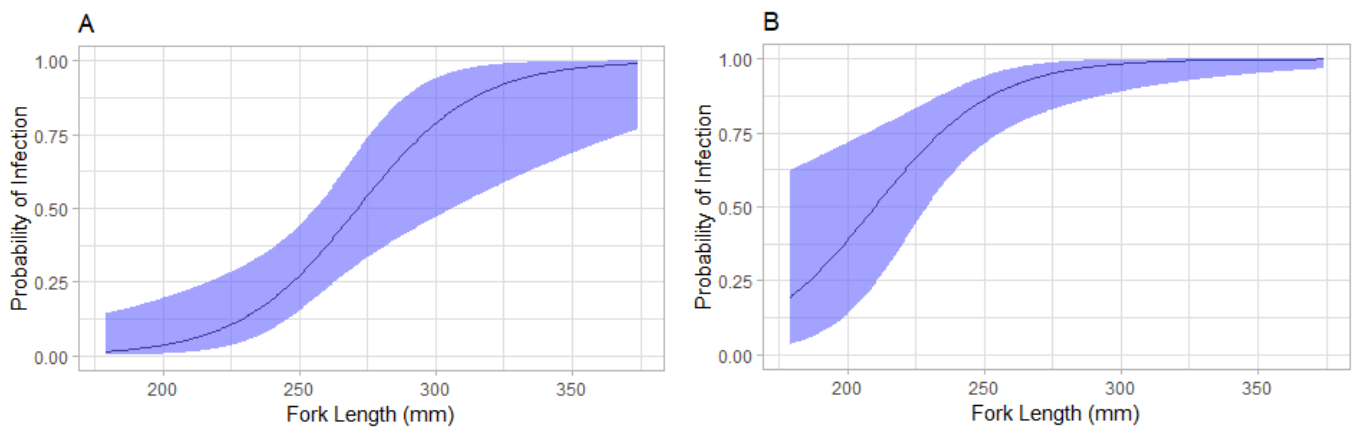


Figure 19: The relationship between the mean (\pm 95% CI) probability of infection of *Tentacularia coryphaenae* and *Chelidonichthys queketti* size (mm) for samples from the western Agulhas Bank (A) and from the southern Benguela (B).

The bar plots (Figure 20) revealed that the probability of infection of *T. coryphaenae* is higher (78%) in fish from the southern Benguela ecosystem than those from the western Agulhas Bank (52%).

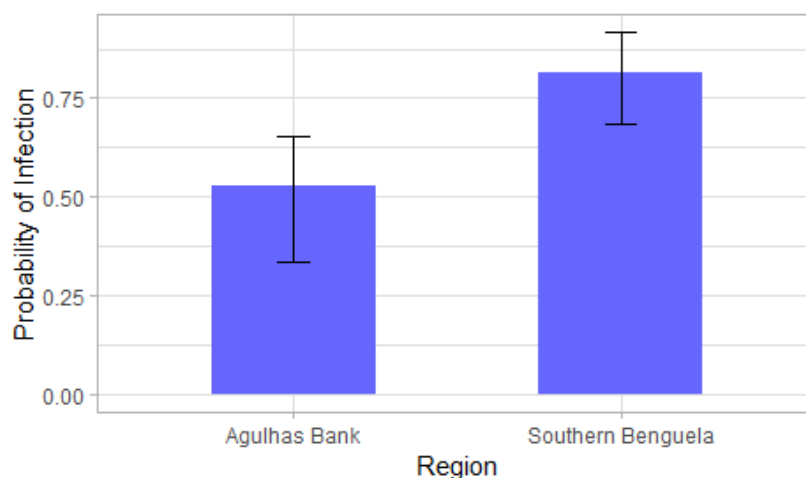


Figure 20: The variability of probability (\pm 95% CI) of infection for *Chelidonichthys queketti* samples from the western Agulhas Bank and southern Benguela ecosystem.

The AIC and analysis of deviance revealed that the most appropriate model for the infection intensity of *T. coryphaenae* consisted of only host size (Table 13). This model was found to only explain 6.7% of the variation and analysis of the residual plots deem the model a suitable fit.

Table 13: Analysis of deviance for the zero-truncated negative binomial GLM for the infection intensity of *Tentacularia coryphaenae* in *C. queketti* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev.	p
Null			51	56.867	
FL	1	3.845	50	53.022	*

p < 0.05 *, p < 0.01 **, p < 0.001 ***

The model output revealed a positive relationship between *C. queketti* size and infection intensity of *T. coryphaenae* (Figure 21). Whereas smaller (<200 mm FL) fish have low (<5 parasites per infected fish) values, infection intensities gradually increase with host size to >15 parasites per infected fish >360 mm FL.

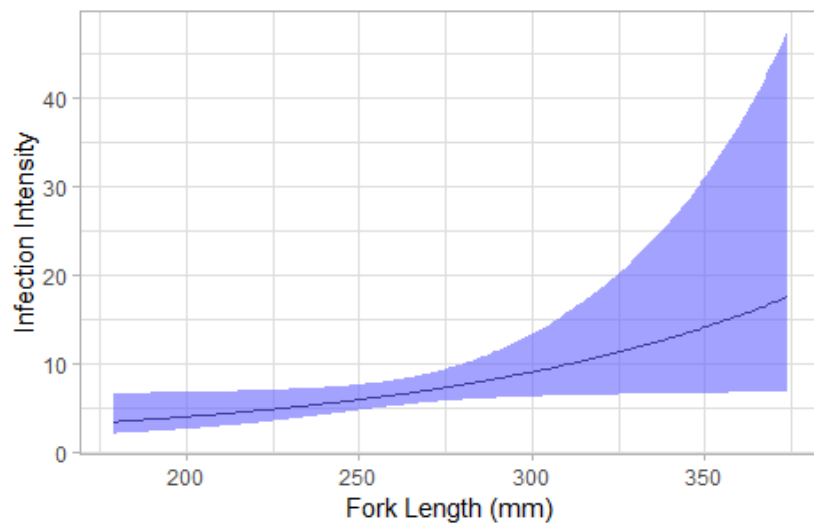


Figure 21: The relationship between *Chelidonichthys queketti* size (mm) and mean (\pm 95% CI) infection intensity of *Tentacularia coryphaenae* (per infected fish).

Anisakis pegreffii

The selection process found that the most appropriate model consisted of sex and region as the explanatory variables best suited to predict *A. pegreffii* prevalence in *C. queketti* (Table 14). Although sex was not a significant variable, this model was chosen as it had the most appropriate AIC value. The model accounted for 40.8% of the variation and analysis of the residuals revealed no extreme deviations from the assumptions of the binomial generalised linear model.

Table 14: Analysis of deviance for the binomial GLM for the prevalence of *Anisakis pegreffii* in *C. queketti* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev	p
Null			86	119.675	
Sex	1	0.96	85	118.715	0.3271
Region	1	47.85	84	70.865	***

p < 0.05 *, p < 0.01 **, p < 0.001 ***

The model output exhibits a marked difference in predicted prevalence between hosts from the western Agulhas Bank and from the southern Benguela (Figure 22), with the Agulhas Bank samples having a higher probability of infection. There is also a difference between sex, as female samples from each region have a slightly lower probability of infection than males.

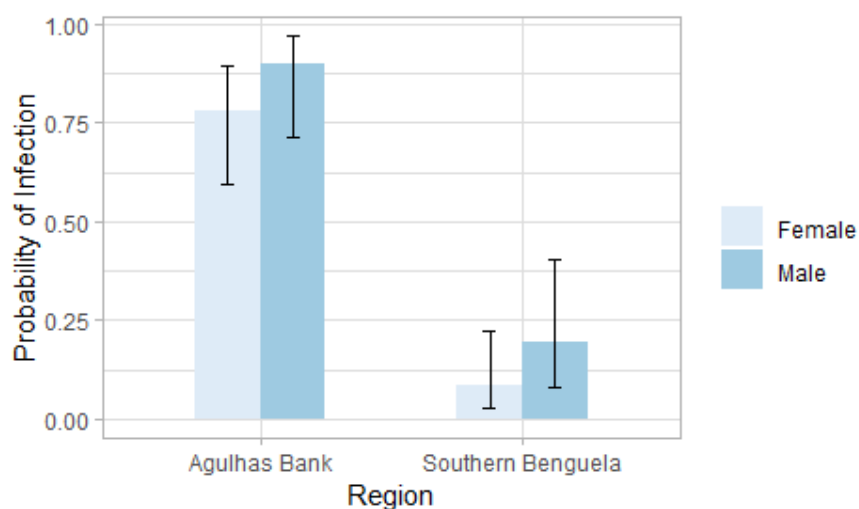


Figure 22: The variation in the mean (\pm 95% CI) probability of infection of *Anisakis pegreffii* between Agulhas Bank and southern Benguela female and male *Chelidonichthys queketti* samples.

Cyst sp.

The AIC and analysis of deviance found that the prevalence of the unidentified cyst species cannot be explained by any of the explanatory variables (Table 15). Analysis of the residuals revealed some deviations from the model assumptions.

Table 15: Analysis of deviance for the binomial GLM for the prevalence of *Anisakis pegreffii* in *C. queketti* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df.	Dev.	Res. df	Res. Dev.	p
Null			86	107.77	

p < 0.05 *, p < 0.01 **, p < 0.001 ***

In terms of infection intensity, the AIC and analysis of deviance revealed that the most appropriate model had only region as an explanatory variable, however this was not significant (Table 16). The residuals of the chosen model do conform to the assumptions of the generalised linear model, although this model only explains 3.1% of the variation.

Table 16: Analysis of deviance for the zero-truncated negative binomial GLM for the infection intensity of the unidentified cyst species in *C. queketti* off South Africa in 2017 and 2018. The degrees of freedom (df), deviance (Dev), residual degrees of freedom (Res. df), residual deviance (Res. Dev.) and significance (p) are summarized from the χ^2 test.

Variable	df	Dev.	Res. df	Res. Dev.	p
Null			59	69.892	
Region	1	2.175	58	67.717	0.1403

p < 0.05 *, p < 0.01 **, p < 0.001 ***

Although region was not a significant variable, a difference in infection intensity of the unidentified cyst species was still detected between samples from the western Agulhas Bank and the southern Benguela ecosystem (Figure 23) – with the latter showing a higher mean infection intensity.

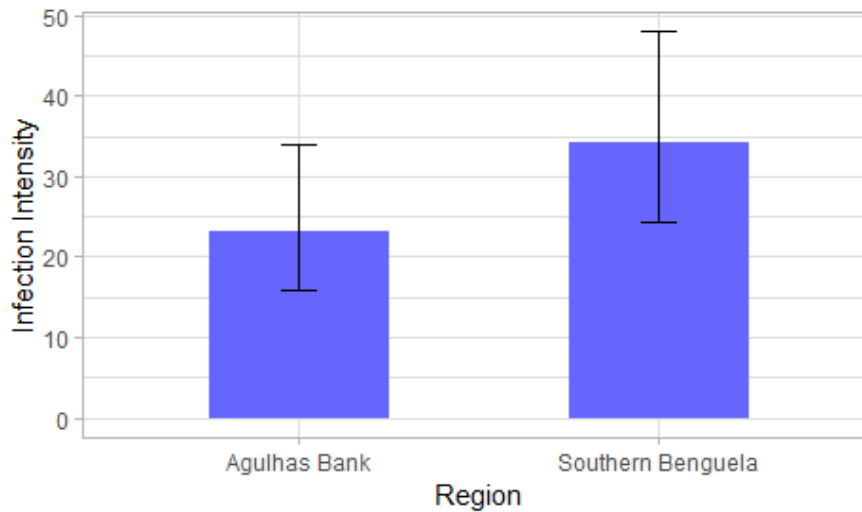


Figure 23: The mean (\pm 95% CI) infection intensity of the unidentified cyst species infecting *Chelidonichthys queketti* samples from the Agulhas Bank and the southern Benguela.

3.3 Interspecific Comparison of Parasite Community Structure

The non-metric multidimensional scaling (NMDS) analysis performed on the abundance data of the parasite communities infecting *Chelidonichthys capensis* and *C. queketti* showed that there was some overlap of the parasite communities infecting the two species (Figure 24). An analysis of similarity (ANOSIM) performed on the parasite community abundance data of the two gurnard species determined that there was a small but highly significant amount of dissimilarity between them ($R^2 = 0.3434$, $p = 0.001$).

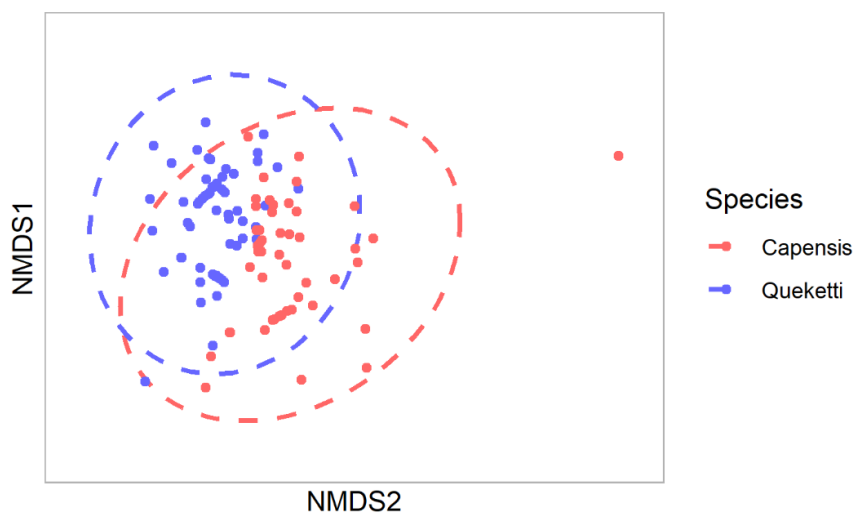


Figure 24: The non-metric multidimensional scaling plot visualising the parasite communities infecting *Chelidonichthys capensis* (in red) and *Chelidonichthys queketti* (in blue). The NMDS output had a stress factor of 0.149 over two dimensions.

Discussion

As the shift towards applied marine parasitology research grows, baseline knowledge of the parasites infecting marine species becomes increasingly important (MacKenzie & Abaunza, 1998; Rohde, 2010; Oliva et al., 2016). Therefore, the primary aim of this study was to determine the parasite assemblages of two South African gurnards, *Chelidonichthys capensis* and *C. queketti*. Secondly, this study seeks to determine whether the degree of parasitism of certain species is linked to the host's biological traits and, lastly, to determine whether there is a significant difference in the parasite communities infecting *C. capensis* and *C. queketti*. Understanding these parasite species and the drivers of parasitism is crucial in improving our knowledge of the role of parasites within the South African marine environment.

4.1 Parasitic Composition and Interactions

This study suggests that the macroparasite community of *C. capensis* is less speciose than that of *C. queketti* with 13 taxa recorded for the former compared with 15 for the latter, although neither gurnard showed an asymptote in their parasite species accumulation curve indicating that their parasite assemblages were not fully documented. Only copepods have previously been described to infect these two gurnard species. This study is thus the first to report their infection by acanthocephalans, cestodes, nematodes, digeneans, monogeneans, leeches and isopods. In total, 18 parasite taxa are now known to infect *C. capensis*, while 17 are known to infect *C. queketti* (Table 17).

4.1.1 Monogenea and Digenea

One species of Monogenea, an ectoparasitic fluke, was recorded from *C. capensis* and two species were recorded from *C. queketti* in this study. These species could not be identified to species level, and the use of molecular techniques is advised. Monogenea sp. 1 was found in the gills of 7.1% of *C. capensis* samples, Monogenea sp. 2 was found in the gills of 6.9% of *C.*

queketti samples, and Monogenea sp. 3 was found in the gills of 2.3% of *C. queketti* samples. Monogeneans have not been previously recorded to infect *C. capensis* or *C. queketti* from South Africa.

Digenea, trematodes with high diversity in teleosts, were only recorded to infect *C. capensis* and could not be identified to species level using morphological characteristics, hence molecular techniques are again recommended in future studies. Three taxa were recorded in South African *C. capensis*; a species from the family Zoogonidae (infecting the buccal cavity and visceral cavity of 4.3% of samples), a species from the family Opecoelidae (infecting the visceral cavity of one sample) and the unidentified Digenea sp. 1 (infecting the visceral cavity of one sample). No digeneans have been previously recorded to infect *C. capensis*.

4.1.2 Cestoda

Two cestode species were found to infect the visceral cavity and stomach of *Chelidonichthys capensis*; *Tentacularia coryphaenae* and unidentified Cestode sp. 1, and two species were also found to infect the visceral cavity of *C. queketti*; *T. coryphaenae* and unidentified Cestode sp. 2, which differed from unidentified Cestode sp. 1 in its morphology. *Tentacularia coryphaenae* was the most prevalent cestode species by far (found in 42.9% of *C. capensis* and 59.8% of *C. queketti*), while Cestode sp. 1 was found in only one *C. capensis* and Cestode sp. 2 was found in 4.6% of *C. queketti*. All three cestode species were new host records.

Tentacularia coryphaenae is a cosmopolitan trypanorhynch, with larvae infecting invertebrates and teleosts and adults infecting elasmobranchs (Palm et al., 2007). This species has been recorded in the visceral cavity, mesenteries, spiral valve and musculature of teleost species (Knoff et al., 2004; Palm et al., 2007; Reed et al., 2012). In *C. capensis* and *C. queketti*, *T. coryphaenae* was recorded inside the visceral cavity and therefore poses no threat to human health or the economic value of the fish.

In both *C. capensis* and *C. queketti*, the prevalence (and infection intensity in *C. queketti*) of *T. coryphaenae* increased with host size, a trend which has been observed in many host species and has come to be generally expected (Poulin, 1999; Poulin, 2000). The increase in prevalence with *C. capensis* size suggests that *T. coryphaenae* is obtained through predation on teleost species rather than predation on crustaceans – as the diets of small *C. capensis* hosts are dominated by crustaceans while large hosts are more likely to prey on teleost species and larger crustaceans (Meyer & Smale, 1991). However, the diet of *C. queketti* is dominated by crustaceans, regardless of the size of the gurnard (Meyer & Smale, 1991). Therefore, it is likely that transmission of *T. coryphaenae* is from predation on crustacean species rather than exclusively from teleost species. The higher prevalence of *T. coryphaenae* in gurnards from the southern Benguela, compared with the Agulhas Bank, indicates that the endemic area of the parasite is likely larger and more easily accessible to *C. capensis* and *C. queketti* in the southern Benguela, therefore hosts in that region are more susceptible to infection and transmission of this parasite species.

The significant differences in the prevalence of *T. coryphaenae* between fish from the Agulhas Bank and southern Benguela, for both gurnard species, as well as its easy detection and identification make it a potential biological tag for population studies of South African *C. capensis* and *C. queketti*, although one disadvantage is its complex life-cycle. However, to determine whether *T. coryphaenae* would be an acceptable biological tag differences in its prevalence between gurnards from the Agulhas Bank and southern Benguela would need to be observed over multiple years, size classes and seasons (MacKenzie & Abaunza, 1998).

4.1.3 Nematoda

Two nematodes were found to parasitize in the visceral cavity, stomach and liver of *C. capensis* in this study; *Anisakis pegreffii* and unidentified Nematode sp. 1, while only *A. pegreffii* was recorded to infect the stomach and visceral cavity of *C. queketti*. While Nematode sp. 1 was

only found in one *C. capensis* individual, *Anisakis pegreffii* was the most prevalent parasite species in *C. capensis* (75.7%) and the third most prevalent in *C. queketti* (44.8%). *Anisakis pegreffii* is a new host record for both gurnard species and Nematode sp. 1 is a new host record for *C. capensis*.

Species of *Anisakis* are commonly found in teleost species, their intermediate hosts, which are preyed upon by marine mammals (specifically cetaceans), their definitive hosts (Mattiucci & Nascetti, 2006). *Anisakis* spp. pose a threat to human health as accidental infection can occur if the parasite is ingested and over-exposure to infected teleosts can cause allergic reactions (Nieuwenhuizen et al., 2006; Mattiucci et al., 2013). In teleosts, *Anisakis* spp. have been recorded in the stomach as well as throughout the visceral cavity (Anderson, 2000; Mattiucci & Nascetti, 2006).

The prevalence of *A. pegreffii* in *C. capensis* increased with host size, although the high prevalence in smaller hosts indicate that hosts are infected from a young age. The modelled infection intensity suggests this and further implies that the infection intensity of *A. pegreffii* increases with size and, therefore, age. *Chelidonichthys capensis* are able to acquire *A. pegreffii* at a young age, likely through predation on small crustaceans, particularly euphausiids that serve as important intermediate hosts to this parasite species (Anderson, 2000).

In *C. queketti* the prevalence of *A. pegreffii* was slightly although not significantly higher in males than in females, as well as significantly higher in fish of both sexes from the Agulhas Bank. The spatial differences in prevalence could be indicative of different diets, since gurnards in the southern Benguela have diets dominated by mysids while those from the Agulhas Bank have diets dominated by brachyurans (Meyer & Smale, 1991).

The regional differences in prevalence of *A. pegreffii* could make this species a potential biological tag for *C. queketti*, however a long term data set is needed before *A. pegreffii* could

be applied as a biological tag for this species. The advantages to using *A. pegreffii* as a biological tag include its easy detection and identification and its well-documented life history (MacKenzie & Abaunza, 1998). *Anisakis* species have previously been used as biological tags in determining the seasonal migration and stock discrimination of several teleost populations (MacKenzie, 2002; Mattiucci et al., 2008).

4.1.4 Acanthocephala

In this study, the acanthocephalan *Corynosoma australe* was recorded in the visceral cavity and kidneys of 42.9% of *C. capensis* samples, while *C. australe* was recorded in the visceral cavity and gastro-intestinal tract of 11.5% of *C. queketti* samples and Acanthocephala sp. 1 was recorded in the visceral cavity of one of the *C. queketti* samples. No previous records of Acanthocephala species from *C. capensis* and *C. queketti* exist, therefore *C. australe* and Acanthocephala sp. 1 constitute new host records.

Although the Acanthocephala phylum is relatively small (Amin, 1998; Rohde, 2005), its members have been used as indicators of heavy metal pollution in marine environments (de Buron et al., 2009) and documented as affecting the behaviour of the host – e.g. making amphipod hosts more susceptible to predation (Poulin, 2010). *Corynosoma* is one of the most speciose genera belonging to Acanthocephala (Hernandez-Orts et al., 2017). *Corynosoma australe* is distributed in the southern hemisphere where it infects amphipods as intermediate hosts, teleosts as paratenic hosts and cetaceans and pinnipeds as definitive hosts (Rohde, 2005).

In *C. capensis*, the prevalence of *C. australe* was not significantly influenced by host size, sex or region, and is seemingly random. The large differences in prevalence between *C. capensis* and *C. queketti* suggests that the endemic area of *C. australe*, where transmission to amphipod hosts occurs, overlaps more with the geographic and depth range of *C. capensis* than with those of *C. queketti*.

4.1.5 Isopoda

Two isopod species were recorded in this study: Isopod sp. 1 was recorded from the body surface of *C. capensis* (in one of sample), while Isopod sp. 2 was a gill-replacing isopod and therefore, the female was recorded in the gills of *C. queketti* and the male was recorded on the body surface. In total, Isopod sp. 2 was recorded in one *C. queketti* sample.

4.1.6 Copepoda

The Copepoda is a highly diverse taxon and its members are extremely abundant within the marine environment (Rohde, 2005). One of the first two copepod species recorded in South Africa was *Medesicaste penetrans*, described by Heller (1865) from *C. capensis* samples (Smit & Hadfield, 2015). Since then, seven more copepod species have been recorded to infest *C. capensis* (*Caligus brevicaudatus*, *C. curtus*, *C. diaphanus*, *C. pelamydis*, *C. tetradontis*, *Charopinus dubius* and *Lernentoma asellina*) and three copepod species have been recorded to infest *C. queketti* (*C. curtus*, *Medesicaste penetrans* and *Parabrachiella supplicans*).

In this study, only three copepod species were found infesting *C. capensis*; *L. asellina* (in the buccal cavity of 7.1% of samples), *M. penetrans* (in the gills of 10% of samples) and a *Caligus* sp. which is thought to be *C. pelamydis* (in the gills of 10% of species). Only two species were recorded to infest *C. queketti*, *L. asellina* (in the buccal cavity of 3.4% of samples) and *M. penetrans* (in the gills of 9.2% of samples). *Lernentoma asellina*, a parasite specific to triglids (Ho, 1994), is a new host record for *C. queketti*.

4.1.7 Hirudinea

There has been little work done on Hirudinea species, commonly known as leeches, in South Africa (Smit & Hadfield, 2015). Only one species of Hirudinea was observed to infest *C. queketti*, *Oceanobdella sexoculata* – found in the buccal cavity of one of sample. This species

constitutes a new host and geographic record, as this species is known to infest teleosts from the Arctic seas and from the northern Atlantic (Appy & Dadswell, 1980).

4.1.8 Unidentified species

The unidentified species remain so due to either that lack of intact samples or, where multiple samples were collected, due to the lack of distinguishable morphological features. Four parasite species recorded to infect *C. queketti* could not be identified; Unidentified species 1, 2 and 3 (each found infecting the visceral cavity of one of the samples), and the Cyst species found infecting the kidneys and spleen of 69% of samples.

The prevalence of the Cyst species, recorded from the liver, kidneys and spleen of host samples, was not influenced by any of the host explanatory variables. The infection intensity, however, was influenced by region as it was higher in southern Benguela samples than in Agulhas Bank samples, but this result was not significant.

4.2 *Chelidonichthys* Parasite Community

The significant difference in the parasite communities of *C. capensis* and *C. queketti* indicates that the ecological and physiological differences between these species affects the presence of parasite species (e.g. the Cyst species) or the prevalence of a parasite species (e.g. *Corynosoma australe*). The similarities shared by *C. capensis* and *C. queketti*, such as habitat and prey, are however significant enough to cause the large overlap in parasite communities observed in this study.

When compared with the parasite species recorded to infect other species of *Chelidonichthys* (Table 17), to date *C. capensis* has the second highest number of parasite species recorded and *C. queketti* has the third highest. *Chelidonichthys lucerna* has the highest number of parasite species, with 22 parasite species recorded to infect samples from various regions (Vaissiere,

1955; Raibaut et al., 1998; Bartoli et al., 2005; Wiecek et al., 2011; Demirkale et al., 2014). There are no reports of the parasite assemblages of *C. gabonensis*, *C. ischyryus* or *C. spinosus*. Several of the parasite species recorded to infect *C. capensis* and *C. queketti* have also been recorded infecting other *Chelidonichthys* species. *Caligus brevicaudatus* has been recorded to infest *C. lucerna* and *C. obscurus* from the Mediterranean Sea, while *Caligus diaphanus* was recorded in *C. cuculus*, *C. lastoviza* and *C. lucerna* (Raibaut et al., 1998). These two parasite species were not found infecting *C. capensis* and *C. queketti* in this study. *Lernentoma asellina* was recorded to infest both *C. capensis* and *C. queketti* and has also been recorded in *C. cuculus*, *C. lastoviza* and *C. lucerna* (Raibaut et al., 1998; Demirkale et al., 2014). Unidentified *Anisakis* species were also recorded from *C. kumu* and *C. obscurus* (Wharton et al., 1998; Serracca et al., 2013).

Table 17: The parasite taxa recorded to infect members of the genus *Chelidonichthys* from various regions.

Species	Region	Parasite Taxa	Reference
<i>Chelidonichthys capensis</i>	South Africa	<i>Medesicaste penetrans</i>	Barnard (1955); This study
		<i>Caligus brevicaudatus</i>	Barnard (1955b)
		<i>Caligus pelamydis</i>	
		<i>Lernentoma asellina</i>	Kensley & Grindley (1973); This study
		<i>Caligus tetradontis</i>	Oldewage (1992)
		<i>Caligus diaphanus</i>	Oldewage (1993)
		<i>Charopinus dubius</i>	
		<i>Caligus curtus</i>	Oldewage & Avenant-Oldewage (1993)
		<i>Tentacularia coryphaenae</i>	This study
		Cestode sp. 1	
		<i>Anisakis pegreffii</i>	
		Nematode sp. 1	
		<i>Corynosoma australe</i>	
		Zoogonidae sp.	
Opecoelidae sp.			
Digenea sp. 1			
Monogenea sp. 1			
Isopod sp. 1			
<i>Chelidonichthys cuculus</i>	England	<i>Parabrachiella bispinosa</i>	Leigh-Sharp (1928)
	Mediterranean	<i>Caligus diaphanus</i>	Raibaut et al. (1998)
		<i>Pandarus bicolor</i>	Koch (2012)
<i>Chelidonichthys gabonensis</i>	-	Not reported	-
<i>Chelidonichthys ischyryus</i>	-	Not reported	-
<i>Chelidonichthys kumu</i>	New Zealand	<i>Anisakis</i> sp.	Wharton et al. (1998)
	China	<i>Hysterothylacium fabri</i>	Li et al. (2008)
	Unknown	<i>Caligus rotundigenitalis</i>	Demirkale et al. (2014)
<i>Chelidonichthys lastoviza</i>	Mediterranean	<i>Parabrachiella triglae</i>	Richiardi (1880)
		<i>Caligus diaphanus</i>	Raibaut et al. (1998)
		<i>Lernentoma asellina</i>	
		<i>Parabrachiella insidiosa</i>	
<i>Chelidonichthys lucerna</i>	Algeria	<i>Caligua uranoscopi</i>	Vaissiere (1955)
	Mediterranean	<i>Acanthochondria triglae</i>	Raibaut et al. (1998)

Species	Region	Parasite Taxa	Reference
		<i>Caligus brevicaudatus</i>	
		<i>Caligus diaphanus</i>	
		<i>Lernentoma asellina</i>	
		<i>Parabrachiella bispinosa</i>	
		<i>Parabrachiella impudica</i>	
		<i>Parabrachiella insidiosa</i>	
		<i>Parabrachiella triglae</i>	
		<i>Thysanote impudica</i>	
	Mediterranean	<i>Helicometra</i> spp.	Bartoli et al. (2005)
		<i>Lecithochirium musculus</i>	
		<i>Prosorhynchoides gracilescens</i>	
		<i>Synaptobothrium caudiporum</i>	
	Baltic Sea	<i>Contracecum osculatum</i>	Wiecaszek et al. (2011)
		<i>Pseudoterranova decipiens</i>	
		<i>Hysterothylacium aduncum</i>	
		<i>Corynosoma strumosum</i>	
	Unknown	<i>Caligus gurnardi</i>	Demirkale et al. (2014)
		<i>Caligus uranoscopi</i>	
		<i>Clavellisa emarginata</i>	
		<i>Medesicaste triglarum</i>	
<i>Chelidonichthys obscurus</i>	Mediterranean	<i>Acanthochondria triglae</i>	Raibaut et al. (1998)
<i>Chelidonichthys obscurus</i>		<i>Caligus brevicaudatus</i>	
		<i>Parabrachiella bispinosa</i>	
		<i>Parabrachiella triglae</i>	
		<i>Triglicola obscurum</i>	Boudaya et al. (2006)
		<i>Plectanocotyle major</i>	
	Ligurian Sea	<i>Anisakis</i> spp.	Serracca et al. (2013)
		<i>Hysterothylacium</i> spp.	
<i>Chelidonichthys queketti</i>	South Africa	<i>Parabrachiella supplicans</i>	Barnard (1955b)
		<i>Medesicaste penetrans</i>	Barnard (1955b); This study
<i>Chelidonichthys queketti</i>		<i>Caligus curtus</i>	Oldewage & Avenant-Oldewage (1993)
		<i>Tentacularia coryphaenae</i>	This study
		Cestode sp. 2	
		<i>Lernentoma asellina</i>	
		<i>Corynosoma australe</i>	
		Acanthocephala sp. 1	
		Monogenea sp. 2	
		Monogenea sp. 2	

Species	Region	Parasite Taxa	Reference
		Isopod sp. 2	
		<i>Oceanobdella sexoculata</i>	
		Cyst sp.	
		Unidentified sp. 1	
		Unidentified sp. 2	
		Unidentified sp. 3	
<i>Chelidonichthys spinosus</i>	-	Not reported	-

4.3 Limitations and Future Research

That the species accumulation curves for both *C. capensis* and *C. queketti* did not asymptote and were still increasing at the maximum sample size of this study demonstrates the need for the processing of further samples until the species accumulation curves flatten out. Samples should also be collected from the full distribution regions of each species. Another limitation of this study was the inability to identify many of the parasites to species level based on morphological techniques, hence it is recommended that a mix of morphological and molecular techniques be used in future research on the parasites of *C. capensis* and *C. queketti*, for clarification of the full parasitological assemblages. In addition, despite smears being taken of the musculature and various organs, no microscopic parasites were found. This could be due to an absence of low prevalence and/or infection intensities of such parasites, or to other factors such as the host samples being frozen rather than fresh. Although microparasites have been recorded from frozen samples of some fish species from South Africa (e.g. sardine *Sardinops sagax*; Reed et al., 2012), future research should examine fresh gurnards, if possible, both to assess whether sample preservation has an effect on parasite detectability and also to aid parasite identification. Samples from each season would also improve future research, allowing for the comparison of parasite infection indices and host biological data across the seasons and determining whether season, and hence seasonality in host characteristics such as condition factor, GSI and HSI, impacts parasite community assemblages.

This study revealed spatial variation in prevalence for *A. pegreffi* and *T. coryphaenae*, in both *C. capensis* and *C. queketti*. Future research should explore the use of these parasite species as potential biological tags for stock assessment for these fishes, expanding sample collection to include multiple years, seasons and regions as well as a variety of size classes. Biological tagging is an ideal tool to assess stock structure and movement in small species such as *C. capensis* and *C. queketti*. Understanding the stock structure of these two important by-catch species is vital as the demersal and inshore trawl fisheries may in future rely more heavily on them.

4.4 Conclusion

Parasite species can reveal a lot about the biology, ecology, and behaviour of their host species, and the health of the marine environment in which they are found in (Marcogliese, 2004; Hudson et al., 2006; Barber, 2007). The opportunistic feeding nature and extended ranges of *C. capensis* and *C. queketti* in benthic ecosystems along the South African coast that cover several bioregions (Meyer & Smale, 1991; Smale & Badenhorst, 1991) are likely to have determined the relatively high parasite diversity observed in this study, and differences in host species biology and ecology appear to be responsible for the difference in their parasite assemblages. Both *Chelidonichthys* species function as intermediate hosts for multiple parasite species, therefore assisting in the transmission and dispersal of these parasite species in the South African marine environment. The new host records of the parasites documented for both *Chelidonichthys capensis* and *Chelidonichthys queketti*, as well as the new geographic record of *Oceanobdella sexoculata*, contributes to our knowledge of these species and of the biodiversity of the South African marine environment.

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