

# **Studies on the Diversity and Distribution of Marine Ichthyoparasites in Southern Africa**

Muhammad Azher Irfan Nunkoo

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Supervisors: Dr. Cecile C. Reed <sup>1</sup>, Assoc. Prof. Sven E. Kerwath <sup>1, 2</sup>, Dr. Carl D. van der Lingen <sup>1, 2, 3</sup>

<sup>1</sup> Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa

<sup>2</sup> Fisheries Research and Development, Branch: Fisheries Management, Department of Agriculture, Forestry and Fisheries, Private Bag X2, Vlaeberg, 8018, Cape Town, South Africa

<sup>3</sup> Marine Research Institute, University of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa

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## Abstract

Parasites are a vital component of ecosystems. However, their contribution to the functioning and structuring of ecosystems has historically been overlooked worldwide. In South Africa, marine ichthyoparasitology has a long history but research has largely been confined to taxonomic studies and the literature pertaining to marine ichthyoparasites is highly fragmented. This situation makes it difficult to gauge advances in marine parasitology, identify knowledge gaps and hampers our understanding of their ecological roles in the marine environments of Southern Africa as well as their use as tools in fisheries science. This thesis aims to explore the diversity of metazoan marine ichthyoparasites reported from Southern African waters and to examine their inter- and intraspecific distribution in marine fishes.

A review of two centuries of parasitological literature, 1818 to 2017, revealed that 378 marine ichthyoparasites have been recorded off South Africa and included taxa from six phyla: Acanthocephala (12), Annelida (6), Arthropoda (210), Cnidaria (11), Nematoda (6) and Platyhelminthes (133). The parasites formed 723 unique host-parasite pairs with 269 host taxa spread across the classes Actinopterygii (186), Elasmobranchii (80), Holocephalii (2) and Myxini (1). Host species with the most diverse parasite assemblages were species of commercial significance, namely *Thyrsites atun* (20) followed by *Merluccius capensis* (17). The dominance of arthropods and platyhelminthes, which together accounted for 90.7% of the parasites found, reflects the interest and expertise of local and foreign researchers who have worked in South Africa.

The parasite assemblage of selected commercially significant fish species was used to assess the degree of interspecific similarity in parasite community structure and identify the drivers of ichthyoparasite community assembly in the Southern Benguela. The examination of 554 specimens comprising six fish species (*Brama brama*, *Chelon richardsonii*,

*Merluccius capensis*, *Merluccius paradoxus*, *Sardinops sagax* and *Thyrsites atun*) caught off the South African west coast revealed that they hosted 41 metazoan parasite taxa. These included 10 new host records and five new geographic records. *Thyrsites atun* and *C. richardsonii* had the most speciose component communities being infected by 17 and 14 taxa respectively. Multivariate analyses revealed that host habitat and identity in conjunction with the host specificity of ectoparasites influenced the community structure of ectoparasitic assemblages. Larval endoparasite community structure, on the other hand, differed between inshore and offshore habitats. Within the offshore habitat, further variation in endoparasite communities were driven by the host species' position in the food web, its trophic ecology and its vulnerability to potential final hosts of larval parasite taxa.

A survey of the metazoan parasites of snoek (*Thyrsites atun*) caught in the Southern Benguela (n = 262) and the Northern Benguela (n = 87) revealed 18 taxa comprising 12 new geographic records for the Northern Benguela. A generalised additive mixed model (GAMM) indicated that infracommunity richness of snoek was determined by host size. Multivariate analyses revealed an ontogenetic shift, driven by an increase in the prevalence and infection intensity of trophically transmitted taxa (*Anisakis* sp., *Corynosoma australe*, *Hepatoxylon trichiuri*, *Molicola uncinatus*), in infracommunity structure as well as in the long-lived larval parasite assemblage. A 'Random Forest' analysis selected *Anisakis* sp. and *M. uncinatus* as potential biological tags for assessing the population structure of snoek in the Benguela ecosystem. GAMMs with binomial and Tweedie error distributions were used to respectively assess the prevalence and abundance of both selected taxa in relation to host traits, seasonality and region of origin. The analyses demonstrated that anisakids were more prevalent and abundant in snoek caught in the Southern Benguela while *M. uncinatus* were more prevalent in snoek from the Northern Benguela. The spatial differences in infection

levels of both parasite taxa suggest the presence of two snoek populations in the Benguela ecosystem.

The information collected, collated and presented in this thesis has enabled an assessment of the present state of marine ichthyoparasitology off Southern Africa. Although the work uncovered a diverse ichthyoparasite fauna, it also revealed a bias towards particular parasitic taxa. The study highlighted a need for wide-ranging parasite surveys not restricted to certain host or parasite taxa in order to improve our knowledge of marine ichthyoparasite diversity in South Africa. The thesis also provided the first assessment of the drivers of parasite community assembly in the Southern Benguela and demonstrated that host ecology and the characteristics of the parasites played an important role in determining their distribution and interspecific distribution. Geographic differences in snoek parasite distribution patterns which reflect ecological variations across ecosystems have also proved useful to inform fishery management.

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This thesis is dedicated to my late grandparents

Nani and Kar

## **Chapter 1. General Introduction**

### **1.1. Marine Parasitology**

Marine ecosystems cover 70% of the planet, extend to great depths and encompass a wide variety of physical conditions. These ecosystems harbour a great diversity of free-living organisms that are, in turn, potential hosts for parasites (Littlewood 2005). Parasites are organisms which rely upon another organism to provide them with a habitat and resources they can exploit (Rohde 2005). Although ubiquitous, parasites have often been overlooked in ecological research for a variety of reasons including their small size, low biomass and perceived inability to affect ecosystem processes (Hudson et al. 2006; Dobson et al. 2008; Lafferty 2008).

Historically, marine parasitology has been restricted to the description of individual parasites and natural history studies (Leach 1818; Milne-Edwards 1834; Poulin et al. 2016a). However, recent developments in epidemiological research and ecological theory have enabled the integration of marine parasitology with other disciplines such as marine ecology, fisheries science, and aquaculture research allowing it to evolve into a hypothesis-driven science (Poulin et al. 2016a). Poulin et al. (2016a) articulate why it has taken so long to integrate parasitology and ecology. The major reason put forward was simply a lack of exposure, whether that be via low representation in general ecology journals or even at the level of university syllabi (Poulin et al. 2016a). Those authors also suggest that parasitologists are guilty of disregarding the main as well as emerging themes in marine ecology, citing the lack of research into the effects of ocean acidification on parasitism as an example (Poulin et al. 2016a; MacLeod 2017).

The uncertainty surrounding the absolute diversity of parasites (Poulin and Morand 2000; Dobson et al. 2008) coupled with unabating rates of parasite discovery in many

taxonomic groups (Randhawa and Poulin 2010; Appeltans et al. 2012) hamper our understanding of the ecological roles of marine parasites. The detection of ecosystem-wide manifestations of parasitism is heavily reliant upon a sound knowledge of the parasite diversity and their respective life cycles within a particular ecosystem (Lafferty et al. 2006; Blasco-Costa and Poulin 2017). Marine parasitology suffers from a lack of reach both in terms of ecosystems and taxa studied, i.e., most research is driven by the proximity of ecosystems (e.g. intertidal and subtidal zones) and the availability or priority of potential study species (Poulin et al. 2016a). Keen to address this gap exposed by Poulin et al. (2016a), Quattrini and Demopoulos (2016) set out to survey the ectoparasite fauna of deep sea fishes using a remotely operated vehicle (ROV) fitted with high definition cameras. Although such innovative techniques have their limits, especially with respect to the resolution of parasite identification that can be achieved (Quattrini and Demopoulos 2016), they have the merit of being a non-invasive, exploratory tool which can be used to plan future research activities. Despite all the methodological and logistical hurdles (Poulin et al. 2016a), the study of marine parasites has made significant contributions to our understanding of the ecological role of parasites and ecosystem functioning.

## **1.2. Marine Parasites: Life Cycles, Roles and Functions**

Despite the diversity of parasites inhabiting the sea (Poulin 2014), their life cycles can be categorised as being either simple or complex (Marcogliese 2004). While parasites with a simple life cycle may have free-living stages, they rely on a single host to ensure the completion of their life cycle (Fig. 1.1). In complex life cycles, the upward or downward inclusion of multiple hosts which harbour a particular life stage in a parasite's life cycle, is thought to have evolved as a means of persistence, although free living stages may still occur (Parker et al. 2003). Upward inclusion of a host, i.e. the adoption of a typically larger free-living taxon as the definitive host in which the parasite reaches maturity, allows the parasite

to attain a greater size at maturity and increase its reproductive output (Parker et al. 2003). On the other hand, the downward addition of an intermediate host (a host harbouring an immature life stage of a particular parasite) facilitates transmission to the definitive host by offering an alternative transmission pathway (Parker et al. 2003). Poulin and Cribb (2002) noted that life cycles comprising several life stages and intermediate hosts are more difficult to complete, and that selective pressures would favour shortened life cycles. Parasites may offset some of the disadvantage by manipulating their intermediate hosts to improve transmission efficiency (Lafferty and Morris 1996; Shaw et al. 2009). For example, the trematode *Euhaplorchis californiensis* affects the behaviour and locomotion of its fish intermediate host in such a way that makes infected fish hosts more conspicuous and therefore facilitates predation by piscivorous birds (Lafferty and Morris 1996; Shaw et al. 2009). Other parasite taxa (e.g. myxozoans) utilize asexual reproduction at one life stage to greatly increase their numbers in intermediate hosts (Poulin and Cribb 2002). Hall et al. (2007) also demonstrated that parasitic castrators benefitted from the increased allocation of energy to the somatic growth of their hosts leading to larger and older hosts which allow for longer infection periods.

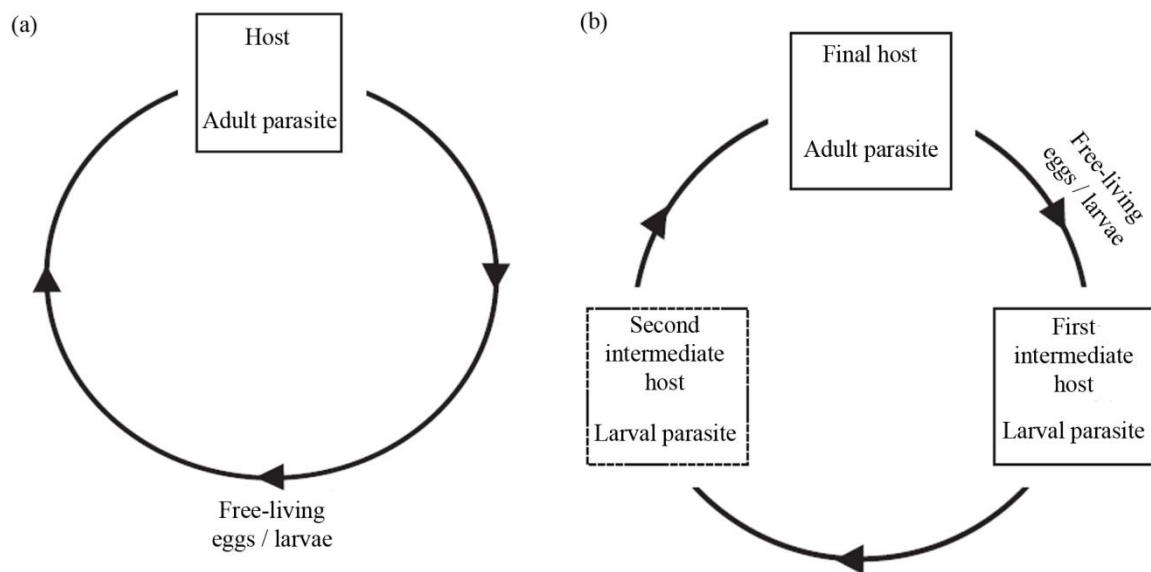


Figure 1.1. Conceptual diagram illustrating the (a) simple and (b) complex life cycles of parasites (after Viney and Cable 2011).

An increasing number of studies have demonstrated that parasites play a significant role in marine ecosystems (e.g. Marcogliese 2004; Leung et al. 2009). Parasites primarily act at the individual host level but these impacts have repercussions across all the levels of biological organisation (Marcogliese 2004). Parasites have physical (Hanafy and Gab-Alla 1998; Blaylock et al. 2004), physiological (Khan and Lacey 1986; Sakuma et al. 1999; Lysne et al. 2006; Fogelman et al. 2009) or behavioural (Miura et al. 2006; Sikkel et al. 2017; Sikkel and Smit 2018) effects on their hosts. At the molecular level, these effects are translated into a selection pressure as parasites favour the recruitment of particular genotypes within a host population (Lafferty 1993; Fogelman et al. 2009). Host populations may also be susceptible to parasite-driven changes in population size and distribution (e.g. Miura et al. 2006) which can in turn affect community structure (Mouritsen and Poulin 2005; Wood et al. 2007). At the ecosystem scale, parasites have the potential to dictate the magnitude of energy flow (Lafferty and Morris 1996; Lafferty 2008) as well as drive ecological engineering through their impacts on keystone species (Thomas et al. 1998; Mouritsen and Poulin 2005).

Parasites are embedded in marine food webs (Lafferty 2013), either as prey items (Grutter 1996; Grutter and Bshary 2003; Lafferty 2008; Artim et al. 2017) or when they take advantage of predator-prey interactions to complete their life cycles (Lafferty 1999). The abundance and diversity of parasites, especially on large predators, has prompted suggestions that they should be considered top predators which make significant contributions to the structure and resilience of the food web (Lafferty et al. 2006; Dunne et al. 2013; Lafferty 2013).

### **1.3. Marine Parasites and Humans**

The omnipresence of parasites in marine ecosystems makes interactions with humans, who are increasingly relying on the sea for resources, inevitable. Most interactions between humans and marine parasites are inconsequential but some do have direct and indirect impacts.

#### **1.3.1. Impacts of Marine Parasites on Humans**

##### **1.3.1.1. Implications in Capture Fisheries**

Worldwide, fisheries exploit a multitude of marine taxa, all of which are potential hosts for parasites. While most parasites in seafood are easily removed or are harmless, some have severe effects on the quality, aesthetic appeal and marketability of marine produce by virtue of their infection sites and biology. Parasites eliciting the most visceral response from potential consumers are without doubt the nematodes (e.g. *Anisakis* spp., *Pseudoterranova* spp.) and cestodes (e.g. *Gymnorhynchus* sp.) which infect the muscles and become visible in the edible flesh (Adams et al. 1997; Wharton et al. 1999). The detection of such parasites in seafood is therefore a critical step in ensuring the quality of the product. Candling, the examination of fish fillets over bright light, is the primary means of mitigating against unacceptably high nematode infection in fish fillets but Levsen et al. (2005) showed that this

method has its limitations, only detecting between 7 – 10% of the nematodes. Other detection methods such as mechanical disruption and pepsin digestion are obviously not practical for use in the fishing industry (Wharton et al. 1999). The implementation of processing protocols designed to limit the migration of nematodes to the surrounding muscles following the host's death are therefore critical in ensuring a catch of acceptable quality (Adams et al. 1997; Wharton and Aalders 2002).

Myxosporeans of the genus *Kudoa* Meglitsch, 1947 are notorious in capture fisheries worldwide primarily due to their effects on product quality. The most characteristic effect of *Kudoa* infections is the post-mortem myoliquefaction, i.e., the breakdown of muscle tissue some of its members (e.g. *K. muscoliquefasciens*, *K. paniformis*, *K. thyrsites*) induce in several commercially important fish species worldwide (Eiras et al. 2014). Myoliquefaction is caused by an accumulation of proteolytic enzymes, whose normal function is to digest surrounding host tissue for the parasite's nutrition, as a direct result of blood flow cessation following the host's death (Moran et al. 1999a). St-Hilaire et al. (1997) showed that a threshold infection intensity was required before signs of myoliquefaction become visible in Atlantic salmon (*Salmo salar*) fillets. The rate of myoliquefaction and infection intensity generally exhibit a positive relationship, i.e., heavily infected fish tend to soften faster than less infected conspecifics (St-Hilaire et al. 1997; Gilman and Eiras 1998). Although myoliquefaction does not render the flesh inedible, its appearance and texture is seriously compromised and such products are invariably rejected by consumers leading to significant economic damage and waste of valuable protein (Henning et al. 2013). The formation of unsightly pseudocysts in the musculature of fish is also a problem sometimes associated with *Kudoa* infections (e.g Kabata and Whitaker 1985; Diamant et al. 2005).

Several commercially significant marine crustaceans such as *Nephrops norvegicus* and a variety of crab species are susceptible to parasitic dinoflagellates of the genus

*Hematodinium* Chatton & poisson, 1930 (Stentiford and Shields 2005; Lafferty et al. 2015). *Hematodinium* infections have physiological effects on their hosts and have been shown to be dependent upon host size and sex. Heavy infections typically result in discolouration of the carapace, muscular degeneration and render the flesh unpalatable (Stentiford and Shields 2005). Moreover, a single infected individual can ruin a whole batch if mixed together, resulting in severe economic losses (Stentiford and Shields 2005).

### **1.3.1.2. Implications for Human Health**

Although a wide variety of parasites are known from marine species that humans harvest for food, only a fraction of these parasites are able to infect humans (Adams et al. 1997). Usually, parasites that require a vertebrate definitive host to complete their life cycles (e.g. *Anisakis* sp., *Diphyllobothrium* sp.) have the most zoonotic potential. The ever-growing popularity of eating raw or lightly processed seafood is increasing the worldwide incidence of human infections by marine parasites (Adams et al. 1994; Nawa et al. 2005; Tokiwa et al. 2018).

The most commonly reported pathogenic helminths are the anisakid nematodes of the genera *Anisakis* Dujardin, 1845, *Contracaecum* Railliet & Henry, 1912 and *Pseudoterranova* Mozgovoi, 1951 which cause a disease referred to as anisakiasis or anisakidosis (Pinel et al. 1996; Adams et al. 1997; Torres et al. 2007; Lim et al. 2015). First reported from the Netherlands, anisakiasis presents itself with acute abdominal pain accompanied by vomiting, nausea and localised internal bleeding as a result of live nematode larvae boring through the gastro-intestinal tract after being ingested along with raw or undercooked seafood (Hochberg and Hamer 2010; Lim et al. 2015). The condition is usually easily treatable by surgical or gastroscopic removal of the offending worm (Adams et al. 1997). Nematodes of the genus *Anisakis* release an assortment of allergens which can, over time, cause acute allergic

reactions as well as anaphylactic shocks, especially in previously sensitized patients (Nieuwenhuizen et al. 2006). This aspect of *Anisakis*' pathology is of most concern for people who work in the seafood processing industry and who regularly come into contact with nematodes. Freezing is a technique commonly used to kill anisakids infecting seafood products; however the efficiency of this technique is temperature and time dependent (Butt et al. 2004; Lanfranchi and Sardella 2010).

Cestodes are the largest known human parasites, adult worms commonly reaching over 2 metres in length (Scholz et al. 2009). Similar to the nematodes, humans acquire cestode infections by ingesting raw or lightly processed fish containing infective plerocercoids which settle and mature in the intestines (Scholz et al. 2009; Scholz and Kuchta 2016). Generally asymptomatic, cestode infections can lead to anaemia and severe vitamin B-12 deficiency, a condition known as diphyllbothriosis (Kuchta et al. 2015). Diphyllbothriosis is caused by some members of the cestode genera *Diphyllbothrium* Cobbold, 1858 and *Adenocephalus* Nybelin, 1931 (Scholz et al. 2009; Kuchta et al. 2015; Scholz and Kuchta 2016). Although diphyllbothriosis is most prevalent in the temperate regions due to the affinity of the implicated parasites for temperate climates, modern practices of shipping fresh fish fillets on ice, human migrations and species introductions facilitate its worldwide spread (Semenas et al. 2001; Scholz et al. 2009; Esteban et al. 2014; Scholz and Kuchta 2016).

Within the last decade it has been suggested that myxosporeans may be pathogenic. *Kudoa septempunctata*, a myxosporean described from cultured Korean olive flounder (*Paralichthys olivaceus*) is strongly suspected of causing food poisoning (Matsukane et al. 2010; Iwashita et al. 2013). Symptoms including abdominal pain, vomiting and diarrhoea generally appear about five hours following the ingestion of raw infected flounder (Iwashita et al. 2013; Chung and Bae 2017). Yahata et al. (2015) determined that a minimum infection

intensity of 72 million kudoid spores per gram of edible flesh was necessary to induce symptoms of food poisoning in patients. Another member of the Kudoidae, *K. hexapunctata* which primarily infects juvenile tunas has also been linked to cases of food poisoning in Japan (Suzuki et al. 2015).

### **1.3.1.3. Implications for Aquaculture**

Aquaculture is the practice of farming aquatic taxa traditionally harvested from the wild. The high stocking densities typically attained in aquaculture settings create the perfect conditions for parasite transmission and persistence (Barber 2007). Parasites encompassing many taxa have been found to be problematic in marine aquaculture (e.g. Moran et al. 1999a; Johnson et al. 2004) where they can impact various stages of development and production (Grossel et al. 2003). For example, the myxosporean *Kudoa neurophila* prevents the production of adequate numbers of fingerlings required for the development of striped trumpeter (*Latris lineata*) aquaculture in Tasmania by causing a fatal inflammation of the central nervous system in fry (Grossel et al. 2005). Other parasites infecting cultured fish species can decrease their growth rates and immunity, alter their behaviour, cause growth abnormalities and even lead to stock mortality (Johnson et al. 2004; Ishimaru et al. 2014), all of which translate into longer grow-out periods and increased financial costs.

Product quality, a key aspect of aquaculture production, can be affected by parasites, particularly those which infect edible tissue. As with wild fisheries, *Kudoa*-induced post-mortem myoliquefaction is a major obstacle in the production of high quality fish fillets, especially in salmonid aquaculture (Moran et al. 1999a). Funk et al. (2007) estimated that the salmon industry in British Columbia incurred losses of \$ 50 million due to *K. thyrssites* infections in 2002 alone. Our lack of knowledge of marine myxozoan life cycles and ecology (Moran et al. 1999b; Esterbauer et al. 2015) is hindering efforts to develop control strategies

although a few advances have been made recently with the use of orally administered nicarbazin and treatment with ultra-violet light (Jones et al. 2012; Cobcroft and Battaglione 2013). Unlike wild fisheries, infection by trophically transmitted parasites (nematodes, cestodes, acanthocephalans) can be controlled to a certain extent by ensuring parasite-free feed is used.

### **1.3.2. Impacts of Humans on Marine Parasites**

Parasitology has traditionally sought to unveil the effects of parasites on free-living wildlife as well as on humans and their activities (Wood et al. 2014). Investigations into the converse relationship, i.e., the impact of humans on parasites, are a relatively novel facet of parasitology which is currently hampered by a dearth of historical data (Wood and Lafferty 2015). Human activities such as fishing and pollution may have direct or indirect effects on parasite infection dynamics within an ecosystem and could lead to parasite extirpation along with a decrease in their contribution to the stability and structuring of the affected ecosystems. For example, King et al. (2007) showed that agricultural activities and urbanisation negatively affected the richness of frog parasite communities. An understanding of the relationship between parasitism and anthropogenic activities is therefore crucial to mitigate against the potential loss of parasite biodiversity and the ecological roles they fulfil.

#### **1.3.2.1. Marine Fisheries**

Fisheries, the harvesting of marine taxa on an industrial scale, is the premier means by which humans affect marine ecosystems globally (Marzoug et al. 2012). The major impact of fisheries is decreasing the abundance of targeted species. This often has consequences that reverberate across ecosystems, not only affecting the free-living biodiversity but also the parasite community. Epidemiological theory predicts that a threshold population density is a pre-requisite for the occurrence of epidemics and that the subsequent probability of disease

outbreaks is directly related to population density. For instance, Lafferty (2004) demonstrated how the removal of lobsters increased the frequency of disease outbreak in sea urchins through a predator release mechanism.

By targeting large, predatory fish species which often serve as definitive hosts for various parasite taxa, fisheries are in direct competition with parasites (Wood and Lafferty 2015). Fishery-induced declines in the abundance of host species implicated in a parasite's life cycle may negatively affect the parasite's transmission and recruitment rates, eventually leading to its extirpation or 'fishing out' (Lafferty et al. 2008; Marzoug et al. 2012). Alarmingly, MacKenzie and Pert (2018) have already documented the first extinction of a marine parasite, the digenean *Stichocotyle nephropis* Cunningham, 1884. The susceptibility and response of parasites to the effects of host overfishing is trait-mediated; parasites with complex life cycles and high host specificity are most vulnerable as they may experience catastrophic declines in host abundances, a situation termed 'life cycle bottleneck' (Lafferty 2004; Lafferty et al. 2008; Wood and Lafferty 2015). The selective removal of old and large individuals that results from fishing activities may decrease the 'carrying capacity' of that population for parasites, since smaller hosts generally harbour fewer parasites (Poulin 2004; Lafferty et al. 2008). Other studies have also demonstrated that due to complex interactions within ecosystems, the effects of fishing on marine parasites are highly variable and difficult to predict (e.g. Sonnenholzner et al. 2011; Wood et al. 2014).

### **1.3.2.2. Marine Pollution**

Pollution in the marine environment which emanates from anthropogenic activities comes in many forms (e.g. thermal, chemical, biological) and impacts both free-living and parasitic biodiversity (Williams and MacKenzie 2003; Sures 2006). Pollution can either stimulate or hinder parasitism via direct or indirect effects. Parasitism may be decreased if

contaminants affect the survival of delicate, free-living stages of parasites (e.g. Morley et al. 2003) or that of adult helminths within a host (Khan and Kiceniuk 1983; Dzikowski et al. 2003). Parasite persistence within an ecosystem can also be challenged by pollution which lowers the abundance of intermediate and final hosts within that ecosystem (Sures 2006). Conversely, pollutants can compromise host immunity thereby facilitating parasitic infections, as suggested by Marcogliese et al. (1998). In general, the effects of pollution on parasitism in the marine realm are highly variable (e.g. Khan and Kiceniuk 1988; Khan 1990; Marcogliese et al. 1998; Pérez-del-Olmo et al. 2007) and are dependent upon the susceptibility of parasites to particular contaminants as well as their respective life cycles (Marcogliese et al. 1998).

### **1.3.3. Applied Marine Parasitology**

Parasites are an integral component of ecosystems whose diversity and abundance within a host population vary in relation to changes in environmental conditions. This property enables parasitologists to utilise parasites as indicators of host biology and ecology and to detect environmental change within ecosystems.

#### **1.3.3.1. Parasites as Biological Markers**

Fisheries management relies heavily on a comprehensive understanding of an exploited species' life history, population structure and ecology. Fisheries scientists have traditionally employed artificial tags, analyses of spatial and seasonal variability in catch, morphometrics, life history characteristics, otolith chemical make-up and shape, molecular data, stomach content and stable isotopes to study exploited populations (Begg and Waldman 1999; Begg et al. 1999; Attwood et al. 2010; Iitembu et al. 2012). However, the holistic utilisation of parasites as biological markers of host biology and ecology along with the traditional parameters is becoming increasingly popular in fisheries research and ichthyology

worldwide (Oliva et al. 2004; Lester et al. 2009; Baldwin et al. 2012; Munster et al. 2015; Vasconcelos et al. 2017).

Parasites make reliable biological markers as they are naturally present in all ecosystems and reflect variations in a host's behaviour and environment (MacKenzie and Abaunza 1998; Marcogliese 2004). Although the collection of parasitological data can be labour intensive, it is relatively inexpensive and depends neither upon host post-tagging survival nor the odds of a recorded recapture (Williams et al. 1992; Mosquera et al. 2003). The use of parasites as biological markers is based on the precept that hosts can only get infected by a particular parasite when in its endemic area (MacKenzie and Abaunza 1998). A parasite's endemic area is that region within which all conditions (biotic and abiotic) necessary to the completion of its life cycle are present (MacKenzie and Abaunza 1998). By studying the parasite assemblages of fish, parasitologists have been able to determine their movement patterns (Lester et al. 2009), unravel their phylogeny and systematics (Williams et al. 1992), follow ontogenetic shifts in their diet (Munster et al. 2015) as well as delineate the stock structure of exploited fish populations (Marcogliese et al. 2003; Williams and Lester 2006; Santos et al. 2009; Braicovich et al. 2012; MacKenzie and Hemmingsen 2015). Despite some limitations (Braicovich et al. 2016) and abuse (Lester and MacKenzie 2009), parasites are proving themselves to be useful biomarkers in ecological and fisheries research.

### **1.3.3.2. Parasites as Bioindicators**

Since the mid-20<sup>th</sup> century, there has been an increasing amount of research into the effects of pollution in marine ecosystems (Williams and MacKenzie 2003). Currently, over 50 techniques including the analysis of water quality parameters and the use of biological indicators are available for monitoring marine pollution (Lafferty 1997; Williams and MacKenzie 2003; Palm et al. 2011). Biological indicators are organisms which owing to their

sensitivity or resistance to disturbance can be used as sentinels to detect ecosystem degradation (MacKenzie 1999; Palm and Ruckert 2009; Vidal-Martínez and Wunderlich 2017). Historically, biological indicators have comprised free-living organisms from a wide range of taxa but there has recently been growing interest in the use of parasites as indicator species to detect and monitor anthropogenic impacts on marine ecosystems (Williams and MacKenzie 2003; Vidal-Martínez and Wunderlich 2017).

Parasites supplant free-living organisms as bioindicators in many ways. Notably, parasites are highly diverse and abundant, their complex life cycles vastly increase the number of possible indicators and fragile, free-living stages can be affected even at low levels of disturbance (MacKenzie 1999). The range of possible outcomes of interactions between parasites and several types of pollution (Lafferty 1997) indicate that by examining variations in a single host species' parasite infracommunities (Bush et al. 1997), information about more than one type of pollutant can be gleaned (Vidal-Martínez and Wunderlich 2017). Additionally, obtaining adequate sample sizes for quantitative studies is generally not problematic with parasites compared to free living bioindicators, especially at higher trophic levels (Vidal-Martínez and Wunderlich 2017). Several authors have also demonstrated the propensity of parasites to bioaccumulate metals more effectively than their hosts, even at very low ambient concentrations (Sures et al. 1999; Sures and Reimann 2003; Pascual and Abollo 2005). However, the magnitude of this effect is dependent upon the 'parasite-metal' relationship being considered while further variation is induced by the differential ability of various host tissues to uptake heavy metals (Sures et al. 1999; Sures and Reimann 2003).

#### **1.4. Thesis Overview**

This thesis aims to improve our knowledge and understanding of marine ichthyoparasitology in southern Africa by assessing its evolution as a field of study,

examining the drivers governing the distribution of parasites amongst marine fishes and evaluating geographic variation in the parasite assemblage of a widely distributed fish in the Benguela ecosystem.

The thesis comprises six chapters, each written as a distinct body of work. Chapter 1, the general introduction, is followed by a description of the study region and dissection protocol and techniques used for the identification of parasites (Chapter 2). To gain an appreciation of the current state of affairs in marine ichthyoparasitology in South Africa, a list of all parasites reported from marine fishes is generated through a survey of literature followed by an examination of spatial and temporal trends in discoveries and infection reports (Chapter 3). Chapter 4 identifies the processes dictating the distribution of parasite diversity and community structure amongst a suite of selected fish hosts in the Southern Benguela. The aim of Chapter 5 is to use snoek (*Thyrsites atun*) as a case study to investigate potential geographical variations in parasite assemblage composition and infection levels in the Benguela ecosystem and use these data to assess snoek population structure, which could contribute to the management of this commercially harvested species. Finally a synthesis of the main findings for each chapter and proposed avenues for future research in the field of marine ichthyoparasitology in Southern Africa is provided in Chapter 6.

## **Chapter 2. Study Region: Currents, Oceanography and Biogeography**

### **2.1. Currents of Southern Africa**

The marine environment around southern Africa is influenced by two major boundary currents; the warm Agulhas Current flowing down the east coast bringing water from the subtropics and the Benguela Current which brings cool Southern Ocean water to the west coast (Fig. 2.1). This thesis focuses on the marine environment of South Africa and Namibia as defined by their respective exclusive economic zones (EEZs) and excluding offshore territories. After gaining independence in 1990, Namibia declared its EEZ and South Africa followed suit in 1994 proclaiming sovereignty over 1 068 659 km<sup>2</sup> spanning both the Atlantic and Indian oceans. Together the EEZs of these two countries cover 1 633 407 km<sup>2</sup>.

#### **2.1.1. The Benguela Current**

The Benguela Current is one of four major eastern boundary currents of the World and flows northwards along the south west coast of Africa (Fig. 2.1) (Garzoli and Gordon 1996; Hutchings et al. 2009; Veitch et al. 2010). The Benguela Current is bound to the north by the poleward flowing Angola Current and to the southeast by the powerful, warm Agulhas Current (Hutchings et al. 2009). It consists of both an offshore and an inshore component. The outer appendage of the Benguela Current forms the northward flowing, easternmost limb of the South Atlantic Subtropical Gyre, thus blurring its outer boundary (Garzoli and Gordon 1996; Veitch et al. 2010). Inshore, the Benguela Current ecosystem comprises discrete, wind-driven upwelling cells of varying intensity and seasonality, the largest of which is located off Lüderitz (Hutchings et al. 2009; Veitch et al. 2010).

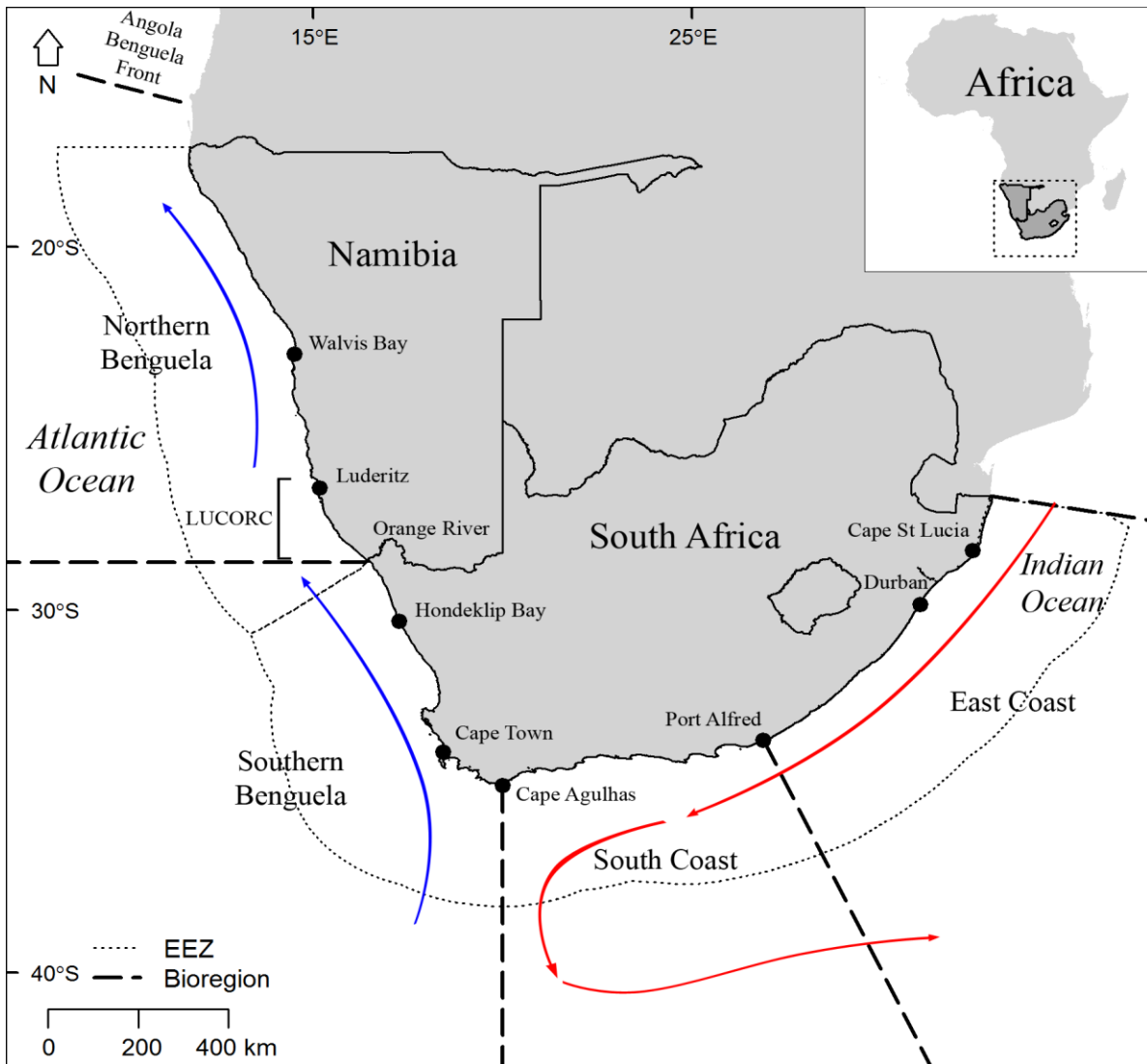


Figure 2.1. Map showing the location and flow direction of the Agulhas (red) and Benguela (blue) currents, marine biogeographic regions and exclusive economic zones (EEZs) off Namibia and South Africa (LUCORC: Lüderitz Upwelling Cell Orange River Cone region).

### 2.1.2. The Agulhas Current

Forming the most southerly limb of the Indian Ocean's western boundary system (Bang et al. 1978), the Agulhas Current flows polewards along the shelf edge off South Africa's east and south coasts before retroflecting back into the southern Indian Ocean as the Agulhas Return Current (Lutjeharms 2007). Born from the mixing of warm water from the Mozambique Current, the East Madagascar Current and the Agulhas Return Current around 27° S (Fig. 2.1), the sea surface temperature in the Agulhas Current varies between 22° - 27°

C (Lutjeharms 2006, 2007). Remote sensing has highlighted the presence of two subsystems within the Agulhas Current: the northern Agulhas where the current flows close to shore due to the narrow shelf and the southern Agulhas Current which starts off Port Elizabeth as the current meanders offshore following the widening of the shelf (Lutjeharms 2007). Upwelling of nutrient-rich waters occurs in both subsystems, notably off Cape St. Lucia and Port Alfred (Lutjeharms 2007). The input of warm Agulhas water in the south Atlantic, via filament and ring leakages, may have global climate implications (Lutjeharms 2006; Lutjeharms and Bornman 2010; Beal et al. 2011).

## **2.2. Marine Ecosystems of South Western Africa**

Climatic (e.g. wind regime), oceanographic (e.g. sea surface temperature) and physical (e.g. shelf width) heterogeneity within the regions influenced by these two major currents has resulted in the formation of distinct ecosystems or subsystems (Fig. 2.1). A recent spatial characterisation of the marine environments off south western Africa, aimed at facilitating marine spatial planning and ecosystem-based management, identified four subsystems (Kirkman et al. 2016). Delineation of the subsystems relied on expert knowledge and the variation in both biotic and abiotic variables (Teske et al. 2011; Kirkman et al. 2016). Subsystem 1, which borders Angola, comprises the northernmost part of the Benguela Current Large Marine Ecosystem and is bound to the south by the Angola-Benguela Front (Cochrane et al. 2009; Kirkman et al. 2016); this subsystem is not considered further in this thesis as it lies outside the boundaries of the Namibian EEZ. Subsystem 2 refers to what is commonly known as the Northern Benguela, Subsystem 3 corresponds to the Southern Benguela and Subsystem 4, also known as the south coast, runs from Cape Agulhas to Port Alfred (Hutchings et al. 2009; Blamey et al. 2015; Kirkman et al. 2016). A further subtropical marine bioregion occurs from Port Alfred northwards and is referred to as the east coast (Blamey et al. 2015).

### 2.2.1. The Northern Benguela

The Northern Benguela extends from 15° S to 29° S along the Namibian coastline (Fig. 2.1). It is bound to the north by the Angola-Benguela Front and to the south by the powerful, perennial Lüderitz Upwelling Cell and the Orange River Cone (LUCORC) (Lett et al. 2007; Hutchings et al. 2009; Veitch et al. 2010). The spatial extent and seasonal persistence of turbulence, mixing and offshore advection in conjunction with a subsurface thermal barrier within the LUCORC hinders the transport of pelagic organisms (e.g. zooplankton, ichthyoplankton) between the Northern Benguela and the Southern Benguela, thus creating a natural boundary for these organisms (Lett et al. 2007). The Northern Benguela is a cool temperate ecosystem characterised by perennial upwelling driven by southerly winds (Heymans et al. 2004; Kirkman et al. 2016).

The thriving sardine (*Sardinops sagax*) fishery which operated in the Northern Benguela crashed in the 1970s due to heavy fishing and that decline was soon followed by a decline in anchovy (*Engraulis encrasicolus*) in the 1990s (Hutchings et al. 2009). The ecological niches left vacant by these two keystone fish species have been taken over by jellyfish (*Aequorea forskalea* and *Chrysaora fulgida*), horse mackerel (*Trachurus capensis*) and the bearded goby (*Sufflogobius bibarbitatus*) which now dominate the system (Shannon and Jarre-Teichmann 1999; Moloney 2010; Roux et al. 2013; Jarre et al. 2015). At lower trophic levels “jellyfication” of the Northern Benguela has resulted in a near 10-fold increase in zooplankton biomass in which copepods dominate (Heymans et al. 2004; Jarre et al. 2015). Predators such as penguins (*Spheniscus demersus*) and gannets (*Morus capensis*) which feed primarily on small pelagic fish and were unable to adapt to these changes have declined severely or have been displaced from the Northern Benguela (Hutchings et al. 2009). Cape fur seal (*Arctocephalus pusillus pusillus*) populations on the other hand, have been expanding as seals are opportunistic predators resilient to the collapse of clupeoid stocks (Hutchings et

al. 2009). The changes in distribution and abundance of ecologically important species in the Northern Benguela has significantly altered food web topology, lowered the efficiency of energy transfer across trophic levels and diminished ecosystem resilience (Shannon and Jarre-Teichmann 1999; Heymans et al. 2004), possibly irreversibly (Roux et al. 2013).

### **2.2.2. The Southern Benguela**

The Southern Benguela is separated from the adjacent Northern Benguela by the LUCORC region and is generally assumed to extend from the Orange River mouth southwards to Cape Agulhas (20 ° E, Fig. 2.1) (Cury and Shannon 2004; Lett et al. 2007; Kirkman et al. 2016). The region is primarily influenced by the Benguela Current and is classified as a cool temperate ecosystem (Hutchings et al. 2009; Kirkman et al. 2016). In contrast to the Northern Benguela, upwelling in the Southern Benguela is seasonal (September to March), peaking in summer (Shannon et al. 2003; Hutchings et al. 2009). Upwelling activity on the west coast promotes high levels of primary productivity which supports major fisheries for species including Cape hakes (*Merluccius capensis* and *M. paradoxus*), anchovy (*Engraulis encrasicolus*) and sardines (*Sardinops sagax*) as well as important nursery grounds such as St Helena Bay off South Africa for many fish species (Shannon et al. 2003; Blamey et al. 2015; Jarre et al. 2015; Kirkman et al. 2016).

Since the 1950s, the Southern Benguela has experienced a number of ecosystem-scale regime shifts driven by climate variability and a long history of anthropogenic activities (Cury and Shannon 2004; Blamey et al. 2015; Jarre et al. 2015). Changes in the abundance of forage fish and community structure of zooplankton (Cury and Shannon 2004) have had cascading impacts at higher trophic levels. Populations of the African jackass penguin (*Spheniscus demersus*) and other seabirds have decreased and shifted East in response to the decline and movement of forage fish stocks (Blamey et al. 2015). As in the Northern

Benguela, Cape fur seals (*Arctocephalus pusillus pusillus*), have proved very adaptable to ecosystem changes and are thriving in the Southern Benguela where they are a protected species (Cury and Shannon 2004; Hutchings et al. 2009). Although there have been a number of ecosystem changes in the Southern Benguela, small pelagic and mesopelagic fish species still dominate the mid-trophic levels of the pelagic food web unlike in the Northern Benguela where they have been replaced by other taxa (Jarre-Teichmann et al. 1998; Roux et al. 2013).

### **2.2.3. The South Coast**

The south coast, extending between Cape Agulhas and Port Alfred (Fig. 2.1), is a region where cool-temperate and warm-temperate taxa from the west and the east coasts of South Africa mix (Branch et al. 2010; Teske et al. 2011). The south coast is largely influenced by the Agulhas Current offshore and by intermittent upwelling inshore (Kirkman et al. 2016). Another dominant feature of the region is the wide and shallow shelf which forms the Central and Eastern Agulhas Bank (Hutchings et al. 2002). Localised upwelling activity fertilises the Agulhas Bank but upwelling and primary production are substantially lower compared to the west coast (Kirkman et al. 2016; Lamont et al. 2018). However, comprising both soft and hard substratum as well as reefs, the Agulhas Bank supports a wide variety of fishes, including many species of economic significance (Hutchings et al. 2002; Götz et al. 2014).

Since the mid-1800s, the south coast has been the theatre for several fishery sectors targeting a range of demersal, pelagic and reef-associated fish species (Griffiths 2000; Yemane et al. 2008; Attwood et al. 2011; Götz et al. 2014; Reed et al. 2017). Over many decades, a lack of quantitative management has led to the collapse of many socio-economically important fish stocks such as geelbek (*Atractoscion aequidens*) and kob (*Argyrosomus* spp.) on the south coast (Griffiths 2000). Ecologically, the south coast serves

as an important spawning and nursery ground for many fish and invertebrate species (Hutchings et al. 2002). The central and eastern Agulhas Bank is a preferred spawning area for offshore, pelagic, shoaling species like sardines, mackerel and hakes (Hutchings et al. 2002). Because this region has often been lumped with the west coast for large scale ecological modelling (e.g. Shannon et al. 2003), it is difficult to tease out trends unique to the south coast. Nonetheless, an increase in gannet population concomitant with the movement of sardines and anchovy onto the central Agulhas Bank has been noted (Kirkman et al. 2016).

#### **2.2.4. The East Coast**

The east coast lies north of Port Alfred and is a subtropical, oligotrophic region characterised by a narrow shelf which is influenced by the Agulhas Current (Bang et al. 1978; Schumann 1987). Interestingly, localised widening of the shelf rather than the wind regime promotes upwelling along the east coast (Lutjeharms et al. 2000). Upwelling brings nutrient-rich water onto the shelf and helps maintain the biological productivity and community of the region (Lutjeharms et al. 2000). Compared to the west and south coast regions, the east coast is a relatively data-poor sub-system whose biological functioning has not been extensively studied (Ayers and Scharler 2011; de Lecea et al. 2016). While the regions influenced by the Benguela Current have a higher harvestable biomass, the east coast's diversity of habitats (coral reefs, sponge reefs, sand bank, soft sediments) harbour a diverse subtropical fish assemblage (Turpie et al. 2000; Celliers and Schleyer 2002; Ayers and Scharler 2011; Fennessy 2016). The Natal Bight region, situated between Durban and Richards Bay, is utilised by several teleost species of commercial importance such as the slinger (*Chrysoblephus puniceps*) as a nursery area (Hutchings et al. 2002).

The east coast supports both crustacean and linefish commercial fisheries (Turpie and Lamberth 2010). A small beach seine fishery has also historically exploited the 'sardine-run',

the annual, eastward winter migration of sardines *Sardinops sagax* (van der Lingen et al. 2010). Two more fishery sectors, namely subsistence and recreational fisheries, operate in the intertidal, sub-tidal and inshore areas targeting a range of seaweeds, invertebrates, crustaceans and fish (Penney et al. 1999; Clark et al. 2002; Sowman 2006; Pradervand et al. 2007; Lamberth et al. 2009).

## **Chapter 3. A Checklist of Metazoan Parasites Associated with Marine Fishes of South Africa**

### **3.1. Introduction**

Marine biodiversity research in South Africa has a long history, dating back to the collections of Carl Peter Thunberg in the 18<sup>th</sup> century (Gilchrist 1923a; Griffiths et al. 2010). The *modus operandi* at the time was to send naturalists on voyages to colonies where they would collect, preserve and send specimens back to various European institutions for classification and description (Gilchrist 1923a). The arrival of John Dow Fisher Gilchrist as state marine biologist in 1895 signalled the start of a new era in South African marine biology (van Sittert 1995).

Although Gilchrist's primary mandate was to develop the fisheries sector, non-ichthyological samples were also regularly retained on board the research trawler *S.S. Pieter Faure* and preserved for later examination (Barnard 1964). By the 1980's, the vast majority of frequently encountered invertebrates and fishes had been catalogued thanks to the efforts of many enthusiastic taxonomists, most notably the prolific Keppel Harcourt Barnard (Gordon 1966; Beckley et al. 2002; Griffiths et al. 2010). From then on, the focus of marine research in South Africa shifted towards elucidating the biology of various organisms (e.g. Griffiths 1996, 2002; Attwood et al. 2010) as well as ecological and phylogenetic investigations (e.g. Kensley 1981; Bally 1987; Shannon et al. 2003; Watermeyer et al. 2008) with the aim of improving management and marine conservation.

#### **3.1.1. Marine Parasitology in South Africa**

While most frequently encountered free-living marine organisms are relatively well known, parasites are lagging behind; as is evident in the latest appraisal of our accumulated knowledge on marine biodiversity in South Africa. Griffiths and his colleagues (2010)

acknowledge the presence of 12 915 species of which approximately one sixth are fishes. The most well documented and speciose taxa, unsurprisingly, are the vertebrates followed by echinoderms, amphipods, decapods, isopods, polychaetes, molluscs, and macro algae. Griffiths et al. (2010) also evaluated the state of knowledge for each taxon and concluded that for some taxa the quality of the data allowed testing of ecological and biogeographic hypotheses to inform management and conservation. Taxa that could clearly be identified as parasites (acanthocephala, aspidogastrea, cestoda, digenea, hirudinea, monogenea, and myxozoa) only accounted for 2.7% of the species known at the time from South African waters (Griffiths et al. 2010). Other parasites may have been included by Griffiths et al. (2010) within the orders Copepoda, Isopoda and Nematoda as these taxa comprise both free-living and parasitic species but this was not specified. The very low diversity of known marine parasites suggests that the development of South African marine parasitology has historically been hindered, probably by a paucity of local experts and the lack of interests of marine scientists in parasites.

The isopod *Anilocra capensis* Leach, 1818 was the first parasite to be recorded from the seas surrounding South Africa (Leach 1818; Smit and Hadfield 2015). For over 150 years, marine parasitology has remained in an explorative and descriptive phase, with all the works published during this time being taxonomic in nature (e.g. Barnard 1914, 1955a; Kensley and Grindley 1973). Dr. Willie Oldewage from the University of Johannesburg was the first to have an interest in assessing the geographical and interspecific distribution of copepod ichthyoparasites off the South African coast (Oldewage and van As 1989; Oldewage 1992a, 1993a). Around the same time, the first investigations into the host-parasite relationships of commercially harvested marine fishes were conducted (Botha 1986; Payne 1986). Much later, some ecological aspects of fish parasitism were examined (Wright et al. 2001; Parker and Booth 2013; Nunkoo et al. 2016) but research in the field has remained patchy. The most

recent development in marine parasitology in South Africa has been the use of parasites as indicators of fish population structure (e.g. Reed et al. 2012; Le Roux 2013; van der Lingen et al. 2015; Weston et al. 2015; Ukomadu 2017) and as an early warning system for pollution in marine ecosystems (Morris et al. 2016). Although marine ichthyoparasitology is gaining ground and recognition in South Africa (Smit and Hadfield 2015) no exhaustive checklist of marine fish parasites exists despite the efforts of several parasitologists based in South Africa (e.g. Oldewage and Avenant-Oldewage 1993; Dippenaar 2004; Hadfield et al. 2014a) and the inception of the SeaKeys project which aims at unlocking marine biodiversity knowledge and opportunities (South African National Biodiversity Institute 2018).

### **3.1.2. Checklists: Benefits and Constraints**

Checklists and synopses are useful sources of primary information in ecological research. They can be used to estimate regional species diversity, determine distribution ranges, harvest data for meta-analyses and in the case of parasite checklists, enable an evaluation of host-specificity (Poulin et al. 2016b). The informative potential of a checklist, however, largely depends on its completeness, a property which can be assessed using a connectance metric or species accumulation curves (Dove and Cribb 2006; Poulin et al. 2016b). While parasite checklists and synopses have, in the past, been sporadic (e.g. Hewitt and Hine 1972; Love and Moser 1983) there has been a flurry of recent publications (e.g. Violante-González et al. 2007; Santos et al. 2008; Alves et al. 2015; Merlo-Serna and García-Prieto 2016). The rate at which parasite checklists are being published appears to have benefitted from the launch of journals which focus on biodiversity, taxonomy and systematics and routinely accept the submission of large monographs (e.g. *Zootaxa*, *Zookeys*). Nevertheless, most of these checklists are geographically restricted or only treat a particular parasitic or host group. The advent of molecular genetics has added a new layer of

complexity to checklists as the discovery of cryptic species dictates that most, if not all, checklists are inherently incomplete (Poulin et al. 2016b).

### **3.1.3. Study Aims**

As the year 2018 marks two centuries of marine parasite research in South Africa, it was deemed an opportune moment to evaluate the status of our knowledge of ichthyoparasite biodiversity in South Africa. This chapter seeks to provide the first comprehensive checklist of metazoan parasites associated with marine fishes of South Africa. Such an effort will hopefully stimulate further research by identifying knowledge gaps and providing a baseline to evaluate progress in our knowledge of marine parasite biodiversity around South Africa.

## **3.2. Materials and Methods**

### **3.2.1. Study Area**

In this chapter, only the marine bioregions bound by the political boundaries of South Africa are considered (Fig. 3.1), i.e., the west coast, the south coast and the east coast (see previous chapter for a description of each bioregion). Parasites infecting hosts from inshore and offshore environments as well as estuaries were included. Only studies conducted around mainland South Africa were considered as no parasitological investigations have been reported from offshore territories administered by South Africa (e.g. Marion Island) to my knowledge.

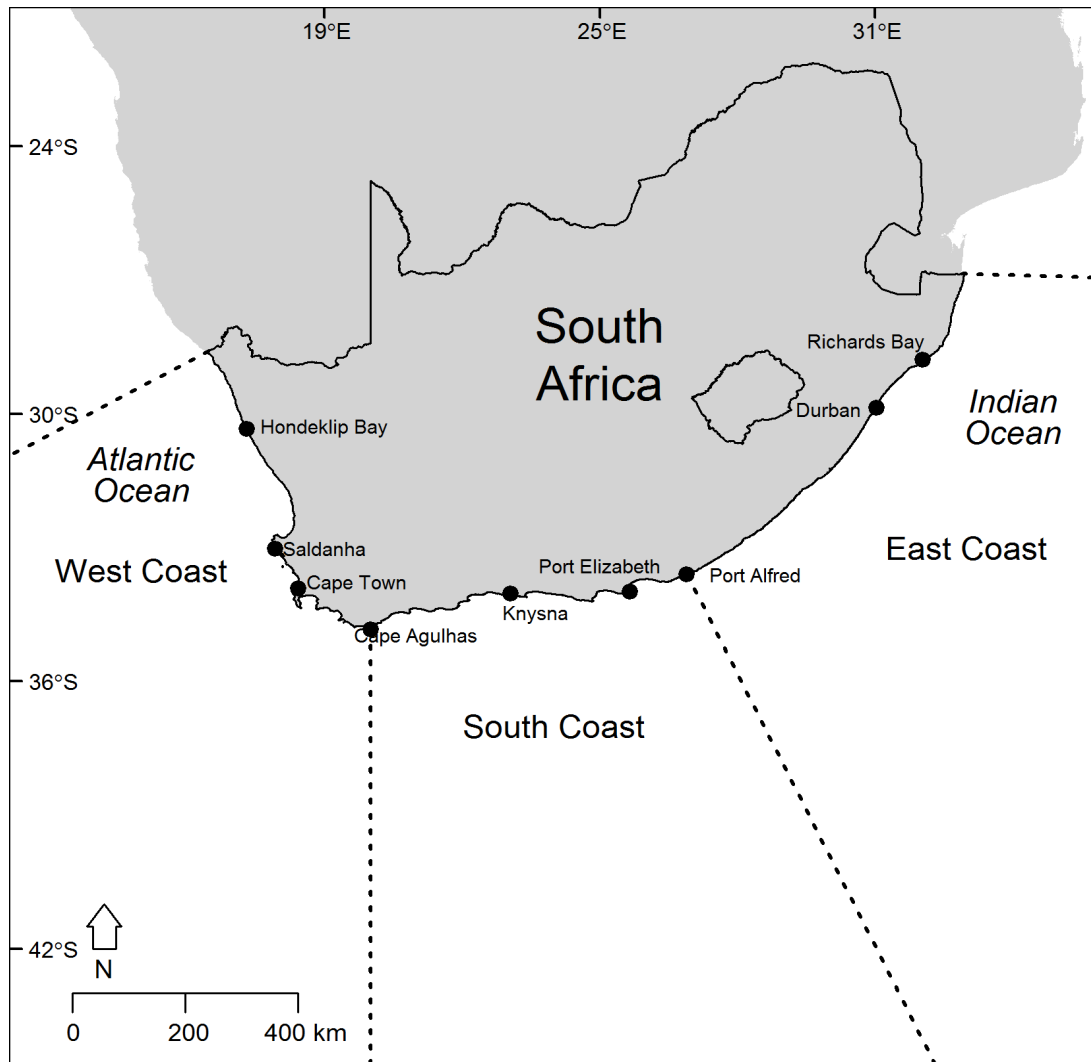


Figure 3.1. Map of the study area showing the three marine bioregions (west coast, south coast, east coast) and the main localities mentioned in the checklist.

### 3.2.2. Generating the Checklist

A review of both published and gray parasitological literature, including postgraduate projects and dissertations, was conducted to generate a list of metazoan parasites associated with marine fishes of South Africa. Pertinent publications were identified via web searches using various keywords singly or in combinations (e.g. parasite, fish, marine, Agulhas, Benguela, South Africa, teleost, metazoan, copepod, nematode, myxozoan, acanthocephala, cestode, monogenea, digenea). Other reports considered in this study that were not available online were requested from the respective authors. New records derived from opportunistic

collections of parasites from a variety of marine fish species that I made over the last six years (2013-2018) have also been included. The distribution of each parasite across the three marine bioregions of South Africa was derived from the localities at which they were reported. Only parasites identified at least to genus level were included.

The parasite checklist is arranged in alphabetical order according to the phylum, class, order, family, genera and species to which they belong. The fish hosts, localities, distribution, year of first record and references used are given for each parasite taxon. Fish and parasite classification and nomenclature follow FishBase (Froese and Pauly 2018) and the World Register of Marine Species (Horton et al. 2019) respectively. The checklist includes records published up to April 2019.

### **3.2.3. Data Analysis**

The host-parasite records reported in the publications consulted were entered in a spreadsheet along with their geographic location and reference. The data were explored and summarised by means of pivot tables and were first used to determine the contribution of different phyla to the checklist within the three bioregions. Next, the number of new geographic records, new host species examined, new host-parasite combinations and publications per year was determined. The cumulative number of parasite taxa, host species, host-parasite pairs and publications was then computed and plotted against time. Records for which hosts were not identified to at least genus level and unpublished records were excluded from the analyses. The same procedure was then applied within each of the different phyla included in the checklist.

Chao2, a non-parametric diversity estimator based on the presence of rare taxa infecting only one or two individual host species within the pool of hosts examined and 10 000 randomisations, was generated to evaluate how many parasite taxa may infect the host

species examined and identified to species level as a measure of how many parasites may have been overlooked (Clarke and Gorley 2006; Dove and Cribb 2006).

### **3.3. Results**

#### **3.3.1. Discovery, Diversity and Distribution**

##### **3.3.1.1. Ichthyoparasites**

A total of 378 parasite taxa comprising members of 6 phyla (Acanthocephala, Annelida, Arthropoda, Cnidaria, Nematoda and Platyhelminthes) have been reported infecting marine fishes in South African waters. Thirty-two taxa included in the list were either not identified to species level or their identification was doubtful. Two phyla, namely the Arthropoda (55.8%) and the Platyhelminthes (35%) account for the vast majority of the known marine ichthyoparasite fauna of South Africa. The dominance of arthropods and platyhelminthes was also apparent within all three bioregions (Fig. 3.2). While all 6 phyla have been recorded from the west and south coasts, nematodes and cnidarians have not been reported infecting fishes from the east coast (Fig. 3.2). The Chao2 diversity estimate revealed that up to 730 parasite taxa may be expected from the 249 hosts identified to species level.

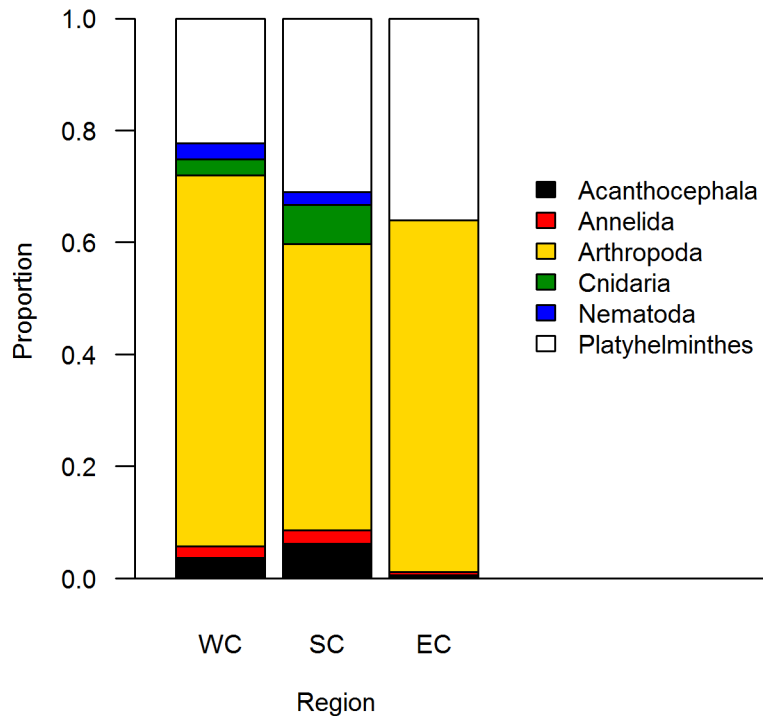


Figure 3.2. The relative contribution of the different phyla towards the composition of the ichthyoparasite fauna of the three marine biogeographic regions (EC: east coast, SC: south coast, WC: west coast) off South Africa.

The description of *Anilocra capensis* by Leach in 1818 was the first South African record of a marine ichthyoparasite (Fig 3.3a). Between 1920 and 1980, four years (1948, 1955, 1973 and 1976) saw the publication of a noticeably large number of parasite records and descriptions. However, from the mid 1980's onwards, the rate at which new parasite records were being published increased, with more than five records per annum on no less than 18 occasions. The years 2007, 2013, 2015, 2017 and 2018 were particularly productive with a total of 82 new South African records published. After a slow start, the rate at which we are adding to our knowledge of marine ichthyoparasite diversity has been increasing steadily since the mid 1950's (Fig.3.3a). The vast majority (> 72%) of parasites have been reported from only one of the three marine bioregions (Fig 3.3b), amongst which the east coast harboured the most speciose parasite assemblage (1413 taxa). A small number of parasites have been reported from more than one bioregion; 17 parasites have been found in

all three bioregions, 37 have been recorded from the south coast and the west coast while the east coast shares 14 and 12 taxa with the south and west coasts, respectively (Fig 3.3b).

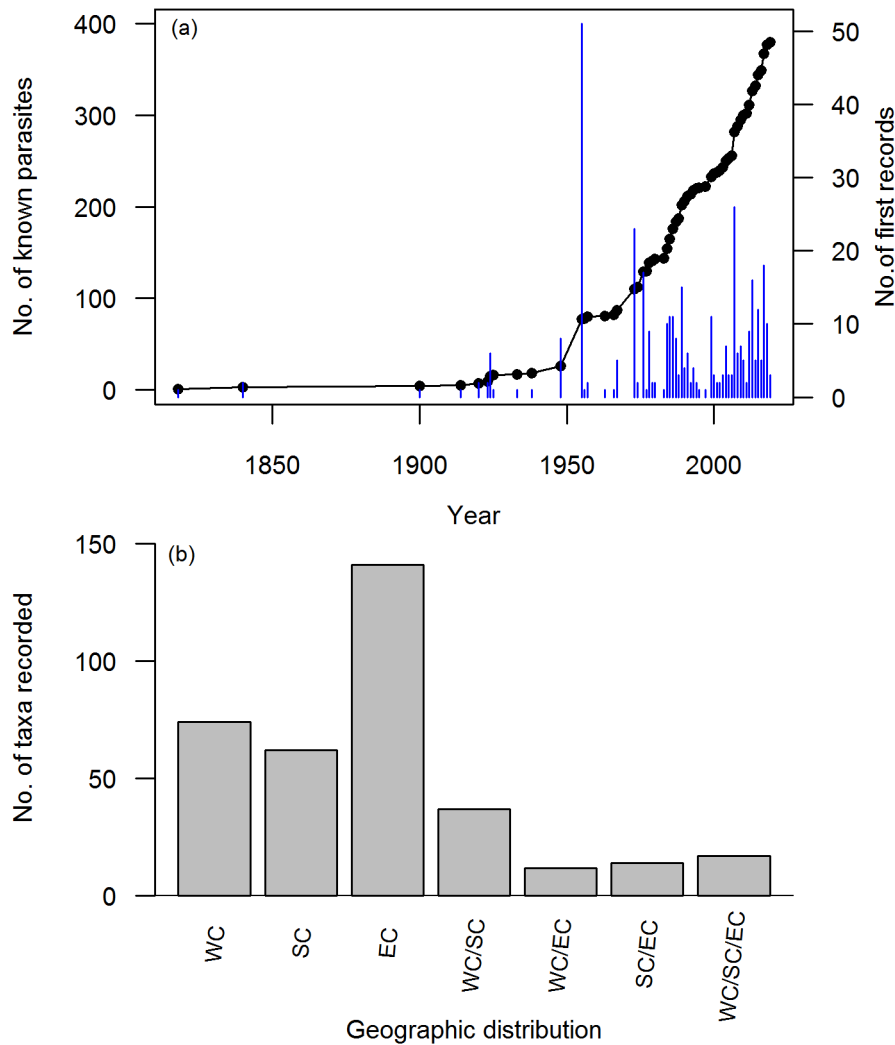


Figure 3.3. (a) The evolution of our knowledge of marine ichthyoparasite diversity shown as the cumulative number of ichthyoparasite taxa recorded from South African marine fish species over the period 1818-2019 (black line) and the number of first South African records per annum (blue bars); and (b) the spatial distribution of the marine ichthyoparasite fauna of South Africa.

### 3.3.1.2. Host taxa

Metazoan parasites have been recorded from 269 fish taxa that were identified at least to genus level and included members of the classes Actinopterygii (72 families, 186 taxa), Elasmobranchii (21 families, 80 taxa), Holocephalii (2 families, 2 taxa) and Myxini (1

family, 1 species). On average, 2.8 different host taxa have been subjected to parasitological examinations every year since 1923. There were nonetheless periods of increased activity (1955, 1973, 1985, 1987, 2007, 2008; Fig 3.4a) when more than 10 new host taxa per annum were examined. While the examination of new host species was slow before 1980, new marine fish taxa have been surveyed for parasites practically every year since (Fig 3.4a). Spatial data was not available for a small proportion (4.8%) of the hosts examined but of those for which geographic information was available, over a third originated from the east coast, the west coast alone contributed to nearly 23% of the fish examined and the south coast had the lowest contribution of the three bioregions (Fig 3.4b). Fifteen host species have been examined in all three bioregions and a further 50 in two of the three regions. While only a single parasite has been recorded from 53% of hosts examined, some fish species had substantially more; *Thyrsites atun* and *Merluccius capensis* are known to host 20 and 17 taxa respectively, while 16 parasites have been recovered from *Carcharodon carcharias* and 14 from *Trachurus capensis*.

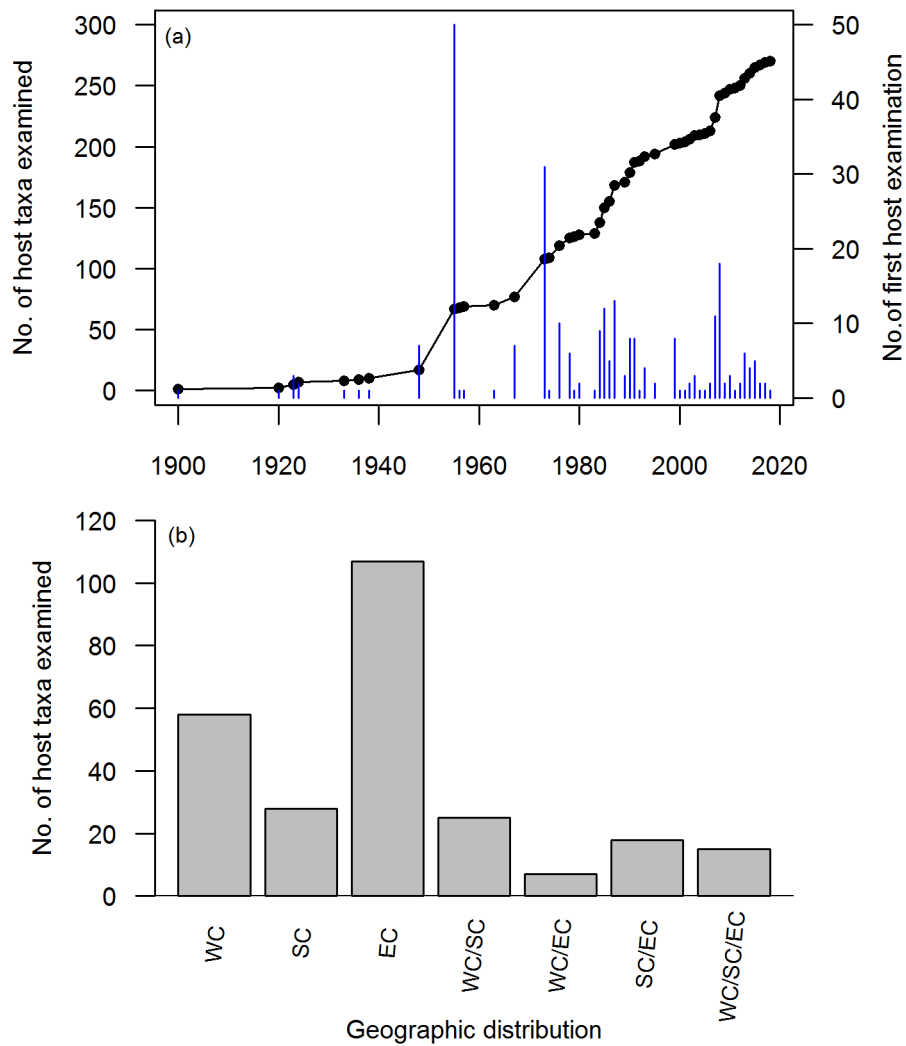


Figure 3.4. (a) The evolution of the number of marine fish taxa examined for parasites shown as the cumulative number of South African marine fish host species examined over the period 1900-2019 (black line) and the number of first host examinations per annum (blue bars); and (b) the spatial distribution of the marine fishes known to host parasites off South Africa.

### 3.3.1.3. Host-Parasite Pairs

The literature survey revealed that 723 unique host-parasite associations have so far been recorded in South African seas. After 150 years of research, by 1968, only 14.2% of the host-parasite pairs had been recorded, an annual average of 0.7 records while over the last 50 years the rate has increased to 12.5 new records per annum (Fig 3.5a). Excluding 55 records for which no spatial data was available, 42.6% of the host-parasite associations were recorded

on the east coast. The west coast accounts for a further 27.3% of the records and 18.2% originate from the south coast (Fig 3.5b). Very few host-parasite pairs have been recorded on more than one coast although the south and west coasts share 57 records.

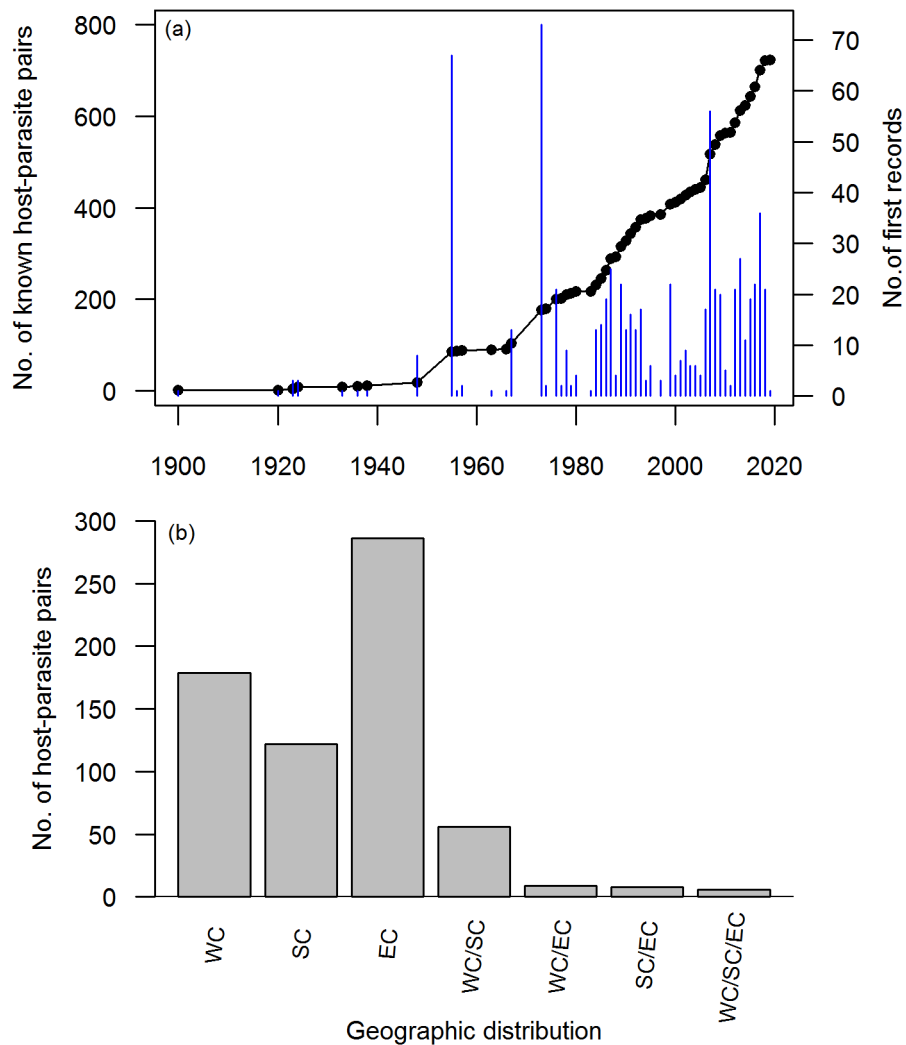


Figure 3.5. (a) The evolution of the number of host-parasite pairs recorded shown as the cumulative number of South African marine fish host species examined over the period 1900-2019 (black line) and the number of host-parasite pairs recorded per annum (blue bars); and (b) the spatial distribution of host-parasite pairs recorded off South Africa.

### 3.3.1.4. Parasitological Publications

One hundred and fifty-three works including published articles, monographs, graduate student projects, dissertations and theses spanning from 1818 to 2019 were included in the

study. The rate at which new parasitological articles were published over the first 150 years of the discipline in South Africa was very low (0.1 works/year). The last 50 years have seen a marked increase in the number and rate (2.6 works/year) of parasitological publications resulting in over 85% of the works included in the present study being published post 1968 (Fig 3.6a). Of the works included, 99 were only concerned with one of the three South African marine biogeographical regions whilst 14 had a wide coverage spanning all three coasts (Fig 3.6b). The south coast was mentioned along with the east coast or the west coast in 18.3% of the manuscripts included. Only four of the works surveyed included both the east and west coasts (Fig 3.6b). No spatial data was available for eight publications. The majority of publications (62.1%) included in the checklist were authored by researchers plying their trade in South Africa at the time of publication whilst 26.1% originated from foreign parasitologists; only 18 articles were borne out of collaboration between South African and foreign scientists.

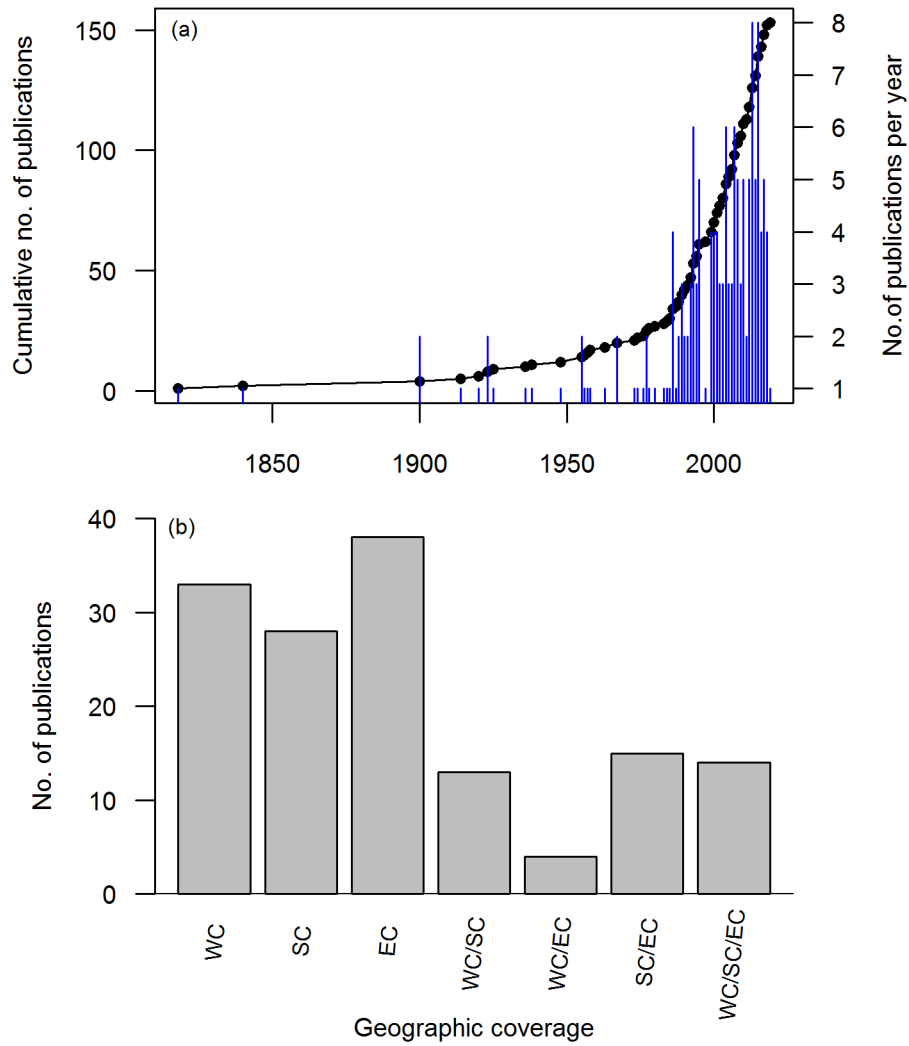


Figure 3.6. (a) The evolution of the number of parasitological publications shown as the cumulative number of South African marine fish host species examined over the period 1818-2019 (black line) and the number of parasitological publications per annum (blue bars); and (b) the spatial coverage of marine ichthyoparasitological publications in South Africa.

Table 3.1. The taxonomic composition of the marine ichthyoparasite fauna of South Africa.

<b>Phylum</b>	<b>Class</b>	<b>Subclass</b>	<b>Order (Suborder)</b>	<b>Family</b>	<b>Genera</b>	
Acanthocephala	Eoacanthocephala		Neoechinorhynchida	Neoechinorhynchidae	1	
			Echinorhynchida	Arhythmacanthidae	1	
	Palaeacanthocephala			Pomporhynchidae	1	
				Rhadinorhynchidae	1	
			Polymorphida	Polymorphidae	2	
Annelida	Clitellata	Hirudinea	Rhynchobdellida	Piscicolidae	6	
Arthropoda	Hexanauplia	Copepoda	Cyclopoida (Poecilostomatoida)	Bomolochidae	4	
				Chondracanthidae	5	
				Ergasilidae	2	
				Siphonostomatoida	Caligidae	8
				Dichelesteiidae	1	
				Eudactylinidae	4	
				Hatschekiidae	1	
				Kroyeriidae	2	
				Lernaeopodidae	15	
				Lernanthropidae	3	
				Pandaridae	13	
				Pennellidae	3	
				Pseudocycnidae	2	
				Sphyrriidae	3	
Trebiidae	1					

Table 3.1 (continued). The taxonomic composition of the marine ichthyoparasite fauna of South Africa.

<b>Phylum</b>	<b>Class</b>	<b>Subclass</b>	<b>Order (Suborder)</b>	<b>Family</b>	<b>Genera</b>				
Arthropoda	Ichthyostraca	Branchiura	Arguloida	Argulidae	1				
				Malacostraca	Eumalacostraca	Isopoda	Cirolanidae	1	
	Cymothoidae	8							
	Gnathiidae	3							
Cnidaria	Myxozoa	Myxosporea	Bivalvulida	Alatasporidae	1				
				Ceratomyxidae	1				
				Myxobolidae	1				
				Sinuolineidae	1				
				Sphaeromyxidae	1				
			Nematoda	Chromadorea	Chromadoria	Multivalvulida	Kudoidae	1	
							Rhabditida	Anisakidae	2
								Cucullanidae	1
								Physalopteridae	1
								Echinobothriidae	2
Platyhelminthes	Cestoda	Eucestoda	Diphyllidea	Gyrocotylidae	1				
				Onchoproteocephalidea	Onchobothriidae	1			
			Phyllobothriidea	Phyllobothriidae	1				
			Rhinebothriidea	Echeneibothriidae	1				
			Tetraphyllidea	Calliobothriidae	2				
				Tetraphyllidae	1				
				Trypanorhyncha	Gymnorhynchidae	1			

Table 3.1 (continued). The taxonomic composition of the marine ichthyoparasite fauna of South Africa.

<b>Phylum</b>	<b>Class</b>	<b>Subclass</b>	<b>Order (Suborder)</b>	<b>Family</b>	<b>Genera</b>				
Platyhelminthes	Cestoda	Eucestoda	Trypanorhyncha	Lacistorhynchidae	2				
				Otobothriidae	1				
				Sphyriocephalidae	1				
				Tentaculariidae	3				
				Monogenea	Monopisthocotylea	Capsalidea	Capsalidae	2	
							Gyrodactylidae	1	
							Gyrodactylidae	1	
							Monocotylidea	Microbothriidae	2
								Monocotylidae	3
							Polyopisthocotylea	Chimaericolidea	Chimaericolidae
	Diclybothriidea	Hexabothriidae	2						
	Mazocraeidea	Discocotylidae	1						
		Gastrocotylidae	1						
	Trematoda	Aspidogastrea	Aspidogastrida	Hexostomatidae	1				
				Mazocraeidae	1				
				Microcotylidae	1				
				Aspidogastridae	1				
				Multicalycidae	1				
		Digenea			Strigeidae	1			
					Acanthocolpidae	2			
Plagiorchiida					Aephniidiogenidae	2			

Table 3.1 (continued). The taxonomic composition of the marine ichthyoparasite fauna of South Africa.

<b>Phylum</b>	<b>Class</b>	<b>Subclass</b>	<b>Order (Suborder)</b>	<b>Family</b>	<b>Genera</b>
Platyhelminthes	Trematoda	Digenea	Plagiorchiida	Azygiidae	1
				Bucephalidae	4
				Cryptogonimidae	1
				Derogenidae	1
				Didymozoidae	1
				Enenteridae	2
				Faustulidae	1
				Fellodistomidae	3
				Gonocercidae	1
				Gorgoderidae	2
				Haplospalchnidae	1
				Hemiuridae	8
				Lecithasteridae	1
				Lepidapedidae	1
				Lepocreadiidae	3
				Mesometridae	1
				Opecoelidae	11
Sclerodistomidae	1				
Zoogonidae	5				

Table 3.2. The classification and number of marine fish taxa recorded as hosts of metazoan parasites in South Africa.

Host Class	Host Family	Host Genus	No. of taxa	Host Class	Host Family	Host Genus	No. of taxa	
<b>Actinopterygii</b>	Acanthuridae	<i>Acanthurus</i>	1	<b>Actinopterygii</b>	Carangidae	<i>Lichia</i>	1	
	Ariidae	<i>Arius</i>	1			<i>Megalaspis</i>	1	
		<i>Galeichthys</i>	1			<i>Pseudocaranx</i>	1	
	Ariommatidae	<i>Ariomma</i>	1			<i>Scomberoides</i>	2	
	Atherinidae	<i>Atherinomorus</i>	1			<i>Seriola</i>	1	
	Belonidae	<i>Ablennes</i>	1			<i>Trachinotus</i>	1	
		<i>Strongylura</i>	1			<i>Trachurus</i>	2	
	Berycidae	<i>Beryx</i>	1			Chaetodontidae	<i>Chaetodon</i>	1
	Blenniidae	<i>Antennablennius</i>	1			Cheilodactylidae	<i>Cheilodactylus</i>	1
		<i>Cirripectes</i>	1			<i>Chirodactylus</i>	1	
		<i>Istiblennius</i>	2		Chirocentridae	<i>Chirocentrus</i>	1	
		<i>Omobranchus</i>	1		Chlorophthalmidae	<i>Chlorophthalmus</i>	2	
		<i>Parablennius</i>	1		Clinidae	<i>Blennioclinus</i>	1	
		<i>Scartella</i>	1			<i>Clinus</i>	6	
	Bramiidae	<i>Brama</i>	1			<i>Muraenoclinus</i>	1	
	Callorhynchidae	<i>Engraulis</i>	1		<i>Pavoclinus</i>	1		
	Carangidae	<i>Alectis</i>	1		<i>Xenopoclinus</i>	2		
		<i>Alepes</i>	1		Clupeidae	<i>Engraulis</i>	1	
		<i>Carangoides</i>	2			<i>Hilsa</i>	1	
		<i>Caranx</i>	2			<i>Sardinops</i>	1	
<i>Decapterus</i>		1	Congiopodidae	<i>Congiopodus</i>	1			

Table 3.2 (continued). The classification and number of marine fish taxa recorded as hosts of metazoan parasites in South Africa.

Host Class	Host Family	Host Genus	No. of taxa	Host Class	Host Family	Host Genus	No. of taxa
<b>Actinopterygii</b>	Coryphaenidae	<i>Coryphaena</i>	1	<b>Actinopterygii</b>	Luvaridae	<i>Luvarus</i>	1
	Dichistiidae	<i>Dichistius</i>	1		Macrouridae	<i>Coelorinchus</i>	1
	Dussumieriidae	<i>Etrumeus</i>	1			<i>Malacocephalus</i>	1
	Elopidae	<i>Elops</i>	1			<i>Unspecified</i>	1
	Engraulidae	<i>Stolephorus</i>	1		Merlucciidae	<i>Merluccius</i>	2
	Gempylidae	<i>Ruvettus</i>	1		Molidae	<i>Masturus</i>	1
		<i>Thyrsites</i>	1			<i>Mola</i>	2
	Gobiesocidae	<i>Chorisochismus</i>	1		Monacanthidae	<i>Aluterus</i>	1
	Gobiidae	<i>Caffrogobius</i>	1			<i>Pervagor</i>	1
		<i>Psammogobius</i>	1		Monodactylidae	<i>Monodactylus</i>	1
	Haemulidae	<i>Pomadasys</i>	4		Moridae	<i>Antimora</i>	1
	Hemigaleidae	<i>Hemipristis</i>	1			<i>Lepidion</i>	1
	Hemiramphidae	<i>Hemiramphus</i>	2		Mugilidae	<i>Chelon</i>	4
		<i>Hyporhamphus</i>	1			<i>Crenimugil</i>	1
	Istiophoridae	<i>Istiompax</i>	2			<i>Liza</i>	1
		<i>Kajikia</i>	1			<i>Mugil</i>	2
	Kyphosidae	<i>Kyphosus</i>	1			<i>Osteomugil</i>	2
		<i>Neoscorpis</i>	1			<i>Pseudomyxus</i>	1
	Labridae	<i>Halichoeres</i>	1			Parupeneus	1
		<i>Thalassoma</i>	1			Muraenesocidae	<i>Muraenesox</i>
Lophiidae	<i>Lophius</i>	1		Muraenidae	<i>Gymnothorax</i>	1	

Table 3.2 (continued). The classification and number of marine fish taxa recorded as hosts of metazoan parasites in South Africa.

Host Class	Host Family	Host Genus	No. of taxa	Host Class	Host Family	Host Genus	No. of taxa	
<b>Actinopterygii</b>	Myctophidae	<i>Gonichthys</i>	1	<b>Actinopterygii</b>	Scombridae	<i>Katsuwonus</i>	1	
		<i>Lampanyctodes</i>	1			<i>Rastrelliger</i>	1	
		<i>Unspecified</i>	1			<i>Sarda</i>	2	
	Nomeidae	<i>Cubiceps</i>	1			<i>Scomber</i>	2	
		<i>Genypterus</i>	1			<i>Scomberomorus</i>	3	
	Ophididae	<i>Neocyttus</i>	1			<i>Thunnus</i>	6	
	Oreosomatidae	<i>Pempheris</i>	1			Scorpaenidae	<i>Pterois</i>	1
			1				<i>Scorpaenodes</i>	1
	Pempheridae	<i>Plotosus</i>	1			Sebastidae	<i>Helicolenus</i>	1
	Plotosidae	<i>Abudefduf</i>	1				<i>Sebastes</i>	1
			1		Serranidae	<i>Epinephelus</i>	3	
	Pomacentridae	<i>Plectroglyphidodon</i>	1			Setarchidae	<i>Lioscorpus</i>	1
	Pomatomidae	<i>Pomatomus</i>	1				Soleidae	<i>Barnardichthys</i>
			1		<i>Solea</i>	1		
	Psychrolutidae	<i>Cottunculus</i>	1		Sparidae	<i>Acanthopagrus</i>	1	
	Psychrolutidae	<i>Psychrolutes</i>	1			<i>Argyrozona</i>	1	
			1			<i>Cheimerius</i>	1	
	Rachycentridae	<i>Rachycentron</i>	1			<i>Chrysoblephus</i>	2	
	Sciaenidae	<i>Argyrosomus</i>	2			<i>Cymatoceps</i>	1	
			1			<i>Diplodus</i>	2	
1			<i>Lithognathus</i>	1				
1								
1								
Sciaenidae	<i>Argyrozona</i>	1						
		1						
		1						
Sciaenidae	<i>Atractoscion</i>	1						
		1						
		1						
		1						
		1						
Sciaenidae	<i>Otolithes</i>	1						
		1						
Sciaenidae	<i>Umbrina</i>	1						
		1						
Scombridae	<i>Acanthocybium</i>	1						
		1						
	<i>Euthynnus</i>	1						

Table 3.2 (continued). The classification and number of marine fish taxa recorded as hosts of metazoan parasites in South Africa.

Host Class	Host Family	Host Genus	No. of taxa	Host Class	Host Family	Host Genus	No. of taxa
<b>Actinopterygii</b>	Sparidae	<i>Pachymetopon</i>	1	<b>Elasmobranchii</b>	Alopiidae	<i>Alopias</i>	1
		<i>Petrus</i>	1		Carcharhinidae	<i>Carcharhinus</i>	10
		<i>Pterogymnus</i>	1		<i>Galeocerdo</i>	1	
		<i>Rhabdosargus</i>	4		<i>Prionace</i>	1	
		<i>Sarpa</i>	1		<i>Rhizoprionodon</i>	1	
		<i>Sparodon</i>	1		<i>Scoliodon</i>	1	
		<i>SpondylIOSoma</i>	1		<i>Triaenodon</i>	1	
	Sphyraenidae	<i>Sphyraena</i>	1		Carcharhinidae	<i>Carcharhinus</i>	1
	Stegostomatidae	<i>Stegostoma</i>	2		Dasyatidae	<i>Dasyatis</i>	2
	Synphobranchi dae	<i>Histiobranchus</i>	1		<i>Himantura</i>	1	
	Syngnathidae	<i>Syngnathus</i>	1		<i>Maculabatis</i>	1	
	Synodontidae	<i>Saurida</i>	1		Etmopteriidae	<i>Etmopterus</i>	1
		<i>Trachinocephalus</i>	1		Gymnuridae	<i>Gymnura</i>	1
	Terapontidae	<i>Terapon</i>	1		Hexanchidae	<i>Hexanchus</i>	1
	Tetraodontidae	<i>Amblyrhynchotes</i>	1		Lamnidae	<i>Carcharodon</i>	1
		<i>Arothron</i>	1		<i>Isurus</i>	2	
		<i>Torquigener</i>	1		<i>Lamna</i>	1	
	Trichiuridae	<i>Lepidopus</i>	1		Myliobatidae	<i>Aetobatus</i>	1
	Triglidae	<i>Chelidonichthys</i>	3		<i>Aetomylaeus</i>	1	
	Xiphiidae	<i>Xiphias</i>	1		<i>Mobula</i>	4	
Zeidae	<i>Zeus</i>	1	Odontaspididae	<i>Carcharias</i>	4		

Table 3.2 (continued). The classification and number of marine fish taxa recorded as hosts of metazoan parasites in South Africa.

Host Class	Host Family	Host Genus	No. of taxa	Host Class	Host Family	Host Genus	No. of taxa	
<b>Elasmobranchii</b>	Odontaspidae	<i>Odontaspis</i>	1	<b>Elasmobranchii</b>	Triakidae	<i>Scylliogaleus</i>	1	
	Pristiophoridae	<i>Pliotrema</i>	1		<b>Holocephali</b>	Callorhynchidae	<i>Callorhynchus</i>	1
	Rajidae	<i>Cruriraja</i>	1	Chimaeridae		<i>Hydrolagus</i>	1	
		<i>Dipturus</i>	1	<b>Myxini</b>		Myxinidae	<i>Eptatretus</i>	1
		<i>Leucoraja</i>	1					
		<i>Raja</i>	3					
		<i>Rajella</i>	2					
	<i>Rostroraja</i>	1						
	Rhincodontidae	<i>Rhincodon</i>	1					
	Rhininae	<i>Rhina</i>	1					
	Rhinobatidae	<i>Acroteriobatus</i>	2					
		<i>Rhinobatos</i>	1					
	Rhynchobatinae	<i>Rhynchobatus</i>	1					
	Scyliorhinidae	<i>Haploblepharus</i>	2					
		<i>Poroderma</i>	2					
	Sphyrnidae	<i>Sphyrna</i>	4					
	Squalidae	<i>Squalus</i>	4					
	Torpedinidae	<i>Tetronarce</i>	1					
		<i>Torpedo</i>	2					
	Triakidae	<i>Galeorhinus</i>	2					
<i>Mustelus</i>		5						

### 3.3.1.5. Acanthocephala

Twelve acanthocephalan taxa, scattered amongst five families, four of which are represented by one genus each (Table 3.1), have been reported infecting South African marine fishes since 1963 (Fig 3.7a), when *Longicollum chabanaudi* Dollfus & Golvan, 1963 was recorded. Acanthocephalans have only been reported from 11 species of bony fishes. Acanthocephalan records have been few and far apart with the richest year being 2017 when four new geographical records were reported (Fig 3.7a). Five acanthocephalan taxa have exclusively been found on the south coast while the east and west coasts harbour much less diverse unique acanthocephalan faunas, and three taxa have distributions straddling both the south and west coasts; only one has been reported from the east coast (Fig 3.7b).

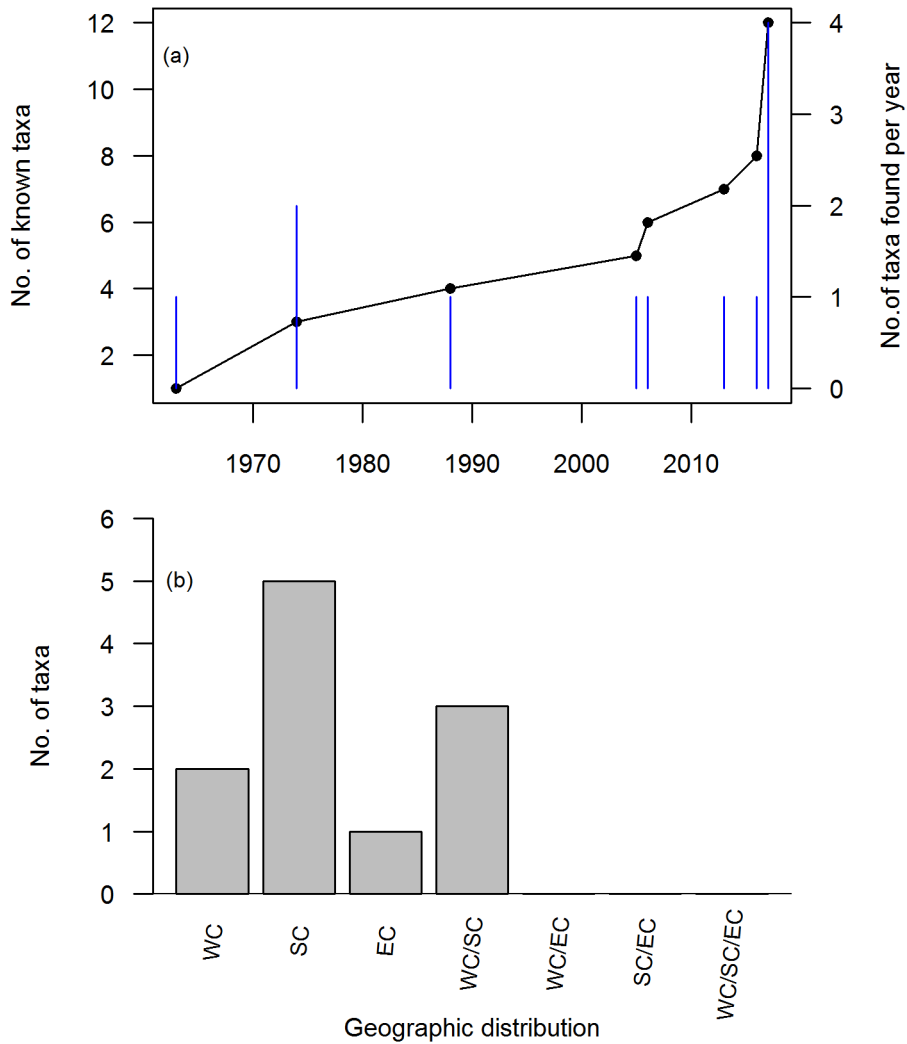


Figure 3.7. (a) The evolution of the number of known acanthocephalans shown as the cumulative number reported from South African marine fish hosts examined over the period 1963-2019 (black line) and the number of acanthocephalans reported per annum (blue bars); and (b) the biogeographical distribution of acanthocephalans reported from South African marine fishes.

### 3.3.1.6. Annelida

Marine ichthyoparasitic annelids were first reported in 1958 (Fig 3.8a) and six genera within the family Piscicolidae (Table 3.1), each comprising one taxon, have so far been found in South Africa (Fig 3.8a). Annelids have been found infecting teleosts (8 species), elasmobranchs (3 species) and holocephalans (1 species). The south and west coasts each

harbour two unique annelid taxa and share a further one while a single species has been found on the east coast (Fig 3.8b).

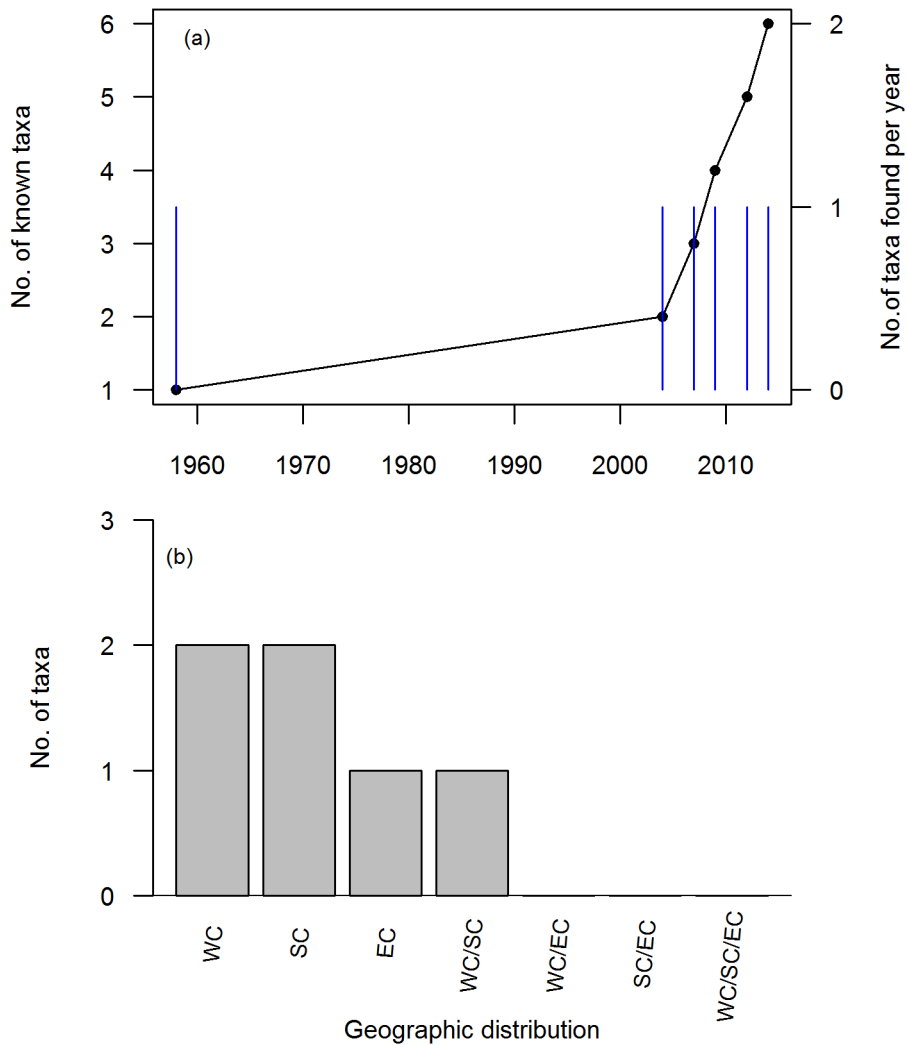


Figure 3.8. (a) The evolution of the number of known annelid parasites shown as the cumulative number reported from South African marine fish hosts examined over the period 1958-2019 (black line) and the number of annelid parasites reported per annum (blue bars); and (b) the biogeographical distribution of annelid parasites reported from South African marine fishes.

### 3.3.1.7. Arthropoda

The South African ichthyoparasitic arthropod fauna reported to date is comprised of 210 taxa spread across four orders, 19 families and 79 genera (Table 3.1). These parasites have been found infecting 118 actinopterygian fishes, 70 elasmobranchs and two members of

the class Holocephali. Following the first record of an arthropod ichthyoparasite in 1818, the addition of new arthropod records was slow until the late 1940's (Fig 3.9a). After that period however, the frequency at which new geographic records were published increased progressively and in three years (1955, 1973, 2007), more than 10 new arthropod records were published, with over 40 taxa in 1955 alone (Fig 3.9a). Over 35% of the arthropods discovered infecting South African marine fish have only been found on the east coast and 21% of the taxa were exclusive to the west coast (Fig 3.9b). Fourteen taxa occurred across all three bioregions while the distribution of 22 taxa included both the south and west coasts. Eighty-three percent of the publications containing arthropod records have been authored by parasitologists working in South Africa, with the difference accounted for by collaborations between South African and foreign parasitologists as well as the work of foreign parasitologists.

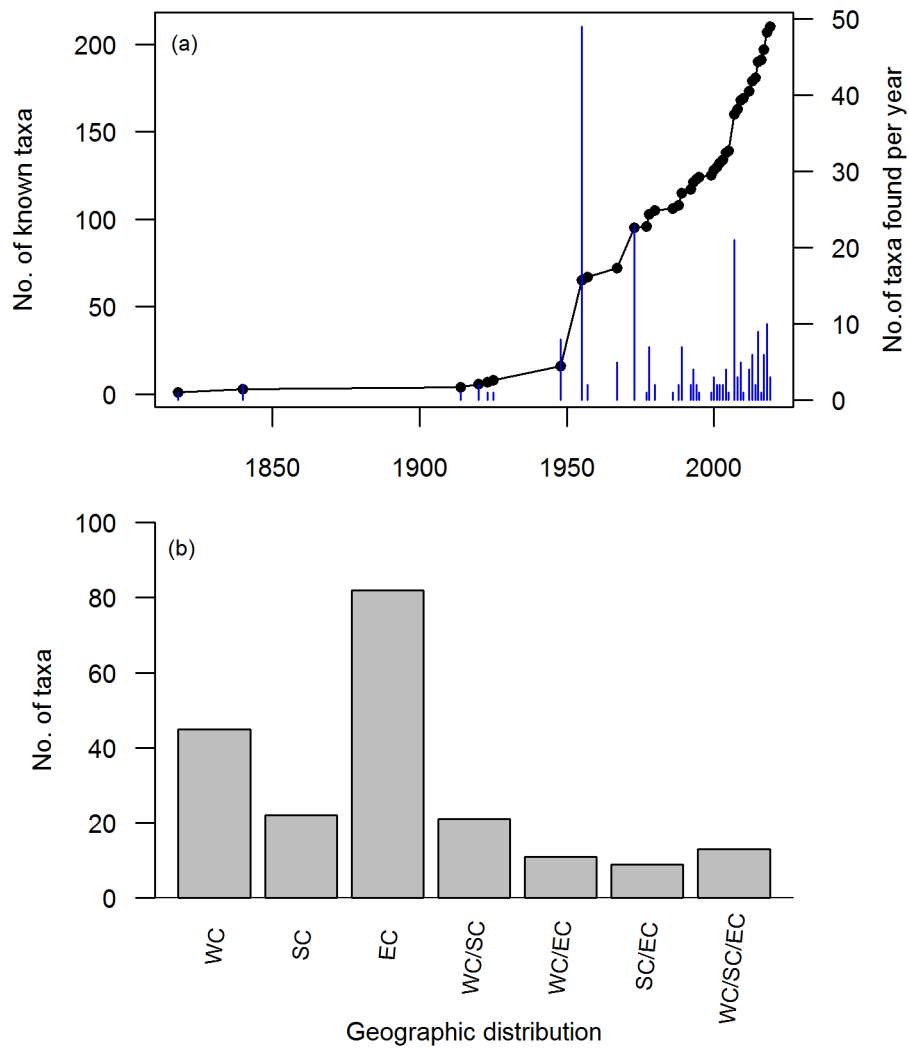


Figure 3.9. (a) The evolution of the number of known arthropod parasites shown as the cumulative number reported from South African marine fish hosts examined over the period 1818-2019 (black line) and the number of arthropod parasites reported per annum (blue bars); and (b) the biogeographical distribution of arthropod parasites reported from South African marine fishes.

### 3.3.1.8. Cnidaria

Parasitic cnidarians of the class Myxozoa, were first reported infecting South African fishes in 1923 (Fig 3.10a), when *Kudoa thyrsites* was described (Gilchrist 1923b). Between 2007 and 2017, a further ten taxa have been reported. Seven of the 11 taxa have been exclusively found on the south coast while only two are unique to the west coast (Fig 3.10b).

*Pseudalataspora vanderlingeni* and *Kudoa thyrsites* on the other hand are known to infect fish on both the south and west coasts.

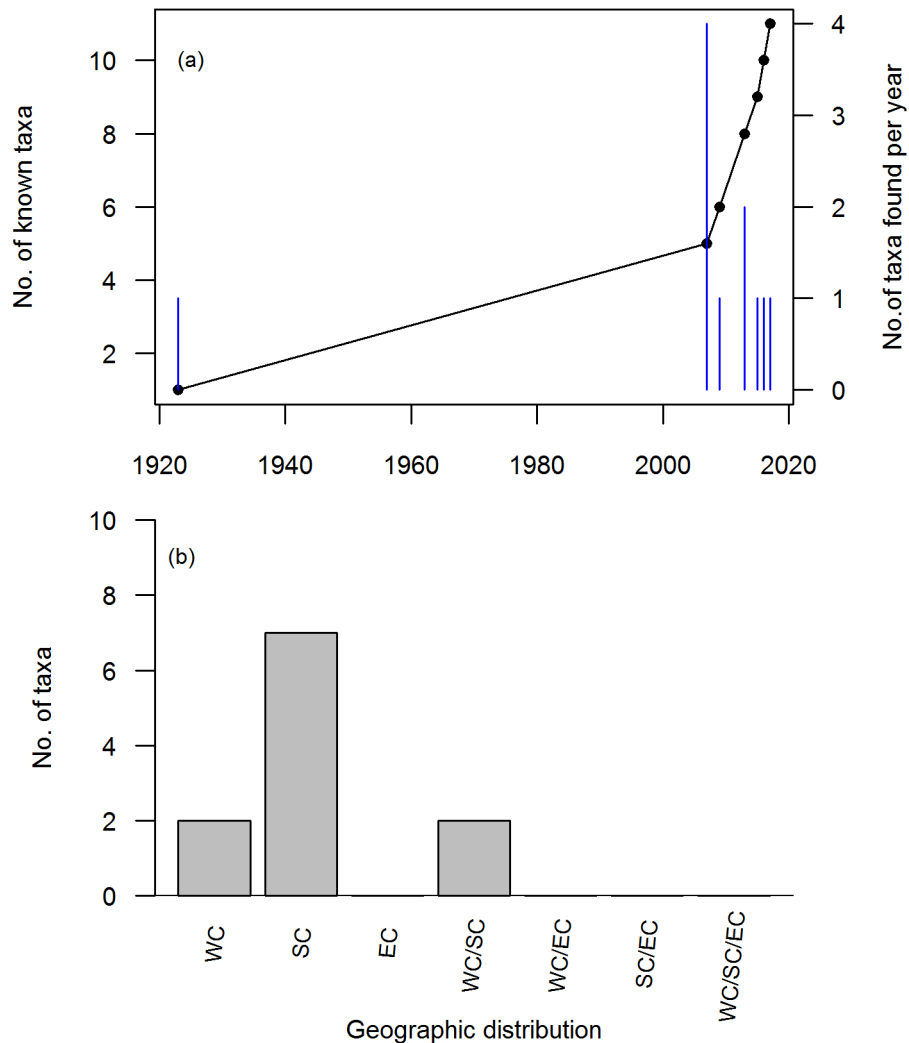


Figure 3.10. (a) The evolution of the number of known cnidarian parasites shown as the cumulative number reported from South African marine fish hosts examined over the period 1923-2017 (black line) and the number of cnidarian parasites reported per annum (blue bars); and (b) the biogeographical distribution of cnidarian parasites reported from South African marine fishes.

### 3.3.1.9. Nematoda

Since 1933, six parasitic nematode taxa representing three families and four genera have been recovered from South African marine fishes (Table 3.1, Fig 3.11a). Infected hosts included 11 teleost species and six elasmobranch taxa. The spatial distribution of half the

nematodes encompasses both the south and west coast (Fig 3.11b). One taxon (*Cucullanus* sp.) has so far only been recorded on the west coast while the remaining two taxa had no spatial data associated with them.

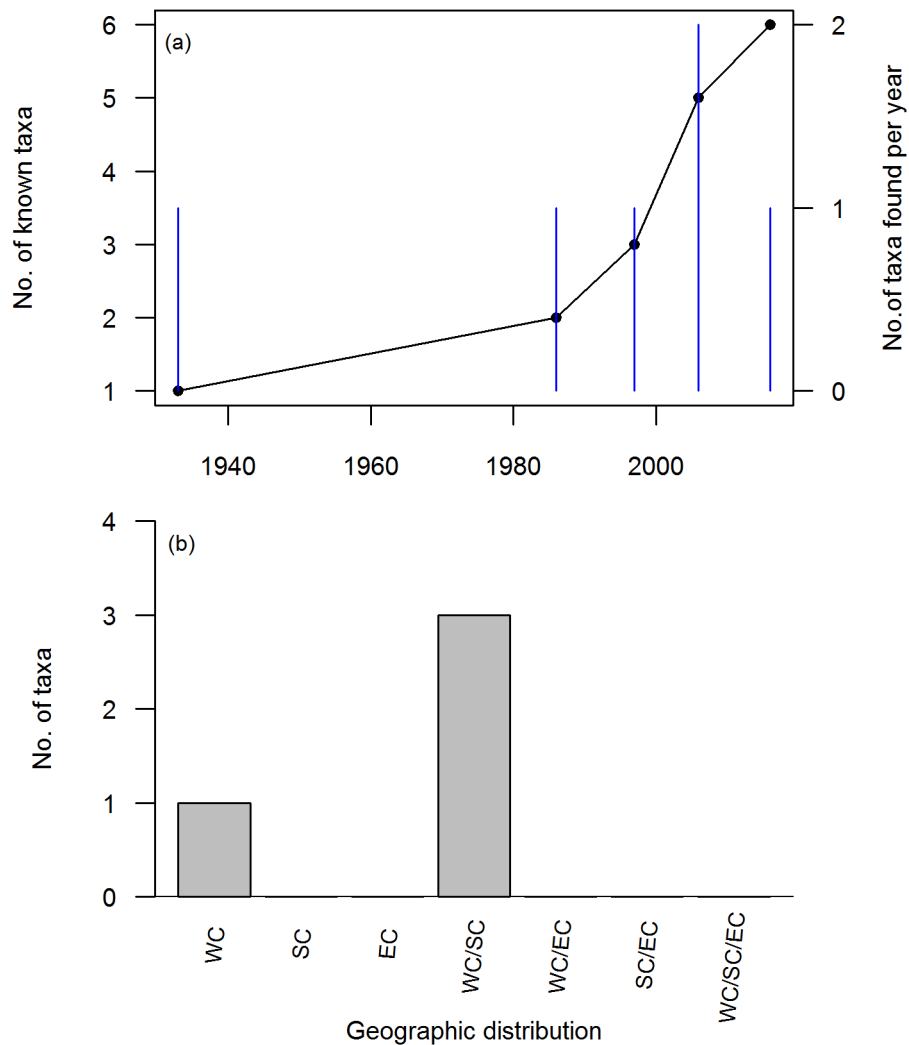


Figure 3.11. (a) The evolution of the number of known nematode parasites shown as the cumulative number reported from South African marine fish hosts examined over the period 1933-2019 (black line) and the number of nematode parasites reported per annum (blue bars); and (b) the biogeographical distribution of nematode parasites reported from South African marine fishes.

### 3.3.1.10. Platyhelminthes

One hundred and thirty-three platyhelminthes, representing three major classes (Cestoda, Monogenea, Trematoda) and 48 families (Table 3.1), parasitise members of the

classes Actinopterygii (92 species), Elasmobranchii (24 species), Holocephali (1 species) and Myxini (1 species) in South Africa. The class Cestoda was comprised of 31 taxa while the class Monogenea could be split between the subclasses monopisthocotylea (11 species) and polyopisthocotylea (9 taxa) and digenetic trematodes comprised 80 taxa. Between 1900 and 1966, only 10 parasitic platyhelminth taxa were recorded but by 2004 the number of known species had grown to 100 (Fig 3.12a). Over the past two decades, a further 45 taxa have been added to our knowledge of South African parasite biodiversity. Over 40% of the platyhelminthes have exclusively been found on the east coast (Fig 3.12b) while the south and west coasts harbour 19.5% and 15.8% respectively of the number of known taxa. Few taxa have been recorded from more than one of the three bioregions; the south coast shares six and five taxa with the west and east coasts respectively while only three have distributions spanning all three bioregions (Fig 3.12b).

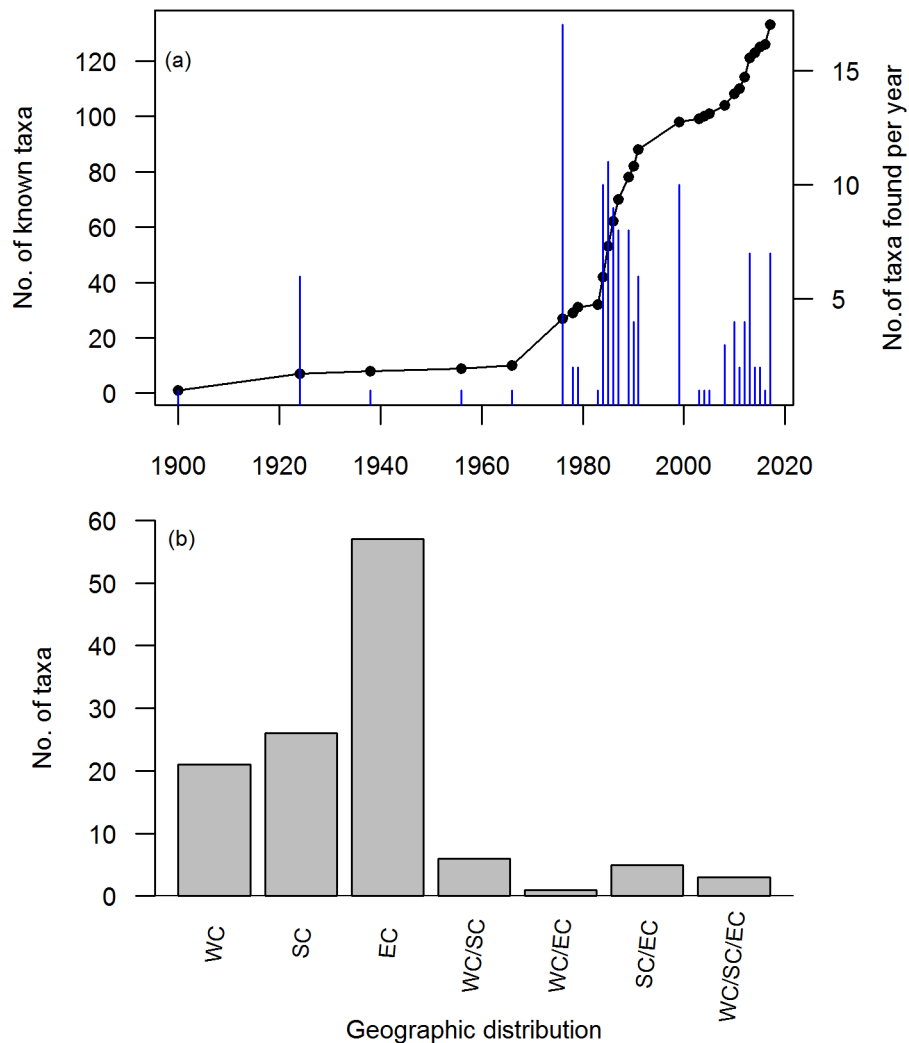


Figure 3.12. (a) The evolution of the number of known platyhelminth parasites shown as the cumulative number reported from South African marine fish hosts examined over the period 1900-2019 (black line) and the number of platyhelminth parasites reported per annum (blue bars); and (b) the biogeographical distribution of platyhelminth parasites reported from South African marine fishes.

### 3.4. Discussion

Two centuries after the inception of marine parasitology in South Africa (Smit and Hadfield 2015), there still exists a scarcity of knowledge relating to the distribution patterns of ichthyoparasite diversity and their ecological roles, despite the documentation of 378 ichthyoparasitic taxa since 1818. At a time when parasites are increasingly being recognised

as essential but threatened components of biological communities (Gómez and Nichols 2013; Carlson et al. 2017) and as a tool in marine research, this study provides a much needed appraisal of marine ichthyoparasite biodiversity in South Africa. Our current lack of knowledge pertaining to marine ichthyoparasite diversity restricts the potential for using parasites to test ecological as well as evolutionary hypotheses and their inclusion in management and conservation strategies.

### **3.4.1. Parasitological Research Effort**

The wide range of environmental conditions prevailing across the South African marine environment (Lutjeharms 2007; Hutchings et al. 2009; Kirkman et al. 2016) and the high diversity of fishes in South African waters (Griffiths et al. 2010) would lead one to expect an equally high diversity of ichthyoparasitic species (Costello 2016). However, since Leach's (1818) description of *Anilocra capensis*, only 377 more taxa parasitic on marine fishes have been added to the South African biodiversity inventory. This number almost certainly underestimates the parasite diversity of the region as less than 14% of the fishes occurring around South Africa have been recorded as host species. This situation is akin to that in Brazil and Peru, where only a small proportion of fishes have parasitological records (Luque et al. 2011, 2016) but is in stark contrast with Canada where over 40% of fishes are known to host parasites (Luque and Poulin 2007).

Before 1990, our knowledge of parasite biodiversity mostly stemmed from the work of a few, highly prolific taxonomists including Dr. Keppel Harcourt Barnard, Brian Frederick Kensley, Professor John Richard Grindley and Dr. Rodney Bray. From then on, research groups focussing on fish parasites were set up at various South African universities, notably at the University of the Free State, the University of Johannesburg, the University of Limpopo, North West University and more recently at the University of Cape Town. These

research groups have contributed to reinvigorate marine parasitology in South Africa, as demonstrated by the rapid increase in the number of host species examined, host-parasite relationships recorded and publications in the last 30 years. However, the fact that a single parasite taxon has been reported from most fish species included in the checklist along with the Chao2 diversity estimator which suggested that only half the parasites potentially infecting hosts identified to species level have been found hint at opportunistic parasite collections or highly taxon-specific research (e.g. Bray 1986a; Dippenaar 2018a). The taxon-specific nature of many ichthyoparasitological studies conducted in South Africa increases the probability of false negatives, i.e, parasites other than the taxon being investigated are not reported even if they infect the host being examined. This situation renders the checklist presented here inadequate to estimate the degree of host specificity of ichthyoparasites in South Africa. Spatial differences were evident both in the breadth of host species surveyed and knowledge of ichthyoparasitic diversity. The east coast is the most well studied bioregion, exhibiting the highest number of host taxa examined, parasite species richness and host-parasite associations. However, parasites recorded from the east coast have been restricted to four phyla (acanthocephala, annelida, arthropoda, platyhelminthes), suggesting that parasitologists working in the region, although highly prolific, have historically only been interested in particular taxa or that they lacked expertise in other ichthyoparasitic taxa (e.g. cnidaria, nematoda). This situation is easily illustrated by Professor Dippenaar's research group at the University of Limpopo which focuses exclusively on siphonostomatoid copepod parasites (Smit and Hadfield 2015). The absence of cnidarians and nematodes from the ichthyoparasite fauna of the east coast could also be the result of rarity, whereby low levels of infection in east coast fish decrease their probability of being detected.

The west coast, being a highly productive region which supports important commercial fisheries (Atkinson et al. 2011), has also garnered significant interest from

biologists since the early days of marine parasitology in South Africa (e.g. Barnard 1914, 1955a; Fantham 1938). Despite having a relatively low ichthyofaunal diversity (Turpie et al. 2000), the west coast ranks second in terms of fish parasite diversity and number of fish species with parasitological records. This might be accounted for by the fact that the Cape has historically been the epicentre of marine research in South Africa (e.g. Gilchrist 1902, 1923a; Day et al. 1970). On the other hand, the south coast, a region considered a transitional zone harbouring a fish fauna exhibiting high levels of endemism amongst coastal species (Turpie et al. 2000), makes the lowest contribution to our knowledge of parasite biodiversity. This might be attributed to the fact that no institution conducting parasitological research is situated in this region of South Africa, thereby making sampling of hosts logistically challenging and costly (e.g. Reed et al. 2007).

Fish species with the most well-documented parasite faunas include commercially important ones such as the hakes (*Merluccius* spp.) and snoek (*Thyrsites atun*). The research into the parasite faunas of commercial fish species has been motivated by the possibility of using parasites as indicators of population structure (Botha 1986; van der Lingen et al. 2015; Weston et al. 2015) while also providing an assessment of parasites which could be detrimental to product quality (Payne 1986; Henning et al. 2013) and those with a zoonotic potential. Sharks, particularly members of the families Carcharinidae, Lamnidae and Odontaspidae, have well-documented arthropod ectoparasite faunas with a few scattered records of platyhelminthes.

The present study revealed that arthropods (210) and platyhelminthes (133) were the most commonly reported marine fish parasites in South Africa (Fig. 3.2). While there are no comparable African checklists, this diversity pattern contrasts with that of Peru where platyhelminthes dominate the marine ichthyoparasitic fauna (Luque et al. 2016). Other taxa,

namely the acanthocephalans (12), annelids (6), cnidarians (11) and nematodes (6), only accounted for a small proportion of marine ichthyoparasitic diversity in South Africa.

### **3.4.2. Parasite Diversity and Distribution**

#### **3.4.2.1. Acanthocephala**

Acanthocephalans have a short history of research in South Africa and are only represented by 12 taxa. Since the first acanthocephalan report in 1963, very little taxonomic work has concerned this phylum (Bray 1974; Bray et al. 1988; Amin and Christison 2005), a situation indicative of a dearth of expertise and interest amongst local parasitologists for this particular taxon. The remaining reports of acanthocephalans from South African marine fishes have emanated from ecological studies (Golvan and de Buron 1988; Le Roux 2013; Nunkoo et al. 2016, 2017; Cruickshank 2017). Acanthocephalans are understudied in all three bioregions, most notably on the east coast where a single taxon has been recorded despite the variety of fish species found in these waters. Undoubtedly, much remains to be discovered and studied within this taxon, both taxonomically and ecologically. Such an endeavour would benefit from international collaborations as parasitologists currently plying their trade in South Africa lack the necessary skills for species identifications and descriptions within this particular phylum.

#### **3.4.2.2. Annelida**

Leeches, parasitic annelids, infecting marine fishes are poorly known in South Africa. Since Moore (1958) described *Janusion stellata* from the east coast, five more taxa have been found, including two new species described by Andrei Utevsky from the Karazin Kharkiv National University in Ukraine (Utevsky 2004, 2007). As is the case with the acanthocephalans, there is a lack of leech-specific taxonomic know-how and interest amongst South African parasitologists, which has led to incomplete or tentative identifications (Yeld

2009; Awa 2012) and limited spatial coverage of surveys targeting marine leeches. The role of marine leeches as vectors of trypanosome infections in fish (Karlsbakk 2004; Hayes et al. 2014) warrants further research, especially with respect to commercially important demersal fish species whose growth and survival could be negatively affected (Khan and Lacey 1986; Hemmingsen et al. 2005).

### **3.4.2.3. Arthropoda**

The Arthropoda is the most diverse ichthyoparasitic phylum in South Africa. This can be accounted for by the long-standing interest of parasitologists, both foreign and local, in this particular taxon. Being ectoparasites, the arthropods are more conspicuous than other parasitic taxa such as acanthocephalans and therefore more easily documented. Our knowledge of arthropods has initially benefitted from the publication of large monographs (e.g. Barnard 1955a; Kensley and Grindley 1973) and more recently from the work of other South African parasitologists (e.g. Dippenaar 2004; Dippenaar and Jordaan 2007; Hadfield et al. 2014a). The present study has increased the number of siphonostomatoids known from South African waters from 136 (Dippenaar 2016a) to 163. Schaeffner and Smit (2019) reported 92 copepod taxa infecting South African chondrichthyans while only 90 are presented in the current study. This discrepancy was due to the fact that Izawa (2010) recognises *A. pinguis* as the only *Achtheinus* occurring off South Africa and therefore earlier reports of *A. oblongus* and *A. dentatus* are considered synonymous with *A. pinguis*. However, there are no adequate resources to gauge advancement in knowledge of less diverse arthropod orders such as the Isopoda and Cyclopoida.

The analysis of spatial distribution revealed that most arthropod taxa (70%) have only been recorded from one of the three bioregions. This may be an artefact of research planning which is in turn dictated by the interest of researchers and funding constraints. Host

specificity and the environmental affinities of the parasitic arthropods and their hosts could also account for this trend. Unsurprisingly, the species recorded from all three regions parasitise widely distributed or migratory hosts (e.g. tunas) or have low host specificity (e.g. *A. pinguis*). Research into parasitic arthropods is still in an exploratory phase as evidenced by the increasing rate of species discovery and addition of new geographical records. However, arthropod ichthyoparasite research appears to be one step ahead compared to other parasitic taxa as some phylogenetic and ecological investigations have been conducted (Dippenaar et al. 2008; Dippenaar 2009; Mangena et al. 2014). Dippenaar (2016c) noted that the main hurdle facing arthropod research was the paucity of local taxonomic expertise and remarked that research focussing on the siphonostomatoids had been mostly directed towards commercially or ecologically important host taxa thereby hampering efforts to reveal the diversity of parasitic copepods and evaluate their roles and impacts within the marine ecosystems of South Africa.

#### **3.4.2.4. Cnidaria**

Worldwide, parasitic members of the phylum Cnidaria, i.e. myxozoans, have primarily been reported from fishes although the completion of their lifecycle requires a definitive invertebrate host (Yokoyama 2003; Lom and Dyková 2006). In South Africa, myxozoans first attracted scientific attention due to their deleterious effects on the quality of commercially harvested fish leading to the description of the notorious *Kudoa thyrsites* (Gilchrist 1923b). Since then, only a handful more myxozoans have been reported infecting marine fishes and our knowledge remains spatially limited (Reed 2003; Reed et al. 2007, 2009; Le Roux 2013). This trend is reminiscent of other parasitic taxa exhibiting low diversity (e.g. acanthocephala, annelida) in that local taxonomic expertise is lacking. At present, Dr. Cecile Reed (University of Cape Town) is the only myxozoan specialist working

in South Africa. Research into the phylogenetics and taxonomy of South African myxozoans has nonetheless benefitted from international collaborations (Bartošová-Sojková et al. 2015, 2018).

#### **3.4.2.5. Nematoda**

Ichthyoparasites of the the phylum Nematoda were first recorded in 1933 from a coastal rhinobatid host (Bayliss 1933 in Schaeffner and Smit 2019).. Despite their economic significance (Levsen et al. 2018) and the health risk nematodes may pose (Adams et al. 1997; Nieuwenhuizen et al. 2006), they are only represented by six taxa indicating that it is a severely understudied group. It is notable that this phylum suffers from a lack of local taxonomic skill with all the systematic and taxonomic publications being authored by foreign parasitologists (Mattiucci et al. 1997; Mattiucci and Nascetti 2006, 2007) with little involvement from South African parasitologists (e.g. Moravec et al. 2002). Reports of nematodes have also been restricted to the south and west coasts, a further indication of the lack of research capacity and interest concerning this phylum. A less likely hypothesis to explain the low number of nematodes reported to date is that they are naturally less diverse and prevalent off South Africa.

#### **3.4.2.6. Platyhelminthes**

The platyhelminthes, represented by members of the classes Cestoda, Monogenea and Trematoda, is the second most species-rich parasite phylum infecting marine fishes in South Africa. They have been reported infecting bony and cartilaginous fish species as well as holocephalans while one monogenean species has been described from hagfishes. However, compared to the high number of fish species found in South Africa (Griffiths et al. 2010), remarkably few (118 taxa) have been reported as hosts of platyhelminthes. Taxonomic work focussing on this phylum has largely been driven by scientists based outside South Africa

(e.g. Bray 1986a; Vaughan and Chisholm 2010a; Caira et al. 2013a) suggesting a scarcity of local taxonomic expertise concerning this phylum. The spatial distribution of platyhelminthes is poorly known as 78.2% of the taxa have only been recorded infecting fishes in one of the three South African marine bioregions. A few more ecologically-inclined studies have helped improve our understanding of their distribution, both within host species and spatially (e.g. Botha 1986; Sibanda 2015; Mackintosh 2016; Nunkoo et al. 2016).

### **3.4.3. Current Challenges and Future Research**

The present study has highlighted how our knowledge of marine ichthyoparasites is skewed towards the arthropods and platyhelminthes while other phyla appear to have largely been neglected. As mentioned before, a potentially naturally low diversity within certain taxa (e.g. acanthocephala, cnidaria, nematoda) may explain their minor contribution to the checklist presented. However, a recurrent theme across all phyla is the dearth of taxonomists, which hampers parasite identifications and descriptions. The use of molecular analyses to elucidate the presence of cryptic species has so far been restricted in South Africa, owing to a lack of funding (Dippenaar 2016a). Specific identifications are critical to improve the completeness of the South African biodiversity inventory and to enable ecological as well as biogeographical studies (Luque and Poulin 2007).

Currently, no credible estimates of marine ichthyoparasitic diversity are possible. Species-accumulation curves, a method often used to estimate biodiversity by extrapolation is not useful in cases such as that we are confronted with in South Africa where the rate of parasite discovery is still increasing (Poulin et al. 2016a). Deriving parasite diversity by using parasites' host-specificity (Costello 2016) is also not a viable option at the moment due to the small number of host species surveyed, a major hurdle to the assessment of parasite host-specificity. While documenting all parasites may be utopic, uncovering biogeographical

patterns and diversity hotspots are essential to the conservation of parasites which are already threatened by human activities and climate change (Poulin 2014; Carlson et al. 2017). There is therefore a need for further surveys of parasite biodiversity in South Africa.

Climate change poses a significant challenge to the survival and persistence of marine parasites (Adlard et al. 2015). The most notable effect of this global phenomenon off South Africa has been the change in sea surface temperature, especially off the south coast (Clark 2006; Rouault et al. 2010; Blamey et al. 2015). This could result in shifts in the distribution of free-living biodiversity which serve as hosts for parasites (e.g. James et al. 2008), a form of habitat loss for parasites, resulting in the extinction or redistribution of parasite diversity within marine ecosystems (Marcogliese 2008; Adlard et al. 2015; Carlson et al. 2017). Research into the potential effects of climate change on marine parasites through experimental approaches, long-term ecological experiments and modelling, is long overdue (Carlson et al. 2017).

#### **3.4.4. Conclusions**

South African marine parasitology has stalled in an exploratory phase for two centuries but the first steps towards integrating this knowledge in ecological and fisheries research have recently been undertaken (e.g. Reed 2015; van der Lingen et al. 2015; Weston et al. 2015; Nunkoo et al. 2016; Weston 2017). However, there is a need for more taxonomists and large scale systematic surveys, the utility of which cannot be stressed enough. Such surveys would benefit our knowledge of marine biodiversity in South Africa, help improve our understanding of the ecological roles of parasitism and evaluation of the impacts of increasing anthropogenic pressure and climate change on marine ecosystems, and support conservation planning.

### **3.5. The Parasite-Host Checklist**

Abbreviations used in the checklist: DHNR - De Hoop Nature Reserve, KZN - KwaZulu-Natal, EC – east coast, SC – south coast, WC – west coast

#### **Phylum Acanthocephala Rudolphi, 1802**

#### **Class Eoacanthocephala Van Cleave, 1936**

#### **Order Neoechinorhynchida Southwell & McFie, 1925**

#### **Family Neoechinorhynchidae (Ward, 1917)**

*Neoechinorhynchus dorsovaginitus* Amin & Christison, 2005

Host (locality): *Argyrosomus japonicus* (Breede River Estuary)

Distribution: SC

References: (Amin and Christison 2005)

#### **Class Palaeacanthocephala Meyer, 1931**

#### **Order Echinorhynchida Southwell & McFie, 1925**

#### **Family Arhythmacanthidae Yamaguti, 1935**

*Acanthocephaloides cyrusi* Bray, Spencer-Jones, Lewis, 1988

Host (locality): *Pomadasys commersonnii*, *Solea bleekeri* (Lake St Lucia),

Distribution: EC

References: (Bray et al. 1988)

#### **Family Pomporhynchidae Yamaguti, 1939**

*Longicollum chabanaudi* Dolfus & Golvan, 1963

Host (locality): *Barnardichthys fulvomarginata*

Distribution: N/A

References: (Golvan and de Buron 1988)

*Longicollum* sp. in nom.

Host (locality): *Solea bleekeri*

Distribution: SC

References: (Bray 1974)

**Family Rhadinorhynchidae Travassos, 1923**

*Rhadinorhynchus cadenati* (Golvan & Houin, 1964)

Host (locality): *Trachurus capensis*, *Thyrsites atun*

Distribution: SC, WC

References: (Le Roux 2013; Nunkoo et al. 2016)

*Rhadinorhynchus capensis* Bray, 1974

Host (locality): *Solea bleekeri*

Distribution: SC

References: (Bray 1974)

*Rhadinorhynchus* sp.

Host (locality): *Brama brama*, *Ruvettus pretiosus*

Distribution: WC

References: (Nunkoo et al. 2017; Mackintosh et al. 2018)

**Order Polymorphida Petrochenko, 1956**

**Family Polymorphidae Meyer, 1931**

*Bolbosoma capitatum* (von Linstow, 1880)

Host (locality): *Ruvettus pretiosus*

Distribution: WC

References: (Nunkoo et al. 2017)

*Bolbosoma vasculosum* (Rudolphi, 1819)

Host (locality): *Thyrsites atun*

Distribution: SC

References: (Nunkoo et al. 2016)

*Bolbosoma* sp.

Host (locality): *Merluccius capensis*

Distribution: SC

References: (Cruickshank 2017)

*Corynosoma australe* Johnston, 1937

Host (locality): *Sebastes capensis*, *Thyrsites atun*

Distribution: SC, WC

References: (González et al. 2006; Nunkoo et al. 2016)

*Corynosoma* sp.

Host (locality): *Merluccius capensis*

Distribution: SC, WC

References: (Cruickshank 2017)

## **Phylum Annelida**

### **Class Clitellata**

#### **Subclass Hirudinea**

#### **Order Rhynchobdellida (Johnston, 1865)**

#### **Family Piscicolidae (Johnston, 1865)**

*Austrobdella oosthuizeni* Utevsky, 2004

Host (locality): N/A (Bloubergstrand)

Distribution: WC

Notes: Specimens were recovered from the crustacean *Jasus lalandii* which is thought to be used as substrate used for cocoon deposition.

References: (Utevsky 2004)

*Branchellion* sp.

Host (locality): *Callorhinchus capensis* (St Helena Bay)

Distribution: WC

References: (Awa 2012)

*Janusion stellata* (Moore, 1958)

Host (locality): N/A (off KZN)

Distribution: EC

References: (Moore 1958)

*Lizabdella africana* Utevsky, 2007

Host (locality): *Chelon dumerili*, *Chelon tricuspidens*, *Chelon richardsonii* (Kowie River Esuary), *Mugil cephalus* (Swartkops Estuary)

Distribution: SC

References: (Utevsky 2007)

*Stibarobdella macrothela* (Schmarda, 1865)

Host (locality): *Haploblepharus edwardsii*, *Haploblepharus pictus*, *Poroderma africanum*

Distribution: SC, WC

Note: Tentative identification of the parasite by Yeld (2009)

References: (Yeld 2009)

*Zeylanicobdella arugamensis* de Silva, 1963

Host (locality): *Clinus cottoides*, *Parablennius cornutus* (DHNR; Tsitsikamma National Park), *Clinus superciliosus*, *Clinus taurus* (Tsitsikamma National Park)

Distribution: SC

References: (Hayes et al. 2014)

## **Phylum Arthropoda von Siebold, 1848**

### **Class Hexanauplia Oakley, Wolfe, Lindgren & Zaharof, 2013**

#### **Subclass Copepoda Milne Edwards, 1840**

#### **Order Cyclopoida Burmeister, 1834**

#### **Family Bomolochidae Claus, 1875**

*Ceratocolax euthynni* Vervoort, 1965

Host (locality): *Sarda sarda* (Port Elizabeth)

Distribution: SC

References: (Cressey and Cressey 1980)

*Hamaticolax maleus* (Oldewage, 1994)

Host (locality): *Malacocephalus laevis*

Distribution: WC

Notes: Originally described as *Holobomolochus maleus* which is now considered a junior synonym

References: (Oldewage 1994)

*Nothobomolochus fradei* Marquès, 1965

Host (locality): *Sardinops sagax* (Agulhas Bank; False Bay; Port Elizabeth), *Thyrsites atun*

Distribution: SC, WC

References: (Reed et al. 2012; Nunkoo et al. 2016)

*Unicolax collateralis* Cressey & Cressey, 1980

Host (locality): *Sarda orientalis* (Durban)

Distribution: EC

References: (Cressey and Cressey 1980)

#### **Family Chondracanthidae Milne Edwards, 1840**

*Acanthochondria lepidionis* Barnard, 1955

Host (locality): *Lepidion capensis* (Cape Point)

Distribution: WC

References: (Barnard 1955a)

*Chondracanthus barnardi* Ho, 1972

Host (locality): *Lophius piscatorius* (Agulhas Bank; Table Bay)

Distribution: SC, WC

Notes: Originally described as *C. lophii* by Barnard (1955a)

References: (Barnard 1955a; Ho 1972; Kensley and Grindley 1973)

*Chondracanthus colligens* Barnard, 1955

Host (locality): *Genypterus capensis* (Table Bay)

Distribution: WC

References: (Barnard 1955b; Weston 2017)

*Chondracanthus merluccii* (Holten, 1802)

Host (locality): *Merluccius capensis*, *Merluccius paradoxus* (Cape of Good Hope)

Distribution: SC, WC

References: (Botha 1986; Cruickshank 2017)

*Chondracanthus neali* Leigh-Sharpe, 1930

Host (locality): *Malacocephalus laevis*

Distribution: WC

References: (Barnard 1955b)

*Chondracanthus tuberculatus* Nordmann, 1832

Host (locality): *Congiopodus torvus* (Table Bay)

Distribution: WC

Note: Originally described as *Chondracanthus congiopodi* by Barnard (1955a)

References: (Barnard 1955a)

*Lernentoma asellina* (Linnaeus, 1758)

Host (locality): *Chelidonichthys capensis* (off Plettenberg Bay; NW of Hondeklip Bay)

Distribution: SC, WC

References: (Oldewage 1992a, 1993a)

*Medesicaste penetrans* Heller, 1865

Host (locality): *Chelidonichthys capensis* (Cape Peninsula; Table Bay), *Chelidonichthys queketti* (False Bay), *Chelidonichthys* sp. (Kalk Bay), *Merluccius capensis* (Agulhas Bank; off Mossel Bay; off Plettenberg Bay)

Distribution: SC, WC

References: (Barnard 1955a, 1955b; Oldewage 1992a)

*Strabax monstrosus* Nordmann, 1864

Host (locality): *Scorpaenodes guamensis* (Port St. Johns)

Distribution: EC

References: (Barnard 1955a)

### **Family Ergasilidae Burmeister, 1835**

*Dermoergasilus mugilis* Oldewage & van As, 1988

Host (locality): *Mugil cephalus* (estuaries of Bushmans River and Keurbooms River)

Distribution: SC

References: (Oldewage and van As 1988)

*Ergasilus ilani* Oldewage & van As, 1988

Host (locality): *Mugil cephalus* (Sodwana Bay)

Distribution: EC

References: (Oldewage and van As 1988)

### **Order Siphonostomatoida Thorell, 1859**

#### **Family Caligidae Burmeister, 1835**

*Alebion carchariae* Krøyer, 1863

Host (locality): *Carcharhinus brevipinna*, *Carcharhinus leucas*, *Carcharhinus obscurus* (Cape Point), *Carcharhinus* sp. (Durban), *Carcharodon carcharias* (off Slangkop), *Carcharias taurus* (Cape Recife), *Isurus oxyrinchus* (Cape Recife), *Odontaspis* sp. (Durban), *Sphyrna lewini*, unspecified shark (Ifafa)

Distribution: EC, SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973; Oldewage and Smale 1993; Oldewage 1995; Dippenaar 2018a)

*Alebion crassus* Wilson C. B., 1932

Host (locality): *Sphyrna lewini*

Distribution: EC

References: (Dippenaar 2018a)

*Alebion difficile* (van Beneden, 1892)

Host (locality): *Carcharhinus obscurus* (off KZN), *Carcharhinus sealei* (off KZN), *Carcharias taurus* (off KZN, off Eastern Cape), *Carcharodon carcharias* (off Western Cape), *Galeorhinus galeus* (off Western Cape), *Mustelus mustelus* (off KZN)

Distribution: EC, WC

References: (Dippenaar 2018a)

*Alebion gracilis* Wilson C. B., 1905

Host (locality): *Carcharhinus obscurus* (Durban)

Distribution: EC

References: (Cressey 1967b)

*Alebion lobatus* Cressey, 1970

Host (locality): *Carcharhinus plumbeus*

Distribution: EC

References: (Dippenaar 2018a)

*Alebion maculatus* Wilson C. B., 1932

Host (locality): *Carcharhinus leucas*, *Carcharhinus limbatus*, *Carcharhinus plumbeus*

Distribution: EC

References: (Dippenaar 2018a)

*Alebion* sp.

Host (locality): *Carcharodon carcharias*

Distribution: N/A

References: (Dippenaar 2018b)

*Caligus acanthopagri* Lin, Ho & Chen, 1994

Host (locality): *Acanthopagrus berda* (Lake St. Lucia; Richards Bay), *Rhabdosargus holubi*  
(Lake St. Lucia; Richards Bay)

Distribution: EC

References: (Grobler et al. 2003a)

*Caligus aesopus* Wilson C.B., 1921

Host (locality): *Seriola lalandi* (False Bay)

Distribution: WC

References: (Kensley and Grindley 1973; Weston 2017)

*Caligus affinis* Heller, 1866

Host (locality): *Pomatomus saltatrix* (Durban)

Distribution: EC

References: (Kensley and Grindley 1973)

*Caligus africanus* Oldewage & van As, 1987

Host (locality): *Arothron hispidus* (Cebe)

Distribution: EC

Notes: *Caligus africanus* was never formally described, the only record is in Dippenaar (2004) who question its validity and considers it as taxon inquirendum.

References: (Dippenaar 2004)

*Caligus asymmetricus* Kabata, 1965

Host (locality): *Katsuwonus pelamis* (Sodwana Bay), *Scomberomorus commerson* (Sodwana Bay)

Distribution: EC

References: (Oldewage and van As 1989)

*Caligus biserioidentatus* Shen, 1957

Host (locality): *Sarda sarda* (Port Elizabeth), *Scomberomorus commerson* (Port Elizabeth)

Distribution: SC

References: (Oldewage and van As 1989)

*Caligus bonito* Wilson C.B., 1905

Host (locality): *Katsuwonus pelamis* (Sodwana Bay), *Sarda sarda* (False Bay; Port Elizabeth), *Sarda orientalis* (Port Elizabeth)

Distribution: EC, SC, WC

References: (Barnard 1955b; Cressey and Cressey 1980; Oldewage and van As 1989; Weston 2017)

*Caligus brevicaudatus* A, Scott, 1901

Host (locality): *Chelidonichthys capensis* (Table Bay)

Distribution: WC

References: (Barnard 1955b)

*Caligus chrysophrysi* Pillai, 1985

Host (locality): *Mobula alfredi* (off KZN), *Mobula kuhlii* (off KZN)

Distribution: EC

References: (Lebepe and Dippenaar 2013)

*Caligus confusus* Pillai, 1961

Host (locality): *Alepes djebaba* (Durban), *Caranx sexfasciatus* (Lake St. Lucia; Richards Bay), *Rhabdosargus holubi* (Lake St. Lucia; Richards Bay)

Distribution: EC

References: (Kensley and Grindley 1973; Grobler et al. 2003a)

*Caligus coryphaenae* Steenstrup & Lütken, 1861

Host (locality): *Katsuwonus pelamis* (Cape Point; Sodwana), *Pomatomus saltatrix* (Cape Infanta), *Thunnus obesus* (Cape Point), *Thyrsites atun*, unspecified shark (Table Bay)

Distribution: EC, SC, WC

References: (Barnard 1955b; Kensley and Grindley 1973; Oldewage and van As 1989; Oldewage 1992a; Nunkoo et al. 2016)

*Caligus curtus* Müller, 1785

Host (locality): *Chelidonichthys capensis*, *Chelidonichthys queketti*

Distribution: SC

References: (Oldewage and Avenant-Oldewage 1993)

*Caligus dakari* van Beneden, 1892

Host (locality): *Pomatomus saltatrix* (False Bay), *Thyrsites atun*, *Trachurus capensis*

Distribution: SC, WC

References: (Barnard 1955a, 1955b; Nunkoo et al. 2016; Weston 2017)

*Caligus diaphanus* von Nordmann, 1832

Host (locality): *Chelidonichthys capensis* (off Port Nolloth), *Trachinotus botla* (Sodwana Bay)

Distribution: EC, WC

References: (Oldewage and van As 1989; Oldewage 1993a)

*Caligus elongatus* von Nordmann, 1832

Host (locality): *Carcharias obscurus* (off KZN), *Carcharias taurus* (off KZN), *Merluccius capensis* (Table Bay), *Mobula kuhlii* (off KZN), *Trachurus capensis* (Table Bay)

Distribution: EC, WC

Notes: Identified as *Caligus rapax* in Barnard (1955b)

References: (Barnard 1955b; Dippenaar 2004; Dippenaar and Jordaan 2007)

*Caligus engraulidis* Barnard, 1948

Host (locality): *Chelon tricuspidens* (Lake St. Lucia), *Mugil cephalus* (Lake St. Lucia), *Stolephorus holodon* (Algoa Bay)

Distribution: EC, SC

References: (Barnard 1948; Grobler 2000)

*Caligus epinepheli* Yamaguti, 1936

Host (locality): *Diplodus capensis* (DHNR), *Rhabdosargus holubi* (Lake St. Lucia)

Distribution: EC, SC

References: (Grobler et al. 2004)

*Caligus hottentotus* Barnard, 1957

Host (locality): *Pachymetopon blochii* (Table Bay)

Distribution: WC

References: (Barnard 1957)

*Caligus infestans* Heller, 1865

Host (locality): *Galeichthys feliceps*, *Scomberomorus commerson* (Sodwana Bay)

Distribution: EC, SC

References: (Oldewage and van As 1989; Oldewage 1992a)

*Caligus labracis* T. Scott, 1902

Host (locality): *Clinus superciliosus* (Table Bay)

Distribution: WC

Notes: identification needs to be confirmed (Dippenaar 2004)

References: (Barnard 1955a)

*Caligus lalandei* Barnard, 1948

Host (locality): *Seriola lalandi* (Kalk Bay)

Distribution: WC

References: (Barnard 1948)

*Caligus lunatus* Wilson C. B., 1924

Host (locality): *Seriola lalandi* (False Bay)

Distribution: WC

References: (Barnard 1955a)

*Caligus mortis* Kensley, 1970

Host (locality): *Chorisochismus dentex* (DHNR; Jeffreys Bay), *Clinus cottoides* (DHNR; Jeffreys Bay), *Clinus superciliosus* (DHNR; Jeffreys Bay), *Chelon richardsonii* (DHNR), *Sarpa salpa* (DHNR)

Distribution: SC

References: (Grobler et al. 2002)

*Caligus pelamydis* Krøyer, 1863

Host (locality): *Chelidonichthys capensis* (Table Bay), *Katsuwonus pelamis* (Simons Bay), *Sarda sarda* (Simons Bay; Port Elizabeth), *Thyrsites atun* (False Bay)

Distribution: SC, WC

References: (Barnard 1955a, 1955b; Cressey and Cressey 1980)

*Caligus productus* Dana, 1852

Host (locality): *Katsuwonus pelamis* (Sodwana Bay), *Scomberomorus commerson* (Sodwana Bay), *Thunnus albacares* (Sodwana Bay)

Distribution: EC

References: (Oldewage and van As 1989)

*Caligus rotundigenitalis* Yü, 1933

Host (locality): *Rhabdosargus holubi* (Lake St. Lucia)

Distribution: EC

References: (Grobler et al. 2004)

*Caligus saucius* Dojiri, 1989

Host (locality): *Cirripectes castaneus* (KwaZulu Reef)

Distribution: EC

References: (Dojiri 1989)

*Caligus tetradontis* Barnard, 1948

Host (locality): *Amblyrhynchotes honckenii* (Knysna), *Arothron hispidus* (Transkei),  
*Chelidonichthys capensis* (DHNR; Jeffreys Bay; off Plettenberg Bay),  
*Torquigener hypselogeneion* (Port Elizabeth)

Distribution: EC, SC

References: (Barnard 1948; Oldewage and van As 1989; Oldewage 1990, 1992a; Grobler 2004)

*Caligus zeii* Norman & Scott T., 1906

Host (locality): *Thyrsites atun*

Distribution: WC

References: (Nunkoo et al. 2016)

*Caligus* sp.

Host (locality): *Argyrosomus japonicus* (DHNR), *Sebastes capensis*, *Thunnus albacares*

Distribution: SC, WC

References: (Grobler et al. 2003b; González and Moreno 2005; Weston 2017)

*Euryphorus brachypterus* (Gerstaecker, 1853)

Host (locality): *Thunnus alalunga*, *Thunnus albacares* (Table Bay), *Thunnus maccoyii*,  
*Thunnus obesus*, *Thunus thynnus* (off Cape Point), unspecified shark (Ifafa)

Distribution: WC

References: (Kensley and Grindley 1973; Oldewage and Avenat-Oldewage 1993; Cressey and Cressey 1980; Weston 2017)

*Gloiopotes huttoni* (Thomson G. M., 1890)

Host (locality): *Kajikia audax* (Cape Peninsula; Mossel Bay), *Istiompax indica* (Cape Point; Mossel Bay; Slangkop), *Istiompax* sp. (Mossel Bay)

Distribution: SC, WC

References: (Barnard 1957; Kensley and Grindley 1973)

*Hermilius pyriventris* Heller, 1865

Host (locality): *Galeichthys feliceps* (Gordons Bay; Table Bay)

Distribution: WC

References: (Barnard 1955b)

*Lepeophtheirus brachyurus* Heller, 1865

Host (locality): *Torquigener hypselogeneion* (Durban)

Distribution: EC

References: (Barnard 1948)

*Lepeophtheirus lalandei* Kensley & Grindley, 1973

Host (locality): *Seriola lalandi* (Vema Seamount)

Distribution: WC

References: (Kensley and Grindley 1973)

*Lepeophtheirus lichiae* Barnard, 1948

Host (locality): *Lichia amia* (KZN)

Distribution: EC

References: (Barnard 1948)

*Lepeophtheirus longispinosus* Wilson C. B., 1908

Host (locality): *Carcharhinus leucas* (KZN), *Carcharhinus limbatus* (KZN), *Squalus megalops* (Agulhas Bank)

Distribution: EC, SC

References: (Kensley and Grindley 1973; Oldewage 1992a; Dippenaar and Jordaan 2007)

*Lepeophtheirus natalensis* Kensley & Grindley, 1973

Host (locality): *Carcharhinus leucas* (KZN), *Carcharias taurus* (KZN)

Distribution: EC

References: (Kensley and Grindley 1973; Dippenaar and Jordaan 2007)

*Lepeophtheirus nordmanni* (Milne Edwards, 1840)

Host (locality): *Masturus lanceolatus* (Sea Point), *Mola mola* (Cape Town; Table Bay; Port Elizabeth), *Mola* sp. (Cape Town), *Thunnus* sp. (Cape Town)

Distribution: SC, WC

Notes: Recorded as *L. insignis* in Kensley & Grindley (1973)

References: (Kensley and Grindley 1973; Oldewage 1993b)

*Lepeophtheirus plotosi* Barnard, 1948

Host (locality): *Plotosus lineatus* (East London)

Distribution: SC

References: Barnard (1948)

*Lepeophtheirus* sp.

Host (locality): *Rhinobatos* sp. (Durban)

Distribution: EC

References: (Barnard 1955a)

*Paralebion elongatus* Wilson C. B., 1911

Host (locality): *Carcharhinus amboinensis* (KZN), *Carcharhinus leucas* (Durban; KZN), *Carcharhinus limbatus* (KZN), *Carcharhinus obscurus* (KZN)

Distribution: EC

References: (Cressey 1967b; Dippenaar and Jordaan 2007)

*Pupulina cliffi* Dippenaar & Lebepe, 2013

Host (locality): *Mobula ereegoodootenkee* (Umdloti; KZN), *Mobula kuhlii* (Umdloti; KZN)

Distribution: EC

References: (Dippenaar and Lebepe 2013)

*Pupulina merira* Dippenaar & Lebepe, 2013

Host (locality): *Mobula ereegoodootenkee* (Karridene; Richards Bay), *Mobula kuhlii* (Richards Bay)

Distribution: EC

References: (Dippenaar and Lebepe 2013)

### **Family Dichelestiidae Milne Edwards, 1840**

*Anthosoma crassum* (Abildgaard, 1974)

Host (locality): *Carcharodon carcharias* (Durban; False Bay; off KZN), *Carcharias* sp. (Durban; False Bay; Table Bay), *Isurus oxyrinchus* (Cape Recife; off KZN; Slangkop), *Isurus* sp. (Cape Point; Durban; East London), *Lamna nasus* (Durban; False Bay; Table Bay), *Manta birostris* (off KZN), *Mobula alfredi* (off KZN), *Odontaspis* sp. (Table Bay), *Prionace glauca* (Cape Point)

Distribution: EC, SC, WC

References: (Barnard 1955a; Cressey 1967b; Kensley and Grindley 1973; Oldewage and Smale 1993; Dippenaar and Jordaan 2007; Lebepe and Dippenaar 2013)

### **Family Eudactylinidae Wilson C. B., 1932**

*Carnifossorius siamensis* Deets & Ho, 1988

Host (locality): *Rhina ancylostoma* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina acanthii* Scott A., 1901

Host (locality): *Squalus megalops*

Distribution: SC

References: (Dippenaar and Molele 2015)

*Eudactylina aspera* Heller, 1865

Host (locality): *Carcharhinus limbatus* (off KZN), *Sphyrna lewini* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina diabolophila* Deets, 1994

Host (locality): *Mobula alfredi* (Karridene; Park Rynie; off San Lameer)

Distribution: EC

References: (Lebepe and Dippenaar 2013)

*Eudactylina dollfusi* Brian, 1924

Host (locality): *Carcharhinus obscurus* (off KZN), *Carcharhinus plumbeus* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina hornbosteli* Deets, 1994

Host (locality): *Aetobatus narinari* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina oliveri* Laubier, 1968

Host (locality): *Mobula kuhlii* (off KZN), *Mobula eregoodootenkee* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007; Lebepe and Dippenaar 2013)

*Eudactylina pollex* Cressey, 1967

Host (locality): *Sphyrna mokarran* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina pusilla* Cressey, 1967

Host (locality): *Galeocerdo cuvier* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Eudactylina* sp.

Host (locality): *Squalus megalops*

Distribution: N/A

References: (Dikgale and Dippenaar 2010 in Schaeffner and Smit 2019)

*Eudactylina vaquetillae* Deets, 1994

Host (locality): *Mobula kuhlii* (off KZN)

Distribution: EC

Notes: *E. vaquetillae* is considered a nomen nudum as the description was not formally published but can be found in Deet's (1994) doctoral thesis (Horton et al. 2019)

References: (Deets 1994; Lebepe and Dippenaar 2013)

*Eudactylinodes niger* (Wilson C. B., 1905)

Host (locality): *Carcharias taurus* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Nemesis lamna lamna* Risso, 1826

Host (locality): *Carcharodon carcharias* (False Bay; off KZN), *Isurus oxyrinchus* (Cape Recife), *Isurus* sp. (Durban)

Distribution: EC, SC, WC

Notes: alternate representation as *Nemesis lamna* Risso, 1826 also accepted (WoRMs 2018)

References: (Cressey 1967b; Kensley and Grindley 1973; Oldewage and Smale 1993; Dippenaar et al. 2008; Weston 2017)

*Nemesis robusta* (van Beneden, 1851)

Host (locality): *Alopias vulpinus* (Table Bay; off west coast), *Prionace glauca* (Fish Hoek)

Distribution: WC

Notes: synonymous with *Nemesis pallida* of Barnard (1955a) and Kensley and Grindley (1973)

References: (Barnard 1955a; Kensley and Grindley 1973)

*Nemesis* sp.

Host (locality): *Squalus megalops*

Distribution: SC

References: (Dippenaar and Molele 2015)

*Nemesis* sp. 1

Host (locality): *Carcharhinus brevipinna* (off KZN), *Sphyrna lewini* (off KZN)

Distribution: EC

References: (Dippenaar 2009; Mangena et al. 2014)

*Nemesis* sp. 2

Host (locality): *Carcharhinus brevipinna* (off KZN)

Distribution: EC

References: (Dippenaar 2009; Mangena et al. 2014)

*Nemesis* sp. 3

Host (locality): *Alopias vulpinus* (off KZN), *Carcharhinus limbatus* (off KZN), *Carcharhinus obscurus* (off KZN), *Carcharhinus sealei* (off KZN), *Sphyrna lewini* (off KZN)

Distribution: EC

References: (Dippenaar 2009; Mangena et al. 2014)

### **Family Hatschekiidae Kabata, 1979**

*Hatschekia conifera* Yamaguti, 1939

Host (locality): *Brama brama* (Fish Hoek; off Hondeklip Bay; off Kleinsee), *Thyrsites atun*

Distribution: WC

References: (Barnard 1955a; Oldewage 1993a, 1993c; Nunkoo et al. 2016; Weston 2017; Mackintosh et al. 2018)

### **Family Kroeyeriidae Kabata, 1979**

*Kroeyerina mobulae* Deets, 1987

Host (locality): *Mobula kuhlii* (off KZN)

Distribution: EC

References: (Lebepe and Dippenaar 2013)

*Kroeyerina scottorum* Cressey, 1970

Host (locality): *Sphyrna lewini* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Kroyeria carchariaeaglauci* Hesse, 1878

Host (locality): *Carangoides equula*, *Carcharhinus amboinensis*, *Carcharhinus leucas* (off KZN), *Prionace glauca* (False Bay; Fish Hoek), unspecified host

Distribution: EC, WC

Notes: synonymous with *K. gracilis* of Cressey (1967b) according to Dippenaar (2004)

References: (Kensley and Grindley 1973; Dippenaar and Jordaan 2007; Mokumo and Dippenaar 2015; Weston 2017)

*Kroyeria decepta* Deets, 1994

Host (locality): *Carcharhinus obscurus* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007; Dippenaar 2009; Mokumo and Dippenaar 2015)

*Kroyeria deetsi* Dippenaar, Benz & Olivier, 2000

Host (locality): *Carcharhinus brevipinna* (Glenmore; Uvongo)

Distribution: EC

References: (Dippenaar et al. 2000)

*Kroyeria dispar* Wilson C. B., 1935

Host (locality): *Galeocerdo cuvier* (Ansteys Beach; off KZN; Umzumbe)

Distribution: EC

References: (Dippenaar and Olivier 1999; Mokumo and Dippenaar 2015)

*Kroyeria gemursa* Cressey, 1967

Host (locality): *Sphyrna mokarran* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Kroyeria lineata* van Beneden, 1853

Host (locality): *Mustelus palumbes*

Distribution: N/A

References: (Mokumo and Dippenaar 2015)

*Kroyeria longicauda* Cressey, 1970

Host (locality): *Carcharhinus limbatus* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Kroyeria papillipes* Wilson C. B., 1932

Host (locality): *Galeocerdo cuvier* (off KZN)

Distribution: EC

References: (Mokumo and Dippenaar 2015)

*Kroyeria procerobscena* Deets, 1994

Host (locality): *Carcharhinus amboinensis* (off KZN), *Carcharhinus leucas* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Kroyeria rrophemophaga* Deets, 1994

Host (locality): *Galeorhinus galeus*

Distribution: N/A

Notes: *K. rrophemophaga* is considered a nomen nudum as the description was not formally published but can be found in Deet' s (1994) doctoral thesis

References: (Mokumo and Dippenaar 2015)

*Kroyeria sphyrnae* Rangnekar, 1957

Host (locality): *Sphyrna lewini* (Amanzimtoti; Zinkwazi; Port Edward; Richards Bay; San Lameer; Winklespruit), *Sphyrna zygaena* (Durban)

Distribution: EC

References: (Dippenaar et al. 2001; Mokumo and Dippenaar 2015)

*Kroyeria* sp.

Host (locality): *Carcharhinus brevipinna*

Distribution: N/A

References: (Dippenaar et al. 2000 in Schaeffner and Smit 2019)

### **Family Lernaepodidae Milne Edwards, 1840**

*Alella pagelli* (Krøyer, 1863)

Host (locality): *Lithognathus lithognathus* (Cape Peninsula), *Pachymetopon blochii* (Cape Peninsula), *Rhabdosargus sarba* (Lake St. Lucia)

Distribution: EC, WC

Notes: synonymous with *Clavella pagelli* of Barnard (1955a) and *Alella gibbosa* of van Niekerk & Olivier (1995) according to (Dippenaar 2004, 2016b)

References: (Barnard 1955a; van Niekerk and Olivier 1995)

*Charopinus dalmanni* (Retzius, 1829)

Host (locality): *Haploblepharus edwardsii* (SW of Cape St. Francis), *Squalus acanthias* (off Hondeklip Bay)

Distribution: SC, WC

References: (Oldewage 1992a, 1993a)

*Charopinus dubius* Scott T., 1901

Host (locality): *Chelidonichthys capensis* (NW of Hondeklip Bay), *Rajella caudaspinosa*, *Rajella leopardus*, *Raja* sp. (Table Bay), Unspecified skate (Port Elizabeth)

Distribution: SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973; Oldewage 1993a)

*Clavella denticis* (Krøyer, 1863)

Host (locality): *Petrus rupestris* (off Cape Peninsula)

Distribution: WC

References: (Barnard 1955a)

*Clavellisa ilishae* Pillai, 1962

Host (locality): *Sardinops sagax* (False Bay; Mossel Bay)

Distribution: SC, WC

References: (Kensley and Grindley 1973; Reed et al. 2012; Weston 2017)

*Clavellisa scombri* (Kurz, 1877)

Host (locality): *Scomber colias* (Table Bay)

Distribution: WC

References: (Barnard 1955b)

*Clavellopsi appendiculata* Kirtisinghe, 1950

Host (locality): *Chirocentrus dorab* (Durban)

Distribution: EC

References: (Kensley and Grindley 1973)

*Clavellopsi hostilis* (Heller, 1865)

Host (locality): *Umbrina ronchus* (off KZN)

Distribution: EC

References: (Barnard 1955a)

*Clavellotis fallax* (Heller, 1865)

Host (locality): *Cymatoceps nasutus* (East London), *Lithognathus lithognathus*

Distribution: SC

References: (Barnard 1955a)

*Clavellotis sargi* (Kurz, 1877)

Host (locality): *Argyrozona argyrozona* (False Bay), *Chrysoblephus laticeps* (False Bay),  
*Pachymetopon blochii* (Table Bay; off west coast)

Distribution: WC

Notes: synonymous with *Clavellopsis sargi* (Horton et al. 2019)

References: (Kensley and Grindley 1973)

*Eobrachiella elegans* (Riciardi, 1880)

Host (locality): *Seriola lalandi*

Distribution: N/A

References: (Weston 2017)

*Lernaeopoda galei* Krøyer, 1837

Host (locality): *Mustelus mustelus* (False Bay), *Rhizoprionodon acutus* (off KZN)

Distribution: EC, WC

Note: misspelt as *Lerneopoda galei* in Barnard (1955a)

References: (Barnard 1955a; Dippenaar and Jordaan 2007)

*Lernaeopoda* sp.

Host (locality): *Squalus megalops*

Distribution: SC

References: (Dippenaar and Molele 2015)

*Naobranchia kabatana* Dippenaar & Jordaan, 2008

Host (locality): *Muraenesox bagio* (Richards Bay)

Distribution: EC

References: (Dippenaar and Jordaan 2008)

*Naobranchia pritchardae* Kensley & Grindley, 1973

Host (locality): *Pomadasys commersonii* (Durban)

Distribution: EC

References: (Kensley and Grindley 1973)

*Neoalbionella etmopteri* (Yamaguti, 1939)

Host (locality): *Etmopterus* sp. (Cape Point)

Distribution: WC

References: (Kensley and Grindley 1973)

*Parabrachiella exilis* (Shiino, 1956)

Host (locality): *Chelon ramada* (Table Bay)

Distribution: WC

Notes: *Chelon ramada* is a synonym of *Mugil capito* of Barnard (1955a) and *Parabrachiella exilis* is synonymous with *Brachiella* sp. of Barnard (1955a)

References: (Barnard 1955a; Lebepe and Dippenaar 2016)

*Parabrachiella insidiosa* (Heller, 1865)

Host (locality): *Merluccius capensis* (off Cape Peninsula; Table Bay), *Merluccius paradoxus* (off Cape Peninsula)

Distribution: WC

Notes: synonymous with *Parabrachiella australis* of Wilson in Barnard (1955a, 1955b) and in Botha (1986) and *Neobrachiella insidiosa* of Dippenaar (2004)

References: (Barnard 1955a, 1955b; Botha 1986)

*Parabrachiella sublobulata* (Barnard, 1955)

Host (locality): *Congiopodus torvus* (Table Bay)

Distribution: WC

Notes: synonymous with *Eubrachiella sublobulata* of Barnard (1955a)

References: (Barnard 1955a)

*Parabrachiella supplicans* (Barnard, 1955)

Host (locality): *Chelidonichthys queketti* (Agulhas Bank), *Genypterus capensis* (Table Bay), *Merluccius capensis* (south of Plettenberg Bay; off Fish Water), *Merluccius paradoxus* (south of Cape St. Francis)

Distribution: SC, WC

Notes: synonymous with *Brachiella supplicans* of Barnard (1955b), Oldewage (1992) and Dippenaar (2004) and *Parabrachiella genypteri* (Capart, 1959)

References: (Barnard 1955a, 1955b; Oldewage 1992a; Lebepe and Dippenaar 2016)

*Parabrachiella* sp. 1

Host (locality): *Seriola lalandi*

Distribution: WC

References: (Weston 2017)

*Parabrachiella* sp. 2

Host (locality): *Seriola lalandi*

Distribution: WC

References: (Weston 2017)

*Pseudocharopinus bicaudatus* (Krøyer, 1837)

Host (locality): *Squalus megalops*,

Distribution: EC, SC

References: (Dippenaar and Molele 2015)

*Pseudocharopinus pteromyiae* Raibaut & Essafi, 1979

Host (locality): *Aetomylaeus bovinus* (Durban)

Distribution: EC

References: (Dippenaar 2012)

*Schistobrachia jordaanae* Dippenaar, Olivier & Benz, 2004

Host (locality): *Gymnura natalensis* (Durban)

Distribution: EC

References: (Dippenaar et al. 2004)

*Schistobrachia kabata* Dippenaar, 2016

Host (locality): *Dipturus batis* (Table Bay), *Leucoraja wallacei*, *Raja straeleni*, *Rostroraja alba*, Unspecified skate (Table Bay)

Distribution: SC, WC

Notes: Barnard (1955b) recorded *S. kabata* as *Charopinus ramosus* and Kensley and Grindley (1973) misidentified *S. kabata* as *S. ramosa* according to Dippenaar (2016c)

References: (Barnard 1955b; Kensley and Grindley 1973; Dippenaar 2016c)

*Sparidicola lithognathi* (Kensley & Grindley, 1973)

Host (locality): *Lithognathus lithognathus* (Milnerton; Table Bay)

Distribution: WC

Notes: synonymous with *Brachiella lithognathae* of Kensley and Grindley (1973)

References: (Kensley and Grindley 1973)

*Vanbenedenia hydrolagae* Oldewage, 1993

Host (locality): *Hydrolagus* sp. (south of Cape Recife)

Distribution: SC

References: (Oldewage 1993d)

#### **Family Lernanthropidae Kabata, 1979**

*Lernanthropodes natalensis* Kensley & Grindley, 1973

Host (locality): *Scomberoides tol* (Durban)

Distribution: EC

References: (Kensley and Grindley 1973)

*Lernanthropus capistroides* Olivier & van Niekerk, 1995

Host (locality): *Otolithes ruber* (Lake St. Lucia)

Distribution: EC

References: (Olivier and van Niekerk 1995a)

*Lernanthropus corniger* Yamaguti, 1954

Host (locality): *Alepes djebaba* (Durban)

Distribution: EC

References: (Kensley and Grindley 1973)

*Lernanthropus ecclesi* Kensley & Grindley, 1973

Host (locality): *Seriola lalandi* (Kalk bay)

Distribution: WC

References: (Kensley and Grindley 1973)

*Lernanthropus paradoxus* (Nordmann, 1832)

Host (locality): *Mugil* sp. (Cape of Good Hope)

Distribution: WC

References: (Barnard 1955a)

*Lernanthropus sarbae* Kensley & Grindley, 1973

Host (locality): *Acanthopagrus berda* (Lake St. Lucia), *Rhabdosargus holubi* (Lake St. Lucia), *Rhabdosargus sarba* (Durban; Lake St. Lucia)

Distribution: EC

References: (Kensley and Grindley 1973; Olivier and van Niekerk 1995b)

*Sagum foliaceum* (Goggio, 1905)

Host (locality): *Acanthocybium solandri*, *Ruvettus pretiosus*

Distribution: WC

Notes: Recorded as *Sagum foliaceus* in Nunkoo et al. (2017) and Toksen et al. (2012)

References: (Toksen et al. 2012; Nunkoo et al. 2017)

### **Family Pandaridae Milne Edwards 1840**

*Achtheinus pinguis* Wilson C. B., 1912

Host (locality): *Carcharias taurus* (Kalk Bay), *Carcharodon carcharias* (Cape Recife; Table Bay), *Haploblepharus edwardsii* (Agulhas Bank; Cape Agulhas; Table Bay), *Haploblepharus pictus*, *Hexanchus griseus* (Cape Agulhas; Cape Recife), *Mustelus canis* (False Bay; Langebaan), *Mustelus mustelus* (Agulhas Bank; Cape Recife), *Mustelus* sp. (Kalk Bay), *Pliotrema warreni* (Cape of Good Hope; Cape Recife; Table Bay), *Sphyrna zygaena* (Strand), *Squalus acanthias* (Dassen Island; False Bay; Table Bay; South of Port Nolloth), *Squalus blainville*, *Squalus megalops* (Agulhas Bank; Cape Recife, off Plettenberg Bay, off PE), *Squalus* sp. (Table Bay)

Distribution: EC, SC, WC

Notes: synonymous with *Achtheinus parvidens* of Wilson (1923), *Perissopus armatus* of Oldewage (1992a), *Perissopus oblongus* of Oldewage (1992b) and *Perissopus oblongatus* of Oldewage and Avenant-Oldewage (1993) and Oldewage and Smale (1993)

References: (Wilson 1923; Barnard 1955a; Kensley and Grindley 1973; Oldewage 1992a, 1992b, 1993a; Oldewage and Smale 1993; Yeld 2009; Dippenaar and Molele 2015; Dippenaar 2018a)

*Cecrops latreillii* Leach, 1816

Host (locality): *Masturus lanceolatus* (Bantry Bay; Sea Point), *Mola mola* (Cape Peninsula)

Distribution: WC

Note: recorded as *C. exiguus* in Kensley and Grindley (1973)

References: (Barnard 1955a; Kensley and Grindley 1973)

*Dinemoura latifolia* (Steenstrup & Lütken, 1861)

Host (locality): *Isurus oxyrinchus* (Durban; off Cape Point; south of Cape Recife), *Isurus* sp.,  
*Mola mola* (Cape Peninsula), *Prionace glauca* (Cape Peninsula), unspecified  
hosts (Durban; Cape Point; Cape Recife)

Distribution: EC, SC, WC

Notes: synonymous with *Dinematura latifolia* in Kensley and Grindley (1973)

References: (Barnard 1955a; Cressey 1967a; Kensley and Grindley 1973; Oldewage 1992c;  
Oldewage and Smale 1993)

*Dinemoura producta* Latreille, 1829

Host (locality): unspecified host (Durban)

Distribution: EC

References: (Barnard 1955a)

*Echthrogaleus coleoptratus* (Guérin-Méneville, 1837)

Host (locality): *Carcharodon Carcharias* (Cape Recife), *Prionace glauca* (Durban; Kalk  
Bay; False Bay; Slangkop)

Distribution: EC, SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973; Oldewage and Smale 1993)

*Echthrogaleus denticulatus* Smith, 1873

Host (locality): *Isurus oxyrinchus* (Cape Recife)

Distribution: SC

References: (Oldewage and Smale 1993)

*Echthrogaleus pellucidus* Shiino, 1963

Host (locality): *Carcharodon carcharias*

Distribution: N/A

References: (Dippenaar 2018a)

*Echthrogaleus torpedinis* Wilson C. B., 1907

Host (locality): *Tetronare nobiliana* (Cape Columbine), *Torpedo* sp. (off Slangkop)

Distribution: WC

References: (Kensley and Grindley 1973)

*Entepherus laminipes* Bere, 1936

Host (locality): *Manta birostris* (off KZN), *Mobula alfredi* (off KZN), *Mobula kuhlii* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007; Lebepe and Dippenaar 2013)

*Nesippus crypturus* Heller, 1865

Host (locality): *Carcharhinus brevipinna* (off Kent Bay, off Ramsgate), *Carcharhinus leucas* (off Richards Bay), *Carcharhinus limbatus* (off Port Edward, off Warner Beach, off Zinkwazi), *Carcharodon carcharias* (off Richards Bay), *Galeocerdo cuvier* (off Amanzimtoti, off Anstey's Beach, off Salt Rocks, off Scottsburgh), *Sphyrna zygaena* (off Leisure Beach), *Sphyrna mokarran* (off Durban, off Umdloti)

Distribution: EC

References: (Dippenaar 2009; Dippenaar and Jordaan 2012)

*Nesippus nana* Cressey, 1970

Host (locality): *Carcharhinus plumbeus* (off Richards Bay)

Distribution: EC

References: (Dippenaar and Jordaan 2012)

*Nesippus orientalis* Heller, 1865

Host (locality): *Alopias vulpinus* (Southbroom), *Carcharhinus brachyurus*, *Carcharhinus brevipinna* (Ramsgate), *Carcharhinus leucas* (Richards Bay), *Carcharhinus limbatus* (Amanzimtoti; Durban; Ramsgate; Richards Bay; Salt Rocks; Scottsburgh; Southbroom; Warner Beach), *Carcharhinus obscurus*, *Carcharias taurus* (Scottsburgh), *Carcharodon carcharias* (Durban; False

Bay), *Isurus oxyrinchus* (Salt Rocks), *Mustelus mustelus* (off KZN), *Sphyrna lewini* (Amanzimtoti), *Sphyrna mokarran* (Durban), *Sphyrna zygaena* (Durban), unspecified host

Distribution: EC, WC

Notes: synonymous with *Nesippus alatus* (WoRMs 2018)

References: (Barnard 1955a; Cressey 1967a; Kensley and Grindley 1973; Oldewage 1993b; Dippenaar and Jordaan 2006; Dippenaar and Jordaan 2012; Dippenaar 2018a)

*Nesippus tigris* Cressey, 1967

Host (locality): *Carcharodon carcharias* (off Richards Bay), *Galeocerdo cuvier* (off Amanzimtoti, Ballito Bay, Brighton Beach Hibberdene, Richards Bay, Salt Rock, Scottsburgh, Trafalgar, T.O. Strand Umdloti, Umzumbe, Umtentweni, Winklespruit)

Distribution: EC

References: (Dippenaar and Jordaan 2007; Dippenaar and Jordaan 2012)

*Nesippus vespa* Cressey, 1964

Host (locality): *Rhina ancylostoma* (off Durban, Richards Bay, Trafalgar), *Rhynchobatus djiddensis* (off Durban)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Orthagoriscicola muricatus* (Krøyer, 1837)

Host (locality): *Masturus lanceolatus* (Table Bay), *Mola mola* (Cape Columbine; Port Elizabeth; Table Bay), *Mola* sp. (Table Bay)

Distribution: SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973)

*Pandarus bicolor* Leach, 1816

Host (locality): *Carcharhinus* sp. (Durban), *Carcharias* sp. (False Bay; Table Bay), *Carcharodon carcharias* (False Bay), *Galeorhinus galeus* (Cape Recife, False Bay), *Galeorhinus* sp. (False Bay; Table Bay), *Odontaspis* sp. (Table Bay), *Squalus acanthias* (NW of Hondeklip Bay), *Squalus* sp. (Sea Point), unidentified shark (Durban), unspecified host (Three Anchor Bay)

Distribution: EC, SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973; Oldewage 1993a; Oldewage and Smale 1993; Dippenaar 2018a)

*Pandarus carcharhini* Ho, 1963

Host (locality): *Carcharhinus leucas* (Durban)

Distribution: EC

References: (Cressey 1967a)

*Pandarus cranchi* Leach, 1819

Host (locality): *Carcharhinus longimanus* (Durban), *Carcharodon carcharias* (Durban), *Poroderma africanum* (Cape of Good Hope), *Sphyrna zygaena* (off KZN), *Sphyrna* sp. (off Tugela River mouth), *Stegostoma fasciatum* (Durban), *Stegostoma* sp. (Durban), unspecified host (off KZN)

Distribution: EC, WC

References: (Barnard 1955a; Cressey 1967a; Kensley and Grindley 1973)

*Pandarus floridanus* Cressey, 1967

Host (locality): *Carcharias taurus* (Cape Recife)

Distribution: SC

References: (Oldewage and Smale 1993)

*Pandarus smithii* Rathbun, 1886

Host (locality): *Carcharhinus* sp. (Durban), *Carcharias* sp. (Table Bay), *Carcharias taurus* (Cape Recife), *Carcharodon carcharias* (Cape Recife; off Slangkop), *Isurus oxyrinchus* (south of Cape Recife; off Slangkop), *Isurus* sp., *Odontaspis* sp. (Durban), *Prionace glauca* (off Slangkop), *Rhincodon typus* (Milnerton), *Rhizoprionodon acutus*, *Scoliodon laticaudus*

Distribution: EC, SC, WC

References: (Barnard 1955a; Kensley and Grindley 1973; Oldewage and Smale 1993; Dippenaar 2018a)

*Pandarus* sp.

Host (locality): *Carcharias taurus*, *Carcharodon carcharias*, *Sphyrna lewini*

Distribution: EC

References: (Dippenaar 2009)

*Pannosus japonicus* (Shiino, 1960)

Host (locality): *Sphyrna lewini* (off KZN)

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Perissopus dentatus* Steenstrup & Lütken, 1861

Host (locality): *Carcharhinus leucas* (Durban), *Carcharhinus limbatus* (off KZN), *Carcharhinus obscurus* (Durban), *Carcharhinus sealei* (off KZN), *Carcharodon Carcharias* (Table Bay), *Haploblepharus edwardsii* (Orange River mouth), *Mustelus canis* (False Bay; Langebaan), *Mustelus mosis* (off KZN), *Mustelus* sp. (Durban), *Rhizoprionodon acutus* (Durban), *Sphyrna zygaena* (Strand), *Squalus blainville*, *Squalus megalops*

Distribution: EC, SC, WC

Notes: *Mustelus canis* reported as a host by Oldewage and Avenant-Oldewage (1993) does not occur in South Africa (Froese and Pauly 2018). Specimens examined must have belonged to one of the other *Mustelus* species that occur in South Africa (*M. mosis*, *M. mustelus*, *M. palumbes*)

References: (Barnard 1955a; Cressey 1967b; Kensley and Grindley 1973; Oldewage 1992a; Oldewage and Avenant-Oldewage 1993; Dippenaar and Jordaan 2007; Dippenaar 2009)

*Philorthragoriscus serratus* (Krøyer, 1863)

Host (locality): *Masturus lanceolatus* (Sea Point), *Mola mola* (Table Bay)

Distribution: WC

References: (Barnard 1948; Kensley and Grindley 1973)

*Phyllothyreus cornutus* (Milne Edwards, 1840)

Host (locality): *Galeocerdo cuvier*, *Isurus oxyrinchus*

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Pseudopandarus gracilis* Kirtisinghe, 1950

Host (locality): *Mustelus mosis*

Distribution: EC

References: (Dippenaar and Jordaan 2007)

*Pseudopandarus longus* (Gnanamuthu, 1951)

Host (locality): *Carcharhinus obscurus*, *Carcharhinus sealei*, *Mustelus mosis*,  
*Rhizoprionodon acutus* (Durban), *Triaenodon obesus* (Durban)

Distribution: EC

References: (Cressey 1967a; Dippenaar and Jordaan 2007)

### **Family Pennellidae Burmeister, 1835**

*Cardiodectes bellottii* (Richiardi, 1882)

Host (locality): *Gonichthys cocco* (off Cape Peninsula), *Lampanyctodes hectoris* (west of  
Saldanha Bay), unspecified myctophid (Cape Point)

Distribution: WC

References: (Barnard 1955a; Kensley and Grindley 1973; Weston 2017)

*Lernaeenicus kabatai* Oldewage, 1989

Host (locality): *Carangoides equula* (Kowie River mouth)

Distribution: SC

References: (Oldewage 1989)

*Pennella filosa* (Linnaeus, 1758)

Host (locality): *Istiompax indica* (off Cape Point), *Mola mola* (Table Bay), *Thunnus*  
*albacares* (False Bay)

Distribution: WC

References: (Kensley and Grindley 1973)

### **Family Pseudocycnidae Wilson C. B., 1922**

*Cybicola armatus* (Bassett-Smith, 1898)

Host (locality): *Scomberomorus maculatus* (Durban), *Scomberomorus plurilineatus* (off  
KZN)

Distribution: EC

Notes: synonymous with. *Pseudocycnoides armatus* of Cressey and Cressey (1980) and *Pseudocycnoides rugosa* of Kensley and Grindley (1973) and in Dippenaar (2004)

References: (Kensley and Grindley 1973; Cressey and Cressey 1980)

*Pseudocycnus appendiculatus* Heller, 1865

Host (locality): *Thunnus alalunga*, *Thunnus albacares*, *Thunnus obesus*

Distribution: WC

References: (Weston 2017)

### **Family Sphyriidae Wilson C. B., 1919**

*Lophoura elongata* Kensley & Grindley, 1973

Host (locality): *Histiobranchus bathybius* (Cape Point)

Distribution: WC

References: (Kensley and Grindley 1973)

*Sphyrion laevigatum* (Quoy & Gaimard, 1824)

Host (locality): *Atractoscion aequidens* (Agulhas Bank), *Coelorinchus fasciatus* (Cape Point), *Genypterus capensis* (Cape Point; Table Bay; off the south east coast of South Africa), unspecified macrurid (Cape Point; Table Bay)

Distribution: EC, WC

References: (Barnard 1955a; Payne 1986)

*Sphyrion lumpi* (Krøyer, 1835)

Host (locality): *Antimora rostrata* (Cape Point), *Cottunculus* sp. (Cape Point), *Psychrolutes macrocephalus* (Cape Point)

Distribution: WC

References: (Barnard 1948, 1955a; Kensley and Grindley 1973)

*Tripaphylus beatricae* Dippenaar 2018

Host (locality): *Mustelus mustelus*

Distribution: WC

References: (Dippenaar 2018c)

*Tripaphylus benzi* Dippenaar, 2018

Host (locality): *Mustelus palumbes*

Distribution: SC

References: (Dippenaar 2018c)

*Tripaphylus elongatus* (Wilson C. B., 1932)

Host (locality): *Carcharhinus obscurus* (Amanzimtoti; Durban; Glenmore; Richards Bay; Southport; Winklespruit; off KZN)

Distribution: EC

Notes: synonymous with *Paeon elongatus* of Dippenaar and Jordaan (2007)

References: (Dippenaar and Jordaan 2007; Dippenaar 2018c)

*Tripaphylus hoi* Dippenaar, 2018

Host (locality): *Mustelus palumbes* (34.17 S, 25.58 E)

Distribution: SC

References: (Dippenaar 2018c)

*Tripaphylus lewisi* Dippenaar, 2018

Host (locality): *Hemipristis elongata* (off Durban)

Distribution: EC

References: (Dippenaar 2018c)

*Tripaphylus vaissierei* Delamare Deboutville & Nunes-Ruivo, 1954

Host (locality): *Sphyrna lewini* (off KZN; off Richards Bay)

Distribution: EC

Notes: *Paeon vaissierei* of Dippenaar and Jordaan (2007) is a synonym

References: (Dippenaar and Jordaan 2007; Dippenaar 2018c)

### **Family Trebiidae Wilson C. B., 1905**

*Trebius benzi* Dippenaar, 2017

Host (locality): *Squalus megalops* (off Mossel Bay)

Distribution: SC

References: (Dippenaar 2017)

*Trebius caudatus* Krøyer, 1838

Host (locality): *Rostroraja alba* (Table Bay), unspecified skate species (Table Bay)

Distribution: WC

References: (Barnard 1948; Kensley and Grindley 1973)

*Trebius* sp.

Host (locality): *Squalus megalops*

Distribution: SC

References: (Dippenaar and Molele 2015)

**Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1997**

**Subclass Branchiura Thorell, 1864**

**Order Arguloida Yamaguti, 1963**

**Family Argulidae Leach, 1819**

*Argulus belones* Kampen, 1909

Host (locality): *Scomberomorus commerson* (off KZN), *Sphyræna barracuda* (off KZN)

Distribution: EC

References: (Barnard 1955a; Kensley and Grindley 1973)

*Argulus izintwala* van As J. G. & van As L. L., 2001

Host (locality): *Hilsa kelee* (Lake St. Lucia)

Distribution: EC

References: (van As and van As 2001)

*Argulus kosus* Avenant-Oldewage, 1994

Host (locality): *Aluterus monoceros* (Port Elizabeth), *Elops machnata* (Lake St. Lucia), *Liza luciae* (Lake St. Lucia), *Mugil cephalus* (Lake St. Lucia), *Otolithes ruber* (Lake St. Lucia), *Pomadasys commersonnii* (Lake St. Lucia), *Pomadasys multimaculatus* (Lake St. Lucia), *Rhabdosargus holubi* (Lake St. Lucia), *Sarpa salpa* (Kosi Bay)

Distribution: EC, SC

Notes: *Argulus smalei* described in Avenant-Oldewage and Oldewage (1995) is considered a synonym of *Argulus kosus* according to van As et al. (1999)

References: (Avenant-Oldewage 1994; Avenant-Oldewage and Oldewage 1995; van As et al. 1999)

*Argulus multipocula* Barnard, 1955

Host (locality): *Chelon richardsonii* (Berg River estuary; Richards Bay)

Distribution: EC, WC

References: (Barnard 1955a; Smit et al. 2005)

## **Class Malacostraca Latreille, 1802**

### **Subclass Eumalacostraca**

### **Order Isopoda Latreille, 1817**

### **Family Cirolanidae Dana, 1852**

*Natatolana hirtipes* (H. Milne Edwards, 1840)

Host (locality): *Carcharias* sp. (Table Bay), Unspecified host (Algoa Bay, Cape of Good Hope, False Bay, Saldanha Bay, off KZN)

Distribution: EC, WC

References: (Milne Edwards 1840; Barnard 1936)

### **Family Cymothoidae Leach, 1818**

*Anilocra capensis* Leach, 1818

Host (locality): *Callorhinchus capensis* (St. Helena Bay), *Pachymetopon blochii* (False Bay), unspecified host

Distribution: WC

References: (Leach 1818; Stebbing 1900; Wright et al. 2001; Awa 2012)

*Anilocra leptosoma* Bleeker, 1857

Host (locality): Unspecified host (St. Lucia)

Distribution: EC

References: (Kensley 1978)

*Ceratothoa africanae* Hadfield, Bruce & Smit, 2014

Host (locality): *SpondylIOSoma emarginatum* (Tsitsikamma to Algoa Bay)

Distribution: SC

References: (Hadfield et al. 2014a)

*Ceratothoa famosa* Hadfield, Bruce & Smit, 2014

Host (locality): *Diplodus hottentotus* (Keiskamma River mouth; Kleinemonde; Knysna; Tsitsikamma National Park), *Diplodus sargus capensis* (Algoa Bay (Swartkops estuary); Cape Agulhas; Kenton on Sea; Morgan Bay; Transkei; Tsitsikamma National Park), *Sparodon durbanensis* (Cape Padrone; Kleinemonde; Knysna; Tsitsikamma National Park)

Distribution: EC, SC

References: (Hadfield et al. 2014a)

*Ceratothoa retusa* (Schioedte & Meinert, 1883)

Host (locality): *Hemiramphus far* (Durban, Knysna), *Hemiramphus* sp. (Durban; Port Elizabeth), unspecified host (Port Natal)

Distribution: EC, SC

References: (Kensley 1978; Hadfield et al. 2014b)

*Cinusa tetrodontis* Schioedte & Meinert, 1884

Host (locality): *Amblyrhynchotes honckenii* (False Bay, Tsitsikamma National Park)

Distribution: SC, WC

References: (Kensley 1978; Hadfield et al. 2010)

*Cymothoa sodwana* Hadfield, Bruce & Smit, 2014

Host (locality): *Trachinotus botla* (Sodwana Bay), unspecified parrot fish (Durban to Mozambique)

Distribution: EC

Notes: *Cymothoa borbonica* in Parker and Booth (2013) is a synonym

References: (Kensley 1978; Hadfield et al. 2013; Parker and Booth 2013)

*Elthusa acutinasa* van der Wal, Smit Hadfield, 2019

Host (locality): Unspecified host (34°38'S, 25°38'E; 30°29'S, 16°0'E; 30°25'S, 16°9'E; 31°8'S, 15°20'E)

Distribution: SC, WC

References: (van der Wal et al. 2019)

*Elthusa raynaudii* (H. Milne Edwards, 1840)

Host (locality): *Chorisochismus dentex* (Hout Bay, Table Bay), unspecified wrasse (Durban),  
unspecified host (Cape of Good Hope, off West Coast, 32°17'S, 16°54'E;  
34°38'S, 25°38'E)

Distribution: EC, SC, WC

Notes: Recorded as *Livoneca raynaudi* in Barnard (1920, 1955b) and as *Lironeca raynaudi* in  
Kensley (1978)

References: (Milne-Edwards 1840; Barnard 1920; Barnard 1955b; Kensley 1978; van der  
Wal et al. 2019)

*Elthusa rotunda* van der Wal, Smit & Hadfield 2019

Host (locality): unspecified host (Sea Point)

Distribution: WC

References: (van der Wal et al. 2019)

*Elthusa xena* van der Wal, Smit & Hadfield 2019

Host (locality): *Clinus superciliosus* (Alexander Bay)

Distribution: WC

References: (van der Wal et al. 2019)

*Mothocya affinis* Hadfield, Bruce & Smit, 2015

Host (locality): *Hyporamphus affinis* (Dog Point; Sodwana)

Distribution: EC

References: (Hadfield et al. 2015)

*Mothocya renardi* (Bleeker, 1857)

Host (locality): *Strongylura leiura* (Durban; St Lucia; Mhlathuze estuary)

Distribution: EC

Notes: recorded as *Irona melanostica* in Barnard (1955b)

References: (Barnard 1955b; Hadfield et al. 2015)

*Nerocila orbignyi* (Guérin-Méneville, 1832)

Host (locality): *Argyrozona argyrozona* (Algoa Bay, False Bay, Table Bay), *Chelidonichthys capensis*, *Mugil* sp. (Agulhas to St Helena Bay), *Pterogymnus laniarus* (Algoa Bay, False Bay, Table Bay), *Rhabdosargus globiceps* (Algoa Bay, False Bay, Table Bay), *Thyrsites atun* (Algoa Bay, False Bay, Table Bay)

Distribution: SC, WC

References: (Kensley 1977; Kensley 1978)

*Nerocila phaiopleura* Bleeker, 1857

Host (locality): *Chirocentrus dorab* (off KZN)

Distribution: EC

References: (Kensley 1978)

*Nerocila serra* Schioedte & Meinert, 1881

Host (locality): *Rhabdosargus* sp. (St. Lucia Bay)

Distribution: EC

References: (Kensley 1978)

*Nerocila trichiura* (Miers, 1877)

Host (locality): Unspecified flying fish (Durban)

Distribution: EC

References: (Kensley 1978)

*Pleopodias nielbrucei* Hadfield & Smit, 2017

Host (locality): Unspecified host (off Cape Town)

Distribution: WC

References: (Hadfield and Smit 2017)

### **Family Gnathiidae Leach, 1814**

*Afrignathia multicavea* Hadfield & Smit, 2008

Host (locality): Unspecified host (Cape Point; False Bay; off Mossel Bay; off Port Alfred; off Stillbay)

Distribution: SC, WC

References: (Hadfield and Smit 2008)

*Caecognathia cryptopais* (Barnard, 1925)

Host (locality): Unspecified host (East London; Port Alfred; Saldanha Bay)

Distribution: EC, SC, WC

References: (Smit et al. 2000)

*Gnathia africana* Barnard, 1914

Host (locality): *Chorisochismus dentex* (Jeffreys Bay), *Clinus cottoides* (DHNR; Jeffreys Bay), *Clinus superciliosus* (DHNR; Jeffreys Bay), unspecified host (DHNR; Jeffreys Bay; McDougall's Bay; off Port Alfred; St. James)

Distribution: SC, WC

References: (Barnard 1914; Smit et al. 1999)

*Gnathia disjuncta* Barnard, 1920

Host (locality): unspecified host (Knysna Heads)

Distribution: SC

References: (Barnard 1920)

*Gnathia nkulu* Smit & van As, 2000

Host (locality): unspecified host (off Port Alfred)

Distribution: SC

References: (Smit and van As 2000)

*Gnathia pantherina* Smit & Basson, 2002

Host (locality): *Haploblepharus edwardsii* (DHNR), *Poroderma pantherinum* (Jeffreys Bay), *Acroteriobatus annulatus* (DHNR), *Torpedo fuscomaculata* (DHNR)

Distribution: SC

References: (Smit and Basson 2002; Hayes et al. 2007)

*Gnathia pilosus* Hadfield, Smit & Avenant-Oldewage, 2008

Host (locality): *Abudefduf sordidus* (Sheffield Beach; Tinley Manor), *Acanthurus triostegus* (Sheffield Beach; Tinley Manor), *Antennablennius bifilum* (Sheffield Beach; Tinley Manor), *Diplodus sargus capensis* (Sheffield Beach; Tinley Manor), *Epinephelus marginatus* (Sheffield Beach; Tinley Manor), *Halichoeres nebulosus* (Sheffield Beach; Tinley Manor), *Istiblennius dussumieri* (Sheffield Beach; Tinley Manor), *Istiblennius edentulus* (Sheffield Beach; Tinley Manor), *Omobranchus banditus* (Sheffield Beach; Tinley Manor), *Plectroglyphidodon leucozoncus* (Sheffield Beach; Tinley Manor), *Psammogobius knysnaensis* (Sheffield Beach; Tinley Manor), *Pterois miles* (Sheffield Beach; Tinley Manor), *Scartella emarginata* (Sheffield Beach; Tinley Manor), *Terapon jarbua* (Sheffield Beach; Tinley Manor), *Thalassoma purpureum* (Sheffield Beach; Tinley Manor)

Distribution: EC

References: (Hadfield et al. 2008)

*Gnathia spongicola* Barnard, 1920

Host (locality): unspecified fish hosts (off Cape Peninsula)

Distribution: WC

Notes: collected from hexactinellid corals

References: (Barnard 1920)

*Gnathia* sp.

Host (locality): *Sebastes capensis*

Distribution: WC

References: (González and Moreno 2005)

**Phylum Cnidaria Verrill, 1865**

**Class Myxozoa (Grassé, 1970)**

**Subclass Myxosporea Bütschli, 1881**

**Order Bivalvulida Shulman, 1959**

**Family Alatasporidae Shulman, Kovaljova & Dubina, 1979**

*Pseudalataspora vanderlingeni* Reed, Kalavati, MacKenzie, Collins & Hemmingsen, 2018

Host (locality): *Merluccius capensis*, *Merluccius paradoxus*

Distribution: SC, WC

References: (Cruickshank 2017)

**Family Ceratomyxidae Doflein, 1899**

*Ceratomyxa australis* Gaevskaya & Kovaleva, 1979

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013)

*Ceratomyxa cottoidi* Reed, Basson, van As & Dykova, 2007

Host (locality): *Clinus cottoides* (DHNR)

Distribution: SC

References: (Reed et al. 2007)

*Ceratomyxa dehoopi* Reed, Basson, van As & Dykova, 2007

Host (locality): *Clinus superciliosus* (DHNR; Jeffreys Bay)

Distribution: SC

References: (Reed et al. 2007)

*Ceratomyxa honckenii* Reed, Basson, van As & Dykova, 2007

Host (locality): *Amblyrhynchotes honckenii* (DHNR; Jeffreys Bay)

Distribution: SC

References: (Reed et al. 2007)

**Family Myxobolidae Thélohan, 1892**

*Henneguya clini* Reed, Basson, van As & Dykova, 2007

Host (locality): *Clinus cottoides* (DHNR), *Clinus superciliosus* (DHNR; Jeffreys Bay)

Distribution: SC

References: (Reed et al. 2007)

**Family Sinuolineidae Shulman, 1959**

*Myxodavisia donecae* (Gayevskaya & Kovaleva, 1979)

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013)

### **Family Sphaeromyxidae Lom & Noble, 1984**

*Sphaeromyxa clini* Bartošová-Sojková, Kodádková, Pecková, Kuchta & Reed, 2015

Host (locality): *Clinus acuminatus* (Mouille Point), *Clinus cottoides* (Kalk Bay), *Clinus superciliosus* (Cape Columbine; Jacobs Bay), *Muraenoclinus dorsalis* (Granger Bay; Kommetjie; Mouille Point)

Distribution: WC

References: (Bartošová-Sojková et al. 2015)

*Sphaeromyxa* sp.

Host (locality): *Pavoclinus graminis* (DHNR)

Distribution: SC

References: (Reed et al. 2009)

### **Order Multivalvulida Shulman, 1959**

#### **Family Kudoidae Meglitsch, 1960**

*Kudoa paniformis* Kabata & Whitaker, 1981

Host (locality): *Merluccius capensis* \*, *Merluccius paradoxus* \*, *Thyrsites atun* \*

Distribution: WC

References: \* personal observations by thesis author (unpublished)

*Kudoa thyrsites* (Gilchrist, 1924)

Host (locality): *Beryx splendens*, *Lepidopus capensis*, *Merluccius capensis*, *Merluccius paradoxus*, *Sardinops sagax*, *Thyrsites atun*, *Zeus capensis*

Distribution: SC, WC

References: (Gilchrist 1923b; Henning et al. 2013; Nunkoo et al. 2016; Cruickshank 2017)

### **Phylum Nematoda**

#### **Class Chromadorea**

##### **Subclass Chromadoria**

#### **Order Rhabditida Chitwood, 1933**

#### **Family Anisakidae Railliet & Henry, 1912**

*Anisakis berlandi* Mattiucci, Cipriani, Webb, Paoletti, Marcer, Bellisario, Gibson & Nascetti, 2014

Host (locality): *Thyrsites atun*

Distribution: N/A

Notes: recorded as *Anisakis simplex* C in Mattiucci and Nascetti (2006, 2007)

References: (Mattiucci and Nascetti 2006, 2007)

*Anisakis pegreffii* Campan-Rouget, & Biocca, 1955

Host (locality): *Brama brama* (off West Coast), *Etrumeus whiteheadi*, *Genypterus capensis*, *Lepidopus caudatus*, *Lophius piscatorius*, *Merluccius capensis*, *Thyrsites atun*, *Trachurus capensis*

Distribution: WC

References: (Mattiucci et al. 1997; Mattiucci and Nascetti 2006, 2007; Mackintosh et al. 2018)

*Anisakis* sp.

Host (locality): *Genypterus capensis* (Agulhas Bank; Algoa Bay; Cape Columbine; Cape Canyon; Childs Bank), *Merluccius capensis* (off Cape of Good Hope), *Merluccius paradoxus* (off Cape of Good Hope), *Ruvettus pretiosus*, *Sebastes capensis*, *Thyrsites atun*, *Trachurus capensis*

Distribution: SC, WC

References: (Botha 1986; Payne 1986; Le Roux 2013; Sibanda 2015; Nunkoo et al. 2016, 2017; Cruickshank 2017)

*Pseudoterranova* sp.

Host (locality): *Thyrsites atun*

Distribution: SC, WC

References: (Nunkoo et al. 2016)

#### **Family Cucullanidae Cobbold, 1864**

*Cucullanus* sp.

Host (locality): *Sebastes capensis*

Distribution: WC

References: (González et al. 2006)

**Family Physalopteridae Railliet, 1893**

*Proleptus obtusus* Dujardin, 1845

Host (locality): *Haploblepharus edwardsii* (DHNR), *Haploblepharus pictus*, *Poroderma africanum*, *Acroteriobatus annulatus* (False Bay; Saldanha Bay), *Acroteriobatus blochii* (False Bay; Saldanha Bay), *Rhinobatos* sp.

Distribution: SC, WC

References: (Bayliss 1933 in Schaeffner and Smit 2019; Moravec et al. 2002; Yeld 2009; Morris et al. 2016)

**Phylum Platyhelminthes Minot, 1876**

**Class Cestoda**

**Subclass Eucestoda**

**Order Diphyllidea**

**Family Echinobothriidae Perrier, 1897**

*Andocadoncum meganae* Abbott & Caira, 2014

Host (locality): *Leucoraja wallacei* (36°31.08'S, 21°12.13'E; 36°17.60'S, 20°6.6'E; 34°10.97'S, 26°26.92'E)

Distribution: SC

References: (Abbott and Caira 2014)

*Echinobothrium dorothyae* Caira, Pickering, Schulman & Hanessian, 2013

Host (locality): *Raja straeleni*

Distribution: EC

References: (Caira et al. 2013a)

*Echinobothrium dougbermani* Caira, Pickering, Schulman & Hanessian, 2013

Host (locality): *Acroteriobatus annulatus*

Distribution: EC

References: (Caira et al. 2013a)

*Echinobothrium joshuai* Rodriguez, Pickering & Caira, 2011

Host (locality): *Cruriraja hullei*

Distribution: EC, SC

References: (Rodriguez et al. 2011)

*Echinobothrium marquesi* Abbott & Caira, 2014

Host (locality): *Leucoraja wallacei* (34°22.26'S, 26°16.94'E; 34°10.27'S, 26°38.96'E)

Distribution: SC

References: (Abbott and Caira 2014)

*Echinobothrium yiae* Caira, Rodriguez & Pickering, 2013

Host (locality): *Raja cf. miraletus*

Distribution: EC

References: (Caira et al. 2013b)

### **Order Gyrocotylidea Poche, 1926**

#### **Family Gyrocotylidae Benham, 1901**

*Gyrocotyle rugosa* Linton, 1924

Host (locality): *Callorhinchus capensis* (False Bay, St Helena Bay)

Distribution: WC

Notes: synonymous with *G. plana* of Awa (2012) and Morris et al. (2016) according to Alves et al. (2017)

References: (Awa 2012; Morris et al. 2016)

### **Order Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014**

#### **Family Onchobothriidae Braun, 1900**

*Acanthobothrium paulum* Linton, 1890

Host (locality): unspecified Rajidae

Distribution: N/A

References: (Linton 1924 in Schaeffner and Smit 2019)

### **Order Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014**

#### **Family Phyllobothriidae Braun, 1900**

*Paraorygmatobothrium angustum* (Linton, 1889) Ruhnke, 2011

Host (locality): *Carcharhinus melanopterus*

Distribution: N/A

References: (Linton 1924 in Schaeffner and Smit 2019)

## **Order Rhinebothriidea Healy, Caira, Jensen, Webster & Littlewood, 2009**

### **Family Echeneibothriidae de Beauchamp, 1905**

*Echeneibothrium austrinum* Linton, 1924

Host (locality): unspecified Rajidae

Distribution: N/A

References: (Linton 1924 in Schaeffner and Smit 2019)

## **Order Tetraphyllidea**

### **Family Calliobothriidae Perrier, 1897**

*Calliobothrium euzeti* Bernot, Caira & Pickering, 2015

Host (locality): *Mustelus palumbes* (34°10.27'S, 26°38.96'E)

Distribution: SC

References: (Bernot et al. 2015)

*Symcallio peteri* Bernot, Caira & Pickering, 2015

Host (locality): *Mustelus palumbes* (34°10.27'S, 26°38.96'E)

Distribution: SC

References: (Bernot et al. 2015)

### **Family Tetraphyllidae incertae sedis**

*Scolex pleuronectis bilocularis* Müller, 1788

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013)

## **Order Trypanorhyncha**

### **Family Gymnorhynchidae Dollfus, 1935**

*Molicola uncinatus* (Linton, 1924) Palm, 2004

Host (locality): *Thyrsites atun*

Distribution: SC, WC

References: (Nunkoo et al. 2016)

### **Family Lacistorhynchidae Guiart, 1937**

*Grillotia erinaceus* (van Beneden, 1857) Guiart, 1927

Host (locality): unspecified Rajidae

Distribution: N/A

References: (Linton 1924 in Schaeffner and Smit 2019)

*Grillotia heptanchi* (Vaullegeard, 1899) Dollfus, 1942

Host (locality): *Merluccius capensis* (off Cape of Good Hope), *Merluccius paradoxus* (off Cape of Good Hope)

Distribution: WC

References: (Botha 1986)

*Pseudogrillotia perelica* (Schuler, 1938) Palm, 2004

Host (locality): *Carcharhinus leucas* (Mbashe estuary), *Chelon dumerili* (Transkei), *Chelon richardsonii* (Transkei), *Chelon tricuspidens* (Transkei), *Mugil cephalus* (Transkei), *Myxus capensis* (Transkei), *Crenimugil buchanani* (Transkei), *Osteomugil cunnesius* (Transkei), *Osteomugil robustus* (Transkei)

Distribution: EC

References: (Schramm 1991)

### **Family Otophthiriidae Dollfus, 1942**

*Poecilancistrum caryophyllum* (Diesing, 1850) Dollfus 1929

Host (locality): *Carcharhinus leucas*

Distribution: N/A

References: (Schramm 1989 in Schaeffner and Smit 2019)

### **Family Sphyriocephalidae Pintner, 1913**

*Hepatoxylon trichiuri* (Holten, 1802) Bosc, 1811

Host (locality): *Brama brama* (off west coast), *Genypterus capensis* (Cape Canyon), *Merluccius capensis* (off Cape of Good Hope), *Merluccius paradoxus* (off

Cape of Good Hope), *Prionace glauca* \*, *Ruvettus pretiosus*, *Squalus acanthias*, *Thunnus alalunga* \*, *Thunnus albacares* \*, *Thyrsites atun*, *Xiphias gladius* \*

Distribution: SC, WC

References: (Botha 1986; Payne 1986; Sibanda 2015; Nunkoo et al. 2016, 2017; Cruickshank 2017; Mackintosh et al. 2018; Linton 1924 in Schaeffner and Smit 2019; \* personal observations by thesis author (unpublished))

### **Family Tentaculariidae Poche, 1926**

*Heteronybelinia estigmena* (Dollfus, 1960) Palm, 1999

Host (locality): *Carcharhinus leucas* (Richards Bay), *Carcharhinus limbatus*

Distribution: EC

References: (Palm 1999)

*Heteronybelinia heteromorphi* Palm, 1999

Host (locality): *Sphyrna mokarran*

Distribution: N/A

References: (Palm 1999)

*Heteronybelinia robusta* (Linton, 1890) Palm, 1999

Host (locality): *Carcharhinus limbatus*

Distribution: N/A

References: (Palm 1999)

*Heteronybelinia yamagutii* (Dollfus, 1960) Palm, 1999

Host (locality): *Sphyrna lewini*

Distribution: N/A

References: (Palm 1999)

*Nybelinia africana* Dollfus, 1960

Host (locality): *Carcharhinus leucas* (Richards Bay), *Carcharhinus obscurus* (Durban), *Scylliogaleus queckettii* (Durban)

Distribution: EC

References: (Palm 1999)

*Nybelinia indica* Chandra, 1986

Host (locality): *Carcharhinus limbatus*

Distribution: N/A

Notes: Recorded as *N. scoliodoni* by Palm (1999)

References: (Palm 1999)

*Nybelinia lingualis* (Cuvier, 1817) Dollfus, 1929

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013)

*Nybelinia riseri* Dollfus, 1960

Host (locality): N/A

Distribution: EC

Notes: host recorded as *Trachyurus felicipes* (unrecognised binomen) in Palm (1999)

References: (Palm 1999; Palm and Walter 2000)

*Nybelinia sakanariae* Palm, 1999

Host (locality): *Genypterus capensis*, *Trachurus trachurus* (Algoa Bay)

Distribution: SC

Notes: The host *G. capensis* originally recorded as *Xiphiurus capensis* and *T. trachurus* does not occur in South African waters, the host was probably *Trachurus trachurus capensis*

References: (Palm 1999)

*Nybelinia schmidtii* Palm, 1999

Host (locality): *Prionace glauca* (Algoa Bay)

Distribution: SC

References: (Palm 1999)

*Nybelinia* sp.

Host (locality): *Coryphaena hippurus* (Cape Vidal)

Distribution: EC

References: (Palm 1999)

*Tentacularia coryphaenae* Bosc, 1802

Host (locality): *Ruvettus pretiosus*, *Sardinops sagax*, *Thyrsites atun*

Distribution: WC

References: (Reed et al. 2012; Nunkoo et al. 2016, 2017)

## **Class Monogenea van Beneden, 1858**

### **Subclass Monopisthocotylea**

#### **Order Capsalidea**

#### **Family Capsalidae Baird, 1853**

*Nasicola klawei* (Stunkard, 1962) Yamaguti 1968

Host (locality): *Thunnus albacares*, *Thunnus obesus*

Distribution: WC

References: (Weston 2017)

*Tristoma adcoccineum* Yamaguti, 1968

Host (locality): *Xiphias gladius*

Distribution: WC

References: (Weston 2017)

#### **Order Gyrodactylidea**

#### **Family Acanthocotylidae Monticelli, 1903**

*Myxinidocotyle eptatreti* Vaughan & Christison, 2010

Host (locality): *Eptatretus hexatrema* (Jacobsbaai; Kommetjie)

Distribution: WC

References: (Vaughan and Christison 2010)

#### **Family Gyrodactylidae Cobbold, 1864**

*Gyrodactylus eyipayipi* Vaughan, Christison, Hansen & Shinn, 2010

Host (locality): *Syngnathus acus* (Simons Town)

Distribution: WC

References: (Vaughan et al. 2010)

### **Order Monocotylidea**

#### **Family Microbothriidae Price, 1936**

*Dermophthirius carcharhini* MacCallum, 1926

Host (locality): *Carcharhinus obscurus* (Umhlanga Rocks)

Distribution: EC

References: (Bullard et al. 2004)

*Pseudoleptobothrium christisoni* Vaughan & Chisholm, 2011

Host (locality): *Acroteriobatus annulatus* (off Cape Agulhas)

Distribution: SC

References: (Vaughan and Chisholm 2011)

#### **Family Monocotylidae Taschenberg, 1879**

*Dendromonocotyle citrosa* Vaughan, Chisholm & Christison, 2008

Host (locality): *Dasyatis chrysonota* (Two Oceans Aquarium), *Maculabatis gerrardi* (uShaka Sea World)

Distribution: EC, WC

References: (Vaughan et al. 2008)

*Dendromonocotyle colorni* Chisholm, Whittington & Kearns, 2001

Host (locality): *Maculabatis gerrardi* (uShaka Sea World)

Distribution: EC

References: (Vaughan et al. 2008)

*Dendromonocotyle ukuthena* Vaughan, Chisholm & Christison, 2008

Host (locality): *Maculabatis gerrardi* (uShaka Sea World), *Maculabatis uarnak* (uShaka Sea World)

Distribution: EC

References: (Vaughan et al. 2008)

*Heterocotyle tokoloshei* Vaughan & Chisholm, 2010

Host (locality): *Dasyatis brevicauda* (caught in Struisbaai and kept at the Two Oceans Aquarium in Cape Town)

Distribution: WC

References: (Vaughan and Chisholm 2010a)

*Neoheterocotyle robii* Vaughan & Chisholm, 2010

Host (locality): *Acroteriobatus annulatus* (off Cape Agulhas)

Distribution: SC

References: (Vaughan and Chisholm 2010b)

### **Subclass Polyopisthocotylea**

#### **Order Chimaericolidea**

##### **Family Chimaericolidae Brinkmann, 1942**

*Callorhynchicola multitesticulatus* Manter, 1955

Host (locality): *Callorhynchus capensis* (St Helena Bay)

Distribution: WC

References: (Awa 2012)

#### **Order Dicybothriidea**

##### **Family Hexabothriidae Price, 1942**

*Branchotentes robinoverstreeti* Bullard & Dippenaar, 2003

Host (locality): *Rhina ancylostoma* (off Trafalgar)

Distribution: EC

References: (Bullard and Dippenaar 2003; Vaughan 2009)

*Callorhynchocotyle callorhynchi* (Manter, 1955)

Host (locality): *Callorhynchus capensis* (St Helena Bay)

Distribution: SC, WC

References: (Vaughan 2009; Awa 2012, Poddubnaya et al. 2015)

**Order Mazocraeidea Bykhovsky, 1957**

**Family Discocotylidae Price, 1936**

*Anthocotyle merluccii* van Beneden & Hesse, 1863

Host (locality): *Merluccius capensis*, *Merluccius paradoxus*

Distribution: SC, WC

References: (Cruickshank 2017; Weston 2017)

**Family Gastrocotylidae Price, 1943**

*Gastrocotyle trachuri* van Beneden & Hesse, 1863

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013; Weston 2017)

**Family Hexostomatidae Price, 1936**

*Hexostoma* sp.

Host (locality): *Thunnus albacares*, *Thunnus obesus*

Distribution: WC

References: (Weston 2017)

**Family Mazocraeidae**

*Mazocraes sardinopsi* (Lebedev & Parukhin, 1969) Mamaev, 1982

Host (locality): *Sardinops sagax* (off Port Elizabeth)

Distribution: SC

References: (Reed et al. 2012)

*Mazocraes* sp.

Host (locality): *Thyrsites atun*

Distribution: WC

References: (Weston 2017)

**Family Microcotylidae Taschenberg, 1879**

*Microcotyle* sp.

Host (locality): *Sebastes capensis* (off Cape Town)

Distribution: WC

References: (González and Moreno 2005)

**Class Trematoda**

**Subclass Aspidogastrea Faust & Tang, 1936**

**Order Aspidogastida Dollfus, 1958**

**Family Aspidogastridae Poche, 1907**

*Cotylogaster basiri* Siddiqui & Cable, 1960

Host (locality): *Rhabdosargus sarba* (Durban)

Distribution: EC

References: (Bray 1984)

**Family Multicalycidae Gibson & Chinabut, 1984**

*Multicalyx cristata* Faust & Tang, 1936

Host (locality): *Carcharias taurus*, *Sphyrna lewini* (Uvongo)

Distribution: EC

References: (Bray 1984)

**Subclass Digenea**

**Order Diplostomida**

**Family Strigeidae Railliet, 1919**

*Cardiocephaloides physalis* (Lutz, 1927)

Host (locality): *Engraulis capensis*, *Sardinops sagax*

Distribution: EC, SC, WC

References: (Reed et al. 2012; van der Lingen et al. 2015; Ukomadu 2017; Parukhin 1976 in Vermaak 2019)

**Order Plagiorchiida La Rue, 1957**

**Family Acanthocolpidae Lühe, 1906**

*Pleorchis sciaenae* Yamaguti, 1938

Host (locality): *Argyrosomus hololepidotus* (Cape Recife)

Distribution: SC

References: (Bray 1986a)

*Stephanostomum ditrematis* (Yamaguti, 1939) Manter, 1947

Host (locality): *Megalaspis cordyla* (Durban)

Distribution: EC

References: (Bray 1985)

*Stephanostomum imparispine* (Linton, 1905) Manter, 1940

Host (locality): *Engraulis capensis*, *Sardinops sagax*

Distribution: N/A

References: (Parukhin 1976 in Vermaak 2019)

*Stephanostomum multispinosum* Manter, 1940

Host (locality): *Merluccius capensis*, *Merluccius paradoxus*

Distribution: SC, WC

References: (Cruickshank 2017)

*Stephanostomum solontschenkae* Parukhin, 1968

Host (locality): *Merluccius capensis* (Cape Recife)

Distribution: SC

References: (Bray 1985)

*Stephanostomum* sp.

Host (locality): *Chaetodon marleyi* (Port Elizabeth Museum Aquarium), *Merluccius capensis*  
(Cape Town)

Distribution: SC, WC

Notes: recorded as encysted metacercaria

References: (Bray 1985)

**Family Aephnidiogenidae Yamaguti, 1934**

*Holorchis pycnopus* Stossich, 1901

Host (locality): *Diplodus sargus capensis* (Port Elizabeth), *Sparodon durbanensis* (Port Elizabeth)

Distribution: SC

References: (Bray 1985)

*Pseudaephnidiogenes rhabdosargi* (Prudhoe, 1956) Yamaguti, 1971

Host (locality): *Rhabdosargus holubi* (Swartkops River estuary), *Rhabdosargus sarba* (Algoa Bay; Durban)

Distribution: SC

References: (Prudhoe 1956; Bray 1985)

*Pseudaephnidiogenes rossi* Bray, 1985

Host (locality): *Caffrogobius nudiceps* (Swartkops River estuary)

Distribution: SC

References: (Bray 1985)

**Family Azygiidae Lühe, 1909**

*Otodistomum* sp.

Host (locality): *Coelorinchus fasciatus*

Distribution: N/A

References: (Parukhin 1976 in Vermaak 2019)

**Family Bucephalidae Poche, 1907**

*Bucephalus margaritae* Ozaki & Ishibashi, 1934

Host (locality): *Carangoides hedlandensis* (Durban), *Caranx heberi* (Sodwana), *Pomatomus saltatrix*

Distribution: EC

References: (Bray 1984, Parukhin 1976 in Vermaak 2019)

*Prosorhynchoides arcuatus* (Linton, 1900) Love & Moser, 1983

Host (locality): *Pomatomus saltatrix* (Sodwana)

Distribution: EC

References: (Bray 1984)

*Prosorhynchus caudovatus* Manter, 1940

Host (locality): *Epinephelus andersoni* (Umvoti)

Distribution: EC

References: (Bray 1984)

*Rhipidocotyle paruchini* Gavriilyuk-Tkachuk, 1979

Host (locality): *Otolithes ruber* (Agulhas Bank)

Distribution: SC

References: (Gavriilyuk-Tkachuk 1979 in Vermaak 2019)

*Rhipidocotyle* sp.

Host (locality): *Ruvettus pretiosus*

Distribution: WC

References: (Nunkoo et al. 2017)

#### **Family Cryptogonimidae Ward, 1917**

*Aphallus rubalo* (Bray, 1986) Bartoli & Bray, 1987

Host (locality): *Cheimerius nufar* (Durban; Port Elizabeth; St Lucia; Umvoti)

Distribution: EC, SC

References: (Bray 1986b)

#### **Family Derogenidae Nicoll, 1910**

*Derogenes varicus* (Müller, 1784) Looss, 1901

Host (locality): *Chelidonichthys capensis*, *Chlorophthalmus agassizi* (Durban), *Coelorinchus fasciatus*

Distribution: EC

References: (Parukhin 1989 in Vermaak 2019)

#### **Family Didymozoidae Monticelli, 1888**

*Skrjabinozoum vodjanitskii* Nikolaeva & Parukhin, 1974

Host (locality): *Ariomma indicum* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

#### **Family Enenteridae Yamaguti, 1958**

*Enenterum elsti* Bray, 1978

Host (locality): *Neoscorpis lithophilus* (Mapelane; Tongaat)

Distribution: EC

References: (Bray 1978, Bray 1986a)

*Enenterum kyphosis* Yamaguti, 1970

Host (locality): *Kyphosus vaigiensis* (Sodwana)

Distribution: EC

References: (Bray 1986a)

*Enenterum mannarensis* Hafeezullah, 1980

Host (locality): *Kyphosus vaigiensis* (Sodwana)

Distribution: EC

References: (Bray 1986a)

*Enenterum prudhoei* Bray, 1978

Host (locality): *Neoscorpis lithophilus* (Tonga)

Distribution: EC

References: (Bray 1978, Bray 1986a)

*Enenterum stinkvis* Bray, 1986

Host (locality): *Neoscorpis lithophilus* (Tonga; Uvongo)

Distribution: EC

References: (Bray 1986a)

*Enenterum tongaatense* Bray, 1986

Host (locality): *Neoscorpis lithophilus* (Tongaat)

Distribution: EC

References: (Bray 1986a)

*Pseudozakia hatampo* Machida & Araki, 1977

Host (locality): *Pempheris oualensis* (Mbibi)

Distribution: EC

References: (Bray 1986a)

### **Family Faustulidae Poche, 1926**

*Paradiscogaster farooqii* Hafeezullah & Siddiqi, 1970

Host (locality): *Monodactylus argenteus* (Sodwana)

Distribution: EC

References: (Bray 1984)

### **Family Fellodistomidae Nicoll, 1909**

*Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911

Host (locality): *Spondyliosoma emarginatum* (Algoa Bay)

Distribution: SC

References: (Bray 1984)

*Tergestia laticollis* (Rudolphi, 1819)

Host (locality): *Decapterus punctatus* (Durban), *Trachurus capensis*

Distribution: EC, SC

References: (Le Roux 2013; Parukhin 1976 in Vermaak 2019)

*Tergestia pauca* Teixeira de Freitas & Kohn, 1965

Host (locality): *Pomatomus saltatrix* (Sodwana)

Distribution: EC

References: (Bray 1984)

*Theledera pectinata* (Linton, 1905) Linton, 1910

Host (locality): *Pomatomus saltatrix*

Distribution: N/A

References: (Parukhin 1976 in Vermaak 2019)

### **Family Gonocercidae Skrjabin & Guschanskaja, 1955**

*Gonocerca crassa* Manter, 1934

Host (locality): Unspecified host (off Cape Town)

Distribution: WC

References: (Parukhin 1989 in Vermaak 2019)

*Gonocerca phycidis* Manter, 1925

Host (locality): *Coelorinchus fasciatus* (off Cape Town)

Distribution: WC

References: (Parukhin 1989 in Vermaak 2019)

### **Family Gorgoderidae Looss, 1899**

*Phyllodistomum tongaatense* Bray, 1985

Host (locality): *Dichistius multifasciatus* (Tongaat)

Distribution: EC

References: (Bray 1985)

*Probolitrema callorhynchi* Parukhin, 1966

Host (locality): *Callorhynchus capensis*

Distribution: N/A

References: (Parukhin 1966, 1968 in Schaeffner and Smit 2019)

*Probolitrema richiardii* (López, 1888) Looss, 1902

Host (locality): *Haploblepharus pictus* (Granger Bay; Saldanha Bay), *Rostroraja alba*,  
Scyliorhinidae gen. sp.

Distribution: WC

References: (Yeld 2009; von Ofenheim 1900 in Schaeffner and Smit 2019; Gibson 1976 in Schaeffner and Smit 2019)

### **Family Haploplanchnidae Poche, 1926**

*Haploplanchnus caudatus* (Srivastava, 1937) Skrjabin & Guschanskaja. 1954

Host (locality): *Mugil cephalus* (Sodwana)

Distribution: EC

References: (Bray 1984)

*Haploplanchnus purii* Srivastava, 1939

Host (locality): *Chelon tricuspides* (Swartkops River estuary)

Distribution: SC

References: (Bray 1984)

### **Family Hemiuridae Looss, 1899**

*Dinurus longisinus* Looss, 1907

Host (locality): *Coryphaena hippurus* (off the Easter Cape)

Distribution: EC

References: (Bray 1990)

*Dissosaccus laevis* (Linton 1898) Manter, 1947

Host (locality): *Helicolenus dactylopterus* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Ectenurus lepidus* Looss, 1907

Host (locality): *Trachurus capensis*

Distribution: SC

References: (Le Roux 2013)

*Ectenurus selari* (Parukhin, 1966)

Host (locality): *Trachurus capensis* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Ectenurus virgula* Looss, 1910

Host (locality): unspecified host (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Elytrophalloides humerus* Bray, 1990

Host (locality): *Trachinotus botla* (Sodwana)

Distribution: EC

References: (Bray 1990)

*Lecithochirium genypteri* Manter, 1954

Host (locality): *Genypterus capensis* (Algoa Bay; off Cape Town; off von Sladens River mouth)

Distribution: EC, SC, WC

References: (Bray 1991)

*Lecithochirium jaffense* Fischthal, 1982

Host (locality): *Blennioclinus brachycephalus* (Port Elizabeth)

Distribution: SC

References: (Bray 1991)

*Lecithochirium kawakawa* Yamaguti, 1970

Host (locality): *Chrysoblephus anglicus* (St. Lucia), *Euthynnus affinis* (Durban; Sodwana)

Distribution: EC

References: (Bray 1991)

*Lecithochirium parafusiforme* Bray, 1991

Host (locality): *Gymnothorax flavimarginatus* (La Mercy)

Distribution: EC

References: (Bray 1991)

*Lecithochirium* sp.

Host (locality): *Alectis ciliaris* (Durban), *Saurida undosquamis* (Richards Bay)

Distribution: EC

Notes: *Lecithochirium* sp. from *Saurida undosquamis* possibly a member of the “*L. synodi*” group according to Bray (1991)

References: (Bray 1991)

*Lecithocladium angustiovum* Yamaguti, 1953

Host (locality): *Rastrelliger kanagurta* (Durban)

Distribution: EC

References: (Bray 1990)

*Lecithocladium excisum* (Rudolphi, 1819) Lühe, 1901

Host (locality): *Scomber japonicus* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Lecithocladium magnacetabulum* Yamaguti, 1934

Host (locality): *Ariomma indicum* (Durban), *Cubiceps whiteleggi* (Durban), *Parupeneus cyclostomus*, *Pseudocaranx dentex* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Parahemiurus merus* (Linton, 1910) Woodcock, 1935

Host (locality): *Chlorophthalmus agassizi* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Plerurus digitatus* (Looss, 1899) Looss, 1907

Host (locality): *Alectis ciliaris* (Durban), *Euthynnus affinis* (Durban; Sodwana), *Lichia amia* (Karridene; Port Elizabeth), *Pomatomus saltatrix* (Sodwana), *Rachycentron canadum* (Umhlanga Rocks), *Saurida undosquamis* (Richards Bay), *Scomberoides commersonianus* (Umhlanga Rocks), *Scomberomorus commerson* (Cape Vidal; Durban), *Thunnus albacares* (Umhlanga Rocks)

Distribution: EC, SC

References: (Bray 1990)

**Family Lecithasteridae Odhner, 1905**

*Aponurus laguncula* Looss, 1907

Host (locality): *Parupeneus cyclostomus*

Distribution: N/A

References: (Parukhin 1976 in Vermaak 2019)

**Family Lepidapedidae Yamaguti, 1958**

*Lepidapedon alvigae* Tkachuk, 2002

Host (locality): *Coelorinchus fasciatus* (Agulhas Bank)

Distribution: SC

References: (Gavrilyuk-Tkachuk 1979 in Vermaak 2019)

**Family Lepocreadiidae Odhner, 1905**

*Clavogalea gaevskayae* Bray, 1985

Host (locality): *Trachinotus botla* (Sodwana)

Distribution: EC

References: (Bray 1985)

*Lepidapedoides nicolli* (Manter, 1934) Yamaguti, 1971

Host (locality): *Epinephelus albomarginatus* (Richards Bay)

Distribution: EC

References: (Bray 1985)

*Prodistomum orientale* (Layman, 1930) Bray & Gibson, 1990

Host (locality): *Scomber japonicus* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

**Family Mesometridae Poche, 1926**

*Elstia stossichianum* (Monticelli, 1892) Bray, 1984

Host (locality): *Sarpa salpa* (Durban)

Distribution: EC

References: (Bray 1984)

#### **Family Opecoelidae Ozaki, 1925**

*Allopodocotyle recifensis* Bray, 1987

Host (locality): *Pterogymnus laniarius* (Cape Recife)

Distribution: SC

References: (Bray 1987)

*Coitocaecum capense* Bray, 1987

Host (locality): *Clinus capensis* (Blue Hole), *Clinus cottoides* (Oudekraal, Blue Hole), *Clinus rotundifrons* (Oudekraal), *Clinus superciliosus* (Oudekraal, Blue Hole), *Xenopoclinus kochi* (Oudekraal), *Xenopoclinus leprosus* (Oudekraal)

Distribution: SC, WC

References: (Bray 1987)

*Dactylostomum griffithsi* Bray, 1987

Host (locality): *Cheilodactylus fasciatus* (Oudekraal)

Distribution: WC

References: (Bray 1987)

*Helicometra fasciata* (Rudolphi, 1819) Odhner, 1902

Host (locality): *Arius feliceps* (Blue Hole), *Chirodactylus brachidactylus* (Blue Hole), *Clinus capensis* (Blue Hole), *Clinus cottoides* (Oudekraal), *Clinus rotundifrons* (Oudekraal), *Clinus superciliosus* (Blue Hole), *Pachymetopon blochii* (Oudekraal), *Pomadasys olivaceum* (Durban), *Pomatomus saltatrix* (Durban), *Xenopoclinus kochi* (Oudekraal), *Xenopoclinus leprosus* (Oudekraal)

Distribution: EC, SC, WC

References: (Bray 1987)

*Helicometrina nimia* Linton, 1910

Host (locality): *Pomadasys furcatus* (Mbibi)

Distribution: EC

References: (Bray 1987)

*Macvicaria obovata* (Molin, 1859) Bartoli, Bray & Gibson, 1989

Host (locality): *Cheilodactylus fasciatus* (Blue Hole), *Diplodus hottentotus* (Blue Hole),  
*Sparodon durbanensis* (Blue Hole)

Distribution: SC

References: (Bray 1987)

*Margolisia vidalensis* Bray, 1987

Host (locality): *Synodus myops* (off Cape Vidal)

Distribution: EC

References: (Bray 1987)

*Neonotoporus decapteri* Parukhin, 1966

Host (locality): Unspecified host (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Opecoelina helicoleni* Manter, 1934

Host (locality): *Helicolenus dactylopterus* (Durban)

Distribution: EC

References: (Parukhin 1989 in Vermaak 2019)

*Opecoelina scorpaenae* Manter, 1934

Host (locality): *Lioscorpus longiceps* (Durban)

Distribution: EC

References: (Parukhin 1989 in Vermaak 2019)

*Opistholebes cotylophorus* Ozaki, 1935

Host (locality): *Amblyrhynchotes honckenii* (Swartkops River estuary)

Distribution: SC

References: (Bray 1987)

*Pseudopecoelus ablennesi* Bray, 1987

Host (locality): *Ablennes hians* (Durban; off St. Lucia)

Distribution: EC

References: (Bray 1987)

*Pseudopecoelus japonicus* (Yamaguti, 1938) von Wicklen, 1946

Host (locality): *Chlorophthalmus punctatus* (Durban)

Distribution: EC

References: (Parukhin 1976 in Vermaak 2019)

*Pseudopecoelus vulgaris* (Manter, 1934) von Wicklen, 1946

Host (locality): *Lioscorpis longiceps* (Durban)

Distribution: EC

References: (Parukhin 1989 in Vermaak 2019)

#### **Family Sclerodistomidae Odhner, 1927**

*Kenmackenzia gigas* (Nardo, 1827)

Host (locality): *Luvarus imperialis* (off Cape Town)

Distribution: WC

References: (Gibson 1983)

#### **Family Zoogonidae Odhner, 1902**

*Cephaloporus bakeri* Bray, 1985

Host (locality): *Pervagor melanocephalus* (Sodwana)

Distribution: EC

References: (Bray 1985)

*Lecithostaphylus retroflexus* (Molin, 1859) Odhner, 1911

Host (locality): *Pachymetopon blochii* (St. James)

Distribution: WC

References: (Fantham 1938)

*Overstreetia sodwanaensis* Bray, 1985

Host (locality): *Atherinomorus lacunosus* (Sodwana)

Distribution: EC

References: (Bray 1985)

*Steganoderma* sp.

Host (locality): *Lioscorpis longiceps* (Durban)

Distribution: EC

References: (Parukhin 1989 in Vermaak 2019)

*Steganodermatoides alloctyti* (Tkachuk, 1979) Bray, 1985

Host (locality): *Neocyttus rhomboidalis* (off Cape Town)

Distribution: WC

References: (Bray 1985)

## **Chapter 4. Community Ecology of Metazoan Parasite Communities of Selected Fishes of the Southern Benguela**

### **4.1. Introduction**

Parasites are ubiquitous in Nature (Poulin and Morand 2000). They are however unevenly distributed in time and space as well as within host populations and communities (Wilson et al. 2002; Poulin 2007a; Timi et al. 2011). Parasitologists have invested considerable effort into understanding which factors determine the patterns of infections observed at different spatial, temporal and ecological scales and evaluating their repeatability (Luque et al. 2004; Poulin 2004; Vignon and Sasal 2010). However, Poulin (2007b) noted that recurrent patterns which could be elevated to the status of ‘laws of parasitology’ have only been found for phenomena detectable at large scales (e.g. aggregation), while no consensus has been reached amongst studies investigating infection patterns and parasite community assembly at smaller scales (e.g. infracommunities).

#### **4.1.1. Ecological Parasitology: the Benefits of Community Analyses**

Ecological parasitology is concerned with uncovering patterns of parasite distributions within and across host populations and revealing the drivers thereof at varying spatial and temporal scales. Studies of parasite community ecology have often restricted themselves to employing simplistic metrics such as species richness, abundance of parasites or taxonomic distinctness (e.g. Luque et al. 2004; Luque and Poulin 2007, 2008; Randhawa and Poulin 2010). However, while the analysis of such metrics is informative, they ignore the identity of parasites and their relative abundances within parasitic assemblages (Gotelli and Colwell 2001; Fleishman et al. 2006). Community analyses on the other hand, take parasite identities and abundances into account and can reveal intricacies not revealed by metrics which tend to condense information into a single value (Timi et al. 2011). Community analyses allow parasitologists to determine whether parasite community structure differs

within and across host populations (Field et al. 1982; Clarke 1993; Carballo et al. 2012). Such analyses can also be employed to evaluate which taxa cause differences, if any, in the community structure of parasite assemblages (Clarke 1993). Another major advantage of community analysis is that it affords parasitologists a chance to evaluate similarities across parasite assemblages and enable correlation of the rate of change in community similarity to variability in host attributes, whether ecological, spatial or phylogenetic (Timi et al. 2011). Community analyses therefore allow a deeper insight into the processes dictating parasite community assembly in Nature.

#### **4.1.2. Drivers of Parasite Community Structure**

The composition of the parasite fauna of a host species is the result of the loss and acquisition of parasite taxa as well as co-adaptation over evolutionary time-scales (Alarcos and Timi 2012). Within an ecosystem where fishes of different species are exposed to the same suite of infective stages, parasite infracommunity structure results from heterogeneities in infection patterns which depend on host susceptibility, which is itself mediated by host traits and the variations therein (Wilson et al. 2002; do Amarante et al. 2015). Several factors including host body size (Alarcos and Timi 2012), diet (Muñoz and Zamora 2011; Munster et al. 2015), phylogeny (Lima et al. 2016), geographic distribution (Alarcos et al. 2016; Gay et al. 2018), age (Lo et al. 1998; Hemmingsen et al. 2000), depth range (Luque et al. 2004; Brickle et al. 2006; Vignon and Sasal 2010), host density (Arneberg et al. 1998), and food web topology (Locke et al. 2014) have been linked to variability in parasite infracommunities amongst sympatric fish host species. Nevertheless, the significance and relative importance of the above named factors varies with the ecosystem and host assemblage being studied. For example, Locke et al. (2014) showed that trophic interactions were more important than host body size in determining the diversity of fish parasite assemblages within a low salinity ecosystem.

The life history of parasites also plays an important role in determining the parasite community structure of a particular host (Timi et al. 2011; Lima et al. 2016). Trophically transmitted endoparasites (e.g. nematodes, cestodes) are embedded in food webs and their distribution amongst potential host species is largely determined by the diet of the host, while ectoparasites have no such restraint but rely on free-living phases to encounter a suitable host for infection to occur (Marcogliese 2002; Thompson et al. 2005; Lima et al. 2016). As previously highlighted by Poulin (2007b), these studies suggest that host characteristics are not the only important determinants of parasitic community structure but that the structure and interactions of the free-living community as well as the local availability of infective stages may subdue co-evolutionary processes and be the major force shaping parasite assemblages. The lack of repeatability amongst the variety of factors known to affect parasite community assembly demonstrates that further research is required at all spatial and temporal scales.

#### **4.1.3. Study Aims**

South African marine parasitology has so far been largely focussed on surveying and describing the biodiversity of parasites infecting fishes (Smit and Hadfield 2015). The ecological aspects of parasitism in marine fishes have received little attention and have often been restricted to investigations of single host-parasite relationships (e.g. Wright et al. 2001; Dippenaar et al. 2008; Parker and Booth 2013). Community analyses have rarely been employed and have almost exclusively dealt with intraspecific variations in fish parasite community structure (van Praag 2004; Sibanda 2015; Nunkoo et al. 2016) with a single study (Yeld 2009) evaluating interspecific differences.

This study aims at providing a comprehensive comparison of the structure and similarity in the parasite communities of selected marine fish species of the southern Benguela. Additionally an assessment of the potential host-dependent drivers of community

structure was also conducted in an attempt to shed some light on the factors governing parasite community assembly in the southern Benguela. Specifically, the following questions were addressed:

- i. Does parasite component community richness differ across host species?
- ii. Do the parasite infracommunities differ with respect to host traits?
- iii. Which factors drive the dissimilarities, if any, in parasite community structure?

## **4.2. Materials and Methods**

### **4.2.1. Host and Parasite Data Collection**

Five hundred and fifty four fish hosts caught between 2012 and 2017 and including members of six species and representing five families were considered in the study (Table 4.1). Data for *Brama brama*, *Merluccius capensis*, *M. paradoxus*, *Sardinops sagax*, and *Thyrsites atun* were obtained from previous studies conducted at the University of Cape Town (Reed et al. 2012; Reed et al. unpublished; Nunkoo 2015; Mackintosh 2016; Cruickshank 2017). All studies from which data were extracted employed the dissection protocol described in Chapter 2. Data for *B. brama* and *T. atun* were supplemented by additional dissections of 15 and 36 fish respectively of specimens caught during research surveys conducted the Department of Agriculture, Forestry and Fisheries in 2016. *Chelon richardsonii* were collected from the Berg River estuary in July 2017 using gill nets and further specimens were obtained from commercial catches made in Yzerfontein. All samples were kept frozen at -20°C in labelled bags prior to dissections. Only specimens collected from the southern Benguela region, i.e. west of Cape Agulhas and south of the Orange River mouth (Fig 4.1) were included to negate the potential effects of spatial differences in hosts susceptibility and parasite availability.

Prior to dissection, fish were thawed to room temperature, measured to the nearest

millimeter (standard length) and weighed to the nearest gram. A full parasitological examination was then conducted. The skin, fins, mouth, nares and opercula were first examined for parasites. Next, the gills and eyes were excised and examined under a dissecting microscope (Nikon SMZ800). The coelom was then cut open and the fish was sexed. The abundance of each parasite taxon present externally, in the body cavity and on various organs was recorded. The gastro-intestinal tract was excised from the coelom, opened longitudinally and examined for parasites, both macroscopically and under a dissecting microscope. The fish were filleted and the number of macroscopic parasites found within the muscle tissue recorded. Squash samples of tissue from the muscles, liver, heart, kidneys, spleen, gonads, and gall bladder were examined for microparasites using a compound microscope (Leica ICC50) at magnifications varying from 40× to 1000×.

Parasite individuals retained as voucher specimens for identification were soaked and refrigerated in tap water overnight to break down the slime covering them. The parasites were then gently cleaned with a fine artist's brush under a dissection microscope. The soaking had the added benefit of promoting the extrusion of acanthocephalan proboscides and cestode tentacles whose armature is critical for identification. Acanthocephalans, copepods, nematodes and cestodes were fixed and preserved in 70% ethanol. Trematodes were flattened between a coverslip and a glass slide and fixed with 10% formalin for 15 minutes before preservation in 70% ethanol. Encysted larval digenetic trematodes were freed from their cysts using fine needles before being processed as described above.

In order to observe diagnostic features of the parasite specimens retained, acanthocephalans, cestodes and trematodes (adults and excysted metacercariae) were stained in Mayer's carmine overnight, dehydrated in an ethanol series, cleared in eugenol and permanently mounted in Canada balsam under a coverslip. Copepods were lightly stained using Mexican Red dissolved in lactic acid, cleared in lactic acid and observed as whole

mounts in lactic acid or appendages were dissected following the wooden slide method and examined at magnifications ranging between 10× and 40× (Humes and Gooding 1964). When necessary, nematodes were cleared in eugenol or lactic acid and observed as whole mounts under a Leica ICC50 compound microscope at magnifications varying between 40× and 400×. The parasites were morphologically identified to the lowest taxonomic level possible using various resources including taxonomic keys and original descriptions.

The identification of acanthocephalans was based on Amin (1987, 2002), Costa et al. (2000), Sardella et al. (2005) and Amin et al. (2011) while that of cestodes relied on Knoff et al. (2004) and Robinson (1959). Myxozoan identifications followed Gilchrist (1923b), Reed (2003), Eiras (2006), Eiras et al. (2014) and Reed et al. (2018). Copepods were identified using Barnard (1955b), Ho (1971), Jones (1985), Boxshall (1986), Margolis and Kabata (1988), Grobler (2004), Tang et al. (2007), Boxshall and El-Rashidy (2009), El-Rashidy and Boxshall (2010) and Lebepe and Dippenaar (2016). Digenetic trematode identification was conducted according to Bray and Reimer (2004) and monogenetic trematodes were classified following Beverley-Burton (1984) and Hendrix (1994). Keys provided by Arai and Smith (2016) were used for the identification of larval and adult nematodes.

The habitat preference of *B. brama*, *M. capensis*, *M. paradoxus*, *S. sagax*, *C. richardsonii* and *T. atun* were obtained from previous research (Whitfield et al. 1981; Botha 1985; Beckley and van der Lingen 1999; Griffiths 2002) and information obtained from FishBase (Froese and Pauly 2018). The bathymetric distribution of *M. capensis*, *M. paradoxus*, *S. sagax* and *T. atun* was derived from previous research (Botha 1985; Beckley and van der Lingen 1999; Griffiths 2002), that of *B. brama* was obtained from FishBase (Froese and Pauly 2018) and expert opinion for *C. richardsonii* (S Lamberth, DAFF, pers. comm.). Each species was assigned to one of three functional feeding groups (FFGs) based on the composition of their respective diets from published studies (Masson and Marais 1975;

Payne et al. 1987; Whitfield 1988; Punt et al. 1992; Griffiths 2002; van der Lingen 2002) in conjunction with stomach contents recovered during dissections. The FFG of *B. brama* was determined using FishBase (Froese and Pauly 2018) as no studies have investigated its feeding ecology in South African waters.

Table 4.1. Characteristics of the fish host species included in the analyses.

<b>Family</b> Host Species	Sample size (n)	Size range (SL / mm)	Habitat	Bathymetric distribution (m)	Functional Feeding Group
<b>Bramidae</b>					
<i>Brama brama</i>	48	327 - 431	Mesopelagic	0-1000	Opportunistic predator
<b>Mugilidae</b>					
<i>Chelon richardsonii</i>	52	162 - 276	Estuarine/ Coastal	0-5	Detritivore
<b>Merlucciidae</b>					
<i>Merluccius capensis</i>	21	227 - 617	Bathydemersal	50-450	Opportunistic predator
<i>Merluccius paradoxus</i>	25	249 - 500	Bathydemersal	150-650	Opportunistic predator
<b>Clupeidae</b>					
<i>Sardinops sagax</i>	194	97 - 202	Epipelagic	0-120	Planktivore
<b>Gempylidae</b>					
<i>Thyrssites atun</i>	214	395 - 997	Benthopelagic	0-550	Opportunistic predator

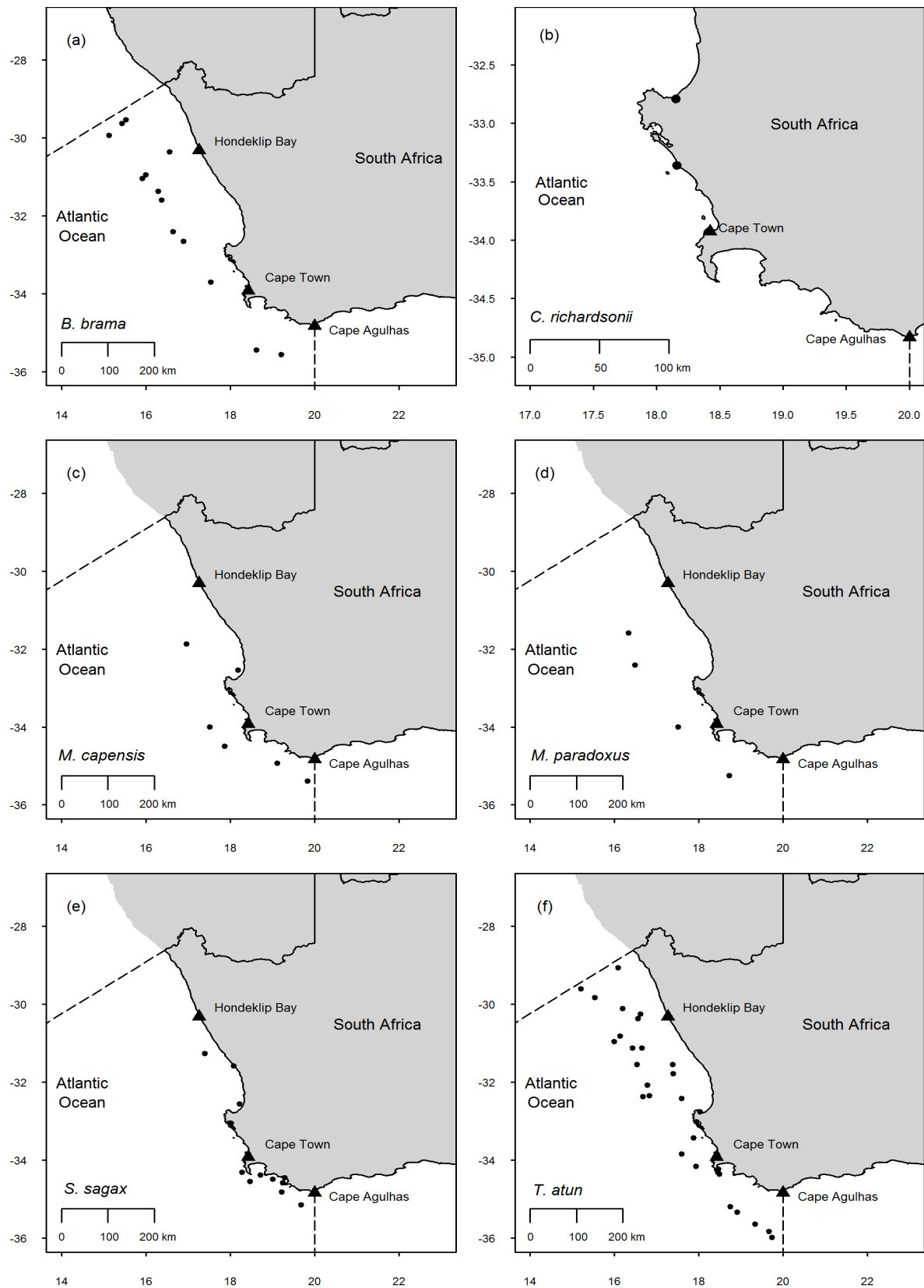


Figure 4.1. The distribution of sampling stations (black dots) for (a) *Brama brama*, (b) *Cheloni richardsonii*, (c) *Merluccius capensis*, (d) *Merluccius paradoxus*, (e) *Sardinops sagax* and (f) *Thyrsites atun* examined in this study.

## **4.2.2. Statistical Analyses**

### **4.2.2.1. Exploratory Data Analysis**

Parasitological data often does not conform to the underlying assumptions of statistical techniques commonly employed in ecological studies. Exploratory Data Analysis (EDA) aims to detect such violations, thus allowing for the most suitable statistical technique for a particular situation to be applied (Zuur et al. 2010; Borcard et al. 2011). Parasites are typically overdispersed within a host population, i.e., a few hosts harbour the majority of parasites (Shaw et al. 1998; Lester 2012). This frequency distribution stems from heterogeneities in host susceptibility coupled with the availability of infective propagules (Wilson et al. 2002) and can have a significant effect on the quality of parasitological data collected. A histogram and the Shapiro-Wilks test were employed to assess overdispersion in the frequency distribution of parasite taxa.

Species accumulation curves which depict the recovery of new taxa as a function of sampling effort (Dove and Cribb 2006) were used to evaluate the completeness of parasite component communities recovered with respect to the number of specimens examined for each host species. Chao2, a non-parametric diversity estimator based on the presence of rare taxa infecting only one or two individual hosts within a sample and 10 000 randomisations, was also generated to evaluate the potential for further parasite taxa to be found infecting each host species (Clarke and Gorley 2006; Dove and Cribb 2006). Because species richness is generally correlated to effort, rarefaction curves which yield the expected diversity within a random subsample were generated for 20 hosts of each species as a means of enabling interspecific species richness comparisons (Heip et al. 1998; Gotelli and Colwell 2001).

### **4.2.2.2. Parasite Infection Indices and Species Richness**

Infection levels were summarised by computing the prevalence and average abundance of each parasite taxon for each host species following Bush *et al.* (1997). The richness of component communities, i.e., the number of different parasitic taxa infecting a particular host species and the proportional contribution of parasites employing different transmission strategies was determined for each host species.

#### **4.2.2.3. Parasite Community Analyses**

Multivariate statistical techniques were used to explore variations in parasite community structure with respect to host identity. Three separate data matrices, comprising only hosts infected by at least one parasite, were generated from the parasite data. First, the whole parasite data matrix was presence-absence transformed as the abundance of microscopic and encysting parasites could not be accurately determined. A resemblance matrix based on Jaccard's index, chosen for its appropriateness in dealing with presence-absence data (Clarke and Gorley 2006), was then computed and formed the basis of analyses considering infracommunities. Second, a subset comprising only ectoparasite abundance was square root transformed and a dissimilarity matrix relying on Bray–Curtis distances was generated. The Bray-Curtis similarity index is well suited for abundance data as it accounts for differences in shared species and is robust to joint absences (Clarke *et al.* 2006). Finally, a matrix including only long-lived and non-specific parasite abundances was obtained and was fourth root transformed to down weight the contribution of highly abundant parasite taxa before Bray-Curtis distances amongst host endoparasite communities was generated. Parasites exhibiting a prevalence below 5% were excluded from the analyses.

The influence of host specific identity on the parasite community structure was assessed by means of Permutational Multivariate Analysis of Variance (PERMANOVA) proposed by Anderson (2001). PERMANOVA has several advantages when compared to the

traditional MANOVA (Multivariate Analysis of Variance) for the analysis of ecological data. Notably, PERMANOVA does not assume multivariate normality in the data, can handle semi-metric distance measures (e.g. Bray-Curtis) and is able to partition variance in multifactorial designs (Anderson 2001; McArdle and Anderson 2001). PERMANOVA tests for differences in the centroid location of multivariate groups but is susceptible to heterogeneity in multivariate dispersion, especially in unbalanced designs (Anderson and Walsh 2013). PERMDISP was therefore used to test for homogeneity in multivariate dispersion between factor levels. An interaction between host size and host identity was also included in the models. In cases where PERMANOVA revealed a significant interaction, a subsequent PERMANOVA was run to assess the influence of host size (SL) on the parasite community of each host species individually. Because of the unbalanced design (unequal number of fish examined per host species) and differences in host sizes both across and within host species, host size (SL) was included as a covariate in the PERMANOVA models and a Type I sequential sum of squares was employed (Anderson et al. 2008).

Similarity Percentage analysis (SIMPER) was then conducted to determine which parasite taxa were responsible for differences in community structure between host species (Clarke and Warwick 1994). Finally, a distance-based redundancy analysis (dbRDA) was performed to visualise the effects of parasite taxa accounting for the first 65% of dissimilarity between pairs of host species in a constrained ordination (Legendre and Anderson 1999). In dbRDA, sample clustering was based on the similarity of their 'constrained' parasite community (only those contributing to the first 65% of dissimilarity) structure and the vectors overlaid on the ordination depict the increasing influence of particular parasite taxa in causing community shifts. Ordinations employing host functional feeding groups and habitat as grouping factors were also generated to explore and support the interpretations of variability in parasite community structure amongst host species. This set of routines was

applied to each of the data sets generated and described above to explore variability in parasite community structure with respect to host identity. Community shifts in ectoparasite communities were not assessed across FFGs as the acquisition of ectoparasites does not depend on a host's diet. All calculations and statistical analyses were conducted in R (R Core Team 2018).

### 4.3. Results

#### 4.3.1. Parasite Assemblages, Infection Indices and Species Richness

Species accumulation curves demonstrated that the parasite assemblages of *T. atun*, *M. paradoxus* and *S. sagax* were adequately surveyed while for *B. brama*, *M. capensis* and *C. richardsonii* the cumulative number of parasites recovered had not yet reached an asymptote (Fig. 4.2). The Chao2 diversity estimator for *M. capensis*, *M. paradoxus* and *S. sagax* converged towards the observed diversity suggesting that sampling was adequate to document their parasite assemblages (Fig 4.2). For *B. brama* and *T. atun*, Chao2 suggested that one more parasite taxon might be revealed by further sampling while for *C. richardsonii* up to four more taxa are expected. Rarefaction curves for *B. brama*, *C. richardsonii* and *M. capensis* suggested that some parasite taxa might not have been found within the examined sample while sampling had adequate coverage for *M. paradoxus*, *S. sagax* and *T. atun* (Fig 4.2).

The parasite assemblages recovered from the six fish host species comprised 41 taxa including members of nine major parasitic taxa (Table 4.2). Of the 41 parasitic taxa, 23 were identified to species level, 12 to genus level, three to family level whilst three could only be assigned to order level. Copepods were the most diverse being represented by 14 taxa followed by acanthocephalans (7 taxa) and parasitic cnidarians (5 taxa). The parasites recorded included five new South African geographical records and 10 new host records

(Table 4.2). The most widespread parasites were *Anisakis* sp. and *Hepatoxylon trichiuri* which were found infecting all four predatory host species (*B. brama*, *M. capensis*, *M. paradoxus*, *T. atun*).

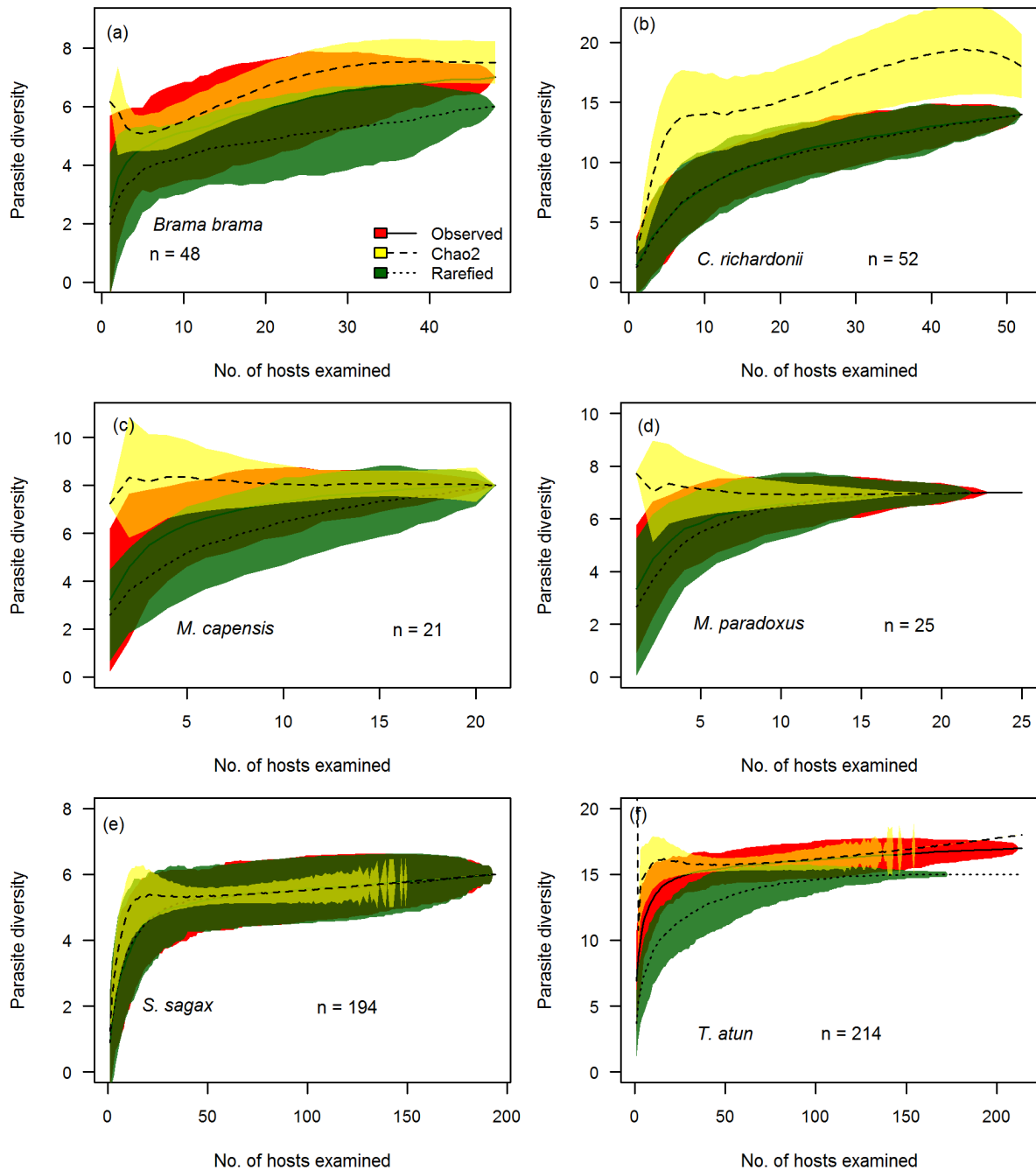


Figure 4.2. Species accumulation curves, Chao2 diversity estimate and rarefaction curves generated from the parasitological data recorded from (a) *Brama brama*, (b) *Chelonia richardsonii*, (c) *Merluccius capensis*, (d) *Merluccius paradoxus*, (e) *Sardinops sagax* and (f) *Thyrsites atun*.

At the component community level, *T. atun* had the most speciose parasite assemblage (17 taxa) followed by *C. richardsonii*, *M. capensis* and *B. brama* with 14, 8 and 7 taxa respectively (Table 4.2). *Merluccius paradoxus* and *S. sagax* were each found to be infected by six parasite taxa in the Southern Benguela. The component community of *C. richardsonii* was dominated by directly transmitted taxa while that of *B. brama* and *T. atun* were mostly composed of trophically transmitted taxa (Fig. 4.3). The transmission pathways utilised by a significant proportion of parasite taxa found infecting *M. capensis*, *M. paradoxus* and *S. sagax* are still to be elucidated.

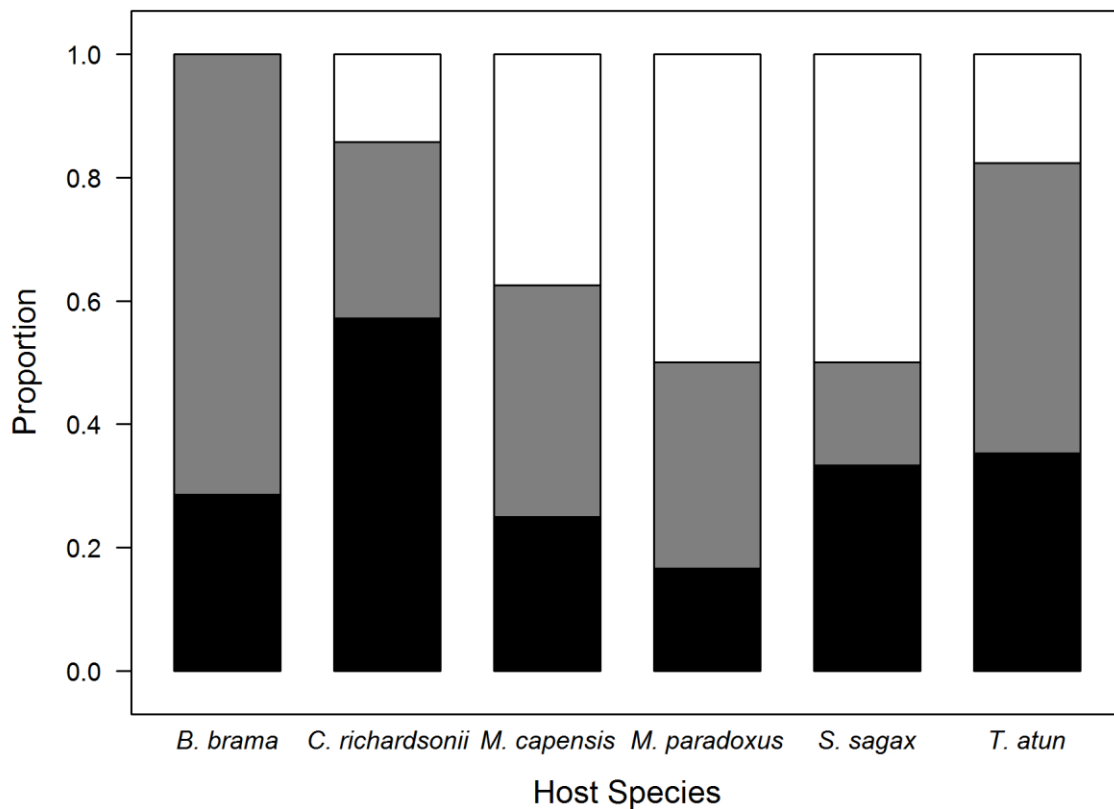


Figure 4.3. The contribution to the component community of fish host species investigated of parasites acquired by direct transmission (black), via trophic interactions (grey) and those whose infection pathways are still unknown (white).

Table 4.2. Taxonomic composition, prevalence and mean abundance  $\pm$  one standard deviation (mean abundance shown in parentheses) of the parasites recovered from the six fish hosts caught in the Southern Benguela and examined in this study (\* new host record, † new geographic record).

Parasite taxon	Life stage	<i>Brama brama</i>	<i>Chelon richardsonii</i>	<i>Merluccius capensis</i>	<i>Merluccius paradoxus</i>	<i>Sardinops sagax</i>	<i>Thyrsites atun</i>
<b>Acanthocephala</b>							
<i>Bolbosoma</i> sp.	Cystacanth	4.2 * (0.04 $\pm$ 0.02)	0	0	0	0	0
<i>Bolbosoma vasculosum</i>	Cystacanth	0	0	0	0	0	6.1 (0.09 $\pm$ 0.4)
<i>Corynosoma australe</i>	Cystacanth	0	0	14.3 (0.7 $\pm$ 1.87)	0	0	34.6 (7.7 $\pm$ 22.82)
<i>Neoechinorhynchus agilis</i>	Adult	0	3.9 *, † (0.1 $\pm$ 0.58)	0	0	0	0
Pomporhynchidae gen. sp.	Adult	0	1.9 * (0.02 $\pm$ 0.14)	0	0	0	0
<i>Rhadinorhynchus cadenati</i>	Adult	0	0	0	0	0	9.4 (0.1 $\pm$ 0.49)
<i>Rhadinorhynchus</i> sp.	Adult	2.1 0.04	0	0	0	0	0
<b>Cestoda</b>							
<i>Hepatoxylon trichiuri</i>	Plerocercoid	54.2 (3.8 $\pm$ 5.69)	0	33.3 (0.5 $\pm$ 0.98)	40.0 (0.5 $\pm$ 0.65)	0	52.3 (1.8 $\pm$ 2.97)
<i>Molicola uncinatus</i>	Plerocercoid	6.3 * (0.06 $\pm$ 0.24)	0	0	0	0	91.6 (30 $\pm$ 32.52)
<i>Tentacularia coryphaenae</i>	Plerocercoid	0	0	0	0	0.5 (0.005 $\pm$ 0.07)	14.5 (0.4 $\pm$ 1.73)

Table 4.2 (continued). Taxonomic composition, prevalence and mean abundance  $\pm$  one standard deviation (mean abundance shown in parentheses) of the parasites recovered from the six fish hosts caught in the Southern Benguela and examined in this study (\* new host record, † new geographic record).

Parasite taxon	Life stage	<i>Brama brama</i>	<i>Chelon richardsonii</i>	<i>Merluccius capensis</i>	<i>Merluccius paradoxus</i>	<i>Sardinops sagax</i>	<i>Thyrsites atun</i>
<b>Cnidaria</b>							
<i>Ceratomyxa minuta</i>	Myxospore	0	0	0	0	0	7.0 † (N/A)
<i>Ceratomyxa</i> sp. 1	Myxospore	0	21.2 * (N/A)	0	0	0	0
<i>Kudoa thyrsites</i>	Myxospore	0	0	0	0	5.7 (N/A)	96.7 (N/A)
<i>Myxobolus</i> sp.	Myxospore	0	15.4 * (N/A)	0	0	0	0
<i>Pseudalataspora vanderlingeni</i>	Myxospore	0	0	33.3 (N/A)	56.0 (N/A)	0	0
<b>Copepoda</b>							
<i>Caligus coryphaenae</i>	Adult	0	0	0	0	0	0.5 (0.005 $\pm$ 0.068)
<i>Caligus dakari</i>	Adult	0	0	0	0	0	46.3 (2.5 $\pm$ 4.69)
<i>Caligus zeii</i>	Adult	0	0	0	0	0	12.2 (0.2 $\pm$ 0.83)
Caligidae gen. sp. 1	Adult	0	1.9 (0.02 $\pm$ 0.014)	0	0	0	0
Caligidae gen. sp. 2	Adult	0	1.9 (0.02 $\pm$ 0.014)	0	0	0	0

Table 4.2 (continued). Taxonomic composition, prevalence and mean abundance  $\pm$  one standard deviation (mean abundance shown in parentheses) of the parasites recovered from the six fish hosts caught in the Southern Benguela and examined in this study (\* new host record, † new geographic record).

Parasite taxon	Life stage	<i>Brama brama</i>	<i>Chelon richardsonii</i>	<i>Merluccius capensis</i>	<i>Merluccius paradoxus</i>	<i>Sardinops sagax</i>	<i>Thyrssites atun</i>
<b>Copepoda</b>							
<i>Chondracanthus merluccii</i>	Adult	0	0	4.8 (0.1 $\pm$ 0.44)	0	0	0
<i>Clavellisa ilishae</i>	Adult	0	0	0	0	9.8 (0.2 $\pm$ 0.76)	0
Ergasilidae gen. sp.	Adult	0	13.5 (0.2 $\pm$ 0.63)	0	0	0	0
<i>Hatschekia conifera</i>	Adult	64.6 (84.8 $\pm$ 109.5)	0	0	0	0	53.7 (2.1 $\pm$ 3.79)
<i>Nothobomolochus fradei</i>	Adult	0	0	0	0	15.0 (0.17 $\pm$ 0.43)	92.5 (13.5 $\pm$ 15.53)
<i>Peniculus fistula</i>	Adult	0	13.5 (0.2 $\pm$ 0.47)	0	0	0	0
<i>Parabrachiella exilis</i>	Adult	0	13.5 *, † (0.2 $\pm$ 0.57)	0	0	0	0
<i>Parabrachiella</i> sp. 1	Adult	0	7.7 * (0.1 $\pm$ 0.36)	0	0	0	0
<b>Digenea</b>							
<i>Cardiocephaloides physalis</i>	Metacercaria	0	0	0	0	54.6 (1.6 $\pm$ 2.25)	0
Digenea sp.	Metacercaria	0	0	0	0	0	36.0 (N/A)
<i>Stephanostomum</i> sp.	Metacercaria	0	0	47.6 (N/A)	36.0 (N/A)	0	0

Table 4.2 (continued). Taxonomic composition, prevalence and mean abundance  $\pm$  one standard deviation (mean abundance shown in parentheses) of the parasites recovered from the six fish hosts caught in the Southern Benguela and examined in this study (\* new host record, † new geographic record).

Parasite taxon	Life stage	<i>Brama brama</i>	<i>Chelon richardsonii</i>	<i>Merluccius capensis</i>	<i>Merluccius paradoxus</i>	<i>Sardinops sagax</i>	<i>Thyrssites atun</i>
<b>Hirudinea</b>							
Hirudinea gen. sp.	Adult	0	1.9 (0.3 $\pm$ 2.36)	0	0	0	0
<b>Monogenea</b>							
<i>Anthocotyle merluccii</i>	Adult	0	0	61.9 (7.6 $\pm$ 8.85)	20.0 (0.3 $\pm$ 0.85)	0	0
Diclidophoridae gen. sp.	Adult	50.0 (2.7 $\pm$ 4.1)	0	0	0	0	0.5 (0.004 $\pm$ 0.068)
Monogenea gen. sp.	Adult	0	13.5 (0.1 $\pm$ 0.35)	0	0	0	0
<b>Myxozoa</b>							
<i>Eimeria sardinae</i>		0	0	0	0	9.3 (N/A)	0
<i>Goussia</i> sp.		0	0	19.1 (N/A)	68.0 (N/A)	0	0
<b>Nematoda</b>							
<i>Anisakis</i> sp.	Larval	91.7 (4.5 $\pm$ 3.56)	0	90.5 (28.1 $\pm$ 33.57)	100.0 (15.9 $\pm$ 11.19)	0	100.0 (144.7 $\pm$ 179.39)
<i>Contracaecum</i> sp.	Larval	0	26.9 *, † (0.8 $\pm$ 1.48)	0	0	0	0
<i>Pseudoterranova</i> sp.	Larval	0	0	0	0	0	11.2 (0.3 $\pm$ 1.06)
<i>Spinitectus</i> sp.	Adult	0	3.9 *, † (0.5 $\pm$ 2.45)	0	0	0	0

## 4.3.2. Parasite Community Analyses

### 4.3.2.1. Infracommunity Level

PERMANOVA results indicated that host SL had a significant impact on parasite infracommunity structure (Table 4.3). The significant interaction indicated that the relationship between host size and infracommunity structure differed across host species. Individual PERMANOVAs revealed a significant ontogenetic shift in infracommunity structure for *B. brama* ( $F = 9.3665$ ,  $df = 1$ ,  $p = 0.002997$ ), *M. capensis* ( $F = 4.3995$ ,  $df = 1$ ,  $p = 0.00999$ ), *S. sagax* ( $F = 5.9402$ ,  $df = 1$ ,  $p = 0.000999$ ) and *T. atun* ( $F = 23.793$ ,  $df = 1$ ,  $p = 0.000999$ ) but not for *C. richardsonii* ( $F = 0.94994$ ,  $df = 1$ ,  $p = 0.5115$ ) and *M. paradoxus* ( $F = 2.3065$ ,  $df = 1$ ,  $p = 0.07093$ ).

Table 4.3. The results of PERMANOVA conducted to test for the influence of host size, and host identity (species) on presence-absence transformed infracommunity data.

Source	df	SS	MS	Pseudo F	R <sup>2</sup>	p(perm)
Host size (SL/mm)	1	44.085	44.085	278.138	0.267	0.000999 *
Species	5	43.553	8.711	54.957	0.264	0.000999 *
Host size × Species	5	4.146	0.829	5.232	0.025	0.000999 *

\* denotes significant results,  $p < 0.05$

PERMANOVA showed that host species identity had a significant effect on the structure of parasite infracommunities (Table 4.3). Significant differences in multivariate dispersion between the host species were also revealed ( $F = 39.274$ ,  $p < 0.0001$ ) and may have affected the PERMANOVA. SIMPER and dbRDA ordinations (Fig. 4.4) showed that bathydemersal predators (*M. capensis*, *M. paradoxus*) were characterised by *Goussia* sp., *S. multispinosum* and *P. vanderlingeni*, mullet (*C. richardsonii*) by *Contracaecum* sp., *Myxobolus* sp. and *Ceratomyxa* sp. 1 while the digenean *C. physalis* was a major driver of

clustering for *S. sagax*. Two taxa, namely *H. conifera* and *Diclidophoridae* sp. were predominantly associated with *B. brama* while *T. atun* could be distinguished from other host taxa by the high prevalences of *Anisakis* sp., *K. thyrsites*, *M. uncinatus*, *N. fradei* and *C. dakari*.

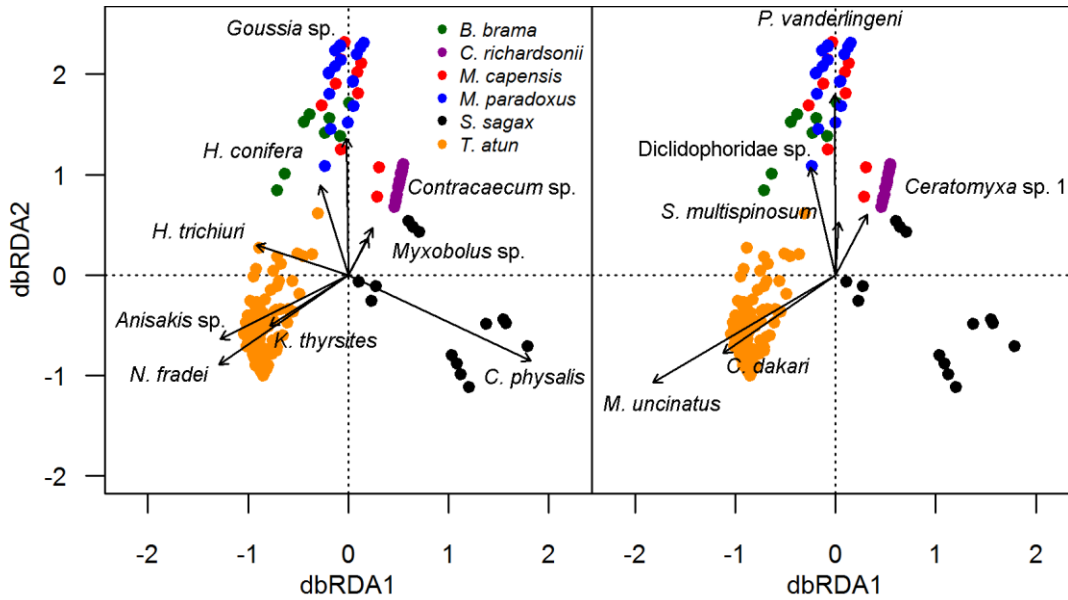


Figure 4.4. Distance-based redundancy analysis (dbRDA) ordination relating constrained parasite infracommunities to host identity (two ordinations were used to avoid overlapping labels).

### 4.3.2.2. Ectoparasite Community

PERMANOVA indicated that host SL had a significant influence on the community structure of ectoparasites (Table 4.4). The lack of a significant interaction between host SL and identity suggested that the effect did not differ across host species. PERMANOVA demonstrated that host identity affected the structure of ectoparasite communities (Table 4.4) although the analysis may have been affected by unequal dispersion amongst host species in the multivariate data ( $F = 41.18, p < 0.0001$ ). SIMPER and dbRDA (Fig. 4.5) revealed that *B. brama* harboured high numbers of *H. conifera*, hakes (*M. capensis, M. paradoxus*) were infected by *A. merlucci*, while mullet (*C. richardsonii*) were characterised by *P. exilis* and Ergasilidae sp. Sardines (*S. sagax*) were separated from other taxa due to their susceptibility to *C. ilishae* and the clustering of *T. atun* was driven by a high abundances of *C. dakari* and *N. fradei*.

Table 4.4. The results of PERMANOVA conducted to test for the influence of host size and host identity (species) on square-root transformed ectoparasite communities.

Source	df	SS	MS	Pseudo F	R <sup>2</sup>	p(perm)
Host size (SL/mm)	1	16.875	16.875	105.488	0.167	0.000999 *
Species	5	31.934	6.3869	39.925	0.315	0.000999 *
Host size × Species	5	1.101	0.220	1.377	0.011	0.09191

\* denotes significant results,  $p < 0.05$

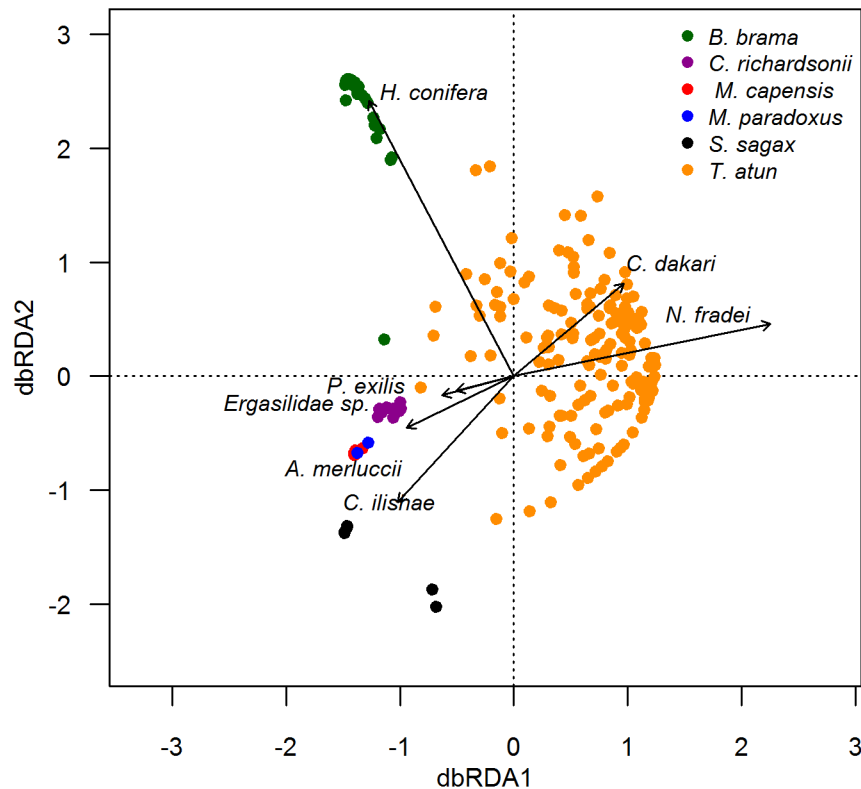


Figure 4.5. Distance-based redundancy analysis (dbRDA) ordination relating ectoparasite abundance to host identity.

#### 4.3.2.3. Long-Lived, Non-Specific Larval Endoparasite Community

PERMANOVA revealed that variations in endoparasite community were linked to variations in host SL and the significant interaction term suggests that the effect varies amongst host species (Table 4.5). Ontogenetic shifts in endoparasite communities were found for *M. capensis* ( $F = 8.6998$ ,  $df = 1$ ,  $p = 0.000999$ ), *M. paradoxus* ( $F = 6.14$ ,  $df = 1$ ,  $p = 0.01399$ ), *S. sagax* ( $F = 19.835$ ,  $df = 1$ ,  $p = 0.000999$ ) and *T. atun* ( $F = 63.145$ ,  $df = 1$ ,  $p = 0.000999$ ) but not for *B. brama* ( $F = 2.6394$ ,  $df = 1$ ,  $p = 0.07193$ ) nor *C. richardsonii* ( $F = 3.1396$ ,  $df = 1$ ,  $p = 0.09391$ ).

Table 4.5. The results of PERMANOVA conducted to test for the influence of host size and host identity (species) on fourth-root transformed endoparasite communities.

Source	df	SS	MS	Pseudo F	R <sup>2</sup>	p(perm)
Host size (SL/mm)	1	50.624	50.624	1328.05	0.444	0.000999 *
Species	5	45.775	9.155	240.17	0.401	0.000999 *
Host size * Species	5	2.017	0.403	10.58	0.018	0.000999 *

\* denotes significant results,  $p < 0.05$

The endoparasite community was found to vary significantly as a function of host identity (Table 4.5). Significant differences in multivariate dispersion between host species were detected ( $F = 52.846$ ,  $p < 0.0001$ ) and could have influenced the results of PERMANOVA. The SIMPER routine and dbRDA (Fig 4.6) ordination revealed that the tight clustering of *C. richardsonii* was driven by *Contracaecum* sp. infections and *S. sagax* was characterised by *C. physalis*. High abundances of anisakids and *H. trichiuri* were typical of predatory species (*B. brama*, *M. capensis*, *M. paradoxus*, *T. atun*) while *M. uncinatus* were exclusively found in *T. atun*.

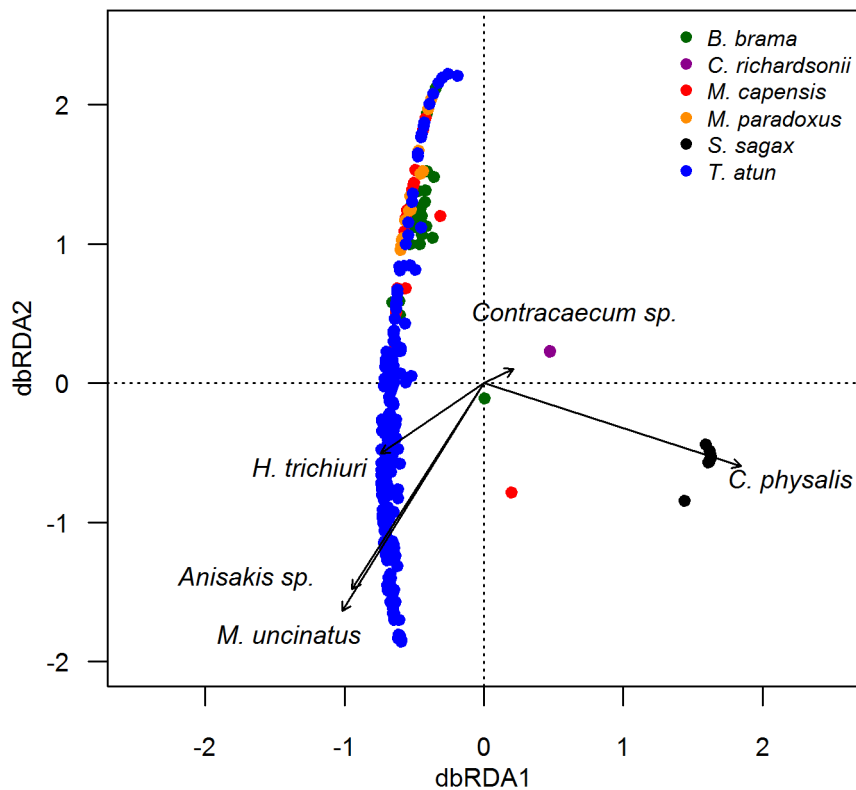


Figure 4.6. Distance-based redundancy analysis (dbRDA) ordination relating long-lived endoparasite abundance to host identity.

#### 4.4. Discussion

##### 4.4.1. Parasite Community Composition

The current study revealed that all major phyla parasitic on marine fish were represented in the suite of parasites recovered from the six fish host species assessed. Amongst these, ectoparasitic copepods were the most diverse taxon (14 taxa) with at least one species found infecting each host species. On the other hand, there was a lack of diversity amongst the monogeneans and digeneans were only recovered in their encysted, larval forms. As adults, these trematodes have delicate bodies and their detection as well as identification may have been curtailed by the host collection protocol which involved freezing the specimens prior to the parasitological examinations. The examination of freshly caught hosts

is therefore recommended to obtain a better idea of trematode biodiversity in fishes of the Southern Benguela.

This study provided the first record of *M. uncinatus* infecting *B. brama* which along with the record of *Bolbosoma* sp. has increased the number of parasites known to infect this fish species in the southern Benguela from five to seven excluding the unidentified taxon reported by Mackintosh et al. (2018). The examination of *C. richardsonii* yielded a remarkable eight new host records despite this host's parasite fauna having been previously investigated (van Praag 2004; Weber 2017). The high number of new records might be explained by the fact that previous studies focused on ectoparasites and lacked taxonomic resolution with respect to parasite identification.

The component communities of the different host species surveyed varied in both their composition and richness, with *T. atun* and *C. richardsonii* being the host species harbouring the most diverse parasite assemblages. For *T. atun*, the high parasite diversity may be attributed to its wide spatial and bathymetric distribution in the southern Benguela (Griffiths 2002) which increases the probability of encountering infective stages of several parasite taxa. The varied diet of *T. atun* (Griffiths 2002; McQueen and Griffiths 2004) also appears to play an important role in determining the composition of its component community, as eight of the 17 parasite taxa rely on predator-prey interactions for transmission. On the other hand, *C. richardsonii* is classified as an iliophagous (detritivorous) species, ingesting few organisms capable of acting as intermediate hosts (Whitfield 1988). This is reflected in its parasite community which includes only four trophically transmitted taxa while ectoparasites dominate. The parasite assemblage of the mesopelagic *B. brama* was dominated by trophically transmitted parasite taxa. Given the lack of studies investigating the diet of *B. brama* in South Africa, the composition of its component community may be used to hypothesise that this species preys on small organisms (e.g. euphausiids, calanoid

copepods) which act as intermediate hosts for a suite of endoparasites (Marcogliese 1995; Gregori et al. 2012, 2015). Further surveys of the parasites of *B. brama* and *C. richardsonii* are necessary as their respective species accumulation curves, Chao2 estimates and rarefaction curves suggested that they may harbour more taxa than reported in this study.

The component community of *M. paradoxus* was nested within that of *M. capensis*. The absence of *Chondracanthus merlucci* and *Corynosoma australe* in *M. paradoxus* could be due to the deeper bathymetric distribution of *M. paradoxus* which precludes his species from encountering the infective stages of the copepod *C. merlucci* and the first intermediate hosts of the acanthocephalan *C. australe*. The less diverse diet of *M. paradoxus* compared to *M. capensis* (Punt et al. 1992; Punt and Leslie 1995) may also account for the absence of *C. australe* infections in *M. paradoxus*. Widespread cannibalism in both merluccid species (Punt and Leslie 1995) may explain the relative conservatism of their parasite assemblages as this would restrict their probability of being exposed to endoparasites transmitted by other prey species. The cestode *Tentacularia coryphaenae* was the only trophically transmitted parasite reported from *S. sagax* and occurred at very low prevalence. This parasite was most likely acquired as a result of feeding on an infected zooplanktonic intermediate host such as calanoid copepods which are known to be vectors of cestode larvae (Marcogliese 1995). The very low incidence of *T. coryphaenae* in *S. sagax* may also be a consequence of the low prevalence of its infective stages within the zooplanktonic community, a trend typical of first intermediate hosts of anisakids, cestodes and acanthocephalans (Gregori et al. 2012, 2013, 2015; Gonzalez-Solis et al. 2013).

#### **4.4.2. Parasite Community Structure**

Previous studies have demonstrated that the structure of ichthyoparasite communities varies according to the hosts' evolutionary history, geographical origin, seasonality in host

physiological cycles and environmental conditions, and host ecology as well as variability in host traits at the individual's level (e.g. Alarcos and Timi 2012; Carballo et al. 2012; Míguez-Lozano et al. 2012; Constenla et al. 2015; Pérez-i-garcía et al. 2015; Braicovich et al. 2017). Aspects of the parasites' biology such as lifestyle (endoparasite, ectoparasite) life cycles (direct, complex), co-evolutionary history (e.g. Desdevises et al. 2000) and ontogenetic variation in host preference (Klimpel et al. 2004; Mikheev et al. 2004; Palm and Caira 2008) also contribute to determining which hosts within an ecosystem can be infected by different life stages of a particular parasite and should not be neglected as drivers of parasite community ecology.

#### **4.4.2.1. Ectoparasite Community**

Host specificity, the range of host species susceptible to a particular parasite, is a ubiquitous phenomenon which nonetheless varies in its magnitude across parasitic taxa and is dependent upon a range of variables such as parasite life stage, host traits, host physiological cycles and geographic distribution (Rohde 1978, 1979; Whittington et al. 2000). Host specificity may stem from the co-evolution of parasites with their host, as demonstrated by Paterson and Poulin (1999) for the copepod genus *Chondracanthus*, but can also be a result of adaptation to a particular environment rather than adaptation to a specific host (Rohde 1979; Desdevises et al. 2002). Rohde (1979) utilised the terms 'phylogenetic' and 'ecological' host specificity to differentiate between the two processes through which host specificity arises.

In the current study, multivariate analyses demonstrated that ectoparasite assemblages differed across host species. The differences in ectoparasite community structure were mainly driven by parasites displaying some form of host specificity (Rohde 1979). For example, the exclusive presence of *A. merlucci* on the merluccids was likely driven its specificity for

members of the genus *Merluccius* (Fernandez 1983; MacKenzie and Longshaw 1995; Luque et al. 2016). Another consequence of the phylogenetic host specificity of parasites is the presence of *C. ilishae* and *P. exilis* in the ectoparasitic assemblages of *S. sagax* and *C. richardsonii*, respectively, as these copepods are known to have an affinity for clupeiform (El-Rashidy and Boxshall 2010; Moreira et al. 2013) and mugilid hosts respectively (Montes et al. 2017).

Other indicator species identified by the analyses exhibited ‘ecological host specificity’ and utilise a wide range of host taxa. Amongst these is *Hatschekia conifera*, a cosmopolitan copepod known to infect fishes from the families Bramidae, Gempylidae, Nomeidae and Stromateidae (Cressey 1968; Jones 1985; Moles 2007; Nunkoo et al. 2016; Mackintosh et al. 2018). In the southern Benguela it infected the gills of both *B. brama* and *T. atun* but occurred at higher infection intensities on *B. brama*. This trend suggests that while it has a well documented high affinity for members of the family Bramidae (e.g. Jones 1985; Ho and Kim 1996; George-Nascimento et al. 2002; Moles 2007; Cantatore et al. 2012; Oliva et al. 2016), *H. conifera* is able to exploit sympatric host species.

Infections by the bomolochid copepod *N. fradei* in the southern Benguela also appear to be driven by ecological rather than phylogenetic factors. This copepod has been reported infecting clupeiform and atheriniid hosts in the Arabian Gulf, the Gulf of Guinea and the Mediterranean Sea (El-Rashidy and Boxshall 2009, 2010, 2014), and was found infecting the pelagic clupeoid *S. sagax* and the predatory *T. atun* in the southern Benguela. However, it occurred at significantly higher abundance on *T. atun*, a trend which may be explained by the larger body size of *T. atun* thereby making it a larger ‘target’ for infective stages. Differences in the site of infection between the two host species may also account for the difference in infection levels; *N. fradei* infects the gill filaments of *S. sagax* and may be dislodged during

filter feeding while they are found in the nares of *T. atun* which offer a more protected microhabitat.

*Caligus dakari* has been reported infecting members of the families Ariidae, Carcharinidae, Carangidae, Gempylidae and Sciaenidae from the tropical waters of India, Mauritania, Mozambique, Senegal, and Sri Lanka as well as the temperate environments of South Africa (Barnard 1955a; Kirtisinghe 1964; Pillai 1985; Kumar 1990; Dippenaar 2004; Boxshall and El-Rashidy 2009; Nunkoo et al. 2016; Weston 2017). This suggests that it does not conform to any of the paradigms proposed to explain host specificity and is a generalist parasite. However, in the southern Benguela, *C. dakari* has only been reported from *T. atun* although it is known to infect the sympatric pelagic horse mackerel (*Trachurus capensis*) on the south coast (Weston 2017).

#### **4.4.2.2. Endoparasite Community**

Most endoparasites have complex (indirect) life cycles involving one or more intermediate hosts and exploit predator-prey interactions for transmission for a least one life stage (Marcogliese 1995, 2002). The evolution of complex life cycles was driven by a need for parasites to survive the death of hosts and as a way to cope with long marine food chains as well as the low concentration of potential hosts (Lafferty 1999; Marcogliese 2002). Long-lived, larval stages which exhibit low host specificity and which use fish as paratenic hosts are characteristic of marine ichthyoparasitic helminths and contribute to their persistence in the marine realm (Marcogliese 1995, 2002). Since they rely on predation events for transmission, trophically transmitted parasites can be used as indicators of the dietary preferences and trophic position of fish (e.g. Munster et al. 2015; Levsen et al. 2016; Zuo et al. 2016).

Two of the host species considered in the study (*C. richardsonii* and *S. sagax*) are unique in both their FFGs and habitats, making it difficult to untangle the effect of each characteristic on their endoparasite assemblage. However, the endoparasite assemblage of *C. richardsonii* was composed of a distinct suite of parasites, none of which were reported from the other hosts species considered. The uniqueness of its endoparasite community composition suggests that *C. richardsonii* is a member of a distinct food web and ecosystem.

On the other hand, *S. sagax* is a component of the lower trophic levels of the pelagic, offshore food web which also includes the predatory fishes considered in this study (van der Lingen 2002; Shannon et al. 2003). Despite *S. sagax* being a small-bodied planktivore, its endoparasite community included *T. coryphaenae* and *K. thyrsites*, two taxa also infecting *T. atun* and *Lepidopus caudatus* (Nunkoo unpublished data), thus indicating that *S. sagax* is exposed to parasites typical of the offshore environment. The high prevalence and abundance of *C. physalis* in *Sardinops sagax* also suggests that it is a key intermediate host in the life cycle of this intestinal parasite of the jackass penguin, *Spheniscus demersus* (Fig 4.7) (Randall and Bray 1983; Crawford et al. 2006; Petersen et al. 2006; Horne et al. 2011).

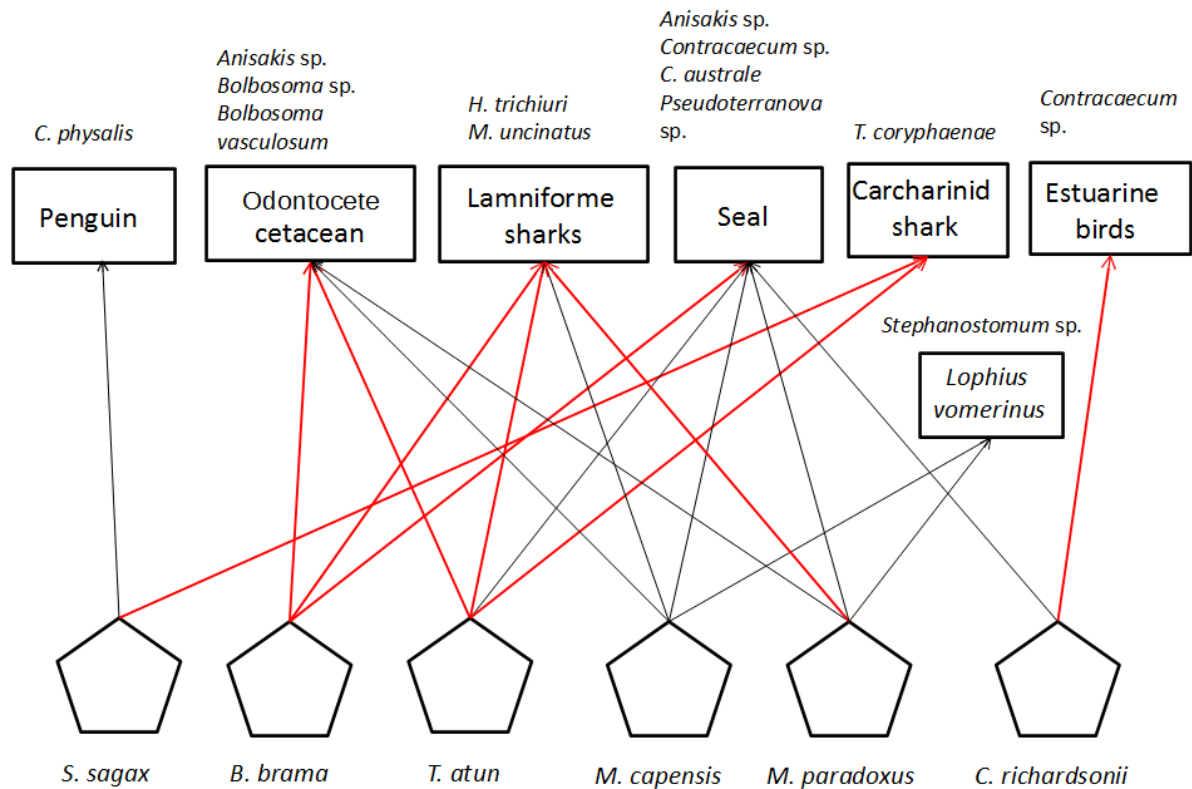


Figure 4.7. Predator-prey interactions inferred from the assemblage of trophically transmitted larval parasites (acanthocephalans, cestodes, nematodes) recovered from fishes of the southern Benguela. Intermediate hosts are indicated by pentagons and definitive hosts by rectangles. Parasites maturing in each definitive host taxa are indicated above the rectangles. Interactions documented through diet analyses are shown in black (David 1987; Sekiguchi 1992; Punt et al. 1995; Smale 2005; Walmsley et al. 2005; Crawford et al. 2006; Hussey et al. 2012) and those inferred from parasitological data are in red.

The guild of predatory fishes examined comprised four species (*B. brama*, *M. capensis*, *M. paradoxus*, and *T. atun*) representing three types of habitats (benthopelagic, mesopelagic, bathydemersal) illustrated how host species traits and ecology interact to determine the parasite community structure. The predatory fishes that were caught offshore were typically infected by non-specific, larval, trophically transmitted nematodes (*Anisakis* sp.) and cestodes (*H. trichiuri*). Amongst the predators, the benthopelagic *T. atun* was the most susceptible to anisakids, a situation which may reflect its reliance on pelagic crustaceans (e.g. euphausiids) which act as first intermediate hosts for anisakids, as prey for much of its

lifespan (Marcogliese 1995; Griffiths 2002). *Thyrsites atun* may also acquire anisakids through the ingestion of infected teleost prey such as *Trachurus capensis* or merluccids (Botha 1986; Griffiths 2002; Le Roux 2013). However, the fact that *M. capensis* and *M. paradoxus* also feed on potentially *Anisakis* sp.-infected prey (Hennig 1974; Botha 1986; Punt and Leslie 1995; Le Roux 2013) suggests that variation in biological and ecological factors not considered in this study could lead to the observed interspecific differences in infection intensities. The high infection intensities recorded in *T. atun* for *Anisakis* sp. and *M. uncinatus*, parasites maturing in odontocete cetaceans and sharks of the order Lamniformes, respectively (Beveridge et al. 1999; Mattiucci and Nascetti 2007; Olson et al. 2010), indicate that this gempylid is an important link in the life cycle of these parasites maturing in pelagic, apex predators of the southern Benguela (Fig 4.7).

Multivariate analyses demonstrated that the endoparasite assemblage of both merluccid species could be distinguished from that of *B. brama* and *T. atun* by the presence of *Goussia* sp., *P. vanderlingeni* and *Stephanostomum* sp. While the life cycles of these taxa are not known, their presence in the merluccids is most likely related to their hosts' demersal lifestyle which exposes the hosts to the infective stages and in the case of *Stephanostomum* sp. also exposes the hosts to predation by potential benthic final hosts such as *Lophius vomerinus* (Fig 4.7) (Bray and Reimer 2004).

The food web inferred from the parasite data and knowledge of the final hosts utilised by the larval helminths gives us an insight into trophic relationships that may not be possible through diet studies. While the analysis of stomach contents often allows diet data to be collected at the species level (e.g. Ebert 1991; Mann and Buxton 1992), it is dependent upon obtaining specimens whose stomachs have not everted during capture (Pillar and Wilkinson 1995), and the degree of prey digestion (Hyslop 1980), and only provides a snapshot of the diet. Obtaining a sufficient number of specimens for certain apex predators is also

problematic due to their iconic and protected statuses (e.g. great white shark, jackass penguin, Cape fur seal) while relying on stranded or recently deceased animals may not provide data representative of healthy specimens. Endoparasites integrate the host's diet over a long period of time and can be used to determine the trophic position and diet breadth of a host. Such an endeavour however depends on a sound knowledge of parasite transmission pathways and highlights the need for parasite surveys of hosts at the low and mid trophic levels and the elucidation of parasite life cycles.

#### **4.4.3. Conclusion**

The current study allowed an assessment of parasite diversity and its partitioning amongst selected fish species while also providing an insight into the factors driving parasite community structure in fishes of the Southern Benguela. The analyses highlighted that the processes responsible for determining the community structure of parasites differed across ichthyoparasite guilds. Ectoparasite infections were largely dependent upon host specificity hinting at the importance of co-evolution through the arms race between hosts and parasites (Bellay et al. 2015; Lima et al. 2016). The make-up of endoparasite communities was primarily influenced by the host's trophic ecology, as also revealed by meta-analyses of parasite networks of freshwater fishes (Bellay et al. 2015; Lima et al. 2016). The use of genetic identification methods is recommended for future studies as it would allow the differentiation of morphologically similar species (e.g. anisakid nematodes) and contribute to our knowledge of parasite biodiversity as well as refining the putative food web.

## **Chapter 5: Stock Discrimination of Snoek *Thyrsites atun* (Perciformes: Gempylidae) in the Benguela Ecosystem using Parasites as Biological Tags**

### **5.1. Introduction**

#### **5.1.1. Parasites in Fisheries Science**

The ‘stock concept’ is a cornerstone of successful stock assessment and fisheries management worldwide (Begg et al. 1999; Booke 1999). Begg and Waldman (1999) define a stock as a population unit assumed to have homogeneous characteristics for management purposes. Stock discrimination is critical to fisheries management as independent management units (stocks) may be of different size, respond differently to exploitation or require different management strategies (Carvalho and Hauser 1994). The delineation of stock structure has traditionally relied on comparative analyses of morphometrics, meristics, life history parameters (e.g. growth, recruitment), catch data, behaviour, tagging studies, the study of hard structures and molecular genetics (Ihssen et al. 1981; Carvalho and Hauser 1994; Coyle 1998; Begg and Waldman 1999; Campana 2005; Mwakiti et al. 2016). However, gathering the data required for the application of techniques mentioned above is often labour intensive, expensive and in the case of tagging may affect the behaviour and mortality of the concerned individuals (Pawson and Jennings 1996; Mosquera et al. 2003). Parasites offer a natural alternative to artificial tags, are inexpensive to sample and circumvent the problems associated with the capture and release of delicate and deep dwelling species (Pawson and Jennings 1996; MacKenzie and Abaunza 1998).

#### **5.1.2. Biological Tags**

The use of parasites as biological tags for population structure studies of commercially harvested fish was pioneered in the late 1930’s and has since been widely applied (Herrington et al. 1939; Sindermann 1961; Williams et al. 1992; Williams and Lester

2006; Cantatore and Timi 2015; MacKenzie and Hemmingsen 2015; Weston et al. 2015). The technique revolves around the concept of the ‘endemic area’, i.e., the area in which conditions allow the transmission of parasites to the focal host species (MacKenzie and Abaunza 1998). However, not all parasites make good biological tags. Over the years, the guidelines for the selection of biological tags to discriminate between stocks have been refined (Sindermann 1982; Williams et al. 1992; Baldwin et al. 2012; Catalano et al. 2014) and are summarised below:

- The parasite should exhibit spatial differences in infection levels, however similarity in infection levels may be used to track migrations (Carballo et al. 2012).
- The life cycle of the parasite should preferably include a single host but parasites with complex life cycles can be used if sufficient information on their life cycle and determinants of infection are available. Information on the life cycle of a biological is essential to allow correct inferences following statistical analyses.
- The parasite should reside on or in its hosts for at least the duration of the study. A parasite with a life span shorter than the study’s duration could lead to underestimations of infection levels in a host population.
- The prevalence and abundance of selected parasites should not exhibit seasonal or inter-annual variations. Seasonal variations in infection levels make comparisons between hosts samples collected at different times problematic.
- The parasite should be easily detected and identified.
- The parasite should not affect the behaviour and mortality of its host. Hosts who experience behavioural changes due to parasite infection are not representative of the whole population and parasite induced host mortalities leads to underestimates of infection levels.

The use of parasites as biological tags also has limitations. The abundance of parasites often exhibits ontogenetic variations and care should be taken to compare hosts of similar ages (MacKenzie and Abaunza 1998). Mosquera et al. (2003) add that to be useful indicators of stock structure, differences in infection levels must be seasonally consistent and that the influence of abiotic and climatic variables on parasite communities must also be accounted for. Variations in parasite infection levels may also represent variations in the distribution of intermediate hosts rather than differences in the host-parasite relationships of the study species (Mosquera et al. 2003).

Used in isolation the techniques mentioned above often fail to grasp the complexity of stock structure or contradict the signal exhibited by a competing stock marker and may lead to erroneous conclusions (Begg and Waldman 1999). A holistic interpretation of the results emanating from studies relying on different techniques to discriminate between stocks is therefore recommended (Begg and Waldman 1999; Baldwin et al. 2012).

### **5.1.3. *Thyrssites atun***

*Thyrssites atun* (Euphrasen, 1791) is a benthopelagic member of the family Gempylidae native to the temperate, shelf waters of the southern hemisphere. *Thyrssites atun* occurs along the southern coast of Australia, off Tasmania, New Zealand, Tristan da Cunha, Argentina, Chile, the Amsterdam and St Paul islands and south-western Africa (Nakamura and Parin 1993). This schooling, predatory species attains a maximum length of 200 cm and can be found from the surface down to depths of 550 m (Nakamura 1981; Griffiths 2002; Stevens et al. 2011).

Archaeological evidence indicates that *Thyrssites atun* has been a source of food for humans for millennia in New Zealand, South Africa and South America (Parkington 1976; Anderson 1982; Zangrando 2009; Tafuri et al. 2017). Initially caught using primitive hooks,

*Thyrsites atun* is nowadays predominantly caught using handlines and in trawls in Australia, New Zealand and South Africa where it is a species of significant commercial importance (Anderson 1982; Nakamura and Parin 1993). The common name of *Thyrsites atun* varies geographically; it is known as ‘barracouta’ in Australia and New Zealand, referred to as ‘sierra’ in South America while in Africa the species is called ‘snoek’.

#### **5.1.4. The Snoek**

##### **5.1.4.1. The Snoek Fishery**

Snoek are widely distributed off south western Africa. Their distribution extends from Angola down to the south coast of South Africa but they are predominantly found in the Northern and Southern Benguela subsystems (Griffiths 2002). In South Africa, snoek have been targeted since the mid 1600’s and provided an important source of proteins for slaves brought to the Cape colony (Isaacs 2013). The abolition of slavery in the early 1800’s coincided with the establishment of a commercial snoek fishery pioneered by freed malay slaves (von Bonde 1931; Isaacs 2013). Since, the fishery has flourished and snoek are now the major target of the inshore line fishery on the west and south coasts of South Africa (Crawford and de Villiers 1985; Attwood and Farquhar 1999; Griffiths 2000; DAFF 2016), where an average of 5500 tons have been caught annually in the last two decades by this fishery. Snoek is also caught in appreciable quantities by the demersal hake–directed trawl fleet and the magnitude of these catches resembles that of the line fishery. Off Namibia, snoek have been targeted since the late 1800’s. Snoek catches reached 70 000 tons per annum in the 1970’s and early 1980’s but have averaged 630 tons since Namibia gained independence in 1990 (Boyer and Hampton 2001). Snoek is a socio-economically and culturally important species, particularly in South Africa where it is an important source of protein for poorer communities and the major means of making a living for line fishermen

(Isaacs 2013). On the other hand, Musaba and Namukwambi (2011) noted that snoek purchases in Namibia were positively correlated with household size and income, a fact they attribute to marketing strategies in Namibia.

#### **5.1.4.2. The Biology and Ecology of Snoek**

*Thyrsites atun* is a fast-growing, schooling, opportunistic predator feeding on a wide range of organisms including annelids, crustaceans, molluscs and teleosts (Mehl 1969; Griffiths 2002; Duarte et al. 2007). In the Benguela ecosystem, schools of snoek exhibit nomadic movement patterns which may be related to the spatio-temporal distribution and movements of their prey (Crawford and de Villiers 1985; Griffiths 2002). Mature specimens (ca. 73 cm) migrate offshore during the winter spawning period which stretches from May to September (Griffiths 2002). Eggs and larvae are then carried to shallow, inshore nursery areas by prevailing currents where juvenile snoek remain until they mature (Griffiths 2002). Snoek are also an ecologically important species occupying an intermediate position in the food web (Heymans et al. 2004; Nunkoo et al. 2016). In the Southern Benguela ecosystem, snoek are a major predator of clupeoids and are capable of ingesting 300 000 tons of anchovy annually with cascading effects on the structure of zooplankton communities (Crawford and de Villiers 1985; Verheye and Richardson 1998). The snoek also serves as prey for several predators including marine birds, sharks and marine mammals (David 1987; Berruti 1991; Ebert 1994; Mecenero et al. 2006).

Over the last three decades, several attempts have been made to determine the population structure and movement patterns of snoek in the Benguela (Crawford et al. 1990; Griffiths 2003). Snoek have traditionally been considered to comprise a single, migratory population (Crawford and de Villiers 1985; Crawford et al. 1990). However, Griffiths (2003) suggested that snoek inhabiting the Northern and Southern Benguela subsystems constitute

two distinct sub-populations. This thesis was based on the analysis of the spatial and seasonal distribution of snoek catches, the presence of spawning and nursery grounds in both subsystems and the nomadic behaviour of mature snoek (Crawford and de Villiers 1985; Crawford et al. 1990; Olivar and Shelton 1993; Griffiths 2003).

#### **5.1.4.3. The Parasitology of *Thyrsites atun***

Worldwide, *T. atun* is host to at least 37 metazoan parasite taxa spread across 8 orders. The majority of the parasites have been recorded from New Zealand and South Africa (Table 5.1). To date, our knowledge of the parasitism of *T. atun* from Australia, South America and oceanic islands is restricted to a few infection records. Interestingly, no parasitological studies have been conducted on this species in Namibian waters despite its significant contribution to the fisheries sector of the region. This disparity in reported parasite richness of *T. atun* between geographical regions most likely reflects the scientific effort afforded to this fish and its parasites within each region.

Parasitological surveys have demonstrated that the richness of the component community of *T. atun* from New Zealand and South Africa was comparable. Studies of host-parasite relationships conducted in New Zealand and South Africa have revealed that the abundance of larval endoparasites is generally linked to the size of the host while seasonality appears to be a key determinant of ectoparasite communities (Mehl 1970; Wierzbicka and Gajda 1984; Nunkoo 2015). Based on the seasonal and spatial stability of parasite infracommunity structure of *T. atun* caught in the Southern Benguela, Nunkoo et al. (2016) postulated that fish from this region constituted a single population. There is however a dearth of biogeographical studies assessing spatial variations in the parasite communities of this widely distributed teleost.

### **5.1.5. Study Aims**

The aim of this chapter was to assess the utility of parasites as a means of discriminating between snoek stocks in the Benguela ecosystem. In order to achieve this goal the following questions were addressed:

- i. Which parasite taxa comprise the component community of snoek in the Northern Benguela?
- ii. Does the structure of parasite infracommunities and endoparasitic guild exhibit spatial variations?
- iii. Which parasites of snoek, if any, constitute suitable biological tags?
- iv. Do the selected parasites indicate the presence of stock separation in snoek of the Benguela?

Table 5.1. Metazoan parasites reported from *Thyrsites atun* worldwide (M: muscle, BC: body cavity, L: liver, G: gills, O: operculum, S: stomach, I: intestine, GB: gall bladder, N: nares; NZ: New Zealand, AUS: Australia, SA: South Africa, ARG: Argentina, CHI: Chile, TDC: Tristan da Cunha; 1: Mehl 1970, 2: Hewitt and Hine 1972, 3: Wierzbicka and Gajda 1984, 4: Nieuwenhuizen et al. 2006, 5: Sobecka 2012, 6: Gilchrist 1923b, 7: Barnard 1955b, 8: Fernandes et al. 2009, 9: Peña-Rehbein de los Rios-Escalante 2012, 10: Nunkoo et al. 2016, 11: Bayliss 1929, 12: Mattiucci and Nascetti 2007, 13: Weston 2017, 14: Kensley 1978).

Parasite	Site of Infection	Country	References
<b>Acanthocephala</b>			
<i>Bolbosoma vasculosum</i>	BC	SA	10
<i>Corynosoma australe</i>	BC	SA	10
<i>Rhadinorhynchus cadenati</i>	I	SA	10
<b>Cestoda</b>			
<i>Lacistorhynchus tenuis</i>	BC	NZ	2
<i>Hepatoxylon trichiuri</i>	BC	NZ, SA	3, 5, 10
<i>Molicola uncinatus</i>	M	NZ, SA	1, 2, 3, 10
<i>Nybelinia thyrsites</i>	BC	NZ	2
<i>Tentacularia coryphaenae</i>	BC	SA	10
<i>Tetrarhynchus</i> sp. 1	M	AUS	1
<i>Tetrarhynchus</i> sp. 2	M	AUS	1
<b>Copepoda</b>			
<i>Caligus coryphaenae</i>	O	SA	10
<i>Caligus dakari</i>	G, O	SA	10
<i>Caligus pelamydis</i>	Not specified	SA	7
<i>Caligus zeii</i>	G, O	SA	7, 10
<i>Hatschekia conifera</i>	G	SA	10
<i>Nothobomolochus fradei</i>	G, N	SA	10
<i>Sagum foliaceum</i>	G	NZ	3

<b>Parasite</b>	<b>Site of Infection</b>	<b>Country</b>	<b>References</b>
<b>Digenea</b>			
<i>Copiatestes thyrstae</i>	G, I, S	NZ	2, 3
Digenea sp.	GA	SA	10
<i>Lampritrema miescheri</i>	I	ARG	8
<i>Lecithochirium australe</i>	S	NZ	2
<b>Isopoda</b>			
<i>Nerocila orbigny</i>	Not specified	SA	14
<b>Monogenea</b>			
<i>Mazocraes</i> sp.	G	SA	13
<i>Winkenthughesia thyrstites</i>	G	NZ	2
<b>Myxozoa</b>			
<i>Ceratomyxa annulata</i>	GB	NZ	2
<i>Ceratomyxa minuta</i>	GB	NZ	2
<i>Ceratomyxa</i> sp.	GB	SA	10
<i>Ceratomyxa</i> sp. a	GB	NZ	2
<i>Kudoa thyrstites</i>	M	AUS, SA	1, 6, 10
<b>Nematoda</b>			
<i>Anisakis pegreffii</i>	BC	SA	4, 12
<i>Anisakis simplex</i>	BC	NZ	3
<i>Anisakis simplex</i> C	Not specified	SA	12
<i>Anisakis</i> sp.	BC, M, S	CHI, NZ, SA, TDC	1, 2, 9, 10, 11
<i>Contracaecum</i> sp.	BC, I, S	NZ	2
<i>Hysterothylacium aduncum</i>	I, S	NZ	2, 3
<i>Pseudoterranova decipiens</i>	M	NZ	3
<i>Pseudoterranova</i> sp.	BC	SA	10

## **5.2. Materials and Methods**

### **5.2.1. Study Area, Host Sampling and Data Collection**

This study was conducted in the temperate and warm-temperate marine environments off Namibia and South Africa, i.e., in the Northern Benguela (NB) and the Southern Benguela (SB) which includes the West and south coasts (see Chapter 2). Although the west coast and the south coast are recognised as distinct subsystems of the Benguela ecosystem (Kirkman et al. 2016), snoek occurring in these two subsystems are considered as a single population based on their nomadic behaviour, spawning migration and homogeneity in parasite assemblage off South Africa (Griffiths 2002; Nunkoo et al. 2016). For the purposes of this study the Southern Benguela was therefore considered to extend from the mouth of the Orange River to the town of Port Alfred on the south coast (Fig 5.1). Snoek were obtained from the catch of commercial line fishermen, the by-catch of trawlers operating offshore and from the catches of research surveys conducted by the Department of Agriculture, Forestry and Fisheries (Fig 5.1). In the Southern Benguela, snoek were sampled in 2011 (April, May), monthly between April 2013 and March 2014 and further samples were obtained in February, March, May and September of 2016. Specimens were obtained from the Northern Benguela in February, March, May, August and September of 2017. For the purposes of modelling and analyses, samples were clustered by seasons; summer comprised November to February, autumn encompassed March and April, winter spanned from May to August while September and October were considered as spring (Table 5.2).

Table 5.2. The number of snoek sampled seasonally from the Northern and Southern Benguela.

Seasons	Summer	Autumn	Winter	Spring	Total
NB	3	55	29	0	87
SB	36	36	96	94	262
Total	39	91	125	94	349

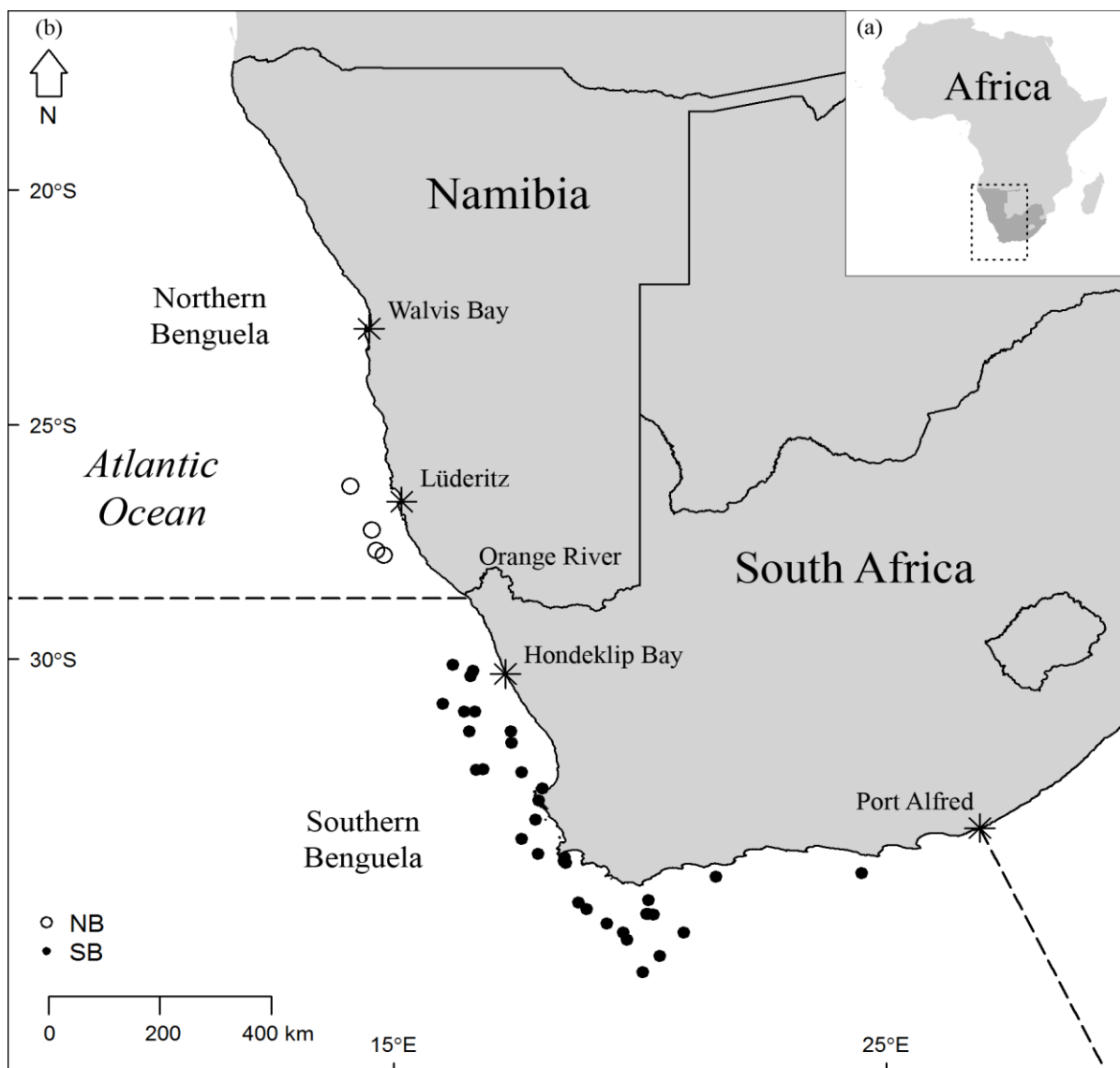


Figure 5.1. (a) The study area within southern Africa and (b) the distribution of snoek sampling stations in the Northern and Southern Benguela.

Snoek were dissected following the protocol described in Chapter 4. Parasites collected were processed in accordance to the protocol described in Chapter 4. Snoek were assigned to size classes 100 mm wide as follows: 300-399 mm, 400-499 mm, 500-599 mm, 600-699 mm, 700-799 mm, 800-899 mm, 900-999 mm. Acanthocephalans were identified using the keys and descriptions provided by Costa et al. (2000), Braicovich et al. (2005), Sardella et al. (2005) and Amin et al. (2011), cestodes were classified following Robinson (1959) and Knoff et al. (2004) while copepods were identified in accordance with Scott and Scott (1912, 1913), Kensley and Grindley (1973), Jones (1985); Boxshall and El-Rashidy (2009) and El-Rashidy and Boxshall (2010). The monogenean was identified using Beverley-Burton (1984), myxozoan identifications followed Gilchrist (1923b) as well as Eiras (2006) and nematode classification relied on Anderson (2000) and Arai and Smith (2016).

## **5.2.2. Statistical Analyses and Modelling**

### **5.2.2.1. Exploratory Data Analysis**

Exploratory data analysis (EDA) is an important preliminary step of statistical analysis (Zuur et al. 2010; Borcard et al. 2011). Exploratory data analysis enables an appreciation of the distribution of variables and their relationships, and the detection of violations that would render an analysis unreliable as its assumptions are not met by the data (Zuur et al. 2010). Data found not to conform to the assumptions of a proposed test can either be pre-treated to meet the assumptions (e.g. Sakuma et al. 1999; Lefebvre et al. 2002; Oliva et al. 2004) or a different, suitable statistical procedure may be employed (e.g. Ganias et al. 2007; Froeschke et al. 2013).

For the current study, histograms in conjunction with the Shapiro-Wilks test were used to examine the normality and homoscedasticity of continuous and discrete variables, i.e., host size (standard length), the abundance of macroscopic parasites and the richness of

infracommunities. Ontogenetic variation in infracommunity richness and parasite abundance was explored by means of scatter plots while gender-specific, seasonal and regional differences were examined graphically through box and whisker plots. Overdispersion, the ratio of the variance to the mean, was computed for parasite abundance and parasite species richness.

#### **5.2.2.2. Host Sample Characteristics**

Given the importance of host characteristics as determinants of parasite infections in fishes (e.g. Amin 1985; Guégan et al. 1992; González et al. 2001; Zuo et al. 2016; Mackintosh et al. 2018), it was important to gain an appreciation of the variability in host size between sexes, regions and seasons to support interpretation of further analyses. Comparisons of host standard length (mm) between sexes and regions were achieved by employing the Mann-Whitney test and the Kruskal-Wallis test with post-hoc comparisons was used to detect seasonal variations as EDA revealed that host standard length (mm) was not normally distributed.

#### **5.2.2.3. Parasite Infection Indices**

Species accumulation curves which depict the recovery of new taxa as a function of sampling effort (Dove and Cribb 2006) were used to evaluate the completeness of parasite component communities recovered with respect to the number of snoek examined in the Northern and Southern Benguela. Rarefaction, the standardisation of species richness by sample size is a useful technique for comparing diversity in uneven samples (Gotelli and Colwell 2011). Rarefaction curves, which were generated via repeated resampling from the pool of hosts examined in one of the two regions (Gotelli and Colwell 2011), were used to determine the expected diversity from 20 host individuals in each regions.

Parasite infection levels were characterised by calculating the prevalence, mean abundance and mean intensity for each parasite taxon within each of the two regions. In accordance with Bush et al. (1997), prevalence is defined as the proportion of hosts examined infected by a particular parasite, mean abundance is the average number of parasites of a particular taxa per host in a given sample and mean infection intensity is defined as the average number of parasites per infected host in a sample.

#### **5.2.2.4. Parasite Species Richness**

Previous research has demonstrated that the richness of ichthyoparasite infracommunities, the number of parasite taxa infecting a host fish, may be influenced by host size, host diet, host ecology, seasonality as well as the geographic origin of hosts (Guégan et al. 1992; Sasal et al. 1997; Morand et al. 2000; Luque and Poulin 2007; Randhawa and Poulin 2010). In this study, the role of host size, sex, seasonality and host biogeographical origin as drivers of the richness of snoek infracommunities, excluding rare species (prevalence < 5%), was evaluated by means of generalised additive modelling (Hastie and Tibshirani 1986; Wood 2006).

Generalised additive models (GAMs) extend the Generalised Linear Model (GLM) proposed by Nelder and Wedderburn (1972) by allowing for non-linear relationships between the response and explanatory variables via the implementation of smooth functions (splines) of the predictor variables (Hastie and Tibshirani 1986; Wood 2006; Zuur et al. 2009). Since snoek are a shoaling species, specimens captured from the same shoal cannot be considered to be statistically independent and represent a form of pseudo-replication induced by the sampling protocol and the ecology of the host species examined. Such a violation of the independence of data can result in parameter overestimation (Thorson and Minto 2015). Generalised additive mixed models (GAMMs), which allow the specification of a random

effect to account for the lack of independence between hosts taken from the same shoal were therefore implemented (Zuur et al. 2009). The model included a smoothing spline for host size (SL), the categorical variables ‘sex’, ‘season’ and ‘region’ as parametric terms while ‘catch location’ (coded as latitude) was used as a random effect. The global GAMM model was of the form:

$$R(\chi_i) \sim \beta_0 + S_1(\text{SL}) + \text{Sex} + \text{Season} + \text{Region} + \alpha_i + \epsilon_i \quad \text{Equation 1}$$

where R is a link function,  $\chi_i$  represents the richness of snoek infracommunities,  $\beta_0$  denotes the intercept,  $S_1$  represents the smoothing function used,  $\alpha_i$  denotes the random effect included for catch location and  $\epsilon_i$  represents the error term. Model selection relied on Akaike’s Information Criterion (AIC), which is a function of the log-likelihood penalised for the number of covariates in the model (Dobson 2002; Fabozzi et al. 2014). Model selection was a two-step process; first the significance of the random effect was evaluated in the global model via AIC and secondly variables not accounting for a significant proportion of explained deviance were dropped in a stepwise fashion and competing models compared through AIC. The most appropriate model was indicated by the lowest AIC and models within 2 AIC were considered equivalent (Fabozzi et al. 2014). GAMMs evaluating the drivers of infracommunity richness assumed a Poisson error distribution and a logarithmic link function as richness exhibited a discrete distribution. An evaluation of the significance of sequentially added predictors in the final model was performed by analysis of deviance relying on F-tests (McCullagh and Nelder 1989). Lastly, predictions of species richness were conducted for each significant predictor variable to visualise the effect of the drivers of infracommunity richness in snoek of the Benguela ecosystem. Predictions with respect to host size were performed for each region separately for the range of host sizes examined while for predicting the effect of categorical variables, host size was set to the average size of

hosts examined (710 mm). Poisson GAMMs were implemented via the ‘`gamm`’ function of package ‘`mgcv`’ using the R statistical computing software (R Core Team 2018).

#### **5.2.2.5. Parasite Community Analyses**

Multivariate techniques were employed to assess and characterise the influence of host traits, seasons and environmental variability on parasite community structure. Permutational Analysis of Variance (PERMANOVA) was applied to assess variability in community structure with respect to host size classes, sex, seasons and biogeographic origin. Implemented through the ‘`adonis2`’ function which allowed the testing of marginal effects, PERMANOVA is appropriate for the analysis of ecological data as it is not dependent upon any statistical distribution but relies on permutation of the data for hypothesis testing (Anderson 2001). Anderson and Walsh (2013) however warn that the method is particularly susceptible to heterogeneity in multivariate dispersion across factor levels for unbalanced designs. Variability in multivariate dispersion across factor levels was therefore tested for significance using the ‘`betadisper`’ function. Sequential (Type I) sum of squares was employed since the number of snook examined differed across factor levels (unbalanced design) (Anderson et al. 2008). In order to account for the lack of statistical independence between hosts sampled from the same shoal, catch location (coded as latitude) was included as a random effect in the PERMANOVA analysis. Parasite taxa responsible for driving the variability in community structure detected by PERMANOVA were identified through Similarity Percentage (SIMPER) analysis. Patterns in parasite community structure were visualised by means of Non-metric multidimensional scaling (nMDS). The correlation between vectors of taxa identified by SIMPER and the nMDS ordination was examined through the ‘`envfit`’ function with 999 permutations. Vectors exhibiting significant correlations ( $p < 0.05$ ) were overlaid on the ordination to indicate the direction and

magnitude of their influence on parasite community structure. Multivariate analyses were supported by the ‘vegan’ R package (Oksanen et al. 2018).

In order to explore variability in infracommunity composition, the routines described above were first applied to a presence-absence transformed matrix consisting of all parasite taxa infecting more than 5% of hosts examined based on Jaccard’s dissimilarities and 999 permutations. The dataset was presence-absence transformed as the abundance of microscopic and encysted parasites could not be determined. Secondly, a subset comprising long-lived, larval endoparasite taxa whose abundance could be accurately determined (*Anisakis* spp., *M. uncinatus*, *H. trichiuri*, *C. australe*, *T. coryphaenae*, *B. vasculosum*, and *Pseudoterranova* sp.) was analysed as they are commonly employed as biological tags due to their long residence time in fish hosts (MacKenzie and Hemmingsen 2015). These analyses were conducted on Bray-Curtis dissimilarities of fourth root transformed abundance data and were based on 999 permutations.

#### **5.2.2.6. Biological Tag Selection and Modelling**

Potential biological tags for fish population studies have traditionally been selected from host species component communities according to the guidelines proposed and refined by several researchers (see Section 5.1.2). In the current study, the traditional selection procedure was applied but was also supported by the use of a classification method known as a ‘random forest’ (RF; Breiman 2001). Random forest is a non-parametric ensemble learning method which combines multiple classification trees generated by recursive binary partitioning of a bootstrap sample of the original data (Breiman 2001; Cutler et al. 2007). Only a subset of the explanatory variables included in the model is used for partitioning at each split in individual trees and trees are combined by majority voting (Breiman 2001; Cutler et al. 2007). Commonly employed multivariate classification techniques assess

variable importance indirectly by relying on statistical significance or Akaike's Information Criterion but RF uses cross-validation to estimate variable importance and thus allows a direct comparison of variable importance (Cutler et al. 2007). This method, which has been used in two previous fish population structure studies has shown promising results (Perdiguero-Alonso et al. 2008; Pérez-del-Olmo et al. 2010), and is here employed to identify parasites potentially allowing for discriminating between snoek caught in the northern and southern Benguela. The analysis was based on parasites whose abundances were recorded and rare species (prevalence < 5%) were excluded. Random forest analyses were conducted in the R programming environment using the 'randomForest' package (Liaw and Weiner 2002).

GAMMs were then employed to model the relationship between two parasite infection statistics (prevalence and abundance) of the proposed biological tags and predictor variables identified by bivariate exploratory data analysis. The global GAMMs used for both the prevalence and abundance analyses were of the form:

$$R(\chi_i) \sim \beta_0 + S_1(\text{SL}) + \text{Sex} + \text{Season} + \text{Region} + \alpha_i + \epsilon_i \quad \text{Equation 2}$$

and where R denotes the link function and  $\chi_i$  represents either prevalence or abundance.  $\beta_0$  denotes the intercept,  $S_1$  represents a smoothing function,  $\alpha_i$  denotes the random effect included for catch location and  $\epsilon_i$  represents the error term. Model selection procedures were AIC-based as described for modelling infracommunity species richness (see Section 5.2.2.3). GAMMs for prevalence and abundance both used a log link function but assumed a binomial and Tweedie error structure, respectively. Analysis of deviance used to evaluate the significance of predictor variables for binomial models utilised the  $\chi^2$  statistic and the deviance in Tweedie models was assessed by the F distribution. Binomial GAMMs were run

using the 'gamm4' function of the 'gamm4' package (Wood and Scheipl 2017) while Tweedie models were run using the 'gamm' function of the package 'mgcv' (Wood 2017).

Finally Random Forest was applied to estimate the rate of correct spatial classification of snoek based on each selected biological tag individually and when they are used in combination.

### **5.3. Results**

#### **5.3.1. Host Sample Characteristics**

Of the 349 snoek examined 190 were female and 159 male. The standard length (SL) of snoek differed significantly between male and female specimens in the Southern Benguela ( $W = 10786$ ,  $p = 0.0001262$ ) but not in the Northern Benguela ( $W = 892$ ,  $p = 0.6497$ ). In the Southern Benguela, female SL averaged  $757.9 \pm 137.09$  mm and males had a mean SL of  $701.6 \pm 143.56$  mm while. In the Northern Benguela females ( $633.7 \pm 103.45$  mm) were, on average, smaller than males ( $642.8 \pm 104.86$  mm) but the difference was not statistically significant. Snoek caught in the Southern Benguela ( $733.2 \pm 142.47$  mm) were significantly ( $W = 6051$ ,  $p < 0.00001$ ) larger than those from the Northern Benguela ( $638.3 \pm 103.66$  mm). Significant seasonal differences in SL were revealed by the Kruskal-Wallis test for snoek caught in the Southern Benguela ( $\chi^2 = 33.33$ ,  $df = 3$ ,  $p < 0.00001$ ) and in the Northern Benguela ( $\chi^2 = 57.01$ ,  $df = 2$ ,  $p < 0.00001$ ) (Fig. 5.2). In the Southern Benguela, the SL of fish caught in summer ( $680.2 \pm 94.66$  mm) did not differ from those sampled in autumn ( $696.6 \pm 125.21$  mm) but were smaller than those caught in winter ( $736.4 \pm 145.63$  mm) and spring ( $764.2 \pm 153.09$  mm). Post-hoc comparisons also revealed that snoek caught in spring were larger than those caught in autumn while no significant differences were found between winter and spring samples. For specimens sampled in the Northern Benguela, the summer ( $653.3 \pm 101.9$  mm) sample did not differ from any other season but autumn ( $572.6 \pm 39.88$  mm) samples were smaller than those caught in winter ( $761.2 \pm 70.94$  mm).

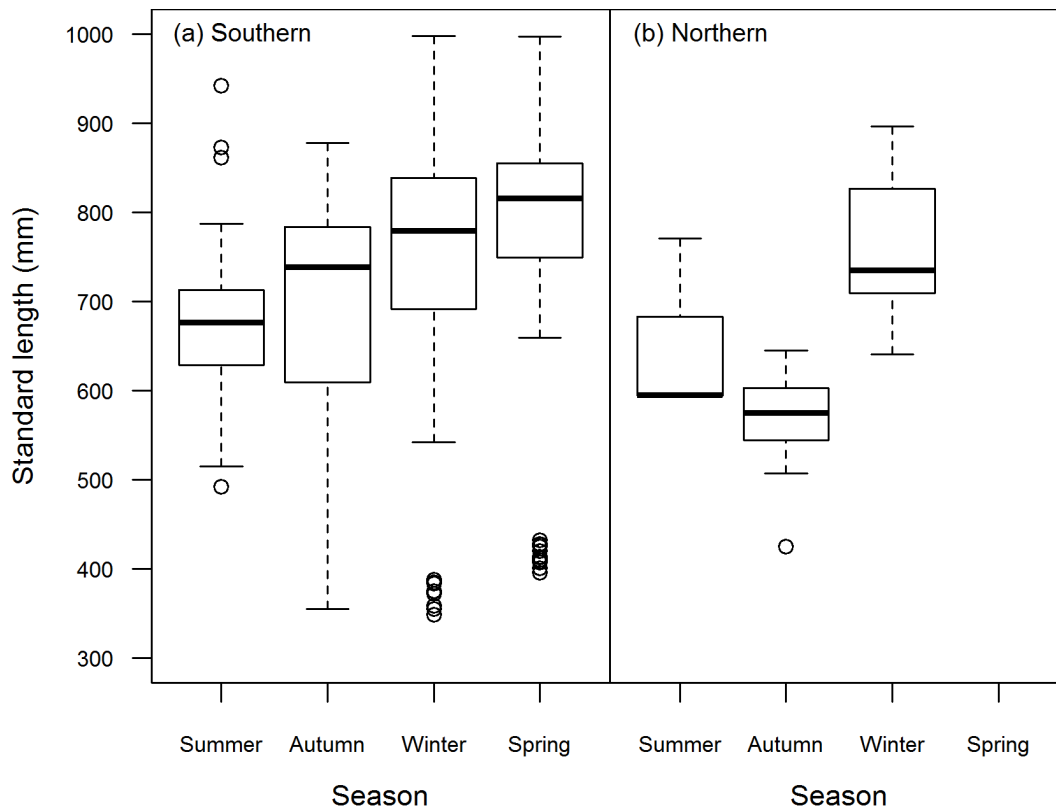


Figure 5.2. Seasonal variation in standard length of snoek caught in (a) the Southern Benguela and (b) the Northern Benguela ecosystem.

### 5.3.2. Parasite Assemblage

The parasite assemblage of snoek in the Benguela comprised 18 taxa representing 7 major parasite groups (Table 5.3). Of these, 13 were identified to species level, 3 to generic level, the monogenean could not be classified further than family level and the encysted digenean could only be assigned to order level. Fourteen taxa infected snoek in both biogeographic regions, 3 were unique to the Southern Benguela and *Caligus* sp. was only recorded from a single snoek in the Northern Benguela. Copepods were the most speciose parasite order in both regions, followed by the acanthocephalans and cestodes which were each represented by three species (Table 5.3). The parasite assemblage of snoek from the Northern Benguela included 12 new geographic records and one new host record while that

of the snoek from the Southern Benguela included 1 new geographic and host record (Table 5.3).

The species accumulation curve for the Northern Benguela showed that 13 of the 15 parasite taxa had been recovered from the first 39 snoek and the remaining 48 hosts yielded two new records (Fig 5.3a). For snoek of the Southern Benguela, the initial 75 specimens yielded 15 parasites and only two further taxa were found infecting the remaining 205 fish dissected (Fig 5.3b). For the Northern Benguela, both the species accumulation and rarefaction curves did not reach an asymptote indicating that further sampling would likely reveal more common and rare parasite taxa (Fig 5.3a). In contrast, the curves for the Southern Benguela tended to flatten out indicating that sampling was adequate to detect the diversity of parasites infecting snoek in this region (Fig 5.3b).

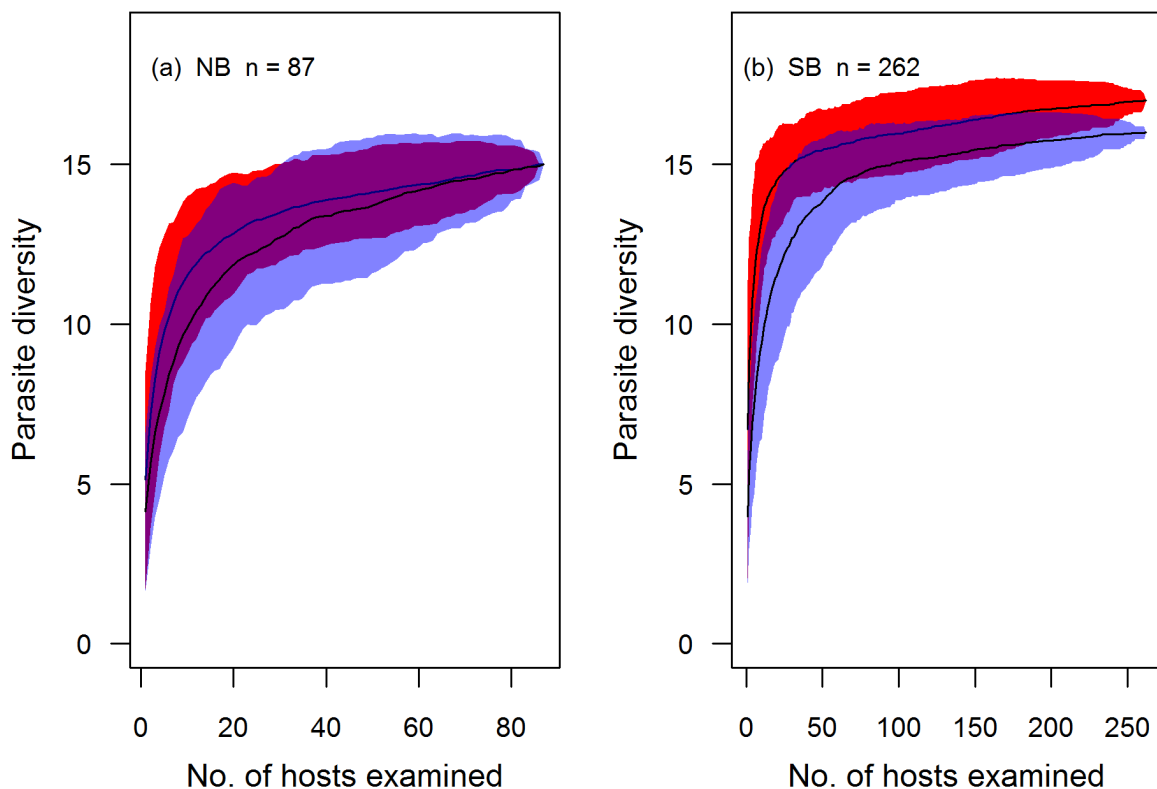


Figure 5.3. Species accumulation (red) and rarefaction (blue) curves showing the relationship between the number of snoek examined and the mean ( $\pm$  95% CI) diversity of parasites recovered in (a) the Northern Benguela and (b) the Southern Benguela.

Table 5.3. Taxonomic composition, site of infection, prevalence, mean abundance ( $\pm$  sd) and the abundance's range of the parasite assemblage of snoek (*Thyrsites atun*) caught in the Northern (NB, n = 87) and Southern (SB, n = 262) Benguela (BC: body cavity, M: muscle, GB: gall bladder, G: gills, O: operculum, N: nares, I: intestines, GA: gill arches, \*: new host record, †: new locality record).

Taxon	Site of Infection	Prevalence (%)		Mean abundance (SD)		Abundance Range	
		NB	SB	NB	SB	NB	SB
<b>Acanthocephala</b>							
<i>Bolbosoma vasculosum</i>	BC	8.1 †	7.6	0.1 ( $\pm$ 0.27)	0.1 ( $\pm$ 0.43)	0 - 1	0 - 3
<i>Corynosoma australe</i>	BC	20.7 †	34.4	4.0 ( $\pm$ 11.37)	9.8 ( $\pm$ 31.86)	0 - 61	0 - 277
<i>Rhadinorhynchus cadenati</i>	I	40.2 †	7.3	2.4 ( $\pm$ 8.40)	0.1 ( $\pm$ 0.46)	0 - 61	0 - 3
<b>Cestoda</b>							
<i>Hepatoxylon trichiuri</i>	BC	32.2	43.5	0.8 ( $\pm$ 1.46)	1.4 ( $\pm$ 2.55)	0 - 6	0 - 17
<i>Molicola uncinatus</i>	M	97.7 †	82.8	24.2 ( $\pm$ 29.35)	25.7 ( $\pm$ 31.70)	0 - 178	0 - 183
<i>Tentacularia coryphaenae</i>	BC	1.1 †	21.4	0.01 ( $\pm$ 0.11)	0.7 ( $\pm$ 2.26)	0 - 1	0 - 24
<b>Copepoda</b>							
<i>Caligus coryphaenae</i>	O	0.0	0.4	0	0.004 ( $\pm$ 0.06)	0	0 - 1
<i>Caligus dakari</i>	G/O	19.5 †	55.0	0.3 ( $\pm$ 0.75)	2.8 ( $\pm$ 4.59)	0 - 3	0 - 33
<i>Caligus zeii</i>	G/O	0.0	18.3	0	0.5 ( $\pm$ 1.84)	0	0 - 23
<i>Caligus</i> sp.	O	1.1	0.0	0.01 ( $\pm$ 0.11)	0	0 - 1	0
<i>Hatschekia conifera</i>	G	37.9 †	44.3	0.5 ( $\pm$ 0.88)	1.6 ( $\pm$ 3.39)	0 - 5	0 - 31
<i>Nothobomolochus fradei</i>	N	90.8 †	93.1	6.9 ( $\pm$ 8.82)	14.0 ( $\pm$ 15.84)	0 - 44	0 - 85
<b>Digenea</b>							
Digenea sp.	GA	0.0	32.8	N/A	N/A	N/A	N/A
<b>Monogenea</b>							
Diclidophoridae sp.	G	11.4 * †	0.8 * †	0.2 ( $\pm$ 0.59)	0.007 ( $\pm$ 0.09)	0 - 3	0 - 1
<b>Myxozoa</b>							
<i>Ceratomyxa minuta</i>	GB	6.9 †	6.9	N/A	N/A	N/A	N/A
<i>Kudoa thyrsites</i>	M	62.1 †	92.7	N/A	N/A	N/A	N/A
<b>Nematoda</b>							
<i>Anisakis</i> sp.	BC	80.5	98.5	35.2 ( $\pm$ 109.47)	126.5 ( $\pm$ 163.54)	0 - 937	0 - 1173
<i>Pseudoterranova</i> sp.	BC	6.9 †	13.7	0.2 ( $\pm$ 0.65)	0.6 ( $\pm$ 1.82)	0 - 4	0 - 13

### 5.3.3. Parasite Species Richness

The AIC-driven model selection indicated that a GAMM only including ‘season’ as a fixed effect and a smooth term for the host size (SL) as predictor variables was the most adequate to model snoek infracommunity richness. Analysis of deviance indicated that host SL was significantly correlated with infracommunity richness ( $F = 82.82$ ,  $edf = 1$ ,  $p < 0.00001$ ) which also varied seasonally ( $F = 3.132$ ,  $df = 3$ ,  $p = 0.0258$ ). The model accounted for 54.4% of the variation in the data and predicted a non-linear, positive relationship between infracommunity richness and host standard length (Fig. 5.4a). The overlap in error bars for seasonal predictions suggests that seasonal variation in infracommunity richness was negligible (Fig. 5.4b).

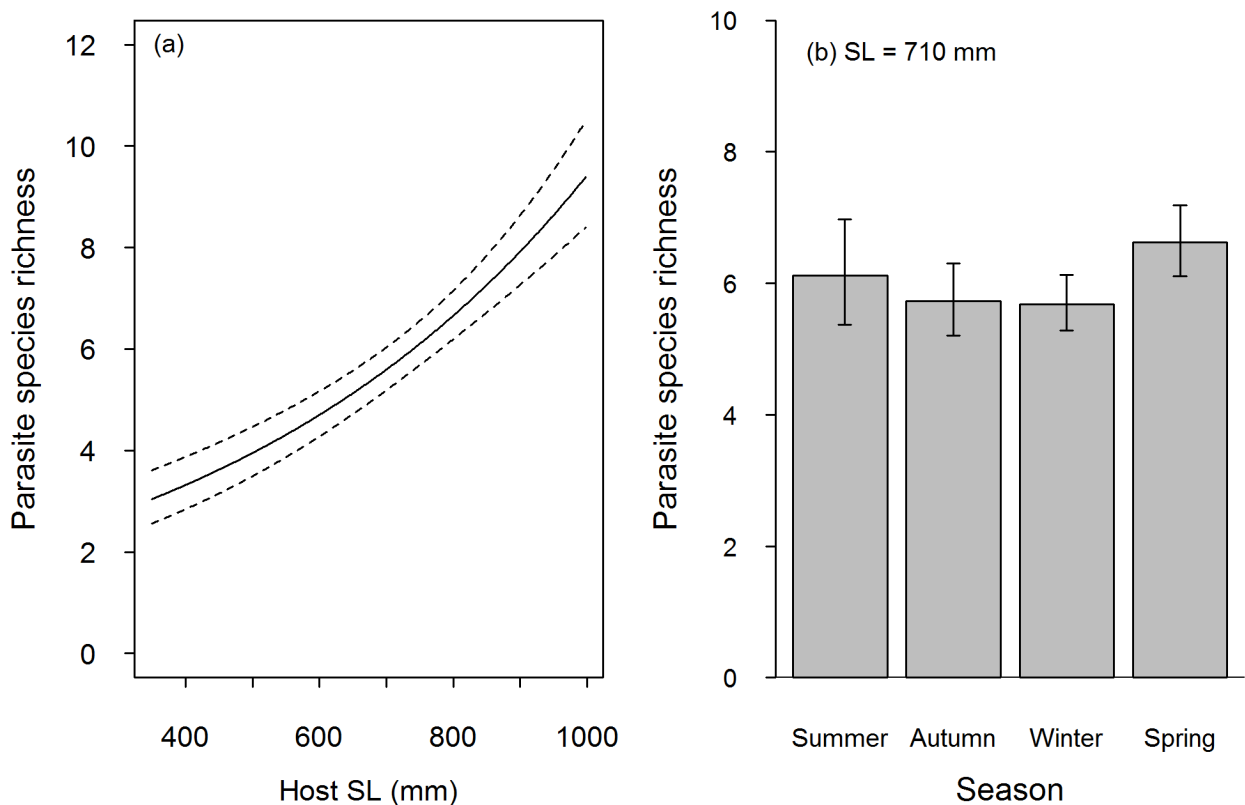


Figure 5.4. (a) The predicted relationship between host standard length and the infracommunity richness ( $\pm 95\%$  CI), (b) the predicted seasonal variation in infracommunity richness ( $\pm 95\%$  CI) of snoek caught in the Benguela ecosystem.

### 5.3.4. Parasite Community Analyses

#### 5.3.4.1. Infracommunity

PERMANOVA revealed that the structure of snoek infracommunities exhibited significant ontogenetic, seasonal and spatial variability (Table 5.4). However, significant differences in multivariate dispersion were detected between host size classes ( $F = 7.0305$ ,  $df = 6$ ,  $p < 0.0001$ ), seasons ( $F = 3.3914$ ,  $df = 3$ ,  $p = 0.01822$ ) and regions ( $F = 4.3103$ ,  $df = 1$ ,  $p = 0.03862$ ) and may have caused Type I errors in the PERMANOVA analysis.

Table 5.4. Results of the PERMANOVA for presence-absence transformed infracommunities of snoek caught in the Benguela ecosystem.

Variable	df	SS	R <sup>2</sup>	Pseudo-F	p(perm)
Size classes	6	6.556	0.131	10.107	0.001 ***
Sex	1	0.094	0.002	0.8718	0.537
Season	3	2.018	0.040	6.2212	0.001 ***
Region	1	1.395	0.028	12.9029	0.001 ***

$p < 0.05$  \*,  $p < 0.01$  \*\*,  $p < 0.001$  \*\*\*

Host size explained 13.1% of the variation in infracommunity structure. Vector fitting demonstrated that the ontogenetic shift in parasite community was driven by an increase in the prevalence of *H. trichiuri* and *C. australei* in larger hosts (Fig 5.5a). The factors sex, season and region only accounted for a small amount of the variation in the data (Table 5.3) and this was evident in the nMDS ordinations which showed large overlaps between clusters representing different sexes (Fig 5.5b), regions (Fig 5.5c) and seasons (Fig 5.5d).

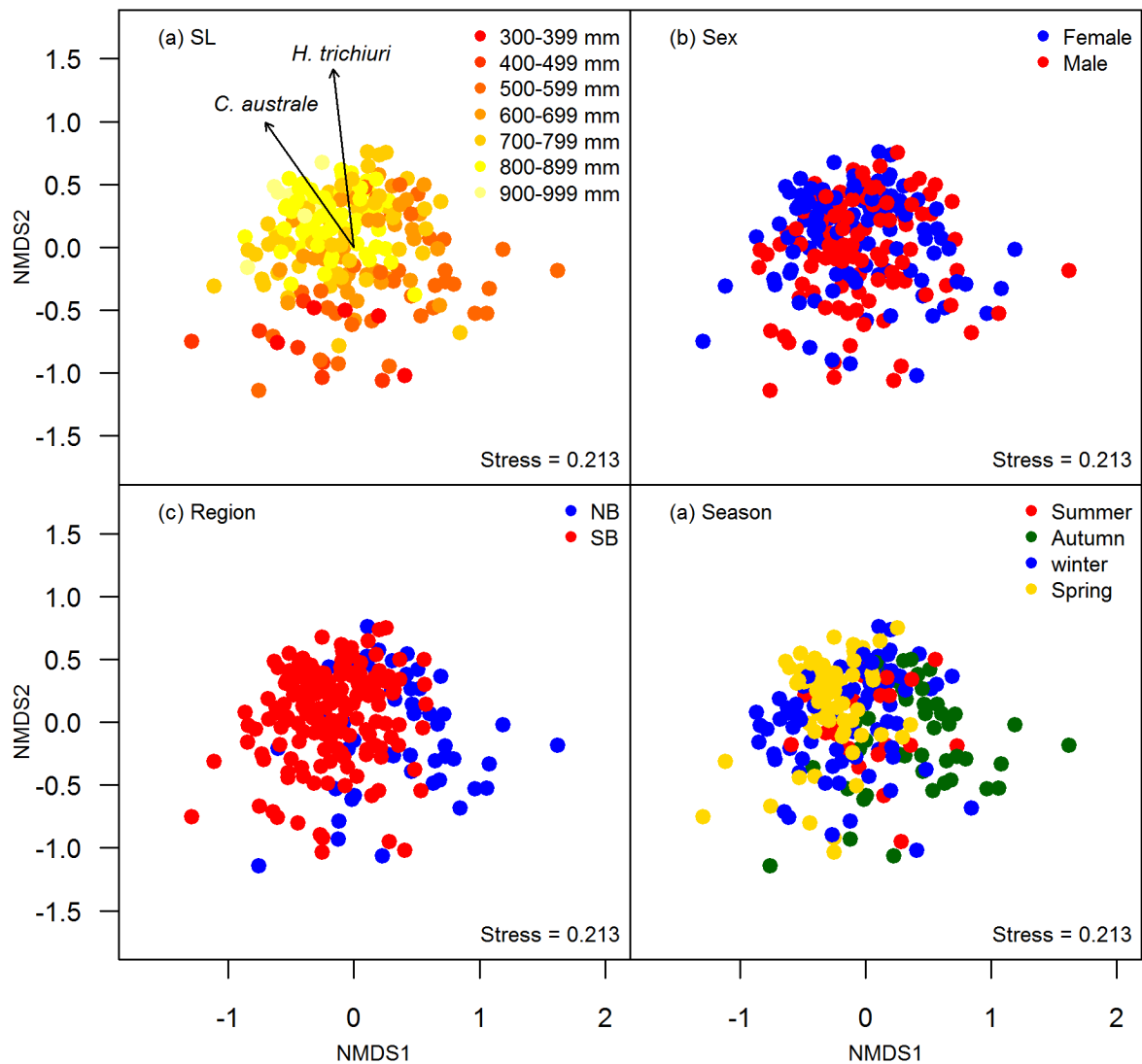


Figure 5.5. nMDS ordinations of presence-absence transformed infracommunities of snoek showing (a) ontogenetic, (b) gender specific, (c) spatial and (d) seasonal variation in parasite community structure.

### 5.3.4.2. Long-Lived Larval Parasites

PERMANOVA indicated that endoparasite communities varied with host size, seasons and across regions (Table 5.5). Significant differences in multivariate dispersion which may have affected the results of PERMANOVA were found across host size classes ( $F = 4.8274$ ,  $df = 6$ ,  $p =$

0.0000959) but not between sexes ( $F = 0.1328$ ,  $df = 1$ ,  $p = 0.7158$ ), seasons ( $F = 0.5285$ ,  $df = 3$ ,  $p = 0.663$ ) and regions ( $F = 3.2487$ ,  $df = 1$ ,  $p = 0.07236$ ).

Table 5.5. Results of the PERMANOVA for fourth-root transformed long-lived, larval endoparasite communities of snoek caught in the Benguela ecosystem.

Variable	df	SS	R <sup>2</sup>	Pseudo-F	p(perm)
Size classes	6	9.878	0.289	31.5198	0.001 ***
Sex	1	0.029	0.0008	0.5519	0.654
Season	3	1.135	0.033	7.2421	0.001 ***
Region	1	1.457	0.043	27.8987	0.001 ***

$p < 0.05$  \*,  $p < 0.01$  \*\*,  $p < 0.001$  \*\*\*

Although heterogeneity in multivariate dispersion may have affected PERMANOVA, the nMDS ordination and vector fitting (Fig. 5.6a) showed that increasing abundance of anisakids, *M. uncinatus*, *C. australe* and *H. trichiuri* drive an ontogenetic shift in the endoparasite community structure of snoek. The biogeographic origin of hosts and seasonality only accounted for a small proportion of the variation in the data as demonstrated by the small R<sup>2</sup> values (Table 5.4) and the overlap between spatial and seasonal clusters (Fig. 5.6 c, d).

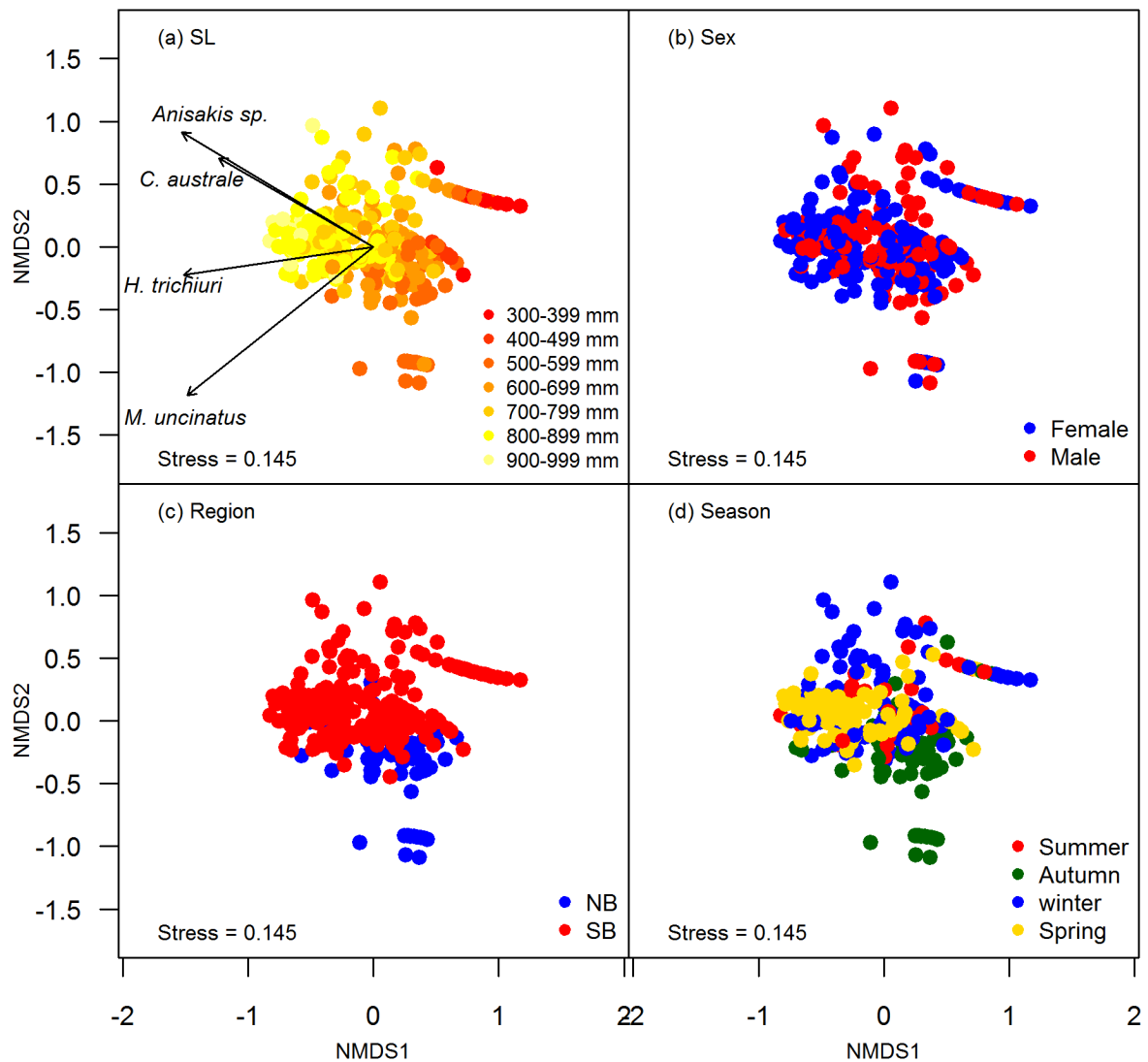


Figure 5.6. nMDS ordinations of fourth-root transformed long-lived, larval endoparasite communities of snoek showing (a) ontogenetic, (b) gender specific, (c) spatial and (d) seasonal variation in long-lived, larval endoparasite community structure.

### 5.3.5. Biological Tags

According to the biological tags selection guidelines, two parasite taxa, namely the nematode *Anisakis sp.* and the cestode *M. uncinatus*, had all the properties required for use as biological tags. This selection procedure was supported by the RF analysis which indicated that the same two taxa had the greatest ability to predict the biogeographic origin of snoek (Fig 5.7).

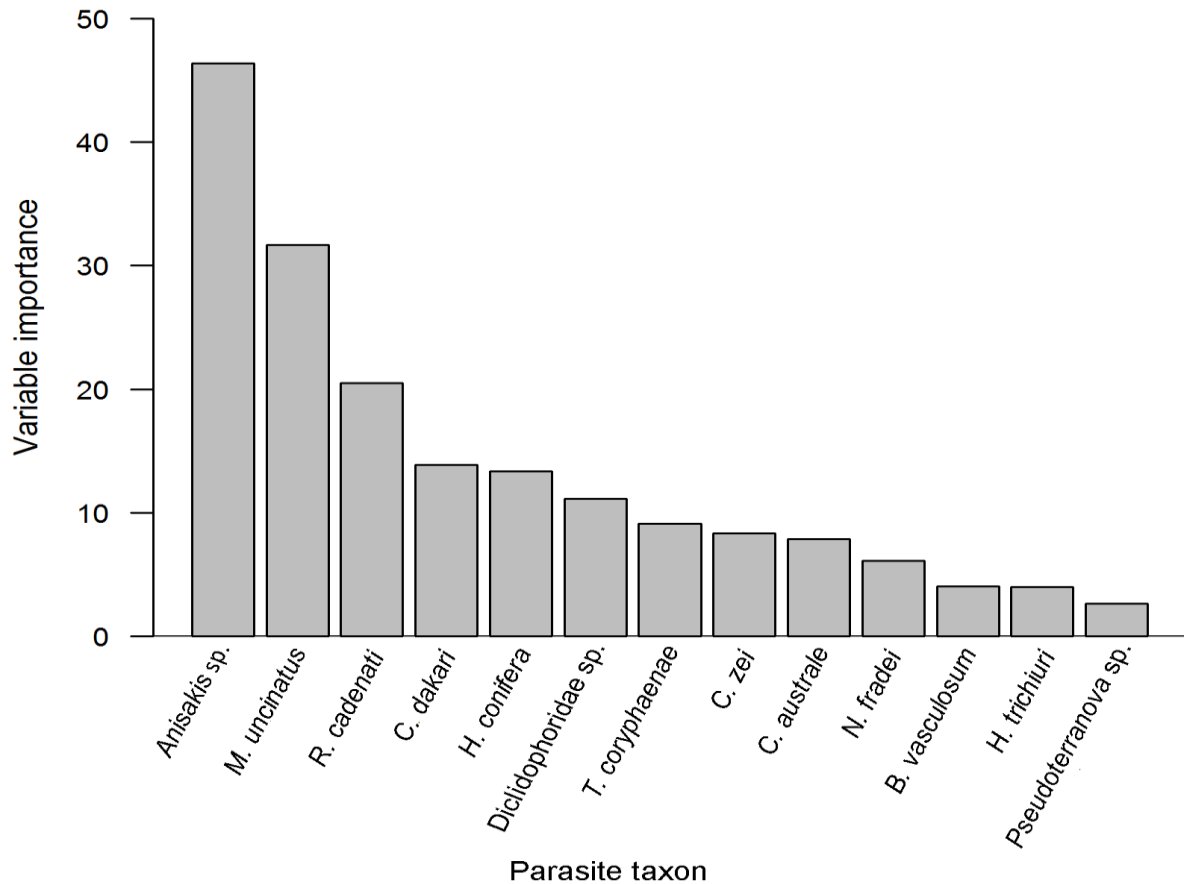


Figure 5.7. Variable importance plot indicating the ability of different parasite taxa to predict the biogeographic origin of snoek in the Benguela ecosystem.

### 5.3.5.1. *Anisakis* sp.

Model selection procedures for the binomial GAMM fitted to the presence-absence data of *Anisakis* sp. indicated that a model comprising a spline for host standard length and a parametric term ‘region’ was the most adequate. Analysis of deviance showed that host size was a significant predictor of *Anisakis* sp. prevalence in snoek of the Benguela and also revealed a spatial effect (Table 5.6). Overall, the model explained 23.9% of the variation in *Anisakis* sp. prevalence.

Table 5.6. Analysis of deviance for the binomial GAMM fitted to the presence-absence data of *Anisakis* sp. infecting snoek in the Benguela ecosystem. The degrees of freedom for parametric terms (df), estimated degrees of freedom for smooth terms (edf), reference degrees of freedom (Ref. df), the Chi-square statistic ( $\chi^2$ ) and its associated significance (p-value) are summarised.

Variable	df	edf	Ref. df	$\chi^2$	p-value
s(SL)		1	1	12.66	0.000373 ***
Region	1			13.94	0.000189 ***

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

The GAMM showed that prevalence was expected to increase with host size in both regions but that the effect was more pronounced for the Southern Benguela (Fig. 5.8a). In the Southern Benguela, 50% of snoek were infected at a standard length of 309.5 mm and in the Northern Benguela this level of infection was reached at 525 mm. No differences in prevalence were apparent in the spatial predictions (Fig. 5.8b); this was due to the fact that the large majority of snoek were infected by *Anisakis* sp. by the time they reach the mean size of the sample (710 mm).

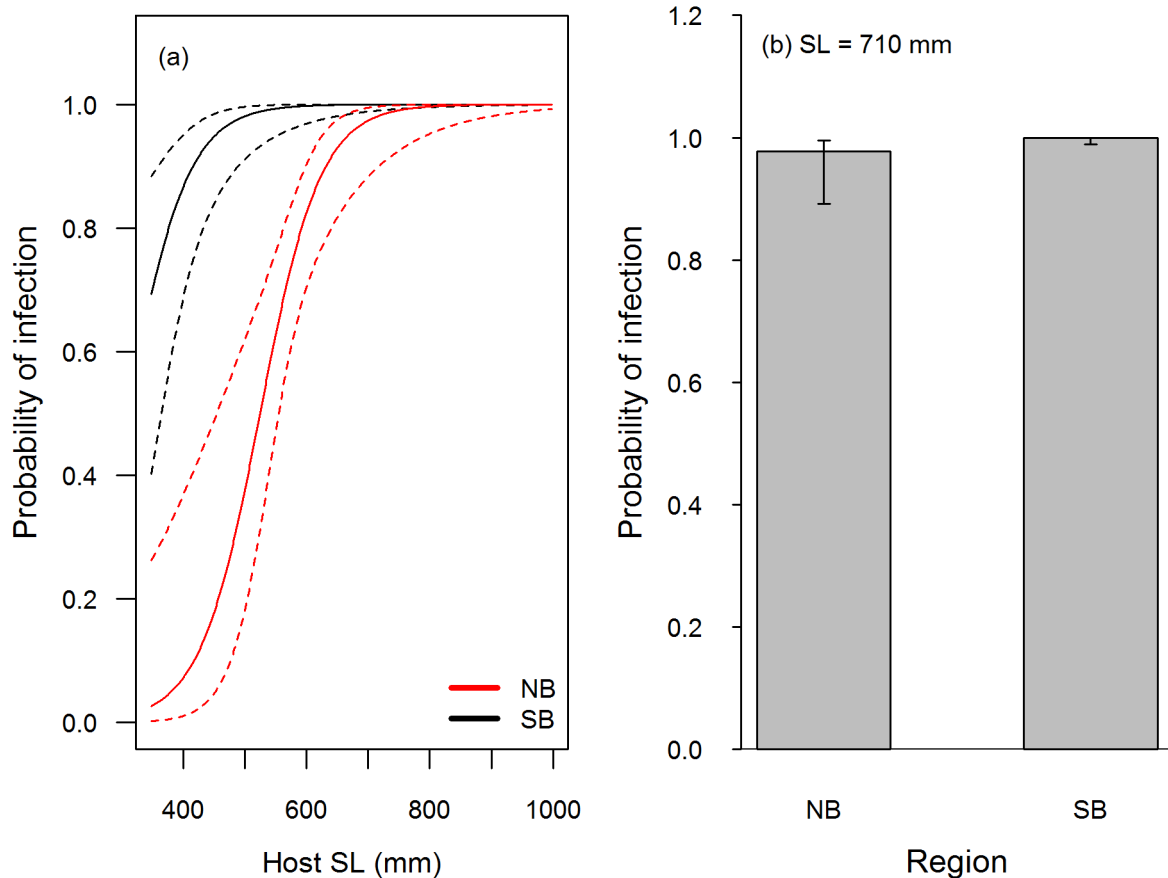


Figure 5.8. (a) The predicted relationship between host standard length and the prevalence of *Anisakis* sp. ( $\pm$  95% CI) and (b) the spatial variation in the prevalence of *Anisakis* sp. ( $\pm$  95% CI) infecting snoek caught in the Benguela ecosystem.

The most parsimonious model selected by AIC for modelling *Anisakis* sp. abundance included a combination of the terms 's(sl)', 'season', 'region' which together accounted for 38.8% of the variation in anisakid abundance (Table 5.7). The size of *Anisakis* sp. infrapopulations of Benguela snoek was expected to increase with increasing host size in both regions (Fig. 5.9a). However, the model predicted that irrespective of size, snoek caught in the Northern Benguela harboured less anisakids than their counterparts from the Southern Benguela (Fig 5.9a, b). The GAMM predicted that the mean abundance of anisakids infecting snoek decreased from summer through to spring and that the effect was consistent across regions (Fig. 5.9c).

Table 5.7. Analysis of deviance for the Tweedie GAMM fitted to the abundance of *Anisakis* sp. infecting snoek in the Benguela ecosystem. The degrees of freedom for parametric terms (df), estimated degrees of freedom for smooth terms (edf), reference degrees of freedom (Ref. df), the F statistic (F) and its associated significance (p-value) are summarised.

Variable	df	edf	Ref. df	F	p-value
s(SL)		1	1	294.8	< 0.00001***
Season	3			3.695	0.012141 *
Region	1			12.113	0.000565 ***

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

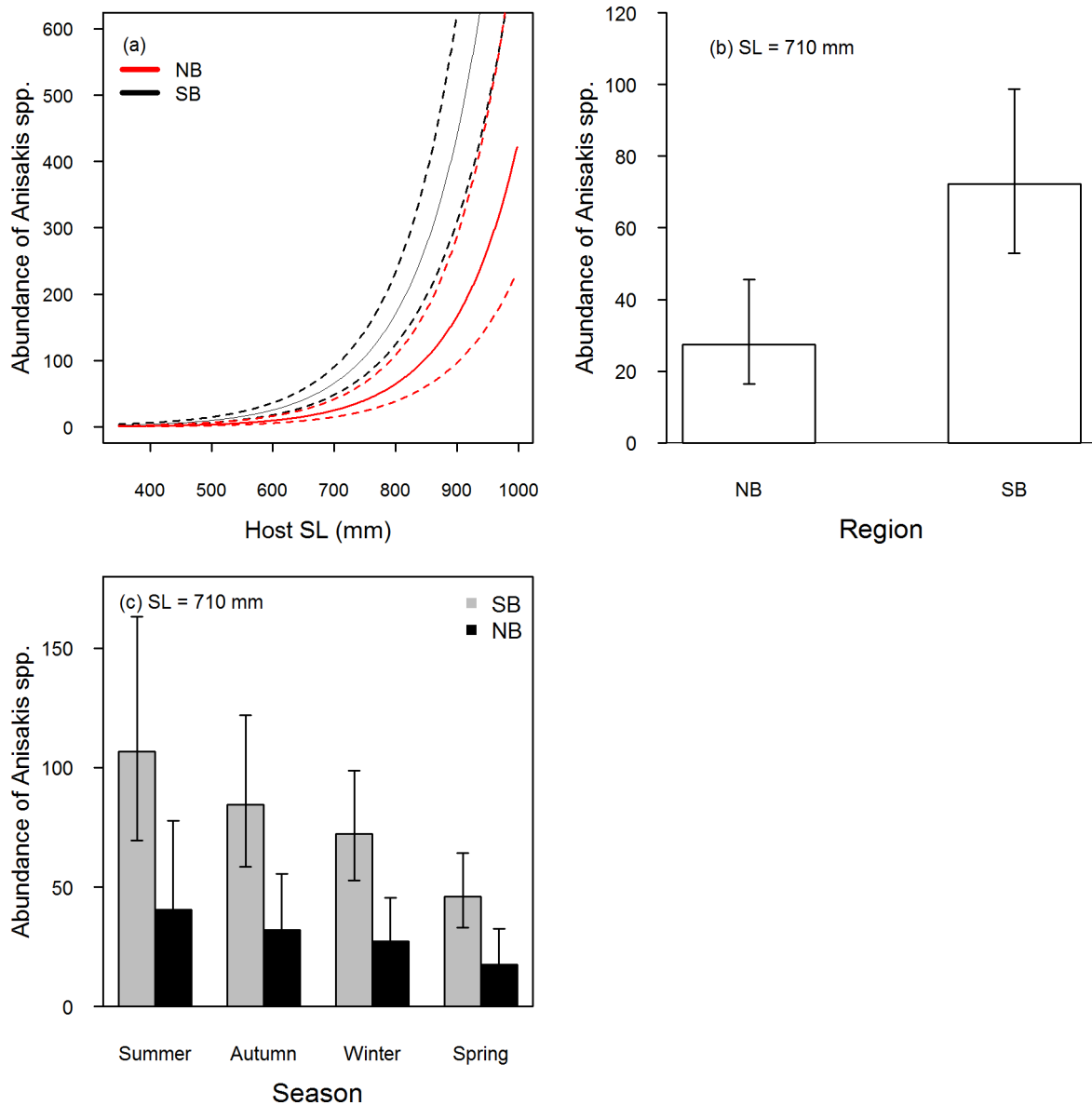


Figure 5.9. (a) The predicted relationship between host size and mean ( $\pm$  95% CI) *Anisakis* sp. abundance in both regions, (b) the spatial and (c) the seasonal variation in the abundance of *Anisakis* sp. infecting snoek in both regions.

### 5.3.5.2. *Molicola uncinatus*

Akaike's Information Criterion indicated that a model explaining 36.2% of the variation and consisting of a smooth term for host size and the parametric term 'region' was the best to predict the prevalence of *M. uncinatus* in snoek. Analysis of deviance identified host size as a significant

predictor of the presence or absence of *M. uncinatus* in snoek and also revealed a spatial effect (Table 5.8).

Table 5.8. Analysis of deviance for the binomial GAMM fitted to the presence-absence data of *Molicola uncinatus* infecting snoek in the Benguela ecosystem. The degrees of freedom for parametric terms (df), estimated degrees of freedom for smooth terms (edf), reference degrees of freedom (Ref. df), the Chi-square statistic ( $\chi^2$ ) and its associated significance (p-value) are summarised.

Variable	df	edf	Ref. df	$\chi^2$	p-value
s(SL)		1	1	37.35	< 0.00001 ***
Region	1			5.55	0.0185 *

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

Snoek standard length was predicted to exhibit a positive correlation with the probability of acquiring *M. uncinatus* but the effects differed spatially (Fig. 5.10a). The model showed that snoek in the Northern Benguela were more susceptible to infection by *M. uncinatus* than snoek from the Southern Benguela. Although analysis of deviance indicated a spatial effect on *M. uncinatus* prevalence, predictions for hosts of average size did not show a marked difference in the probability of infection of snoek by *M. uncinatus* (Fig. 5.10b).

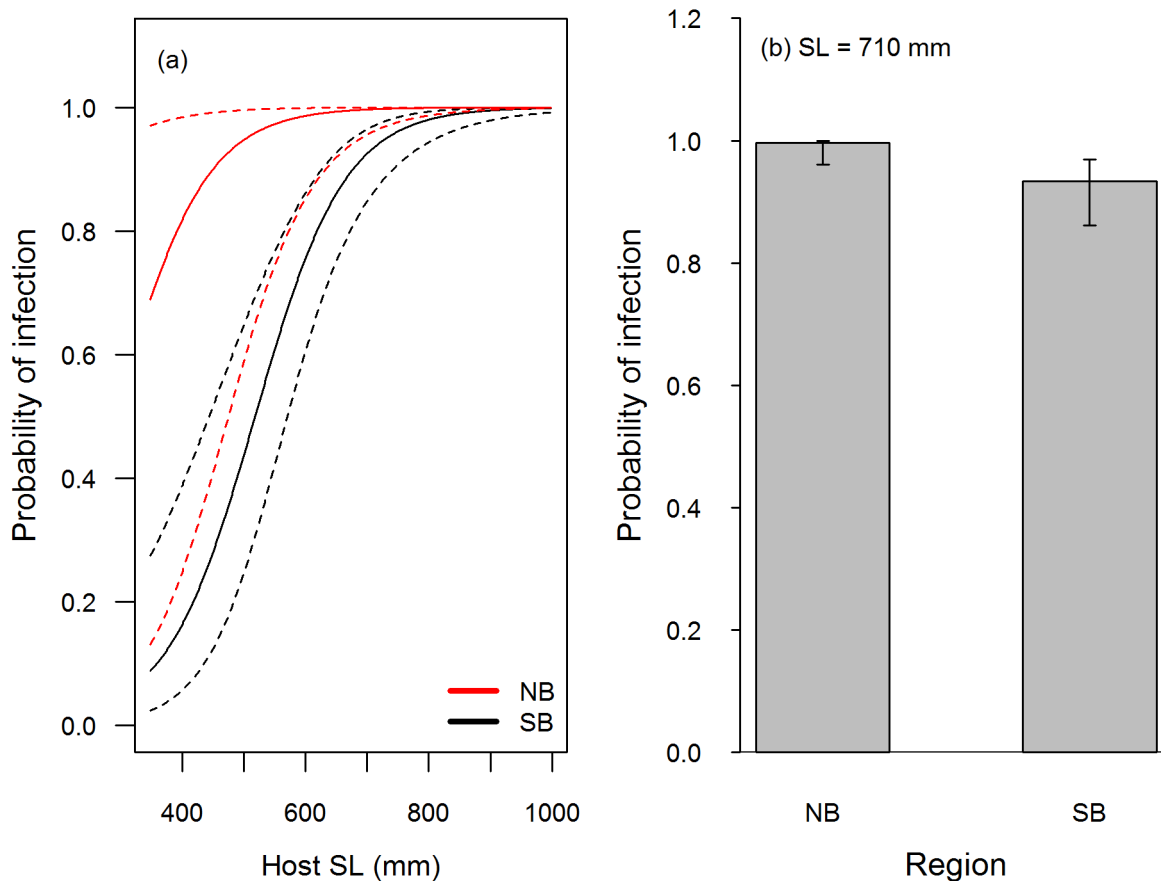


Figure 5.10. (a) The predicted relationship between host standard length and the prevalence of *M. uncinatus* ( $\pm$  95% CI) and (b) the spatial variation in the prevalence of *M. uncinatus* ( $\pm$  95% CI) infecting snoek caught in the Benguela ecosystem.

AIC-based model selection indicated that the abundance of *M. uncinatus* in snoek was best modelled by a GAMM comprising the parametric term ‘region’ and a smooth term for host size. The model explained 23.4% of the variation in the abundance data and showed that there was a significant ontogenetic and spatial effect on the abundance of *M. uncinatus* (Table 5.9). Irrespective of host standard length, a higher abundance of *M. uncinatus* was expected in snoek of the Northern Benguela compared to fish caught in the Southern Benguela (Fig 5.11 a, b).

Table 5.9. Analysis of deviance for the Tweedie GAMM fitted to the abundance of *Molicola uncinatus* infecting snoek in the Benguela ecosystem. The degrees of freedom for parametric terms (df), estimated degrees of freedom for smooth terms (edf), reference degrees of freedom (Ref. df), the F statistic ( $\chi^2$ ) and its associated significance (p-value) are summarised.

Variable	df	edf	Ref. df	F	p-value
s(SL)		1	1	314.3	< 0.00001 ***
Region	1			6.113	0.0139 *

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

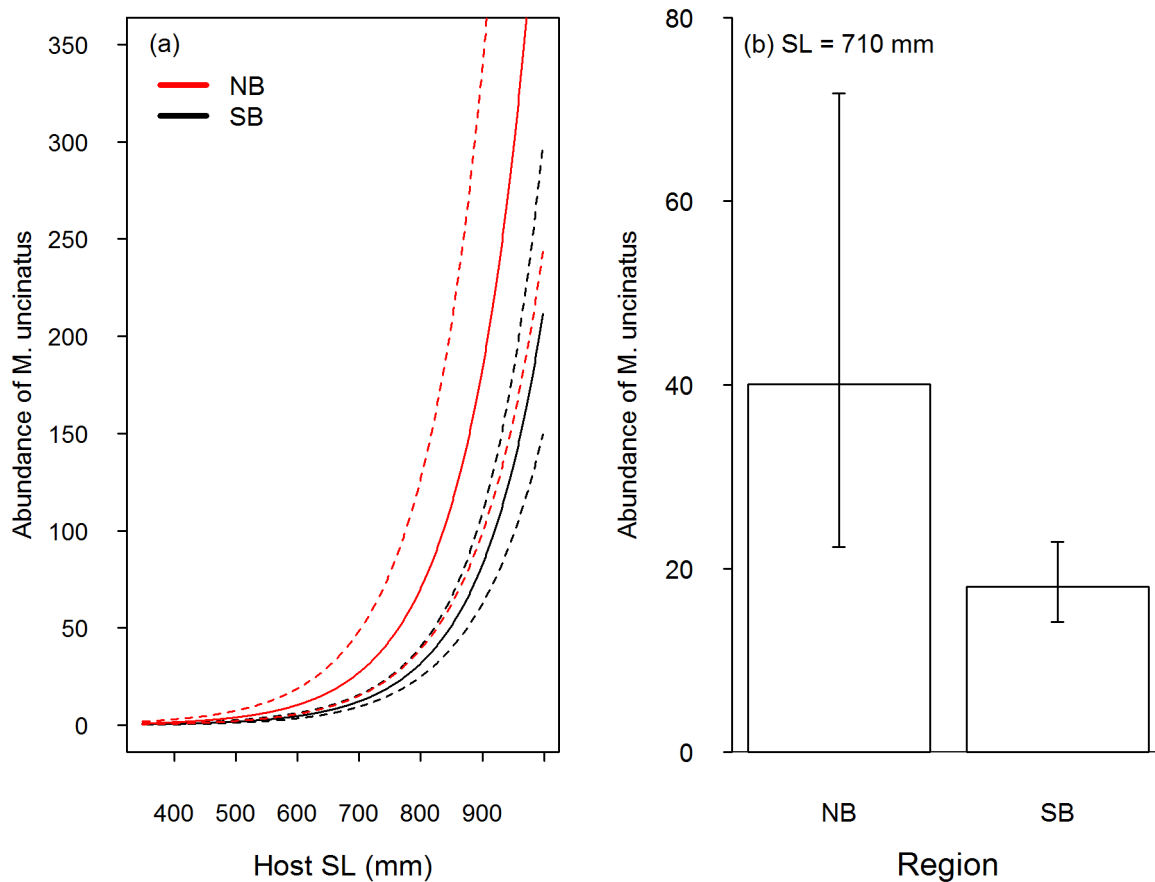


Figure 5.11. (a) The predicted relationship between host standard length and the mean ( $\pm$  95% CI) abundance of *Molicola uncinatus* and (b) the spatial variation in the mean ( $\pm$  95% CI) abundance of *M. uncinatus* infection snoek in the Benguela.

### **5.3.5.3. Classification based on Biological Tags**

The Random Forest analysis based on *Anisakis* sp. only yielded a correct classification rate of 54% and 84.7% for the Northern Benguela and Southern Benguela respectively. When considering *M. uncinatus*, the rate of correct classification for the Northern Benguela dropped to 29.9% while 84% of the Southern Benguela fish were correctly assigned to their region of origin. When used in combination, the biological tags improved the correct classification rate of Northern Benguela snoek to 63.2% and that of hosts from the Southern Benguela to 93.5%.

## **5.4. Discussion**

In the last decade, marine parasitology has contributed to better our understanding of the biodiversity and ecology of the Benguela ecosystem (Nunkoo et al. 2016, 2017) and has also been integrated in fisheries management in South Africa (Reed et al. 2012; van der Lingen et al. 2015; Weston et al. 2015). This study, which focused on the parasites of snoek, *Thyrsites atun*, exploited the intimate relationship between parasites and their hosts as a means of gaining an insight into the host-parasite relationships and ecology of this economically (Griffiths 2002; Isaacs 2013; DAFF 2016), ecologically (Verheye and Richardson 1998; Pecquerie et al. 2004) and culturally (Norton 2013) important fish species in the Benguela ecosystem.

### **5.4.1. Parasite Community of Snoek in the Benguela**

#### **5.4.1.1. Component Community Composition**

Community structure is a multi-faceted feature of biological communities and can be studied at various spatial and temporal scales as well as at different hierarchical levels of its organisation. Parasite communities exhibit a hierarchical organisation where infracommunities are nested within component communities themselves being a subset of the supracommunity (Bush et al. 1997). The composition of the component community of a host population is driven by its

evolutionary history, its life history parameters as well as ecosystem-level biotic and abiotic features, which together determine its susceptibility to different parasite taxa (Timi and Poulin 2003; Alarcos and Timi 2012).

Snoek sampled off South Africa, i.e. in the Southern Benguela, harboured a more diverse parasite component community than snoek from the Northern Benguela. The absence of *C. zei* from the Northern Benguela snoek may be due to seasonal variability in the availability of its infective stages while that of *C. coryphaenae* might be explained by the fact that it is considered to be an accidental infection due to its affinity for scombrid hosts (Cressey 1991; Nunkoo 2015). On the other hand, the absence of the encysted digenean metacercariae in snoek of the Northern Benguela may be a consequence of its lifestyle. The life cycle of marine digeneans typically involves a mollusc as first intermediate host, a fish second intermediate host and the final host may be a predatory fish or marine bird (Cribb 2005). In the present case, where snoek act as second intermediate host, the digenean's absence may be attributed to a lack of suitable first or final hosts in the Northern Benguela. This situation would prevent the transmission and persistence of this parasite in the Northern Benguela. However, the absence of these taxa from the parasite assemblage of Northern Benguela snoek may also be an artefact of the smaller sample size of fish examined as the species accumulation and rarefaction curves (Fig 5.3a) indicated that further surveys are recommended. Nonetheless, the majority of parasite taxa infected snoek from both biogeographic regions (Table 5.3) indicating that their endemic areas straddled both the Northern and the Southern Benguela.

#### **5.4.1.2. Infracommunity Richness**

Species richness is a simple yet fundamental and commonly employed measure of the diversity of biological communities (Gotelli and Colwell 2001; Fleishman et al. 2006). One advantage of species richness over other diversity metrics such as Simpson's diversity index is that

it does not take into account relative abundances and is therefore suited to the analysis of data sets comprised of both abundance and presence/absence data (Heip et al. 1998; Morris et al. 2014). Infracommunity richness, a function of the exposure and susceptibility of individual hosts to parasite infective stages, has generally been associated with host traits such as ontogeny, diet, condition, sex and distribution range as well as seasonality (e.g. Poulin 2004; Timi et al. 2010; Violante-González et al. 2010; Muñoz and Randhawa 2011; Losee et al. 2014). However, general laws governing the species richness of infracommunities still elude parasitologists (Poulin 2004, 2007b).

Parasite species richness of snoek of the Southern Benguela is known to exhibit an ontogenetic increase (Nunkoo et al. 2016). The current study demonstrated that this effect is independent of the biogeographic origin of hosts and suggests that irrespective of host size the ‘carrying capacity’, i.e. the number of parasite taxa an individual host can harbour, of snoek as a host does not vary in the Benguela ecosystem. As a host individual grows, it presents a larger target for parasite attachment and has been exposed to parasites for a longer period of time, thus increasing the probability of colonisation by parasite taxa (Poulin 2004; Soares et al. 2014). Ontogenetic shifts in a host’s ecology may also contribute to the diversification of its parasite assemblage (Timi et al. 2010; Muñoz and Zamora 2011). In the Benguela snoek recruit in inshore nursery areas and expand their range into offshore areas as they reach maturity (Griffiths 2002). Such a broadening of their distribution may expose them to parasites not present in the nursery areas and contribute to the observed increase in the richness of their parasite assemblages. The ontogenetic shift in the diet of snoek could also contribute to the observed increase in parasite species richness (Griffiths 2002). A wider diet in conjunction with the ingestion of larger quantities of prey would make larger snoek more susceptible to trophically transmitted parasite taxa.

## **5.4.2. Parasite Community Structure**

### **5.4.2.1. Infracommunity Structure**

The structure of parasite infracommunities results from the acquisition and loss of parasites during an individual host's lifespan. Several factors such as host traits, geographic origin, depth and seasonality are known to influence ichthyoparasite community structure (e.g. Míguez-Lozano et al. 2012; Santoro et al. 2014; Pérez-i-garcía et al. 2015). Infracommunities of snoek exhibited a slight shift in community structure with increasing host size. This change was driven by an increase in the prevalence of trophically transmitted taxa (*H. trichiuri*, *C. australe*) in larger snoek and suggests that the ontogenetic shift in the diet of snoek (Griffiths 2002) plays a role in infracommunity variability by increasing the probability of infection by these two taxa. A high prevalence of the copepod *C. dakari* was also indicative of the infracommunity of larger snoek. This effect might be attributable to the fact that larger specimens are more easily infected by free-living infective stages or that the wider movement patterns of adult snoek (Griffiths 2002) improved chances of infection. However, the second hypothesis is less plausible as *C. dakari* is known to have a wide distribution spanning inshore and offshore environments in the Benguela ecosystem (Nunkoo 2015). Although multivariate analyses suggested both a seasonal and a biogeographic effect on infracommunity structure, ordinations revealed that these effects were negligible. This result indicates that snoek in the Northern and Southern Benguela are exposed to the same suite of parasites throughout the year.

### **5.4.2.2. Long-Lived, Larval Parasite Guild Structure**

This guild of parasites was exclusively comprised of taxa relying on predator-prey interactions for transmission and whose residence time in the host exceeds the length of the study. Such an assemblage might potentially be useful at discriminating between host populations (Lester and MacKenzie 2009). However, although the PERMANOVA indicated strong support for seasonal and regional effects on community structure, the nMDS ordinations showed that the

parasite assemblages largely overlapped both in space and time and did not allow a delineation of snoek population. Nonetheless, ontogenetic variability driven by increases in the abundances of larval nematodes (*Anisakis* sp.), acanthocephalans (*C. australe*) and cestodes (*H. trichiuri*, *M. uncinatus*) was detected in the structure of this trophically transmitted assemblage. The increasing abundances of these taxa are most probably a consequence of the increased feeding activity, both in terms of diversity and quantity, of larger snoek (Griffiths 2002), as well as the accumulation of parasites over the host's life span (Nunkoo 2015; Gay et al. 2018).

#### **5.4.3. Biological Tags**

Patterns of parasite infections are a useful tool for the study of host population structure and ecology (e.g. Balbuena et al. 1995; MacKenzie and Longshaw 1995; Moore et al. 2003; Lester et al. 2009; Vasconcelos et al. 2017). Similarities and dissimilarities in infection patterns are equally informative; the former indicating that the hosts examined have similar exposure to particular parasites while the latter implies that the hosts exhibit differential susceptibility to parasites which results from differences in their ecology.

The results of criteria-based biological tag selection and Random Forest analysis concurred and indicated that *Anisakis* sp. and *M. uncinatus* were the best candidates for discriminating between snoek populations. The adult acanthocephalan *Rhadinorhynchus cadenati*, which was more prevalent and abundant in the Northern Benguela fish, was ranked as the third best candidate biological tag but was not considered due to its short residence time in fish hosts (Smith et al. 2005; Costa et al. 2013). Generalised Additive Mixed Models revealed spatial differences in both the prevalence and abundance of the two selected biological tags, namely *Anisakis* sp. and *M. uncinatus*. Such differences in parasite infestation levels may reflect ecosystem-level variability in their life-history traits, ecology and environment (Brattey et al. 1990; Timi and Lanfranchi 2009; Munster et al. 2015).

#### 5.4.3.1. *Anisakis* sp.

Nematodes of the widely distributed genus *Anisakis* have a complex life cycle including crustacean intermediate hosts while pinnipeds and cetaceans serve as final hosts (Anderson 2000). Anisakids also make use of fishes and squid as paratenic hosts to improve their persistence within an ecosystem as well as transmission rates to final hosts (Abollo et al. 1998; Anderson 2000; Strømnes and Andersen 2003). Of the nine taxa constituting this genus, six have been recorded in South African waters infecting fishes, squid and marine mammals (Mattiucci and Nascetti 2006, 2007). Snoek caught off South Africa are known to be susceptible to at least two of the anisakid taxa, namely *Anisakis pegreffii* and *Anisakis simplex* C (Mattiucci and Nascetti 2006; Nieuwenhuizen et al. 2006). Anisakids recovered during snoek dissections were not identified to species level for logistical and budgetary reasons as the use of molecular techniques is essential for their classification at the specific level (Mattiucci and Nascetti 2006).

The contrasting infection levels of *Anisakis* sp. between snoek caught in the Northern and Southern Benguela may be explained by ecological differences between the two regions. Since *Anisakis* sp. relies on predation events for transmission, the higher susceptibility of Southern Benguela snoek to this nematode may be due to spatial variability in the diet of snoek. However, the dearth of diet studies for snoek in the Northern Benguela precludes any comparisons and inferences with regards to diet composition. Spatial differences in *Anisakis* sp. infection rates in euphausiids, the major intermediate hosts of anisakids and a common prey of snoek (Marcogliese 1995; Anderson 2000; Griffiths 2002), could also account for the contrasting infection patterns found in snoek of the Northern and Southern Benguela. Although no studies have yet investigated parasite infestations in macro-zooplankton in the Benguela ecosystem, the lower abundance of odontocete cetacean final hosts in the Northern Benguela (Findlay et al. 1992) suggests that the availability of anisakid eggs and free-living propagules in this region is limited compared to the Southern Benguela. This would result in a lower prevalence and abundance of anisakids in

crustacean intermediate hosts in the Northern Benguela leading to lowered nematode infections in snoek. The seasonal trend predicted by the abundance model may have been caused by the difference in the size range of snoek examined in each season as a long-lived, larval parasite's abundance is not expected to vary seasonally.

Since anisakids were not identified to species level, the possibility that different *Anisakis* species infect snoek in the Northern and Southern Benguela and may have resulted in the observed spatial differences in infection levels should be considered. Although anisakids exhibit low specificity in their first crustacean intermediate hosts (e.g. Gregori et al. 2015), their abundance within a particular ecosystem might be dictated by the abundance of specific final hosts. A better understanding of anisakid diversity and distribution in the Benguela ecosystem would improve their value as biological tags.

#### **5.4.3.2. *Molicola uncinatus***

The trypanorhynch cestode *Molicola uncinatus* was described from *T. atun* in New Zealand and is one of three species within the genus (Robinson 1959, Horton et al. 2019). Although its life cycle has not been elucidated, adults have been recovered from the gastro-intestinal tract of thresher sharks (*Alopias vulpinus*) and plerocercoids infect teleosts as second intermediate hosts while it is hypothesised that pelagic crustaceans (e.g. euphausiids) serve as first intermediate hosts (Dollfus 1976; Love and Moser 1983; Marcogliese 1995; Gonzalez-Solis et al. 2013; Pollerspöck and Staube 2014). The current study demonstrated that infection levels of *M. uncinatus* varied spatially, both in terms of prevalence and abundance. Given the complex life cycle of *M. uncinatus* and its reliance on predation events for successful transmission, the trophic ecology of snoek as well as the distribution of intermediate and final hosts are suspected of playing a major role in determining infection levels.

As with anisakids, no plausible explanation with regards to the snoek's trophic ecology in the Benguela may be proposed due to the lack of diet studies of snoek in the Northern Benguela. First putative intermediate euphausiid hosts are widely distributed in both biogeographic regions and are therefore not thought to have a limiting effect on the transmission of *M. uncinatus* in either region (Barange et al. 1992). On the other hand, the abundance of final hosts (*Alopias vulpinus*) may differ spatially. Thresher sharks are not commercially targeted in the Benguela and there are no records of catches which would allow an estimation of its distribution within the Northern and Southern subsystems of the Benguela ecosystem (DAFF 2013). However, catch data for two commonly targeted pelagic sharks (*Isurus oxyrinchus* and *Prionace glauca*) suggest that sharks are more abundant in the Northern Benguela (BCC 2011). If thresher shark abundance follow the same pattern, their higher abundance in the Northern Benguela would facilitate the completion of the life cycle of *M. uncinatus* leading to an increased shedding of parasite eggs into the environment which in turn would result in higher infections levels in first intermediate hosts and in snoek.

#### **5.4.3.3. Snoek Population Structure**

Until quite recently, snoek was considered to occur as a single, migratory stock in the Benguela ecosystem (Crawford et al. 1990). However, a synthesis of all available information suggested that snoek in the Northern and Southern Benguela constitute two distinct stocks which experience limited mixing (Griffiths 2003). The results of the current study showed that spatially distinct snoek populations could not be delineated based on the composition and structure of their parasite assemblages. On the other hand, the analysis of the host-parasite relationships of both selected biological tags revealed spatial heterogeneity in infection patterns with respect to host ontogeny. This most probably reflects ecosystem variability between the Northern and Southern Benguela which affects the transmission of *Anisakis* sp. an *M. uncinatus* in converse ways and

support the notion that snoek occur as two discrete stocks off South-Western Africa. The results of Random Forest analyses indicated that the use of a combination of both biological tags yielded better classification rates than either of the selected parasite taxa when used singly. The consistently lower correct classification rate of snoek from the Northern Benguela may be due to the smaller host sample examined from this particular region and further sampling is recommended.

While this study did not show any evidence of the movement of snoek between the two regions, long-term surveys of the parasite fauna of snoek are recommended and may provide a means of assessing the movement patterns of the two putative populations of snoek in the Benguela ecosystem. Future surveys should however not be restricted to *Anisakis* sp. and *M. uncinatus* as other taxa might be useful indicators of north-south migration of snoek in the Benguela ecosystem. For instance the presence of the encysted digenean, which was exclusively found in the Southern Benguela, in snoek caught in the Northern Benguela would indicate northward movement of the southern stock. Similarly, *Rhadinorhynchus cadenati* which occurred at higher prevalence and abundance in the Northern Benguela may prove useful in assessing southward movement of snoek over short time scales. Studies of snoek migration based on biological tags should also include an assessment of classification rates to evaluate the probability of correct spatial assignment of hosts and the discriminatory power of the chosen biological tags.

#### **5.4.4. Conclusions**

The present study provided the first survey of the parasite assemblage of snoek in the Northern Benguela. This exercise revealed significant similarities in the parasite communities of snoek in the Northern and Southern Benguela and demonstrated that community analyses were inadequate for population structure studies of snoek. However, analyses considering individual biological tags provided a consistent signal which allowed the assessment of population structure of snoek in the Benguela. Nonetheless, the biological reasons for the spatial differences in infection

levels of both biological tags are unclear and would benefit from surveys of the parasite fauna of first intermediate and final hosts. This study also highlighted the usefulness of biological tags for fish population structure studies in Southern Africa and supports its inclusion in the fishery scientist's arsenal of techniques.

## Chapter 6: Synthesis and Conclusions

Parasites are an essential component of all ecosystems (Gómez and Nichols 2013). They play important roles as regulators of host populations, are a major driving force of free-living community structure and contribute to ecosystem stability (Marcogliese 2004; Sures et al. 2017). Surprisingly, parasites are often omitted from ecosystem studies and knowledge of the distribution and interactions with their hosts is still poor. Given their prevalence and importance in mediating ecosystem processes, documenting their diversity and assessing their host-parasite relationships as well as their biogeography ought to be common practice in ecological studies, environmental monitoring, fisheries management and conservation efforts (MacKenzie and Abaunza 1998; Williams and MacKenzie 2003; Gómez and Nichols 2013). While marine parasitology is a relatively well-developed discipline in some regions of the World (e.g. Australia, Europe, New Zealand, South America), it is a discipline still in its explorative phase in Southern Africa (Jones 1988; Hine et al. 2000; Moore et al. 2003; Podolska and Horbowy 2003; Williams and Lester 2006; Timi 2007; Leung et al. 2009; Malovic et al. 2010; Cantatore and Timi 2015; MacKenzie and Hemmingsen 2015; Lanfranchi et al. 2016; Luque et al. 2017).

This thesis aimed to contribute towards a better understanding of marine fish parasite ecology in southern Africa with a particular emphasis on fishes found in South African waters. In order to achieve this, the first step was to consolidate the highly fragmented body of research and produce a checklist of metazoan parasitic taxa known to infect marine fish off South Africa (Chapter 3). A total of 378 parasite taxa comprising members of the Acanthocephala, Annelida, Arthropoda, Cnidaria, Nematoda, and Platyhelminthes have been reported, with the majority belonging to either the Arthropoda (55.8%) or the Platyhelminthes (35%). More than 72% of parasite taxa have been reported from only one of the three marine bioregions (west, south and east coasts) off South Africa with the east Coast having the most speciose parasite assemblage, and only a small proportion (4.5%) of parasite taxa being found in all three bioregions. The checklist

revealed that metazoan parasites have been recorded from 270 host fish taxa, primarily members of the class Actinopterygii. While over half of the host species examined are only known to host a single parasite taxon, some (e.g. *Merluccius capensis*, *Thyrsites atun*) had highly diverse assemblages. The number of host species examined represents a small proportion (13%) of South African marine fish species, which together with the finding that the state of knowledge is highly variable amongst ichthyoparasitic phyla, indicates relatively limited knowledge of South African marine ichthyoparasite biodiversity and a dearth of research capacity with regards to most marine ichthyoparasite taxa. This constrains comparisons of marine ichthyoparasite diversity between South Africa and other regions. Despite these shortcomings, the checklist provides a baseline against which to gauge advances in our knowledge of marine ichthyoparasite biodiversity in South African waters. This work also highlighted the lack of taxonomic expertise for several parasite taxa (e.g. Annelida, Cestoda, Cnidaria, and Nematoda) and suggested a bias towards commercially significant host species. Addressing these issues will enable a better understanding of parasite biodiversity in South African waters and contribute to marine conservation planning as highlighted by Adlard et al. (2015).

The current study also provided an insight into the factors determining the make-up of parasite communities in selected fish species of the Southern Benguela. Parasite surveys revealed several new host records, even in species whose parasite communities have previously been surveyed, thus highlighting the benefits of regular parasite surveys. Multivariate analyses indicated that endoparasite and ectoparasite community structure were driven by different factors, with the former largely dependent on host trophic ecology and the latter on host specificity. The composition of the larval endoparasite communities of examined fishes also enabled the construction of a putative food web. Food webs, patterns of predator-prey interactions, are key to our understanding of ecosystem dynamics as they map energy flow (Shannon et al. 2003). Food webs are generally derived from extensive studies of the animal component of the studied ecosystem (Shannon et al. 2003) but as discussed in Chapter 4, acquiring a large enough sample

size which yields a reliable picture of a species' diet may be problematic, especially for high trophic level, endangered species. On the other hand, the examination of the trophically transmitted parasite fauna of a single specimen (e.g. a stranded individual) would yield long term information about its diet. The study of the trophically transmitted parasite assemblages of lower trophic levels coupled with knowledge of their respective life cycles is therefore an alternative means of estimating trophic interactions within the Southern Benguela which should be further explored and integrated into ecosystem modelling.

Fisheries management is a data intensive science. It relies on information pertaining to a harvested species' life history, ecology and population structure to determine the best management strategies to ensure sustainability of the resource. In Southern Africa, fishery management and fish conservation has relied on traditional indicators of population structure and movement such as life history parameters, catch statistics and tagging studies (e.g. Griffiths 2003; Burmeister 2005; Attwood et al. 2010; da Silva et al. 2013). Parasites have already proved to be valuable indicators of population structure for sardines off South Africa (van der Lingen et al. 2015; Weston et al. 2015). The current study demonstrates that despite strong similarity in the composition of parasite communities of snoek in the Northern and Southern Benguela sub-systems, application of individual parasites as biological tags corroborated results from previous recent studies that used traditional indicators and indicated discrete snoek populations in the Northern and Southern Benguela ecosystems. The use of biological tags for fishery management purposes in Southern Africa should be encouraged and expanded to other species, in particular those which have a transboundary distribution and are commercially exploited and managed by different national governments, such as the Cape hakes.

At present, there is much scope for the development of marine parasitology as a discipline in Southern Africa. Taking South Africa, where the vast majority (87%) of marine fish species have never been examined for parasites, as an example, much undoubtedly remains to be discovered and

many new species described. The identification and classification of ichthyoparasites would benefit from a wider application of molecular techniques as well as the development of shape recognition algorithms as is widely used in otolith shape analysis (e.g. Tracey et al. 2006). Knowledge of the diversity, distribution and ecology of marine ichthyoparasites in Southern Africa should also be included in ecosystem modelling thus contributing to a deeper insight into the ecology of the Southern African marine realm. Parasites also have the potential to be used as indicator species in climate change research to detect shifts in faunal distributions (Adlard et al. 2015) and abundances while also being employed as biological tags in fisheries research. Adlard et al. (2015) also note that studying the potential impacts of climate change on the biology and host-parasite relationships of South African marine ichthyoparasite is also of paramount importance to enable their conservation as critical components of the marine ecosystem.

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## Appendix

### Parasite photographs

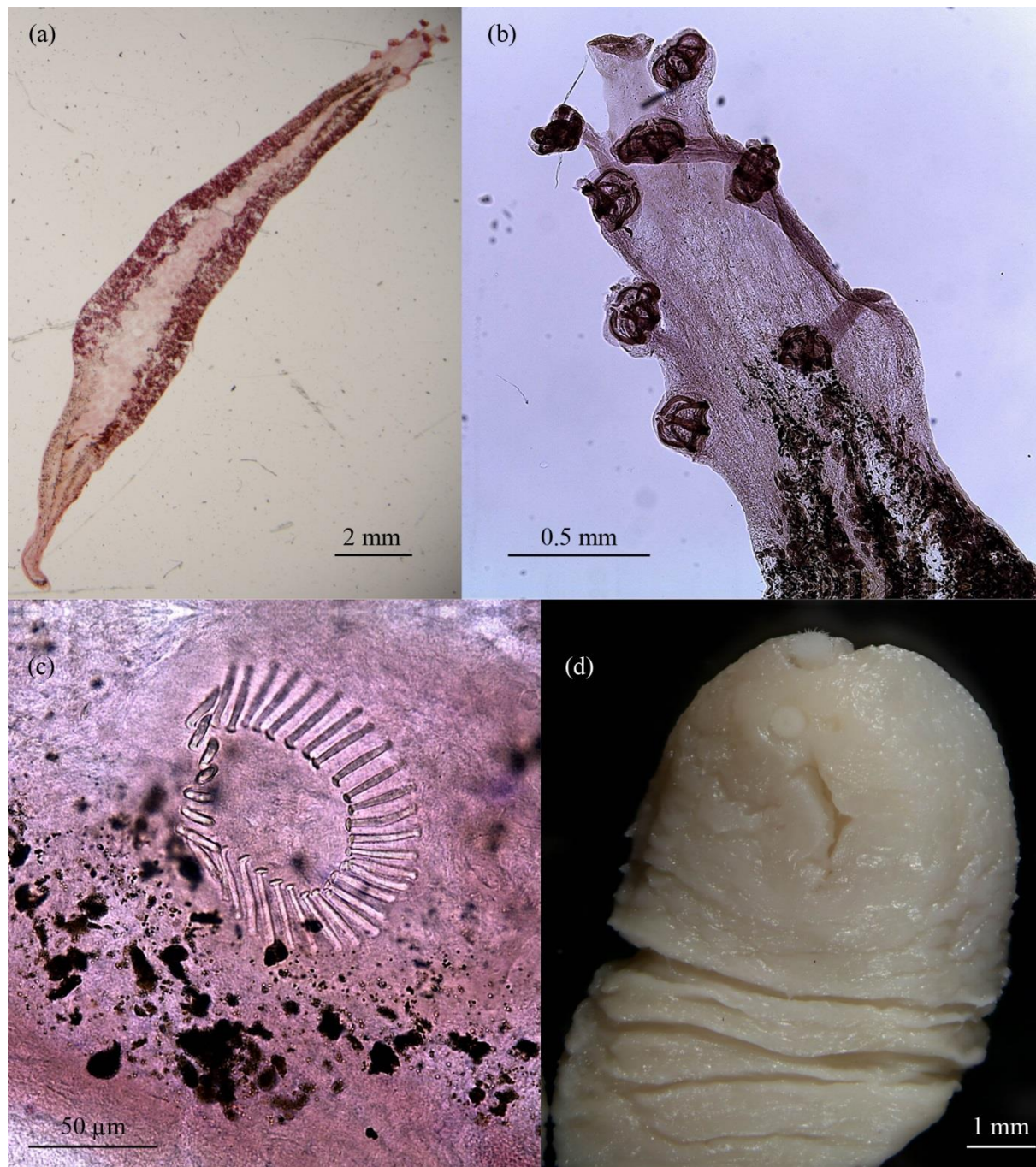


Figure 1. Diclidophoridae gen. sp. (a: whole organism, b: ventral view of haptor, c: genital corona and (d) anterior section of *Hepatoxylon trichiuri* showing armed tentacle.

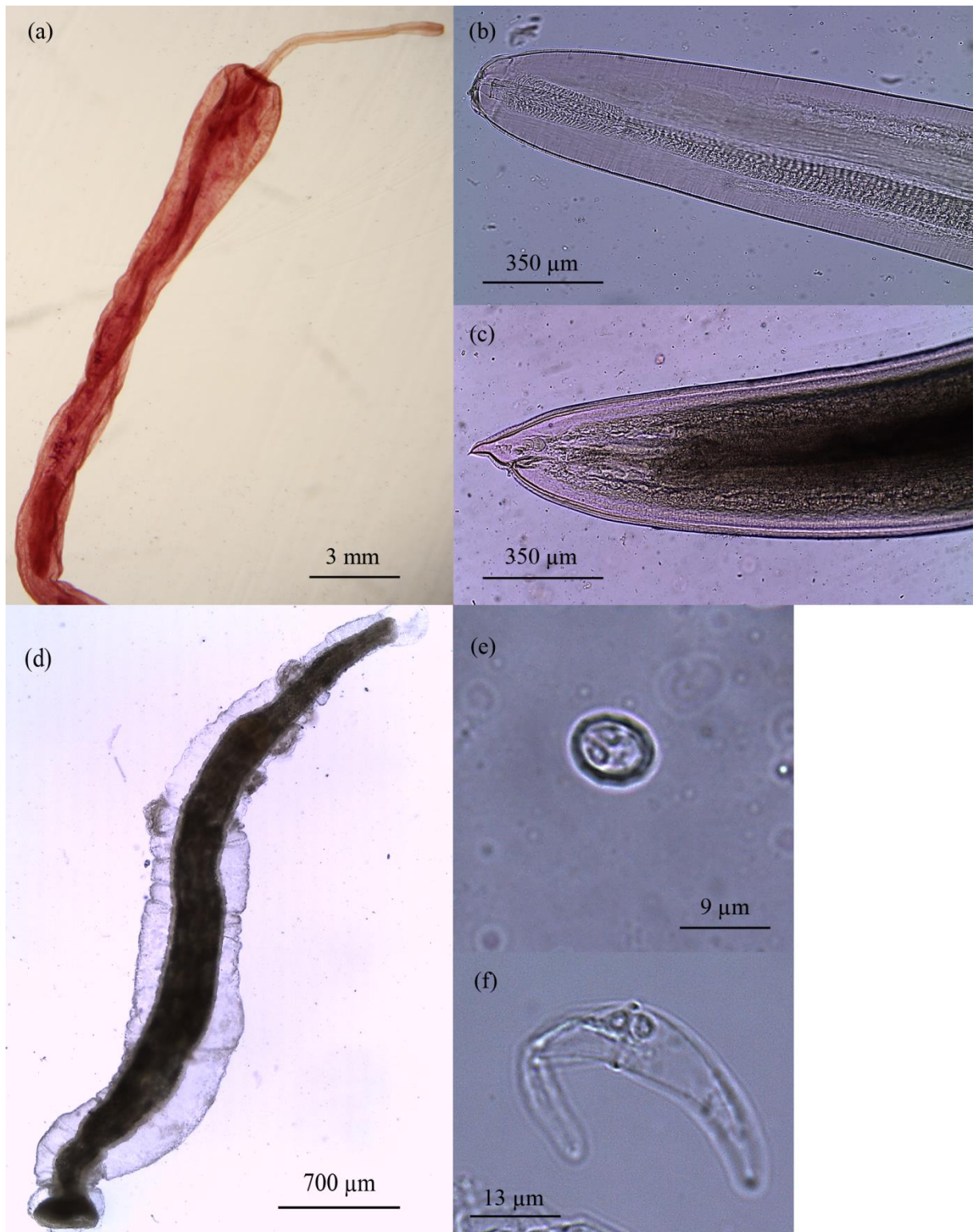


Figure 2. Parasites of *Chelon richardsonii*: (a) Pomporhynchidae gen. sp. with everted proboscis, (b) anterior section of *Contracaecum* sp., (c) posterior section of *Contracaecum* sp., (d) whole Hirudinea gen. sp., (e) *Myxobolus* sp. myxospore and (f) *Ceratomyxa* sp. 1 myxospore.

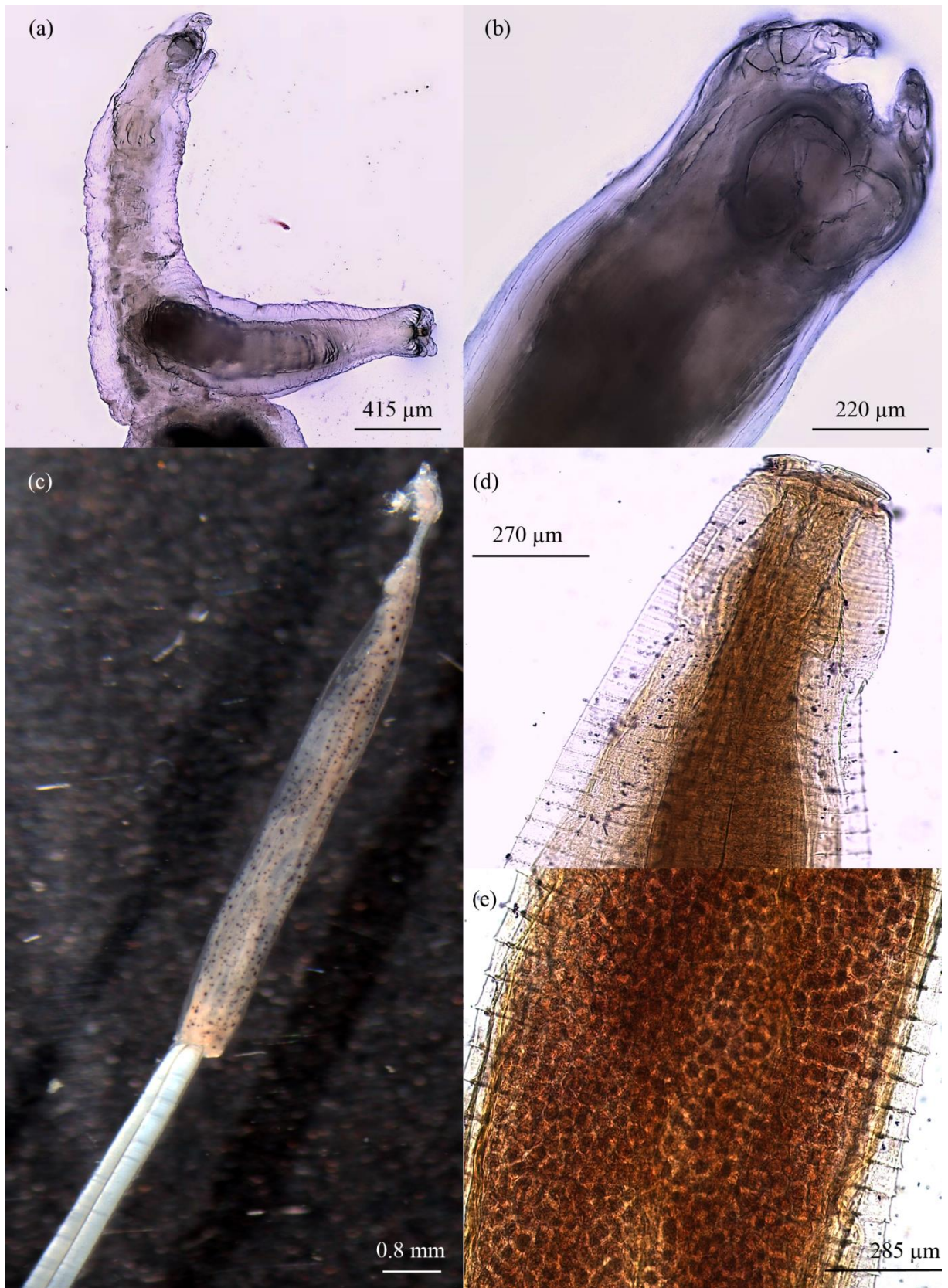


Figure 3. Parasites of *Chelon richardsonii*: (a) anterior section of *Parabradiella exilis* showing cephalothorax and maxilla, (b) , detail of *P. exilis* maxilliped, (c) *Peniculus fistula* with egg strings, (d) anterior section of *Spinitectus* sp., (e) mid-section of *Spinitectus* sp. showing ridged cuticle.

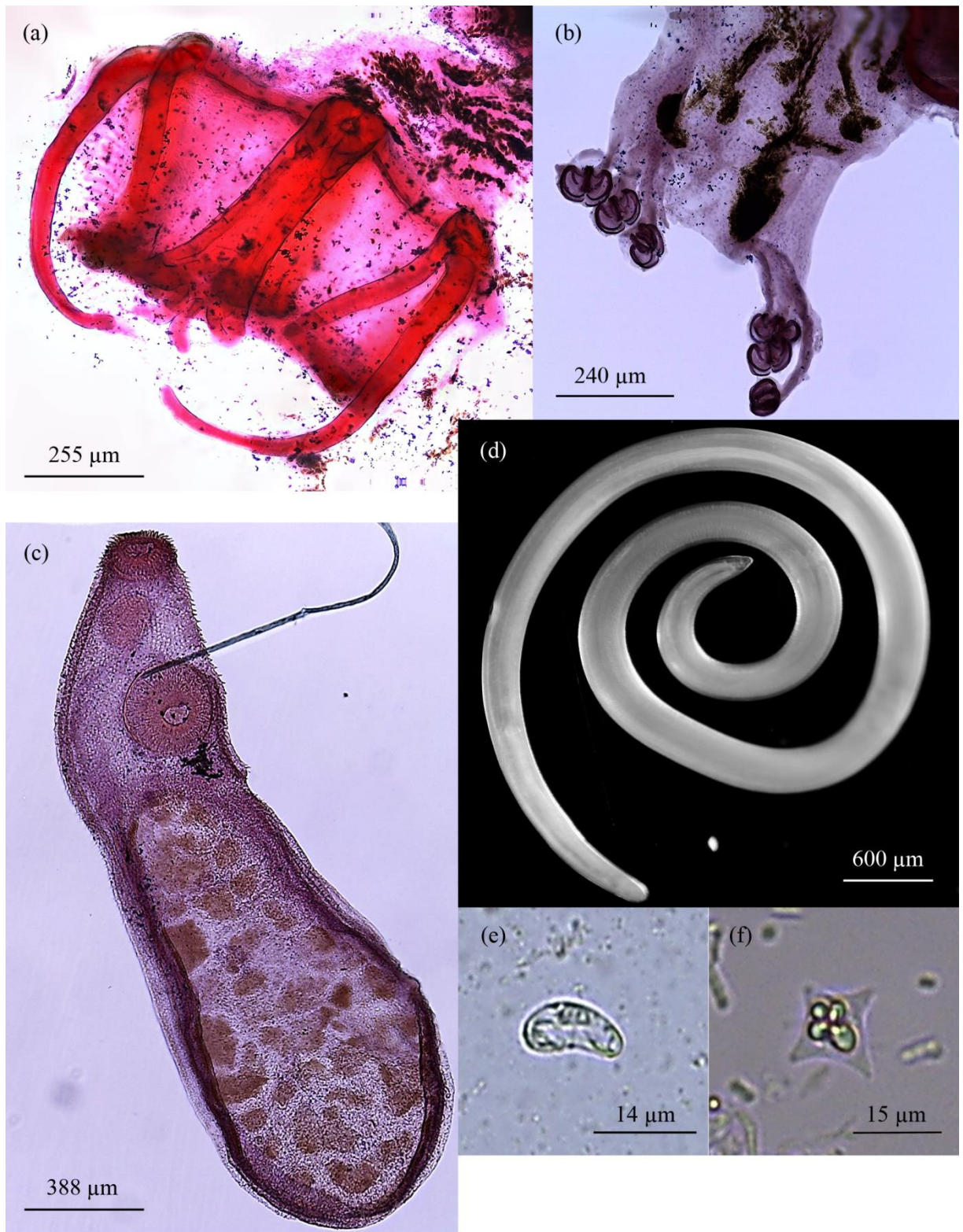


Figure 4. *Anthocotyle merluccii* (a: sclerites, b: detail of lappet), (c) *Stephanostomum* sp. metacercaria, (d) *Anisakis* sp. L3 larva, (e) *Ceratomyxa minuta* myxospore, (f) *Kudoa thyrsites* myxospore.



Figure 5. Parasite of *Thyrsites atun*: *Bolbosoma vasculosum* (a: habitus with retracted proboscis, b: everted proboscis), (c) female *Caligus dakari*, (d) male *Caligus dakari*.

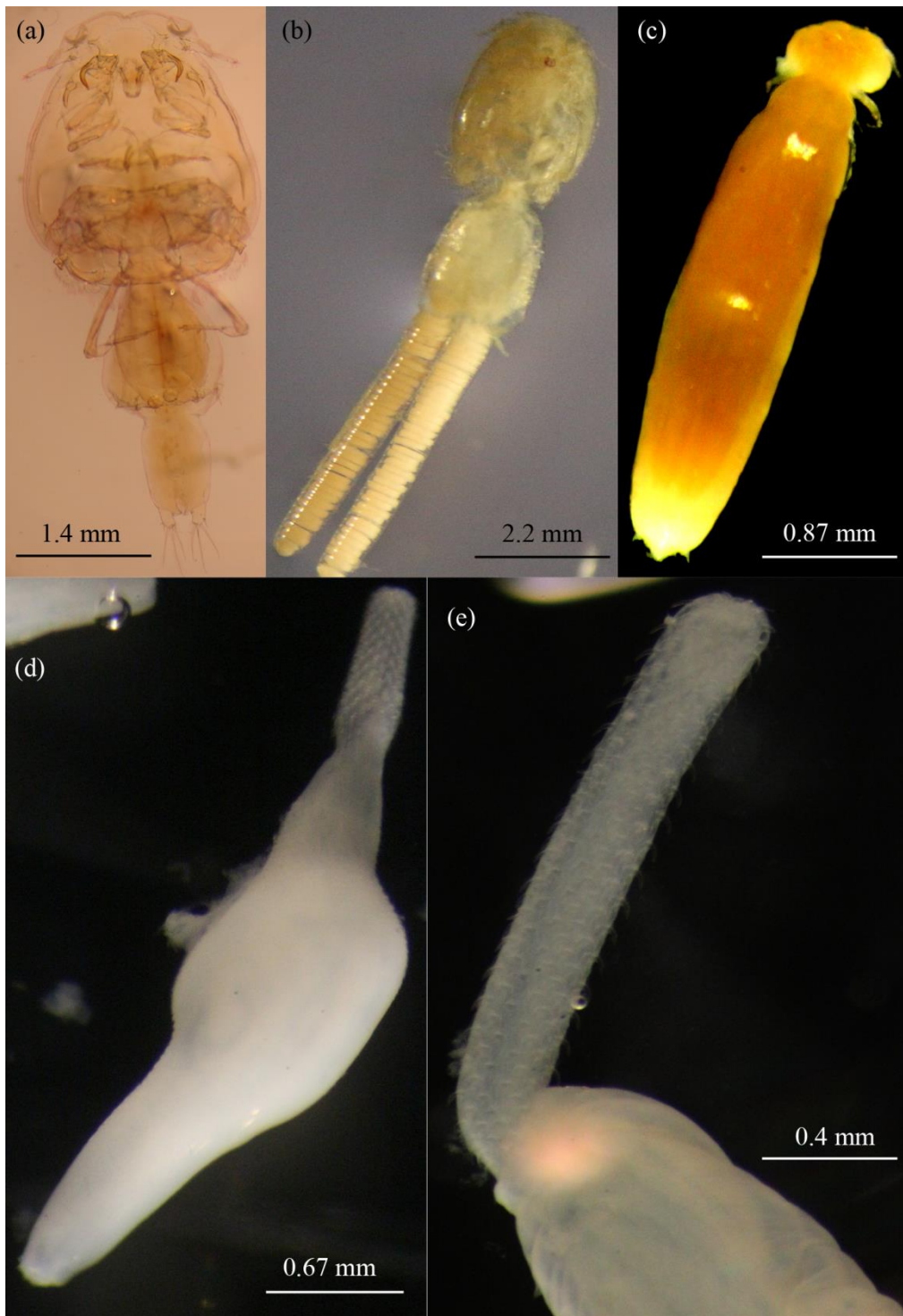


Figure 6. Parasite of *Thyrsites atun*: (a) *Caligus* sp. recovered from *T. atun* caught off Namibia, (b) *Caligus zeii*, (c) *Hatschekia conifera*, (d) *Corynosoma australe*, (e) proboscis of *Rhadinorhynchus cadenati*.

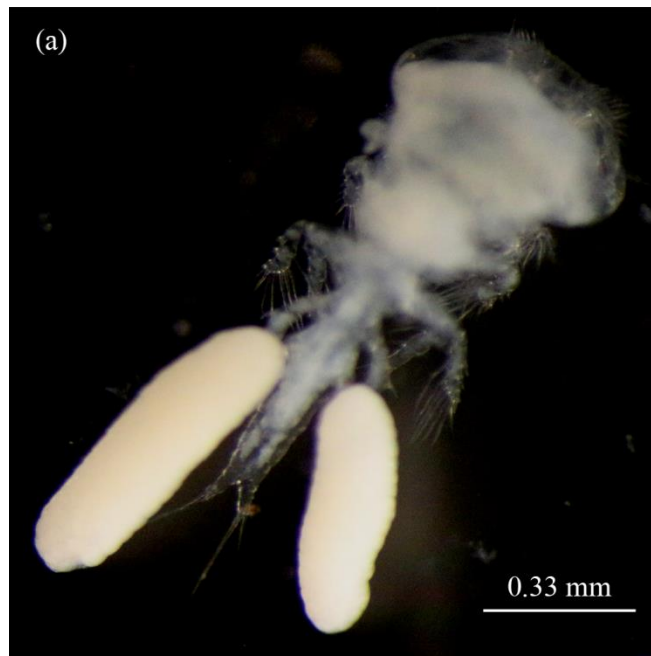


Figure 6. Parasite of *Thyrsites atun*: (a) *Nothobomolochus fradei* and (b) scolex of *Molicola uncinatus* showing armature of tentacles.