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Meta-Analytic Summary of Parasites and Diseases of Elasmobranchs Found in Florida Waters

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

META-ANALYTIC SUMMARY OF PARASITES AND DISEASES OF ELASMOBRANCHS FOUND IN FLORIDA WATERS

By
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Submitted to the Faculty of Halmos College of Natural Sciences and Oceanography in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

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Abstract

Elasmobranchs have conservational and commercial importance. There is a need for a more complete understanding of their health, due to their ability to **s**hape trophic webs and their money-making potential with fishers and ecotourists. Sharks have been known to influence the strength of food webs, including reef ecosystems where many fish species are harvested for food. The investigation of pathogenic agents and diseases in elasmobranchs has been biased to favor those natural enemies that inhabit the digestive system and epidermal surfaces. Certain groups of parasites such as cestodes, copepods, and monogeneans, were most often recorded in this study. The bacterial microbiota of elasmobranchs is currently being researched, but much information is lacking in the field, with the exception of certain well-known strains, such as members of the genus *Vibrio*. In addition, information on the 22 species of sharks included in this study is more in depth than that which can be found for the 11 ray species and three skates. A semi-quantitative study was undertaken to investigate relationships between taxonomic Order and Family, as well as the relationship between diet and number of natural enemies with the use of the statistical package R. It was found that number of natural enemies present in an elasmobranch species correlates with the number of sources available. This first attempt at an exhaustive study of elasmobranch natural enemies from Florida waters includes over 400 pathogens.
Keywords: parasite, bacteria, disease, pathology, elasmobranch.

Introduction

Many elasmobranchs have commercial as well as conservation importance (Vélez-Zuazo and Agnarsson 2011). There is a need for a more complete understanding of their health, due to their ability to shape trophic webs and their money-making potential with fishers and ecotourists. Sharks have been known to influence the strength of food webs, including reef ecosystems where many fish species are harvested for food (NOAA 2001). Jameson et al. (1995) notes that some causes of population decline of reef organisms include anthropogenic stressors such as: overfishing, pollution, and increased sedimentation. Natural enemy information is critical to managing species of both conservation and commercial importance. Dobson and May (1987) attempted to predict how pathogens affect the dynamics of exploited fisheries and found that the ability for a pathogen to establish itself is dependent on the host's current parasite density. Related to that same study, Winemiller (2005) created a model for predicting population resilience, production potential, and conformity to density dependent regulation in fish and found that his models can be useful in understanding traits as adaptations to environmental variation. He investigated three major life history strategies because this gives a more comprehensive view of adaptation to environmental variation than if one strategy was examined at a time. Burge et al. (2014) investigated another complicated factor for use within mathematical modelling of host-pathogen relationships: climate change. Burge et al. noted that marine ecosystems are among the most valuable and heavily used natural systems in the world, and provide many services, such as water filtration, food from fisheries and aquaculture, and tourism revenue. Effective management of species of interest requires understanding the factors that influence their populations, including their natural enemies.

This study is a meta-analytic summary of the parasites and diseases of elasmobranchs known to inhabit Florida coastal waters. Although there are many reports of individual parasite taxa in elasmobranchs, no single study has compiled an exhaustive data search on natural enemy communities from as many countries as this study, nor has there been any attempt to explore such data using a meta-analytical approach. The scope of this project includes all parasites as well as viral, fungal, and bacterial infections found in selected elasmobranch species; it therefore represents a first attempt at an exhaustive inventory of the natural enemies of 36 species of elasmobranchs from Florida. A meta-analysis was undertaken to investigate the structure of these natural enemy communities, and explore relationships with life history, broad feeding patterns, pathogen abundance, and vulnerability. The current study comprises information taken from elasmobranchs in both captive and wild situations. Pathogenic data comes from numerous countries, including: The United States, the United Kingdom, Mexico, Africa, Germany, Japan, Saudi Arabia, Russia, and Australia.

The key conclusion of the capstone is that current understanding of the natural enemies of elasmobranchs is likely strongly distorted by bias in the species studied: for example, larger elasmobranch species tend to be more frequently studied than their smaller counterparts, and sharks are more often studied than rays and skates. This bias may be due in part to the accessibility of some elasmobranchs, for example large individuals may be easier to sample in the wild than their smaller relatives. This in turn has shaped understanding of their natural enemies: a major finding of this summary is the strong positive correlation between the number of studies on a given species, and the number of natural enemies it is reported to have. I conclude with a discussion of the likely sources of this bias, and its management and conservation implications.

Significance of Elasmobranchs

The importance of sharks as both apex and meso-predators has a large effect on ecosystem trophic webs. For example, blue shark *Prionace glauca* and white shark *Carcharodon carcharias* are mentioned as species known to have large distributions and can have profound effects on trophic webs and shaping them, especially in the open ocean (Wood et al. 2010). Wood et al. (2010) mentions that the removal of fish from the world's oceans can be driving a long term and global decline in their parasites as well. In this same study the authors go on to say, "Because fishing reduces the density of fish (reducing transmission efficiency of directly transmitted parasites), selectively removes large fish (which tend to carry more parasites than small fish), and reduces food web complexity (reducing transmission efficiency of trophically transmitted parasites), the removal of fish from the world's oceans over the course of hundreds of years may be driving a longterm, global decline in fish parasites."

From a trophic perspective, Heithaus et al. (2008) investigated ecological consequences when marine top predator populations decline. While the reported effects varied, the loss of apex predators such as large sharks were often found to have large cascading effects. For example, with an increase in the number of cownose rays, *Rhinoptera bonasus,* caught the number of shark catches has decreased. This increase in the population of cownose rays can cause a collapse in certain fisheries such as those for bivalves (an important fisheries resource), but this influence has not been studied in depth.

Phylogeny

Members of Chondrichthyes - cartilaginous fishes- include sharks, rays, skates, and chimaeras. Camhi et al. (2008) noted sharks and rays are some of the oldest vertebrates in the oceans, with elasmobranchs surviving for more than 400 million years. About 360 million years ago, ancestral sharks diversified extensively (Bright 2011). Vélez-Zuazo and Agnarsson (2011) studied the phylogeny of shark and ray species in an attempt to resolve phylogenetic discrepancies due the creation of tree models based on morphology rather than molecular evidence. Vélez-Zuazo and Agnarsson (2011) note that as the field of molecular biology advances, the previous tree models that were based on morphology will be updated based on molecular and genetic information. There are some agreements on major classifications, such as taxonomic Order. In the present meta-analytical study, the Orders included are: Carcharhiniformes, Orectolobiformes, Lamniformes, Myliobatiformes, Rajiformes, Rhinopristiformes, and Squatiniformes. Vélez-Zuazo and Agnarsson go on to say that Carcharhiniformes was considered a sister taxa to Lamniformes, supported by morphology and molecular evidence, as well as sister to Orectolobiformes (Naylor et al. 2005; Compagno, 1973; de Carvalho 1996; Douady et al., 2003; Human et al., 2006; Heinicke et al., 2009; Mallatt and Winchell 2007; as cited by Vélez-Zuazo and Agnarsson 2011).

Taxonomic Family is considered more controversial. Within the Carcharhiniformes, for example, the families Scyliorhinidae and Triakidae appear to be paraphyletic (Iglésias et al., 2005; Human et al., 2006; Lopez et al., 2006 as cited by Vélez-Zuazo) and they go on to say that Odontaspididae and Carcharhinidae, often considered a single family (reviewed in Shimada et al., 2009), form divergent branches in

Lamniformes (Martin et al., 2002), and within the Squaliformes, the monophyly and relationships among most of the families were more or less completely unresolved until very recently (Klug and Kriwet, 2010). While the current study does not attempt to parse phylogeny, the families included in this study are: Carcharhinidae, Cetorhinidae, Dasyatidae, Ginglymostomatidae, Gymnuridae, Lamnidae, Mobulidae, Myliobatidae, Narcinidae, Pristidae, Rajidae, Rhincodontidae, Rhinobatidae, Scyliorhinidae, Sphyrnidae, Squatinidae, Torpedinidae, Triakidae.

Species Included In This Study

Study species are the same as those reported as existing within Florida waters by the Florida Fish and Wildlife Commission ; source websites included the Florida Fish and Wildlife Commission website, Wikipedia, a general Google search including subsequent websites and forums focusing on museum collections in Florida and sport fishing websites. Terms used include: *Florida fish*, Southeastern US fish*, subtropical fish**, and *typical Florida fish*.*

Blacknose shark *Carcharhinus acronotus*

A member of Order Carcharhiniformes and Family Carcharhinidae, the blacknose shark is named for the black spot on its snout and can be found in coastal marine waters of the western Atlantic Ocean from the southern United States and the Gulf of Mexico, throughout the Caribbean, and down to Brazil (Carlson et al. 2009). *C. acronotus* is considered a tropical to warm temperate climate shark and has been known to be a species affected by fishery bycatch. A number of other species included in this study are affected by this as well. *C. acronotus* was assessed as Near Threatened by the IUCN (International Union for the Conservation of Nature (2009)).

Spinner shark *Carcharhinus brevipinna*

The Spinner Shark is a schooling species inhabiting tropical and subtropical waters from the northeastern United States to Brazil, as well as the Mediterranean Sea, Indian Ocean, and western Pacific near Australia (Burgess 2009). *C. brevipinna* is both a coastal and pelagic species, and preys upon a variety of fishes. The Spinner Shark is a commercially targeted shark species caught for its meat and fins and is considered Near Threatened by the IUCN (2009).

Finetooth Shark *Carcharhinus isodon*

C. isodon is a shallow water shark, although its full distribution remains unknown (Carlson et al. 2009). It can be found commonly in the western Atlantic, especially around Mexico. Records of its appearance in South America are lacking, but the Finetooth shark's distribution includes this area as well (IUCN 2009). Schooling of individuals has been reported, and *C. isodon* have been known to migrate to warmer waters during the colder months of the year. While this shark is a target of recreational anglers and is subject to accidental bycatch, it is categorized as being of Least Concern by the IUCN (2009).

Bull Shark *Carcharhinus leucas*

The Bull shark has been reported in marine, estuarine, and freshwater environments, and is one of the only species of shark to be found in such a range of salinities (Simpfendorfer and Burgess 2009). *Carcharhinus leucas* can be found in tropical and warm, temperate waters. It has a global distribution and preys upon may types of fish, birds, and invertebrates. Migratory habitats have been found in pregnant females who travel into estuarine environments to give birth, and adults in general will move northward during warmer seasons. The IUCN assessed this species as Near Threatened (2009).

Blacktip Shark *Carcharhinus limbatus*

The Blacktip shark is vulnerable to fishing pressure as it frequents inshore waters and has inshore nurseries that are susceptible to anthropogenic effects (Burgess and Branstetter 2009). *C. limbatus* is a loosely schooling species and has been recorded as having migratory habits (IUCN 2009). *C. limbatus* mostly preys upon fish and invertebrates. Blacktip meat, liver oil, and fins are commercially harvested from this species and they have been categorized as being Near Threatened (IUCN 2009).

Sandbar Shark *Carcharhinus plumbeus*

Sandbar sharks are long lived and have low fecundity, making them vulnerable to overfishing (Musick et al. 2009). This shark can be typically found in muddy areas, bays, and estuaries, where there is shallow water for foraging. It mainly feeds on benthic fishes and invertebrates. With this species being considered Vulnerable to extinction (IUCN 2009), some countries have put management plans into action to conserve local populations. Such countries include: Canada, the United States, and Australia. Sandbar sharks eat a wide variety of fishes and invertebrates.

Night Shark *Carcharhinus signatus*

The Night shark is heavily fished off the coast of Brazil, where this species is known to aggregate (Santana et al. 2006). Populations of this shark species have declined in fisheries off Florida, Cuba, and in the Caribbean. This shark prefers depths ranging from the surface down to 600m at depth, with individuals coming nearer the surface at night. It is believed there are few refuges for this species, however, the Brazilian and US governments have both imposed fisheries restrictions on this species. *C. signatus* is considered Vulnerable by the IUCN (2006).

White Shark *Carcharodon carcharias*

The White shark is a globally distributed species, but is most commonly sighted near Australia, South Africa, the northeastern United States, and California (Fergusson et al. 2009). White sharks have a torpedo-shaped body with an irregular line between their dark gray dorsal surface coloring and their white underside (Bright 2011). *C. carcharias* can be found in marine and estuarine environments, nearshore and pelagic waters, and eats a variety of fish including other elasmobranchs. The White shark is a member of the Lamnidae family. The IUCN notes that multiple countries have protections in place for this species, however, enforcement is an issue. The IUCN lists this species as Vulnerable (2009).

Basking Shark *Cetorhinus maximus*

The Basking shark is one of the few species in this study that is commonly found in cold waters and is known to filter feed. This shark swims through the water at 3-5 km/h sieving through up to 7,000 L of water in an hour (Bright 2011). Compagno (1984a as cited by Fowler 2005), wrote of this species that it is possibly more vulnerable to anthropogenic effects than other sharks due to its slow growth rate, long gestation periods (speculated at a year), long maturation times, and possible low populations. The IUCN lists this shark as being Vulnerable (2009). It is considered to be a deepwater shark, undertaking vertical migrations and only basking at the surface in good weather (Sims et al. 2003 as cited by Fowler 2005).

Tiger Shark *Galeocerdo cuvier*

The Tiger shark is considered omnivorous and eats a wide variety of organisms and trash (Randall 1992 as cited by Simpfendorfer 2009). They have been called the "ocean's garbage collector" (Bright 2011). *G. cuvier* has a global distribution, but is most often found in tropical and temperate waters. Tiger sharks grow quickly, have high fecundity, and are caught as a target species and bycatch. Fisheries include: western Atlantic, Australia, India, Papua New Guinea, Brazil, and Taiwan (Simpfendorfer 2009).

They are called the Tiger shark due to the striped pattern on their bodies and are considered Near Threatened by the IUCN (2009).

Nurse Shark *Ginglymostoma cirratum*

The Nurse shark is coastal and can often be found resting on the benthos among coral (Cervigón and Alcalá 1999; Compagno 2001; as cited by Rosa et al. 2006). Nurse sharks are vulnerable to overfishing as they have a sedentary or docile nature and large size (210 to 308 cm). Diet primarily consists of small fish, sea urchins, cephalopods and other invertebrates, but many other life history parameters are considered data deficient such as length at reproductive maturity (IUCN 2006). Locally, nurse sharks are known to frequent areas such as the Florida Keys (Caira and Gavarrino 1990, Karns et al. 2017, Bright 2011). The IUCN categorizes nurse sharks as Data Deficient (2006).

Shortfin Mako Shark *Isurus oxyrinchus*

Shortfin Mako sharks are coastal and can be found up to 500m at depth, including near areas with large populations such as Long Island, New York (Compagno 2001 as cited by Cailliet et al. 2009; Caira and Bardos 1996). They are considered a pelagic as well as migratory species. Shortfin Mako meat is considered very valuable, as are its liver, oil, teeth, and leather. *I. oxyrinchus* has a diet mainly consisting of teleosts and invertebrates; it is very active and has to eat about 1.8 kg (4 lbs.) every day (Bright 2011 The IUCN lists this species as Vulnerable (2009).

Dusky Smoothhound *Mustelus canis*

The Dusky Smoothhound's geographic range includes the western Atlantic from the northeastern United States to Argentina in South America (Compagno 1984b as cited by Contrath 2005) and it is a demersal, coastal shark. *M. canis* has a diet mostly comprised of teleosts, bivalves and crustaceans, as such, they have flattened teeth that are used for crushing. The spiral valve portion of their digestive system is known to have eight chambers to it, with the parasites *Protochristianella, Lacistorhyncus,* and *Calliobothrium* inhabiting the first three (Bright 2011). *M. canis* is considered Near Threatened by the IUCN (2009).

Lemon Sharks *Negaprion brevirostris*

Lemon sharks can be found in the Atlantic and eastern Pacific oceans, with habitat preference for shallow waters such as coral reefs, mud flats, bays, and river mouths (Compagno 1984b as cited by Sundström 2015). Lemon sharks feed at night generally, on fish, smaller sharks, invertebrates, birds, and rays (Bright 2011). Lemon sharks are listed as Near Threatened (IUCN 2015).

Blue Shark *Prionace glauca*

The Blue shark is one of the most studied elasmobranch species included, and is considered to have one of the largest distributions, frequenting tropical and temperate waters (Last and Stevens 1994 as cited by Stevens 2009). This shark has a streamlined body and a blue coloring (Bright 2011). They are highly migratory and feed on mainly fish and invertebrates, but will eat birds and crustaceans as well. Schooling behavior has been observed, in groups made of hundreds of individuals (Bright 2011). Blue sharks are Near Threatened (IUCN 2009).

Whale Shark *Rhincodon typus*

The Whale shark is the largest living fish with about 75% of this globally distributed species located in the Indo-Pacific oceans and the remaining 25% in the Atlantic. They prefer tropical and warm temperate waters, and have a characteristic white spotting pattern on their back. Whale sharks filter feed on plankton, small fishes, and krill as they swim through the water column. The IUCN lists whale sharks as Endangered (2016).

Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*

The IUCN (2009) lists *R. terraenovae* as Least Concern due to this species being abundant in the western Atlantic Ocean. The common name for this species is the Atlantic Sharpnose shark and it can be found from Canada to the Yucatan Peninsula (Cortes 2009). While this shark is subjected to accidental targeting via bycatch, it has relatively high fecundity and matures faster than some shark species (Cortes 2009). Adults are typically 80-100 cm in length and prefer muddy or sandy bottom habitats near beaches and bays.

Chain Catshark *Scyliorhinus retifer*

The Chain Catshark is similarly categorized by the IUCN (2006) as being of Least Concern and this species prefers rough bottom habitat on the continental shelf below 450 m. *S. retifer* eats many benthic organisms, including polychaetes, crustaceans, and fish (Sherrill-Mix 2006). A number of this species' life parameters are unknown, such as age at maturity and average reproductive age. There are no conservation plans set in place for them specifically, and they are not harvested for their meat or fins, but are caught accidently during trawling of fisheries.

Scalloped Hammerhead *Sphyrna lewini*

Baum et al. (2007) describes the Scalloped Hammerhead as coastal with a circumglobal distribution and can be found from the surface and intertidal areas to a depth of 275 m. The diet of *S. lewini* is diverse. Juveniles prey upon benthic fishes and crustaceans, while adults eat mesopelagic fish, cephalopods, and rays. Scalloped hammerheads are Endangered (IUCN 2009).

Great Hammerhead *Sphyrna mokarran*

Denham et al. (2007) describes *S. mokarran* as widely distributed in tropical waters, but most often restricted to the continental shelf. This species migrates and has nursery areas in estuaries and mangroves. They feed upon many demersal fishes, crustaceans, cephalopods, and have been observed eating a ray (Strong et al. 1990 as cited by Denham et al. 2007). All three members of the genus *Sphyrna* included in this study have the distinct hammer shape to their heads. A few countries have put protections in place for this shark species, such as the United States, South Africa, and Australia. *S. mokarran* is endangered (IUCN 2007).

Bonnethead *Sphyrna tiburo*

Cortes et al. (2016) describes the Bonnethead as being incredibly abundant, with a very high population growth rate. This species is generally only found around the Americas, with a preference for bays and estuaries. Their total length typically reaches around 150 cm, and they are known to be one of the smallest hammerhead species. The Bonnethead is not a very aggressive sharks species, and displays schooling behaviors (Bright 2011). The IUCN lists the Bonnethead as Least Concern (2016).

Atlantic Angel Shark *Squatina dumeril*

The IUCN (2006) lists the Atlantic Angel shark as being Data Deficient, this is mirrored in the present study. *Squatina dumeril* inhabits the western Atlantic from the northeastern United States to Venezuela (Heupel and Carlson 2006) with many of its life history characteristics unknown. Diet is mostly made up of benthic organisms such as flounders and crustaceans. Members of the Family Squatinidae are known as flat sharks, due to their dorsoventrally compressed body and lengthened pectoral and pelvic fins similar to rays (Bright 2011).

Spotted Eagle Ray *Aetobatus narinari*

The Spotted Eagle ray is named as such due to the white spots on its dorsal surface. Like most rays, *A. narinari* has a body shape that appears to have wing-like structures as if it were stretched laterally. Spotted Eagle rays have a large distribution across the Indo-Pacific and Atlantic oceans (Kyne et al. 2006), but may be made of a species-complex. Widespread in tropical and subtropical waters, they can be found in shallow waters near coral reefs, as well as pelagically. Individuals are considered mature at around four to six years of age. Spotted Eagles rays are considered Near Threatened by the IUCN (2006).

Southern Stingray *Dasyatis americana*

Often found in the western Atlantic, the Southern stingray is a coastal and estuarine species preferring seagrass, reef, and sandy habitats (Grubbs 2016). *D. americana* preys upon benthic crustaceans and demersal teleosts. Males mature when their disc width is about 50 cm wide and females mature at approximately 75 cm. Southern stingrays are abundant near the United States and the species is considered of Least Concern by the IUCN (2016).

Atlantic Stingray *Dasyatis sabina*

The Atlantic stingray is found in estuaries and in marine waters throughout the East Coast of the United States, the Gulf of Mexico and in Mexican fisheries (Piercy et al. 2016). It is a smaller ray, with a disc width of around 35 cm, and a gestation time of four months. Like many rays, this species will typically survive after being released if caught as bycatch. The IUCN lists this ray as Least Concern (2016).

Bluntnose Stingray *Dasyatis say*

The Bluntnose stingray is found in rather shallow waters, for example in bays, estuaries, and lagoons up to 20 m in depth (Snelson et al. 2016). Males become mature at approximately 30 cm disc width, and females are mature around 50 cm. *D. say* is a benthic predator and eats demersal fish and invertebrates. Similar to *D. sabina, D. say* also is most commonly found on the East Coast of the United States, down to Mexico. This species is not considered vulnerable to fishing. *D. say* is listed as Least Concern by the IUCN (2016).

Smooth Butterfly Ray *Gymnura micrura*

Extensive life history parameters are not known about this species of ray, however, it is known to inhabit both the eastern and western Atlantic (Grubbs and Ha 2006). The Smooth Butterfly ray can be found up to an approximate depth of 40 m and births 4 to 6 pups at a time. This species is considered Data Deficient by the IUCN (2006).

Giant Manta *Manta birostris*

Marshall et al. (2011) describes the Giant Manta ray as being circumglobal and prefers tropical and subtropical waters. There are multiple populations across the globe, with some countries (Mozambique, Mexico, and Japan) aggregating photos for identification and in addition to mark-recapture studies for estimation of local population sizes. Individuals are considered to be migratory and have a maximum disc width of 700 cm with maturation around 400 cm. These rays are large and are known to aggregate, making them vulnerable to overfishing. A number of countries have legislation in place to protect this species and to deter depletion of stocks (IUCN 2018). The IUCN lists this ray as Vulnerable (2018).

Caribbean Electric Ray *Narcine bancroftii*

Narcine bancroftii's distribution includes the southern United States, the Gulf of Mexico, and as far South as the northern coast of South America (Carvalho et al. 2007). The Lesser Electric ray is found up to depths of 35 m, and prefers soft substrates in shallows or intertidal areas. *N. bancroftii* is an electric ray and a sluggish swimmer. This ray is Critically Endangered (IUCN 2007).

Smalltooth Sawfish *Pristis pectinata*

The Smalltooth Sawfish is labelled as Critically Endangered by the IUCN (2013) and inhabits the western Atlantic Ocean with some information from the eastern Atlantic. *P. pectinata* is one species of shark known to survive in aquaria long term (McDavitt 1996 as cited by Carlson et al. 2013). This elasmobranch species has a long protruding rostrum and teeth that look similar to teeth on a saw blade. Many of this species life history characteristics are unknown.

Atlantic Guitarfish *Rhinobatos lentiginosus*

The Atlantic Guitarfish is found from the southeast United States south to Nicaragua, and has a body form that appears to be a mix between a shark and ray, in that it looks like an elongated triangle. *R. lentiginosus* prefers inshore, shallow (less than 30 m), soft bottom habitats (Casper et al. 2016). This benthic elasmobranch eats mostly benthic crustaceans and invertebrates. Fecundity is somewhat low, at approximately 6 pups per litter. This species is Near Threatened (IUCN 2016).

Cownose Ray *Rhinoptera bonasus*

The Cownose ray inhabits shallow, warm, temperate and tropical waters from the New England region of the United States to Brazil in South America and frequents bays and estuaries (Barker 2006). This ray usually grows to a disc width of around 70 cm and is one of the medium sized rays in this study. *R. bonasus* is a migratory species and shows schooling behavior with other individuals. The IUCN considers this ray species to be Near Threatened (2006).

Great Torpedo Ray *Tetronarce nobiliana*

This is the 2nd electric ray included in this study and is commonly referred to as the Atlantic Torpedo ray. It has a more rounded body shape than a typical ray and is darkly colored. *T. nobiliana* has a wide distribution in the Atlantic Ocean and has been recorded in the Mediterranean Sea as well. This ray species can be found up to 800 m at depth, but juveniles prefer more shallow water (up to 50 m). Gestation takes about one year, but some life history parameters are lacking information, hence why the IUCN lists this particular ray as being Data Deficient. Llewellyn (1960) notes that electric rays are known to harbor monogeneans on their gills.

Barndoor Skate *Dipturus laevis*

The first of three skates species included in this study, the Barndoor skate can be thought of as shaped like a ray, but with a more pointed nasal area. Length at maturity was estimated by Dulvy (2003) to be approximately 115 cm and this species has been found to weigh up to 20 kg. This skate eats mostly benthic invertebrates and fishes. As such, this species is at risk of being caught as bycatch in fisheries were trawling occurs, but some fisheries do target skates for their meat as use for bait. Most often found in the northwest Atlantic Ocean, *D. laevis* prefers cooler, more temperate waters such as those near Canada. The IUCN lists this skate as Endangered (2003).

Clearnose Skate *Raja eglanteria*

Sporting the same pointed ray body form, the Clearnose skate has a milky and clear area near its nose. This skate's distribution includes most of the eastern United States coast, including the Gulf of Mexico (Ha et al. 2009). *R. eglanteria* is usually found in depths less than 100 meters, however, they have been recorded as deep as 330 meters. Maturity is believed to occur around 50 cm in total length, at approximately 4 years of age. This skate is considered Least Concern (2009).

Roundel Skate *Raja texana*

The Roundel skate occurs in the southern United States coastal waters, south to Mexico, including the Gulf waters. It eats benthic invertebrates and may be found up to depth of 183 m (Bethea et al. 2009). Juveniles can be found in more shallow waters than adults, and prefer soft, muddy bottoms. The IUCN lists this skate species as being Data Deficient (2009).

Pathogen Background

Natural elasmobranch populations are exposed to a wide range of viral, bacterial, and parasitic enemies due to their diverse distributions mentioned above. While some natural enemies have limited pathologies, others can be so pathogenic as to regulate their hosts' populations, such as the bacterial genus *Vibrio* found in teleost fishes (Austin and Austin 2007).

Parasites, bacteria, and viruses are ubiquitous, however, strains of pathogenic microorganisms can be very damaging when they enter the body of an elasmobranch. Both acute diseases of individuals and chronic outbreaks are possible, especially in fish farms (Austin and Austin 2016) and other captive situations. In many cases, a lesion or soft tissue damage is the perfect entryway for bacteria (most commonly of the genus Vibrio) to infiltrate the host and begin causing immune responses.

Bacteria

A bacterium is a member of a large group of unicellular microorganisms that may be pathogenic. Vibrio bacteria have been well studied in marine fishes, with four included in this study: *Vibrio anguillarum, V. charchariae, V. cholarae, and V. parahaemolyticus*. *V. anguillarum* has been considered part of normal microflora in aquatic environments (West and Lee, 1982 as cited by Austin and Austin 2016, Hurst 2016), but strains of it have been found to contain virulent plasmids. *V. carchariae* has been found isolated from a sandbar shark (*Carcharhinus plumbeus*) and these are commonly found in Florida waters. Vibrosis is possibly caused by a number of *Vibrio* species, and infection by *V. carchariae* causes lethargy, disorientation, subdermal cysts, and organ necrosis. Another elasmobranch included in this study, the lemon shark (*Negaprion brevirostris*) has shown to be resistant to this type of infection. Other bacteria reported from sharks include: *Corynebacterium* spp., *Escheria coli, Flavobacterium* spp., *Kordia* spp., *Mycobacterium chelonae, Mycobacterium fortuitum, Mycobacterium marinum, Salmonella enterica, and Streptococcus* spp (Austin and Austin 2016; Karns et al unpublished). Along with the genus *Vibrio*, the genus *Mycobacterium* is also known to commonly live on and in elasmobranchs (Anderson et al. 2012).

Parasites

Parasites are eukaryotic organisms that share a symbiotic relationship with a host and cause harm to that host (Crofton 1971). Parasites are the most studied natural enemies of elasmobranchs, particularly cestodes recovered from the spiral intestine and the epidermis (Borucinska 1993, Borucinska and Dunham 2000, Carrier 2004, Caira et al. 1996, Caira et al. 1999, Caira et al. 2001, Bright 2011).

The spiral intestine is a specialized section in the digestive system of elasmobranchs (Bright 2011). This organ has spiral, corkscrew shape, and allows for more surface area in the digestive system for nutrient absorption (Campbell and Reece 2014).

There are a number of parasites included in this study, such as the cestodes, trematodes, and nematodes. Caira and Jensen (2014) describe elasmobranch tapeworms as being very diverse. Ecto-parasites are commonly found, as well as pathogens typically living in the digestive system. When an organism has a heavy parasite load, it is possible that they would experience negative health/survival effects; indeed, parasites are known to regulate host populations (Austin and Austin 2016). Hurst (2016) notes that the degree of severity of infection can vary depending on the type of parasite. For example, nematodes can be confined within granulomas without any obvious harm to the host, but some nematodes and their larvae can cause meningitis, encephalitis, or metritis (Borucinska and Heger 1999, Credille et al. 1993, Borucinska and Frasca 2002, Borucinska and Adams 2013 as cited by Hurst 2016). In fact, the presence of nematodes in fish populations has been recorded since the 13th century (Myers 1976 as cited by Abollo et al. 2001).

A major factor of parasitism is the method by which the parasite attaches to the internal or external portions of an organism. Parasites have adaptations for the area they tend to be found. For example, many parasites have mouth appendages such as hooks that allow them to maintain their position within or on their host. Similarly, copepods of the genus *Kroyeria* only infest gills of elasmobranchs (Benz and Deets 1986). Some nestle themselves between rough body coverings, such as the denticles of shark skin (Benz 1988).

Parasitic Life Cycles

Monogeneans

Monogeneans are parasitic flukes that can often be found on gills of sharks, with 58 included in the present study (Cheung and Ruggieri 1983, Chisholm et al. 2001, Hendrix 1994, Kearn et al. 2010, Kohn et al. 1989, Llewellyn 1960). Monogenetic flukes are host-specific and have one generation in their life cycle (Reed et al. 2009). Monogeneans are often found on gill filaments.

Digeneans

Digeneans are another type of parasitic fluke, but these have a life cycle including multiple hosts (Gordy et al. 2016). Adults produce an egg which travels via water until it penetrates a mollusc or is eaten by one (intermediate host). Their swimming larval stage may encrust on vegetation, however, the definitive host of a digenean is a vertebrate, typically a fish.

Cestodes

Often referred to as tapeworms, cestodes are often found in the digestive system of their hosts (Natural History Museum 2018). This group of parasitic worms is the best studied parasitic group on elasmobranchs based on the information recorded in the present study. The United Kingdom's Natural History Museum goes on to note that there are over 5200 described species of cestodes in the collection, but there is no single compilation of cestode life cycles and the collection included non-elasmobranch organisms. They also mention that cestodes have a variety of intermediate hosts, but reproduce in vertebrate digestive tracts.

Caira and Jensen (2014) investigated evolution of parasites with an emphasis on tapeworms and noted that the tapeworms and their hosts are now among the most well documented host-parasite relationships. Similarly, the present study has also found within the selected species, that tapeworms are one of the most studied parasites found infecting elasmobranchs. Multiple articles focus on endo-parasites of sharks, such as tapeworms (cestodes) (Adamson and Caira 1991, Anderson et al. 2012, and many others). Consequently, the cestodes are likely the best known and most reported shark parasites, with 205 species reported.

Protists

The taxonomic kingdom of Protista is diverse, with many unicellular organisms that do not fit into any other category (Encyclopedia of Life 2008). The term protist refers to three groups: an animal group of Protozoa, unicellular algae, and slime molds (EOL 2008). The Protozoa are often grouped by their type of locomotive adaptation (e.g., ciliates, flagellates, pseudopods). Reproduction can be asexual, such as with binary fission, or sexual during a protists life cycle (EOL 2008). In addition, protists are capable of digesting food particles including nearby bacteria.

Acanthocephalans

Adult acanthocephalans are vertebrate intestinal parasites (thus considered trophically acquired), with eggs passing from the host to be eaten later by an arthropod intermediate host (Bricknell 2017). Development continues within the intermediate host until eaten by a definitive host, where the encysted acanthocephalan breaks free and attaches to the intestinal wall (University of Alberta 2018). Acanthocephalans are believed to modify the behavior of their intermediate host in order to enhance the chance they are eaten by an appropriate definitive host.

Nematodes

Nematodes have a complex life cycle involving multiple stages, which have been investigated by the Bricknell (2017). There is a parasitic and pre-parasitic phase. The parasitic phase takes place in the definitive host while the pre-parasitic takes place in the external environment while free-living, or inside a second intermediate host. A nematode life cycle seven stages: an egg, four larval stages, and two adult stages. Sexual reproduction by adults in the definitive host takes place, eggs are passed to the external environment where they develop and infect a new host.

Arthropods

The most prevalent member of Arthropoda included in the study are those of the group Copepoda (89 records). Copepods copulate in the water, with the female eventually shedding eggs that go through five to six developmental stages (Food and Agriculture of the United Nations 2018). Development can take one week up to a year; adulthood is reached when molting ceases.

Viruses

A virus is an infective agent that is too small to be seen with light microscopy and can only multiply within a living host cell. In the present study, *Mustelus canis* was the only shark recorded with a virus, that of herpes. Leibovitz and Lebouitz (1985) recorded a viral dermatitis in the smooth dogfish in wild, laboratory, and aquaria populations. Due to this being the only recorded case found in the present study, there is not enough information available on elasmobranch viral infections to perform any statistical tests. The authors Leibovitz and Lebouitz (1985) ask an important question of whether age, nutrition, heredity, and the environment affect the pathogenesis and expression of the herpes virus; a question requiring more research.

Current Work on Natural Enemies

Presently, there are few encompassing studies of the natural enemy communities of elasmobranchs. Garner (2013) published a summary of elasmobranch diseases, including several caused by parasites and other infectious agents, with special emphasis on microbial pathogens and their associated histopathology. Terrell (2004) and Goertz (2004) compiled a general list of pathogens for elasmobranchs commonly held in captivity, but the emphasis was on methods to treat some of the more prevalent infections (their reviews were part of a larger husbandry guide that listed more than 300 "taxa" of potential infectious agents). Cheung (1993) compiled a list of hundreds of elasmobranch species globally and their reported parasites, including some species covered in the present study; however, that study included some misnamed elasmobranchs and inconsistently-identified parasites. However, as will be shown below, the literature is heavily biased in favor of a limited number of elasmobranch species; this in turn has likely distorted our understanding of their natural enemies.

Another commonly studied elasmobranch ectoparasite is the copepod (Benz and Deets 1986, Benz and Deets 1988, Benz 1989, Benz and Dupre 1987, Benz et al 2001, Dippenaar et al. 2008, and many others). In contrast, the information on bacterial inhabitants of elasmobranchs can be lacking, with the exception of the genus Vibrio being well documented (Austin and Austin 2007). This past year, a fellow graduate student's defense focused on the microbiome of shark mouths taken via swabs of sharks sampled near the Pompano Beach, Fl area (Karns 2017).

Some bodies of water are more studied than others, for example, areas found to be common fisheries would have the most available data. There is a plethora of information for elasmobranch parasites from areas such as the Sea of Japan and areas near Southeast Asia (Cheung 1993). Luckily, South Florida is a popular fishing destination and the universities have ample access to perform research on many of the resident elasmobranch species, with elasmobranch-related papers used in this study focusing on the Florida Keys and Gulf of Mexico areas (Caira and Gavarrino 1990, Cheung 1993, Karns et al. 2017).

The objective of this capstone was to synthesize published accounts of natural enemies reported from elasmobranchs common to Florida, and to use a meta-analytical approach to explore how their life histories shape their communities of natural enemies. The host / natural enemy list compiled in the present study will be of interest to resource managers and wildlife biologists who study elasmobranchs; providing much-needed information on potential natural causes of morbidity and mortality in local shark populations. Knowledge gaps focusing on individual elasmobranch species will be investigated and identified, which may open the door to further research by scientists and students.

Materials and Methods

Species selection

A preliminary search of online resources identified 36 elasmobranchs that frequent Florida waters; these are listed in Table 1 by Family with their common name, and naming authority. Published accounts of the viruses, bacteria, and parasites of these species were obtained from online databases (Web of Science and EBSCO Host), as well as Google Scholar. The host-parasite database compiled by the Museum of Natural History in London was used to cross-reference any sources already found, and provided an additional 30+ sources of information used in the study's dataset. The following keywords were used in the database search: parasit*, bacter*, diseas*, patho*, elasmobranch*, as well as all the scientific names of the 36 shark, ray, and skate species.

Table 1. List of elasmobranch species included in this study. Although individual publications may use alternate common names based on historical or geographic variations, all common names below conform to the American Fisheries Society (AFS) standards.

Family	**Scientific name**	**Common Name**	**Naming Authority**
Carcharhinidae	*Carcharhinus acronotus*	Blacknose shark	Poey 1860
	Carcharhinus brevipinna	Spinner shark	Muller & Henle 1839
	Carcharhinus isodon	Finetooth shark	Muller & Henle 1839
	Carcharhinus leucas	Bull shark	Muller & Henle 1839
	Carcharhinus limbatus	Blacktip shark	Muller & Henle 1839
	Carcharhinus plumbeus	Sandbar shark	Nardo 1827
	Carcharhinus signatus	Night shark	Poey 1868
	Negaprion brevirostris	Lemon shark	Poey 1868
	Galeocerdo cuvier	Tiger shark	Peron & Lesueur 1822

	Prionace glauca	Blue shark	Linnaeus 1758
	Rhizoprionodon terraenovae	Atlantic Sharpnose shark	Richardson 1836
Cetorhinidae	*Cetorhinus maximus*	Basking shark	Gunnerus 1765
Dasyatidae	*Dasyatis americana*	Southern stingray	Hildebrand & Schroeder 1928
	Dasyatis sabina	Atlantic Stingray	Lesueur 1824
	Dasyatis say	Bluntnose stingray	Lesueur 1817
Ginglymostomatidae	*Ginglymostoma cirratum*	Nurse shark	Bonnaterre 1788
Gymnuridae	*Gymnura micrura*	Smooth Butterfly ray	Bloch & Schneider 1801
Lamnidae	*Carcharodon carcharias*	White shark	Linnaeus 1758
	Isurus oxyrinchus	Shortfin mako shark	Rafinesque 1810
Myliobatidae	*Aetobatus narinari*	Spotted Eagle ray	Euphrasen 1790
	Manta birostris	Manta ray	Walbaum 1792
	Rhinoptera bonasus	Cownose ray	Mitchill 1815
Narcinidae	*Narcine bancroftii*	Lesser Electric ray	Griffith & Smith 1834
Pristidae	*Pristis pectinata*	Smalltooth Sawfish	Latham 1794
Rajidae	*Dipturus laevis*	Barndoor skate	Mitchill 1818
	Raja eglanteria	Clearnose skate	Bosc 1800
	Raja texana	Roundel skate	Chandler 1921
Rhincodontidae	*Rhincodon typus*	Whale shark	Smith 1828
Rhinobatidae	*Rhinobatos lentiginosus*	Atlantic Guitarfish	Garman 1880
Scyliorhinidae	*Scyliorhinus retifer*	Chain Dogfish	Garman 1881
Sphyrnidae	*Sphyrna lewini*	Scalloped Hammerhead	Griffith & Smith 1834
	Sphyrna mokarran	Great Hammerhead	Ruppell 1837

	Sphyrna tiburo	Bonnethead	Linnaeus 1758
Squatinidae	*Squatina dumeril*	Atlantic Angel shark	Lesueur 1818
Triakidae	*Mustelus canis*	Smooth Dogfish	Mitchill 1815
Torpedinidae	*Tetronarce nobiliana*	Atlantic Torpedo	Bonaparte 1835

The International Union for the Conservation of Nature (IUCN), FishBase, and WoRMS (World Register of Marine Species) websites were used to resolve any ambiguity of common names in elasmobranchs with large or global distributions. These databases were also used to clarify any name changes related to the natural enemies, due to regular revisions and synonymization of taxa. Additional databases such as Zoological Record were consulted, as well as any ‘grey’ literature sources available online, including unpublished government surveys and academic theses and dissertations. It is worth noting that some ambiguity in identifying specimens, whether elasmobranch or pathogen, may be due to: lack of quality specimens for examination as was the case for Beveridge (1993) with brittle parasites and low number of specimens in museum or personal collections or inability to identify the specimen caught by another party such as for Cheung (1993). If the species cannot be named due it being degraded or for any reason, this is very important as one of the goals of the present meta-analytical summary, was to attempt an exhaustive search of natural enemies. In addition, the name may be considered *nomina dubia/species inquirenda* or the taxonomic category may be under review (Beveridge and Campbell 1988, Beveridge and Campbell 1998, Beveridge and Campbell 2010).

Data and data analysis

A database was assembled in a spreadsheet as a matrix of elasmobranch species names with a complete presence/absence inventory of their natural enemies. Wherever possible, the abundance or other measure of infection intensity or prevalence was recorded and summarized; however, the current study is primarily concerned with which pathogens are present, so most analyses used presence-absence approaches.

These data were analyzed using two different strategies: first, the host-natural enemy data was used in multivariate analyses to explore how host factors shaped overall community structure; second, these data were then used to calculate more general indices of overall natural enemy diversity (i.e., the number of natural enemies recorded from each elasmobranch species in the literature), which were then tested against host factors (see below) using univariate statistical approaches such as regression.

Elasmobranch life history parameters were also determined from the literature and Fishbase.org (http://www.fishbase.us/ July 13, 2018), to establish a pool of possible predictor variables shaping natural enemy communities. Factors include size, preferred temperatures by the selected species with behavior and biological range information, diet, biometrics such as age at maturity, and average lifespan. Data on the feeding ecology of each elasmobranch species was collected from published accounts summarized in FishBase (Froese and Pauly 2017). Data was also collected on trophic level. For example, a simple search for "lemon shark" returns eight global records, including an American record that places this species at trophic level 4.3. Similar information was retrieved for all elasmobranchs, as well as more detailed information on preferred prey items.

Presence-absence data was imported into R studio (version 1.1.447, vegan package add-on, https://www.rstudio.com/products/rstudio2/).

Univariate Approaches

Regression was used to assess the effects of univariate host factors (number of prey items, number of reports) on overall number of natural enemies.

Multivariate Approaches

First, Sorensen similarity indices were calculated for their natural enemy communities in each elasmobranch species. The Sorensen index is a metric of community similarity that is specifically structured for use with presence-absence data. Sorensen indices were used to establish a triangular matrix of natural enemy community similarities among elasmobranch species. This triangular matrix was then used to statistically compare pathogen community structure in different elasmobranch taxa using an NMDS (Non-metric multidimensional scale) to search for possible patterns based on the presence or absence data. Clustering by taxonomic Family and Order were used as well in R, using hierarchical clusters with the hclust command. Hierarchical clustering in R is done using complete linkage, this method defines the cluster distance between two clusters to be the maximum distance between their individual components.

Results

Database Results

Much of the information on elasmobranch natural enemies has been produced by a select number of authors (see Figure 1 and Figure 2) and some of the 17 natural enemy types have been more widely studied (e.g., cestodes, with hundreds of species described in the literature). Only five protists have been included in this study: *Haemogregarina, Paronatrema vaginicola, Trichodina rajae, Trypanosoma*, and *Uronema marinum*, but the elasmobranchs with very few recorded natural enemies (less than 10) were not used to make figures as there is so little available information. The 10 most prolific authors included in this study have been displayed in Figure 2, in order of decreasing number of publications cited. In addition, Table 2 (below) lists the 36 elasmobranch species by Family, their scientific name, the geographic region from which the species was recorded, and the associated sources. Some sources recorded a species as having been cataloged in more than one geographic region, and sources included both wild and captive elasmobranchs. In the situation that information used in a source was from a museum collection that did not identify geographic region, other (O) was indicated.

Table 2. Peer-reviewed and other scientific literature found for 36 target species of elasmobranchs in a preliminary search. For geographic region, A=Atlantic Ocean, P=Pacific Ocean, I= Indian Ocean, M= Mediterranean Sea, and O=Other; numbers in parentheses indicate the number of individual references.

Family	**Scientific name**	**Geographic Region**	**Sources**
Carcharhinidae	*Carcharhinus acronotus*	A(2), O(2)	Caira et al. (2017), Caira and Jensen (2009), Garner (2013), Schwartz (1984)
	Carcharhinus brevipinna	O(4), P(2), A(1), I(1)	Al Kawari et al. (1996), Benz and Bullard (2004), Bruce and Cannon (1993), Bullard et al. (2004), Caira et al. (2017), Caira and Jensen (2009), Dippenaar et al. (1999), Vassiliades (1985)
	Carcharhinus isodon	P(1)	Caira and Jensen (2009)
	Carcharhinus leucas	O(4), A(2), P(1), I(3)	Benz and Bullard (2004), Borucinska and Bullard et al. (2004), Caira (2006), Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Cheung (1993), Healy (2003), Moravec and Little (1988), Palm (1995), Palm (1999), Schramm (1991)
	Carcharhinus limbatus	P(4), A(6), O(5), I(1)	Argumendo (1997), Beveridge and Campbell (1993), Bruce and Cannon (1993), Bullard et al. (2004), Bullard et al. (2006), Bullard and Jensen (2008), Cheung (1993), Olson et al. (2010), Owens (2008), Palm (1995), Palm (1999), Palm and Beveridge (2002), Ritter

			(2003), Schmidt and Beveridge (1990)
	Carcharhinus plumbeus	A(7), P(3), O(4), I(1)	Austin and Austin (2007), Benz et al. (1987), Benz (1989), Benz and Bullard (2004), Beveridge and Campbell (1993), Bullard et al. (2012), Caira et al. (2017), Caira and Jensen (2009), Cheung (1993), Goertz (2004), Healy (2003), Newbound and Knott (1999), Palm (1995), Rokicki and Bychawska (1991), Rosa-Molinar et al. (1983), Schramm (1991)
	Carcharhinus signatus	A(2)	Benz and Deets (1986), Knoff et al. (2001)
	Negaprion brevirostris	A(4), O(6), P(1)	Austin and Austin (2007), Benz and Bullard (2004), Bullard et al. (2004), Beveridge and Campbell (1993), Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Cheung (1993), Cheung and Ruggieri (1983), Palm (1995), Poynton et al. (1997), Ruhnke and Thompson (2006), Vassiliades (1985)
	Galeocerdo cuvier	A(1), O(3), P(4)	Al Kawari et al. (1996), Benz and Bullard (2004), Bruce and Cannon (1993), Bruce (1994), Caira et al. (1999), Caira et al. (2017), Cheung (1993), Newbound and Knott (1999)
	Prionace glauca	P(2), A(11), O(5)	Abollo et al. (2001), Adamson et al. (1987),

			Benz and Dupre (1987), Benz and Bullard (2004), Beveridge and Campbell (2003), Borucinska and Dunham (2000), Bruce (1994), Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Cheung (1993), Cousin et al. (2006), Curran and Caira (1995), Escalante (1986), Henderson et al. (2002), Knoff et al (2002), Olson et al. (2010), Palm (1995), Rokicki and Bychawska (1991), Threlfall (1969), Vassiliades (1985)
	Rhizoprionodon terraenovae	A(11), O(1)	Benz et al. (2001), Beveridge and Campbell (1993), Borucinska and Adams (2013), Bullard et al. (2006), Bullard and Jensen (2008), Cheung (1993), Karns et al. (2017), Karsten and Rice (2006), Kohn (1989), Palm (1995), Ruiz and Bullard (2013), Short (1954)
Cetorhinidae	*Cetorhinus maximus*	P(1), O(2), I(1), M(2), A(1)	Beveridge and Duffy (2005), Bruce (1994), Bullard et al. (2006), Bullard and Jensen (2008), Caira et al. (1999), Caira et al. (2017), Cheung (1993)
Dasyatidae	*Dasyatis americana*	A(9), O(2)	Amin (1998), Bruce (1994), Caira et al. (1999), Caira et al. (2001),

			Campbell and Beveridge (1996), Chisholm et al. (2001), Garner (2013), Goertz (2004), Cheung (1993), Chisholm (1993), Ruhnke (1994)
	Dasyatis sabina	A(6), O(1)	Amin (1998), Bruce (1994), Bullard and Jensen (2008), Buron and Euzet (2005), Goertz (2004), Cheung (1993), Chisholm (1993), Olson et al. (2010)
	Dasyatis say	P(1), O(1), A(5), M(1)	Amin (1998), Benz and Bullard (2004), Bullard et al. (2004), Campbell and Beveridge (1996), Cheung (1993), Olson et al. (2010)
Ginglymostomatidae	*Ginglymostoma cirratum*	A(9), O(6), P(2)	Adamson and Caira (1991), Argumendo (1997), Benz and Bullard (2004), Borucinska and Caira (1993), Bruce and Cannon (1993), Bruce (1994), Caira and Gavarrino (1990), Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Cheung (1993), Credille et al. (1993), Garner (2013), Karns et al. (2017 unpublished), Olson et al. (2010), Palm (1995), Waldoch et al. (2010)
Gymnuridae	*Gymnura micrura*	A(1), P(2), O(2), I(1)	Benz and Bullard (2004), Beveridge (1996), Campbell and Cheung (1993), Sarada et al. (1993)
Lamnidae	*Carcharodon carcharias*	P (5), I(1), A(1), O(1)	Benz et al. (2003), Caira et al. (1999), Caira et al. (2017), Cheung (1993), Dippenaar et al. (2008),

			Hewitt (1979), Hogans and Dadswell (1985), Randhawa (2011)
	Isurus oxyrinchus	A(6), P(1), O(1)	Benz and Bullard (2004), Caira and Bardos (1996), Caira et al. (1999), Cheung (1993), Knoff et al (2002), Olson et al. (2010), Palm and Beveridge (2002), Ruhnke (1993), Williams (1978)
Myliobatidae	*Aetobatus narinari*	P(10), O(5), I(1), A(1)	Al Kawari et al. (1996), Beveridge and Campbell (1988), Beveridge and Campbell (1998), Butler (1987), Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Campbell and Beveridge (2002), Cheung (1993), Ghoshroy and Caira (2001), Goertz (2004), Janse and Borgsteede (2003), Marie and Justine (2005), Morales-Serna et al. (2016), Olson et al. (2010), Whittington (1990)
	Manta birostris	O(1), P(1)	Benz and Deets (1988), Cheung (1993)
	Rhinoptera bonasus	A(7), O(3),	Benz and Bullard (2004), Borucinska and Bullard (2011), Caira et al. (2017), Cheung (1993), Garner (2013), Goertz (2004), Ivanov and Campbell (2000), Olson et al. (2010), Stamper et al. (1998), Stidworthy (2017), Thoney and Burreson (1986)
Narcinidae	*Narcine bancroftii*	A(2)	Caira et al. (1999), Cheung (1993)
Pristidae	*Pristis pectinata*	A(1), O(2)	Benz and Bullard (2004), Cheung

			(1993), Kearn et al. (2010)
Rajidae	*Dipturus laevis*	A(1), O(1), P(1)	Benz and Bullard (2004), Cheung (1993)
	Raja eglanteria	A(1)	Becker and Overstreet (1979), Bruce (1994)
	Raja texana	A(1)	Valdo-Zalik and Campbell (2011)
Rhincodontidae	*Rhincodon typus*	P(3)	Cheung (1993), Dyer (1988), Norman et al. (2000)
Rhinobatidae	*Rhinobatos lentiginosus*	A(2), O(1),	Anderson et al. (2012), Derome and Borucinska (2016), Valdo-Zalik and Campbell (2011)
Scyliorhinidae	*Scyliorhinus retifer*	A(2)	Cheung (1993), Khan and Newman (1981)
Sphyrnidae	*Sphyrna lewini*	O(7), A(5), P(2)	Argumendo (1997), Benz and Bullard (2004), Beveridge and Campbell (1993), Bruce (1994), Caira et al. (2001), Healy (2003), Cheung (1993), Karns et al. (2017), Palm (1995), Palm (1999), Palm (2000), Palm and Beveridge (2002), Rokicki and Bychawska (1991), Sao Clemente and Gomes (1992), Shields (1985), Vassiliades (1985)
	Sphyrna mokarran	A(2), O(8), P(3)	Argumendo (1997), Beveridge and Campbell (1989), Beveridge and Campbell (1993), Caira et al. (1996), Caira et al. (2001), Cheung (1993), Maranick et al. (2011), Olson et al. (2010), Palm (1995), Palm (1999), Palm (2000), Schmidt

			and Beveridge (1990)
	Sphyrna tiburo	A(3), O(5)	Benz and Bullard (2004), Beveridge and Campbell (2010), Bullard et al.(2001), Cheung (1993), Derome and Borucinska (2016), Garner (2013), Olson et al. (2010), Stidworthy (2017)
Squatinidae	*Squatina dumeril*	O(1)	Cheung (1993)
Triakidae	*Mustelus canis*	A(6), O(7), P(1), M(2),	Caira et al. (1999), Caira et al. (2001), Caira et al. (2017), Cheung (1993), Cislo and Caira (1993), Leibovitz and Lebouitz (1985), Palm (1995), Palm (1999), Garner (2013), Goertz (2004), Knoff et al. (2001), Vardo-Zalik and Campbell (2011), Vassiliades (1985)
Torpedinidae	*Tetronarce nobiliana*	A(2), O(1),	Cheung (1993), Llewellyn (1960), Vassiliades (1985)

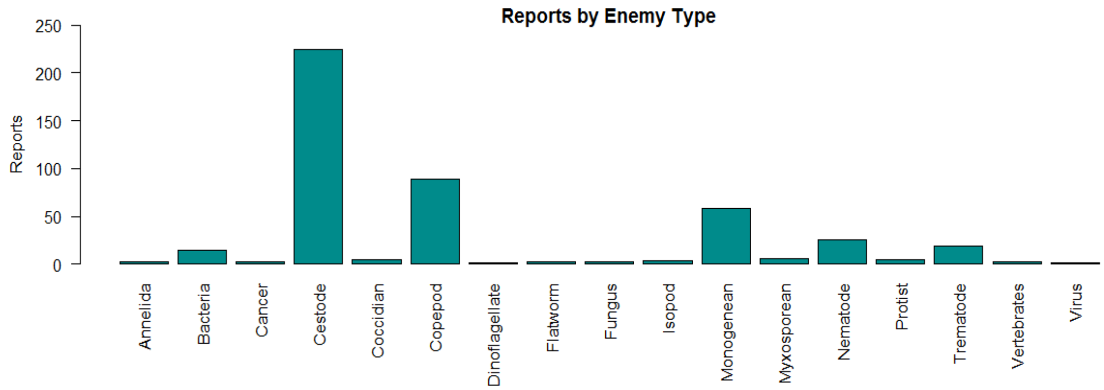

Figure 1. Reports by enemy type included in the study. Certain enemy types have a high number of species described of that type.

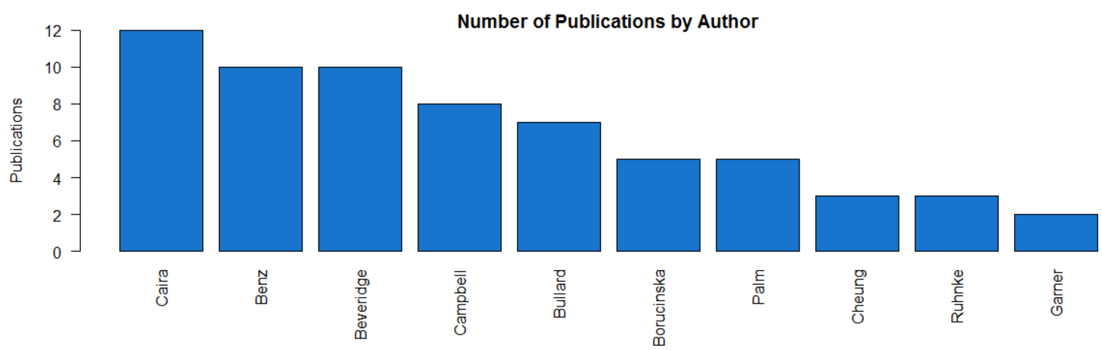

Figure 2. Number of publications by author in decreasing order.

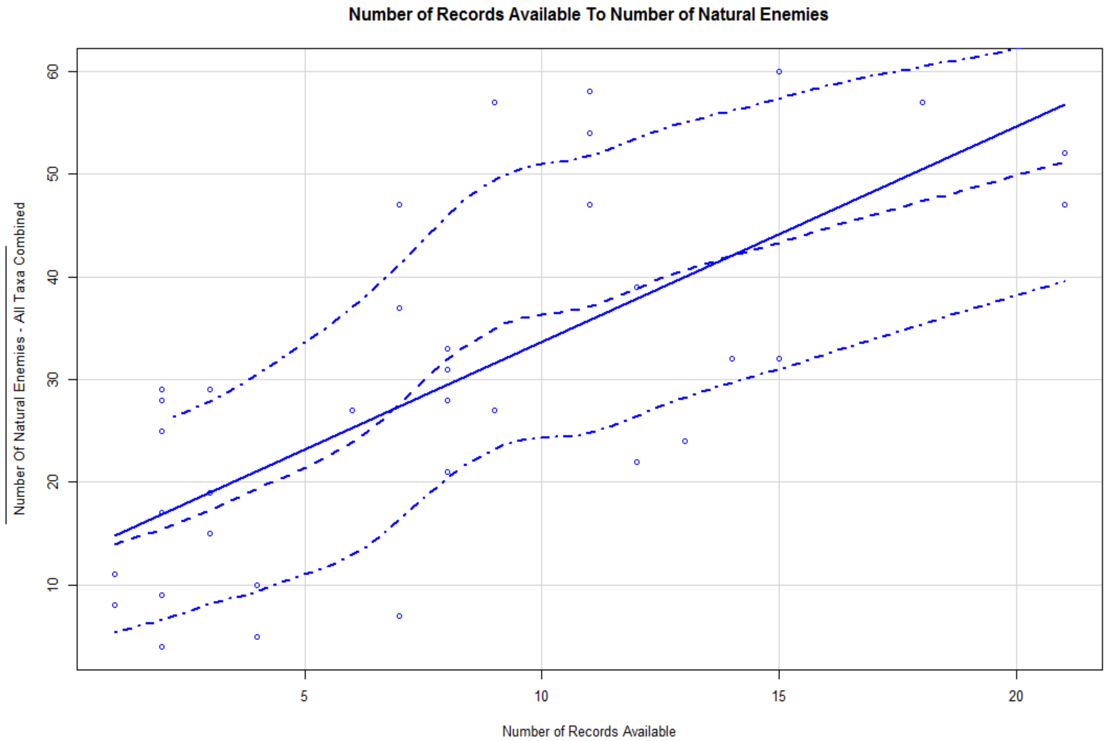

Figure 3. Linear Regression comparing number of records available of each elasmobranch to the number of natural enemies. (R squared = 0.67, p-value <0.001, d.f. = 1,34; F = 67.64). There is a significant relationship between number of records available about an elasmobranch and the number of natural enemies found. Dotted lines are LOWESS smoothing lines used to try and show possible relationships within the data. Box plots indicate data distribution.

Regression analysis found a significant positive correlation between the number of studies conducted on a given species and the number of natural enemies reported for that species (R squared = 0.492, p < 0.001, Df= 1,34; F=32.86). This relationship is depicted in Figure 3. Regression also detected a significant relationship between the number of recorded prey items preferred by an elasmobranch species and the number of natural enemies (R squared= 0.13, p value = 0.026, df= 1 and 34; F=5.457). This relationship is depicted in Figure 4.

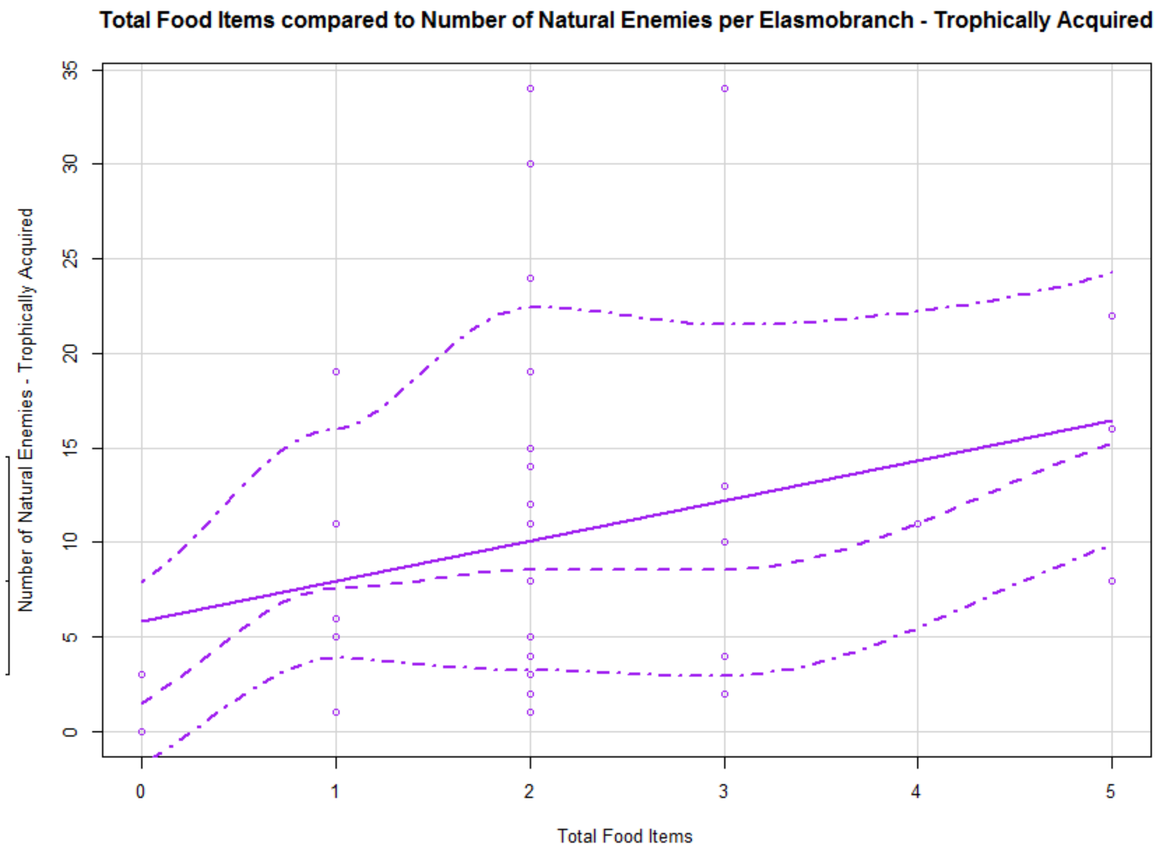

Figure 4. Linear regression between total food items and natural enemies trophically acquired. (R squared: 0.075, p value: 0.105, df= 1 and 34; F=2.775). There is not a significant relationship between food items eaten by an elasmobranch and trophically acquired parasites. Dotted lines are LOWESS smoothing lines used to try and show possible relationships within the data. Box plots indicate distribution of data.

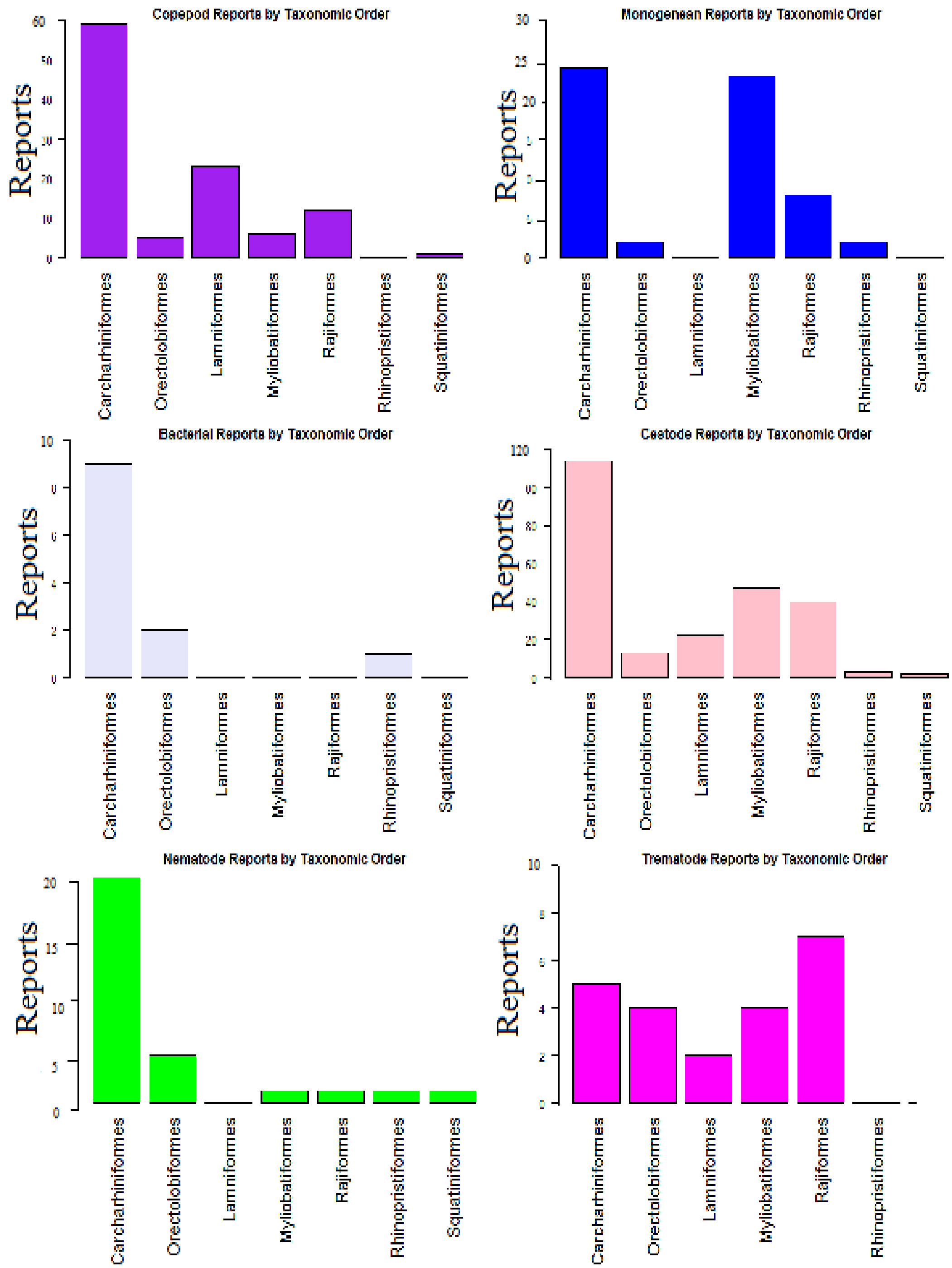

Figure 5. Reports of natural enemy type categorized by taxonomic order, from left to right: Carcharhiniformes, Orectolobiformes, Lamniformes, Myliobatiformes, Rajoformes, Rhinopristiformes, and Squatiniformes.

Figure 5 depicts the elasmobranchs of the study, grouped by their taxonomic Order and indicates the most reported natural enemies of each. Of the six natural enemy groups depicted (Bacteria, Cestodes, Copepods, Monogeneans, Nematodes, and Trematodes), the order with the most reports is the Carcharhiniformes. The Myliobatiformes and Orectolobiformes have information available, but not to the extent to that of the Carcharhiniformes.

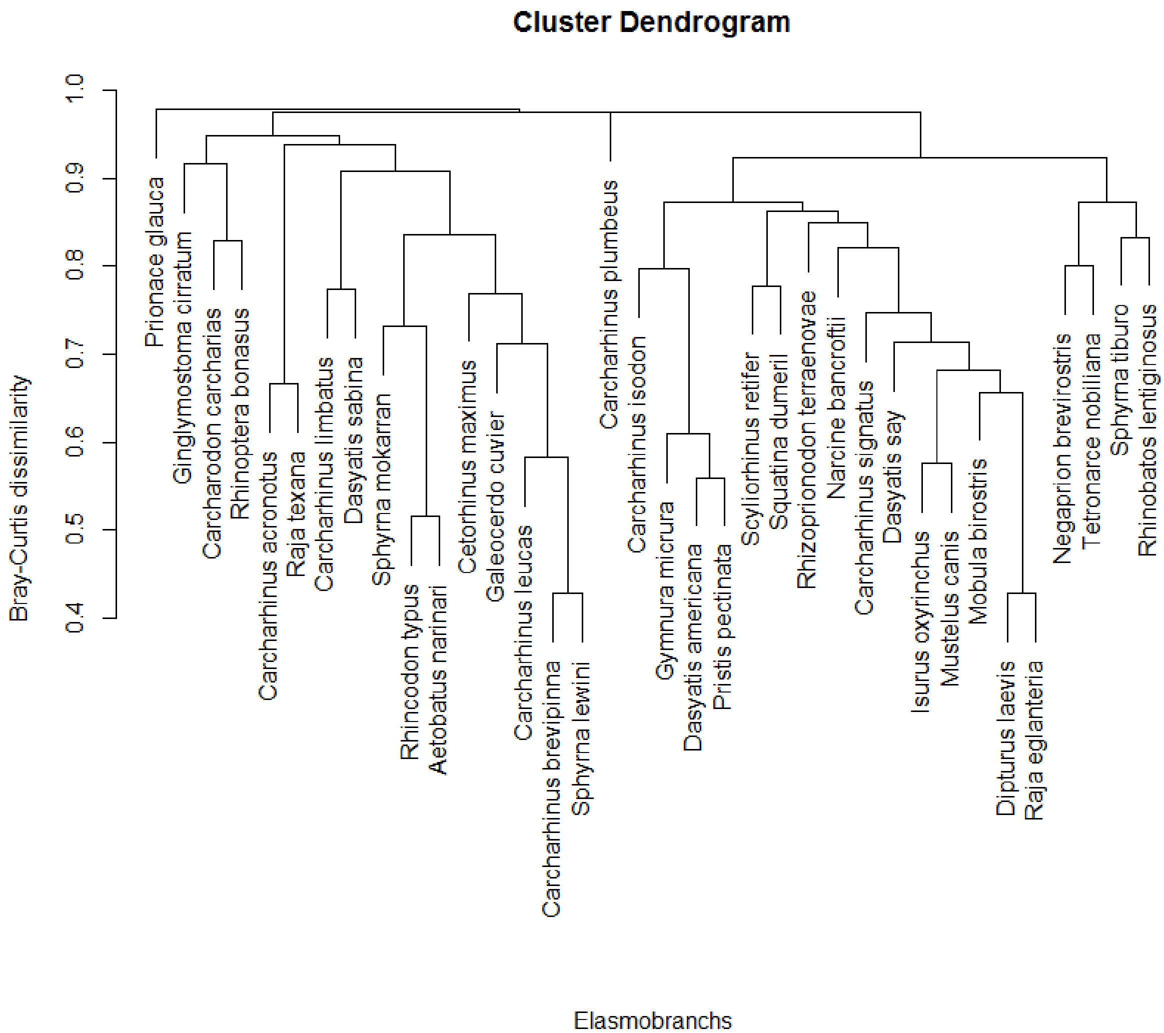

Figure 6. Species hierarchical cluster. No overt patterns appear, with the exception of the figure being split by *C. plumbeus.*

Figure 6 used the species level of elasmobranch with all natural enemies and clustered by using Bray-Curtis dissimilarity. A Bray-Curtis dissimilarity matrix ranges from zero to one, with zero indicating two samples as being identical; in Figure 6, there seems to be some clustering as in *C. plumbeus* splits the clusters. Similarly, Figure 7 depicts clustering by taxonomic Family using all natural enemies, where about four clusters appeared.

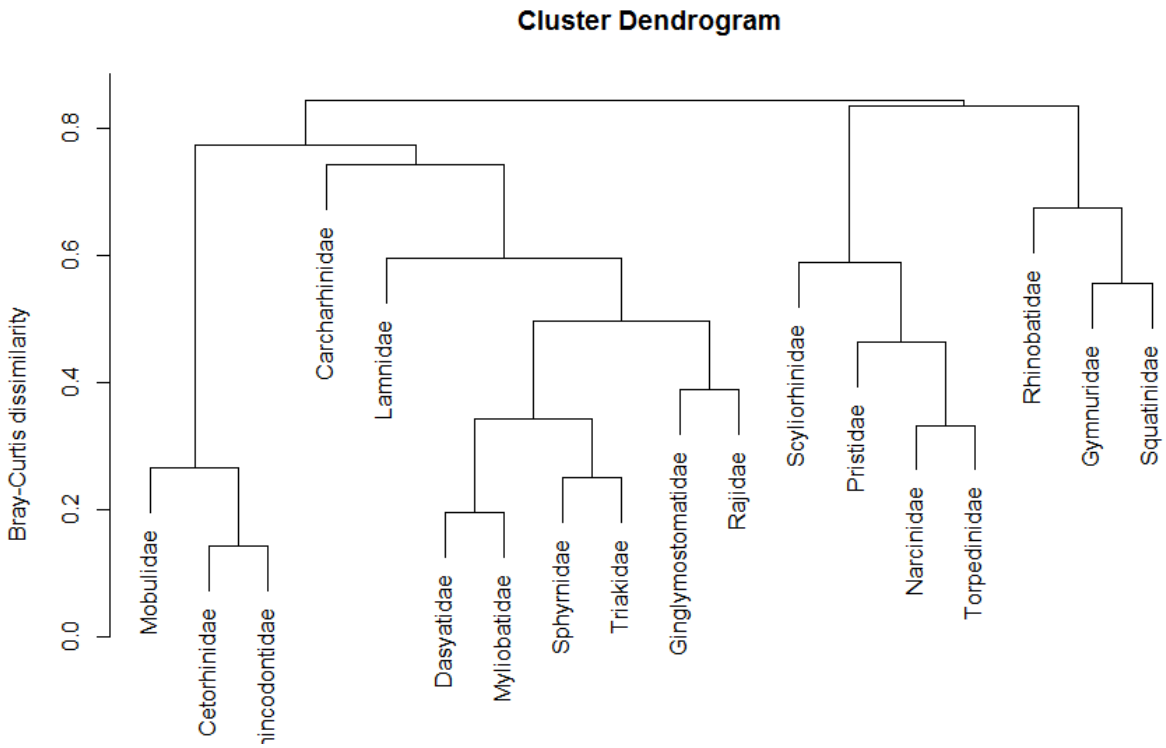

Figure 7. Hierarchical cluster by taxonomic family, split using natural enemy reports. There are about four clusters appearing.

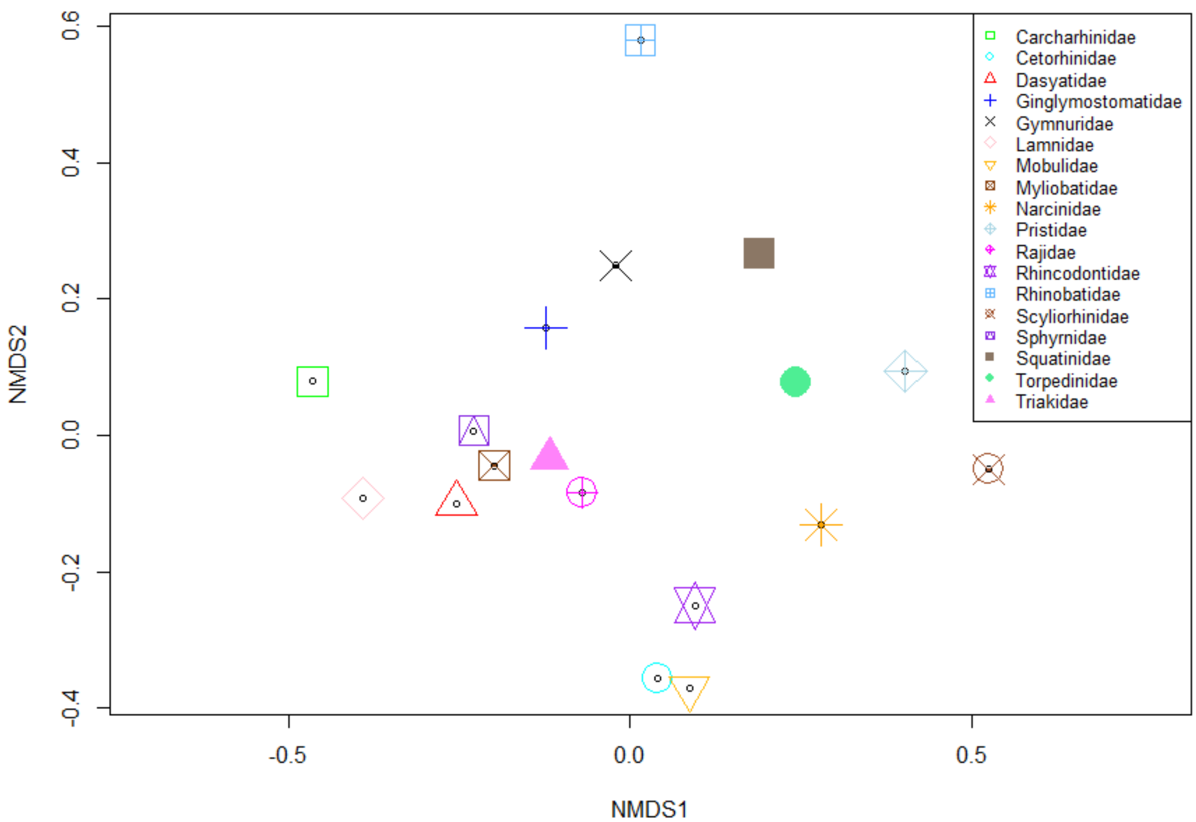

Figure 8. NMDS using elasmobranch taxonomic order. Some clustering appears, such as Cetorhinidae, Mobulidae, and Rhincodontidae near the bottom of the figure.

The NMDS produced was used to examine the patterns between taxonomic order and natural enemy community similarity between samples. A cluster formed near the bottom of the figure as well as center-left between Triakidae, Scyliorhinidae, Rajidae, Dasyatidae, and Sphyrnidae. Rhinobatidae appeared alone near the top of the figure.

Discussion

Database Aggregation and Exploration

A statistically significant relationship was found between the number of natural enemies and number of records available. This indicates that with an increase in the number of publications related to natural enemies, there are new natural enemies described. The relationship indicates that the best way to learn more about elasmobranch disease and pathogens is to study them.

In addition, there were differences in data available between the species reviewed (22 sharks, 11 rays, and three skates). For example, *Carcharhinus isodon* (Finetooth Shark), *Rhincodon typus* (Whale Shark), *Scyliorhinus retifer* (Chain catshark), and *Squatina dumeril* (Atlantic Angelshark) have less than four records documenting their pathogens. In comparison, the ray species of this study which are the most understudied include: *Manta birostris* (Manta), Narcine bancroftii (Lesser electric ray), *Rhinobatos lentiginosus* (Atlantic Guitarfish), and *Tetronarce nobiliana* (Atlantic torpedo). Each with two, one, three and three sources, respectively, documenting their pathogens and the diseases with which they are found. Lastly, all three species of skates included in the scope of this study have very few documented sources of the pathogens and diseases. The species are *Dipturus laevis* (Barndoor skate), *Raja eglanteria* (Clearnose skate), and *Raja texana* (Roundel skate), each skate has less than three sources documenting natural enemies.

The highest number of reports per enemy type belong to the cestodes, a group that is extensively studied by the most prolific author as labelled in Figure 9, Janine Caira. Copepods, nematodes, trematodes, and monogeneans are the next most studied natural enemies in Figure 8. The other authors generating research in this field are pictured in Figure 9. Taken together, both of these figures indicate there is a small number of authors generating most of the information and hopefully new researchers will move into the field. New researchers interested in health of ecosystems would benefit from increased knowledge of elasmobranchs due to their ability to shape trophic webs.

Bias in the Literature

Viruses, fungal infections, and bacteria are data deficient; there is little information on these pathogens infecting elasmobranchs. Availability and economic importance may play a role in the bias in host species studied (Baum and Worm 2009). Adamson and Caira (1991) noted that another reason for some elasmobranch species having less information may be due to the size of sharks and that performing thorough necropsies on sharks may not be a viable option. Anatomical areas that are not typically thought to harbor many parasites may be overlooked completely, such as the circulatory system. Al Kawari et al. (1996) explored helminths in the Arabian Gulf and noticed a bias toward studying larger organisms, species which do not require complex instrumentation, and those which are easiest to locate. This can lead to a vast underestimation of microorganisms in the less accessible species.

Diet and Trophically Acquired Natural Enemies

There was no significant relationship between the number of trophically acquired natural enemies as well as number of prey items, however it is important to note that these analyses are being run with data that is fragmented due to species being understudied. For example, this relationship may be a statistically significant one, but that investigation would require more records on natural enemies of understudied sharks, rays, and skates. Examination of stomach contents by necropsy of elasmobranchs may provide more information on trophically acquired parasites as can the continued research into the spiral valve portion of shark digestive systems (Borucinska and Dunham 2000, Borucinska and Caira 1993, Cislo and Caira 1993, Curran and Caira 1995). Level of vulnerability, and trophic level as recorded by Fishbase, did not show any type of pattern due to Fishbase categorizing many of the elasmobranchs similarly across life history factors.

Reports of Enemy Type Filtered by Taxonomic Order

Overall reports of natural enemies filtered by taxonomic order show that cestodes are the most researched parasite in this study. Some of the elasmobranchs do not have any record of certain pathogens at this current time. Aside from the cestodes, all other pathogen groups have elasmobranch orders where no record exists (Figure 5). Certain pathogens had such low numbers of recorded cases in elasmobranchs, they were not used in making figures. Taxonomic Order in this figure contains many of the more accessible, larger, and better studied sharks such as the Bull shark, Sandbar shark, and Lemon shark. Included in Order Carcharhiniformes are some understudied sharks, such as the Blacknose shark and Scyliorhinus retifer, indicating that while examination of natural enemies by Order provides some useful information, the problem of knowledge gaps in these species' pathogens persists.

Clustering of Elasmobranchs

Figure 6 did not display any tight clusters, this may be due to some elasmobranchs being more studied than others. In Figure 7, the clusters are separated more clearly than in Figure 6. The clusters may also have been related to the same bias in the literature mentioned earlier. Two of the most studied families, Carcharhinidae and Lamnidae, are clustered near each other, however, this may be due in part to any number of factors. These Families include the Basking shark, the Manta ray, and the Whale shark. These elasmobranchs are known to be more sluggish and slow moving individuals, which may explain why they would have similar natural enemies as each other. Carcharhinidae and Lamnidae clustered together. Both of these taxonomic Families include high energy, well studied shark species such as: Bull sharks, Blacktips, Sandbar sharks, White sharks, the Shortfin Mako shark, etc.

This cluster has a number of well studied and under studied species. Nurse sharks, Dusky Smoothhounds, Hammerheads and some rays have a large amount of information on natural enemies available. This cluster also includes skates and it is possible that this cluster formed as a type of midpoint between elasmobranchs with a lot of information and those lacking information. The second to last cluster includes Scyliorhinidae, Pristidae, Narcinidae, and and Torpedinidae. The last cluster comprises: Rhinobatidae, Gymnuridae and Squatinidae. These final two clusters represent the least studied species, with the exception of the Rajidae family grouped elsewhere.

The generated NMDS is Figure 8. The generated ordination plot of this NMDS (not pictured had a very high r squared value (0.987, non-metric fit) indicating it was a good model to use for this data. The NMDS attempted to find patterns within the data, but the lack of information on Orders presents itself in the lack of very tight groupings. When more information on natural enemies is compiled and added to the database created in this study, a new NMDS should be run to look for new patterns based on dissimilarity between elasmobranchs.

The host or natural enemy list compiled in the present study will be of interest to resource managers and wildlife biologists who study elasmobranchs, providing much-needed information on potential natural causes of morbidity and mortality in local shark populations. The subsequent meta-analysis has provided further insight into the broad factors that shape natural enemy communities in these fish. Knowledge gaps focusing on individual elasmobranch species have been investigated and identified, which may open the door to further research by scientists and students.

Summary and Conclusions

The above mentioned data deficient species would benefit from increased study by researchers and scientists in order to better understand and document the natural enemies of elasmobranch species. Some elasmobranchs are of commercial importance and this may be related to the difference in sampling effort (Camhi et al. 2008). With each new parasite description or recorded case of illness in an elasmobranch, the field of marine conservation gains insight into how to better conserve and protect at-risk species.

This literature review and meta analysis accomplished both research objectives of: creating the first comprehensive database of natural enemies from the selected Florida elasmobranchs, and the exploration of relationships between natural enemy community structure and life history traits, such as diet with regressions, hierarchical clustering, and a non-metric multi-dimensional scale model. Statistically significant relationships were found between the number of sources available and number of natural enemies present in an elasmobranch. The discovery of knowledge gaps pertaining to natural enemies and elasmobranch species has been uncovered, and discussion of underlying causes to bias leads to the indication that there is a lot of research needed in this field of study.

References

Adamson, M. and Caira, J. (1991) Lockenloia sanguinis n. gen., n. sp. (Nematoda: Dracunculoidea) from the Heart of a Nurse Shark, Ginglymostoma cirratum, in Florida. *The Journal of Parasitology*, 77(5), p.663. DOI: 10.2307/3282695

Adamson, M., Deets, G. and Benz, G. (1987) Description of male and redescription of female Phlyctainophora squali Mudry and Dailey, 1969 (Nematoda; Dracunculoidea) from elasmobranchs. *Canadian Journal of Zoology*, 65(12), pp.3006-3010. Available from: https://doi.org/10.1139/z87-455

Al Kawari KS, Saoud MFA, Ramadan MM (1996) Biodiversity of helminth parasites of fishes in the Arabian Gulf, with special reference to digenetic trematodes and cestodes. *Qatar University Science*, 16(1), pp. 141-153. Available from: http://hdl.handle.net/10576/9849

Altizer, S., Bartel, R. and Han, B. (2011) Animal Migration and Infectious Disease Risk. *Science*, 331(6015), pp.296-302. DOI: 10.1126/science.1194694

Amin O.M. (1998) *Marine flora and fauna of the Eastern United States: Acanthocephala.* National Oceanic and Atmospheric Association. Report number: 135. Available from: http://spo.nwr.noaa.gov/tr135.pdf

Anderson, E., Frasca, S., Asakawa, M., Fatzinger, M., Johnson, J., Marchetere, K., Goodale, L., Risatti, G. and Harms, C. (2012) Splenic mycobacteriosis in an Atlantic guitarfish, Rhinobatos lentiginosus Garman. *Journal of Fish Diseases*, 35(7), pp.541-544. Available from: https://doi.org/10.1111/j.1365-2761.2012.01367.x

Argumendo, R. (1997) *Catálogo de la colección nacional de helmintos*. Mexico City, Universidad Nacional Autonoma de Mexico.

Austin, B. and Austin, D.A., (2007) Characteristics of the diseases. *Bacterial Fish Pathogens: Diseases of Farmed and Wild Fish*, pp.15-46. Available from: https://doi.org/10.1007/978-1-4020-6069-4_2

Barker, A.S., (2006*) Rhinoptera bonasus*. [Online] Available from: http://www.iucnredlist.org/details/60128/0 [Accessed 18 May 2018].

Bates, R.M., 1990. *A checklist of the Trypanorhyncha (Platyhelminthes: Cestoda) of the world (1935-1985)* (No. 1). National Museum of Wales.[Online] Available from: http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/cestode-life-cycle/index.html [Accessed September 9 2018].

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. and Doherty, P.A., (2003) Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, *299*(5605), pp.389-392. DOI: 10.1126/science.1079777

Baum, J., Clarke, S., Domingo, A., Ducrocq, M., Lamónaca, A.F., Gaibor, N., Graham, R., Jorgensen, S., Kotas, J.E., Medina, E. and Martinez-Ortiz, J., (2012) *Sphyrna lewini*. [Online] Available from: http://www.iucnredlist.org/details/39385/0 [Accessed 18 May 2018].

Baum, J.K. and Worm, B., (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology, 78*(4), pp.699-714. doi: 10.1111/j.1365-2656.2009.01531.x

Becker, C.D. and Overstreet, R.M., (1979) Haematozoa of marine fishes from the northern Gulf of Mexico. *Journal of Fish Diseases, 2*(6), pp.469-479. Available from: https://doi.org/10.1111/j.1365-2761.1979.tb00408.x

Benz, G.W., (1989) Developmental stages of Alebion lobatus Cressey, 1970 (Copepoda: Euryphoridae) found parasitic on the sandbar shark (Carcharhinus plumbeus (Nardo, 1827)) in the western North Atlantic, and a phylogenetic analysis of the genus Alebion Krøyer, 1863. *Canadian Journal of Zoology, 67*(6), pp.1578-1598. Available from: https://doi.org/10.1139/z89-224

Benz, G.W. and Bullard, S.A., (2004) Metazoan parasites and associates of chondrichthyans with emphasis on taxa harmful to captive hosts. In: *The Elamobranch Husbandry Manual: Captive Care of Sharks, Rays, and their Relatives.* Columbus, OH, Ohio Biological Survey, pp.325-416.

Benz, G.W. and Deets, G.B., (1986) Kroyeria caseyi sp. nov.(Kroyeriidae: Siphonostomatoida), a parasitic copepod infesting gills of night sharks (Carcharhinus signatus (Poey, 1868)) in the western North Atlantic. *Canadian Journal of Zoology*, *64*(11), pp.2492-2498. Available from: https://doi.org/10.1139/z86-369

Benz, G.W. and Deets, G.B., (1988). Fifty-one years later: an update on Entepherus, with a phylogenetic analysis of Cecropidae Dana, 1849 (Copepoda: Siphonostomatoida). *Canadian Journal of Zoology*, *66*(4), pp.856-865. Available from: https://doi.org/10.1139/z88-127

Benz, G.W. and Dupre, K.S., (1987) Spatial distribution of the parasite Kroyeria carchariaeglauci Hesse, 1879 (Copepoda: Siphonostomatoida: Kroyeriidae) on gills of the blue shark (Prionace glauca (L., 1758)). *Canadian Journal of Zoology*, *65*(5), pp.1275-1281. Available from: https://doi.org/10.1139/z87-199

Benz, G.W., Mollet, H.F., Ebert, D.A., Davis, C.R. and Van Sommeran, S.R., (2003) Five species of parasitic copepods (Siphonostomatoida: Pandaridae) from the body surface of a white shark captured in Morro Bay, California. *Pacific Science, 57*(1), pp.39-43. doi: 10.1353/psc.2003.0002

Benz, G.W., Pratt, H.L. and Adamson, M.L., (1987) Larval philometrid nematodes (Philometridae) from the uterus of a sandbar shark, Carcharhinus plumbeus.

In: *Proceedings of the Helminthological Society of Washington* (Vol. 54, pp. 154-155). Available from: http://bionames.org/bionames-archive/issn/0018-0130/54/154.pdf

Benz, G.W., Smith, B.E. and Bullard, S.A., (2001) Kroeyerina deetsorum n. sp.(Copepoda: Kroyeriidae) from the olfactory sacs of Atlantic sharpnose sharks (Rhizoprionodon terraenovae) captured in the Gulf of Mexico and northwestern Atlantic and first report of copepodids representing Kroyeriidae. *Journal of Parasitology*, *87*(6), pp.1279-1290. Available from: https://doi.org/10.1645/0022-3395(2001)087[1279:KDNSCK]2.0.CO;2

Bethea, D.M., Carlson, J. & Sulikowski, J. (2009) *Raja texana*. [Online] Available from: http://www.iucnredlist.org/details/161686/0 [Accessed May 19 2018]

Beveridge, I., (1991) The distribution of Echinocephalus overstreeti Deardorff and KO (Nematoda), a parasite of Elasmobranch fishes in Australian waters.[Brief communication]. *Transactions of the Royal Society of South Australia (Australia)*.

Beveridge, I. and Campbell, R.A., (1989) Chimaerarhynchus ng and Patellobothrium ng, two new genera of trypanorhynch cestodes with unique poeciloacanthous armatures, and a reorganisation of the poeciloacanthous trypanorhynch families. *Systematic Parasitology*, *14*(3), pp.209-225. Available from: https://doi.org/10.1007/BF02187055

Beveridge, I. and Campbell, R.A., (1993) A revision of Dasyrhynchus Pintner (Cestoda: Trypanorhyncha), parasitic in elasmobranch and teleost fishes. *Systematic Parasitology*, *24*(2), pp.129-157. Available from: https://doi.org/10.1007/BF00009597

Beveridge, I. and Campbell, R.A., (1998) Re-examination of the trypanorhynch cestode collections of AE Shipley, J. Hornell and T. Southwell, with the erection of a new genus, Trygonicola, and redescriptions of seven species. *Systematic Parasitology*, *39*(1), pp.1-34. Available from: https://doi.org/10.1023/A:10058525

Beveridge, I. and Campbell, R.A., (2010) Validation of Christianella Guiart, 1931 (Cestoda: Trypanorhyncha) and its taxonomic relationship with Grillotia Guiart, 1927. *Systematic parasitology*, *76*(2), pp.111-129. Available from: https://doi.org/10.1007/s11230-010-9239-x

Beveridge, I. and Campbell, R.A., (1988) A review of the Tetrarhynchobothriidae Dollfus, 1969 (Cestoda: Trypanorhyncha) with descriptions of two new genera, Didymorhynchus and Zygorhynchus. *Systematic Parasitology*, *12*(1), pp.3-29. Available from: https://doi.org/10.1007/BF00182025

Beveridge, I. and Campbell, R.A., (2003) Review of the Rhopalothylacidae Guiart, 1935 (Cestoda: Trypanorhyncha), with a description of the adult of Pintneriella musculicola Yamaguti, 1934 and a redescription of P. gymnorhynchoides (Guiart, 1935) comb. n. *Folia parasitologica*, *50*(1), pp.61-71.

Beveridge, I. and Duffy, C., (2005). Redescription of Cetorhinicola acanthocapax Beveridge & Campbell, 1988 (Cestoda: Trypanorhyncha) from the basking shark Cetorhinus maximus (Gunnerus). *Systematic Parasitology*, *62*(3), pp.191-198. Available from: https://doi.org/10.1007/s11230-005-5492-9

Biodiversity Institute of Ontario. *Protozoa*. In: Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment). Encyclopedia of Earth.

Borucinska, J.D. and Adams, D.H., (2013) Parasitic metritis and oophoritis associated with nematode larvae in an Atlantic sharpnose shark, Rhizoprionodon terraenovae (Richardson), collected in the western Atlantic off Florida. *Journal of fish diseases*, *36*(9), pp.811-817. Available from: https://doi.org/10.1111/jfd.12085

Borucinska, J.D. and Bullard, S.A., (2011) Lesions associated with plerocerci (Platyhelminthes: Cestoda: Trypanorhyncha) in the gastric wall of a cownose ray, Rhinoptera bonasus (Mitchill),(Myliobatiformes: Rhinopteridae) from the northern Gulf of Mexico. *Journal of fish diseases*, *34*(2), pp.149-157. Available from: https://doi.org/10.1111/j.1365-2761.2010.01223.x

Borucinska, J. and Caira, J.N., (1993) A comparison of mode of attachment and histopathogenicity of four tapeworm species representing two orders infecting the spiral intestine of the nurse shark, Ginglymostoma cirratum. *The Journal of parasitology*, pp.238-246. DOI: 10.2307/3283514

Borucinska, J.D. and Caira, J.N., (2006) Mode of attachment and lesions associated with trypanorhynch cestodes in the gastrointestinal tracts of two species of sharks collected from coastal waters of Borneo. *Journal of Fish Diseases*, *29*(7), pp.395-407. Available from: https://doi.org/10.1111/j.1365-2761.2006.00730.x

Borucinska, J. and Dunham, A., (2000) Lesions associated with attachment of the cestode Tentacularia sp. to the duodeno-spiral junction in the blue shark, Prionace glauca (L.), with a description of the intestinal morphology of the shark. *Journal of Fish Diseases*, *23*(5), pp.353-359. Available from: https://doi.org/10.1046/j.1365-2761.2000.00253.x

Bricknell, I., (2017) Types of Pathogens in Fish, Waterborne Diseases. In: *Fish Diseases.* Orono, Maine, Univeristy of Maine, pp. 53-80. Available from: https://doi.org/10.1016/B978-0-12-804564-0.00003-X

Bright, M. (2011) *Sharks*. Buffalo, New York, Firefly Books.

Bruce, N.L., Adlard, R.D. and Cannon, L.R., (1994) Synoptic checklist of ascaridoid parasites (Nematoda) from fish hosts. *Invertebrate Systematics*, *8*(3), pp.583-674. Available from: https://doi.org/10.1071/IT9940583

Bruce, N.L. and Cannon, L.R.G., (1990) Ascaridoid nematodes from sharks from Australia and the Solomon Islands, southwestern Pacific Ocean. *Invertebrate Systematics*, *4*(4), pp.763-783. Available from: https://doi.org/10.1071/IT9900763

Bullard, S.A., Dippenaar, S.M., Hoffmayer, E.R. and Benz, G.W., (2004) New locality records for Dermophthirius carcharhini (Monogenea: Microbothriidae) and Dermophthirius maccallumi and a list of hosts and localities for species of Dermophthirius. *Comparative Parasitology*, *71*(1), pp.78-80. Available from: https://doi.org/10.1654/4093

Bullard, S.A., Frasca Jr, S. and Benz, G.W., (2001) Gill lesions associated with Erpocotyle tiburonis (Monogenea: Hexabothriidae) on wild and aquarium-held bonnethead sharks (Sphyrna tiburo). *Journal of Parasitology*, *87*(5), pp.972-977. Available from: https://doi.org/10.1645/0022-3395(2001)087[0972:GLAWET]2.0.CO;2

Bullard, S.A. and Jensen, K., (2008) Blood flukes (Digenea: Aporocotylidae) of stingrays (Myliobatiformes: Dasyatidae): Orchispirium heterovitellatum from Himantura imbricata in the Bay of Bengal and a new genus and species of Aporocotylidae from Dasyatis sabina in the northern Gulf of Mexico. *Journal of Parasitology*, *94*(6), pp.1311-1321. Available from: https://doi.org/10.1645/GE-1498.1

Bullard, S.A., Overstreet, R.M. and Carlson, J.K., (2006) Selachohemecus benzi n. sp.(Digenea: Sanguinicolidae) from the blacktip shark Carcharhinus limbatus (Carcharhinidae) in the northern Gulf of Mexico. *Systematic Parasitology*, *63*(2), p.141. Available from: https://doi.org/10.1007/s11230-005-9010-x

Bullard, S.A., Payne, R.R. and Braswell, J.S., (2004) New genus with two new species of capsalid monogeneans from dasyatids in the Gulf of California. *Journal of Parasitology*, *90*(6), pp.1412-1427. Available from: https://doi.org/10.1645/GE-304R

Bullard, S.A., Ruiz, C.F., McElwain, A., Murray, M.J., Borucinska, J.D. and Benz, G.W., (2012) Huffmanela cf. carcharhini (Nematoda: Trichosomoididae: Huffmanelinae) from skin of a sandbar shark, Carcharhinus plumbeus, in the Pacific Ocean. *Journal of Parasitology*, *98*(2), pp.333-340. Available from: https://doi.org/10.1645/GE-2962.1

Burge, C.A., Eakin, C.M., Friedman, C.S., Froelich, B., Hershberger, P.K., Hofmann, E.E., Petes, L.E., Prager, K.C., Weil, E., Willis, B.L. and Ford, S.E., (2014) *Climate change influences on marine infectious diseases: implications for management and society*. [Online] Ithaca, New York, Cornell Univeristy. Available from: https://www.annualreviews.org/doi/pdf/10.1146/annurev-marine-010213-135029 [Accessed May 23 2018].

Burgess HG (2009). *Carcharhinus brevipinna*.[Online] Available from: http://www.iucnredlist.org/details/39368/0 [Accessed May 18 2018].

Burgess HG & Branstetter S (2009) *Carcharhinus limbatus*. [Online] Available from: http://www.iucnredlist.org/details/3851/0 [Accessed May 18 2018].

Butler, S.A., (1987) Taxonomy of some tetraphyllidean cestodes from elasmobranch fishes. *Australian Journal of Zoology*, 35(4), pp.343-371. Available from: https://doi.org/10.1071/ZO9870343

Cailliet GM, Cavanagh RD, Kulka DW, Stevens JD, Soldo A, Clo S, Macias D, Baum J, Kohin S, Duarte A, Holtzhausen JA, Acuña E, Amorim A & Domingo A (2009) *Isurus oxyrinchus*. [Online] Available from: http://www.iucnredlist.org/details/39341/0 [Accessed May 18 2018].

Caira, J.N. and Jensen, K., (2017) *Planetary biodiversity inventory (2008–2017): Tapeworms from vertebrate bowels of the earth*. Natural History Museum, University of Kansas.

Caira, J.N. and Jensen, K., (2014) A digest of elasmobranch tapeworms. *The Journal of Parasitology*, *100*(4), pp.373-391. Available from: https://doi.org/10.1645/14-516.1

Caira, J.N., Jensen, K. and Healy, C.J., (2014) Interrelationships annong tetraphyllidean and lecanicephalidean cestodes. *Interrelationships of the Platyhelminthes*, p.135.

Caira, J.N., Jensen, K. and Healy, C.J., (1999) On the phylogenetic relationships among tetraphyllidean, lecanicephalidean and diphyllidean tapeworm genera. *Systematic Parasitology*, *42*(2), pp.77-151. Available from: https://doi.org/10.1023/A:1006192603349

Caira, J.N. and Jensen, K., (2009) Erection of a new onchobothriid genus (Cestoda: Tetraphyllidea) and the description of five new species from whaler sharks (Carcharhinidae). *Journal of Parasitology*, *95*(4), pp.924-940. Available from: https://doi.org/10.1645/GE-1963.1

Caira, J.N., Healy, C.J. and Swanson, J., (1996) A new species of Phoreiobothrium (Cestoidea: Tetraphyllidea) from the great hammerhead shark Sphyrna mokarran and its implications for the evolution of the onchobothriid scolex. *The Journal of parasitology*, pp.458-462. DOI: 10.2307/3284086

Caira, J.N. and Bardos, T., (1996) Further information on Gymnorhynchus isuri (Trypanorhyncha: Gymnorhynchidae) from the shortfin mako shark. *Journal of the Helminthological Society Washington*, *63*, pp.188-192. Available from: http://bionames.org/bionames-archive/issn/1049-233X/63/188.pdf

Caira, J.N. and Gavarrino, M.M., (1990) Grillotia similis (Linton, 1908) comb. n.(Cestoda: Trypanorhyncha) from nurse sharks in the Florida Keys. *Journal of* *the Helminthological Society of Washington*, *57*(1), pp.15-20. url: Available from: http://bionames.org/bionames-archive/issn/1049-233X/57/15.pdf

Campbell, R.A. and Beveridge, I., (2002) The genus Acanthobothrium (Cestoda: Tetraphyllidea: Onchobothriidae) parasitic in Australian elasmobranch fishes. *Invertebrate Systematics*, *16*(2), pp.237-344. https://doi.org/10.1071/IT01004

Campbell, R.A. and Beveridge, I., (1996) Revision of the family Pterobothriidae Pintner, 1931 (Cestoda: Trypanorhyncha). *Invertebrate Systematics, 10*(3), pp.617-662. Available from: https://doi.org/10.1071/IT9960617

Carlson J, Kyne P.M. & Valenti. SV (2009) *Carcharhinus isodon*. [Online] Available from: http://www.iucnredlist.org/details/161524/0 [Accessed May 18 2018].

Carlson J, Wiley T & Smith K (2013) *Pristis pectinata*. [Online] Available from: http://www.iucnredlist.org/details/18175/0 [Accessed May 18 2018].

Carrier, J.C., Musick, J.A. and Heithaus, M.R. eds., (2012) *Biology of sharks and their relatives*. Boca Raton, Florida, CRC press.

De Carvalho, M.R., McCord, M.E. and Myers, R.A., (2007) *Narcine bancroftii*. [Online] Available from: http://www.iucnredlist.org/details/63142/0 [Accessed May 19 2018].

Casper B, Burgess GH & Shepherd T (2016) *Pseudobatos lentiginosus*. [Online] Available from: http://www.iucnredlist.org/details/161743/0 [Accessed May 19 2018].

Castro, J.I., (1983) The sharks of North American waters, Texas A & M University Press, College Station. 180 pp. *Google Scholar*.[Online] Available from: http://www.tamupress.com/product/Sharks-of-North-American-Waters,1784.aspx

Cheung, P., (1993) Eimeria southwelli Halawani, 1930 (Apicomplexa: Coccidia) from a new host, the cownose ray, Rhinoptera bonasus Mitchill. *Journal of Aquariculture & Aquatic Sciences*, *6*(3), pp.68-75. Url: Available from: https://www.cabdirect.org/cabdirect/abstract/19950803106

Cheung, P., (1993) Parasitic diseases of elasmobranchs. M.Stoskopf, (ed.)*Fish Medicine*. Philadelphia, Pennsylvania, pp.782-807.

Cheung, P.J. and Ruggieri, G.D., (1983) Dermophthirius nigrellii n. sp.(Monogenea: Microbothriidae), an ectoparasite from the skin of the lemon shark, Negaprion brevirostris. *Transactions of the American Microscopical Society*, pp.129-134. DOI: 10.2307/3225882

Chisholm, L.A., (1998) A revision of Monocotyle Taschenberg, 1878 (Monogenea: Monocotylidae) with descriptions of three new species from Australia. *Journal of*

Natural History, *32*(9), pp.1259-1290. Available from: https://doi.org/10.1080/00222939800770631

Chisholm, L.A., Whittington, I.D. and Kearn, G.C., (2001) Dendromonocotyle colorni sp. n.(Monogenea: Monocotylidae) from the skin of Himantura uarnak (Dasyatididae) from Israel and a new host record for D. octodiscus from the Bahamas. *Folia Parasitologica*, *48*(1), pp.15-20. Available from: https://www.researchgate.net/profile/Ian_Whittington/publication/12067130_Dendromonocotyle_colorni_sp_n_Monogenea_Monocotylidae_from_the_skin_of_Himantura_uarnak_Dasyatididae_from_Israel_and_a_new_host_record_for_D_octodiscus_from_the_Bahamas/links/0fcfd50b2775b06a22000000/Dendromonocotyle-colorni-sp-n-Monogenea-Monocotylidae-from-the-skin-of-Himantura-uarnak-Dasyatididae-from-Israel-and-a-new-host-record-for-D-octodiscus-from-the-Bahamas.pdf

Cislo, P.R. and Caira, J.N., (1993) The parasite assemblage in the spiral intestine of the shark Mustelus canis. *The Journal of parasitology*, pp.886-899. DOI: 10.2307/3283727

Clarke, K.R. and Gorley, R.N., (2006) Primer v6: User Manual/Tutorial. *Primer-E, Plymouth*.

Conrath C. (2005) *Mustelus canis*. [Online] Available from: http://www.iucnredlist.org/details/39359/0 [Accessed May 18 2018].

Cortés, E., (2000) Life history patterns and correlations in sharks. *Reviews in Fisheries Science*, *8*(4), pp.299-344. Available from: https://doi.org/10.1080/10408340308951115

Cortés E, Lowry D, Bethea D & Lowe CG (2016) *Sphyrna tiburo*. [Online] Available from: http://www.iucnredlist.org/details/39387/0 [Accessed May 18 2018].

Cousin, J.C.B., Pereira Junior, J. and Gonzales, J.F., (2003) Histopatologia no fígado de Prionace glauca (Chondrichthyes, Squaliformes, Carcharhinidae) causada por Hepatoxylon trichiuri (Eucestoda, Trypanorhyncha). *Biociencias,* 11(2), pp.167-172. Available from: http://repositorio.furg.br/handle/1/451

Crawley, M.J., (2012). *The R book.* John Wiley & Sons.

Credille, K.M., Johnson, L.K. and Reimschuessel, R., (1993) Parasitic meningoencephalitis in nurse sharks (Ginglymostoma cirratum). *Journal of wildlife diseases*, *29*(3), pp.502-506. Available from: https://doi.org/10.7589/0090-3558-29.3.502

Crofton, H.D., (1971) A model of host–parasite relationships. *Parasitology*, *63*(3), pp.343-364. Available from: https://doi.org/10.1017/S0031182000079890

Curran, S. and Caira, J.N., (1995) Attachment site specificity and the tapeworm assemblage in the spiral intestine of the blue shark (Prionace glauca). *The Journal of parasitology*, pp.149-157. DOI: 10.2307/3283913

de Buron, I. and Euzet, L., (2005) A new species of Thaumatocotyle (Monogenea: Monocotylidae) from Dasyatis sabina (Myliobatiformes: Dasyatidae) off the coast of South Carolina. *Journal of Parasitology*, *91*(4), pp.791-793. Available from: https://doi.org/10.1645/GE-428R.1

Denham J., Stevens J.D., Simpfendorfer C., Heupel M.R., Cliff G., Morgan A., Graham R., Ducrocq M., Dulv N.K., Seisay M., Asber M., Valenti S.V., Litvinov F., Martins P., Lemine Ould Sidi M., Tous P. & Bucal D. (2007) *Sphyrna mokarran*. [Online] Available from: http://www.iucnredlist.org/details/39386/0 [Accessed May 18 2018].

Derome, N., Gauthier, J., Boutin, S. and Llewellyn, M., (2016) Bacterial opportunistic pathogens of fish. In *The Rasputin Effect: When Commensals and Symbionts Become Parasitic* (pp. 81-108). Springer. DOI https://doi.org/10.1007/978-3-319-28170-4_4

Dippenaar, S., van Tonder, R., Wintner, S. and Zungu, P., (2008) Spatial distribution of Nemesis lamna Risso 1826 (Copepoda: Siphonostomatoida: Eudactylinidae) on the gills of white sharks Carcharodon carcharias off KwaZulu-Natal, South Africa. *African Journal of Marine Science*, *30*(1), pp.143-148. Available from: https://doi.org/10.2989/AJMS.2008.30.1.14.464

Dippenaar, S.M., Benz, G.W. and Olivier, P.A., (2000) Kroyeria deetsi n. sp.(Kroyeriidae: Siphonostomatoida), a parasitic copepod infecting gills of spinner sharks, Carcharhinus brevipinna (Müller & Henle, 1839), in the Indian Ocean. *African Zoology*, *35*(2), pp.185-192. Available from: https://doi.org/10.1080/15627020.2000.11657089

Dobson, A.P. and May, R.M., (1987) The effects of parasites on fish populations—theoretical aspects. *International journal for parasitology*, *17*(2), pp.363-370. Available from: https://doi.org/10.1016/0020-7519(87)90111-1

Dyer, W.G., Williams Jr, E.H. and Williams, L.B., (1988) Digenetic trematodes of marine fishes of Okinawa, Japan. *The Journal of parasitology*, pp.638-645. Available from: 10.2307/3282183

E., A., C., G. and S., P. (2001) Anisakis infestation in marine fish and cephalopods from Galician waters: an updated perspective. *Parasitology Research*, 87(6), pp.492-499. Available from: https://doi.org/10.1007/s004360100389

Escalante, H.E.R.M.E.S., (1986) Cestodes de elasmobranquios de la costa peruana. *Revista de Ciencias (Lima)*, *74*, pp.70-74.

Fergusson I., Compagno L.J.V. & Marks M. (2009) *Carcharodon carcharias*. [Online] Available from: http://www.iucnredlist.org/details/3855/0 [Accessed May 18 2018].

Fowler S.L. (2005) *Cetorhinus maximus*. [Online] Available from: http://www.iucnredlist.org/details/4292/0 [Accessed May 18 2018].

Garner, M.M., (2013) A retrospective study of disease in elasmobranchs. *Veterinary pathology*, *50*(3), pp.377-389. Available from: https://doi.org/10.1177/0300985813482147

Ghoshroy, S. and Caira, J.N., (2001) Four new species of Acanthobothrium (Cestoda: Tetraphyllidea) from the whiptail stingray Dasyatis brevis in the Gulf of California, Mexico. *Journal of Parasitology*, *87*(2), pp.354-372. Available from: https://doi.org/10.1645/0022-3395(2001)087[0354:FNSOAC]2.0.CO;2

Goertz, C.E., (2004) Protozoal diseases of elasmobranchs. *The elasmobranch husbandry manual: captive care of sharks, rays and their relatives*. Columbus, OH,Ohio Biological Survey, pp.417-426.

Gordy, M.A., Kish, L., Tarrabain, M. and Hanington, P.C., (2016) A comprehensive survey of larval digenean trematodes and their snail hosts in central Alberta, Canada. *Parasitology research*, *115*(10), pp.3867-3880. DOI Available from: https://doi.org/10.1007/s00436-016-5152-9

Grubbs R.D., Snelson F.F., Piercy A., Rosa R. & Furtado M. (2016) *Hypanus americanus*. [Online] Available from: http://www.iucnredlist.org/details/60149/0 [Accessed May 19 2018].

Grubbs R.D. & Ha D.S. (2006) *Gymnura micrura*. [Online] Available from: http://www.iucnredlist.org/details/60115/0 [Accessed May 19 2018].

Ha D., Luer C. & Sulikowski J. (2009) *Raja eglanteria*. [Online] Available from: http://www.iucnredlist.org/details/161658/0 [Accessed May 19 2018].

Healy, C.J., (2003) A revision of Platybothrium Linton, 1890 (Tetraphyllidea: Onchobothriidae), with a phylogenetic analysis and comments on host-parasite associations. *Systematic Parasitology*, *56*(2), pp.85-139. DOI Available from: https://doi.org/10.1023/A:1026135528505

Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B., (2008) Predicting ecological consequences of marine top predator declines. *Trends in ecology & evolution*, *23*(4), pp.202-210. Available from: https://doi.org/10.1016/j.tree.2008.01.003

Henderson, A.C., Flannery, K. and Dunne, J., (2002) Parasites of the blue shark (Prionace glauca L.), in the North-East Atlantic Ocean. *Journal of Natural History*, *36*(16), pp.1995-2004. Available from: https://doi.org/10.1080/00222930110078834

Hendrix, S.S., (1994) *Marine Flora and Fauna of the Eastern United States: Platyhelminthes, Monogenea.* National Oceanic and Atmospheric Association. Report number: 121. Available from: http://aquaticcommons.org/id/eprint/2694

Heupel M.R. & Carlson J.K. (2006) *Squatina dumeril*. [Online] Available from: Available from: http://www.iucnredlist.org/details/60248/0 [Accessed may 19 2018].

Hewitt, G.C., (1979) Eight species of parasitic Copepoda on a white shark. *New Zealand Journal of Marine and Freshwater Research*, *13*(1), pp.171-171. Available from: https://doi.org/10.1080/00288330.1979.9515790

Hogans, W.E. and Dadswell, M.J., (1985) Parasitic copepods of the white shark (Carcharodon carcharius L.) from the Bay of Fundy. *Canadian journal of zoology*, *63*(3), pp.740-741. Available from: https://doi.org/10.1139/z85-106

Ivanov, V.A. and Campbell, R.A., (2000) Emendation of the generic diagnosis of Tylocephalum (Cestoda: Lecanicephalidea: Tetragonocephalidae), and description of Tylocephalum brooksi n. sp. *Journal of Parasitology*, *86*(5), pp.1085-1092. Available from: https://doi.org/10.1645/0022-3395(2000)086[1085:EOTGDO]2.0.CO;2

Jameson, S.C., McManus, J.W. and Spalding, M.D., (1995) *State of the reefs: regional and global perspectives*. Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Administration, US Department of Commerce.

Janse, M. and Borgsteede, F.H., (2003) Praziquantel treatment of captive white-spotted eagle rays (Aetobatus narinari) infested with monogean trematodes. *Bulletin of the European Association of Fish Pathologists*, *23*(4), pp.152-156. url: Available from: https://library.wur.nl/WebQuery/wurpubs/362707

Karns RC, Shivji M (2017) *Microbial Community Richness Distinguishes Shark Species Microbiomes in South Florida* (unpublished).

Karsten, A.H. and Rice, C.D., (2006) Serum IgM levels against select marine bacteria in the Atlantic sharpnose shark (Rhizoprionodon terraenovae) from three estuaries. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *143*(3), pp.355-361. Available from: https://doi.org/10.1016/j.cbpc.2006.04.011

Kearn, G., Whittington, I. and Evans-Gowing, R., (2010) A new genus and new species of microbothriid monogenean (Platyhelminthes) with a functionally enigmatic reproductive system, parasitic on the skin and mouth lining of the largetooth sawfish, Pristis microdon, in Australia. *Acta Parasitologica*, *55*(2), pp.115-122. Available from: https://doi.org/10.2478/s11686-010-0019-1

Khan, R.A. and Newman, M.W., (1982) Blood parasites from fish of the Gulf of Maine to Cape Hatteras, Northwest Atlantic Ocean, with notes on the distribution of fish hematozoa. *Canadian Journal of Zoology*, *60*(3), pp.396-402. Available from: https://doi.org/10.1139/z82-054

Knoff M., Carmona De Sao Clemente S., Magalhaes Pinto R., Correa Gomes D. (2002) Prevalência e intensidade de infecção de cestóides Trypanorhyncha de elasmobrânquios nos estados do Paraná e Santa Catarina, Brasil. *Parasitología latinoamericana* 57:149-157

Knoff, M., São Clemente, S.C.D., Pinto, R.M. and Gomes, D.C., (2001) Nematodes of elasmobranch fishes from the southern coast of Brazil. *Memórias do Instituto Oswaldo Cruz*, *96*(1), pp.81-87. Available from: http://dx.doi.org/10.1590/S0074-02762001000100009

Kohn, A. and Santos, C.P., (1989) Brazilian Monogenea-List of Species, Hosts and Geographical Distribution. *International Journal of Parasitology 28(10*), pp. 1517-1554. DOI: 10.1016/S0020-7519(98)00083-6

Kyne P.M., Ishihara H., Dudley S.F.J. & White, W.T. (2006) *Aetobatus narinari. [Online]* Available from: http://www.iucnredlist.org/details/39415/0 [Accessed May 19 2018].

Leibovitz, L. and Lebouitz, S.S., (1985) A viral dermatitis of the smooth dogfish, Mustelus canis (Mitchill). *Journal of Fish Diseases*, *8*(3), pp.273-279. Available from: https://doi.org/10.1111/j.1365-2761.1985.tb00943.x

Llewellyn, J., (1960) Amphibdellid (monogenean) parasites of electric rays (Torpedinidae). *Journal of the Marine Biological Association of the United Kingdom*, *39*(3), pp.561-589. Available from: https://doi.org/10.1017/S0025315400013552

Lyons, K. and Adams, D.H., (2017) First evidence of persistent organic contaminants as potential anthropogenic stressors in the Barndoor Skate Dipturus laevis. *Marine pollution bulletin*, *116*(1-2), pp.534-537. Available from: https://doi.org/10.1016/j.marpolbul.2017.01.007

Marancik, D.P., Berliner, A.L., Cavin, J.M., Clauss, T.M., Dove, A.D., Sutton, D.A., Wickes, B.L. and Camus, A.C., (2011) Disseminated fungal infection in two species of captive sharks. *Journal of Zoo and Wildlife Medicine*, *42*(4), pp.686-693. Available from: http://www.zoowildlifejournal.com/doi/abs/10.1638/2010-0175.1?code=zvet-site

Margolis, L. and Arthur, J.R., (1979) Synopsis of the parasites of fishes of Canada. *Nanaimo, British Columbia, Canadian Agriculture Library.* Available from: https://www.cabdirect.org/cabdirect/abstract/19790865410

Marie, A.D. and Justine, J.L., (2005) Monocotylids (Monogenea: Monopisthocotylea) from Aetobatus cf. narinari off New Caledonia, with a description of Decacotyle elpora n. sp. *Systematic Parasitology*, *60*(3), pp.175-185. Available from: https://doi.org/10.1007/s11230-004-6345-7

Marshall A., Bennett M.B., Kodja G., Hinojosa-Alvarez S., Galvan-Magana F., Harding M., Stevens G. & Kashiwagi T. (2011) *Manta birostris*. [Online] Available from: http://www.iucnredlist.org/details/198921/0 [Accessed May 19 2018].

Meyer, W. and Seegers, U., (2012) Basics of skin structure and function in elasmobranchs: a review. *Journal of Fish Biology*, *80*(5), pp.1940-1967. Available from: https://doi.org/10.1111/j.1095-8649.2011.03207.x

Morales-Serna, F.N., Rodríguez-Santiago, M.A. and Gómez, S., (2016) Euryphorus suarezi n. sp.(Copepoda: Caligidae) parasitic on an elasmobranch from the Gulf of Mexico. *Systematic parasitology*, *93*(1), pp.91-99. Available from: https://doi.org/10.1007/s11230-015-9608-6

Moravec F, Little MD (1988) Granulinema gen. n. a new dracunculoid genus with two new species (G. carcharhini sp. n. and G. simile sp. n.) from the bull shark Carcharhinus leucas (Valenciennes), from Louisiana, U.S.A. *Folia Parasitologica (Ceske Budejovice)* 35:113-120 Available from: Available from: https://europepmc.org/abstract/med/3169642

Morgan M., Carlson J., Kyne P.M. & Lessa R. (2009) *Carcharhinus acronotus*. [Online] Available from: http://www.iucnredlist.org/details/161378/0 [Accessed May 18 2018].

Musick J.A., Stevens J.D., Baum J.K., Bradai M., Clò S., Fergusson .I, Grubbs R.D., Soldo A., Vacchi M. & Vooren C.M. (2009) *Carcharhinus plumbeus*. [Online] Available from: http://www.iucnredlist.org/details/3853/0 [Accessed May 18 2018].

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. and Peterson, C.H., (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*(5820), pp.1846-1850. DOI: 10.1126/science.1138657

Myfwc.com. (2018) Sharks and Fishing. [Online] Available at: http://myfwc.com/research/saltwater/sharks-rays/shark-fisheries/fishing/ [Accessed 18 Jan. 2015].

Natural History Museum (2018) *Cestode Life Cycle Database*. London. Available from: http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/cestode-life-cycle/index.html

Newbound, D.R. and Knott, B., (1999) Parasitic copepods from pelagic sharks in western Australia. *Bulletin of marine science*, *65*(3), pp.715-724. Available from:

https://www.ingentaconnect.com/content/umrsmas/bullmar/1999/00000065/00000003/art00011

Norman, B.M., Newbound, D.R. and Knott, B., (2000) A new species of Pandaridae (Copepoda), from the whale shark Rhincodon typus (Smith). *Journal of Natural History*, *34*(3), pp.355-366. Available from: https://doi.org/10.1080/002229300299534

Notarbartolo di Sciara, G., Serena, F., Ungaro, N., Ferretti, F., Holtzhausen, H.A. & Smale, M.J. (2009). *Tetronarce nobiliana*. [Online] Available from: http://www.iucnredlist.org/details/161580/0 [Accessed May 19 2018].

Olson, P.D., Caira, J.N., Jensen, K., Overstreet, R.M., Palm, H.W. and Beveridge, I., (2010) Evolution of the trypanorhynch tapeworms: parasite phylogeny supports independent lineages of sharks and rays. *International Journal for Parasitology*, *40*(2), pp.223-242. Available from: https://doi.org/10.1016/j.ijpara.2009.07.012

Owens, H.L., (2008) *Multiple species of Phoreiobothrium from the blacktip shark, Carcharhinus limbatus, in the Gulf of Mexico* (Doctoral dissertation, University of Kansas). Available from: http://hdl.handle.net/1808/4559

Palm, H., (1995) *Untersuchungen zur Systematik von Rüsselbandwürmern (Cestoda: Trypanorhyncha) aus atlantischen Fischen* (Doctoral dissertation, Institut für Meereskunde). Available from: http://oceanrep.geomar.de/21882/1/IFM-BER_275.pdf

Palm, H.W. and Beveridge, I., (2002) Tentaculariid cestodes of the order Trypanorhyncha (Platyhelminthes) from the Australian region. *Records of the South Australian Museum*, *35*(1), pp.49-78.

Palm, H.W., (1999) Nybelinia Poche, 1926, Heteronybelinia gen. nov. and Mixonybelinia gen. nov.(Cestoda, Trypanorhyncha) in the collections of the Natural History Museum, London. *Bulletin of the Natural History Museum of London (Zoology)*, *65*, pp.133-153. Available from: http://www.marineparasitology.com/papers/palm%201999%20nybelinia.pdf

Palm, H.W. and Walter, T., (2000) Tentaculariid cestodes (Ord. Trypanorhyncha) from the Muséum d'Histoire Naturelle Paris. *Zoosystema*, *22*(4), pp.641-666. Available from: http://eprints.uni-kiel.de/2285/1/z2000n4a1.pdf

Pierce, S.J. and Norman, B., (2016) *Rhincodon typus*. [Online] Available from: http://www.iucnredlist.org/details/19488/0 [Accessed May 18 2018].

Piercy A., Snelson F.F. & Grubbs R.D. (2016) *Hypanus sabinus*. [Online] Available from: http://www.iucnredlist.org/details/60158/0 [Accessed May 19 2018].

Poynton, S.L., Campbell, T.W. and Palm, H.W., (1997) Skin lesions in captive lemon sharks Negaprion brevirostris (Carcharhinidae) associated with the monogenean Neodermophthirius harkemai Price, 1963 (Microbothriidae). *Diseases of Aquatic Organisms*, *31*(1), pp.29-33. Available from: https://www.int-res.com/abstracts/dao/v31/n1/p29-33/

Randhawa, H.S., (2011) Insights using a molecular approach into the life cycle of a tapeworm infecting great white sharks. *The Journal of parasitology*, *97*(2), pp.275-280. Available from: https://doi.org/10.1645/GE-2530.1

Randhawa, H.S. and Poulin, R., (2009) Determinants and consequences of interspecific body size variation in tetraphyllidean tapeworms. *Oecologia*, *161*(4), pp.759-769. Available from: https://doi.org/10.1007/s00442-009-1410-1

Reed, P., Francis-Floyd, R., Klinger, R. and Petty, D., 2009. Monogenean parasites of fish. *Fisheries and Aquatic Sciences. University of Florida UF, IFAS Extension. FA28, USA*, *4*, pp.1-4.

Ritter, E.K., (2002) Analysis of sharksucker, Echeneis naucrates, induced behavior patterns in the blacktip shark, Carcharhinus limbatus. *Environmental Biology of Fishes*, *65*(1), pp.111-115. Available from: https://doi.org/10.1023/A:1019642221755

Rokicki, J. and Bychawska, D., (1991) Parasitic copepods of Carcharhinidae and Sphyridae (Elasmobranchia) from the Atlantic Ocean. *Journal of Natural History*, *25*(6), pp.1439-1448. Available from: https://doi.org/10.1080/00222939100770911

Rosa-Molinar, E., Williams, C.S. and Lichtenfels, J.R., (1983) Larval nematodes (Philometridae) in granulomas in ovaries of black-tip sharks, Carcharhinus limbatus (Valenciennes). *Journal of wildlife diseases*, *19*(3), pp.275-277. Available from: http://www.jwildlifedis.org/doi/pdf/10.7589/0090-3558-19.3.275

Rosa R.S., Castro A.L.F., Furtado M., Monzini J. & Grubbs R.D. (2006) *Ginglymostoma cirratum*. [Online] Available from: http://www.iucnredlist.org/details/60223/0 [Accessed May 18 2018].

Ruhnke, T.R., (1993) A new species of Clistobothrium (Cestoda: Tetraphyllidea), with an evaluation of the systematic status of the genus. *The Journal of parasitology*, pp.37-43. Available from: https://www.jstor.org/stable/3283274

Ruhnke, T.R., (1994) Resurrection of Anthocephalum Linton, 1890 (Cestoda: Tetraphyllidea) and taxonomic information on five proposed members. *Systematic Parasitology*, *29*(3), pp.159-176. Available from: https://doi.org/10.1007/BF00009673

Ruhnke, T.R. and Thompson, V.A., (2006) Two new species of Paraorygmatobothrium (Tetraphyllidea: Phyllobothriidae) from the lemon sharks Negaprion brevirostris and Negaprion acutidens (Carcharhiniformes: Carcharhinidae). *Comparative Parasitology*, *73*(1), pp.35-41. Available from: https://doi.org/10.1654/4198.1

Ruiz, C.F. and Bullard, S.A., (2013) Huffmanela markgracei sp. n.(Nematoda: Trichosomoididae) from buccal cavity of Atlantic sharpnose shark, Rhizoprionodon terraenovae (Carcharhiniformes: Carcharhinidae), in the northwestern Gulf of Mexico off Texas. *Folia parasitologica*, *60*(4), p.353. Available from: http://sfaas.auburn.edu/ash-bullard/wp-content/uploads/sites/158/2016/10/2013-Huffmanela-markgracei.pdf

Santana F.M., Lessa R. & Carlson J. (2006) *Carcharhinus signatus*. [Online] Available from: http://www.iucnredlist.org/details/60219/0 [Accessed May 19 2018].

São Clemente, S.C.D. and Gomes, D.C., (1992) Description of the adult form of Nybelinia (Syngenes) rougetcampanae Dollfus, 1960 and some new data on n.(n.) bisculata (Linton, 1889)(Trypanorhyncha: Tentaculariidae). *Memórias do Instituto Oswaldo Cruz*, *87*, pp.251-255. Available from: http://dx.doi.org/10.1590/S0074-02761992000500047

Sarada S, Vijaya Lakshmi C, Hanumantha Rao K (1993) Description of a new species of Acanthobothrium giganticum from Gymnura micrura from Waltair Coast. *Rivista di Parassitologia* 54:371-374

Schmidt, G.D. and Beveridge, I., (1990) Cathetocephalus australis n. sp.(Cestoidea: Cathetocephalidae) from Australia, with a Proposal for Cathetocephalidea n. ord. *The Journal of Parasitology*, pp.337-339. DOI: 10.2307/3282661

Schramm, M., (1991) Grillotia perelica (Cestoda: Trypanorhyncha) plerocercoids in mullet (Pisces: Mugilidae) from estuaries in Transkei, southern Africa. *South African Journal of Marine Science*, *11*(1), pp.169-178. Available from: https://doi.org/10.2989/025776191784287493

Schwartz, F.J., (1984) Occurrence, abundance, and biology of the blacknose shark, Carcharhinus acronotus, in North Carolina. *Gulf of Mexico Science*, *7*(1), p.2. Available from: https://doi.org/10.18785/negs.0701.02

Shepherd, T.D. and Myers, R.A., (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology letters, 8(10),* pp.1095-1104. Available from: https://doi.org/10.1111/j.1461-0248.2005.00807.x

Sherrill-Mix S.A., Myers R.A. & Burgess G.H. (2006) *Scyliorhinus retifer*. [Online] Available from: http://www.iucnredlist.org/details/60233/0 [Accessed May 18 2018].

Shields, J.D., (1985) Surface morphology and description of Otobothrium kurisi new species (Cestoda: Trypanorhyncha) from a hammerhead shark, Sphyrna lewini. *International journal for parasitology*, *15*(6), pp.635-643. Available from: https://doi.org/10.1016/0020-7519(85)90009-8

Short, R.B., (1954) A new blood fluke, Selachohemecus olsoni, ng, n. sp.(Aporocotylidae) from the sharp-nosed shark, Scoliodon terra-novae. *Proceedings of the Helminthological Society of* Washington, 21(2), pp.78-82. Available from: https://www.cabdirect.org/cabdirect/abstract/19540801313

Simpfendorfer C. & Burgess G.H. (2009) *Carcharhinus leucas*. [Online] Available from: http://www.iucnredlist.org/details/39372/0 [Accessed May 18 2018].

Simpfendorfer C. (2009) *Galeocerdo cuvier*. [Online] Available from: http://www.iucnredlist.org/details/39378/0 [Accessed May 18 2018].

Smith, M., Warmolts, D., Thoney, D. and Hueter, R., (2004) The elasmobranch husbandry manual: captive care of sharks, rays and their relatives. *Special Publication of the Ohio Biological Survey, Columbus, Ohio*.

Snelson F.F., Piercy A. & Grubbs R.D. (2016) *Hypanus say*. [Online] Available from: http://www.iucnredlist.org/details/60159/0 [Accessed May 19 2018].

Stamper, M.A., Lewbart, G.A., Barrington, P.R., Harms, C.A., Geoly, F. and Stoskopf, M.K., (1998) Eimeria southwelli infection associated with high mortality of cownose rays. *Journal of Aquatic Animal Health, 10*(3), pp.264-270. Available from: https://doi.org/10.1577/1548-8667(1998)010<0264:ESIAWH>2.0.CO;2

Stevens J. (2009) *Prionace glauca*. [Online] Available from: http://www.iucnredlist.org/details/39381/0 [Accessed May 18 2018].

Sundström L.F. (2015*) Negaprion brevirostris*. [Online] Available from: http://www.iucnredlist.org/details/39380/0 [Accessed May 18 2018].

Thoney D.A., Burreson E.M. (1986) Ecological aspects of Multicalyx cristata (Aspidocotylea) infections in northwest Atlantic elasmobranchs. *Proceedings of the Helminthological Society of Washington* 53:162-165 Available from: http://bionames.org/bionames-archive/issn/0018-0130/53/162.pdf

Threlfall, W., (1969) Some parasites from elasmobranchs in Newfoundland. *Journal of the Fisheries Board of Canada*, *26*(4), pp.805-811. Available from: https://doi.org/10.1139/f69-078

Vardo-Zalik, A.M. and Campbell, R.A., (2011) Five new species of Acanthobothrium van Beneden, 1849 (Cestoda: Tetraphyllidea) in elasmobranchs from the northwest Atlantic and Gulf of Mexico with first records from smooth-hound sharks and guitarfish. *Zootaxa*, *2838*(1), pp.41-64. Available from: http://www.mapress.com/j/zt/article/view/11023

Vassiliades, G., (1982) Helminthes parasites des poissons de mer des côtes du Sénégal. *Bulletin de l'Institut Fondamental d'Afrique Noire. Série A: Sciences Naturelles*, *44(1-2),* pp.78-99. Available from: http://agritrop.cirad.fr/398039/

Waldoch, J.A., Burke, S.S., Ramer, J.C. and Garner, M.M., (2010). Melanoma in the skin of a nurse shark (Ginglymostoma cirratum). *Journal of Zoo and Wildlife Medicine*, *41*(4), pp.729-731. Available from: http://www.zoowildlifejournal.com/doi/abs/10.1638/2010-0014.1

Whittington, I.D., (1990) Empruthotrema kearni n. sp. and observations on Thaumatocotyle pseudodasybatis Hargis, 1955 (Monogenea: Monocotylidae) from the nasal fossae of Aetobatus narinari (Batiformes: Myliobatidae) from Moreton Bay, Queensland. *Systematic Parasitology*, *15*(1), pp.23-31. Available from: https://doi.org/10.1007/BF00009915

Williams, E.H., (1978) Conchoderma virgatum (Spengler)(Cirripedia Thoracica) in association with Dinemoura latifolia (Steenstrup & Lutken)(Copepoda, Caligidea), a parasite of the shortfin mako, Isurus oxyrhynchus Rafinesque (Pisces, Chondrichthyes). *Crustaceana*, *34*(1), pp.109-110. Available from: https://www.jstor.org/stable/20103258

Winemiller, K.O., (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(4), pp.872-885. Available from: https://doi.org/10.1139/f05-040

Wood, C.L., Lafferty, K.D. and Micheli, F., (2010) Fishing out marine parasites? Impacts of fishing on rates of parasitism in the ocean. *Ecology Letters*, *13*(6), pp.761-775. Available from: https://doi.org/10.1111/j.1461-0248.2010.01467.x

Appendix

SUPPLEMENTARY LIST

S1. The following lists all 448 pathogens found in the study, categorized by enemy type.

Annelida

Branchellion ravenelii	*Branchellion torpedinis*	*Hirudinae sp.*

Bacteria

Corynebacterium sp.	*Salmonella enterica*	*Vibrio sp.*
Escherichia coli	*Serratia marcescens*	
Flavobacterium sp.	*Streptococcus*	
Kordia sp.	*Vibrio anguillarium*	
Mycobacterium chelonae	*Vibrio charchariae*	
Mycobacterium fortuitum	*Vibrio cholarae*	
Mycobacterium marinum	*Vibrio parahaemolyticus*	

Cancer

Melanoma

Cestode

Acanthobothrium sp.	*Acanthobothrium dysbiotos*	*Acanthobothrium mathiasi*	*Acanthobothrium westi*	*Anthocephalum alicae*

Acanthobothrium aetiobatidis	*Acanthobothrium electricolum*	*Acanthobothrium micracantha*	*Anthobothrium*	*Anthocephalum cairae*
Acanthobothrium americanum	*Acanthobothrium floridensis*	*Acanthobothrium monksi*	*Anthobothrium auriculatum*	*Bombycirhynchus sphyraeniaicum*
Acanthobothrium arlenae	*Acanthobothrium fogeli*	*Acanthobothrium nicoyaense*	*Anthobothrium cornucopia*	*Calliobothrium lintoni*
Acanthobothrium brevissime	*Acanthobothrium giganticum*	*Acanthobothrium paulum*	*Anthobothrium laciniatum*	*Calliobothrium nodosum*
Acanthobothrium colombianum	*Acanthobothrium lentiginosum*	*Acanthobothrium tortum*	*Anthobothrium minutum*	*Calliobothrium verticillatum*
Acanthobothrium coronatum	*Acanthobothrium lineatum*	*Acanthobothrium triacis*	*Anthobothrium quadribothria*	*Callitetrarhynchus gracilis*
Acanthobothrium crassicolle	*Acanthobothrium lintoni*	*Acanthobothrium ulmeri*	*Anthobothrium spinosum*	*Calycobothrium typicum*

Cestode	**continued**			
Calyptrobothrium occidentale	*Dasyrynchus variouncinatus*	*Echeneibothrium minimum*	*Heteronybelinia estigmena*	*Nybelinia africana*
Calyptrobothrium riggii	*Dermophthirioides pristidis*	*Echinobothrium typus*	*Heteronybelinia heteromorphi*	*Nybelinia estigmena*
Cathetocephalus sp.	*Dicranobothrium spinulifera*	*Echinobothrium*	*Heteronybelinia nipponica*	*Nybelinia goreensis*
Cathetocephalus australis	*Didymorhynchus southwelli*	*Eutetrarhynchus ruficollis*	*Heteronyebelinia robusta*	*Nybelinia indica*
Cathetocephalus thatcheri	*Diesingium lomentaceum*	*Floriceps saccatus*	*Heteronybelinia yamagutii*	*Nybelinia lingualis*
Cephalobothrium	*Dinobothrium*	*Gastrolecithus*	*Hispidorhynchus*	*Nybelinia pinteri*

aetobatidis	*keilini*	*planus*	*australiensis*	
Ceratobothrium xanthocephalum	*Dinobothrium paciferum*	*Glyphobothrium zwerneri*	*Hornellobothrium cobraformis*	*Nybelinia schmidti*
Cetorhinicola acanthocapax	*Dinobothrium septaria*	*Grillotia erinaceus*	*Hexacanalis abruptus*	*Nybelinia sphyrnae*
Christianella sp.	*Dioecotaenia*	*Grillotia pastinacae*	*Kotorella pronosoma*	*Orygmatobothrium musteli*
Clistobothrium carcharodoni	*Dioecotaenia cancellata*	*Grillotia similis*	*Lacistorhynchus tenuis*	*Otobothrium australe*
Clistobothrium montaukensis	*Dioecotaenia campbelli*	*Gymnorhynchus gigas*	*Lecanicephalum peltatum*	*Otodistomum cestoides*
Crossobothrium dohrnii	*Discocephalum linton*	*Gymnorhynchus isuri*	*Mecistobothrium brevispine*	*Otobothrium cysticum*
Cylindrophorus typicus	*Disculiceps pileatus*	*Halysioncum boisii*	*Metanisakis tricupola*	*Otobothrium insigne*
Dasyrhynchus giganteus	*Dollfusiella lineata*	*Halysioncum bonasum*	*Mixonybelinia edwinlintoni*	*Otobothrium minutum*
Dasyrhynchus ingens	*Dollfusiella tenuispinis*	*Halysioncum rhinoptera*	*Molicola horridus*	*Otobothrium mugilis*
Dasyrhynchus magnus	*Duplicibothrium minutum*	*Hepatoxylon megacephalum*	*Monorygma galeocerdonis*	*Otobothrium penetrans*
Dasyrynchus pacificus	*Echeneibothrium cancellatum*	*Hepatoxylon trichiuri*	*Myzophyllobothrium rubrum*	*Otobothrium pronosomum*
Dasyrhynchus talismani	*Echeneibothrium javanicum*	*Nybelinia eureia*	*Nybelinia aequidentata*	*Otobothrium propecysticum*

Cestode	continued		
Parachristianella monomegacantha	*Phyllobothrium lactuca*	*Prochristianella*	*Rhinebothrium flexile*
Parachristianella trygonis	*Phyllobothrium microsomum*	*Prochristianella hispida*	*Rhinoptericola megacantha*
Paragrillotia similis	*Phyllobothrium minutum*	*Prochristianella tenuispine*	*Rhodobothrium sp*
Paraorygmatobothrium arnoldi	*Phyllobothrium pammicrum*	*Prochristianella tumidula*	*Shirleyrhynchus aetobatidis*
Paraorygmatobothrium prionacis	*Phyllobothrium tumidum*	*Proemotobothrium southwelli*	*Spiniloculus mavensis*
Paraorygmatobothrium roberti	*Phyllobothrium unilaterale*	*Progillotia dollfus*	*Symcallio violae*
Pedibothrium brevispine	*Pintneriella gymnorhynchoides*	*Prosobothrium adherens*	*Tentacularia coryphaenae*
Pedibothrium globicephalum	*Platybothrium angelbahiense*	*Prosobothrium armigerum*	*Tetrarhynchobothrium striatum*
Pedibothrium hutsoni	*Platybothrium auriculatum*	*Pseudogrillota perelica*	*Thysanocephalum thysanocephalum*
Pedibothrium longispine	*Platybothrium baeri*	*Pseudogilquina microbothria*	*Triloculatum geeceearelensis*
Pelichnibothrium speciosum	*Platybothrium cervinum*	*Pseudolacistorhynchus noodti*	*Triloculatum triloculatum*
Phoreiobothrium	*Platybothrium coshtaprum*	*Pterobothrium acanthotruncatum*	*Trygonicola macropora*
Phoreiobothrium exceptum	*Platybothrium hypoprioni*	*Pterobothrium filicolle*	*Trypanorhyncha sp.*

Phoreiobothrium lasium	*Platybothrium parvum*	*Pterobothrium heteracanthum*	*Tylocephalum aetiobatidis*
Phoreiobothrium manirei	*Platybothrium spinulifera*	*Pterobothrium kingstoni*	*Tylocephalum bonasum*
Phoreiobothrium tiburonis	*Platybothrium tantatulum*	*Pterobothrium lesteri*	*Tylocephalum brooksi*
Phyllobothrium sp.	*Poecilancistrium caryophyllum*	*Pterobothrium lintoni*	*Tylocephalum marsupium*
Phyllobothrium dagnalium	*Polypocephalus sp.*	*Pterobothrium southwelli*	*Tylocephalum pingue*
Phyllobothrium dasybati	*Polypocephalus medusia*	*Rhabdotobothrium dollfusi*	*Tylocephalum yorkei*

Coccidian

Eimeria sp.	*Eimeria quentini*	*Eimeria southwelli*	*Haemogregarina dasyatis*	*Haemogregarina delagei*

Copepod

Acanthochondrites annulatus	*Echthrogaleus coleoptratus*	*Kroyeria carchariaeglauca*	*Nemesis lamna lamna*	*Pandarus satyrus*
Acespadia pomposa	*Echthrogaleus denticulatus*	*Kroyeria deetsi*	*Nemesis macrocephalus*	*Pandarus sinuatus*
Achtheinus oblongus	*Echthrogaleus disciarai*	*Kroyeria dispar*	*Nemesis pallida*	*Pandarus smithii*
Alebion carchariae	*Eudactylina aspera*	*Kroyeria elongata*	*Nemesis robusta*	*Perissopus dentatus*

Alebion crassus	*Eudactylina breviabdomina*	*Kroyeria lineata*	*Nemesis vermi*	*Pharodes tortugensis*
Alebion echinatus	*Eudactylina carchariaeglauci*	*Kroyeria papillipes*	*Nessipus borealis*	*Phyllothyreus cornutus*
Alebion elegans	*Eudactylina longispina*	*Kroyeria spatulata*	*Nesippus crypturus*	*Prosaetes rhinodontis*
Alebion lobatus	*Eudactylina minuta*	*Kroyeria sphyrnae*	*Nesippus orientalis*	*Pseudocharopinus bicaudatus*
Anthosoma crassum	*Eudactylina pusilla*	*Kroyerina deetsorum*	*Nesippus tigris*	*Pseudocharopinus malleus*
Caligus coryphaenae	*Eudactylina spinula*	*Lepeophtheirus longispinosus*	*Nogagus borealis*	*Pupulina*
Caligus elongatus	*Eudactylina squamosa*	*Lepeophtheirus thompsoni*	*Otobothrium curtum*	*Siphonostomatoida sp.*
Caligus mutabilis	*Eudactylina valei*	*Lernaeopoda bidiscalis*	*Ommatokoita elongata*	*Tripaphylus musteli*
Caligus praetextus	*Eudactylinodes niger*	*Lernaeopoda galei*	*Paeon ferox*	*Trebius exilis*
Charopinus dubius	*Euryphorus brachypterus*	*Lernaeopodina longimana*	*Pandarus sp.*	
Conchoderma virgatum	*Euryphorus suarezi*	*Lernaeopodina relata*	*Pandarus bicolor*	
Dalbergia latifolia	*Gangliopus pyriformis*	*Luetkenia asterodermi*	*Pandarus carcharhini*	
Dimemoura latifolia	*Irodes gracilis*	*Nemesis atlantica*	*Pandarus cranchii*	

Dinemoura producta	*Kroyeria sp.*	*Nemesis carchariaeglauci*	*Pandarus floridanus*
Dysgamus limbatus	*Kroyeria caseyi*	*Nemesis lamna*	*Pandarus katoi*

Dinoflagellate

Amyloodinium ocellatum

Flatworm

Micropharynx sp.	*Paraorygmatobothrium arnoldi*

Fungus

Exophiala pisciphila	*Fusarium solani*	*Paecilomyces lilacinus*

Isopod

Conchoderma auritum	*Gnathiidae sp.*	*Gnathia piscivora*	*Natatolana borealis*	*Pandarus rhincodonicus*

Monogenean

Amphibdella flavolineata	*Decacotyle floridana*	*Empruthotrema raiae*	*Heterocotyle sp.*	*Loimos scitulus*
Amphibdella torpedinis	*Decacotyle octona*	*Erpocotyle antarctica*	*Heterocotyle aetobatis*	*Loimos scoliodoni*
Amphibdelloides	*Dendromonocotyle*	*Erpocotyle*	*Heterocotyle*	*Loimosina*

maccallumi	*octodiscus*	*carcharhini*	*americana*	*parawilsoni*
Amphibdalloides narcine	*Dermophthirius carcharhini*	*Erpocotyle catenulata*	*Heterocotyle minima*	*Merizocotyle concinna*
Benedeniella macrocolpa	*Dermophthirius maccallumi*	*Erpocotyle ginglymostomae*	*Heterocotyle pastinacae*	*Merizocotyle longicirrus*
Benedeniella posterocolpa	*Dermophthirius nigrelli*	*Erpocotyle laevis*	*Heterocotyloides prici*	*Merizocotyle pseudodasybatis*
Calicotyle stossichi	*Dermophthirius penneri*	*Erpocotyle maccallumi*	*Hexabothriinae*	*Merizocotyle retorta*
Capsalid monopisthocotylean	*Dermophthirius pristidis*	*Erpocotyle macrohystera*	*Hexabothrium incertae sedis musteli*	*Merizocotyle roumillati*
Clemacotyle australis	*Dionchus postoncomiracidia*	*Erpocotyle microstoma*	*Listrocephalos corona*	*Monocotyle diademalis*
Dasyoncocotyle spiniphallus	*Dionchus remorae*	*Erpocotyle sphyrnae*	*Loimopapillosum dasyatis*	*Monocotyle pricei*
Decacotyle elpora	*Empruthotrema kearni*	*Erpocotyle tiburonis*	*Loimopapillosum diadema*	*Multicalyx cristata*

Monogenean	**continued**	
Multicalyx multicristatus	*Neodermophthirius harkemai*	*Neoheterocotyle inpristi*

Mycotic Infection		
Bronchitis	Dermatitis	Hepatitis

Myxosporean

Ceratomyxa lubati	*Ceratomyxa mesospora*	*Chloromyxum sphyrnae*
Ceratomyxa lunata	*Chloromyxum leydigi*	*Kudoa sp.*

Nematode

Anisakis sp.	*Granulinema carcharhini*	*Mexiconema cichlasomae*	*Pseudanisakis tricupola*	*Terranova ginglymostomae*
Anisakis pegreffii	*Granulinema simile*	*Parascarophis sphyrnae*	*Pseudoterranova*	*Terranova rochalimai*
Anisakis simplex	*Huffmanela carcharhini*	*Philometridae*	*Pulchrascaris*	
Contracaecum	*Huffmanela markgracei*	*Phlyctainophora lamnae*	*Pulchrascaris chiloscyllii*	
Contracaecum plagiostomorum	*Hysterothylacium hospitum*	*Phylcytainophora squali*	*Terranova brevicapitata*	
Echinocephalus	*Lockenloia sanguinis*	*Proleptus obtusus*	*Terranova galeocerdonis*	

Protist

Haemogregarina	*Paronatrema vaginicola*	*Trichodina rajae*	*Trypanosoma sp.*	*Uronema marinum*

Trematode

Amphibelloides narcine	*Hyperandrotrema cetorhini*	*Nagmia larga*	*Paronatrema mantae*	*Selachohemecus sp.*

Anaporrhutum albidum	*Multicalyx cristata*	*Otodistomum cestoides*	*Paronatrema vaginicola*	*Selachohemecus benzi*
Bermophthirius nigrelli	*Myliobaticola richardheardi*	*Otodistomum pristiophori*	*Ptychogonimus megastomum*	*Staphylorchis pacificus*
Bothriocephalus squali glauci	*Nagmia floridensis*	*Otodistomum veliporum*	*Sanguinicola sp.*	*Stichocotyle nephropis*

Vertebrate

Echeneis naucrates	*Petromyzontiform*	*Simenchelys parasitica*

Virus

Herpes

Carcharhiniformes - Bacteria

Flavobacterium sp.

Mycobacterium fortuitum

Mycobacterium marinum

Streptococcus

Vibrio sp.

Vibrio anguillarium

Vibrio charchariae

Vibrio cholarae

Vibrio parahaemolyticus

Orectolobiformes - Bacteria

Kordia sp.
Salmonella enterica

Rhinopristiformes - Bacteria

Mycobacterium chelonae

Carcharhiniformes - Cestodes

Acanthobothrium sp.	*Diesingium lomentaceum*
Acanthobothrium mathiasi	*Dinobothrium keilini*
Acanthobothrium triacis	*Dinobothrium septaria*
Anthobothrium sp.	*Discocephalum linton*
Anthobothrium auriculatum	*Disculiceps pileatus*
Anthobothrium cornucopia	*Echinobothrium sp.*

Anthobothrium laciniatum

Anthobothrium minutum

Anthobothrium spinosum

Bombycirhynchus sphyraeniaicum

Calliobothrium lintoni

Calliobothrium nodosum

Calliobothrium nodosum

Callitetrarhynchus gracilis

Cathetocephalus sp.

Cathetocephalus australis

Cathetocephalus thatcheri

Clistobothrium carcharodoni

Crossobothrium dohrnii

Dasyrhynchus giganteus

Dasyrhynchus giganteus

Dasyrhynchus giganteus

Dasyrynchus pacificus

Dasyrhynchus talismani

Dasyrynchus variouncinatus

Dicranobothrium spinulifera

Eutetrarhynchus ruficollis

Floriceps saccatus

Hepatoxylon trichiuri

Heteronybelinia eureia

Heteronybelinia estigmena

Heteronybelinia heteromorphi

Heteronybelinia nipponica

Heteronyebelinia robusta

Heteronybelinia yamagutii

Lacistorhynchus tenuis

Mixonybelinia edwinlintoni

Molicola horridus

Nybelinia africana

Nybelinia estigmena

Nybelinia goreensis

Nybelinia indica

Nybelinia lingualis

Nybelinia sphyrnae

Orygmatobothrium musteli

Otobothrium australe

Otobothrium cysticum

Otobothrium insigne

Otobothrium minutum

Otobothrium mugilis

Otobothrium penetrans

Paragrillotia similis

Paraorygmatobothrium arnoldi

Paraorygmatobothrium prionacis

Paraorygmatobothrium roberti

Pedibothrium hutsoni

Pedibothrium longispine

Pelichnibothrium speciosum

Phoreiobothrium sp.

Phoreiobothrium exceptum

Phoreiobothrium lasium

Phoreiobothrium manirei

Phoreiobothrium tiburonis

Phyllobothrium sp.

Phyllobothrium dagnalium

Phyllobothrium dasybati

Platybothrium baeri

Platybothrium cervinum

Platybothrium coshtaprum

Platybothrium hypoprioni

Platybothrium parvum

Platybothrium spinulifera

Platybothrium tantatulum

Poecilancistrium caryophyllum

Prochristianella sp.

Prochristianella tumidula

Proemotobothrium southwelli

Progillotia dollfus

Prosobothrium adherens

Prosobothrium armigerum

Pseudogrillota perelica

Pseudogilquina microbothria

Pterobothrium acanthotruncatum

Pterobothrium filicolle

Pterobothrium heteracanthum

Spiniloculus mavensis

Phyllobothrium lactuca	*Symcallio violae*
Phyllobothrium minutum	*Tentacularia coryphaenae*
Phyllobothrium pammicrum	*Tetrarhynchobothrium striatum*
Phyllobothrium tumidum	*Thysanocephalum thysanocephalum*
Pintneriella gymnorhynchoides	*Triloculatum geeceearelensis*
Platybothrium angelbahiense	*Triloculatum triloculatum*
Platybothrium auriculatum	*Trypanorhyncha sp.*
Platybothrium baeri	

Orectolobiformes - Cestodes
Dollfusiella lineata
Grillotia similis
Monorygma galeocerdonis
Pedibothrium brevispine
Pedibothrium globicephalum
Pedibothrium hutsoni
Pedibothrium longispine
Phyllobothrium microsomum
Prochristianella tenuispine
Pseudolacistorhynchus noodti

Lamniformes - Cestodes

Ceratobothrium xanthocephalum	*Hepatoxylon trichiuri*
Cetorhinicola acanthocapax	*Molicola horridus*
Clistobothrium montaukensis	*Nybelinia lingualis*
Cylindrophorus typicus	*Nybelinia pinteri*
Dinobothrium paciferum	*Nybelinia schmidti*
Dinobothrium septaria	*Phyllobothrium lactuca*
Gastrolecithus planus	*Phyllobothrium tumidum*
Gymnorhynchus gigas	*Platybothrium parvum*
Gymnorhynchus isuri	*Pterobothrium heteracanthum*
Hepatoxylon megacephalum	*Tentacularia coryphaenae*

Myliobatiformes - Cestodes

Acanthobothrium aetiobatidis	*Kotorella pronosoma*
Acanthobothrium americanum	*Lecanicephalum peltatum*
Acanthobothrium arlenae	*Myzophyllobothrium rubrum*
Acanthobothrium brevissime	*Otobothrium pronosomum*

Acanthobothrium colombianum

Acanthobothrium crassicolle

Acanthobothrium dysbiotos

Acanthobothrium monksi

Acanthobothrium nicoyaense

Acanthobothrium paulum

Acanthobothrium tortum

Anthobothrium quadribothria

Anthocephalum alicae

Anthocephalum cairae

Calycobothrium typicum

Cephalobothrium aetobatidis

Didymorhynchus southwelli

Dollfusiella tenuispinis

Echeneibothrium minimum

Echinobothrium typus

Grillotia pastinacae

Halysioncum boisii

Hispidorhynchus australiensis

Hornellobothrium cobraformis

Parachristianella monomegacantha

Parachristianella trygonis

Polypocephalus sp.

Polypocephalus medusia

Prochristianella hispida

Pterobothrium filicolle

Pterobothrium heteracanthum

Pterobothrium kingstoni

Pterobothrium lintoni

Rhabdotobothrium dollfusi

Rhinebothrium flexile

Rhodobothrium sp.

Shirleyrhynchus aetobatidis

Thysanocephalum thysanocephalum

Trygonicola macropora

Tylocephalum aetiobatidis

Tylocephalum marsupium

Tylocephalum yorkei

Hexacanalis abruptus

Rajiformes - Cestodes

Acanthobothrium brevissime	*Echeneibothrium javanicum*
Acanthobothrium coronatum	*Echeneibothrium minimum*
Acanthobothrium electricolum	*Glyphobothrium zwerneri*
Acanthobothrium floridensis	*Grillotia erinaceus*
Acanthobothrium fogeli	*Halysioncum bonasum*
Acanthobothrium giganticum	*Halysioncum rhinoptera*
Acanthobothrium lentiginosum	*Lecanicephalum peltatum*
Acanthobothrium lineatum	*Mecistobothrium brevispine*
Acanthobothrium lintoni	*Metanisakis tricupola*
Acanthobothrium micracantha	*Nybelinia aequidentata*
Acanthobothrium paulum	*Otodistomum cestoides*
Acanthobothrium ulmeri	*Phyllobothrium dagnalium*
Acanthobothrium westi	*Pterobothrium lesteri*
Calyptrobothrium occidentale	*Pterobothrium southwelli*
Calyptrobothrium riggii	*Rhinoptericola megacantha*
Dioecotaenia sp.	*Trypanorhyncha sp.*
Dioecotaenia cancellata	*Tylocephalum bonasum*

Dioecotaenia campbelli	*Tylocephalum brooksi*
Duplicibothrium minutum	*Tylocephalum pingue*
Echeneibothrium cancellatum	

Rhinopristiformes - Cestodes

Acanthobothrium lentiginosum
Dermophthirioides pristidis
Lecanicephalum peltatum

Squatiniformes - Cestodes

Christianella sp.
Phyllobothrium unilaterale

Carcharhiniformes - Copepods

Alebion carchariae	*Gangliopus pyriformis*
Alebion crassus	*Irodes gracilis*
Alebion echinatus	*Kroyeria caseyi*
Alebion elegans	*Kroyeria carchariaeglauca*

Alebion lobatus

Anthosoma crassum

Caligus elongatus

Caligus praetextus

Dimemoura latifolia

Dinemoura producta

Dysgamus limbatus

Echthrogaleus coleoptratus

Echthrogaleus denticulatus

Eudactylina breviabdomina

Eudactylina carchariaeglauci

Eudactylina longispina

Eudactylina pusilla

Eudactylina valei

Eudactylinodes niger

Euryphorus brachypterus

Nemesis robusta

Nessipus borealis

Nesippus crypturus

Nesippus orientalis

Kroyeria deetsi

Kroyeria dispar

Kroyeria elongata

Kroyeria lineata

Kroyeria papillipes

Kroyeria spatulata

Kroyeria sphyrnae

Kroyerina deetsorum

Lepeophtheirus longispinosus

Lernaeopoda bidiscalis

Lernaeopoda galei

Luetkenia asterodermi

Nemesis carchariaeglauci

Nemesis lamna

Nemesis macrocephalus

Nemesis pallida

Pandarus cranchii

Pandarus floridanus

Pandarus satyrus

Pandarus sinuatus

Nesippus tigris	*Pandarus smithii*
Otobothrium curtum	*Perissopus dentatus*
Ommatokoita elongata	*Pharodes tortugensis*
Paeon ferox	*Phyllothyreus cornutus*
Pandarus bicolor	*Tripaphylus musteli*
Pandarus carcharhini	

Orectolobiformes - Copepods
Acespadia pomposa
Eudactylina aspera
Nemesis atlantica
Pandarus sp.
Prosaetes rhinodontis

Lamniformes - Copepods

Achtheinus oblongus	*Nesippus crypturus*
Anthosoma crassum	*Nesippus orientalis*

Caligus coryphaenae	*Nogagus borealis*
Conchoderma virgatum	*Pandarus bicolor*
Dalbergia latifolia	*Pandarus cranchii*
Dimemoura latifolia	*Pandarus floridanus*
Dinemoura producta	*Pandarus katoi*
Echthrogaleus coleoptratus	*Pandarus satyrus*
Echthrogaleus denticulatus	*Pandarus sinuatus*
Nemesis lamna	*Pandarus smithii*
Nemesis lamna lamna	*Phyllothyreus cornutus*
Nemesis vermi	

Myliobatiformes - Copepods
Eudactylina minuta
Euryphorus suarezi
Lepeophtheirus thompsoni
Nemesis robusta
Pseudocharopinus bicaudatus
Pseudocharopinus malleus

Rajiformes - Copepods

Acanthochondrites annulatus	*Trebius exilis*
Caligus elongatus	
Caligus mutabilis	
Charopinus dubius	
Echthrogaleus disciarai	
Eudactylina squamosa	
Kroyeria sp.	
Lernaeopodina longimana	
Lernaeopodina relata	
Pupulina sp.	
Siphonostomatoida sp.	

Squatiniformes - Copepod

Eudactylina spinula

Carcharhiniformes - Monogeneans

Calicotyle stossichi	*Erpocotyle macrohystera*
Dermophthirius carcharhini	*Erpocotyle microstoma*
Dermophthirius maccallumi	*Erpocotyle sphyrnae*
Dermophthirius nigrelli	*Erpocotyle tiburonis*
Dermophthirius penneri	*Heterocotyle sp.*
Dionchus postoncomiracidia	*Hexabothrium incertae sedis musteli*
Dionchus remorae	*Loimos scitulus*
Erpocotyle antarctica	*Loimos scoliodoni*
Erpocotyle carcharhini	*Loimosina parawilsoni*
Erpocotyle catenulata	*Multicalyx cristata*
Erpocotyle laevis	*Multicalyx multicristatus*
Erpocotyle maccallumi	*Neodermophthirius harkemai*

Orectolobiformes - Monogeneans

Erpocotyle ginglymostomae
Loimos scitulus

Myliobatiformes - Monogeneans

Clemacotyle australis	*Listrocephalos corona*
Dasyoncocotyle spiniphallus	*Loimopapillosum dasyatis*
Decacotyle elpora	*Loimopapillosum diadema*
Decacotyle floridana	*Merizocotyle concinna*
Decacotyle octona	*Merizocotyle longicirrus*
Dendromonocotyle octodiscus	*Merizocotyle pseudodasybatis*
Empruthotrema kearni	*Merizocotyle retorta*
Heterocotyle aetobatis	*Merizocotyle roumillati*
Heterocotyle americana	*Monocotyle diademalis*
Heterocotyle minima	*Monocotyle pricei*
Heterocotyle pastinacae	
Heterocotyloides prici	
Hexabothriinae sp.	

Rajiformes - Monogeneans

Amphibdella flavolineata
Amphibdella torpedinis

Amphibdelloides maccallumi
Amphibdalloides narcine
Benedeniella macrocolpa
Benedeniella posterocolpa
Capsalid monopisthocotylean
Empruthotrema raiae

Rhinopristiformes - Monogeneans

Dermophthirius pristidis
Neoheterocotyle inpristi

Carcharhiniformes - Nematodes

Anisakis sp.	*Parascarophis sphyrnae*
Anisakis pegreffii	*Philometridae sp.*
Anisakis simplex	*Phlyctainophora lamnae*
Contracaecum sp.	*Phylcytainophora squali*
Echinocephalus sp.	*Pseudoterranova sp.*
Granulinema carcharhini	*Pulchrascaris sp.*
Granulinema simile	*Pulchrascaris chiloscyllii*

Huffmanela carcharhini	*Terranova brevicapitata*
Huffmanela markgracei	*Terranova galeocerdonis*
Hysterothylacium hospitum	

Orectolobiformes - Nematodes
Lockenloia sanguinis
Mexiconema cichlasomae
Terranova galeocerdonis
Terranova ginglymostomae

Myliobatiformes - Nematode
Proleptus obtusus

Rajiformes - Nematode
Pseudanisakis tricupola

Rhinopristiformes - Nematode
Terranova rochalimai

Squatiniformes - Nematode

Anisakis sp.

Carcharhiniformes - Trematodes

Bothriocephalus squali glauci
Paronatrema vaginicola
Ptychogonimus megastomum
Selachohemecus benzi
Staphylorchis pacificus

Orectolobiformes - Trematodes

Nagmia larga
Otodistomum pristiophori
Paronatrema mantae
Selachohemecus sp.

Lamniformes - Trematodes

Hyperandrotrema cetorhini

Sanguinicola sp.

Myliobatiformes - Trematodes

Anaporrhutum albidum

Myliobaticola richardheardi

Nagmia floridensis

Nagmia larga

Rajiformes - Trematodes

Amphibelloides narcine

Multicalyx cristata

Nagmia larga

Otodistomum cestoides

Otodistomum veliporum

Paronatrema mantae

Stichocotyle nephropis