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# Trophic Ecology and Parasitism of a Mesopelagic Fish Assemblage

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Thesis of  
Matthew Woodstock

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University  
Halmos College of Natural Sciences and Oceanography

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Approved:  
Thesis Committee

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Woodstock Thesis

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Trophic Ecology and Parasitism of a Mesopelagic Fish Assemblage

By

Matthew S. Woodstock

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:

Marine Biology

Nova Southeastern University

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### **Abstract**

Mesopelagic (open ocean, 200-1000 m depth) fishes are important consumers of zooplankton and are prey of oceanic predators. Some mesopelagic fishes (e.g., myctophids and stomiids) undertake a diel vertical migration where they ascend to the near-surface waters during the night to feed and descend into the depths during the day to avoid predators. Other mesopelagic fishes (e.g., *Sternoptyx* spp.) do not vertically migrate and remain at deep depths throughout the day. While in the epipelagic zone (surface – 200 m depth), vertically migrating fishes become prey to upper-trophic level predators, such as: tunas and billfishes. Benthic fishes (e.g., macrourids) often vertically migrate as well, ascending into the pelagic zone to feed on pelagic organisms. Fishes of different depths and vertical migration habits likely have a different ecological role in food webs. The relationship between parasites and gut contents provides insights into ecological processes occurring within assemblages, as prey items are often vectors for parasites. This study examined the differences between the prey items present in the gastrointestinal cavity and parasites of 26 mesopelagic fish species in the Gulf of Mexico. Results showed that based on the proportionally dominant prey items per species, six different feeding guilds existed within this assemblage, five based on planktivory: copepodivores, predators of copepods and other zooplankton, predators of copepods and euphausiids, gelatinivores, generalists, crustacean decapodivores, and upper-trophic level predators. Larger fishes preyed on larger prey items and harbored more parasites. *Sigmops elongatus* exhibited an ontogenetic diet shift at 75 mm standard length, progressing from eating primarily copepods at small sizes to eating primarily euphausiids at large sizes. Compared to similar studies, this study revealed a higher parasitic infestation by trematodes, an endoparasite (parasite within the host) class often restricted to nearshore hosts, in Gulf of Mexico fishes. *Helicometrina nimia*, the dominant parasite of the gempylid *Nealotus tripes*, has not previously been recorded in hosts below 200 m depth, suggesting a foodweb pathway that transitions from nearshore to offshore. These data can be used to develop and refine models aimed at understanding ecosystem structure and connectivity.

**Keywords:** Ecosystem connectivity, mesopelagic fishes, parasitology, trophic ecology

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## 1. Introduction

### 1.1. Mesopelagic fishes

The ichthyofauna of the mesopelagic zone serve as important trophic mediators between the zooplankton and higher trophic levels. Many mesopelagic (200 – 1000 m depth) fishes are diel vertical migrators, living at mesopelagic depths during the daytime to avoid predators and ascending into the epipelagic zone (0 – 200 m) to feed during the night (Angel 1989; Lampert 1989, Herring 2001). It is estimated that one of the most biomass-dominant vertically migrating families, the lanternfishes (Actinopterygii: Myctophiformes: Myctophidae), accounts for the removal of one-third of the daily zooplankton production in the eastern Gulf of Mexico (hereafter referred to as GoM; Hopkins and Gartner 1992). Vertical migrators transport material such as parasites and organic matter between the epipelagic and mesopelagic zones (Houston and Haedrich 1986; Marcogliese 2002), blending the stratification that would normally exist between depth zones. Other mesopelagic fishes do not vertically migrate and remain at depth to feed. The non-migrating genus *Cyclothone* spp. (Actinopterygii: Stomiiformes: Gonostomatidae) dominates the biomass of the mesopelagic ichthyofauna (32.1% total fish biomass; Sutton et al. in prep). Regardless of diel-migration habits, many deep-pelagic fishes undergo an ontogenetic migration, in which larva begin life at the surface and settle deeper with growth (Sutton and Hopkins 1996a). Depth changes widen the depth range for prey groups and predators, adding to open-ocean food web connectivity.

### 1.2. Resource partitioning of fishes

Mesopelagic fishes account for a daily consumption of 2.5-4.3 kg C km<sup>-2</sup> in the upper 1000 m in the eastern GoM (Hopkins et al. 1996). Approximately 80% of this daily consumption is zooplankton, primarily copepods (Hopkins et al. 1996). Hopkins and Gartner (1992) suggest that for myctophids alone, 50 species ascend into the epipelagic waters each night to feed. Given both diet and spatial similarity, niche separation might seem unlikely. However, resource partitioning occurs even among size classes within species (Hopkins and Gartner 1992; Hopkins and Sutton 1998), but is only evident through discrete-depth sampling. Four zooplanktivorous sternoptychids (Actinopterygii:

Stomiiformes: Sternoptychidae), *Argyropelecus aculeatus* Valenciennes 1850, *Argyropelecus hemigymnus* Cocco 1829, *Sternoptyx diaphana* Hermann 1781, and *Sternoptyx pseudobscura* Baird 1971, also partition resources by having subtle diet differences and occupying different depths (Hopkins and Baird 1985). The diverse mesopelagic fishes of the GoM occupy a variety of feeding guilds, suggesting these fishes have evolved to minimize competition.

### 1.3. Parasites

Differences among daily ration and feeding guild are reflected in the parasite load of a fish species. Parasites are ubiquitous in the marine environment, from the surface to the seafloor, and can provide useful information about the life histories of fishes, such as diet diversity, migratory behaviors, and general trophic position (Klimpel et al. 2006; Busch et al. 2008). As depth increases, parasite diversity generally decreases until reaching the seafloor (Noble and Orias 1975; Marcogliese 2002; Klimpel et al. 2006). At the seafloor, parasite diversity increases because the diversity of potential hosts increases with more available niches (e.g., benthic prey; Marcogliese 2002; Klimpel et al. 2006). In addition to parasite diversity, parasite abundance within individual fish decreases with increasing depth (Zubchenko 1981). The incorporation of parasite analysis with other trophic analysis techniques (e.g., gut content analysis, stable isotope analysis) increases the robustness of food web models (Cone et al. 1993; Huxham et al. 1995, Lafferty et al. 2006). Analyses of the parasite fauna and prey found in hosts' guts have revealed relationships between specific parasite species and the host's prey taxa (Hoberg 1996; MacKenzie and Abaunza 1998). When a parasite has a specific geographic range, the presence of that parasite suggests that the host (or host's prey) was at one point within that range (MacKenzie and Abaunza 1998).

Factors associated with parasite distribution are likely related to intermediate host availability (Campbell et al. 1980), suggesting host community structure can have the greatest effect on parasite distribution and abundance (Conneely and McCarthy 1986). The surface waters contain myriad predators that prey upon phytoplankton, zooplankton, and nekton (fishes, shrimps, and pelagic mollusks). At mesopelagic depths, there are a variety

of zooplanktivores and micronektonivores, some of which feed on vertically migrating organisms. Historically, it was thought that bathypelagic organisms do not undergo diel vertical migration, but recent evidence has shown that this generalization may not be universally true (Cook et al. 2013). Diel vertical migration also occurs among demersal organisms as they migrate upwards to feed on holoplanktonic organisms (Klimpel et al. 2006). Hypothetically, a connection from the surface to the bottom could exist through multiple trophic pathways (Figure 1).

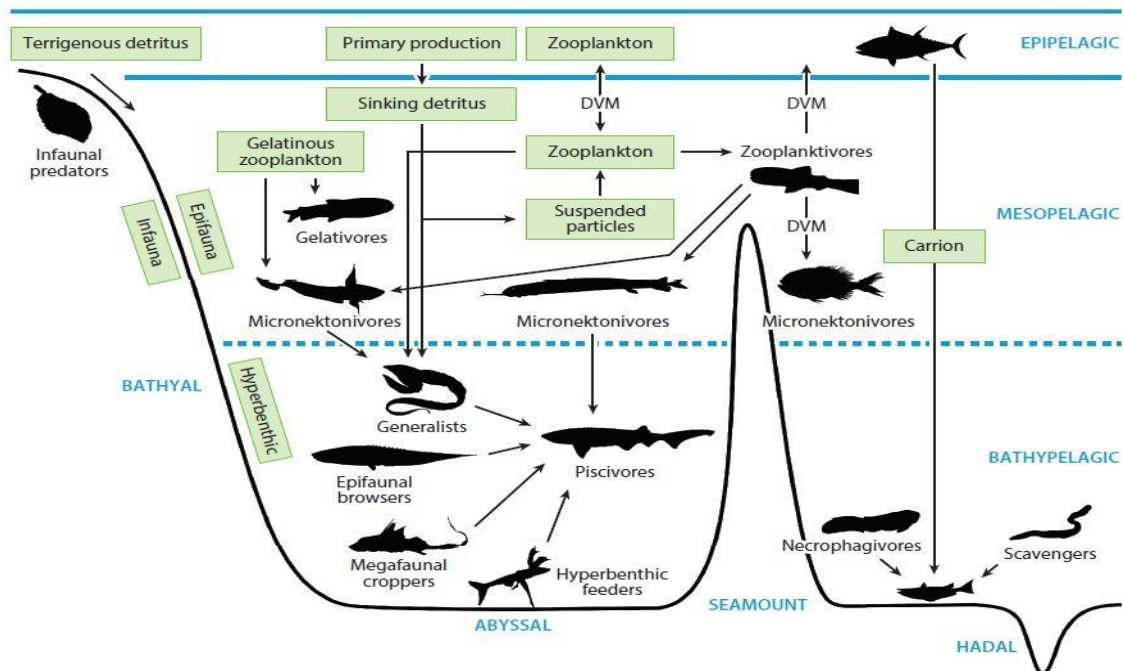


Figure 1. A representation of an oceanic food web depicting numerous trophic levels and feeding guilds (after Drazen and Sutton 2017, with permission of the author).

The feeding strategy of the host plays a significant role in determining the parasite load and diversity (Bush et al. 1997). High daily rations and a wide variety of prey items increases the quantity and diversity of parasites within a host (Marcogliese 2002). In contrast, a selective predator with a small daily ration will have a lesser parasite load. The zooplankton diversity of the pelagic is less diverse than the benthos (Marshall 1954), therefore the parasite fauna of the pelagic realm is expected to be less diverse. A higher parasite diversity reflected in deep-demersal predators is caused by a generalist feeding

strategy that incorporates a wider array of prey taxa (Sedberry and Musick 1978; Palm and Klimpel 2008).

In order to advance through the food web, parasites often progress through many taxon-specific stages and hosts before metamorphosing into an adult (Bush et al. 1997). Each parasite class uses a different taxon as a primary host and intermediate host before settling in their definitive host. For example, trematodes typically use a mollusk as primary host, an array of invertebrates as intermediate hosts, and a teleost as another intermediate or a definitive host (Bray et al. 1999; Klimpel et al. 2010). Many cestodes utilize a pelecypod mollusk as a primary host, molluscivorous gastropods as second hosts, and finish development in elasmobranchs (Cake Jr 1977). In pelagic fishes, larval cestodes are common and display low host specificity (Ñacari and Oliva 2016). Acanthocephalans, another group of parasitic worms, are typically connected to amphipods at an early life stage (Campbell et al. 1980). However, acanthocephalans do not appear to use other crustaceans as intermediate hosts (Gregori et al. 2012). *Anisakis* spp. conducts its larval stages in euphausiaceans and copepods before completing its life cycle in a fish (Campbell et al. 1980; Manooch et al. 1984; Busch et al. 2008). Regardless of parasite species, fishes are typically involved in the completion of the life history of aquatic parasites (Hendrix and Overstreet 1977). Some deep-pelagic parasites appear to take a generalist approach through the food web, suggesting it is much more likely that parasites of this realm have evolved to inhabit a taxon and not a specific species (Bray et al. 1999).

Endoparasites (parasites within the host) infect pelagic fishes through the consumption of a parasitized organism (Lester et al. 2001). Aquatic endoparasites directly and indirectly progress through the food web. Directly, endoparasites infect zooplankton after the ingestion of a free-living planktonic parasite larva or egg (Kennedy et al. 1992; Kjøie 1993). Indirect infections occur when a suitable potential host consumes a prey organism that has already been infected (Kennedy et al. 1992, Bush et al. 1997). Parasite accumulation throughout the host's lifetime is a function of the intake of parasites through ingestion and the removal of parasites through the host's immune system, suggesting older fishes that have eaten more prey items may have a greater parasite abundance.



*1.4. Food web connectivity*

Parasitism has historically been omitted from food web models, likely because parasites are difficult to quantify compared to free-living species (Lafferty et al. 2006). Food web models that include parasitism display a greater species richness, more food web links, and an overall more complex web (Hudson et al. 2006; Figure 2). Low-trophic level organisms have the least chance to be infected because of the larger abundance of zooplankton compared to the free-living, soon-to-be parasitic organisms in the water column. As the trophic-level of an organism increases, the ration increases (Petipa 1978), increasing the probability of consuming an infected organism. Therefore, upper-trophic level organisms (e.g., large predatory fishes) have greater opportunity to take in a larger abundance and diversity of parasites than lower-trophic level organisms (Lafferty et al. 2006).

## Deep-Pelagic Parasites

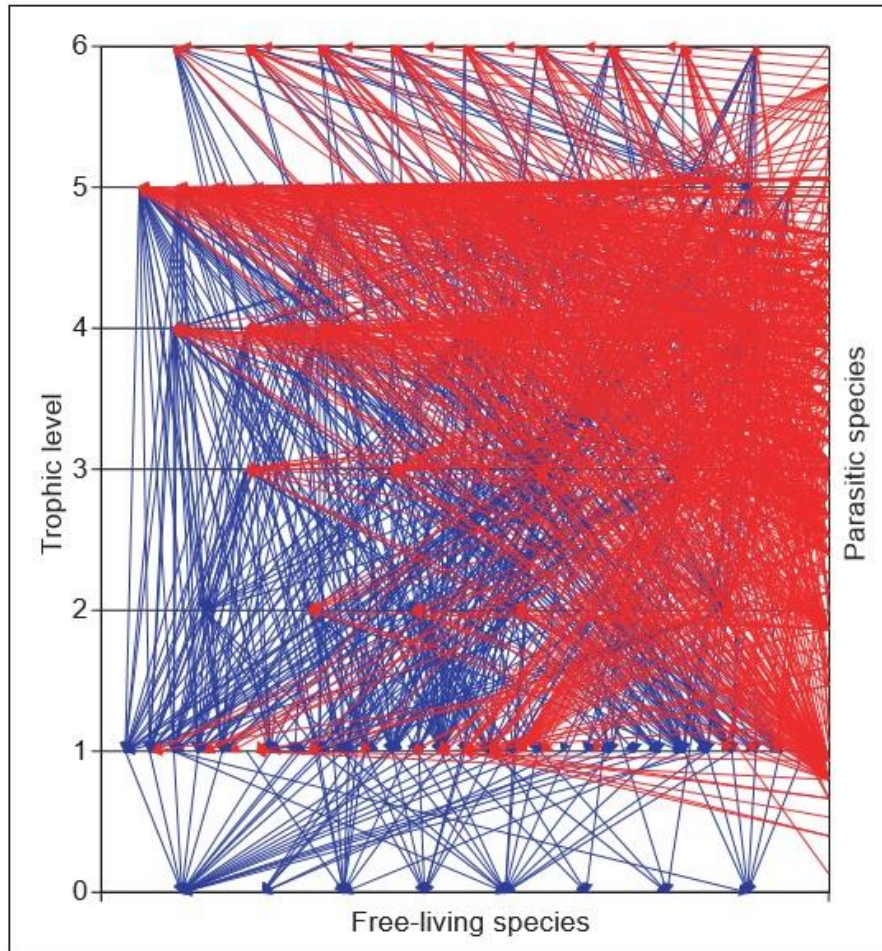


Figure 2. Parasite complexity as related to food webs, represented by the Carpinteria salt marsh in California, USA. Blue lines are trophic interactions between free-living species (blue nodes); red lines are the parasitic interactions between species. (after Hudson et al. 2006).

### 1.5. The ecosystem of the oceanic Gulf of Mexico

The oceanic GoM is a highly diverse system with species overlap among depth occupancy in the water column and diets. Niche overlap suggests a low number of unrealized niches exist in an ecosystem, and competition for resources is high (Hutchinson 1959). Tucker trawl surveys by Hopkins (1982) revealed that the upper 1000 m of the eastern GoM has 21 zooplankton genera with biomass greater than 1% of the total zooplankton biomass. The 794-fish species that have been found in midwater trawls since the 2010 *Deepwater Horizon* oil spill rank the GoM as one of the most diverse oceanic

ecosystems in the world (Sutton et al. 2017). The fish components of the deep-pelagic GoM are a composite of deepwater fishes found in the Caribbean and Sargasso Seas (Bangma and Haedrich 2008), suggesting the GoM is an important ecotone with influences from equatorial currents (Loop Current) and freshwater input (Mississippi River) that provide a suitable habitat for temperate, tropical, and subtropical fish species.

### *1.6. Oceanographic characteristics of the Gulf of Mexico*

The dynamics of plankton, and thus the geographic ranges of pelagic ecoregions, is dependent upon ocean currents (McManus and Woodson 2012). The biota of the deep-pelagic GoM are likely influenced by the Loop Current. The Loop Current is a warm-water current that enters the GoM from the south between Cuba and the Yucatan Peninsula, often meandering north towards Louisiana, and exits through the Florida Straits. Mesoscale eddies, circular oceanographic features with different temperature and salinity signatures than surrounding waters, are produced by the Loop Current, concentrating larval fishes and zooplankton near their boundaries (Bakun 2006). From the north, outflow from the Mississippi River enters the GoM, introducing nutrients and increasing phytoplankton production. Increased phytoplankton production enhances the biomass of zooplankton assemblages, and consequently provides nutrients to organisms at deep depths in the form of marine snow (Eppley and Peterson 1979). However, increased phytoplankton production at the surface can increase oxygen consumption rates, depleting oxygen levels at mesopelagic depths (Wyrki 1962). This depletion can affect growth, development, reproductive success, and migratory behaviors of organisms (Ekau et al. 2010). Fishes are more vulnerable to low oxygen levels than crustaceans and mollusks (Vaquer-Sunyer and Duarte 2008). The oceanographic features of the GoM make this region a unique and diverse ecological location for organisms of all trophic levels and depths.

## **2. Project Aims and Significance**

This study aims to be the most robust deep-pelagic parasite study for the GoM and one of the few deep-pelagic studies globally to combine diet and parasite analyses. This project focuses on the parasites and gut contents of mesopelagic fishes with the following objectives: (1) describe the parasite fauna that occupies mesopelagic fishes of the GoM;

(2) discriminate fishes into feeding guilds based on their preferential prey items; (3) examine the potential connection between diet and the parasite fauna among feeding guilds and among species; (4) determine whether ontogenetic changes in diet and parasites exist for species with a sufficient sample size; (5) model factors that drive parasite prevalence and abundance in deep-pelagic fishes; and (6) create a host-parasite interaction list for 26 host species and an updated list of deep-sea parasites recorded in the GoM. These data are important for the understanding of the connectivity of deep-pelagic ecosystems, which are the world's largest, yet least known ecosystems.

### **3. Methods**

#### *3.1. Study location and dates.*

Four cruises were conducted in the GoM (27° N to 29° N, 87.5° W to 91° W; Figure 3) aboard the NOAA FRV *Pisces* during four seasons between 2010-2011 as part of the NOAA-supported Offshore Nekton Sampling and Analysis Program (ONSAP): *Pisces* 8 (PC8), *Pisces* 9 (PC9), *Pisces* 10 (PC10), and *Pisces* 12 (PC12). Each *Pisces* survey lasted approximately three weeks. Seventeen stations were sampled repeatedly over the four cruises. Sampling stations were equidistant from each other at 30 nautical miles apart (55.6 km), most being seaward of the 1000-m isobath (Figure 4). Cruise dates, gear type, and the number of tows conducted on each cruise are displayed in Table 1. Fishes from PC8, PC10, and PC12 were used in this project.

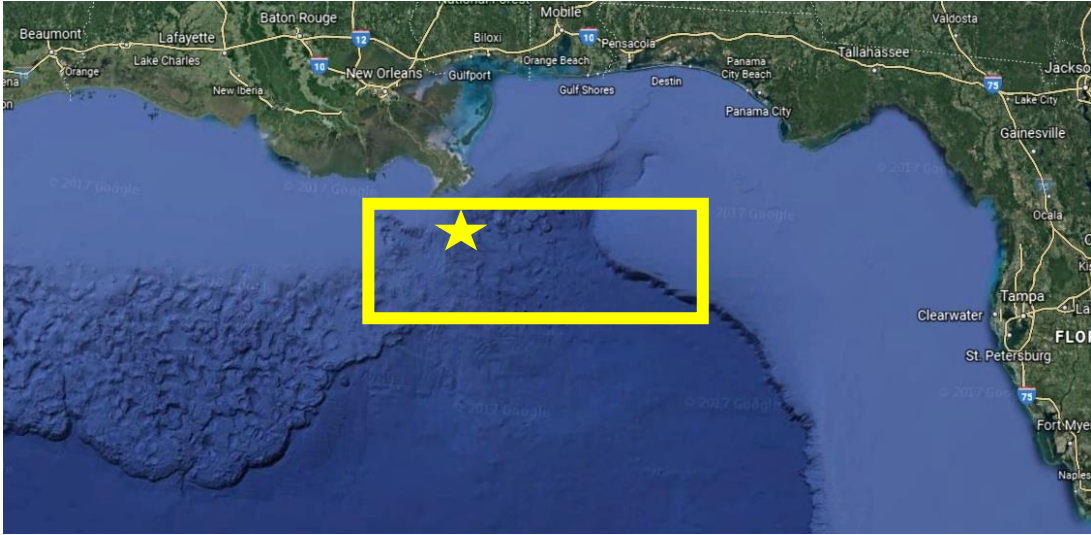


Figure 3. Sampling location (yellow box) for the FSV *Pisces* and R/V *Point Sur* cruises (2010-2017). The star indicates the approximate location of the 2010 *Deepwater Horizon* oil spill (Accessed from Google Earth on December 28, 2017).

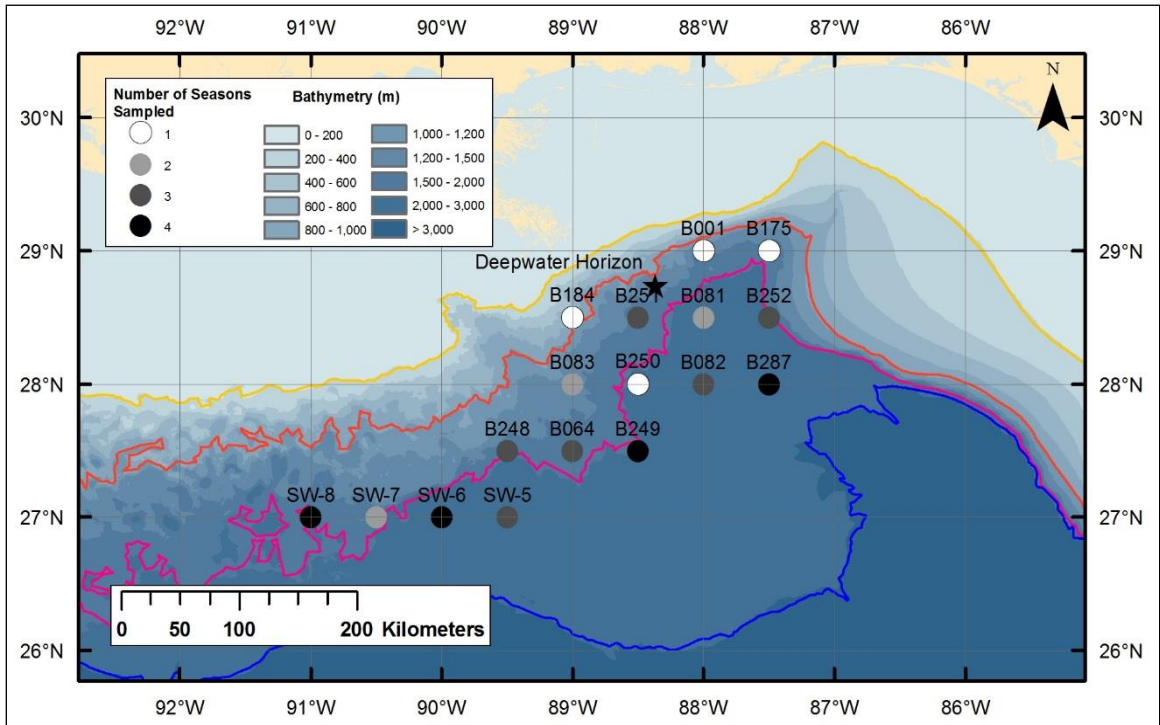


Figure 4. Stations sampled during ONSAP cruises aboard the FRV *Pisces*, conducted seasonally between December 2010 and September 2011. The darkest dots represent the most heavily sampled stations. The orange line represents the 1000-m isobath.

Table 1. Sample data for specimens used in this study. IHT = Irish Herring Trawl

<b>Cruise</b>	<b>Cruise Date</b>	<b>Gear Type</b>	<b>No. of Tows</b>	<b>No. of Fishes</b>
<i>Pisces</i> (PC8)	December 2010	IHT	37	12
<i>Pisces</i> (PC10)	June – July 2011	IHT	48	43
<i>Pisces</i> (PC12)	September 2011	IHT	50	8
<i>Point Sur</i> (DP03)	April - May 2016	MOCNESS	21	386
<i>Point Sur</i> (DP04)	August 2016	MOCNESS	26	188
<i>Point Sur</i> (DP05)	April – May 2017	MOCNESS	25	62

Five additional cruises were conducted on the R/V *Point Sur* biannually during May and August 2015-2017: DEEPEND (DP) 01, DP02, DP03, DP04, and DP05. Sample sites were chosen in the weeks prior to setting sail to match current oceanographic features (e.g., mesoscale eddies, Loop Current waters). Many of the stations sampled during *Pisces* cruises were also sampled during DEEPEND cruises. All of the *Point Sur*-caught fishes examined in this study came from DP03, DP04, and DP05 cruise stations seaward of the 1000-m isobath (Figure 5).

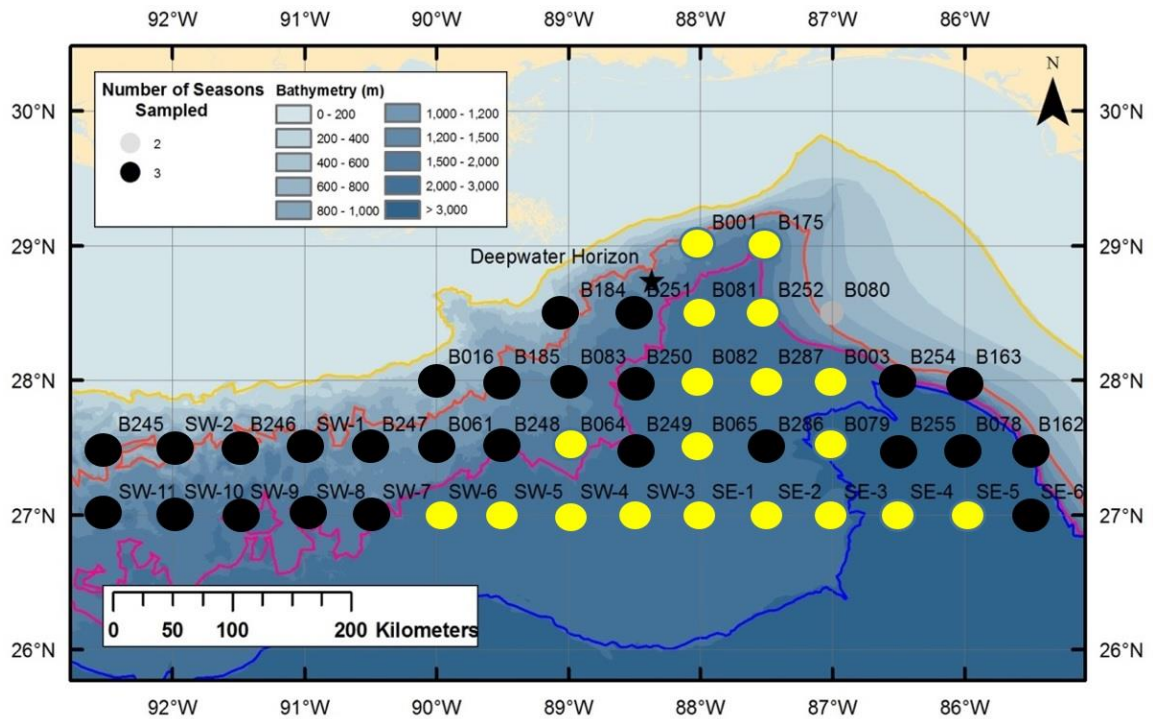


Figure 5. Stations sampled during DEEPEND cruises DP03, DP04 and DP05 in 2016 and 2017. Yellow dots are the sampled station locations.

### 3.2. Sample acquisition

On all *Pisces* cruises, a commercial-sized midwater trawl with an effective mouth area of 165.47 m<sup>2</sup> (Sutton and Mercier 2012) and a graded mesh size of 3.2 m at the mouth and 5 mm at the cod end was utilized. This large, non-closing net obliquely sampled the water column from the surface to depth and back to the surface. At each sampling station (Figure 4), four deployments were conducted; one shallow (0-600 m) during the day, one shallow during the night, one deep (0-1500 m) during the day, and one deep during the night. Sampling during *Point Sur* cruises used a 10-m<sup>2</sup> mouth area MOCNESS, or Multiple Opening and Closing Environmental Sampling System (Wiebe et al. 1985). Each net had a 3-mm uniform mesh size. The unit used six nets that opened and closed via an electronic signal from the ship for discrete-depth sampling. Upon deployment, the first net sampled

obliquely from the surface to max depth (typically 1500 m). For most tows, the succeeding nets fished at consistent depth bins as displayed in Figure 6. Discrete-depth sampling during both the day and night has previously provided results towards the vertical migration habit and daytime depth of fishes (McEachran and Fechhelm 1998, McEachran and Fechhelm 2010, and Sutton et al. 2017). After capture, fish identification was completed by T. Sutton at sea and samples were frozen at  $-20^{\circ}\text{C}$ .

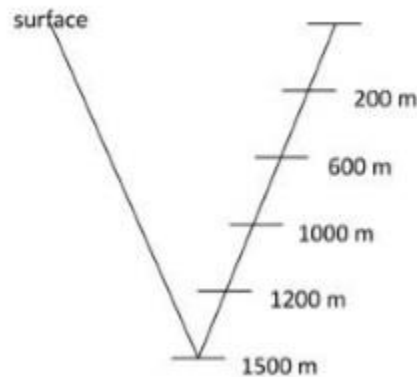


Figure 6. Discrete-depth sampling scheme used during MOCNESS sampling. Horizontal lines represent depths at which nets were switched.

### 3.3. Specimen processing

Specimens from DEEPEND cruises were the first to be analyzed and therefore, fishes from the *Pisces* cruises were selected based on known ecological information (i.e. assumed-diet and vertical migratory habit) that rendered them complementary to this project. The fishes came from 28 stations, sampled during both day and night (Table 2). Although sampling was conducted at each station during each stage of the solar cycle, fishes were selected non-randomly.



Table 2. Sample sizes of migrating and non-migrating fishes by station location

<b>Station ID</b>	<b>Non-Migrator</b>			<b>Vertical Migrator</b>			<b>Grand Total</b>
	Day	Night	Total	Day	Night	Total	
B001	-	-	-	-	3	3	3
B003	12	11	23	35	-	35	58
B064	-	-	-	11	8	19	19
B065	3	17	20	-	4	4	24
B079	17	10	27	19	22	41	68
B081	8	-	8	60	21	81	89
B082	-	-	-	3	1	4	4
B083	-	-	-	-	5	5	5
B163	4	-	4	-	-	-	4
B175	25	10	35	8	20	28	63
B242	-	2	2	-	-	-	2
B245	1	-	1	-	-	-	1
B247	-	4	4	-	-	-	4
B248	-	-	-	1	-	1	1
B249	-	-	-	7	12	19	19
B251	-	-	-	11	-	11	11
B252	18	15	33	68	39	107	140
B286	-	1	1	-	-	-	1
B287	-	3	3	8	4	12	15
SE 1	-	-	-	-	11	11	11
SE 2	-	-	-	-	3	3	3
SE 3	-	9	9	6	-	6	15
SE 4	17	34	51	5	5	10	61
SE 5	2	6	8	11	18	29	37
SW 3	-	-	-	-	11	11	11
SW 5	-	-	-	3	8	11	11
SW 6	-	-	-	4	-	4	4
SW 7	-	-	-	2	13	15	15
<b>Grand Total</b>	<b>107</b>	<b>122</b>	<b>229</b>	<b>257</b>	<b>204</b>	<b>470</b>	<b>699</b>

Prior to dissection, each individual specimen was thawed, a process that typically took ten minutes, but varied by species and size of the fish. For each individual fish, the standard length (SL, in mm), wet weight (g), and stomach weight (g) was measured. For all fishes, a first cut was made near the isthmus and continued posteriorly on the ventral

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surface beyond the anus (Figure 7). A second cut began at the isthmus and continued dorsally, separating the gastrointestinal tract from the body. A final cut was made anterior of the isthmus to free the gill rakers for removal. The stomach and intestine were opened separately, contents removed, and prey were identified to major taxon. Stomach and intestinal contents were treated separately in quantitative analyses. Upon opening, stomachs were given a fullness value from zero (completely empty) to five (completely full) and prey items were given a digestion value of one (newly eaten) to five (completely digested/unrecognizable). Post-identification, recognizable prey items were preserved in 70% ethanol, and stored for future reference. Any prey items that were not immediately recognizable (e.g., shrimp mandibles, crustacean pleopods) were preserved on a slide with an acid fuchsin/glycerol mixture to stain chitinous material.

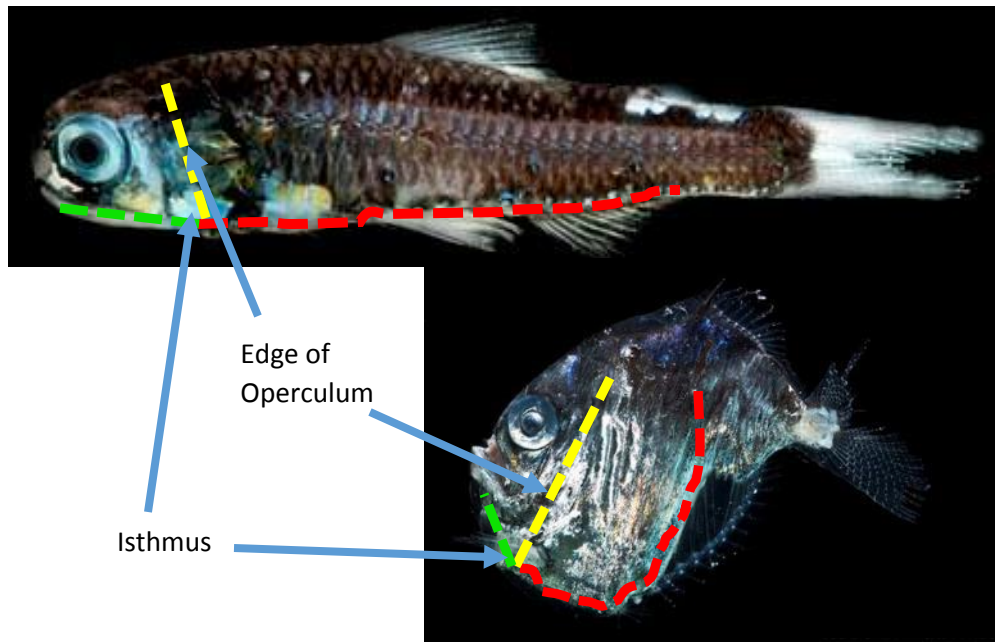


Figure 7. Examples of the cuts made during dissections in this study. The first cut (red dash) began at the isthmus and continued posteriorly past the anus. The second cut (yellow dash) cut dorsally up the edge of the operculum. The third cut (green dash) began at the isthmus and progressed anteriorly to free the gill rakers for removal.

In parallel with trophic analysis, parasitological examination was conducted. The exterior of the fish was washed with tap water to remove any ectoparasites that may be attached to scales. Fin rays were inspected for larval parasites, particularly trematode metacercaria (early larval stage). Organs of the alimentary tract were separated and examined under a stereomicroscope. Gill rakers and eyes were examined in the same fashion as the fin rays. Candling, the process of placing a specimen in between two glass plates and inspecting for parasites using an upwards-illuminating light source (Mackenzie and Abaunza 1998), was used to find endohelminths hidden within muscle tissue. Parasites were identified to the lowest taxonomic level possible and stored in 70% ethanol.

Staining and mounting techniques were used to identify parasites to lower taxonomic levels (Table 3). For platyhelminths and acanthocephalans, the sample was placed in a mixture of acetocarmine (~20 drops) and 70% ethanol for 20 minutes. The sample was then processed through a dehydrating ethanol series (70% to 99% in four steps) for approximately five minutes at each step. Note the purest ethanol available should be used for the 99% ethanol washes (Table 3: steps 4 and 5). Clove oil was used as a clearing agent to add transparency to unstained portions of the sample. The sample was kept in clove oil for approximately one minute before being transferred onto a slide and mounted using Permount. The staining process made internal organs visible for further identification (Figure 8). Trematodes were identified to genus using taxonomic keys of Gibson et al. (2002), Jones et al. (2005), and Bray et al. (2008). Cestodes were identified to genus using keys of Schmidt (1986) and Khalil et al. (1994). Acanthocephalans were identified using the key of Amin (1998).

Table 3. Staining, clearing and mounting procedure for parasites in the phyla Platyhelminthes and Acanthocephala

Step	Treatment	Time
1	Acetocarmine	20 min
2	70% EtOH	5 min
3	95% EtOH	5 min
4	99% EtOH	5 min
5	99% EtOH	5 min
6	Clove Oil	1 min
7	Permount	30 sec
8	Cover slip	30 sec
9	Set	2 days



Figure 8. The result of staining a digenean trematode showing the illumination of internal organs.

Nematodes were cleared using a different process (Table 4) than described in Table 3. Nematodes were placed in a 70:30 ethanol: glycerol mixture. The container was covered, but not sealed, to exclude external particles (e.g., dust and mold spores) and to allow the ethanol to evaporate. Nematodes were placed in this mixture until the ethanol fully evaporated and the organism had begun to absorb glycerol (approximately two weeks). The cleared nematodes were temporarily mounted in a glycerin jelly, a medium similar to the clearing agent, and examined using a stereomicroscope. Nematodes were identified to genus using keys of Anderson et al. (2009).

Table 4. Clearing and mounting procedure for parasites in the phylum Nematoda

<b>Step</b>	<b>Treatment</b>	<b>Time</b>
1	70:30 Ethanol: Glycerol	2 – 3 weeks
2	Glycerin jelly	Temporarily

### 3.4. Statistical analysis

All statistical analyses were performed using R Studio and Primer 7. Figures were created using Primer 7 and JMP 12. Test statistics were considered significantly different at  $p < 0.05$ . For all species that had a sample size greater than 40, a binomial regression for the proportion of small prey items (e.g., copepods, ostracods, pteropods) compared to large prey items (i.e. fishes, amphipods, and euphausiids) was conducted to determine if a diet shift from small prey to large prey occurred with fish growth. If a significant diet shift was found, fishes within that species were separated into size classes at the standard length the model revealed a shift occurred. The two size classes were treated as different operational taxonomic units for diet analyses. The sums of major prey taxa in the diets of each species were converted into proportions of the total prey items. A Bray-Curtis similarity matrix (Bray and Curtis 1957) was created to determine similarity among samples. A multivariate similarity profile (SIMPROF) analysis comparing the similarity of diets among all species was conducted to discriminate feeding guilds based on preferred prey taxa.

Binomial models were used to test for the differences in parasite prevalence (either zero for no parasites, or one for the presence of at least one parasite) among fishes due to biotic and abiotic factors, including: cruise number (temporal and spatial), station location (spatial), species, vertical migration habit, standard length, and feeding guild (a factor created by the results of the aforementioned SIMPROF analysis). Based on the multiple factors listed above, Kruskal-Wallis tests (cruise number, station location, species, and feeding guild), a Mann-Whitney Wilcoxon test (vertical migration), and a linear model (standard length) were conducted to determine differences in parasite abundance among the levels of each factor. When significant differences occurred among levels within a factor, post-hoc tests were conducted to determine which levels housed the highest parasite

abundances. Average digestion index values were compared to stage of the solar cycle (night or day) for each feeding guild (excluding gelatinivores) and tested with a Wilcoxon Rank Sums test.

Analyses of similarities (ANOSIMs) were used to compare the abundance of parasite taxa to the factors mentioned above using 9999 permutations and a Bray-Curtis distance matrix. The ANOSIM analysis tested for differences in the parasite communities among all levels of the response variable. If a level within a factor had zero parasites, it was removed prior to analysis.

#### 4. Results

A total of 699 specimens representing 26 mesopelagic fish species and eight families were analyzed in this study, the majority of which (n = 637) were collected on *Point Sur* cruises. Through dissections, 298 endoparasites and 366 ectoparasites were identified.

##### 4.1. Fish taxa examined and parasite prevalence.

The daytime depth, mean standard length, migration habit, and parasite prevalence were determined for all fish species. Parasite prevalence is presented for each fish family in Table 5. Four taxa (*Chauliodus sloani*, *Echiostoma barbatum*, *Lampadena luminosa*, and *Nannobranchium* spp.) included only one individual and thus do not have a range of lengths.

Most of the parasites found in this study were at an immature life stage and could not be given a species-level identification, but each parasite was identified to major taxon. Of the parasites identified, 55.1% were ectoparasitic copepods, 18.4% were trematodes, 13.6% were cestodes, 11.4% were nematodes, and 1.5% were acanthocephalans. Table 6 displays the number and percentage of parasite taxa recovered from host families, genera, species, and specimens. Trematodes were the most diverse taxon of parasite found in this study. Cestodes were less diverse and consisted primarily of *Tentacularia coryphaenae* and unidentified tetraphyllidean larvae. All but one nematode was from the family Anisakidae. Every acanthocephalan found in this study was from the genus *Floridosentis*.

A list of parasites found in this study organized by host species is presented in Table 7. A list of host-parasite interactions for all occurrences below 200 m in the GoM is presented in Appendix 1 and a global host-parasite interaction record for the fishes examined in this study is presented in Appendix 2

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Table 5. Fishes examined in this study. Daytime depths were reported from McEachran and Fechhelm (1998, 2010; Sutton et al. in prep). All fish lengths measured as standard length (SL, in mm). Mean standard lengths were rounded to the nearest mm. Y = Vertical Migrator, N = Non-Migrator. Note: recent taxonomic revisions preclude depth determinations for the genus *Nannobranchium* (*sensu* Zahuranec 2000); previous depth records were ascribed to the genus *Lampanyctus*)

Species	Migratory pattern	Daytime Depth (m)	Mean SL (range)	No. Parasitized /	Prevalence of Infection
<b>Bathylagidae</b>				<b>0 / 17</b>	<b>0.0%</b>
<i>Dolicholagus longirostris</i>	Y	600 - 1000	116 (69 – 148)	0 / 17	0.0%
<b>Gempylidae</b>				<b>12 / 14</b>	<b>85.7%</b>
<i>Nealotus tripes</i>	Y	100 - 600	148 (123 – 185)	12 / 14	85.7%
<b>Gonostomatidae</b>				<b>26 / 159</b>	<b>11.9%</b>
<i>Cyclothone obscura</i>	N	1200 - 1500	42 (22 – 53)	0 / 74	0.0%
<i>Cyclothone pallida</i>	N	0 - 1500	46 (40 – 51)	0/15	0.0%
<i>Sigmops elongatus</i>	Y	200 - 600	79 (26 – 195)	19 / 67	28.4%
<b>Melamphaidae</b>				<b>2 / 2</b>	<b>100%</b>
<i>Melamphaes simus</i>	Y	600 - 1000	26 (25 – 26)	2 / 2	100%
<b>Myctophidae</b>				<b>45 / 253</b>	<b>17.8%</b>
<i>Benthoosema suborbitale</i>	Y	200 - 600	24 (17 – 31)	4 / 23	17.4%
<i>Ceratoscopelus warmingii</i>	Y	600 - 1000	28 (21 – 42)	3 / 13	23.1%
<i>Diaphus dumerilii</i>	Y	200 - 600	39 (21 – 58)	3 / 9	33.3%
<i>Diaphus lucidus</i>	Y	200 - 600	75 (57 – 98)	6 / 6	100%



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<i>Diaphus mollis</i>	Y	200 - 600	41 (32 – 51)	4 / 4	100%
<i>Lampadena luminosa</i>	Y	600 - 1000	57	0/1	0.0%
<i>Lampanyctus alatus</i>	Y	600 - 1000	32 (18 – 55)	12 / 145	8.3%
<i>Lepidophanes guentheri</i>	Y	600 - 1000	39 (15 – 60)	10 / 47	21.3%
<i>Myctophum affine</i>	Y	600 - 1000	41 (35 – 46)	2 / 2	100%
<i>Nannobranchium</i> spp.	Y	-	128	0/1	0.0%
<i>Notoscopelus resplendens</i>	Y	600 - 1000	29 (28 – 30)	1 / 2	50.0%
<b>Scombrolabracidae</b>				<b>30 / 31</b>	<b>96.8%</b>
<i>Scombrolabrax heterolepis</i>	Y	560 - 1340	118 (76 – 214)	30 / 31	96.8%
<b>Sternoptychidae</b>				<b>33 / 210</b>	<b>15.7%</b>
<i>Argyropelecus aculeatus</i>	Y	200 - 600	21 (8 – 45)	4 / 30	13.3%
<i>Argyropelecus hemigymnus</i>	N	200 - 600	17 (8 – 31)	3 / 45	6.67%
<i>Sternoptyx diaphana</i>	N	600 - 1000	20 (9 – 46)	9 / 62	14.5%
<i>Sternoptyx pseudobscura</i>	N	600 - 1000	27 (13 – 47)	17 / 35	48.6%
<i>Valenciennellus tripunctulatus</i>	Y	200 - 600	26 (19 – 30)	0 / 38	0.0%
<b>Stomiidae</b>				<b>2 / 16</b>	<b>12.5%</b>
<i>Chauliodus sloani</i>	Y	200 - 600	147	0/1	0%
<i>Echiostoma barbatum</i>	Y	1000 +	208	1 / 1	100%
<i>Photostomias guernei</i>	Y	600 - 1000	72 (37 – 114)	1 / 14	7.1%
<b>Totals</b>				<b>141 / 699</b>	<b>20.2%</b>

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Table 6. Major parasite taxa and higher orders of classification associated with the taxonomic grouping of hosts. The numbers in parentheses represent the number of each taxonomic grouping examined

	Family (8)		Genera (21)		Species (26)		Specimen (699)	
	No	%	No	%	No	%	No	%
<b>Nematoda</b>	<b>6</b>	<b>75.0</b>	<b>12</b>	<b>57.1</b>	<b>14</b>	<b>53.8</b>	<b>30</b>	<b>4.3</b>
Anisakidae indet.	4	50.0	9	28.6	10	30.8	14	2.0
<i>Anisakis</i> spp.	2	25.0	2	9.5	5	19.2	7	1.0
<i>Contracaecum</i> spp.	2	25.0	2	9.5	2	7.7	2	0.3
<i>Procamallanus</i> spp.	1	12.5	1	4.8	1	3.8	1	0.1
Spirurida	1	12.5	1	4.8	1	3.8	1	0.1
<b>Cestoda</b>	<b>5</b>	<b>62.5</b>	<b>10</b>	<b>47.6</b>	<b>11</b>	<b>42.3</b>	<b>42</b>	<b>6.0</b>
Lecanicephalidae indet.	1	12.5	1	4.8	1	3.8	1	0.1
Tetraphyllidea indet.	4	50.0	5	23.8	6	23.1	15	2.1
<i>Tentacularia coryphaenae</i>	5	62.5	7	33.3	8	30.8	23	3.3
<i>Nybelinia</i> spp.	1	12.5	1	4.8	1	3.8	1	0.1
<i>Paranybelinia otophriodes</i>	1	12.5	1	4.8	1	3.8	1	0.1
<i>Hepatoxylon trichiuri</i>	1	12.5	1	4.8	1	3.8	1	0.1
<b>Trematoda</b>	<b>5</b>	<b>62.5</b>	<b>11</b>	<b>52.4</b>	<b>13</b>	<b>50.0</b>	<b>68</b>	<b>9.7</b>
<i>Proisorhyncus</i> spp.	1	12.5	1	4.8	1	3.8	1	0.1
Didimyzoidae juv. Type 1	1	12.5	1	4.8	1	3.8	3	0.4
Didimyzoidae juv. Type 2	1	12.5	1	4.8	1	3.8	1	0.1
Hemiuridae indet.	3	37.5	3	14.3	3	11.5	6	0.9
<i>Dissosaccus laevis</i>	2	25.0	2	9.5	2	7.7	3	0.4
<i>Lecithochirum</i> spp.	1	12.5	1	4.8	1	3.8	1	0.1
<i>Hirudinella</i> spp.	1	12.5	1	4.8	1	3.8	1	0.1
Lepocreadiidae juv.	1	12.5	1	4.8	1	3.8	1	0.1
Opecoelidae indet.	1	12.5	1	4.8	1	3.8	2	0.3
<i>Helicometra</i> spp.	2	25.0	2	9.5	2	7.7	5	0.7
<i>Helicometrina nimia</i>	2	25.0	2	9.5	2	7.7	9	1.3
Digenea indet.	5	62.5	9	42.9	12	46.2	36	5.1
<b>Acanthocephalan</b>	<b>4</b>	<b>50.0</b>	<b>7</b>	<b>33.3</b>	<b>7</b>	<b>26.9</b>	<b>8</b>	<b>1.1</b>
<i>Floridosentis</i> spp.	4	50.0	7	33.3	7	26.9	8	1.1
<b>Copepoda</b>	<b>3</b>	<b>37.5</b>	<b>3</b>	<b>14.3</b>	<b>6</b>	<b>23.1</b>	<b>36</b>	<b>5.2</b>
<i>Caligus</i> spp.	1	12.5	1	4.8	1	3.8	29	4.1
<i>Sarcotretes scopeli</i>	2	25.0	2	9.5	4	15.4	6	0.9

Table 7. The host-parasite interactions discovered among the fishes in this study. A global host-parasite interaction list for these species is presented in Appendix 2

<b><i>Argyrolepecus aculeatus</i></b>	Opecoelidae	<i>Paranybelinia</i>
Anisakidae	<i>Helicometrina nimia</i>	<i>otobothriodes</i>
<i>Contracaecum</i> spp.	Digenea indet.	Tetraphyllidea indet.
Cestoda indet.	<b><i>Myctophum affine</i></b>	<i>Tentacularia coryphaenae</i>
Hemiuridae	<i>Floridosentis</i> spp.	<i>Helicometra</i> spp.
Digenea indet.	<b><i>Nealotus tripes</i></b>	Digenea indet.
<i>Floridosentis</i> spp.	Anisakidae	<i>Sarcotretes scopeli</i>
<b><i>Argyrolepecus hemigymnus</i></b>	Tetraphyllidea indet.	<b><i>Sternoptyx pseudobscura</i></b>
Nematoda indet.	<i>Tentacularia coryphaenae</i>	Nematoda indet.
Digenea indet.	Trypanorhyncha indet.	Tetraphyllidea indet.
<b><i>Benthosema suborbitale</i></b>	<i>Helicometrina nimia</i>	<i>Tentacularia coryphaenae</i>
Tetraphyllidea indet.	Digenea indet.	<i>Prosorhyncus</i> spp.
Digenea indet.	<b><i>Notoscopelus resplendens</i></b>	Didimyzoidae Type 1
<i>Floridosentis</i> spp.	<i>Floridosentis</i> spp.	Didimyzoidae Type 2
<b><i>Ceratoscopelus warmingii</i></b>	<b><i>Photostomias guernei</i></b>	Digenea indet.
Cestoda indet.	<i>Contracaecum</i> spp.	Hemiuridae
Digenea indet.	<b><i>Scombrobrax heterolepis</i></b>	<i>Lecithochirum</i> spp.
<b><i>Diaphus dumerilii</i></b>	Nematoda indet.	<i>Hirudinella</i> spp.
Anisakidae	Tetraphyllidea indet.	Lepocreadiidae
Spirurida indet.	<i>Tentacularia coryphaenae</i>	<i>Floridosentis</i> spp.
<i>Sarcotretes scopeli</i>	<i>Dissosaccus laevis</i>	<i>Sarcotretes scopeli</i>
<b><i>Diaphus lucidus</i></b>	Hemiuridae	
<i>Anisakis</i> spp.	Opecoelidae	
Tetraphyllidea indet.	Digenea indet.	
<i>Tentacularia coryphaenae</i>	<i>Floridosentis</i> spp.	
Digenea indet.	<i>Caligus</i> spp.	
<b><i>Diaphus mollis</i></b>	<i>Hepatoxylon trichiuri</i>	
<i>Helicometra</i> spp.	<b><i>Sigmops elongatus</i></b>	
<b><i>Echiostoma barbatum</i></b>	<i>Procamallanus</i> spp.	
<i>Anisakis</i> spp.	Nematoda indet.	
<b><i>Lampanyctus alatus</i></b>	<i>Tentacularia coryphaenae</i>	
<i>Tentacularia coryphaenae</i>	<i>Nybelinia</i> spp.	
<i>Dissosaccus laevis</i>	Digenea indet.	
Digenea indet.	<i>Floridosentis</i> spp.	
<b><i>Lepidophanes guentheri</i></b>	<i>Sarcotretes scopeli</i>	
Anisakidae	<b><i>Sternoptyx diaphana</i></b>	
<i>Tentacularia coryphaenae</i>	Lecanicephalidae	

#### 4.2. Fish feeding ecology

Most of the fish specimens in this study had at least one prey item in their stomach (77%; Table 8). Of specimens with empty stomachs ( $n = 161$ ), 74 were of the genus *Cyclothone*. Of the 89 *Cyclothone* examined in this study, 15 specimens (16.9%) contained the remnants of at least one prey item, and only seven fishes had two prey items. Other than *Cyclothone*, *Dolicholagus longirostris* is the only fish that had an average stomach fullness index value lower than one. However, despite a low average stomach fullness value, 12 *D. longirostris* intestines (71%) contained prey remains. Four of the 14 *Photostomias guernei* specimens (29%) had prey items, and only one fish contained two prey items. With the few exceptions, most of the species examined in this study rarely had empty stomachs.

In the 699 fish specimens examined in this study, 2405 total prey items were found (mean = 3.59 prey items fish<sup>-1</sup>; Table 9). Fifty-eight prey items (2.4%) could not be identified and were classified as “unidentified.” Unidentified prey items were predominately chitinous material that have no distinguishing features. Identified prey items were apportioned into major taxonomic groups, such as: amphipod, copepod, decapod, euphausiid, fish, gelatinous zooplankton, mysid, ostracod, polychaete, pteropod, and squid.

*Sternoptyx pseudobscura* consumed the greatest proportion of amphipods (34.1%) in their diet. Many fishes consumed a large proportion of copepods, but *Valenciennellus tripunctulatus* consumed the largest (90%). Fishes comprised greater than 45% of the diets of *Scombrolabrax heterolepis* and *Nealotus tripes*. *Dolicholagus longirostris* was the only species that had multiple occurrences of gelatinous zooplankton prey. *Argyropelecus aculeatus* and *Sternoptyx diaphana* were the only species that had a diet of greater than 25% ostracod prey. *Argyropelecus aculeatus* was also the only species whose diet contained greater than 20% pteropod prey (31.6%).

Table 8. Summary statistics of fish feeding including the percentage of occupied stomachs, average stomach fullness rating and average number of prey items per species. Positive = specimens with at least one prey item

Species	No. Empty Stomachs	No. Fishes	Percent Positive	Average Stomach Fullness Index	Prey Items Per Fish
<i>Argyropelecus aculeatus</i>	3	30	90	2.73	5.10
<i>Argyropelecus hemigymnus</i>	5	45	89	1.66	1.82
<i>Benthoosema suborbitale</i>	1	23	96	2.30	3.91
<i>Ceratoscopelus warmingii</i>	0	13	100	2.31	2.46
<i>Chauliodus sloani</i>	0	1	100	4.00	2.00
<i>Cyclothone obscura</i>	61	74	18	0.38	0.19
<i>Cyclothone pallida</i>	13	15	13	0.73	0.13
<i>Diaphus dumerilii</i>	0	9	100	3.67	8.33
<i>Diaphus lucidus</i>	0	6	100	3.67	3.50
<i>Diaphus mollis</i>	0	4	100	3.25	4.25
<i>Dolicholagus longirostris</i>	5	17	71	0.71	0.71
<i>Echiostoma barbatum</i>	0	1	100	1.00	3.00
<i>Lampadena luminosa</i>	0	1	100	5.00	7.00
<i>Lampanyctus alatus</i>	23	145	84	2.08	2.12
<i>Lepidophanes guentheri</i>	3	47	94	2.79	3.49
<i>Melamphaes simus</i>	0	2	100	3.50	1.50
<i>Myctophum affine</i>	0	2	100	2.50	4.00
<i>Nannobranchium</i> spp.	0	1	100	5.00	3.00
<i>Nealotus tripes</i>	5	14	64	1.71	1.64
<i>Notoscopelus resplendens</i>	0	2	100	3.50	7.50
<i>Photostomias guernei</i>	10	14	29	1.07	0.36
<i>Scombrolabrax heterolepis</i>	8	31	74	1.97	1.48
<i>Sigmops elongatus</i>	12	67	82	1.85	1.46
<i>Sternoptyx diaphana</i>	3	62	95	3.24	9.06
<i>Sternoptyx pseudobscura</i>	2	35	94	3.46	14.11
<i>Valenciennellus tripunctulatus</i>	7	38	82	2.59	2.84

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Table 9. The sums of prey items per fish species. Prey items are abbreviated as follows: Amp = amphipod, Cop = copepod, Dec = decapod, Eup = euphausiid, Gel = gelatinous zooplankton, Mys = mysid, Ost = ostracod, Poly = polychaete, Pte = pteropod, Squi = squid, Sto = stomatopod and Unk = unknown. (“-“ = not found in diet)

Species	n	Amp	Cop	Dec	Eup	Fish	Gel	Mys	Ost	Poly	Pte	Squi	Sto	Unk	T
<i>Argyropelecus aculeatus</i>	30	6	42	-	6	3	-	-	46	1	49	-	-	2	155
<i>Argyropelecus hemigymnus</i>	45	-	69	-	2	-	-	-	10	-	1	-	-	2	84
<i>Benthoosema suborbitale</i>	23	1	78	-	5	4	-	-	2	-	-	-	-	2	92
<i>Ceratoscopelus warmingii</i>	13	3	21	-	1	-	-	-	1	-	6	-	-	1	33
<i>Chauliodus sloani</i>	1	1	-	-	-	1	-	-	-	-	-	-	-	-	2
<i>Cyclothone obscura</i>	74	-	12	-	1	-	-	-	1	-	-	-	-	5	19
<i>Cyclothone pallida</i>	15	-	-	-	2	-	-	-	-	-	-	-	-	1	3
<i>Diaphus dumerilii</i>	9	7	50	1	3	1	-	-	5	-	7	-	1	2	77
<i>Diaphus lucidus</i>	6	-	7	4	7	3	-	-	-	-	-	-	-	-	21
<i>Diaphus mollis</i>	4	-	10	-	1	-	-	-	4	1	1	-	-	1	18
<i>Dolicholagus longirostris</i>	17	-	1	-	-	-	11	-	-	-	-	-	-	-	12
<i>Echiostoma barbatum</i>	1	-	-	1	-	2	-	-	-	-	-	-	-	-	3
<i>Sigmops elongatus</i>	67	4	59	4	20	5	-	-	5	-	1	-	-	-	98
<i>Lampadena luminosa</i>	1	1	5	-	1	-	-	-	-	-	-	-	-	-	7
<i>Lampanyctus alatus</i>	145	4	258	-	28	2	1	-	12	-	2	-	1	7	315
<i>Lepidophanes guentheri</i>	47	4	130	-	13	-	-	-	12	-	5	-	-	6	170
<i>Melamphaes simus</i>	2	-	2	-	-	1	-	-	-	-	-	-	-	-	3
<i>Myctophum affine</i>	2	-	7	-	1	-	-	-	-	-	-	-	-	-	8
<i>Nannobrachium</i> spp.	1	1	-	-	1	1	-	-	-	-	-	-	-	-	3
<i>Nealotus tripes</i>	14	1	1	4	-	11	-	2	-	-	-	4	-	-	23
<i>Notoscopelus resplendens</i>	2	-	13	-	-	1	-	-	1	-	-	-	-	-	15
<i>Photostomias guernei</i>	14	-	1	4	-	-	-	-	-	-	-	-	-	-	5
<i>Scombrobrax heterolepis</i>	31	-	1	6	-	31	-	1	-	-	-	5	2	-	46
<i>Sternoptyx diaphana</i>	62	82	201	-	70	38	-	4	164	2	1	-	-	21	583
<i>Sternoptyx pseudobscura</i>	35	170	158	10	83	38	1	9	10	12	-	2	1	4	498
<i>Valenciennellus tripunctulatus</i>	38	3	101	-	3	-	-	-	1	-	-	-	-	4	112

A binomial analysis for the proportion of large prey and small prey detected a significant diet shift for *Sigmops elongatus* from copepods, ostracods, and pteropods to euphausiids, fish, and decapods at 75 mm SL ( $p < 0.001$ , Figure 9). Multivariate diet analyses showed that *S. elongatus* could be split into two operational units, one less than 75 mm SL, and one greater than or equal to 75 mm. This prey shift was not detected for *Sternoptyx diaphana* ( $p = 0.724$ ) and *Lampanyctus alatus* ( $p = 0.483$ ; Figure 10), and these species comprised single operational units.

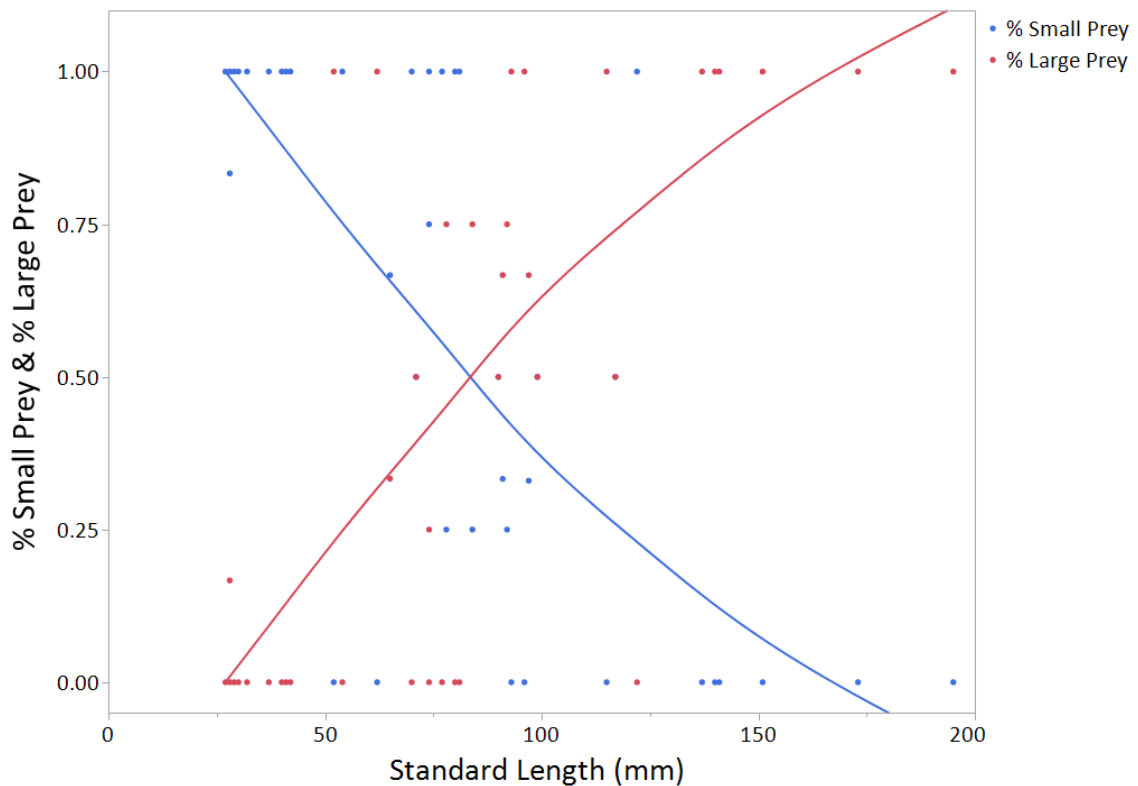


Figure 9. The proportion of large and small prey items per fish for *Sigmops elongatus*.

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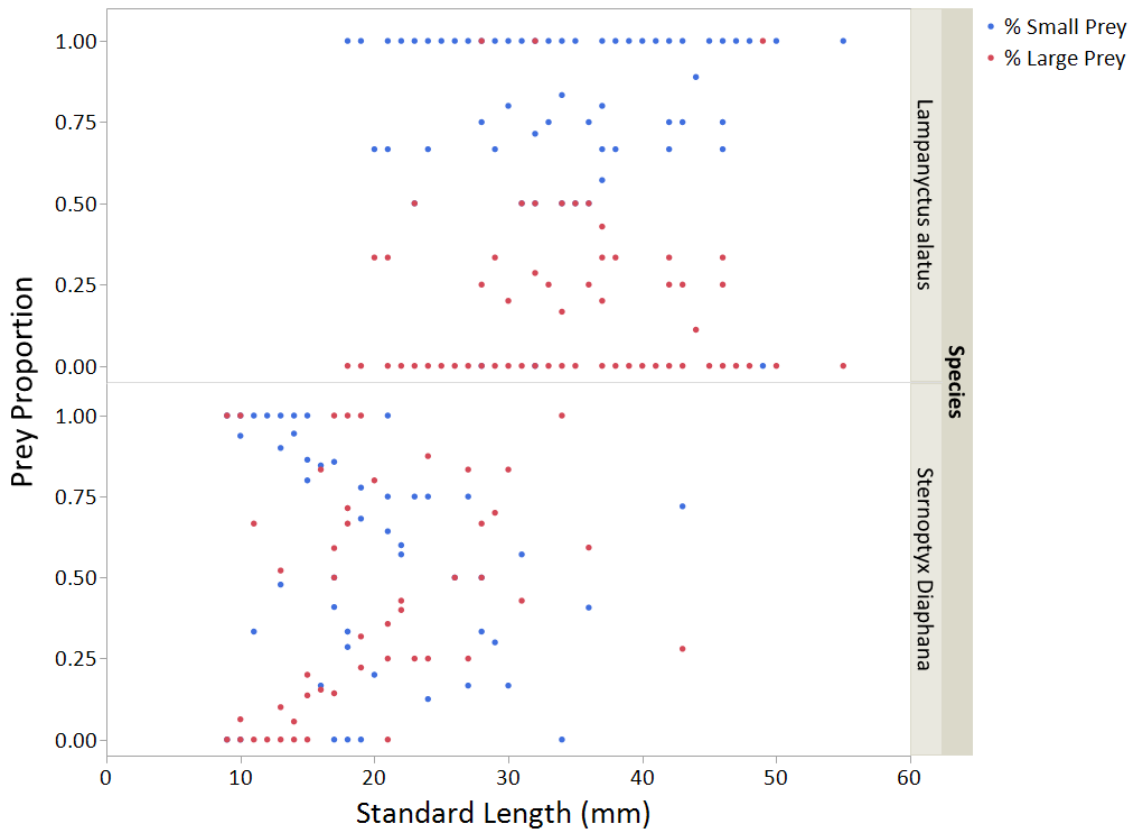


Figure 10. The proportion of large and small prey items in individual fishes for *Lampanyctus alatus* and *Sternoptyx diaphana*.

A multivariate similarity profile analysis (SIMPROF) determined six significantly differentiable feeding guilds within the assemblage of fish species examined. Of these, five guilds were centered on planktivory. An upper-trophic level feeding guild consisted of the gempylid, *Nealotus tripes*, and the scombrilacrid, *Scombrobrax heterolepis*. A gelatinivore feeding guild, consisting of the bathylagid *Dolicholagus longirostris*, was the most dissimilar to all other guilds (95% dissimilarity). Planktivory focused on shrimp and copepod feeding was exhibited by *Diaphus lucidus*, *Photostomias guernei*, and large (>75 mm SL) *Sigmops elongatus*. A feeding guild focused on the consumption of copepods and various other zooplankton comprised two myctophids, *Ceratoscopelus warmingii* and *Diaphus dumerilii*. Another feeding guild centered on the consumption of calanoid copepods included: *Argyropelecus hemigymnus*, *Benthoosema suborbitale*, *Cyclothone obscura*, *Lampanyctus alatus*, *Lepidophanes guentheri*, *Sigmops elongatus* less than 75 mm SL, and *Valenciennellus tripunctulatus*. A final feeding guild focused on generalist



feeding was exhibited by three sternoptychids, *Argyropelecus aculeatus*, *Sternoptyx diaphana*, and *Sternoptyx pseudobscura*. A cluster diagram (Figure 11) and a non-metric dimensional scaling ordination (nMDS; Figure 12) emphasize the dissimilarity among feeding guilds and the species within guilds. A stress value of 0.08 indicated that the nMDS plot was able to effectively discriminate feeding guilds in multidimensional space.

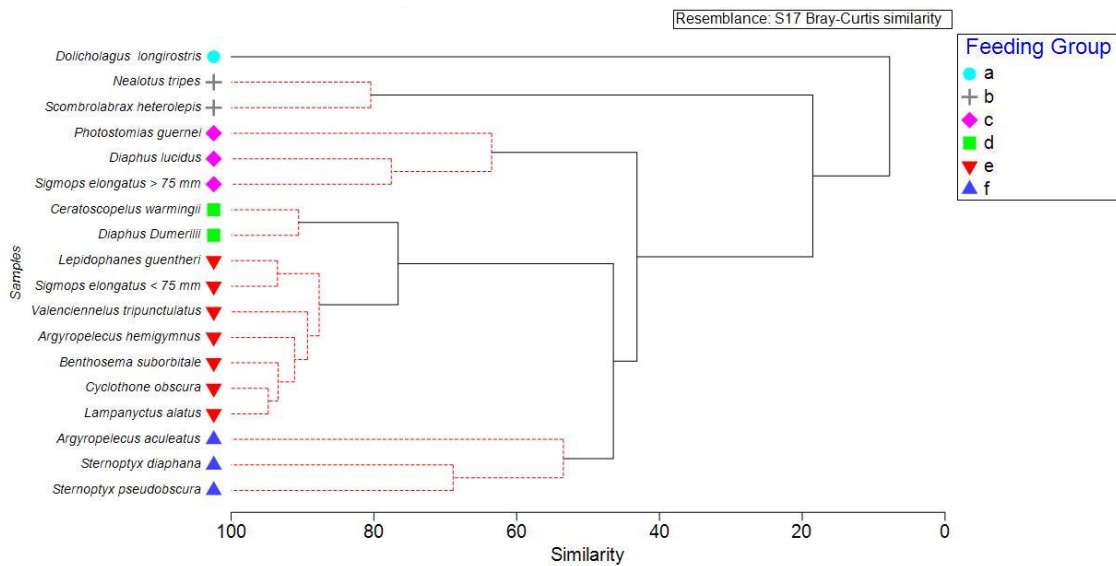


Figure 11. Classification of feeding guilds among the fishes in this study. Feeding guilds are represented by unique symbols.

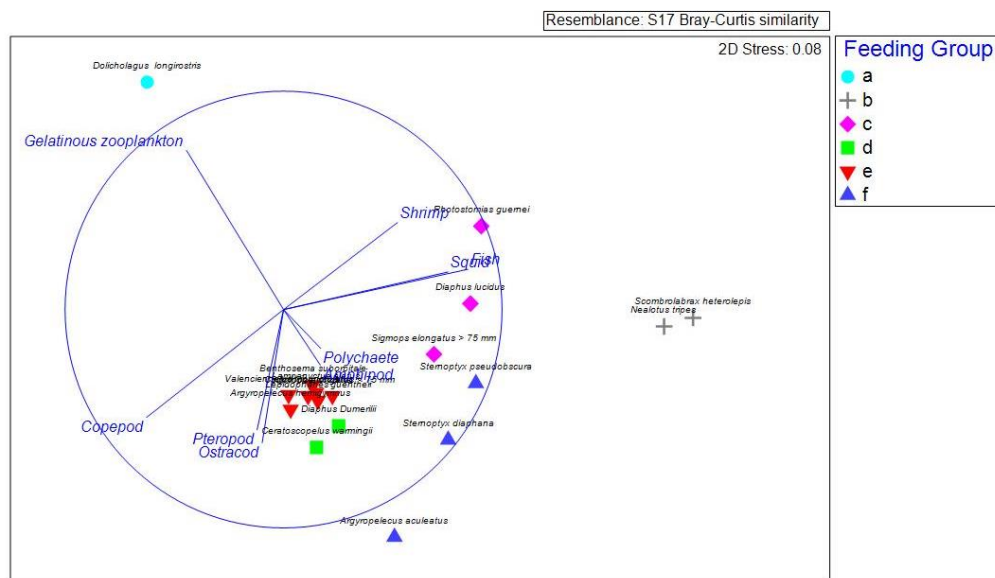


Figure 12. Ordination (nMDS) of feeding guilds discriminated by cluster analysis. Feeding guild symbols are as in Figure 11. Vector lines represent the prey factor with the greatest effect on feeding guild dissimilarity.

#### 4.3. *Factors affecting endoparasitism*

Six biotic and abiotic variables, including cruise, feeding guild, sample location, species, standard length, and vertical migration behavior, were analyzed to determine their effect on parasite prevalence, parasite abundance, and parasite similarity.

##### 4.3.1. Parasite prevalence and abundance as a function of diet

A binomial model (presence/absence), with the prevalence value of parasites as the response variable and counts of prey items per each prey category as dependent variables, revealed the prey taxa that increase the probability of a fish having at least one parasite. Predators of fishes and squids exhibited a significantly higher parasite prevalence ( $p < 0.001$  each; Table 10). Predators of shrimp were marginally higher in parasite prevalence ( $p = 0.056$ ). Predators of other major zooplankton groups did not exhibit significant relationships with respect to parasite prevalence ( $p > 0.3$ ). Based on the feeding guilds created by diet clustering, an ANOVA of parasite abundance revealed that the feeding guild of a fish was also significantly related to the abundance of parasites within fishes ( $p < 0.001$ ; Figure 13). Fishes that consumed larger (upper-trophic level) prey items were more often parasitized and the number of parasites that infect these fishes increased as well.

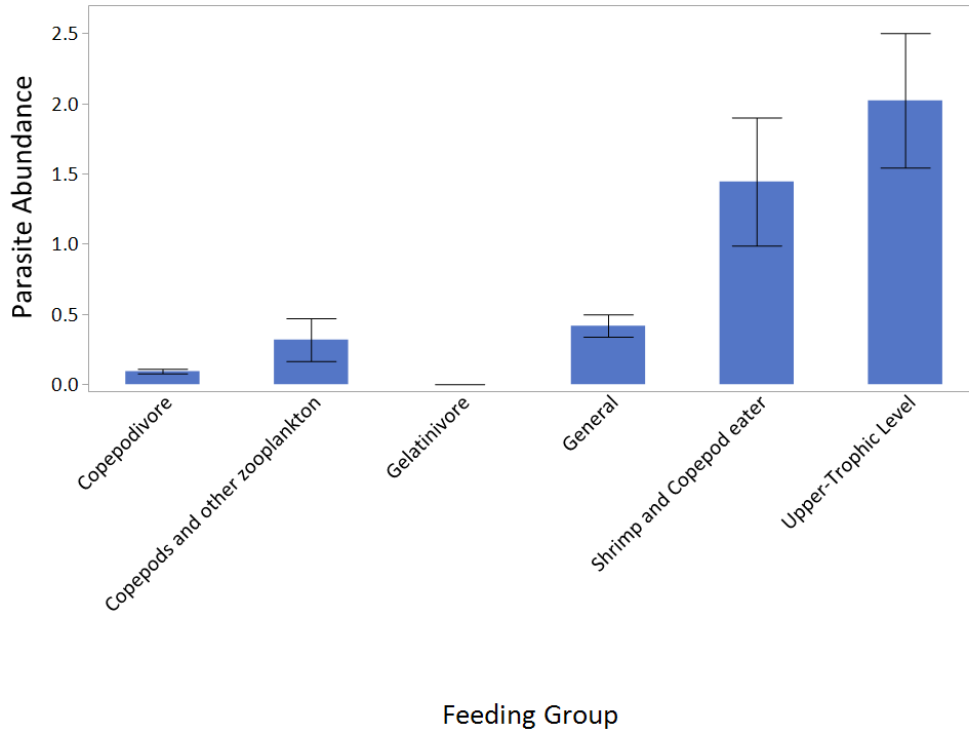


Figure 13. Mean parasite abundance (number per fish) relative to feeding guilds of mesopelagic fishes. The mean abundance is the top of the bar and whiskers represent standard error for each guild

Table 10. Binomial model results for parasite prevalence relative to prey taxon of mesopelagic fishes

<b>Prey Taxon</b>	<b>Estimate</b>	<b><i>p</i> - value</b>
Amphipod	-0.017	0.534
Copepod	-0.019	0.312
Fish	0.048	<0.001***
Gelatinous Zooplankton	-0.324	0.410
Ostracod	-0.039	0.268
Polychaete	-0.440	0.143
Pteropod	-0.028	0.715
Shrimp	0.073	0.056
Squid	1.312	<0.001***

A binomial model for parasite prevalence by fish species revealed that some host species exhibited a higher degree of parasitism than others (Table 11). Positive effect values from this model corresponded to a species having more parasitized individuals, while negative

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effect values corresponded to fewer. *Diaphus dumerilii* ( $p = 0.017$ ), *D. lucidus* ( $p < 0.001$ ), *Diaphus mollis* ( $p < 0.001$ ), *Echiostoma barbatum* ( $p = 0.017$ ), *Myctophum affine* ( $p < 0.001$ ), *Nealotus tripes* ( $p < 0.001$ ), *Scombrobrax heterolepis* ( $p < 0.001$ ), and *Sternoptyx pseudobscura* ( $p < 0.001$ ) exhibited a significantly greater likelihood of having at least one parasite per individual than other fishes. *Cyclothone obscura* ( $p = 0.026$ ), *Dolicholagus longirostris* ( $p = 0.046$ ), and *Lampanyctus alatus* ( $p = 0.04$ ) exhibited a significantly lesser likelihood of having parasitized individuals than other fishes.

Table 11. Binomial model results for parasite prevalence by host species displaying the likelihood of particular fish species having a parasite

Species	Effect	Std. Error	Z-value	p-value
<i>Argyropelecus aculeatus</i>	-0.12	0.09	-0.32	0.092
<i>Argyropelecus hemigymnus</i>	-0.13	0.08	-1.72	0.087
<i>Benthoosema suborbitale</i>	-0.03	0.09	-0.29	0.775
<i>Ceratoscopelus warmingii</i>	0.03	0.11	0.28	0.779
<i>Chauliodus sloani</i>	-0.2	0.34	-0.58	0.551
<i>Cyclothone obscura</i>	-0.16	0.07	-2.24	0.026**
<i>Cyclothone pallida</i>	-0.2	0.1	-1.92	0.055
<i>Diaphus dumerilii</i>	0.8	0.34	2.39	0.017**
<i>Diaphus lucidus</i>	0.8	0.15	5.43	<0.001***
<i>Diaphus mollis</i>	0.8	0.18	4.56	<0.001***
<i>Dolicholagus longirostris</i>	-0.2	0.1	-2.00	0.046*
<i>Echiostoma barbatum</i>	0.8	0.34	2.39	0.017**
<i>Lampadena luminosa</i>	-0.2	0.34	-0.58	0.551
<i>Lampanyctus alatus</i>	-0.13	0.07	-1.98	0.048*
<i>Lepidophanes guentheri</i>	0.012	0.08	0.17	0.868
<i>Melamphaes simus</i>	-0.2	0.24	-0.83	0.406
<i>Myctophum affine</i>	0.8	0.24	3.32	<0.001***
<i>Nannobranchium</i> spp.	-0.2	0.33	-0.6	0.551
<i>Nealotus tripes</i>	0.66	0.11	6.16	<0.001***
<i>Notoscopelus resplendens</i>	0.3	0.24	1.25	0.213
<i>Photostomias guernei</i>	-0.13	0.11	-1.21	0.229
<i>Scombrobrax heterolepis</i>	0.77	0.08	9.1	<0.001***
<i>Sigmops elongatus</i>	0.11	0.07	1.58	0.118
<i>Sternoptyx diaphana</i>	-0.02	0.07	-0.31	0.758
<i>Sternoptyx pseudobscura</i>	0.29	0.08	3.48	<0.001***
<i>Valenciennellus tripunctulatus</i>	-0.15	0.08	-1.83	0.068

When all species were considered, the standard length of fishes was significantly related to the likelihood of parasitism ( $p < 0.001$ ; Figure 14). This pattern was exhibited by the three numerically dominant fish species in this study, *L. alatus*, *S. diaphana*, and *S. elongatus* ( $p < 0.001$ ,  $p = 0.03$ , and  $p = 0.002$  respectively, Figure 15).

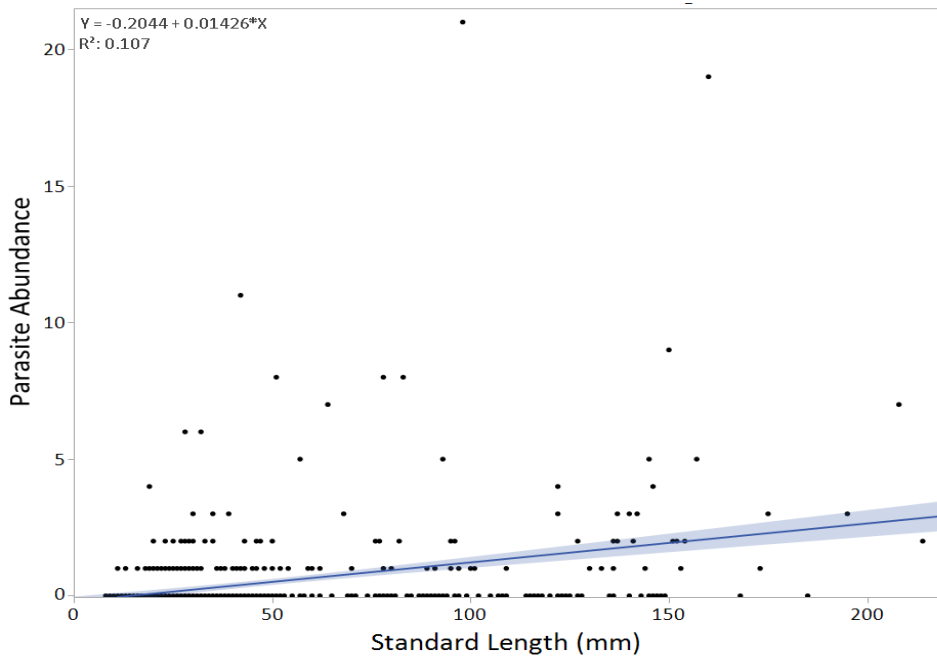


Figure 14. The relationship of parasite abundance and standard length for all fishes.

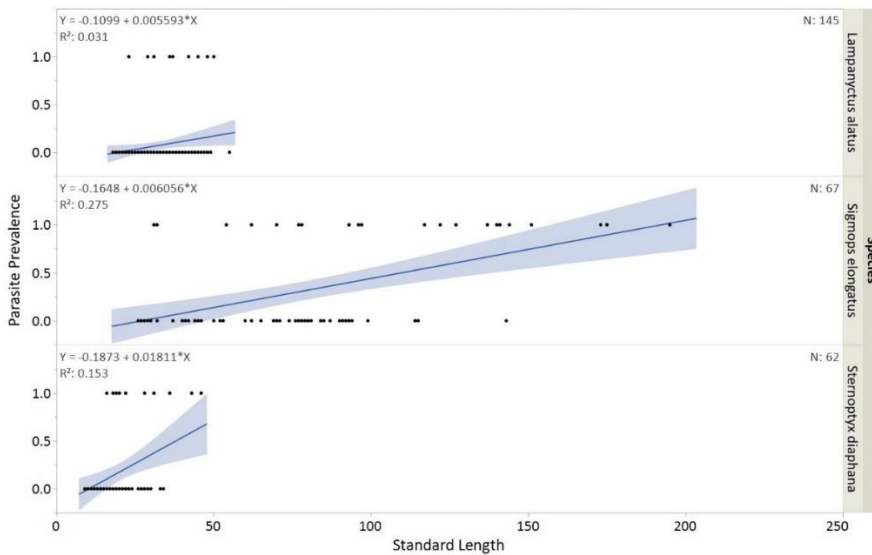


Figure 15. The relationship of parasite prevalence and standard length for *Lampanyctus alatus*, *Sigmops elongatus*, and *Sternoptyx diaphana*.

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The prevalence of parasites was significantly higher in diel vertical migrators compared to non-migrating species ( $p = 0.002$ ). A Mann-Whitney Wilcoxon test revealed that vertically migrating fishes also had a significantly greater number of parasites per fish ( $W = 48075$ ,  $p < 0.001$ ; Figure 16).

Samples from three DEEPEND cruises (DP03, DP04, and DP05) were used to assess a spatio-temporal change in the abundance of parasites in mesopelagic fishes. The prevalence of parasites was not significantly different among the three cruises ( $z = -1.433$ ,  $p = 0.152$ ) and among sample locations ( $p = 0.571$ ). The abundance of parasites significantly differed among sample location ( $p < 0.001$ ; Figure 17). The station locations that had no parasites were not adjacent. Station B083 had a greater mean abundance than the other sample locations. As DEEPEND cruises progressed, parasites were found in the same proportion of fishes, but the number of parasites per fish increased.

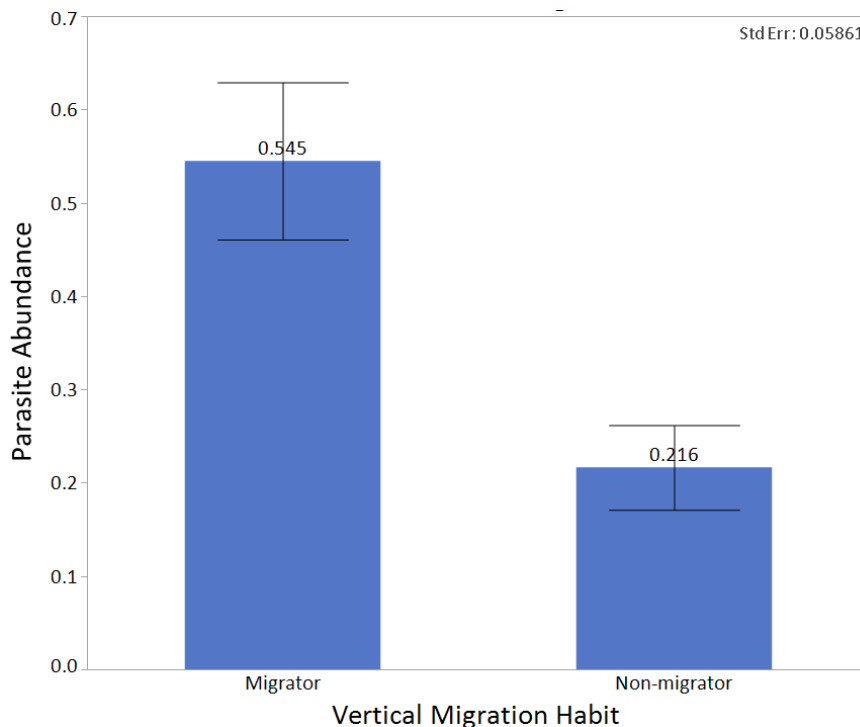


Figure 16. Mean parasite abundance (number of parasites per fish) of vertically migrating and non-migrating fishes. The mean abundance is the top of the bar and whiskers represent standard error for each migration behavior.

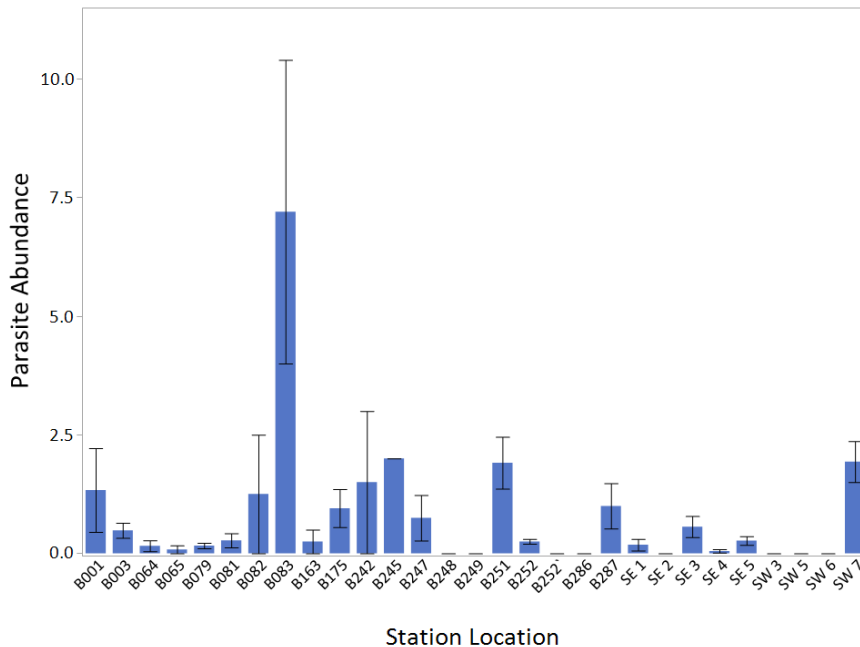


Figure 17. The mean abundance (number per fish) of parasites among station locations sampled during ONSAP and DEEPEND cruises. The mean abundance is the top of the bar and whiskers represent standard error.

#### 4.3.2. The differences in parasites of mesopelagic fishes

Due to difficulties in identifying parasites to species level, the parasite taxonomic levels used for analysis were: Nematoda, Lecanicephalidea (Cestode), Tetrphyllidea (Cestode), Trypanorhyncha (Cestode), Digenea (Trematoda), and Acanthocephalan. The binomial model results and ANOSIM results for parasite differences among fishes are displayed in Table 16.

An ANOSIM revealed that the previously described feeding guilds exhibited significantly different parasite faunas ( $p = 0.001$ ; Table 12). The gelatinivore feeding guild did not have any parasites and was excluded from this analysis. The feeding guild centered on shrimp and copepod prey differed from the other feeding guilds in parasite content, owing to a larger abundance of trypanorhynch cestodes and nematodes. Upper-trophic level fishes had more tetrphyllidean cestodes than the other feeding guilds. Three feeding guilds (Copepodivore, Generalist, and Upper-Trophic Level predator) had many digeneans compared to the shrimp-and copepod-feeding guild.

Table 12. The number of parasites from each major parasite taxon that were found in each fish feeding guild

<b>Feeding Guild</b>	<b>Nem.</b>	<b>Lecan.</b>	<b>Tetra.</b>	<b>Trypano.</b>	<b>Digen.</b>	<b>Acanth.</b>
Copepodivore	7	0	1	7	20	1
Copepods and other zooplankton	4	0	1	0	2	0
Gelatinivore	0	0	0	0	0	0
General	11	1	8	7	26	2
Shrimp and copepod feeder	36	0	1	30	5	1
Upper-Trophic Level	8	0	31	4	47	1

An ANOSIM for parasite taxa among species revealed that certain species of fishes contained specific parasites ( $p < 0.001$ ). Species in which no parasites were found were excluded from this analysis. The summed number of each parasite taxon for each fish species is presented in Table 13. *Diaphus lucidus* had many more trypanorhynch cestodes and nematodes than other fishes. *Sternoptyx diaphana* had the lone occurrence of a lecanicephalidean cestode. *Diaphus mollis* had more digeneans than other zooplanktivores, despite a sample size of four fishes. *Nealotus tripes* was unique with 23 tetraphyllidean cestodes and 32 digeneans. *Myctophum affine* contained four acanthocephalans in two fish specimens.

Despite a greater endoparasite abundance in vertically migrating fishes compared to non-migrators, the major parasite taxa within vertically migrating fishes was not significantly different from those in non-migrating fishes ( $p = 0.5$ ; Table 14). The parasite taxa within fishes was not significantly different among the three DEEPEND cruises ( $p = 0.167$ ; Table 15). All eight acanthocephalans were from one cruise, DP03, but the variation among the other parasite groups was not great enough to result in a significant difference.



Table 13. The cumulative number of major parasite taxa for fish species included in analyses of similarity

<b>Species</b>	<b>Nem.</b>	<b>Lecan.</b>	<b>Tetra.</b>	<b>Trypano.</b>	<b>Digen.</b>	<b>Acanth.</b>
<i>Argyropelecus aculeatus</i>	2	0	0	0	3	1
<i>Argyropelecus hemigymnus</i>	2	0	0	0	2	0
<i>Benthoosema suborbitale</i>	0	0	1	0	3	1
<i>Ceratoscopelus warmingii</i>	0	0	0	0	2	0
<i>Cylothone obscura</i>	5	0	0	0	0	0
<i>Diaphus dumerilii</i>	4	0	0	0	0	0
<i>Diaphus lucidus</i>	31	0	1	17	0	0
<i>Diaphus mollis</i>	0	0	0	0	23	0
<i>Echiostoma barbatum</i>	5	0	0	0	0	0
<i>Lampanyctus alatus</i>	3	0	0	5	2	0
<i>Lepidophanes guentheri</i>	2	0	0	2	6	0
<i>Myctophum affine</i>	0	0	0	0	0	4
<i>Nealotus tripes</i>	1	0	23	1	32	0
<i>Notoscopelus resplendens</i>	0	0	0	0	0	1
<i>Photostomias guernei</i>	1	0	0	0	0	0
<i>Scombrolabrax heterolepis</i>	7	0	8	3	15	1
<i>Sigmops elongatus</i>	4	0	0	12	10	1
<i>Sternoptyx diaphana</i>	3	1	6	4	5	0
<i>Sternoptyx pseudobscura</i>	6	0	1	2	17	1

Table 14. The sum of each major parasite taxon found within vertically migrating fishes and non-migrating fishes

<b>Migration Habit</b>	<b>Nem.</b>	<b>Lecan.</b>	<b>Tetra.</b>	<b>Trypano.</b>	<b>Digen.</b>	<b>Acanth.</b>
Non-migrator	16	1	7	6	24	1
Vertical Migrator	60	0	33	40	98	9

Table 15. The sum of each major parasite taxon found within three DEEPEND cruises aboard the R/V *Point Sur*

<b>Cruise Number</b>	<b>Nem.</b>	<b>Lecan.</b>	<b>Tetra.</b>	<b>Trypano.</b>	<b>Digen.</b>	<b>Acanth.</b>
DP03	19	0	1	13	18	8
DP04	4	1	1	3	18	0
DP05	31	0	6	24	29	0

Table 16. Summary statistics of parasite occurrence in fishes and ANOSIM results showing different parasite taxa among levels within the listed factors. \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$

Factor Tested	Parasite Prevalence	Parasite Dissimilarity
Feeding Guild	< 0.001***	< 0.001***
Species	< 0.001***	< 0.001***
Standard length	< 0.001***	NC
Vertical Migration Habit	0.002**	0.50
Cruise Number	0.003**	0.167
Station Location	NC	< 0.001***

## 5. Discussion

Divergent diets among zooplanktivores have been shown to be related to differences in parasite faunas (Lafferty et al. 2006). The parasites of deep-pelagic fishes in the GoM have not been studied extensively. Andres et al (2016) examined five stomiiform fishes (all zooplanktivores) from the continental-shelf region of the northern GoM and found a low parasite abundance, similar to this study. In the Norfolk Submarine Canyon, Gartner and Zwerner (1989) found greater parasite abundances, particularly in fishes that feed at a higher trophic level.

The parasite assemblage and gut contents of the mesopelagic fishes in this study suggests that the diet of these fishes is consistent per species, meaning individuals of the same species eat the same prey items on a nightly basis, despite the presumed competition for resources in the GoM. Other species preferred other prey items. Most myctophid species selectively preferred calanoid copepods, but *Diaphus lucidus* fed more regularly on euphausiids, and two other species *Diaphus dumerilii* and *Ceratoscopelus warmingii* fed upon a diverse array of zooplankton. The fishes that did not feed on copepods had a greater abundance of nematodes and trypanorhynch cestodes, suggesting these diet differences are a pattern than exists for the lifespan of the species. With over fifty myctophid species (and other zooplanktivores) in the epipelagic zone each night, and many myctophids consuming similar prey items, these myctophids would likely occupy the same niche and compete. However, myctophids are vertically partitioned in the water column, occupying specific 25-m depth intervals per species (Hopkins and Gartner 1992), reducing

interspecific competition. The myctophids in this study had varying diets that correspond with divergent parasite taxa, suggesting diet differences are consistent among species within this assemblage.

The hatchetfishes of the family Sternoptychidae are the third most abundant micronekton fish family in the oceanic GoM (6.9% of all fishes) behind the Gonostomatidae (69.2%) and Myctophidae (15.5%; Sutton et al. in prep). Within the Sternoptychidae, two genera and four dominant species are found in the GoM: *Argyropelecus aculeatus*, *Argyropelecus hemigymnus*, *Sternoptyx diaphana*, and *Sternoptyx pseudobscura*. The diets of the four sternoptychids varied; no species specialized on the same prey taxon. In this study, *A. hemigymnus* ate far more copepods than any other taxon (82.1% prey abundance), which is an uptick from Hopkins and Baird (1985) where *A. hemigymnus* consumed 59.9% copepods and 35.2% ostracods. Based on diet, *A. hemigymnus* occupies a niche more similar to small myctophids than to other members of the Sternoptychidae. *A. hemigymnus* hypothetically remains at mesopelagic depths during the night to avoid competition with the many myctophid species that ascend to epipelagic depths to feed on copepods. *Argyropelecus aculeatus*, *S. diaphana*, and *S. pseudobscura* belong to the generalist feeding guild when compared to other fishes, but there were differences in prey taxa abundances between the three species. In this study and Hopkins and Baird (1985), *A. aculeatus* and *S. diaphana* both preferred copepods and ostracods, but *S. diaphana* preyed upon amphipods more regularly than *A. aculeatus*. The prey taxa that the sternoptychids of this study eat is different than the other numerically-dominant zooplanktivores of the mesopelagic zone, removing competition with other mesopelagic fishes of the GoM.

The copepod-eater, *A. hemigymnus*, had a particularly low parasite prevalence (6.67%), compared to the generalist predators, *A. aculeatus*, *S. diaphana*, and *S. pseudobscura*. *Sternoptyx pseudobscura* was infected with more digeneans than most fishes in this study, and the digeneans that did infect these *S. pseudobscura* were diverse. Five individual parasites from the poorly understood trematode family, Didimyzoidae, separated *S. pseudobscura* from the other fishes in this study. Divergence among the diet and parasites of the four biomass-dominant sternoptychids in the GoM suggest these four

fishes occupy a slightly different niche from each other, as well as the other zooplanktivores of the GoM.

*5.1. Species-specific patterns of parasite infestation in mesopelagic fishes.*

The 26-fish species examined in this study vary in their ecology. A synopsis of the feeding ecology and then parasite dynamics for each species is presented below.

*5.1.1. Sigmops elongatus*

*Sigmops elongatus* provided a case study of ontogenetic change in both diet and parasite abundance. A binomial proportion analysis comparing small prey items to large prey items revealed a significant diet shift at 75 mm standard length. Small *S. elongatus* (< 75 mm SL) were parasitized less than large *S. elongatus* ( $\geq$  75 mm SL) and those parasites were in early life stages. Larger *S. elongatus* also had a greater abundance of parasites and a more diverse array of parasite taxa. The parasites of small *S. elongatus* were all digenean metacercariae while the parasites of large *S. elongatus* included: trypanorhynch cestodes (11 *Tentacularia coryphaenae*, two *Nybelinia* spp.), *Procamallanus* spp., and other anisakid nematodes. Three *S. scopeli* copepods were found on three separate *S. elongatus*, all fishes greater than 90 mm SL. *Sigmops elongatus* was one of the most parasitized vertically migrating zooplanktivores in this study.

*5.1.2. Diaphus lucidus*

*Diaphus lucidus* has a tropical distribution and is less common in the GoM than other myctophids (Backus et al. 1977). All *D. lucidus* specimens were parasitized (one containing 21 parasites). The parasite mix of *D. lucidus* was exclusive to anisakid nematodes and encysted trypanorhynch cestodes (all *Tentacularia coryphaenae*). The *Tentacularia coryphaenae* specimens found within *D. lucidus* were all plerocercoids, a larval cestode stage, suggesting *D. lucidus* is an intermediate host for this species. Both endohelminth taxa simultaneously occupy the external lining of the intestine and the mesentery of their host, suggesting competition within *D. lucidus* is not a factor. In this study, the primary prey items for *D. lucidus* were euphausiids and calanoid copepods. Decapod shrimps and fishes were consumed to a lesser degree, in agreement with Hopkins et al. (1996). Although rare in the GoM, *D. lucidus* had a large parasite abundance (8.83 parasites per fish), suggesting a consistent diet.

### 5.1.3. *Diaphus dumerilii*

*Diaphus dumerilii* is a common tropical myctophid in the Atlantic Ocean that migrates from the lower mesopelagial to the epipelagic zone at night (Backus et al. 1977). *Diaphus dumerilii* has a diet preference similar to that of *Ceratoscopelus warmingii*, but had a greater feeding ration (8.67 prey items fish<sup>-1</sup>). Congruent with Hopkins et al. (1996), this study found calanoid copepods (primarily *Pleuromamma* spp.) as the dominant prey item. All of the endohelminths found in *D. dumerilii* were nematodes (three Spirurida and one Anisakidae). One ectoparasite, *Sarcotretes scopeli* was found attached to the dorsal side of its host, penetrating the exterior and probing the stomach lining. All *Diaphus* species were well parasitized compared to other myctophids.

### 5.1.4. *Diaphus mollis*

Despite feeding on copepods (Hopkins et al. 1996), *Diaphus mollis* was one of the most abundantly parasitized species in this study (6.5 parasites fish<sup>-1</sup>). All endoparasites within *D. mollis* were the digenean, *Helicometra* spp. An increased abundance of parasitism in *D. mollis* compared to other copepodivorous fishes suggests other life history factors (e.g., geographic location) have an effect on the parasite fauna for this species. Bakus et al. (1977) found *D. mollis* to be a common myctophid in subtropical, temperate, and tropical waters of the Atlantic Ocean, and a species that can be caught at the 10-m depth mark during the night, although the mean nighttime depth was around 100 m. The abundance results of Gartner et al. (1989) suggest that the geographic range of *D. mollis* populations (and other tropical myctophids) are heavily influenced by surface currents, as juveniles appear to follow Gulf Stream waters out of the GoM. *Helicometra* are most commonly found in neritic species, suggesting some portion of *D. mollis*'s life history may exist in shallower waters than were sampled during this study.

### 5.1.5. *Scombrobrax heterolepis*

*Scombrobrax heterolepis*, the lone species within the family Scombrobracidae, is a cosmopolitan species that occupies epi- and mesopelagic depths (Parin 1986). *Scombrobrax heterolepis* is an upper-trophic level predator, consuming primarily fishes, decapods, and squids (Parin 1986). *Scombrobrax heterolepis* specimens had a parasite abundance of 12.7 parasites per fish, much larger than any other fish in this study. Within 31 *S. heterolepis*, nine nematodes, eight tetrathyllideans, eight trypanorhynch, sixteen

digeneans, and one acanthocephalan were found. A few digeneans found in *S. heterolepis* were adults, unlike the digeneans found in fishes that predated upon copepods. A caligid copepod (*Caligus* sp.) was found in large abundance in the opercular cavities of all but one specimen. Excluding ectoparasites, *S. heterolepis* has a parasite complement similar to *Nealotus tripes*, another upper-trophic level predator.

#### 5.1.6. *Nealotus tripes*

The vertically migrating snake mackerel, *N. tripes*, has a cosmopolitan distribution and reaches maturity around 150 mm SL (Parin and Nakamura 2002). All of the fishes examined in this study are near this maturity length (123 – 185 mm SL). With 12 of the 14-studied fish parasitized (85.7%), *N. tripes* was one of the most regularly parasitized fishes in this study. Most parasitized fish contained the digenean, *Helicometrina nimia*. Fish that did not have a high abundance of *H. nimia* harbored many tetraphyllidean cestodes in their intestines. *Helicometrina nimia* and tetraphyllideans never occurred in high abundances in the same fish, a potential indicator of competition between two parasites that occupy the same location of the host. *Nealotus tripes* also contained the only parasite in this study that was an infector of the liver, a larval anisakid nematode. Predominately a piscivore, *N. tripes* also feeds on squids and decapods, primarily of the family Sergestidae (Parin and Nakamura 2002). The high rate of parasitism found in this study aligns with the characterization of this species as a dominant predator of the mesopelagic zone.

#### 5.1.7. *Sternoptyx diaphana*

The non-migrating *Sternoptyx diaphana* is most abundant between 700 and 1000 m depth (Baird 1971). The voraciousness of *S. diaphana* ranked second highest among fishes in this study, with 9.39 prey items per fish. Almost all the individuals that contained prey items had a stomach fullness rating of 4 or greater, suggesting *S. diaphana* eats often. The diversity of prey found in *S. diaphana* stomachs placed this species in the generalist feeding guild, in agreement with Hopkins and Baird (1985). Despite feeding on many items, the parasite abundance was not particularly high. Gartner and Zwerner (1989) found parasites in 52.6% (10/19) of the specimens they investigated. However, the mean standard length of *S. diaphana* was 30 mm SL in Gartner and Zwerner (1989) compared to 20.1 mm SL in this study, potentially explaining this disparity. Collard (1968) studied *S. diaphana*

from throughout the Pacific Ocean and found parasite abundances similar to those of this study. The parasite taxa found in *S. diaphana*, including Digenea (Trematoda), Tetraphyllidea (Cestoda), Trypanorhyncha (Cestoda), Lecanicephalidea (Cestoda), Nematoda, and Siphonostomatoida (Copepoda) reflected the generality of the prey items eaten. The generalist feeding strategy of *S. diaphana* did not result in a greater parasite abundance.

#### 5.1.8. *Sternoptyx pseudobscura*

*Sternoptyx pseudobscura* lives deeper than the other sternoptychids examined in this study, between 800 and 1500 m depth (Baird 1971). *Sternoptyx pseudobscura* is a generalist predator, eating every major prey taxon observed in this study, except pteropods, without specificity. A greater abundance of alciopid polychaetes in the diet of *S. pseudobscura* may differentiate this fish from other fishes of a similar ecological niche, reducing the competition among other non-migrating zooplanktivores. Seventeen digeneans were found in *S. pseudobscura* stomachs and body cavities including: *Hirudinella* spp., *Lecithochirum* spp., *Prosorhyncus* metacercaria, two types of Didimyzoidae juvenile, unidentified hemiurids, an unidentified Lepocreadiidae, and two unidentified digeneans. Other parasites found included six nematodes, two trypanorhynchs, and *Sarcotretes scopeli*. *Sternoptyx pseudobscura* has a diverse diet and a parasite mix that reflected such. Many of these parasites were digeneans, suggesting that some factor beyond the generalist feeding strategy (potentially polychaete feeding) drives the parasite dynamics within these fishes.

#### 5.1.9. *Benthoosema suborbitale*

*Benthoosema suborbitale* is a small vertically migratory myctophid found between 500 – 700 m depth during the day and reaches the near-surface water (~10 m depth) at night (Backus et al. 1977). In this study and Hopkins et al. (1996), *B. suborbitale* clearly specialized in the consumption of calanoid copepods (> 80% prey abundance). McClain-Counts et al. (2017) found *B. suborbitale* in the north-central GoM eat a mixture of zooplankton, but copepods comprised approximately 50% of the diet. Five juvenile parasites were found in *B. suborbitale* including, a single acanthocephalan (*Floridosentis* spp.), three trematode metacercariae, and a tetraphyllidean plerocercoid. Despite the lack

of resolution in these parasite identifications, all parasites found within *B. suborbitale* are new host-parasite records.

5.1.10. *Ceratoscopelus warmingii*

*Ceratoscopelus warmingii* is a common myctophid throughout the Atlantic Ocean and GoM (Backus et al. 1977). *Ceratoscopelus warmingii* can reach 75 mm SL when fully grown (Backus et al. 1977), much larger than many of the other myctophids in this study (e.g., *Lampanyctus alatus* and *Lepidophanes guentheri*). However, most of the *C. warmingii* used in this study were immature specimens between (21 – 42 mm SL). McClain-Counts et al. (2017) found *C. warmingii* to be a generalist feeder, predating on all available prey items. Robison (1984) found evidence of herbivory in nine *C. warmingii* stomachs from the North Pacific gyre. Hopkins et al. (1996) saw ontogenetic changes in the diet of *C. warmingii*; progressing from a small crustacean eater, to gelatinivore, to large crustacean feeder with increasing body size. In this study, the primary prey item for *C. warmingii* was calanoid copepods, but six pteropods, a euphausiid, an ostracod, and a hyperiid amphipod were found as well. In summation, *C. warmingii* appears to be an opportunistic zooplanktivore that capitalizes on prey availability. Three *C. warmingii* specimens were parasitized, each containing a single parasite: one immature cestode and two digenean metacercariae. Gartner and Zwerner (1989) examined *C. maderensis* (a related species that is common in the north Atlantic Ocean, but rare in the GoM) and recorded a much higher parasite prevalence (55.6 % prevalence) than was found in this study, but the mean length of those fishes was 61 mm SL as opposed to 28 mm SL in this study. Despite its high abundance in GoM waters and opportunistic feeding strategy, *C. warmingii* was not infected with many parasites.

5.1.11. *Lampanyctus alatus*

*Lampanyctus alatus* is one of the most numerically abundant myctophids in the GoM (Backus et al. 1977) and was the most thoroughly examined fish in this study (n =145). A nearly complete size range was sampled (18-55 mm SL), and all sizes predominately preferred calanoid copepods, and to a lesser degree, cyclopoid copepods. Larger specimens occasionally contained a euphausiid or other zooplankter in their stomach, but not enough to indicate a statistically significant ontogenetic diet change. However, McClain-Counts et al. (2017) and Hopkins et al. (1996) did observe a slight diet



change with increasing body size for *L. alatus*, progressing from a copepodivore to a mixed zooplanktivore (preferentially euphausiids). The parasite abundances were low for *L. alatus* (0.08 parasites fish<sup>-1</sup>), especially considering a full-size range was sampled. A larval hemiurid, *Dissosaccus laevis*, was observed from the stomach of one *L. alatus*, a new host record. Other parasites include five *Tentacularia coryphaenae*, two nematodes, and a digenean metacercariae. Despite being the best-examined species in this study, *L. alatus* was depauperate in terms of parasite fauna.

#### 5.1.12. *Lepidophanes guentheri*

Backus et al. (1977) described *L. guentheri* as the most abundant myctophid in the Atlantic tropical region, and a common fish in the GoM. Hopkins et al. (1996) found an ontogenetic change in diet, from small copepods to euphausiids. In this study, *L. guentheri* predominately consumed copepods and rarely contained empty stomachs, suggesting these fish feed daily. There was no sign of a dominant parasite species or taxon in *L. guentheri*. Ten of the 47 *L. guentheri* specimens examined in this study had at least one parasite (21.3% prevalence) and all of these parasites were at immature life stages: two anisakid nematodes, two trypanorhynch cestodes, five digenean metacercariae, and a juvenile *Helicometrina nimia*. The trophic niche of *L. guentheri* appears similar to *L. alatus*, but Hopkins and Gartner (1992) found the maximum abundance of *L. guentheri* to be 26 – 50 m depth during the night, while the maximum nighttime abundance of *L. alatus* was 51 – 75 m depth. Compared to other copepodivores, *L. guentheri* has an above-average parasite abundance.

#### 5.1.13. *Argyropelecus aculeatus*

*Argyropelecus aculeatus* is a vertically migrating sternoptychid that is common in subtropical waters worldwide (Baird 1971). *Argyropelecus aculeatus* has a maximum size exceeding 70 mm SL (Baird 1971), much larger than the *A. aculeatus* specimens observed in this study (45 mm SL maximum). In this study, *A. aculeatus* was classified a generalist planktivore, specializing on calanoid copepods, pteropods, and ostracods. Hopkins and Baird (1985) listed (in order of decreasing abundance) ostracods, copepods, and mollusks as important prey items for *A. aculeatus*. In Hopkins and Baird (1985), *A. aculeatus* specimens 29 mm SL and less preyed upon ostracods and copepods, while larger fishes ate larger crustaceans, fishes, and mollusks. The current study did not observe an ontogenetic

diet shift in *A. aculeatus*, but with a mean SL of 21 mm SL, the larger size classes examined by Hopkins and Baird (1985) were absent from our analyses. Gartner and Zwerner (1989) and Andres et al. (2016) studied the parasites of *A. aculeatus* from the Norfolk Submarine Canyon and the northern GoM respectively, and found low parasite abundances, similar to this study (0.23 parasite abundance). Mollusks were preferred as prey by *A. aculeatus* more than any other species in this study, suggesting pelagic mollusks (pteropods) are not necessarily hosts for parasites in the deep-pelagic zone. Despite the classification of a diel-vertical migrator and generalist feeding strategy, *A. aculeatus* had a low parasite abundance that did not reflect the typical parasite dynamics given these life history characteristics.

### 5.1.14. *Argyropelecus hemigymnus*

During the day, both *Argyropelecus* species overlap in their distributions between 300 and 400-m depth (Hopkins and Baird 1985). During the night, *A. aculeatus* ascends to the epipelagic zone to feed while *A. hemigymnus* remains at mesopelagic depths, with a few catch records in the lower epipelagic zone (Baird 1971). Premetamorphic larvae can occur as shallow as 50 m depth, but once the fish settle, they remain at upper-mesopelagic depths (Baird 1971). In this study, *A. hemigymnus* primarily preyed upon copepods. Hopkins and Baird (1985) also noted the selective behavior of copepod feeding, but ostracods were a secondary prey item that resulted in a greater biomass consumption. In this study, the size range of this species was nearly complete (8 – 31 mm SL). *Argyropelecus hemigymnus* did not have many parasites (0.09 parasite abundance), two early larval stage nematodes and two trematode metacercariae. All parasites are new host-parasite interactions for this species. As is true with other fishes that primarily feed on copepods, *A. hemigymnus* had a low, non-dominant parasite mix that is reflective of zooplanktivores that feed in deep-pelagic waters.

### 5.1.15. *Photostomias guernei*

*Photostomias guernei* is a circumglobal species and is the dominant stomiid fish in the eastern GoM (Sutton and Hopkins 1996a). *Photostomias guernei* is an asynchronous vertical migrator, meaning only a portion of the population ascends to the surface each night to feed. For *P. guernei* in the eastern GoM, 50% of the population vertically migrates each night (Sutton and Hopkins 1996a). Sutton and Hopkins (1996b) found a lack of diel periodicity in the feeding strategy of *P. guernei* when plotting the digestion rate of prey

items over time, suggesting this species either has no common timeframe in which the entire population eats, or these fishes feed one night and digest their prey for multiple days. In this study, many empty stomachs were found in *P. guernei* specimens (71% vacuity index), suggesting this fish does not feed every day. The fishes that do not migrate have likely not digested the food from the previous few days, leaving no reason to spend the energy associated with vertical migration. Sutton and Hopkins (1996b) described *P. guernei* as an obligatory-shrimpivore, consuming penaeids and sergestids. The shrimp-eating *Photostomias guernei* contained only one parasite, a single nematode infecting the exterior portion of the intestine. Gartner and Zwerner (1989) examined just five *P. guernei* specimens but found two to be parasitized. One parasite was a spuriid nematode, *Johnstonmawwnia* spp., and the other was an ectoparasitic copepod, *Sarcotretes scopeli*. Despite feeding on large crustaceans, *P. guernei* did not have many parasites, an anomaly for a species that feeds on large prey.

#### 5.1.16. *Dolicholagus longirostris*

Seventeen *Dolicholagus longirostris* specimens were examined in this study, none of which contained any parasites. The greater story for this species lies within the diet, with nearly all stomachs containing gelatinous material, indicating that *D. longirostris* feed often. Gelatinous prey organisms are typically hard to identify because gelatinous prey items dissolve within minutes and digestion continues post-mortem (Jackson et al. 1987; Arai et al. 2003). *Dolicholagus longirostris* has elongate papillae in their stomach that appear to trap prey tissue and leftover nematocysts (Figure 18). In some specimens, evidence of feeding on siphonophores was found in the stomach and intestine. One calanoid copepod (*Pleuromamma* sp.) was found in the stomach of one fish. Hopkins et al. (1996) reported *D. longirostris* as a consumer of salps and gastropods.



Figure 18. The interior lining of a *Dolicholagus longirostris* stomach post-dissection. The right image is magnified 2x to show individual cartilaginous spines.

#### 5.1.17. *Valenciennellus tripunctulatus*

*Valenciennellus tripunctulatus* lives at lower-epipelagic and upper-mesopelagic depths and does not vertically migrate (Sutton et al. in prep.). The abundance maximum for *V. tripunctulatus* is between 290 – 460 m depth (Hopkins and Baird 1981). Large individuals live at deeper depths than juveniles, like many other deep-pelagic fishes (Sutton and Hopkins 1996a). Despite not vertically migrating, *V. tripunctulatus* most actively feeds during the afternoon-nighttime hours between 1200 and 2200, although daytime feeding occasionally occurs (Hopkins and Baird 1981). McClain-Counts et al. (2017), Hopkins and Baird (1981), and this study characterize *V. tripunctulatus* as a copepod specialist (particularly *Pleuromamma* sp.) that will occasionally prey on other mesozooplankton (e.g., conchoecid ostracods). No parasites were found in any of the 38 *V. tripunctulatus* specimens, suggesting this fish is not an obligatory intermediate host for any parasites in the deep-pelagic GoM.

#### 5.1.19. *Cyclothone obscura*

*Cyclothone obscura* is a cosmopolitan species in tropical and subtropical seas that numerically dominates GoM ichthyofauna below 1000 m (Badcock 1984). A small fish with no photophores, *C. obscura* does not appear to be a very active predator. Of 74 individuals, only 14 prey items were consumed, leaving a vacuity index (percent of empty stomachs) of 82%. *Cyclothone obscura* also did not contain any parasites, similar to the report of Mauchline and Gordon (1984) for other *Cyclothone* species. This is the first parasite study of *C. obscura*.

#### 5.1.20. *Cyclothone pallida*

The most abundant vertebrate in the mesopelagic zone of the GoM, *Cyclothone pallida* numerically dominates the ichthyofauna above 1000 m (Sutton et al. in prep.). Badcock (1984) lists the maximum size of *C. pallida* males at 48 mm SL and females at 70 mm SL. These fishes are potentially protandrous hermaphrodites like other *Cyclothone* species (*Cyclothone acartia*; Miya and Nemoto 1985), switching from male to female. Most of the stomachs of *C. pallida* examined in this study were empty, similar to other studies of congenetics (Gordon et al. 1985; DeWitt Jr. and Calliet 1972). *Cyclothone pallida* was omitted from diet analyses comparing species because only two prey items were found in fifteen individuals (two euphausiids). Previous studies of the diet of *Cyclothone* spp. characterize these fishes as mesozooplanktivores, eating primarily copepods and ostracods (Gordon et al. 1985). Collard (1968) found one parasite, a 19 mm anisakid nematode in a 32 mm SL *C. pallida* specimen (likely an accidental infection), but no other parasites. No parasites were found in *C. pallida* during this study. *Cyclothone pallida* has a high abundance in the GoM, but the trophic impact of this species appears to be low.

#### 5.1.21. *Melamphaes simus*

*Melamphaes simus* was the lone stephanoberyciform fish in this study. The maximum size of *M. simus* is 29 mm SL (Ebeling and Weed 1973), meaning the two individuals examined in this study (25 and 26 mm SL) were nearly full grown. Prior literature suggests *M. simus* is a vertically migrating zooplanktivore that specializes in copepod feeding (Hopkins et al. 1996). This is the first parasite study that examined *M. simus*, but neither fish had a parasite.

#### 5.1.22. *Myctophum affine*

*Myctophum affine* is a tropical species, common to the GoM, with a nighttime distribution that extends to near the surface (can be caught in neuston tows) and a daytime distribution between 300 and 650 m depth (Backus et al. 1977, Hopkins and Sutton 1998). The size at maturity for *M. affine* females is likely between 46 and 58-mm SL (Backus et al. 1977), meaning both fish in this study (35 and 46 mm SL) were maturing fishes. Hopkins et al. (1996) reported that *M. affine* feeds on small crustaceans, predominately copepods, at all sizes. Only two *M. affine* specimens were examined in this study; both

fishes were parasitized by two acanthocephalans (*Floridosentis* sp.) in their intestinal cavity, one near the intestinal mouth and the other nestled in the median of the intestine. No correlation to diet can be made for the parasites of *M. affine*, but this is a new host-parasite relationship for this species.

### 5.1.23. *Notoscopelus resplendens*

*Notoscopelus resplendens* is a common myctophid species in the GoM and upwelling zones but appears to be less abundant in the portions of the Atlantic with low productivity (Backus et al. 1977). Vertical distribution patterns suggest *N. resplendens* abundance maximums are a few hundred meters deeper than most other myctophids examined in this study (daytime depth of 700 -1200 m depth; Backus et al. 1977). Individuals have also been recorded below 1500 m depth near the Canary Islands (Backus et al. 1977). Small *N. resplendens* (< 29 mm SL) prefer copepods as a prey item, but large crustaceans enter their diet with growth (Hopkins et al. 1996). The two *N. resplendens* examined in this study were found at upper-bathypelagic depths (1000 – 1200 m). In the two fish, one parasite was found, an acanthocephalan (*Floridosentis* spp.) located at the mouth of the intestine. No correlation can be made between the diet and parasites of these fishes at this time, but other fishes that contained acanthocephalans also fed upon copepods.

## 5.2. Parasite life histories

Prior to this study, many of the species examined had no previous record of parasite-host interactions. In this study and others, the deep-pelagic has proven to be a realm of low parasite abundance. Among the parasites that have been found, a high amount of diversity is present. The flatworm class Digenea is typically a shallow-water taxon that is not commonly found in deep-sea organisms (Bray et al. 2004). However, four digenean families have members that are found in deep-pelagic studies: Fellodistomidae, Hemiuridae, Lepocreadiidae, and Opecoelidae. No fellodistomids were found in this study, but the other three deep-sea digenean families made up the dominant number of trematodes found. In Campbell (1980), Gartner and Zwerner (1989), and this study, trypanorhynch cestodes within the family Tentacularidae were the dominant tapeworms. Deep-pelagic nematodes are largely from the family Anisakidae; Acanthocephalans are rare (Klimpel et al. 2001). Many of the parasites found in this study are new records for the species they infect, but have previously been found in other deep-water hosts.

### 5.2.1. *Opecoelidae*

The most taxonomically diverse digenean family is the Opecoelidae, comprising greater than 800 species and 85 genera (Jones et al. 2005). Opecoelids are not immediately recognizable because they are not defined by a single taxonomic character. Instead, opecoelids are recognized by multiple characters, such as: a smooth tegument, two-to-ten testes, two ceca, an I-shaped excretory vesicle, and extensive vitelline follicles that typically occupy the fore- and hindbody (Jones et al. 2005). The life history of opecoelids is as diverse as the taxonomic characters that define them. Typically, eggs are passed through feces, hatch into miracidium that infect prosobranch snails, develop into free-living cercariae, penetrate a wide range of hosts (particularly crustaceans), and passively enter its final host (often marine and freshwater fishes) through the ingestion the previous host (Cribb 1985). Most opecoelid cercariae are not swimmers, but instead crawl in a leach-like motion to infect their host, suggesting these parasites have a benthic or neritic origin (Jones et al. 2005). The subfamily Plagioporinae is more common in deepwater fishes than the other three opecoelid subfamilies, and was more regularly found in this study.

### 5.2.2. *Helicometrina nimia*

*Helicometrina nimia* is a cosmopolitan opecoelid that generally infects fish hosts from the families Clinidae, Pomodasyidae, Scorpaenidae, and Serranidae (Roumbedakis et al. 2014). *Helicometrina nimia* was discovered by Edwin Linton in the Florida Keys, USA during an expedition of reef fish parasites in the early 20<sup>th</sup> century (Linton 1910). Linton (1910) focused on fishes that comprised the shallow water reef systems, but Manter (1934) examined fishes that lived on the reefs and deep-benthic Dry Tortugas, FL, USA down to 350 fathoms (~640 m) depth. Manter (1934) found *H. nimia* to be a “shallow-water” parasite that had a depth maximum shallower than 200 m, despite finding other trematodes that occupy both shallow and deep depths. Since then, *H. nimia* has been found in the coastal waters of every ocean basin, but is more common in the GoM (Sparks 1957, Salgado-Maldonado and Kennedy 1997, Oliva et al. 2004). Once stained, *H. nimia* is easily recognizable by the presence of nine testes. In this study, *H. nimia* were a dominant parasite in the piscivorous snake mackerel, *N. tripes*. Given the dominant nature of this infection compared to other parasites in this realm (3.63 mean abundance), this infection displays a consistent food-web connection that occurs laterally, from the near-shore, reef environment

to the mesopelagic realm of the GoM. One *H. nimia* specimen was also present in a *Lepidophanes guentheri*, but this occurrence appears to be rare. These host-parasite interactions are the first for *H. nimia* recorded globally below 200 m depth.

#### 5.2.3. *Helicometra*

*Helicometra* is the most speciose genus within the subfamily Plagioporinae, consisting of greater than forty species. *Helicometra* can be differentiated from other genera within the Opecoelidae by the presence of a polar filament on the eggs, a helical uterus, and two testes. The lanternfish, *Diaphus mollis*, had a large number of *Helicometra* species in the intestinal cavity. Each of the four *D. mollis* specimens that were examined were infected with a mean of 5.75 parasites per fish, suggesting this infection is a consistent act of parasitism for this host species. None of the *Helicometra* specimens in this study were adults, shown by a lack of eggs, suggesting that *D. mollis* is an intermediate host for this parasite.

#### 5.2.4. *Hemiuridae*

Historically, the digenean family Hemiuridae has been a complex assortment of parasitic forms that have undergone taxonomic revision. The Hemiuridae is an incredibly diverse group which consists of 12 subfamilies separated by a suite of characters. The life history of many hemiurids is variable depending on the host; some genera have been found in both freshwater and saltwater hosts (*Clupenurus*; Gibson et al. 2002). With the exception of a juvenile *Dissosaccus laevis* found in *Lampanyctus alatus*, hemiurids were exclusively found in *Scombrobrax heterolepis* and *Sternoptyx pseudobscura* in this study. The hemiurids were found in low abundances, suggesting these parasites are generalists that can survive in the mesopelagic zone because of their ability to live in a variety of hosts, including many not examined in this study.

#### 5.2.5. *Dissosaccus laevis*

Three *Dissosaccus laevis* specimens were found in this study, two from *Scombrobrax heterolepis* and one from *Lampanyctus alatus*. The two specimens found in *S. heterolepis* were clearly adults as evidenced by the possession of eggs. The *D. laevis* found in *L. alatus* was in very poor condition, but was much smaller than the *D. laevis* found in *S. heterolepis*, suggesting this specimen was a juvenile. Many Lecithochiriinae members are deep-water generalist parasites. Little is known about the life history of *D.*



*laevis*, but previous literature has shown this hemiurid infects deep-sea fishes at low prevalences and intensities, suggesting *D. laevis* is a general parasite that can infect many hosts in the deep-water realm (Campbell et al. 1980, Blend et al. 1996, Bray et al. 2004).

#### 5.2.6. *Lepocreadiidae*

A single lepocreadiid (Trematoda: Digenea) juvenile was found in the stomach of a *Sternoptyx pseudobscura*. One subfamily of the Lepocreadiidae that has previously been found in deep-sea hosts is the Lepidapedinae (Klimpel et al. 2001). The Lepidapedinae are commonly associated with deep-demersal teleosts, such as macrourids, gadiids, and ophiidiids (Jones et al. 2005). Members of the Lepidapedinae are have not been found in many deep-pelagic parasite studies, but this may be due to the scarcity of deep-pelagic studies, compared to benthic studies. The lone lepocreadiid found in this study has not been identified further, but given the previous host records of this family, this specimen likely belongs to the subfamily Lepidapedinae. The lepocreadiid occurrence in this study suggests that this parasite family is not as common in the mesopelagic fishes of the GoM as the Opecoelidae and Hemiuridae.

#### 5.2.7. *Hirudinella*

A single *Hirudinella* (Hirudinellidae) specimen was found in a *Sternoptyx pseudobscura*. The life history of hirudinellids is poorly understood, but the members of the family are generally found in large, pelagic fishes such as *Acanthocybium solandri* (Manooch III and Hogarth 1983). Manooch III and Hogarth (1983) proposed that the life history of *H. ventricosa* is likely similar to *Lecithaster confusus*, another digenean in the superfamily Hemiuroidea. In *L. confusus*, the cercariae develop in the digestive gland of a marine snail before being released, consumed by a copepod, and reach its final host in a large, epipelagic predator (Manooch III and Hogarth 1983). A zooplanktivorous link is missing from the proposed life history of *L. confusus*. In this study, the *Hirudinella* found was noticeably smaller than typical specimens from this genus and did not contain any eggs (an indication of a juvenile). Given the similar morphological characteristics among species within the genus, it is difficult to determine if the *Hirudinella* found in this study is one of the undescribed species presented by Calhoun et al. (2013), or if it is a juvenile *H. ahi* or *H. ventricosa*. A singular occurrence of *Hirudinella* in *S. pseudobscura* and the dominance of *Hirudinella* in large epipelagic consumers suggests this genus possibly

displays low host specificity at the zooplanktivore trophic level, but a zooplanktivore is necessary for the completion of the *Hirudinella* life cycle.

5.2.8. *Didimyzoidae* juv. indet.

The digenean family Didimyzoidae is a relatively unknown family that can parasitize the tissues and organs of fishes either as larvae or adults (Kohn and Justo 2008; Felizardo et al. 2011). Three individuals were taken from two *Sternoptyx pseudobscura* specimens and were tentatively identified as two didimyzoid types. The presence of glandular objects throughout the hindbody (sometimes reaching into the forebody) were a key feature in the identification of these parasites as Didimyzoidae. Unfortunately, the presence of ventral glands, and the juvenile life stage of these parasites, prevent further identification.

5.2.9. *Lecanicephalidae* (*Stoibocephalum*?)

Redescribed by Cielocha and Jensen (2013), the lecanicephalid cestode genus *Stoibocephalum* is poorly known. The two traits that distinguish *Stoibocephalum* from other lecanicephalids are only recognizable through cross-section, so the lone individual found in this study is given a family-level identification. However, this individual most closely resembles *Stoibocephalum*-like lecanicephalids.

5.2.10. *Tentacularia coryphaenae*

A recent revision of the genus *Tentacularia* has reduced the number of accepted species within this genus from 14 to one, *T. coryphaenae*. Postlarvae are widespread throughout plankton and teleost fishes with a cosmopolitan distribution (Khalil et al. 1994). As an adult, *T. coryphaenae* will infect the stomach and intestine of elasmobranchs (Schmidt 1986, Borucinska and Dunham 2000). *Tentacularia coryphaenae* has been found in many deep-sea fishes, including *Aphanopus carbo*, *Chauliodus sloani*, *Deania calcea*, *Deania profundorum*, *Heptranchias perlo*, *Sternoptyx diaphana*, and *Stomias boa ferox* (Klimpel et al. 2001). *Tentacularia coryphaenae* was the most dominant trypanorhynch found in this study, predominately infecting vertically migrating fishes (e.g., *Diaphus lucidus* and *Sigmops elongatus*). All of the *T. coryphaenae* specimens found in this study were encysted in the post-larval stage, commonly associated with the exterior margin of the host's intestine, suggesting the zooplanktivorous fishes these tapeworms infect are intermediate hosts for *T. coryphaenae*.

#### 5.2.11. *Hepatoxylon trichiuri*

Larval *Hepatoxylon* are found in large pelagic fishes, such as *Thunnus alalunga* (Albacore; Jones 1991), *Thunnus albacares* (Yellowfin Tuna; Ward 1962), and *Thunnus thynnus* (Bluefin Tuna; Mladineo 2006). Large sharks are infected by *H. trichiuri* through the ingestion of fishes, like other trypanorhynchs (Campbell and Callahan 1998). Jones (1991) found a greater abundance of *H. trichiuri* in smaller, coastal *T. alalunga* than larger, offshore fishes, suggesting *Hepatoxylon* use an invertebrate (e.g., euphausiids, hyperiid amphipods, cephalopods) as an intermediate host. In this study, a single *H. trichiuri* larvae was encysted and attached to the intestine of a *Scombrolabrax heterolepis*. This host-parasite interaction is the first for *H. trichiuri* below 200 m globally, and is the second reported occurrence in the Gulf of Mexico (*T. albacares*; Ward 1962).

#### 5.2.12. *Caligus*

Commonly nicknamed “sea lice,” the ectoparasitic copepods from the family Caligidae are of importance to fish farmers worldwide because they are damaging to fish stocks (Pike and Wadsworth 1999, Butler 2002). In this study, *Caligus* specimens were found in the opercular cavity of *Scombrolabrax heterolepis*. No parasites were found on the exterior portion of any fish, but this absence could be a product of the trawling sampling method. Fishes captured in trawl nets can be abraded by the net, potentially removing ectoparasitic organisms. It is impossible to know if the *Caligus* found in this study are exclusive to the opercular cavity of *S. heterolepis*, or if they occupy other locations around the host as well. Most of the *Caligus* found in this study were egg-bearing females, but adult males and copepodites were also present. The abundance of these copepods inside *S. heterolepis* was much larger than other parasite abundances observed in this study (11.55 parasites fish<sup>-1</sup>), suggesting *S. heterolepis* individuals are commonly infected with *Caligus* spp.

#### 5.2.13. *Sarcotretes scopeli*

The mesoparasitic (parasitic during part of the life cycle) copepod *Sarcotretes scopeli* is commonly found on mesopelagic fishes. The specimen found in our study are all *S. scopeli* based on species descriptions and a key to *Sarcotretes* species provided by Uyeno et al. (2012). *Sarcotretes scopeli* has a wide geographical range and low host specificity (Hogans 1988). Many host records for this species come from myctophiform fishes

(Gjørøseter 1971; Boxshall 1998). In this study, some hosts were infected from the dorsal side while some were infected from the ventral side. In all cases, a long proboscis penetrated the scales and was buried in the gastrointestinal cavity, presumably to feed on digested food particles. It appears that the location of infection is not a host-specific response, but instead a random event that allows the parasite to be successful as long as it can reach the internal organs. The prevalence and abundance of *S. scopeli* in this study was low, with only four fishes parasitized. These results are in agreement with Gjørøseter (1971), who found 31 *S. scopeli* on 989 *Benthosema glaciale* (3.1% abundance). When dividing fishes into size classes, Gjørøseter (1971) found a lesser abundance of *S. scopeli* in larger fishes and noted a negative effect on infected host's gonads, suggesting *S. scopeli* can significantly affect their host's health.

#### 5.2.14. *Floridosentis*

A rarely occurring parasite in this study was the spiny-head worm, *Floridosentis* spp. (Family: Neoechinorhynchidae). Aside from their presence in mullets, the life history of *Floridosentis* is not well known. However, mullets are planktivorous feeders that migrate offshore annually (Ditty and Shaw 1996), so *Floridosentis* larvae are likely transmitted through small zooplankton (e.g., copepods, ostracods, and amphipods), and eggs are potentially deposited in offshore waters. The acanthocephalans found in this study all resemble the characteristics of *Floridosentis*, but given the taxonomic uncertainty of the genus, a species-level classification was not made. All occurrences of *Floridosentis* in this study are new host-parasite records for the genus below 200-m depth.

#### 5.2.15. *Anisakis*

The cosmopolitan anisakid genus *Anisakis* was the most commonly found nematode in this study. Morphometric identification to species is difficult, so molecular techniques are often employed (Klimpel and Palm 2011). A genus-level distinction has been made in this study. *Anisakis* spp. were found in *Diaphus lucidus* and *Echiostoma barbatum*, two fishes that selectively feed on larger prey items (euphausiids and fishes, respectively). Many unidentified anisakids were also found in this study. These anisakids are larval forms that have not developed the features that allow for a genus-level distinction (count and directionality of caeca), but potentially are of the genus *Anisakis*. *Anisakis* are believed to follow a pelagic life style, utilizing invertebrate and vertebrate hosts before

infecting a marine mammal as a definite host (Nascetti et al. 1986). In the Norwegian Deep, Klimpel et al. (2004) determined the calanoid copepod, *Paraeuchaeta norvegica*, and sternoptychid, *Mauroliticus muelleri*, were obligatory intermediate hosts for *Anisakis simplex*. A euphausiid, *Meganycitiphanes norvegica*, was notably not infested by *A. simplex* larvae (Klimpel et al. 2004). However, at the Mid-Atlantic Ridge, euphausiids appear to have a more important role in the life cycle of anisakids (Klimpel et al. 2008). Myctophids and other pelagic zooplanktivores are likely teleost intermediate hosts for *Anisakis* spp. (Klimpel et al. 2007). These parasites are commonly found at mesopelagic depths, occupying fish hosts from the surface to the benthos (Klimpel et al. 2001; Blend et al. 1996).

#### 5.2.16. *Contracaecum*

Similar to *Anisakis*, another anisakid genus *Contracaecum* is present in many different animals (e.g., birds, fishes, mammals, and reptiles), suggesting low host specificity (Sprent 1954). After larval *Contracaecum* are ingested by fishes, some larvae will penetrate through the intestinal wall before encapsulating themselves in the mesentery of its host (Huizinga 1966). *Contracaecum* spp. were found in two species in this study: *Argyropelecus hemigymnus* and *Photostomias guernei*. Both *Contracaecum* found in this study occupied the mesentery of their host. Copepods, shrimp, and small fishes appear to be intermediate hosts for *Contracaecum* in the pelagic zone (Sprent 1954). Marine mammals, particularly the Hawaiian Monk Seal, are heavily infested by *Contracaecum* (Kenyon and Rice 1959). *Contracaecum* spp. has previously been recorded in deep-sea macrourids in the GoM (Klimpel et al. 2001), but not in the deep-pelagic GoM. Gartner and Zwerner (1989) reported an occurrence of *Contracaecum* spp. in *Chauliodus sloani* in the Norfolk Submarine Canyon. *Contracaecum* utilizes similar hosts to the aforementioned *Anisakis*, but is not as common in the mesopelagic GoM.

#### 5.2.17. *Procamallanus*

A single *Procamallanus* specimen was found in a 173 mm SL *Sigmops elongatus* during this study. *Procamallanus* has both freshwater and saltwater forms worldwide, but in both, uses a copepod at an early life history stage (Li 1935, Moravec et al. 1995). *Procamallanus cricotus* was described in the northern GoM and found in at least 13 teleost

host species (Fusco and Overstreet 1978), but no species-level identification could be made in the current study. The presence of *Procamallanus* in *Sigmops elongatus* is the first record of this parasite in a host below 200 m depth.

### 5.3. Feeding guild descriptions

The eighteen species analyzed for diet were classified into six feeding guilds. This section includes a description of each feeding guild and its species complement.

#### 5.3.1. Copepod specialists

The most speciose feeding guild in this study was that of the copepod specialists. The copepod specialist guild includes all fishes that consumed copepods as greater than 70% of the prey items in their diet. Seven species made up this guild: *Argyropelecus hemigymnus*, *Benthoosema suborbitale*, *Cyclothone obscura*, *Lampanyctus alatus*, *Lepidophanes guentheri*, *Sigmops elongatus* < 75 mm SL, and *Valenciennellus tripunctulatus*. The typical prey size of these copepods was 1 – 3 mm total carapace length. Many copepodivorous fishes contained one or two prey items per stomach, but almost always at least one prey item (except *C. obscura*). Most of the consumed copepods were from the order Calanoida, followed by Cyclopoida, and a single representative from Harpacticoida. A majority of the calanoid copepods were *Pleuromamma* spp., which can be identified by a large, black, metasomal spot. Four of the seven species that made up the copepodivorous feeding guild are vertical migrators. The non-migrating fishes of this feeding guild feed on deeper-dwelling copepods. The parasites found within the fishes of this feeding guild are all larval-stage endohelminths, primarily digenean metacercariae. Based on these results, the copepods of the pelagic GoM may be early-stage hosts for digeneans, but low parasite abundances and host species-specific ecologies make this distinction unclear.

#### 5.3.2. Gelatinivores

This guild consists of fish that consume gelatinous zooplankton. The gelatinivore guild was the most statistically dissimilar from any other guild (95% dissimilarity) because of the absence of copepod prey. The lone gelatinivore observed in this study was *Dolicholagus longirostris*. This species contained cnidarian nematocysts and amorphous gelatinous material. A few occurrences of siphonophore prey were observed, as well as a single calanoid copepod. However, this copepod was soft, devoid of any chitinous material

and potentially could have been prey of a gelatinous zooplankter before ingestion. Hopkins et al. (1996) also found limited evidence of gelatinous feeders in the eastern GoM midwater fish assemblage, including *D. longirostris*, *Scopelogadus mizolepis mizolepis*, and *Poromitra gibbsi*. Gelatinous feeding is difficult to quantify in gut content studies because prey items dissolve much more quickly than chitinous prey items (Jackson et al. 1987). Digeneans have been observed in gelatinous zooplankton in the southern Atlantic Ocean (Martorelli 2001), but no parasites were found in gelatinivores in this study.

### 5.3.3. Upper-trophic level predators

This study focused mainly on zooplanktivorous fishes, but the inclusion of two upper-trophic level predators, *Nealotus tripes* and *S. heterolepis*, added the potential for inter-trophic level analyses. Two stomiids, *Chauliodus sloani* and *Echiostoma barbatum*, would likely belong in this feeding guild, but were excluded from diet analysis because of a small sample size (one fish per species). Sutton and Hopkins (1996b) determined most stomiids belong to the piscivore feeding guild, with a few exceptions (e.g., *Astronesthes* spp., *Photostomias guernei*, and *Malacosteus niger*). Fishes were the dominant prey of this guild. Sergestid decapods and squids also occurred as prey, but in lower numbers. Most prey fishes were unrecognizable, only identified by their hard eye-lenses, but a well-preserved *Diaphus lucidus*, several clupeiform fishes, and a juvenile *N. tripes* was found in the stomach *N. tripes*, the latter being a rare display of cannibalism. *Nealotus tripes* and *S. heterolepis* had greater abundances of tetraphyllidean cestodes and digeneans than other feeding guilds. The digeneans found within these fishes were at a later stage of development than the parasites found in zooplanktivorous fishes. Parasite abundances were also greater in *N. tripes* and *S. heterolepis* than most of the other fishes in this study. Upper-trophic level fishes prey upon larger prey items that are more likely to have parasites, thus having more parasites themselves.

### 5.3.4. Copepods and euphausiid predators

The copepod and euphausiid feeding guild represented trophic intermediaries between upper-trophic level predators and copepod specialists. Three species were represented in this guild: *Photostomias guernei*, *Diaphus lucidus*, and large *Sigmops elongatus*. All of the fishes in this feeding guild had a mean standard length greater than

70 mm and are considered vertical migrators. Sutton and Hopkins (1996b) determined *P. guernei* primarily preyed upon decapods in the families Sergestidae (greatest prey biomass) and Penaeidae (greatest prey abundance). Many mesopelagic fishes display a diet shift with increasing growth (Hopkins et al. 1996), as has been observed with *S. elongatus* in this study. Only six *D. lucidus* specimens were examined, all greater than 55 mm SL. If a wider range of lengths had been examined, a diet shift may have been observed, as Hopkins et al. (1996) reported for *D. lucidus*. This euphausiids found as prey were larger than the copepods, typically 5-6 mm carapace length. Larger prey items provide more nutrition, likely prompting deep-pelagic fishes to target euphausiids once the fish grows to a size at which they can catch and consume these prey. Anisakid nematodes and trypanorhynch cestodes (*Nybelinia* spp., *Tentacularia coryphaenae*) were the primary parasite taxa found within this feeding guild. The presence of anisakids and tentacularid trypanorhynchs in this feeding guild and not the copepod feeding guild suggests that euphausiids are used as vectors in the life cycle of these parasites.

### 5.3.5. Predators of copepods and other zooplankton

Two myctophids, *Ceratoscopelus warmingii* and *Diaphus dumerilii*, represented the copepod-and-other-zooplankton feeding guild. This guild comprised fishes that consumed copepods, but also a diverse assortment of other zooplankton (e.g., amphipods, ostracods, and pteropods). Literature records for the diet of *C. warmingii* are variable. McClain-Counts et al. (2017) listed *C. warmingii* as a true generalist predator, consuming various prey taxa in nearly equal amounts. Hopkins et al. (1996) showed that *C. warmingii* shifted its diet to become more general with increasing body size, and Robison (1984) observed herbivory in *C. warmingii* in the Pacific. Hopkins et al. (1996) classified *D. dumerilii* as a small crustacean eater, similar to this study. Both *C. warmingii* and *D. dumerilii* were represented by a small sample size, 13 and 9 fishes, respectively, which may have resulted in differences in diet breadth compared to other studies. *Ceratoscopelus warmingii* and *D. dumerilii* are likely opportunistic zooplanktivores, feeding on the dominant available prey. The parasites of this feeding guild were representative of the copepodivores that were parasitized. All parasites were in a larval stage, again suggesting that fishes preying upon copepods will not have a large parasite abundance because pelagic copepods of the GoM are not heavily infected by parasites.



### 5.3.6. Generalists

The predators with the greatest ration in this study (9.64 prey items fish<sup>-1</sup>) were classified as generalists, including *A. aculeatus*, *S. diaphana*, and *S. pseudobscura*. *Argyropelecus aculeatus* was unique in eating an equal portion of pteropods as copepods and ostracods. In all three species almost every fish had at least one prey item in their stomach and did not seem to prefer any particular food source. *Sternoptyx pseudobscura* consumed more alciopid polychaete worms, euphausiids, and amphipods than *S. diaphana*, but this difference was not statistically significant. Hopkins and Baird (1985) also noted a greater abundance of polychaete worms in the diet of *S. pseudobscura* than *S. diaphana*. These fishes belong to the Sternoptychidae and have large eyes, potentially aiding in detection of a wide range of prey groups. As a function of their general diet, these fishes had the most diverse parasite fauna of all fishes in this study.

### 5.4. Other life history parameters affecting parasitism

For many fishes, an increase in body size results in an increase in endoparasites (Lo et al. 1998). Deep-pelagic fishes overall contain less parasites than fishes in coastal habitats, but display a similar trend with increasing body size (Marcogliese 2002). Assuming standard length is a suitable proxy for age within species, the older fishes in this study contained more parasites, and these parasites were in more advanced stages of maturity than the parasites of the smaller fishes. The gape of fishes' mouths increases with body size, allowing for the consumption of a greater variety of prey items. Further, the swimming speed of a fish is directly related to its size because of the interplay of Reynold's number dynamics with growth (Ware 1978). Larger fishes within species will have the ability to catch larger, faster prey items that are more likely to be infected with a parasite. Therefore, parasitism rates of fishes would be predicted to increase with increasing body size, as was found in this study.

The greatest size-class range of any fish in this study was that of *Sigmops elongatus* (26 – 195 mm SL). The diet of *S. elongatus* shifted with ontogeny, transitioning from primarily copepods at small lengths to euphausiids and fishes at large sizes. The abundance of parasites in these fishes shifted with increasing size as well. As with most fishes in this study, the smallest size class had a low parasite prevalence. The first parasites detected in

*S. elongatus* were digenean metacercariae in fishes less than 75 mm standard length. Fish in the largest size classes showed a dominance of nematodes and trypanorhynch. The introduction of euphausiids into the diet of *S. elongatus* greater than 75 mm SL influenced the influx of nematodes and trypanorhynch in the parasite fauna of this species.

Parasites are more abundant in epipelagic waters where the biomass and diversity of free-living organisms (potential hosts) is greater (Marshall 1954), than the deep-pelagial (Marcogliese, 2002). As vertically migrating organisms ascend into the epipelagic zone to feed, these organisms are leaving a parasite-poor environment and entering a comparatively parasite-rich environment. The parasite abundance and taxa that infect mesopelagic fishes will be determined primarily by the depth a fish occupies during its feeding time. In this study, vertically migrating fishes had a greater abundance of parasites than non-migrators, but the parasite taxa that were found between these two groups were similar. These results provide another piece of evidence that suggests more parasites occupy the epipelagic zone than mesopelagic depths (Marcogliese 2002, Bray 2004, Klimpel et al. 2006). However, parasite similarity suggests the parasites that exist in the oceanic GoM are either general parasites that can occupy a variety of different hosts, or the zooplankton trophic-level of the oceanic GoM is so complex and well-connected between the epi- and mesopelagic depth boundaries that the parasites in these zones are homogenized among zooplanktivorous fishes.

Diet specifications among species would be expected to regulate the parasites found within feeding guilds but differences in parasite taxon among species within feeding guilds suggest other species-specific life history factors are likely at play as well. In just four *Diaphus mollis* specimens, 23 *Helicometra* spp. were present. Compared to other copepodivores, *D. mollis* was an outlier in terms of parasite abundance. In this study, feeding ration of *D. mollis* was slightly higher than most other fishes within the copepodivore feeding guild, but this factor alone does not likely explain this unique parasite load. The geographic location of fishes has been shown to be a factor in the parasite load of a species (MacKenzie and Abaunza 1998), because in order for a fish to be infected by a parasite, the geographic range of the two organisms must overlap. For example, *Scombrobrax heterolepis* had a large abundance of *Caligus* spp. in their opercular cavity.

Although caligid copepods are not endoparasites and thus not transmitted through the food web, the abundance of these copepods in *S. heterolepis* (and absence in all other fishes) suggests divergence in the distribution/life history characteristics of *S. heterolepis* from the other mesopelagic fishes in this study.

#### 5.5. Offshore movement of prey

The biota and oceanographic features of the GoM provide an interesting case study in ecosystem connectivity. The trematode *Helicometrina nimia* is a shallow-water parasite that, prior to this study, had never been found in fishes deeper than 200 m depth. *Nealotus tripes* is an oceanic, mesopelagic predator that does not live on the continental shelf at any life stage (Beckett and Barrett 1967). Within *N. tripes* stomachs, the dissolved remains of clupeiform fishes (e.g., anchovies, sardines) were occasional occurrences. Many clupeiform are known to undergo an ontogenetic offshore migration, from the nearshore to offshore waters (Modde 1980). Engraulid fishes (anchovies) have been caught in the offshore waters of the GoM (Sutton et al. 2017). The offshore movement and predation of engraulids may provide a vector that connects *H. nimia* and *N. tripes*. Aside from this offshore movement hypothesis, the movement of mesoscale eddies along the outer continental shelf may funnel neritic water offshore, transporting small fishes and plankton from a neritic to an oceanic habitat. Whatever the vector method, the presence of multiple *H. nimia* specimens inside *N. tripes* demonstrate that the nearshore and offshore ecosystems of the GoM are connected by trophic pathways. Therefore, natural and anthropogenic events that affect the nearshore environment may influence the mesopelagic GoM as well.

## 6. Conclusions

Currently, this study is the most extensive deep-pelagic parasite study in the GoM in terms of both number of fishes and species. Among the fishes of this mesopelagic assemblage, six feeding guilds were recognized based on their preferential prey items. Fishes that prey upon larger prey items (macrozooplankton and micronekton) were more likely to have a parasite than fishes that prey upon mesozooplankton. The parasites that were found within these fishes varied according to size (age) of the fish, both within and among species. Euphausiids appeared to be a host for anisakid nematodes and *Tentacularia*

*coryphaenae* based on the dominance of these parasites in fishes that feed upon this prey taxon. A generalist diet resulted in a parasite fauna with high diversity and low dominance. Digeneans appeared to use copepods as life-history vectors, and because copepods are preferred prey for the largest number of mesopelagic fish species, digeneans were the most common endoparasites. Finally, the dominance of a parasite that typically infects neritic fishes in a mesopelagic piscivore suggests a consistent foodweb pathway exists between the nearshore and offshore waters of the GoM.

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**Appendices**

Deep-Pelagic Parasites

APPENDIX TABLE 1. The host-parasite interactions of the deep (> 200) Gulf of Mexico including the Dry Tortugas, Florida, USA

Host-Parasite Interactions	Original Source
Acropomatidae	
<b><i>Synagrops bellus</i></b>	
<i>Distomum fenestratum</i>	Manter 1934
<i>Rhipidocotyle longleyi</i>	Manter 1934
Alepocephalidae	
<b><i>Xenodermichthys copei</i></b>	
<i>Steringophorus spp.</i>	Manter 1934
<i>Sterrhurus profundus</i>	Manter 1934
Argentinidae	
<b><i>Argentina striata</i></b>	
<i>Fellodistomum profundum</i>	Manter 1946
<i>Parasterrhurus anurus</i>	Manter 1934
<i>Steringophorus profundus</i>	Manter 1934
Bothidae	
<b><i>Monolene antillarum</i></b>	
<i>Lomasoma monolenei</i>	Manter 1934
<b><i>Trichopsetta ventralis</i></b>	
<i>Sterrhurus floridensis</i>	Manter 1934
Bythitidae	
<b><i>Diplacanthopoma brachysoma</i></b>	
<i>Hemiperina nicollia</i>	Manter 1934
<i>Megenteron crassum</i>	Manter 1934
Chaunacidae	
<b><i>Chaunax pictus</i></b>	
<i>Adinosoma robustum</i>	Manter 1934
<i>Aponurus intermedius</i>	Manter 1946
<i>Hemiperina nicollia</i>	Manter 1934
<i>Sterrhurus floridensis</i>	Manter 1934
<i>Sterrhurus robustus</i>	Manter 1934
Chlorophthalmidae	



<b><i>Parasudis truculenta</i></b>	
<i>Adinosoma robustum</i>	Manter 1946
<i>Sterrhurus robustus</i>	Manter 1934
Epigonidae	
<b><i>Epigonus occidentalis</i></b>	
<i>Lepidapedon elongatum</i>	Manter 1934
Gempylidae	
<b><i>Nealotus tripes</i></b>	
Anisakidae	This Study
Tetraphyllidea indet.	This Study
<i>Tentacularia coryphaenae</i>	This Study
Trypanorhyncha indet.	This Study
<i>Helicometrina nimia</i>	This Study
Digenea indet.	This Study
Gonostomatidae	
<b><i>Sigmops elongatus</i></b>	
<i>Procamallanus</i> spp.	This Study
Nematoda indet.	This Study
<i>Tentacularia coryphaenae</i>	This Study
<i>Nybelinia</i> spp.	This Study
Digenea indet.	This Study
<i>Floridosentis</i> spp.	This Study
<i>Sarcotretes scopelii</i>	This Study
Macrouridae	
<b><i>Bathygadus favosus</i></b>	
<i>Macrourimegatrema brayi</i>	Blend <i>et al.</i> 2004
<b><i>Bathygadus macrops</i></b>	
<i>Adinosoma robustum</i>	Blend 1996
<i>Anisakis</i> spp.	Armstrong 1974
<i>Aponurus</i> sp.	Blend 1996
<i>Ascarophis</i> sp.	Armstrong 1974
<i>Contracaecum</i> spp.	Armstrong 1974
Digenea indet.	Armstrong 1974
<i>Dinosoma robustum</i>	Armstrong 1974
<i>Dissosaccus laevis</i>	Blend 1996
<i>Echinorhynchus</i> sp.	Armstrong 1974
<i>Gonocerca phycidis</i>	Armstrong 1974

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Hemiuridae indet.	Klimpel <i>et al.</i> 2001
<i>Lecithochirium robustus</i>	Klimpel <i>et al.</i> 2001
<i>Lethadena profunda</i>	Blend 1996
<i>Macrourimegatrema brayi</i>	Blend <i>et al.</i> 2004
<i>Nybelinia</i> sp. (Pleurocercoïd)	Armstrong 1974
Opecoelidae indet.	Klimpel <i>et al.</i> 2001
<i>Podocotyle pearsei</i>	Armstrong 1974
Tetraphyllidea ident. (larva)	Armstrong 1974
<i>Tentacularia</i> spp. (Pleurocercoïd)	Armstrong 1974
<b><i>Bathygadus melanobranchus</i></b>	
Digenea indet.	Klimpel <i>et al.</i> 2001
<i>Macrourimegatrema brayi</i>	Blend <i>et al.</i> 2004
Opecoelidae indet.	Klimpel <i>et al.</i> 2001
<i>Podocotyle</i> sp.	Blend 1996
<i>Scolex pleuronectis</i> form I	Armstrong 1974
Trematode indet.	Blend 1996
<b><i>Coelorinchus carminatus</i></b>	
<i>Cymbephallus fimbriatus</i>	Manter 1934
<i>Gonocerca crassa</i>	Manter 1934
<i>Gonocerca phycidis</i>	Manter 1946
<i>Lepidapedon elongatum</i>	Manter 1934
<i>Lepidapedon rachion</i>	Manter 1934
<i>Lomasoma wardi</i>	Manter 1934
<i>Otodistomum</i> spp	Manter 1934
<b><i>Coelorinchus caelorhincus</i></b>	
<i>Echinobreviceca caelorhynchae</i>	Dronen <i>et al.</i> 1994
<b><i>Coryphaenoides mexicanus</i></b>	
<i>Gonocerca phycidis</i>	Blend 1996
<b><i>Coryphaenoides zaniophorus</i></b>	
<i>Gonocerca phycidis</i>	Blend 1996
<b><i>Coryphaenoides</i> spp.</b>	
<i>Lepidapedon desotoensis</i>	Armstrong 1974
<b><i>Gadomus arcuatus</i></b>	
<i>Dissosaccus laevis</i>	Armstrong 1974
<i>Macrourimegatrema brayi</i>	Blend <i>et al.</i> 2004
<i>Macrourimegatrema gadoma</i>	Armstrong 1974
<i>Nybelinia</i> spp. (Pleurocercoïd)	Armstrong 1974
<i>Podocotyle pearsei</i>	Armstrong 1974
Tetraphyllidea indet.	Armstrong 1974
<b><i>Gadomus longifilis</i></b>	
<i>Anisakis</i> spp.	Armstrong 1974

<i>Contracaecum</i> spp.	Armstrong 1974
<i>Nybelinia</i> spp. (Pleurocercoid)	Armstrong 1974
Tetraphyllidea indet.	Armstrong 1974
<b><i>Malacocephalus occidentalis</i></b>	
<i>Buticulotrema stenauchenus</i>	Blend <i>et al.</i> 1993
<i>Glomericirrus macrouri</i>	Armstrong 1974
<i>Gonocerca phycidis</i>	Blend 1996
<i>Podocotyle pearsei</i>	Blend 1996
<i>Pseudopecoelus tortugae</i>	Armstrong 1974
<b><i>Maurolicus weitzmani</i></b>	
<i>Hysterothylacium fortalezae</i>	Andres <i>et al.</i> 2016
Tetraphyllidea ident.	Andres <i>et al.</i> 2016
<b><i>Merluccius</i> spp.</b>	
<i>Adinosoma robustum</i>	
<i>Derogenes varicus</i>	Manter 1934
<i>Distomum fenestratum</i>	Manter 1934
<i>Gonocerca crassa</i>	Manter 1934
<i>Gonocerca phycidis</i>	Manter 1946
<i>Sterrhurus praeclarus</i>	Manter 1934
<i>Sterrhurus robustus</i>	Manter 1934
<b><i>Nezumia aequalis</i></b>	
<i>Anisakis</i> spp.	Armstrong 1974
<i>Ascarophis</i> spp.	Armstrong 1974
<i>Buticulotrema stenauchenus</i>	Blend <i>et al.</i> 1993
<i>Contracaecum</i> spp.	Armstrong 1974
<i>Dissosaccus laevis</i>	Armstrong 1974
Opecoelidae indet.	Blend 1996
<i>Glomericirrus macrouri</i>	Armstrong 1974
<i>Gonocerca phycidis</i>	Armstrong 1974
<i>Johnstonmawsonia</i> spp.	Armstrong 1974
<i>Lepidapedon nezumiatis</i>	Armstrong 1974
<i>Myxobolus mexicanus</i>	Moser 1977
<i>Nybelinia</i> spp.	Armstrong 1974
<i>Podocotyle</i> spp.	Armstrong 1974
<i>Podocotyle nimoyi</i>	Armstrong 1974
Tetraphyllidea indet.	Armstrong 1974
<i>Tellervotrema armstrongi</i>	Armstrong 1974
<b><i>Nezumia cyrano</i></b>	
<i>Dissasaccus laevis</i>	Blend 1996
<i>Lepidapedon nezumiatis</i>	Blend 1996
<i>Tellervotrema armstrongi</i>	Blend 1996

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Trematoda indet.	Blend 1996
<b><i>Sphagemacrurus grenadae</i></b>	
<i>Dissosaccus laevis</i>	Armstrong 1974
<i>Podocotyle nimoyi</i>	Armstrong 1974
Moridae	
<b><i>Laemonema barbatulum</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Eurycreadium vitellosum</i>	Manter 1934
<i>Lepidapedon elongatum</i>	Manter 1934
<i>Stephanostomum lineatum</i>	Manter 1934
Myctophidae	
<b><i>Benthoosema suborbitale</i></b>	
Tetraphyllidea indet.	This Study
Digenea indet.	This Study
<i>Floridosentis</i> spp.	This Study
<b><i>Ceratoscopelus warmingii</i></b>	
Cestoda indet.	This Study
Digenea indet.	This Study
<b><i>Diaphus dumerilii</i></b>	
Anisakidae	This Study
Spirurida indet.	This Study
<i>Sarcotretes scopelii</i>	This Study
<b><i>Diaphus lucidus</i></b>	
<i>Anisakis</i> spp.	This Study
Tetraphyllidea indet.	This Study
<i>Tentacularia coryphaenae</i>	This Study
Digenea indet.	This Study
<b><i>Diaphus mollis</i></b>	
<i>Helicometra</i> spp.	This Study
<b><i>Lampanyctus alatus</i></b>	
<i>Tentacularia coryphaenae</i>	This Study
<i>Dissosaccus laevis</i>	This Study
Digenea indet.	This Study
<b><i>Lepidophanes guentheri</i></b>	
Anisakidae	This Study
<i>Tentacularia coryphaenae</i>	This Study
Opecoelidae	This Study
<i>Helicometrina nimia</i>	This Study
Digenea indet.	This Study

<b><i>Myctophum affine</i></b>	
<i>Floridosentis</i> spp.	This Study
<b><i>Notoscopelus resplendens</i></b>	
<i>Floridosentis</i> spp.	This Study
Ogcocephalidae	
<b><i>Dibranchus atlanticus</i></b>	
<i>Hemiperina nicollia</i>	Manter 1934
Ophidiidae	
<b><i>Brotula barbata</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Gonocerca crassa</i>	Manter 1934
<i>Lissoloma brotulae</i>	Manter 1934
<i>Siphodernia brotulae</i>	Manter 1934
<i>Sterrhurus floridensis</i>	Manter 1934
<b><i>Monomitopus agassizii</i></b>	
<i>Megenteron manteri</i>	Harris and Dronen 1999
Paralichthyidae	
<b><i>Ancylopsetta dilecta</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<b><i>Hippoglossina oblonga</i></b>	
<i>Adinosoma robustum</i>	Manter 1946
<i>Gonocerca crassa</i>	Manter 1934
<i>Sterrhurus robustus</i>	Manter 1934
Percophidae	
<b><i>Bembrops gobioides</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
Peristediidae	
<b><i>Peristedion brevirostre</i></b>	
<i>Brachyenteron peristedioni</i>	Manter 1934
<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Dissosaccus laevis</i>	Manter 1946
<i>Sterrhurus laevis</i>	Manter 1934
<b><i>Peristedion longispatha</i></b>	
<i>Dissosaccus laevis</i>	Manter 1946
<i>Sterrhurus laevis</i>	Manter 1934
<b><i>Peristedion miniatum</i></b>	

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<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Dissosaccus laevis</i>	Manter 1946
<i>Lomasoma gracilis</i>	Manter 1934
<i>Sterrhurus laevis</i>	Manter 1934
Phosichthyidae	
<b><i>Pollichthys maui</i></b>	
<i>Anisakis brevispiculata</i>	Andres <i>et al.</i> 2016
<i>Hysterothylacium fortalezae</i>	Andres <i>et al.</i> 2016
Tetraphyllidea ident.	Andres <i>et al.</i> 2016
<b><i>Polymetme corythaeola</i></b>	
<i>Anisakis typica</i>	Andres <i>et al.</i> 2016
Phycidae	
<b><i>Phycis chesteri</i></b>	
<i>Adinosoma robustum</i>	Manter 1946
<i>Lepidapedon elongatum</i>	Manter 1934
<i>Podocotyle pearsei</i>	Manter 1934
<i>Sterrhurus robustus</i>	Manter 1934
<b><i>Urophycis cirrata</i></b>	
<i>Stephanostomum lineatum</i>	Manter 1934
<i>Sterrhurus floridensis</i>	Manter 1934
<b><i>Urophycis regia</i></b>	
<i>Adinosoma robustum</i>	Manter 1946
<i>Derogenes varicus</i>	Manter 1934
<i>Dinosoma rubrum</i>	Manter 1934
<i>Gonocerca crassa</i>	Manter 1934
<i>Gonocerca phycidis</i>	Manter 1937
<i>Lecithochirium</i> spp.	Manter 1934
<i>Lomasoma wardi</i>	Manter 1934
<i>Stephanostomum lineatum</i>	Manter 1934
<i>Sterrhurus robustus</i>	Manter 1934
Polymixiidae	
<b><i>Polymixia lowei</i></b>	
<i>Sterrhurus floridensis</i>	Manter 1934
Scombrlacidae	
<b><i>Scombrlabrax heterolepis</i></b>	
Nematoda indet.	This Study
Tetraphyllidea indet.	This Study

<i>Tentacularia coryphaenae</i>	This Study
<i>Dissosaccus laevis</i>	This Study
Hemiuridae	This Study
Opecoelidae	This Study
Digenea indet.	This Study
<i>Floridosentis</i> spp.	This Study
<i>Caligus</i> spp.	This Study
<i>Hepatoxylon trichiuri</i>	This Study
Scorpaenidae	
<b><i>Pontinus longispinis</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<b><i>Scorpaena maderensis</i></b>	
<i>Dissosaccus laevis</i>	Manter 1946
Sebastidae	
<b><i>Helicolenus dactylopterus</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Derogenes varicus</i>	Manter 1934
<i>Dissosaccus laevis</i>	Manter 1946
<i>Opecoelina helicoleni</i>	Manter 1934
<i>Sterrhurus laevis</i>	Manter 1934
<b><i>Trachyscorpia cristulata</i></b>	
<i>Derogenes varicus</i>	Manter 1934
<i>Opecoelina scorpanae</i>	Manter 1934
Serranidae	
<b><i>Hyporthodus niveatus</i></b>	
<i>Prosorhynchus ozakii</i>	Manter 1937
<i>Stephanostomum microstephanum</i>	Manter 1946
<b><i>Pronotogrammus</i> spp.</b>	
<i>Cymbephallus vulgaris</i>	Manter 1934
<i>Sterrhurus profundus</i>	Manter 1934
<i>Distomum fenestratum</i>	Manter 1934
Setarchidae	
<b><i>Setarches guentheri</i></b>	
<i>Derogenes varicus</i>	Manter 1934
<i>Gonocerca crassa</i>	Manter 1934
Sternoptychidae	

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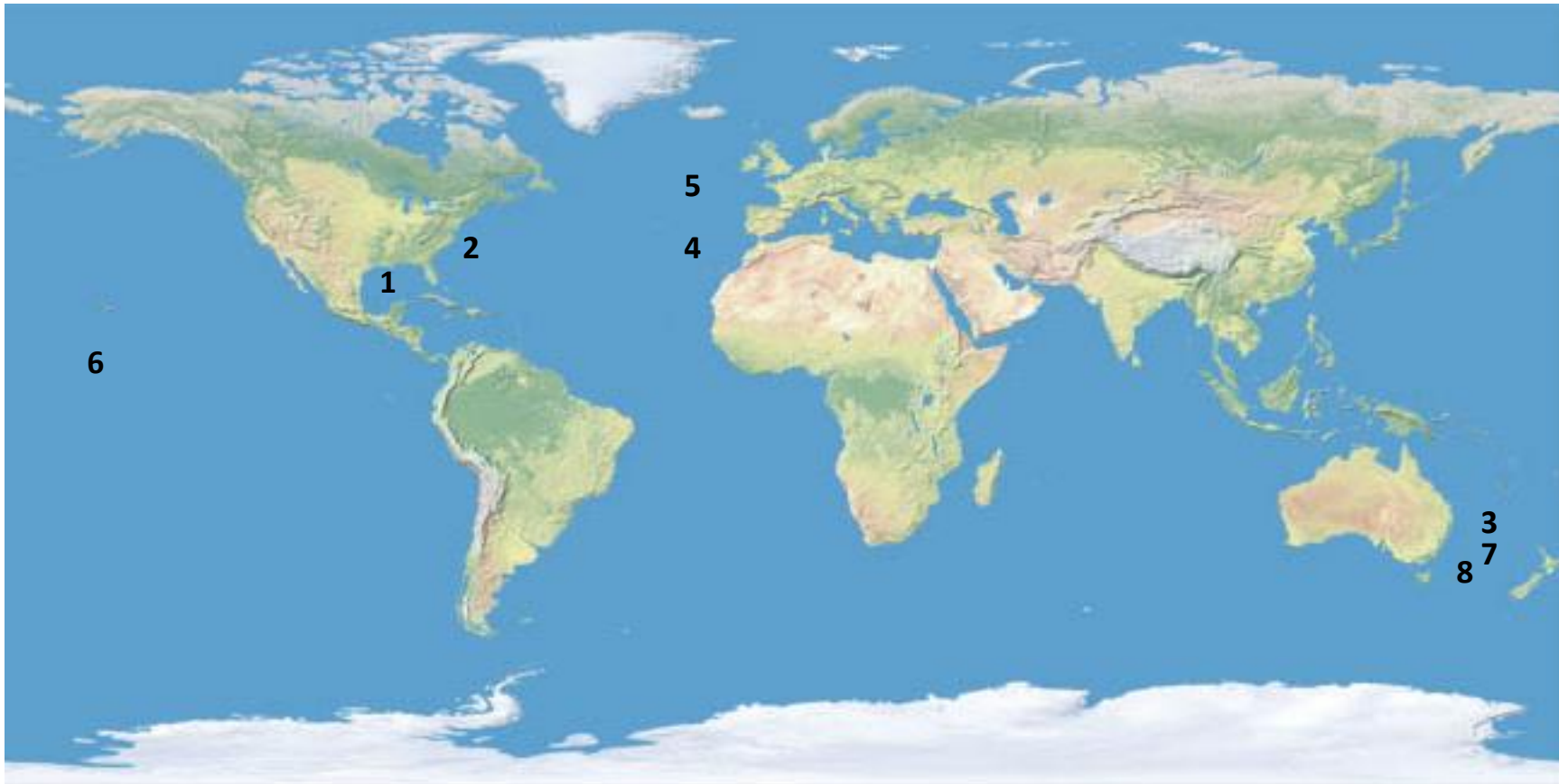
<b><i>Argyrolepecus aculeatus</i></b>	
<i>Anisakis brevispiculata</i>	Andres <i>et al.</i> 2016
Anisakidae	This Study
<i>Contracaecum</i> spp.	This Study
Cestoda indet.	This Study
Digenea indet.	This Study
<i>Floridosentis</i> spp.	This Study
Hemiuridae	This Study
<i>Hysterothylacium fortalezae</i>	Andres <i>et al.</i> 2016
<b><i>Argyrolepecus hemigymnus</i></b>	
Nematoda indet.	This Study
Digenea indet.	This Study
<b><i>Polyipnus clarus</i></b>	
<i>Anisakis brevispiculata</i>	Andres <i>et al.</i> 2016
<i>Hysterothylacium fortalezae</i>	Andres <i>et al.</i> 2016
Tetraphyllidea ident.	Andres <i>et al.</i> 2016
<b><i>Sternoptyx diaphana</i></b>	
Lecanicephalidae	This Study
<i>Paranybelinia otobothrioides</i>	This Study
Tetraphyllidea indet.	This Study
<i>Tentacularia coryphaenae</i>	This Study
<i>Helicometra</i> spp.	This Study
Digenea indet.	This Study
<i>Sarcotretes scopelii</i>	This Study
<b><i>Sternoptyx pseudobscura</i></b>	
Nematoda indet.	This Study
Tetraphyllidea indet.	This Study
<i>Tentacularia coryphaenae</i>	This Study
Digenea indet.	This Study
<i>Prosorhyncus</i> spp.	This Study
Didimyzoidae Type 1	This Study
Didimyzoidae Type 2	This Study
Hemiuridae	This Study
<i>Lecithochirum</i> spp.	This Study
<i>Hirudinella</i> spp.	This Study
Lepocreadiidae	This Study
<i>Floridosentis</i> spp.	This Study
<i>Sarcotretes scopelii</i>	This Study
Stomiidae	
<b><i>Echiostoma barbatum</i></b>	



<i>Anisakis</i> spp.	This Study
<b><i>Photostomias guernei</i></b>	
<i>Contracaecum</i> spp.	This Study
Synaphobranchidae	
<b><i>Synaphobranchus oregoni</i></b>	
<i>Hypertrema ambovatum</i>	Overstreet and Martin 1974
Trichiuridae	
<b><i>Benthodesmus simonyi</i></b>	
<i>Cymbephallus vulgaris</i>	Manter 1934

## Deep-Pelagic Parasites

APPENDIX FIGURE 1. Approximate locations of studies that have contributed host-parasite interactions that are included in appendix table 2. 1 = Andres et al. 2016, 2 = Gartner and Zwerner 1989, 3 = Heath 1989, 4 = Hogans 1988, 5 = Mordvinova 1988, 6 = Rohde 1988, 7 = Rohde et al. 1995, 8 = Rohde and Williams 1997. Mordvinova 2000 is included in the table, but did not have a specified location.



APPENDIX Table 2. Global host-parasite interaction list for all fishes examined in this study. A – acanthocephalan, C – cestode, Co – copepod, D - digenean, M – monogenean, N – nematode

Species	Parasite Taxon	Source
<b><i>Argyrolepecus aculeatus</i></b>		
<i>Anisakis brevispiculata</i>	N	Andres et al. 2016
<i>Hysterothylacium fortalezae</i>	N	Andres et al. 2016
Pseudophyllidean plerocercoid	C	Heath 1989
<i>Heteronybelinia robusta</i>	C	Gartner and Zwerner 1989
<i>Anisakis</i> sp. (larva)	N	Heath 1989
<i>Lampritrema miescheri</i>	D	Heath 1989
Nematoda indet.	N	This Study
<i>Contracaecum</i> spp.	N	This Study
Cestoda	C	This Study
Hemiuridae	D	This Study
Digenea indet.	D	This Study
<i>Floridosentis</i> spp.	A	This Study
<b><i>Argyrolepecus hemigymnus</i></b>		
Nematoda indet.	N	This Study
Digenea indet.	D	This Study
<b><i>Benthoosema suborbitale</i></b>		
Tetraphyllidea indet.	C	This Study
Digenea indet.	D	This Study
<i>Floridosentis</i> spp.	A	This Study
<b><i>Ceratoscopelus warmingii</i></b>		
<i>Neorhadinorhynchus myctophumi</i>	A	Mordvinova 2000
<i>Rhadinorhynchus</i> sp.	A	Mordvinova 2000
<i>Scolex pleuronectis</i>	C	Heath 1989
<i>Heterovitellus atlanticus</i>	C	Mordvinova 2000
Phyllobothriidae sp.	C	Mordvinova 2000
<i>Nybelinia</i> sp. (larva)	C	Mordvinova 2000
Monogenea sp.	M	Rohde et al. 1995
<i>Reimericotyle ceratoscopeli</i>	M	Rohde 1988
<i>Anisakis simplex</i>	N	Mordvinova 2000
<i>Anisakis</i> sp. (larva)	N	Heath 1989
<i>Ascarophis</i> sp. (larva)	N	Heath 1989
Spiurata sp.	N	Mordvinova 2000
<i>Lethadena profunda</i>	D	Heath 1989
<i>Lethadena</i> sp.	D	Mordvinova 2000
Cestoda indet.	C	This Study
Digenea indet.	D	This Study

Deep-Pelagic Parasites

<b><i>Chauliodus sloani</i></b>		
Pseudophyllidean pleroceroid	C	Gartner and Zwerner 1989
Tetraphyllidea indet.	C	Gartner and Zwerner 1989
<i>Scolex pleuronectis</i>	C	Heath 1989
<i>Nybelinia</i> sp. (larva)	C	Gartner and Zwerner 1989
<i>Tentacularia coryphaenae</i>	C	Gartner and Zwerner 1989
<i>Contracaecum</i> sp.	N	Gartner and Zwerner 1989
Digenea sp.	D	Gartner and Zwerner 1989
Hirudinellidae sp.	D	Gartner and Zwerner 1989
<i>Anisakis</i> sp. (larva)	N	Gartner and Zwerner 1989
<b><i>Diaphus dumerilii</i></b>		
<i>Rhadinorhynchus</i> sp.	A	Mordvinova 2000
<i>Scolex pleuronectis</i>	C	Mordvinova 2000
Phyllobothriidae sp.	C	Mordvinova 2000
<i>Anisakis simplex</i>	N	Mordvinova 2000
Anisakidae	N	This Study
Spirurida	N	This Study
<i>Sarcotretes scopelii</i>	Co	This Study
<b><i>Diaphus lucidus</i></b>		
<i>Anisakis</i> sp.	N	This Study
Tetraphyllidea indet.	C	This Study
<i>Tentacularia coryphaenae</i>	C	This Study
<b><i>Diaphus mollis</i></b>		
<i>Helicometra</i> sp.	D	This Study
<b><i>Echiostoma barbatum</i></b>		
<i>Anisakis</i> sp.	N	This Study
<b><i>Lampanyctus alatus</i></b>		
<i>Nybelinia</i> sp. (larva)	C	Heath 1989
Nematoda	N	This Study
<i>Tentacularia coryphaenae</i>	C	This Study
<i>Dissosaccus laevis</i>	D	This Study
Trematoda metacercariae	D	This Study
<b><i>Lepidophanes guentheri</i></b>		
Anisakidae	N	This Study
Trypanorhyncha indet.	C	This Study
<i>Helicometrina nimia</i>	D	This Study
Digenea metacercariae	D	This Study
<b><i>Myctophum affine</i></b>		
<i>Neorhadinorhynchus myctophumi</i>	A	Mordvinova 1988
<i>Scolex pleuronectis</i>	C	Mordvinova 2000
<i>Pseudomazocraeoides ceratoscopeli</i>	M	Mordvinova 2000

<i>Anisakis simplex</i>	N	Mordvinova 2000
<i>Pseudomonilicaecum</i> sp.	D	Mordvinova 2000
<i>Floridosentis</i> spp.	A	This Study
<b><i>Nealotus tripes</i></b>		
Anisakidae	N	This Study
Tetraphyllidea indet.	C	This Study
<i>Scolex pleuronectis</i>	C	This Study
Trypanorhyncha indet.	C	This Study
<i>Helicometrina nimia</i>	D	This Study
Digenea indet.	D	This Study
<b><i>Notoscopelus resplendens</i></b>		
<i>Neorhadinorhynchus myctophumi</i>	A	Mordvinova 2000
<i>Bolobosoma</i> sp.	A	Heath 1989
<i>Rhadinorhynchus</i> sp.	A	Mordvinova 2000
Trypanorhynch sp.	C	Heath 1989
<i>Scolex pleuronectis</i>	C	Mordvinova 2000
<i>Polyipnicola hygophi</i>	M	Rohde and Williams 1987
<i>Pseudomazocraeoides ceratoscopeli</i>	M	Mordvinova 2000
<i>Anisakis simplex</i>	N	Mordvinova 2000
<i>Hysterothylacium</i> sp. (larva)	N	Heath 1989
<i>Ascarophis</i> sp. (larva)	N	Heath 1989
<i>Pseudomonilicaecum</i> sp.	D	Mordvinova 2000
<i>Lethadena profunda</i>	D	Heath 1989
<i>Sarcotretes scopeli</i>	Co	Hogans 1988
<i>Floridosentis</i> spp.	A	This Study
<b><i>Photostomias guernei</i></b>		
Tetraphyllidea sp.	C	Gartner and Zwerner 1989
Nematoda sp.	N	Gartner and Zwerner 1989
Rhabdochonidae sp.	N	Gartner and Zwerner 1989
<i>Johnstonmawsonia</i> sp.	N	Gartner and Zwerner 1989
<i>Contracaecum</i> sp.	N	This Study
<i>Sarcotretes scopeli</i>	Co	Gartner and Zwerner 1989
<b><i>Scombrolabrax heterolepis</i></b>		
Nematoda	N	This Study
Tetraphyllidea indet.	C	This Study
<i>Scolex pleuronectis</i>	C	This Study
Trypanorhyncha indet.	C	This Study
<i>Dissosaccus laevis</i>	D	This Study
Hemiuridae	D	This Study
Opecoelidae	D	This Study
Digenea indet.	D	This Study

Deep-Pelagic Parasites

<i>Floridosentis</i> spp.	A	This Study
<i>Caligus</i> spp.	Co	This Study
<b><i>Sigmops elongatus</i></b>		
<i>Nybelinia yamagutii</i>	C	Gartner and Zwerner 1989
Nematoda sp.	N	Gartner and Zwerner 1989
Anisakidae sp.	N	Gartner and Zwerner 1989
<i>Anisakis</i> sp. (larva)	N	Gartner and Zwerner 1989
<i>Procamallanus</i> spp.	N	This Study
Nematoda	N	This Study
<i>Tentacularia coryphaenae</i>	C	This Study
<i>Nybelinia</i> spp.	C	This Study
Digenea indet.	D	This Study
<i>Floridosentis</i> spp.	A	This Study
<i>Sarcotretes scopelii</i>	Co	This Study
<b><i>Sternoptyx diaphana</i></b>		
Tetraphyllidea sp.	C	Gartner and Zwerner 1989
<i>Ceratobothrium xanthocephalum</i>	C	Gartner and Zwerner 1989
<i>Heteronybelinia robusta</i>	C	Gartner and Zwerner 1989
<i>Nybelinia robusta</i>	C	Gartner and Zwerner 1989
<i>Tentacularia coryphaenae</i>	C	Gartner and Zwerner 1989
<i>Anisakis</i> sp. (larva)	N	Gartner and Zwerner 1989
<i>Pseudoterranova</i> sp.	N	Gartner and Zwerner 1989
Digenea sp.	D	Gartner and Zwerner 1989
<i>Sarcotretes scopeli</i>	Co	Hogans 1988
Nematoda	N	This Study
Lecanicephalidae	C	This Study
Trypanorhyncha indet.	C	This Study
Tetraphyllidea indet.	C	This Study
<i>Helicometra</i> spp.	D	This Study
Digenea metacercariae	D	This Study
<i>Sarcotretes scopelii</i>	Co	This Study
<b><i>Sternoptyx pseudobscura</i></b>		
Nematoda	N	This Study
Tetraphyllidea indet.	C	This Study
Trypanorhyncha indet.	C	This Study
<i>Prosorhyncus</i> spp.	D	This Study
Didimyzoidae Type 1	D	This Study
Didimyzoidae Type 2	D	This Study
Hemiuridae	D	This Study
<i>Lecithochirum</i> sp.	D	This Study
<i>Hirudinella</i> sp.	D	This Study

Lepocreadiidae	D	This Study
<i>Floridosentis</i> sp.	A	This Study
<i>Sarcotretes scopelii</i>	Co	This Study