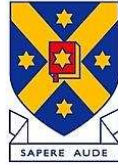


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Te Whare Wānanga o Ōtāgo

**Does host diet govern the structure and diversity of
tapeworm assemblages in sharks? Insights from the
literature and a model shark species; *Cephaloscyllium
isabellum***

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**A thesis submitted for the degree of Masters of Science in Ecology
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Abstract

Previous research has shed some light on what phylogenetic and ecological factors may be important determinants of tapeworm parasite diversity in elasmobranchs (sharks, skates and rays). However, several potentially key factors for tapeworm transmission, including the breadth and composition of host's diets, have been recognised as crucial gaps in our understanding.

The main objective of this research was to investigate the relative importance of sharks' diets for the structure and diversity of their tapeworm assemblages. First, the literature was searched for information on tapeworms and host features for a large subset of different shark species, and aspects of shark's diets (including their diet breadth, diet composition and trophic level) were assessed for their relative importance as predictors of tapeworm diversity. Second, literature records were used to conduct a comprehensive analysis of the relationship between shark's diet compositions and tapeworm compositions. Finally, the importance of host diet was examined as a potential encounter filter for restricting tapeworm diversity in a model shark species, *Cephaloscyllium isabellum*.

The results of this study revealed diet breadth to be a key predictor of tapeworm richness in sharks, indicating that sharks with broader diets generally harbour more tapeworm species. The composition of tapeworms infecting a shark species was found to be related to its diet composition, and moreover, certain tapeworm taxa were found to be useful indicators of the host species' ecology and evolutionary history. The research on *C. isabellum* here offered only limited insights into the potential importance of diet as an encounter filter for the shark, but provided some new important data on both the diet and parasites of this species.

Ultimately, the observational studies carried out within this research emphasise that aspects of sharks' diets can have important implications for their tapeworm parasite assemblages. Further exploration of these patterns with experimental research may be able to validate the influence of these patterns in nature.

Acknowledgements

I would firstly like to thank the University for selecting me as a candidate for an MSc Research Year Scholarship, which supported me throughout this project. To my supervisors Haseeb Randhawa and Steve Wing, I cannot thank you enough for providing me with your critical support and feedback. Overall, I could not have hoped for better mentors. Thanks to Haseeb for his constant guidance and advice all the way from the inception of ideas for this research to the analyses and final stages of writing. Thanks to Steve for his advice and ideas, especially on the scientific methods for data collection, and for his support in overseeing the logistics for conducting this research.

I would like to say a big thank you to the staff in the Marine Science and Botany departments for helping me to setup and carry out the practical parts of this research. Thanks to Doug Mackie, Daryl Coup and Sean Heseltine for their help in organising shark prey collections, and to Peter Batson and Adelle O'Neill for their assistance in collection trips and setup of my laboratory workspace. In addition, thanks to Gavin Heineman (Echo F/V) for his help in collections of sharks and some invertebrates. I am grateful for Vickey Tomlinson of the Botany department, for helping to provide me with the needed workspace and resources for some of the practical work, and for Michelle McKinlay (Botany) and Christoph Matthaei (Zoology) for their guidance on the logistics of completing and submitting this project.

Thank you to my colleagues and professors who got involved with this research throughout various stages. I would like to thank Keith Probert for his advice regarding some of the identifications of collected invertebrate species and my fellow students Thibaut Anglade, Steph Bennington and Zuri Burns who helped me with some of the practical work. I would also like to extend my thanks to Robert Poulin and various members of the Evolutionary and Ecological Parasitology Group for their valuable discussions and insights regarding some of the ideas and methods used in this project.

Finally, I would like to thank my partner Ashley, and my friends and family for being there for me during each stage of this project. My long and arduous journey towards completing this thesis was made possible thanks to their continued support and encouragement.

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Chapter 1: Introduction

1.1. General introduction

Parasites comprise an extremely diverse group of organisms and account for a large portion of our total global biodiversity (Dobson et al. 2008; Poulin & Morand 2014). Traditionally, parasites have been viewed as a massive burden to our environment. We have sought, and in many cases, we have succeeded in their eradication (see Bowman 2006). Nevertheless, many ecological studies have shown that parasites are a critical part of ecosystems, serving an important role in the regulation of food webs and host populations, and mediating energy flow through trophic levels (Lafferty et al. 2006; Lafferty et al. 2008; Amundsen et al. 2009). Recent notions in parasite ecology have also highlighted the potential consequences of parasite loss from our ecosystems, indicating that the influence of parasites on overall communities and ecosystems may often be underestimated (Holt 2010; Wood & Johnson 2015). With these points in mind, there is a clear need for further research to better describe the parasite diversity in our ecosystems, and likewise, to determine what factors govern parasite diversity.

Determining what host features influence parasite species richness has been the subject of a broad range of ecological studies, conducted in different ecosystems and animal groups. A recent meta-analysis looking at parasite richness across animal, plant and fungal hosts found that three features of hosts, namely body size, population density and geographical range, could be generally considered as universal predictors of parasite species richness (Kamiya et al. 2014). However, notwithstanding the general significance of these features, their relative influence on parasite diversity can vary considerably among different studies, and in many cases, other less prominent variables may be better predictors of parasite richness among host species e.g. temperature (Poulin & Rohde 1997), anthropogenic changes to land (Mitchell et al. 2010), diet breadth and vulnerability of hosts to predators (Locke et al. 2014). The significance, direction and strength of predictors may largely depend on what type of hosts and parasites are involved (Lindenfors et al. 2007; Poulin & Morand 2014). It is also worth noting that several host features with potentially large impacts on parasite diversity are seldom included in studies looking at determinants of parasite diversity. For instance, it is difficult to evaluate the predictive strength of host diet, home range size or metabolic rate on parasite richness, because they have rarely been taken in

account in comparative studies (Kamiya et al. 2014). To gauge the generality of these factors, more emphasis must be put on their inclusion in research going forward.

Sharks are important apex predators in all of the world's oceans and are distributed across a broad range of depths, latitudes and habitats (Froese & Pauly 2017). Their exploitation over the past few decades has left many sharks vulnerable and endangered, producing unpredictable and ecosystem-wide consequences (Stevens et al. 2000; Ward & Myers 2005, Myers et al. 2007; Ferretti et al. 2010). Sharks present an important system for studying determinants of parasite diversity, due not only to their importance as apex predators and integral role in food webs, but also because their associated tapeworms are an extremely diverse and significant group of parasites (Caira & Healy 2004). These parasites may offer key insights from an evolutionary perspective given that elasmobranchs have been hosts of tapeworms for an estimated 270 million years, and they represent the earliest fossil record of tapeworm parasitism of vertebrates (Dentzien-Dias et al. 2013). Previous records show there are about one thousand tapeworm species so far described from elasmobranchs (Caira & Jensen 2014), with thousands more to be described (Randhawa & Poulin 2010). These parasites hold additional importance in marine ecosystems in that they are all trophically transmitted through food webs and affect an array of other marine species as larvae (Caira & Jensen 2017). Hundreds of intermediate hosts have already been described for elasmobranch tapeworms, including various species of teleost fishes, cephalopods, crustaceans and reptiles (Palm 2004; Caira & Jensen 2017).

Previous research has begun to shed some light on what phylogenetic and ecological factors may be important determinants of tapeworm infections in elasmobranchs (McVicar & Fletcher 1970; Randhawa et al. 2007; Randhawa & Burt 2008; Randhawa & Poulin 2010). A recent study found that host size, latitude and depth may each influence tapeworm diversity in elasmobranchs (Randhawa & Poulin 2010). However, the influence of these factors clearly depends on the type of elasmobranch host involved (shark or batoid), and after correcting for phylogenetic influences in sharks, only host size has been demonstrated to significantly impact tapeworm richness (Randhawa & Poulin 2010). Notably, there are still many factors that remain to be comparatively tested for their influence on tapeworm diversity. It has been

pointed out that host diet breadth and composition especially warrant further investigation (Randhawa & Poulin 2010).

The aim of this thesis is to assess what factors govern the structure and diversity of tapeworm parasite assemblages in sharks, with particular reference to the importance of host diet. Two main approaches will be used to achieve this. The first will be to look at records from the literature across many shark species and their prey to determine whether aspects of host diet are strong predictors of tapeworm diversity and composition in comparison with other relevant host features. This approach will serve to tell us whether factors such as diet breadth, diet composition and trophic level appear to be generally important barriers for tapeworm establishment in sharks. The second approach will complement the first approach by more specifically analysing the importance of diet for parasite composition in a local shark species, the draughtsboard shark *Cephaloscyllium isabellum*. This species could be a good model for investigating what factors restrict parasite establishment in sharks because it is known to have a broad diet (Horn 2016), but has fewer tapeworm species than would be expected for a shark of its size (Randhawa 2014, unpublished data; see also Poulin et al. 2011b). Thus, it can be investigated whether its diet is a large factor restricting encounters with different tapeworm parasites, or alternatively, whether strong compatibility filters in the species prevent parasite associations. Notably, this investigation could also provide valuable biological information on the shark, which is currently scarce (Horn 2016).

1.2. Host specificity and barriers to parasite establishment

As described in the above introduction, testing what factors predict parasite richness among host species can help us to understand patterns of parasite biodiversity. For a complementary approach to understanding these patterns of diversity, we can look at a trait known as "host specificity" and analyse what factors act as barriers to infection for certain parasites. Host specificity is a fundamental property of parasites (Kosoy et al. 1997; Dyer et al. 2007; Poulin 2011). Although there are many definitions for this property (see Poulin & Mouillot 2005; Poulin et al. 2011a), it can generally be defined as the extent to which different host species are used by a parasite (Combes 2001). Host specificity exhibits great variation among different species and groups of

parasites. At one end of the spectrum, we have parasites which infect only one species. Most monogenean ecto-parasites of fish, for example, are restricted to a single host species (Šimková et al. 2006). On the other end, some parasites infect a multitude of different hosts. For instance, the Asian tapeworm *Bothriocephalus acheilognathi* has been described from more than a hundred different fish species (Salgado Maldonado & Pineda-López 2003).

Understanding what ecological and evolutionary factors determine parasite-host specificity is a common goal for research in parasitology. On the theoretical side, knowing what factors prevent a parasite from expanding its host range is key to learning about the community structure of parasites and host-parasite co-evolution (Poulin et al. 2011a). On the practical side, knowing what ecological and evolutionary factors underpin host specificity may guide scientists towards better prediction and control of the transmission of infectious diseases (Poulin 1992; Taraschewski 2006; Lootvoet et al. 2013). Of course, the ability of a parasite to successfully spread and establish in a new area largely depends on what ecological or phylogenetic barriers may prevent the parasite from establishing and spreading to alternative hosts (Taraschewski 2006; Dunn 2009).

Euzet and Combes' filter paradigm offers a simple but effective illustration of what factors determine the host specificity of a parasite (Euzet & Combes 1980). The idea is that there is a two-step filter for parasite-host compatibility. The first step is an 'encounter filter', which excludes hosts from a parasite's potential host spectrum that don't come in physical contact with the parasite (illustrated by circles in Figure 1.1). A host may not be encountered by a parasite either because they live in different ecosystems, or alternatively, because host behaviours such as diet and niche segregation prevent contact with infective stages of the parasite (Combes 2001). The second step of the filter paradigm is a 'compatibility filter', which excludes any hosts from a parasite's potential host spectrum that are incompatible with the parasite (illustrated by triangular section in Figure 1.1). Hosts may be incompatible either because they do not provide adequate spatial or metabolic resources for the parasite, or because immunological or other defense mechanisms of the host kill the parasite (Combes 2001). Upon consideration of each of these filters, it is clear that the range of hosts actually used by a parasite represents only a small subset of their potential

host species (small shaded triangular area in Figure 1.1).

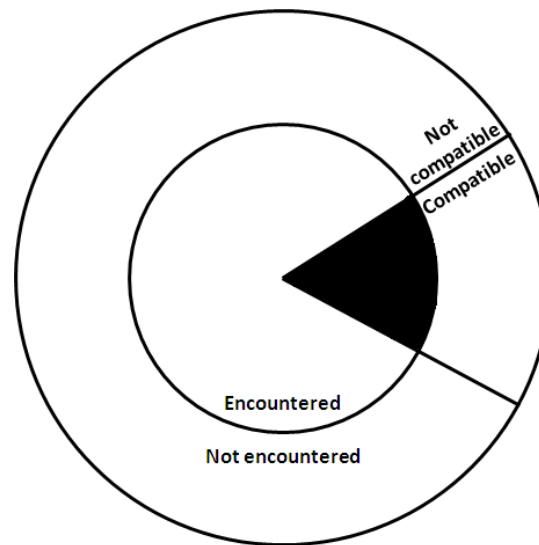


Figure 1.1: Diagram illustrating the filter paradigm of host-parasite specificity. (adapted from Combes 2001). A parasite's host spectrum (range of hosts it uses) represents a small subset of its potential host species (small shaded area) that are encountered (within the small inner circle) as well as compatible (within the triangular area).

The compatibility filter concept has been applied in research over the past few decades as a basic tool for understanding determinants of host specificity (Kuris et al. 2007; Randhawa & Burt 2008; Lagrue et al. 2011). A handful of studies have shown that the high specificity of tapeworms in elasmobranchs is, to some extent, the result of compatibility filters. For example, immune response in elasmobranchs has been demonstrated to cause mortality for certain tapeworm species (McVicar & Fletcher 1970; Randhawa & Burt 2008). Attachment site morphology in elasmobranch host mucosa may also determine whether some tapeworm species can live in the host (Williams 1960, 1966, 1968). Although it has been suggested that attachment site morphology is more of a determinant for attachment site specificity rather than for host specificity (Randhawa and Burt 2008). These studies clearly demonstrate that compatibility filters have an influence in restricting the host specificity of elasmobranch tapeworms. However, the role of these compatibility filters in comparison with encounter filters is unclear.

It is unknown whether encounter filters (e.g. diet) are as restrictive for tapeworm establishment in elasmobranchs as parts of the compatibility filters (e.g. immune response). This is an important gap in knowledge since some encounter filters, such as host substrate preference and diet, have been suggested as potentially important ecological determinants of host specificity (Randhawa et al. 2008). It is likely that both filters play key roles as barriers to parasite establishment, but by assessing the relative importance of each filter we may be able to better predict the consequences of ecological changes on the transmission of these parasites to other hosts in future.

1.3. The influence of host diet on parasite diversity

Helminth parasites with complex life cycles rely on trophic interactions for transmission to their final host (Simkova et al. 2001; Cirtwill et al. 2016).

Thus, the diversity of these parasites is unlikely to be randomly distributed in food webs, but is rather expected to be concentrated in parts of a food web that favour transmission (Locke et al. 2014). Following from this, it would make sense that hosts diets have a large influence on their acquisition of parasites, and consequently, the diversity of their parasite assemblages. Many previous studies support this notion, showing that variation in diet breadth and trophic positions among host species can explain a large amount of interspecific variation in the richness of their trophically-transmitted parasites (Klimpel et al. 2006; Chen et al., 2008; Poulin & Leung, 2011; Locke et al., 2014).

Diet breadth could be one of the most important factors in determining the diversity of fish parasites. In theory, a fish species that feeds on many different prey species should be exposed to a greater range of larval parasites compared to a host species with a restricted or specialised diet. Because of this, fish species with broad diets could accumulate a larger variety of trophically transmitted adult parasites (Kennedy et al. 1986; Lo et al. 1998; Locke et al. 2014). The trophic level of a host might be similarly important, since fish occupying higher trophic positions have access to more prey, and parasites tend to exploit host species that are highly connected (Chen et al. 2008). The diet composition of a host may also play a large role in its accumulation of different parasites. Trophically transmitted parasites typically infect a limited number of intermediate hosts, meaning that the variety of parasites in the final host may

depend on whether these intermediate hosts are an important component of the definitive host's diet (Kennedy et al. 1986; Marques et al. 2011).

The influence of dietary factors on the diversity of tapeworms infecting sharks is currently unknown (Randhawa & Poulin 2010). There is good reason, however, to think that diet may be an important factor for tapeworms in elasmobranchs, since all tapeworm species are acquired by elasmobranchs via trophic transmission from intermediate or paratenic hosts (Willams 2002).

1.4. Life cycles of shark tapeworms

From what is currently known of tapeworms infecting sharks, the life cycles of these parasites are typically complex and involve several invertebrate and vertebrate intermediate hosts (Sakanari & Moser 1989; Palm 2004; Randhawa 2011; Caira & Jensen 2017). In general, these parasites are highly host specific as adults (i.e. are restricted to one or a few host species), but show considerably lower host specificity in intermediate hosts (Palm & Caira 2008; Jensen & Bullard 2010). There also appears to be considerable variation in life cycles among different tapeworm species, where some species use many more intermediate and paratenic hosts than others (Palm 2004).

To get an idea of a general shark tapeworm life cycle, we can look at one of the earliest described examples involving the trypanorhynch tapeworm *Lacistorhynchus dollfusi* infecting the leopard shark *Triakis semifasciata*. Adult tapeworms live in the spiral intestine of its definitive elasmobranch host (Figure 1.2a), and once mature, pass eggs out through the shark's faeces (Figure 1.2b-c). These eggs are then consumed by a first intermediate host, which is often a small crustacean such as a copepod or amphipod (Palm 2004) (Figure 1.2d). The first intermediate host is consumed by a second, larger intermediate host, such as a teleost fish, where the tapeworm develops from a proceroid to a plerocercoid larva (Figure 1.2e). The tapeworm then completes its life cycle once the shark host eats the plerocercoid-infected fish (Figure 1.2). Life cycles of tapeworms can be more complex than the one described above, and prey other than crustaceans and fish, including reptiles, mammals and cephalopods, have also been identified as intermediate hosts (Palm

2004; Randhawa 2011; Caira & Jensen 2017). Moreover, there are variations in life cycles where the second intermediate host is not a fish, and is instead another larger invertebrate like a shrimp or crab (Palm 2004).

An overwhelming majority of the life cycles of elasmobranch tapeworms are still unknown or poorly described (Caira & Reyda, 2005; Jensen & Bullard 2010). The main reason for this is the difficulty of identifying larval stages, since most tapeworms have larvae that don't look like the adult based on morphology (trypanorhynchs are an exception) (Jensen & Bullard 2010). This difficulty has sparked the need for alternative approaches to identify tapeworm larvae, including molecular tools (Poulin & Keeney 2008; Jensen & Bullard 2010; Randhawa 2011) and in-vitro growth (e.g. Presswell et al. 2012). These alternatives to morphological identification could be pivotal for researchers aiming to better understand the ecology and evolution of tapeworm life cycles in future (Palm & Caira 2008).

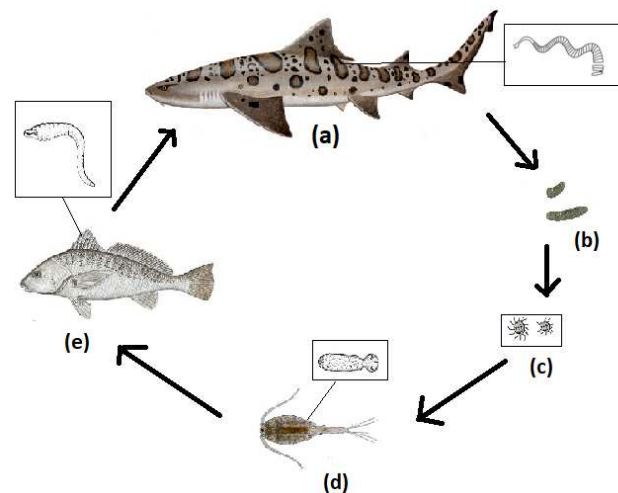


Figure 1.2: Diagram illustrating the life cycle of a shark trypanorhynch tapeworm: *Lacistorhynchus dollfusi* infecting the leopard shark *Triakis semifasciata* (Modified from Sakanari & Moser (1989)). (a) Adult tapeworms live in the spiral valve of the definitive shark host. (b) gravid proglottids pass out in shark faeces, releasing eggs. (c) Ciliated coracidia hatch from operculated eggs and are consumed by copepods (d), where they develop into proceroid larvae. Copepods are eaten by teleosts such as white croakers (e), and the proceroids develop into plerocerci inside blastocysts. When infected fish is consumed by the shark host, the tapeworm lifecycle is completed.

1.5. Biology of the model species: *Cephaloscyllium isabellum*

The draughtsboard shark *Cephaloscyllium Isabellum* (Bonnaterre, 1788) is a scyliorhinid catshark species, of the Order Carcharhiniformes, that is thought to be endemic to New Zealand (Cox & Francis 1997) (Figure 1.3). This species is sometimes referred to as the New Zealand carpet shark, but it is not a member of the carpet shark Order Orectolobiformes. To avoid confusion, the species will be hereafter referred to as the draughtsboard shark or *C. isabellum*.



Figure 1.3: Image of the New Zealand draughtsboard shark (*Cephaloscyllium isabellum*). Image credit: Chris 2012, <http://www.surfcaster.co.nz/>

Like other members of the *Cephaloscyllium* genus, *C. isabellum* is oviparous (Dulvy & Reynolds 1997), and is it thought to have year-round reproduction (Horn 2016). Individuals of this species generally range from 20cm in length as juveniles up to a metre in length as adults, with male sharks generally not growing as large as females (Cox & Francis 1997; Horn 2016). Draughtsboard sharks live around New Zealand coasts in shallow depths out to around 200 metres, but also occur (mostly as larger individuals) in deeper waters out to 500 metres (Francis et al. 2002; Horn 2016). They are known to be demersal hunter and scavenger, and feed on a variety of prey including fishes, crustaceans, molluscs and other invertebrates (Horn 2016). *Cephaloscyllium* species can detect weak bioelectric fields of prey (Tricas 1982), which likely assists them in their ambush predation and scavenging. Like other species of this genus, *C. isabellum* is thought to forage mainly at night, whilst taking refuge in caves or reefs during the day (Nelson & Johnson, 1970; Awruch et al. 2012; Horn 2016).

Several endoparasite species have been described in *C. isabellum*; two digenean trematodes (in the stomach), three nematodes (in the stomach and sometimes intestine), and one tapeworm species, *Calyptrobothrium chalarosomum* (in the spiral

intestine) (Hewitt & Hine 1972; Hine et al. 2000). *Cephaloscyllium isabellum* has a notably low diversity of intestinal tapeworms (one) compared to other sharks, which on average, are infected by around 6 different tapeworm species (Randhawa and Poulin 2010). This shark species has also been identified as a cold spot in shark tapeworm diversity, which means that it has fewer tapeworm species than would be expected for a shark of its size (Poulin et al. 2011b). This is surprising given that the species demonstrates a broad diet (Horn 2016), and it could potentially encounter many tapeworm larvae in different prey. It is unknown, however, whether many different tapeworm larvae are present in its favoured prey. The above points indicate that *C. isabellum* should be a useful model for looking at determinants of tapeworm host specificity. Its diet may be a large factor restricting encounters with different tapeworm parasites, or alternatively, there are perhaps strong compatibility filters in the species preventing parasite establishment. This poses a key question: Which filter is more restrictive of parasite establishment in *C. isabellum*?

1.6. Study location

All samples for this research were obtained between the Otago Peninsula region of Dunedin, and Curio Bay in Southland, New Zealand (Figure 1.4). Draughtsboard sharks and their prey were sampled from between Curio Bay and Taiaroa Head, Dunedin. Lab work, including most measurements and dissections, was conducted at Portobello Marine Lab, which is in close proximity to the sampling sites (Figure 1.4). However, some practical work, primarily the identification of shark prey items, also took place in the University of Otago Botany Department.



Figure 1.4: Map of the Otago region displaying the sampling site locations; Curio Bay to Nugget Point to Taiaroa Head, and the sites for lab work; Portobello Marine Lab and the University of Otago Botany Department.

1.7. Aims, objectives and hypotheses

The overall aim of this research was to provide insights into what factors govern the composition and diversity of tapeworm parasites in sharks, with particular reference to the influence of host diet. This aim was explored on a large scale by using published literature to conduct comparative analyses across a broad range of different shark species. In addition, this aim was examined on a smaller scale, by testing links between the diet and tapeworms of a model shark species (*C. isabellum*).

The objective of the comparative analyses was to determine whether certain aspects of host diet (such as diet breadth, composition or trophic level) are important predictors of tapeworm diversity or composition, particularly in comparison with other host variables. Additionally, larval shark tapeworm records in the literature were investigated to ascertain whether intermediate hosts of shark tapeworms show strong links with the diet of their shark hosts. These objectives were carried out by compiling comprehensive datasets on diet and other features of shark species from the literature and testing the variables of interest for their predictive strength on measures of tapeworm diversity among host species (e.g. tapeworm richness).

The objective of research on the model species *Cephaloscyllium isabellum* was to find out what factors act to restrict parasite establishment in the species, something which may also be relevant for other sharks. Moreover, this part of the study attempted to elucidate parts of the life cycle of the shark's only known tapeworm (*Calyptrobothrium chalarosomum*). To complete these objectives, a number of individual sharks were examined for their diets and parasite fauna, and their known prey items were surveyed for parasite larvae to determine their potential as intermediate hosts. This was done to give some indication of how many larval parasites are likely to be encountered via their diet, and thus, whether there are mechanisms other than diet (e.g. host immune response) that heavily restrict parasite establishment.

1.8. Overview of thesis chapters

This thesis is presented in five chapters; a general introduction (this chapter), three chapters devoted to three individual studies, and a general discussion chapter.

Chapter two investigated aspects of host diet as determinants of tapeworm diversity in sharks. Data was obtained from the literature on the diet breadth, trophic level and diet composition of as many shark species as possible in order to test whether these variables are strong predictors of tapeworm diversity. The importance of these factors were also assessed relative to many other potentially significant host features (e.g. host size and phylogeny).

Chapter three examined the influence of diet on the composition of shark tapeworm assemblages. Similarly to chapter two, this involved compiling data from the literature on the diet composition of different sharks. However, this chapter analysed what factors may shape shark tapeworm compositions rather than analysing which factors are important for general tapeworm diversity. This chapter also examined larval shark tapeworm records in the literature to determine whether known intermediate hosts of shark tapeworms show a strong presence in the diets of their definitive shark hosts.

Chapter four focused on the model species *C. isabellum*, and primarily investigated whether this shark's diet is an important factor restricting its encounters with potential tapeworm parasites. This involved a look at both the parasites and diet of this shark species, and an examination of larval parasites in its known prey items, which could serve as potential intermediate hosts.

The final chapter summarised key findings from all of these thesis chapters, discussed their implications, and provided suggestions for further research.

Chapter 2: Host diet as a determinant of tapeworm diversity in sharks

2.1. Introduction

The diversity of parasite species in a host, like the diversity of free-living species in an ecosystem, is shaped by a range of different ecological and evolutionary features. Exploring how these features relate to parasite diversity is fundamental to our understanding of why particular host species evolve with richer or more diverse parasite faunas than others (Poulin 2004). Research over the past several decades has already identified several widely important host features that can influence the diversity of parasite assemblages, including body size, lifespan, population density, geographical range and diet (Morand et al. 2000; Vitone et al. 2004; Kamiya et al. 2014). A few of these features; body size, population density and geographical range, have even been recognised as ‘universal’ determinants of parasite species richness (Kamiya et al. 2014). Despite the general significance of these few host features, however, their relative importance is known to vary considerably among different host-parasite systems (e.g. Poulin et al. 2011). Depending on what hosts and parasites are involved, other less-generalised factors may also have a large influence on parasite diversity. For instance, in anthropoid primates, parasite species richness is influenced largely by social group size (Vitone et al. 2004). In addition, a number of host features, which could potentially have a significant impact on parasite diversity, are often left out of studies looking at determinants of parasite diversity. For example, host basal metabolic rate (BMR) is potentially a very important factor for parasite diversity. Higher BMRs are associated with higher rates of energy processing and resource availability, and consequently, animals with a high BMR may be able to support richer parasite assemblages (Brown et al. 2004). However, since BMR has been scarcely included as a factor in comparative analyses of parasite diversity, it is difficult to assess its predictive strength and relative importance compared to other factors (Kamiya et al. 2014). Likewise, host diet breadth may be an important predictor of parasite diversity because species with broad diets can encounter a greater range of parasite species from different prey (Locke et al. 2014). Yet, diet breadth has been rarely included in comparative analyses of parasite diversity, making it difficult to know how important diet breadth is for parasite diversity on a larger scale (Kamiya et al. 2014). In light of these issues, there remains a need for research to assess the relative importance of many different host features in various host-parasite systems to

better understand emerging diseases and their transmission dynamics.

Sharks and their tapeworm species assemblages provide a useful system for looking at large-scale patterns of parasite diversity for a number of reasons. First, the tapeworm parasites of these elasmobranchs show substantial diversity and exhibit high host specificity. They are the most diverse group of parasites infecting elasmobranchs, with 977 different species and 201 genera known from nine established orders (Caira and Healy 2004; Caira and Jensen 2014). Based on the number of host species sampled for parasites to date, it is also estimated that an astounding 3600 tapeworm species in described elasmobranchs have yet to be recorded (Randhawa and Poulin 2010). Almost all tapeworm species exhibit a high degree of host specificity in sharks, with most being restricted to a single host species or a few closely related hosts (Caira and Jensen 2014). However, it is also worth noting that these tapeworms are generally less specific in intermediate hosts and can have consequences for thousands of marine species other than elasmobranchs, including a broad range of teleost fishes, molluscs, crustaceans, mammals, reptiles and other invertebrates (Palm and Caira 2008; Jensen 2009). Second, sharks are a group of animals that have features with broad and easily measurable variation across species. Shark species display a broad range of sizes, are found at nearly all marine habitats, depths and latitudes, and show marked variation in the breadth of their depth and latitudinal distributions (Froese and Pauly 2015). There is also considerable variation in diet and trophic level among different species (Cortés 1999). Third and finally, sharks are apex predators of marine ecosystems and they, along with their many parasites, exert considerable influences throughout marine food-webs. Thus, sharks and their parasites stand as an important model for understanding determinants of marine diversity.

From previous research looking at tapeworm diversity in sharks, several host features, including latitude, depth, and habitat, appear to have little influence on their parasite diversity (Randhawa and Poulin 2010). Host size has been identified as a significant predictor, but no other ecological or host biological features examined so far have demonstrated significant effects on shark tapeworm diversity (Randhawa and Poulin 2010). Additionally, it has been shown that shared host evolutionary history, i.e. shark phylogeny, outweighs ecological variables as a predictor of tapeworm diversity in sharks (Poulin et al. 2011). Nevertheless, there are a number of potentially important

host features that have yet to be examined for their influence on tapeworm diversity. Host population density is a feature of likely importance, but data on population density is generally unavailable for different shark species, making it difficult to investigate its influence on parasite diversity. Of the features for which data are available, aspects of host diet are arguably the prominent features warranting investigation. Host diet hasn't previously been assessed as a determinant of shark tapeworm diversity, but it is likely to have a large impact considering that all tapeworm species in elasmobranchs are acquired via ingestion of infected prey (which are intermediate or paratenic hosts) (Williams et al. 1994). Essentially, the number of tapeworm species that infect a shark species should directly depend on what prey, and ultimately how many different prey, a shark consumes as part of its regular diet.

2.1.1. Objectives of chapter 2

The main aim of this chapter was to examine whether three major aspects of host diet; (1) breadth of diet, (2) trophic level, and (3) diet composition, influence the species diversity of tapeworm assemblages in sharks. Although all three of these factors convey information on the diet of sharks, each is distinctly different in what it tells us. Breadth of diet is a general measure of how many different prey are consumed by a shark species. It was hypothesised that shark species with broader diets (diets including more different prey taxa) would harbour a greater diversity of tapeworm species than those with restricted diets. This was based on the fact that they would encounter more tapeworm intermediate hosts through their diet, and thus, could come in contact with a greater diversity of parasites. Trophic level is a measure of a species' position in food webs, and indicates overall what type of ecological groups are most important in their diet (see Cortés 1999). It was hypothesised that shark species occupying higher trophic levels would harbour more diverse tapeworm assemblages than those occupying lower trophic levels, since they have access to more trophic links and additional intermediate hosts from higher trophic levels. Diet composition is a measure of what specific taxa are the most dominant in the diet of a host species. In contrast to trophic level, which reflects the position of a shark's prey in the food web, diet composition tells us which specific taxonomic groups of prey (e.g. teleosts, cephalopods, crustaceans) comprise most of the diet. I predicted that shark species feeding predominantly on teleost fishes would have more tapeworm species than

other groups because most currently described intermediate hosts for marine tapeworms are teleost fishes (Palm 2004; Jensen 2009). Overall, it was predicted that each of these measures of host diet would have more significant, higher magnitude impacts on tapeworm diversity than host features examined in previous studies.

2.2. Methods

2.2.1. Tapeworm data collection

All tapeworm species diversity data used in this study were compiled by revising and updating a comprehensive elasmobranch tapeworm dataset made available by Randhawa and Poulin (2010). This original data set obtained tapeworm richness estimates for a large range of shark species by searching through Zoological Records on ISI Web of Knowledge and compiling available data from 1864 to 2008. To ensure that the data set would be accurate and up to date, the original data set was revised by changing tapeworm richness estimates to include all new shark-tapeworm records published in Zoological Records from 2008 to 2017. Notably, a number of shark species were included in the present data set for which tapeworm species records had become available since 2008. Using the same method as Randhawa and Poulin (2010), new tapeworm records for each host species were found by searching the shark taxa (Latin name plus all known synonyms) combined with keywords “Parasit* OR disease OR pathog*”.

Since measures of parasite diversity are often greatly influenced by sampling/study effort (Walther et al. 1995), correcting for sampling effort can give a more accurate measure of diversity (Poulin 2004; Luque and Poulin 2007). An ideal measure of parasite diversity sampling effort would be the sum of host individuals examined for parasites, but unfortunately, these data are seldom available from studies describing parasite records. As such, sampling effort for parasite diversity of each host species was measured as the total number of references obtained by searching the host’s tapeworm records on ISI Web of Knowledge (using the search parameters defined above). Compared with other estimates of sampling effort, this measure has been previously demonstrated as a stronger correlate with tapeworm richness (Randhawa and Poulin 2010).

To complement tapeworm species richness as a measure of parasite diversity, the average taxonomic distinctness (TD) of tapeworm assemblages was also calculated for each shark species. This index is used to measure the average taxonomic distance between the parasite species of an assemblage, with greater TD values indicating greater average taxonomic difference between species in the assemblage (Luque et al. 2004). TD is a different measure of diversity to richness in that is thought to be more sensitive to host ecology (Luque et al. 2004, Luque and Poulin 2008). It is measured as the average number of steps up the taxonomic hierarchy (Phylum, Class, Order, Family, Genus, and Species) in order to reach a taxonomic level common to two species, and is calculated for all pairs of species in the assemblage being examined (Warwick and Clarke 2001). Variance in TD was computed to accompany the measure of average TD for each shark species. Variance in TD can be used to provide information on the taxonomic heterogeneity among host species, basically showing how even the distribution of taxa across the taxonomic tree is (Warwick and Clarke 2001). Tapeworm TD was calculated (with the associated variance) for each host species harbouring at least 3 tapeworm species, using the programme 'Taxobiodiv 1.2' (available at <www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>).

2.2.2. Host features data collection

For all shark species with an available estimate of tapeworm richness, a number of important host features were recorded: (1) diet breadth, measured as the total number of prey families in a shark's diet; (2) diet TD, measured as the average taxonomic distance between all prey families in a shark's diet; (3) trophic level, measured as the number of energy-transfer steps to the shark's food chain position; (4) diet composition, given as the taxonomic prey category composing most of the diet (of nine groups: teleost fishes, cephalopods, crustaceans, mammals, chondrichthyan fishes, reptiles, birds, other molluscs, other invertebrates); (5) habitat, given as which zone of the ocean a shark species is most associated with inhabiting (of seven categories: reef-associated, demersal, pelagic-oceanic, pelagic-neritic, benthopelagic, bathypelagic, bathydemersal); (6) host total length (cm); (7) latitudinal range, measured by the number of degrees of latitude spanning the shark's geographic distribution; (8) depth range, measured as the distance in metres between shallowest and deepest points at which they occur; (9) depth mid-point, measured as the mid-

point of the shark's preferred depth distribution; and (10) phylogeny, represented by the Genus, Family and Order of the host. It is worth noting that many of these host characteristics (host length, latitudinal range, depth range, depth mid-point, and habitat) have been previously assessed as predictors of tapeworm diversity (Randhawa and Poulin 2010), and were also included in the present data set to determine their relative importance compared with the dietary features of primary interest here.

Data on most host features (phylogeny, trophic level, host length, latitudinal range, depth range, depth mid-point, and habitat) were obtained directly from recent species records listed on FishBase in March 2017 (Froese and Pauly 2017). In cases where data on one or more of these host features were not available for a species, the shark species was excluded from the data set. For all data on host diet, a comprehensive dataset was compiled from ISI Web of Knowledge. To do this, the taxa of each shark was searched (Latin name plus all known synonyms) combined with keywords “diet* OR feed* OR prey*” on ISI Web of Knowledge (all databases) and all available references from 1864 to 2017 were compiled (Searches were conducted April 2017). Every reference listed was searched for information on the diet of sharks, and out of 2,081 references listed across all species, 361 had relevant data on diet that could be included in this study (see references in Table A.1 in Appendix).

Unsurprisingly, the level of taxonomic definition for prey varied among studies; where some sharks had prey recorded mostly to Family or Order level, others had prey items known to the level of species. Considering this potential bias in records, it was decided that the best measure of diet breadth would be at the taxonomic level of Family. At this level there were records for most species that had tapeworm diversity estimates and there was also a large range of taxonomic groups (603 different families of prey) to give a good measure of variability in diet breadth among sharks. To ensure further accuracy in diet breadth comparisons, the final data set was also restricted to only include host species with at least one family of prey recorded ($n = 91$). Every family of prey identified for each shark species was recorded from each reference. Notably, some diet records were old, and taxonomic changes had been made to certain prey taxa since their publication. To address this, all prey taxa were checked in

the World Register of Marine Species (WoRMS) database and updated to their current taxonomical nomenclature (WoRMS Editorial Board 2017).

Similarly to measures of parasite diversity, measures of diet breadth may be substantially affected by sampling effort (Randall and Myers 2001). Diet breadth is likely to increase as more individual hosts are examined for diet contents. Correcting for this influence of sampling effort should therefore provide a better measure of host diet (Cortés 1999). In contrast to studies describing parasites from sharks, the standard protocol for dietary studies is to include the number of hosts examined. Thus, it was possible to measure diet sampling effort as the sum of stomachs containing food (i.e. the number of non-empty stomachs) examined across all diet records for each shark species. For a few references, the number of non-empty stomachs examined was not provided, and therefore had to be excluded from further analyses. All the references were checked thoroughly in the methods and results sections to make sure that diet information was not duplicated among studies. In cases where studies gave duplicate data, the data was cited from the original reference only, and the number of hosts examined was only included for the original reference to avoid overestimation of sampling efforts.

Taxonomic distinctness (TD) of diet was calculated to complement number of prey families as a measure of diet breadth. This was measured as the average number of steps up the taxonomic hierarchy in order to reach a taxonomic level common to two prey families, and was calculated for all prey family pairs in a shark's prey assemblage. Similarly to the TD calculations for tapeworm assemblages, TD of prey family assemblages and associated variance were computed for each shark species with at least 3 families of prey in their diet, using 'Taxobiodiv 1.2'. For information on diet composition, the percentage composition of nine different prey groups was recorded from each reference (teleost fishes, cephalopods, crustaceans, mammals, chondrichthyan fishes, reptiles, birds, other molluscs, other invertebrates). The overall composition of these groups for each shark species was then calculated by taking the average compositions across all studies, weighted by the number of non-empty stomachs examined for diet. Similar to the approach of Cortés (1999), compound indices were used to estimate composition where available (e.g. the index of relative importance %IRI), and otherwise, single indices, such as percent frequency of

occurrence (%O), percent number (%N) percent weight (%W), or percent volume (%V) were used individually. Where two of these single indices were available, an average was calculated (e.g. $\%O + \%W/2$). Plant materials, detritus and non-organic materials were not included in composition estimates as the present study was only interested in prey which are potential intermediate hosts for shark tapeworms.

2.2.3. Data analysis

All statistical tests were carried out in the R environment (R Development Core Team 2012). Prior to analysing relationships between measures of tapeworm diversity and recorded host features, regressions were run to determine the influence of sampling effort on measures of tapeworm diversity and diet breadth. As expected, for both tapeworm richness and diet breadth, the relationships between diversity and sampling effort were best characterized by positive curves where diversity increased with increasing sampling effort, slowing towards an asymptote at higher effort values. To determine the significance of the associations, simple quadratic regressions were run for each diversity measure on their associated measures of sampling effort. Host-parasite sampling effort was found to have a significant influence on tapeworm species richness ($r^2 = 0.539$, $p < 0.001$), but not on tapeworm TD ($r^2 = 0.007$, $p = 0.825$). To correct for this influence in further analyses, tapeworm richness was from here on measured by residuals for its quadratic regression on host-parasite sampling effort (a plot of this regression can be seen in Appendix Figure A.1.). Diet breadth was also influenced by sampling effort. The number of stomachs sampled for diet showed a strongly positive association with number of recorded prey families ($r^2 = 0.601$, $p < 0.001$), although not with prey family TD ($r^2 = 0.047$, $p = 0.272$). Thus, there was a need to correct diet breadth, but not diet TD, in further analyses. From this point forwards, diet breadth (prey family richness) was measured by residuals for its quadratic regression on diet sampling effort (see regression plot for diet breadth and associated study effort in Appendix Figure A.2.).

Linear mixed-effects models (LMMs) were used to analyse relationships between measures of tapeworm diversity and all recorded host features, each with identity link functions and Gaussian error distribution. The first main LMM looked at the influence of host features on tapeworm richness (response variable). This model included seven

continuous (fixed) predictor variables (diet breadth, diet TD, trophic level, host length, depth mid-point, depth range, and latitudinal range) and three categorical (random) predictor variables (habitat type, dominant diet group, and host phylogeny [which was measured as host genus nested within host family, nested within host order]). The second main LMM looked at tapeworm TD as a response with the same predictors as the above model. To supplement the analysis of tapeworm TD, a model was also run where tapeworm TD and prey TD variables were replaced with associated variances in TD. This was done to gauge the taxonomic ‘evenness’ among host species. In addition to these LMMs, a “tips” analysis was performed, which involved re-running each model with the random effects removed. This analysis serves as an approach to examining differences to the importance of predictor variables when the phylogenetic relationships among hosts are not considered (See Figure 2.1 for species phylogeny).

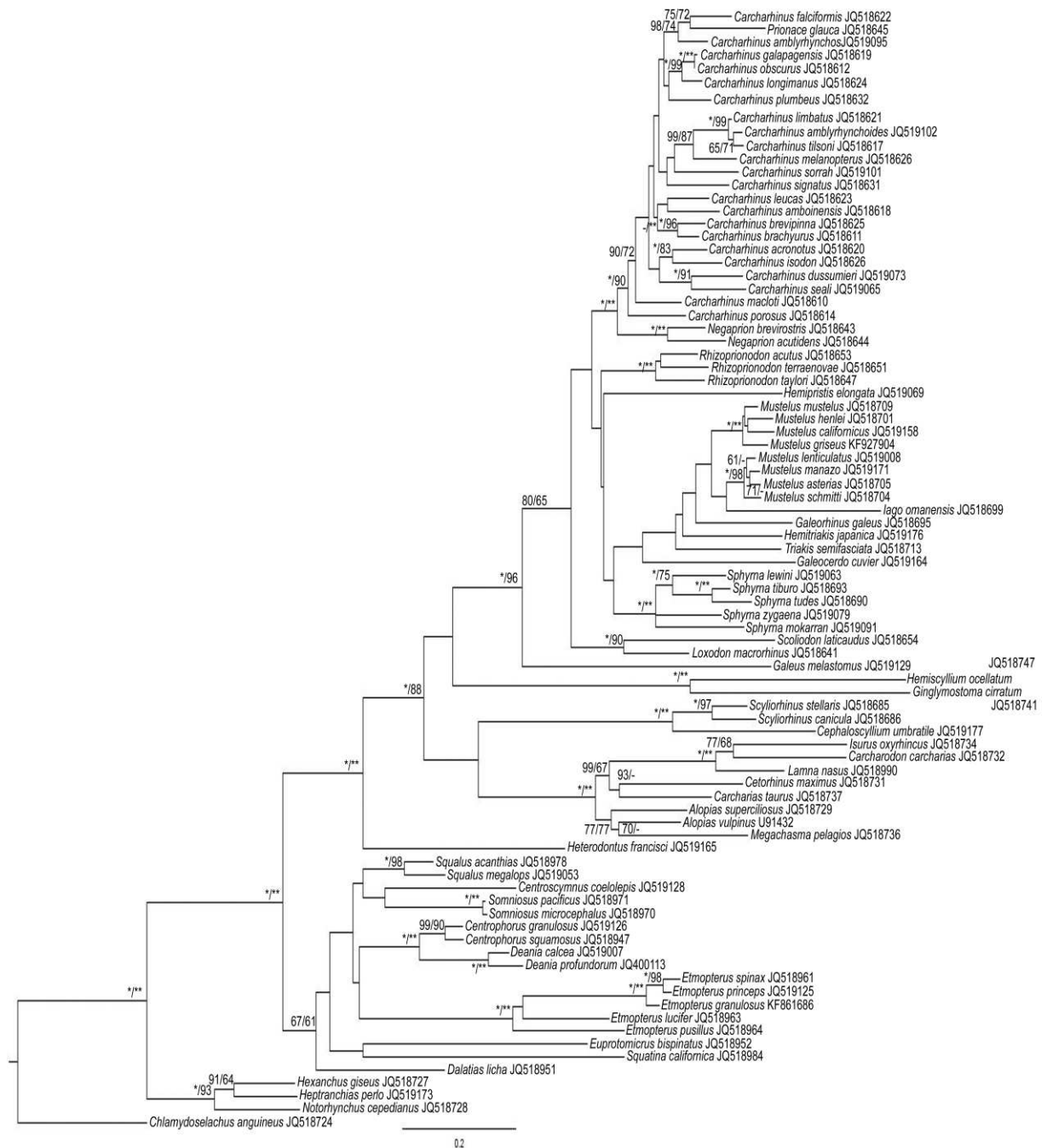


Figure 2.1: Phylogenetic tree displaying relationships among hosts included in this study (taken from Rasmussen and Randhawa 2017, submitted). The shark phylogeny was generated using Bayesian Inference from which contrasts were derived for phylogenetic independent contrast analyses (Rasmussen & Randhawa 2017, submitted). Numbers next to species names correspond to GenBank accession numbers for individual NADH2 sequences. Nodal support is expressed as posterior probabilities/bootstrapped support; *, 100% posterior probability; **100% bootstrap support.

LMMs were each analysed in detail using the “MuMIn” package in R (Barton 2013). Corrected Akaike’s information criterion (AICc) and Akaike model-averaged weights (w_{+i}) were calculated for all possible linear regression models (models with all possible combinations of the predictors), and used to determine the best models as well as the rank and relative importance of each individual predictor in each model. Model averaged parameter estimates and 95% confidence intervals were also calculated for each variable using methods summarised in Anderson (2008). To determine the interaction terms to be included in each model, a priori sets of second order interactions were selected for combinations of predictor variables that were thought to be relevant based on biological and ecological principles. For instance, there is a known association between host size and trophic level that should be accounted for (Poulin and Leung 2011). AICc values were compared between models including these sets and the models with only combinations of individual predictors to determine whether the inclusion of the interaction terms significantly improved models. All other potential interactions between predictors were assessed in the same way to make sure that no important interactions were missed. From these analyses it was decided that four interaction terms were to be included in the model predicting tapeworm richness (habitat & depth mid-point, diet breadth & diet TD, diet breadth & trophic level, trophic level & host size) and three were to be included in the model predicting tapeworm TD (diet breadth & diet TD, host size & trophic level, latitudinal range & depth range).

2.3. Results

Across the 91 different shark species analysed in the present data set, there was a total of 570 tapeworm-host associations. Based on the raw data, shark species harboured 6.26 tapeworm species on average (± 6.00 SD, range = 1 to 24) (Figure 2.2), and the average TD (taxonomic distinctness) and variance in TD of tapeworm assemblages was 3.39 (± 0.39 SD, range = 1.90 to 4.17) and 0.74 (± 0.51 SD, range = 0.00 to 2.53) hierarchical steps, respectively. Host species were commonly infected by a single tapeworm species and there was a positive skew in the number of tapeworm species infecting sharks (frequency of shark species decreased with increasing tapeworm richness) (Figure 2.2). In total, the host-parasite study effort across the 91 shark

species included 2068 records, which equated to 22.73 mean records per host (± 35.67 SD).

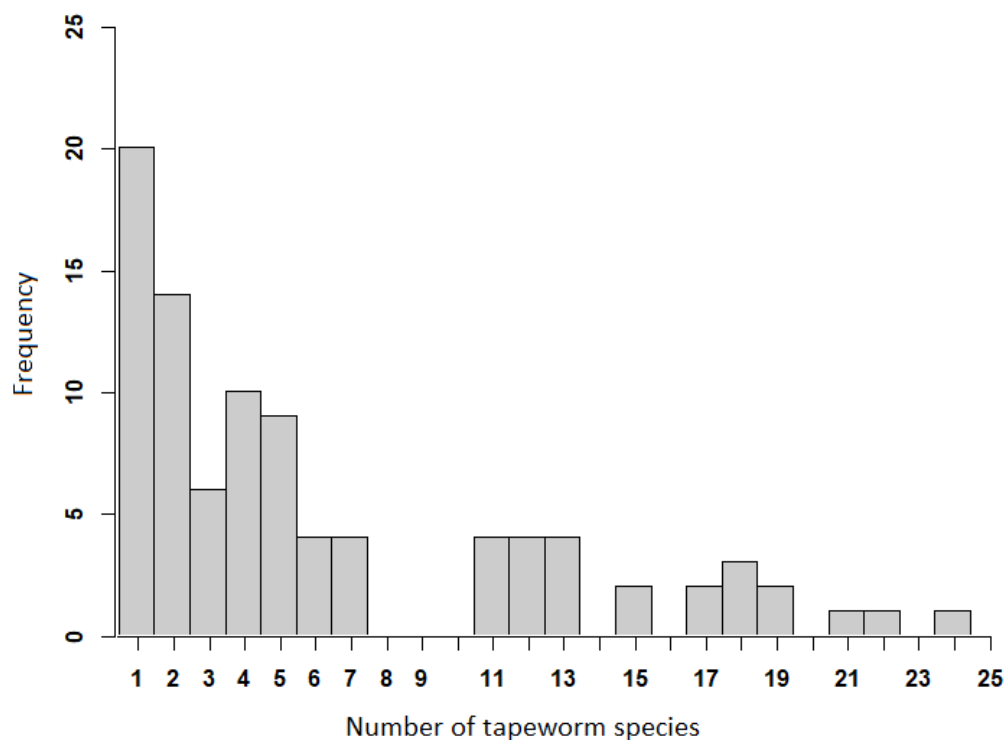


Figure 2.2. Frequency distribution of the number of shark species infected with different numbers of tapeworm species (n=91).

A total of 603 families of prey (within 163 orders; 39 classes; 16 phyla) were recorded in the data set. Shark species had records, on average, of 39.49 families of prey (± 34.16 SD, range = 1 to 145) (Figure 2.3), and the average TD and variance in TD of prey family assemblages was 2.81 (± 0.56 SD, range = 0 to 4.00) and 1.12 (± 0.42 SD, range = 0 to 2.05) hierarchical steps, respectively. As illustrated by Figure 2.3, diet breadth (prey family richness) was distributed with a positive skew across the shark species examined. In total, the number of stomachs examined across all shark species was more than 170,000, with 110,005 stomachs containing food. Notably, the number of stomachs with food examined was highly variable among species (mean = 1208.85 ± 4502.72 SD), and the spiny dogfish *Squalus acanthias* on its own had data from 40,698 stomachs containing food. The average trophic level of sharks in this dataset was 4.14 (± 0.34 SD, range = 3.20 to 4.94).

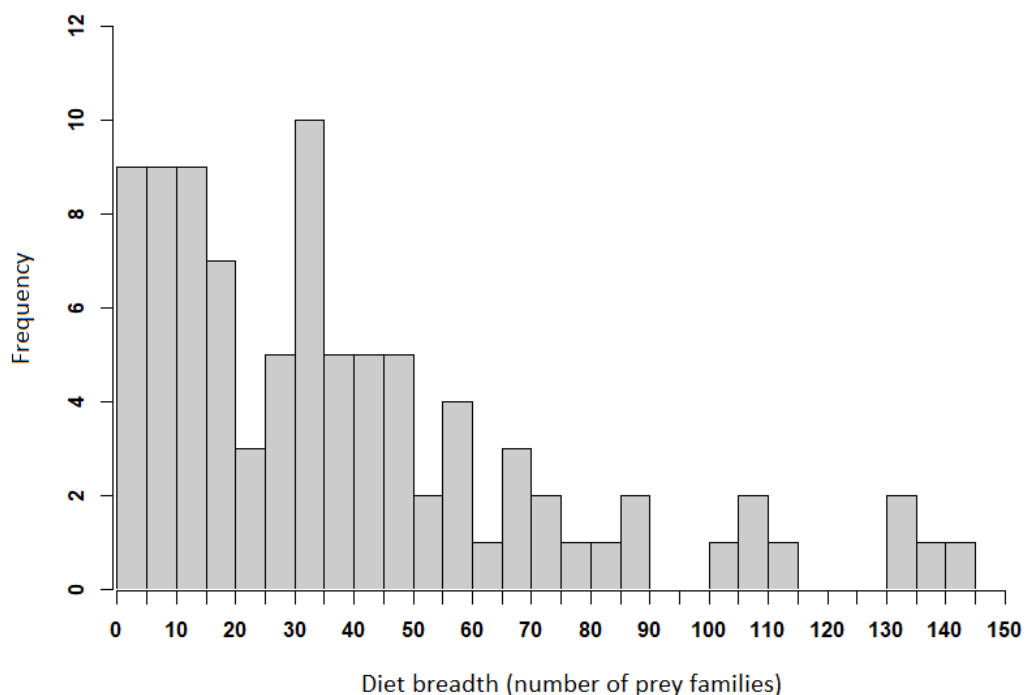


Figure 2.3. Frequency distribution of the number of shark species consuming various quantities of prey families (n=91).

2.3.1. Determinants of tapeworm richness

In the LMM analysis looking at tapeworm richness, it was found that random effects explained a total of 19.1% of observed variation in tapeworm richness, with the interaction of habitat and depth mid-point explaining 13.26%, host phylogeny explaining 5.84%, but habitat and diet composition each did not explain any variation (Table 2.1). The top AIC model explaining variation in shark tapeworm richness (AICc = 508.59) included a combination of only three fixed predictors, diet breadth, diet TD and trophic level. The top five best AICc models were very close ($\Delta\text{AICc} < 1$), and included various combinations of diet breadth, diet TD, trophic level and the interaction effect of diet breadth and diet TD. The model-averaged Akaike weights analysis also showed that these diet related variables were the best predictors of tapeworm richness. The factor with the highest relative variable weight was diet breadth ($w_{+}(i) = 0.99$), followed by diet TD ($w_{+}(i) = 0.71$), trophic level ($w_{+}(i) = 0.59$), and the interaction between diet breadth and diet TD ($w_{+}(i) = 0.37$) (Table 2.1). It was interesting to note that although the association between diet breadth and tapeworm richness was positive (tapeworm increased with increasing diet breadth), the association between diet TD and tapeworm richness was negative (diet TD

decreased with increasing tapeworm richness) (Table 2.1). Most other variables, including latitudinal range, depth mid-point, depth range and host size, were generally poor predictors of tapeworm richness in comparison (all $w+(i) \leq 0.01$).

Table 2.1. Summary of host features as predictors for tapeworm species richness in sharks. The relative importance of predictors is compared by model-averaged weights ($w+(i)s$), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Random effects				
Variable		Number of levels	Variance explained (%)	
Host Phylogeny (Genus/Family/Order)		(n=40)	5.84%	
Habitat		(n=7)	0.00%	
Diet composition		(n=6)	0.00%	
Habitat*Depth Mid-Point		(n=81)	13.26%	
Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Diet Breadth	0.99	1	0.288	(-0.332, 0.909)
Diet TD	0.71	2	-2.047	(-4.705, 0.611)
Trophic Level	0.59	3	0.806	(-1.758, 3.369)
Diet Breadth*Diet TD	0.37	4	-0.124	(-0.213, -0.037)
Diet Breadth*Trophic Level	0.14	5	-0.115	(-0.211, -0.019)
Latitudinal Range	0.01	6	0.005	(-0.020, 0.031)
Depth Range	<0.01	7	-0.001	(-0.002, -0.000)
Host Size	<0.01	8	-0.003	(-0.007, 0.002)
Depth Mid-Point	<0.01	9	-0.001	(-0.004, 0.001)
Host Size*Trophic Level	<0.01	10	0.000	(-0.000, 0.000)

Three predictors had significant effects on tapeworm richness, the interaction between diet breadth and diet TD, the interaction between diet breadth and trophic level, and depth range (their 95% confidence intervals were all bounded away from “0”) (Table 2.1). However, it should be noted that the effect size for depth range was small and it

was only marginally significant (95% CI = (-0.002, -0.000), $p = 0.044$) (Table 2.1). The relationship between diet breadth and tapeworm richness was further analysed to determine the strength of the association. From a plotted linear regression (see Figure 2.4) it can be seen that there is a significant positive correlation between the variables with a moderate amount of variability surrounding the linear trend line ($r^2 = 0.220$, $p < 0.001$). When the analysis was repeated with phylogeny and the other random effects removed, diet breadth, diet TD, the interaction between diet breadth and diet TD, and the interaction between diet breadth and trophic level all became highly significant predictors of tapeworm richness ($p < 0.001$, Table 2.2). In contrast, depth range became non-significant ($p = 0.276$, Table 2.2).

Table 2.2. Summary of “tips” analysis assessing predictors of tapeworm richness (random effects of main models are excluded in this analysis). The relative importance of predictors is compared by model-averaged weights ($w+(i)s$), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Tapeworm Richness Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Diet Breadth	1.00	1	0.926	(0.279, 1.574)
Diet TD	0.98	2	-3.046	(-5.118, -1.115)
Diet Breadth*Diet TD	0.94	3	-0.124	(-0.219, -0.043)
Trophic Level	0.89	4	0.283	(-2.074, 2.714)
Diet Breadth*Trophic Level	0.84	5	-0.109	(-0.221, -0.039)
Depth Range	0.71	6	-0.001	(-0.002, 0.000)
Depth Mid-Point	0.30	7	0.000	(-0.003, 0.004)
Host Size	0.29	8	0.000	(-0.017, 0.017)
Latitudinal Range	0.28	9	0.002	(-0.017, 0.034)
Host Size*Trophic Level	0.06	10	0.000	(-0.010, 0.008)

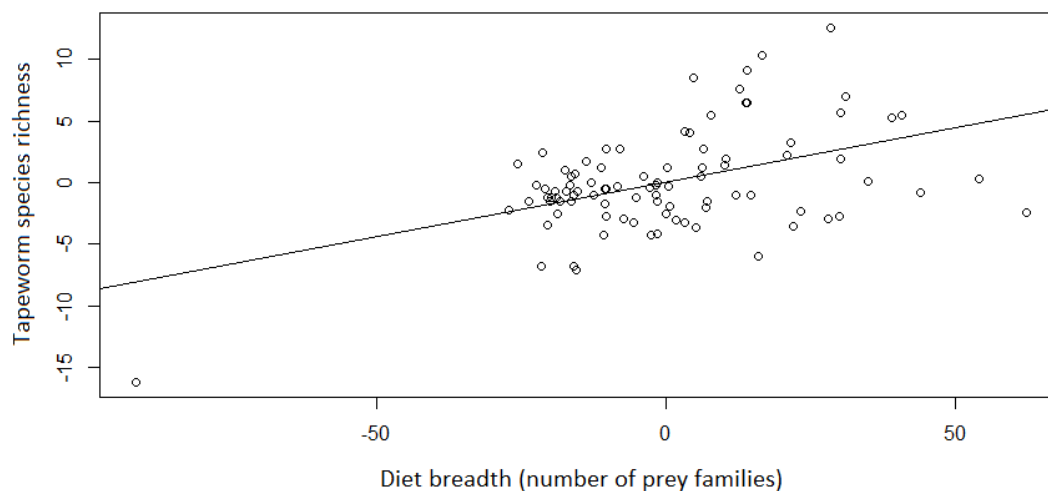


Figure 2.4. Scatter plot showing the association between tapeworm richness (measured as the residuals for the quadratic regression of number of tapeworm species on parasite sampling effort) and shark diet breadth (measured as the residuals for the quadratic regression of number of prey families on prey sampling effort). Solid line shows linear regression between the variables ($r^2 = 0.220$, $p < 0.001$).

2.3.2. Determinants of tapeworm TD

In the LMM analysis looking at predictors of tapeworm taxonomic distinctness (TD), it was found that random effects overall accounted for 26.91% of the variation in tapeworm TD, and host phylogeny explained a much larger proportion of variation in tapeworm TD (20.15%) compared to tapeworm richness (Table 2.3). The top AIC model explaining variation in tapeworm TD ($AICc = 71.75$) was the null model (model including none of the fixed predictors in the data set). Notably, the null model was considerably better than all other AIC models (all others $\Delta AICc > 2$). Diet TD and trophic level were the best predictors of tapeworm TD included in the model, with the highest relative variable weights across all models (diet TD ($w_{+i} = 0.23$) and trophic level ($w_{+i} = 0.10$)). However, these model weights were still low, and ultimately, all variables included in the analysis were poor predictors of tapeworm TD. In addition, no variables demonstrated statistical significance for tapeworm TD (Table 2.3).

Table 2.3. Summary of various host features as predictors for tapeworm species taxonomic distinctness (TD) in sharks. Relative importance of these predictors is compared by model-averaged weights ($w+(i)$ s), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Random effects				
Variable		Number of levels	Variance explained (%)	
Host Phylogeny (Genus/Family/Order)		(n=29)	20.15%	
Habitat		(n=6)	2.25%	
Diet composition		(n=5)	4.51%	
Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Diet TD	0.23	1	-0.210	(-0.447, 0.027)
Trophic Level	0.10	2	0.012	(-0.331, 0.356)
Diet Breadth	<0.01	3	0.001	(-0.004, 0.005)
Latitudinal Range	<0.01	4	-0.001	(-0.004, 0.002)
Host Size	<0.01	5	0.000	(-0.001, -0.001)
Depth Mid-Point	<0.01	6	0.000	(-0.000, 0.001)
Depth Range	<0.01	7	-0.000	(-0.000, 0.000)
Diet Breadth*Diet TD	0.00	8	0.000	(-0.000, 0.000)
Host Size*Trophic Level	0.00	8	0.000	(-0.000, 0.000)
Latitudinal range*Depth Range	0.00	8	0.000	(-0.000, 0.000)

When the analysis was repeated with phylogeny and the other random effects removed, Latitudinal range ($w+(i) = 0.45$) and depth range ($w+(i) = 0.41$) became the best predictors of tapeworm TD (Table 2.4). However, all variables remained poor predictors of tapeworm TD overall, and none of the host features included demonstrated significance in this analysis (Table 2.4).

Table 2.4. Summary of “tips” analysis assessing predictors of the average TD of shark tapeworm assemblages (random effects of main models are excluded in this analysis). The relative importance of predictors is compared by model-averaged weights ($w+(i)s$), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Tapeworm TD Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Latitudinal Range	0.45	1	-0.003	(-0.009, 0.002)
Depth Range	0.41	2	-0.000	(-0.001, 0.000)
Depth Mid-Point	0.36	3	0.000	(-0.000, 0.001)
Trophic Level	0.33	4	-0.151	(-0.548, 0.246)
Diet TD	0.32	5	-0.097	(-0.355, 0.162)
Host Size	0.27	6	-0.000	(-0.003, 0.002)
Diet Breadth	0.26	7	-0.001	(-0.021, 0.018)
Latitudinal range*Depth Range	0.15	8	0.000	(-0.000, 0.000)
Host Size*Trophic Level	0.03	9	0.001	(-0.001, 0.002)
Diet Breadth*Diet TD	0.03	10	0.006	(-0.008, 0.020)

The model looking at determinants of variance in tapeworm TD was similar to the LMM for TD, with the null model being favoured. A large portion of variation (58.64%) in variance of TD was explained by host phylogeny (no other random effects explained variance), but all fixed variables were non-significant and poor predictors of variance in TD (Table 2.5). When the analysis was repeated with random effects removed, all factors remained poor predictors of variance in tapeworm TD (Table 2.6).

Table 2.5. Summary of host features as predictors for variance in the taxonomic distinctness (TD) of tapeworm assemblages in sharks. The relative importance of predictors is compared by model-averaged weights ($w+(i)s$), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Random effects				
Variable		Number of levels	Variance explained (%)	
Host Phylogeny (Genus/Family/Order)		(n=29)	58.64%	
Habitat		(n=6)	0.00%	
Diet composition		(n=5)	0.00%	
Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Trophic Level	0.22	1	-0.270	(-0.661, 0.121)
Variance in Diet TD	0.10	2	0.046	(-0.292, 0.385)
Diet TD	0.09	3	-0.061	(-0.365, 0.243)
Latitudinal Range	<0.01	4	-0.003	(-0.008, 0.002)
Diet Breadth	<0.01	5	0.002	(-0.004, 0.008)
Host Size	<0.01	6	-0.000	(-0.001, 0.000)
Depth Mid-Point	<0.01	7	-0.000	(-0.001, 0.000)
Depth Range	<0.01	8	-0.000	(-0.000, 0.000)
Diet Breadth*Diet TD	0.00	9	0.000	(-0.000, 0.000)
Host Size*Trophic Level	0.00	9	0.000	(-0.000, 0.000)
Latitudinal range*Depth Range	0.00	9	0.000	(-0.000, 0.000)

Table 2.6. Summary of “tips” analysis assessing predictors of variance in TD of shark tapeworm assemblages (random effects of main models are excluded in this analysis). The relative importance of predictors is compared by model-averaged weights ($w+(i)s$), ranks, parameter estimates, and 95% confidence intervals (CIs). 95% CIs in bold indicate statistical significance.

Variance in TD Fixed effects				
variable	$w+(i)$	Rank	Parameter estimate	95% CI
Depth Range	0.39	1	0.000	(-0.000, 0.001)
Trophic Level	0.33	2	-0.172	(-0.618, 0.274)
Latitudinal Range	0.27	3	-0.000	(-0.006, 0.006)
Diet Breadth	0.27	4	0.004	(-0.022, 0.031)
Diet TD	0.26	5	0.029	(-0.312, 0.371)
Depth Mid-Point	0.25	6	0.000	(-0.001, 0.001)
Host Size	0.25	7	0.000	(-0.002, 0.002)
Variance in Diet TD	0.24	8	-0.066	(-0.312, 0.371)
Latitudinal range*Depth Range	0.04	9	0.000	(-0.000, 0.000)
Diet Breadth*Diet TD	0.03	10	-0.010	(-0.028, 0.009)
Host Size*Trophic Level	0.02	11	-0.000	(-0.002, 0.001)

2.4. Discussion

The main objective of this study was to determine what host features influence the diversity of tapeworm assemblages in sharks, with focus on the influence of certain aspects of host diet, such as diet breadth, composition, and trophic level. In accordance with this, it was found that the breadth of a shark’s diet, measured by its diversity of prey families, was a better predictor of tapeworm richness than any other host feature examined to date (Table 2.1). This outcome was robust with both parasite richness and diet breadth corrected to prevent confounding by their associated sampling efforts. Moreover, diet breadth showed a highly significant positive association with tapeworm richness after adjusting data to account for phylogenetic relationships between shark species (Table 2.2). Thus, the findings here support the hypothesis that shark species with broader diets encounter and subsequently acquire more tapeworm species than those with restricted diets. So far only a few empirical

studies in other host-parasite systems have shown diet breadth to be important for the diversity of trophically-transmitted parasites (e.g. Chen et al. 2008; Locke et al. 2014). However, it is also worth noting that other studies looking at determinants of parasite diversity have rarely included diet breadth, and in fact, too few comparative studies have involved diet for meta-analysis to sufficiently assess its strength as a predictor of parasite richness (Kamiya et al. 2014). In such cases, there is an eminent need for more research into the diet of hosts. Where diet records are available, on the other hand, it is suggested that future studies involving trophically-transmitted parasites should consider finding ways to analyse diet breadth as a potential predictor of parasite richness among host species.

Using the average taxonomic distinctness (TD) of species assemblages to complement simpler measures of species diversity (i.e. species richness) has been a common practice in ecological studies for the past couple of decades (Von Euler & Svensson 2001; Heino et al. 2005; Winter et al. 2013). But despite its potential application as a measure for diversity in species diets, to my knowledge TD has only been implemented as a measure of diet breadth in one recent diet study involving the diet of turtles (Stringell et al. 2016). In the present study it was found that diet TD (the taxonomic distinctness among prey families in the diet) was the second most important predictor of tapeworm species richness in sharks following diet breadth (prey family richness). Interestingly, diet TD displayed a negative estimate in the LMM of tapeworm richness, entailing a net decrease in tapeworm richness with increasing diet TD. In addition, there was a significant negative interaction between diet breadth and diet TD. These results are somewhat peculiar given that prior to the analyses I predicted that tapeworm richness would increase with both the general diet breadth and diet TD of sharks. One possible reason for this discrepancy could be that most of these shark tapeworms have a high host specificity (Palm & Cairns 2008), and from an evolutionary perspective, these tapeworms are likely to exploit a narrower (more closely related) range of intermediate hosts than other more generalist parasites. Thus, if transmission of tapeworms is generally limited to more closely related intermediate hosts (low diet TD), perhaps parasite speciation has also been favoured more in closely related hosts, leading to infection with multiple congeners in these hosts (i.e. high tapeworm richness within low diet TD). This could mean that certain

taxonomic groups are generally devoid of tapeworm larval stages and may inflate prey TD to be higher in certain sharks that eat them, despite not being relevant for tapeworm transmission. Nevertheless, without knowing the relative importance of these taxonomic groups as intermediate hosts for tapeworms, reasons for the discrepancy found between diet breadth and diet TD here can only be speculated. Importantly, for many elasmobranch tapeworm species, intermediate hosts are completely unknown (Palm 2004; Jensen & Bullard 2010; Caira & Jensen 2014), and further research on the life cycles of these tapeworms could be key towards better understanding the relative importance of these diet aspects for tapeworm richness in sharks.

Large-scale food web analyses have previously highlighted trophic level as an important aspect of host diet that can drive patterns of parasite richness (Lafferty et al. 2006; Chen et al. 2008). Trophic level was found to be the third best predictor of shark tapeworm richness in this study (Table 2.1), but unlike measures of diet breadth, trophic level did not have a significant effect when data were adjusted to account for phylogenetic relationships between hosts (Table 2.2). It is worth noting, however, that trophic level and diet breadth had a significant interaction in the model, indicating that although these variables measure different diet aspects (trophic level reflects the position of a shark's prey in the food web, where general diet breadth does not), they are related on some level, and may both gauge how broad a shark's diet is. When considering this, one could posit that tapeworm richness in sharks is determined more by the breadth of different prey in a host species' diet than by the position of these prey in food webs. A study of other marine fishes has also observed trophic level to have less impact on parasite richness compared with breadth of diet (Locke et al. 2014). Even so, there is a question of why trophic level has shown to be a key driver of parasite richness in network studies, while appearing to be of less importance here. Locke et al. (2014) have offered a few plausible explanations: (1) trophic level is less relevant in the context of a fish community because it varies much less than in larger networks of species, and (2) links found between parasite richness and trophic level in other studies may reflect their association with diet breadth, meaning that diet breadth may actually be the underlying predictor of significance for parasite richness. It is also worth considering that trophic level may not appear as important in vertebrates where species at higher trophic levels have their parasite faunas restricted by more complex

and effective immune responses (Benesh et al. 2014). There may be some truth to each of these explanations. In any case, further research will be necessary to fully understand the relative influences of diet breadth and trophic level on parasite richness, and considering the results here, it is recommended that such studies look simultaneously at both factors as predictors of parasite richness (and account for their interaction).

All variables other than host diet breadth, trophic level, and diet TD were comparatively poor predictors of tapeworm species richness in this study. However, it is worth pointing out that when the effect of phylogeny was removed from the analyses, many factors became more important (Table 2.2). The depth range of a shark species was a poor predictor of tapeworm richness (despite being marginally significant), but became considerably more important when data were adjusted to remove host phylogeny. Little is known about how depth factors regulate parasite diversity in the marine environment, but it has been suggested that depth-driven temperature gradients could influence tapeworm richness in elasmobranchs (Randhawa & Poulin 2010). Prior to this study, I also thought that differences in depth might reflect differences in habitat or diet among hosts. Yet, the results here showed conversely that although there was an interaction between habitat and the mid-point of shark depth ranges, habitat itself did not explain any variation in tapeworm richness. Likewise, diet composition, which was represented by the shark's preferred taxonomic group of prey, did not account for any variation in tapeworm richness (Table 2.1). As such, despite measures of diet breadth demonstrating large influences on tapeworm species richness in sharks, the importance of the sharks' preferred prey and habitats appeared to be negligible (Table 2.1).

Prior to this study, it was predicted that shark species feeding predominantly on teleost fishes would have more tapeworm species than sharks feeding mainly on other prey groups because most currently described intermediate hosts for tapeworms are teleost fishes (Palm 2004; Jensen 2009). With the present results running counter to this proposal, there is a question of why the dominant prey group of sharks does not appear to be a major determinant of tapeworm richness. One thing worth noting is that crustaceans and cephalopods (the two most commonly dominant prey groups of sharks other than teleosts) have been described as intermediate hosts for many

tapeworms, but are generally less studied for parasites than teleost fishes, meaning that they likely harbour larval stages of substantially more species of tapeworms than have been currently described (Jensen 2009). Another possibility is that the lack of importance for diet composition reflects the limitations of simplifying composition into such large taxonomic groups. Perhaps more specific diet composition involving comparisons at the species or genus level could more accurately reflect differences in tapeworm richness. Analysing diet composition at this level would prove extremely challenging, however, since a large portion of studies on shark diets do not provide composition for individual species, genera, families, or even orders, and instead only estimate the full composition of major taxonomic groups. The importance of habitat for tapeworm richness may similarly be limited by the simplification of shark's ecologies. Although habitat categories such as "Demersal" and "Benthopelagic" summarise the areas where these sharks are distributed, there can be substantial differences in the foraging behaviours, dietary preferences and distributions of sharks living in these same habitats.

The lack of importance of host size for parasite richness in this study was surprising given that host size is a key predictor of parasite richness for a vast range of taxa (Kamiya et al. 2014). Larger host species generally provide more space and a greater diversity of niches for parasites to exploit (Kuris et al. 1980; Poulin & Morand 2004). Interestingly, however, Randhawa and Poulin (2010) have found host size to be a non-significant predictor of tapeworm richness in sharks, but found that it became a highly significant predictor when using Phylogenetic Independent Contrasts analyses to control confounding of host's phylogenetic relationships (Randhawa & Poulin 2010). Here a different method was used to examine the importance of variables without the influence of phylogeny (a "tips" analysis to remove phylogeny from the LMM), but host size was still non-significant for tapeworm richness (Table 2.2). This inconsistency highlights the difference between these methods to adjust for phylogenetic relationships. Phylogeny in the analysis here was measured by host genus nested within family, nested within order, and this assumes that species in these groups are equally related. On the other hand, the PIC method uses a phylogenetic tree which accounts for the genetic differences within each of these taxonomic groups (see Figure 2.1). Based on this, perhaps one could say that host size is probably a key predictor of tapeworm richness after accounting for phylogeny, because the

Phylogenetic Independent Contrasts result corrects for the effects of phylogeny using more precise data. However, it must be also be noted that Phylogenetic independent contrasts analyses are more sensitive to phylogeny due to the assumptions of accurate branch lengths and correct topology (Felsenstein 1985, Ackerly 2000), so any taxon bias or phylogenetic uncertainty, e.g. polytomies, might lead to questionable results that should be interpreted with caution (Ackerly & Reich 1999). In any case, increased sampling of shark diets and parasite assemblages across all shark orders should provide further insight into the importance of phylogeny and host size for tapeworm richness.

Like host size, geographical range is generally known to be a key predictor of parasite richness for a broad range of taxa (Kamiya et al. 2014), but latitudinal range was found to be of little importance for tapeworm richness in sharks here. It was thought that shark species spanning greater ranges of latitude would likely encounter more prey taxa, and consequently encounter a greater diversity of parasite species than sharks with covering limited ranges in latitude. Yet, given that diet breadth, but not latitudinal range, had a significant influence on tapeworm richness, perhaps latitudinal range is not a good predictor since latitude indicates only one dimension of a shark's distribution, whereas the diversity of prey taxa encountered by a shark would also vary with their longitudinal and depth distributions, in addition to their temporal patterns in foraging. Some other measures may be much better proxies for total geographical range of shark species (e.g. total area distribution). However, information on these other aspects of geographical range are unknown for many sharks, and would need to become available for further analysis.

The LMM looking at predictors of the average taxonomic distinctness (TD) of tapeworm assemblages found that no factors included in this study were good predictors of tapeworm TD (Table 2.3). This was somewhat surprising given that a few of the same variables (especially diet breadth) were considerably more important predictors of tapeworm species richness (Table 2.1), but as previous research has illustrated, parasite richness and average TD of parasite assemblages are sensitive to different host features (Luque et al. 2004; Heino et al. 2005; Luque & Poulin 2008; Randhawa & Poulin 2010). It is possible that diet breadth has much less influence on tapeworm TD than tapeworm richness because the distinctness of tapeworm

assemblages is driven more by other factors that were not accounted for in this study. For instance, tapeworm TD may be driven more by the compatibility of tapeworms with shark hosts. From an evolutionary perspective, hosts are more likely to be compatible with closely related tapeworm species, and as such, a shark could have a broad diet and encounter many tapeworm species, but only tapeworms within a limited range of taxa may actually be able to exploit the shark i.e. they could have species rich parasite assemblages with overall low TD consisting of many congener species. Notably, immune response has already been demonstrated to prevent infection by certain cestode species in elasmobranchs (McVicar & Fletcher 1970; Randhawa & Burt 2008). However, the importance of host compatibility in determining the taxonomic diversity of tapeworms in sharks warrants further investigation. In line with the results for average tapeworm TD, there were no good predictors observed for variance in tapeworm TD. This indicates that the taxonomic evenness of tapeworm assemblages in sharks is unlikely to be influenced by the factors examined. However, the present dataset including variance in tapeworm TD was considerably more restricted (n= 57 species) and this variable may be worth revisiting in future when more shark tapeworm records are described.

2.4.1. Conclusions

A total of 91 different shark species were examined in this study, which is less than a fifth of all described shark species known to date (Randhawa et al. 2015). However, a more complete analysis of diet's influence on tapeworm richness would require host diet and tapeworm records to become available for many more shark species which are currently data deficient. The present study is the first to examine the influence of host diet and trophic level on parasite diversity in elasmobranchs, and to my knowledge, is the most comprehensive analysis of parasite diversity in sharks thus far. This gives credence to the key finding that the diet of a shark species, and particularly the breadth of its diet, has important consequences for the diversity of its trophically transmitted parasites. The intricacies of this link between host diet breadth and tapeworm diversity in sharks warrant deeper exploration. Despite having records of prey for the shark species examined here, the parasites of these prey items are generally unknown, and it remains uncertain whether these prey are actually intermediate hosts contributing to shark tapeworm richness. Indeed, several studies

have pointed out that there are major gaps in our knowledge of the life cycles of elasmobranch tapeworms (Palm 2004; Jensen & Bullard 2010; Randhawa & Brickle 2011; Caira & Jensen 2014). These life cycles will need to be elucidated for a more in-depth understanding of diet breadth's influence on tapeworm diversity.

Chapter 3: Linking the diet composition of sharks to their tapeworm compositions and use of prey as intermediate hosts

3.1. Introduction

In the past few decades parasites have gained increased appreciation as a vital component of food webs (Marcogliese and Cone 1997; Lafferty et al. 2008; Dunne et al. 2013). The collective biomass of parasites distributed throughout a food web has been shown to exceed that of top predators in certain ecosystems (Kuris et al. 2008) and contribute substantially to energy flow through species networks (Johnson et al. 2010; Goedknecht et al. 2012; Thielts et al. 2013). Moreover, parasites can largely influence the structure of free-living communities and impact the strength of trophic links among species (Marcogliese 2003; Thompson et al. 2005; Lefèvre et al. 2009; Poulin 2010). For instance, larval trematode parasites have been shown to induce behavioral changes in their intermediate hosts that increase their susceptibility to bird definitive hosts, consequently strengthening the link between these different animals (Lafferty & Morris 1996). This is one of many examples of this type of influence (Aeby 1991; Thomas and Poulin 1998; Thomas et al. 2010; Bakker et al. 2017). On the flip side of these interactions, the structure of food webs may shape the ecology of these parasites, and their ability to strengthen trophic links may have ultimately arisen from selection pressures on parasites to reach their definitive hosts (Lafferty 1999; Lefèvre et al. 2009). Food web structure especially may have implications for the ecology of parasites with highly complex life cycles that depend on several different interactions among free-living species to reach their definitive hosts.

Certain prey in food webs provide better routes than others for trophically-transmitted parasites to the definitive hosts (Thompson et al. 2013). For trophically-transmitted parasites, infecting intermediate hosts that are closely linked with their desired definitive hosts should increase the probability of completing their life cycle.

Therefore, we might expect larval stages of trophically-transmitted parasites to occur more frequently in intermediate hosts that are abundant, high in biomass, or constitute a large proportion of their definitive host's diet (Cirtwill et al. 2017). However, parasites also face phylogenetic constraints that limit which prey are suitable intermediate hosts (Euzet and Combes 1980; Combes 2001). Acanthocephalan parasites, for instance, are restricted to using arthropod intermediate hosts to reach their vertebrate definitive hosts (Near 2002). In some cases, host evolutionary history may be even more important in determining the range of intermediate hosts used by

parasites than the strength of their trophic links to the definitive host (Cirtwill et al. 2017). Nevertheless, the importance of ecology and host evolutionary history for intermediate host-use may vary considerably among different parasites and hosts, and is yet to be investigated in many ecosystems.

Tapeworms infecting elasmobranchs (sharks, skates and rays) represent an incredibly diverse and speciose group of marine parasites (Caira and Healy 2004; Caira and Jensen 2014). These parasites all have complex life-cycles and use a range of different invertebrate and vertebrate prey as intermediate (or paratenic/non-obligate) hosts, including, but not limited to, a variety of teleost and elasmobranch fishes, crustaceans, and molluscs (Palm 2004; Caira and Jensen 2017). In general, these tapeworms are highly host specific as adults, living in the spiral intestines of their definitive elasmobranch hosts, but show much lower specificity as larval stages in their respective intermediate hosts (Palm & Caira 2008; Jensen & Bullard 2010). Several cosmopolitan elasmobranch tapeworm species with lower host specificity may be exceptions to this, but these species also show considerably lower specificity in intermediate hosts (Palm & Caira 2008). *Tentacularia coryphaenae*, for instance, has been described as adults from more than 10 different elasmobranch species. Their larval stages have been described from more than 80 different intermediate host species in more than 40 different taxonomic families (Palm & Caira 2008). From what is currently known of elasmobranch tapeworm life cycles, different taxonomic groups of the parasites may use distinctly different types of intermediate hosts (Palm 2004; Palm & Caira 2008). For example, certain trypanorhynch tapeworms in the families Eutetrarhynchidae and Aporhynchidae are known to use almost exclusively crustaceans (e.g. crabs and shrimps) as their second intermediate hosts, whereas trypanorhynch tapeworms of the family Lacistorhynchidae seem to use generally teleost fishes as their second intermediate hosts (Palm 2004). These patterns have been established from limited information on certain species, however, and until further research is done to elucidate the life cycles of more tapeworms, it cannot be said whether these patterns of intermediate host use are consistent within taxonomic groups (Palm 2004). Notably, the life cycles of different elasmobranch tapeworms have been poorly described, and in many cases their intermediate hosts are completely unknown (Caira & Reyda 2005; Jensen & Bullard 2010).

Ongoing research in parasitology is continuing to reveal new records for elasmobranch tapeworms in both intermediate and definitive hosts (Caira and Jensen 2017). However, there remain significant gaps in knowledge regarding what factors underpin these patterns of host use. Questions remain as to which described intermediate hosts may represent “dead ends” for the parasites (ecological sinks), and which hosts are likely to transmit parasites to suitable paratenic or definitive hosts (ecological links) (Jensen and Bullard 2010). Likewise, it is unknown whether intermediate host use by these parasites is strongly linked to the diets of their definitive elasmobranch hosts, or alternatively, whether the links between intermediate and definitive hosts are dynamically weak as has been observed in other food webs (Cirtwill et al. 2017). Palm et al. (2017) have provided some recent insights, showing that the depth, diet, and habitat of sharks are major factors influencing the composition of their trypanorhynch tapeworm assemblages. Yet, the influence of diet has only been examined at a very coarse level (between vertebrate and invertebrate feeding sharks) (Palm et al. 2017), and many questions remain about how more specific taxonomic groups of prey in shark diets might influence their tapeworm compositions. Answering these questions may be critical towards better understanding and predicting the life cycles of these important marine parasites.

3.1.1. Objectives of chapter 3

In chapter two of this thesis, it was found that the dominant prey group in shark diets (e.g. crustaceans, cephalopods or teleosts) had little bearing on the overall diversity of their tapeworm assemblages. Diet composition may be substantially more important for the composition of their respective tapeworm assemblage, however, since as noted above, tapeworms in different taxonomic groups may use different types of intermediate hosts (i.e. some tapeworms may only use crustaceans as second intermediate hosts whereas others may use cephalopods or teleosts). The objective of this chapter was to investigate association between the diet and tapeworm composition of sharks. The first part of this chapter involved the use of ordination methods to map known tapeworm and prey taxa across different shark species. These methods served to analyse whether similarities in diet composition among sharks are correlated with their similarities in tapeworm composition, and more specifically, whether tapeworm assemblages show distinct differences among different feeding

groups of sharks (e.g. teleost-feeding and cephalopod-feeding sharks). The second part of this chapter looked more specifically at whether intermediate host use by tapeworm species is associated with their contribution to shark diets i.e. whether families of prey that harbour many different tapeworms are also important contributors to the diets of sharks that the tapeworms infect as adults. This entailed searching the literature for tapeworm records in families of intermediate hosts that could be compared with shark diet records for the same animal families. Only trypanorhynch tapeworms (Order Trypanorhyncha) were examined for their larval records in this part because unlike other tapeworms, they have consistent morphology between larval stages and adults, and thus, have been more consistently identified from intermediate hosts (Palm 2004; Jensen & Bullard 2010). Intermediate host records for other tapeworms are rare due to their reliance on molecular tools for identification, making it difficult to explore their life cycle patterns based on current records (Jensen & Bullard 2010). In any case, patterns of intermediate host use by trypanorhynchs especially warrant investigation because the Order Trypanorhyncha is a basal tapeworm group of elasmobranchs and is the most speciose tapeworm Order in elasmobranchs known to date (Mariaux & Olson 2001; Hoberg & Klassen 2002; Caira & Jensen 2017; Palm et al. 2017).

3.2. Methods

3.2.1. Data collection of shark diets and tapeworms

All data on tapeworms infecting sharks were compiled from a revised dataset of tapeworms in elasmobranchs that is publicly available from Randhawa and Poulin (2010). The final dataset included tapeworm species records for more than a hundred different shark species listed in Zoological Records on ISI Web of Knowledge from 1864 to 2017 (see methods in 2.2.1 for more detail). Searches for tapeworm records were conducted for each shark species on ISI Web of Knowledge by searching its Latin name and all known synonyms combined with keywords “Parasit* OR disease OR pathog*”. All data on prey families of sharks were compiled in a similar fashion; for each shark species which had tapeworm records, prey records were obtained from all published records listed across all databases on ISI Web of Knowledge from 1864 to 2017. Diet records were obtained for individual shark species by searching its Latin name and all known synonyms combined with keywords “diet* OR feed* OR

prey*’’. The final dataset included all known prey families for each of 91 different shark species (for a list of prey families for each of the sharks see Table A.1 in Appendix). Given that many diet studies were published decades ago and taxonomic changes had been made to certain prey taxa since their publication, all prey taxa recorded were checked in the World Register of Marine Species (WoRMS) database and updated to reflect their currently accepted taxonomical nomenclature (WoRMS Editorial Board 2017). For information on the dominant prey groups of each shark species, the percentage composition of nine different prey groups were recorded from each diet reference (teleost fishes, cephalopods, crustaceans, mammals, chondrichthyan fishes, reptiles, birds, other molluscs, other invertebrates). The overall composition of these groups for each shark species was calculated by taking the average compositions across all studies, weighted by the number of non-empty stomachs examined for diet (See 2.2.2 for details on how composition was quantified). Overall diet composition was also recorded for the five families of prey most dominant in each shark species’ diet (this was relevant for later analyses linking intermediate hosts of trypanorhynch tapeworms to shark prey; see 3.2.4.).

In preparation for ordination analyses, tapeworm and diet data were formatted into presence/absence matrices in Microsoft Excel. For tapeworm data, a binary matrix was constructed giving the presence/absence of tapeworm families for each shark species (shark species x tapeworm families), where presence of a tapeworm family was indicated by “1” and absence of a tapeworm family was indicated by “0”. Tapeworm composition was analysed at the family level since tapeworms are highly host specific in elasmobranchs and, consequently, there is generally low overlap of tapeworms among different shark species (Caira and Jensen 2008). There is considerably more overlap of tapeworm families among sharks, allowing more meaningful comparisons in composition among hosts. Presence/absence of tapeworm families was used to represent composition rather than the species richness per family because the main interest of the present study was to explore the influence of diet on tapeworm composition in sharks, rather than tapeworm diversity which was already explored in detail within chapter two of this thesis. Only shark species with at least two available adult tapeworm records were included in the final matrix (akin to the methodology of Palm et al. 2017). This restriction was made to ensure more reliable comparisons in the ordination since species with fewer than two tapeworm records

could have just been poorly studied for parasites. Based on this minimum criterion, the analysis of tapeworm composition included a total of 272 host/tapeworm family records, involving 22 different tapeworm families recorded across 61 different shark species.

For diet data, a binary matrix was constructed giving the presence/absence of prey families for each shark (shark species x prey families), where presence of a prey family was indicated by “1” and absence of a prey family was indicated by “0”. Consistent with the tapeworm data, only shark species with at least two prey families described were included in the final matrix. This restriction was made because shark species with fewer than two prey family records may have been poorly studied for diet, and thus, removing them ensured more reliable comparisons in the ordination. Based on this minimum criterion, the analysis of diet composition included a total of 2,793 shark/prey family records, involving 398 different families of prey recorded across 61 different shark species (importantly, these 61 shark species were the same species analysed for tapeworm composition).

3.2.2. Analysis of diet vs. tapeworm composition

All statistical tests were carried out in the R environment (R Development Core Team 2012). Prey and tapeworm family matrices were uploaded into R and the package “betapart” (Baselga & Orme 2012) was used to transform each presence-absence matrix into a distance matrix of pair-wise dissimilarities among shark species. The Jaccard similarity index was used to generate dissimilarities. This index was selected for its simplicity and widespread application to presence/absence data, and for this study, it specifies the number of prey (or tapeworm) families shared by two shark species divided by the total number of prey (or tapeworm) families found across both shark species. Similarity measures are usually not independent of richness gradients among sites (in the case of this research, similarity would not be independent of gradients in prey and tapeworm family richness among shark species), meaning that differences in composition among sites can be obscured by differences in richness among sites (Baselga et al. 2007; Carvalho et al. 2012). One method that has been proposed to resolve this issue is to quantify dissimilarities by two different components; nestedness and turnover (Baselga 2010). The nestedness component of

dissimilarity accounts for differences in composition that are due to species loss between sites (in this case, prey/tapeworm family loss between shark species), whereas the turnover component, which is independent of potential differences in richness between sites, reflects replacement of species between sites (in this case, the replacement of prey/tapeworm families by other families between sharks) (Koleff et al. 2003; Baselga 2010; Baeten et al. 2012). For this study, both prey and tapeworm distance matrices were partitioned into nestedness and turnover components of dissimilarity using the “betapart” package (Baselga & Orme 2012), and since the main interest was in quantifying differences in tapeworm composition among sharks (not differences in richness), further analyses of prey and tapeworm composition were conducted specifically on turnover dissimilarities.

The “metaMDS” function of the “vegan” package in R (Oksanen 2013) was used to generate two-dimensional nMDS ordinations plotting dissimilarities in tapeworm and prey composition among shark species. Both prey and tapeworm nMDS ordinations found global solutions within 20 runs. Initial ordinations displayed the species names for each shark, but they were subsequently re-plotted with two factors (dominant diet group and shark order) superimposed on the plot to show composition differences among sharks with different dominant prey groups and different orders (each shark species was coded with a symbol to represent its associated group). To test for significant differences in composition among sharks with different dominant prey groups and sharks with different orders, the “adonis” function was used to run non-parametric (permutational) MANOVAs for both factors (999 permutations). Pairwise dissimilarities among the groups were calculated by re-running the function on each individual pair of groups (e.g. for the difference among two shark orders, the data was adjusted to include only sharks from those two orders). In instances where significant differences were seen between groups, SIMPER analyses (Clarke 1993) were performed to explore which prey families, or which tapeworm families, contributed most to compositional differences. In these analyses prey and tapeworm families were ordered by increasing contribution (%) to the total dissimilarity observed between groups. To determine overall correlation between the tapeworm and prey dissimilarities of sharks, the Mantel statistic was used (function “mantel” in the “vegan” package).

3.2.3. Data collection on intermediate host families

A list of trypanorhynch tapeworm species was compiled for the 91 shark species with recorded diet information (only tapeworms known to infect spiral valves of these sharks as adults). Intermediate host records were obtained for each species from Palm (2004), which provides a comprehensive list of intermediate hosts described for trypanorhynchs up until 2004. Additional records published after 2004 (between 2004 and 2017) were compiled from all databases of ISI Web of Knowledge. References were found on Web of Knowledge by searching the taxa of each tapeworm (Latin name plus all known synonyms) combined with keywords “larva* OR plerocerc* OR merocerc* OR procerc* OR cysticerc* OR "intermediate host"” (searches were all conducted in September 2017). Overall, 186 different animal families were recorded as intermediate hosts across 74 of the 139 trypanorhynch species infecting the 91 included shark species (see hosts and associated references in Appendix Table A.2).

The occurrence of animal families as intermediate hosts to trypanorhynch tapeworms is likely to be substantially influenced by each family’s sampling effort for parasites. Considering this, a measure of sampling effort was obtained for each animal family from ISI Web of Knowledge by searching each family name and all its described genera (all currently accepted genera described on WoRMS) combined with keywords “Parasit* OR disease OR pathog*”. Several different genera were synonymous with taxa from unrelated families. In light of this potential error in searches, the list of taxa returned for each search was checked to make sure all included species and genera were part of the family in question. Where taxa were not part of the family, the search was refined to exclude them and their associated references. Families of terrestrial mammals recorded from shark diets were not included due to their potential inflation of sampling effort, and their unlikelihood to serve as intermediate hosts to shark tapeworms.

3.2.4. Analysis of intermediate host importance

All statistical tests were conducted in the R environment. To investigate the relationship between intermediate host use by trypanorhynch tapeworms and importance to shark’s diets, a linear mixed model (LMM) was run with trypanorhynch richness of animal families as a response. To correct for the influence of sampling

effort, trypanorhynch richness was measured by the residuals for its quadratic regression on sampling effort (a plot of this regression can be seen in Appendix Figure A.3). Prey phylogeny was included as a random effect in the model (measured as prey order, nested within prey class, nested within prey phylum). Two fixed predictors were included; (1) the overall occurrence of the animal family as prey across the 91 shark's diets, and (2) the occurrence of the animal family as important prey across the 91 shark's diets (important prey families were defined as those within a shark's top five prey families by overall composition). The interaction between these fixed effects was included in the model since common prey families are also likely to be important in shark's diets.

To determine whether sharks feeding on trypanorhynch-rich prey had more trypanorhynch tapeworms as adults, the average trypanorhynch richness across a shark's top five prey families by composition (adjusted for sampling effort as stated above) was plotted against its richness of adult trypanorhynchs (measured as residuals for the quadratic regression of richness on sampling effort (regression plot available in Appendix, Figure A.4). Significance was determined by a linear regression between these variables.

3.3. Results

3.3.1. The influence of sharks' diets on their tapeworm compositions

The 61 different shark species included in the analyses comparing diet and tapeworm compositions (Figures 3.1 & 3.2) showed considerable bias towards shark species with certain diets. Sharks with diets dominated by teleost fishes were by far the most frequent in the data (n=38), followed by sharks with diets dominated by crustaceans (n=14), and sharks with diets dominated by cephalopods (n=5). Sharks with diets dominated by other groups were poorly represented in comparison (chondrichthyan fishes (n=2) and other invertebrates (n=2)). The species were also biased towards certain taxonomic orders. Notably, more than two thirds of the sharks included were of the Order Carcharhiniformes (n=41). Lamniformes (n=7) and Squaliformes (n=6) were reasonably well represented, but all other orders (Hexanchiformes, Heterodontiformes, Orectolobiformes and Squatiniformes) were poorly represented, each with three or fewer species included.

There was a significant difference in prey family compositions among sharks with different dominant prey groups (ADONIS; $R^2=0.188$, $p<0.001$) (Figure 3.1B).

Pairwise comparisons indicated that there was a notably large difference in prey family composition between crustacean-feeding and teleost-feeding sharks (ADONIS; $R^2=0.124$, $p<0.001$), and between crustacean-feeding and cephalopod-feeding sharks (ADONIS; $R^2=0.191$, $p=0.002$). However, prey composition was not significantly different between teleost-feeding and cephalopod-feeding sharks (ADONIS; $R^2=0.035$, $p=0.161$) (Figure 3.1B), indicating substantial overlap in the families of prey consumed between sharks feeding primarily on teleosts and sharks feeding primarily on cephalopods.

Prey family composition showed a significant difference among sharks' taxonomic orders (ADONIS; $R^2=0.179$, $p<0.001$) (Figure 3.1C). Pairwise comparisons revealed significant differences in prey family composition between squaliform and lamniform sharks (ADONIS; $R^2=0.141$, $p=0.032$), between carcharhiniform and squaliform sharks (ADONIS; $R^2=0.082$, $p<0.001$), and between carcharhiniform and lamniform sharks (ADONIS; $R^2=0.044$, $p=0.021$), (comparisons for other orders were not included due to their small sample sizes). SIMPER analysis determined that the five prey families contributing most to dissimilarity between lamniform and squaliform sharks were teleost fish families Macrouridae (cumsum=0.015, $p<0.001$), Myctophidae (cumsum=0.027, $p=0.017$), and Callionymidae (cumsum=0.061, $p=0.005$), and the cephalopod families Histioteuthidae (cumsum=0.050, $p=0.031$) and Sepiolidae (cumsum=0.039, $p=0.003$). All five of these families were significantly more common in the diets of squaliform sharks (in 100%, 100%, 66.7%, 100% and 66.7%, respectively) than in the diets of lamniform sharks (in 14.3%, 28.6%, 0.0%, 42.9% and 0.0%, respectively). The five prey families contributing most to dissimilarity between carcharhiniform and squaliform sharks were the teleost fish families Macrouridae (cumsum=0.014, $p<0.001$), Myctophidae (cumsum=0.038, $p=0.002$), and Gadidae (cumsum=0.057, $p=0.008$), and the cephalopod families Histioteuthidae (cumsum=0.026, $p=0.002$) and Sepiolidae (cumsum=0.048, $p=0.003$). All five of these families were significantly more common in the diets of squaliform sharks (in 100%, 100%, 66.7%, 100% and 66.7%, respectively) than in the diets of carcharhiniform sharks (in 12.2%, 22.0%, 19.5%, 42.9% and 19.5%, respectively).

The five families contributing most to dissimilarity between carcharhiniform and lamniform sharks were the teleost fish families Merlucciidae (cumsum=0.011, $p<0.001$), Sebastidae (cumsum=0.022, $p<0.001$), Sciaenidae (cumsum=0.041, $p=0.084$) and Paralepididae (cumsum=0.050, $p=0.004$), and the crustacean family Penaeidae (cumsum=0.032, $p=0.196$). The teleost families (Merlucciidae, Sebastidae, Sciaenidae and Paralepididae) were more common in the diets of lamniform sharks (in 85.7%, 71.4%, 71.4% and 57.1%, respectively) than in the diets of carcharhiniform sharks (in 26.8%, 7.3%, 51.2% and 2.4%, respectively). Conversely, Penaeidae was present more in the diets of carcharhiniform sharks (68.3%) than in lamniform sharks (42.9%).

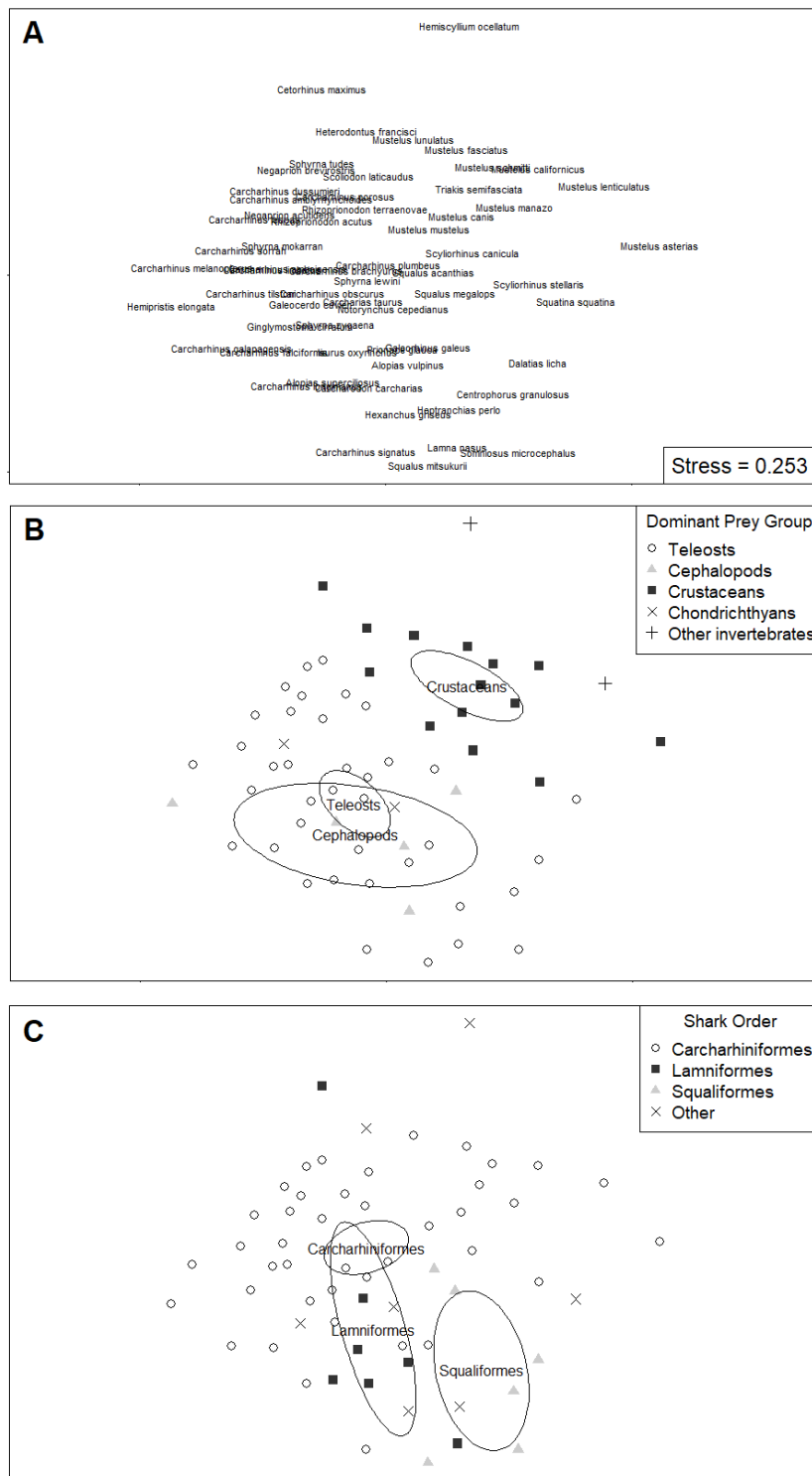


Figure 3.1. Non-metric multidimensional scaling (nMDS) plots displaying the similarity in diet (prey family) composition among shark species ($n=61$), grouped by shark species (A), shark diet composition (B), and shark Order (C). Distances are based on Jaccard similarities of spatial turnover among shark species. In B and C, 95% CI ellipses are displayed to compare groups.

The tapeworm family assemblages of sharks were substantially different among dominant prey groups (ADONIS; $R^2=0.167$, $p<0.001$) (Figure 3.2B). However, pairwise comparisons revealed that there was only a significant difference in tapeworm composition between crustacean-feeding and teleost-feeding sharks (ADONIS; $R^2=0.430$, $p<0.001$), and not between crustacean-feeding and cephalopod-feeding sharks (ADONIS; $R^2=0.099$, $p=0.162$), or teleost-feeding and cephalopod-feeding sharks (ADONIS; $R^2=0.022$, $p=0.487$). These differences can be clearly seen in the associated nMDS plot (Figure 3.2B), which shows relatively distinct groupings for teleost-feeding and crustacean-feeding sharks, with cephalopod-feeding sharks in-between and overlapping both groups. Notably, the two chondrichthyan-feeding sharks overlapped with teleost-feeding sharks in their tapeworm composition, whereas the two sharks feeding on other invertebrates were closest to crustacean-feeding sharks (Figure 3.2B).

SIMPER analysis revealed that the five tapeworm families contributing most to dissimilarity between teleost-feeding and crustacean-feeding sharks were the diphyllidean family Echinobothriidae (cumsum=0.116, $p<0.001$), the trypanorhynch families Lacistorhynchidae (cumsum=0.212, $p=0.245$) and Tentaculariidae (cumsum=0.300, $p=0.728$), the phyllobothriidean family Phyllobothriidae (cumsum=0.388, $p=0.682$), and the onchoproteocephalidean family Onchobothriidae (cumsum=0.473, $p=0.771$). Echinobothriidae was particularly common in the tapeworm assemblages of crustacean-feeding sharks (harboured by 71.4% of crustacean-feeding sharks) but completely absent from assemblages of teleost feeding sharks. Tentaculariidae and Phyllobothriidae were also more common in crustacean-feeding sharks (harboured by 71.4% and 85.7% of crustacean-feeding sharks, respectively) than in teleost-feeding sharks (harboured by 57.9% and 55.2%, respectively). On the other hand, Lacistorhynchidae and Onchobothriidae were more common in teleost-feeding sharks (harboured by 71.1% and 44.7%, respectively) than in crustacean-feeding sharks (each harboured by 42.9% of crustacean-feeding sharks).

Tapeworm family composition showed a significant difference among shark orders (ADONIS; $R^2=0.319$, $p<0.001$) (Figure 3.2C). Pairwise comparisons demonstrated that tapeworm compositions were significantly different between carcharhiniform and lamniform sharks (ADONIS; $R^2=0.145$, $p<0.001$), and between carcharhiniform and

squaliform sharks (ADONIS; $R^2=0.122$, $p<0.001$), but not between lamniform and squaliform sharks (ADONIS; $R^2=0.132$, $p=0.203$). SIMPER analysis revealed that the five tapeworm families contributing most to dissimilarity between carcharhiniform and lamniform sharks were all trypanorhynch families; Sphyricephalidae (cumsum=0.110, $p<0.001$), Tentaculariidae (cumsum=0.200, $p=0.331$), Lacistorhynchidae (cumsum=0.289, $p=0.388$), Otophthriidae (cumsum=0.374, $p=0.260$) and Gymnorhynchidae (cumsum=0.452, $p<0.001$). Sphyricephalidae and Gymnorhynchidae were significantly more common in lamniform sharks (71.4% and 57.1%, respectively) compared with carcharhiniform sharks (each harboured by only 2.4% of carcharhiniform sharks). Conversely, Tentaculariidae, Lacistorhynchidae and Otophthriidae were all more common in the assemblages of carcharhiniform sharks (73.2%, 65.9% and 51.2%, respectively) than in the assemblages of lamniform sharks (42.9%, 42.9% and 14.3%, respectively). SIMPER analysis determined that the five tapeworm families contributing most to tapeworm dissimilarity between carcharhiniform and squaliform sharks were the trypanorhynch families Tentaculariidae (cumsum=0.116, $p=0.002$), Lacistorhynchidae (cumsum=0.216, $p=0.023$), Sphyricephalidae (cumsum=0.313, $p=0.004$) and Otophthriidae (cumsum=0.405, $p=0.045$), and the phyllobothriidean family, Phyllobothriidae (cumsum=0.492, $p=0.216$). Tentaculariidae, Lacistorhynchidae and Otophthriidae were all more common in carcharhiniform sharks (73.2%, 65.9%, and 51.2%, respectively) than in squaliform sharks (16.7%, 33.3%, and 0.0%, respectively). In contrast, Sphyricephalidae and Phyllobothriidae were more common in squaliform sharks (50.0% and 66.7%, respectively) than in carcharhiniform sharks (2.4% and 63.4%, respectively).

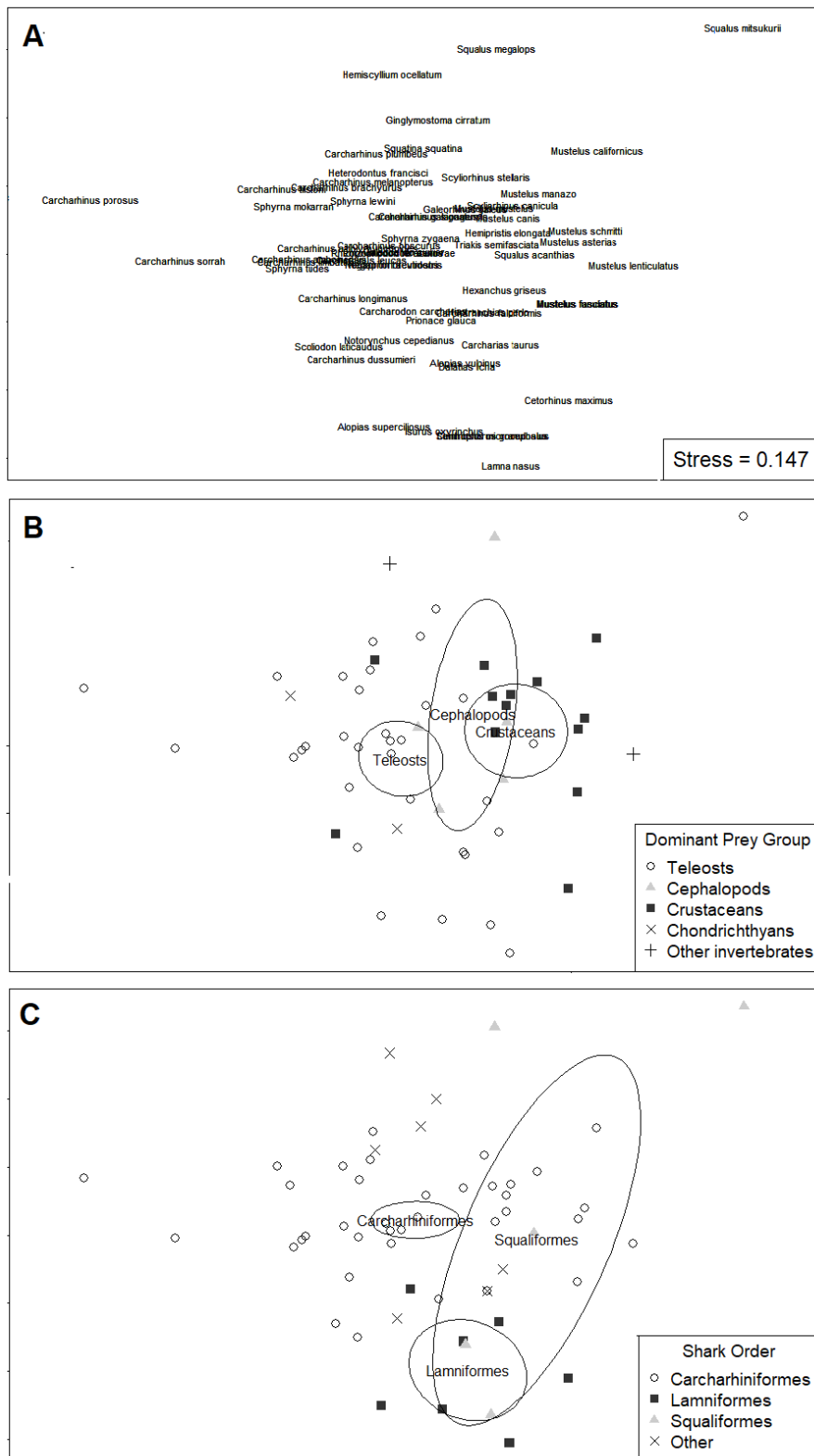


Figure 3.2. Non-metric multidimensional scaling (nMDS) plots displaying the similarity in tapeworm family composition among shark species ($n=61$), grouped by shark species (A), shark diet composition (B), and shark order (C). Distances are based on Jaccard similarities of spatial turnover among shark species. In B and C, 95% CI ellipses are displayed to compare groups.

Overall, dissimilarity in tapeworm family composition was significantly positively correlated with dissimilarity in prey family composition (Mantel $R^2=0.118$, $p<0.001$, permutations=999). In other words, tapeworm family assemblages were more similar in composition between sharks with similar diets (Figure 3.3).

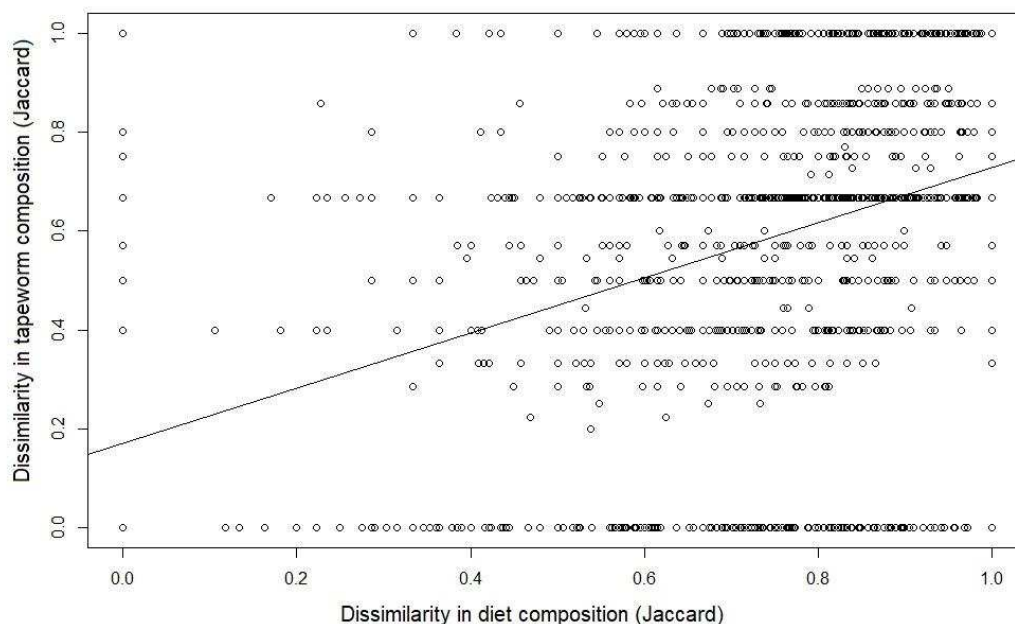


Figure 3.3. Scatter plot showing the relationship between similarity in diet composition (prey family assemblages) and similarity in tapeworm composition (tapeworm family assemblages) among sets of shark species ($n=61$ sharks, 3721 comparisons). Dissimilarities were derived using the Jaccard index and specifically reflect spatial turnover. Solid line shows linear regression between the two variables.

3.3.2. Linking trypanorhynch intermediate hosts with shark diet composition

Data on diet and tapeworm composition was obtained for a total of 91 different shark species and across these shark species there were 139 different trypanorhynch tapeworm species described as adults from spiral valves. Seventy-four (53.2%) of these trypanorhynch species had one or more families of marine animals described as their intermediate hosts in the literature. Overall, these trypanorhynch larvae were recorded across 186 different families of marine animals (Appendix Table A.2). Most of these intermediate host families were teleost fishes ($n=134$), and the remainder were comprised of families of chondrichthyan fishes ($n=23$), crustaceans ($n=16$), cephalopods ($n=7$), other molluscs ($n=3$) and reptiles ($n=3$). After cross referencing trypanorhynch intermediate host families with families recorded from the diets of the 91 shark host species analysed, a sum of 613 animal families could be compared for

their use as intermediate hosts of shark trypanorhynch and their use as prey by sharks.

The number of trypanorhynch species described to infect prey families as larval stages ranged from 0 in most families, up to more than 20 species in some families of teleost fishes. Once this number was corrected by each family's associated sampling effort (using residuals for the quadratic regression of trypanorhynch species richness on sampling effort), it was revealed that the families with the most trypanorhynch species larvae described per sampling effort were teleost fishes of the Order Perciformes (Figure 3.4A). In fact, of the 20 families with the highest species richness of shark trypanorhynch larvae (per sampling effort), 13 families were perciform fishes, five were families of teleost fishes from other orders, and only two families were of other taxonomic groups (elasmobranchs and cephalopods, respectively) (Figure 3.4A). There was considerable overlap between the most trypanorhynch-rich intermediate hosts and the most common prey of sharks (Figure 3.4B). Seven of the 20 families most rich in shark trypanorhynch tapeworm larvae (Carangidae, Sciaenidae, Scombridae, Trichiuridae, Serranidae, Merlucciidae, and Ommastrephidae) were also observed among the twenty most common prey families recorded from the diets of sharks (Figures 3.4A & 3.4B). Similarly, there was considerable overlap between the most trypanorhynch-rich families and the families most commonly comprising important shark prey (important prey families were defined as one of the five prey families with overall highest composition in a shark's diet) (Figures 3.4A & 3.4C). In contrast with the 20 families most rich in shark trypanorhynch tapeworm larvae, there was more variation in taxonomy among the 20 families most common as shark prey and important shark prey, with several families of cephalopods and crustaceans being much more common as shark prey than as intermediate hosts to their trypanorhynch tapeworm larvae (Figure 3.4).

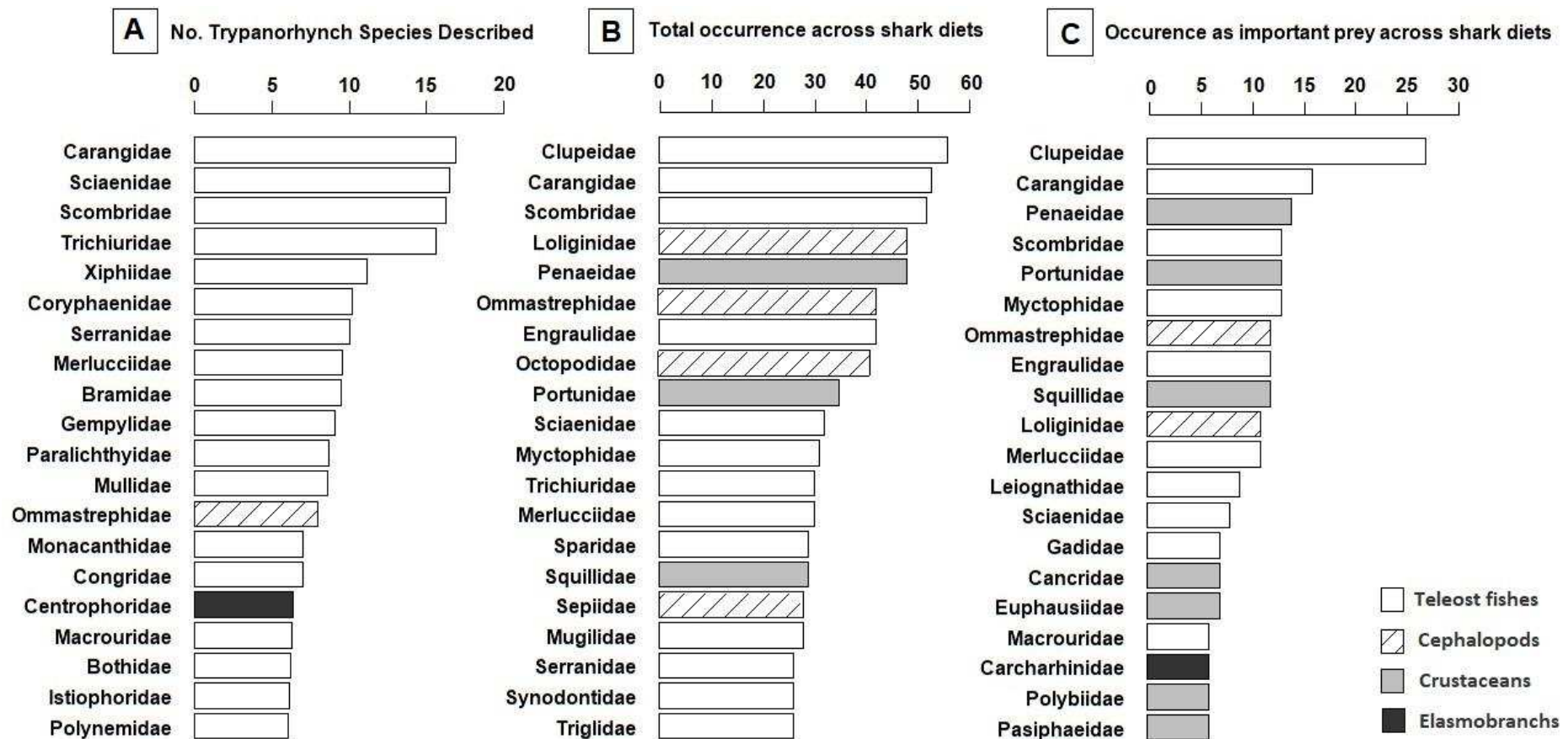


Figure 3.4: Frequency distributions showing the twenty animal families with (A) the most described larval trypanorhynch tapeworm species known to infect 91 different shark species as adults (adjusted to show highest numbers of trypanorhynch tapeworm species described per sampling effort), (B) the highest total occurrence as prey across the same 91 shark species, and (C) the highest occurrence as important prey across the same 91 shark species, defined by their frequency as one of the top five prey families by overall composition in shark's diets. Legend (lower right) gives the higher taxonomic groupings of prey families.

For the LMM looking at factors influencing richness of shark trypanorhynch tapeworm larvae, the full model (AICc = 2600.139) was considerably better than the null model (AICc = 2817.743) and the model including the random effect only (AICc = 2740.764). The evolutionary history of intermediate host families (measured as prey order nested within prey class nested within prey phylum) was found to explain a considerable amount of the variance in richness (11.39%). Of the fixed effects, occurrence as shark prey had a significant positive influence on trypanorhynch richness ($t_{448} = 8.315$, $P < 0.001$), but occurrence as important shark prey, and the interaction between the fixed effects, were both statistically non-significant (Table 3.1).

Table 3.1: Summary of Linear mixed model (LMM) showing the effects of variables on the number of shark Trypanorhynch tapeworm species (corrected for sampling effort) known to infect various families of marine animals as larval stages. Frequency of shark prey is the overall number of occurrences of an animal family across the diets of 91 different shark species, and frequency as important shark prey represents the number of occurrences in the top five prey families of sharks by composition. The model estimates, t-values, degrees of freedom (df) and p-values are shown for each variable.

Random effect				
Variable	Number of levels	Variance explained (%)		
Prey Phylogeny (Order/Class/Phylum)	(n=162)	11.39%		
Fixed effects				
Variable	Estimate	t-value	df	p-value
Occurrence as shark prey	0.138	8.315	448	<0.001
Occurrence as important shark prey	0.010	0.099	448	0.921
Fixed effects interaction	0.000	0.086	448	0.932

It was found that the average trypanorhynch tapeworm richness across a shark's most important prey (top 5 prey families by composition) was positively associated with

the overall richness of trypanorhynch tapeworms known to infect the shark ($t_{69}=2.592$, $P=0.012$) (Figure 3.5). In other words, sharks infected by high numbers of trypanorhynch species as adults appeared to feed often on families of prey harbouring more trypanorhynch species as larval stages. However, it must be noted that this association was relatively weak overall ($R^2=0.089$), and there was considerable variation among sharks (Figure 3.5).

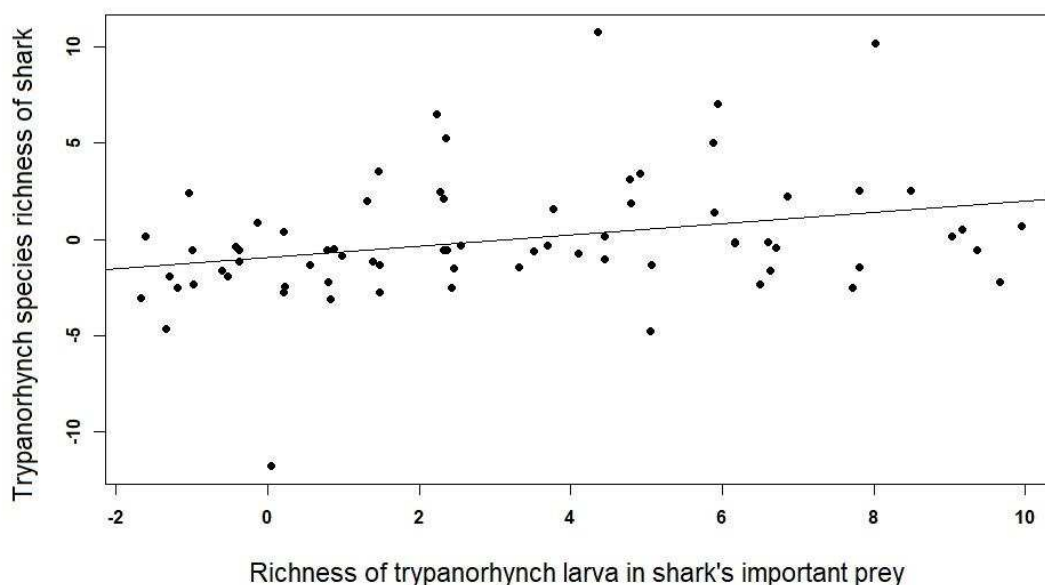


Figure 3.5. Scatter plot showing the relationship between number of trypanorhynch tapeworm species infecting shark species and number of trypanorhynch tapeworm species infecting their important prey families as larval stages (important prey families are defined as families that are in the top five families by overall composition in the shark's diet). Both measures of trypanorhynch tapeworm richness represent the residuals for their quadratic regressions on sampling effort.

3.4. Discussion

The results of this study reveal some important links between the diet of sharks and their tapeworm assemblages. First, tapeworm families were found to have substantially more overlap between shark species with similar diets. This pattern was demonstrated by a significantly positive correlation between shark similarities in tapeworm composition and similarities in diet composition (Figure 3.3). Additionally, nMDS analyses revealed distinct differences in shark species' tapeworm compositions depending on what taxonomic group of prey was dominant in their diets (Figure 3.2B). Taken together, these findings support the notion that tapeworms may be

useful indicators of the feeding ecology of their definitive shark hosts, and vice versa (Palm et al. 2017). However, these findings must also be viewed in light of host evolutionary histories. Tapeworm compositions showed significant differences among sharks of different taxonomic orders (Figure 3.2C), and shark diets were also largely dependent on their evolutionary history (Figure 3.1C). These relationships make it difficult to decipher the relative impacts of host ecology and evolutionary history on the structure of shark tapeworm assemblages. Ultimately, tapeworm assemblages may be similar between related shark species partly due to their shared evolutionary history with tapeworms, and partly due to the fact that they feed on the same type of intermediate hosts. Nevertheless, host ecology is evidently more important in some cases. In the present study, for example, there was substantial variation in tapeworm families among different lamniform shark species, and some lamniform sharks were shown to have tapeworm compositions closer to those of some squaliform shark species with similar feeding ecologies than those of other lamniform sharks. Likewise, other research has found that trypanorhynch tapeworms show substantial overlap among ecologically similar shark species even when they are phylogenetically-distant hosts (Palm et al. 2017). These instances likely reflect the occurrence of host switches between shark species with different evolutionary histories (Palm et al. 2017). Phylogenetic research of trypanorhynch tapeworms suggests that host switches have occurred for tapeworms even between exceptionally different elasmobranchs e.g. host switches between sharks and rays (Palm et al. 2009).

3.4.1. The influence of sharks' diets on their tapeworm compositions

Tapeworm families were observed to be remarkably different between crustacean-feeding and teleost-feeding sharks in this study (Figure 3.2B). This pattern is likely the result of life-cycle differences among tapeworm families, since some tapeworm taxa appear to exclusively use crustaceans as second intermediate hosts, whereas others may only use teleosts as second intermediate hosts (see Palm 2004). For illustration, the trypanorhynch family *Lacistorhynchidae* was observed to be much more common among teleost-feeding shark species than crustacean-feeding species, which is consistent with previous findings that tapeworms of this family generally use teleosts as their second intermediate hosts (Palm 2004; Jakob & Palm 2006; Jensen

2009; see also Appendix Table A.2). In contrast, diphyllidean tapeworms of the family Echinobothriidae were observed to be very common in crustacean-feeding shark species, but completely absent from teleost-feeding sharks. A majority of the echinobothriid tapeworms infecting sharks in this study were of the genus *Coronocestus*, for which intermediate hosts are completely unknown. In other genera of echinobothriid tapeworms, crustaceans and molluscs have been described as second intermediate hosts (Vivares 1971; Cake 1976; Tyler 2006), and based on findings here, it is likely that *Coronocestus* species also use these invertebrates as second intermediate hosts. Phyllobothriid tapeworms were also more common in crustacean-feeding sharks than teleost-feeding sharks. However, larval stages of phyllobothriid tapeworms have been recorded from a range of different marine fauna including crustaceans (Vivares 1971), mammals (Aznar et al. 2007), teleost fishes, and molluscs (cephalopods and bivalves) (Jensen 2009; Jensen & Bullard 2010; Randhawa & Brickle 2011). Notably, these records from different fauna involve different phyllobothriid genera, indicating that different taxa within this family could have very different life cycles. Certain phyllobothriid genera may typically use crabs as second intermediate hosts (Vivares 1971), whereas others infecting primarily lamniform sharks (e.g. *Clistobothrium*) use squid as second intermediate hosts (Randhawa & Brickle 2011). However, further research is needed to elucidate their poorly studied life cycles.

The families Tentaculariidae and Onchobothriidae showed minor differences in their presence between teleost-feeding and crustacean-feeding sharks (tentaculariids were present more in crustacean-feeders, whereas onchobothriids were slightly more common in teleost-feeders), and overall both families were relatively common amongst sharks of both feeding types. This is perhaps unsurprising for tentaculariid tapeworms, which generally use teleosts as second intermediate hosts, but show cosmopolitan distributions across a range of other marine animals including cephalopods, other molluscs, chondrichthyans and reptiles (Palm 2004; Palm & Cairns 2008; Jensen 2009; see also Appendix Table A.2). Some genera within Tentaculariidae are probably more host specific than others, but most members of this family have low host specificity, and some species (e.g. *Tentacularia* sp.) appear to have flexible life cycles with many potential paratenic hosts (Palm 2004; Palm & Cairns 2008). The typically low host specificity of these species perhaps explains why

they are common across shark species with very different feeding habits. Interestingly, onchobothriid tapeworms are characterised by a high degree of host specificity (Caira & Jensen 2001; Caira et al. 2001), but are also common across sharks with different feeding habits. As described above for Phyllobothriidae, it is likely that different genera within this family have contrasting life-cycles. For example, the genus *Acanthobothrium* is found in crustacean-feeding carcharhiniform sharks (*Mustelus* and *Scyliorhinus* spp.), and some species in this genus have been found to commonly use benthic molluscs (gastropods and bivalves) as intermediate hosts (although it must be noted that there is a paucity of information on the life cycles of most *Acanthobothrium* species) (Cake 1976; Holland & Wilson 2009; Jensen 2009). Sharks with diets dominated by crustaceans are generally benthic foragers that often eat families of bivalves and gastropods (see *Mustelus* and *Scyliorhinus* species in Appendix Table A.1 for examples), and thus, crustacean-feeding sharks are likely to also frequently encounter tapeworm larval stages from these mollusc intermediate hosts. On the other hand, the onchobothriid genus *Phoreiobothrium* is known from teleost-feeding carcharhiniform sharks (e.g. *Carcharhinus* and *Sphyrna* spp.) and has been recorded to generally utilise teleost second intermediate hosts (Jensen & Bullard 2010). Based on these different associations, the feeding ecology of shark hosts could provide useful insights for onchobothriid genera with completely unknown life cycles. For instance, intermediate hosts have not been described for tapeworms of the genus *Platybothrium* (Healy 2003), but given that tapeworms of this genus are common in teleost-feeding sharks (e.g. *Carcharhinus* spp. and *Sphyrna* spp.) and are frequently found in co-infections with species of *Phoreiobothrium* (Caira et al. 2017), they most likely use teleosts as intermediate hosts.

The nMDS analyses revealed that tapeworm families of cephalopod-feeding sharks were not distinctly different from those of either teleost-feeding or crustacean-feeding sharks (Figure 3.2B). This pattern may be in part due to the low sample size here for sharks feeding primarily on cephalopods ($n = 5$). However, there was also strong overlap in the prey families of cephalopod-feeding and teleost-feeding sharks (Figure 3.1B), indicating that sharks with these different dominant prey groups have very similar diets overall. This pattern was also anecdotally supported by the diet composition data obtained for this study, which showed that the diet of sharks feeding

mainly on cephalopods typically had high overall compositions of teleost fishes (15-30%). Pelagic cephalopods are commonly intermediate hosts to trypanorhynch tapeworms that also use teleost second intermediate hosts (Palm 2004; Appendix Table A.2), and many studies suggest that cephalopods are frequent paratenic hosts for these trypanorhynch tapeworms (Stunkard 1977; Brickle et al. 2001; Shukhgalter & Nigmatullin 2001; Palm et al. 2017). Hence, tapeworm assemblages may not be distinctly different between cephalopod-feeding and teleost-feeding sharks since cephalopods are often used as second intermediate hosts (facultative or obligate) and paratenic hosts in the same life-cycles as teleost fishes. Notably, this would not explain why no significant difference was observed in tapeworm compositions between cephalopod-feeding and crustacean-feeding sharks. The diet composition data showed that cephalopod-feeding sharks had variable, but generally lower diet compositions of crustaceans (0-15%), compared to teleosts (15-30%). Based on this, there is less support for cephalopods and crustaceans being intermediate or paratenic hosts in the same life cycles. However, given the current paucity of information on marine tapeworm life cycles, further investigation is needed.

Tapeworm families showed strong distinctions among the different shark Orders, with significant differences observed between carcharhiniform and lamniform sharks, as well as between carcharhiniform and squaliform sharks. The analyses revealed that carcharhiniform sharks were characterised by the trypanorhynch tapeworm families Tentaculariidae, Lacistorhynchidae and Obothriidae. These findings mirrored those of Palm et al. (2017), who found that genera within these and other trypanorhynch families could be useful indicators of the ecology of carcharhiniform shark hosts. For example, the genera *Tentacularia* and *Heteronybelinia* (Tentaculariidae), *Obothrium* (Obothriidae), *Callitetrarhynchus*, *Floriceps* and *Dasyrhynchus* (Lacistorhynchidae) are all typical of pelagic teleost-feeding carcharhiniform sharks, whereas the genera *Dollfusiella* and *Trigonolobium* (Eutetrarhynchidae), *Lacistorhynchus* and *Diesingium* (Lacistorhynchidae) are all typical of benthic invertebrate-feeding carcharhiniform sharks (Palm et al. 2017). Although these disparities are also underpinned by further phylogenetic differences within the Order e.g. sharks of the Family Carcharhinidae are typically teleost-feeding sharks, whereas sharks of the Family Triakidae are typically invertebrate-feeding sharks (Palm et al. 2017), these tapeworm genera could clearly be very useful for predicting the general

feeding habits of a host species. To illustrate this, there is a paucity of information on the feeding habits of the triakid shark *Mustelus mento* (Fishbase 2017), but this species is known to harbour tapeworms of the trypanorhynch genera *Lacistorhynchus* (Gibson et al. 2005) and *Dollfusiella* (Alves et al. 2017), which both suggest that this shark has a diet dominated by benthic invertebrates. In a similar vein, the feeding habits of a shark host could be used for making inferences about their tapeworm assemblages. For example, to my knowledge the carcharhinid shark *Rhizoprionodon longurio* has not yet been studied for tapeworm parasites, but it is known to feed mainly on pelagic teleost fishes (Márquez-Farías et al. 2005). From this we could infer that the tapeworm assemblage of this shark is likely to include tapeworms of the aforementioned genera common to teleost-feeding carcharhiniform sharks.

Both squaliform and lamniform sharks were characterised by the trypanorhynch tapeworm family *Sphyriocephalidae* (which was rare in carcharhiniform sharks). The common occurrence of this family across both lamniform and squaliform sharks may at least partially explain why tapeworm compositions were overall not significantly different among sharks of these orders. Tapeworms of this family are known to use teleost fishes, elasmobranchs, and cephalopods as intermediate or paratenic hosts (Jensen & Bullard 2010; Dallarés et al. 2017; Appendix Table A.2). Interestingly, sphyriocephalid tapeworms have also been described from many of the same intermediate host species as tapeworms characteristic of carcharhiniform sharks (species of tentaculariids, lacistorhynchids and otobothriids) (see Appendix Table A.2). Considering this overlap in intermediate hosts, one might ask why sphyriocephalid tapeworms are not common in carcharhiniform shark species too. One possibility is that these tapeworms might be incompatible with carcharhiniform sharks due to differences in immune response (McVicar & Fletcher 1970; Randhawa & Burt 2008) or other filters that have yet to be examined in this host-parasite system. However, this can only be speculated without further investigation. Importantly, the patterns of host use established here are based on small subsets of shark species from all orders other than Carcharhiniformes, and may become much clearer with larger sample sizes. This will require increased sampling of sharks' diets and parasite assemblages across different orders in future.

3.4.2. Linking trypanorhynch intermediate hosts with shark diet composition

One of the primary aims of this study was to investigate links between intermediate host use by trypanorhynch tapeworms and the diets of their definitive shark hosts. The present study demonstrated considerable overlap between the most trypanorhynch-rich families of intermediate hosts and the most common prey families of sharks (Figure 3.4). Moreover, the occurrence of animal families as shark prey was overall statistically significant and positively correlated with the number of trypanorhynch species known to infect them (adjusted by the family's sampling effort for parasites) (Table 3.1). Based on these findings, trypanorhynch tapeworms of sharks appear to use intermediate hosts which have a high likelihood of being consumed by shark definitive hosts. From an evolutionary standpoint, this could suggest that these tapeworms increase the probability of completing their life cycles by infecting intermediate hosts which have strong trophic links to suitable definitive hosts (Cirtwill et al. 2017). However, this is not to say that trypanorhynch tapeworms specifically target prey with strong trophic links to their definitive shark hosts. Notably, many of the families of marine animals that are important hosts of trypanorhynch larvae are also some of the most common, speciose, and widespread animals across marine ecosystems (e.g. Scombridae and Sciaenidae (Nelson et al. 2016)), and consequently, are likely to be frequently encountered by sharks. Thus, it is possible that the links observed between intermediate host use in trypanorhynch tapeworms and shark's diets are a product of the wide distribution and abundance of these prey families (see Cirtwill et al. 2017).

The evolutionary history of an animal has an important influence on its use by trypanorhynch tapeworm species (Table 3.1). In line with previous records, families of teleost fishes were by far the most common intermediate hosts for shark trypanorhynch tapeworms (Palm 2004; Jensen & Bullard 2010), and made up more than two thirds of all described intermediate host families in the present study. Fishes of the Order Perciformes were particularly important intermediate hosts (Figure 3.4a, which as noted above, may partly be a consequence of the size, abundance and wide distributions of members within the Order. Families of perciform fishes could also be more suitable intermediate hosts for phylogenetic reasons e.g. they may provide more adequate resources for larval development. Although most trypanorhynch tapeworms

exhibit low host specificity as larval stages, some species (e.g. *Gymnorhynchus gigas*) appear to have higher host specificity as larvae, perhaps due to such phylogenetic constraints (Palm & Caira 2008). Nevertheless, trypanorhynch tapeworm patterns of host use in teleosts are almost certainly more influenced by the ecology, rather than the phylogeny, of their intermediate hosts (Jakob and Palm 2006). Based on the comparative findings here it is difficult to establish the extent to which phylogenetic constraints might influence patterns of host use, and further insights would require experimental infection studies which could test compatibility of larval tapeworms among different potential intermediate hosts. To my knowledge, no such studies have been conducted to date.

The average richness of trypanorhynch tapeworms (larval stages) across a shark's preferred families of prey was found to be positively associated with the richness of adult trypanorhynch tapeworm species known to infect the shark (Figure 3.5). However, it must also be cautioned that the overall association between these factors was relatively weak ($r^2 = 0.089$), and there was a large amount of variation among different species. Many factors might account for this variation, including all the factors analysed within chapter two of this thesis (e.g. the phylogeny, size, trophic level, and overall diet breadth of the shark), as well as factors which have not yet been examined, such as host-parasite compatibility. It is also possible that some of this variability is the result of limitations in the diet records obtained for this study. The overall diet compositions of shark species here reflect the sum of their feeding habits across all examined individuals for a species, regardless of their sex, size and locality. Unfortunately, many further diet studies of shark species would be required to assess the influence of these factors because a substantial amount of currently published records have not provided data on shark's feeding habits for each of these sub-populations. Furthermore, it is very uncommon for studies of elasmobranch stomach contents to include information on the intestinal parasites of individuals (see the following for some notable exceptions; Klimpel et al. 2003; Gracan et al. 2014; Isbert et al. 2015).

3.4.3. Conclusions

The present study revealed several important links between the diets of shark species and their tapeworm parasite assemblages. Firstly, there was substantial overlap found between the tapeworm families infecting a shark species and the prey families comprising their diet. Second, it was established that certain tapeworm lineages may serve as useful indicators of the feeding habits and evolutionary history of shark host species. Finally, it was observed that trypanorhynch tapeworm species that mature in sharks often use intermediate hosts which are commonly preyed upon by shark hosts. As a whole these findings demonstrate that both evolutionary history and ecology have important influences in shaping the tapeworm parasite assemblages of shark species. Importantly, the patterns of host use established here are conspicuously biased towards shark species of the Order Carcharhiniformes. Sharks of this order are generally the most well-studied and are arguably some of the most important, abundant and widespread species inhabiting our oceans (Compagno 2001). However, to further our understanding of the evolution of parasitic life cycles in sharks, it is recommended that sampling of diets and parasite assemblages prioritise shark species across more different Orders in future.

**Chapter 4: Analysing host diet and parasites
in a model species; the draughtsboard shark
*Cephaloscyllium isabellum***

4.1. Introduction

Parasite species demonstrate substantial heterogeneity in their distributions among host species, and consequently, certain hosts harbour disproportionately more parasite species than others (Poulin 2011). This heterogeneity in parasite diversity among host species is underpinned by a number of ecological and phylogenetic factors, which act to restrict the range of hosts that can be used by parasite species i.e. their host specificity (Combes 2001; Poulin 2011; Poulin et al. 2011a). In 1980, Euzet and Combes proposed that these determinants of host use can be thought of as two types of “filters”; namely encounter filters, which are factors that prevent physical contact between hosts and parasites, and compatibility filters, which are factors that prevent parasites from forming an association with hosts, even if they do come in contact (Euzet & Combes 1980; Combes 2001). Testing the relative strength of encounter and compatibility filters has since become a common feature of studies aiming to understand patterns of host use by different parasites (Kuris et al. 2007; Lagrue et al. 2011; Medeiros et al. 2013). By assessing the relative importance of these filters, researchers may gain key insights towards understanding, predicting and controlling outbreaks of infectious diseases in the future (Poulin 1992; Taraschewski 2006; Lootvoet et al. 2013).

A common method used to test the relative importance of compatibility and encounter filters is to control for the encounter filter via experimental infection of a host with a parasite it does not naturally encounter (Komar et al. 2003; Perlman & Jaenike 2003; Kuris et al. 2007; Dick et al. 2009; Van Oosten et al. 2016). A number of studies employing this method have established the importance of encounter filters, showing that many parasites are compatible with hosts that they don't normally come in contact with (Komar et al. 2003; Perlman & Jaenike 2003; Dick et al. 2009). However, this is not to say compatibility filters are less important in preventing parasite infections. Studies have also demonstrated substantial variation in the compatibility of parasites among different host species, with compatibility suggested to depend heavily on the taxonomic distance between hosts (Komar et al. 2003; Perlman & Jaenike 2003; Medeiros et al. 2013). Unfortunately, assessing the importance of encounter and compatibility filters relative to each other has proven more challenging, largely due to the difficulty of quantifying host-parasite encounters

(Combes 2001). Although the natural distribution of parasites in different hosts gives some clue as to how many parasites are encountered by a host, the full extent of encounters cannot be estimated without knowing how many parasites are encountered that fail to infect the host (Kuris et al. 2007). Researchers must address this issue and look for ways to reliably measure host-parasite encounters in order to gain a better understanding of the relative roles of encounter and compatibility filters in different ecosystems.

Tapeworms (cestodes) are arguably the most important group of parasites infecting elasmobranchs. These parasites are known to have typically high host specificity as adults (are limited to one or a few host species) and showcase an incredible diversity of species across various elasmobranch hosts (Caira & Healy 2004; Caira & Jensen 2010). Several studies have demonstrated that the high specificity of tapeworms in elasmobranchs is at least partially the consequence of compatibility filters. For example, immune response in elasmobranchs has been shown to reject certain tapeworm species (McVicar & Fletcher 1970; Randhawa & Burt 2008). On the other hand, the importance of encounter filters for tapeworm infection is generally unknown, and it is possible that some encounter filters, such as host diet, are more restrictive for tapeworm establishment than compatibility filters (Randhawa et al. 2008). These tapeworms all have complex life-cycles, involving at a minimum three different host species, and are trophically-transmitted to elasmobranchs from their intermediate or paratenic host prey (Williams 2002), and thus, it would not be surprising for their diet to play a large role in restricting parasite encounters.

The draughtsboard shark *Cephaloscyllium isabellum* (Bonnaterre, 1788) is a scyliorhinid catshark species, of the Order Carcharhiniformes, endemic to New Zealand (Cox & Francis 1997). This species is abundant around New Zealand's continental shelf, and acts as a demersal hunter and scavenger, foraging down to depths of 500 m (Francis et al. 2002; Horn 2016). Their diet is dominated by benthic invertebrates, but overall consists of a broad range of prey species, including but not limited to, fishes, crustaceans, molluscs, tunicates, echinoderms and priapulid worms (Horn 2016). Despite their broad diet, however, only one tapeworm species, *Calypotrobothrium chalarosomum*, has been described from *C. isabellum* (Hewitt and Hine 1972; Hine et al. 2000). This is interesting given that most other studied sharks

harbour several different tapeworm species on average (Randhawa and Poulin 2010). Moreover, *C. isabellum* has been identified as a cold spot in shark tapeworm diversity, entailing that it is infected by fewer tapeworm species than expected for a shark of its size (~1m in length) (Randhawa 2014, unpublished data; see Poulin et al. 2011b for details on hot and cold spots in parasite diversity). In essence, this makes *C. isabellum* a good model for studying the importance of encounter and compatibility filters for elasmobranch tapeworms. On one hand, the shark species could be a coldspot for tapeworm diversity because it does not encounter other tapeworm species through its diet, and conversely, different tapeworm species may be encountered through its diet, but their infection of the shark could be inhibited by strong compatibility filters such as host immune response. The life cycle of the shark's known tapeworm *C. chalarosomum* is completely unknown, and the intermediate hosts used by this tapeworm could consist of any number of the many different species included in the shark's diet. It is also unknown whether any of its prey species harbour the larval stages of other tapeworm species, although given the breadth of its diet, there is a high possibility that other tapeworms are also encountered by the shark.

4.1.1. Objectives of chapter 4

The primary objective of this chapter was to provide some insight into the importance of encounter and compatibility filters for the tapeworm infection of the draughtsboard shark *C. isabellum*. This objective was addressed through a series of steps. The first step was to analyse the diet and parasites of *C. isabellum* individuals to get an idea of what prey the shark encounters, and thus determine which prey species might serve as intermediate hosts for tapeworms. Previous research has shown that the intermediate hosts of trophically transmitted parasites are not always important prey of their final host (Cirtwill et al. 2017). However, important shark prey were targeted for parasite examination in this study to give some indication of how many parasites *C. isabellum* might regularly encounter via its diet. The second step was to examine samples of the sharks favoured prey, to determine whether they host any larval tapeworms. This included looking for larval stages of the shark's only known tapeworm species, *C. chalarosomum*. The third and final step relied on whether any tapeworm larvae other than *C. chalarosomum* were recovered from the prey of *C. isabellum*. If other

tapeworm larvae were found in prey, they were tested for their compatibility with the shark host via exposure to the host's blood serum (following procedures described in Randhawa and Burt 2008).

4.2. Methods

4.2.1. Surveying parasites of *C. isabellum*

A total of 24 adult draughtsboard sharks were examined for this study. These sharks were trawled from approximately 80 metres deep by local fishermen off the coast of Otago, New Zealand, on two separate trips. Thirteen of the sharks were caught on the 25th of April 2015, between Curio Bay (46°66S, 169°10E), and Dunedin (45°87S, 170°54E). The other 11 sharks were caught on the 26th of June 2015, a few kilometres north of Nugget Point (46°44S, 169°82E). Individuals were collected from the fishermen immediately following each trip and transported to the laboratory to be necropsied without delay.

Prior to dissection, each individual shark was measured for total length (in cm) and sex was determined based on the presence of distinct claspers in males (Horn 2016). Following these measurements, the individuals were flipped upside down and an incision was made along the ventral body surface to allow inspection of the body and organs for any parasites. The entire spiral valve was removed, carefully cut open, and placed inverted into a 1L container filled with saline solution and 1 tsp of sodium bicarbonate (baking soda). This container was sealed and shaken vigorously for a few minutes to separate tapeworms from mucous, then left to sit for at least 2 hours. Any tapeworms not detached from the gut mucosa were extracted from the tissue using forceps. All recovered parasites were then placed in formalin to be later counted under a dissection microscope.

4.2.2. Diet analysis of *C. isabellum*

Once measured and surveyed for parasites, the stomach of each shark was removed and opened via an incision along the dorsal surface. Stomach contents were placed into a fine sieve (500µm mesh size), rinsed with tap water, and transferred into a container with 70% ethanol for later measurement and identification. Prey were identified under dissection microscope to the lowest taxonomic level possible. A

range of available guides and taxonomic keys from literature were used to aid in identifications for crustaceans (Schembri & McLay 1983; Naylor et al. 2005; Ahyong 2012; Wilkens & Ahyong 2015), molluscs (Powell 1979) and teleosts (Lourie et al. 2004; Roberts et al. 2014). Prey items were counted and weighed (wet weight, to nearest .01 g) for subsequent quantitative analyses.

The diet composition of different shark prey groups was quantified by percentage number (%N), percentage mass (%M), and frequency of occurrence (%O). These indices were also used to calculate the index of relative importance [IRI = (%N + %M) × %O] (Cortés 1997). % IRI was calculated for the contribution of overall groups (teleosts, molluscs, crustaceans, unidentified organic matter and plants) as well as separately for individual prey within each group.

4.2.3. Surveying known prey items for parasites

Based on the quantitative diet analyses here, combined with findings of Horn's (2016) diet analysis on a larger subset of *C. isabellum* individuals, it was decided that parasite surveys of prey should focus on crab species, and especially, hermit crabs (Paguridae), which make up a considerable amount of the diet of *C. isabellum*. Most of the prey collected for this study were obtained on the 14th of March 2016 by the vessel "RV Polaris II" operating Northeast of Taiaroa Head, off Otago's Shelf (45°48S, 170°55E). More than a hundred individual hermit crabs, as well as small numbers (n<25) of several other crab species and ascidians, were caught as by-catch in beam trawls at 92 metres depth. A small sample (n=10) of long-legged masking crabs (*Leptomithrax longipes*) was obtained separately from local fishermen, who found the crabs in a trawl with draughtsboard sharks. This trawl was conducted on the 7th of December 2015 offshore Otago peninsula at 50 m depth (45°87S, 170°75E).

All invertebrates were kept alive on capture and transported to an aerated holding tank with seawater in Portobello Marine Lab, where they were surveyed for macroparasites within two weeks of capture. It was important they were kept alive so that any parasites were still alive upon inspection. Similar with the stomach contents of *C. isabellum*, invertebrates were identified to the lowest taxonomic level possible using guides and taxonomic keys from literature (Schembri & McLay 1983; Naylor et al.

2005; Ahyong 2012; Wilkens & Ahyong 2015). Tunicates were measured by length and dissected via longitudinal incision to reveal internal organs. Crabs were euthanised by piercing the cephalic ganglion with a knife, measured (carapace length) and determined for sex where possible. Following measurements, crabs were placed in a petri dish with seawater and the carapace was removed to expose organs for dissection. The full body was checked for macroparasites under a light dissection microscope and any recovered worms were placed in 5ml Eppendorf tubes containing 70% ethanol.

4.2.4. Host compatibility tests

Due to the complete absence of any tapeworm larval stages recovered from prey items, serological tests to analyse host compatibility (exposure of parasites to the host's blood serum) could not be carried out in this study.

4.3. Results

Of the 24 sharks caught in this study, there were 14 males and 10 females. The mean length of individuals was 72.40cm (± 6.25 cm SD, range = 53.6-82.1cm). There was no significant difference in size between males (72.05 ± 3.81 cm SD) and females (72.88 ± 8.85 cm SD) ($t^{22} = 0.31$, $p = 0.76$), although size was notably more variable among female sharks.

4.3.1. Parasites of *C. isabellum*

All 24 draughtsboard sharks were infected by the tapeworm *Calyptrorhynchium chalarosomum* in their spiral valves (100% prevalence), but no other tapeworm species were recovered from the sharks' intestines. In total, 1,609 adult *C. chalarosomum* were recovered. The mean abundance of tapeworms per shark was 67.04 (± 49.90 SD) and intensity ranged from 16 to 241 tapeworms per host. Sharks caught between Curio Bay and Dunedin in April generally had a higher intensity of infection (mean = 82.46 ± 60.17 SD) compared with sharks caught North of Nugget Point in June (mean = 48.82 ± 26.59 SD) (Figure 4.1). However, there was considerable variation among individuals from each location and the difference was statistically non-significant between the two samples ($t^{22} = 1.71$, $p=0.10$). Male sharks

had generally higher intensity of infection (mean = 82.79 ± 58.15 SD) than females (mean = 45.00 ± 23.53 SD) (Figure 4.1), but there was a similarly high variation within each sex and the overall difference was marginally non-significant ($t^{22} = 1.94$, $p=0.06$). There was also no significant association between infection intensity and host length (Figure 4.2) ($R^2 = 0.0003$, $p=0.94$).

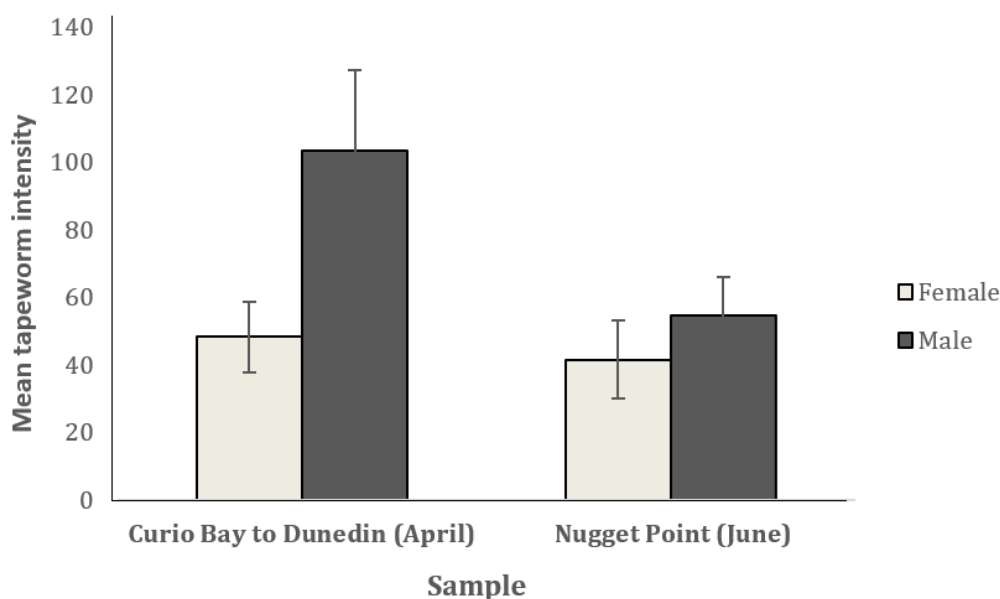


Figure 4.1. Mean infection intensity of the tapeworm *Calyptrobothrium chalarosomum* and the sex and sample of their draughtsboard shark hosts (*Cephaloscyllium isabellum*). Sample sizes for the Curio Bay to Dunedin sharks were (n=5) for females and (n=8) for males. Sample Sizes for the Nugget Point sharks were (n=5) for females and (n=6) for males. Error bars show ± 1 Standard Error.

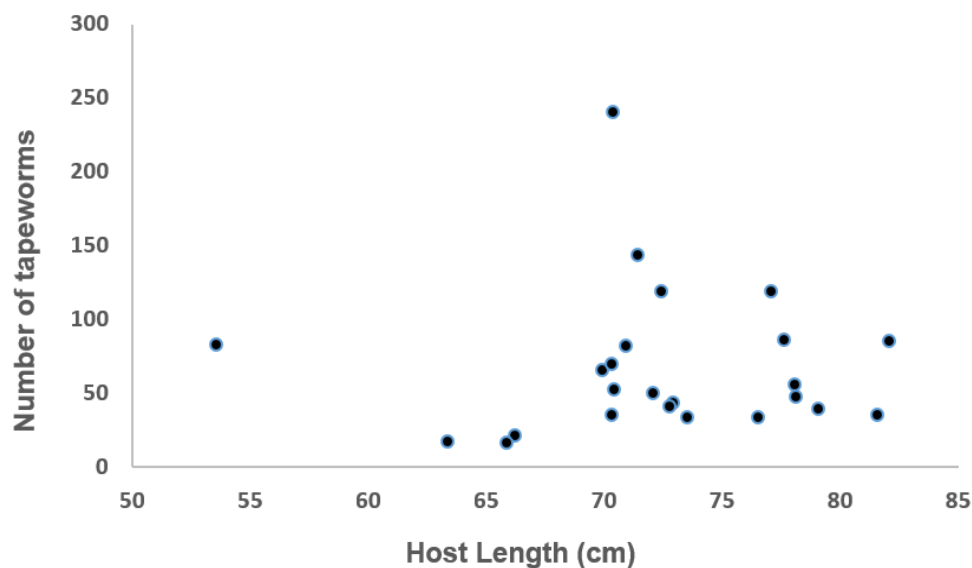


Figure 4.2. Relationship between the infection intensity of the tapeworm *Calyptrorobothrium chalarosomum* and the total length (cm) of their draughtsboard shark hosts (*Cephaloscyllium isabellum*). There was no significant relationship between the variables ($R^2 = 0.0003$, $p=0.94$).

Although no parasite other than *C. chalarosomum* was recovered from the spiral valve of *C. isabellum*, there were a few parasites recovered from other parts of the shark. Five individuals were each infected by a single digenean trematode in the stomach (Prevalence = 20.83%). This trematode species was not identified, but could possibly be *Otodistomum veliporum*, which has been previously described from the stomach of *C. isabellum* (Hewitt & Hine 1972). Two female sharks (both from North of Nugget Point) also had a few (3 and 4) larval *Anisakis* sp. nematodes embedded in their body wall. The only other parasite recovered from *C. isabellum* was a singular immature (plerocercoid) tapeworm, identified as *Hepatoxylon trichiuri* (Palm 2004), which was found in the body cavity of a male shark caught North of Nugget Point.

4.3.2. The diet of *C. isabellum*

All 24 sharks sampled in this study had stomachs containing food. Stomach contents included remains from a variety of different taxa, including teleost fishes, bivalves, cephalopods, crabs and shrimps (Table 4.1). Overall, teleosts, molluscs and crustaceans were all similarly important prey groups in diet of *C. isabellum*, with their %IRI's being 29.69%, 38.39%, and 29.73%, respectively (Table 4.1). Crustaceans were the most important prey group by frequency of occurrence (%O) with 16 of the

24 sharks sampled (66.67%) containing some crustacean remains in their stomachs. Teleosts were most important in terms of overall mass (%M) (49.68% of total prey mass), and molluscs contributed the most to the diet by percentage in number (%N) (Table 4.1).

Table 4.1. Diet composition of 24 draughtsboard sharks (*Cephaloscyllium isabellum*) caught off the Coast of Otago, New Zealand. Composition is expressed as percentage in number (%N), mass (%M), percentage occurrence (%O), and by index of relative importance (%IRI).

Prey group	Species	%N	%M	%O	%IRI
Teleosts		15.15	49.68	41.67	29.69
Sea horse (Syngnathidae)	<i>Hippocampus abdominalis</i>	1.52	0.03	4.17	0.12
Unidentified teleost remains		13.64	49.37	37.5	42.29
Molluscs		42.42	41.39	41.67	38.39
Bivalve siphons (Hiatellidae)	<i>Panopea zelandica</i>	31.82	40.64	29.17	37.83
Unidentified Cephalopods		4.55	0.25	12.5	1.07
Unidentified Mollusc remains		6.06	0.5	12.5	1.47
Crustaceans		33.33	7.24	66.67	29.73
Policeman crabs (Goneplacidae)	<i>Neommatocarcinus huttoni</i>	4.55	2.00	8.33	0.98
Hairy red swimming crab (Ovalipidae)	<i>Nectocarcinus antarcticus</i>	3.03	1.70	8.33	0.71
Hermit crabs (Paguridae)	<i>Pagurus sp.</i>	6.06	0.51	16.67	1.96
Unidentified crabs		13.64	1.84	33.33	9.24
Banded mantis shrimp (Lysiosquillidae)		1.52	1.15	4.17	0.20
Unidentified shrimp		1.52	0.01	4.17	0.11
Other crustacea remains		3.03	0.03	8.33	0.46
Unidentified organic matter		7.58	1.68	20.83	2.12*
Plant material		1.52	0.00	4.17	0.07*
Total number of prey items	66				
Total mass of prey	494.76g				
Number of stomachs sampled (none empty)	24				

*Calculated as overall group IRIs, not compared against individual components

Teleosts and crustaceans found in stomach contents included a range of different species, although most were unidentifiable parts, or their digestion was too far advanced for specific identification. In contrast, molluscs were represented almost

entirely by a single bivalve species, *Panopea zelandica* (Table 4.1). Only siphons of this bivalve were found in stomachs, except for one individual which had its shell attached. Crabs were the most important group of crustaceans within the diet of *C. isabellum*, and of the identified crabs, hermit crabs (*Pagurus* sp.) made up the most %O (Table 4.1). The only teleost species identified from stomach contents was the seahorse *Hippocampus abdominalis*, but it was of low overall importance to the diet with only one specimen observed (Table 4.1).

4.3.3. Survey of prey items

Five different crab species and one ascidian species were trawled off the coast of Otago at depths where *C. isabellum* is common (50-100m) (Table 4.2). Most of the crabs sampled (n=128) were hermit crabs (*Pagurus* sp.), which as described above, make up a large component of the diet of *C. isabellum*. The other crab species and ascidian that were sampled in smaller numbers (n=5-25) have not been explicitly identified from the shark's stomach contents. However, given that other ascidians and a large amount of unidentified crabs are important parts of its diet, *C. isabellum* is very likely to encounter and eat these species too.

There was a general absence of parasites in these invertebrates, and overall, no tapeworm larval stages were recovered from any of the sampled crabs or ascidians. All species were found to have some individuals with very small nematodes (≤ 1 mm in size), and some individual hermit crabs and ascidians also harboured small mites. The prevalence and abundance of these small nematodes was generally low for each crab species (Prevalence mostly below 20%), except for camouflage crabs (prevalence = 76.92%) (Table 4.2). A few mites were recovered from one orange ascidian and two individual hermit crabs, and their total prevalence and abundance also was very low (Table 4.2). Only one other symbiont was recovered from the invertebrates examined; a nematode found only in orange ascidians. This unidentified nematode species was much larger than the other nematode observed from crabs and ascidians (it reached a few millimetres in length). Four specimens of this nematode were recovered from each of four individual ascidians (26.67% prevalence).

Table 4.2. Prevalence and abundance of symbionts recovered from crabs and ascidians caught off the Coast of Otago, New Zealand. All prey species were caught via beam trawl from the Otago Shelf, ~NE off Taiaroa Head, at 92 m depth, except for long-legged masking crabs (*Leptomithrax longipes*), which were caught in a trawl with sharks offshore Otago peninsula, at 50 m depth. Mean host size given represents the carapace length of crabs, and the longest width dimension of ascidians. Numbers in parentheses indicate associated standard deviations.

Prey (Species)	Sample size (n)	Mean host size (mm)	Nematodes ($\leq 1\text{mm}$)		Mite symbionts	
			Prevalence	Abundance	Prevalence	Abundance
Orange Ascidian (<i>Cnemidocarpa bicornuta</i>)	15	51.67 (16.01)	40.00%	0.87 (1.30)	6.67%	0.07 (0.26)
Hermit crabs (<i>Pagurus spinulimanus</i>)	128	11.02 (3.58)	3.91%	0.06 (0.39)	1.56%	0.03 (0.28)
Triangle crabs (<i>Eurynolambrus australis</i>)	25	27.40 (9.45)	8.00%	0.28 (1.21)	-	-
Long-legged masking crabs (<i>Leptomithrax longipes</i>)	11	67.45 (17.49)	9.09%	0.18 (0.60)	-	-
Long-handed masking crabs (<i>Leptomithrax longimanus</i>)	5	23.60 (7.64)	20.00%	0.60 (1.34)	-	-
Camouflage crabs (<i>Notomithrax sp.</i>)	13	36.38 (8.90)	76.92%	3.00 (3.36)	-	-

4.4. Discussion

The main objective of this study was to provide some insight into the importance of encounter and compatibility filters for tapeworm infection in the draughtsboard shark *Cephaloscyllium isabellum*. Regarding this aim, the findings of this study offer a small glimpse into the importance of diet as an encounter filter, showing that some of the most important prey items of draughtsboard sharks (hermit crabs *Pagurus spinulimanus*) are unlikely to be intermediate hosts to tapeworms. It is possible that despite their broad diet, draughtsboard sharks have a low diversity of tapeworms because the prey species they exploit generally don't harbour many tapeworm larvae. However, this can only be speculated based on the data analysed in this study. As demonstrated here and in other research, this shark consumes a variety of teleost, mollusc and other invertebrate prey (Horn 2016), none of which have been surveyed

for parasites. Consequently, a far more comprehensive survey of prey would be needed to fully quantify the shark's tapeworm encounters, and accordingly, to determine the full importance of diet as an encounter filter for tapeworms. As highlighted by previous research on parasite encounter and compatibility filters, quantifying all parasite encounters is logistically challenging and requires a considerable amount of time and resources (Combes 2001; Kuris et al. 2007). Nevertheless, the data here provide a useful starting point for such research.

Prior to this research, *C. isabellum* was considered a cold spot in shark tapeworm diversity because it has fewer described tapeworm species than expected for a shark of its size (Randhawa 2014, unpublished data). The results here are consistent with this notion, given that all 24 of the sharks' spiral valves examined were exclusively infected by their only known tapeworm, *Calyptrobothrium chalarosomum*. It is still possible that the parasite assemblages of *C. isabellum* vary on a greater spatial scale. These sharks are known to occur across the entire coastal shelf around the North, South and Stewart Islands of New Zealand (Horn 2016), but so far records of their tapeworms have only been obtained from sharks examined off the east coast in Otago (present study), Oamaru, and from sharks inhabiting waters at the bottom of the North Island (Alexander 1963). To fully confirm the shark's low diversity of tapeworm species, individuals should be examined across their entire range, including waters off the West Coast, upper North Island, and offshore islands.

There was considerable variation in the intensity of *Calyptrobothrium chalarosomum* infection among the sharks inspected in this study, but the size, sex and sample of individuals did not significantly affect intensity. The intensity of tapeworm infections has been shown to generally increase with host size in fishes (see Poulin 2000). However, studies of elasmobranchs have shown mixed results (Cislo & Caira 1993; Sanmartin et al. 2000; Friggens & Brown 2005), and consistent with findings herein, some demonstrate that host length has little impact on tapeworm intensity of infection (Cislo & Caira 1993; Randhawa and Poulin 2009). It has been noted that the relationship may be in part masked by differences in tapeworm size, since there is a trade-off between the size and number of worms in the limited space and resources of a host, i.e. "crowding effect" (Read 1951; Roberts 2000; Randhawa and Poulin 2009). Regarding the effect of host sex on tapeworm intensity, it was interesting that

although the difference was marginally non-significant here, male draughtsboard sharks generally harboured more tapeworms than females. Differences in infection intensity between sexes may reflect physiological or behavioural differences between male and female hosts (Zuk 1990; Poulin 1996). It is possible for example, that male and female draughtsboard sharks have different dietary preferences, whereby males are exposed to more tapeworm larva in their prey. Diet has not been analysed per sex in *C. isabellum*, however (Horn 2016), and in any case, high variation in tapeworm intensity was also observed within each sex and sample of sharks. Thus, larger sample sizes are needed to determine whether the differences seen here are consistent on a larger scale.

The overall diet composition of *C. isabellum* showed substantial overlap with previous records, reinforcing the notion that crustaceans, teleosts and molluscs are all important prey groups for this shark (Graham 1956; Horn 2016). Much like Horn's (2016) New Zealand-wide diet analysis, the present study showed that crabs dominate the diet in terms of occurrence (%O), and several crab species identified here had already been described as prey of *C. isabellum*. On the other hand, it was found here that the siphons of geoduck clams (*Panopea zelandica*) constituted a large part of the diet for individuals caught off Otago; this is the first record of these molluscs as prey. Given that there was a general absence of the clam's shells and other parts in stomach contents, it is suggested that the sharks likely bite off *P. zelandica* siphons while foraging, rather than eating them whole. Horn (2016) noted that similarly with findings here, despite feeding on many hermit crabs and gastropods, there are rarely shells or shell fragments in *C. isabellum* stomach contents. Like other scyliorhinid sharks, draughtsboard sharks may actively use their snouts to flip over protected invertebrates and eat only the exposed prey (Brightwell 1953; Horn 2016). This would allow them to avoid hard shells and materials that are difficult to digest and have little to no nutritional value. Remarkably, many other bivalve species have been recorded as intermediate hosts of elasmobranch tapeworms, but the infection of tapeworm larvae is generally restricted to the gonads, digestive gland and digestive tract of these bivalve hosts (Lauckner 1983; Hine & Thorne 2000; Vázquez & Cremonte 2017). This indicates that feeding on these siphons is unlikely to yield in tapeworm transmission for *C. isabellum*.

The complete absence of tapeworm larval stages that was observed in hermit crabs *Pagurus spinulimanus* suggests that they are unlikely intermediate hosts of elasmobranch tapeworms off the coast of Otago. By having a diet that consists largely of these hermit crabs, *C. isabellum* may inadvertently avoid potential encounters with tapeworms. However, this is not to say that all hermit crabs in their diet are scarce sources of tapeworms, since *C. isabellum* probably eat many other species which have not been surveyed for parasites. Overseas, several hermit crab species have been confirmed to host proceroid and plerocercoid larval stages of tapeworms that mature in sharks (Abbott 1987; Cherry et al. 1991; Smolowitz et al. 1993; McDermott et al. 2010). The most studied tapeworm species in hermit crabs, *Calliobothrium verticillatum*, has showed more than 95% prevalence in *Pagurus* sp. from the Woods Hole region, Massachusetts (Cherry et al. 1991). Interestingly, these tapeworms have also been described from brachyuran crabs (Fyler 2007), highlighting the potential for both hermit crabs and brachyuran crabs to be intermediate hosts of the same tapeworm larva. In the several small samples of brachyuran crabs examined for parasites in this study, no tapeworm larval stages were found. Nevertheless, the crab species examined from this area of Otago may harbour tapeworm larvae at a low prevalence, and hence, considerably larger sample sizes of these species must be surveyed to determine whether they host tapeworm larval stages. It is also worth noting that individuals in other areas may be more heavily infected, given that the prevalence and abundance of marine parasites often varies substantially across spatial and temporal scales (Smith 2001; Latham & Poulin 2003; Byers et al. 2008). Accordingly, further research on the parasites of these crabs would likely benefit from surveying individuals across other areas and during different seasons.

Despite not recovering any larval tapeworms from the ascidians, hermit crabs and brachyuran crabs examined, it is worth noting that all species were found to be infected with small nematodes, and some individual hermit crabs and ascidians also harboured small mites. Hermit crabs and other decapod crustaceans are known to sometimes harbour juvenile nematodes that mature in marine fishes (Poinar and Kuris 1975; Moravec et al. 2003; McDermott et al. 2010). Conversely, the nematodes of crabs examined herein were not encysted, and are probably not parasitic. However, further insights into the nature of this relationship will require additional studies and molecular tools for specific identification of the nematodes. Based on mites known

from other hermit crabs, the mites found on *P. spinulimanus* in this study are also unlikely to be parasitic, and are probably symbiotic or commensal associates (McDermott 2010). Though it has been pointed out that the nature of relationships between mites and hermit crabs are generally unknown and warrant further investigation (O'Connor 1982, McDermott 2010).

4.4.1. Conclusions

The limited application of this study toward determining the importance of encounter filters for *C. isabellum* emphasises that analysing encounter filters for parasite infection is a very challenging task. Difficulties in estimating parasite encounters have been acknowledged by many researchers seeking to understand the importance of encounter and compatibility filters in hosts (Combes 2001; Kuris et al. 2007; Lagrue et al. 2011; Medeiros et al. 2013). In some host-parasite systems it may be possible to find good proxies for parasite encounter rates (Medeiros et al. 2013), but this is not possible for trophically transmitted parasites that use many different intermediate hosts to encounter their final host. In tapeworms of elasmobranchs, for example, the importance of encounter filters is hard to estimate without conducting comprehensive surveys of parasites from all of the elasmobranch's prey. Surveys can focus on prey species that are known to be most important in the final host's diet, since these species are the most encountered, and therefore, the quantity of larval parasites they harbour should be good indicators of how many parasites are typically encountered by the host. However, the most important prey in the diet are not necessarily the most important intermediate hosts (Cirtwill et al. 2017), and as illustrated by the findings here, there may be important prey which don't harbour larval stages of parasites known to infect the final host as adults. Ultimately, where there is sufficient time and resources available for researchers to quantify a host's encounters with trophically-transmitted parasites, it would be ideal to survey as many of their common prey for parasites as possible. However, it is suggested that smaller scale studies can still prove to be a valuable tool for analysing parasite encounters. Despite not finding any links in the life-cycles of local elasmobranch tapeworms, the results of this study provide new ecological and parasitological data for draughtsboard sharks and some of their selected prey, and offer some important insights that may aid further research towards better understanding the influence of encounter and compatibility filters of

tapeworms in the model species *C. isabellum* and other South Island (NZ) elasmobranchs.

Chapter 5: Discussion

5.1. Summary of main findings and their implications

The overall objective of this thesis was to assess what factors influence the structure and diversity of tapeworm parasite assemblages in sharks, with focus on the importance of host diet. Previous research has already provided insights on several important determinants for tapeworm infections in elasmobranchs. These include a combination of phylogenetic factors, such as the interface between tapeworm attachment structures and host gut morphology (Williams 1960; 1966; 1968; Randhawa & Burt 2008), immune response (McVicar & Fletcher 1970; Randhawa & Burt 2008) and ecological factors, such as host size, depth, and latitude (Randhawa & Poulin 2010). However, a number of potentially key determinants, including the breadth and composition of host diet, have been recognised as crucial gaps in knowledge (Randhawa & Poulin 2010). The present research aimed to investigate these gaps on a broad scale by assessing the relative importance of host diet features (diet breadth, diet composition and trophic level) as predictors of tapeworm diversity across a large subset of different shark species (Chapter 2). Furthermore, literature records were used to conduct a comprehensive analysis of the relationship between shark's diet compositions and tapeworm compositions (Chapter 3). And finally, these gaps in knowledge were investigated on a smaller scale by analysing the importance of host diet for tapeworm encounter in a local shark species, *Cephaloscyllium isabellum* (Chapter 4). This shark species was selected as a model given its relatively broad diet and restricted tapeworm diversity.

The present research revealed that the diet breadth of a shark species, measured as its number of known prey families, is a better predictor of tapeworm species richness than other host features examined to date (Chapter 2). Thus, it is suggested that shark species with broad diets generally encounter and become infected with more tapeworm species than those with restricted or specialised diets. This has important implications not only for tapeworm diversity in sharks, but also for the diversity of trophically transmitted parasites in general. This study is the first to examine the influence of host diet on tapeworm diversity in elasmobranchs, and to my knowledge, is the most comprehensive analysis of tapeworm diversity in sharks to date. Few empirical studies in other host-parasite systems have demonstrated diet breadth to be important for the diversity of trophically-transmitted parasites (e.g. Chen et al. 2008;

Locke et al. 2014). Moreover, other comparative studies looking at determinants of parasite diversity have rarely analysed diet breadth as a factor (Kamiya et al. 2014). Thus, the findings herein emphasise that diet breadth could be very important for parasite diversity in other systems too, and should be more seriously considered in comparative studies among other commonly tested predictors of parasite diversity (e.g. host size, geographical range and population density).

Although the findings here establish diet breadth to be a key determinant of tapeworm richness in sharks, it was also made evident that it cannot be considered as a universal determinant of tapeworm diversity in all shark species. There are some shark species which are clear exceptions to the rule, demonstrated in chapter four with the model species *C. isabellum*. *C. isabellum* was found to have a relatively broad diet consisting of a variety of teleost fishes, crustaceans and other benthic invertebrates. Yet, it was shown to have a limited tapeworm fauna, with all individuals examined being exclusively infected by one species; *Calypotrobothrium chalarosomum*. This finding ultimately reinforces the notion that *C. isabellum* is a cold spot in shark tapeworm diversity, meaning that it harbours fewer tapeworm species than is expected for a shark of its size (Randhawa 2014, unpublished data; see Poulin et al. 2011b). Prior to this research, it was thought that *C. isabellum* could be a cold spot in tapeworm diversity due to compatibility filters (e.g. immune response) that eliminate potential tapeworm infections. However, given that no larval tapeworms were recovered in this research, testing for such compatibility filters was beyond the scope of the present study and still requires further investigation. The lack of tapeworm larval stages observed in some of the local prey species of this shark (hermit crabs and various brachyuran crabs) could also indicate that *C. isabellum* is a cold spot in tapeworm diversity because its preferred prey taxa are not intermediate hosts for tapeworms that mature in elasmobranchs. Without further surveys of its other prey, this can only be speculated. However, these results highlight the fact that certain prey taxa in a shark's diet are likely to be considerably more relevant for tapeworm encounters than others.

The potential for highly variable distributions of tapeworm larval stages among prey is perhaps best illustrated in chapter three, where it was found that certain families of perciform fishes are substantially more important intermediate hosts of

trypanorhynch-species larvae than other prey families. This notion has also been supported by extensive surveys of some fish families which have revealed particular taxa to be devoid of any tapeworm larvae (Beveridge et al. 2014). In chapter two, a negative relationship was found between the tapeworm richness of sharks and the average TD (taxonomic distinctness) of prey in their diets, which could also reflect this minor importance of certain prey as intermediate hosts. It was reasoned that sharks eating very unique and taxonomically different prey might often consume taxa that are irrelevant for tapeworm transmission, therefore resulting in species-poor tapeworm assemblages. Whether or not this is the case, this result clearly demonstrates that general diet breadth (richness of prey families) and diet TD, despite both being relative measures of diversity, reflect very different properties. Although the average TD of species assemblages is often included in ecological studies to complement simpler measures of diversity (i.e. species richness) (Von Euler & Svensson 2001; Heino et al. 2005; Winter et al. 2013), to my knowledge TD has only been implemented to measure aspects of diet in one other study comparing the diets of turtles (Stringell et al. 2016). The different patterns observed in this research for diet breadth and diet TD indicate that diet TD can provide unique and interesting insights into the feeding ecology of animals. As such, I encourage future comparative diet studies to consider investigating diet TD in conjunction with other aspects of diet.

It was clear from the present research that sharks' diets not only have important implications for the diversity of their tapeworms, but also have large consequences for the structure and composition of their tapeworm assemblages (Chapter 3). A significant positive correlation was found between similarities in shark diet composition and similarities in tapeworm composition, meaning that shark species are more likely to share tapeworm taxa if they have similar diets. This relationship supports the idea that tapeworms can be useful indicators of the feeding ecology of their definitive shark hosts (Palm et al. 2017). Further support for this point can be seen in comparisons of tapeworm families among sharks with different dominant prey groups. Tapeworm families were observed to be remarkably different between crustacean-feeding and teleost-feeding shark species, reflecting underlying differences in the life cycles of their tapeworms. Chapter three used several examples to illustrate that the tapeworm families common in crustacean-feeding sharks generally use crustaceans as second intermediate hosts, whereas tapeworm families of

teleost-feeding sharks generally use teleosts or cephalopods as second intermediate hosts (see Palm 2004). These associations have important implications for ecologists who want to know the general feeding habits of poorly studied shark species. Notably, certain tapeworm taxa may be used to make predictions about a host's diet. For example, if a host is known to harbour echinobothriid tapeworm species, we could say that its diet is likely dominated by crustaceans and other benthic invertebrates, which are known to be their second intermediate hosts (Vivares 1971; Cake 1976; Tyler 2006) (see 3.4.1 for more examples). In some cases, these predictions may also work in reverse to inform ecologists of the likely intermediate hosts of certain tapeworms. Such information is extremely valuable given the current paucity of information on the life cycles of marine tapeworms (Caira & Reyda 2005; Jensen & Bullard 2010; Caira & Jensen 2017). Research on tapeworm life cycles has also been declining over the last few decades and is failing to keep up with new species descriptions, further highlighting the importance of this research (Blasco-Costa & Poulin 2017).

Tapeworm compositions were demonstrated to significantly differ between sharks of different taxonomic Orders, with carcharhiniform sharks being characterised by different tapeworm families than both lamniform and squaliform sharks (Chapter 3). This highlights the fact that tapeworm assemblages are fundamentally shaped both by host ecology and host evolutionary history, and emphasises the need to consider both aspects when looking at parasites as indicators of host ecology. Although previous research has given some insight into the importance of host diet and evolutionary history for the structure of trypanorhynch tapeworm assemblages in sharks (see Palm et al. 2017), the present research is the first to use ecological and phylogenetic data of host species to make inferences about the potential life cycles of tapeworms in other taxonomic Orders. Furthermore, this research offers new insights on more specific aspects of host diets, which have only been examined prior at a very basic level (between vertebrate and invertebrate feeding sharks) (Palm et al. 2017). For instance, the tapeworms of cephalopod-feeding sharks were found to overlap considerably with both teleost-feeding and crustacean-feeding sharks, indicating that perhaps cephalopods are commonly intermediate or paratenic hosts in the same life cycles of teleosts and crustaceans. Overall, these insights provide a considerable step towards a better understanding of the complex relationships that exist between the ecology and

evolution of elasmobranch hosts and the composition of their tapeworm parasite assemblages.

A more comprehensive survey of the prey of *C. isabellum* is still clearly needed to determine the relative importance of its diet as an encounter filter for tapeworm parasite diversity. However, although the prey survey conducted here offered very limited insights regarding the life-cycles of local elasmobranch tapeworms, important new data were provided on both the parasites and diet of *C. isabellum*. The geoduck clam *Panopea zelandica* was revealed as a new diet record for *C. isabellum*, and was found to be very important prey for individuals inhabiting the Otago region. *Panopea zelandica* has been recognised to lack current ecological information, but has recently gained increased attention as a potential target for commercial exploitation (Gribben & Heasman 2015). Likewise, *C. isabellum* has been identified as one of the shark species most at risk to commercial fishery impacts in New Zealand, but is also acknowledged that significant knowledge gaps remain regarding its basic biology and ecology (Ford et al. 2015; Horn 2016). Thus, the diet information herein may be of use for fisheries involving these species. On top of this, these findings provide a small step for further research towards better understanding the influence of encounter and compatibility filters of tapeworms in *C. isabellum* and other South Island (NZ) elasmobranchs.

5.2. Further research

The current research established some strong ecological patterns that demonstrate host diet as an important factor governing tapeworm assemblages in sharks. These patterns were established by large-scale comparative analyses across different species and by some limited observations in the model shark species *C. isabellum*.

Nevertheless, there is still great room for future comparative studies to extend on this work and provide a better understanding of the intricacies within these patterns.

Furthermore, there is a need for the patterns established here to be backed up with experimental evidence. Notably, questions remain as to whether encounter filters or compatibility filters are more important barriers to tapeworm infections in *C.*

isabellum and other elasmobranchs. These questions cannot be fully answered by

observational studies alone, and will require explorations of host-parasite compatibility in future experimental studies.

This research identified several key knowledge gaps in the literature that, if addressed, may considerably improve our understanding of the relationship between the diet of shark hosts and the diversity and structure of their parasite assemblages. First and foremost, available data on hosts' diets and parasites are conspicuously biased towards shark species of the Order Carcharhiniformes. It could be argued that this is the result of carcharhiniform species being some of the most important, abundant and widespread sharks inhabiting our oceans (Compagno 2001). However, to further our knowledge of the diversity and evolution of parasite lineages in sharks, there is a need to prioritise the sampling of diets and parasites across shark species of other taxonomic Orders. The diets of some lesser-studied shark species could be poorly known for conservational or ethical reasons (since most diet sampling is lethal). However, several studies have demonstrated the efficacy of non-lethal methods of diet sampling e.g. gastric lavage (Foster 1977; Barnett et al. 2010; Hammerschlag & Sulikowski 2011). These methods warrant consideration in further research aiming to elucidate the diets of important shark species, especially those that are endangered or identified as conservation risks.

Another key knowledge gap that may be of interest to future research is how intraspecific variation in the diets of elasmobranchs affects their tapeworm assemblages. In the present study, tapeworms and prey were viewed for each shark species as the sum of all records known for the species. However, diets may vary substantially with the size or age of individuals (e.g. Lowe et al. 1996; Ebert 2002), between different sexes (e.g. Klimley 1987; Borrell 2011), between seasons (e.g. Cortes et al. 1996), and between different geographical areas (e.g. Simpfendorfer et al. 2001; Bethea et al. 2007). The present research indicates that disparities in diet among these different sub-populations could have large consequences for their parasite assemblages. Though diet studies often look at differences in sharks' stomach contents among these different sub-populations, few diet studies have looked at the intestinal parasites of individuals in conjunction with their diets (for notable exceptions see Klimpel et al. 2003; Gracan et al. 2014; Isbert et al. 2015). I recommend that future studies examining elasmobranch stomach contents should also

examine the spiral valves of individuals for any potential parasites. Such studies will provide valuable insights into the effects of intra-specific diet variation on the diversity and composition of elasmobranch tapeworm assemblages. Furthermore, even where researchers are specifically interested in revealing species diets (i.e. have no interest in parasitological data), as demonstrated within this research, tapeworms can provide additional information on species' feeding habits. In some cases, tapeworm assemblages could be even more informative given that stomach contents provide only a limited snapshot of a host's last meal, whereas tapeworms have the potential to reflect their longer-term feeding habits. The inclusion of parasite data in future diet studies will require raising the awareness of marine ecologists to these potential insights, and ultimately, better collaborations between marine ecologists and marine parasitologists (Poulin et al. 2016).

Future studies integrating diet and parasite data could perhaps also benefit from looking at how diet variation among closely related elasmobranchs affects their respective tapeworm assemblages. In chapter three of this thesis it was shown that deciphering the relative influence of feeding ecology and host evolutionary history on shark tapeworm assemblages can be very challenging. However, it would be possible to explore the relative influence of host ecology and evolutionary history in some species by looking at how tapeworm compositions vary among closely related sharks with different feeding habits. For example, in hammerhead sharks (*Sphyrna* sp.), there are some clear differences in feeding habits between species. *Sphyrna lewini*, *S. mokkaran* and *S. zygaena* all feed predominantly on fishes and cephalopods (Stevens & Lyle 1989; Smale 1991), whereas *S. tiburo* is a durophagous predator that feeds mainly on crustaceans (Cortés et al. 1996; Bethea et al. 2007). The dataset herein indicates that the three teleost-feeding hammerhead species each have relatively high tapeworm species richness, but *S. tiburo* appears to have low tapeworm richness (although it requires further study for parasites). A possible reason for this discrepancy could be that the ancestors of *S. tiburo* were mainly teleost-feeders, but *S. tiburo* has gone down an evolutionary path where it switched to feeding on crustaceans (see Lim et al. 2010). Considering this, the evolution of *S. tiburo* may have broken life cycles of ancestral tapeworms involving teleost fishes, resulting in a lower diversity of tapeworms for the species compared with other *Sphyrna* species.

These points can only be speculated without further research looking more specifically at the variations in diet and parasites among these species.

The present research showed a novel approach towards understanding encounter and compatibility filters for parasites in *C. isabellum*, by analysing host diet to determine parasite encounters. However, there is still a long way to go before the relative importance of these filters can be established. More comprehensive parasite surveys of the shark's prey will be needed to determine the relative influence of encounter filters. This will demand a considerable amount of time and resources (Combes 2001; Kuris et al. 2007). Nevertheless, no previous studies have quantified parasite encounters for elasmobranchs in this way, and the findings of such research could significantly advance our understanding of parasite filters in elasmobranchs. In addition, where larval parasites are recovered from prey in these surveys, this would open opportunities for experimental studies to test the strength of compatibility filters in elasmobranch hosts. For instance, larval tapeworms from known prey could be exposed to the host's blood sera and observed for mortality to determine whether immune response restricts potential tapeworm establishment i.e. whether immune response is a strong compatibility filter for the species (McVicar & Fletcher 1970; Randhawa & Burt 2008). Other compatibility filters could also be tested by setting up experiments where sharks are held in vivo and given anthelmintic drugs to remove their tapeworms. Subsequently, prey infected by larval tapeworms (that are not naturally found in the host) could be fed to individual hosts and assessed for whether they can successfully establish in the shark's digestive system as mature adult worms. These tests could potentially be done in species other than *C. isabellum*. However, the findings of this thesis reinforce that *C. isabellum* would be an ideal model for these studies given its relatively broad diet and low tapeworm diversity.

5.3. Conclusions

The observational studies carried out within this project emphasise that various aspects of sharks' diets can have important implications for their tapeworm parasite assemblages. It was demonstrated that the diversity of tapeworms infecting a shark species largely depends on the breadth of its diet. Furthermore, it was shown that certain prey taxa are considerably more important as intermediate hosts for

tapeworms than others, and ultimately, even sharks with broad diets may have a limited diversity of tapeworm species depending on their dietary preferences. Finally, it was found that certain tapeworm taxa in sharks are useful indicators of their ecology and evolutionary history, and may be used to make predictions about the host's feeding habits. Together these findings demonstrate some strong ecological patterns that establish host diet as an important determinant of tapeworm composition and diversity in sharks. However, there is a need for further exploration of these patterns with experimental research to validate the influence of these patterns in nature.

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Appendix

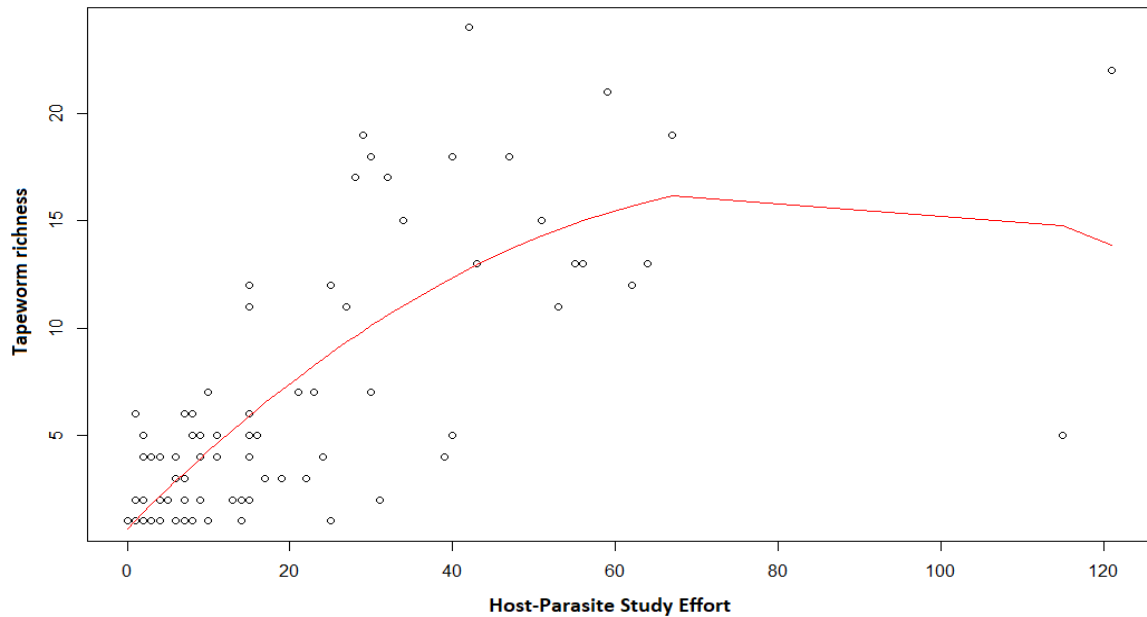


Figure A.1. Scatter plot showing the relationship between tapeworm richness and host-parasite study effort of shark species ($n = 91$). Tapeworm richness represents the sum of all tapeworm species known to infect the shark species (as adult stages) and host-parasite study effort is the total number of references obtained by searching parasite records for the host species on ISI Web of Knowledge. The solid line shows the fit of a quadratic regression of tapeworm richness on study effort.

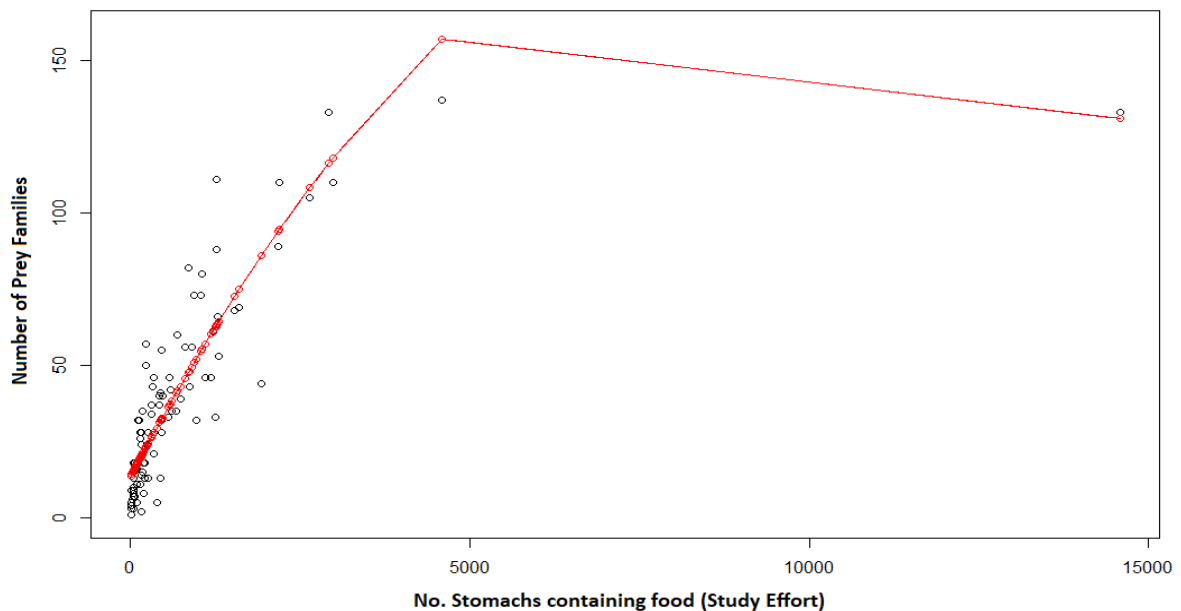


Figure A.2. Scatter plot showing the relationship between number of prey families (diet breadth) and the number of stomachs examined containing food (study effort for diet) for 91 shark species. Number of prey families is how many different taxonomic families were recorded across all diet references available for a species on ISI Web of Knowledge and number of stomachs containing food represents the sum of how many stomachs were examined for diet contents across these references. The solid line shows the fit of a quadratic regression of number of prey families on study effort.

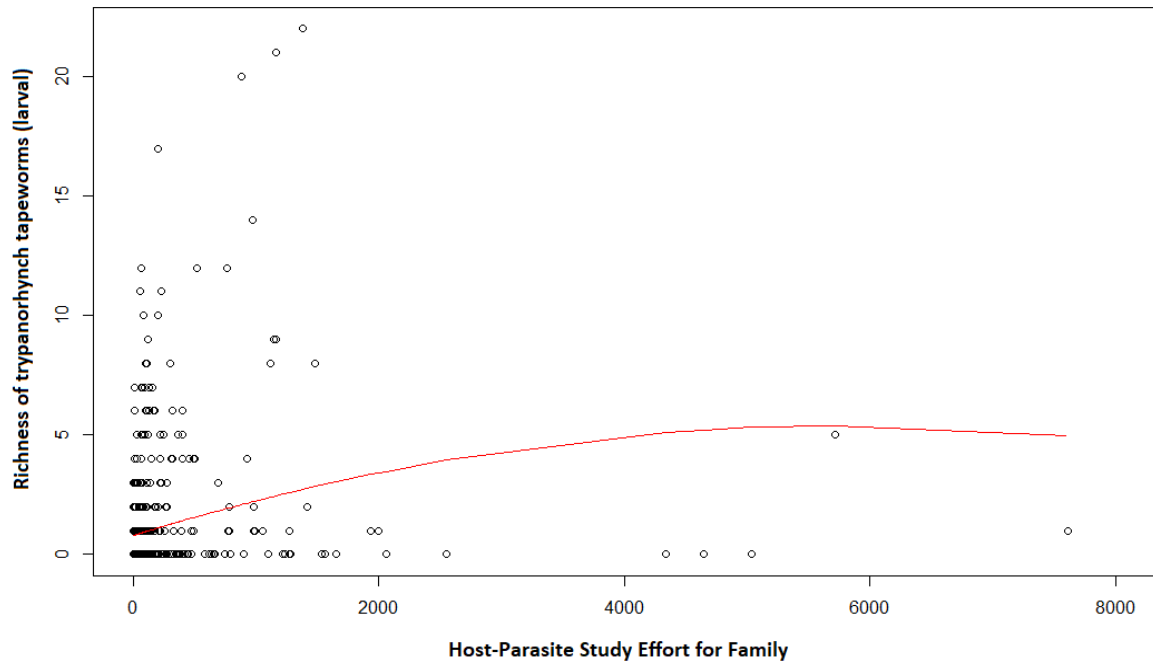


Figure A.3. Scatter plot showing the relationship between richness of trypanorhynch tapeworms (larval stages) known to infect an animal family and the study effort of the family for parasites ($n = 626$). Study effort represents the total number of references obtained by searching parasite records for the animal family on ISI Web of Knowledge. The solid line shows the fit of a quadratic regression of trypanorhynch tapeworm richness on study effort.

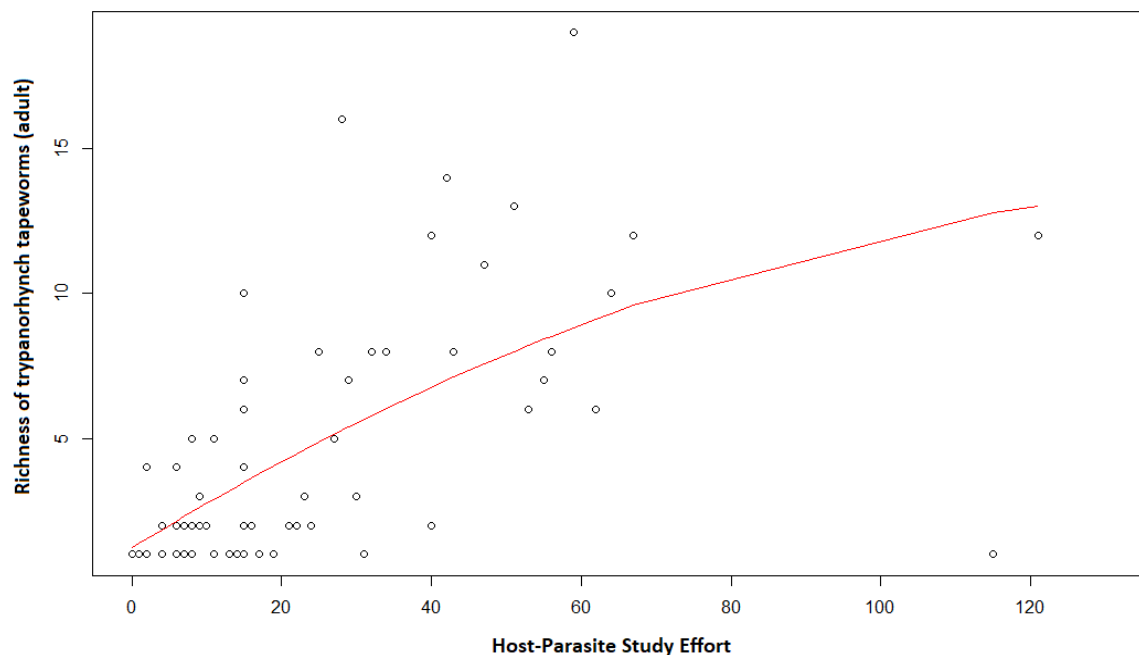


Figure A.4. Scatter plot showing the relationship between richness of trypanorhynch tapeworms (adult stages) known to infect a shark species and the study effort of the shark species for parasites ($n = 71$). host-parasite study effort is the total number of references obtained by searching parasite records for the shark species on ISI Web of Knowledge. The solid line shows the fit of a quadratic regression of trypanorhynch tapeworm richness on study effort.

Table A.1. Table displaying tapeworm species richness and diet breadth (prey family richness) for 91 different shark species. For each shark host species, families of prey are listed with their respective references indicated in brackets following each name. This dataset on shark families was obtained from ISI Web of Knowledge. Taxa of each shark here (Latin name plus all known synonyms) combined with keywords “diet* OR feed* OR prey*” were searched on ISI Web of Knowledge (all databases) and all available references from 1864 to 2017 were perused for records on shark diets (Searches conducted April 2017). The total number of references listed, references with diet information, and sum of stomachs examined containing food are given for each shark species. The total sum of stomachs examined (including empty stomachs) is included in parentheses and indicates minimum estimates.

Shark Species	Total No. Prey Families	List of prey families in diet of shark species [references]	Total No. Refs	Refs with diet info	Stomachs examined with food (total Inc. empty)
<i>Alopias superciliosus</i>	42	Alepisauridae [8], Ancistrocheiridae [1-2,6], Belonidae [1-2,5-6], Carangidae [4], Clupeidae [1-2,4-6,8], Coryphaenidae [1-2,5-6], Cranchiidae [4], Echeenidae [1-2,5], Engraulidae [4], Enopoteuthidae [1-2,6], Exocoetidae [1,5-6], Fistulariidae [1-2,5-6], Gonatidae [4], Hemiramphidae [5], Histioteuthidae [1-2,4-6], Istiophoridae [8], Loliginidae [2,4-5], Lutjanidae [1,6], Mastigoteuthidae [1-2,5-6], Merlucciidae [1-2,4-6], Munididae [4], Myctophidae [1-2,5], Octopoteuthidae [1,4,6], Ommastrephidae [1-2,4-7], Ophichthidae [1-2,6], Ophidiidae [5], Paralepididae [4], Penaeidae [5], Pholidoteuthidae [2], Sciaenidae [1-2,5-6], Scomberesocidae [4], Scombridae [1-2,4-6,8], Scorpaenidae [1,6], Sebastidae [4], Serranidae [1,6], Solenoceridae [6], Steniteuthidae [1], Synodontidae [1], Tetraodontidae [1-2,5-6], Thysanoteuthidae [2], Trachipteridae [4,6], Trichiuridae [3],	26	8	448 (523)
<i>Alopias vulpinus</i>	21	Arripidae [9], Atherinidae [10,12], Berycidae [9], Carangidae [9-10,12-13], Clupeidae [9-12], Engraulidae [9-12], Gadidae [13], Gonatidae [12], Loliginidae [10-12], Luvaridae [12], Merlucciidae [10-12], Munididae [12], Ommastrephidae [10-11], Paralepididae [10], Paralichthyidae [10,12], Sciaenidae [12], Scomberesocidae [10], Scombridae [11-13], Sebastidae [10-12], Sphyraenidae	31	5	349 (506)

[12], Stromateidae [12]						
<i>Carcharhinus acronotus</i>	5	Loliginidae [14], Muraenidae [14], Octopodidae [14], Pomacentridae [14], Serranidae [14]	12	1	19 (86)	
<i>Carcharhinus amblyrhynchoides</i>	14	Ariidae [17], Carangidae [17], Clupeidae [17], Hemiramphidae [36], Labridae [17], Leiognathidae [17,36], Ophichthidae [17], Penaeidae [17,36], Platycephalidae [17], Plotosidae [17], Scombridae [17], Sillaginidae [17], Squillidae [17], Terapontidae [17]	2	2	163 (241)	
<i>Carcharhinus amblyrhynchos</i>	24	Acanthuridae [16], Apogonidae [37], Ariidae [38,285], Carangidae [38,285], Chaetodontidae [16], Clupeidae [38], Elapidae [37], Gerreidae [36], Hemiramphidae [38], Holocentridae [16], Leiognathidae [36], Monacanthidae [16], Mugilidae [38], Mullidae [36], Muraenidae [16,37-38], Octopodidae [37], Palinuridae [15], Penaeidae [36,285], Pomacentridae [16], Scaridae [16], Scombridae [17], Scorpaenidae [16], Sepiidae [37], Zanclidae [16]	25	9	173 (400)	
<i>Carcharhinus amboinensis</i>	50	Acanthuridae [19], Ariidae [17-19], Carangidae [18-19], Carcharhinidae [18-20], Chanidae [18], Chirocentridae [19], Clupeidae [17], Cynoglossidae [18], Dasyatidae [19], Delphinidae [18], Diodontidae [18], Elapidae [19-20], Engraulidae [20], Gobiidae [19], Gymnuridae [18], Haemulidae [18], Istiophoridae [17], Labridae [19], Leiognathidae [18-19], Loliginidae [17,19], Megalopidae [19], Mugilidae [18], Myliobatidae [18], Octopodidae [18], Ommastrephidae [19], Oplegnathidae [18], Penaeidae [19], Platycephalidae [18], Pomacanthidae [19], Pomatomidae [18], Polynemidae [17,19-20], Portunidae [17], Psettodidae [19], Rhinobatidae [18], Sciaenidae [18-19], Scombridae [17-19], Scyliorhinidae [18], Sepiidae [18-19], Sepiolidae [19], Serranidae [18], Sparidae [18-19], Sphyrnidae [18], Squatinidae [18], Squillidae [19], Synodontidae [18], Terapontidae [19], Tetraodontidae [19], Triacanthidae [20], Triacanthodidae [20], Trichiuridae [18]	9	4	227 (338)	
<i>Carcharhinus brachyurus</i>	56	Alcyoniidae [22], Apogonidae [23], Arhynchobatidae [22], Arripidae [9], Atherinidae [22-23], Batrachoididae [22], Callianassidae [23], Callorhynchidae [22-23], Carangidae [9,21,23], Cheilodactylidae [23], Clupeidae [9,21-23],	12	4	895 (2264)	

Congridae [22], Delphinidae [21], Dussumieriidae [21,23], Engraulidae [9,22-23], Gadidae [9], Gempylidae [9], Haemulidae [21,23], Hemiramphidae [9], Labridae [9], Loliginidae [9,21,23,39], Merlucciidae [23], Monacanthidae [9], Mugilidae [9,21,23], Mullidae [21], Myliobatidae [21-23], Nassariidae [22], Octopodidae [23], Odacidae [9], Ommastrephidae [9,23], Ophidiidae [9,23], Ovalipidae [9], Penaeidae [9,23], Pentanchidae [21], Percophidae [22], Pinguipedidae [22], Platycephalidae [9], Plotosidae [9], Pomatomidae [21], Rajidae [9,22], Rhinobatidae [21,23], Sciaenidae [9,22-23], Scombridae [9,21,23], Scorpaenidae [9], Sepiidae [9,21,23], Serranidae [22-23], Sillaginidae [9], Sparidae [9,21-23], Sphyaenidae [9], Squalidae [21,23], Squatinidae [21-22], Stromateidae [22], Terapontidae [9], Triakidae [22], Trichiuridae [21], Urolophidae [9]

<i>Carcharhinus brevipinna</i>	33	Ancistrocheiridae [26], Ariidae [25-26], Carangidae [17,24,26], Carcharhinidae [26], Clupeidae [17,24-25], Engraulidae [24-27], Exocoetidae [24], Gerreidae [17,26], Haemulidae [24,26], Leiognathidae [17,26], Loliginidae [26], Monacanthidae [17], Monodactylidae [26], Mugilidae [24,26], Mullidae [17,26], Muraenidae [24], Nemipteridae [17], Octopodidae [24,26], Paralichthyidae [24], Pomacanthidae [26], Pomatomidae [26], Rhinobatidae [26], Sciaenidae [25-26], Scombridae [17,24,26-27], Sepiidae [26], Soleidae [26], Sparidae [26], Sphyaenidae [24,26], Sphyrnidae [26], Syngnathidae [25], Synodontidae [24,26], Trichiuridae [26], Triglidae [26]	27	6	559 (2038)
<i>Carcharhinus dussumieri</i>	40	Anguillidae [17], Apogonidae [17], Balistidae [17], Bothidae [17], Bregmacerotidae [17], Callianassidae [17], Callionymidae [17], Carangidae [38], Centriscidae [17], Clupeidae [17], Congridae [17], Cynoglossidae [17], Engraulidae [17,38,40], Fistulariidae [17], Gerreidae [36], Gobiidae [17,38], Hemiramphidae [36], Hypoptychidae [17], Labridae [17,38], Leiognathidae [17,36,38,40], Loliginidae [17], Monacanthidae [17,36], Mugilidae [17,36], Mullidae [17], Muraenesocidae [17], Muraenidae [17], Myctophidae [17], Nemipteridae [17], Ogcocephalidae [17], Penaeidae [17,36, 40], Platycephalidae [17], Portunidae [17], Priacanthidae [17], Raninidae [17], Scombridae [17],	4	4	470 (695)

		Scorpaenidae [17], Squillidae [17], Synodontidae [17], Tetraodontidae [17], Uranoscopidae [17]			
<i>Carcharhinus falciformis</i>	44	Alloposidae [29], Amphitretidae [29], Ancistrocheiridae [2,28-30], Argonautidae [2,17,28-30], Balistidae [2,17,28,30-31], Carangidae [2,28-30], Clupeidae [30], Coryphaenidae [2,28-30], Diodontidae [29], Echeneidae [29], Enoploteuthidae [28], Exocoetidae [29-31], Galatheidae [29], Gempylidae [28], Gobiidae [31], Gonatidae [2,30], Haemulidae [30], Hemiramphidae [29], Histioteuthidae [2,30], Istiophoridae [29], Kyphosidae [29], Labridae [2,30], Mastigoteuthidae [29], Molidae [29], Monacanthidae [17,28], Mugilidae [41], Munididae [29-30], Myctophidae [28-29], Nomeidae [28-29], Octopodidae [28], Octopoteuthidae [29], Ommastrephidae [2,28-31], Onychoteuthidae [2,28-29], Ostraciidae [29], Penaeidae [2], Polynemidae [31], Portunidae [17,28-29,31], Priacanthidae [2,28,30], Scombridae [2,27-31], Sepiidae [17], Sphyraenidae [28,30], Tetraodontidae [29-30], Tremoctopodidae [29], Vitreledonellidae [29]	31	7	864 (1447)
<i>Carcharhinus galapagensis</i>	16	Acanthuridae [32], Balistidae [32], Belonidae [32], Carangidae [32], Clupeidae [32], Diodontidae [32], Holocentridae [32], Lethrinidae [32], Monacanthidae [32], Muraenidae [32], Pomacentridae [32], Priacanthidae [32], Scaridae [32], Scombridae [32], Serranidae [32], Synodontidae [32]	10	3	96 (178)
<i>Carcharhinus isodon</i>	11	Carangidae [25,33], Carcharhinidae [34], Clupeidae [25,33-35], Elopidae [25], Engraulidae [25], Penaeidae [34-35], Portunidae [33], Sciaenidae [25,33-34], Scombridae [33-34], Sparidae [25], Syngnathidae [25]	10	4	142 (293)
<i>Carcharhinus leucas</i>	73	Achiridae [46], Ambassidae [19], Anguillidae [19], Ariidae [19,42,45-47], Batrachoididae [46], Bradypodidae [44], Carangidae [19,42,45-46], Carcharhinidae [19,42,45-46], Centropomidae [19,44], Characidae [44], Cheilodactylidae [42], Cheloniidae [42,44,47], Cichlidae [42,44], Clariidae [42], Clupeidae [42-43,46-47], Coryphaenidae [42], Crocodylidae [47], Dasyatidae [19,42,45-46], Dermochelyidae [42], Dinopercidae [42], Drepaneidae [42], Elapidae [43], Eleotridae [44], Elopidae [46], Engraulidae [42], Ephippidae [42], Gecarcinidae [44], Gerreidae [45], Gobiidae [19,45], Haemulidae [42,44-45],	88	7	1034 (1967)

Hemiramphidae [47], **Hominidae [42]**, Labridae [42], Lamnidae [42], Latidae [47],
 Leiognathidae [19], Lepisosteidae [44], Lutjanidae [44], Megalopidae [44],
 Monodactylidae [42], Mugilidae [42,44,46-47], Muraenidae [42], Myliobatidae
 [42,45], Octopodidae [42], Odontaspidae [42], Ophichthidae [46],
 Osteoglossidae [19,47], Ovalipidae [42], Palaemonidae [19,47], Penaeidae [46],
 Platycephalidae [42], Plotosidae [42], Polynemidae [47], Pomatomidae [42],
 Portunidae [45-46], Pristidae [44,47], Rhinobatidae [42], Sciaenidae [42,45-47],
 Scombridae [19,42,45], Scyliorhinidae [42], Sepiidae [42], Serranidae [42],
 Sesarmidae [42], Sparidae [42,46], Sphyrnidae [42,45], Squalidae [42],
 Squatinidae [42], Stegostomatidae [42], Suidae [47], Synbranchidae [19],
 Synodontidae [42,46-47], Triakidae [42], Tyrannidae [44]

<i>Carcharhinus limbatus</i>	72	Acanthuridae [54], Achiridae [33], Albulidae [54,56], Ariidae [25,38,48,51,55], Atherinopsidae [53], Balistidae [48,50,56], Batrachoididae [55], Belonidae [48,54], Berycidae [48], Blenniidae [48], Bothidae [33,53], Carangidae [25,48,50,53-54], Carcharhinidae [48,55], Chaetodontidae [54,56], Cichlidae [48], Clupeidae [25,33,35,38,40,48,50-51,53-56], Cynoglossidae [38,48], Dasyatidae [33], Delphinidae [48], Dinopercidae [48], Echeneidae [48], Elopidae [25,48], Engraulidae [25,48,50,53], Ephippidae [51], Gerreidae [54,56], Gymnuridae [48], Haemulidae [48,50,54,56], Hemiramphidae [50], Holocentridae [56], Kyphosidae [48], Labridae [48], Leiognathidae [40,48], Lethrinidae [38], Loliginidae [25,48,50,53], Lutjanidae [25,48,54,56-57], Megalopidae [51], Monodactylidae [48], Mugilidae [48], Mullidae [56], Muraenidae [49], Myliobatidae [50,55], Octopodidae [48], Ophichthidae [33], Oplegnathidae [48], Ostraciidae [48], Palinuridae [48], Paralichthyidae [50-51,55], Penaeidae [25,33,50-53], Plotosidae [48], Pomacanthidae [48], Pomacentridae [48,54], Pomatomidae [48], Rajidae [50], Rhinobatidae [48], Scaridae [54,56], Sciaenidae [25,33,38,48,50-51,53,55], Scombridae [27,48,55-57], Scyliorhinidae [48], Sepiidae [48], Serranidae [48], Sillaginidae [38], Sparidae [25,48,54,56-57], Sphyaenidae [49], Sphyrnidae [48,55], Squillidae [52], Stromateidae [33,53], Syngnathidae [25], Synodontidae	64	16	1624 (3056)
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		[25,40,48], Terapontidae [40], Tetraodontidae [48], Triacanthidae [38], Trichiuridae [33,48,50,53]			
<i>Carcharhinus longimanus</i>	9	Alepisauridae [58], Berycidae [27], Bramidae [58], Carangidae [27], Clupeidae [58], Coryphaenidae [59], Pomatomidae [27], Scombridae [58], Sparidae [27]	20	3	44 (89)
<i>Carcharhinus macroti</i>	11	Carangidae [17], Chirocentridae [17], Clupeidae [17], Dasyatidae [17], Engraulidae [17], Hoplichthyidae [17], Leiognathidae [17], Nemipteridae [17], Platycephalidae [17], Scombridae [17], Synodontidae [17]	2	1	91 (216)
<i>Carcharhinus melanopterus</i>	37	Acanthuridae [60], Aplysinidae [60], Apogonidae [63], Acrochordidae [63], Atherinidae [37], Balistidae [60], Carangidae [36], Chanidae [63], Elapidae [37,63], Ephippidae [63], Fistulariidae [37], Gerreidae [36], Haemulidae [36], Haliotidae [37], Labridae [37,60,63], Leiognathidae [36], Lethrinidae [60], Loliginidae [37], Lutjanidae [37,63], Monacanthidae [63], Mullidae [36,60], Muraenidae [37], Muridae [61] , Octopodidae [37], Platycephalidae [63], Pomacanthidae [37], Portunidae [60], Scaridae [37,60], Sparidae [63], Sternidae [37], Sulidae [61], Synodontidae [37],	45	6	133 (231)
<i>Carcharhinus obscurus</i>	105	Acanthuridae [67,319], Achiridae [66], Albulidae [65], Anguillidae [65,319], Apogonidae [65], Ariidae [23,64], Atherinidae [66], Aulopidae [65], Balistidae [64,66], Belonidae [319], Cancridae [66], Carangidae [9,50,64-65,67], Carcharhinidae [27,50,64-65,67], Cheilodactylidae [64-65], Cheloniidae [50], Chirocentridae [64], Chlorophthalmidae [64], Cichlidae [64], Clupeidae [9,23,64-65,67], Congridae [50,319], Cynoglossidae [64-65], Dactylopteridae [319], Dasyatidae [23,64-66], Delphinidae [64], Elopidae [64,67], Engraulidae [23,50,64,66-67], Enoploteuthidae [319], Ephippidae [50,319], Exocoetidae [64], Fistulariidae [68], Gempylidae [9,64], Gerreidae [64-65], Gobiidae [23,67], Gymnuridae [64], Haemulidae [23,64,67], Hemiramphidae [65], Heterodontidae [9,65], Istiophoridae [319], Kyphosidae [64-65], Labridae [65], Lamnidae [319], Leiognathidae [64], Lethrinidae [67], Limulidae [66], Loliginidae [23,50,64,66-67], Lophiidae [66], Lutjanidae [50], Lycoteuthidae [319], Macrouridae [64], Matutidae [67], Monacanthidae [65], Mugilidae [23,64-65,67], Mullidae [50,64-	41	10	2466 (6467)

65,67], Muraenidae [64], Myctophidae [319], Myliobatidae [64-65], Nassariidae [66-67], Neosebastidae [65], Octopodidae [9,23,64,67,319], Octopoteuthidae [319], Odacidae [9], Odontaspidae [64], Ommastrephidae [9,64], Ophidiidae [9], Oplegnathidae [64], Ostraciidae [64,68], Ovalipidae [9,66], Palinuridae [23,64,67], Paralichthyidae [50,65-66], Penaeidae [9,67], Pentacerotidae [65], Pentanchidae [64], Peristediidae [319], Platycephalidae [65,319], Pleuronectidae [319], Plotosidae [64-65], Pomacentridae [65,319], Pomatomidae [64,66-68], Priacanthidae [319], Pristigasteridae [64], Rajidae [50,64,66], Rhinobatidae [23,64-65], Scaridae [65], Sciaenidae [23,50,64,66-67], Scombridae [9,23,64-65,67], Scyliorhinidae [319], Sepiidae [9,23,64,67], Serranidae [23,64-65], Sillaginidae [9], Sparidae [9,23,64,67], Sphyrinae [9,64,67], Sphyrnidae [64-65], Spirulidae [67], Squalidae [319], Squatinidae [64], Stromateidae [66], Syngnathidae [65,319], Synodontidae [50,64,67], Terapontidae [319], Triakidae [64-65,67], Trichiuridae [23,50,67,319], Triglidae [50,66-67,319], Uranoscopidae [9,65-66], Urolophidae [65], Zeidae [23]

<i>Carcharhinus plumbeus</i>	110	Acanthuridae [70], Achiridae [69], Acropomatidae [73], Ammodytidae [17,69], Anguillidae [69,74-75], Apogonidae [73], Atherinopsidae [74], Aulostomidae [70], Balistidae [17,70,72], Belonidae [70,72], Bothidae [17,70-71], Callianassidae [69], Callionymidae [70], Cancridae [69,71,75], Caproidae [17], Carangidae [17,69-73], Carcharhinidae [69], Carcinidae [69], Centrolophidae [73], Chaetodontidae [70], Champsodontidae [17], Chauliodontidae [71], Clupeidae [69,71-72,74-75,81], Congridae [17,69-71,73], Cottidae [71], Crangonidae [69], Cynoglossidae [69], Dasyatidae [69,71], Diodontidae [70], Engraulidae [69,73-74,81], Ehippidae [69], Epialtidae [69], Exocoetidae [70], Fistulariidae [69-70], Fundulidae [69,74-75], Gadidae [71], Gonatidae [71], Holocentridae [70], Labridae [17,70-71], Leiognathidae [17], Lethrinidae [17], Leucosiidae [69], Limulidae [69], Littorinidae [69], Loliginidae [17,69,72,74,81], Lophiidae [69,71], Lutjanidae [70], Lysmatidae [69], Mactridae [69], Majidae [69], Merlucciidae [71], Monacanthidae [70], Monocentridae [17], Moronidae [69], Mugilidae [69,72-	87	10	2022 (2757)
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73,81], Mullidae [17,70,72], Muraenidae [70], Myliobatidae [69], Mytilidae [69], Nassariidae [69], Naticidae [69], Nemipteridae [17], Nuculidae [69], Octopodidae [72,76], Ommastrephidae [69,71,73], Ophidiidae [69,71], Ophichthidae [71], Ophiuridae [70], Ostraciidae [70], Ovalipidae [69,74-75], Paguridae [69], Paralichthyidae [69,74], Penaeidae [17,69,72], Pharidae [69], Phocoenidae [70], Phycidae [69,81], Pinguipedidae [17], Pleuronectidae [69,71], Pomacanthidae [17], Pomatomidae [69,71,74-75], Portunidae [69,74-75], Priacanthidae [17,70], Rachycentridae [69], Rajidae [69,71-72], Scaridae [70,76], Sciaenidae [69,74-75,81], Scombridae [17,70-72], Scopthalmidae [69], Scorpaenidae [70], Scutellidae [71], Scyliorhinidae [17], Sepiidae [72], Serranidae [69], Soleidae [72], Sparidae [69,72,81], Sphyrinaeidae [70], Squalidae [71], Squatinidae [81], Squillidae [69,72,74-75], Stromateidae [71,73,81], Syngnathidae [69-70,74], Synodontidae [17,70-71], Tetraodontidae [17,69-70,75], Triakidae [69,71,74,81], Trichiuridae [17,73], Triglidae [69-71,81], Upogebiidae [69], Uranoscopidae [69], Zanclidae [70], Zoarcidae [71]

<i>Carcharhinus porosus</i>	15	Achiridae [77], Ariidae [77], Carcharhinidae [77], Clupeidae [77], Dasyatidae [77], Engraulidae [77], Ephippidae [77], Loliginidae [77], Mugilidae [77], Penaeidae [77], Polynemidae [77], Portunidae [77], Sciaenidae [77], Stromateidae [77], Trichiuridae [77]	4	1	171 (684)
<i>Carcharhinus sealei</i>	6	Carangidae [78], Clupeidae [78], Hemiramphidae [78], Labridae [78], Lutjanidae [78], Nemipteridae [78]	1	1	30 (108)
<i>Carcharhinus signatus</i>	13	Acanthuridae [79], Bramidae [79], Chiroteuthidae [79], Cranchiidae [79], Histiotteuthidae [79], Howellidae [79], Myctophidae [79], Octopodidae [79], Octopoteuthidae [79], Ommastrephidae [79], Scombridae [79], Serranidae [79], Xiphiidae [79]	6	1	215 (415)
<i>Carcharhinus sorrah</i>	39	Ammodytidae [80], Apogonidae [20], Ariidae [80], Balistidae [80], Bothidae [20,80], Carangidae [20,36,80], Centriscidae [80], Chirocentridae [80], Clupeidae [20,80], Congridae [80], Dactylopteridae [80], Diodontidae [80], Exocoetidae [80], Fistulariidae [80], Gerreidae [20,80], Haemulidae [20,36], Leiognathidae	6	5	731 (1388)

		[20,36,40,80], Lethrinidae [80], Loliginidae [20], Menidae [20,80], Monacanthidae [36,80], Mullidae [20,36,80], Nemipteridae [80], Ostraciodontidae [80], Penaeidae [20,36,38,40], Polynemidae [20], Portunidae [80], Priacanthidae [80], Scaridae [80], Sciaenidae [20], Scombridae [80], Sillaginidae [20], Soleidae [20], Spirulidae [20], Synodontidae [40,80], Terapontidae [20], Tetraodontidae [20,80], Trichiuridae [80], Triglidae [80]			
<i>Carcharhinus tilstoni</i>	46	Anguillidae [80], Ariidae [20,38,80], Balistidae [80], Bothidae [80], Carangidae [20,80], Carcharhinidae [80], Clupeidae [20,38,40,80], Coryphaenidae [80], Cynoglossidae [38], Dactylopteridae [80], Diodontidae [80], Elapidae [80], Engraulidae [20], Exocoetidae [80], Gerreidae [20,36], Haemulidae [36,80], Hemigaleidae [80], Hemiramphidae [36,80], Leiognathidae [20,36,40,80], Lethrinidae [38,80], Loliginidae [20,80], Lutjanidae [80], Monacanthidae [80], Mullidae [20,36,80], Muraenesocidae [80], Myctophidae [80], Nemipteridae [80], Paralepididae [80], Penaeidae [20,36], Platycephalidae [80], Polynemidae [20], Priacanthidae [80], Psettodidae [80], Scaridae [80], Sciaenidae [36,38,80], Scombridae [20,40,80], Scorpaenidae [80], Sillaginidae [38], Sphyraenidae [80], Synodontidae [20,80], Terapontidae [40], Tetraodontidae [80], Triacanthidae [38,80], Trichiuridae [80], Triglidae [80], Uranoscopidae [80]	4	5	1192 (2402)
<i>Carcharias taurus</i>	56	Achiridae [66], Aphroditidae [83], Arhynchobatidae [83], Ariidae [82], Atherinidae [83], Batrachoididae [81,83], Bothidae [82], Carangidae [81-83], Carcharhinidae [66,81,82], Cheilodactylidae [82-83], Clupeidae [66,81-83], Congridae [83], Ctenodiscidae [83], Cynoglossidae [82], Dasyatidae [82], Dussumieriidae [82], Echeineidae [82], Gonorynchidae [82], Haemulidae [82], Hexanchidae [83], Labridae [66], Loliginidae [39,66,81-82], Lophiidae [66], Merlucciidae [82], Mugilidae [82], Myliobatidae [66,82-83], Nassariidae [83], Octopodidae [82], Ophidiidae [66,82], Paguridae [66,83], Paralichthyidae [66,83], Pentanchidae [82], Percophidae [81,83], Phycidae [83], Pinguipedidae [83], Platyxanthidae [83], Pomatomidae [66,82-83], Rajidae [66,82-83], Rhinobatidae [82], Sciaenidae [66,81-83], Scombridae [66,81-82], Scophthalmidae [66],	46	5	801 (1000)

Scyliorhinidae [82], Sepiidae [82], Serranidae [83], Soleidae [82], Sparidae [66,81-82], Squalidae [82], Squatinidae [66,83], Stromateidae [66,81,83], Synodontidae [66], Torpedinidae [82], Triakidae [66,81-83], Trichiuridae [81], Triglidae [66,82-83], Uranoscopidae [83]

<i>Carcharodon carcharias</i>	43	Acipenseridae [94], Alopiidae [91], Ariidae [84], Asteriidae [85], Bursidae [94], Cancridae [85,88,94], Carcharhinidae [84], Cetorhinidae [89,94], Chiroteuthidae [91], Clupeidae [84-85,89,94], Cottidae [89,94], Dasyatidae [84,94], Delphinidae [84,90], Engraulidae [94], Haemulidae [91], Hexagrammidae [89,94], Loliiginidae [91], Merlucciidae [85,88], Moronidae [94], Myliobatidae [84,89,94,96], Odontaspidae [84], Otariidae [84,87,94-95], Phocidae [88,92-94,97], Phocoenidae [86], Phycidae [85], Pleuronectidae [85,92], Pomatomidae [85], Rajidae [85], Rhincodontidae [91], Rhinobatidae [84], Salmonidae [88,92,94], Sciaenidae [84,89,94,96], Scombridae [84,96,98], Sebastidae [88,94], Sepiidae [84], Serranidae [91], Sparidae [84], Sphyrinae [84], Sphyrnidae [84,91], Squalidae [84,89,94], Stromateidae [85], Triakidae [85,89,94,96], Triglidae [85]	266	17	329 (512)
<i>Centrophorus granulosus</i>	28	Apogonidae [100], Argentinidae [99], Brachioteuthidae [100], Calappidae [99], Callionymidae [99], Clupeidae [100], Cranchiidae [100], Etmopteridae [99], Gadidae [99], Geryonidae [99], Histioteuthidae [100], Lepidoteuthidae [100], Macrouridae [99], Myctophidae [99], Nephropidae [99], Octopoteuthidae [100], Ommastrephidae [99], Pandalidae [99], Pentanchidae [99], Phosichthyidae [99], Phycidae [99], Polybiidae [99], Rajidae [99], Scombridae [100], Sepiidae [99], Sepiolidae [99], Soleidae [100], Trachichthyidae [99]	11	3	153 (194)
<i>Centrophorus squamosus</i>	16	Alepocephalidae [102], Argentinidae [104], Bramidae [101], Carangidae [101,103], Chimaeridae [102], Congridae [101], Diretmidae [103], Gadidae [102], Macrouridae [102-104], Merlucciidae [101,103], Moridae [104], Onychoteuthidae [103], Oreosomatidae [101], Penaeidae [103], Sebastidae [101,104], Squalidae [101]	12	4	85 (466)
<i>Centroscymnus coelolepis</i>	18	Acanthephyridae [105], Alepocephalidae [102], Bramidae [103], Epigonidae [103], Gadidae [102], Histioteuthidae [105], Ipnopidae [105], Lotidae [104],	14	4	222 (379)

		Lycoteuthidae [103], Macrouridae [102,104], Merlucciidae [103], Moridae [104], Myctophidae [104], Octopoteuthidae [103], Ommastrephidae [105], Pleuronectidae [104] Sepiolidae [105], Stomiidae [105]			
<i>Cephaloscyllium isabellum</i>	28	Buccinidae [106], Cancridae [106], Carangidae [106], Centriscidae [106], Engraulidae [106], Goneplacidae [106], Macrouridae [106], Monacanthidae [106], Moridae [106], Munidae [106], Octopodidae [106], Ommastrephidae [106], Ophidiidae [106], Ostreidae [106], Ovalipidae [106], Palinuridae [106], Percophidae [106], Pinguipedidae [106], Pleuronectidae [106], Pseudarchasteridae [106], Pyuridae [106], Rajidae [106], Scyllaridae [106], Squalidae [106], Squillidae [106], Syngnathidae [106], Triakidae [106], Urechidae [106]	1	1	261 (278)
<i>Cetorhinus maximus</i>	3	Penaeidae [107], Sergestidae [108], Temoridae [109]	87	3	3 (6)
<i>Chlamydoselachus anguineus</i>	7	Chiroteuthidae [110], Gonatidae [110], Histioteuthidae [110], Mastigoteuthidae [110], Ommastrephidae [110], Onychoteuthidae [110], Rostellariidae [110]	6	1	37 (139)
<i>Dalatias licha</i>	26	Alpheidae [111], Aristeidae [111], Axiidae [111], Carapidae [113], Centrophoridae [101], Chlorophthalmidae [112], Epigonidae [111], Etmopteridae [111,113], Gadidae [111], Histioteuthidae [111], Loliginidae [112,115], Macrouridae [111], Merlucciidae [101,112,114], Moridae [111,113], Myctophidae [111-112], Nephropidae [113], Paralepididae [111], Pasiphaeidae [111,113], Penaeidae [112], Pentanchidae [111-113], Phycidae [111], Pyrosomatidae [113], Sepiolidae [111-112,114], Sergestidae [111], Stomiidae [111], Trichiuridae [115]	16	8	151 (210)
<i>Deania calcea</i>	32	Acanthephyridae [116], Alepocephalidae [117], Aphroditidae [117], Carangidae [116,118], Clupeidae [120], Cranchiidae [116], Cyttidae [116], Gadidae [102,117], Gempylidae [120], Gonostomatidae [117], Histioteuthidae [117], Lotidae [102], Macrouridae [116], Merlucciidae [116], Myctophidae [102-103,116-120], Notosudidae [116], Ommastrephidae [116-117,119], Onychoteuthidae [116],	11	7	455 (814)

Oplophoridae [116], Pandalidae [120], Paralepididae [103], Pasiphaeidae [116-117], Penaeidae [103], Phosichthyidae [116], Phycidae [102], Scombridae [102,117], Sebastidae [102], Sergestidae [102,116-117], Sternoptychidae [116], Stomiidae [103,117], Trachichthyidae [116], Zeidae [116]

<i>Deania profundorum</i>	3	Enoploteuthidae [103], Myctophidae [103], Ommastrephidae [103]	1	1	43 (78)
<i>Etmopterus granulosus</i>	7	Batoteuthidae [121], Brachioteuthidae [121], Histioteuthidae [103,121], Mastigoteuthidae [121], Myctophidae [103,121], Paralepididae [103], Penaeidae [103]	1	2	67 (191)
<i>Etmopterus lucifer</i>	5	Enoploteuthidae [122], Euphausiidae [122-123], Histioteuthidae [122], Lophogastridae [123], Myctophidae [122]	8	2	385 (681)
<i>Etmopterus princeps</i>	7	Acanthephyridae [124], Bathylagidae [102], Gadidae [124], Myctophidae [124], Notosudidae [124], Ommastrephidae [124], Paralepididae [124]	5	2	55 (98)
<i>Etmopterus pusillus</i>	13	Enoploteuthidae [125], Gadidae [125], Gonostomatidae [125], Histioteuthidae [125], Merlucciidae [103], Myctophidae [103,125], Ommastrephidae [125], Onychoteuthidae [125], Pandalidae [125], Pasiphaeidae [125], Polybiidae [125], Sepiolidae [125], Trichiuridae [125]	1	2	448 (605)
<i>Etmopterus spinax</i>	35	Alepocephalidae [127], Alpheidae [133], Aristeidae [126,133], Callionymidae [126], Centrolophidae [127], Crangonidae [126,131,133], Enoploteuthidae [133], Etmopteridae [126], Euphausiidae [102,117,127-133], Gadidae [102,117,126,131], Gnathophausiidae [117,127], Gobiidae [129], Goneplacidae [126], Histioteuthidae [117,129-130,133], Munididae [127], Myctophidae [102,126-127,129-130,133], Mysidae [102], Oplophoridae [117], Pandalidae [126,128,130-131], Paralepididae [130], Pasiphaeidae [127-131,133], Pentanchidae [126], Phosichthyidae [126], Phycidae [102,126-127], Processidae [127], Scombridae [128], Sepiidae [126], Sepiolidae [126,128-130,133], Sergestidae [102,129-130,133], Solenoceridae [127], Sternoptychidae [102,128,131-132], Stomiidae [130,133], Synaphobranchidae [102],	42	12	533 (866)

Trachichthyidae [126], Trichiuridae [130]					
<i>Euprotomicrus bispinatus</i>	5	Bramidae [136], Myctophidae [136], Oncaeiidae [136], Phosichthyidae [136], Sternoptychidae [136]	3	1	12 (12)
<i>Galeocerdo cuvier</i>	111	Acanthuridae [138], Ancistrocheiridae [332], Anguillidae [17,148], Argonautidae [332], Ariidae [76], Aulostomidae [138], Balistidae [17,50,76,138,140], Batrachoididae [137,143], Belonidae [138,143], Bovidae [138,141,147,153-155] , Busyconidae [150], Canidae [138] , Carangidae [27,50,137-138,147,156], Carcharhinidae [50,62,137,154], Chelonibiidae [17], Cheloniidae [137-138,149,153-154], Chirocentridae [156,332], Cirolanidae [139], Clupeidae [27,62,140,154,156], Columbidae [150,152] , Congridae [138], Coryphaenidae [138], Cranchiidae [332], Cuculidae [150] , Cycloteuthidae [332], Dasyatidae [50,76,145,154], Delphinidae [17,27,137], Diodontidae [27,50,76,137-138,143,145,147], Diomedeidae [17], Dugongidae [143,145,148], Elapidae [17,143,145,148,151], Elopidae [144], Engraulidae [156], Enoploteuthidae [332], Ehippidae [50,140], Equidae [138,153] , Fasciariidae [150], Felidae [138] , Fistulariidae [138,147], Gerreidae [50,140], Gorgoniidae [137], Haemulidae [140], Hemiramphidae [143,145], Herpestidae [138] , Histioteuthidae [332], Hominidae [138,146] , Istiophoridae [17,138], Joubiniteuthidae [332], Labridae [138], Lamnidae [141], Laridae [137], Limulidae [137], Loliginidae [50,140,332], Luidiidae [137], Lutjanidae [145], Meropidae [141] , Molidae [27], Monacanthidae [138,140], Muridae [138] , Mugilidae [50,137], Mullidae [138], Muraenidae [138], Myliobatidae [50,145,154], Naticidae [137], Octopodidae [137,332], Octopoteuthidae [332], Ommastrephidae [332], Onychoteuthidae [332], Ostraciidae [17,138], Ovalipidae [137], Palinuridae [138,145], Paralichthyidae [137], Parulidae [150] , Pelecanidae [149], Phalacrocoracidae [137], Phocidae [157], Phocoenidae [154], Pholidoteuthidae [332], Platycephalidae [27], Pleuronectidae [138], Pomacanthidae [17], Pomacentridae [138], Pontoporiidae [144], Portunidae [17,27,50,137,149], Pristidae [62], Procellariidae [27], Rachycentridae [137], Rajidae [137], Rallidae [142],	208	30	1359 (1944)

Raninidae [147], Rhinobatidae [17,145], Sciaenidae [27,50,137,140,144,156],
 Scaridae [138], Scombridae [17,27,137-138,154], Scyllaridae [17,138,147],
 Sepiidae [332], Serranidae [137], Sparidae [50,137], Sphyraenidae [138],
 Sphyrnidae [50,154], Squillidae [17,137], **Suidae [147]**, Sulidae [140],
 Stromateidae [137,144,156], Syngnathidae [145], **Tachyglossidae [17]**,
 Tetraodontidae [17,27,60,138,140,145], Trichiuridae [156], Triglidae [50],
Turdidae [150], Volutidae [145]

<i>Galeorhinus galeus</i>	66	Agonidae [163], Argentinidae [101], Arhynchobatidae [158], Atherinidae [158], Batrachoididae [158-159], Belonidae [159], Bramidae [101], Callionymidae [163], Callorhynchidae [158], Caproidae [161], Carangidae [81,101,158,161,164], Centriscidae [161], Chimaeridae [159], Clinidae [159], Clupeidae [81,158- 160,162-163], Congridae [158], Cottidae [159,162], Cynoglossidae [158], Eledonidae [163], Embiotocidae [159], Engraulidae [81,158-160,162], Exocoetidae [159], Gadidae [163], Gempylidae [160,164], Gonatidae [162], Kyphosidae [159], Loliginidae [158,163,165], Macrouridae [101,161], Merlucciidae [81,101,160,162], Moridae [101], Mugilidae [158], Mullidae [158], Myliobatidae [158], Nephropidae [101], Nototheniidae [159], Octopodidae [158,161], Ommastrephidae [101,158,160,165], Onychoteuthidae [101], Ophidiidae [158], Palinuridae [164], Pandalidae [101], Paralichthyidae [158,160], Percophidae [81,158], Phycidae [161], Pinguipedidae [158], Pleuronectidae [162-163], Pomacentridae [159], Pomatomidae [81,158], Porpitidae [162], Rajidae [158], Salmonidae [159], Salpidae [101], Sciaenidae [81,158-159], Scombridae [159,161,163], Sebastidae [101], Sepiolidae [163], Serranidae [158], Sparidae [159,161], Sphyraenidae [159], Squatinidae [81], Sternoptychidae [161], Stromateidae [158], Synodontidae [161], Triakidae [81,158], Trichiuridae [81,161], Triglidae [81,163]	34	12	1280 (1976)
<i>Galeus melastomus</i>	110	Acanthephyridae [105,117,166], Alepocephalidae [117,167], Alpheidae [105,129- 130,167], Aphroditidae [117], Argentinidae [169], Argonautidae [166,171], Aristeidae [130,166], Astorhizidae [169], Axiidae [105,129-130,169],	49	14	2983 (3431)

Bathypolypodidae [105,117], Benthescycymidae [129-130,166], Bothidae [166],
Brachioteuthidae [130,166,171], Bythitidae [166], Carangidae [117,167],
Chiroteuthidae [105,166], Chlorophthalmidae [166], Chtenopterygidae [166],
Ciolanidae [105,117], Cliidae [166], Cranchiidae [105], Crangonidae
[117,129,169,359], Cymbuliidae [117], Cynoglossidae [166], Diphyidae [105],
Eledonidae [172], Enoploteuthidae [130,166,171], Epimeriidae [117], Eucopiidae
[105], Euphausiidae [105,117,129-130,169], Eusiridae [169], Gadidae
[117,130,166-167,169,359], Gammaridae [169], Geryonidae [105,117,130],
Gnathophausiidae [117], Gobiidae [166,169], Goneplacidae [167],
Gonostomatidae [130], Hauerinidae [105], Histioteuthidae [105,129,166,170-
171], Hyperiidae [105,117], Ipnopidae [166], Leuconidae [105], Loliginidae [166],
Lophogastridae [129-130,169], Lotidae [105,166,169], Lysianassidae [169],
Macrouridae [105,117,129,166,359], Merlucciidae [166-167], Moridae
[105,117,359], Munididae [102,117,166-167,169], Myctophidae
[102,105,117,129-130,166-167,170], Mysidae [105,169], Nassariidae [166],
Nebaliidae [169], Nemichthyidae [129], Octopodidae [166,172],
Octopoteuthidae [166], Ommastrephidae [105,117,129-130,166,168],
Onuphidae [169], Onychoteuthidae [129-130,166], Opisthoteuthidae [172],
Oplophoridae [129,166], Paguridae [105,117,129-130,167], Pandalidae
[129,166,169,359], Paralepididae [105,166], Parapaguridae [117], Parasquillidae
[166], Pardaliscidae [105], Pasiphaeidae [105,117,129-130,166-167,170,359],
Penaidae [130], **Phasianidae [105]**, Phosichthyidae [166], Phronimidae
[105,129], Phrosinidae [105], Phycidae [117], Platyscelidae [105], Pleuronectidae
[129], Polybiidae [117,130,167], Polychelidae [117,129], Poromyidae [166],
Processidae [105,129-130,166-167], Pyrosomatidae [129,166], Pyroteuthidae
[166,359], Rajidae [130], Rhabdamminidae [105,169], Rissoidae [105],
Saccamminidae [169], Salpidae [105,117,129], Scinidae [105], Scomberesocidae
[167], Scombridae [167], Scorpaenidae [166], Scyllaridae [166], Sebastidae [166],
Sepiidae [172], Sepiolidae [105,129-130,166,168-169,171-172,359], Sergestidae

[105,117,129-130,166-167,170], Serpulidae [105], Sigalionidae [169], Solenoceridae [167,359], Sternoptychidae [117,129,167,169], Stomiidae [105,129-130,166], Synaphobranchidae [117], Terebratulidae [105], Trachichthyidae [166], Tubulariidae [166], Uristidae [117,169], Uvigerinidae [105], Xanthidae [105]

<i>Ginglymostoma cirratum</i>	18	Batrachoididae [173], Belonidae [173], Carangidae [173], Epialtidae [173], Haemulidae [173], Labridae [173], Lolinidae [173], Lutjanidae [173], Majidae [173], Octopodidae [173], Ophichthidae [173], Palinuridae [173], Rachycentridae [173], Rajidae [173], Scaridae [173], Scombridae [173], Sparidae [173], Syngnathidae [173]	80	1	41 (91)
<i>Hemipristis elongata</i>	5	Congridae [17], Dasyatidae [17], Diodontidae [17], Lutjanidae [17], Muraenidae [17]	2	2	86 (114)
<i>Hemiscyllium ocellatum</i>	10	Alpheidae [174], Amphinomidae [174], Callionymidae [174], Gammaridae [174], Gonodactylidae [174], Lysiosquillidae [174], Ocypodidae [174], Portunidae [174], Terebellidae [174], Xanthidae [174]	15	1	51 (53)
<i>Hemitriakis japonica</i>	13	Alpheidae [175], Bothidae [175], Callianassidae [175], Engraulidae [175], Gobiidae [175], Hippolytidae [175], Mysidae [175], Ogyrididae [175], Palaemonidae [175], Pasiphaeidae [175], Penaeidae [175], Sciaenidae [175], Upogebiidae [175]	3	2	51 (57)
<i>Heptranchias perlo</i>	18	Acropomatidae [176], Centrolophidae [176], Enoploteuthidae [176], Gempylidae [176], Macrouridae [176], Merlucciidae [176], Myctophidae [176], Narcinidae [176], Octopodidae [176], Ommastrephidae [176-177], Ophidiidae [176], Oplophoridae [176], Paraulopidae [176], Scombridae [177], Serranidae [176], Solenoceridae [176], Trichiuridae [176], Triglidae [176]	9	2	89 (117)
<i>Heterodontus francisci</i>	8	Aegidae [178-179], Calyptraeidae [178-179], Fissurellidae [178], Octopodidae [178-179], Penaeidae [178-179], Portunidae [178-179], Sipunculidae [178-179], Syngnathidae [178-179]	30	2	193 (219)
<i>Hexanchus griseus</i>	28	Callorhynchidae [180], Carangidae [181], Chimaeridae [184], Clupeidae [180-181], Delphinidae [180], Dussumieriidae [180], Echinorhinidae [184], Engraulidae	33	8	90 (162)

[180,182], Gempylidae [180], Inachoididae [183], Loliginidae [180-181], Lophiidae [183], Macrouridae [180,183], Merlucciidae [180-182,184], Myctophidae [180], Myxinidae [184], Ommastrephidae [180], Otariidae [180], Petromyzontidae [184], Pomatomidae [182], Phycidae [183], Rajidae [180], Scombridae [180-182], Scyliorhinidae [180], Sebastidae [180], Squalidae [180-184], Triakidae [180-181], Xiphiidae [181]

<i>Iago omanensis</i>	12	Cranchiidae [185], Eledonidae [185], Enoploteuthidae [185], Histioteuthidae [185], Loliginidae [185], Majidae [185], Myctophidae [185-186], Ommastrephidae [185], Portunidae [185], Sepiolidae [185], Solenoceridae [186], Squillidae [185]	11	2	256 (279)
<i>Isurus oxyrinchus</i>	89	Alepisauridae [190,193,195,197,202], Ammodytidae [194], Amphitretidae [10], Ancistrocheiridae [1,201], Anguillidae [202], Argentinidae [73], Argonautidae [10], Atelecyclidae [197], Axiidae [197], Balistidae [190,197], Belonidae [1,191,197,201], Berycidae [27], Bramidae [10,190,192-193,195,199], Carangidae [1,9-10,27,73,191,193,195,197,199-201], Carcharhinidae [10,191,194,201-202], Centrolophidae [27], Cheloniidae [190], Clupeidae [10,27,191,194,198,202], Coryphaenidae [1], Dalatiidae [195], Dasyatidae [191], Delphinidae [9-10,189,193,196], Diodontidae [27,195], Diomedeidae [193], Engraulidae [10,73], Enoploteuthidae [10], Ehippidae [191], Gadidae [202], Gempylidae [3,9,27,191,195,199], Gnathophausiidae [192], Gonatidae [10,202], Haemulidae [1,191,201], Histioteuthidae [1,10,165,193,197,199,201-202], Istiophoridae [191,195,201], Kyphosidae [10], Lamnidae [191,193], Loliginidae [10,191,194,197,201-202], Lycoteuthidae [165,199,201], Macrouridae [10], Malacanthidae [194], Mastigoteuthidae [1], Merlucciidae [191,194,202], Monacanthidae [1,9], Mugilidae [10,27,73], Myliobatidae [1,191,201-202], Nomeidae [1,193,195], Octopoteuthidae [1,10,201], Odontaspidae [191], Ommastrephidae [1,9-10,73,165,192-194,197,199,201-203], Onychoteuthidae [1,10,202], Ophidiidae [10,191], Opisthoteuthidae [1], Oplegnathidae [191], Ostraciidae [201], Otariidae [188], Paralepididae [10], Paralichthyidae [10],	106	23	2177 (3776)

		<p>Penaeidae [27], Phycidae [197], Pomatomidae [194,202], Priacanthidae [1], Pseudocarchariidae [193], Rajidae [197,202], Regalecidae [1,27], Sciaenidae [191,201], Scomberesocidae [10,190,197-198,202], Scombridae [1,3,9-10,27,73,190-195,197,199-202], Scorpaenidae [202], Scyliorhinidae [191,201], Sebastidae [10,202], Sepiidae [187,201], Serranidae [194], Solenoceridae [193-194], Sparidae [27,191,194,197,202], Sphyrnidae [191,201], Spirulidae [197], Squalidae [191,194,201], Squillidae [197], Stromateidae [202], Syngnathidae [202], Tetragonuridae [195], Tetraodontidae [1,27], Thysanoteuthidae [1], Trachipteridae [199], Trichiuridae [3,27,73,199], Triglidae [194,202], Xiphiidae [193-195,197,202], Zeidae [191], Zoarcidae [194,202]</p>			
<i>Lamna nasus</i>	44	<p>Alepisauridae [204], Ammodytidae [204], Anarhichadidae [204], Anguillidae [204], Anopteroideae [204], Argentinidae [209], Belonidae [209], Brachioteuthidae [121], Bramidae [200,206], Carangidae [200], Centrolophidae [200], Channichthyidae [121], Chiroteuthidae [121], Clupeidae [204,208-209,211], Congiopodidae [121], Cottidae [204], Cranchiidae [121], Cyclopteridae [204], Eledonidae [208], Euphausiidae [207], Gadidae [204,209], Gempylidae [121], Gonatidae [121], Hemitriptidae [204], Histioteuthidae [121], Loliginidae [211], Mastigoteuthidae [121], Merlucciidae [204,206], Myctophidae [121,204], Nemichthyidae [204], Neoteuthidae [121], Ommastrephidae [121,200,204], Onychoteuthidae [121,205,210], Oregoniidae [204], Paralepididae [200], Petromyzontidae [204], Phosichthyidae [206], Pleuronectidae [209], Scomberesocidae [204], Scombridae [204,208,211], Sebastidae [204,211], Squalidae [204], Stomiidae [121], Trachipteridae [206]</p>	30	10	1928 (4891)
<i>Loxodon macrorhinus</i>	46	<p>Alpheidae [17], Ammodytidae [17], Apogonidae [17], Bothidae [17], Bregmacerotidae [17], Caesionidae [17], Calappidae [212], Callianassidae [17], Callionymidae [17,212], Carangidae [17], Champsodontidae [17], Congridae [17], Creediidae [212], Engraulidae [213], Euphausiidae [17], Gobiidae [17], Labridae [17,212], Leiognathidae [17], Loliginidae [212-213], Mugilidae [212], Mullidae [17], Mussidae [213], Nannosquillidae [212], Ocyrodidae [213], Ophichthidae</p>	4	3	345 (449)

		[212], Palinuridae [213], Pegasidae [17,212], Penaeidae [17,212-213], Phascolosomatidae [213], Platycephalidae [17], Portunidae [212-213], Scaridae [17], Scombridae [212], Scorpaenidae [17], Sepiidae [213], Sepiolidae [17,212], Siganidae [212], Sillaginidae [212], Sparidae [212], Squillidae [17,212], Syngnathidae [17], Synodontidae [212], Tetraodontidae [17,212], Triglidae [17,212], Upogebiidae [17], Uranoscopidae [17]			
<i>Megachasma pelagios</i>	1	Euphausiidae [214-216]	19	3	3(3)
<i>Mustelus asterias</i>	15	Agonidae [163], Atelecyliidae [163], Axiidae [163], Cancridae [163], Corystidae [163], Donacidae [163], Galatheidae [207], Majidae [163], Oregoniidae [163], Paguridae [163], Pandalidae [163], Pilumnidae [163], Polybiidae [163,207], Upogebiidae [163], Xanthidae [163]	8	2	48 (49)
<i>Mustelus californicus</i>	8	Batrachoididae [217], Blepharipodidae [217], Callianassidae [217], Cancridae [217], Clupeidae [217], Crangonidae [217], Urechidae [217], Varunidae [217]	5	1	49 (52)
<i>Mustelus canis</i>	55	Achiridae [66], Ammodytidae [66,218], Anguillidae [218], Ariidae [222], Atherinopsidae [224], Busyconidae [66], Calappidae [223], Cancridae [66,218-220,224], Carcinidae [224], Clupeidae [218], Congridae [223], Crangonidae [66,220,224], Diodontidae [223], Diogenidae [223], Engraulidae [220,222], Epialtidae [66,219-220,224], Fundulidae [224], Gadidae [66], Gammaridae [220], Geryonidae [223], Glyceridae [220], Gonodactylidae [223], Limulidae [66,219], Loliginidae [66,165,218,220,223], Majidae [218,223], Merlucciidae [218], Munididae [223], Mysidae [220], Mytilidae [219-220], Naticidae [218,220], Nephropidae [218-219], Octopodidae [223], Ommastrephidae [218], Ophidiidae [66], Ovalipidae [66,219,224], Paguridae [66,218-220,224], Palaemonidae [224], Panopeidae [218-219,224], Paralichthyidae [66,218,220], Parasquillidae [223], Penaeidae [220], Pharidae [220,224], Portunidae [66,223-224], Priacanthidae [223], Rajidae [218], Sciaenidae [220], Sepiolidae [165], Solenidae [66], Sparidae [66,218], Squalidae [218], Squillidae [66,219-220,222-223], Stromateidae [218], Triglidae [218], Upogebiidae [219-220,224], Xanthidae [223]	45	8	453 (514)

<i>Mustelus fasciatus</i>	9	Aethridae [225], Batrachoididae [225], Diogenidae [225], Epialtidae [225], Leucosiidae [225], Olividae [225], Paralichthyidae [225], Penaeidae [225], Portunidae [225]	1	1	14 (17)
<i>Mustelus griseus</i>	35	Alpheidae [175], Bothidae [175], Callianassidae [175], Callionymidae [175], Cancridae [175], Carangidae [175], Crangonidae [175], Diogenidae [175], Dorippidae [175], Epialtidae [175], Euryplacidae [175], Galatheidae [175], Galenidae [175], Hexapodidae [175], Hippolytidae [175], Holognathidae [175], Leucosiidae [175], Lysmatidae [175], Menippidae [175], Mysidae [175], Ogyrididae [175], Ommastrephidae [175], Palaemonidae [175], Parthenopidae [175], Pasiphaeidae [175], Penaeidae [175], Pinnotheridae [175], Polybiidae [175], Portunidae [175], Sepiidae [175], Sepiolidae [175], Squillidae [175], Upogebiidae [175], Urechidae [175], Varunidae [175]	3	1	181 (187)
<i>Mustelus henlei</i>	42	Blepharipodidae [217], Bothidae [217,227], Calappidae [226-227], Callianassidae [229-230], Cancridae [217,229-230], Chasmocarcinidae [228], Cottidae [229], Crangonidae [217,229-230], Diogenidae [226], Dromiidae [228], Embiotocidae [230], Engraulidae [217,229-230], Epialtidae [229], Ethusidae [227], Eurysquillidae [226], Galatheidae [226-227], Gobiidae [217,230], Grapsidae [230], Loliginidae [217,228], Lophiidae [227], Molgulidae [230], Munididae [226,228], Nereididae [230], Octopodidae [226], Ophidiidae [227], Paguridae [228], Pandalidae [227], Paralichthyidae [226-227,230], Parasquillidae [227], Penaeidae [227-228], Pinnotheridae [229], Portunidae [226-228], Scombridae [226], Scorpaenidae [226], Serranidae [226-227], Sicyoniidae [228], Solenoceridae [226-227], Squillidae [226-228], Syngnathidae [229], Upogebiidae [229-230], Uranoscopidae [226], Varunidae [217,229-230]	13	6	585 (768)
<i>Mustelus lenticulatus</i>	37	Aphroditidae [232], Arenicolidae [232], Axiidae [232], Cancridae [232], Crangonidae [232], Diogenidae [232], Eunicidae [232], Glyceridae [232], Goneplacidae [232], Goniadidae [232], Hiatellidae [232], Hymenosomatidae [232], Laomedidae [232], Macrophthalmidae [232], Majidae [232], Maldanidae [232], Mesodesmatidae [232], Olividae [232], Ommastrephidae [232], Ovalipidae	2	1	428 (428)

[232], Paguridae [232], Palaemonidae [232], Palinuridae [232], Pinnotheridae [232], Priapulidae [232], Sabellariidae [232], Sigalionidae [232], Squillidae [232], Struthiolariidae [232], Terebellidae [232], Tetrasquillidae [232], Trochidae [232], Turritellidae [232], Upogebiidae [232], Urechidae [232], Varunidae [232], Volutidae [232]

<i>Mustelus lunulatus</i>	37	Aethridae [233-234], Albulidae [233], Axiidae [228], Batrachoididae [235], Blepharipodidae [235], Buccinidae [234], Calappidae [228,235], Cancridae [233], Carangidae [233], Chasmocarcinidae [228], Congridae [235], Dromiidae [228], Dussumieriidae [233], Gobiidae [228], Hemiramphidae [233], Hemisquillidae [233], Hippidae [234], Kyphosidae [233], Leucosiidae [228], Loliginidae [228], Munididae [228,233], Octopodidae [233], Paguridae [228], Palaemonidae [234], Parthenopidae [228], Penaeidae [228,234], Portunidae [228,234], Pseudorhombilidae [228], Pseudosquillidae [234], Scombridae [233], Scorpaenidae [235] Sicyoniidae [228,233], Squillidae [228,234], Stromateidae [233], Synodontidae [233], Terebridae [234], Xanthidae [228]	7	4	309 (498)
<i>Mustelus manazo</i>	68	Aegidae [236], Alpheidae [175,236-237], Ammodytidae [175,236], Axiidae [236], Blepharipodidae [237], Calappidae [175,236], Callianassidae [175], Cancridae [73,175,236-237], Carangidae [236-237], Carditidae [236], Cheiragonidae [236], Cirolanidae [175], Clupeidae [236-237], Cottidae [236], Crangonidae [175,236-237], Diogenidae [175,236-237], Dorippidae [175,236-237], Engraulidae [73,236], Epialtidae [175], Euphausiidae [236], Euryplacidae [175,236], Galatheididae [175,236], Galenidae [175], Gobiidae [236], Goneplacidae [73,175,236], Hexapodidae [175], Hippolytidae [175], Holognathidae [175], Inachidae [236], Leucosiidae [175,236-237], Lysmatidae [175], Majidae [236], Menippidae [175], Monacanthidae [237], Moridae [237], Munididae [73], Mysidae [175], Nephropidae [236], Ogyrididae [175], Ommastrephidae [73], Ophiolepididae [236], Oregoniidae [236], Ovalipidae [237], Paguridae [236-237], Palaemonidae [175], Pandalidae [236], Parthenopidae [175,236], Pasiphaeidae [175], Penaeidae [175,236-237], Pinnotheridae [236], Polybiidae [73,175,236],	12	4	1539 (1602)

Porcellanidae [175], Portunidae [175,236-237], Raninidae [236-237],
 Scomberesocidae [73,236], Scombridae [237], Scyllaridae [175], Semelidae [236],
 Sicyoniidae [237], Solenoceridae [73], Squillidae [175,236-237], Synodontidae
 [236], Trichiuridae [73], Trichopeltariidae [236], Upogebiidae [175,236-237],
 Urechidae [175], Varunidae [175], Xanthidae [175,236-237]

<i>Mustelus mustelus</i>	88	Alpheidae [238-239], Aphroditidae [242], Atelecyclidae [238,242], Belonidae [239], Bothidae [238], Calappidae [238-240], Callianassidae [240], Carangidae [239-240,242], Carcinidae [241], Centranchidae [239-240,242], Cerithiidae [238], Cheilodactylidae [240], Clupeidae [238-240,242], Congridae [238-239], Congiopodidae [240], Corystidae [238], Crangonidae [238-239,242], Dairoididae [240], Dentaliidae [238], Diodontidae [240], Diogenidae [238], Donacidae [238], Dorippidae [238-239], Dromiidae [239], Dussumieriidae [240], Eledonidae [239], Engraulidae [238,240-242], Enteractopodidae [240], Eriphiidae [239], Ethusidae [238-239], Euryplacidae [239], Gadidae [241-242], Geryonidae [239], Gobiidae [239], Goneplacidae [238-240,242], Haemulidae [240], Inachidae [238], Labridae [239], Leucosiidae [238,240], Loliginidae [168,238-240,242], Lophogastridae [238], Mactridae [238], Majidae [238-239], Merlucciidae [240,242], Mugilidae [238-240], Mullidae [239], Munididae [242], Mytilidae [240], Nannosquillidae [238], Nephropidae [242], Nuculidae [238], Octopodidae [239-240], Ommastrephidae [168,242], Ophichthidae [238], Ophiotrichidae [240], Ovalipidae [240], Paguridae [238-239], Palaemonidae [239], Palinuridae [240], Parasquillidae [238], Parthenopidae [238-239], Pectinidae [238], Penaeidae [238-240], Pilumnidae [241], Plagusiidae [240], Polybiidae [238-239,241-242], Pomatomidae [240], Portunidae [238-241], Processidae [238], Sciaenidae [240], Scombridae [238-239], Scorpaenidae [239], Scyllaridae [238,240], Sebastidae [240], Sepiidae [238-241], Sepiolidae [242], Serranidae [239], Sicyoniidae [238-239], Soleidae [239], Sparidae [238-240,242], Squillidae [238-242], Syngnathidae [239-240], Tellinidae [238], Thiidae [240], Turritellidae [238], Upogebiidae [238-241], Varunidae [238,240], Xanthidae [239,242]	22	8	1271 (1444)
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<i>Mustelus schmitti</i>	80	Alpheidae [247], Ampeliscidae [243], Ampharetidae [243], Atherinidae [247], Balanidae [243], Batrachoididae [243], Belliidae [243,245], Blepharipodidae [243,246], Branchiostomatidae [243], Calappidae [243], Capitellidae [243], Caprellidae [245], Carangidae [243], Cirolanidae [243,245], Clupeidae [247], Columbidae [243], Cynoglossidae [243], Diogenidae [243,245], Echiuridae [243], Engraulidae [243,246], Epiplatidae [243,245], Eunicidae [243], Flabelligeridae [243], Gammaridae [243,245], Glyceridae [243-244,246], Goniadidae [243], Idoteidae [246], Inachoididae [243], Lithodidae [243], Loliginidae [243-245,247], Lumbrineridae [243], Mactridae [243], Majidae [243,247], Maldanidae [243], Marginellidae [243], Merlucciidae [243], Munididae [243], Muricidae [244], Mytilidae [243], Myxinidae [243], Nassariidae [243], Naticidae [243], Nephtyidae [243], Nereididae [243], Nototheniidae [246], Octopodidae [243,245-246], Ommastrephidae [243], Onuphidae [243,246], Opheliidae [243], Ophidiidae [243], Paguridae [243-244], Panopeidae [243], Paralichthyidae [243], Pectinariidae [243], Penaeidae [243,245-246], Phyllodocidae [243], Pilumnidae [243], Pilumnoididae [243,245], Pinnotheridae [243], Platyxanthidae [243,245], Polybiidae [243], Porcellanidae [243,246], Portunidae [243], Sabellidae [243], Sergestidae [243,245], Serolidae [243,245,247], Serranidae [243], Sesarmidae [243], Sipunculidae [243,245], Solenidae [243,245], Solenoceridae [243], Spionidae [243], Squillidae [243], Tetrasquillidae [243,245-246], Traviidae [243], Trichopeltariidae [243,247], Varunidae [245-247], Veneridae [243,245], Volutidae [243], Zoarcidae [247]	12	5	1056 (1126)
<i>Negaprion acutidens</i>	18	Ariidae [38], Atherinidae [248], Balistidae [60], Belonidae [38,248], Carangidae [38], Clupeidae [38,248], Drepaneidae [38], Gobiidae [38], Labridae [248], Mugilidae [38], Penaeidae [38], Portunidae [248], Rhinobatidae [248], Scaridae [60], Scombridae [38], Sillaginidae [248], Sparidae [248], Syngnathidae [248]	22	4	68 (98)
<i>Negaprion brevirostris</i>	46	Albulidae [249], Alpheidae [249,253], Arenicolidae [249], Ariidae [250], Atherinidae [249-250], Atherinopsidae [251], Balistidae [249], Batrachoididae [249-251], Belonidae [249-250], Blenniidae [250], Bothidae [249], Carangidae	164	5	576 (855)

[249-250,253], Centropomidae [250], Clupeidae [253], Cyprinodontidae [249-251], Dasyatidae [249], Elopidae [250], Engraulidae [251], Ephippidae [250], Fundulidae [253], Gerreidae [249-251,253], Gobiidae [249-250], Gonodactylidae [249], Haemulidae [249-251], Hemiramphidae [249-250], Labridae [249], Loliginidae [249], Lutjanidae [249-250], Monacanthidae [250], Mugilidae [250,252], Octopodidae [250], Ocypodidae [249], Ophichthidae [249-250,253], Ostraciidae [250], Palinuridae [249], Penaeidae [249-251], Pomacentridae [249], Portunidae [249-250,253], Pseudosquillidae [249], Scaridae [249-250], Soleidae [249-250], Sparidae [249-251], Sphyraenidae [249-250], Synodontidae [249], Tetraodontidae [250], Xanthidae [249]

<i>Notorynchus cepedianus</i>	82	Acipenseridae [259], Aegidae [176], Anguillidae [254], Aplodactylidae [176], Arhynchobatidae [256], Ariidae [258], Arripidae [176,254], Atherinidae [255-257,259], Balaenopteridae [254], Batrachoididae [81], Callorhynchidae [176,254,257-258], Cancridae [259], Carangidae [176,254,256-258], Carcharhinidae [258], Centriscidae [176], Centrolophidae [176,254,257], Cheilodactylidae [176], Clupeidae [81,254,258], Congridae [254,258], Cottidae [259], Dasyatidae [254,258], Delphinidae [254,258], Embiotocidae [259], Emmelichthyidae [254], Engraulidae [254], Enteractinoptera [259], Gempylidae [176,254], Geotriidae [254], Gobiidae [176], Haemulidae [258], Hexanchidae [176,254,258-259], Labridae [254], Latridae [254], Loliginidae [81,176,258], Macropodidae [254] , Merlucciidae [257-258], Moridae [254], Mugilidae [254,258], Myliobatidae [176,254,256,258-259], Mytilidae [258], Myxinidae [257-258], Narcinidae [254], Narkidae [258], Nassariidae [256,258], Octopodidae [258], Odacidae [254], Ommastrephidae [176,254,257], Ophidiidae [257-258], Otariidae [176,255-258], Paguridae [256], Palinuridae [176], Paralichthyidae [257], Parascylliidae [176], Pentacerotidae [176], Percophidae [81], Petromyzontidae [259], Phocidae [257,259], Pinguipedidae [257], Plagusidae [258], Platycephalidae [254], Polyprionidae [257], Pontoporiidae [256], Pristiophoridae [176,254], Rajidae [176,254,256-259], Rhinobatidae [258],	38	8	855 (1371)
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Salmonidae [254,259], Sciaenidae [81,256,258], Scombridae [254,257-258],
 Scyliorhinidae [176,254,258], Sebastidae [259], Serranidae [176,254,257],
 Sertulariidae [256], Sillaginidae [176], Sparidae [176,258], Squalidae
 [176,254,257-259], Squatinidae [81,176,256], Stromateidae [257], Torpedinidae
 [258], Triakidae [81,176,254,256-259], Trichiuridae [258], Triglidae [176,254],
 Urolophidae [176,254]

<i>Prionace glauca</i>	133	Alepisauridae [58,192,200,261,264,268,274], Alloposidae [2,10,165,199,260-262,266,268,271-272], Amphitretidae [2,10,260-262,268,272], Ancistrocheiridae [1-2,165,199,260,262,266,268,272], Anoplopomatidae [275], Anopteridae [280], Architeuthidae [165,199,260-261], Argonautidae [1-2,10,165,192,199,260,262,270,272,275], Ariommatidae [261], Balistidae [265], Bathylagidae [260], Batrachoididae [260,275], Belonidae [260,278], Brachioteuthidae [271], Brachyscelidae [192], Bramidae [192,199,261,264,268,274], Buccinidae [278], Cancridae [260], Caproidae [272], Carangidae [1-2,10,27,192,199,200,260-262,264,277-278], Carcharhinidae [262,264], Centriscidae [272], Chiroteuthidae [165,199,260-261,265-266,268,272,277], Chtenopterygidae [272], Cionidae [278], Cinclidae [262] , Cirolanidae [199], Cirroteuthidae [264,268], Clupeidae [10,27,58,162,192,260,269,271,275,278], Congridae [199], Coryphaenidae [1], Cottidae [260], Cranchiidae [2,260-262,266,268,272,277,279], Cyclopteridae [269,276], Cycloteuthidae [268,272], Dasyatidae [261], Delphinidae [192,260,264], Dermochelyidae [264], Diodontidae [27,192,199,261,265], Diretmidae [272], Echeneidae [2,58,262], Embiotocidae [281], Engraulidae [1,162,260,262,267,270,275,277,281], Enoploteuthidae [10,260-261,268], Euphausiidae [10,266,275], Exocoetidae [268,277], Gadidae [269,271,278], Galatheidae [278], Gempylidae [192,199,261,264,274], Gnathophausiidae [260,274], Gonatidae [1-2,10,260-262,266,268,271-272,274-275,279], Halosauridae [271], Hexagrammidae [260], Histioteuthidae [1-2,10,165,192,199,260-262,266,268,271-273,275,277,279], Hyperiididae [266,271],	167	34	2921 (4259)
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Idoteidae [260], Istiophoridae [261], Joubiniteuthidae [272], Lamnidae [261,264],
 Lampridae [10,261], Loliginidae [10,260,275,277], Lophiidae [269],
 Lophogastridae [262], Luvaridae [10], Lycoteuthidae [165,199], Lysianassidae
 [277], Macrouridae [272], Mastigoteuthidae [1-2,260,272,277], Merlucciidae [1-
 2,10,162,260,262,269,275,277], **Mimidae [263]**, Molidae [10,260],
 Monacanthidae [199,261,265], Moronidae [278], Mugilidae [10,260,278],
 Munididae [2,10,260,262], Muraenidae [272], Myctophidae [58,260-
 261,268,272,274-275,280], Neoteuthidae [260], Nomeidae [260,264],
 Octopodidae [192,260-261,275,277], Octopoteuthidae [1,10,165,199,260-
 261,268,271-272,275,279], Ocythoidae [200,260-261,266,272,274],
 Ommastrephidae [1-2,10,165,192,199,260-262,264-265,267,271,274-
 275,277,279], Onuphidae [278], Onychoteuthidae [1-2,10,162,165,199,260-
 262,266,268,272,274-275,277], Ophidiidae [1,275], Opisthoteuthidae [1,10],
 Ostraciidae [58], Otariidae [265], Pandalidae [275,277], Paralichthyidae
 [162,275], Pentacerotidae [274], Petromyzontidae [275], Pholidoteuthidae [1-
 2,261-262], Platyscelidae [199,261], Pleuronectidae [162,269,271,275,278],
 Polybiidae [278], Pomacentridae [277], Procellariidae [261,271], Psammobiidae
 [278], Rajidae [269], Regalecidae [27], Renillidae [277], Salmonidae [268-269],
 Salpidae [261], Sciaenidae [275,281], Scomberesocidae [10,260,269,271,280],
 Scombridae [1-2,10,27,192,200,260-262,264,268-269,271,276,278], Sebastidae
 [10,260,269,275,277], Sepiidae [278-279], Sepiolidae [279], Solenoceridae [264],
 Sphyraenidae [272], Squalidae [10,269,275,277], Squillidae [2,262], Sternidae
 [10], Stauroteuthidae [268], Sternoptychidae [260,268,274], Stomiidae [260],
 Sulidae [58], Syngnathidae [271,275-277], Tetragonuridae [192], Tetraodontidae
 [1,264], Thysanoteuthidae [261-262,277], Trachichthyidae [192], Trachipteridae
 [2,261-262], Tremoctopodidae [165,199,261], Triakidae [10,270], Trichiuridae
 [192,199,265,271-272], Triglidae [278], Vampyroteuthidae [1-2,10,260-
 262,264,266,268,272,275,277], Veneridae [278], Xiphiidae [261,264]

Rhizoprionodon

61

Alpheidae [38], Apogonidae [38], Ariidae [17], Aristeidae [282], Atherinidae

20

8

1223 (4656)

acutus

[38,248], Batrachoididae [17], Bothidae [20], Bregmacerotidae [17],
Callionymidae [20], Carangidae [17,38,213,282], Centropomidae [248],
Clupeidae [17,20,38,40,213,248,282], Congridae [17], Cynoglossidae [282],
Dactylopteridae [17], Draconettidae [20], Elapidae [20], Elopidae [282],
Engraulidae [20,38,40,213,282], Gerreidae [36,38,213,282], Gobiidae [38],
Haemulidae [20,36,282], Hemiramphidae [36,38], Labridae [248,282],
Leiognathidae [17,20,36,38,40], Lethrinidae [213], Loliginidae [17,20], Lutjanidae
[213], Monacanthidae [17,36], Monocentridae [17], Moronidae [282], Mugilidae
[20,36,213,282], Mullidae [17,20,36,282], Muraenesocidae [282], Muraenidae
[17,282], Nassariidae [282], Nemipteridae [17], Octopodidae [282],
Ommastrephidae [282], Penaeidae [17,20,36,38,40,248], Pinguipedidae [17],
Platycephalidae [17,38], Polybiidae [282], Polynemidae [282], Pomatomidae
[282], Portunidae [248,282], Pristigasteridae [17], Ranellidae [282], Sciaenidae
[38,282], Scombridae [17,20], Scorpaenidae [17], Sepiidae [213,282], Sillaginidae
[17,38,248], Soleidae [20,282], Sparidae [282], Sphyradenidae [282], Strombidae
[282], Syngnathidae [17], Synodontidae [17,20], Terapontidae [38,248],
Tetraodontidae [17]

<i>Rhizoprionodon terraenovae</i>	53	Aethridae [51,283], Alpheidae [284], Ariidae [25,33,51,284], Balistidae [283], Bothidae [33,283], Calappidae [24], Cancridae [66], Carangidae [24- 25,33,51,284], Cerithiidae [25], Cheloniidae [283], Clupeidae [25,33,51,66,283- 284], Congridae [283], Cynoglossidae [25,66,284], Dasyatidae [33,284], Elopidae [24,33], Engraulidae [24-25,33,51,66,283-284], Epialtidae [66], Gerreidae [284], Gobiidae [51], Gonodactylidae [24], Haemulidae [24,66,283-284], Hippidae [284], Loliginidae [24-25,33,66,284], Lutjanidae [25,51], Lysiosquillidae [283], Mugilidae [51], Muraenidae [24,283], Nassariidae [66], Naticidae [284], Octopodidae [24], Ophichthidae [25,33,51,284], Ophidiidae [66], Ovalipidae [66], Paguridae [66,283], Paralichthyidae [24,51,66,284], Penaeidae [25,33,51,66,283- 284], Portunidae [25,33,51,284], Priacanthidae [66], Rajidae [283], Sciaenidae [25,33,51,66,283-284], Scombridae [24,33,51,283], Scopthalmidae [66],	35	8	1306 (2287)
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		Serranidae [51,66], Sicyoniidae [283], Sparidae [51,66,284], Sphyraenidae [283], Squillidae [25,33,51,283], Syngnathidae [33,284], Synodontidae [51,283-284], Terebellidae [284], Triacanthodidae [283], Trichiuridae [33,51], Triglidae [33,66]			
<i>Rhizoprionodon taylori</i>	24	Apogonidae [286], Chirocentridae [286], Clupeidae [17,20,286], Cynoglossidae [286], Engraulidae [20,285-286], Haemulidae [286], Hemiramphidae [286], Leiognathidae [17,20,286], Leptobramidae [286], Loliginidae [286], Monacanthidae [17], Mullidae [20,286], Penaeidae [17,286], Plotosidae [286], Polynemidae [20,286], Portunidae [286], Pristigasteridae [17], Scombridae [17,20], Sillaginidae [286], Syngnathidae [286], Synodontidae [286], Terapontidae [286], Triacanthidae [286], Trichiuridae [286]	8	4	238 (536)
<i>Scoliodon laticaudus</i>	32	Ambassidae [287], Bregmacerotidae [287], Carangidae [287], Clupeidae [287-288,290-291], Cynoglossidae [288], Cyprinidae [290], Engraulidae [287-288,290-291], Eucalanidae [290], Glyceridae [290], Gobiidae [287-288], Hyperidae [290], Leiognathidae [287], Loliginidae [287-288], Mugilidae [287,290], Muraenesocidae [290], Nereididae [290], Ophichthidae [290], Palaemonidae [290], Pasiphaeidae [290], Penaeidae [287-288,290-291], Sciaenidae [287-288,290-291], Scyllaridae [291], Sepiidae [288], Sergestidae [287-288], Solenoceridae [288,290], Sphyraenidae [290], Squillidae [288,290-291], Synodontidae [288,290], Temoridae [290], Trachipteridae [291], Trichiuridae [287-288,290], Triglidae [290]	10	4	964 (1867)
<i>Scyliorhinus canicula</i>	135	Aegidae [300], Alepocephalidae [167], Alpheidae [129,167,294-297,301], Agonidae [163,292], Ammodytidae [163,292], Ampeliscidae [294,298], Aphroditidae [129,163,292,298,301], Arenicolidae [163,302], Argentinidae [129,163,300], Atelecyclidae [129,163,292,294], Axiidae [163], Belonidae [296], Bonelliidae [301], Bothidae [295,301], Branchiostomatidae [292], Buccinidae [163,292,298], Callianassidae [163], Callionymidae [129,163,292,294,296,298], Cancridae [163], Caproidae [129,297], Carangidae [129,163,167,295-297,301], Cardiidae [292], Centranchidae [129], Centriscidae [301], Cepolidae [129,295-297], Cerithiidae [302], Chaetopteridae [300], Chlorophthalmidae [300],	164	14	14579 (16876)

Cirolanidae [294,300], Clupeidae [163,292,294,300-301], Corystidae [163,302], Cottidae [292], Crangonidae [129,163,292,298], Cucumariidae [294,298], Cynoglossidae [129], Diogenidae [129,294,301], Echinasteridae [292], Eledonidae [163], Engraulidae [297,300-301], Eriphiidae [301], Eunicidae [292], Euphausiidae [129,294-296], Euphosinidae [300], Gadidae [129,163,167,292,294-297,300,302], Galatheidae [129,163,292,295,300-302], Gammaridae [292], Glyceridae [292,301], Glycymerididae [292], Gobiesocidae [292], Gobiidae [129,163,292,295,300], Golfingiidae [292], Goneplacidae [129,163,167,294,297,300], Gonostomatidae [300], Haliotidae [294], Inachidae [163,301], Laomediidae [163,294], Leucosiidae [129,292,294], Liparidae [163], Loliginidae [163,294,300], Lophogastridae [129,294-296], Lumbrineridae [292], Macrouridae [300], Mactridae [292], Majidae [163], Merlucciidae [167,295,297,300-302], Mullidae [301], Munididae [129,163,167,295-297], Myctophidae [167,300], Myidae [163,292], Mysidae [295], Mytilidae [163], Naticidae [300], Nephropidae [163,295,301-302], Nephtyidae [292,298], Nereidae [163], Nereididae [292,301-302], Octopodidae [294,297,301], Oenonidae [292], Ommastrephidae [168,295,300-301], Opheliidae [292], Ophichthidae [129,301], Ophiidiidae [163], Ophiuridae [292], Onuphidae [294], Oregoniidae [163,292,298], Paguridae [129,163,167,292,294,296-298,301-302], Palaemonidae [302], Palinuridae [129], Pandalidae [129,163,292,296-298,300], Parechinidae [301], Parthenopidae [129], Pasiphaeidae [129,163,167,294,297], Pectinidae [292], Penaeidae [300-301], Peristediidae [300], Pharidae [163,292], Pholidae [163,292], Phronimidae [129], Phyllophoridae [292,302], Pinnotheridae [292], Pleuronectidae [129,163,292,294], Polybiidae [129,163,167,292,294-298,300-302], Polynoidae [292], Porcellanidae [292], Portunidae [129,294,300], Processidae [129,167,295,297], Rajidae [294], Sabellidae [302], Salpidae [129], Scomberesocidae [167], Scombridae [163,167,294], Scopthalmidae [129], Scyliorhinidae [292,297], Scyllaridae [129,301], Sepiidae [168,294-295,300-301], Sepiolidae [129,163,292,295,300-301], Sergestidae [167], Sipunculidae [129,293-

294,301], Soleidae [163,301], Solenoceridae [129,167,294-295,297], Sparidae [129,301], Squillidae [129,163,295], Sternaspidae [294-295], Sternoptychidae [167,295], Stichaeidae [163,292], Stomiidae [129], Synphobranchidae [296], Syngnathidae [129,294], Thiidae [294], Thoridae [292], Trachinidae [163], Triglidae [163,301-302], Upogebiidae [163,292,294-295,298,301-302], Xanthidae [129,163,292]

<i>Scyliorhinus stellaris</i>	32	Ammodytidae [303], Aphroditidae [303], Atelecyclidae [303], Buccinidae [163,303], Callionymidae [303], Cancridae [163], Carangidae [303], Clupeidae [303], Crangonidae [303], Eledonidae [163], Gadidae [163,303], Galatheidae [163], Loliginidae [163], Majidae [163], Merlucciidae [163,303], Myidae [163], Nephropidae [163], Nephtyidae [303], Oregoniidae [163], Paguridae [163,303], Palaemonidae [303], Pandalidae [303], Parechinidae [303], Pleuronectidae [163], Polybiidae [163,303], Rajidae [163], Scombridae [163,303], Sepiolidae [163], Soleidae [303], Squillidae [163], Triglidae [163], Upogebiidae [163]	13	2	112 (126)
<i>Somniosus microcephalus</i>	57	Acanthephyridae [304], Agonidae [304], Anarhichadidae [304-307,309], Architeuthidae [121], Argentinidae [309], Arhynchobatidae [121], Balaenopteridae [305], Bathylagidae [304], Bathypolypodidae [304], Brachioteuthidae [121], Buccinidae [308], Chimaeridae [309], Clupeidae [309], Cottidae [304,307-308], Cranchiidae [121], Cyclopteridae [304,307-309], Cycloteuthidae [121], Etmopteridae [309], Gadidae [304-305,307,309], Gonatidae [121,305,307], Gorgonocephalidae [305,307], Histioteuthidae [121], Liparidae [304], Lithodidae [307], Lotidae [304,309], Lysianassidae [306], Macrouridae [304,307,310], Mastigoteuthidae [121], Monodontidae [306], Myctophidae [309], Myxinidae [307], Neoteuthidae [121], Nototheniidae [121], Octopodidae [304], Octopoteuthidae [121], Ommastrephidae [121], Onychoteuthidae [121], Ophiactidae [305], Ophiuridae [306], Opisthoteuthidae [304], Oplophoridae [304], Oregoniidae [305,307], Otariidae [121], Pandalidae [304], Phocidae [304-305,307-308,310-312], Pleuronectidae [304-305,307-309,311], Psychrolutidae [304], Rajidae [304-305,307-309], Salmonidae	41	10	230 (256)

		[310,312], Sebastidae [304-305,307,309], Solasteridae [310], Somniosidae [305-306,310], Stichaeidae [304], Strongylocentrotidae [305,308], Uristidae [306], Ursidae [307,309], Zoarcidae [304,307-308,310]			
<i>Somniosus pacificus</i>	28	Anoplopomatidae [314], Cirolanidae [304], Clupeidae [316], Cranchiidae [316], Crangonidae [315], Delphinidae [317], Enteroctopodidae [304,314-315], Gadidae [304,313-316], Gonatidae [304,316], Liparidae [313,316], Macrouridae [304,313,316], Myctophidae [316], Nototheniidae [317], Octopodidae [318], Ommastrephidae [304], Onychoteuthidae [316], Oregoniidae [318], Paguridae [315], Phocidae [314,318], Pleuronectidae [314-316], Psychrolutidae [316], Ranellidae [315,318], Salmonidae [313-316], Sebastidae [314-315], Spongiidae [316], Squalidae [314], Uristidae [316], Zoarcidae [316]	28	9	461 (545)
<i>Sphyrna lewini</i>	137	Acanthuridae [2,320-321,329-330], Achiridae [325,328], Alloposidae [79,165], Alpheidae [50,323,329-330], Amphitretidae [79], Ancistrocheiridae [2,321,326,332], Anguillidae [319], Apogonidae [329-331], Argonautidae [321,324,326,328], Ariidae [320,323], Atherinidae [329-330], Aulostomidae [49], Balistidae [50,319,321,324,328,331], Batrachoididae [2,321], Belonidae [320-321,331], Bothidae [320,323-324,328,330-331], Brachioteuthidae [332], Callionymidae [2,331], Carangidae [2,24,79,320-326,328,331], Carcharhinidae [320], Centropomidae [328], Chaetodontidae [330], Champsodontidae [331], Chanidae [330], Cheilodactylidae [320], Chirocentridae [319], Chiroteuthidae [79,332], Chlorophthalmidae [319], Cichlidae [319], Clupeidae [2,320-324,326,328-329,331], Congridae [320,330-331], Coryphaenidae [2,321,326,328], Cranchiidae [79,332], Cynoglossidae [320,325,328], Dactylopteridae [320,331], Dasyatidae [320], Delphinidae [319], Diodontidae [331], Dussumieriidae [2,320], Echeneidae [321], Elopidae [319], Engraulidae [40,50,320,323-326,328-330], Enoploteuthidae [2,320-321,324,328,330], Ehippidae [319], Exocoetidae [2,320-321,323,326,331], Gempylidae [2,79,319], Gerreidae [319,322-323,328], Gobiidae [329-330], Gonatidae [2,321,326], Gymnuridae [320], Haemulidae [24,50,320,323], Hemiramphidae	106	28	4157 (5320)

[2,321,326,328,330], Histioteuthidae [2,79,235,326,330,332], Holocentridae [328], Istiophoridae [319], Kyphosidae [320], Labridae [321,324,328,330], Lamnidae [319], Leiognathidae [40,320,331], Lethrinidae [331], Loliginidae [2,50,320-321,323-328,332], Lutjanidae [2,79,325,331], Lycoteuthidae [165,320,332], Lysiosquillidae [329], Malacanthidae [328], Mastigoteuthidae [2,321,326], Menidae [331], Merlucciidae [2,320,326], Monacanthidae [79,331], Mugilidae [24,320,322,324-326,328-329], Mullidae [235,320,328,330-331], Munididae [2,321,324,328], Muraenesocidae [27,320], Muraenidae [2,24,79,319,321,324,326,328], Muricidae [325], Myctophidae [319,326], Myliobatidae [319], Nemipteridae [331], Octopodidae [2,79,235,320,325-326,332], Octopoteuthidae [2,79,320,326,332], Odontaspidae [319], Ommastrephidae [2,79,165,319,321,326,328,330,332], Onychoteuthidae [326], Ophichthidae [2,324,326,328], Ophidiidae [328], Opisthoteuthidae [332], Oplegnathidae [320], Ostraciidae [320,331], Palaemonidae [323,329], Pandalidae [2], Paralichthyidae [24,50,321-324,326,328], Penaeidae [2,24,40,50,321-326,328,331], Pentanchidae [320], Peristediidae [320], Pholidoteuthidae [2,326], Pinguipedidae [320], Platycephalidae [320,331], Pleuronectidae [320,328], Plotosidae [320], Polynemidae [331], Pomacentridae [320,330], Pomatomidae [320], Portunidae [50,323,328-329], Priacanthidae [2,320,331], Processidae [325,328], Pseudocarchariidae [320], Rajidae [50,320], Rhinobatidae [320], Scaridae [79,329-331], Sciaenidae [2,50,320,322-326,328], Scombridae [2,79,235,320-324,326,328,331], Scorpaenidae [2], Scyliorhinidae [320], Sepiidae [320,331-332], Sepiolidae [165], Serranidae [2,24,320-321,326,328], Sicyoniidae [323-325,328], Sillaginidae [331], Solenoceridae [2,50,325], Sparidae [50,320,323], Sphyrnidae [79,320,328], Sphyrnidae [319,330], Squalidae [27,320-321,323,331], Squillidae [235,324-325,327-329,331], Squatinidae [320], Stromateidae [324,328], Syngnathidae [320], Synodontidae [2,50,320-321,323-324,326,328-331], Terapontidae [320], Tetraodontidae [331], Thysanoteuthidae [2,325-326], Triacanthidae [331], Trichiuridae [50,320,331], Triglidae [24,320],

Vampyroteuthidae [235], Xanthidae [2], Yoldiidae [323]					
<i>Sphyrna mokarran</i>	40	Ancistrocheiridae [332], Ariidae [333], Balistidae [331], Carcharhinidae [333], Cynoglossidae [331], Dasyatidae [333], Diodontidae [331], Echeneidae [333], Gymnuridae [333], Haemulidae [331,333], Istiophoridae [331], Labridae [331], Latidae [331], Loliginidae [332], Lutjanidae [331], Myliobatidae [333], Nemipteridae [331], Octopodidae [332], Octopoteuthidae [332], Ommastrephidae [332], Oplegnathidae [333], Ostraciidae [331], Palinuridae [331,333], Penaeidae [331], Pentanchidae [333], Platycephalidae [333], Portunidae [331], Psettodidae [331], Rajidae [333], Rhinobatidae [333], Sciaenidae [331,333], Scombridae [331], Scyliorhinidae [333], Scyllaridae [331], Sepiidae [332-333], Sphyrnaenidae [331], Squillidae [331], Tetraodontidae [331], Trichiuridae [331], Triglidae [333]	27	3	423 (493)
<i>Sphyrna tiburo</i>	33	Aethridae [334], Batrachoididae [334], Bothidae [334], Calappidae [334], Callianassidae [334], Cancridae [334], Clupeidae [51], Congridae [337], Elopidae [334], Engraulidae [337], Epialtidae [334,336], Leucosiidae [334,336], Limulidae [336], Loliginidae [51,334,336], Menippidae [336], Mithracidae [334], Mugilidae [51], Octopodidae [334], Onuphidae [334], Ophichthidae [334,336], Ophirolepididae [51], Ovalipidae [334], Paguridae [334,336], Palinuridae [334,337], Pandalidae [334], Panopeidae [334], Penaeidae [51,334-337], Portunidae [51,334-337], Sciaenidae [51,334,337], Sicyoniidae [334], Squillidae [51,334,336], Syngnathidae [334], Xanthidae [51,334]	65	5	1262 (1317)
<i>Sphyrna tudes</i>	2	Ariidae [338], Penaeidae [338]	8	1	155 (155)
<i>Sphyrna zygaena</i>	73	Achiridae [340], Amathinidae [340], Amphitretidae [2,340], Anisakidae [341], Ancistrocheiridae [2,332,340], Argonautidae [2,23,332], Ariidae [23], Arripidae [9], Atherinopsidae [50], Balistidae [2,339], Belonidae [9,27,235], Berycidae [9,27], Carangidae [2,23,27,49-50,340-341], Chaetodontidae [23], Chiroteuthidae [23,339], Clupeidae [2,23,27,50,340-341], Congiopodidae [23], Congridae [23], Coryphaenidae [2,340], Cranchiidae [235,332], Cynoglossidae [23], Diodontidae [339], Dussumieriidae [23], Engraulidae [9,23,340], Enoploteuthidae [2,332],	45	13	943 (1463)

Exocoetidae [2,340], Fistulariidae [2], Gempylidae [2,9], Gerreidae [2], Gonatidae [2,340], Haemulidae [340-341], Hemiramphidae [2,9,50,340-341], Histioteuthidae [2,235,332,340], Loliginidae [2,9,23,39,50,332,340-341], Lycoteuthidae [23,332], Macrouridae [23], Mastigoteuthidae [2,340], Merlucciidae [2,23], Monacanthidae [9,27,339], Mugilidae [2,23,27,50], Myctophidae [340], Myliobatidae [235], Naticidae [340], Nuculanidae [340], Octopodidae [332], Octopoteuthidae [2,332,340], Ocythoidae [23], Ommastrephidae [2,9,23,50,332,339-340], Onychoteuthidae [2,235,332,340], Ophichthidae [2,340], Ophidiidae [2,23,340], Ovalipidae [9], Paralichthyidae [2,340], Pempheridae [9], Penaeidae [9], Pholidoteuthidae [2], Phosichthyidae [2], Platycephalidae [27], Portunidae [341], Sciaenidae [2,23,50,340-341], Scomberesocidae [23,27], Scombridae [2,23,27,50,58,340], Sepiidae [9,23,332], Serranidae [2], Sparidae [9,23,50], Sphyraenidae [27], Squalidae [23], Syngnathidae [9], Synodontidae [2], Terapontidae [9], Thysanoteuthidae [2,340], Trichiuridae [23,50,341], Triglideae [23,27,340]

<i>Squalus acanthias</i>	145	Actiniidae [342], Alpheidae [343], Ammodytidae [163,218,221,345,348,352,357-358], Ampeliscidae [346], Anguillidae [218,346], Anoplopomatidae [357], Aphroditidae [351,354], Argentinidae [116], Atherinidae [346], Batrachoididae [342,351,357], Belonidae [163], Beroidae [353,358], Bolinopsidae [353,357], Bothidae [343], Buccinidae [358], Callianassidae [163], Callionymidae [103,163,352,358], Cancridae [162-163,218,221,348,355,358], Carangidae [116,163,342-343,349,358], Centracanthidae [343], Centriscidae [116], Centrolophidae [342], Cepolidae [343], Cheilodactylidae [354], Chimaeridae [116,357], Cirolanidae [342], Clupeidae [103,162-163,218,221,342-349,352-353,355,357-358], Congridae [342-343], Cottidae [345,348], Cranchiidae [116], Crangonidae [116,163,349], Cryptacanthodidae [221], Cylopodidae [116], Cymothoidae [346], Cynoglossidae [344-345], Echiuridae [342], Dussumieriidae [103], Eledonidae [163,343,352], Embiotocidae [357], Emmelichthyidae [116], Engraulidae [103,162-163,342-344,346,348-349,351,354], Enteropodidae	334	23	40827 (72204)
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[351,353], Epialtidae [342,354], Eunicidae [116], Euphausiidae [116,162,221,342,345,347-348,350,354-355,357], Gadidae [163,221,342-343,347,349,352,357-358], Gammaridae [221,342], Gempylidae [346], Glyceridae [342,346], Gobiidae [343,345-346,349], Gonatidae [353], Goneplacidae [116], Hexagrammidae [162,347], Histioteuthidae [348], Hoplichthyidae [116], Hyperiididae [116,162,342,351,353-355], Latridae [346], Limacinidae [162], Lithodidae [342], Litocheiridae [346], Loliginidae [163,218,221,342-343,351,353-354,357], Lophiidae [221], Lotidae [349], Macrouridae [116], Majidae [116,342], Merlucciidae [103,116,162,218,221,342-343,348,351-354,356-358], Metridiidae [358], Moridae [116,342,355], Moronidae [344], Mullidae [343,349], Munididae [116,342,351,353-355], Muricidae [349], Myctophidae [103,116,342,354-355], Myxinidae [342,354], Nassariidae [346], Naticidae [345], Nephropidae [116,163], Nereididae [358], Nototheniidae [342,351,353-354], Octopodidae [342-343,346,352,354-355,357], Ommastrephidae [103,116,218,221,342-343,346,351,353-355], Onuphidae [116,343], Onychoteuthidae [116], Ophiidiidae [116,342,345,351], Oplophoridae [116], Oreosomatidae [116], Osmeridae [348,357], Ovalipidae [355], Paguridae [163,354,358], Palaemonidae [343], Palinuridae [116], Pandalidae [116,162-163,357], Paralichthyidae [162,218,221,344-345,351], Pasiphaeidae [163], Penaeidae [103,346,354], Percophidae [342,355], Petromyzontidae [348], Phycidae [221,345], Phyllodocidae [346], Pleurobrachiidae [351,355,357-358], Pleuronectidae [162-163,221,352,354], Polybiidae [163], Polymixiidae [345], Polyprionidae [342], Porpitidae [162], Portunidae [345], Rajidae [342], Salmonidae [347], Salpidae [353-355], Sciaenidae [342,344], Scomberesocidae [103,352], Scombridae [163,221,342,352,358], Scopthalmidae [221], Scorpaenidae [116,343,347,349,357], Sebastidae [116,221,342], Sepiadariidae [355], Sepiidae [343], Sepiolidae [116,163,345,351,353-354], Sergestidae [342], Serolidae [342,351,354], Serranidae [116,342], Sillaginidae [346], Sipunculidae [342], Soleidae [343], Solenoceridae [342,351,354], Sparidae [218,342-343],

Squalidae [103,342,346,349,355,357], Squillidae [103,346], Sternoptychidae [103,116], Stichaeidae [163], Stromateidae [218,342,351,353], Syngnathidae [345,349], Terebellidae [346], Tetrarogidae [346], Tetrasquillidae [355], Thalasseleotrididae [355], Trichiuridae [103], Trichopeltariidae [116,353-354], Triglidae [218,342-343,345,351,358], Upogebiidae [163,349], Uranoscopidae [349], Urechidae [355], Varunidae [346], Zeniontidae [342], Zoarcidae [221,351,357]

<i>Squalus blainville</i>	46	Alpheidae [294,360], Aphroditidae [360], Argentinidae [359-360], Astropectinidae [360], Atelecyclidae [360], Blenniidae [360], Bothidae [360], Callionymidae [360], Calliostomatidae [294], Carangidae [360], Centranchidae [360], Cepolidae [360-361], Cirolanidae [294], Citharidae [360], Clupeidae [360-361], Congridae [360], Crangonidae [360], Echinasteridae [360], Eledonidae [360], Engraulidae [360-361], Euprosinidae [361], Gadidae [359-360], Gobiidae [360-361], Goneplacidae [360-361], Haliotidae [294], Inachidae [360], Leucosiidae [360], Loliginidae [294,360], Merlucciidae [360], Mullidae [360-361], Nereididae [360], Octopodidae [294,360], Paguridae [294], Palaemonidae [294], Penaeidae [360-361], Polybiidae [294,360-361], Portunidae [294], Scyliorhinidae [361], Sepiidae [294,360-361], Sepiolidae [360], Serranidae [360], Sicyoniidae [360], Sipunculidae [294,360], Soleidae [294,360], Sparidae [360], Squillidae [360]	11	4	1103 (1471)
<i>Squalus megalops</i>	60	Acropomatidae [299], Alpheidae [299], Aphroditidae [299], Apogonidae [299], Argentinidae [73,299], Callionymidae [103], Carangidae [299], Centriscidae [299], Cirolanidae [299], Clupeidae [299], Congridae [299], Crangonidae [73], Cyttidae [299], Diogenidae [299], Dussumieriidae [103], Engraulidae [73,103], Eunicidae [299], Fasciolariidae [299], Gempylidae [299], Gerreidae [299], Histiotteuthidae [299], Leucosiidae [299], Loliginidae [73], Lumbrineridae [299], Macrouridae [299], Merlucciidae [299], Myctophidae [73,103,299], Nannosquillidae [299], Narcinidae [299], Nereididae [299], Octopodidae [73,103,299], Ommastrephidae [73,299], Ophichthidae [299], Otariidae [299], Paguridae [299], Palaemonidae	9	3	694 (1076)

		[299], Palinuridae [299], Paraulopidae [299], Penaeidae [103,299], Philinidae [299], Pilumnidae [299], Platycephalidae [299], Portunidae [299], Rajidae [299], Scomberesocidae [73], Scombridae [73,299], Scorpaenidae [299], Sebastidae [299], Serrivomeridae [299], Sillaginidae [299], Sipunculidae [299], Solenoceridae [299], Squalidae [299], Squillidae [103,299], Triakidae [299], Trichiuridae [73,103], Triglidae [299], Turbinidae [299], Urolophidae [299], Volutidae [299]			
<i>Squalus mitsukurii</i>	34	Benthescymidae [289], Berycidae [289], Bothidae [289], Callanthiidae [289], Calappidae [103], Callionymidae [103], Clupeidae [103], Congridae [103,289], Echeneidae [289], Emmelichthyidae [103,289], Enoploteuthidae [289], Epigonidae [289], Euphausiidae [289], Gnathophausiidae [289], Histioteuthidae [289], Macrouridae [103], Merlucciidae [103], Monacanthidae [289], Myctophidae [103,289], Ommastrephidae [103,289], Oplophoridae [289], Paralepididae [289], Parapaguridae [103], Phronimidae [289], Pyrosomatidae [289], Salpidae [289], Scomberesocidae [103], Sebastidae [103], Sepiolidae [289], Sergestidae [289], Sternoptychidae [289], Stomiidae [289], Trichiuridae [103], Zeidae [103]	10	2	312 (564)
<i>Squatina californica</i>	18	Batrachoididae [231], Carangidae [231], Clupeidae [231], Dussumieriidae [231], Enoploteuthidae [231], Holocentridae [231], Labridae [231], Mastigoteuthidae [231], Mugilidae [231], Muraenidae [231], Ophidiidae [231], Pomacentridae [231], Scombridae [231], Serranidae [231], Sicyoniidae [231], Stromateidae [231], Synodontidae [231], Triglidae [231]	9	1	190 (414)
<i>Squatina squatina</i>	4	Majidae [163], Pleuronectidae [163], Polybiidae [163], Triglidae [163]	7	1	18 (19)
<i>Triakis semifasciata</i>	35	Atherinidae [62,230], Batrachoididae [62,230], Blepharipodidae [62], Bothidae [62], Callianassidae [62,230], Cancridae [62,134-135,230], Clupeidae [62,230], Cottidae [62,135], Crangonidae [62,230], Cynoglossidae [62], Embiotocidae [62,135,230], Engraulidae [62,230], Gobiidae [62,230], Grapsidae [62,134], Hippidae [62], Loliginidae [135], Mactridae [135], Myliobatidae [135,230], Nereididae [230], Octopodidae [62,230], Ophidiidae [135], Paralichthyidae [135,230], Petromyzontidae [135], Pinnotheridae [135], Rajidae [135],	49	4	676 (827)

Rhinobatidae [62], Sciaenidae [62], Scorpaenidae [62], Solenidae [135],
Squalidae [135], Syngnathidae [135], Triakidae [230], Upogebiidae [62,135,230],
Urechidae [62,134-135,230], Varunidae [62,134]

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Table A.2. Table showing intermediate hosts of trypanorhynch tapeworms, which infect various shark species with known diet information. For each tapeworm species, the larval stage(s) are given alongside the known definitive hosts and intermediate hosts obtained via the extensive records in Palm (2004) and from ISI Web of Knowledge references 2004-present.

Trypanorhynch tapeworm species	Tapeworm Family	Definitive shark hosts with diet records	Intermediate hosts (family -species) listed with references
<i>Aporhynchus norvegicus</i>	Aporhynchidae	<i>Etmopterus spinax</i>	Key to larval stage: pro = proceroid, pls = plerocercus, pld = plerocercoid, mer = merocercoid
<i>Dollfusiella lineata</i>	Eutetrarhynchidae	<i>Ginglymostoma cirratum</i>	<u>Crustaceans:</u> Euphausiidae - <i>Meganyctiphanes norvegica</i> (pls) [1]; Calanidae - <i>Calanus finmarchicus</i> (pro) [1]
<i>Dollfusiella martini</i>	Eutetrarhynchidae	<i>Carcharhinus brachyurus</i>	<u>Teleosts:</u> Sciaenidae - <i>Sciaenops ocellatus</i> (pls) [1] <u>Crustaceans:</u> Carcinidae - <i>Carcinus maenas</i> (pld) [2-3]
<i>Eutetrarhynchus ruficollis</i>	Eutetrarhynchidae	<i>Mustelus canis</i> , <i>Mustelus mustelus</i> , <i>Squalus acanthias</i>	<u>Crustaceans:</u> Cancriidae - <i>Cancer pagurus</i> (pls) [1]; Carcinidae - <i>Carcinus maenas</i> (pls) [1]; Oregoniidae - <i>Hyas araneus</i> (pls) [1]; Inachidae - <i>Inachus dorsettensis</i> (pls) [1], <i>Macropodia longirostris</i> (pls) [1], <i>Macropodia rostrata</i> (pls) [1] Polybiidae - <i>Liocarcinus marmoreus</i> (pls) [1], <i>Liocarcinus depurator</i> (pls) [1]; Paguridae - <i>Pagurus bernhardus</i> (pls) [1]; Penaeidae - <i>Penaeus kerathurus</i> (pls) [1]; Pilumnidae - <i>Pilumnus hirtellus</i> (pls) [1]; <u>Other mollusks:</u> Ostreidae - <i>Ostrea edulis</i> (pls) [1];

<i>Parachristianella dimegacantha</i>	Eutetrarhynchidae	<i>Sphyrna zygaena</i>	<u>Crustaceans:</u> Penaeidae - <i>Penaeus aztecus</i> (pls) [1], <i>Penaeus duorarum</i> (pls) [1]; <u>Other mollusks:</u> Veneridae - <i>Chione cancellate</i> (pls) [1]; Mactridae - <i>Spisula solidissima</i> (pls) [1]
<i>Prochristianella tumidula</i>	Eutetrarhynchidae	<i>Carcharhinus obscurus</i> , <i>Mustelus canis</i> , <i>Mustelus mustelus</i>	<u>Teleosts:</u> Batrachoididae - <i>Opsanus tau</i> (pls) [1];
<i>Gilquinia squali</i>	Gilquiniidae	<i>Etmopterus granulosus</i> , <i>Mustelus mustelus</i> , <i>Scyliorhinus stellaris</i> , <i>Squalus acanthias</i> , <i>Squalus blainville</i>	<u>Teleosts:</u> Gadidae - <i>Merlangius merlangus</i> (pls) [1]; Salmonidae - <i>Oncorhynchus tshawytscha</i> (pls) [1];
<i>Gymnorhynchus gigas</i>	Gymnorhynchidae	<i>Carcharodon carcharias</i> , <i>Isurus oxyrinchus</i> , <i>Lamna nasus</i>	<u>Teleosts:</u> Bramidae - <i>Brama brama</i> (mer) [1]; Xiphiidae - <i>Xiphias gladius</i> (pld) [4]; Trichiuridae - <i>Lepidopus caudatus</i> (pld) [5]
<i>Molicola horridus</i>	Gymnorhynchidae	<i>Carcharodon carcharias</i> , <i>Isurus oxyrinchus</i> , <i>Prionace glauca</i>	<u>Teleosts:</u> Diodontidae - <i>Cylichthys orbicularis</i> (mer) [1], <i>Diodon holocanthus</i> (mer) [1], <i>Diodon hystrix</i> (mer) [1,11], <i>Diodon liturosus</i> (mer) [11]; Molidae - <i>Masturus lanceolatus</i> (mer) [1], <i>Mola mola</i> (mer) [1,7]; Xiphiidae - <i>Xiphias gladius</i> (pld) [4,6];
<i>Molicola uncinatus</i>	Gymnorhynchidae	<i>Alopias vulpinus</i>	<u>Teleosts:</u> Scombridae - <i>Allothunnus fallai</i> (mer) [1]; Molidae - <i>Mola mola</i> (mer) [1]; Bramidae - <i>Taractes rubescens</i> (mer) [1], <i>Taractichthys steindachneri</i> (mer) [1]; Gempylidae - <i>Thyrsites atun</i> (mer) [1,8]; Xiphiidae - <i>Xiphias gladius</i> (mer) [1]

***Callitetrarhynchus
gracilis***

Lacistorhynchidae

*Carcharhinus
amblyrhynchoides,
Carcharhinus
amboinensis,
Carcharhinus leucas,
Carcharhinus limbatus,
Carcharhinus
melanopterus,
Carcharhinus obscurus,
Mustelus canis,
Negaprion brevirostris,
Prionace glauca,
Rhizoprionodon acutus,
Rhizoprionodon
terraenovae, Sphyrna
lewini, Sphyrna zygaena*

Teleosts:

Belonidae -*Ablenes hians* (pls) [1], *Tylosurus crocodilus crocodilus* (pls) [1];
Carangidae -*Alepes djedaba* (pls) [1], *Alectis alexandrina* (pls) [1], *Carangoides otrynter* (pls) [1], *Carangoides bajad* (pls) [1], *Carangoides fulvoguttatus* [11], *Caranx crysos* (pls) [1], *Caranx hippos* (pls) [1], *Caranx ignobilis* (pls) [1], *Caranx rhonchus* (pls) [1], *Caranx ruber* (pls) [1], *Caranx senegallus* (pls) [1], *Caranx sexfasciatus* (pls) [1], *Caranx papuensis* [11], *Caranx sp.* (pls) [1] *Caranx latus* (pls) [19], *Chloroscombrus chrysurus* (pls) [1], *Lichia amia* (pls) [1], *Megalaspis cordyla* (pls) [1,11], *Oligoplites palometa* (pls) [1], *Oligoplites saurus* (pls) [1], *Scomberoides commersonianus* (pls) [1], *Scomberoides lysan* (pls) [1], *Scomberoides tala* (pls) [1], *Selene vomer* (pls) [1], *Seriola quinqueradiata* (pls) [1], *Seriola sp.* (pls) [1], *Trachinotus goodei* (pls) [1], *Trachinotus ovatus* (pls) [1], *Trachurus capensis* (pls) [1], *Trachurus trachurus* (pls) [1], *Atule mate* [11];
Serranidae -*Alphestes afer* (pls) [1], *Cephalopholis fulva* (pls) [1], *Cephalopholis taeniops* (pls) [1], *Cephalopholis miniata* (pls) [11,17], *Cephalopholis boenak* [11], *Cephalopholis cyanostigma* [11], *Cephalopholis spiloparaea* [11], *Hyporthodus niveatus* (pls) [1], *Epinephelus adscensionis* (pls) [1], *Epinephelus aeneus* (pls) [1], *Epinephelus akaara* (pls) [1], *Epinephelus maculatus* (pls) [1], *Epinephelus striatus* (pls) [1], *Epinephelus chlorostigma* [11], *Epinephelus fasciatus* [11], *Epinephelus retouti* [11], *Epinephelus rivulatus* [11], *Epinephelus polyphemadion* (pls) [17] *Epinephelus summana* (pls) [17], *Epinephelus sp.* (pls) [1], *Hemilutjanus macrophthalmos* (pls) [1], *Mycteroperca bonaci* (pls) [1], *Mycteroperca interstitialis* (pls) [1], *Mycteroperca tigris* (pls) [1], *Mycteroperca venenosa* (pls) [1], *Paralabrax humeralis* (pls) [1], *Paranthias furcifer* (pls) [1], *Cromileptes altivelis* [11], *Plectropomus maculatus* [11], *Variola louti* [11];
Sciaenidae -*Argyrosomus regius* (pls) [1], *Cynoscion guatucupa* (pls) [1,20], *Cynoscion jamaicensis* (pls) [1], *Larimus breviceps* (pls) [1] *Macrodon ancylodon* (pls) [1,20], *Micropogonias furnieri* (pls) [1,20], *Otolithes ruber* (pls) [1,13,15], *Paralanchurus peruanus* (pls) [1], *Pennahia anea* (pls) [1], *Pennahia argentata* (pls)

[1], *Paralonchurus peruanus* (pls) [1], *Sciaena deliciosa* (pls) [1], *Johnius borneensis* [11];

Ariidae -*Ariopsis felis* (pls) [1], *Netuma thalassina* (pls) [1], *Bagre marinus* (pls) [1], *Genidens barbatus* (pls) [1];

Arripidae -*Arripis truttacea* (pls) [1];

Scombridae -*Auxis rochei rochei* (pls) [1], *Euthynnus affinis* (pls) [1], *Euthynnus alletteratus* (pls) [1,9], *Euthynnus sp.* (pls) [1], *Scomber colias* (pls) [1], *Scomberomorus cavalla* (pls) [1], *Scomberomorus commerson* (pls) [1,11,21], *Scomberomorus guttatus* (pls) [1], *Scomberomorus maculatus* (pls) [1], *Scomberomorus munroi* (pls) [1], *Scomberomorus nipponius* (pls) [1], *Scomberomorus queenslandicus* [11], *Thunnus albacares* (pls) [1], *Thunnus thynnus* (pls) [1], *Thunnus sp.* (pls) [1];

Balistidae -*Balistes sp.* (pls) [1];

Bramidae -*Brama brama* (pls) [1];

Centropomidae -*Centropomus undecimalis* (pls) [1];

Bothidae -*Chascanopsetta lugubris* (pls) [1];

Psettodidae - *Psettodes erumei* (pls) [10,15],

Chirocentridae -*Chirocentrus dorab* (pls) [1,11], *Chirocentrus nudus* (pld) [15];

Chlorophthalmidae -*Chlorophthalmus agassizi* (pls) [1];

Sparidae -*Chrysoblephus puniceus* (pls) [1], *Chrysophrys auratus* (pls) [1], *Pagrus pagrus* (pls) [1], *Parcostoma dentata* (pls) [1];

Labridae -*Bodianus axillaris* (pls) [1], *Choerodon cyanodus* [11];

Exocoetidae -*Cypselurus poecilopterus* (pls) [1];

Moronidae -*Dicentrarchus labrax* (pls) [1];

Dinopercidae -*Dinoperca petersi* (pls) [1];

Elopidae -*Elops saurus* (pls) [1];

Engraulidae -*Engraulis japonicus* (pls) [1];

Clupeidae -*Ethmalosa fimbriate* (pls) [1], *Harengula clupeola* (pls) [1],
Opisthonema oglinum (pls) [1], *Sardina pilchardus* (pls) [1], *Sardinella maderensis*
(pls) [1];

Ammodytidae -*Gymnammodytes cicerelus* (pls) [1];

Haemulidae -*Haemulon aurolineatum* (pls) [1];

Istiophoridae - *Istiophorus platypterus* (pls) [1], *Istiompax indica* (pls) [1], *Makaira mazara* (pls) [1];

Latidae - *Lates calcarifer* (pls) [1];

Leiognathidae - *Leiognathus equulus* (pls) [1], *Secutor ruconius* (pls) [1];

Trichiuridae -*Lepturacanthus savala* (pls) [1], *Trichiurus lepturus* (pls, pld)
[1,14,56];

Macrouridae -*Malacocephalus laevis* (pls) [1];

Lethrinidae -*Lethrinus erythracanthus* (pls) [1], *Lethrinus miniatus* [11], *Lethrinus nebulosus* [15], *Lethrinus mahsena* (pls) [17], *Lethrinus variegatus* (pls) [17];

Lutjanidae -*Lutjanus analis* (pls) [1], *Lutjanus campechanus* (pls) [1], *Lutjanus fulgens* (pls) [1], *Lutjanus gorensis* (pls) [1], *Lutjanus griseus* (pls) [1], *Lutjanus vitta* (pls) [1,11], *Lutjanus carponotatus* [11], *Lutjanus johnii* (pls) [15], *Lutjanus sp.* (pls) [1], *Ocyurus chrysurus* (pls) [1], *Pristipomoides multidens* (pls) [1];

Merlucciidae -*Merluccius gayi peruanus* (pls) [1], *Merluccius gayi gayi* (pls) [1];

Mullidae -*Mullus barbatus* (pls) [1];

Muraenesocidae -*Muraenesox cinereus* (pls) [1];

Nemipteridae - *Nemipterus japonicus* (pls) [1], *Nemipterus furcosus* [11];

Paralichthyidae -*Paralichthys dentatus* (pls) [1], *Paralichthys olivaceus* (pls) [1],
Paralichthys isosceles (pls) [18];

Platycephalidae -*Platycephalus fuscus* (pls) [1];

Pomatomidae -*Pomatomus saltatrix* (pls) [1,11,19];

Priacanthidae -*Priacanthus hamrur* (pls) [1];

Rachycentridae -*Rachycentron canadum* (pls) [1];

Synodontidae -*Saurida tumbil* (pls) [1,15], *Saurida undosquamis* (pls) [1], *Synodus lucioceps* (pls) [1];

Sphyraenidae - *Sphyraena acutipinnis* (pls) [1], *Sphyraena barracuda* (pls) [1], *Sphyraena guachancho* (pls) [1], *Sphyraena novaehollandiae* (pls) [1], *Sphyraena pinguis* (pls) [1], *Sphyraena obtusata* [11];

Monacanthidae -(unidentified) (pls) [1];

Pomacentridae -*Abudefduf whitleyi* [11];

Apogonidae -*Apogon poecilopterus* [11], *Ostorhinchus fasciatus* [11];

Caesionidae -*Caesio cuning* [11];

Moridae -*Lotella rhacina* [11];

Acanthuridae -*Naso vlamingii* [11];

Polynemidae -*Filimanus heptadactyla* [11], *Eleutheronema tetradactylum* [16];

Triodontidae -*Triodon macropterus* [11];

Phycidae -*Urophycis brasiliensis* [12];

Ophidiidae -*Genypterus brasiliensis* (pls) [22];

Coryphaenidae -*Coryphaena hippurus* [28], *Coryphaena equiselis* [28];

Chondrichthyan fishes

Ginglymostomatidae -*Nebrius ferrugineus* (pls) [1];

Reptiles:

Colubridae -*Cerberus rynchops* (pls) [1];

Callitetrarhynchus speciosus Lacistorhynchidae *Carcharhinus obscurus*,
Negaprion brevirostris

Teleosts:

Ariidae -*Netuma thalassina* (pls) [1], *Genidens barbatus* (pls) [1];

Platycephalidae -*Cociella punctata* (pls) [1], *Cymbacephalus beauforti* [11], *Platycephalus indicus* (pls) [1];

Congridae -*Conger cinereus* (pls) [17];

Pomatomidae -*Pomatomus saltatrix* (pls) [1,19];

Sciaenidae -*Cynoscion guatucupa* (pls) [1,20], *Cynoscion regalis* (pls) [1], *Micropogonias furnieri* (pls) [1,20], *Nibeal biflora* (pls) [1];

Balistidae -*Canthidermis maculata* (pls) [1];

Serranidae -*Cephalopholis hemistiktos* (pls) [1], *Epinephelus adscensionis* (pls) [1],
Epinephelus areolatus (pls) [1], *Epinephelus maculatus* (pls) [1], *Epinephelus morio*
(pls) [1], *Epinephelus multinotatus* (pls) [1], *Epinephelus striatus* (pls) [1],
Epinephelus tukula (pls) [1], *Mycteroperca interstitialis* (pls) [1], *Mycteroperca*
phenax (pls) [1], *Mycteroperca venenosa* (pls) [1];
Sparidae -*Chrysolephus anglicus* (pls) [1];
Coryphaenidae -*Coryphaena hippurus* (pls) [1];
Echeneidae -*Echeneis naucrates* (pls) [1],
Haemulidae -*Haemulon album* (pls) [1];
Priacanthidae -*Heteropriacanthus cruentatus* (pls) [1], *Priacanthus arenatus* (pls)
[23];
Scombridae -*Katsuwonis pelamis* (pls) [1], *Scomber japonicus* (pls) [1],
Scomberomorus commerson (pls) [1], *Scomberomorus guttatus* (pls) [1], *Thunnus*
thynnus (pls) [1];
Labridae -*Lachnolaimus maximus* (pls) [1];
Lethrinidae -*Lethrinus nebulosus* (pls) [1];
Lutjanidae -*Lutjanus analis* (pls) [1], *Lutjanus campechanus* (pls) [1], *Lutjanus*
griseus (pls) [1], *Lutjanus synagris* (pls) [1], *Lutjanus argentimaculatus* [25],
Ocyurus chrysurus (pls) [1];
Muraenesocidae -*Muraenesox cinereus* (pls) [1];
Triglidae -*Prionotus carolinus* (pls) [1];
Carangidae -*Selene vomer* (pls) [1], *Seriola dumerili* (pls) [1], *Trachinotus goodei*
(pls) [1];
Monacanthidae -*Stephanolepis hispidus* (pls) [1], *Aluterus monoceros* (pls) [24];
Trichiuridae -*Trichiurus lepturus* (pls) [1];
Xiphiidae -*Xiphias gladius* (pls) [1];

Dasyrhynchus
giganteus

Lacistorhynchidae

Carcharhinus leucas,
Carcharhinus
melanopterus,

Teleosts:

Carangidae -*Caranx hippos* (pls) [1], *Oligoplites saliens* (pls) [1], *Seriola dumerili*
(pls) [1];

		<i>Carcharhinus plumbeus</i> , <i>Negaprion brevirostris</i> , <i>Rhizoprionodon</i> <i>terraenovae</i>	Polynemidae - <i>Polydactylus quadrifilis</i> (pls) [1]; Xiphiidae - <i>Xiphias gladius</i> (pls) [1];
<i>Dasyrhynchus pacificus</i>	Lacistorhynchidae	<i>Carcharhinus brachyurus</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus obscurus</i> , <i>Carcharhinus plumbeus</i> , <i>Sphyrna lewini</i>	<u>Teleosts:</u> Sciaenidae - <i>Cynoscion guatucupa</i> (pls) [1,20], <i>Cynoscion jamaicensis</i> (pls) [1], <i>Macrodon ancylodon</i> (pls) [1,20], <i>Micropogonias furnieri</i> [20], <i>Menticirrhus americanus</i> (pls) [1,20], <i>Argyrosomus japonicus</i> (pls) [1], <i>Argyrosomus hololepidotus</i> (pls) [1], <i>Sciaena deliciosa</i> (pls) [1]; Monacanthidae - <i>Acanthaluteres brownie</i> (pls) [1]; Lutjanidae - <i>Aprion virescens</i> (pls) [1]; Lethrinidae - <i>Lethrinus mahsena</i> (pls) [1]; Mugilidae - <i>Mugil curema</i> (pls) [1], <i>Mugil cephalus</i> (pls) [1];
<i>Dasyrhynchus talismani</i>	Lacistorhynchidae	<i>Carcharhinus brachyurus</i> , <i>Carcharhinus leucas</i> , <i>Carcharhinus longimanus</i> , <i>Prionace glauca</i>	<u>Teleosts:</u> Scombridae - <i>Thunnus albacares</i> (pls) [1], <i>Thunnus obesus</i> (pls) [1];
<i>Dasyrhynchus varioucinatus</i>	Lacistorhynchidae	<i>Carcharhinus amblyrhynchoides</i> , <i>Carcharhinus amblyrhynchos</i> , <i>Carcharhinus falciformis</i> , <i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus plumbeus</i> , <i>Carcharodon carcharias</i> , <i>Negaprion brevirostris</i>	<u>Teleosts:</u> Scombridae - <i>Euthynnus affinis</i> (pls) [1]; Carangidae - <i>Carangoides ciliarius</i> (pls) [1], <i>Caranx sexfasciatus</i> (pls) [1], <i>Caranx sp.</i> (pls) [1];

<i>Diesingium lomentaceum</i>	Lacistorhynchidae	<i>Galeorhinus galeus</i> , <i>Mustelus canis</i> , <i>Mustelus mustelus</i>	<u>Teleosts:</u> Carangidae - <i>Carangoides fulvoguttatus</i> [11]; Serranidae - <i>Epinephelus chlorostigma</i> [11]
<i>Floriceps minacanthus</i>	Lacistorhynchidae	<i>Carcharhinus amblyrhynchos</i> , <i>Carcharhinus amboinensis</i> , <i>Carcharhinus brachyurus</i> , <i>Carcharhinus melanopterus</i>	<u>Teleosts:</u> Serranidae - <i>Cephalopholis hemistiktos</i> (pls) [1], <i>Cephalopholis urodeta</i> [11], <i>Cephalopholis miniate</i> (pld) [11,26-27], <i>Cephalopholis boenak</i> [11], <i>Cephalopholis cyanostigma</i> [11], <i>Cephalopholis sonnerati</i> [11], <i>Epinephelus quoyanus</i> [11], <i>Epinephelus coioides</i> [11], <i>Epinephelus cyanopodus</i> [11], <i>Epinephelus maculatus</i> [11], <i>Plectropomus areolatus</i> [11], <i>Plectropomus leopardus</i> (pls) [1,11], <i>Plectropomus laevis</i> [11], <i>Variola louti</i> [11]; Scombridae - <i>Euthynnus affinis</i> (pls) [1,11], <i>Euthynnus alletteratus</i> (pls) [1,11], <i>Grammatorcynus bicarinatus</i> [11], <i>Gymnosarda unicolor</i> (pls) [1]; Lethrinidae - <i>Lethrinus miniatus</i> (pls) [1,11], <i>Lethrinus mahsena</i> (pls,pld) [1,26]; Nemipteridae - <i>Nemipterus furcosus</i> (pls) [1,11]; Sphyraenidae - <i>Sphyraena flavicauda</i> [11], <i>Sphyraena putnamae</i> [11], <i>Sphyraena jello</i> [11], <i>Sphyraena novaehollandiae</i> (pls) [1]; Belonidae - <i>Tylosurus crocodilus crocodilus</i> [11]; Carangidae - <i>Carangoides bajad</i> (pls,pld) [1,26]; Platycephalidae - <i>Platycephalus bassensis</i> (pls) [1], <i>Platycephalus laevigatus</i> (pls) [1], <i>Platycephalus sp.</i> (pls) [1]
<i>Floriceps saccatus</i>	Lacistorhynchidae	<i>Carcharhinus limbatus</i> , <i>Carcharhinus obscurus</i> , <i>Carcharhinus plumbeus</i> , <i>Carcharhinus signatus</i> , <i>Negaprion brevirostris</i> , <i>Notorynchus cepedianus</i> , <i>Prionace glauca</i>	<u>Teleosts:</u> Carangidae - <i>Caranx papuensis</i> [11], <i>Caranx hippos</i> (pls) [1], <i>Seriola lalandi</i> (pls) [1], <i>Trachinotus ovatus</i> (pls) [1]; Diodontidae - <i>Diodon holocanthus</i> (pls) [1], <i>Diodon liturosus</i> [11], <i>Diodon hystrix</i> (pls) [1,11]; Monacanthidae - <i>Aluterus monoceros</i> (pls) [24], <i>Aluterus sp.</i> (pls) [1]; Coryphaenidae - <i>Coryphaena hippurus</i> (pls) [1,28], <i>Coryphaena equiselis</i> (pls) [1]; Sciaenidae - <i>Argyrosomus regius</i> (pls) [1]; Centropomidae - <i>Centropomus nigrescens</i> (pls) [1];

			<p>Gempylidae -<i>Gempylus serpens</i> (pls) [1,56]; Pleuronectidae -<i>Glyptocephalus stelleri</i> (pls) [1]; Scombridae -<i>Katsuwonis pelamis</i> (pls) [1]; Molidae -<i>Mola mola</i> (pls) [1]; Tetraodontidae -<i>Takifugu porphyreus</i> (pls) [1]; Trichiuridae -<i>Trichiurus lepturus</i> (pls) [1];</p>
<i>Grillotia acanthoscolex</i>	Lacistorhynchidae	<i>Hexanchus griseus</i>	<p><u>Teleosts:</u> Scorpaenidae -<i>Scorpaena scrofa</i> (pls) [1]; Lophiidae -<i>Lophius piscatorius</i> (pls) [29]; <u>Chondrichthyan fishes:</u> Torpedinidae -<i>Tetronarce nobiliana</i> (pls) [1]; Centrophoridae -<i>Deania hystricosa</i> (pls) [1], <i>Deania profundorum</i> (pls) [1]; Hexanchidae -<i>Heptranchias perlo</i> (pls) [1];</p>
<i>Grillotia amblyrhynchos</i>	Lacistorhynchidae	<i>Carcharhinus amblyrhynchos</i>	<p><u>Chondrichthyan fishes:</u> Etmopteridae -<i>Etmopterus sp.</i> (pls) [1];</p>
<i>Grillotia dolichocephala</i>	Lacistorhynchidae	<i>Centrophorus squamosus</i>	<p><u>Chondrichthyan fishes:</u> Somniosidae -<i>Centroscymnus coelolepis</i> (pls) [29]; Centrophoridae -<i>Centrophorus squamosus</i> (pls) [29], <i>Deania profundorum</i> (pls) [29];</p>
<i>Grillotia dollfusi</i>	Lacistorhynchidae	<i>Carcharhinus signatus</i> , <i>Heptranchias perlo</i>	<p><u>Teleosts:</u> Macrouridae -<i>Nezumia aequalis</i> (pls) [1]; Merlucciidae -<i>Merluccius gayi gayi</i> (pls) [1];</p>
<i>Grillotia erinaceus</i>	Lacistorhynchidae	<i>Squalus acanthias</i>	<p><u>Teleosts:</u> Agonidae -<i>Agonus cataphractus</i> (pls) [1]; Anarhichadidae -<i>Anarhichas lupus</i> (pls) [1]; Bothidae -<i>Arnoglossus laterna</i> (pls) [1]; Lotidae -<i>Brosme brosme</i> (pls) [1], <i>Enchelyopus cimbrius</i> (pls) [1], <i>Lota lota</i> (pls) [1], <i>Molva molva</i> (pls) [1]; Macrouridae -<i>Coelorinchus fasciatus</i> (pls) [1], <i>Malacocephalus laevis</i> (pls) [1];</p>

Callionymidae -*Callionymus lyra* (pls) [1];
Caproidae -*Capros aper* (pls) [1];
Cepolidae -*Cepola macrophthalma* (pls) [1];
Triglidae -*Chelidonichthys cuculus* (pls) [1], *Chelidonichthys lucerna* (pls) [1],
Eutrigla gurnardus (pls) [1], *Trigloporus lastoviza* (pls) [1], *Prionotus carolinus* (pls)
[1];
Clupeidae -*Clupea harengus* (pls) [1];
Congridae -*Conger conger* (pls) [1];
Serranidae -*Epinephelus marginatus* (pls) [1];
Gadidae -*Gadus morhua* (pls) [1], *Melanogrammus aeglefinus* (pls) [1], *Merlangius
merlangus* (pls,pld) [1,30-31], *Pollachius pollachius* (pls) [1], *Pollachius virens* (pls)
[1], *Trisopterus esmarkii* (pls) [1], *Trisopterus minutus* (pls) [1];
Pleuronectidae -*Glyptocephalus cynoglossus* (pls) [1], *Hippoglossoides
platessoides* (pls) [1], *Hippoglossus hippoglossus* (pls) [1], *Limanda aspera* (pls) [1],
Limanda ferruginea (pls) [1], *Limanda limanda* (pls) [1] *Microstomus kitt* (pls) [1],
Platichthys flesus (pls) [1], *Pleuronectes platessa* (pls) [1], *Reinhardtius
hippoglossoides* (pls) [1];
Ateleopodidae -*Guentherus altivela* (pls) [1];
Scophthalmidae -*Lepidorhombus
Whiffiagonis* (pls) [1], *Scophthalmus aquosus* (pls) [1], *Scophthalmus maximus* (pls)
[1], *Scophthalmus rhombus* (pls) [1];
Lophiidae -*Lophius piscatorius* (pls) [1];
Merlucciidae -*Merluccius bilinearis* (pls) [1], *Merluccius merluccius* (pls) [1];
Cottidae -*Myoxocephalus scorpius* (pls) [1], *Taurulus bubalis* (pls) [1];
Pholidae -*Pholis gunnellus* (pls) [1];
Batrachoididae -*Porichthys porosissimus* (pls) [1];
Salmonidae -*Salmo salar* (pls) [1];
Scombridae -*Scomber scombrus* (pls) [1];
Scorpaenidae -*Scorpaena plumieri* (pls) [1];

Sebastidae -*Sebastes norvegicus* (pls) [1], *Sebastes mentella* (pls) [1], *Sebastes viviparus* (pls) [1];

Soleidae -*Solea solea* (pls) [1];

Carangidae -*Trachurus capensis* (pls) [1], *Trachurus trachurus* (pls) [1];

Phycidae -*Urophycis tenuis* (pls) [1];

Xiphiidae -*Xiphias gladius* (pls) [1];

Nototheniidae -*Dissostichus eleginoides* (pld) [32,34];

Eleginopsidae -*Eleginops maclovinus* (pld) [33];

Crustaceans

Acartidae -*Acartia longiremis* (pro) [1];

Paracalanidae -*Paracalanus parvus* (pro) [1];

Clausioalanidae -*Pseudocalanus elongatus* (pro) [1];

Temoridae -*Temora longicornis* (pro) [1];

Chondrichthyan fishes:

Odontaspidae -*Carcharias Taurus* (pls) [1];

Centrophoridae -*Centrophorus squamosus* (pls) [1];

Rajidae -*Dipturus batis* (pls) [1];

Arhynchobatidae -*Sympterygia bonapartii* (pls) [1];

Grillotia heptanchi Lacistorhynchidae *Dalatias licha*,
Heptranchias perlo,
Hexanchus griseus

Teleosts:

Scophthalmidae -*Lepidorhombus*

Whiffiagonis (pls) [29];

Lotidae -*Molva dypterygia* (pls) [1,29];

Ophidiidae -*Genypterus chilensis* (pls) [1];

Trachichthyidae -*Hoplostethus atlanticus* (pls) [1];

Sciaenidae -*Johnius coitor* (pls) [1];

Trichiuridae -*Lepidopus caudatus* (pls) [1];

Lophiidae -*Lophius piscatorius* (pls) [1];

			<p>Merlucciidae -<i>Macruronus magellanicus</i> (pls) [1], <i>Merluccius australis</i> (pls) [1,47], <i>Merluccius capensis</i> (pls) [1], <i>Merluccius gayi gayi</i> (pls) [1], <i>Merluccius merluccius</i> (pls) [1], <i>Merluccius paradoxus</i> (pls) [1];</p> <p>Gadidae -<i>Merlangius merlangus</i> (pls) [1], <i>Gadus chalcogrammus</i> (pls) [1];</p> <p>Centrarchidae -<i>Micropterus salmoidesi</i> (pls) [1];</p> <p>Hexagrammidae -<i>Ophiodon elongatus</i> (pls) [1];</p> <p><u>Chondrichthyan fishes:</u></p> <p>Hexanchidae -<i>Hexanchus griseus</i> (pls) [1];</p>
Grillotia smaris-gora	Lacistorhynchidae	<i>Squatina californica</i> , <i>Squatina squatina</i>	<p><u>Teleosts:</u></p> <p>Gadidae -<i>Microgadus tomcod</i> (pls) [1];</p> <p>Paralichthyidae -<i>Paralichthys dentatus</i> (pls) [1];</p> <p>Centrarchidae -<i>Spicara maena</i> (pls) [1], <i>Spicara smaris</i> (pls) [1];</p> <p>Sparidae -<i>Stenotomus chrysops</i> (pls) [1];</p> <p>Carangidae -<i>Trachurus sp.</i> (pls) [1];</p>
Grilotiella exile	Lacistorhynchidae	<i>Galeocerdo cuvier</i>	<p><u>Teleosts:</u></p> <p>Scombridae -<i>Scomberomorus commerson</i> [11];</p>
Lacistorhynchus dollfusi	Lacistorhynchidae	<i>Galeorhinus galeus</i> , <i>Mustelus californicus</i> , <i>Mustelus henlei</i> , <i>Mustelus lunulatus</i> , <i>Triakis semifasciata</i>	<p><u>Teleosts:</u></p> <p>Sciaenidae -<i>Atractoscion nobilis</i> (pls) [1], <i>Genyonemus lineatus</i> (pls) [1], <i>Cheilotrema fasciatum</i> (pls) [1];</p> <p>Labridae -<i>Choerodon cyanodus</i> (pls) [1];</p> <p>Clupeidae -<i>Clupea pallasii</i> (pls) [1];</p> <p>Embiotocidae -<i>Cymatogaster aggregata</i> (pls) [1], <i>Cymatogaster sp.</i> (pls) [1], <i>Embiotoca jacksoni</i> (pls) [1], <i>Rhacochilus vacca</i> (pls) [1];</p> <p>Poeciliidae -<i>Gambusia affinis</i> (pls) [1];</p> <p>Atherinidae -<i>Leuresthes tenuis</i> (pls) [1];</p> <p>Moronidae -<i>Morone saxatilis</i> (pls) [1];</p> <p>Hexagrammidae -<i>Ophiodon elongatus</i> (pls) [1];</p> <p>Paralichthyidae -<i>Paralichthys adspersus</i> (pls) [1], <i>Paralichthys californicus</i> (pls) [1], <i>Citharichthys sordidus</i> (pld) [35-36];</p>

			<p>Pleuronectidae -<i>Platichthys stellatus</i> (pls) [1];</p> <p>Sebastidae -<i>Sebastes atrovirens</i> (pls) [1], <i>Sebastes flavidus</i> (pls) [1], <i>Sebastes goodei</i> (pls) [1], <i>Sebastes paucispinis</i> (pls) [1];</p> <p>Synodontidae -<i>Synodus lucioceps</i> (pls) [1];</p> <p><u>Chondrichthyan fishes</u></p> <p>Triakidae -<i>Triakis semifasciata</i> (pls) [1];</p> <p><u>Crustaceans:</u></p> <p>Harpacticidae -<i>Tigriopus californicus</i> (pro) [1];</p>
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Lacistorhynchus tenuis	Lacistorhynchidae	<p><i>Alopias vulpinus,</i> <i>Galeorhinus galeus,</i> <i>Mustelus canis, Mustelus mustelus, Squalus acanthias</i></p>	<p><u>Teleosts:</u></p> <p>Mugilidae -<i>Aldrichetta forsteri</i> (pls) [1];</p> <p>Monacanthidae -<i>Aluterus schoepfii</i> (pls) [1];</p> <p>Anguillidae -<i>Anguilla rostrata</i> (pls) [1];</p> <p>Belonidae -<i>Belone belonei</i> (pls) [1];</p> <p>Triglidae -<i>Chelidonichthys cuculus</i> (pls) [1], <i>Eutrigla gurnardus</i> (pls) [1], <i>Chelidonichthys lucerna</i> (pls) [1], <i>Trigloporus lastoviza</i> (pls) [1], <i>Trigla lyra</i> (pls) [1], <i>Trigla sp.</i> (pls) [1];</p> <p>Clupeidae -<i>Clupea harengus</i> (pls) [1,37];</p> <p>Congridae -<i>Conger conger</i> (pls) [1];</p> <p>Moronidae -<i>Dicentrarchus labrax</i> (pls) [1];</p> <p>Trachinidae -<i>Echiichthys vipera</i> (pls) [1], <i>Trachinus draco</i> (pls) [1];</p> <p>Lotidae -<i>Enchelyopus cimbrius</i> (pls) [1], <i>Molva macrophthalma</i> (pls) [1];</p> <p>Gadidae -<i>Gadus morhua</i> (pls) [1], <i>Melanogrammus aeglefinus</i> (pls) [1], <i>Merlangius merlangus</i> (pls) [1], <i>Pollachius pollachius</i> (pls) [1], <i>Trisopterus luscus</i> (pls) [1];</p> <p>Poeciliidae -<i>Gambusia affinis</i> (pls) [1];</p> <p>Gasterosteidae -<i>Gasterosteus aculeatus aculeatus</i> (pls) [1];</p> <p>Gobiidae -<i>Gobius sp.</i> (pls) [1];</p> <p>Labrisomidae -<i>Labrisomus philippii</i> (pls) [1,38];</p> <p>Labridae -<i>Labrus bergylta</i> (pls) [1], <i>Labrus merula</i> (pls) [1], <i>Symphodus tinca</i> (pls) [1], <i>Tautoga onitis</i> (pls) [1];</p>
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Pleuronectidae -*Limanda limanda* (pls) [1];
Lophiidae -*Lophius piscatorius* (pls) [1];
Scophthalmidae - *Scophthalmus aquosus* (pls) [1];
Merlucciidae -*Merluccius gayi gayi* (pls) [1], *Merluccius merluccius* (pls) [1],
Merluccius gayi peruanus (pls) [1];
Mullidae -*Mullus barbatus* (pls) [1];
Cottidae -*Myoxocephalus octodecemspinosus* (pls) [1], *Myoxocephalus Scorpius*
(pls) [1];
Atherinidae -*Odontesthes regia* (pls) [1];
Osmeridae -*Osmerus eperlanus* (pls) [1];
Scombridae -*Scomber scombrus* (pls) [1], *Scomberomorus maculatus* (pls) [1];
Sparidae -*Sparus aurata* (pls) [1];
Gempylidae -*Thyrsites atun* (pls) [1];
Carangidae -*Trachurus trachurus* (pls) [1];
Zeidae -*Zenopsis nebulosa* (pls) [1], *Zeus faber* (pls) [1];
Chondrichthyan fishes:
Etmopteridae -*Etmopterus spinax* (pls) [1];
Triakidae -*Mustelus canis* (pls) [1];
Cephalopods:
Loliginidae -*Doryteuthis (Amerigo) pealeii* (pls) [1];
Ommastrephidae -*Illex illecebrosus* (pls) [1];
Crustaceans:
Acartiidae -*Acartia (Acanthacartia) tonsa* (pro) [1];
Harpacticidae -*Tigriopus fulvus* (pro) [1];

<i>Pseudogrillotia basipunctata</i>	Lacistorhynchidae	<i>Carcharhinus amblyrhynchos</i>	<u>Teleosts:</u> Diodontidae - <i>Diodon hystrix</i> (pls) [1];
<i>Pseudogrillotia epinepheli</i>	Lacistorhynchidae	<i>Carcharhinus leucas</i>	Serranidae - <i>Epinephelus flavocaeruleus</i> (pls) [1], <i>Epinephelus marginatus</i> (pls) [1], <i>Serranus atricauda</i> (pls) [39]; Muraenidae - <i>Muraena Helena</i> (pls) [1];

<i>Pseudogrillotia perelica</i>	Lacistorhynchidae	<i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Negaprion brevirostris</i>	<u>Teleosts:</u> Carangidae - <i>Caranx senegallus</i> (pls) [1]; Mugilidae - <i>Liza dumerili</i> (pls) [1], <i>Liza macrolepis</i> (pls) [1], <i>Liza richardsonii</i> (pls) [1], <i>Mugil cephalus</i> (pls) [1], <i>Myxus capensis</i> (pls) [1], <i>Valamugil buchanani</i> (pls) [1], <i>Valamugil cunnesius</i> (pls) [1], <i>Valamugil robustus</i> (pls) [1];
<i>Pseudolacistorhynchus noodti</i>	Lacistorhynchidae	<i>Ginglymostoma cirratum</i>	<u>Teleosts:</u> Monacanthidae - <i>Aluterus schoepfii</i> (pls) [1]; Muraenidae - <i>Gymnothorax funebris</i> (pls) [1]; Mullidae - <i>Pseudupeneus maculatus</i> (pls) [1]; Scombridae - <i>Scomberomorus maculatus</i> (pls) [1];
<i>Otobothrium alexanderi</i>	Otobothriidae	<i>Carcharhinus melanopterus</i>	<u>Teleosts:</u> Belonidae - <i>Tylosurus crocodilus crocodilus</i> (pls) [1,11,40];
<i>Otobothrium carcharidis</i>	Otobothriidae	<i>Carcharhinus amblyrhynchoides</i> , <i>Carcharhinus brachyurus</i> , <i>Carcharhinus dussumieri</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus macloti</i> , <i>Carcharhinus melanopterus</i> , <i>Carcharhinus sealei</i> , <i>Carcharhinus sorrah</i> , <i>Rhizoprionodon acutus</i> , <i>Rhizoprionodon taylori</i> , <i>Scoliodon laticaudus</i> , <i>Sphyrna lewini</i>	<u>Teleosts:</u> Balistidae - <i>Abalistes stellatus</i> (pls) [1]; Lethrinidae - <i>Lethrinus ornatus</i> (pls) [1];

Otobothrium cysticum Otobothriidae

Carcharhinus
amboinensis,
Carcharhinus leucas,
Carcharhinus longimanus,
Carcharhinus
melanopterus,
Carcharhinus obscurus,
Galeocerdo cuvier,
Rhizoprionodon
terraenovae, *Sphyrna*
zygaena

Teleosts:

Ophidiidae -*Genypterus brasiliensis* (pls) [22];
Scombridae -*Scomberomorus commerson* (pls) [1,21], *Euthynnus alletteratus* (pls) [1,40], *Sarda sarda* (pls) [1,40], *Scomberomorus cavalla* (pls) [1,40], *Scomberomorus regalis* [40], *Scomberomorus maculatus* (pls) [1];
Coryphaenidae -*Coryphaena hippurus* (pls) [1,28,40];
Acanthuridae -*Acanthurus coeruleus* (pls) [1,40];
Monacanthidae -*Aluterus schoepfii* (pls) [1,40];
Ariidae -*Ariopsis felis* [40], *Bagre marinus* (pls) [1,40], *Neoarius graeffei* (pls) [1], *Arius latiscutatus* (pls) [1];
Sciaenidae -*Bairdiella chrysoura* (pls) [1,40], *Cynoscion nebulosus* (pls) [1,40], *Cynoscion regalis* (pls) [1,40], *Cynoscion arenarius* (pls) [1], *Leiostomus xanthurus* (pls) [1,40], *Micropogonias undulatus* (pls) [1,40], *Pseudolithus elongatus* (pls) [1], *Pseudolithus senegallus* (pls) [1], *Pseudolithus typus* (pls) [1];
Balistidae -*Balistes capriscus* (pls) [1,40];
Carangidae -*Caranx crysos* (pls) [1,40], *Caranx senegallus* (pls) [1], *Trachurus trecae* (pls) [1];
Sparidae -*Diplodus sargus sargus* (pls) [1,40], *Lagodon rhomboides* (pls) [1,40], *Dentex macrophthalmus* (pls) [1], *Pagrus pagrus* (pls) [1];
Fundulidae -*Fundulus heteroclitus heteroclitus* (pls) [1,40];
Triglidae -*Lepidotrigla faurei* (pls) [1,40];
Lobotidae -*Lobotes surinamensis* (pls) [1,40];
Acropomatidae -*Neoscombrops cynodont* [40];
Lutjanidae -*Ocyurus chrysurus* (pls) [1,40], *Lutjanus campechanus* (pls) [1];
Batrachoididae -*Opsanus tau* (pls) [1,40];
Haemulidae -*Orthopristis chrysoptera* (pls) [1,40], *Haemulon parra* (pls) [1];
Paralichthyidae -*Paralichthys albigutta* (pls) [1,40], *Paralichthys dentatus* (pls) [1,40], *Paralichthys lethostigma* (pls) [1];

Stromateidae -*Peprilus paru* (pls) [1,40], *Peprilus burti* (pls) [1], *Peprilus triacanthus* (pls) [1,40];

Pomatomidae -*Pomatomus saltatrix* (pls) [1,40];

Trichiuridae -*Trichiurus lepturus* (pls) [1,40];

Siluridae -*Wallago attu* (pls) [1,40];

Xiphiidae -*Xiphias gladius* (pls) [1,40];

Cepolidae -*Cepola macrophthalma* (pls) [1];

Muraenesocidae -*Cynoponticus ferox* (pls) [1];

Serranidae -*Epinephelus striatus* (pls) [1], *Mycteroperca bonaci* (pls) [1], *Sacura boulengeri* (pls) [1];

Lophiidae -*Lophius piscatorius* (pls) [1];

Merlucciidae -*Merluccius capensis* (pls) [1], *Merluccius merluccius* (pls) [1];

Monodactylidae -*Monodactylus sebae* (pls) [1];

Sphyraenidae -*Sphyraena guachancho* (pls) [1];

Uranoscopidae -*Uranoscopus scaber* (pls) [1], *Uranoscopus sp.* (pls) [1];

Chondrichthyans:

Carcharhinidae -*Carcharhinus melanopterus* (pls) [1,40], *Carcharhinus limbatus* (pls) [1,40], *Carcharhinus obscurus* (pls) [1,40], *Carcharhinus plumbeus* (pls) [1], *Rhizoprionodon terraenovae* (pls) [1,40];

Dasyatidae -*Dasyatis margarita* (pls) [1];

Triakidae -*Mustelus canis* (pls) [1,40], *Mustelus mustelus* (pls) [1,40];

Squalidae -*Squalus acanthias* (pls) [1,40];

Lamnidae -*Carcharodon carcharias* (pls) [1];

Cephalopods:

Ommastrephidae -*Illex illecebrosus* (pls) [1];

Loliginidae -*Doryteuthis pealeii* (pls) [1,40];

Reptiles:

Crocodyllidae -*Osteolaemus tetraspis* (pls) [1];

Cheloniidae -*Eretmochelys imbricata* (pls) [1], *Chelonia mydas* (pls) [1];

<i>Otobothrium insigne</i>	Otobothriidae	<i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus obscurus</i> , <i>Rhizoprionodon</i> <i>terraenovae</i> , <i>Sphyrna</i> <i>tudes</i>	<u>Teleosts:</u> Ariidae - <i>Ariopsis felis</i> (pls) [1,40], <i>Arius sp.</i> (pls) [1]; Balistidae - <i>Balistes polylepis</i> [40]
<i>Otobothrium minutum</i>	Otobothriidae	<i>Carcharhinus limbatus</i> , <i>Carcharhinus macloti</i> , <i>Rhizoprionodon acutus</i>	<u>Teleosts:</u> Carangidae - <i>Parastromateus niger</i> (pls) [1];
<i>Otobothrium mugilis</i>	Otobothriidae	<i>Carcharhinus limbatus</i> , <i>Sphyrna mokarran</i>	<u>Teleosts:</u> Mugilidae - <i>Mugil cephalus</i> (pls) [1,40]; Ariidae - <i>Neoarius graeffei</i> (pls) [1,40], <i>Netuma thalassina</i> (pls) [1], <i>Arius sp.</i> (pls) [1]; Sciaenidae - <i>Otolithes ruber</i> (pls) [1,40]; Clupeidae - <i>Tenualosa ilisha</i> (pls) [1];
<i>Otobothrium penetrans</i>	Otobothriidae	<i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus longimanus</i> , <i>Carcharhinus melanopterus</i> , <i>Carcharodon carcharias</i> , <i>Negaprion brevirostris</i> , <i>Rhizoprionodon</i> <i>terraenovae</i> , <i>Sphyrna</i> <i>lewini</i> , <i>Sphyrna zygaena</i>	<u>Teleosts:</u> Belonidae - <i>Tylosurus crocodilus crocodilus</i> (pls) [1,11,40,56], <i>Tylosurus acus acus</i> (pls) [1,40], <i>Platybelone sp.</i> (pls) [1,40]; Hemiramphidae - <i>Hyporhamphus dussumieri</i> (pls) [1,40];
<i>Poecilancistrum caryophyllum</i>	Otobothriidae	<i>Carcharhinus brachyurus</i> , <i>Carcharhinus leucas</i> ,	<u>Teleosts:</u>

Carcharhinus limbatus,
Negaprion brevirostris,
Rhizoprionodon acutus,
Rhizoprionodon
terraenovae

Sciaenidae -*Micropogonias furnieri* [20], *Micropogonias altipinnis* (pls) [1],
Micropogonias undulatus (pls) [1]; *Macrodon ancylodon* (pld) [41] *Argyrosomus*
hololepidotus (pls) [1], *Argyrosomus japonicus* (pls) [1], *Bairdiella chrysoura* (pls)
[1], *Cilus gilberti* (pls) [1], *Cynoscion arenarius* (pls) [1], *Cynoscion nebulosus* (pls)
[1], *Cynoscion nothus* (pls) [1], *Cynoscion regalis* (pls) [1], *Leiostomus xanthurus*
(pls) [1], *Menticirrhus americanus* (pls) [1], *Nibea maculata* (pls) [1], *Pennahia*
anea (pls) [1], *Pennahia argentata* (pls) [1], *Pogonias cromis* (pls) [1], *Protonibea*
diacanthus (pls) [1], *Pseudotolithus senegalensis* (pls) [1], *Sciaenops ocellatus* (pls)
[1], *Umbrina coroides* (pls) [1];

Polynemidae -*Eleutheronema tetradactylum* (pls) [1], *Polydactylus opercularis*
(pls) [1];

Serranidae -*Epinephelus coioides* (pls) [1];

Latidae -*Lates calcarifer* (pls) [1];

Pomatomidae -*Pomatomus saltatrix* (pls) [1];

Sillaginidae -*Sillago robusta* (pls) [1];

Clupeidae -*Tenuulosa ilisha* (pls) [1];

Crustaceans:

Acartiidae -*Acartia (Acanthacartia) tonsa* (pro) [1];

Pseudodiaptomidae -*Pseudodiaptomus sp.* (pro) [1];

Harpacticidae -*Tigriopus californicus* (pro) [1];

Proemotobothrium Otophthriidae *Carcharhinus limbatus*
southwelli

Teleosts:
Sciaenidae -*Johnius borneensis* (pls) [1,11];
Istiophoridae -*Istiophorus platypterus* (pls) [1];

Pterobothrium Pterobothriidae *Mustelus manazo*
pearsoni

Teleosts:
Sphyraenidae -*Sphyraena jello* [11],
Polynemidae -*Eleutheronema tetradactylum* [16];
Sciaenidae -*Cynoscion virescens* (pls) [1], *Otolithes ruber* (pls) [1], *Protonibea*
diacanthus (pls) [1];
Leiognathidae -*Gazza minuta* (pls) [1];

			<p>Carangidae -<i>Pseudocaranx dentex</i> (pls) [1]; Scombridae -<i>Scomberomorus guttatus</i> (pls) [1]; Clupeidae -<i>Tenualosa ilisha</i> (pls) [1];</p>
<i>Pintneriella musculicola</i>	Rhopalothylacidae	<i>Carcharias taurus</i>	<p><u>Teleosts:</u> Sparidae -<i>Chrysophrys auratus</i> (pls) [1]; Serranidae -<i>Epinephelus akaara</i> (pls) [1], <i>Epinephelus chlorostigma</i> (pls) [1], <i>Epinephelus tauvina</i> (pls) [1]; Lethrinidae -<i>Lethrinus nebulosus</i> (pls) [1];</p>
<i>Hepatoxylon megacephalum</i>	Sphyrnocephalidae	<i>Carcharodon carcharias</i> , <i>Notorynchus cepedianus</i> , <i>Prionace glauca</i>	<p><u>Teleosts:</u> Gadidae -<i>Pollachius virens</i> (pld) [1]; Scorpaenidae -<i>Scorpaena porcus</i> (pld) [1]; Trichomycteridae -<i>Trichomycterus punctulatus</i> (pld) [1]; Xiphiidae -<i>Xiphias gladius</i> (pld) [1]; <u>Chondrichthyan fishes:</u> Squalidae -<i>Squalus acanthias</i> (pld) [1], <i>Squalus megalops</i> (pld) [1]; Squatinae -<i>Squatina australis</i> (pld) [1]; Torpedinidae -<i>Torpedo marmorata</i> (pld) [1]; Scyliorhinidae -<i>Scyliorhinus canicula</i> (pld) [1], <i>Scyliorhinus stellaris</i> (pld) [1]; Sphyrnidae -<i>Sphyrna zygaena</i> (pld) [1]; Carcharhinidae -<i>Carcharhinus obscurus</i> (pld) [1], <i>Prionace glauca</i> (pld) [1]; Dalatiidae -<i>Dalatias licha</i> (pld) [1]; Centrophoridae -<i>Deania calcea</i> (pld) [1]; Rajidae -<i>Dipturus oxyrinchus</i> (pld) [1], <i>Raja clavata</i> (pld) [1], <i>Raja sp.</i> (pld) [1]; Etmopteridae -<i>Etmopterus spinax</i> (pld) [1]; Triakidae -<i>Galeorhinus galeus</i> (pld) [1], <i>Mustelus mustelus</i> (pld) [1]; Pentanchidae -<i>Galeus melastomus</i> (pld) [1]; Hexanchidae -<i>Heptranchias perlo</i> (pld) [1], <i>Hexanchus griseus</i> (pld) [1], <i>Notorynchus cepedianus</i> (pld) [1]; Lamnidae -<i>Isurus oxyrinchus</i> (pld) [1];</p>

Hepatoxylon trichiuri

Sphyriocephalidae

Alopias vulpinus,
Carcharodon carcharias,
Isurus oxyrinchus, *Lamna*
nasus, *Prionace glauca*,
Somniosus microcephalus

Teleosts:

Diodontidae -*Diodon hystrix* [11];

Istiophoridae -*Tetrapturus angustirostris* [11];

Scombridae -*Thunnus obesus* [11], *Thunnus alalunga* (pld) [1], *Thunnus albacares* (pld) [1], *Thunnus thynnus* (pld) [52], *Katsuwonus pelamis* (pld) [1], *Scomber japonicus* (pld) [1];

Ophidiidae -*Genypterus brasiliensis* (pld) [1,22], *Genypterus blacodes* (pld) [1], *Genypterus chilensis* (pld) [1];

Coryphaenidae -*Coryphaena hippurus* (pld) [1,28];

Nototheniidae -*Dissostichus eleginoides* (pld) [34,48];

Alepisauridae -*Alepisaurus ferox* (pld) [1];

Argentinidae -*Argentina elongata* (pld) [1];

Berycidae -*Beryx splendens* (pld) [1];

Bramidae -*Brama brama* (pld) [1], *Taractes rubescens* (pld) [1], *Taractichthys steindachneri* (pld) [1], *Brama australis* [1], *Unidentified bramid* (pld) [1];

Macrouridae -*Coelorinchus australis* (pld) [1], *Coelorinchus chilensis* (pld) [51], *Lepidorhynchus denticulatus* (pld) [1];

Serranidae -*Caesioperca lepidoptera* (pld) [1], *Lepidoperca pulchella* (pld) [1];

Cyttidae -*Cyttus novaezealandiae* (pld) [1], *Cyttus traversi* (pld) [1];

Gadidae -*Gadus morhua* (pld) [1], *Melanogrammus aeglefinus* (pld) [1], *Micromesistius australis* (pld) [1,47], *Pollachius virens* (pld) [1];

Gempylidae -*Gempylus serpens* (pld) [1,56], *Rexea solandri* (pld) [1], *Thyrsites atun* (pld) [1];

Geotriidae -*Geotria australis* (pld) [1];

Pleuronectidae -*Hippoglossus hippoglossus* (pld) [1];

Hoplichthyidae -*Hoplichthys haswelli* (pld) [1];

Trachichthyidae -*Hoplostethus atlanticus* (pld) [1];

Centrolophiidae -*Hyperoglyphe antarctica* (pld) [1];

Haemulidae -*Isacia conceptionis* (pld) [1];

Trichiuridae -*Lepidopus caudatus* (pld) [1];
Merlucciidae -*Macruronus novaezelandiae* (pld) [1], *Macruronus magellanicus* (pld) [46-47], *Merluccius australis* (pld) [1,45,47], *Merluccius capensis* (pld) [1], *Merluccius gayi gayi* (pld) [1,47], *Merluccius hubbsi* (pld) [1], *Merluccius merluccius* (pld) [1], *Merluccius paradoxus* (pld) [1], *Merluccius polli* (pld) [1];
Lotidae -*Molva sp.* (pld) [1];
Moridae -*Mora moro* (pld) [1], *Pseudophycis bachus* (pld) [1];
Cheilodactylidae -*Nemadactylus macropterus* (pld) [1];
Salmonidae -*Oncorhynchus keta* (pld) [1], *Oncorhynchus tshawytscha* (pld) [1], *Salmo salar* (pld) [1], *Salmo carpio* (pld) [1], *Salmo trutta trutta* (pld) [1];
Oplegnathidae -*Oplegnathus conwayi* (pld) [1];
Polyprionidae -*Polyprion oxygeneios* (pld) [1];
Scophthalmidae -*Scophthalmus maximus* (pld) [1];
Sebastidae -*Sebastes norvegicus* (pld) [1], *Sebastes mentella* (pld) [1];
Carangidae -*Seriola lalandi* (pld) [1], *Trachurus murphyi* (pld) [1];
Trachipteridae -*Trachipterus arcticus* (pld) [1];
Xiphiidae -*Xiphias gladius* (pld) [1,43];
Notacanthidae -*Notacanthus sexspinis* [51];
Chondrichthyan fishes:
Alopiidae -*Alopias vulpinus* (pld) [1], *Alopias superciliosus* (pld) [1];
Carcharhinidae -*Carcharhinus plumbeus* (pld) [1], *Prionace glauca* (pld) [1,42];
Lamnidae -*Carcharodon carcharias* (pld) [1], *Isurus oxyrinchus* (pld) [1], *Lamna nasus* (pld) [1];
Somniosidae -*Centroscymnus coelolepis* (pld) [1], *Centroscymnus owstonii* (pld) [1], *Somniosus microcephalus* (pld) [1], *Somniosus pacificus* (pld) [1];
Chlamydosechalidae -*Chlamydoselachus anguineus* (pld) [1];
Dalatiidae -*Dalatias licha* (pld) [1];
Centrophoridae -*Deania calcea* (pld) [1];
Triakidae -*Galeorhinus galeus* (pld) [1], *Mustelus mustelus* (pld) [1];

			<p>Pentanchidae -<i>Galeus melastomus</i> (pld) [1]; Hexanchidae -<i>Hexanchus griseus</i> (pld) [1]; Squalidae -<i>Squalus acanthias</i> (pld) [1], <i>unidentified squalid</i> (pld) [1]; Torpedinidae -<i>Tetronarce fairchildi</i> (pld) [1]; Scyliorhinidae -<i>Scyliorhinus canicula</i> (pld) [1]; <u>Cephalopods:</u> Architeuthidae -<i>Architeuthis dux</i> (pld) [1]; Ommastrephidae -<i>Illex argentinus</i> (pld) [1], <i>Sthenoteuthis pteropus</i> (pld) [1], <i>Todarodes angolensis</i> (pld) [1], <i>Dosidicus gigas</i> (pld) [49-50]; <u>Mammals:</u> Hominidae -<i>Homo sapiens</i> (pld) [1];</p>
<i>Heterosphyriocephalus tergestinus</i>	Sphyriocephalidae	<i>Alopias vulpinus</i> , <i>Euprotomicrus bispinatus</i> , <i>Isurus oxyrinchus</i>	<p><u>Teleosts:</u> Trichiuridae -<i>Aphanopus carbo</i> (pld) [1], <i>Lepidopus caudatus</i> (pld) [1], <i>Aphanopus carbo</i> [54]; Bramidae -<i>Brama brama</i> (pld) [1], <i>Brama dussumieri</i> (pld) [1,56], <i>Taractichthys steindachneri</i> (pld) [1]; Merlucciidae -<i>Macruronus novaezelandiae</i> (pld) [1]; Carangidae -<i>Trachurus picturatus</i> (pld) [1]; Congridae -<i>Conger conger</i> [53]; Scombridae -<i>Sarda chiliensis</i> (pld) [55];</p>
<i>Sphyriocephalus dollfusi</i>	Sphyriocephalidae	<i>Alopias superciliosus</i>	<p><u>Teleosts:</u> Alepisauridae -<i>Alepisaurus ferox</i> (pld) [1,56]; Bramidae -<i>Taractichthys steindachneri</i> (pld) [1]; Scombridae -<i>Thunnus obesus</i> (pld) [1];</p>
<i>Sphyriocephalus viridis</i>	Sphyriocephalidae	<i>Alopias superciliosus</i> , <i>Alopias vulpinus</i> , <i>Centrophorus granulosus</i> ,	<p><u>Teleosts:</u> Xiphiidae -<i>Xiphias gladius</i> [43]; Alepocephalidae -<i>Alepocephalus rostratus</i> (pld) [1]; Synphobranchidae -<i>Synphobranchus brevidorsalis</i> (pld) [1]; Macrouridae -<i>Trachyrincus scabrus</i> (pld) [1];</p>

		<i>Dalatias licha</i> , <i>Isurus oxyrinchus</i>	<u>Chondrichthyan fishes:</u> Centrophoridae - <i>Centrophorus granulosus</i> (pld) [1]; Somniosidae - <i>Centroscymnus coelolepis</i> (pld) [1]; Dalatiidae - <i>Dalatias licha</i> (pld) [1]; Pentanchidae - <i>Galeus melastomus</i> (pld) [1]; Pseudotriakidae - <i>Pseudotriakis microdon</i> (pld) [1]; Squalidae - <i>Squalus acanthias</i> (pld) [1];
<i>Heteronybelinia estigmene</i>	Tentaculariidae	<i>Carcharhinus amblyrhynchoides</i> , <i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus obscurus</i> , <i>Prionace glauca</i>	<u>Teleosts:</u> Scombridae - <i>Sarda australis</i> (pld) [1,11], <i>Scomberomorus maculatus</i> (pld) [1], <i>Thunnus albacares</i> (pld) [1]; Carangidae - <i>Atule mate</i> [11], <i>Selar crumenophthalmus</i> (pld) [1,11], <i>Alectis alexandrina</i> (pld) [1], <i>Caranx rhonchus</i> (pld) [1], <i>Selene setapinnis</i> (pld) [1], <i>Seriola dumerili</i> (pld) [1], <i>Trachurus murphyi</i> (pld) [1]; Sciaenidae <i>Cynoscion jamaicensis</i> (pld) [1,20], <i>Genyonemus lineatus</i> (pld) [1], <i>Otolithes ruber</i> (pld) [1]; Clupeidae - <i>Herklotsichthys quadrimaculatus</i> [11]; Sphyraenidae - <i>Sphyraena putnamae</i> [11], <i>Sphyraena guachancho</i> (pld) [1]; Trichiuridae - <i>Trichiurus lepturus</i> [11]; Coryphaenidae - <i>Coryphaena hippurus</i> (pld) [1,28], <i>Coryphaena equiselis</i> (pld) [1,28]; Monacanthidae - <i>Aluterus monoceros</i> (pld) [1]; Sparidae - <i>Boops boops</i> (pld) [1]; Bramidae - <i>Brama dussumieri</i> (pld) [1,56], <i>Taractichthys steindachneri</i> (pld) [1], <i>Unidentified Bramid</i> (pld) [1]; Echeneidae - <i>Echeneis naucrates</i> (pld) [1], <i>Remora sp.</i> (pld) [1]; Serranidae - <i>Epinephelus fasciatus</i> (pld) [1]; Fistulariidae - <i>Fistularia tabacaria</i> (pld) [1]; Haemulidae - <i>Haemulon plumierii</i> (pld) [1], <i>Pomadasys incisus</i> (pld) [1]; Pomatomidae - <i>Pomatomus saltatrix</i> (pld) [1];

			Xiphiidae - <i>Xiphias gladius</i> (pld) [1];
<i>Heteronybelinia heteromorphi</i>	Tentaculariidae	<i>Sphyrna mokarran</i>	<u>Teleosts:</u> Bothidae - <i>Bothus podas</i> (pld) [1]; Nemipteridae - <i>Nemipterus furcosus</i> (pld) [1];
<i>Heteronybelinia nipponica</i>	Tentaculariidae	<i>Carcharhinus signatus</i> , <i>Sphyrna lewini</i>	<u>Teleosts:</u> Paralichthyidae - <i>Paralichthys isosceles</i> (pls) [18], <i>Pseudorhombus pentophthalmus</i> (pld) [1]; Sciaenidae - <i>Menticirrhus americanus</i> (pld) [1,20], <i>Umbrina canosai</i> (pld) [1,20]; Ophidiidae - <i>Genypterus brasiliensis</i> (pls) [22], <i>Neobythites macrops</i> (pld) [1]; Argentinidae - <i>Argentina kagoshimae</i> (pld) [1]; Macrouridae - <i>Coelorinchus caelorhincus</i> (pld) [1]; Pleuronectidae - <i>Eopsetta grigorjewi</i> (pld) [1]; Sebastidae - <i>Helicolenus dactylopterus</i> (pld) [1]; Trachichthyidae - <i>Hoplostethus mediterraneus mediterraneus</i> (pld) [1]; Tetraodontidae - <i>Sphoeroides pachygaster</i> (pld) [1];
<i>Heteronybelinia overstreeti</i>	Tentaculariidae	<i>Carcharhinus limbatus</i>	<u>Teleosts:</u> Mullidae - <i>Pseudupeneus maculatus</i> (pld) [1];
<i>Heteronybelinia palliata</i>	Tentaculariidae	<i>Notorynchus cepedianus</i> , <i>Sphyrna zygaena</i>	<u>Teleosts:</u> Alepisauridae - <i>Alepisaurus ferox</i> (pld) [1]; Sciaenidae - <i>Cynoscion regalise</i> (pld) [1]; Paralichthyidae - <i>Paralichthys dentatus</i> (pld) [1]; <u>Chondrichthyan fishes:</u> Triakidae - <i>Mustelus canis</i> (pld) [1];
<i>Heteronybelinia perideraeus</i>	Tentaculariidae	<i>Notorynchus cepedianus</i>	<u>Teleosts:</u> Leiognathidae - <i>Secutor ruconius</i> (pld) [1];
<i>Heteronybelinia robusta</i>	Tentaculariidae	<i>Carcharhinus limbatus</i> , <i>Mustelus asterias</i>	<u>Teleosts:</u> Carangidae - <i>Caranx rhonchus</i> (pld) [1]; Bothidae - <i>Chascanopsetta lugubris</i> (pld) [1];

			<p>Lophiidae -<i>Lophiodes mutilus</i> (pld) [1], <i>Lophius piscatorius</i> (pld) [1];</p> <p>Merlucciidae -<i>Merluccius capensis</i> (pld) [1];</p> <p>Polymixiidae -<i>Polymixia nobilis</i> (pld) [1];</p> <p>Congridae -<i>Bassanago albescens</i> (pld) [1];</p> <p>Peristediidae -<i>Satyrichthys adeni</i> (pld) [1];</p> <p>Synodontidae -<i>Saurida undosquamis</i> (pld) [1];</p>
<i>Heteronybelinia yamagutii</i>	Tentaculariidae	<i>Carcharhinus signatus</i> , <i>Sphyrna lewini</i>	<p><u>Teleosts:</u></p> <p>Trichiuridae -<i>Aphanopus carbo</i> [54], <i>Benthodesmus elongatus</i> (pld) [1];</p> <p>Berycidae -<i>Beryx splendens</i> (pld) [1];</p> <p>Macrouridae -<i>Coelorinchus flabellispinnis</i> (pld) [1];</p> <p>Chaunacidae -<i>Chaunax pictus</i> (pld) [1];</p> <p>Coryphaenidae -<i>Coryphaena hippurus</i> (pld) [1];</p> <p>Derichthyidae -<i>Derichthys serpentinus</i> (pld) [1];</p> <p>Gempylidae -<i>Gempylus serpens</i> (pld) [1,56], <i>Thyrsitoides marleyi</i> (pld) [1,56];</p> <p>Gonostomatidae -<i>Gonostoma elongatum</i> (pld) [1];</p> <p>Lycoteuthidae -<i>Lycoteuthis springeri</i> (pld) [1];</p> <p>Myctophidae -<i>Metelectrona ventralis</i> (pld) [1];</p> <p>Nemichthyidae -<i>Nemichthys scolopaceus</i> (pld) [1];</p> <p>Derichthyidae -<i>Nessorhamphus ingolfianus</i> (pld) [1];</p> <p>Sternoptychidae -<i>Polyipnus polli</i> (pld) [1];</p> <p>Polymixiidae -<i>Polymixia nobilis</i> (pld) [1];</p> <p>Synodontidae -<i>Saurida undosquamis</i> (pld) [1];</p> <p>Tetraodontidae -<i>Sphoeroides pachygaster</i> (pld) [1];</p> <p><u>Cephalopods:</u></p> <p>Ommastrephidae -<i>Sthenoteuthis oualaniensis</i> (pld) [1], <i>Sthenoteuthis pteropus</i> (pld) [1], <i>Todarodes angolensis</i> (pld) [1];</p> <p>Loliginidae -<i>Doryteuthis (Amerigo) pealeii</i> (pld) [1];</p>
<i>Mixonybelinia californica</i>	Tentaculariidae	<i>Isurus oxyrinchus</i>	<p><u>Teleosts:</u></p> <p>Pleuronectidae -<i>Eopsetta jordani</i> (pld) [1];</p>

<i>Mixonybelinia edwinlintoni</i>	Tentaculariidae	<i>Sphyrna lewini</i> , <i>Sphyrna tudes</i>	<p>Sciaenidae -<i>Genyonemus lineatus</i> (pld) [1];</p> <p><u>Teleosts:</u></p> <p>Bothidae -<i>Arnoglossus sp.</i> (pld) [1];</p> <p>Mullidae -<i>Pseudupeneus maculatus</i> (pld) [1];</p> <p><u>Chondrichthyan fishes</u></p> <p>Carcharhinidae -<i>Carcharhinus melanopterus</i> (pld) [1], <i>Carcharhinus sorrah</i> (pld) [1];</p> <p>Rhinobatidae -<i>Rhynchobatus djiddensis</i> (pld) [1];</p>
<i>Mixonybelinia lepturi</i>	Tentaculariidae	<i>Alopias superciliosus</i> , <i>Sphyrna lewini</i>	<p><u>Teleosts:</u></p> <p>Alepisauridae -<i>Alepisaurus ferox</i> (pld) [1,56];</p> <p>Coryphaenidae -<i>Coryphaena hippurus</i> (pld) [1];</p> <p>Gempylidae -<i>Gempylus serpens</i> (pld) [1,56], <i>Thyrsitoides marleyi</i> (pld) [1,56];</p> <p>Trichiuridae -<i>Trichiurus lepturus</i> (pld) [1,56];</p> <p>Bramidae -<i>Brama dussumieri</i> (pld) [56];</p> <p><u>Cephalopods:</u></p> <p>Ommastrephidae -<i>Sthenoteuthis oualaniensis</i> (pld) [1];</p>
<i>Mixonybelinia southwelli</i>	Tentaculariidae	<i>Galeocerdo cuvier</i>	<p><u>Teleosts:</u></p> <p>Labridae -<i>Choerodon venustus</i> (pld) [1,11];</p> <p>Serranidae -<i>Epinephelus longispinis</i> (pld) [1];</p> <p>Istiophoridae -<i>Istiompax indica</i> (pld) [1];</p> <p>Trichiuridae -<i>Trichiurus lepturus</i> (pld) [1];</p> <p>Mullidae -<i>Upeneus sulphureus</i> (pld) [1], <i>Upeneus vittatus</i> (pld) [1];</p>
<i>Nybelinia africana</i>	Tentaculariidae	<i>Alopias superciliosus</i> , <i>Carcharhinus leucas</i> , <i>Carcharhinus melanopterus</i> , <i>Carcharhinus obscurus</i> , <i>Mustelus canis</i>	<p><u>Teleosts:</u></p> <p>Gempylidae -<i>Gempylus serpens</i> (pld) [1,56], <i>Thyrsitoides marleyi</i> (pld) [1];</p> <p>Trichiuridae -<i>Trichiurus lepturus</i> (pld) [1,56], <i>Benthodesmus elongatus</i> (pld) [1];</p> <p>Bramidae -<i>Brama dussumieri</i> (pld) [1,56];</p> <p>Alepisauridae -<i>Alepisaurus ferox</i> (pld) [1,56];</p> <p>Paralepididae -<i>Arctozenus risso</i> (pld) [1], <i>Lestrolepis intermedia</i> (pld) [1];</p> <p>Congridae -<i>Conger cinereus</i> (pld) [1];</p>

			<p>Coryphaenidae -<i>Coryphaena hippurus</i> (pld) [1]; Polynemidae -<i>Galeoides decadactylus</i> (pld) [1]; Mullidae -<i>Mullus barbatus</i> (pld) [1], <i>Pseudupeneus maculatus</i> (pld) [1]; Sparidae -<i>Pagellus sp.</i> (pld) [1]; Sternoptychidae -<i>Polyipnus polli</i> (pld) [1]; Polymixiidae -<i>Polymixia nobilis</i> (pld) [1]; Serranidae -<i>Serranus cabrilla</i> (pld) [1]; Triglidae -<i>Trigla sp.</i> (pld) [1]; <u>Cephalopods:</u> Ommastrephidae -<i>Sthenoteuthis oualaniensis</i> (pld) [1], <i>Todarodes angolensis</i> (pld) [1];</p>
<i>Nybelinia anthicosum</i>	Tentaculariidae	<i>Heterodontus francisci</i> , <i>Prionace glauca</i> , <i>Triakis semifasciata</i>	<p><u>Teleosts:</u> Embiotocidae -<i>Amphistichus rhodoterus</i> (pld) [1], <i>Cymatogaster aggregata</i> (pld) [1], <i>Hyperprosopon argenteum</i> (pld) [1], <i>Rhacochilus vacca</i> (pld) [1]; Sciaenidae -<i>Genyonemus lineatus</i> (pld) [1]; Pleuronectidae -<i>Glyptocephalus zachirus</i> (pld) [1], <i>Lyopsetta exilis</i> (pld) [1]; Paralichthyidae -<i>Paralichthys californicus</i> (pld) [1]; Cottidae -<i>Scorpaenichthys marmoratus</i> (pld) [1]; <u>Chondrichthyan fishes:</u> Squalidae -<i>Squalus acanthias</i> (pld) [1];</p>
<i>Nybelinia gopalai</i>	Tentaculariidae	<i>Sphyrna lewini</i> , <i>Sphyrna zygaena</i>	<p><u>Teleosts:</u> Macrouridae -<i>Coelorinchus flabellispinnis</i> (pld) [1], <i>Ventrifossa nasuta</i> [1]; Hoplichthyidae -<i>Hoplichthys acanthopleurus</i> (pld) [1]; Peristediidae -<i>Satyrichthys adeni</i> (pld) [1], <i>Satyrichthys welchi</i> (pld) [1]; Synodontidae -<i>Saurida undosquamis</i> (pld) [1];</p>
<i>Nybelinia gorensis</i>	Tentaculariidae	<i>Sphyrna lewini</i>	<p><u>Teleosts:</u> Lethrinidae -<i>Lethrinus genivittatus</i> [11], <i>Lethrinus rubrioperculatus</i> [11]; Nemipteridae -<i>Nemipterus furcosus</i> (pld) [1,11];</p>

			<p>Mullidae - <i>Parupeneus barberinus</i> [11], <i>Parupeneus multifasciatus</i> [11], <i>Upeneus vittatus</i> (pld) [1];</p> <p>Paralichthyidae - <i>Pseudorhombus arsius</i> (pld) [1], <i>Pseudorhombus dupliciocellatus</i> (pld) [1];</p>
<i>Nybelinia indica</i>	Tentaculariidae	<p><i>Alopias superciliosus</i>, <i>Carcharhinus leucas</i>, <i>Carcharhinus limbatus</i>, <i>Rhizoprionodon acutus</i></p>	<p><u>Teleosts:</u></p> <p>Carangidae - <i>Caranx sexfasciatus</i> [11], <i>Alepes djedaba</i> (pld) [1], <i>Selar crumenophthalmus</i> (pld) [1];</p> <p>Diodontidae - <i>Diodon hystrix</i> (pld) [1,11], <i>Diodon liturosus</i> (pld) [1];</p> <p>Tetraodontidae - <i>Lagocephalus sceleratus</i> [11];</p> <p>Leiognathidae - <i>Leiognathus fasciatus</i> [11];</p> <p>Nemipteridae - <i>Nemipterus furcosus</i> [11], <i>Nemipterus japonicus</i> (pld) [1];</p> <p>Polynemidae - <i>Eleutheronema tetradactylum</i> [16];</p> <p>Gempylidae - <i>Gempylus serpens</i> (pld) [1,56];</p> <p>Balistidae - <i>Balistes capriscus</i> (pld) [1];</p> <p>Congridae - <i>Conger cinereus</i> (pld) [1];</p> <p>Coryphaenidae - <i>Coryphaena hippurus</i> (pld) [1];</p> <p>Serranidae - <i>Epinephelus coioides</i> (pld) [1], <i>Epinephelus tauvina</i> (pld) [1];</p> <p>Istiophoridae - <i>Istiophorus platypterus</i> (pld) [1], <i>Istiompax indica</i> (pld) [1];</p> <p>Latidae - <i>Lates calcarifer</i> (pld) [1];</p> <p>Sciaenidae - <i>Pennahia anea</i> (pld) [1];</p> <p>Platycephalidae - <i>Platycephalus indicus</i> (pld) [1];</p> <p>Sternoptychidae - <i>Polyipnus polli</i> (pld) [1];</p> <p>Priacanthidae - <i>Priacanthus hamrur</i> (pld) [1];</p> <p>Paralichthyidae - <i>Pseudorhombus dupliciocellatus</i> (pld) [1];</p> <p>Mullidae - <i>Pseudupeneus maculatus</i> (pld) [1], <i>Upeneus japonicus</i> (pld) [1], <i>Upeneus sulphureus</i> (pld) [1], <i>Upeneus tragula</i> (pld) [1], <i>Upeneus vittatus</i> (pld) [1];</p> <p>Synodontidae - <i>Saurida undosquamis</i> (pld) [1], <i>Trachinocephalus myops</i> (pld) [1];</p> <p>Scombridae - <i>Scomberomorus commerson</i> (pld) [1];</p> <p>Trichiuridae - <i>Trichiurus lepturus</i> (pld) [1];</p>

			<u>Cephalopods:</u> Ommastrephidae - <i>Sthenoteuthis pteropus</i> (pld) [1];
<i>Nybelinia jayapaulazariahi</i>	Tentaculariidae	<i>Rhizoprionodon terraenovae</i>	<u>Teleosts:</u> Cynoglossidae - <i>Cynoglossus sp.</i> (pld) [1]; Synodontidae - <i>Harpadon nehereus</i> (pld) [1]; Soleidae - <i>Synclidopus macleayanus</i> (pld) [1], <i>Brachirus niger</i> (pld) [1];
<i>Nybelinia lingualis</i>	Tentaculariidae	<i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus melanopterus</i> , <i>Carcharhinus obscurus</i> , <i>Carcharhinus plumbeus</i> , <i>Carcharodon carcharias</i> , <i>Hexanchus griseus</i> , <i>Isurus oxyrinchus</i> , <i>Mustelus canis</i> , <i>Mustelus schmitti</i> , <i>Notorynchus cepedianus</i> , <i>Scyliorhinus canicula</i>	<u>Teleosts:</u> Paralichthyidae - <i>Paralichthys isosceles</i> (pld) [18], <i>Paralichthys californicus</i> (pld) [1]; Trichiuridae - <i>Aphanopus carbo</i> (pld) [1,54], <i>Lepidopus caudatus</i> (pld) [1]; Bothidae - <i>Arnoglossus imperialis</i> (pld) [1]; Berycidae - <i>Beryx splendens</i> (pld) [1]; Bramidae - <i>Brama japonica</i> (pld) [1], <i>Unidentified Bramid</i> (pld) [1]; Triglidae - <i>Eutrigla gurnardus</i> (pld) [1], <i>Chelidonichthys lucerna</i> (pld) [1], <i>Trigla lyra</i> (pld) [1]; Congridae - <i>Conger conger</i> (pld) [1]; Embiotocidae - <i>Cymatogaster aggregata</i> (pld) [1]; Sciaenidae - <i>Cynoscion leiarchus</i> (pld) [1], <i>Genyonemus lineatus</i> (pld) [1]; Ammodytidae - <i>Hyperoplus lanceolatus</i> (pld) [1]; Merlucciidae - <i>Merluccius bilinearis</i> (pld) [1]; Soleidae - <i>Microchirus variegatus</i> (pld) [1], <i>Pegusa lascaris</i> (pld) [1]; Mullidae - <i>Mullus barbatus</i> (pld) [1], <i>Mullus surmuletus</i> (pld) [1], <i>Pseudupeneus maculatus</i> (pld) [1]; Salmonidae - <i>Oncorhynchus gorboscha</i> (pld) [1], <i>Oncorhynchus keta</i> (pld) [1]; Phycidae - <i>Phycis blennoides</i> (pld) [1]; Batrachoididae - <i>Porichthys porosissimus</i> (pld) [1]; Scombridae - <i>Sarda sarda</i> (pld) [1], <i>Scomber scombrus</i> (pld) [1], <i>Thunnus thynnus</i> (pld) [1]; Cottidae - <i>Scorpaenichthys marmoratus</i> (pld) [1];

Centracanthidae -*Spicara smaris* (pld) [1];
Tetraodontidae -*Torquigener pleurogramma* (pld) [1];
Carangidae -*Trachurus capensis* (pld) [1], *Trachurus murphyi* (pld) [1], *Trachurus picturatus* (pld) [1,57], *Trachurus trachurus* (pld) [1];
Chondrichthyan fishes:
Rajidae -*Zearaja nasuta* (pld) [1], *Raja sp.* (pld) [1];
Arhynchobatidae -*Sympterygia bonapartii* (pld) [1];
Scyliorhinidae -*Scyliorhinus canicula* (pld) [1];
Carcharhinidae -*Prionace glauca* (pld) [1];
Cephalopods:
Eledonidae -*Eledone cirrhosa* (pld) [1], *Eledone moschata* (pld) [1];
Ommastrephidae -*Eucleoteuthis luminosa* (pld) [1], *Ommastrephes bartramii* (pld) [1], *Sthenoteuthis oualaniensis* (pld) [1], *Sthenoteuthis pteropus* (pld) [1], *Todarodes angolensis* (pld) [1], *Todaropsis eblanae* (pld) [1];
Loliginidae -*Loligo vulgaris* (pld) [1];
Octopodidae -*Octopus vulgaris* (pld) [1];
Sepiidae -*Sepia elegans* (pld) [1,58], *Sepia officinalis* (pld) [1];

<i>Nybelinia pinteri</i>	Tentaculariidae	<i>Prionace glauca</i>	<u>Teleosts:</u> Paralichthyidae - <i>Paralichthys olivaceus</i> (pld) [1];
<i>Nybelinia queenslandensis</i>	Tentaculariidae	<i>Carcharhinus melanopterus</i>	<u>Teleosts:</u> Nemipteridae - <i>Nemipterus furcosus</i> [11]; Apogonidae - <i>Ostorhinchus cookie</i> [11], <i>Ostorhinchus properuptus</i> [11];
<i>Nybelinia strongyla</i>	Tentaculariidae	<i>Sphyrna tudes</i>	<u>Teleosts:</u> Sciaenidae - <i>Johnius borneensis</i> (pld) [1,11], <i>Argyrosomus hololepidotus</i> (pld) [1]; Tetraodontidae - <i>Sphoeroides pachygaster</i> (pld) [1];
<i>Nybelinia syngenes</i>	Tentaculariidae	<i>Sphyrna zygaena</i>	<u>Teleosts:</u> Scorpaenidae - <i>Dendrochirus zebra</i> (pld) [1]; <u>Chondrichthyan fishes:</u> Sphyrnidae - <i>Sphyrna zygaena</i> (pld) [1];

<i>Nybelinia thyrsites</i>	Tentaculariidae	<i>Carcharhinus brachyurus</i> , <i>Carcharhinus longimanus</i> , <i>Galeorhinus galeus</i>	<u>Teleosts:</u> Trichiuridae - <i>Aphanopus carbo</i> [54], <i>Lepidopus caudatus</i> (pld) [1]; Arripidae - <i>Arripis truttacea</i> (pld) [1]; Gempylidae - <i>Thyrsites atun</i> (pld) [1]; Carangidae - <i>Trachurus declivis</i> (pld) [1], <i>Trachurus novaezelandiae</i> (pld) [1]; Zeidae - <i>Zeus faber</i> (pld) [1]; <u>Chondrichthyan fishes:</u> Squalidae - <i>Squalus sp.</i> (pld) [1];
<i>Tentacularia coryphaenae</i>	Tentaculariidae	<i>Carcharhinus galapagensis</i> , <i>Carcharhinus limbatus</i> , <i>Carcharhinus melanopterus</i> , <i>Carcharhinus obscurus</i> , <i>Carcharhinus plumbeus</i> , <i>Carcharodon carcharias</i> , <i>Galeocerdo cuvier</i> , <i>Prionace glauca</i> , <i>Rhizoprionodon acutus</i> , <i>Sphyrna zygaena</i>	<u>Teleosts:</u> Ophidiidae - <i>Genypterus brasiliensis</i> (pls) [22]; Coryphaenidae - <i>Coryphaena hippurus</i> (pld) [1,28,61], <i>Coryphaena equiselis</i> (pld) [1,28]; Trichiuridae - <i>Aphanopus carbo</i> (pld) [1,54], <i>Trichiurus lepturus</i> (pld) [1,56]; Scombridae - <i>Sarda chiliensis</i> (pld) [1,55], <i>Sarda sarda</i> (pld) [1], <i>Acanthocybium solandri</i> (pld) [1], <i>Euthynnus affinis</i> (pld) [1], <i>Euthynnus alletteratus</i> (pld) [1], <i>Katsuwonis pelamis</i> (pld) [1], <i>Orcynopsis unicolor</i> (pld) [1], <i>Scomber japonicus</i> (pld) [1], <i>Scomber scombrus</i> (pld) [1], <i>Scomberomorus cavalla</i> (pld) [1], <i>Scomberomorus commerson</i> (pld) [1], <i>Scomberomorus guttatus</i> (pld) [1], <i>Thunnus alalunga</i> (pld) [1], <i>Thunnus albacares</i> (pld) [1], <i>Unidentified bonito</i> (pld) [1]; Gempylidae - <i>Gempylus serpens</i> (pld) [1,56], <i>Thyrsitoides marleyi</i> (pld) [1,56], <i>Lepidocybium flavobrunneum</i> (pld) [1], <i>Ruvettus pretiosus</i> (pld) [1], <i>Thyrsites atun</i> (pld) [1,62]; Bramidae - <i>Brama dussumieri</i> (pld) [1,56], <i>Brama brama</i> (pld) [1], <i>Taractichthys steindachneri</i> (pld) [1]; Alepisauridae - <i>Alepisaurus ferox</i> (pld) [1,56]; Sciaenidae - <i>Atractoscion aequidens</i> (pld) [1]; Centropomidae - <i>Centropomus nigrescens</i> (pld) [1]; Stomiidae - <i>Chauliodus sloani</i> (pld) [1], <i>Stomias boa</i> (pld) [1]; Chaunacidae - <i>Chaunax pictus</i> (pld) [1];

Carangidae -*Decapterus sp.* (pld) [1], *Scomberoides commersonianus* (pld) [1], *Seriola dumerili* (pld) [1], *Trachurus capensis* (pld) [1], *Trachurus murphyi* (pld) [1], *Trachurus picturatus* (pld) [1], *Trachurus declivis* (pld) [1], *Unidentified Carangid* (pld) [1];

Echeneidae -*Echeneis naucrates* (pld) [1], *Remora remora* (pld) [1];

Gadidae -*Gadus morhua* (pld) [1];

Pleuronectidae -*Hippoglossus hippoglossus* (pld) [1];

Trachichthyidae -*Hoplostethus atlanticus* (pld) [1];

Lampridae -*Lampris guttatus* (pld) [1];

Lobotidae -*Lobotes surinamensis* (pld) [1];

Lophiidae -*Lophius piscatorius* (pld) [1];

Merlucciidae -*Macruronus novaezelandiae* (pld) [1], *Merluccius capensis* (pld) [1], *Merluccius gayi gayi* (pld) [1], *Merluccius gayi peruanus* (pld) [1];

Salmonidae -*Oncorhynchus tshawytscha* (pld) [1], *Salmo salar* (pld) [1];

Paralichthyidae -*Paralichthys dentatus* (pld) [1];

Nomeidae -*Psenes cyanophrys* (pld) [1];

Polynemidae -*Polydactylus opercularis* (pld) [1];

Polyprionidae -*Polyprion oxygeneios* (pld) [1];

Rachycentridae -*Rachycentron canadum* (pld) [1];

Peristediidae -*Satyrichthys adeni* (pld) [1];

Sternoptychidae -*Sternoptyx diaphana* (pld) [1];

Istiophoridae -*Kajikia albida* (pld) [1];

Cyprinidae -*Tinca tinca* (pld) [1];

Xiphiidae -*Xiphias gladius* (pld) [1,60];

Clupeidae -*Sardinops sagax* (pld) [59];

Chondrichthyan fishes:

Carcharhinidae -*Carcharhinus obscurus* (pld) [1], *Galeocerdo cuvier* (pld) [1];

Centrophoridae -*Centrophorus moluccensis* (pld) [1], *Deania calcea* (pld) [1], *Deania profundorum* (pld) [1];

Somniosidae -*Centroscymnus coelolepis* (pld) [1];

Rajidae -*Raja sp.* (pld) [1], *Rajella caudaspinosa* (pld) [1];

Rhinobatidae -*Rhynchobatus sp.* (pld) [1];

Hexanchidae -*Hepttranchias perlo* (pld) [1];

Cephalopods:

Ommastrephidae -*Dosidicus gigas* (pld) [1,49-50,63], *Illex illecebrosus* (pld) [1],

Ommastrephes bartramii (pld) [1,64], *Sthenoteuthis pteropus* (pld) [1],

Sthenoteuthis oualaniensis (pld) [1], *Todarodes angolensis* (pld) [1];

Sepiidae -*Sepia unguiculata* (pld) [1];

Reptiles:

Cheloniidae -*Chelonia mydas* (pld) [1];

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