A survey of the metazoan parasite assemblage of snoek, *Thyrsites atun* (Euphrasen, 1791), off South Africa with an assessment of host-parasite relationships and potential biological tags

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Abstract

Parasites are a ubiquitous but often unseen, unacknowledged and understudied component of biological communities. However, their roles in structuring ecosystems, their influence on the evolutionary history of host species and their potential applications are slowly being uncovered. The snoek, *Thyrsites atun*, is a nomadic predator native to the cold coastal waters of the southern Hemisphere. Being a major target of the South African inshore linefishery, the snoek is a socioeconomically important species whose ecological significance in the southern Benguela should not be underestimated. This study aimed to survey the metazoan parasite community of snoek off South Africa, assess host-parasite relationships and evaluate the potential of parasites as biological tags for stock structure studies.

Examination of 210 snoek (FL 411 – 1040 mm) revealed them to be host to 16 parasite taxa. These included 9 new host records (*Tentacularia coryphaenae*, *Caligus coryphaenae*, *Caligus dakari*, *Corynosoma australe*, *Nothobomolochus fradei*, *Hatschekia conifera*, *Bolbosoma vasculosum*, *Rhadinorhynchus cadenati,* Digenea sp.) and 4 new locality records (*Molicola uncinatus*, *Pseudoterranova* sp., *C. dakari*, *B. vasculosum*). A further three cosmopolitan taxa (*Anisakis* sp., *Kudoa thyrsites*, *Hepatoxylon trichiuri*) as well as *Caligus zei* were also recorded. The parasite assemblage of snoek off South Africa was less speciose than that of New Zealand *T. atun* populations. The high prevalence of *Anisakis* sp. (100 %), *M. uncinatus* (90 %), *K. thyrsites* (97.1 %) and *N. fradei* (96.2 %) hinted that these parasites were acquired early in the snoek's life history. In contrast, the low prevalence of *Ceratomyxa* sp., *C. coryphaenae*, *B. vasculosum* and *R. cadenati* suggested that they were accidental infections. The diversity of prey taken by snoek, which included teleosts, pelagic crustaceans, cephalopods and invertebrates, associated to its nomadic behaviour are proposed as major factors contributing to the composition of its infracommunity.

Prevalence and infection intensity in relation to biological and environmental factors were assessed by means of Generalized linear models (GLMs) with binomial and negative binomial error distribution, respectively. Models were selected for their ability to deal with presence-absence data and the overdispersion observed in infection intensity data. Results of modelling and dietary analysis suggested that anisakids and *M. uncinatus* are acquired and accumulated throughout the host's life. In contrast, the prevalence of *H. trichiuri* and *T. coryphaenae* was dependent upon both host size and seasonality which suggests that infection by these cestodes is linked with the behaviour and condition of fish in relation to spawning activity. Infection by ectoparasitic copepods (*H. conifera*, *C. dakari*, *C. zei*) was best predicted by seasonality, mesenteric fat content and investment in gonad development. This could either be linked to changes in environmental factors triggered by the snoek's offshore spawning migration or be the result of seasonal differences in the host's immunity. Infection intensity of *H. conifera* was also dependent upon host sex and suggests behavioural differences between male and female snoek.

Community analyses, performed via multivariate techniques (MDS, ANOSIM, SIMPER) suggested no differences in the structure of the infracommunity between male and female snoek (Global R = 0.0129, p = 0.117). The snoek's infracommunity also exhibited seasonal stability (Global R = 0.1705, p = 0.001) which was ascribed to the nomadic behaviour of snoek off South Africa. The analyses also suggested a slight ontogenetic shift (Global R = 0.09088, p = 0.005) and nestedness in the parasitic community structure of snoek. Simpson's diversity index indicated that parasitic diversity increased with host size.

Four parasitic taxa (*Anisakis* sp., *N. fradei*, *M. uncinatus*, *K. thyrsites*) were considered valuable as potential biological tags but whether differences in prevalence and infection intensity exist between putative snoek stocks in the south eastern Atlantic remains to be investigated.

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Introduction

1.1: Parasites, Humans and Nature

Parasitism is a singular type of relationship, distinct from predation, commensalism and symbiosis. Parasites live in or on other organisms (the hosts) and, in contrast to commensals and symbionts, decrease the fitness of their host while deriving some form of benefit. They were first recorded in antiquity (3000 to 400 BC) and have, since then, been linked to diseases in humans as well as in domestic and wild animals (Bush *et al.* 2001; Cox 2002; Poulin 2002; Marcogliese 2004, 2005). Some parasites can cause severe illness and even death in both humans and animals. The protozoan malarial parasite, *Plasmodium falciparum*, kills about 2.7 million people each year (Gardner *et al.* 2002). The guinea worm, *Dracunculus medinensis*, although rarely fatal can be highly incapacitating and was responsible for over 3 million cases of dracunculiasis per annum in the 1980's (Hopkins *et al.* 2014). However, successful eradication campaigns have brought the number of cases down to 148 in 2013 (Hopkins *et al.* 2014). The Rinderpest virus, which affects the ruminants of Africa, can have severe consequences for the animal and plant communities and even the ecosystem (Chapin *et al.* 1997).

Consequently, parasites have generally been considered with disdain and disgust by the media and the general public and have often been the focus of eradication campaigns on a global scale (Hopkins & Ruiz-Tiben 1991; Hopkins *et al.* 1993; Dowdle 1998; Baumhover 2002; Barrett 2003). Viewed as pests and unimportant, parasites have historically been ignored by ecologists (Rohde 2010). Parasites are smaller than their hosts, often by an order of magnitude, and account for only a fraction of the biomass in an ecosystem (Marcogliese 2004; Hudson *et al.* 2006; Dobson *et al.* 2008; Lafferty 2008). For this reason, ecologists have for a long time underestimated the capabilities and roles of parasites. However, after it was proposed that parasites could account for more than 50% of the World's biodiversity (Poulin & Morand 2000;

Hudson *et al.* 2006), extensive research has been conducted to uncover the roles of parasites in natural communities and ecosystems (Poulin 1999). Parasites are now a recognized component of biodiversity in both the terrestrial and aquatic realms.

1.2: The Parasitic Lifestyle

A countless number of organisms have adopted a parasitic lifestyle, making parasitism the most successful mode of life on Earth (Poulin & Morand 2000; Palm & Klimpel 2006; Dobson *et al.* 2008). Parasites can either be endoparasitic (inside the host) or ectoparasitic (on the external surface of the host) (Marcogliese 2004; Poulin 2004). Parasites can have multiple hosts (generalists) or be restricted to a single or a few related host species (specialists) (Palm & Klimpel 2006; Poulin *et al.* 2011). Generalist parasites thrive to increase their host range through the process of cumulative evolution and are more resilient to extinction than specialist species (Poulin *et al.* 2011).

The life cycle of parasites can be direct (simple) or indirect (complex), which has significant consequences on the mode of transmission. Parasites with a direct life cycle (e.g. copepods) only live on or in its definitive host and propagules are acquired by contact or as free swimming larvae (Marcogliese 2004). The indirect life cycle involves one or more intermediate hosts in which the parasite develops to a certain ontogenetic stage before being transmitted to its next host via a predation event (Marcogliese 2002; Poulin 2004).

1.3: The Diversity and Biogeography of Parasites

1.3.1: The Diversity of Parasites

Parasites encompass organisms from most phyla (Rohde 2005; Roberts *et al.* 2009) and it is most likely that only a fraction of them have been discovered and described to date. A wide literature review undertaken by Poulin and Morand (2000) suggested that at least 102 220 species of metazoans parasitize metazoan hosts while Dobson *et al.* (2008) estimated that there are anywhere between 75 000 and 300 000 helminth species. As illustrated by the two examples above, estimating parasite diversity is fraught with difficulties and remains inaccurate (Rohde, 2005).

Methodological hurdles will have to be overcome before a credible estimate is possible. The major difficulties encountered in discovering new parasite species are low and geographically biased scientific effort, inadequate sampling of the host populations, their small size, low prevalence and the presence of cryptic species which are often not detected by conventional taxonomic methods (Poulin & Morand 2000; Poulin 2004; Dobson *et al.* 2008; Rohde 2010).

1.3.2: The Origins of Parasite Diversity

Understanding how parasite diversity arises is central to uncovering their evolutionary history and improves our knowledge of their interactions with their hosts. Three major theories have been put forward to explain the radiation of parasite lineages (Poulin 2004; Huyse *et al.* 2005; Poulin *et al.* 2011). Firstly, host-parasite co-evolution, secondly sympatric host switching and finally intrahost speciation of parasites.

When an ancestral host lineage diversifies, some parasites are passed down to the daughter species. These parasites then co-evolve with their new host and eventually split off completely from the ancestral species (Poulin 2004; Poulin & Mouillot 2004). Host switching, the second theory, is the process by which a parasite is transmitted to a sympatric host that it manages to colonize (Poulin & Mouillot 2004). This can only happen if the newly infected host is physiologically and immunologically similar to the donor host. Intrahost speciation, as postulated by the third theory, occurs when parasites are subjected to more selection pressures than free-living organisms (Huyse *et al.* 2005). The host, without itself undergoing cladogenesis (Hoberg 2005a), offers a dynamic environment and thereby increases the number of diversifying factors which can significantly contribute to intrahost speciation.

1.3.3: The Theory of Parasite Diversity

Explaining biodiversity patterns in natural communities is a central theme in ecology. The factors determining parasitic species richness and community structure of a host species has been at the centre of attention for at least two decades (Poulin 2002). Two theoretical frameworks have been extensively used in generating hypotheses about factors affecting the diversity of parasites in a particular host species. Firstly, the island biogeography theory and secondly the epidemiological theory that arose from mathematical modeling of host-parasite interactions (Poulin 2002, 2004).

The island biogeography theory postulates that the species diversity of an island is dependent upon the rate of colonization and extinction of species on the island (Poulin 2004). These rates are affected by the island's features, or when adapted for parasitological research, the host's traits. No single trait has been found to be the determinant of parasitic community structure; instead several traits interact at various spatial and temporal scales (Poulin & Morand 2000). These are host geographical range, body size, behaviour, life-span, diet, population density and host mobility (Poulin & Morand 2000; Poulin 2004; Huyse *et al.* 2005).

Generally, a larger geographical range, larger body size (Guégan *et al.* 1992), longer life-span (Lo *et al.* 1998), active behaviour, broad diet (Lo *et al.* 1998) and high population density (Arneberg *et al.* 1998) have been correlated to higher parasite species richness. These factors increase the probability that the host will be exposed to and colonized by a new species of parasite but the effects of phylogeny must not be ignored (Poulin & Morand 2000; Poulin *et al.* 2011). When a phylogenetically independent contrast method (Felsentein 1985) is used, often the patterns that were obvious disappear, suggesting that host-specificity plays a major role in determining the parasite infracommunity structure of a host species. One major drawback is that the island biogeography theory does not allow one to generate quantitative hypotheses; e.g. parasite diversity doubles with a doubling of host body size.

The epidemiological theory has grown out of medical research targeting parasitic diseases and has only recently been employed in ecological parasitology (Poulin & Morand 2000; Poulin 2004). Entrenched in mathematics, this method allows one to derive a measure of reproductive success (R_0) of a single parasite introduced in an uninfected host population (Poulin 2004). An $R_0 > 1$ indicates that the parasite will be able to colonize and persist in a particular host population. Predictions based on this framework are, as with the island biogeography theory, qualitative and overlap greatly with those of the former theory (Arneberg *et al.* 1998; Poulin 2002, 2004). In practice, it is difficult to distinguish between the two frameworks as they both rely on the same principle, the probability that a parasite will establish itself on a new host.

1.3.4: The Biogeography of Marine Parasites

The goal of biogeography is to map and understand patterns of biodiversity at large spatial and temporal scales (Poulin *et al.* 2011). The current distribution of organisms is the result of historical events coupled to geological processes that have altered abiotic conditions within an environment and caused the extinction of some species while others adapted and subsequently radiated. Adopting the parasitic lifestyle comes with its constraints (Poulin *et al.* 2011). Due to the intimate relationship parasites have with their host, the spatial distribution and dispersal of parasites is entirely dependent on the host's geographic range. Consequently, the diversity of parasitic life within an ecosystem often tends to mirror host species diversity (Thieltges *et al.* 2011). Host specificity is not the only determinant of parasite distribution, the lifecycle and environmental requirements are also important (Poulin *et al.* 2011). All three factors interact, resulting in the realized niche or distribution of a particular parasite.

The most obvious pattern in oceanic biodiversity is the latitudinal gradient of species diversity and parasites make no exception to this trend (Poulin 2004; Rohde 2010; Poulin *et al.* 2011). Monogenean species richness increases faster than their host diversity at low latitudes whereas trematodes show no significant variation in number of species per host species at all latitudes (Rohde 1999, 2010) This suggests that endoparasite community diversity is a function of host diversity. Therefore, ectoparasitic diversity is much higher at low than at high latitudes, whereas infracommunity richness of endoparasites is relatively stable at all latitudes. Parasitic traits including host specificity, life history and impact on host also vary with latitude (Moller 1998; Rohde 2010; Poulin *et al.* 2011).

The possible causes of latitudinal gradients are diverse and are often inferred from theory developed for free-living organisms. One explanation often invoked, is that tropical areas are simply larger, have a long undisturbed history, offer more niches and therefore foster increased biodiversity compared to temperate and Arctic regions (Rohde 2010). But as Gaston (2000) stated, “no single mechanism adequately explains all examples of a given pattern”. Species diversity in a given area is under hierarchical control from a number of interacting biotic and abiotic factors. Therefore, the species diversity-area theory is not likely to be the only plausible explanation for latitudinal gradients of species diversity. Poulin and Rohde (1997) found that temperature significantly correlated with diversification rates in marine fish ectoparasites. Rohde (2010) argued that higher temperatures led to faster mutation rates, shorter generation time and faster selection and result in faster speciation at low latitudes. This is thought to be the major explanation for the latitudinal pattern of marine biodiversity on a global scale. Multiple factors and processes, other than temperature and area, including climate change, genetic drift, speciation type, physiological tolerance, dispersal ability, strength and importance of biotic interactions have been proposed to explain faster speciation in the tropics (Rohde 2010). None of these explanations have universal support and must be investigated further.

Longitudinal and depth diversity gradients have also been documented, albeit much less frequently than latitudinal gradients (Rohde 2010). Longitudinal gradients may be maintained by barriers to dispersal of species (e.g. islands, open ocean) as demonstrated by the biogeography of parasites of coastal scombrid fish species (Rohde 2010). Depth gradients are more easily explained as being a function of increasingly harsh environmental conditions (e.g. light penetration, temperature, food supply, pressure) as depth increases. Further studies at various spatial and temporal scales are required to improve our understanding of parasite biogeography.

1.4: The Ecological Significance and Consequences of Parasitism

A growing body of literature is demonstrating that parasites are ecologically significant at all levels of biological organization (Figure 1) and impact many taxonomic groups, both directly and indirectly (Bakker *et al.* 1997; Barber *et al.* 2000; Dawson & Bortolotti 2000; Hurd *et al.* 2001; Latham & Poulin 2002; Decaestecker *et al.* 2005; Barber 2007; Sitjà-Bobadilla 2009).

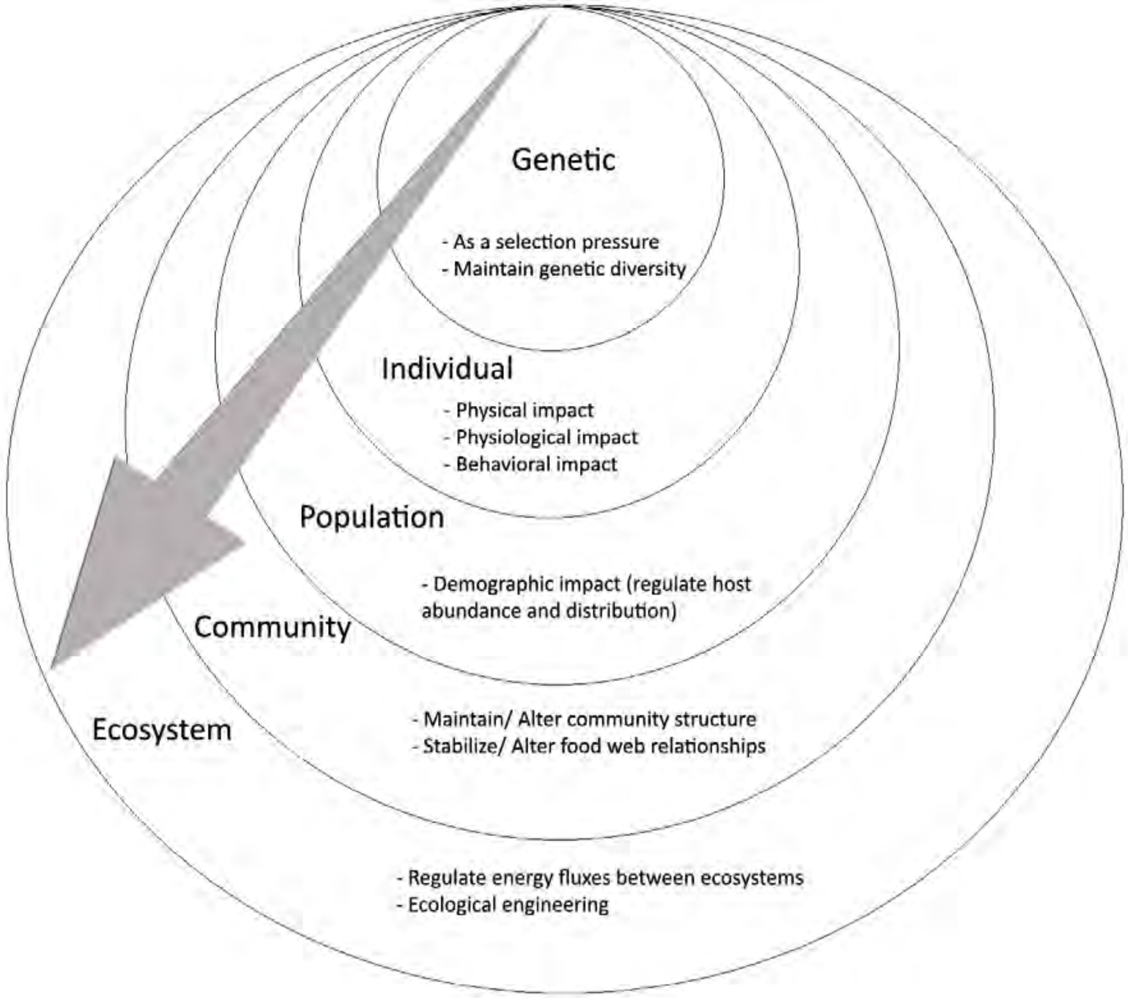

Figure 1. Schematic representation of the ecological significance of parasites at the five levels of biological organization (genetic, individual, population, community, and ecosystem). The arrow indicates that the significance of parasites is often not restricted to one particular level but instead cascades across multiple hierarchical levels.

1.4.1: The Ecological Significance of Parasites

Impacts of parasites are apparent at the genetic (as a selection pressure), individual (physical, physiological, behavioral) and population (regulate host demography) levels (Lemly & Esch 1984; Kennedy *et al.* 1987; Lafferty 1992; Lafferty & Morris 1996; Hurd *et al.* 2001; Torchin *et al.* 2002; Diggles 2003; Wegner *et al.* 2003; Wagner *et al.* 2005; Cable & van Oosterhout 2007; Shah *et al.* 2009; Sitjà-Bobadilla 2009). The impact that parasites have on their hosts is determined by the intrinsic qualities of the parasite and the characteristics of the host.

We have no means of predicting the effects of parasitism on a host. Host-parasite interactions thus require careful study, at a range of spatial and temporal scales and at all levels of biological organization, in order to improve our knowledge on the ecological impacts and roles of parasites in an attempt to inform management and conservation planning.

The impact of parasites at the genetic, individual and population levels inevitably cascade through to higher levels of biological organization, this is where parasites take all their significance. Parasites have been shown to be key in the maintenance of biological community structure in marine and freshwater ecosystems (Mouritsen & Poulin 2005; Wood *et al.* 2007; Hernandez & Sukhdeo 2008a). In biological invasion scenarios, parasites can be responsible for decreased fitness and extinction of native species as well as the modification of food web relationships and community structure of a given ecosystem (Torchin *et al.* 2002, 2003; de Castro & Bolker 2005; Hudson *et al.* 2006). Some evidence also suggests that parasites are of high ecological significance in the food web dynamics of freshwater and marine ecosystems (Marcogliese 2002; Kagami *et al.* 2007; Hernandez & Sukhdeo 2008b; Sato *et al.* 2012). They can alter energy fluxes between ecosystems (Kagami *et al.* 2007; Sato *et al.* 2011a, 2011b), thereby providing or limiting energy input and flow in the ecosystem and contribute to the structuring of the biological community. The consequences of parasitism are not restricted to the natural world.

1.4.2: Economic and Health Impacts of Fish Parasites

Parasites have negative economic impacts both in the aquaculture and fishing industries and can also have health implications for humans (Langdon *et al.* 1992; Piccolo *et al.* 1999; Barber *et al.* 2000; Ravichandran *et al.* 2009). Economically, the aquaculture industry is particularly at risk. Space restrictions and high fish densities increase the chances of parasite transmission and negate selection against infected shoalmates (Barber 2007). Parasites which cause physical degradation of their fish host muscle (e.g. *Kudoa thyrsites*), can trigger a decrease in marketability of the catch (Langdon *et al.* 1992). Other parasites such as the nematode *Anisakis pegreffii* (Campana-Rouget & Biocca, 1955) and *Anisakis simplex* (Rudolphi, 1809) can be a human health hazard if ingested. Anisakis infections in humans and repeated exposure to the nematode may lead to a condition known as anisakiasis, allergic reactions and potentially fatal anaphylactic shocks in sensitive people (Piccolo *et al.* 1999; Nieuwenhuizen *et al.* 2006). Further research is required to develop novel control measures for parasites in the aquaculture and wild-caught industry and also to better our understanding of diseases caused by 'trophically' transmitted parasites in humans.

1.5: Parasitology, Fisheries Biology and Environmental Monitoring

1.5.1: Parasites as Biological Tags

The stock concept is fundamental to the rational and successful management of fisheries (MacKenzie & Abaunza 1998; Begg *et al.* 1999; Mosquera *et al.* 2003; Baldwin *et al.* 2011). By delineating discrete stocks (subpopulations) of commercially significant marine species, it is possible to refine existing management strategies and devise novel methods for the management and conservation of marine resources. Mathematical and statistical analysis of morphometrics, artificial tagging data, catch data, otolith microchemistry and shape, genetics and life-history parameters have traditionally been used to elucidate the stock structure of marine species (Begg & Waldman 1999; Begg & Brown 2000; Mosquera *et al.* 2003; Attwood *et al.* 2010; Baldwin *et al.* 2011). Collection of data required by the above mentioned methods is labour intensive, expensive and often impacts the organism studied (Mosquera *et al.* 2003). Consequently, the use of parasites as biological tags is an alternative that is increasingly being attempted in fishery management worldwide (Moser & Hsieh 1992; Pascual & Hochberg 1996; Castro-Pampillon *et al.* 2002; Oliva & Ballon 2002; MacKenzie *et al.* 2008; Luque *et al.* 2010; McClelland & Melendy 2011). Due to the evolution and refinement of the stock concept over the years (Begg & Waldman 1999) an up-to-date working definition is necessary.

Begg and Waldman (1999) stated that "… the stock concept describes the characteristics of the units assumed homogeneous for particular management purposes" and also made the distinction between the goals of fisheries management and endangered species management. From a parasitological point of view, a fish stock is considered to be 'a group of individuals whose parasite infracommunities (Bush *et al.* 1997) are more similar to each other than to any individual outside this group at any time'.

Parasites make ideal tags as they occur naturally, are ubiquitous, integrate variation in environmental conditions over time and can only infect fish within their endemic region (MacKenzie & Abaunza 1998). Parasites can yield information about the host's nursery grounds, migration and diet (Mosquera *et al.* 2003; Baldwin *et al.* 2011), thereby proving useful in discriminating between stocks. The characteristics of the ideal parasite to be used as a biological tag following the guidelines given by MacKenzie and Abaunza (1998), Mosquera *et al.* (2003) and Baldwin *et al.* (2011) are summarized in Figure 2. However, this method also has its shortcomings. The distribution of a particular parasite may only reflect the distribution of its intermediate host and not the actual species being studied (Mosquera *et al.* 2003). MacKenzie and Abaunza (1998) also warn against age-dependent intensity of infection and recommend only comparing fish from similar age classes. Used cautiously and holistically, the use of parasites as biological tags could prove very useful in fishery management and research.

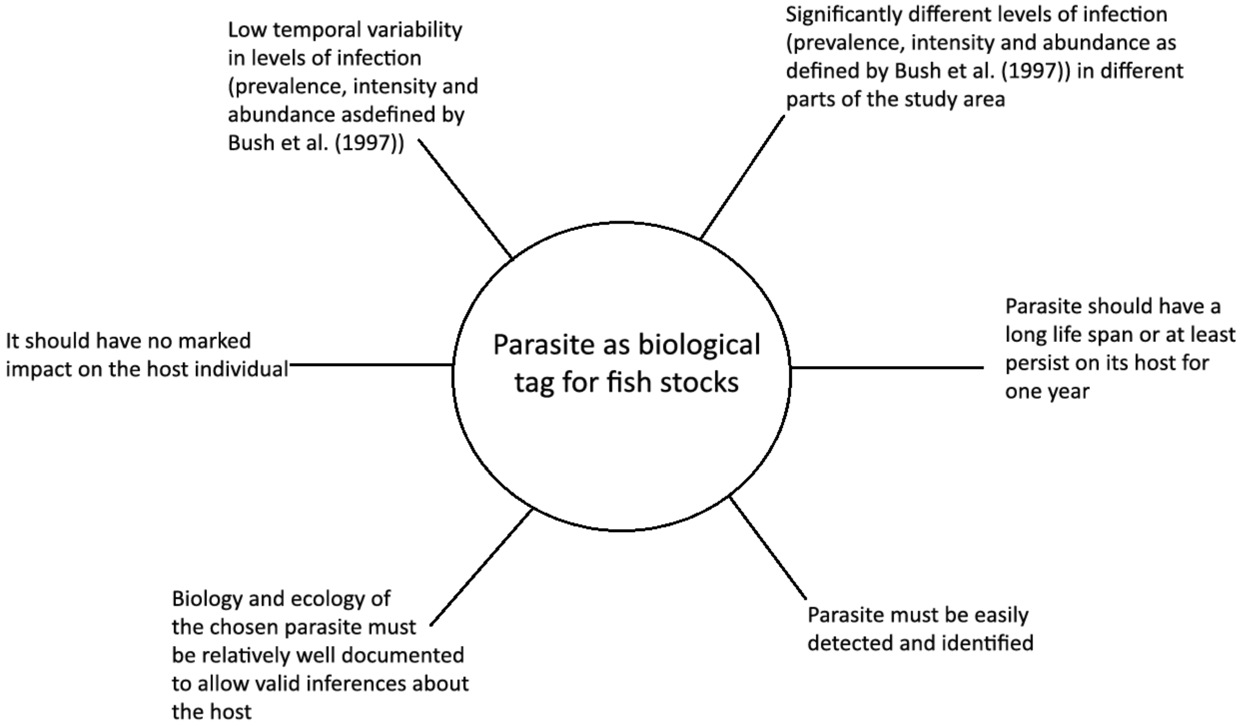

Figure 2. The theoretical characteristics of the ideal parasite to use as biological tag. After MacKenzie & Abaunza (1998), Mosquera *et al.* (2003) and Baldwin *et al.* (2011).

1.5.2: Parasites as Bioindicators

Pollution of aquatic ecosystems, both freshwater and marine, can have lethal and sublethal impacts on the biological community, including parasites (MacKenzie 1999; Bayoumy *et al.* 2008; Sures 2008). Pollution can either increase or decrease parasitism in an ecosystem. Generally, the abundance of ectoparasites tends to increase with increasing levels of pollution, whereas endoparasites tend to decrease in numbers (Sures 2005). The diversity and magnitude of the response of parasites to pollutants makes them good candidates for use as bioindicators and could provide ecologists with an early warning of impending pollution-mediated change in an ecosystem.

Bioindicators are species that respond to changes in their environment in such a way as to reflect the 'health' of the system (Vidal-Martínez *et al.* 2010). The criteria and guidelines for choosing an appropriate parasite for use as a bioindicators were originally proposed by MacKenzie (1999) and have since then been refined by Williams and MacKenzie (2003). Bioindicators can be classified either as effect or accumulation indicators (Pascual & Abollo 2005; Sures 2005). Effect indicators respond physiologically and/or behaviourally to pollution whereas accumulation indicators bioaccumulate pollutants to in their tissues and allow their early detection, even at low ambient concentrations.

The use of parasites as pollution indicators is still hotly debated (Williams & MacKenzie 2003; Sures 2005; Vidal-Martínez *et al.* 2010). Sures (2005) argued that parasitic communities may be subject to stochastic changes not related to environmental conditions. This situation would make interpretation of parasitological data for use in biological monitoring unreliable. Also, a relatively good knowledge of the biology and ecology of the parasite species used as bioindicator is vital for valid interpretation of data. However, compared to free-living indicators, parasites may be advantageous as they integrate conditions experienced across multiple trophic levels and can possibly respond to small, otherwise undetectable, changes in environmental conditions (Sures 2005). Further research is required to overcome methodological, practical and conceptual hurdles that plague this young but promising interdisciplinary field.

1.6: Marine Parasitology in South Africa

Marine parasitology in South Africa has a long history (Gilchrist 1924), but research in this field has been patchy. The infamous myoliquefactive myxozoan, *Kudoa thyrsites,* was first described from snoek (*Thyrsites atun*) in 1924 by J. D. F Gilchrist while he was Head of the Zoology Department at the University of Cape Town (Brown 2003). Early studies were mostly of taxonomic nature (Barnard, 1955a, 1955b, Bray 1984, 1985, 1986, 1987; Avenant-Oldewage 1994) although the host-parasite relationships of a few species have been investigated more thoroughly (e.g. Botha 1986; Payne 1986; Wright *et al.* 2001; Yeld 2009; Tang 2010, Bowker

2013; Le Roux 2013). Recently, the potential use of parasites as biological tags for pelagic species of the Benguela ecosystem has been investigated (Reed *et al.* 2012, Van der Lingen *et al.* 2014) with promising results.

While some aspects of the host-parasite relationships of a few commercially significant species, including hottentot (*Pachymetopon blochii*) (Wright *et al.* 2001), kingklip (*Genypterus capensis*) (Payne 1986) and the two hake species (Botha 1986) have been studied, there is little information available on snoek (*Thyrsites atun*). This is especially surprising when considering the iconic status of snoek in the Western Cape and the fact that a closed season has been observed in the past due to low fish condition attributed to high levels of parasitism (Botha 1986; Payne 1986). Although the nematodes which commonly infest the body cavity are not considered a health hazard in South Africa (van der Elst 1993), despite one study suggesting otherwise (Nieuwenhuizen *et al.* 2006), the parasites of this species could well be of significant ecological importance and may provide clues to improve fishery management strategies in South Africa.

1.7: Thyrsites atun

Thyrsites atun (Euphrasen, 1791), is a medium sized, pelagic, predatory gempylid (2000 mm SL, max. weight 9 kg) native to coastal waters of the southern hemisphere (Branch *et al.* 2010; FishBase 2013). The species occurs off Australia, New Zealand, southern South America, Tristan da Cunha, the Amsterdam and St. Paul islands and southern Africa (Nakamura & Parin 1993). The biology of *T. atun* has been relatively well studied both in Australia (Grant *et al.* 1978) and New Zealand (Mehl 1970, 1971; Hurst & Bagley 1989; Bull *et al.* 2001; Trella 2004) where it is known as the barracouta. This is in stark contrast with the southern African population of *T. atun*, for which research is lacking despite its ecological (Olivar & Shelton 1993; Verheye & Richardson 1998), commercial (Attwood & Farquhar 1999) and socioeconomic significance (Dudley 1987; Griffiths 2002, Isaacs 2013) in this part of the world.

1.7.1: The Cape Snoek

Thyrsites atun, commonly referred to as snoek in southern Africa, occurs from Angola to Algoa Bay, on the southern coast of South Africa, but are mostly found along the South Western coast, i.e., in the Benguela ecosystem (Griffiths 2002, 2003). The first recorded snoek catch came from Saldanha Bay in the 1600's and two centuries later, this fish became the major source of protein for many in Cape Town (Gilchrist 1905; Crawford 1989). The bulk of the catch was, at the time, salted and exported to Mauritius but it has also been directed towards canning factories in war times (Crawford 1989). The snoek fishery has grown in prominence and is currently the largest handline fishery on the West and South coasts (Attwood & Farquhar 1999; Griffiths 2002) although exports have dwindled. In 1982, snoek made up a record 85% of the total West coast catch (Crawford 1989). Between 2001 and 2010, an average of 4515 tons of snoek were landed per annum by line fishermen (DAFF 2012). A substantial amount of snoek is also caught as part of trawler by-catch in South African and Namibian waters (Griffiths 2002). Efficiency now being of essence in business, the snoek fishery has evolved from a harbour-based decked boat fleet to a mobile ski-boat fleet (Dudley 1987).

The ecological importance of snoek should not be underestimated; it is both predator and prey in the Benguela ecosystem. Snoek are capable of consuming up to 300 000 tons of anchovy (*Engraulis capensis* Gilchrist, 1913) per annum and can have significant top-down effects on the lower levels of the food web (Crawford 1989; Verheye & Richardson 1998). The availability of snoek to fishermen has been shown to depend upon the availability of anchovy (Crawford 1989). The snoek fishery cannot therefore be adequately managed in isolation. The major prey species, *E. capensis* and *Sardinops sagax* (Jenyns, 1842), which are commercially exploited must also be carefully managed so as not to compromise a flourishing handline fishery on the South African West coast. Understanding the stock structure of snoek in the Benguela, something still debatable (Crawford 1989; Crawford *et al.* 1990; Griffiths 2002, 2003), is critical to the successful management of this fishery.

A number of attempts have been made to elucidate the stock structure of snoek in the Benguela (e.g. Dudley 1987; Crawford *et al.* 1990; Griffiths 2002, 2003). Snoek of the south eastern Atlantic have historically been considered to consist of a single stock (Crawford 1989; Crawford *et al.* 1990) but recent evidence suggests the presence of two sub-populations separated by the Lüderitz upwelling cell (Figure 3) (Griffiths 2002, 2003). Previous studies have used catch data (Crawford *et al.* 1990), analysis of spatial and temporal distribution, diet, distribution of eggs and larvae (Dudley 1987) and life history traits (Griffiths 2002) as indicators of the stock structure. Employing a holistic approach, as encouraged by Begg and Waldman (1999), and integrating parasitological data to the analysis could shed some further light on the stock structure of snoek in the Benguela.

The terms 'snoek' and 'barracouta' are hereafter used to distinguish between the African and Australasian populations of the focal species of this study while *Thyrsites atun* refers to the species as a whole.

1.7.2: Parasites of *Thyrsites atun*: what do we know?

Despite the ecological and economic importance of *T. atun* and fish parasites, few publications report on the parasites of this pelagic predator. Twenty-four parasite taxa have been recorded from *T. atun* worldwide (Table 1), but little is known about their host-parasite relationships. It appears that the intensity of nematode and cestode infections is positively correlated to host size (Mehl 1970; Wierzbicka & Gajda 1984). The most notorious parasites of *T. atun* are without doubt *K. thyrsites* and anisakid nematodes. *Kudoa thyrsites* can cause the myoliquefaction of up to 5% of the catch, a condition known locally in South Africa as 'pap-snoek' (Crawford 1989), while anisakid nematodes can be a human health hazard (Nieuwenhuizen *et al.* 2006). Further investigations are required to establish the potential ecological, economic and health significance of parasite infracommunities of *Thyrsites atun* in southern Africa.

1.8: Objectives of this Dissertation

This dissertation seeks to improve our knowledge on the composition and structure of parasite infracommunities of snoek in southern Africa and evaluate potential implications for fishery management and conservation of marine resources in South Africa. More specifically, the following questions are addressed:

- Which species of parasites use snoek (*T. atun*) as host?
- What are the determinants of infection?
- How does the parasitic community vary with host sex, size and seasonality of capture?
- Which parasite species could serve as biological tags for snoek in the Benguela?

Table 1. Parasites known to use *Thyrsites atun* as host for at least one life-stage. (M: muscle, BC: body cavity, L: liver, G: gills, O: operculum, S: stomach, I: intestine, GB: gall bladder; NZ: New Zealand, AUS: Australia, SA: South Africa, ARG: Argentina; 1: Mehl 1970, 2: Hewitt & Hine 1972, 3: Wierzbicka & Gajda 1984, 4: Nieuwenhuizen *et al.* 2006, 5: Sobecka 2012, 6: Gilchrist 1924, 7: Barnard 1955b, 8: Fernandes *et al.* 2009).

Parasite	**Site of Infection**	**Country**	**References**
Cestoda			
Molicola uncinatus (Linton 1924)	M	NZ	1, 2, 3
Lacistorhynchus tenuis (van Beneden, 1858)	M, BC	NZ	2
Nybelinea thyrsites Korotaeva, 1971	M, BC	NZ	2
Tetrarhynchus sp. 1	M	AUS	1
Tetrarhynchus sp. 2	M	AUS	1
Hepatoxylon trichiuri (Holten, 1802)	BC, L	NZ	3, 5
Copepoda			
Caligus pelamydis Kroyer, 1863	O	NZ	2
Paralernanthropus foliaceus (Goggio, 1905)	G	NZ	2, 3
Caligus zei Normann & Scott T., 1906	Not specified	SA	7
Digenea			
Lampritrema meischeri (Zschokke, 1890) Margolis, 1962	S	ARG	8
Lecithochirium australis Manter, 1954	S	NZ	2
Syncoelium thyrsitae (Crowcroft, 1948)	G, S, I	NZ	2, 3
Monogenea			
Winkenthughesia thyrsites (Hughes, 1928)	G	AUS, NZ	2, 3
Udonella caligorum Johnson, 1835	G	NZ	2
Nematoda			
Anisakis sp. (thought *simplex*)	M	NZ	1
Anisakis pegreffii (Campana-Rouget & Biocca, 1955)	BC	SA	4
Thynnascaris aduncum (Rudolphi, 1802)	S, I	NZ	2, 3
Contracaecum sp. larva	S, BC	NZ	2
Pseudoterranova decipiens (Krabbe, 1878)	M	NZ	3
Porrocaecum sp. larva	M, BC	NZ	2, 3
Myxozoa			
Ceratomyxa minuta (Meglitsch, 1960)	GB	NZ	2
Ceratomyxa sp. *a*	GB	NZ	2
Leptotheca annulata (Meglitsch, 1960)	GB	NZ	2
Kudoa thyrsites (Gilchrist, 1924)	M	AUS, SA	1

Materials and Methods

2.1: Study Area

The South African marine environment, which harbours approximately 12, 915 species, is a recognized hotspot of marine biodiversity (Roberts *et al.* 2002). This high level of diversity has been attributed to the contrasting oceanic regimes prevailing off the East and West coasts respectively (Branch *et al.* 2010; Griffiths *et al.* 2010). The west coast is influenced by the cold, north-flowing Benguela Current and the east coast is dominated by the warm Agulhas current (Figure 3), although its influence is limited inshore south of Durban due to a widening of the shelf (Branch *et al.* 2010).

The Benguela system, situated along the south-western coast of Africa, is the primary habitat of snoek off Africa (Griffiths 2002, 2003). The Benguela ecosystem can be divided into two subsystems (northern and southern) separated by the Lüderitz upwelling cell and the Orange River Cone, a region referred to as the LUCORC (Lett *et al.* 2007). The LUCORC can act as a barrier to the dispersal of marine species (Lett *et al.* 2007) and is thought to be a major driver of fish population structure in the Benguela ecosystem (Griffiths 2003).

2.2: Sampling of Host Population

Snoek examined during this study were caught mainly within the southern Benguela ecosystem, i.e., west of Cape Agulhas. A single sample was obtained from the south coast, inshore of the warm Agulhas current (Figure 3). Snoek were sampled monthly over a one year period (April 2013 – March 2014, Table 2), from commercial handline catches that were landed at various slipways and harbours along the South African coast (Figure 3). Samples were also collected by on-board observers from the by-catch obtained by commercial trawlers operating further offshore. Fish were kept frozen at -20°C in labelled bags prior to processing. While every attempt was made to obtain samples from a number of locations for each month, the nomadic nature of snoek and its associated directed fishery (Dudley 1987; Griffiths 2002) precluded this (Table 2). For the purposes of statistical analysis, samples were aggregated by seasons; March and April were considered as autumn, winter encompassed May through to August, spring covered September and October and summer ran from November through to February (Table 2).

2.3: Processing Samples

2.3.1: Host dissection and data collection

Prior to processing, fish were thawed to room temperature, measured to the nearest millimeter (total length and fork 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 the presence of parasites. Next, the gills and eyes were removed and examined under a dissecting stereomicroscope (Nikon SMZ800). The otoliths were removed, washed in water and dried before being stored in a labelled vial for later age determination. The body cavity was cut open and mesenteric fat lining the stomach was scored on a three-staged scale (Table 3). At that point the fish was sexed and the gonads were weighed to the nearest gram. Gonad maturity stages were assigned following the five macroscopic stage system described by Griffiths (2002) (Table 4).

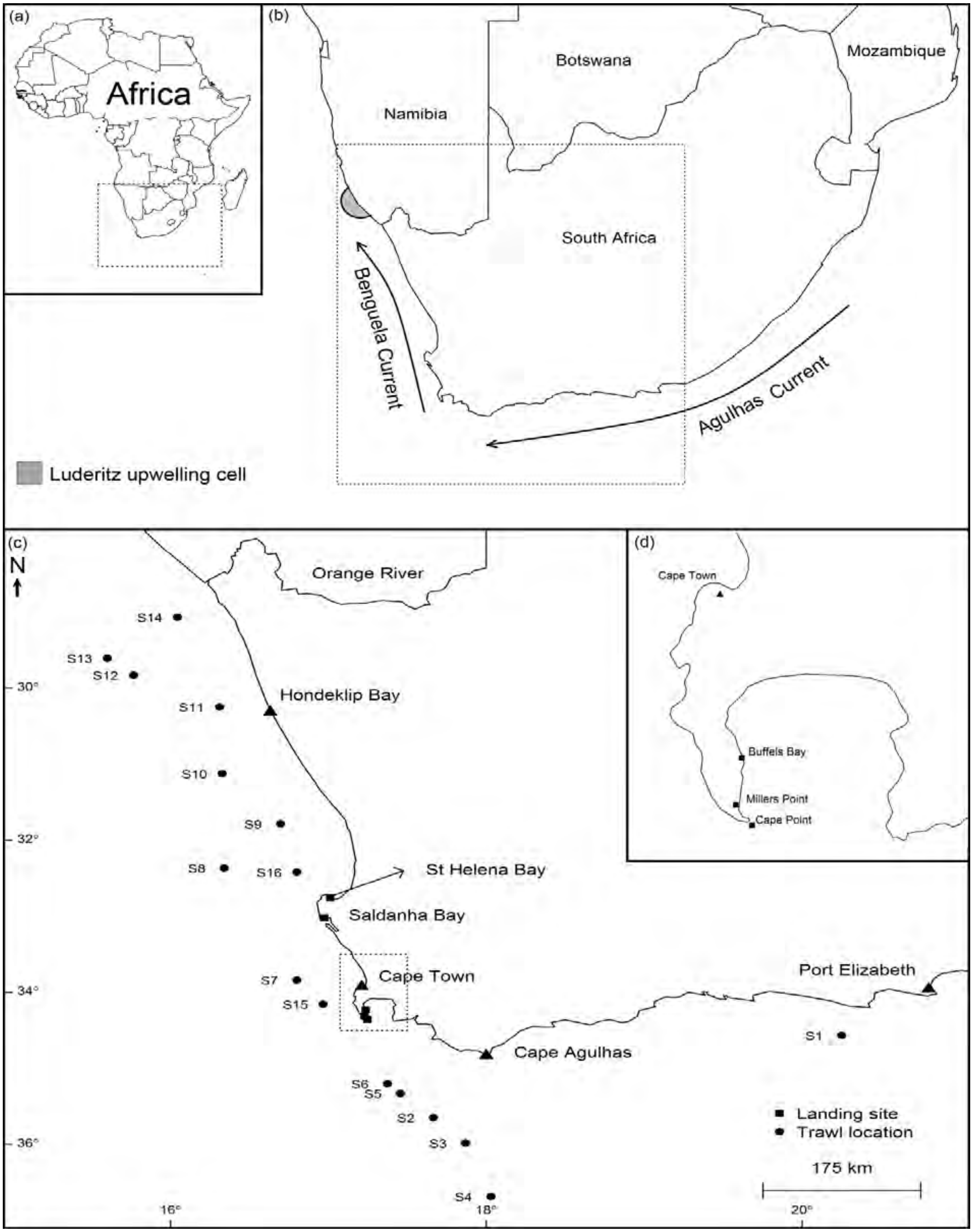

Figure 3. (a) The study area within southern Africa (b) showing major oceanographic features and (c, d) the snoek sampling sites off South Africa.

Table 2. The seasonality and number of snoek sampled from each trawl station and landing site around the South African coast between 2013 and 2014 (n: the number of snoek sampled per season).

Trawl stations/ Landing sites	Autumn n = 31	Winter n = 75	Spring n = 78	Summer n = 26
S1		23		
S2			27	
S3			6	
S4			9	
S5			12	
S6			14	
S7	3			
S8	2			
S9	2			
S10	1			
S11	1			
S12	2			
S13	3			
S14	3			
S15				3
S16				3
Buffels Bay		10	10	
Cape Point				20
Miller's Point		12		
Saldanha Bay		10		
St Helena Bay	14	20		

The weight of the host's stomach contents was recorded and the proportions, by weight, of the different prey items present were calculated after accounting for any bait present. For the purposes of diet analysis, prey items were assigned to one of the five categories described in Table 5. The diversity and abundance of parasites present externally, in the body cavity and on various organs was recorded. The gastro-intestinal tract was opened 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.

Table 3. Description of the fat stages for *Thyrsites atun* based on fat cover on internal organs. Fat strings refer to mesenteric fat deposits along the internal organs of snoek (Griffiths 2002).

Fat stage	Description
1	No or very small (< 5 mm) fat strings lining the internal organs
2	Fat strings cover < 50% of the internal organs
3	Fat strings cover > 50% of the internal organs

Squash samples of tissue from the dorsal muscle, liver, heart, kidneys, spleen, gonads, brain and gall bladder were examined using a compound microscope (Leica ICC50) at magnifications varying from 40x to 1000x. The presence of any parasites on the slides was noted and an attempt at quantification of infection intensity was made by recording the abundance of the particular parasite on five fields of view at 400x magnification. In order to ensure consistency, tissue for microscopy was always sampled from the same position on the fish or its organs.

2.3.2: Preservation and identification of parasites

Voucher specimens of each macroparasite species encountered were preserved in 70 % ethanol for identification purposes. Copepods and nematodes were cleaned of excess mucus and debris using a fine brush before fixation and preservation in 70 % ethanol. Acanthocephalans and cestodes were relaxed in cold, fresh water to induce tentacle extrusion and were then preserved in 70 % ethanol. Micrographs of microscopic parasites infecting the gall bladder and the muscle tissue were taken with a Leica ICC50 compound microscope and the necessary software (LAS EZ Suite) (Leica Microsystems 2008).

Parasites were identified to the lowest possible taxonomic level based on their morphological features. Literary resources used for the identification of parasites are given in the appendix. The expert knowledge of Prof. McKenzie (University of Aberdeen) and Dr. Reed (University of Cape Town) was also put to contribution during the identification process.

Table 4. Macroscopic appearance of snoek (*T. atun*) gonad maturity stages (after Griffiths 2002).

Stage	Ovaries	Testes
1. Immature and resting	Ovaries appear as clear, pinkish, or translucent orange tubes. Eggs are not visible to the naked eye	Testes thread-like and clear, to ribbon-like and pinkish white in colour
2. Active	Eggs, visible to the naked eye as yellow granules, do not occupy all the space in ovaries. Little increase in ovary diameter	Testes are wider, triangular in cross-section, and beige or cream in colour. Sperm extruded if gonad cut and squeezed
3. Ripe	Ovaries opaque and orange to yellow in colour. Increase in ovary diameter. Eggs occupy all the available space	Testes still larger in cross-section, softer. Testes become creamier due to large amounts of sperm
4. Ripe or running	Ovaries considerably larger in diameter, amber in colour with a substantial proportion of hydrated eggs	Sperm is freely extruded when pressure is applied to the abdomen of the whole fish
5. Spent	Ovaries are reduced in size, similar to stage-1 ovaries. A few aspherical yolked oocytes may be present	Testes are shrivelled in appearance. Mottled beige and cream in colour. Semen may still ooze out if pressure is applied to the abdomen

2.4: Statistical Analyses

2.4.1: Exploratory data analysis

Exploratory data analysis (EDA) is a crucial first step in the analysis of any type of data, a step often by-passed by less statistically aware researchers worldwide (Zuur *et al.* 2010; Borcard *et al.* 2011). Ecological data, in its raw form, regularly violates the underlying assumptions of statistical techniques commonly used. EDA is aimed at detecting such violations, thereby enabling one to choose the most appropriate statistical technique for a particular situation (Zuur *et al.* 2010; Borcard *et al.* 2011). When the most common assumptions (e.g. normality, collinearity, heteroscedasticity, independence of observations) are not conformed to, two options are available to the ecologist. The data can either be transformed in an attempt to coerce it into normality and apply normal parametric methods (e.g. Latham & Poulin 2002; Rombouts *et al.* 2009) or a different technique (e.g. non-parametric tests, generalized linear model) can be applied to the untransformed data (e.g. Podolska & Horbowy 2003; Paterson *et al.* 2012; Cañás *et al.* 2013). The EDA protocol recommended by Zuur *et al.* (2007, 2010) was used as a guideline.

The normality and heteroscedasticity of continuous variables (fl, mass, condition, gsi) and those of the parasite abundance data were assessed graphically via histograms and by means of the Shapiro-Wilks test. Potential outliers were identified with boxplots. Pair-wise scatterplots and simple linear regression were employed to detect collinearity between continuous variables. Chi-square tests of independence were used to assess whether there was a relationship between categorical variables (fat stage, gonad stage, seasons).

Table 5. Description of the prey categories used to characterize the stomach contents of snoek.

Category	Prey items
Clupeoid	*Engraulis capensis*, *Etrumeus whiteheadi*, unidentified clupeoid
Mackerel	*Trachurus trachurus capensis*
Pelagic crustaceans	*Euphausia lucens, Themisto gaudichaudii*
Merluccius sp.	*Merluccius* sp.
Invertebrates	*Pterygosquilla armata*, unidentified squid species

2.4.2: The hosts' characteristics

An understanding of the basic biology of a host species is critical to any parasitological investigation. As mentioned earlier, variability in life-history traits of fish hosts can have a significant impact on the rate of acquisition and loss of parasites (Sasal *et al.* 1997; Arneberg *et al.* 1998; Lo *et al.* 1998). The sex, size, condition, mesenteric fat reserves, reproductive status and diet of the snoek examined were analysed, as described below, in order to gain an understanding of the host sample's characteristics to support or refute parasitological interpretations.

As expected, EDA revealed the non-normal distribution of host size, non-parametric tests were employed. The Mann-Whitney test was used to assess whether there were any differences in host size between the sexes and seasonal variation was evaluated by means of the Kruskal-Wallis test with post-hoc pairwise comparisons.

Fish weight is commonly used to report catch data (e.g. during angling competitions, commercial fishing) as well as to assess growth and production of fish populations (Anderson & Neumann 1996). Variation in the weight of fish of similar lengths makes direct interpretation of length and weight data complicated and may lead to erroneous conclusions (Anderson &

Neumann 1996). An index of condition integrates both parameters and may make interpretation easier. In this study, Fulton's condition factor (K) was calculated for each fish, according to the equation given below, where W is the weight of fish in grams and FL is the fork length of fish in millimeters (Anderson & Neumann 1996).

$$K = \frac{W}{FL^3} \times 100\,000 \qquad \text{Equation 1}$$

One of the drawbacks of using K is that it varies with length of fish, such as *T. atun*, that do not display isometric growth (Froese 2006). Therefore comparisons should be constrained to fish of similar lengths. Seasonality in condition, within sexes, was then investigated using the Kruskal-Wallis test with post-hoc pairwise comparisons. The seasonality in mesenteric fat content, which is expected to track body condition, was assessed by way of a Chi-square test.

The spawning season of *T. atun* was determined using a combination of the visual assessment of gonad maturity stage and seasonality in the gonado-somatic index (GSI). The GSI, a measure of the size and development of fish gonads relative to the weight of the fish, can be used to detect the spawning season. Its monthly progression was assessed visually and statistically via the Kruskal-Wallis test with post-hoc pairwise comparisons. The GSI was calculated following Griffiths (2002) using the equation below:

$$\mathrm{GSI} = \frac{\text{Gonad Mass}}{\text{Fish Mass} - (\text{Gonad Mass} + \text{Stomach Content Mass})} \qquad \text{Equation 2}$$

The analysis of stomach contents is widely used to determine the dietary preferences of fish and assess their trophic ecology although other techniques such as stable isotope analysis are now available (Smale 1992; De Crespin De Billy *et al.* 2000; Jardine *et al.* 2003; Sinisalo *et al.* 2006). Analysis of stomach contents allows data to be recorded at a better resolution, often at the species level. The diet of fish has been shown to be a major determinant of its endoparasite

parasite diversity (e.g. Klimpel *et al.* 2006; Bertrand *et al.* 2008; Lagrue *et al.* 2011). It is therefore important to take ontogenetic, seasonal and spatial variability in the host's diet into account during a parasitological investigation.

In a comprehensive review of fish stomach content analysis, Hyslop (1980) emphasized the need for both "the amount and the bulk" of the food items to be recorded and analyzed together. An index of relative importance (IRI), which integrates both measures, was calculated for each prey category as the product of % W and % F. % W is the total mass of a particular prey type over the total prey mass and % F is the frequency of stomachs containing a particular prey item over the total number of guts examined, both are expressed as a percentage.

$$\mathrm{IRI} = \%W \times \%F \qquad \text{Equation 3}$$

Following Griffiths (2002), the numerical abundance of food items was not used to calculate the IRI as it could bias the results of the analysis towards small prey items, such as euphausiids, that are preyed upon in large quantities.

2.4.3: Determinants of Parasite Infestation

This study focuses on the relationship between parasite prevalence and infection intensity with variables and host traits that have been identified from previous studies and preliminary analyses as potential predictors of parasite infestation level in fish (Lo *et al.* 1998; Neff & Cargnelli 2004; Paterson *et al.* 2012; Le Roux 2013; Cañás *et al.* 2013). The influence of these variables and their interactions (Table 6) on the prevalence and infection intensity of snoek parasites was investigated by means of generalized linear models (GLMs). Due to the nomadic nature of snoek and previous research strongly suggesting the presence of a single stock off South Africa (Griffiths 2002), no analyses in relation to capture localities were conducted.

Table 6. Description of the candidate variables considered for the analysis of parasite prevalence and infection intensity utilizing GLMs.

Variable	Description
FL	Host size (fork length (mm))
Condition	Condition factor of host
GSI	Gonado somatic index of host (proxy for reproductive status)
Fat	Mesenteric fat stage
Maturity	Based on Griffiths (2002), juveniles < 730 mm FL, adults ≥ 730 mm FL
Sex	Host sex
Season	Season during which sample was collected
Sex × FL	Interaction between sex and host size
Sex × Condition	Interaction between sex and host condition
Sex × GSI	Interaction between sex and host reproductive status
Sex × Season	Interaction between sex and season
FL × Season	Interaction between host size and season

Generalized linear modelling, pioneered by Nelder and Wedderburn (1972), proposes a unified framework for the application of techniques previously thought to be incompatible with one another (McCulloch 2000). By utilizing available techniques, such as the use of link functions and iterative model fit, Nelder & Wedderburn (1972) seamlessly put together probit regression, linear models and contingency tables. A GLM has three components: (i) the response variable, (ii) explanatory variables and their associated coefficients and (iii) a monotone link function (Dobson 2002). Another major advantage of GLMs is that they can handle non-normal, binomial and overdispersed data through the use of the appropriate link function and quasi-likelihood estimation methods (Nelder & Wedderburn 1972; McCulloch 2000). GLMs also allow for specific interactions to be modeled, although the link function inherently induces interactions between explanatory variables (Tsai & Gill 2013). The difference between the effects of interactions induced by the link function and that specified by the user can be considerable (Tsai & Gill 2013). A cautious interpretation of interaction coefficients is therefore required.

Previously curtailed by lacking computational power (McCulloch 2000), the use of GLMs has now been made widely accessible with the advent of increasingly powerful computers.

Two generalized linear models were used to investigate the relationship between parasite infection measures (prevalence and infection intensity) and predictor variables (Table 6). The global model used for each analysis was of the form:

$$G(\chi_i) = FL + Condition + GSI + Fat + Maturity + Sex + Season + Sex \times FL + Sex \times Condition + Sex \times GSI + Sex \times Season + FL \times Season + \varepsilon_i \quad \text{Equation 4}$$

where G is a link function and χ represents either prevalence or infection intensity. The link function is used to specify the relationship between the mean of the response variable to each linear predictor included in the model (McCullagh & Nelder 1989; Lindsey 1974). The link function is an aid to computation for models with a linear part and becomes obsolete when dealing with nonlinear models (Lindsey 1974). The logit link function was used for models assessing prevalence, for which the error structure was assumed to be binomial and the logarithmic link function was employed for the analysis of parasite infection intensity as a zero-truncated negative binomial error structure was assumed due to high overdispersion of the response variable.

The Akaike's information criterion (AIC) is an information theoretic approach to model selection (Lindsey 1974; Dobson 2002). The AIC, a function of the log-likelihood function adjusted for the number of covariance parameters (Dobson 2002), reports the difference observed between competing models in expected predictive power (Bolker *et al.* 2009). This allows for an easy comparison between models, with the model exhibiting the lowest AIC being considered the most appropriate. The quasi-AIC (QAIC), a variant of the traditional AIC was preferred to AIC for its ability to cope with overdispersed data for the analysis of infection intensity. The Durbin-

Watson test was used to detect autocorrelation amongst the selected set of explanatory variables. When autocorrelation was detected, the variables most likely to be the cause of autocorrelation were dropped sequentially and the model was reassessed with the AIC and a goodness-of-fit measure (pseudo R^2). If a more parsimonious, nested, combination of variables exhibiting no autocorrelation was found within 2 AIC of the top-ranked model, it was adopted as the preferred model. Otherwise, the model initially selected by the AIC was carefully interpreted.

Analysis of deviance was conducted to test the significance of sequentially adding each selected explanatory variable to the preferred model (McCullagh & Nelder 1989). This test uses the deviance of linear models, deviance being approximated by a Chi-squared distribution, as a measure of goodness of fit (Lindsey 1974). Both McCullagh & Nelder (1989) and Lindsey (1974) warn about its use with non-normal models and recommend careful interpretation. The deviance or goodness of fit, explained by the final model can be expressed as a pseudo coefficient of variation (R^2) (Weston 2013), which is the ratio of the final model to the deviance of the null model, expressed as:

$$R^2 = 1 - \frac{Residual\ deviance}{Null\ deviance} \qquad \text{Equation 5}$$

Before any interpretations could be made it was important to validate the models. Dobson (2002) recommended the use of residual plots to ensure the adequacy of the final model. Residuals were plotted against explanatory variables used as well as the fitted values to assess models.

In order to ensure that the models were fed an adequate sample, infection intensity was only modelled for parasite taxa exhibiting a prevalence of more than 45% and for which abundance data was available (*Anisakis* spp., *M. uncinatus*, *N. fradei*, *C. dakari*, *H. conifera*) while the prevalence of all taxa infecting at least 20% of the sample was modelled. The prevalence of *Anisakis* spp. and *Kudoa thyrsites* was not modelled since both occurred at a very high prevalence, 100% and 97.1% respectively, and would not have lent themselves well to modelling.

2.4.4: Parasite community structure

The gender-specific, ontogenetic and seasonal variation in the snoek's parasite infracommunity was investigated by way of multivariate statistical techniques, as outlined by Field *et al.* (1982). Since a parasite's absence or presence was recorded as either abundance or presence-absence data, the whole parasite data matrix was presence-absence transformed. A resemblance matrix, based on Jaccard's index for its suitability to deal with presence-absence data, was then generated (Clarke & Gorley 2006). Nonmetric multidimensional scaling (MDS) was used to depict variability in the parasite infracommunity with respect to seasons, sex and size class. Community composition variability was tested for significance using ANOSIM (analysis of similarity). ANOSIM is analogous to the univariate ANOVA, but it has no distribution and compares rank similarity, tests pre-selected groups against random groups in ordination space and generates an R value which lies between -1 and +1 (Chapman & Underwood 1999). An R value of zero (0) indicates that there is no difference among groups, while a value of one (+1) indicates that all samples within groups are more similar to one another than any samples from other groups (Clarke & Gorley 2006). Negative values of R occur under specific circumstances (e.g. patchy distribution) and should not be dismissed as anomalous as it may hold clues to identifying issues with the sampling procedure or the underlying ecological processes at work (Chapman & Underwood 1999). Finally, the SIMPER analysis was used to identify which parasite species were characteristic of significant shifts in community structure between seasons. The ontogenetic and seasonal variation in diversity was tracked by means of the Simpson's diversity index.

All calculations and statistical procedures were conducted in R (R Development Core Team 2014), unless otherwise clearly stated in the text. R packages used for EDA, analyses and modelling include ‘MASS’ (Venables & Ripley 2002), ‘MuMIN’ (Barton 2013), ‘pgirmess’(Giraudoux 2013), ‘lmtest’ (Zeilis & Hothorn 2002), ‘vcd (Meyer *et al.* 2013)’, ‘vcdExtra’ (Friendly 2014), ‘gplots’ (Gregory *et al.* 2014), ‘maps’(Becker *et al.* 2013a), ‘mapdata’ (Becker *et al*. 2013b), ‘sp’ (Bivand *et al.* 2013), ‘maptools’ (Bivand & Lewin-Koh 2014). Multivariate analyses were supported by the packages ‘vegan’ (Oksanen *et al.* 2013) and ‘picante’ (Kembel *et al.* 2010).

Results

3.1: Exploratory Data Analysis

Between April 2013 and March 2014, 210 snoek caught in South African waters (Figure 3, Table 2) were examined for biological and parasitological data. The fish ranged from 411 mm to 1040 mm FL and weighed between 323 and 5687 grams. The sample comprised 120 females and 90 males.

A visual assessment of the distribution of fork length (FL) and the GSI, by means of histograms, showed that both were non-normally distributed. FL was biased towards larger hosts while the GSI was strongly right skewed. The Shapiro-Wilk test, conducted on FL and GSI also suggested a strong deviation from normality ($p < 0.0005$). Host weight conformed to the assumptions of normality ($p = 0.3846$). Condition appeared to be reasonably normally distributed but the results of the Shapiro-Wilk test disagreed ($p = 0.001179$). The distribution of parasite species recorded as abundance data as well as species richness displayed a severe right skewness in their distribution and their non-normal nature was confirmed by the Shapiro-Wilks test ($p < 0.0001$). The assessment of collinearity between the continuous explanatory variables (fork length, mass, GSI and condition) showed that only FL and mass displayed a significant correlation ($R^2 = 0.84$, df = 208, $p < 0.0001$).

3.2: Host Sample Characteristics

The sex ratio of line caught snoek was significantly biased in favour of females ($\chi^2 = 6.2402$, df = 1, $p = 0.01249$) while for trawl caught snoek the sex ration did not differ from unity ($\chi^2 = 0.0702$, df = 1, $p = 0.791$). The fork length (FL) of fish differed significantly between the sexes ($U = 6987$, $p = 0.0002718$). Females had a mean FL of 833.3 ± 77.78 mm while males averaged 779.2 ± 108.11 mm. Seasonally, fork length varied significantly for both females ($\chi^2 = 28.9112$, df = 3, $p < 0.0001$) and males ($\chi^2 = 33.0673$, df = 3, $p < 0.0001$) (Figure 4). Post hoc pairwise tests showed that females caught in summer (749.4 ± 91.5 mm) were significantly ($p < 0.05$) smaller than those caught in winter (825.5 ± 69.7 mm) and spring (874.4 ± 63.8 mm) but did not differ from the autumn sample (817.2 ± 39.2 mm). Significantly smaller male hosts were sampled in summer (670.0 ± 64.9 mm) and autumn (689.3 ± 146.8 mm) compared to winter (809.1 ± 79.1 mm) and spring (831.9 ± 59.8 mm).

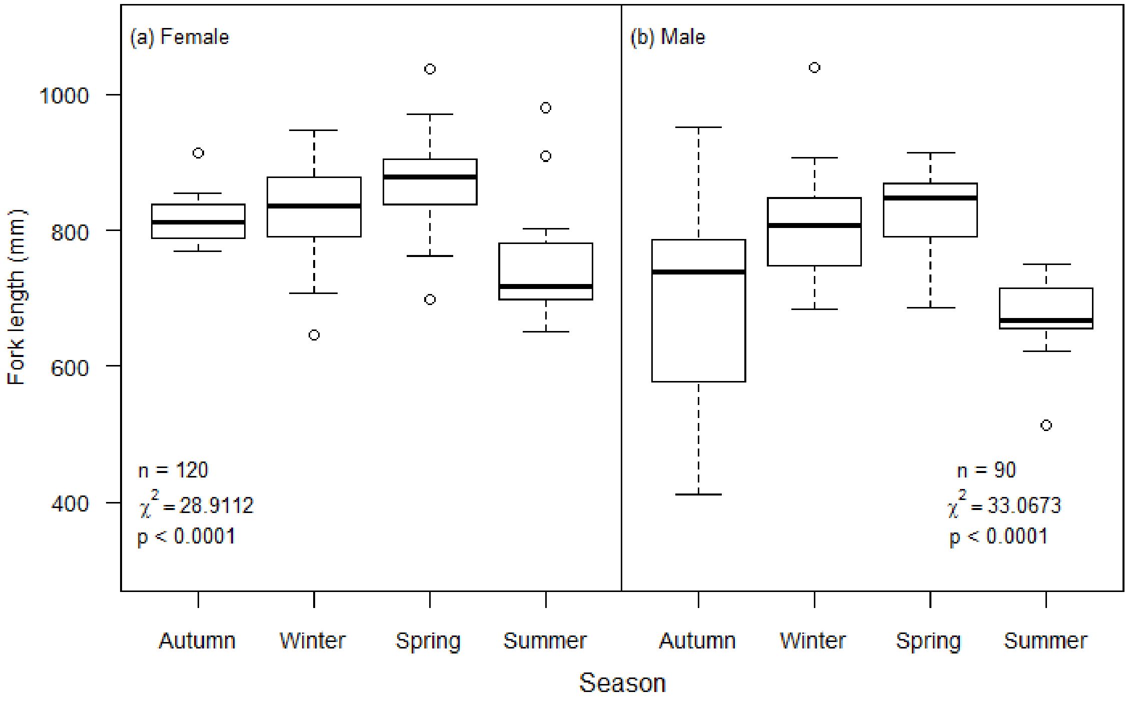

Figure 4. The seasonal variation in fork length of both (a) female and (b) male snoek examined between April 2013 and March 2014.

The condition (k) of both female ($\chi^2 = 19.4884$, df = 3, $p = 0.0002166$) and male ($\chi^2 = 25.5466$, df = 3, $p < 0.0001$) snoek exhibited significant seasonal variability. For both sexes, condition was at its highest in winter before decreasing rapidly to a minimum in spring before recovering throughout summer and autumn (Figure 5). Irrespective of host sex, the proportion of each mesenteric fat score varied seasonally ($\chi^2 = 90.3885$, df = 6, $p < 0.00001$). From November to June samples were dominated by hosts with a fat score of 2 while the incidence of fat score 1 increased between July and October. Mesenteric fat covering more than 50% of the stomach (score 3) were only recorded between February and June (Figure 6).

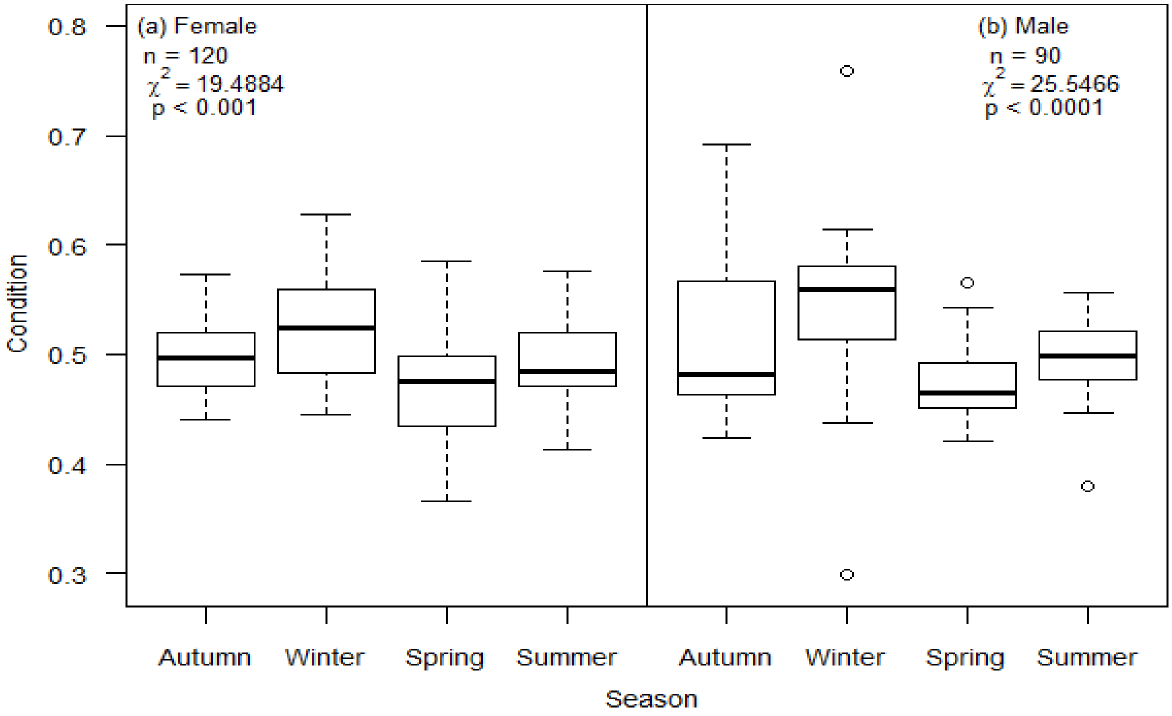

Figure 5. The seasonal variation in the condition of (a) female and (b) male snoek examined between April 2013 and March 2014.

The gonadosomatic index (GSI), an index of gonad maturity, showed significant variation across seasons for both females ($\chi^2 = 14.8143$, df = 3, $p = 0.001982$) and males ($\chi^2 = 21.6545$, df = 3, $p < 0.0001$). The significantly ($p < 0.05$) higher GSI observed in winter and spring, indicating increased investment in gonad development, suggest that the spawning season of snoek spans from May to October (Figure 7).

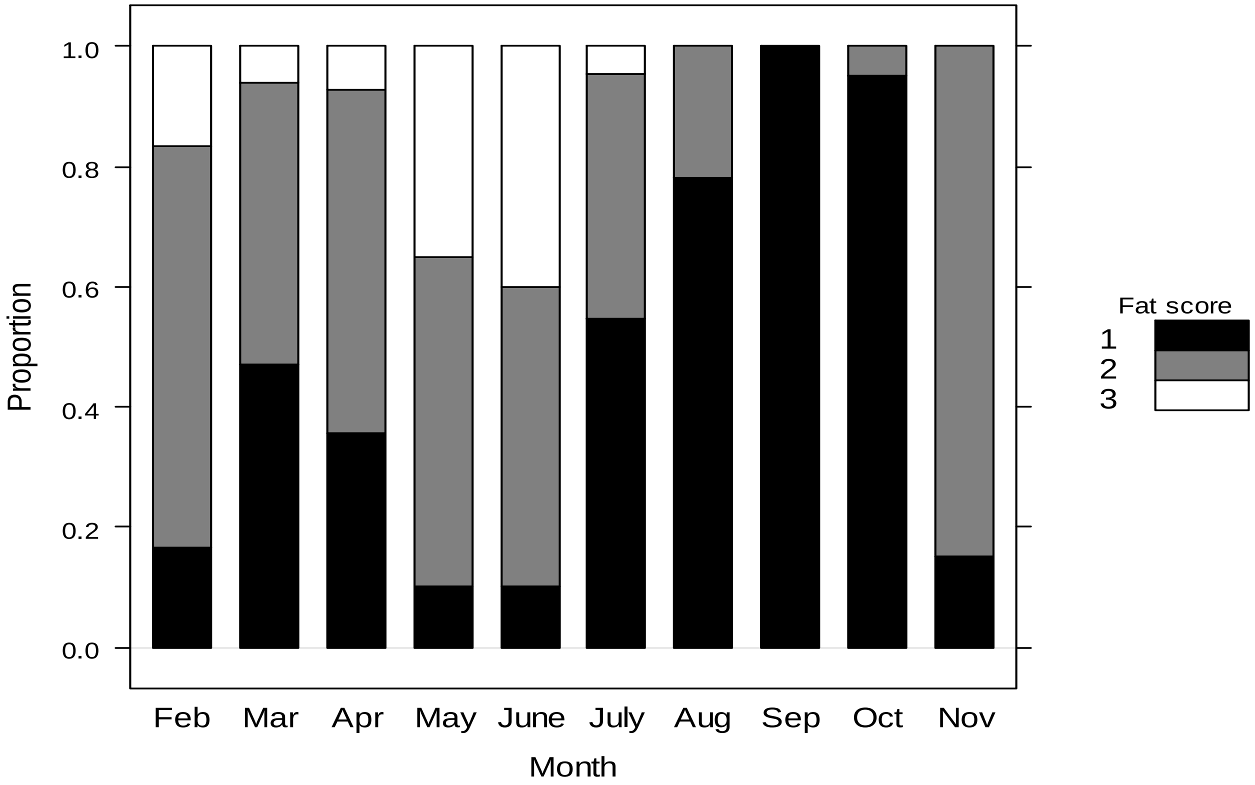

Figure 6. The proportion of different fat scores recorded in snoek over the course of the study.

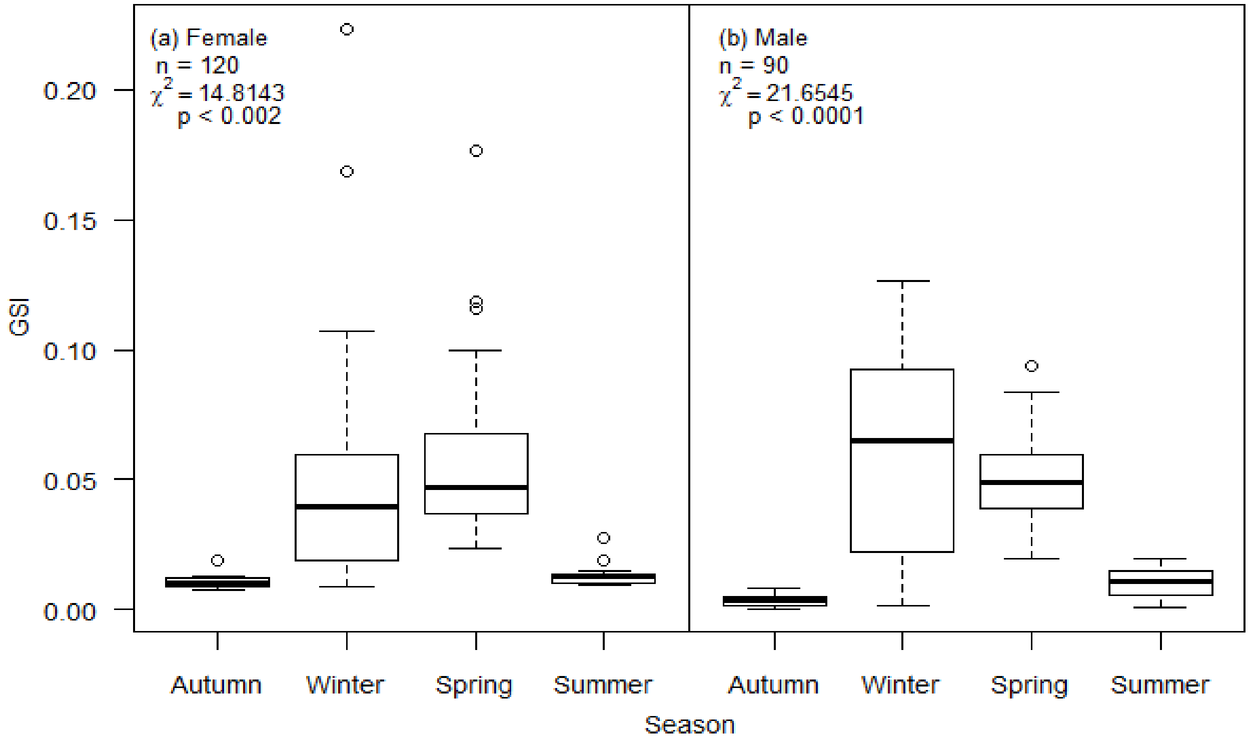

Figure 7. The seasonal variation in the gonadosomatic index (GSI) of (a) female and (b) male snoek examined between April 2013 and March 2014.

Sixty of the 210 snoek examined had empty stomachs. From the remaining 150 stomachs, 9 prey types (*Euphausia lucens*, *Themisto gaudichaudii*, *Engraulis capensis*, *Etrumeus whiteheadi*, unidentified clupeoids, *Trachurus trachurus capensis*, *Merluccius spp*., squid and *Pterygosquilla armata*) were distinguishable and were assigned to one of the five prey categories described in the methods section. Ranked by percentage frequency, clupeoids (53.3 %) dominated the snoek's diet, followed by *Trachurus* sp. (20 %), pelagic crustaceans (19.3 %), invertebrates (7.3 %) and *Merluccius* sp. (4.7 %). The index of relative importance (IRI) suggested a slightly different picture, with the invertebrates prey category ranking last instead of the merluciids (Figure 8).

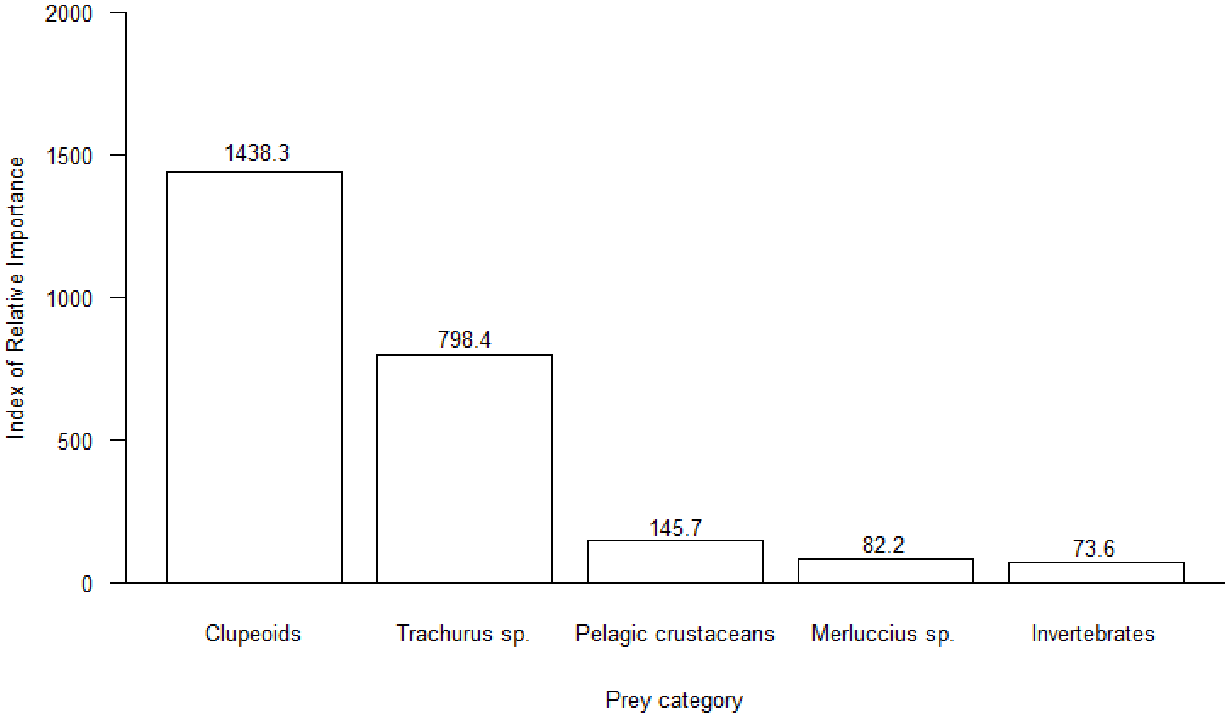

Figure 8. The contribution of different prey categories, according to their respective IRI (given above bars), to the diet of snoek examined between April 2013 and March 2014.

3.3: Parasite Assemblage

The parasite assemblage recovered from snoek comprised 16 taxa belonging to 6 parasitic orders (Table 7). Of these, 12 were identified to species level, another 3 to genus level and one could not be classified further than order level. The parasitic assemblage included 9 new host records and 4 new records for the Southern Benguela (Table 7). The endoparasitic assemblage included 3 acanthocephalans (*Bolbosoma vasculosum* Rudolphi, 1819, *Corynosoma australe* Johnston, 1937, *Rhadinorhynchus cadenati* (Golvan & Houin, 1964)), 3 cestodes (*Molicola uncinatus* (Linton 1924), *Hepatoxylon trichiuri* (Holten, 1802), *Tentacularia coryphaenae* Bosc, 1802), 2 nematodes (*Anisakis* spp. (Dujardin, 1845), *Pseudoterranova* sp. (Mosgovoi, 1951)), 2 myxosporean species (*Kudoa thyrsites* (Gilchrist, 1924), *Ceratomyxa* sp. (Thélohan, 1892)) and one unidentified digenean cyst (Digenea sp.). Five members of the Copepoda (*Caligus zei* Norman & T. Scott, 1906, *Caligus coryphaenae* Steenstrup & Lütken, 1861, *Caligus dakari* van Beneden 1892, *Hatschekia conifera* Yamaguti, 1939, *Nothobomolochus fradei* Marques, 1965) made up the ectoparasitic community. One epiparasitic species', *Udonella* sp., egg cases were recovered from the body surface of 13 out of 640 *C. dakari* specimens examined. No pathologies associated to parasitism were observed in snoek.

Table 7. Taxonomic composition, site of infection, overall prevalence, mean intensity (± sd) and the abundance's range of the parasite assemblage of snoek (*Thyrsites atun*) caught off South Africa (BC: body cavity, M: muscle, GB: gall bladder, G: gills, O: operculum, N: nares, I: intestine, GA: gill arches, [1]: new host record, [2]: new locality record).

Species	Site of Infection	Overall prevalence (%)	Mean infection intensity (± sd)	Range
Nematoda				
Anisakis spp.	BC	100.0	139 ± 170.19	0 - 1173
Pseudoterranova sp. [2]	BC	17.1	4.2 ± 3.06	0 - 13
Myxozoa				
Kudoa thyrsites	M	97.1		
Ceratomyxa sp.	GB	6.7		
Cestoda				
Molicola uncinatus [2]	M	90.0	31.5 ± 31.9	0 - 183
Hepatoxylon trichiuri	BC	47.1	3.2 ± 3.17	0 - 17
Tentacularia coryphaenae [1]	BC	26.7	3.2 ± 4.04	0 -24
Copepoda				
Nothobomolochus fradei [1]	N, G	96.2	16.2 ± 16.72	0 - 85
Hatschekia conifera [1]	G	51.0	3.3± 3.97	0 - 31
Caligus coryphaenae [1]	O	0.5	1	0 - 1
Caligus dakari [1, 2]	G, O	55.2	4.93 ± 5.08	0 - 33
Caligus zei	G, O	21.0	3.2 ± 2.11	0 -10
Acanthocephala				
Bolbosoma vasculosum [1, 2]	BC	7.6	1.5 ± 0.73	0 - 3
Corynosoma australe [1]	BC	41.4	21.4 ± 3.5	0 - 211
Rhadinorhynchus cadenati [1]	I	6.7	1.5 ± 0.76	0 - 3
Digenea				
Digenea sp. [1]	GA	38.1		

3.4: Determinants of Infection

3.4.1: *Anisakis* spp.

The AIC-based stepwise selection procedure identified a model consisting of three main effects and one interaction term as the most appropriate to model anisakid infection intensity (Table 8). Analysis of residual plots did not reveal any significant departures from the assumptions of the zero-truncated model used and no autocorrelation was detected ($D = 2.076$, $p = 0.5959$). Overall the model explained 47.3% of the observed variation. Analysis of deviance indicated that the infection intensity of *Anisakis* spp. in snoek was most strongly influenced by host length and to a lesser degree by sampling season, and host condition.

Table 8. Analysis of deviance for the zero-truncated negative binomial GLM fitted to the infection intensity of *Anisakis* spp. in snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	P
Null	209		434.21			
FL	208	1	260.64	173.57	39.97	***
Condition	207	1	252.30	8.34	1.92	**
Season	204	3	237.30	15.00	3.45	**
FL × Season	201	3	228.73	8.57	1.97	*

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

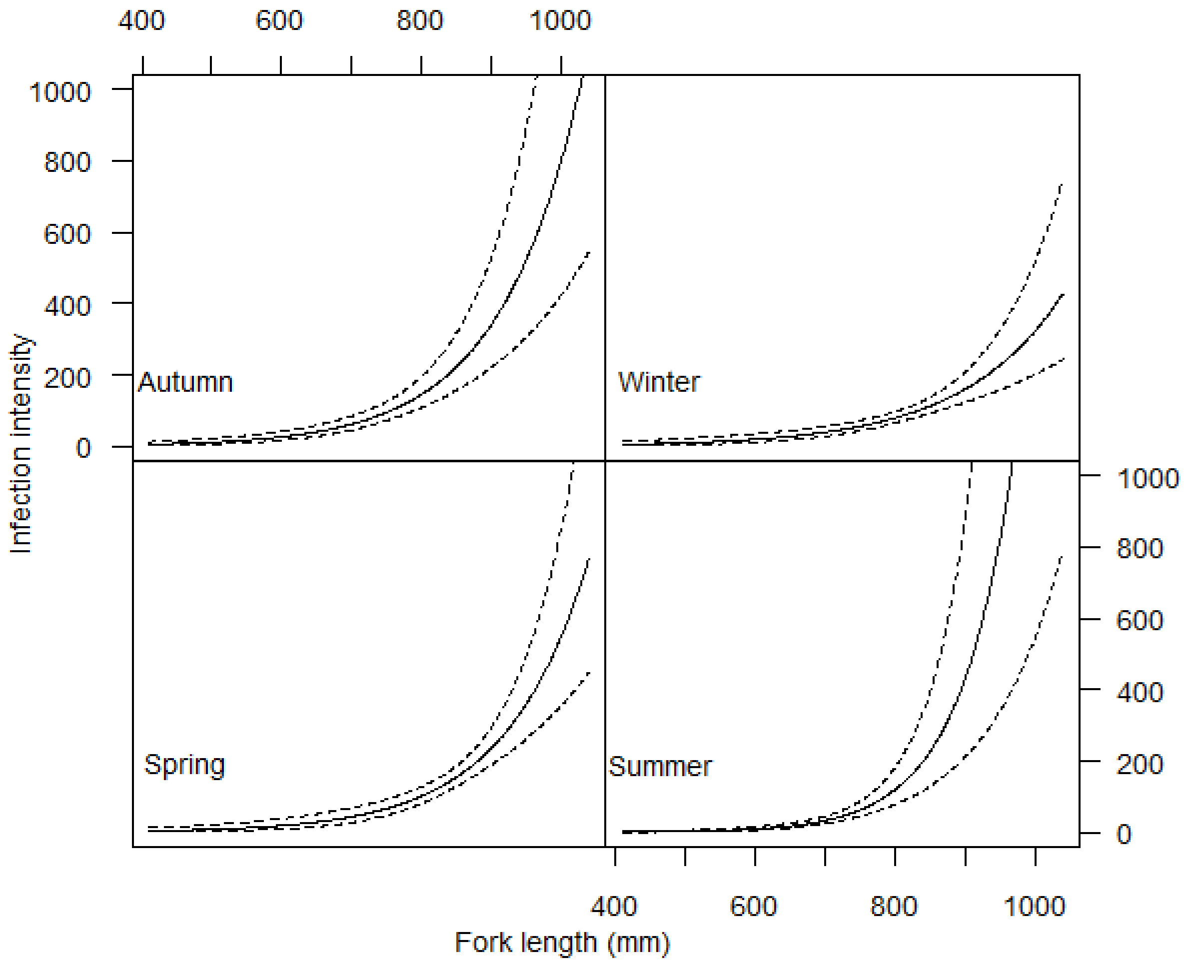

Figure 9. The predicted relationship between host size and *Anisakis* spp. infection intensity (± 95% CI) in snoek caught off South Africa.

The model predicted a non-linear, positive relationship between host length and *Anisakis* spp. infection intensity for all seasons (Figure 9). Irrespective of season and host size, a positive relationship between host condition and infection intensity was also predicted, as illustrated in Figure 10a. The model suggested significant seasonal variability in mean *Anisakis* spp. infection intensity in snoek (Figure 10b). Mean infection intensity was predicted highest in autumn and summer while snoek sampled in winter and spring were expected to harbour lower and less variable numbers of the parasitic nematode.

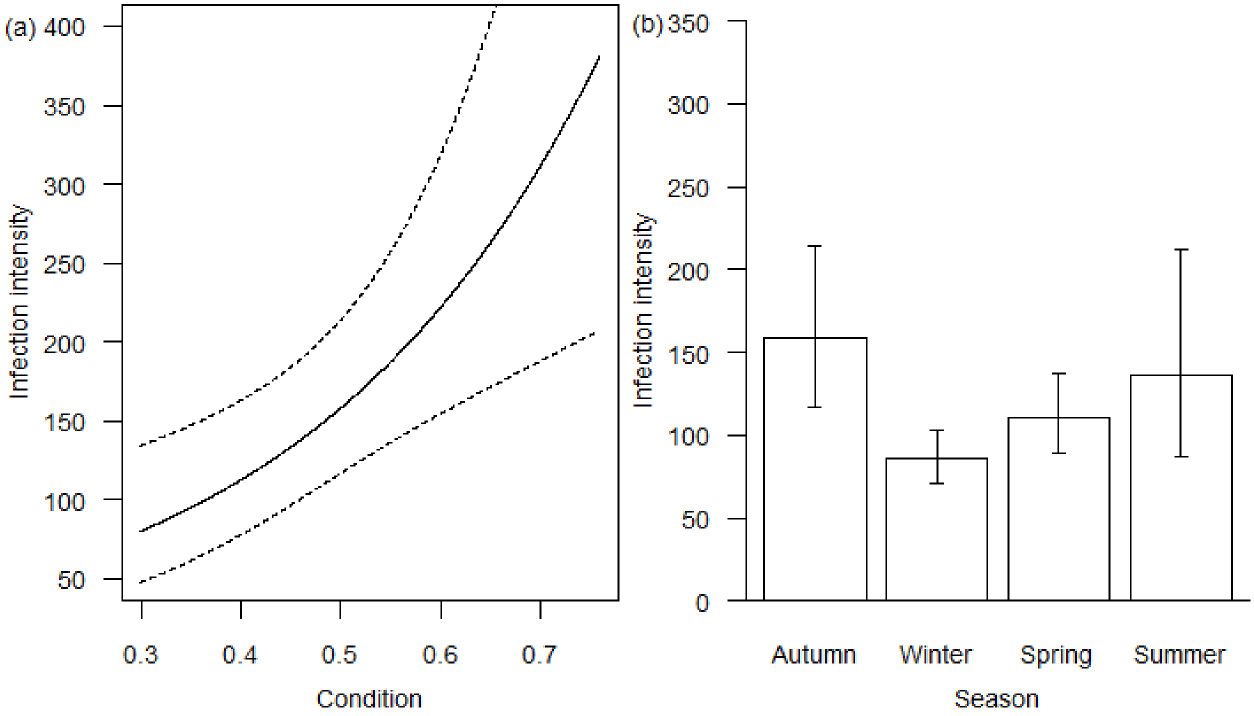

Figure 10. (a) The relationship between host condition and predicted mean infection intensity (± 95% CI) and (b) the predicted seasonal variability in *Anisakis* spp. mean infection intensity (± 95% CI) in snoek caught off South Africa.

3.4.2: *Molicola uncinatus*

According to the AIC, the combination of 'FL', 'Season' and 'FL × Season' make up the 'best' model for predicting *M. uncinatus* prevalence in snoek. No autocorrelation was detected amongst the selected explanatory terms (D = 1.922, p = 0.2016) and the residual plots revealed no unacceptable deviations from the assumptions of a GLM with binomial error structure. The model accounted for 30.3% of the variation in the data. Host length and seasonality strongly influenced the prevalence of *M. uncinatus* in snoek (Table 9).

Table 9. Analysis of deviance for the binomial GLM fitted to the prevalence of *Molicola uncinatus* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	P
Null	209		136.535			
FL	208	1	119.535	17.00	12.45	***
Season	204	3	105.909	13.63	9.98	**
FL × Season	201	3	95.156	10.75	7.88	*

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

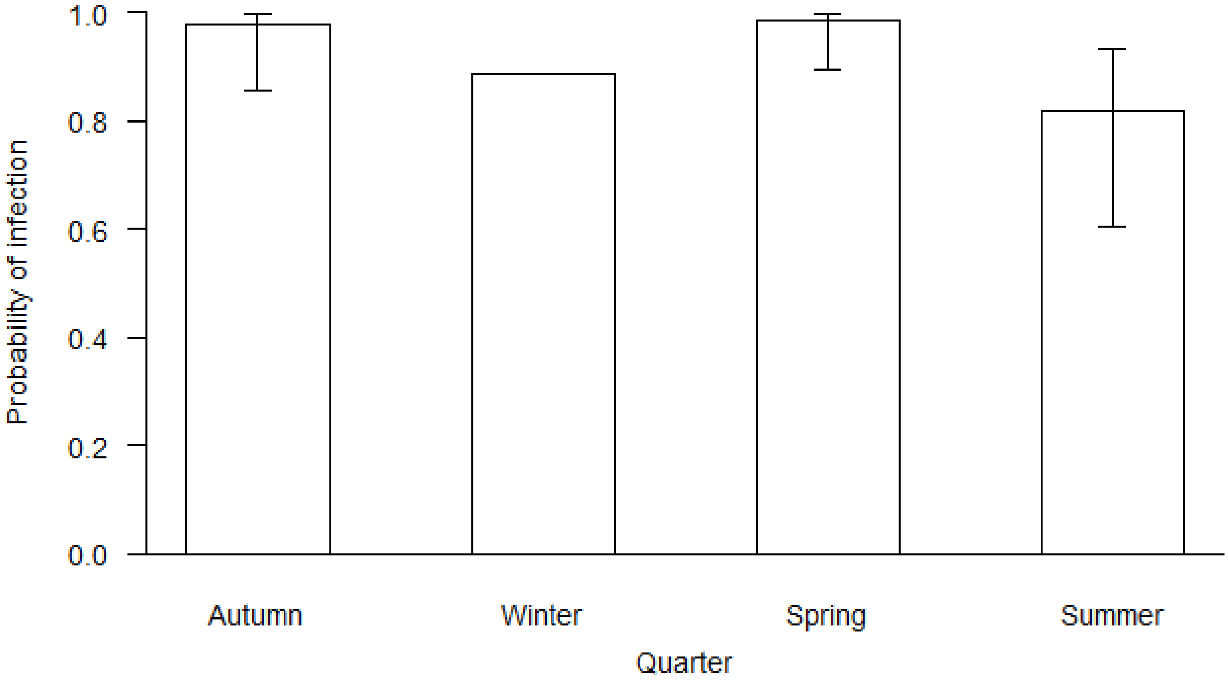

Figure 11. The predicted seasonal variability in mean (± 95% CI) probability of infection for *Molicola uncinatus* in snoek caught off South Africa

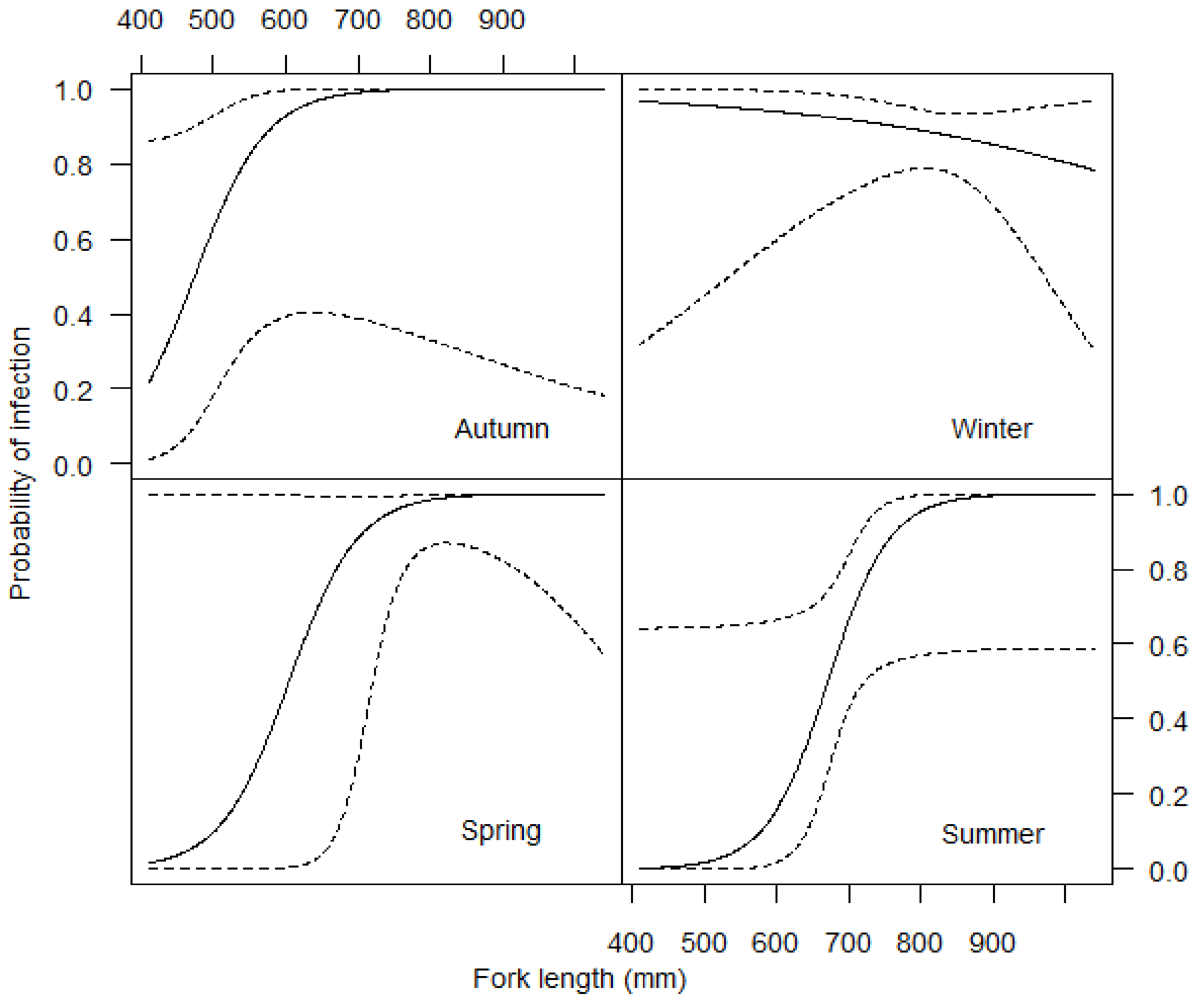

Figure 12. The relationship between host body size and the mean (± 95% CI) probability of infection for *Molicola uncinatus* in snoek caught off South Africa for all four quarters.

The model predicted a high (> 80%) mean probability of infection for snoek sampled in all seasons (Figure 11). The uncertainty in prevalence predictions was highest in summer, the same period during which the widest range of host sizes was examined (411 mm – 981 mm). A positive ontogenetic shift in probability of infection was predicted. The effect was only apparent in autumn, spring and summer since, irrespective of host size, high probabilities of infection were predicted for snoek caught in winter (Figure 12). The size-at-mean-50% infection for snoek caught in autumn, spring and summer was predicted at 474 mm, 605 mm and 671 mm respectively.

Table 10. Analysis of deviance for the zero-truncated negative binomial GLM fitted to the infection intensity of *Molicola uncinatus* in snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	P
Null	188		399.85			
FL	187	1	242.9	156.953	39.25	***
Condition	186	1	241.92	0.973	0.24	
GSI	185	1	229.75	12.177	3.05	***
Season	182	3	219.09	10.655	2.66	*
FL × Season	179	3	202.33	16.757	4.19	***

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

For the intensity model, variable selection according to the AIC, revealed that the infection intensity for *M. uncinatus* was best predicted by a combination of 'FL', 'Condition', 'GSI', 'Season' and 'FL*Season' (Table 10). A Durbin-Watson test revealed no autocorrelation in the preferred model (D = 1.926, p = 0.1986). Examination of residual plots highlighted no trends in the variance and revealed that the residuals were almost normally distributed, thereby validating the model. Overall, the model explained 49.4% of the variance in observed infection intensity. Host body size (FL), which alone accounted for 79.5% of the explained deviance, was by far the strongest predictor of infection intensity. The terms 'GSI', 'Season' and the interaction term only explained a small but nonetheless significant amount of the deviance.

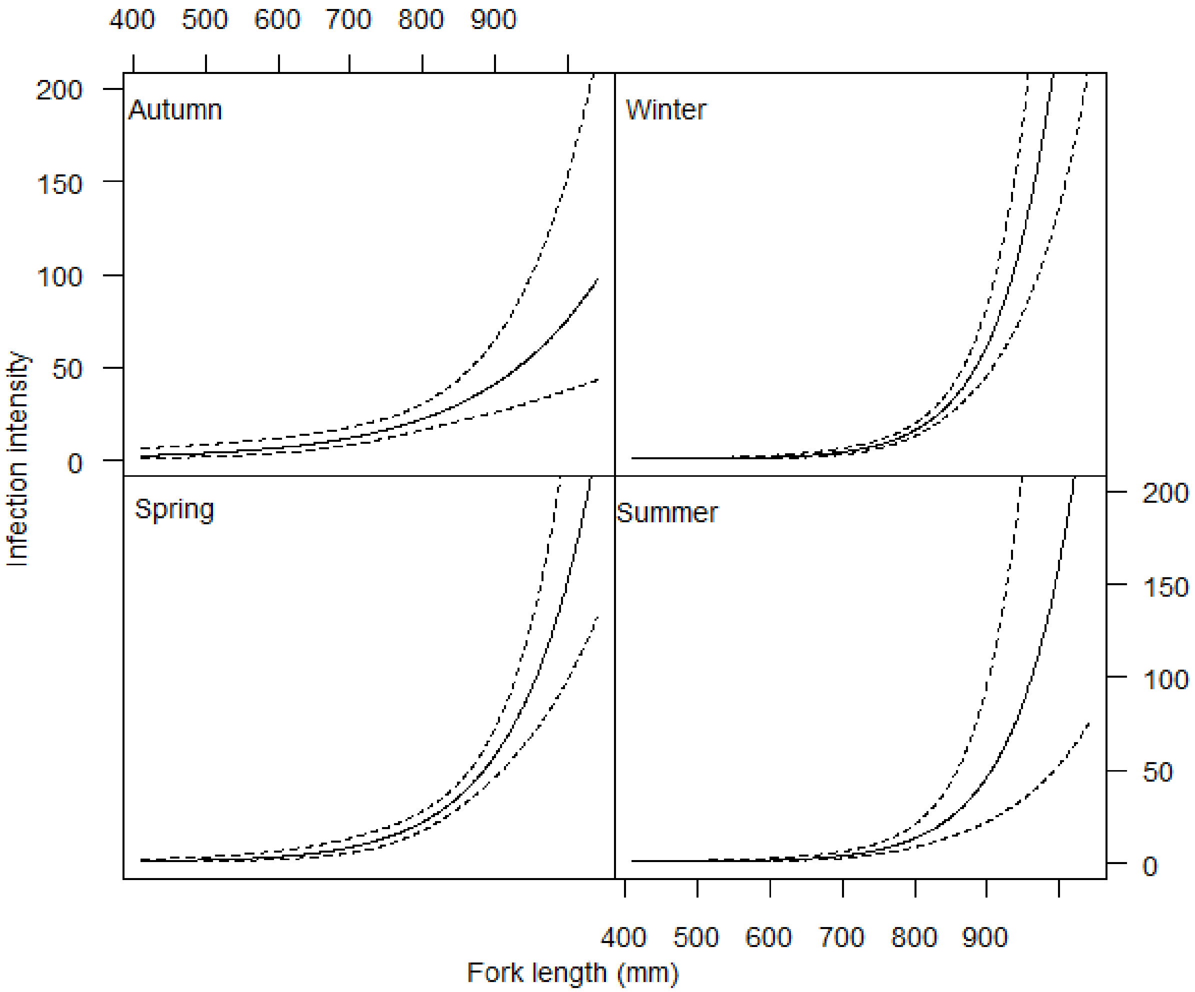

Figure 13. The relationship between host body size and the mean (± 95% CI) predicted infection intensity for *Molicola uncinatus* in snoek caught off South Africa for all four seasons.

Host fork length was predicted to correlate positively with the intensity of *M. uncinatus* infection in snoek (Figure 13). The significant interaction between host length and season indicated that the rate at which snoek acquire *M. uncinatus* may differ seasonally, as depicted in Figure 13. A lower accumulation rate than in any other season was expected in autumn. Higher infection intensities were predicted for hosts sampled in autumn and spring than in winter and summer (Figure 14a). Irrespective of host length and sampling season, an improvement in the host's GSI was expected to correlate with a decline in mean infection intensity of *M. uncinatus* in snoek (Figure 14b).

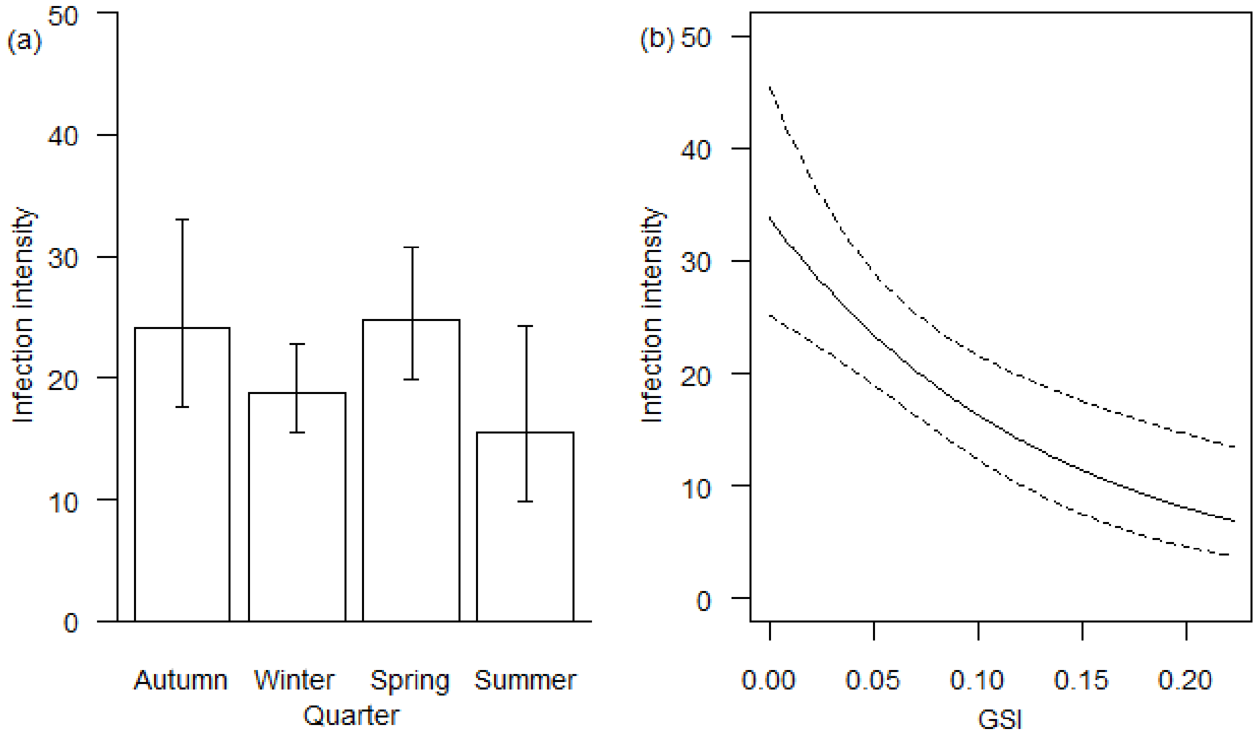

Figure 14. (a) The predicted seasonal variability in mean (± 95% CI) predicted infection intensity and (b) the relationship between host gonado somatic index and mean (± 95% CI) predicted infection intensity for *Molicola uncinatus* in snoek caught off South Africa.

3.4.3: *Hepatoxylon trichiuri*

The results of the analysis of deviance conducted on the binomial GLM selected by the AIC-based procedure, suggested that the prevalence of the cestode *Hepatoxylon trichiuri* in snoek was significantly dependent upon its length, reproductive status, the sampling season, the mesenteric fat content and an interaction between host size and sex (Table 11). A Durbin-Watson test revealed no significant autocorrelation between the selected explanatory variables (D = 1.9886, p = 0.3669). Overall, the model accounted for 28.8% of the variation in the data. Host size (FL) and sampling season alone accounted for more than 50% of the explained variation.

Table 11. Analysis of deviance for the binomial GLM fitted to the presence-absence data for *Hepatoxylon trichiuri* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		290.44			
FL	208	1	263.92	26.52	9.13	***
GSI	207	1	258.23	5.69	1.96	*
Sex	206	1	256.73	1.50	0.52	
Season	203	3	236.07	20.66	7.11	***
Fat	201	2	230.43	5.64	1.94	
FL × Sex	200	1	213.50	16.93	5.83	***
Sex × Season	197	3	206.90	6.60	2.27	

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

Keeping other variables constant, increasing host length was predicted to have a positive effect on the probability of a snoek harbouring at least one *H. trichiuri* individual. This positive correlation was predicted for both sexes (Figure 15) although the change in susceptibility with increasing size of male and female snoek differed.

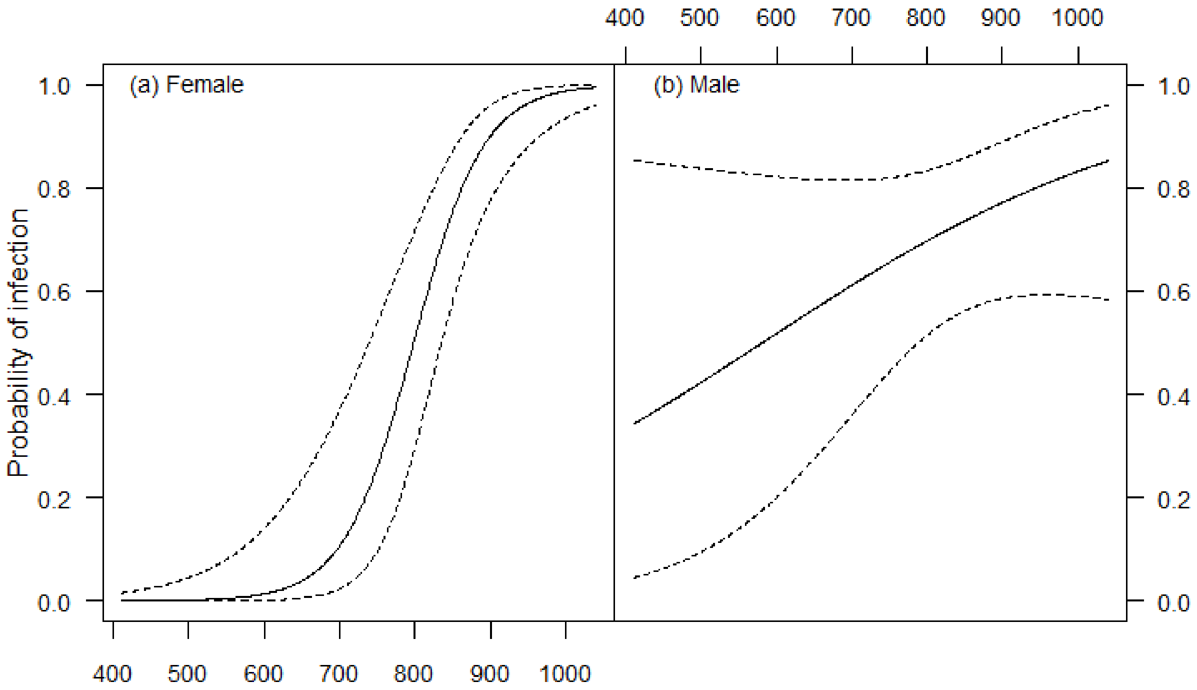

Figure 15. The relationship between host body size and the mean (± 95% CI) predicted probability of infection for *Hepatoxylon trichiuri* in snoek caught during spring off South Africa.

The probability of infection was also dependent upon the host's reproductive status, as depicted in Figure 16a. The probability of infection was expected to decrease with increasing GSI, i.e., adult fish sampled close to or during the spawning period were less likely to be infected by *H. trichiuri*. Seasonally, the probability of infection was predicted to vary for both males and females (Figure 16b). Female snoek were predicted to exhibit a year-long trend in the probability of acquiring *H. trichiuri*. Prevalence increased from a minimum in autumn to a peak in spring before decreasing again in summer. On the other hand, males displayed a 6 month cycle in the boom and bust of mean expected prevalence of *H. trichiuri*.

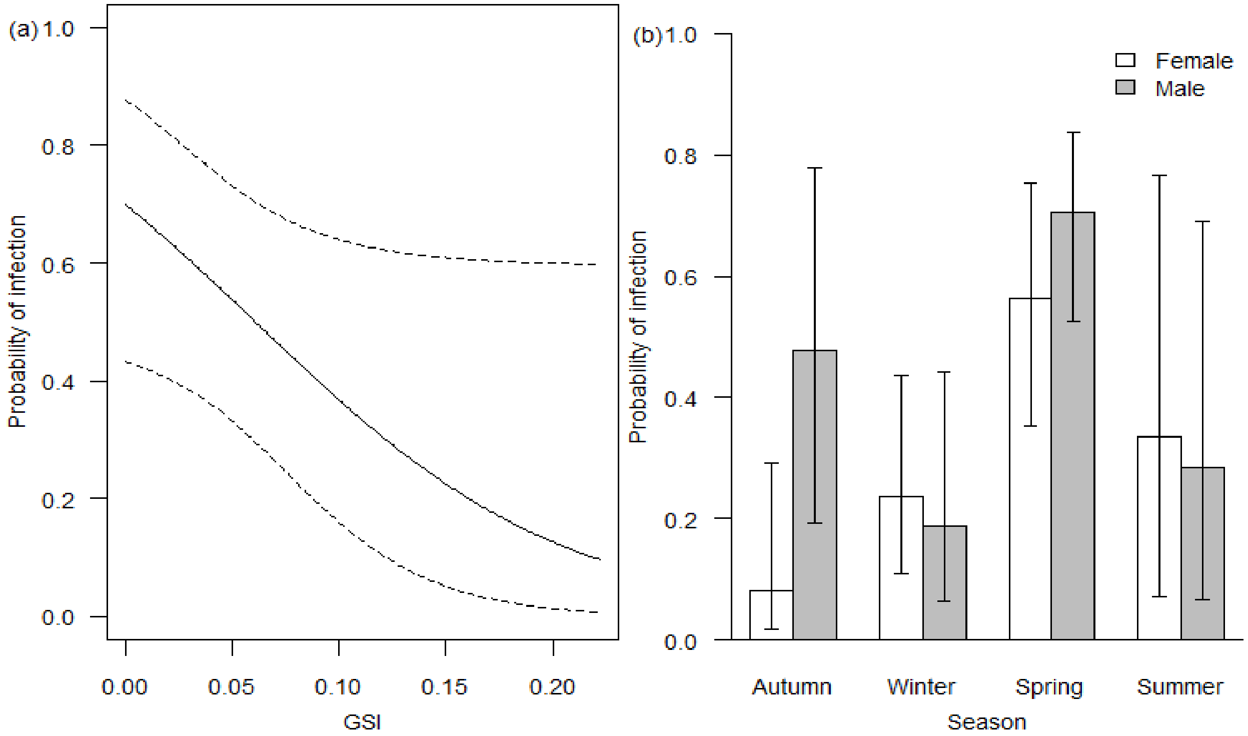

Figure 16. The relationship between (a) host gonado-somatic index and the mean (± 95% CI) predicted probability of infection and (b) the seasonal variability in the mean (± 95% CI) predicted probability of infection for *Hepatoxylon trichiuri* in snoek caught off South Africa.

3.4.4: *Tentacularia coryphaenae*

The AIC identified a set of six variables as the most adequate to model the prevalence of *T. coryphaenae* in snoek (Table 12). The Durbin-Watson test revealed no autocorrelation between the selected variables (D = 2.1342, p = 0.8058) and residuals plots showed no marked deviations from the assumptions of a GLM with binomial error structure. The model accounted for 32.5% of the observed variation. Host length and its interaction with season explained most of the variation in the model. Host GSI and fat reserves accounted for a small but nonetheless significant amount of variation.

Table 12. Analysis of deviance for the binomial GLM fitted to the presence-absence data for *Tentacularia coryphaenae* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		243.56			
FL	208	1	217.44	26.127	10.73	***
Condition	207	1	213.66	3.780	1.55	
GSI	206	1	200.63	13.027	5.35	***
Season	203	3	198.02	2.612	1.07	
Fat	201	2	188.85	9.171	3.77	*
FL × Season	198	3	164.51	24.339	9.99	***

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

A positive ontogenetic shift in the probability of infection of *T. coryphaenae* was predicted for all seasons except winter where it was expected to be constant across the size range of hosts examined (Figure 17). An improvement in the host's GSI, irrespective of sex, was expected to exhibit a positive correlation with the probability of infection (Figure 18a) while improved fat reserves are expected to decrease the odds of a snoek becoming infected by *T. coryphaenae* (Figure 18b).

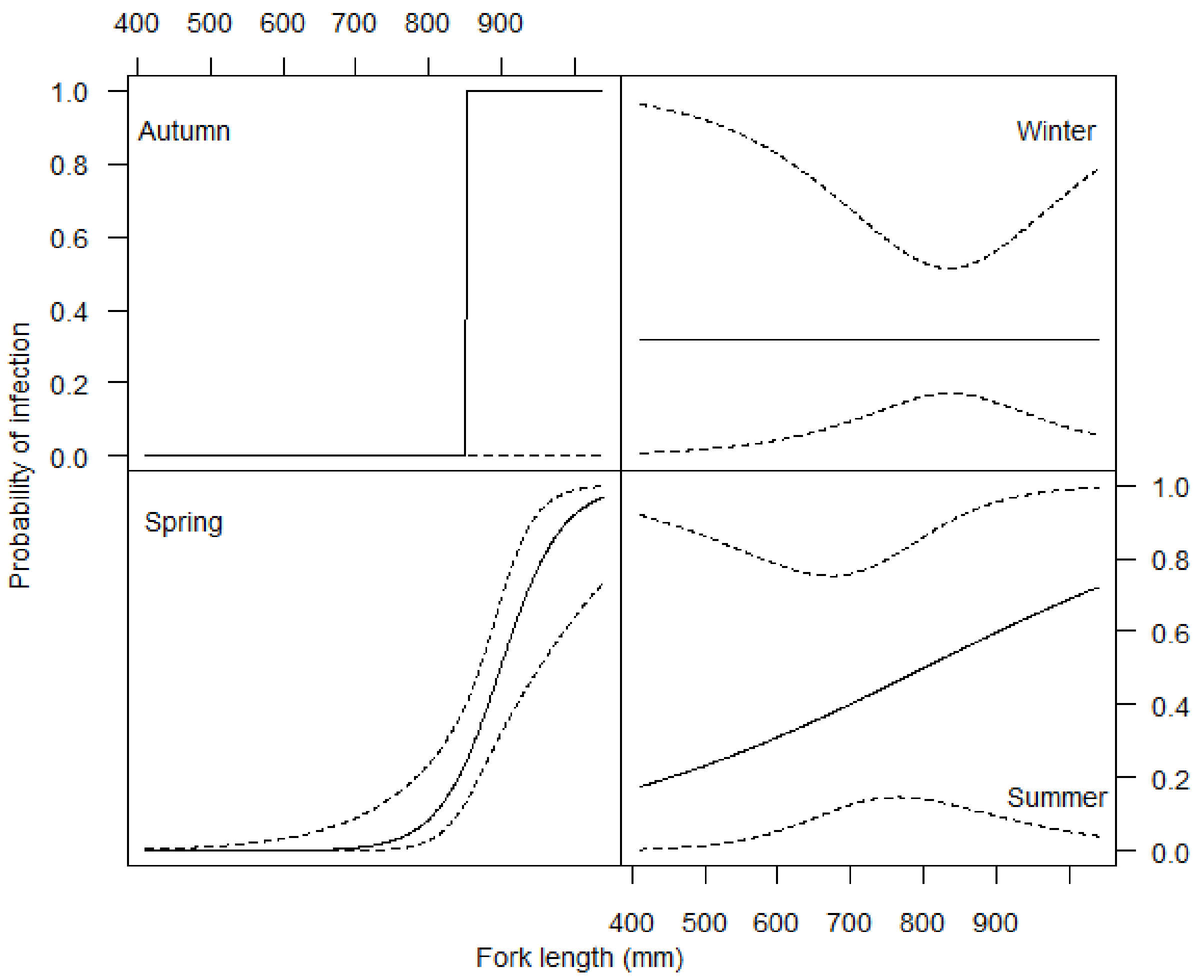

Figure 17. The relationship between host body size and the mean (± 95% CI) probability of infection for *Tentacularia coryphaenae* in snoek caught off South Africa for all four seasons.

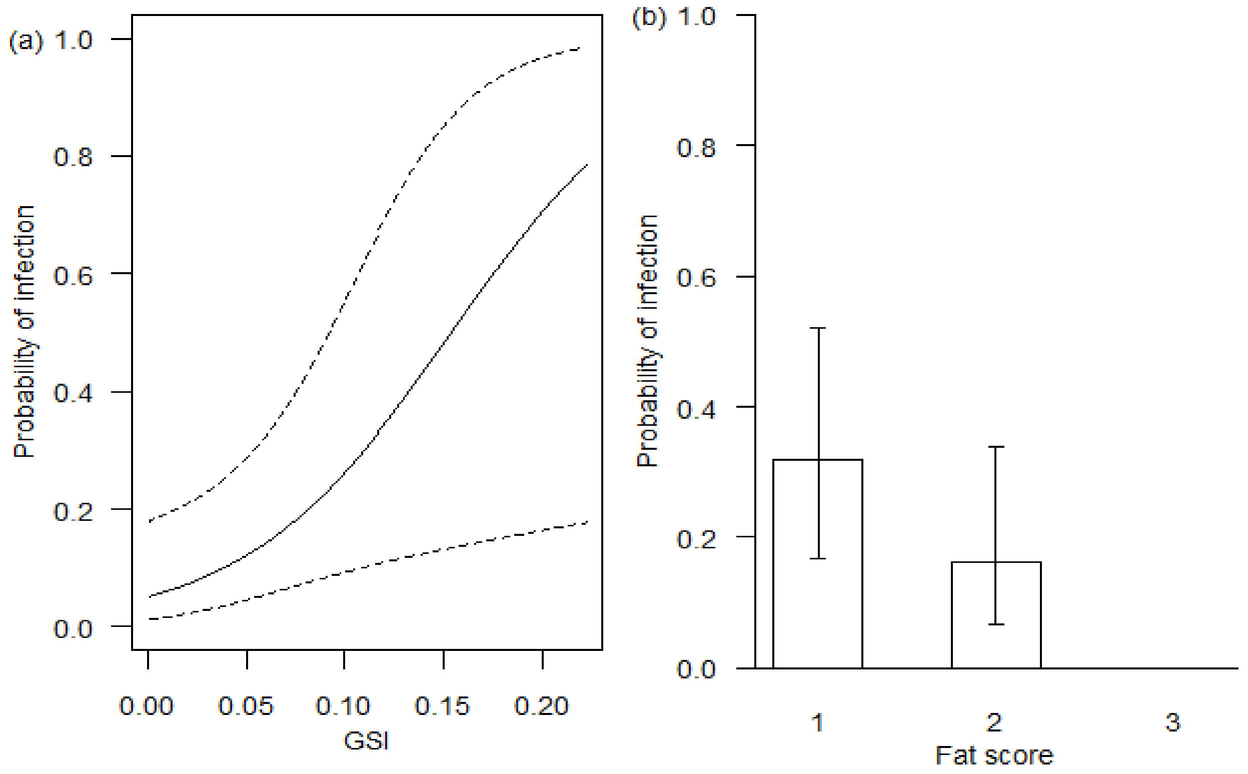

Figure 18. (a) The relationship between host GSI and the mean (± 95% CI) probability of infection for *Tentacularia coryphaenae* and (b) the variability in mean probability (± 95% CI) of infection with respect to fat score in snoek caught off South Africa.

3.4.5: *Nothobomolochus fradei*

The most parsimonious model to predict the prevalence of *N. fradei* on snoek included four main effects and two interaction terms (Table 13). An examination of residual plots revealed no significant departures from the assumptions of the GLM and no autocorrelation was detected (D = 2.045, p = 0.538). The model explained 32.6 % of the variation in *N. fradei* prevalence. Host condition and the sampling season were found to be the only significant predictors of *N. fradei* prevalence on snoek (Table 13). The susceptibility of snoek to *N. fradei* was expected to decrease with improving body condition and a high (> 95%) prevalence of *N. fradei* was predicted for all seasons (Figure 19).

Table 13. Analysis of deviance for the binomial GLM fitted to predict the prevalence of *Nothobomolochus fradei* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		67.97			
Condition	208	1	63.41	4.56	6.71	*
GSI	207	1	62.16	1.25	1.84	
Sex	206	1	61.79	0.37	0.55	
Season	203	3	53.60	8.19	12.04	*
GSI × Sex	202	1	53.30	0.30	0.44	
Sex × Season	199	3	45.83	7.47	10.99	

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

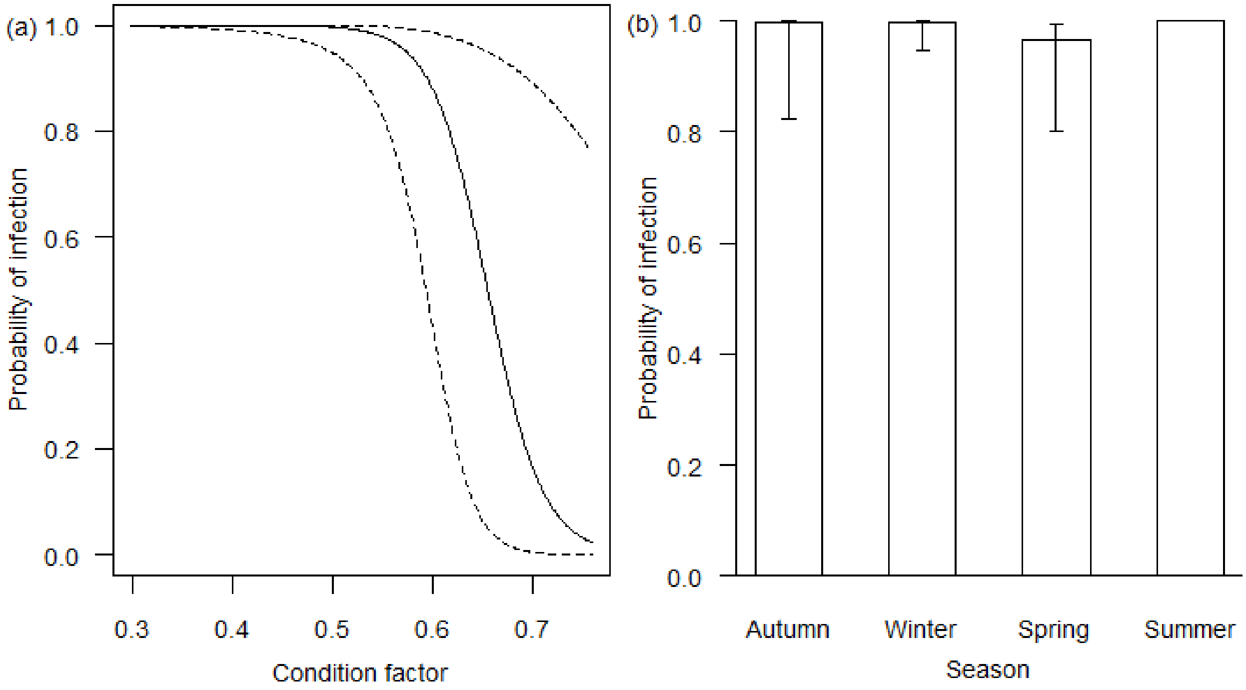

Figure 19. (a) The relationship between host size and predicted mean probability of infection (± 95% CI) and (b) the predicted seasonal variability in *Nothobomolochus fradei* mean probability of infection (± 95% CI) on snoek caught off South Africa.

The stepwise, AIC-based variable selection indicated that variation in *N. fradei* infection intensity was best predicted by a model comprising five main effects and four interaction terms (Table 14). No autocorrelation amongst the variables included in the model was detected (D = 2.0678, p = 0.5803). An examination of residual plots revealed no marked departures from the assumptions of the negative binomial GLM. The model accounted for 15.2% of the variation in the data. The interaction of host condition and sampling season with sex significantly influenced the infection intensity of *N. fradei* on snoek (Table 14).

Table 14. Analysis of deviance for the zero-truncated negative binomial GLM fitted to the infection intensity of *Nothobomolochus fradei* on snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	201		258.37			
FL	200	1	255.05	3.32	1.29	
Condition	199	1	252.46	2.59	1.00	
GSI	198	1	252.05	0.41	0.16	
Sex	197	1	251.33	0.72	0.28	
Season	194	3	247.71	3.62	1.40	
Condition × Sex	193	1	240.69	7.025	2.72	**
GSI × Sex	192	1	240.69	0.00	0.00	
FL × Season	189	3	235.22	5.46	2.11	
Sex × Season	186	3	219.03	16.19	6.27	**

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

The relationship between host condition and infection intensity was expected to differ between the sexes (Figure 20a). Infection intensity was predicted to remain stable for females across the range of observed condition factors. On the other hand, infection intensity was expected to increase with improving condition for male hosts (Figure 20a). During summer and autumn, male snoek were predicted to harbour more *N. fradei* than females whereas over winter and spring the trend was reversed (Figure 20b). The overlapping 95% confidence intervals suggest no overall differences between sexes and seasons.

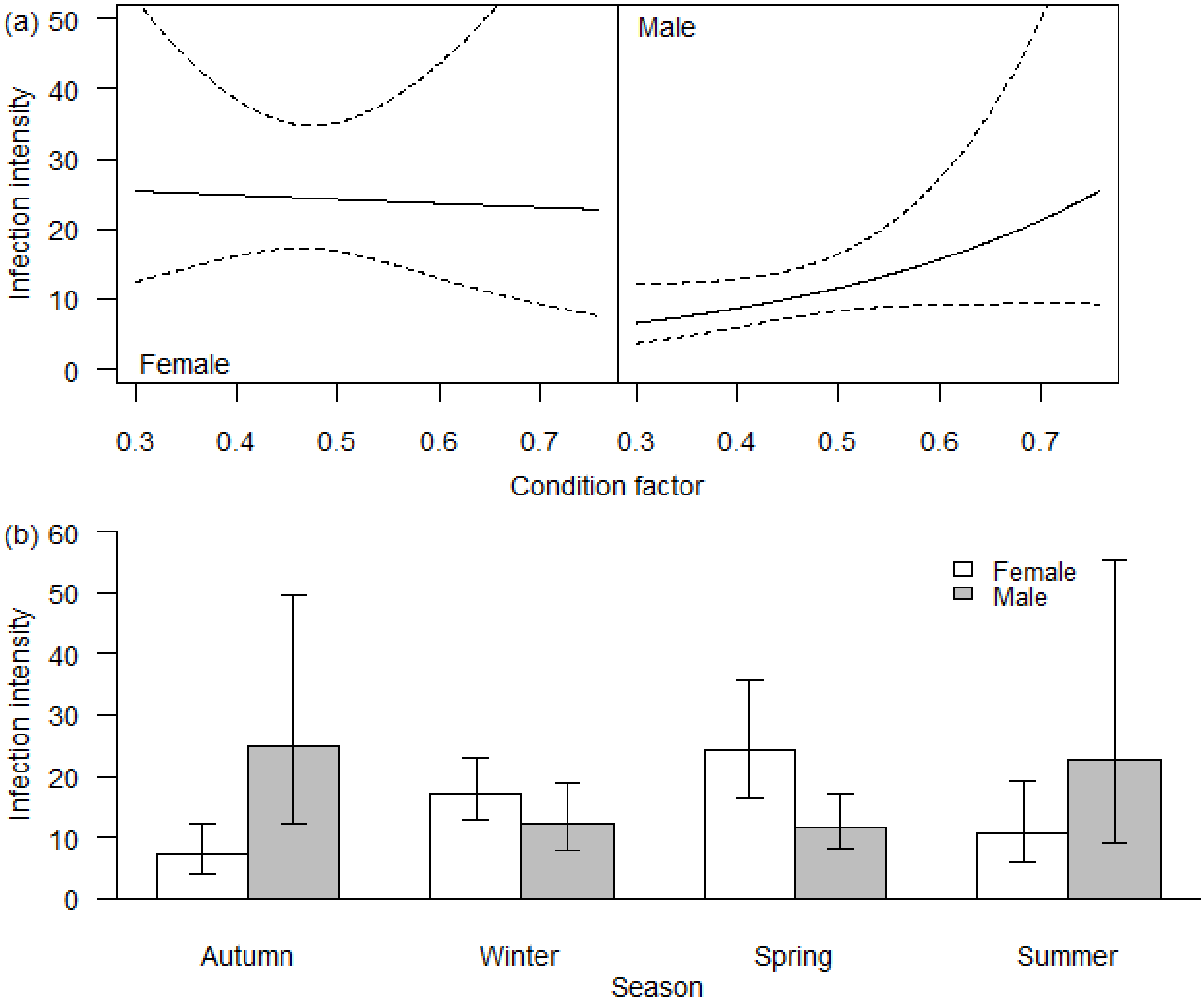

Figure 20. The predicted mean (± 95% CI) infection intensity for *Nothobomolochus fradei* on snoek caught off South Africa with respect to the interaction between (a) host condition and (b) sex and season.

3.4.6: *Hatschekia conifera*

Model selection procedures identified a set of eleven explanatory variables for the model best predicting the prevalence of *H. conifera* on snoek (Table 15). The residual plots revealed no significant trends and no autocorrelation was detected ($D = 2.178$, $p = 0.8633$). The model explained 22.2% of the variability in observations. Analysis of deviance indicated that the host's GSI, sampling seasonality, fat reserves, maturity and an interaction between host sex and season were the strongest predictors of *H. conifera* prevalence although host FL also had a significant effect (Table 15).

Table 15. Analysis of deviance for the binomial GLM fitted to the prevalence of *Hatschekia conifera* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		291.05			
FL	208	1	286.47	4.576	1.57	*
Condition	207	1	284.47	2.004	0.69	
GSI	206	1	272.46	12.006	4.12	***
Sex	205	1	270.38	2.078	0.71	
Season	202	3	261.28	9.104	3.13	*
Fat	200	2	254.45	6.825	2.34	*
Maturity	199	1	246.22	8.235	2.83	**
FL × Season	196	3	240.45	5.773	1.98	
FL × Condition	195	1	236.80	3.646	1.25	
GSI × Sex	194	1	234.32	2.477	0.85	
Sex × Season	191	3	226.33	7.993	2.75	*

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

The susceptibility of snoek to *H. conifera* was expected to increase with host length (Figure 21a). The size-at-mean-50% infection probability was predicted at 749 mm fork length. The probability of a snoek being infected by *H. conifera* was predicted to decrease with an increase in the host's GSI (Figure 21b). Hosts with little or no fat reserves (fat score 1) were predicted to, on average, be 35% less susceptible to the copepod parasite than hosts with a fat score of 2 or 3 (Figure 22a). Adult snoek were predicted to be more susceptible to *H. conifera* (Figure 22b). Seasonally, the expected mean prevalence of *H. conifera* exhibited a bimodal distribution for female snoek while for males a unimodal distribution was predicted (Figure 22c). Female snoek caught in autumn and spring were expected to have an increased chance of being infected by *H. conifera* compared to females caught in winter or summer. Males were predicted to be most susceptible to *H. conifera* in spring. However, the overlaps in 95% confidence intervals suggest no significant seasonal differences in the incidence of *H. conifera* on snoek in South Africa (Figure 22c).

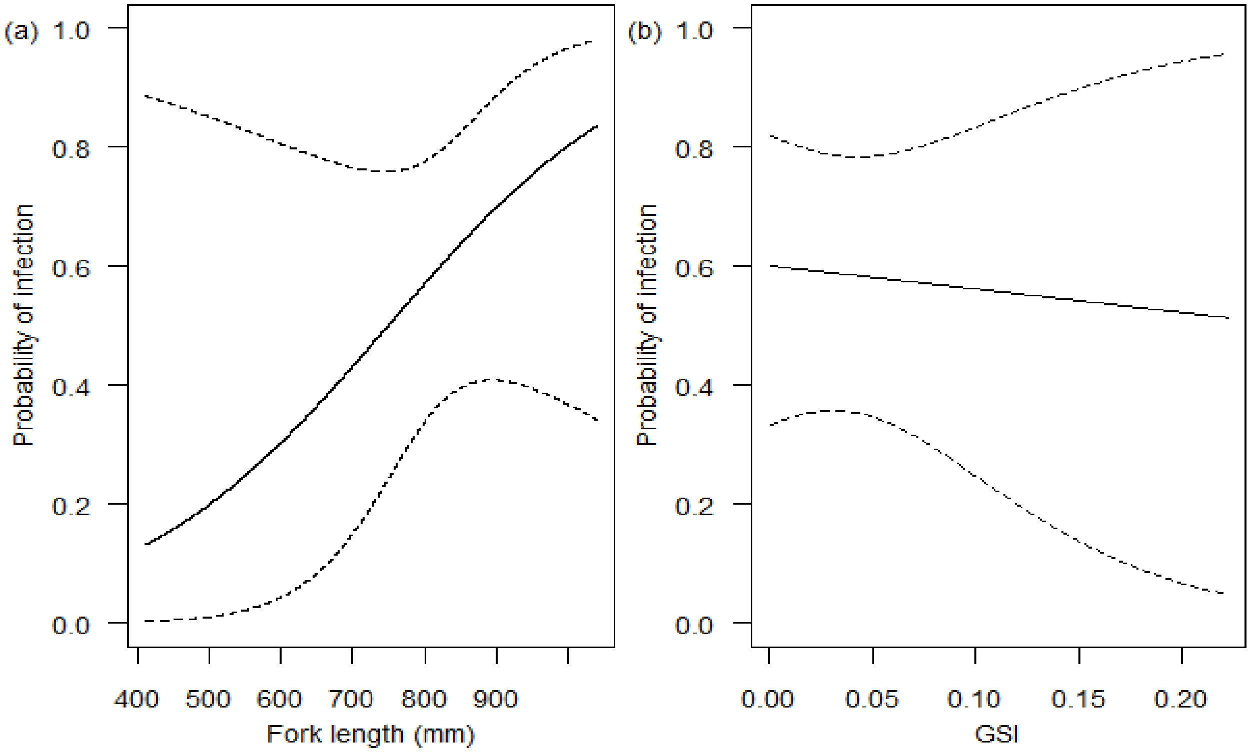

Figure 21. The predicted relationship between the mean (± 95% CI) probability of infection for *Hatschekia conifera* on snoek caught off South Africa with respect to (a) host size and (b) GSI.

The results of AIC- based model selection indicated that the most parsimonious set of variables adequate for modelling the intensity of *H. conifera* included host size, reproductive status, sex and seasons (Table 16). There was no autocorrelation between the selected set of explanatory variables (D = 1.7196, p = 0.05457). Host length, GSI and sex each explained a significant proportion of the 27% of the variability explained by the model.

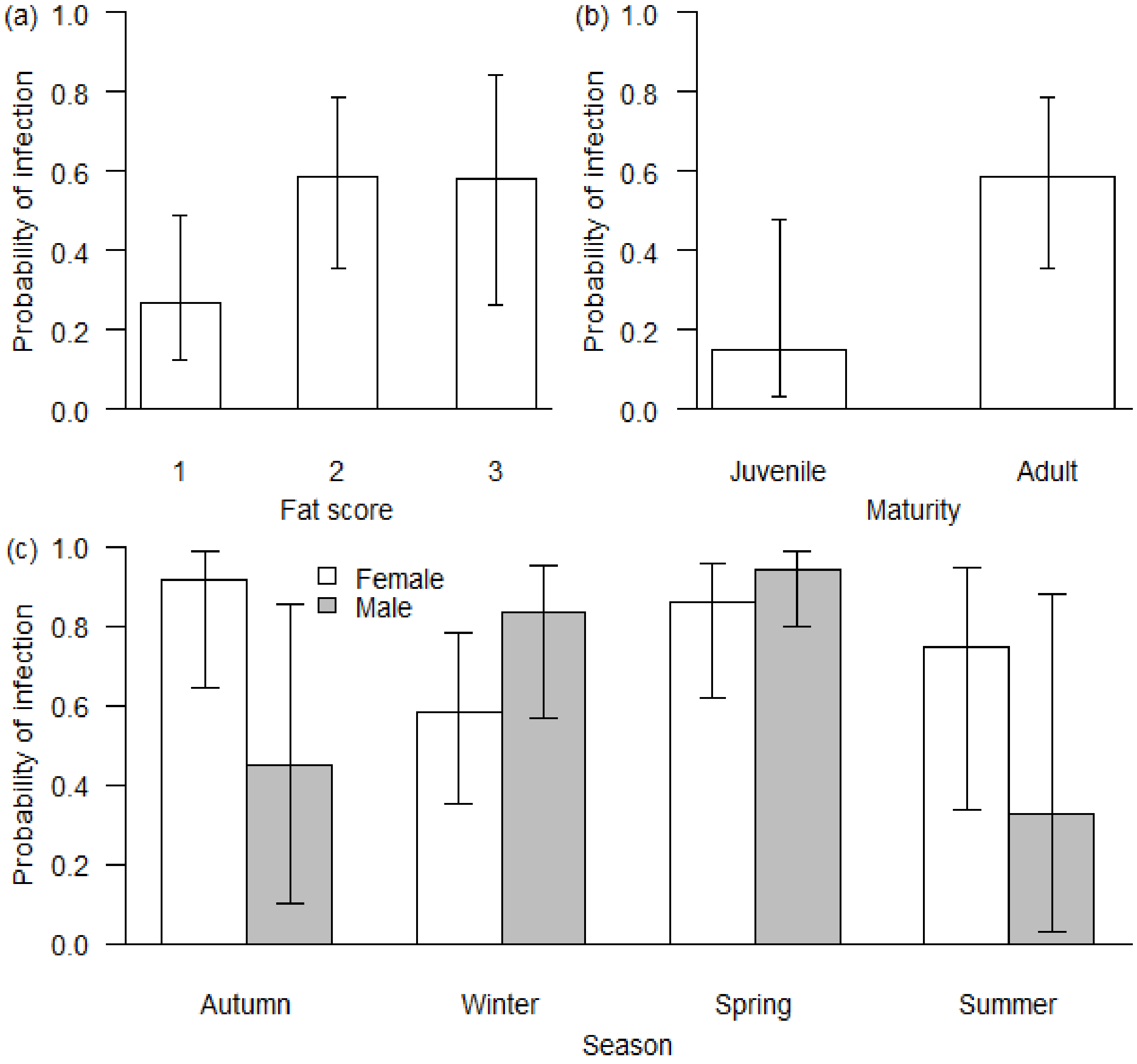

Figure 22. The predicted relationship between (a) mesenteric fat reserves, (b) maturity and (c) the gender-specific seasonal variability in mean (± 95% CI) probability of infection for *Hatschekia conifera* on snoek caught in South African waters.

Table 16. Analysis of deviance for the zero-truncated negative binomial GLM fitted to the infection intensity of *Hatschekia conifera* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	106		127.658			
FL	105	1	119.061	8.597	6.73	**
GSI	104	1	106.936	12.1248	9.50	***
Sex	103	1	99.283	7.6539	6.00	**
Season			93.233	6.0493	4.74	

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

The size of *H. conifera* infrapopulations on both male and female snoek was expected to increase with increasing host length (Figure 23a). Holding FL constant, an increase in the host's GSI correlated negatively with predicted mean infection intensity for both sexes (Figure 23b). For any given size and GSI, males were always predicted to be more susceptible to *H. conifera* than females. Male snoek were expected to, on average, harbour two more individuals compared to females of the same size and reproductive status (Figure 23c).

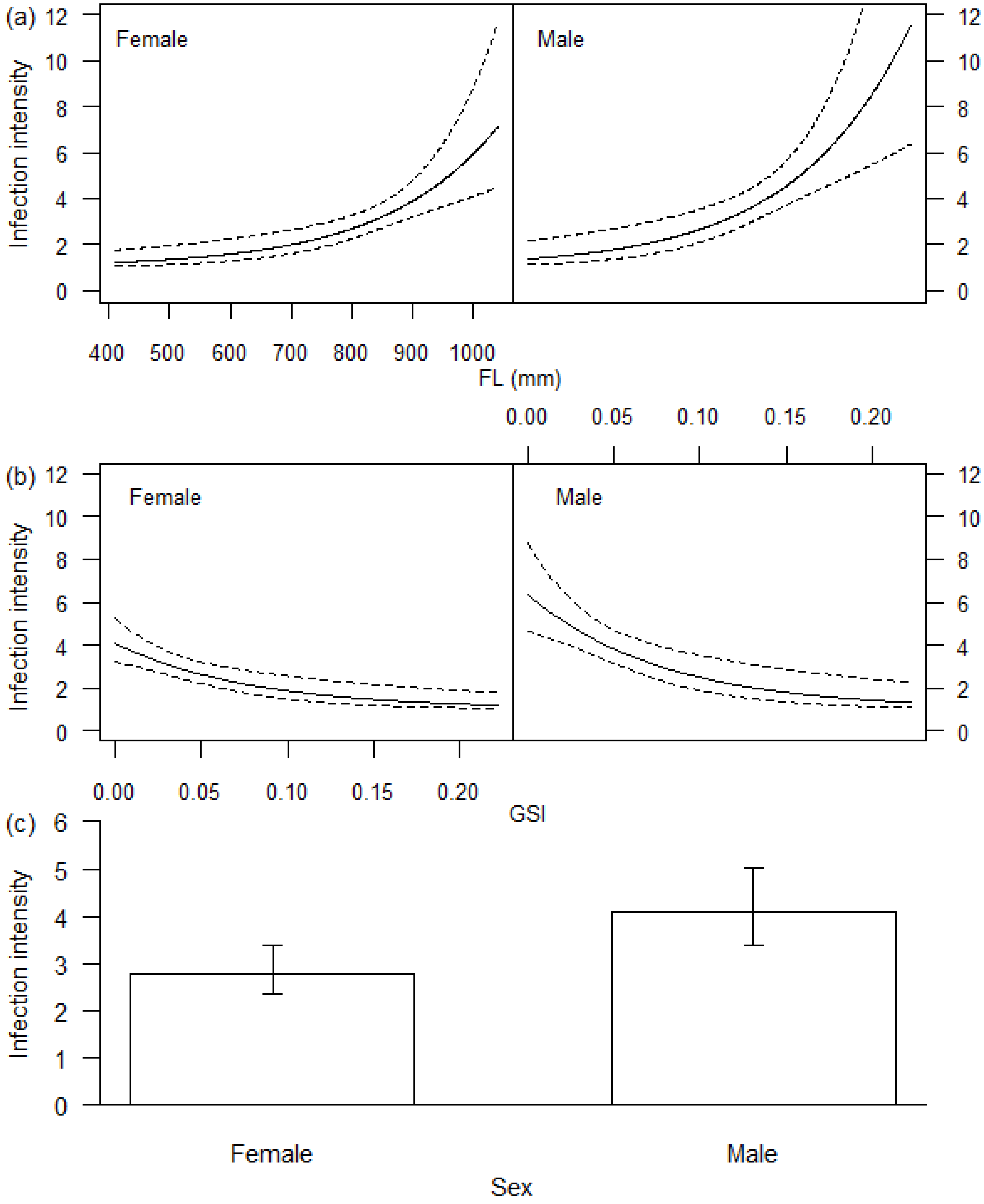

Figure 23. The relationship between *Hatschekia conifera* mean (± 95% CI) predicted intensity of infection and (a) host size, (b) host reproductive status and (c) sex for snoek caught off South Africa

3.4.7: *Caligus dakari*

Stepwise, AIC-based variable selection yielded a simple model including 'GSI', 'Season', 'Fat' and host maturity as explanatory variables. A Durbin-Watson test revealed no autocorrelation amongst the selected combination of variables (D = 2.0097, p = 0.491) and an examination of residual plots revealed no marked departure from the assumptions of the model. The model accounted for 21.2% of the variation in the data, the majority of which (56%) could be explained by 'Season' alone (Table 17). The host's GSI, fat reserves and maturity appeared to have a small but significant influence on the susceptibility of snoek to *C. dakari*.

Table 17. Analysis of deviance for the binomial GLM fitted to the prevalence of *Caligus dakari* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		288.81			
GSI	208	1	279.11	9.702	3.36	**
Season	205	3	244.82	34.286	11.87	***
Fat	203	2	232.05	12.771	4.42	**
Maturity	202	1	227.66	4.389	1.52	*

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

Host GSI was predicted to exhibit a weak positive correlation with the probability of infection for *C. dakari* (Figure 24a) irrespective of seasonality. *C. dakari* was expected to parasitize snoek year-round although significant seasonal variability in the probability of infection was predicted. Prevalence was predicted lowest in autumn, it was then expected to peak in spring before decreasing again in summer (Figure 24b). Within seasons, the mean probability of infection was expected to decrease steadily as the fat score increased (Figure 24c) and juveniles (FL < 730 mm) appeared to be more susceptible to the caligid (Figure 24d).

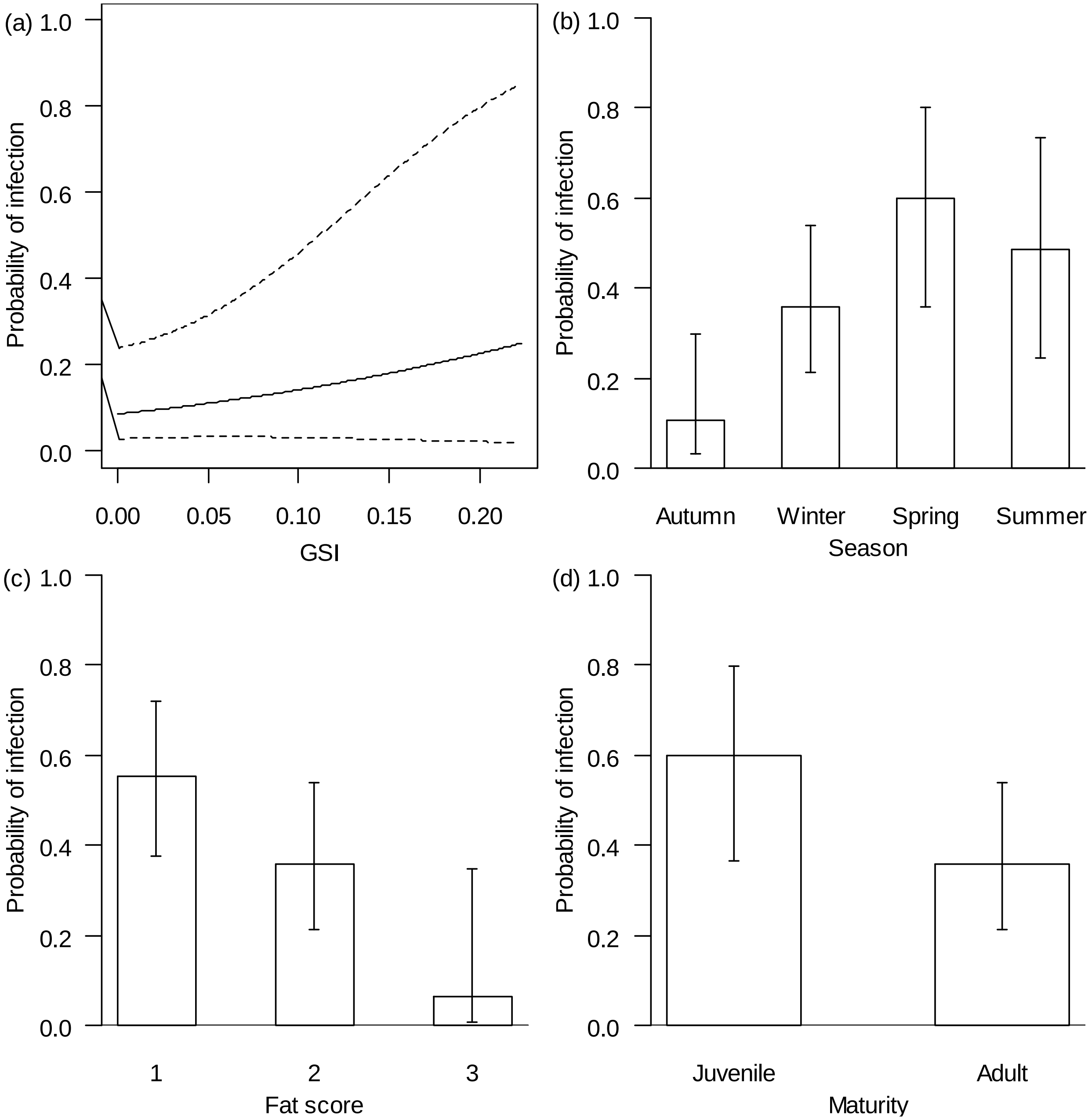

Figure 24. (a) The relationship between host GSI and mean (± 95% CI) probability of infection and the variability in the mean (± 95% CI) predicted probability of infection with respect to (b) seasons, (c) fat score and (d) host maturity for *Caligus dakari*.

According to the AIC, the observed intensity of *C. dakari* infection on snoek off South Africa was best predicted by sampling seasonality ($\chi^2 = 15.976$, df = 3, $p < 0.002$). An examination of diagnostic plots revealed no significant departures from the assumptions of a GLM with negative binomial error structure. Overall the model explained 12.5% of the variation in observed infection intensity. The average size of *C. dakari* infrapopulations on snoek was expected to vary little between autumn and winter before peaking in spring (Figure 25).

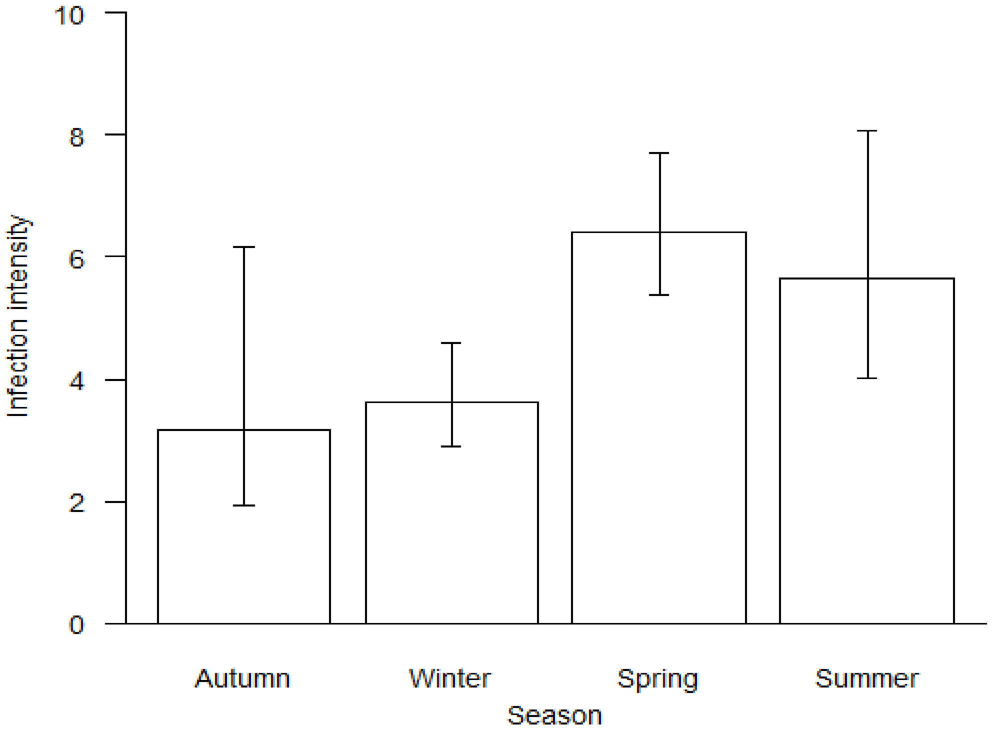

Figure 25. The predicted variation in mean (± 95% CI) infection intensity for *Caligus dakari* on snoek caught off South Africa.

3.4.8: *Caligus zei*

The model with the lowest AIC, which was also the most parsimonious alternative within 2 AIC, identified seasonality, mesenteric fat score and maturity as variables significantly influencing the prevalence of *C. zei* on snoek (Table 18). No significant autocorrelation was detected amongst the selected explanatory variables Analysis of deviance suggested that host size was the strongest predictor of infection followed by seasonality and the mesenteric fat content.

Table 18. Analysis of deviance for the binomial GLM fitted to the presence-absence data for *Caligus zei* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		215.60			
Season	206	3	192.24	23.3603	10.84	***
Fat	204	2	177.1	15.1328	7.02	***
Maturity	203	1	170.53	6.5745	3.05	*

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

Snoek were only predicted to have a chance of being infected by *C. zei* in winter, spring and summer (Figure 26a). This is consistent with the relationship predicted with respect to host fat score which showed that the probability of infection decreased with improving fat reserves, which are at their highest in autumn (Figure 26b). Mature snoek were expected to be more susceptible to *C. zei* than juveniles (Figure 26c).

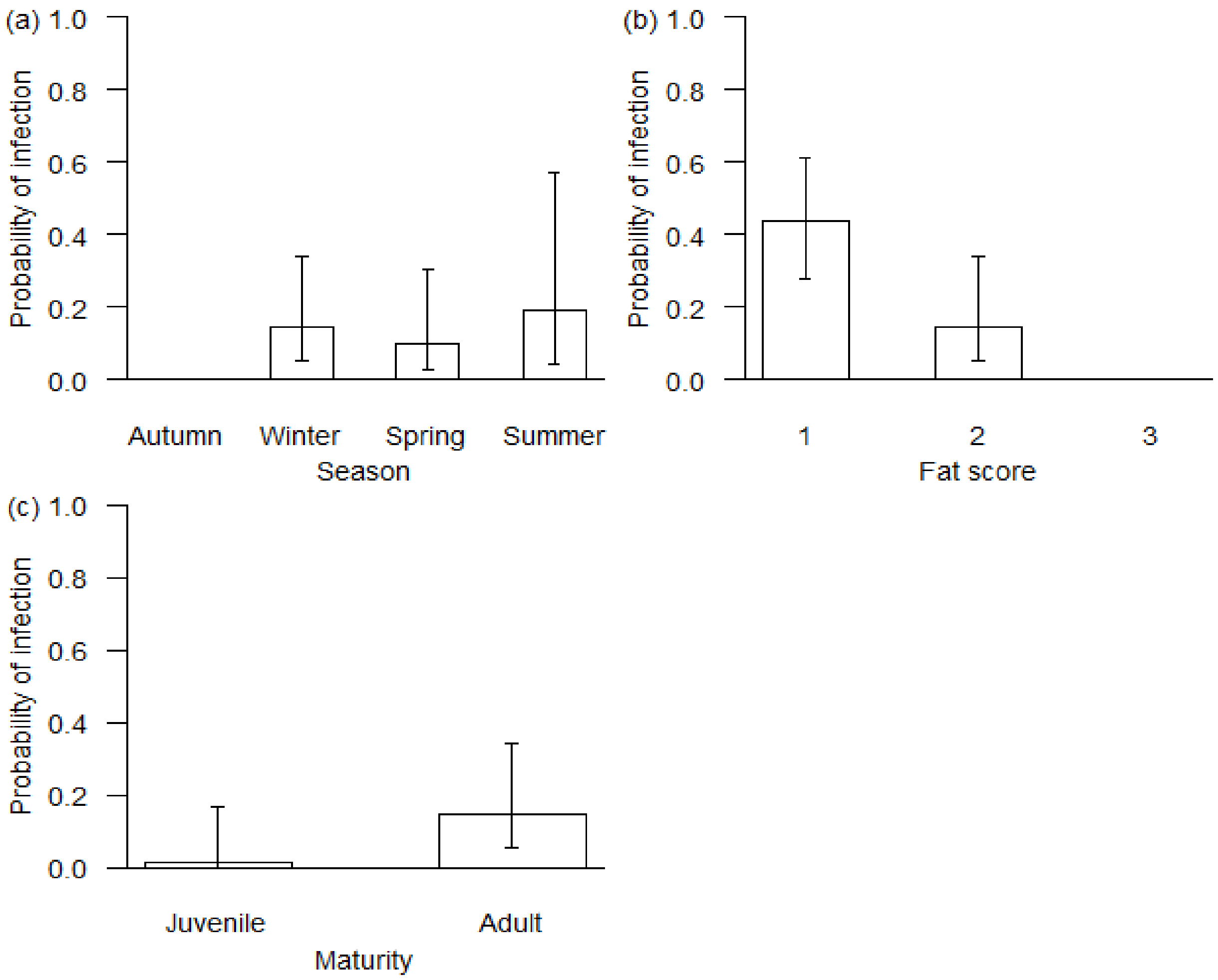

Figure 26. The variability in the mean (± 95% CI) predicted probability of infection with respect to (a) seasons, (b) mesenteric fat content and (c) host maturity for *Caligus zei* on snoek caught off South Africa.

3.4.9: *Corynosoma australe*

The preferred model, comprising three main effects (FL, condition, GSI), was the most parsimonious of three models ranked within 0.2 AIC of the model with the lowest AIC. Analysis of residuals did not suggest any marked departures from the assumptions of the binomial error structure GLM and the Durbin-Watson test revealed no autocorrelation (D = 1.825, p = 0.0904). The model explained 14.9% of the variation in the observed prevalence of *C. australe* in snoek. Host fork length was the strongest predictor of prevalence followed by condition and GSI (Table 19).

Table 19. Analysis of deviance for the binomial GLM fitted to the presence-absence data for *Corynosoma australe* infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		284.92			
FL	208	1	256.31	28.61	10.04	***
Condition	207	1	248.27	8.04	2.82	**
GSI	206	1	242.41	5.8582	2.06	*

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

The susceptibility of snoek to *C. australe* was expected to correlate positively with host length (Figure 27a). The size-at-50% mean prevalence of *C. australe* in snoek was predicted at 883 mm fork length. A decrease in the risk of a snoek being infected by *C. australe* was expected to be linked to improving body condition (Figure 27b). Conversely, hosts with higher GSIs and therefore lower condition, were more likely to be infected by *C. australe* (Figure 27c).

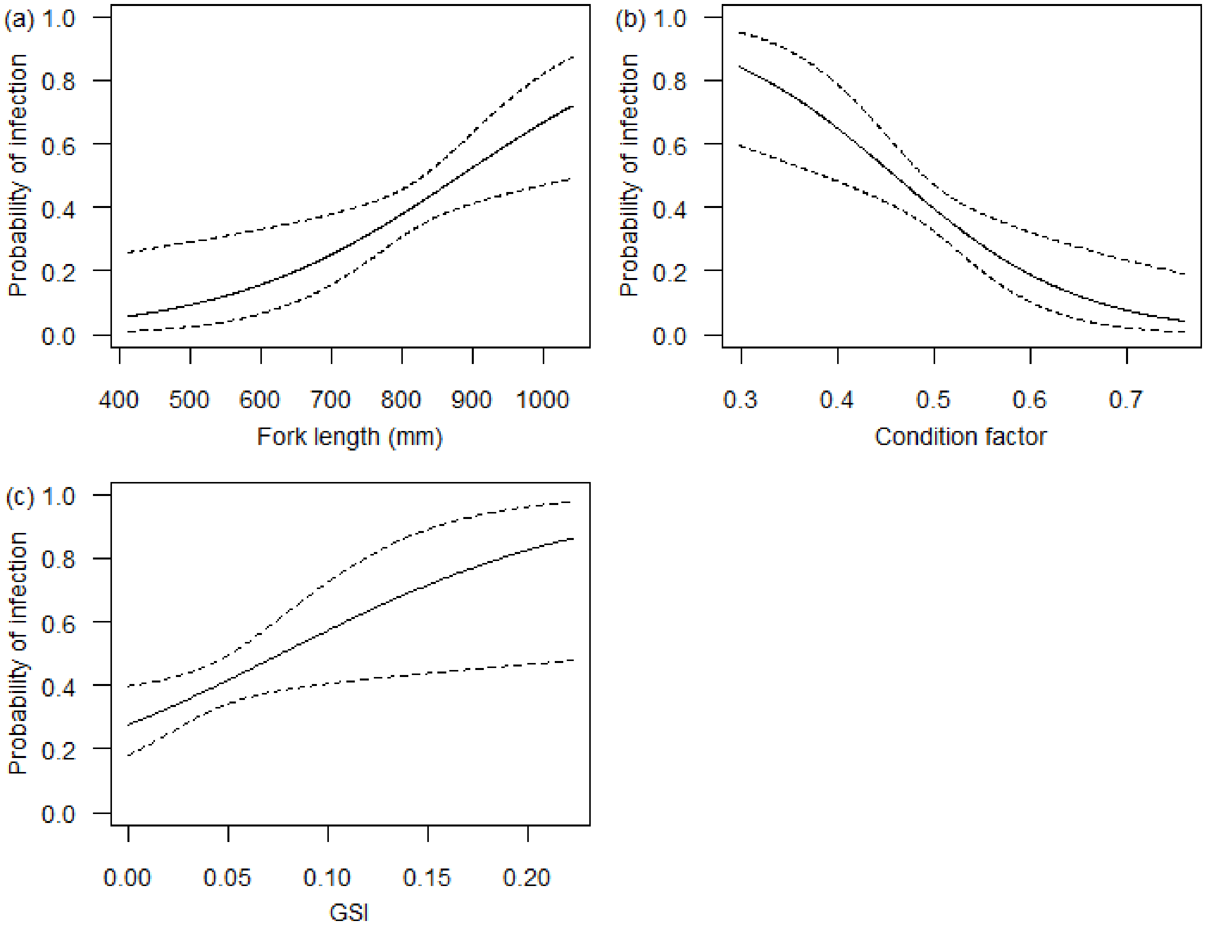

Figure 27. The relationship between (a) host size, (b) host condition, (c) host GSI and the predicted mean (± 95% CI) probability of infection for *Corynosoma australe* infecting snoek off South Africa.

3.4.10: Digenea sp.

Of the models ranked within 2 AIC of the 'best' model (AIC = 259.49), the most parsimonious and therefore preferred alternative indicated that host sex, seasonality and an interaction between host FL and season significantly influenced the prevalence of *Digenea* sp. in snoek (Table 20). Overall the model accounted for 13.4% of the variation in the data. The analysis of residual plots and the Durbin-Watson (D = 1.845, p = 0.09171) test revealed no significant departures from the assumptions of the GLM, thereby validating the model.

Table 20. Analysis of deviance for the binomial GLM fitted to the presence-absence data for *Digenea* sp. infecting snoek off South Africa. The residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and the associated significance (p) for a χ^2 test are summarized.

Variable	Res. df	df	Res. Dev.	Δ Dev.	% explained	p
Null	209		279.1			
Sex	208	1	268.36	10.743	3.85	**
Season	205	3	257.07	11.285	4.04	*
FL × Season	201	3	241.81	15.261	5.47	**

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

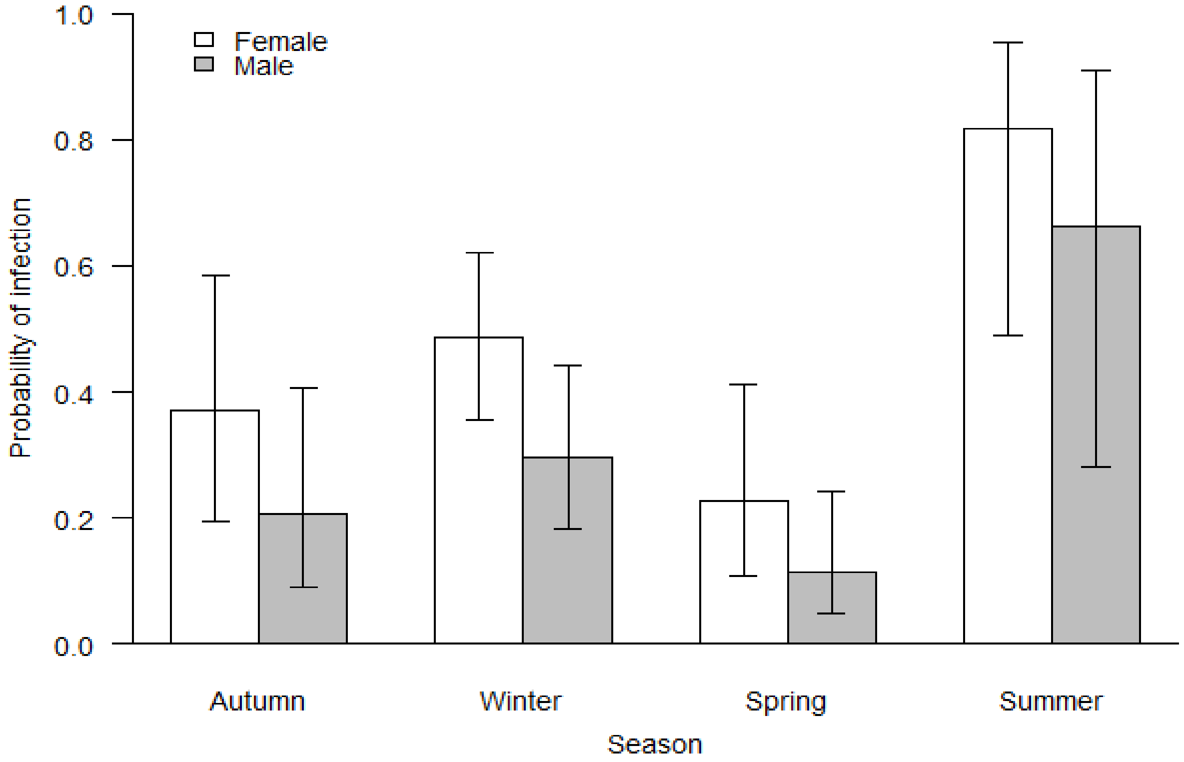

Figure 28. The predicted seasonal variation in the mean (± 95% CI) prevalence of *Digenea* sp. in snoek caught off South Africa.

The probability of infection was expected to differ between the sexes (Figure 28). Males were predicted to be less susceptible to the digenean parasite than females. This effect was expected to be consistent across all seasons, although significant seasonal variability in the prevalence of *Digenea* sp. was predicted (Figure 28). The expected relationship between host size and the chances of a snoek acquiring the digenean parasite displayed seasonal variation (Figure 29). In autumn, spring and summer the probability of infection correlated positively with host length while the opposite was predicted for snoek caught in winter.

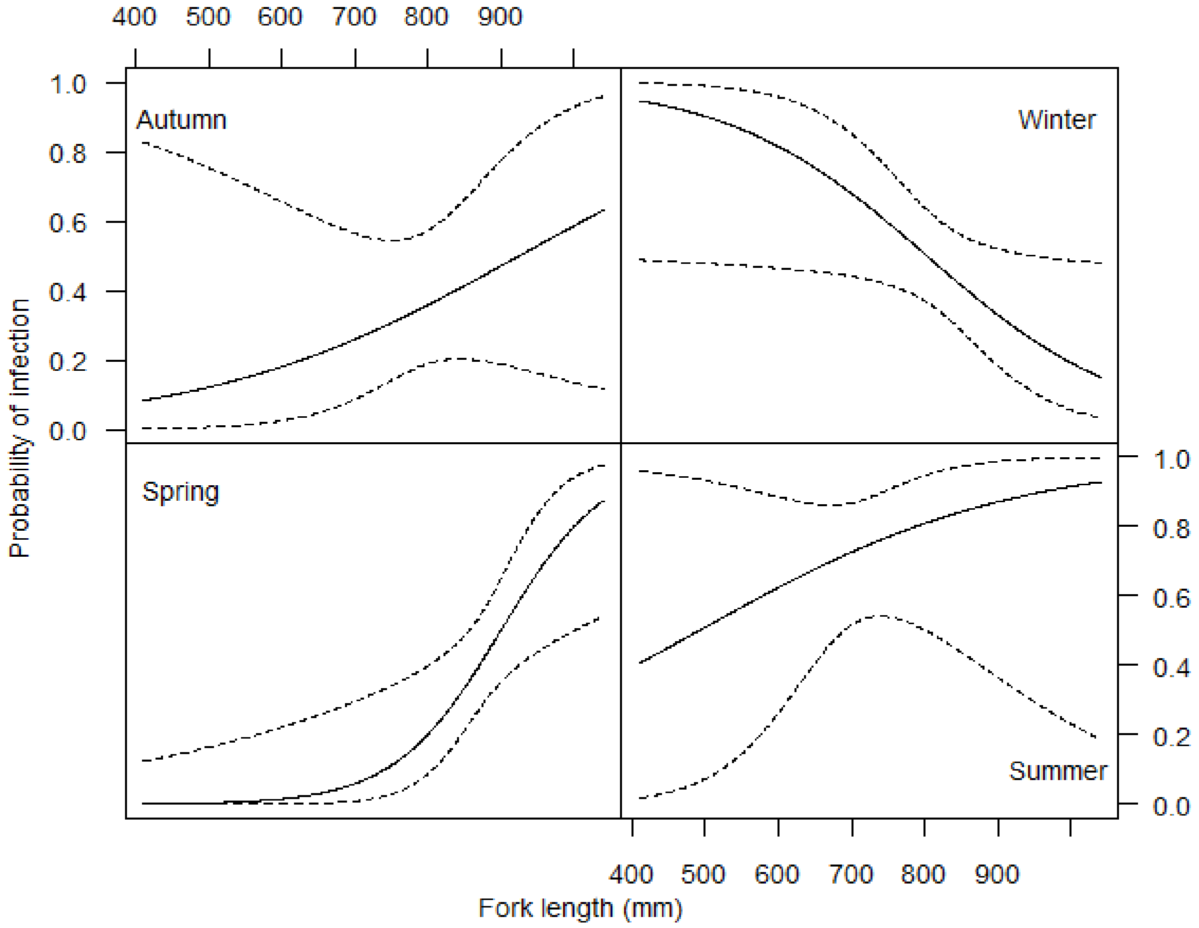

Figure 29. The predicted relationship between the mean (± 95% CI) probability of infection for *Digenea* sp. in snoek caught off South Africa with respect to host size for each season.

3.5: Community Analysis

Fifteen of the 16 parasite taxa recorded during this study were recovered from the first 50 hosts examined (Figure 30). A single parasite taxon was recovered for the first time from the remaining 160 hosts examined. This suggests that sampling was adequate to cover the range of parasite species using snoek as hosts in South African waters.

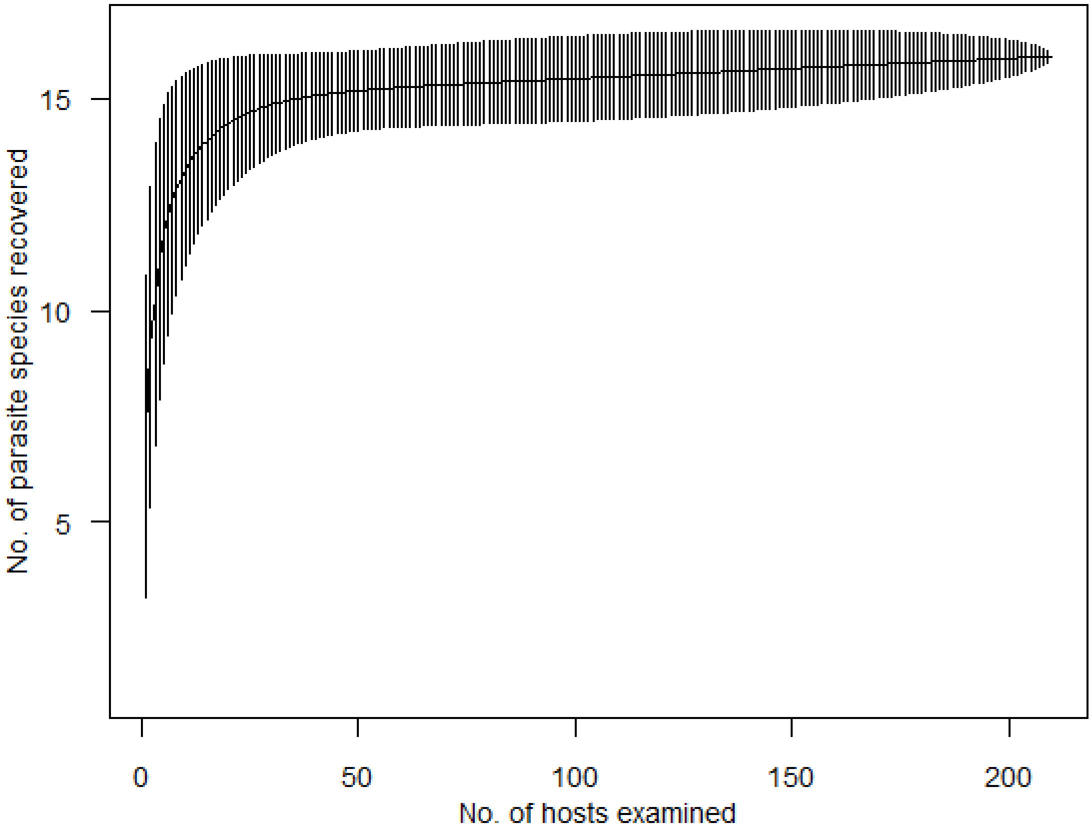

Figure 30. The species accumulation curve generated from the parasitological data collected from snoek caught off South Africa between 2013 and 2014.

Analysis of similarity (Global R = 0.0129, p = 0.117) indicated that the parasite community structure of male and female snoek did not differ. Hosts of both sexes were therefore pooled for subsequent analyses. The NMDS ordination did not reveal any clear seasonal trends or clusters (Figure 31), although the ANOSIM routine indicated that parasite community structure did differ slightly between seasons (Global R = 0.1705, p = 0.001). Pairwise analysis of similarity revealed a slight but significant shift in parasite community structure from autumn to winter and from winter to spring (Table 21). On the other hand, no significant differences in parasite community structure were detected between spring and summer as well as between summer and autumn. The diversity of the parasite assemblage did not vary much over the course of the study (Simpson's index: 0.816 - 0.866).

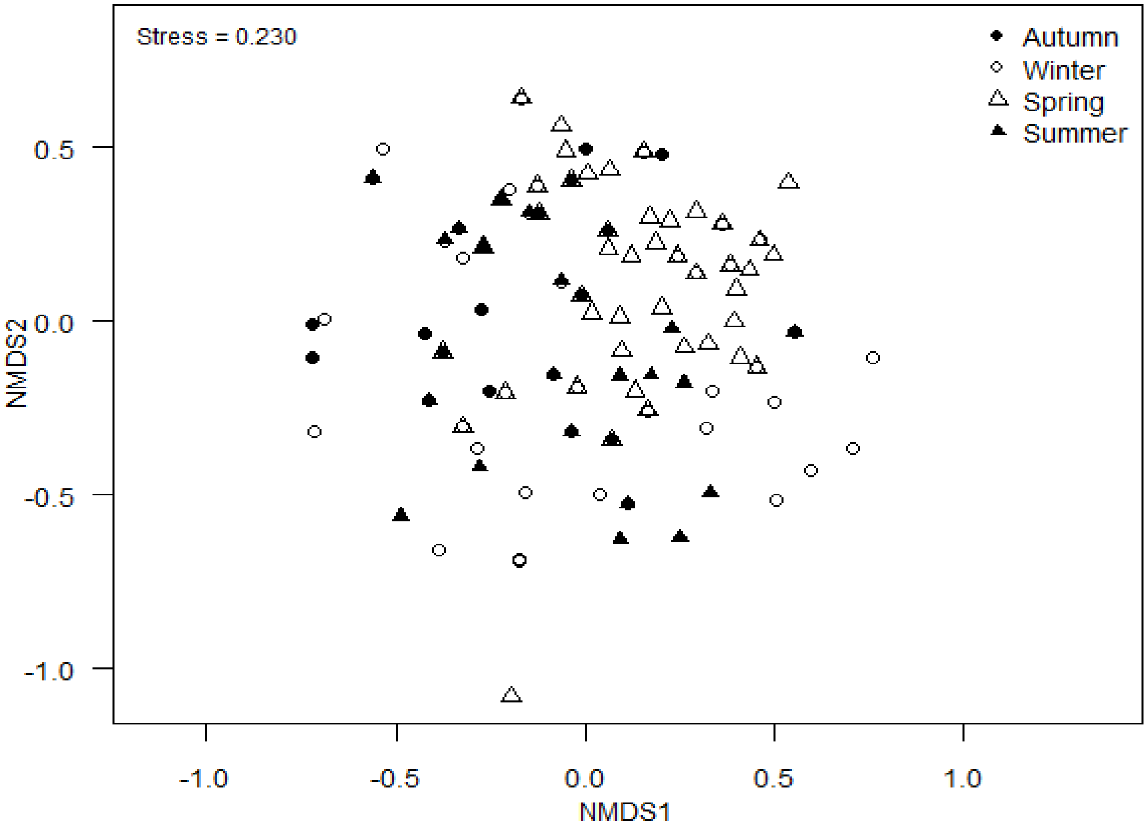

Figure 31. NMDS depicting the seasonal variability in parasite communities of snoek caught off South Africa.

Table 21. The results of seasonal, pairwise analysis of similarity (ANOSIM) conducted on the parasite community of snoek caught off South Africa (* denotes significant results, $p < 0.05$).

Seasons	Global R	p value
Autumn - Winter	0.2001	0.001*
Winter - Spring	0.1207	0.001*
Spring - Summer	0.04272	0.207
Summer - Autumn	0.09918	0.059

The SIMPER routine indicated that the same 5 parasite species, namely, *H. conifera*, *C. dakari*, *H. trichiuri*, *C. australe* and Digenea sp. were responsible for at least 65 % of the dissimilarity in snoek parasite community structure between autumn and spring although their ranking differed between pairwise comparisons (Figure 32).

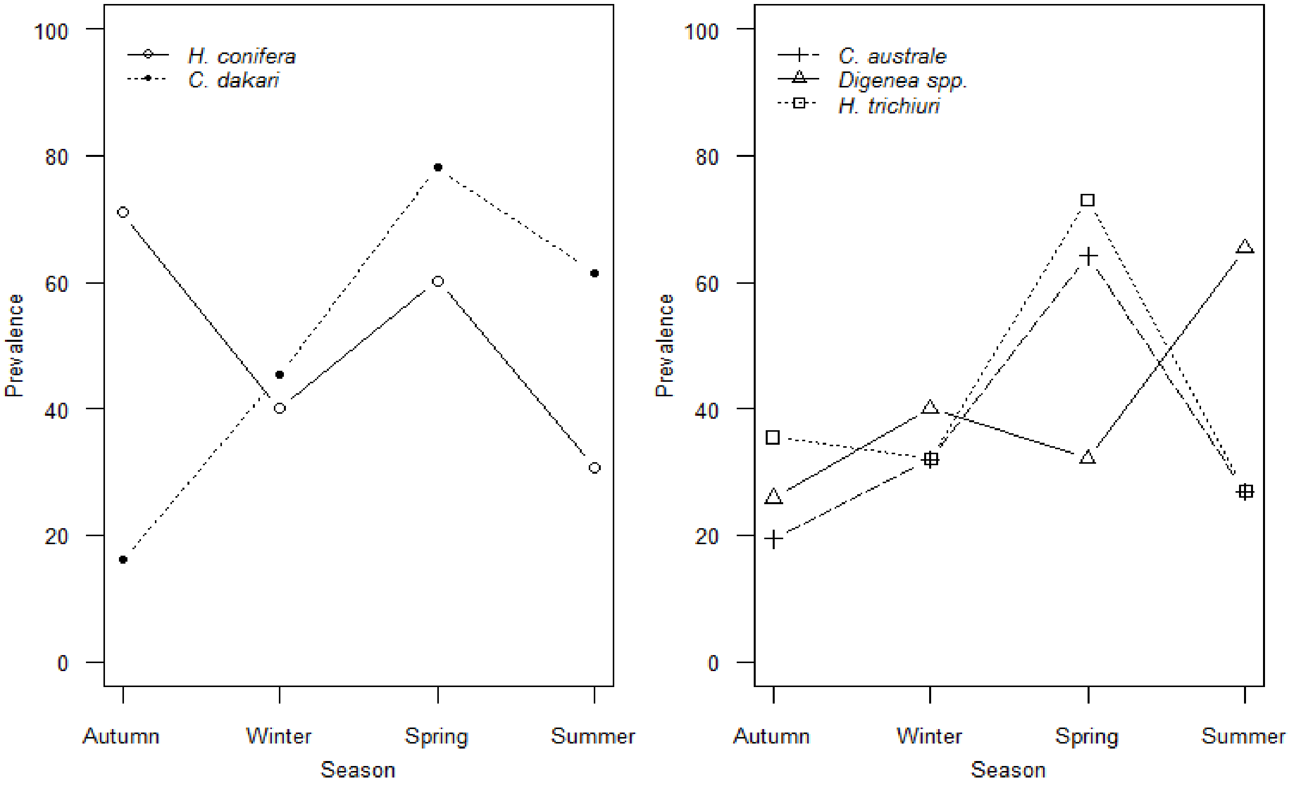

Figure 32. The seasonal variation in prevalence of parasite species contributing to at least 65% of the dissimilarity in community structure between successive seasons.

The analysis of similarity suggested a very small but significant ontogenetic shift in the parasite community structure of snoek off South Africa (Global R = 0.09088, p = 0.005). On the other hand, the pairwise ANOSIM did not reveal significant differences in community structure between snoek of successive size classes. The NMDS suggested that the parasite community of juvenile snoek (< 700 mm FL) was nested within that of adult specimens (Figure 33). Simpson's diversity index revealed that there was a small ontogenetic increase (0.806 to 0.874) in the diversity of the parasite assemblage between the smallest and largest host size classes.

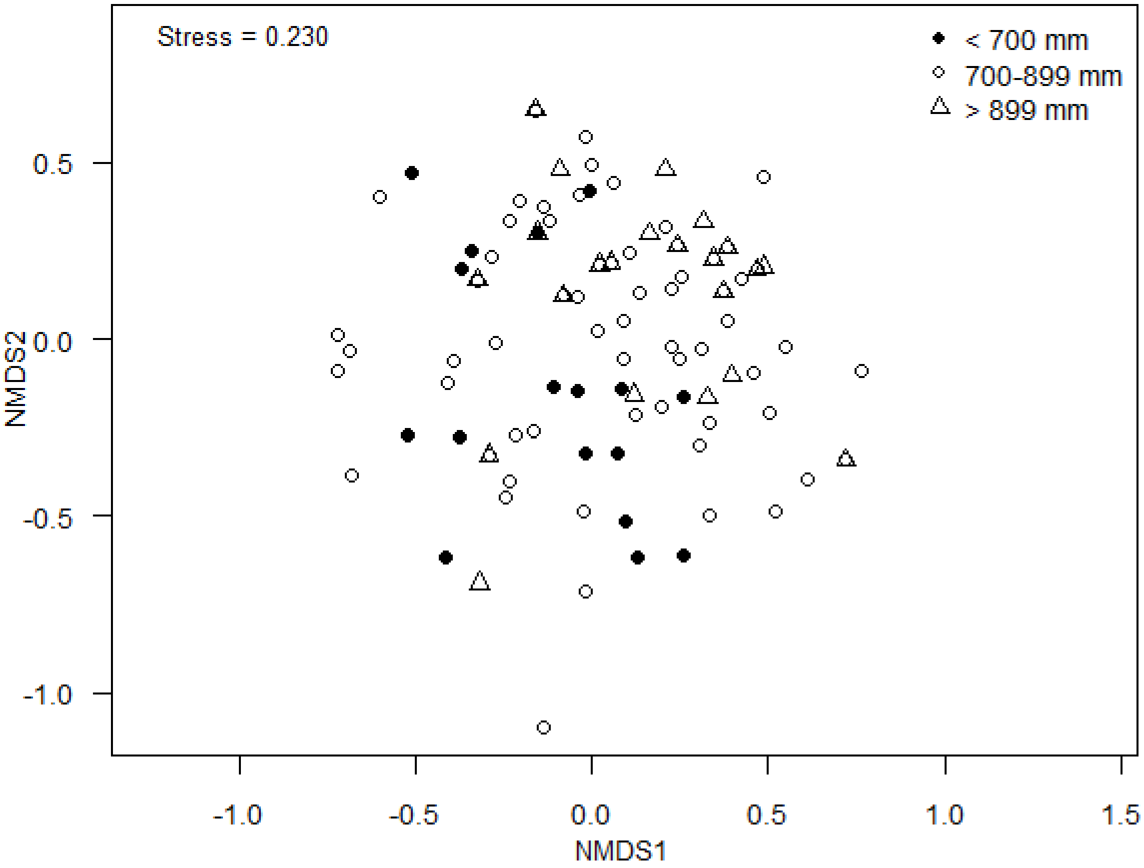

Figure 33. NMDS ordination depicting the ontogenetic shift in the parasite communities of snoek caught off South Africa.

Discussion

As fish parasitology gains momentum in both marine ecology and fisheries management, this study focusing on snoek, *Thyrsites atun*, undertaken between 2013 and 2014 seeked to improve our knowledge on the parasitic biodiversity and ecology of the Southern Benguela as well as to provide further information for management purposes. The economic impacts and the role of fish parasites as drivers of population and community structure have been demonstrated by numerous studies (Johnson *et al.* 2004; Thompson *et al.* 2005; Lafferty *et al.* 2006; Milligan 2008; Henning *et al.* 2013). The degree of parasitism in fish has been intimately linked to host traits including host size, sex, condition, reproductive status and diet, but no universal rules of assembly for fish infrapopulations have emerged. It is therefore crucial to understand the variability in the host sample characteristics as well as the life cycle of the concerned parasite before inferring about the potential causes and consequences of parasitism.

4.1: The Host Sample's Characteristics

The snoek is an iconic species in the Western Cape (Norton 2013). Its life-history has previously been investigated but questions remain about its stock structure and movement patterns in the Southern Benguela (Dudley 1987; Crawford *et al.* 1990; Griffiths 2002, 2003). Answering these questions could improve current management measures for this economically and ecologically significant species in the Southern Benguela. The linefishery landings of the Western Cape for the past decade have been dominated by snoek (DAFF 2012).

The female biased sex ratio of line-caught snoek examined during this study and the increase in mean host size observed in winter and spring (May – October), which coincide with the spawning period, lend further support to Griffiths' (2002) hypothesis that adult female snoek migrate inshore in search of food between spawning events. The proposed spawning period is one month short of that (May – November) postulated by Griffiths (2002) but may have been caused by an unintentional bias towards smaller, juvenile hosts being sampled in summer. Although the analysis of stomach contents only provided a snapshot of the snoek's diet, previous studies suggest that snoek are generalist predators exhibiting an ontogenetic shift in their feeding behaviour (Dudley 1987; Griffiths 2002). Griffiths (2002) reported that juvenile snoek in the Southern Benguela favoured pelagic crustaceans and that the importance of teleosts, both pelagic and demersal, as prey item increased with fish size. Given that the sample examined consisted mostly of adult snoek (80%), the results which suggested a largely piscivorous diet are therefore consistent with previous findings.

4.2: The Host-Parasite Relationships of Snoek

The infracommunity of snoek in South Africa was found to be less speciose but more diverse at the order level than that of New Zealand barracouta (Table 2, 6). Acanthocephalans are reported for the first time from *T. atun* although two of the three species seem to be accidental infections (*B. vasculosum* and *R. cadenati*). Rather surprisingly, no monogeneans were found on snoek although they have routinely been recorded from other active pelagic and demersal fish species (Llewellyn 1962; Hutson *et al.* 2007; Rodríguez-Marín *et al.* 2008; Vaughan & Chisholm 2010). Thirty-four parasite taxa are now known to use *Thyrsites atun* as host for at least one stage in their respective life cycles.

4.2.1: Nematoda

Two nematode taxa were recorded from snoek examined during this study, namely *Anisakis* spp. and *Pseudoterranova* sp. Both are widespread parasite taxa which have been recorded in over 80 fish and mammalian hosts worldwide (Anderson 2000; McClelland 2002; Colón-Llavina *et al.* 2009).

Members of the cosmopolitan genus *Anisakis*, which currently comprises 9 taxa, have a complex life cycle involving a crustacean intermediate host and marine mammals (cetaceans and pinnipeds) as final hosts. (Mattiucci & Nascetti 2006, 2007). In South Africa, six of the nine taxa have been recorded from various hosts, including oceanic dolphins, sperm whales, fur seals and a number of teleosts (Stewardson & Fourie 1998; Anderson 2000; Mattiucci & Nascetti 2006). Two species, *Anisakis pegreffi* and *Anisakis simplex C*, have previously been recorded from *T. atun* in South Africa and New Zealand respectively (Wharton *et al.* 1999; Nieuwenhuizen *et al.* 2006). Anisakids recorded during this study were not identified to species level due to time constraints as well as practical and budgetary reasons since larval anisakids can only be differentiated using molecular techniques (Colón-Llavina *et al.* 2009).

As suggested by the results of this study and past research, squid and fish, including snoek, act as paratenic hosts for L3 anisakid larvae in the Southern Benguela (Botha 1986; Abollo *et al.* 1998; Anderson 2000; Podolska & Horbowy 2003; Le Roux 2013). Although the results of modelling indicate that snoek only acquire anisakids when they reach 700mm FL, the 100% prevalence and high infection intensities observed for *Anisakis* spp. suggest that snoek acquire the parasite at an early age. This discrepancy may be ascribed to the small number of snoek below 700 mm present in the sample examined. Early acquisition of anisakids is consistent with juvenile snoek having a crustacean dominated diet, the major intermediate host of anisakids (Wharton *et al.* 1999; Anderson 2000). Transmission from a paratenic fish host (e.g. *Merluccius* sp., *Trachurus trachurus capensis*) to snoek, or post-cyclic transmission, is also possible (Botha 1986; Le Roux 2013). Euphausiids (*Euphausia lucens*) were the third most important prey type ingested by snoek and appear to be major intermediate hosts of anisakid larvae parasitizing snoek off South Africa. The seasonal variation in *Anisakis* spp. infection intensity may be correlated to the host’s condition (Figure 10). The peak in condition observed in winter coincided with the lowest mean predicted infection intensity and could have been the result of a stronger immune response to the anisakid larvae during that period. The seasonal variation in infection intensity of anisakids may also have been caused by the phenomenon termed 'spring rise' (Strømnes & Andersen 2000) which results in an increase in the incidence of infected euphausiids concomitant with changes in water temperature. Within seasons though, host condition and anisakid infection intensity were positively correlated. This finding contrasted with our expectation that hosts in better condition would harbour less parasites as well as the results of previous studies (Kortet & Taskinen 2004; Neff & Cargnelli 2004). This effect could be due to the fact that fish in better condition feed more aggressively and are thus more susceptible to infection following the ingestion of intermediate and paratenic hosts.

In contrast, *Pseudoterranova* sp., here recorded for the first time in Southern Africa (McClelland 2002), occurred at a much lower incidence (16.4%) than *Anisakis* spp. in snoek. Despite both nematode taxa maturing in pinnipeds and cetaceans, fundamental differences in the bathymetric distribution of their larval stages and intermediate hosts (pelagic versus demersal) could explain the contrasting pattern of nematode parasitism observed in snoek (Anderson 2000; McClelland 2002). As reported by Palm (1999), the inability of *Pseudoterranova* larvae to swim translated into demersal foragers being more susceptible to this particular nematode. Consistent with the results of stomach content analysis and previous studies (Dudley 1987; Griffiths 2002), this suggested that snoek do not rely heavily on benthic organisms as prey items and that *Pseudoterranova* infection may have been acquired via the ingestion of a sympatric teleost paratenic host (e.g. *Merluccius* sp.) (David 1987; Sardella & Timi 2004). Abiotic conditions prevailing within the study area may also have contributed to the low incidence of *Pseudoterranova* sp. in snoek. The wind induced upwelling of cold bottom water off South Africa's West coast during summer could decrease the settling and development of

Pseudoterranova sp. eggs and larvae while also resulting in the dispersal of eggs outside the distribution of snoek off Southern Africa (McClelland *et al.* 2000; McClelland 2002; Hauksson 2011).

Although the pathogenic potential of nematodes in humans as well as their economic impacts are well documented (Pinel *et al.* 1996; Piccolo *et al.* 1999; Scholz 1999; Anderson 2000; Chai *et al.* 2005; Nieuwenhuizen *et al.* 2006; Roberts *et al.* 2009), nematodes parasitizing snoek were never found within the muscle tissue and therefore do not represent a major health hazard for consumers since gutting and thorough cleaning should dislodge any larvae from within the coelom. People employed in the fish processing industry are more at risk as repeated and prolonged exposure to anisakid larvae can result in mucosal irritations and allergic reactions (Nieuwenhuizen *et al.* 2006). Further research is required to evaluate the health risk posed by nematodes and uncover their ecology in the southern Benguela.

4.2.2: Myxozoa

Myxozoans are mainly parasites of fish, both freshwater and marine (Fomena & Bouix 1997; Lom 2005). Myxozoans have an indirect, two-host life cycle, but questions remain about their biology, ecology and diversity in many parts of the World (Moran *et al.* 1999a, 1999b; MacKenzie & Kalavati 2014). To date, the life cycles of only 6 marine species have been elucidated (MacKenzie & Kalavati 2014). Two myxozoan taxa, the histozoic *Kudoa thrysites* and coelozoic *Ceratomyxa* sp. were found infecting snoek in the southern Benguela.

Kudoa thyrsites is a cosmopolitan myxozoan exhibiting low host specificity and is known to infect at least 37 teleost species, including *Thyrsites atun*, worldwide (Whipps & Kent

2006; Burger & Adlard 2011). First described as *Chloromyxum thyrsites* from snoek by Gilchrist (Gilchrist 1924), *K. thyrsites* is infamous for the post-mortem myoliquefaction it induces in a number of commercially important fish species (St-Hilaire *et al.* 1997; Dawson-Coates *et al.* 2003; Henning *et al.* 2013). Off South Africa, two myoliquefactive kudoid species have been recorded, *K. paniformis* in merluciids (Henning *et al.* 2013) and *Trachurus capensis* (Le Roux 2013) and *K. thyrsites* in the muscles of *Sardinops sagax* (Reed *et al.* 2012), *Zeus capensis* (Henning *et al.* 2013) and snoek (Gilchrist 1924). In both the sardine and snoek fisheries operating off South Africa, the post-mortem myoliquefaction induced by *K. thyrsites* is responsible for significant economic losses and waste of animal protein (Henning *et al.* 2013).

While *K. paniformis* was not detected during this study using microscopy although it has recently been recorded in snoek by St Claire-Henning (2014) using molecular identification methods. The small dorsal muscle samples screened for *Kudoa* infections are susceptible to Type I error, i.e., *K. paniformis* may have been present in the host but was not detected. This could also be due to interspecific differences in the preferred site of infection between *K. paniformis* and *K. thyrsites* (Tamkee 1999; Henning *et al.* 2013). The high prevalence (97%) of *K. thyrsites* recorded during this study suggest that snoek acquire the infection at an early age, most probably while still on nursery grounds (Griffiths 2002). Little can be safely inferred about the ecology of *K. thyrsites* in the Southern Benguela due to the paucity of knowledge pertaining to its life cycle (Moran *et al.* 1999a). Further studies, both laboratory and field based, are required to shed some light on the life cycle and ecology of *K. thyrsites* and as acknowledged by Henning *et al.* (2013) there is a need for an early detection system to be developed.

The genus *Ceratomyxa*, whose members generally parasitise the gall bladder of marine fish, is one of the most speciose genera within the myxosporea (Eiras 2006). To date, 252 nominal species have been reported from marine fish worldwide despite lower discovery rates outside the North Atlantic (MacKenzie & Kalavati 2014). Before 2007, only *Ceratomyxa schulmanii* had been reported from South African waters (Reed *et al.* 2007). Since then, *C. australis* was found infecting the gall bladder of horse mackerel off South Africa (Le Roux 2013) and 3 species (*C. dehoopi*, *C. cottoidii*, *C. honckenii*) have been described from intertidal fish (Reed *et al.* 2007). Although sympatry between species of the genus *Ceratomyxa* is possible (George-Nascimento *et al.* 2004; Hutson *et al.* 2007), a single species, only identified to genus level, was recovered from snoek. Initial observations and measurements indicated that *Ceratomyxa* sp. found in snoek constitute a new host and locality record while the very low observed incidence of this parasite suggests that it may have been an accidental infection.

4.2.3: Cestoda

Marine trypanorhynch cestodes have an indirect life-cycle involving two intermediate hosts, a crustacean and a teleost, before maturing in the spiral valves or intestines of a suitable vertebrate final host, generally an elasmobranch (Caira & Reyda 2005). Larval forms, plerocercoids and plerocerci, infect the muscles and various other organs of a wide range of commercially important fish species including barracouta (Mehl 1970; Seyda 1976; Williams & Bunkley-Williams 1996; Felizardo *et al.* 2010). Muscle-infecting species are responsible for considerable losses in the seafood industry, mostly due to the severely impacted visual appeal of infected fish fillets (Muscolino *et al.* 2012; Giarratana *et al.* 2014). Off South Africa, three trypanorhynch species were recovered from snoek, namely, *Molicola uncinatus*, *Hepatoxylon trichiuri* and *Tentacularia coryphaenae*.

The plerocercoids of *Molicola uncinatus*, which uses the thresher shark (*Alopias vulpinus*) as final host, have been observed infecting the muscles of several teleosts including swordfish (*Xiphias gladius*), sunfish (*Mola mola*) and barracouta (Robinson 1959a; Love &

Moser 1983; Williams & Bunkley-Williams 1996). The current study, during which *M. uncinatus* was recovered from the musculature of snoek caught off South Africa, therefore constitutes a new geographical record for the species. Given its widespread and conspicuous nature (Williams & Bunkley-Williams 1996), it is surprising that *M. uncinatus*, commonly referred to as 'melkaare' (milk vein) in South Africa, was only identified to species level in the course of this study. In contrast to New Zealand, where the barracouta fishery is severely affected by the presence of *M. uncinatus*, the South African snoek linefishery is thriving despite the high year-round prevalence of *M. uncinatus* (DAFF 2012). This could be due to the longstanding and still perpetuated myth that the cestode is part of the fish tissue and therefore does not warrant an investigation or as suggested by Reed's (2014) review it might just be a reflection of the low effort afforded to marine parasitology in Southern Africa.

The results suggested that as snoek aged they became more susceptible to *M. uncinatus* and that they accumulated the parasite within their muscle tissue, as reported by Mehl (1970) from barracouta in New Zealand. Snoek may acquire the infection by either preying on the intermediate crustacean host or on a fish acting as second intermediate host. The small amount of variation accounted for by the reproductive status of hosts and sampling seasonality indicate that these two variables have a negligible influence on the infection intensity of *M. uncinatus* in snoek off South Africa.

Hepatoxylon trichiuri is a cosmopolitan species whose plerocercoids infect the body cavity of a wide range of commercially valuable teleosts while the adults infect the spiral valves of elasmobranchs (Botha 1986; Payne 1986; Beveridge & Campbell 1996; Campbell & Callahan 1998; Munday *et al.* 2003; Knoff *et al.* 2004; Gonzalez *et al.* 2006; Jakob & Palm 2006; Mladineo 2006; MacKenzie *et al.* 2013). By virtue of its preferred site of infection, both as plerocercoids and adults, *H. trichiuri* is not a cause for concern in the fishing and seafood industries (Mladineo 2006). The species has previously been reported from *T. atun* in off New Zealand (Wierzbicka & Gajda 1984).

The analyses revealed a difference in mean size-at-50%-infection and the seasonal variation pattern in prevalence between the sexes. These differences suggest that infective stages of *H. trichiuri* are available all year round but that subtle differences exist in the behaviour and feeding patterns of male and female snoek off South Africa. Such differences in feeding patterns have been previously reported (Dudley 1987; Griffiths 2002). Long-lived parasites whose biology is relatively well known such as *H. trichiuri* (Waterman & Sin 1991; Beveridge & Campbell 1996; MacKenzie *et al.* 2013), provide insight into a fish's diet and behaviour over a longer time frame than the study of stomach contents (Jacobson *et al.* 2012) and can prove useful in the assessment of stock structure (Oliva & Ballon 2002).

Tentacularia coryphaenae

Tentacularia coryphaenae is a widely distributed trypanorhynch (Palm 2007) whose plerocercoids have been reported from both teleosts and cephalopods (Williams & Bunkley-Williams 1996; Pardo-Gandarillas *et al.* 2009) while adults infect sharks. Previously reported from two Indonesian gempylids (Jakob & Palm 2006), *Gempylus serpens* and *Thyrsitoides marleyi*, this study provides a new host record for *T. coryphaenae*. In teleosts, *T. coryphaenae* infects the body cavity, mesenteries as well as the musculature (Palm 2000; Munday *et al*. 2003; Reed *et al*. 2012) and can be of commercial significance. In snoek, *T. coryphaenae* plerocercoids were restricted to the coelom and therefore neither represent a human health hazard nor an economic problem. *Tentacularia coryphaenae* may aggressively compete with sympatric cestodes such as *H. trichiuri* (Williams & Bunkley-Williams 1996) although in snoek examined during the course of this study no such interactions were observed.

The ontogenetic increase in prevalence predicted by modelling suggests that snoek acquire *T. coryphaenae* via predation on secondary intermediate teleost hosts such as clupeoids (Reed *et al*. 2012) rather than through predation on a crustacean intermediate host which dominate the diet of juvenile snoek (Griffiths 2002). The positive relationship between host GSI and *T. coryphaenae* prevalence suggests that as fish invest more energy in reproduction their immunity to the cestode is decreased. This claim is also supported by the increased prevalence predicted for fish with smaller fat reserves, although the possibility that plerocercoids were covered by heavy fat deposits (fat score 3) and therefore not recorded cannot be dismissed. Despite *T. coryphaenae* being employed as a biological tag for stock discrimination of commercially important teleosts in the Atlantic (Castro-Pampillon et al. 2002; Serrano Gordo et al. 2009), the parasite appears of limited use for elucidating snoek stock structure off Africa due to it not being easily detectable because of its small size relative to other cestodes and its susceptibility to being covered by fat deposits.

4.2.4: Copepoda

The Copepoda is a highly diverse taxon, comprising over 12 000 species, parasitizing an array of hosts across most phyla and exhibiting a mind-boggling diversity in their respective ecologies (Dippenaar 2004; Boxshall 2005; Suarez-Morales & Carrera-Parra 2012). Worldwide, parasitic copepods, especially members of the family Caligidae, are the cause of considerable losses in the fin-fish aquaculture and fishing industries.(Payne 1986; Scholz 1999; Cruz-Lacierda *et al.* 2011). In South Africa, the study of parasitic copepods was pioneered by Barnard (1955a, 1955b). Since then, a number of attempts at documenting the known biodiversity of parasitic copepods occurring off South Africa have been undertaken (Kensley & Grindley 1973; Oldewage 1992, 1993a; Oldewage & Smale 1993; Dippenaar 2004) and a number of new species have been described from marine fish hosts (Kensley 1970; Dojiri 1989; Avenant-Oldewage

1994; Van As *et al.* 1999; Dippenaar *et al.* 2000, 2001; Grobler *et al.* 2002; Smit *et al.* 2005; Dippenaar & Jordaan 2006, 2008; Dippenaar & Lebepe 2013). A single copepod species, *Caligus zei*, has previously been reported from snoek (Barnard 1955b). Four out of the five ectoparasitic copepods recorded during this study, *Nothobomolochus fradei*, *Hatschekia conifera*, *C. dakari* and *C. coryphaenae*, therefore all constitute new host records although all have been previously recorded off South Africa from different hosts (Dippenaar 2004; Reed *et al.* 2012).

Nothobomolochus fradei is a little known but widespread parasitic copepod favouring clupeoid hosts (Ho & Lin 2004; El-Rashidy & Boxshall 2010; Reed *et al.* 2012). The majority of publications in which *Nothobomolochus fradei* is mentioned are of taxonomic nature (Ho & Lin 2004; El-Rashidy & Boxshall 2010, 2011, 2012), only two reported prevalence figures (El-Rashidy & Boxshall 2009; Reed *et al.* 2012). While only 10% of the sardines (*Sardinops sagax*) examined by Reed *et al.* (2012) harboured *N. fradei* at low mean intensity, a very high year-round incidence and mean intensity was predicted for snoek, a sympatric, predatory gempylid. The preferred site of infection also differed between sardines and snoek (Reed *et al.* 2012); in sardines *N. fradei* was only recorded from the opercular cavity and gills while on snoek most infections occurred in the nares. The active nature of snoek may preclude attachment of *N. fradei* inside the operculum and on the gills, whereas the nares provide a more sheltered environment. These findings contrast with the suggestion of Ho & Lin (2004) that bomolochid copepods exhibit some degree of host specificity and suggest that ecology rather than phylogeny dictates which fish species within the endemic area (MacKenzie *et al.* 2008) of *N. fradei* off South Africa are susceptible to it. The predicted effects of seasonality and condition in conjunction with host sex on the infection intensity of *N. fradei*, once again, suggest that male and female snoek exhibit significant differences in their movement patterns. This effect may be explained by a difference in the amount of time male and female snoek spend within the endemic area of *N. fradei* within each season or by differences in their immunity to *N. fradei*.

Members of the widely distributed genus *Hatschekia*, which comprised at least 97 species, exhibit a high level of specificity in their preferred site of infection by only parasitizing the gill filaments of marine fish (Jones 1985; Ho & Kim 2001; Hermida *et al.* 2012; Moon & Kim 2013). The genus is also characterized by a lack of taxonomic features and considerable intraspecific variation in size, segmentation and setation (Jones 1985; Oldewage 1993b). Size and colour are also not appropriate taxonomic features to distinguish between species due to the potential effect of fixing agents (Jones 1985). This prompted Oldewage (1993b) to propose body shape as a defining feature of hatschekiids. In his enthusiasm to document marine biodiversity off South Africa, Barnard (1955a) briefly described *Hatschekia acuta* from *Brama brama* caught off South Africa, although he himself noted a resemblance to *H. conifera*. *H. acuta* has since been relegated to junior synonym of *Hatschekia conifera* (Jones 1985). This copepod has previously been recorded from Japan, Java, New Zealand, Argentina, Chile and South Africa from a variety of hosts (Jones 1985; Oldewage 1993b; Dippenaar 2004; Jakob & Palm 2006; Cantatore *et al.* 2012). Although Jakob & Palm (2006) recorded an unidentified *Hatschekia* species from a gempylid (*Thyrsitoides marleyi*) caught off the Javan coast, this study constitutes a new host record for *H. conifera*.

The prevalence and mean infection intensity (48.6%, 3.5) of *H. conifera* on snoek were in line with that reported by Oldewage (1993a) from sympatric angelfish (*Brama brama*, 46%, 4.3) caught off the West Coast of South Africa. The slight differences observed in both indices could be reflecting ecological differences between host species (Jakob & Palm 2006) or be an artefact of the smaller spatial and temporal scale of Oldewage's study (1993a). Given that *H. conifera* has only been recorded off Hondeklip Bay and in False Bay, the results of the present survey extend the known distribution range of *H. conifera* off South Africa. Worldwide, few studies of host-parasite relationships have focused on species of *Hatschekia* (Lo *et al.* 1998; Hermida *et al.* 2012; Henriquez & Gonzalez 2014) with contrasting results. In snoek, both prevalence and infection intensity increased with host size as expected by standard parasitological theory (Poulin 1999), although negative correlations have also been reported, albeit for a different hatschekiid species, *H. pagellibogneravei* (Hermida *et al.* 2012). Despite the models suggesting that snoek of all sizes are susceptible to *H. conifera*, exploratory data analysis showed that a single fish smaller than 650 mm FL was infected. This suggests that juvenile snoek are not susceptible to the infective stages of *H. conifera*, i.e., they do not venture into the endemic area of the parasite or that they are resistant to the infection. While the predicted seasonal variation was considered negligible, the reproductive status and the mesenteric fat score of hosts appeared to be major determinants of both prevalence and intensity but since they are known to inversely co-vary (Griffiths 2002), it is difficult to tease the effect of one from the other without laboratory studies. This covariation in GSI and mesenteric fat reserves of fish hosts could explain why snoek with high GSI and low fat score were both predicted to be less susceptible to *H. conifera*. Behavioural differences, as reported by Griffiths (2002), or a stronger immune response associated with the process of gonad development and spawning could lower the chance of snoek acquiring hatschekiid parasites. Behavioural differences may either result in the loss of parasites already present as fish hosts move outside the range of environmental conditions tolerated by *H. conifera* (Hermida *et al.* 2012) or decrease the probability of acquiring new parasites by avoiding the endemic area of the parasite. The first hypothesis seems more plausible given the wide distribution and year-round availability of *H. conifera* infective stages suggested by the analyses.

Of the three caligids recorded, *Caligus dakari* was the most prevalent and abundant. Initial identification of this copepod using Barnard’s key (1955a) led to it being identified as

Caligus arii Bassett-Smith 1898 but a comparison with Bassett-Smith's (1898) original description strongly suggested that this was incorrect, as noted by Kumar (1990). The two species, *C. dakari* and *C. arii*, differ in the segmentation of the abdomen having a one and two jointed abdomen respectively. The copepod was subsequently identified as *Caligus dakari* using the redescription of Boxshall & El-Rashidy (2009). *Caligus arii* of Barnard (1955) and *C. mauritanicus* Brian, 1924 are now accepted as synonyms of *C. dakari* (Dippenaar 2004; Boxshall & El-Rashidy 2009). *Caligus dakari* is a large caligid (Özak *et al.* 2010) which has been reported from India, Mauritania, Senegal, Sri Lanka and South Africa from the teleost families Ariidae and Carangidae as well as elasmobranchs of the carcharinid family (Thompson & Scott 1903; Kumar 1990; Dippenaar 2004; Boxshall & El-Rashidy 2009). This study provides the first record of *C. dakari* on a gempylid host and also constitutes a new locality record.

Previously only reported from the mouth of the Zambezi River (Barnard 1955a) and off the coast of West Africa (Boxshall & El-Rashidy 2009), a third African population, from the west and south coasts of South Africa, is here reported from snoek. The results greatly extend the known distribution of the species although it is impossible, at this stage, to establish whether there is any exchange between the three populations. Given that the parasite occurs off South Africa year-round, the results of this study strongly suggest that the prevalence and infection intensity of *C. dakari* on snoek are dependent upon the host's traits rather than seasonality in the parasite's life cycle. The peak predicted for prevalence and intensity in spring both coincided with lowest mean host body condition while within seasons, fish with less energy reserves, in the form of fat deposits, were predicted to be more susceptible to *C. dakari*. Fish with low body condition and small fat reserves may be weak swimmers and/or have a diminished immune response to ectoparasitic infections (Kennedy *et al.* 1987), thereby providing a better platform for infection. These findings, along with those of Neff & Cargnelli (2004) who reported lower parasite densities with increasing body condition in bluegill sunfish (*Lepomis macrochirus*), support the hypothesis that infection of snoek by *C. dakari* is dependent upon host fat reserves and possibly the strength of the associated immune response (Sitjà-Bobadilla 2008; Simková *et al.* 2008). Yet, the little knowledge we have on the caligid life cycle (Boxshall 2005) does not allow one to completely discard the possibility that the seasonal variation in *C. dakari* prevalence and infection is due to recruitment of the copepod rather than seasonal variation in the host's traits or even a combination of the two alternatives.

Caligus zei, originally described from the dory (*Zeus faber*) (Scott & Scott 1912, 1913), has previously been recorded from snoek (Barnard 1955b) although doubts exist about the validity of Barnard's identification (Dippenaar 2004). The positive identification reported here supports the findings of Barnard (1955b) that snoek are susceptible to *C. zei* and extend their known range off South Africa from a spot sample taken in Table Bay to the entire West coast southwards to the Western Agulhas Bank. The ontogenetic shift in the prevalence of *C. zei* on snoek is consistent with the hypothesis that a larger body size offers a larger 'target' for parasite infections in marine fish (Luque *et al.* 2004) although a number of studies suggest otherwise (Poulin 2000; Poulin & Leung 2011). The seasonal prevalence pattern predicted for *C. zei* suggest that the species has a year-long life cycle with infective stages being available from winter through to spring but the paucity of information pertaining to *C. zei* hampers inference. The relationship between *C. zei* prevalence and host mesenteric fat content indicates that like *C. dakari*, *C. zei* infection is dependent upon host condition. The infection could also have resulted from the occasional interaction between snoek and the most probable reservoir host (Langdon *et al.* 1992) of *C. zei* off South Africa, the demersal Cape dory *Zeus capensis* (Smale & Badenhorst 1991; Smale 1992). Such interactions could arise from deep water feeding forays by adult snoek while on offshore spawning grounds.

A single specimen of the circumtropical *Caligus coryphaenae*, constituting a new host record, was recovered from snoek examined during this study (Kensley & Grindley 1973; Hogans 1985; Jones 1988; Cressey 1991; Luque & Tavares 2007; Maran & Ohtsuka 2008; Justine *et al.* 2010; Özak *et al.* 2012). Primarily a parasite of scombrids (Cressey *et al.* 1983), it has also been recorded from other widely distributed teleosts such as dolphinfishes *Coryphaena sp*. (Jensen 1967; Pillai 1984; Williams & Bunkley-Williams 1996; Carbonell *et al.* 1999) and one elasmobranch species (Dippenaar 2004). Off southern Africa, *C. coryphaenae* occurs all the way from the coast of Mozambique to Table Bay on the west coast of South Africa (Dippenaar 2004). Given its wide distribution off South Africa it is rather surprising that a single snoek was infected and the infection should be considered accidental. The parasite could have been acquired via interactions between snoek and potential, commonly infected hosts on the Western Agulhas Bank (Pecquerie *et al.* 2004).

4.2.5: Acanthocephala

Acanthocephala is a relatively small phylum (Amin 1998) whose members primarily parasitise the gastro-intestinal tract (GIT) of fish (Tarachewski 2005) although both bird (Van Cleave 1918) and mammalian (Van Cleave 1953a) final hosts have been recorded. Acanthocephalans, commonly referred to as ‘spiny-headed’ worms, have an indirect life cycle involving a crustacean first host and in which fish serve either as final or paratenic hosts depending on the concerned parasite taxon (Tarachewski 2005). Acanthocephalans are known to affect the behaviour (Lafferty & Shaw 2013) and the mortality (Latham & Poulin 2002; Kennedy 2006) of their hosts. They do not usually represent a health hazard in the seafood industry since they either encapsulate within the body cavity or are restricted to the GIT of fish hosts (Kennedy 2006) and are therefore easily removed through gutting and cleaning. No previous records of acanthocephalans from *Thyrsites atun* exist. All three species recovered during the course of this study (*Bolbosoma vasculosum*, *Corynosoma australe*, *Rhadinorhynchus cadenati*) therefore constitute new host records.

Bolbosoma vasculosum has previously only been reported from the northern hemisphere where it is widespread and infects a number of teleost as an immature while adults parasitise the intestines of odontocete cetaceans (Love & Moser 1983; Williams & Bunkley-Williams 1996; Amin 1998; Costa *et al.* 2000; Fernandez *et al.* 2004; Klimpel *et al.* 2006). The life cycle of this species most likely involves an intermediate crustacean first host such as euphausiids, as proposed by Gregori *et al.* (2012), while fish serve as paratenic hosts. Cystacanths, the late immature and infective stage of *B. vasculosum*, appear to exhibit low host specificity in their choice of fish paratenic hosts (Williams & Bunkley-Williams 1996) and have successfully been employed as biological tags in a stock structure study of the black scabbardfish (*Aphanopus carbo*) in the northern Atlantic Ocean (Serrano Gordo *et al.* 2009). The very low level of infection detected in snoek suggests that this was an accidental infection that could have resulted from snoek predation on a paratenic fish host species although a potential intermediate host, *Euphausia lucens*, is common within the study area and is preyed upon by snoek. In addition to a new host record, this survey also serves as a new geographic record, the first in the southern hemisphere, for *B. vasculosum*.

Members of the genus *Corynosoma* utilize either mammals or birds as definitive hosts (Van Cleave 1953b; Laskowski *et al.* 2008). Initially thought to be restricted to the southern hemisphere (Shaughnessy & Ross 1980; González *et al.* 2001; Alves *et al.* 2003; Timi *et al.* 2005; Rocka 2006), *Corynosoma australe* has recently been recorded from the northern Atlantic (Costa *et al.* 2011) in chub mackerel (*Scomber colias*). It has an indirect life cycle in which crustaceans serve as first intermediate host, fish as paratenic or second intermediate host while seals act as definitive hosts (Zdzitowiecki 1986; Braicovich *et al.* 2005). The cystacanth stage of

C. australe displays low host specificity in its choice of paratenic host (Zdzitowiecki 1986; Sardella & Timi 2004; Santos *et al.* 2008; Vales *et al.* 2011) and has proved a promising biological tag in population structure and migration studies of various teleosts (Timi *et al.* 2005; Luque *et al.* 2010; Costa *et al.* 2011; Carballo *et al.* 2012). Despite the fact that *C. australe* cystacanths have often been reported and employed as biological tag, a single study evaluated the ontogenetic shift in prevalence and abundance of this acanthocephalan in a fish paratenic host (Alves *et al.* 2003).

In snoek, *C. australe* exhibited an ontogenetic increase in prevalence. This finding contrasts with that of Alves *et al.* (2003) who reported no significant correlation in either prevalence or infection intensity with host size, although their analyses may have been hampered by the small size range of hosts examined. The effects reported with respect to condition and GSI are most probably linked since these two variables generally display a negative relationship. The results of modelling also suggest that although the infective stage of *C. australe* may be available for most of the year, snoek with low body condition were more at risk of being infected. This would be beneficial to *C. australe* as snoek in lower condition may be more at risk of being preyed upon (Booth & Beretta 2004) and therefore improve transmission rates of *C. australe* to its proposed final host (Shaughnessy & Ross 1980), the fur seal *Arctocephalus pusillus pusillus*, in South African waters.

Rhadinorhynchus is a small acanthocephalan genus comprising 38 species, many of which parasitise the intestines of teleosts as adults (Amin *et al.* 2011). Scombrids are the primary definitive host for *Rhadinorhynchus cadenati* although sparids (e.g. *Boops boops*) are also susceptible (Troncy & Vassiliadès 1973; Love & Moser 1983; Munday *et al.* 2003; Pérez-del-Olmo 2008). Off South Africa, *R. cadenati* was previously only known from horse mackerel *Trachurus trachurus capensis* (Le Roux 2013). Although this acanthocephalan has previously been employed as a biological tag for population structure studies of mackerel species in the northern Atlantic (Shukhgalter & Rodjuk 2007; MacKenzie & Hemmingsen 2014), the proposed short residence time in the definitive host may reduce its usefulness and hamper inference (Costa *et al.* 2013). The low prevalence of *R. cadenati* in snoek suggests that it was an accidental infection acquired via post-cyclic transmission (Kennedy 2006) and therefore is of low importance for management purposes.

4.2.6: Digenea

The digenean metacercariae (Digenea sp.) recovered from snoek gill arches could not be identified to species using morphological characteristics; the use of molecular and genetic techniques is recommended. A tentative identification as *Cardiocephaloides physalis*, a parasite of the African jackass penguin (*Spheniscus demersus*) (Brandão *et al.* 2014), is proposed based upon the findings of Reed *et al.* (2012). *Cardiocephaloides physalis* is a rare example of a digenean infecting pelagic bird species (Hoberg 2005b) and which can potentially seriously affect penguin chick survival (Horne *et al.* 2011). The long residence time, site specificity and the large size of digenean metacercariae recovered from clupeoids in the southern Atlantic (Timi 2007; Weston 2013; van der Lingen *et al.* 2014) make them useful biological tags. In South African waters, sex, seasonality and host size appeared to be significant drivers of *Digenea* sp. infection in snoek. The lower prevalence predicted for male snoek could either be related to behavioural differences between host sexes (Griffiths 2002) which lower encounter rates with the parasite or a stronger immune response in males which decrease the chances of parasite establishment. The seasonal variability in prevalence may indicate a seasonal peak in the release of eggs and/or the development of infective stages of the digenean, although, little is known about its life cycle and different obligate hosts (Horne *et al.* 2011). Caution must be exercised if this parasite is used as a biological tag, since the ontogenetic shift in prevalence could lead to erroneous conclusions should fish of different size class be compared.

4.3: Parasite Community Structure

The community structure of parasites of free ranging organisms is widely considered to be a function of the host's phylogeny, ecology and various individual level traits such as diet, sex and body size (Muñoz *et al.* 2006; Timi *et al.* 2010; Marques *et al.* 2011; Lagrue *et al.* 2011). The high degree of similarity between the infracommunity structure of male and female snoek off South Africa suggested that although gender specific differences in ecology and physiology may determine infection levels of some parasite species (e.g. *H. conifera*, Digenea sp.), these differences were too subtle to significantly affect the infracommunity of snoek as a whole.

Irrespective of size, snoek appeared to be exposed to the same suite of core parasite infective stages but larger hosts seemed susceptible to a wider range of parasites, as evidenced by the slight ontogenetic increase in diversity index and the nested nature of the infracommunity (Figure 34). The increased susceptibility of large, mature snoek to parasites, could be the result of a trade-off between immunity and fecundity (Sitjà-Bobadilla 2008) or be related to an ontogenetic shift in behaviour and diet (Dudley 1987; Griffiths 2002). Young snoek may invest more in immunity and parasite avoidance to improve their chances of reaching sexual maturity, at which point the trade-off is reversed in favour of fecundity.

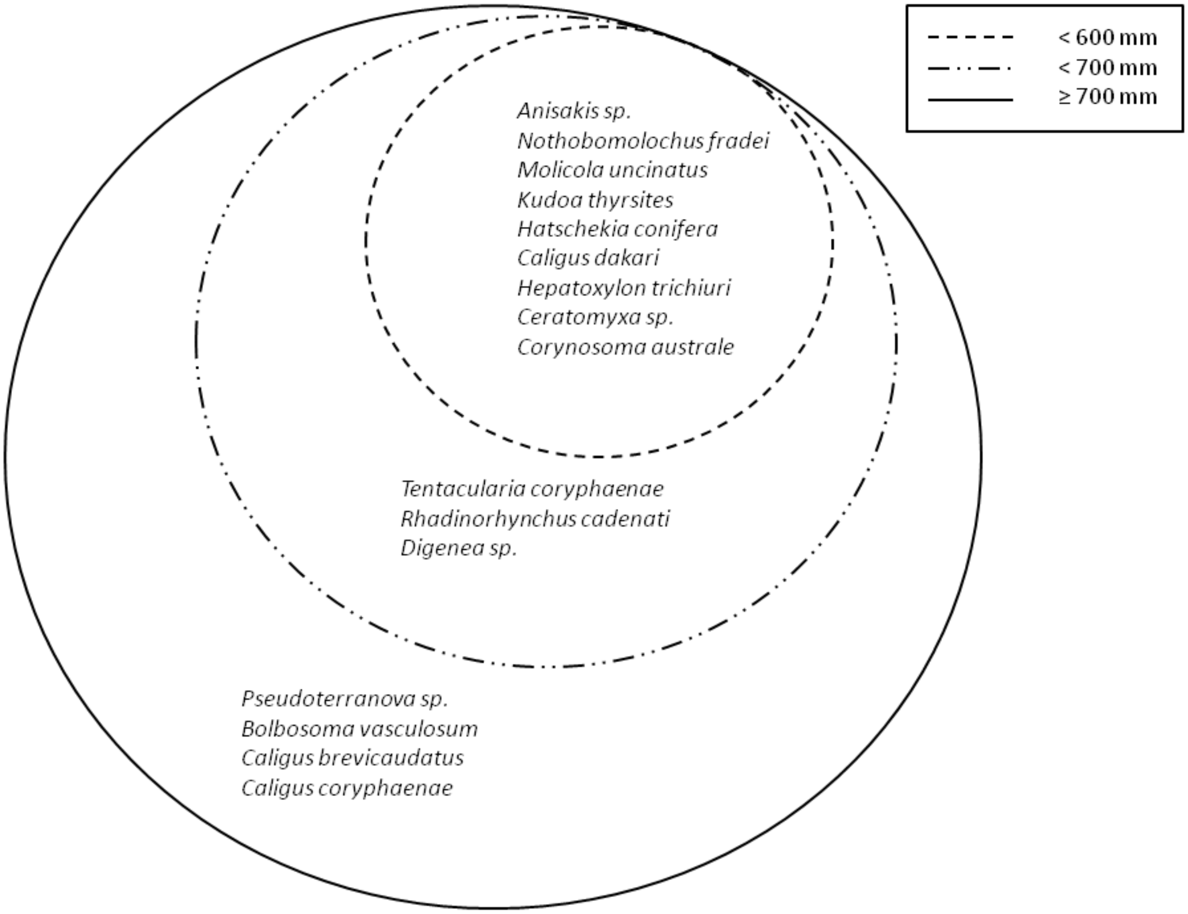

Figure 34. Ontogenetic nestedness of the parasite community of snoek caught off South Africa.

Seasonally, the parasite assemblage of snoek exhibited low variability in taxonomic composition and diversity. The slight seasonal differences in parasite community structure could be attributed to fluctuations in the prevalence of indicator species rather than the increase in infracommunity richness and diversity. The widely acknowledged relationship between effort and observed diversity (Hechinger & Lafferty 2005; Luque & Poulin 2007) could explain the higher parasite diversity observed in winter and spring samples since 73% of the snoek examined were caught during this period. The seasonal stability in the infracommunity may be a result of the nomadic nature of snoek off South Africa. By moving over vast distances rapidly, snoek may well go beyond the range of environmental factors tolerated by parasites with strict environmental and biological requirements (Luque *et al.* 2004; Luque & Poulin 2008) thereby applying an ecological filter to its parasite community. This could also explain the dominance of non-specific endoparasitic larval taxa with long residence time as these should be more resilient to environmental change than ectoparasites and specialist endoparasites.

The dominance of larval anisakids and cestodes in the snoek's infracommunity suggest that snoek serve as an important intermediate or paratenic host for many parasite species by providing an alternative route which can improve transmission rates to definitive hosts (Rohde 2010). Snoek may be a key species in South African waters as they do not only act as ecological 'bridges' for parasites (Abollo *et al.* 1998), their nomadic nature and the results of the current study suggest that they play a major role in the dispersal and transmission of parasites. *Pseudoterranova* sp. infection, which relies on benthic larvae and intermediate hosts, for example suggest that snoek may have a significant effect on the bathymetric distribution of some parasites.

4.4: Population Structure and Biological Tags

Parasites are increasingly employed as biological tags to study the population structure and movement patterns of wild, commercially exploited marine hosts of various taxa (Moser & Hsieh 1992; Pascual & Hochberg 1996; Lester *et al.* 2001; Oliva & Ballon 2002; MacKenzie & Hemmingsen 2014). As more information on parasite life cycles and host-parasite relationships becomes available, the guidelines for the use of parasites as biological tags (Figure 2) have been refined accordingly (MacKenzie 1983; MacKenzie & Abaunza 1998; Mosquera *et al.* 2003; Lester & MacKenzie 2009).

The relative stability of the snoek's parasite community structure with respect to sex, size and season suggest that snoek occurring off South Africa comprise a single stock, as hypothesized by Griffiths (2003). A comparison of the parasite assemblage of snoek between the northern and southern Benguela is long overdue. Assessing whole parasite assemblages has its pros and cons. While it results in more data being collected, it is a time consuming process. The identification of single species as biotags is therefore desirable. Three parasite taxa recorded during this study fit five of the criteria summarized in figure 2. These are *Anisakis* spp., *N. fradei*, *M. uncinatus* and *K. thyrsites*. Whether or not infestation levels differ between the two proposed snoek stocks is not known at this point and was not considered as a criterion to select candidate biotags.

Each of the proposed species has its advantages and disadvantages. *Kudoa thyrsites* can only be analysed in terms of prevalence since evaluating infection intensity via microscopy proved at best unreliable but it does not require the examination of whole specimens. The cestode, *M. uncinatus*, is a long lived, conspicuous species but the fact that it parasitizes the muscles may stymie its effectiveness as a biotag. A thorough assessment of each myomere is required to assert infection intensity although presence-absence data is relatively easily collected. *Anisakis* spp. fits five of the criteria and there is good reason to think that infestation levels between fish stocks in the northern and southern Benguela differ. Le Roux (2013) reported spatial variations in the infection intensity and abundance of anisakids in *T. capensis* caught in the northern and southern Benguela. For both *M. uncinatus* and *Anisakis* spp., spatial comparisons should be constrained to fish of the same size class to negate the ontogenetic increase they exhibit in both prevalence and infection intensity.

4.5: Recommendations and Conclusions

4.5.1: Constraints & Future research

One of the shortcomings of this project was that not all the parasite taxa recovered were identified to species level. This could possibly have improved the inferential power of analyses. Identification based on both morphological features and genetic techniques is recommended to clarify the composition of the snoek's infracommunity. Parasites identified to species level should also be considered in biodiversity assessments. No protistan parasites were observed, possibly because host samples were frozen. Although otoliths were taken during processing, the hosts were not aged due to time constraints. Using age rather than host length, which is commonly used as a proxy for age, may improve our understanding of the ontogenetic dynamics of snoek parasites. Future studies should aim to assess the effect of age on the degree of parasitism experienced by wild fish hosts. A study assessing the parasite assemblage of snoek over a longer time-frame is also recommended to assess potential inter-annual variation in parasite infestation levels. Our ecological understanding of the southern Benguela would also benefit from a comparison of the parasite assemblage of sympatric fish species. Such an analysis could possibly highlight trends, especially with respect to trophic relationships and spatial distribution, not detected by previous studies (Shannon *et al.* 2003; Drapeau *et al.* 2004; Pecquerie *et al.* 2004).

4.5.2: Conclusions

In the early 1990's, Guégan *et al.* (1992) lamented the paucity of studies focusing on the relationship between parasite infestation levels and host traits. The flurry of research that followed (e.g. Poulin & Rohde 1997; Sasal *et al.* 1997; Arneberg 2002; Luque *et al.* 2004; Neff & Cargnelli 2004; Poulin & Leung 2011) has shed little light on the determinants of parasite diversity and abundance. Inconsistencies and contradictions between investigations prevent generalization from one host species to another as well as between parasitic species; this was once more illustrated by the results of the present study. The results of modelling suggest that the determinants of parasite infestation in snoek exhibit a hierarchical nature and are taxon-specific. Seasonality, host body size, body condition and investment in gonad development were the most common predictors of parasite infection levels in snoek but their effects differed between parasite taxa.

Parasites can reveal a lot about the biology, evolutionary history and ecology of their hosts, as much as their hosts can reveal about them. The indiscriminate, predatory feeding behaviour and nomadic nature suggested by past studies (Dudley 1987; Hurst & Bagley 1989; Crawford *et al.* 1990; Griffiths 2002) and results of the present study are most probably the reasons for the high diversity of parasites reported from snoek in the Southern Hemisphere (Robinson 1959a, 1959b; Mehl 1970; Hewitt & Hine 1972; Wierzbicka & Gajda 1984; Waterman & Sin 1991; Beveridge & Campbell 1996; Wharton *et al.* 1999; Mattiucci & Nascetti 2007; Sobecka 2012). The apparently harmonious relationship snoek have with their parasites is indicative of a long, shared evolutionary history. The role snoek play in the dispersal and transmission of parasites, as suggested by the present study, highlight its ecological importance in South African waters. As parasites are increasingly being incorporated into ecosystem models (Britton 2013), environmental assessments (MacKenzie 1999; Malek *et al.* 2007; Sures 2008) and fisheries research (Van der Lingen *et al.* 2014), understanding the dynamics of parasite communities with respect to host traits is essential to improve the management and conservation of marine resources. Further studies are required to better comprehend the host-parasite relationships of fish and determinants of infection.

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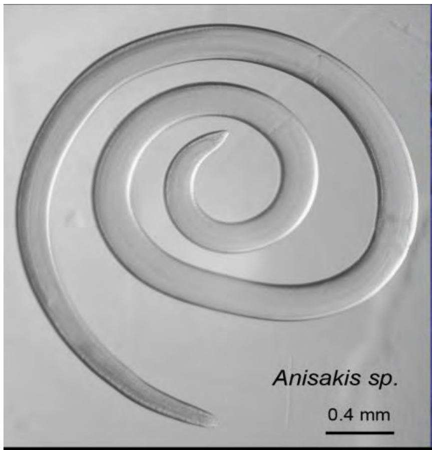
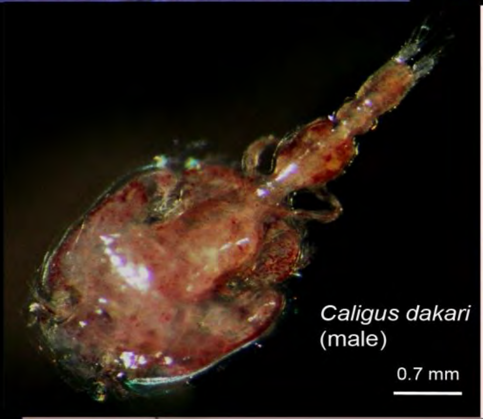
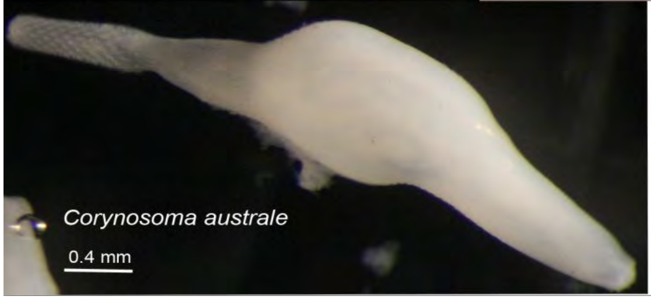
Appendices

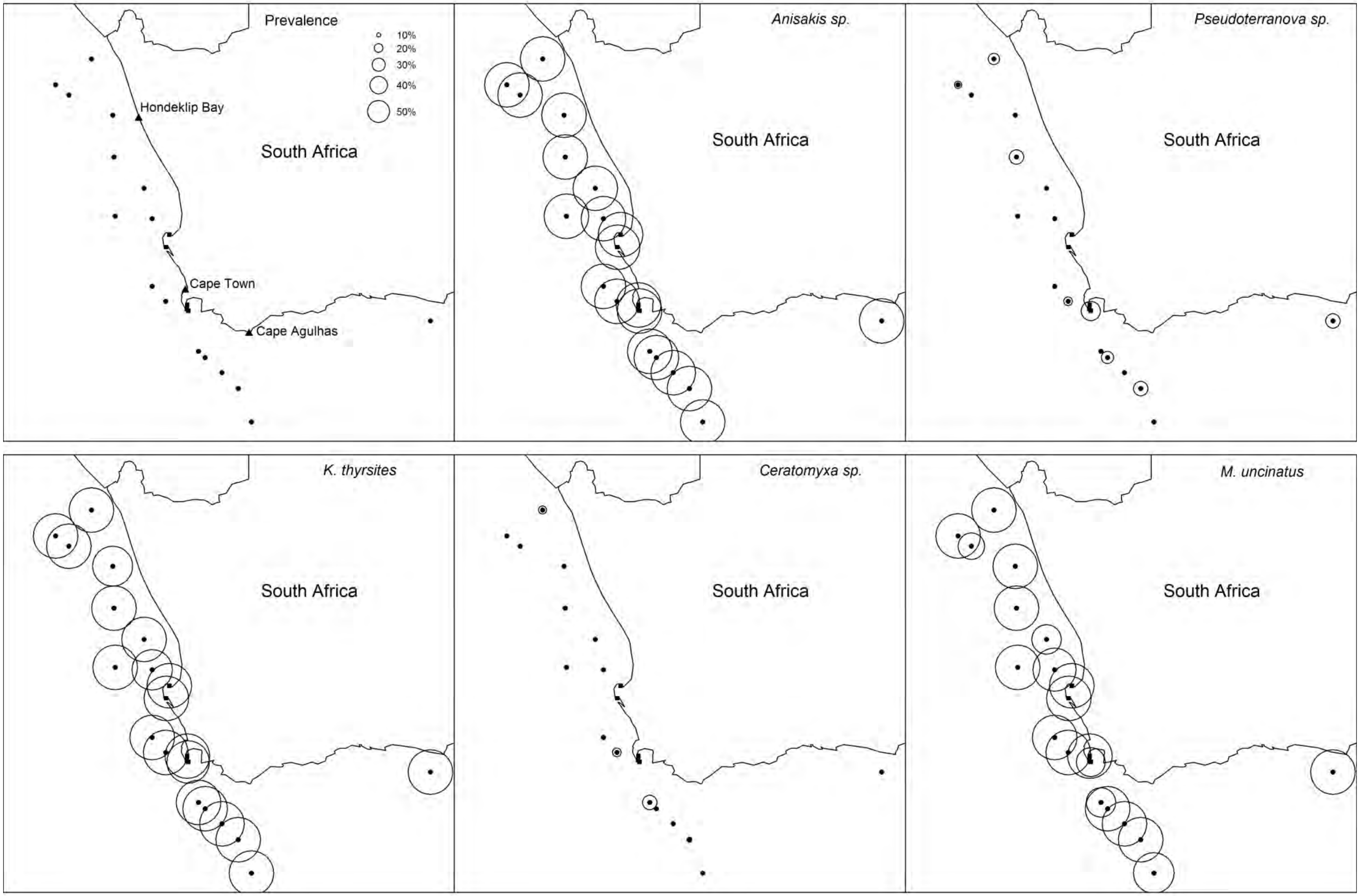
Appendix 1: Parasite Photographs

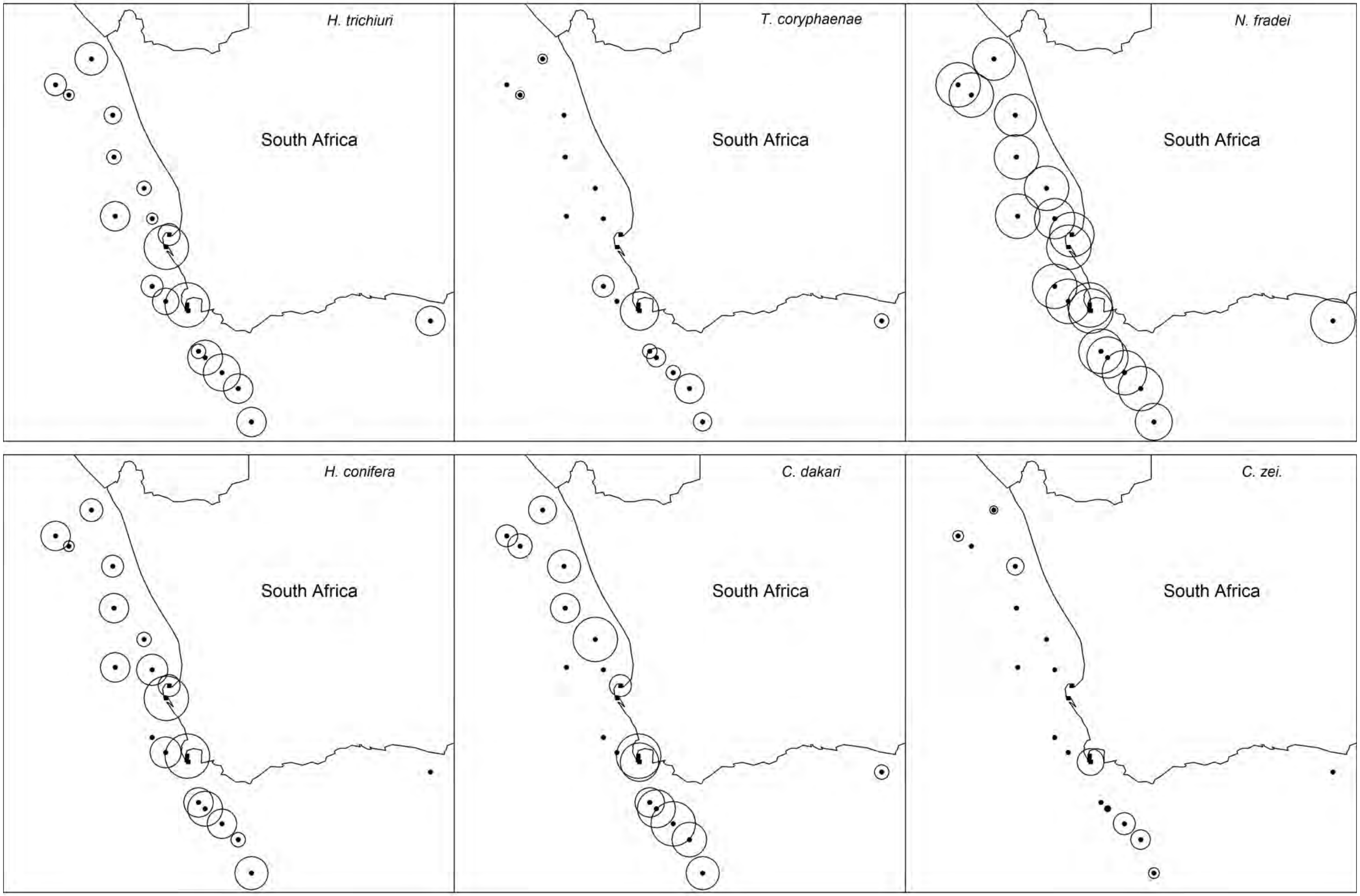




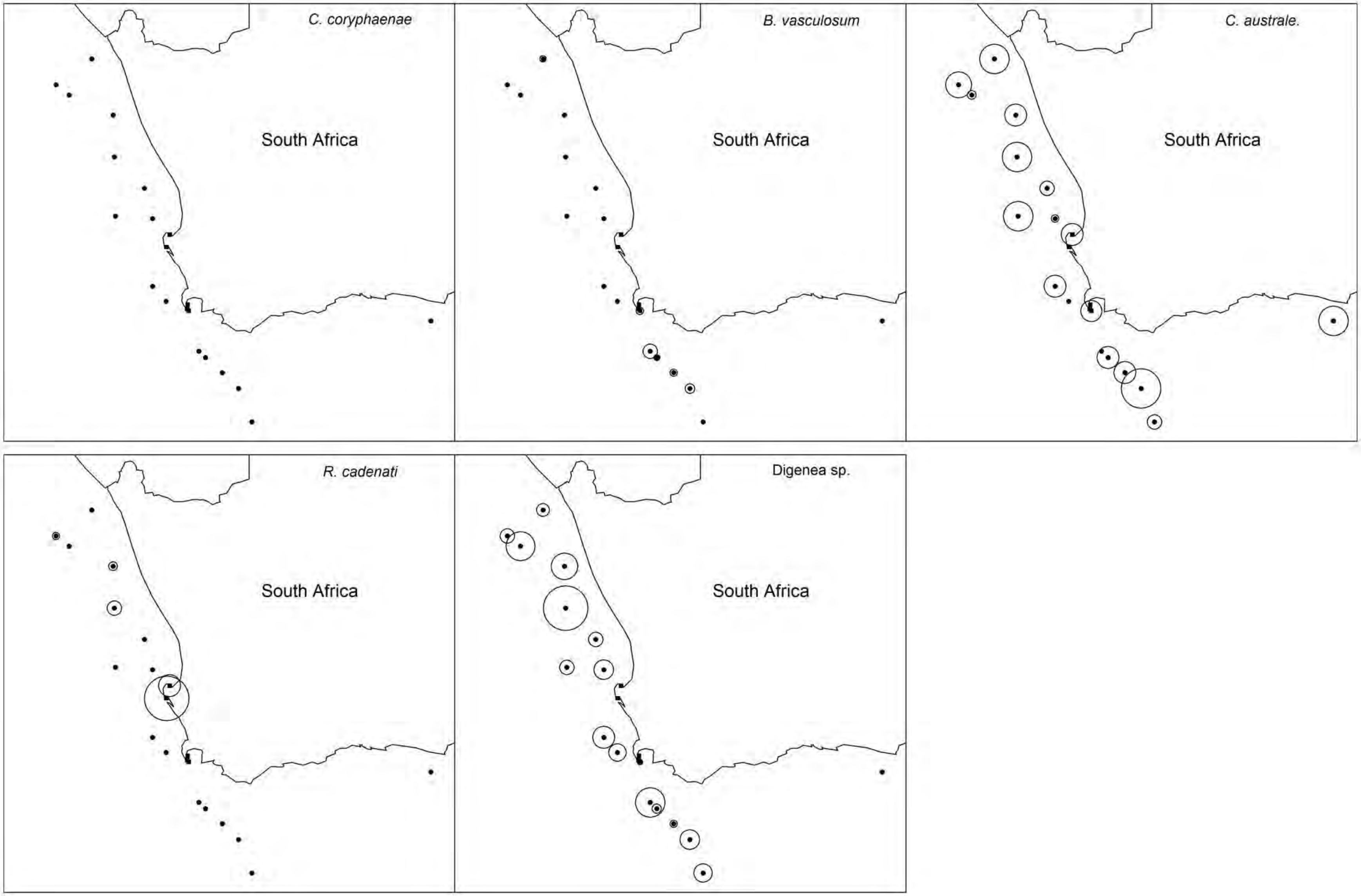


Appendix 2: Parasite Distribution Maps





H. trichiuri
South Africa
T. coryphaenae
South Africa
N. fradei
South Africa
H. conifera
South Africa
C. dakari
South Africa
C. zei.
South Africa


C. coryphaenae
South Africa
B. vasculosum
South Africa
C. australe.
South Africa
R. cadenati
South Africa
Digenea sp.
South Africa

Appendix 3. Summary of seasonal variation in host length and infection statistics

Host sex	Female			
Variable	Mean ± sd (prevalence)			
	Autumn (n = 15)	Winter (n = 45)	Spring (n = 45)	Summer (n = 15)
Fork length (mm)	817.2 ± 39.2	825.5 ± 69.7	874.4 ± 63.81	749.4 ± 91.48
Anisakis spp.	195.5 ± 257.4 (100%)	133.4 ± 125.48 (100%)	179.3 ± 178.3 (100%)	144.2 ± 307.13 (100%)
Pseudoterranova sp.	0.0 ± 0.0 (0%)	1.0 ± 2.56 (24.4%)	1.0 ± 2.35 (22.2%)	0.3 ± 1.05 (13.3%)
*Kudoa thyrsites**	86.7%	97.8%	100%	100%
*Ceratomyxa sp.**	0%	6.7%	13.3%	0%
Molicola uncinatus	31.7 ± 24.89 (100%)	29.1 ± 33.16 (91.1%)	41.3 ± 32.36 (97.8%)	19.5 ± 46.63 (66.7%)
Hepatoxylon trichiuri	2.1 ± 5.46 (20%)	1.2 ± 2.19 (40%)	2.2 ± 1.97 (75.6%)	1.2 ± 3.84 (26.7%)
Tentacularia coryphaenae	0.5 ± 1.25 (13.3%)	0.7 ± 1.55 (24.4%)	1.5 ± 3.18 (42.2%)	0.3 ± 0.59 (20%)
Nothobomolochus fradei	7.5 ± 8.52 (93.3%)	16.4 ± 18.62 (95.6%)	20.3 ± 15.98 (95.6%)	13.1 ± 13.69 (100%)
Hatschekia conifera	3.8 ± 3.38 (86.7%)	1.0 ± 2.15 (40%)	1.3 ± 2.58 (53.3%)	1.3 ± 2.89 (40%)
Caligus brevicaudatus	0 (0%)	0.6 ± 1.63 (20%)	0.7 ± 1.44 (40%)	0.1 ± 0.26 (6.7%)
Caligus coryphaenae	0 (0%)	0 (0%)	0.02 ± 0.15 (2.2%)	0 (0%)
Caligus dakari	0.3 ± 1.29 (6.7%)	1.4 ± 2.32 (40%)	4.8 ± 5.32 (80%)	2.9 ± 3.33 (73.3%)
Bolbosoma vasculosum	0.1 ± 0.52 (6.7%)	0.1 ± 0.33 (4.4%)	0.3 ± 0.72 (15.6%)	0.1 ± 0.26 (6.7%)
Corynosoma australe	0.5 ± 1.13 (20%)	8.5 ± 23.51 (33.3%)	15.8 ± 33.62 (71.1%)	2.5 ± 6.9 (33.3%)
Rhadinorhynchus cadenati	0.1 ± 0.26 (6.7%)	0.1 ± 0.50 (8.9%)	0.02 ± 0.15 (2.2%)	0 (0%)
Digenea sp.*	40%	42.2%	48.9%	66.7%

* only prevalence reported as only presence-absence data collected.

Host sex	Male			
Variable	Mean ± sd (prevalence)			
	Autumn (n = 16)	Winter (n = 30)	Spring (n = 33)	Summer (n = 11)
Fork length (mm)	689.3 ± 146.75	809.1 ± 79.14	831.9 ± 59.81	670.0 ± 64.88
Anisakis spp.	112.8 ± 147 (100%)	85.2 ± 92.83 (100%)	159.52 ± 155.59 (100%)	35.5 ± 35.41 (100%)
Pseudoterranova sp.	0.25 ± 1.0 (6.3%)	0.9 ± 2.45 (16.7%)	0.7 ± 1.62 (18.2%)	0.3 ± 0.90 (9.1%)
*Kudoa thyrsites**	100%	90%	100%	100%
*Ceratomyxa sp.**	6.3%	3.3%	9.1%	0%
Molicola uncinatus	24.1 ± 29.41 (87.5%)	18.6 ± 26.65 (83.3%)	31.2 ± 26.88 (100%)	3.5 ± 3.21 (63.6%)
Hepatoxylon trichiuri	2.1 ± 3.61 (50%)	0.3 ± 0.76 (20%)	1.9 ± 2.45 (69.7%)	0.4 ± 0.67 (27.3%)
Tentacularia coryphaenae	0.3 ± 1 (6.3%)	1.5 ± 4.45 (40%)	0.5 ± 1.66 (21.2%)	0.1 ± 0.30 (9.1%)
Nothobomolochus fradei	13.3 ± 12.84 (100%)	18.3 ± 21.77 (96.7%)	10.1 ± 13.36 (93.9%)	19.4 ± 16.1 (100%)
Hatschekia conifera	2.9 ± 3.84 (56.3%)	0.8 ± 1.21 (40%)	2.9 ± 5.58 (69.7%)	0.4 ± 0.92 (18.2%)
Caligus brevicaudatus	0 (0%)	0.7 ± 1.6 (26.7%)	0.5 ± 1.35 (21.2%)	0.2 ± 0.6 (9.1%)
Caligus coryphaenae	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Caligus dakari	0.5 ± 1.27 (25%)	1.5 ± 1.96 (53.3%)	4.7 ± 6.65 (75.7%)	3.6 ± 6.31 (45.5%)
Bolbosoma vasculosum	0 (0%)	0.1 ± 0.40 (6.7%)	0.1 ± 0.29 (9.1%)	0 (0%)
Corynosoma australe	4.7 ± 12.3 (18.8%)	8.4 ± 29.16 (30%)	11.4 ± 24.41 (54.5%)	2.1 ± 5.26 (18.2%)
Rhadinorhynchus cadenati	0.3 ± 0.79 (18.8%)	0.1 ± 0.40 (6.7%)	0.1 ± 0.38 (6.1%)	0.2 ± 0.60 (9.1%)
Digenea sp.*	12.5%	36.7%	9.1%	63.6%

* only prevalence reported as only presence-absence data collected.

Appendix 4: Literary resources used for parasite identification

Parasite taxon	References
Anisakis spp.	Anderson 2000
Pseudoterranova sp.	Anderson 2000
Kudoa thyrsites	Gilchrist 1924
Ceratomyxa sp.	Eiras 2006, Gunter & Adlard 2010
Molicola uncinatus	Robinson 1959b, Williams & Bunkley-Williams 1996
Hepatoxylon trichiuri	Knoff *et al.* 2004, Mladineo 2006, Williams & Bunkley-Williams 1996
Tentacularia coryphaenae	Knoff *et al.* 2004, Williams & Bunkley-Williams 1996
Nothobomolochus fradei	El-Rashidy & Boxshall 2010
Hatschekia conifera	Jones 1985
Caligus coryphaenae	Kensley & Grindley 1973
Caligus dakari	Boxshall & El-Rashidy 2009
Caligus zei	Scott & Scott 1912, Scott & Scott 1913
Bolbosoma vasculosum	Costa *et al.* 2000
Corynosoma australe	Sardella *et al.* 2005, Braicovich *et al.* 2005
Rhadinorhynchus cadenati	Amin *et al.* 2011, Troncy & Vassiliades 1973

Appendix 5a. Biological, spatial and temporal data collected for Thyrsites atun off South Africa.

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
1	St Helena Bay	Handline	April	Autumn	Female	810	2985	2	29	1
2	St Helena Bay	Handline	April	Autumn	Female	820	2690	2	24	1
3	St Helena Bay	Handline	April	Autumn	Male	780	2216	2	9	2
4	St Helena Bay	Handline	April	Autumn	Female	847	2770	2	26	1
5	St Helena Bay	Handline	April	Autumn	Female	769	2332	2	17	2
6	St Helena Bay	Handline	April	Autumn	Male	760	2207	2	5	1
7	St Helena Bay	Handline	April	Autumn	Female	837	2629	2	32	2
8	St Helena Bay	Handline	April	Autumn	Female	770	2613	2	22	3
9	St Helena Bay	Handline	April	Autumn	Female	826	2923	2	22	2
10	St Helena Bay	Handline	April	Autumn	Male	793	2405	2	12	2
11	St Helena Bay	Handline	April	Autumn	Female	804	2525	2	31	2
12	St Helena Bay	Handline	April	Autumn	Male	767	2649	2	13	2
13	St Helena Bay	Handline	April	Autumn	Female	813	2641	2	29	1
14	St Helena Bay	Handline	April	Autumn	Female	805	2615	2	30	2
15	Buffels Bay	Handline	May	Winter	Female	735	2203	2	19	2
16	Buffels Bay	Handline	May	Winter	Male	835	4420	5	430	2
17	Buffels Bay	Handline	May	Winter	Female	645	1292	4	58	2
18	Buffels Bay	Handline	May	Winter	Male	685	1663	3	17	2
19	Buffels Bay	Handline	May	Winter	Female	708	1854	3	40	3
20	Buffels Bay	Handline	May	Winter	Female	811	3038	4	60	3
21	Buffels Bay	Handline	May	Winter	Female	712	2014	3	23	1
22	Buffels Bay	Handline	May	Winter	Female	727	2135	4	81	2
23	Buffels Bay	Handline	May	Winter	Female	707	1886	2	17	2
24	Saldanha Bay	Handline	May	Winter	Male	878	3510	5	318	2
25	Saldanha Bay	Handline	May	Winter	Female	870	3903	2	53	3
26	Saldanha Bay	Handline	May	Winter	Male	835	3382	5	249	3
27	Saldanha Bay	Handline	May	Winter	Female	811	2984	2	38	2
28	Saldanha Bay	Handline	May	Winter	Male	875	3755	3	65	3
29	Saldanha Bay	Handline	May	Winter	Male	830	3226	4	176	3
30	Saldanha Bay	Handline	May	Winter	Female	835	2982	3	44	3

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
31	Saldanha Bay	Handline	May	Winter	Male	903	4108	5	461	2
32	Saldanha Bay	Handline	May	Winter	Female	885	3643	4	105	1
33	Saldanha Bay	Handline	May	Winter	Female	795	2833	4	134	2
34	Buffels Bay	Handline	May	Winter	Female	855	3013	3	41	2
35	St Helena Bay	Handline	June	Winter	Female	947	4709	3	118	3
36	St Helena Bay	Handline	June	Winter	Female	924	4290	3	106	3
37	St Helena Bay	Handline	June	Winter	Female	878	3788	4	139	2
38	St Helena Bay	Handline	June	Winter	Female	840	3524	3	131	2
39	St Helena Bay	Handline	June	Winter	Male	770	2242	2	27	1
40	St Helena Bay	Handline	June	Winter	Female	827	2847	3	42	3
41	St Helena Bay	Handline	June	Winter	Female	820	3228	4	128	2
42	St Helena Bay	Handline	June	Winter	Male	807	2461	4	78	2
43	St Helena Bay	Handline	June	Winter	Female	792	2601	3	45	3
44	St Helena Bay	Handline	June	Winter	Male	742	2315	4	84	2
45	St Helena Bay	Handline	July	Winter	Female	729	1822	2	23	2
46	St Helena Bay	Handline	July	Winter	Male	720	2199	4	131	3
47	St Helena Bay	Handline	July	Winter	Female	741	2073	4	33	2
48	St Helena Bay	Handline	July	Winter	Female	777	2192	3	40	2
49	St Helena Bay	Handline	July	Winter	Male	687	1812	3	52	2
50	St Helena Bay	Handline	July	Winter	Male	721	1658	2	27	2
51	St Helena Bay	Handline	July	Winter	Female	763	2788	5	213	2
52	St Helena Bay	Handline	July	Winter	Female	796	2594	5	101	2
53	St Helena Bay	Handline	July	Winter	Male	696	2070	4	102	2
54	St Helena Bay	Handline	July	Winter	Male	700	1752	4	44	1
55	Millers Point	Handline	July	Winter	Male	847	3218	4	269	1
56	Millers Point	Handline	July	Winter	Female	863	2950	5	205	1
57	Millers Point	Handline	July	Winter	Female	901	3317	4	133	1
58	Millers Point	Handline	July	Winter	Female	857	2864	4	94	1
59	Millers Point	Handline	July	Winter	Female	877	3260	4	176	1
60	Millers Point	Handline	July	Winter	Female	892	3364	4	164	1

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
61	Millers Point	Handline	July	Winter	Female	837	3095	4	132	2
62	Millers Point	Handline	July	Winter	Female	940	3892	4	182	1
63	Millers Point	Handline	July	Winter	Female	854	3049	4	168	1
64	Millers Point	Handline	July	Winter	Female	818	2434	4	92	1
65	Millers Point	Handline	July	Winter	Female	900	3443	5	211	1
66	Millers Point	Handline	July	Winter	Male	873	2913	5	168	1
67	Buffels Bay	Handline	September	Spring	Female	900	2988	5	119	1
68	Buffels Bay	Handline	September	Spring	Female	858	2857	4	80	1
69	Buffels Bay	Handline	September	Spring	Female	820	2453	4	96	1
70	Buffels Bay	Handline	September	Spring	Female	883	2871	5	81	1
71	Buffels Bay	Handline	September	Spring	Female	901	3058	4	76	1
72	Buffels Bay	Handline	September	Spring	Female	930	3016	4	93	1
73	Buffels Bay	Handline	September	Spring	Female	938	3021	4	78	1
74	S1	Trawl	August	Winter	Female	893	4012	6	732	1
75	S1	Trawl	August	Winter	Male	845	3373	6	265	1
76	S1	Trawl	August	Winter	Female	858	3123	5	241	1
77	S1	Trawl	August	Winter	Male	787	2787	5	188	1
78	Buffels Bay	Handline	September	Spring	Female	891	3204	5	126	1
79	Buffels Bay	Handline	September	Spring	Female	885	2758	4	76	1
80	Buffels Bay	Handline	September	Spring	Female	855	2681	5	70	1
81	S1	Trawl	August	Winter	Female	890	4001	6	576	1
82	S1	Trawl	August	Winter	Female	914	3896	6	339	1
83	S1	Trawl	August	Winter	Male	781	2922	5	284	1
84	S1	Trawl	August	Winter	Female	824	3103	5	173	1
85	S1	Trawl	August	Winter	Male	808	3053	6	249	2
86	S1	Trawl	August	Winter	Male	845	3598	6	302	1
87	S1	Trawl	August	Winter	Male	800	2886	6	255	1
88	S1	Trawl	August	Winter	Male	1040	5687	6	318	1
89	S1	Trawl	August	Winter	Male	749	2523	5	212	2
90	S1	Trawl	August	Winter	Male	774	2692	6	302	2

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
91	S1	Trawl	August	Winter	Male	805	2767	5	181	2
92	S1	Trawl	August	Winter	Male	834	3063	5	258	2
93	S1	Trawl	August	Winter	Female	830	3029	4	103	1
94	S1	Trawl	August	Winter	Female	790	2843	6	272	1
95	S1	Trawl	August	Winter	Male	895	3682	6	267	1
96	S1	Trawl	August	Winter	Female	754	2217	6	156	1
97	S1	Trawl	August	Winter	Female	885	3890	6	207	1
98	S1	Trawl	August	Winter	Male	907	2230	6	218	1
99	S1	Trawl	August	Winter	Female	839	2904	5	196	1
100	S2	Trawl	September	Spring	Female	838	2639	5	130	1
101	S2	Trawl	September	Spring	Male	858	2794	6	127	1
102	S2	Trawl	September	Spring	Female	871	2730	6	175	1
103	S2	Trawl	September	Spring	Female	827	2849	6	195	1
104	S2	Trawl	September	Spring	Male	860	3138	6	243	1
105	S2	Trawl	September	Spring	Male	880	3321	6	267	1
106	S2	Trawl	September	Spring	Male	865	3183	5	202	1
107	S2	Trawl	September	Spring	Female	845	3004	5	128	1
108	S2	Trawl	September	Spring	Female	855	3093	5	145	1
109	S2	Trawl	September	Spring	Female	860	3138	4	110	1
110	S2	Trawl	September	Spring	Female	895	3463	6	312	1
111	S2	Trawl	September	Spring	Male	823	2815	5	102	1
112	S2	Trawl	September	Spring	Male	847	2754	5	196	1
113	S2	Trawl	September	Spring	Female	822	2284	5	116	1
114	S2	Trawl	September	Spring	Male	806	2207	7	84	1
115	S2	Trawl	September	Spring	Female	843	2964	6	269	1
116	S2	Trawl	September	Spring	Female	900	3163	5	139	1
117	S2	Trawl	September	Spring	Male	855	2821	5	181	1
118	S2	Trawl	September	Spring	Male	715	1789	4	85	1
119	S2	Trawl	September	Spring	Male	883	3738	3	218	1
120	S2	Trawl	September	Spring	Male	910	3415	4	178	1

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
121	S2	Trawl	September	Spring	Female	959	3888	6	411	1
122	S2	Trawl	September	Spring	Female	896	3465	6	118	1
123	S2	Trawl	September	Spring	Male	845	2998	4	106	1
124	S2	Trawl	September	Spring	Female	892	3426	5	222	1
125	S3	Trawl	October	Spring	Male	829	2723	4	69	1
126	S3	Trawl	October	Spring	Female	843	2831	5	175	1
127	S3	Trawl	October	Spring	Female	800	2393	3	71	1
128	S2	Trawl	September	Spring	Female	1039	4894	5	211	1
129	S2	Trawl	September	Spring	Male	849	2800	4	154	1
130	S3	Trawl	October	Spring	Female	878	3836	5	172	1
131	S3	Trawl	October	Spring	Male	885	3125	5	157	1
132	S3	Trawl	October	Spring	Male	843	2971	4	57	1
133	S4	Trawl	October	Spring	Female	917	4239	4	167	1
134	S4	Trawl	October	Spring	Female	970	4827	5	261	1
135	S4	Trawl	October	Spring	Female	818	2083	5	128	1
136	S4	Trawl	October	Spring	Female	960	4734	6	711	1
137	S4	Trawl	October	Spring	Male	885	3538	4	204	1
138	S4	Trawl	October	Spring	Female	877	3634	6	213	1
139	S4	Trawl	October	Spring	Female	824	2769	3	89	1
140	S4	Trawl	October	Spring	Male	782	2223	3	98	1
141	S5	Trawl	October	Spring	Male	793	2365	3	107	1
142	S5	Trawl	October	Spring	Female	773	2244	2	58	1
143	S4	Trawl	October	Spring	Female	905	3903	5	256	1
144	S5	Trawl	October	Spring	Male	744	2000	3	116	1
145	S5	Trawl	October	Spring	Female	698	1655	3	66	1
146	S6	Trawl	October	Spring	Male	909	3479	7	163	1
147	S6	Trawl	October	Spring	Male	864	2817	7	104	1
148	S6	Trawl	October	Spring	Male	870	2907	7	149	1
149	S6	Trawl	October	Spring	Male	792	2295	3	101	1
150	S6	Trawl	October	Spring	Male	780	2284	4	129	1

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
151	S5	Trawl	October	Spring	Female	885	3900	5	404	1
152	S5	Trawl	October	Spring	Female	866	3090	4	149	1
153	S5	Trawl	October	Spring	Male	763	2266	4	75	1
154	S6	Trawl	October	Spring	Male	858	2931	4	130	1
155	S6	Trawl	October	Spring	Male	850	2716	4	139	1
156	S6	Trawl	October	Spring	Male	772	2117	7	97	1
157	S6	Trawl	October	Spring	Male	726	1885	2	39	2
158	S6	Trawl	October	Spring	Male	686	1825	3	65	2
159	Cape Point	Handline	November	Summer	Male	750	1883	2	20	2
160	Cape Point	Handline	November	Summer	Female	696	1780	2	16	2
161	Cape Point	Handline	November	Summer	Female	695	1589	2	21	1
162	Cape Point	Handline	November	Summer	Male	653	1446	2	7	2
163	Cape Point	Handline	November	Summer	Female	650	1298	2	16	2
164	Cape Point	Handline	November	Summer	Female	706	1975	2	22	2
165	Cape Point	Handline	November	Summer	Female	721	1757	2	16	2
166	Cape Point	Handline	November	Summer	Female	735	2037	3	38	2
167	Cape Point	Handline	November	Summer	Male	710	1784	2	11	1
168	Cape Point	Handline	November	Summer	Female	650	1331	2	18	1
169	Cape Point	Handline	November	Summer	Female	802	2309	2	30	2
170	Cape Point	Handline	November	Summer	Female	776	2255	2	22	2
171	Cape Point	Handline	November	Summer	Male	733	1940	3	37	2
172	Cape Point	Handline	November	Summer	Male	663	1458	2	20	2
173	Cape Point	Handline	November	Summer	Male	667	1400	2	16	2
174	Cape Point	Handline	November	Summer	Female	703	1774	3	47	2
175	Cape Point	Handline	November	Summer	Male	656	1572	2	9	2
176	Cape Point	Handline	November	Summer	Male	681	1666	2	25	2
177	Cape Point	Handline	November	Summer	Female	711	1626	2	17	2
178	Cape Point	Handline	November	Summer	Male	623	1167	2	19	2
179	S6	Trawl	October	Spring	Female	950	3466	5	149	1
180	S6	Trawl	October	Spring	Female	917	3357	3	129	1

Fish no.	Locality	Gear	Month	Season	Sex	Fork length (mm)	Mass (g)	Gonad stage	Gonad mass (g)	Fat score
181	S6	Trawl	October	Spring	Male	915	3399	7	87	1
182	S6	Trawl	October	Spring	Male	911	3247	4	152	1
183	S5	Trawl	October	Spring	Female	946	4021	5	233	1
184	S5	Trawl	October	Spring	Female	972	4452	6	303	1
185	S5	Trawl	October	Spring	Female	762	2591	2	53	1
186	S5	Trawl	October	Spring	Female	804	2688	4	134	1
187	S5	Trawl	October	Spring	Female	780	2498	5	165	1
188	S16	Trawl	February	Summer	Female	981	3903	7	50	2
189	S16	Trawl	February	Summer	Female	788	2494	2	26	3
190	S16	Trawl	February	Summer	Male	721	1966	2	8	2
191	S7	Trawl	March	Autumn	Female	915	3374	3	62	2
192	S7	Trawl	March	Autumn	Male	706	2067	2	15	2
193	S7	Trawl	March	Autumn	Male	536	842	1	2	2
194	S12	Trawl	March	Autumn	Female	773	2292	2	18	3
195	S12	Trawl	March	Autumn	Male	635	1173	1	2	1
196	S11	Trawl	March	Autumn	Male	809	2451	2	11	1
197	S10	Trawl	March	Autumn	Male	716	2211	7	7	2
198	S13	Trawl	March	Autumn	Male	953	3666	7	14	1
199	S13	Trawl	March	Autumn	Male	512	617	1	0.25	1
200	S13	Trawl	March	Autumn	Male	465	499	1	0.3	1
201	S15	Trawl	February	Summer	Female	909	4332	2	56	2
202	S15	Trawl	February	Summer	Female	718	2086	2	17	2
203	S15	Trawl	February	Summer	Male	513	513	1	0.2	1
204	S8	Trawl	March	Autumn	Female	839	3076	7	27	2
205	S8	Trawl	March	Autumn	Female	855	3324	3	39	1
206	S14	Trawl	March	Autumn	Male	792	2389	7	12	2
207	S14	Trawl	March	Autumn	Female	775	2062	2	18	2
208	S14	Trawl	March	Autumn	Male	620	1144	1	0.2	1
209	S9	Trawl	March	Autumn	Male	774	3210	7	23	2
210	S9	Trawl	March	Autumn	Male	411	323	1	0.1	1

Appendix 5b. Prey items collected from Thyrsites atun as percentages of the total mass of stomach contents.

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
1	100	0	0	0	0	0	0	0	0	2
2	0	0	100	0	0	0	0	0	0	9
3	0	0	0	0	0	0	0	0	0	0
4	0	0	100	0	0	0	0	0	0	5
5	0	0	0	0	0	0	0	0	0	0
6	0	0	100	0	0	0	0	0	0	114
7	0	0	100	0	0	0	0	0	0	6
8	0	0	0	0	0	0	0	0	0	0
9	100	0	0	0	0	0	0	0	0	6
10	0	0	100	0	0	0	0	0	0	28
11	100	0	0	0	0	0	0	0	0	12
12	0	0	100	0	0	0	0	0	0	59
13	0	0	100	0	0	0	0	0	0	1
14	0	0	0	0	0	0	0	0	0	0
15	0	100	0	0	0	0	0	0	0	58
16	0	0	0	0	100	0	0	0	0	45
17	0	100	0	0	0	0	0	0	0	39
18	0	0	100	0	0	0	0	0	0	44
19	0	0	100	0	0	0	0	0	0	12
20	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0
22	100	0	0	0	0	0	0	0	0	44
23	100	0	0	0	0	0	0	0	0	3
24	0	0	0	0	0	0	0	0	0	0
25	50	0	50	0	0	0	0	0	0	14
26	0	0	0	0	0	0	0	0	0	0
27	100	0	0	0	0	0	0	0	0	32
28	0	0	0	0	0	0	0	100	0	182
29	0	0	0	0	0	0	0	100	0	13
30	85	0	15	0	0	0	0	0	0	35

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
31	0	0	0	0	0	0	0	100	0	346
32	85	0	0	0	0	15	0	0	0	36
33	0	0	0	0	0	100	0	0	0	5
34	100	0	0	0	0	0	0	0	0	8
35	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0
37	100	0	0	0	0	0	0	0	0	14
38	100	0	0	0	0	0	0	0	0	13
39	0	0	0	0	0	0	100	0	0	128
40	100	0	0	0	0	0	0	0	0	7
41	100	0	0	0	0	0	0	0	0	20
42	0	0	0	0	0	0	0	0	0	0
43	100	0	0	0	0	0	0	0	0	35
44	0	0	0	0	0	0	0	0	0	0
45	0	100	0	0	0	0	0	0	0	5
46	0	0	0	0	0	0	0	0	0	0
47	0	0	100	0	0	0	0	0	0	3
48	0	0	100	0	0	0	0	0	0	13
49	0	0	0	0	0	0	100	0	0	158
50	0	0	100	0	0	0	0	0	0	28
51	0	0	100	0	0	0	0	0	0	11
52	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0
56	100	0	0	0	0	0	0	0	0	4
57	0	0	0	0	0	0	100	0	0	93
58	100	0	0	0	0	0	0	0	0	35
59	100	0	0	0	0	0	0	0	0	20
60	100	0	0	0	0	0	0	0	0	14

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
61	95	0	5	0	0	0	0	0	0	17
62	0	0	0	0	0	0	100	0	0	52
63	0	0	100	0	0	0	0	0	0	3
64	100	0	0	0	0	0	0	0	0	105
65	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0
68	0	0	100	0	0	0	0	0	0	12
69	0	0	100	0	0	0	0	0	0	16
70	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	100	0	0	0	0	201
72	0	0	0	0	0	0	100	0	0	9
73	0	0	0	0	0	0	100	0	0	60
74	0	0	100	0	0	0	0	0	0	2
75	0	0	100	0	0	0	0	0	0	50
76	50	50	0	0	0	0	0	0	0	6
77	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0
79	0	0	100	0	0	0	0	0	0	25
80	0	0	100	0	0	0	0	0	0	5
81	100	0	0	0	0	0	0	0	0	9
82	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0
84	0	0	100	0	0	0	0	0	0	8
85	0	0	0	0	0	0	0	0	0	0
86	0	0	100	0	0	0	0	0	0	11
87	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	100	0	231
89	0	0	0	0	0	0	0	0	0	0
90	0	0	100	0	0	0	0	0	0	8

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
91	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0
93	0	100	0	0	0	0	0	0	0	4
94	0	0	100	0	0	0	0	0	0	18
95	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	100	0	0	0	0	26
99	0	0	100	0	0	0	0	0	0	7
100	0	0	100	0	0	0	0	0	0	16
101	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0
107	0	0	100	0	0	0	0	0	0	6
108	0	0	100	0	0	0	0	0	0	7
109	0	0	100	0	0	0	0	0	0	2
110	0	0	100	0	0	0	0	0	0	15
111	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0
115	0	0	100	0	0	0	0	0	0	3
116	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	100	0	0	134
120	0	0	0	0	100	0	0	0	0	8

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
121	0	0	0	0	0	0	100	0	0	112
122	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	100	0	0	111
124	0	0	0	0	0	0	100	0	0	5
125	0	0	100	0	0	0	0	0	0	7
126	0	0	0	0	0	0	100	0	0	5
127	0	0	0	0	0	0	100	0	0	17
128	0	0	0	0	0	0	100	0	0	21
129	0	0	0	0	0	0	100	0	0	11
130	0	0	100	0	0	0	0	0	0	16
131	0	0	100	0	0	0	0	0	0	13
132	0	0	100	0	0	0	0	0	0	257
133	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0
135	0	0	100	0	0	0	0	0	0	3
136	0	0	100	0	0	0	0	0	0	1
137	0	0	0	0	0	0	0	0	0	0
138	0	0	100	0	0	0	0	0	0	14
139	0	0	0	0	0	0	100	0	0	2
140	0	0	100	0	0	0	0	0	0	28
141	0	0	0	0	0	0	0	100	0	56
142	0	0	0	0	0	0	100	0	0	38
143	0	0	0	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0
145	0	0	0	0	100	0	0	0	0	10
146	0	0	100	0	0	0	0	0	0	66
147	0	0	0	0	0	0	100	0	0	74
148	0	0	100	0	0	0	0	0	0	74
149	0	0	0	0	0	0	0	0	0	0
150	0	0	100	0	0	0	0	0	0	7

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
151	0	0	0	0	0	0	100	0	0	97
152	0	0	0	0	0	0	100	0	0	17
153	0	0	100	0	0	0	0	0	0	20
154	0	0	100	0	0	0	0	0	0	32
155	0	0	100	0	0	0	0	0	0	40
156	0	0	100	0	0	0	0	0	0	200
157	0	0	100	0	0	0	0	0	0	6
158	0	0	0	0	45	0	0	55	0	367
159	0	0	0	0	0	0	0	0	0	0
160	100	0	0	0	0	0	0	0	0	20
161	85	0	0	15	0	0	0	0	0	29
162	0	0	0	0	100	0	0	0	0	150
163	100	0	0	0	0	0	0	0	0	12
164	0	0	25	0	0	0	75	0	0	487
165	0	0	0	0	0	0	100	0	0	14
166	0	0	0	0	0	0	0	0	0	0
167	0	0	95	0	0	5	0	0	0	20
168	100	0	0	0	0	0	0	0	0	7
169	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0
171	0	0	0	0	0	0	100	0	0	425
172	0	0	0	0	0	0	0	0	0	0
173	0	0	0	0	0	0	0	0	0	0
174	0	0	0	0	0	0	100	0	0	177
175	0	0	100	0	0	0	0	0	0	51
176	0	0	0	0	0	0	0	0	100	64
177	0	0	0	0	0	0	100	0	0	26
178	0	0	0	0	0	0	0	0	0	0
179	0	0	0	0	0	0	100	0	0	57
180	0	0	0	0	0	0	0	0	0	0

Fish no.	*Euphausia lucens*	*Engraulis capensis*	Unidentified clupeoid	*Pterygosquilla armata*	Squid	*Themisto gaudichaudii*	*Trachurus trachurus capensis*	*Merluccius spp.*	*Etrumeus whiteheadi*	Total Prey Mass (g)
181	0	0	0	0	0	0	100	0	0	194
182	0	0	0	0	0	0	0	0	0	0
183	0	0	0	0	0	0	0	0	0	0
184	0	0	0	0	0	0	0	0	0	0
185	0	0	0	0	0	0	100	0	0	7
186	0	0	0	0	0	0	100	0	0	75
187	0	0	0	0	0	0	100	0	0	58
188	0	0	0	0	100	0	0	0	0	1
189	0	0	100	0	0	0	0	0	0	77
190	0	0	0	0	0	0	0	100	0	243
191	0	0	0	0	0	0	100	0	0	342
192	0	0	100	0	0	0	0	0	0	115
193	0	0	0	0	0	0	0	0	0	0
194	0	0	100	0	0	0	0	0	0	3
195	0	0	100	0	0	0	0	0	0	14
196	0	0	0	0	0	0	0	0	0	0
197	0	0	100	0	0	0	0	0	0	20
198	0	0	100	0	0	0	0	0	0	75
199	0	0	0	0	100	0	0	0	0	3
200	0	0	100	0	0	0	0	0	0	24
201	0	0	100	0	0	0	0	0	0	17
202	0	0	100	0	0	0	0	0	0	10
203	0	0	0	0	0	0	0	0	100	53
204	0	0	100	0	0	0	0	0	0	8
205	0	0	100	0	0	0	0	0	0	15
206	0	0	0	0	0	0	0	0	0	0
207	0	0	0	0	0	0	0	0	0	2
208	0	0	100	0	0	0	0	0	0	25
209	0	0	0	0	0	0	0	0	0	0
210	0	0	0	0	100	0	0	0	0	152

Appendix 5c. Endoparasite data collected from Thyrsites atun off South Africa (Digenea sp. and Ceratomyxa sp. only recorded as presence-absence data).

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
1	72	19	0	0	0	1	0	0	0	0	0
2	167	37	0	0	0	2	0	0	0	0	0
3	63	13	0	0	0	2	0	0	0	0	0
4	15	26	0	0	0	6	0	0	0	0	0
5	86	35	0	0	0	1	0	0	0	0	0
6	24	6	0	0	0	3	0	0	0	1	0
7	118	19	0	0	0	1	0	0	0	0	0
8	47	13	0	0	0	0	0	0	0	0	0
9	123	15	0	0	0	0	0	0	0	0	0
10	16	35	0	0	0	13	0	0	0	0	0
11	173	9	0	0	0	1	1	0	0	0	0
12	181	33	0	0	0	1	1	0	0	0	0
13	27	19	0	0	0	7	1	0	0	0	0
14	24	16	0	0	0	1	1	0	0	0	0
15	123	7	0	0	0	2	1	0	0	0	0
16	131	23	0	0	0	0	1	0	0	0	0
17	49	2	0	0	0	4	1	0	0	1	0
18	27	2	0	0	0	0	1	0	0	2	0
19	15	14	0	0	0	4	1	0	0	0	0
20	187	17	1	0	0	6	1	0	0	1	0
21	43	8	0	0	0	3	1	0	0	0	0
22	24	4	0	0	0	4	0	0	0	0	0
23	162	2	0	0	1	5	1	0	0	0	0
24	41	24	0	0	0	2	0	0	0	0	0
25	136	57	3	0	0	2	0	1	0	0	0
26	23	31	0	0	0	3	1	0	0	0	0
27	79	47	2	0	0	2	1	0	2	0	0
28	287	61	1	0	0	1	1	0	0	0	0
29	77	29	1	0	0	1	0	0	0	0	0
30	37	65	3	0	0	1	0	1	0	0	0

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
31	64	53	0	0	0	1	0	0	0	0	0
32	413	84	12	0	0	6	1	0	2	0	0
33	291	33	0	0	0	1	0	0	0	0	0
34	41	17	0	0	0	7	0	0	0	0	0
35	641	97	3	0	0	1	1	0	0	0	0
36	63	111	1	92	0	2	0	0	0	0	0
37	91	67	3	0	0	1	1	0	0	0	0
38	188	42	1	0	1	2	0	0	0	1	0
39	49	27	0	0	0	1	1	0	0	0	0
40	88	16	2	0	0	0	1	3	0	0	0
41	33	39	4	1	0	4	0	0	0	0	0
42	71	32	0	0	0	2	0	0	0	0	0
43	127	26	4	0	0	1	1	0	0	0	0
44	153	14	0	0	0	1	0	0	0	0	0
45	3	4	0	0	0	1	0	0	0	0	0
46	21	9	0	0	0	1	1	0	0	0	0
47	32	2	0	0	0	18	0	0	0	0	0
48	8	2	0	0	0	17	0	0	0	0	0
49	29	1	1	53	0	11	1	0	0	0	0
50	21	0	0	6	0	3	0	0	0	0	0
51	121	23	0	18	0	8	1	2	0	0	0
52	279	26	4	5	0	6	1	0	8	0	0
53	65	2	0	0	0	13	1	0	0	0	0
54	36	5	0	0	0	6	1	0	7	0	0
55	249	113	2	0	0	11	0	0	0	1	0
56	219	47	0	0	0	9	0	0	0	0	0
57	181	113	3	4	1	11	0	0	0	0	0
58	11	36	0	0	0	5	0	0	0	0	0
59	49	7	1	0	0	8	1	0	0	0	0
60	111	13	0	45	0	6	1	0	0	0	0

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
61	89	52	0	0	0	3	0	0	0	0	0
62	387	117	5	53	0	4	0	0	0	3	0
63	137	32	0	115	0	15	1	0	0	0	0
64	59	37	1	3	0	37	0	1	0	0	0
65	247	27	2	23	0	16	1	6	0	0	0
66	27	14	0	3	0	14	0	0	0	0	0
67	65	54	1	15	0	3	0	0	11	0	0
68	58	3	0	47	0	21	1	0	0	0	0
69	27	8	0	11	0	2	0	0	0	0	0
70	113	91	3	23	0	21	1	0	0	0	0
71	337	63	4	21	0	3	1	4	0	0	0
72	47	12	0	11	0	92	1	0	0	0	0
73	13	38	1	9	0	97	0	0	0	1	0
74	143	3	0	3	1	8	1	0	0	0	0
75	33	0	0	3	0	4	0	0	0	0	0
76	71	0	0	7	3	5	0	13	0	0	0
77	17	2	0	0	1	4	0	0	0	0	0
78	97	24	3	7	1	21	0	0	0	0	0
79	45	25	1	3	0	3	0	0	26	0	0
80	39	31	1	2	0	3	0	0	0	0	0
81	61	2	0	7	0	4	0	5	0	0	0
82	76	0	0	0	0	11	0	0	0	0	0
83	57	1	0	2	1	3	0	0	0	0	0
84	71	0	0	0	6	131	0	1	0	0	0
85	26	1	0	0	2	31	0	0	0	0	0
86	99	29	2	21	1	3	1	0	0	0	0
87	77	1	0	0	6	0	0	5	0	0	1
88	427	0	0	0	24	57	0	11	0	0	0
89	51	0	0	0	1	12	0	0	0	0	0
90	98	5	0	0	1	7	0	1	0	0	2

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
91	3	0	0	7	2	5	0	0	0	0	0
92	38	1	0	5	3	18	0	4	0	0	0
93	164	1	0	3	2	9	0	0	0	0	1
94	183	5	0	3	6	2	0	2	0	0	2
95	87	75	3	153	3	4	0	0	0	0	0
96	27	0	0	0	2	19	0	0	0	0	0
97	312	3	0	0	5	273	0	9	0	0	0
98	173	3	0	0	1	213	1	6	0	0	0
99	131	2	0	0	3	3	0	0	0	0	0
100	151	8	0	0	0	4	0	0	0	0	0
101	3	3	0	11	0	4	0	0	9	0	0
102	62	18	3	7	0	4	1	0	13	0	0
103	59	4	0	0	0	18	0	0	0	0	0
104	453	69	2	33	0	11	0	6	0	0	0
105	54	21	2	21	1	4	0	0	0	0	0
106	63	21	1	0	0	88	1	0	27	0	0
107	564	83	8	7	0	5	0	0	0	0	0
108	181	18	2	18	0	17	0	0	0	0	0
109	427	46	4	17	1	13	0	0	0	0	1
110	51	29	0	0	0	5	0	0	0	0	0
111	77	43	2	31	0	3	0	0	0	0	0
112	267	41	6	5	0	13	0	4	0	0	1
113	63	26	2	2	0	5	1	3	0	0	0
114	91	51	1	2	0	2	0	0	0	0	0
115	72	28	1	0	0	15	0	3	4	0	0
116	39	63	7	2	0	8	1	0	0	0	1
117	287	4	4	0	0	6	0	0	0	0	0
118	81	9	0	2	0	5	0	0	0	0	0
119	221	22	0	3	0	19	0	0	0	2	0
120	387	74	3	17	1	7	0	0	0	0	0

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
121	527	89	5	0	2	7	1	2	8	0	0
122	174	47	4	0	1	5	1	0	0	0	0
123	72	26	2	21	0	11	0	0	0	0	0
124	541	149	3	7	0	8	1	3	0	0	0
125	13	25	0	0	0	27	0	0	0	0	0
126	131	27	1	11	0	13	0	0	0	0	0
127	77	12	1	0	0	28	0	0	0	0	0
128	511	89	6	7	16	32	1	3	0	0	3
129	69	68	0	0	0	9	0	0	0	0	0
130	82	29	1	23	7	3	1	0	0	0	0
131	473	111	4	71	9	4	0	0	0	0	1
132	83	11	1	0	0	9	0	0	0	0	0
133	183	63	4	211	1	37	0	0	0	0	2
134	227	69	2	37	1	29	1	13	3	0	1
135	54	29	3	7	1	3	1	0	0	0	0
136	323	43	3	27	1	77	1	0	0	0	0
137	257	55	2	121	0	1	0	0	0	0	0
138	137	37	0	83	3	3	1	6	0	0	0
139	61	13	0	0	0	7	0	0	0	0	0
140	4	4	0	7	0	3	0	0	0	0	0
141	167	32	6	0	0	51	0	0	0	0	0
142	99	2	0	0	0	17	0	0	0	0	0
143	147	23	3	3	1	39	0	4	0	0	0
144	63	17	0	0	0	4	0	0	0	1	0
145	61	4	0	0	0	11	0	0	0	0	0
146	512	47	12	0	1	39	0	4	0	0	0
147	53	6	0	0	0	63	0	0	0	0	0
148	153	27	4	9	0	82	0	4	3	0	0
149	53	8	2	5	0	29	0	0	0	0	0
150	62	13	2	0	0	19	0	0	0	0	0

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
151	177	49	3	29	4	3	0	0	0	0	0
152	361	24	3	4	0	9	0	0	0	0	0
153	197	3	1	0	0	2	0	0	0	0	0
154	113	48	2	0	0	2	0	0	0	0	0
155	62	12	1	5	0	83	1	3	0	0	0
156	18	19	2	2	1	11	0	0	0	0	0
157	41	7	1	0	0	14	0	0	0	0	0
158	53	8	0	0	0	23	0	0	0	0	0
159	113	4	2	0	0	8	0	3	0	0	0
160	22	0	0	0	0	1	0	0	0	0	0
161	37	0	0	0	0	4	1	0	0	0	0
162	27	5	1	0	0	4	1	0	0	0	0
163	13	0	0	0	0	47	0	0	0	0	0
164	44	3	1	0	0	19	0	0	0	0	0
165	21	0	0	0	0	3	1	0	0	0	0
166	31	4	0	0	0	4	1	0	0	0	0
167	19	5	0	0	0	43	1	0	0	0	0
168	27	2	0	0	0	13	1	0	0	0	0
169	74	23	0	4	1	4	0	0	0	0	0
170	69	9	1	0	2	3	1	1	0	0	0
171	62	8	0	0	0	17	1	0	0	0	0
172	8	0	0	0	0	7	1	0	0	0	0
173	4	6	0	6	0	11	0	0	0	0	0
174	84	8	0	2	1	4	1	0	0	0	1
175	34	2	0	0	1	1	1	0	0	0	0
176	44	0	1	0	0	3	0	0	0	0	0
177	11	0	0	3	0	2	1	0	0	0	0
178	3	0	0	0	0	1	1	0	0	0	0
179	47	58	3	13	6	37	1	0	0	0	1
180	331	47	1	13	3	9	0	0	0	0	0

Fish no.	*Anisakis spp.*	*Molicola uncinatus*	*Hepatoxylon trichiuri*	*Corynosoma australe*	*Tentacularia coryphaenae*	*Kudoa thyrsites*	Digenea sp.	*Pseudoterranova sp.*	*Ceratomyxa sp.*	*Rhadinorhynchus cadenati*	*Bolbosoma vasculosum*
181	531	82	1	9	3	4	1	3	0	0	1
182	231	43	0	0	2	9	0	0	0	0	0
183	669	78	4	4	12	14	1	3	0	0	3
184	498	117	1	31	3	13	1	0	0	0	0
185	61	0	0	0	0	4	1	0	0	0	0
186	11	53	3	0	1	11	1	0	0	0	0
187	69	37	2	0	1	13	1	0	0	0	0
188	1173	183	15	27	0	6	1	4	0	0	0
189	21	17	0	0	0	2	1	0	0	0	0
190	74	8	0	17	0	3	1	0	0	2	0
191	587	83	14	0	3	2	1	0	0	0	2
192	117	3	0	0	0	4	1	0	0	0	0
193	6	0	0	0	0	2	0	0	3	0	0
194	157	29	1	2	0	7	0	0	0	1	0
195	27	7	0	0	0	17	0	0	0	0	0
196	241	38	2	0	0	3	0	0	0	1	0
197	115	38	4	0	0	4	0	0	0	0	0
198	537	113	13	17	4	37	0	4	0	0	0
199	29	2	0	0	0	9	0	0	0	0	0
200	3	12	1	47	0	2	0	0	0	0	0
201	479	41	1	0	0	3	1	0	0	0	0
202	57	3	0	2	0	13	0	0	0	0	0
203	2	0	0	0	0	4	0	0	0	0	0
204	297	89	0	3	0	37	1	0	0	0	0
205	967	53	17	0	4	9	0	0	0	0	0
206	81	19	3	11	0	3	0	0	0	0	0
207	73	13	0	3	0	13	1	0	0	0	0
208	28	8	1	0	0	13	0	0	0	0	0
209	328	59	8	0	0	17	0	0	0	3	0
210	8	0	2	0	0	5	0	0	0	0	0

Appendix 5d. Ectoparasite data collected from Thyrsites atun off South Africa

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
1	0	1	0	0	0	0
2	1	12	0	0	0	0
3	2	8	0	0	0	0
4	2	1	0	0	0	0
5	8	4	0	0	0	0
6	12	2	0	0	0	0
7	1	7	0	0	0	0
8	14	3	0	0	0	0
9	9	2	0	0	0	0
10	13	9	0	0	0	0
11	3	5	0	0	0	0
12	24	4	0	0	0	0
13	13	5	0	0	0	0
14	1	2	0	0	0	0
15	0	1	0	0	0	0
16	85	0	0	0	0	0
17	2	0	3	0	0	0
18	12	1	2	0	0	0
19	12	0	0	0	0	0
20	1	0	0	0	0	0
21	9	0	4	0	0	0
22	54	1	1	0	0	0
23	1	0	0	0	0	0
24	29	3	0	0	0	0
25	1	4	0	0	0	0
26	47	4	0	0	0	0
27	12	3	0	0	0	0
28	11	3	0	0	0	0
29	6	1	0	0	0	0
30	3	0	0	0	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
31	12	0	0	0	0	0
32	1	11	4	0	0	0
33	11	0	0	0	0	0
34	17	1	12	0	0	0
35	1	8	0	0	0	0
36	0	1	0	0	0	0
37	8	0	0	0	0	0
38	25	4	0	0	0	0
39	3	2	0	0	0	0
40	2	0	0	0	0	0
41	36	0	0	0	0	0
42	7	1	0	0	0	0
43	6	0	0	0	0	0
44	0	1	2	0	0	0
45	5	0	0	0	0	0
46	1	0	0	0	0	0
47	6	1	0	0	0	0
48	9	0	0	0	0	0
49	9	2	0	0	0	0
50	3	0	0	0	0	0
51	4	1	0	0	0	0
52	7	0	0	0	0	0
53	8	3	3	0	0	0
54	6	0	0	0	0	0
55	2	2	5	0	0	5
56	23	2	2	1	0	0
57	78	0	0	0	0	0
58	43	1	2	0	0	0
59	2	1	0	0	0	0
60	21	3	0	0	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
61	53	1	0	0	0	0
62	18	2	1	5	0	1
63	34	1	0	0	0	0
64	22	0	3	0	0	0
65	48	0	3	1	0	0
66	8	0	0	0	0	0
67	43	1	2	1	0	0
68	34	2	19	2	0	0
69	32	1	3	1	0	1
70	23	0	5	1	0	1
71	46	0	7	5	0	1
72	18	0	3	1	0	0
73	23	2	1	1	0	0
74	5	0	0	0	0	0
75	23	0	0	0	0	0
76	6	0	5	1	0	0
77	45	0	1	1	0	0
78	4	1	4	0	0	1
79	21	0	1	0	0	0
80	15	1	7	8	0	1
81	14	0	1	1	0	0
82	4	0	0	0	0	0
83	12	0	7	4	0	0
84	53	0	4	0	0	0
85	5	0	2	0	0	0
86	8	0	1	1	0	0
87	6	0	2	0	0	0
88	9	0	2	1	0	0
89	2	0	1	0	0	0
90	51	0	2	2	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
91	73	0	5	1	0	0
92	27	0	2	4	0	0
93	42	0	5	9	0	0
94	3	0	3	1	0	0
95	5	0	1	0	0	0
96	8	0	5	4	0	0
97	21	0	1	2	0	0
98	34	2	6	7	0	0
99	6	0	2	0	0	0
100	8	1	6	0	0	0
101	6	0	0	0	0	0
102	9	0	0	0	0	0
103	22	0	1	0	0	0
104	1	6	3	0	0	0
105	43	0	3	0	0	0
106	4	0	3	0	0	0
107	51	0	2	0	0	0
108	12	2	7	0	0	0
109	4	3	0	0	0	0
110	17	0	0	0	0	0
111	0	2	0	0	0	0
112	1	2	0	0	0	0
113	4	0	1	0	0	0
114	14	5	0	0	0	0
115	13	3	2	1	0	0
116	27	2	8	0	0	0
117	1	0	7	1	0	0
118	6	0	3	1	0	0
119	13	0	0	0	0	0
120	1	0	3	0	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
121	13	5	0	1	0	0
122	8	1	0	0	0	0
123	12	5	2	0	0	0
124	3	2	4	0	0	0
125	17	2	7	0	0	0
126	12	0	2	2	0	0
127	2	2	19	1	0	0
128	13	0	9	0	0	0
129	3	2	7	1	0	0
130	27	0	1	0	0	0
131	61	1	1	0	0	1
132	1	1	2	3	0	0
133	2	0	1	1	0	0
134	36	0	14	1	0	0
135	42	1	0	0	0	0
136	2	0	9	0	0	0
137	8	1	4	7	0	0
138	23	0	0	0	0	0
139	67	0	8	0	0	0
140	6	1	6	0	0	0
141	5	8	18	0	0	0
142	13	5	4	0	1	0
143	31	0	5	2	0	1
144	13	2	0	0	0	0
145	33	1	8	0	0	0
146	1	1	9	1	0	0
147	27	2	1	2	0	0
148	3	0	0	0	0	0
149	4	1	1	0	0	0
150	7	1	0	0	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
151	0	1	7	1	0	1
152	7	1	1	0	0	0
153	27	0	3	0	0	0
154	1	6	1	0	0	0
155	7	1	5	0	0	1
156	6	8	12	0	0	0
157	0	2	1	0	0	0
158	25	0	6	0	0	2
159	29	1	0	0	0	0
160	3	4	3	0	0	0
161	2	0	6	0	0	0
162	56	0	0	0	0	0
163	23	0	3	0	0	0
164	12	0	0	0	0	0
165	7	0	12	0	0	0
166	4	0	3	0	0	0
167	3	0	0	0	0	0
168	11	0	0	0	0	0
169	3	0	1	1	0	0
170	2	1	0	0	0	0
171	6	0	0	2	0	0
172	23	0	7	0	0	0
173	7	0	5	0	0	0
174	7	1	3	0	0	0
175	32	3	21	0	0	0
176	7	0	0	0	0	0
177	28	0	1	0	0	0
178	24	0	0	0	0	0
179	53	16	12	0	0	0
180	11	0	21	0	0	0

Fish no.	*Nothobomolochus fradei*	*Hatschekia conifera*	*Caligus dakari*	*Caligus zei*	*Caligus coryphaenae*	*Udonella sp.*
181	2	31	33	0	0	0
182	6	6	13	0	0	0
183	31	0	5	1	0	0
184	5	1	5	0	0	0
185	0	0	0	1	0	0
186	26	3	2	0	0	0
187	27	2	0	0	0	0
188	15	11	0	0	0	0
189	29	2	1	0	0	0
190	21	0	2	0	0	0
191	21	7	5	0	0	0
192	13	0	0	0	0	0
193	13	1	5	0	0	0
194	6	7	0	0	0	0
195	5	0	1	0	0	0
196	33	2	0	0	0	0
197	7	6	1	0	0	0
198	3	0	0	0	0	0
199	2	0	1	0	0	0
200	9	0	0	0	0	0
201	1	1	7	0	0	0
202	49	0	4	0	0	0
203	5	0	5	0	0	0
204	29	0	0	0	0	0
205	3	0	0	0	0	0
206	45	2	0	0	0	0
207	1	1	0	0	0	0
208	1	0	0	0	0	0
209	28	12	0	0	0	0
210	3	0	0	0	0	0