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Trophic Ecology and Functional Morphology of the Scaleless Black Dragonfishes (Family Stomiidae; Subfamily Melanostomiinae)

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Thesis of
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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

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ABSTRACT

Dragonfishes (Family Stomiidae) are considered the most numerically important and diverse taxon of higher-level meso- and bathypelagic predators in oceanic food webs, with the subfamily Melanostomiinae contributing 220 of the 317 species. The Stomiidae is also the most speciose fish family in the Gulf of Mexico. The relationship between diversity (both systematic and morphological) and feeding of the Melanostomiinae has not been previously examined due to sample size limitation. Here the diet and morphology of 16 species of dragonfishes in the Gulf of Mexico was examined to address the question, "Does the extraordinary speciation in this most-diverse deep-pelagic fish clade reflect specialization in its primary limiting resource – food?" Gut content analysis revealed three feeding guilds by major prey taxon, with most species grouped into a piscivorous guild and two other guilds that selected for cephalopods. Piscivorous dragonfishes were further categorized into feeding groups by fish family, where four feeding groups were identified. Within this feeding guild, most dragonfishes were grouped into a myctophid-eating cluster, with three additional clusters including predation upon bristlemouths (Family Gonostomatidae), oceanic basslets (Family Howellidae), bigscales (Family Melamphaidae), and dragonfishes. Regarding functional morphology, five morphotype groups were identified, with dissimilarity driven by barbel length, vertical oral gape, and horizontal maxillary oral gape. There were no obvious morphological-dietary relationships amongst melanostomiines, suggesting that morphology and diet are not strictly correlated in extant species. Diet specialization may have influenced the hyperspeciation exhibited by melanostomiines, but other factors like species-specific bioluminescence, interspecific competition, and predator avoidance also influenced this speciation.

Keywords: trophic ecology, diet analysis, morphology, morphometrics, morphological-dietary relationships

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1. INTRODUCTION

1.1 Systematics

Deep-sea dragonfishes are classified as Class Actinopterygii, Order Stomiiformes, Family Stomiidae, and are distributed throughout the world oceans (Gibbs 1969; Fink 1985; Sutton 2003; Kenaley 2007). There are two historical classifications of dragonfishes. Weitzman (1974) classified six families, including the Astronesthidae (snaggletooths), Chauliodontidae (viperfishes), Idiacanthidae (black dragonfishes), Malacosteidae (loosejaws), Melanostomiatidae (scaleless dragonfishes), and Stomiatidae (barbeled dragonfishes). Stomiatidae was later revised to Stomiidae, per Latin nomenclatural rules. Fink (1985) later classified all dragonfishes in one family (Stomiidae, the senior Family name), with six subfamilies derived from the original classification (Figure 1). The Stomiidae is the most speciose fish family within the Gulf of Mexico with 18 genera and 83 recorded species (Sutton & Hopkins 1996a). Stomiids comprise the majority of species within the Order Stomiiformes, with 317 of the 453 species. The subfamily of focus in this study (Melanostomiinae) is the largest subfamily, comprising 220 of the 317 species within the family Stomiidae (Fricke et al. 2021). Moreover, genus *Eustomias,* within the subfamily Melanostomiinae, accounts for half of the species within the Stomiidae (Sutton 2003).

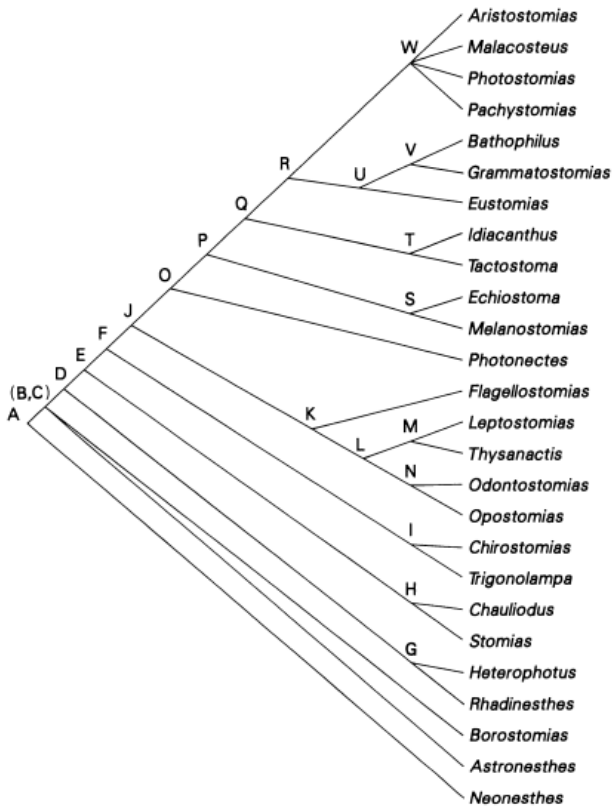

Figure 1. Cladogram of the interrelationships of 26 stomiid genera with clades A through W representing genera (from Fink, 1985).

1.2 Review of Life History and Ontogenetic Morphology of Melanostomiines

The life cycle of stomiid fishes includes egg, pre-larva, larva, post-larva, adolescent, and adult (Beebe & Crane 1939). Dragonfishes are oviparous, with planktonic eggs and larvae occurring in the upper water column (Kawaguchi & Moser 1984; Watson & Moser 2011). As development progresses, stomiids undergo ontogenetic changes in foraging ability, swimming, and body size (Hunter 1976; Margulies 1989). Eggs of dragonfishes have only been identified for three genera (*Chauliodus*, *Stomias*, and *Tactostoma*). Of these, *Tactostoma* is classified within the subfamily Melanostomiinae. The eggs of *Tactostoma* are spherical, contain one oil globule, have a wide perivitelline space, and have a smooth chorion (Moser 1996; Richards 2006; Watson & Moser 2011). The larvae of 18 genera of dragonfishes have been identified and studied. Stomiid larvae are typically slender and elongate, with some genera more deep-bodied than others. Larvae of dragonfishes range in pigmentation, from no pigmentation to heavy pigmentation. The larvae

of some species have trailing guts that can be up to 100% of their body length. The eyes of larval stomiids are elliptical and may be stalked (Watson & Moser 2011).

Each subfamily has diagnostic larval characteristics. Melanostomiinae larvae are elongate with guts that either do not trail or slightly trail with an exception for *Eustomias* larvae which have a trailing gut. The head of melanostomiines is moderately large with small oval eyes. Melanostomiine larvae are moderate to heavily pigmented with melanophores on the dorsal surface of each myomere and on the hypaxial myosepta (Richards 2006; Watson & Moser 2011). *Bathophilus* larvae are deep-bodied with one or more dorsal melanophores per myomere. *Bathophilus* larvae have moderate eye size and have a large slightly trailing gut. The barbel forms in late postflexion *Bathophilus* larvae. The gut of larval *Echiostoma* is voluminous and does not trail. The shape of the eyes of *Echiostoma* range from elliptical to round. *Eustomias* larvae have a trailing gut, a flat elongate head with a broad snout, moderately sized slightly elliptical eyes, and a slender round body. *Flagellostomias* larvae have a large, slightly trailing gut, large deep head with a sloped snout, and large jaws. Larvae of *Leptostomias* have a slender slightly trailing gut, small eyes, and both the head and body are deep. *Melanostomias* larvae have a short head, short snout, and a slender body. *Photonectes* larvae have a deep body, moderate head length, moderate snout length, and small highly elliptical eyes (Richards 2006).

Larval stomiids undergo metamorphosis, transforming into the juvenile stage at around 20 mm in most melanostomiids (Beebe & Crane 1939; Kawaguchi & Moser 1984). In the adolescent stage of melanostomiids, the intestine is enclosed within the body cavity, a loss of larval pigment spots occurs, the organs approach adult conditions, and the fin rays fully develop. The adolescent stage is highlighted by the growth of the organism with a size range of 20 – 30 mm in most melanostomiids and 30 – 50 mm in *Flagellostomias*, *Leptostomias*, and *Eustomias* (Beebe & Crane 1939). Stomiids descend to the meso- and bathypelagic zones at some point in the juvenile stage as they grow and become more easily detected by epipelagic predators (Moser 1996; Sutton 2013). Juveniles of melanostomiids look similar to adults externally in the latter end of adolescence but juveniles are smaller with undeveloped reproductive organs, thus indicating immaturity (Beebe & Crane 1939). The reproductive ecology of dragonfishes is understudied due to inadequate sample size of mature adults resulting from the gear type most commonly used (but see Marks et al., 2020). There have been a few reproductive studies indicating size at maturity in some stomiid species.

For example, females of *Tactostoma macropus* spawn near 301 mm standard length (SL; Fisher & Pearcy 1983) and *Photostomias guernei* become mature at 125 mm SL in waters off Hawaii (Clarke 1974). At 50% maturity, females of *Eustomias hypopsilus*, *Malacosteus niger*, *Chauliodus sloani*, *Eustomias schmidti*, *and Echiostoma barbatum* were 106.4 mm, 110.9 mm, 151.9 mm, 166.6 mm, and 200.5 mm SL, respectively (Marks et al. 2020). Juvenile and adult dragonfishes exhibit diel vertical migration (DVM), ostensibly to feed (Gibbs 1969; Clarke 1974; Clarke 1982; Sutton & Hopkins 1996a; Sutton et al. 2010).

1.3 Trophic Ecology of Dragonfishes

Trophic ecology is the study of how energy and nutrients are exchanged on ecological scales and accounts for mechanistic and evolutionary processes (Garvey & Whiles 2016). Aspects of trophic ecology involve the nature of the diet, feeding chronology, feeding selectivity, biochemical composition of the prey (e.g., caloric content), feeding behaviors, and adaptations to feeding at depth (Gartner et al. 1997). The nature of the diet involves the types of prey an organism eats, which is a function of feeding strategy. Hyatt (1979) described some species as being generalists, which consume any organism they come across, or as specialists, which only consume a specific prey type. Feeding strategies influence how selective predators are with respect to prey. Many fishes selectively feed on larger prey, enhancing growth and decreasing mortality as fishes become larger (Keeley & Grant 2001; Schabetsberger et al. 2003). Originally, dragonfishes were thought to have a wide range in diet, utilizing a generalist feeding strategy (Beebe & Crane 1939; Haffner 1952; Merrett & Roe 1974). This view has evolved with increased interest in the extent of prey selectivity in deep-sea animals. In order to categorize prey selectivity, feeding guilds have been established by ichthyologists to group together species that exploit the same prey items. Three main feeding guilds exist for deep-pelagic species: micronektonivores, zooplanktivores, and generalists (Gartner et al. 1997).

A second aspect of trophic ecology is feeding chronology, which describes when and how often species feed. Predation by stomiids is thought to occur mostly in the epipelagic zone at night (Sutton & Hopkins 1996b; Hopkins & Sutton 1998), with lanternfishes (Myctophidae) as dominant prey. Myctophids vertically migrate to the epipelagic zone at night to feed on zooplankton, and thus myctophid predators, such as dragonfishes, follow (Hopkins & Gartner 1992; Sutton & Hopkins 1996b). Studies have investigated the metabolic rates of both lanternfishes and

dragonfishes. Results showed that dragonfishes have lower metabolic rates than lanternfishes, even though both species vertically migrate (Torres et al. 1979; Childress et al. 1980).

There is an extensive scientific literature on trophic ecology and feeding in deep-sea fishes. Diet, morphological specializations for feeding, and feeding guilds were the primary focus in earlier trophic ecology studies (reviewed by Drazen & Sutton 2017). An extensive review of feeding at depth was conducted by Gartner et al. (1997), covering feeding habits, patterns in the diet, sources of food, and energetics of species in the deep sea. Previously, little was known about feeding habits of deep-sea fishes, with few investigations of feeding in the mesopelagic zone and no studies into the bathypelagic trophic complex (Borodulina 1972). Clarke (1982) conducted a study in Hawaii on feeding habits of stomiids. Earlier midwater (i.e. mesopelagic zone) trophic studies focused on numerically dominant zooplanktivorous groups, with little focus on deep-sea predators. Hopkins et al. (1996) conducted a trophic analysis on the midwater fish assemblage in the eastern Gulf of Mexico that included common genera within the Melanostomiinae. Sutton & Hopkins (1996b) conducted a trophic study specifically on the Gulf of Mexico stomiid assemblage, providing information on diet, strategies, feeding selectivity, and impacts of stomiid predation. Through these studies, it was determined that most dragonfishes fed primarily on myctophids and only a small portion of the diets consisted of fishes from the families Gonostomatidae, Sternoptychidae, Bregmacerotidae, Argentinidae, and the order Beryciformes. Common eastern Gulf of Mexico myctophid species identified in the stomiid diets were *Diaphus dumerilii*, *Notolychnus valdiviae*, *Lampanyctus alatus*, *Lepidophanes guentheri*, and *Myctophum affine* (Sutton & Hopkins 1996b). Trophic ecology studies have advanced in the last twenty years, with the traditional gut content analyses being complemented by new approaches (e.g., biomarkers and isotopic analyses; Choy et al. 2012; Drazen & Sutton 2017).

Trophic studies within the family Stomiidae have generally pooled species into genera due to low sample sizes, excepting three dominant species, none of which are melanostomiines. Currently, no trophic studies have solely focused on the Melanostomiinae. This study aimed to focus on dominant species of the Melanostomiinae within the Gulf of Mexico, facilitated by increased sample size resulting from intensive sampling. According to Hyslop (1980), stomach content analyses represent only a "snap-shot" of what an animal has eaten recently. Thus, obtaining stomach content data from numerous specimens and assessing feeding chronology through

variable digestion of prey provides information currently lacking on the "what, when, and where" of melanostomiine feeding. Additionally, more data from trophic analyses (e.g., quantitative gut content analysis and bioenergetic modeling) will aid in estimating feeding rates of deep-sea fishes (Drazen & Sutton 2017). Sutton & Hopkins (1996b) noted a correlation between the barbel structure and diet of dragonfishes, finding that species with reduced barbels preyed on zooplankton or larger invertebrates and species with more developed barbels preyed on fishes. Other feeding morphometric characteristics have yet to be analyzed with respect to morphological-dietary relationships of stomiids.

1.4 Functional Morphology of Stomiidae

Functional morphology involves the study of the physical characteristics of an organism and how they relate to that organism's ecology (Bock 1994). Studies of functional morphology are difficult to perform with deep-sea taxa, leaving many areas (e.g., behavioral aspects of morphology) unexplored. Most of the data available on the associations between morphology and feeding in deep-sea taxa are derived through dissection and manipulation of preserved specimens (Tchernavin 1953; Günther & Deckert 1959). Members within the Stomiiformes are morphologically diverse, ranging from elongate and slender bodies to laterally compressed and deep-bodied. Dragonfishes are generally elongate and slender. The family Stomiidae has no true gill rakers in adults, photophores without lumen or ducts, a mental barbel along the hyoid apparatus, and most are darkish in color (Nelson et al. 2016). Characteristics of the subfamily Melanostomiinae include an absence of scales, a dorsal fin origin over the anal fin and far behind the pelvic fin, and most with the barbel adorned on the chin (Morrow & Gibbs 1964; Nelson et al. 2016). Sutton & Hopkins (1996b) outlined the Stomiidae trophic lineage and phylogeny with basal and derived characters (Figure 2).

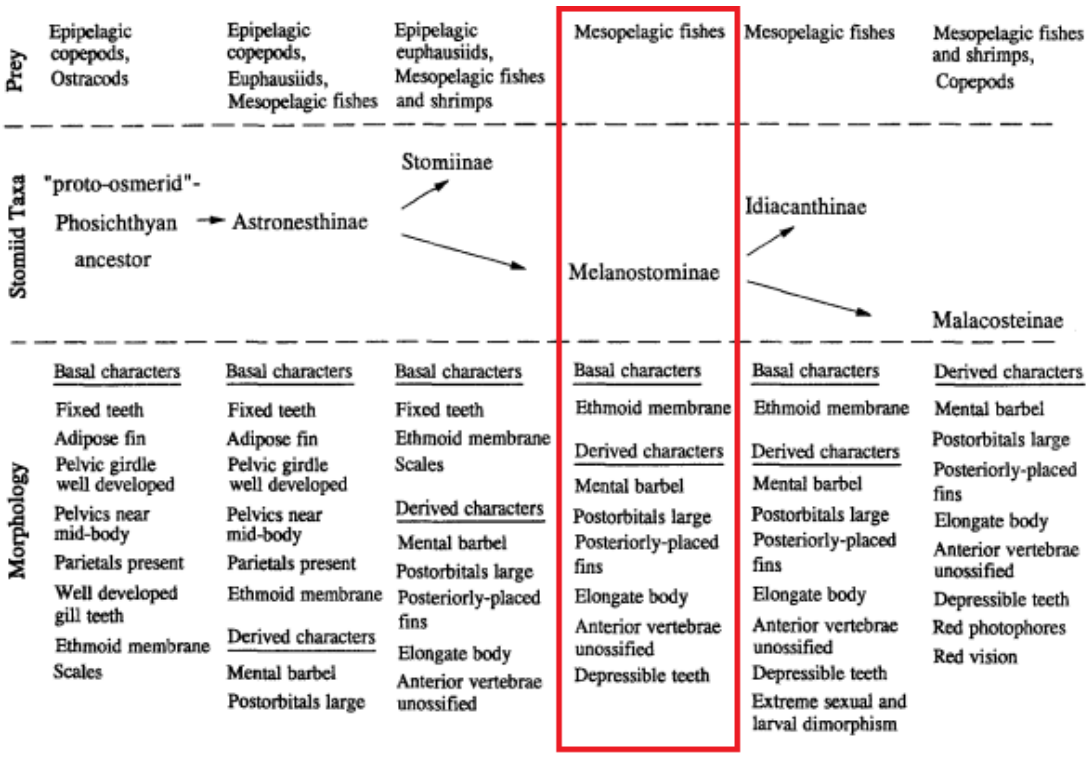

Figure 2. Proposed trophic lineage diagram with morphological characters of the subfamilies within the Stomiidae with the Melanostomiinae highlighted (from Sutton & Hopkins, 1996b).

The physical characteristics of dragonfishes exemplify a predatory lifestyle in the deep sea. First, dentition is an important factor in determining the relative prey size preference of organisms. Small-item predators usually have more teeth that are small, while large-item predators have fewer, longer jaw teeth. Dragonfishes have large mouths with a limited number of fang-like teeth that aid in larger prey capture (Sutton 2005). The dentition of the malacosteine *Aristostomias scintillans* was determined to have a nanostructured design of the transparent teeth which show no contrast to their darker body or dark waters around (Velasco-Hogan et al. 2019). The lack of contrast enables the teeth to be practically invisible, which is thought to allow *Aristostomias scintillans* to be an effective successful predator (Velasco-Hogan et al. 2019). Thus, dentition characteristics are important, as encounters with prey can be rare in the deep sea.

An additional feature of a predatory lifestyle is the form of dragonfish bioluminescence. Most dragonfishes lure prey by use of a chin barbel bearing luminescent structures at the terminus. A recent study showed that the tissue forming the chin barbel in *Stomias boa* has adrenaline within the tissue, strongly supporting the hypothesis of adrenergic control of light emission (Mallefet et

al. 2019). Most deep-sea fishes have visual pigments sensitive to blue bioluminescence and dim residual sunlight. Three derived species (*Aristostomias* sp., *Malacosteus niger*, and *Pachystomias microdon*) not only emit blue bioluminescence but also emit a far-red bioluminescence (Douglas et al. 1998). *Pachystomias microdon* is a melanostomiine and the far-red bioluminescence allows this species to actively hunt prey, as red light is visually undetectable by other deep-sea animals. Both *Aristostomias* and *Pachystomias* emit red bioluminescence and detect it using three or four long-shifted rhodopsins (Partridge & Douglas 1995; Douglas et al. 1998).

A detailed description of the osteology of stomiid jaws and dentition was provided by Fink (1985). Only melanostomiine genera will be discussed here. Figure 3 in that work illustrates the jaws and teeth of four melanostomiine species for reference. Most stomiid jaws are slender and elongate, but some genera such as *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis* have jaws that are short and heavy. The supramaxillae of *Chirostomias* and *Trigonolampa* are reduced. The supramaxilla of other stomiid genera are variously sized but never as small as *Chirostomias* and *Trigonolampa*. In *Echiostoma*, the supramaxilla and antorbital are rugose. *Opostomias* has a large foramen located in the premaxilla that a mandibular tooth extends into when the mouth is closed. Other stomiids do not have the foramen and have teeth that extend anterior to the premaxilla. In *Bathophilus*, *Eustomias*, *Grammatostomias*, *Pachystomias*, *Tactostoma*, and *Thysanactis*, the mesopterygoid is absent, while present in other stomiiforms. *Photonectes* species have an elongate posterior process of the anguloarticular. *Eustomias* is distinctive in jaw osteology compared to most teleosts. The ectopterygoid and palatine of *Eustomias* are separate from the quadrate, metapterygoid, and other jaw apparatus bones. Other stomiids have the ectopterygoid bound to the quadrate and metapterygoid. The premaxilla of *Bathophilus* has a process that articulates along the anterodorsal margin of the maxilla, as opposed to other stomiids where the process articulates along the anteroventral surface. Most stomiids have teeth that are widely spaced and large. Some melanostomiines, such as *Bathophilus*, *Eustomias*, *Grammatostomias*, and *Pachystomias*, have teeth that are small and closely set on the maxilla. Dentition in melanostomiine genera are classified as Type 3 or Type 4 with respect to tooth attachment. Type 3 tooth attachment describes hinged teeth with an anterior axis of rotation, while Type 4 tooth attachment describes hinged teeth with a posterior axis of rotation. *Tactostoma* species have Type 4 tooth attachment in juveniles and adults. While Type 4 tooth attachment is seen in other stomiids, Type 4 tooth attachment is only seen in early post-larval ontogenetic stages

in other dragonfishes, and therefore this is considered a paedomorphic feature in *Tactostoma*. Dentary teeth in most stomiids do not project at large angles, with the exception of some melanostomiines such as *Flagellostomias*, *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*. The second large tooth in the dentary of these genera projects at an angle of 60 degrees (Fink 1985).

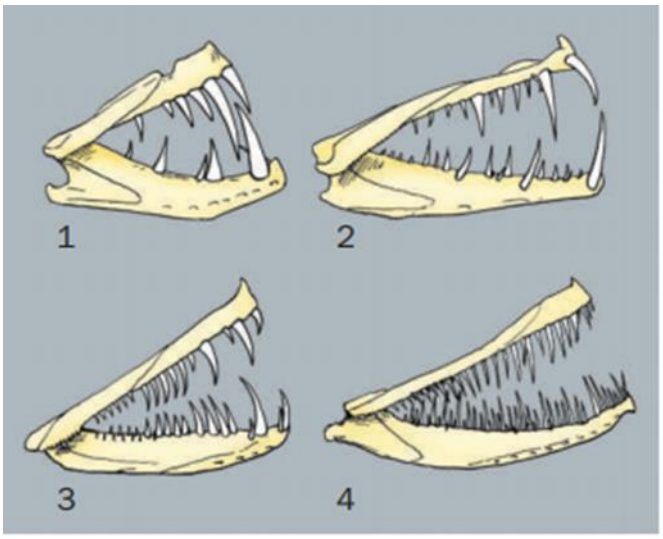

Figure 3. The jaws and teeth of four melanostomiine species: 1. *Leptostomias gladiator*; 2. *Grammatostomias dentatus*; 3. *Echiostoma barbatum*; 4. *Tactostoma macropus* (Illustration by Joseph E. Trumpey; reproduced from Sutton, 2003).

There have been several studies that have examined basic morphological characteristics of dragonfishes (e.g., fang-like teeth and long jaws), with follow-on studies looking into evolution of their morphology and biomechanics (Günther & Deckert 1959; Borodulina 1972; Merrett & Roe 1974; Clarke 1982; Roe & Badcock 1984; Schnell et al. 2010; Kenaley 2012; Kenaley et al. 2014). Most of the studies on the morphology of dragonfishes have focused on the family Stomiidae, with emphasis placed on the most derived subfamily, Malacosteinae. The Melanostomiinae has yet to be the sole focus of a functional morphological analysis.

1.5 Significance of Work

Two concepts that apply to ecosystem interactions are top-down and bottom-up control. Top-down control involves higher trophic levels controlling lower trophic levels through intense, closely linked predation, while bottom-up control involves lower trophic levels limiting the biomass of higher trophic levels through resource limitation. The reality of top-down vs. bottom-up control in the open ocean remains unclear (Worm & Myers 2003); however, it is generally accepted that predation shapes oceanic food webs (Verity & Smetacek 1996; Pace et al. 1999).

In terms of biomass, lanternfishes are among the two dominant micronektonic fish taxa in the mesopelagic zone (Brodeur & Yamamura 2005; De Forest & Drazen 2009), the other being bristlemouths (Gonostomatidae) due to the preponderance of the genus *Cyclothone*. Stomiids and myctophids both are important mediators of organic carbon transfer between trophic levels within the water column and on continental margin benthic communities because stomiids and myctophids vertically migrate (Hidaka et al. 2001; Gartner et al. 2008). With consumption of myctophids, stomiids convert micronekton biomass into stomiid biomass. Dragonfishes have been found in the diets of other fishes (e.g., epipelagic and benthopelagic fishes) as well as epipelagic mammals. Therefore, with vertical migration tied to feeding, dragonfishes play an essential role in interzonal energy transfer between the epi-, meso-, and bathypelagic zones (Sutton & Hopkins 1996b).

1.6 Project Aims

The first aim of this study was to examine morphological characteristics among species in the subfamily Melanostomiinae. Morphological characteristics among melanostomiine species were analyzed in order to establish morphotypes to group species into respective clusters. The second aim was to perform a detailed trophic analysis on species classified under the subfamily Melanostomiinae. The trophic analysis included analyses of gut contents, feeding chronology, and feeding selectivity. The trophic analysis conducted in this study is the most complete trophic study to date on the Melanostomiinae. The sample sizes in previous trophic studies of the Melanostomiinae were not large enough to avoid pooling species by genus. The third aim was to determine if there is a relationship between Melanostomiinae prey composition and feeding morphology. The morphotypes were compared to the diet classified via trophic analysis.

2. *METHODS*

2.1 Sample Collection and Processing

Following the *Deepwater Horizon* oil spill in the Gulf of Mexico in 2010, the NOAA-supported Offshore Nekton Sampling and Analysis Program (ONSAP) was created to assess the impact to deep-pelagic fishes and invertebrates in the Gulf of Mexico. Seven research cruises were conducted in this program aboard two research vessels, the NOAA FRV *Pisces* and the M/V *Meg Skansi* in 2010 – 2011 (Table 1). The 'cruises' aboard the M/V Meg Skansi were very long and represented several legs assembled into a single cruise series.

Table 1. Research cruises conducted for the Offshore Nekton Sampling and Analysis Program listed in chronological order.

Research Vessel	Cruise Identification	Duration
Pisces	PC8	12/02/2010 – 12/19/2010
Meg Skansi	MS6	01/28/2011 – 03/30/2011
Pisces	PC9	03/23/2011 – 04/06/2011
Meg Skansi	MS7	04/14/2011 – 06/30/2011
Pisces	PC10	06/23/2011 – 07/13/2011
Meg Skansi	MS8	07/18/2011 – 09/30/2011
Pisces	PC12	09/08/2011 – 09/27/2011

The NOAA FRV *Pisces* and M/V *Meg Skansi* each used a different collection method to obtain specimens of deep-pelagic fishes and invertebrates. On the NOAA FRV *Pisces* vessel, a midwater trawl with a 165-m^2 mouth and a graded mesh (3.2-m to 19-mm) was used to sample the water column nekton and micronekton. This midwater trawl sampled both day and night with shallow tows from the surface to 700 m and deep tows from the surface to 1500 m. On the M/V *Meg Skansi*, a 10-m^2 mouth area, 3-mm mesh Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) was used to sample the water column micronekton (and occasional nekton). The MOCNESS used six nets, which opened and closed at targeted depths (Wiebe et al. 1985). The MOCNESS sampled consecutive depth intervals day and night: surface to 1500 m (Net 0; N0), 1500 – 1200 m (N1), 1200 – 1000 m (N2), 1000 – 600 m (N3), 600 – 200 m (N4), and lastly, 200 m to the surface (N5).

Initial specimen processing occurred at sea, and specimens were further identified to species level and curated by members of the Oceanic Ecology Laboratory at the Halmos College of Arts and Sciences, Nova Southeastern University (NSU). Specimens were initially fixed with 10% buffered formalin onboard and later transferred to 70% ethanol:water in lab. This collection represents the world's largest research sample set with respect to melanostomiine dragonfishes. Melanostomiinae species with 20 or more specimens at NSU (excluding those only identified to genus) were used in this study (Table 2).

Table 2. Counts and standard length (SL) size range (mm) of Melanostomiinae specimens used in this study.

Specimen	**Sum of Counts**	**SL Size Range (mm)**
Eustomias schmidti	91	72 – 275
Echiostoma barbatum	89	40 – 315
Eustomias hypopsilus	62	81 – 142
Melanostomias melanops	41	63 – 223
Eustomias fissibarbis	33	56 – 170
Leptostomias gladiator	23	61 – 403
Melanostomias valdiviae	19	55 – 200
Eustomias brevibarbatus	18	70 – 112
Leptostomias bermudensis	16	86 – 420
Bathophilus pawneei	15	49 – 126
Photonectes margarita	15	49 – 290
Eustomias acinosus	14	59 – 174
Eustomias filifer	12	74 – 131
Flagellostomias boureei	10	66 – 286
Melanostomias tentaculatus	10	46 – 214
Bathophilus longipinnis	5	65 – 112
Grand Total	**473**	

2.2 Diet Analysis

The methods described by Sutton & Hopkins (1996b) were followed for dissection and trophic analyses. Specimens of the subfamily Melanostomiinae were blotted dry and weighed to the nearest 0.01 g. During dissection, one transverse incision was made at the isthmus. A shallow

ventral incision was made from the anterior incision of the isthmus to the anus to extract the entire gastrointestinal (GI) tract. For diet analysis, the GI tract was removed and the stomach and intestine separated. After dissection, prey items in the stomach and intestine were identified to the lowest taxonomic level possible. Each prey item was measured to the nearest 0.1 mm SL where applicable (Sutton & Hopkins 1996b).

2.3 Feeding Chronology

Prior to dissection, stomach fullness was graded on a scale of 0 – 5, with zero being empty and five being completely full (Sutton & Hopkins 1996b). In order to determine feeding chronology of melanostomiines, state of digestion was recorded for every prey item in the stomachs of dragonfishes. Prey items were graded on a scale from 0.5 – 5, with 0.5 being mostly digested and five being relatively undigested (prey items showing no digestion, compression, or mucus-coating were omitted from analysis, as these would likely represent net feeding) (Sutton & Hopkins 1996b). With respect to prey items, a state of digestion value of five was classified as some compression and a mucus coating on the prey were present, a value of four indicated that up to half of the skin on the prey was digested, a value of three indicated that most of the skin on the prey was digested, a value of two indicated that up to half of the muscle tissue on the prey was digested, a value of one indicated that most of the muscle tissue on the prey was digested, and a value of 0.5 was classified as prey remains such as hard parts and scales. Since stomiids are predators, all prey items were assumed to be alive and whole at the time of ingestion by the predator. The state of digestion of the prey and the time interval that the melanostomiine was captured (i.e. trawl end time) were plotted to determine feeding chronology (Swenson & Smith 1973; Eggers 1977).

2.4 Feeding Selectivity

Feeding selectivity of dragonfishes was measured using Chesson's selectivity index equation (1978):

$$\alpha_i = \frac{(\frac{r_i}{p_i})}{\sum(\frac{r}{p})}, i = 1, \dots, n$$

where α_i indicates selectivity for prey type i, r indicates the relative abundance of the prey item in the diet, p indicates the relative abundance of the prey item in the environment, and n is

the number of prey types. In this study, the relative abundance of prey in the environment was estimated using the collection data of samples in the Oceanic Ecology Laboratory at the NSU Oceanographic Center. The values for α_i ranged between 0 – 1, with a value greater than 0.5 indicating prey preference, a value near 0.5 indicating non-selective feeding, and a value less than 0.5 indicating prey avoidance.

2.5 Instantaneous Ration

Instantaneous ration is defined as how much weight a predator consumes in one feeding bout in relation to their own weight. Instantaneous ration estimates were calculated per species by dividing the wet weight of prey by the wet weight of predators in cases of prey-positive stomachs (Sutton & Hopkins 1996b). It should be noted that in some cases stomiid specimens had been fixed in formalin and then transferred to ethanol, whereas in other cases specimens were fixed and curated long-term in formalin. Given that ration estimates are ratios, it is assumed that differences in fixation methodology would be negligible. It should also be noted that instantaneous ration, expressed as a percentage of the stomiid body weight, would always be considered an underestimate due to digestion effects on the prey at the time of predator collection.

2.6 Morphometric Measurements

For each specimen, morphometric analyses were based on SL, mouth gape size, dentition, head length, jaw protrusibility, barbel length, lure complexity, and eye size (see below). Most of the morphometric characteristics were measured using a Vernier caliper to the nearest 0.1 mm; however, smaller characteristics (e.g., dentition) were measured using a Stemi 2000-C dissecting microscope outfitted with a camera system and Zen image analysis software if needed (2012 Blue Edition).

Standard length was measured from the tip of the longest jaw (upper or lower) to the end of the hypural bone (Howe 2002). For oral mouth gape, there were three morphological measurements: the vertical oral gape, horizontal articular oral gape, and the horizontal maxillary oral gape. All measurements were taken with the mouth open maximally, just shy of head deformation. The vertical oral gape is the vertical distance between the anteriormost upper jaw and lower jaw (Figure 4a), the horizontal articular oral gape is the distance between the two articular bones measured at the dorsoposterior margin (Figure 4b), and the horizontal maxillary oral gape

is the distance between the left and right maxilla-premaxilla complexes (Figure 4c; Mihalitsis & Bellwood 2017).

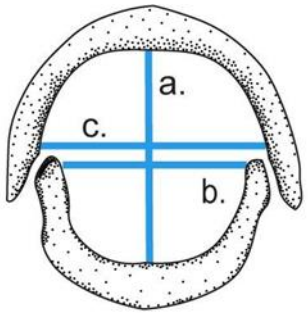

Figure 4. Oral mouth gape measurements: a. Vertical Oral Gape, b. Horizontal Articular Oral Gape, and c. Horizontal Maxillary Oral Gape (from Mihalitsis & Bellwood, 2017).

Dentition and head length measurements followed the methodology of Gibbs et al. (1983), where only the longest premaxillary tooth and mandibular tooth were measured. Head length was measured from the tip of the upper jaw to the posteriormost part of the fleshy operculum (Gibbs et al. 1983). Relative mouth size was represented by the ratio of each mouth gape size to head length. Eye size was measured as the diameter from the rostral to caudal ends of the orbit (De Busserolles et al. 2013). The barbels of dragonfishes have structures such as bulbs, filaments, and branching (Figure 5). Barbel length was measured from the barbel origin on the ventral head surface to the distal end of the distal bulb of the lure, excluding the filaments. Both lure complexity and jaw protrusibility were analyzed qualitatively. Lure complexity was determined by counting and reporting the number of main branches from the main stem of the barbel. Dragonfishes have barbels of variable complexity, especially for species within the genus *Eustomias* (Figure 6; Sutton & Hartel 2004). Jaw protrusibility was characterized as no protrusion, slight protrusion, or full protrusion by manipulating the stomiid jaws with forceps.

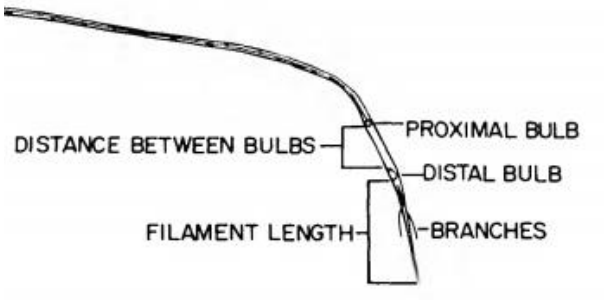

Figure 5. Lateral view of *Eustomias austratlanticus* lure displaying barbel structures (from Gibbs et al., 1983).

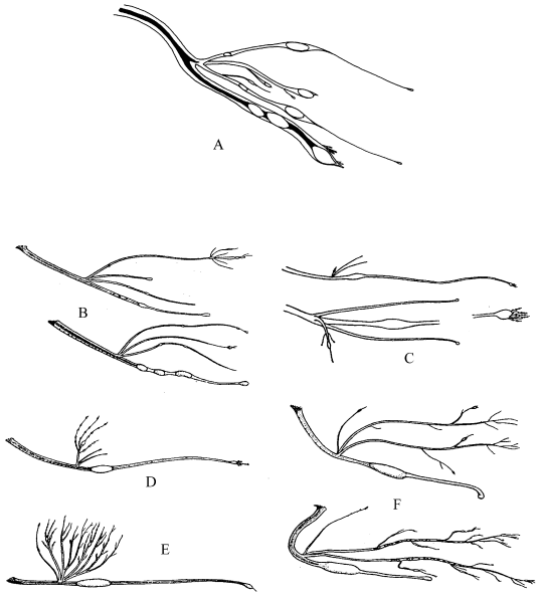

Figure 6. Illustrations of barbels of several *Eustomias* (*Neostomias*) species. (A) *Eustomias jimcraddocki*; (B) *Eustomias tetranema*; (C— E) *Eustomias filifer*; (F) *Eustomias monodactylus*. (from Sutton & Hartel, 2004; with illustration A drawn by T. Sutton and illustrations B–F from Regan & Trewavas, 1930).

2.7 Statistical Analysis

All statistical analyses were performed using the statistical analysis programs R Studio and PRIMER (Field et al. 1982). For trophic ecology analyses, a Bray-Curtis similarity index (Bray & Curtis 1957) was computed after standardizing feeding data as a percentage of all prey items. Two multivariate techniques, (1) an unweighted pair-group method using arithmetic averages (UPGMA; Romesburg 1990) cluster analysis and (2) non-parametric multi-dimensional scaling (MDS; Kruskal & Wish 1978), were used to group melanostomiines into feeding guilds. Prey type was analyzed at two levels: 1) Teleostei, Crustacea, and Cephalopoda; and 2) prey fish family for teleost consumers. Two t-tests were used to assess significant differences in gut fullness and state of digestion of prey items as a function of time of day (i.e. day versus night). The t-test statistic was considered significant at $p < 0.05$. The results of the t-tests were used to determine if patterns exist between feeding, space, and distribution of predators and prey. Larger prey items can take more than a day to digest and thus the pattern between feeding, space, and distribution can be difficult to determine. For morphological analyses, a Bray-Curtis similarity index was also computed using ratio values of morphological measurements. The Bray-Curtis similarity index for both the trophic ecology and morphological analyses were not computed by size class due to inadequate sample size of each taxon. Both analyses were conducted for each treatment. Groupings within each treatment (feeding and morphology) were defined by concordance of the two analyses (UPGMA and MDS), following the methods of Sutton et al. (2008; Figure 7). In order to determine the morphological-dietary relationships of melanostomiines, concordance of the treatment groupings was assessed using the same method.

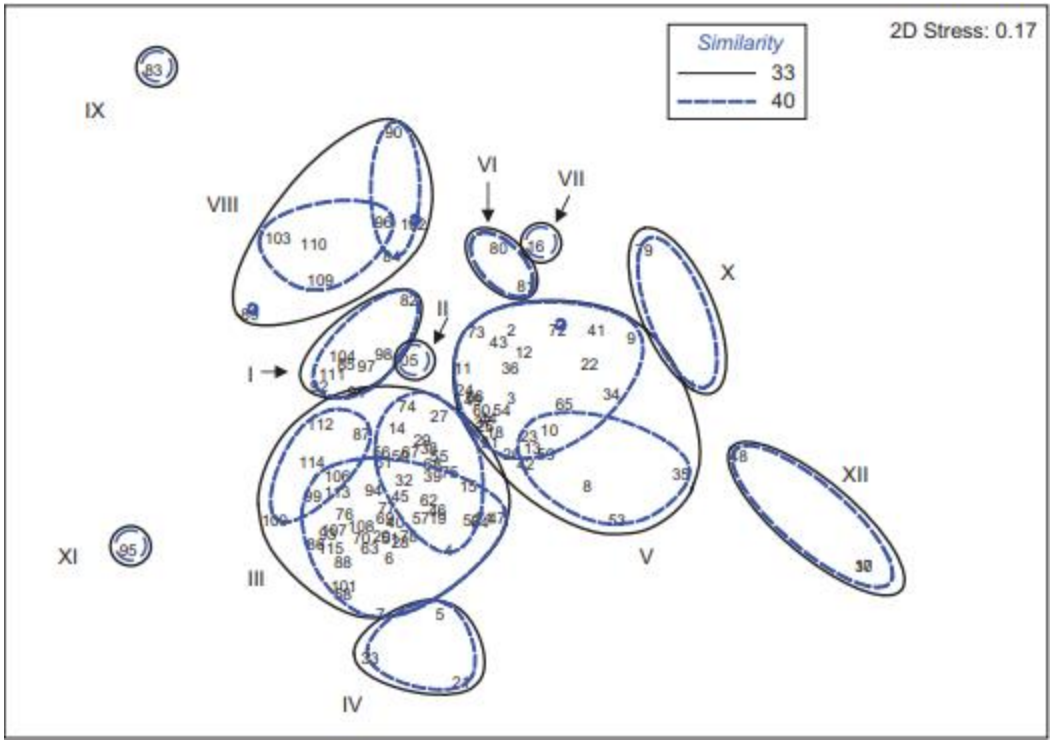

Figure 7. Results of MDS comparing deep-pelagic fish trawl samples taken during the 2004 MAR-ECO expedition (from Sutton et al., 2008) with cluster analysis groupings overlain at two similarity levels to assess MDS-cluster analysis concordance.

3. RESULTS

A total of 473 specimens were examined in the morphological analyses, representing 16 species. Of those 473 specimens, 451 specimens were examined for diet (22 specimens were not included in diet analysis due to damaged GI tracts sustained during collection or previous experiments). During dissections, 155 prey items were identified, including prey categorized as "net feeds" (ingestion within the collection net) (Table 3).

3.1 Trophic Ecology

3.1.1 Eustomias schmidti

Eustomias schmidti was the most abundant melanostomiine species collected from the Gulf of Mexico, hereby referred to as GoM, with a total of 27 prey items found across 88 dissected specimens. Of the 27 prey items, 24 were only identified to Teleostei due to the digested condition of the prey. There were three additional fish prey items identified further to family Myctophidae (one of which was identified as *Diaphus rafinesquii*; Table 3).

Of the 88 specimens dissected, there were 17 prey-positive stomachs (19.3%) and nine prey-positive intestines (10.2%; Table 4). The average stomach fullness was 0.6. Stomach fullness as a function of time of day was not significant ($p = 0.90$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.28$; Table 6). The state of digestion values of 17 prey items were plotted on a 24-hour time scale and showed a negative trend during the late-night hours and a positive trend during the day to early night (Figure 8). Per feeding event, *E. schmidti* ingested meals that were 7.0% of their body weight (Table 7) and 27.9% of their own body size (Table 8).

The feeding selectivity analysis of *E. schmidti* suggested high selectivity for teleosts (Table 9). *Eustomias schmidti* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. schmidti* was highly selective for myctophids (Table 10). *Eustomias schmidti* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.2 Echiostoma barbatum

Echiostoma barbatum was the second-most abundant melanostomiine species collected from the GoM, with a total of 26 prey items found in 83 dissected specimens. Of these 26 prey items, 17 were only identified to Teleostei due to the digested condition of the prey. There were four additional fish prey items identified further to the family level and included two myctophids (one of which was identified as *Lepidophanes guentheri*), one melamphaid, and one stomiid. All other prey items (n = 5) were cephalopods (Table 3). Two prey items (both crustaceans – a copepod and a *Cystisoma* specimen) were determined to be net feeds and were, therefore, excluded from analyses.

Of the 83 specimens dissected, there were 19 prey-positive stomachs (22.9%) and seven prey-positive intestines (8.4%; Table 4). The average stomach fullness was 0.6. Stomach fullness as a function of time of day was not significant ($p = 0.38$; Table 5). State of digestion as a function of time of day was also not significant ($p = 0.10$; Table 6). The state of digestion values for 20 prey items were plotted on a 24-hour time scale and showed no trend (Figure 8). Per feeding event, *E. barbatum* ingested meals that were 4.2% of their body weight (Table 7) and 35.8% of their body size (Table 8).

The feeding selectivity analysis of *E. barbatum* suggested high selectivity for cephalopods and negative selectivity for teleosts (Table 9). *Echiostoma barbatum* was grouped into their own feeding guild (feeding guild “b”) in UPGMA clustering (Figure 9). However, in multidimensional space, *E. barbatum* was grouped within the piscivorous guild (Figure 10). With respect to fishes consumed, *E. barbatum* was highly selective for melamphaids, negatively selective for stomiids, and highly selective against myctophids (Table 10). *Echiostoma barbatum* was grouped separately from other myctophid-eating dragonfishes (feeding group “d”) in UPGMA clustering (Figure 11) but were grouped with other myctophid-eating dragonfishes in multidimensional space (Figure 12).

3.1.3 Eustomias hypopsilus

Eustomias hypopsilus was the third-most abundant melanostomiine species collected from the GoM, with a total of 17 prey items found in 61 dissected specimens. Of those 17 prey items, 12 were only identified to Teleostei due to the digested condition of the prey. There were five

additional fish prey items identified further to family Myctophidae (two of which were identified as *Bolinichthys*; Table 3).

Of the 61 specimens dissected, there were 14 prey-positive stomachs (22.9%) and three prey-positive intestines (4.9%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.81$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.63$; Table 6). The state of digestion values of 14 prey items were plotted on a 24-hour time scale and demonstrated a relatively decreased trend during the night, a plateau during early morning, and then an increased trend during the day (Figure 8). Per feeding event, *E. hypopsilus* ingested meals that were 9.0% of their body weight (Table 7) and 27.5% of their body size (Table 8).

The feeding selectivity analysis of *E. hypopsilus* suggested high selectivity for teleosts (Table 9). *Eustomias hypopsilus* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. hypopsilus* was highly selective for myctophids (Table 10). *Eustomias hypopsilus* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.4 Melanostomias melanops

Melanostomias melanops was the most abundant *Melanostomias* species collected from the GoM, with a total of 13 prey items found in 40 dissected specimens. Of those 13 prey items, 11 were only identified to Teleostei due to the digested condition of the prey. There were two additional fish prey items identified further to the family level and included one gonostomatid, *Cyclothone acclinidens*, and the other prey item was a myctophid (Table 3).

Of the 40 specimens dissected, there were eight prey-positive stomachs (20.0%) and three prey-positive intestines (7.5%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.26$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.22$; Table 6). The state of digestion values of nine prey items were plotted on a 24-hour time scale and showed no trend (Appendix Figure 1). Per feeding

event, *M. melanops* ingested meals that were 6.7% of their body weight (Table 7) and 43.1% of their body size (Table 8).

The feeding selectivity analysis of *M. melanops* suggested high selectivity for teleosts (Table 9). *Melanostomias melanops* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *M. melanops* was highly selective for gonostomatids and negatively selective for myctophids (Table 10). *Melanostomias melanops* was grouped with *E. barbatum* (feeding group "d") in UPGMA clustering (Figure 11) separate from the other dragonfishes that preyed preying primarily upon myctophids. However, *M. melanops* was grouped with other myctophid-eating dragonfishes in multidimensional space (Figure 12).

3.1.5 Eustomias fissibarbis

There were 12 prey items found in 32 dissected *Eustomias fissibarbis* specimens collected from the GoM. Of those 12 prey items, 10 were only identified to Teleostei due to the digested condition of the prey. There were two additional fish prey items identified further to family Myctophidae (one of which was identified as *Notoscopelus resplendens*; Table 3).

Of the 32 specimens dissected, there were 10 prey-positive stomachs (31.2%) and one prey-positive intestine (3.1%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.79$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.78$; Table 6). The state of digestion values of 10 prey items were plotted on a 24-hour time scale and exhibited no trend (Appendix Figure 1). Per feeding event, *E. fissibarbis* ingested meals that were 10.5% of their body weight (Table 7) and 31.1% of their own body size (Table 8).

The feeding selectivity analysis of *E. fissibarbis* suggested high selectivity for teleosts (Table 9). *Eustomias fissibarbis* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. fissibarbis* was highly selective for myctophids (Table 10). *Eustomias fissibarbis* was grouped with seven other

dragonfishes (feeding group “c”) in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.6 Leptostomias gladiator

Leptostomias gladiator was the most abundant *Leptostomias* species collected from the GoM, with a total of three prey items found in 17 dissected specimens. All three prey items were only identified to Teleostei due to the digested condition of the prey (Table 3).

Of the 17 specimens dissected, there were three prey-positive stomachs (17.6%) and zero prey-positive intestines (0.0%; Table 4). The average stomach fullness was 0.5. Stomach fullness as a function of time of day was not significant (p = 1.00; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values of three prey items were plotted on a 24-hour time scale and displayed no trend (Appendix Figure 1). Per feeding event, *L. gladiator* ingested meals that were 1.3% of their body weight (Table 7). Percentage of body size consumed was unable to be calculated due to the digested condition of all prey found.

The feeding selectivity analysis of *L. gladiator* suggested high selectivity for teleosts (Table 9). *Leptostomias gladiator* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild “c”) in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). No prey items were identified to family level and thus *L. gladiator* was excluded from prey fish family analysis.

3.1.7 Melanostomias valdiviae

There was only one prey item found in 19 dissected *Melanostomias valdiviae* specimens collected from the GoM. This prey item was only identified to Teleostei due to the digested condition of the prey (Table 3).

Of the 19 specimens dissected, there were zero prey-positive stomachs (0.0%) and one prey-positive intestine (5.3%; Table 4). The average stomach fullness was 0.0. Stomach fullness as a function of time of day was not significant (p = NA; Table 5). State of digestion as a function of time of day was unable to be analyzed. State of digestion values also were not able to be graphed for *M. valdiviae*. Instantaneous ration and percent of body size consumed were not able to be calculated as the prey item was the remnant of a fish scale (i.e. unable to be measured or weighed).

The feeding selectivity analysis of *M. valdiviae* suggested high selectivity for teleosts (Table 9). *Melanostomias valdiviae* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). No prey items were identified to family level and thus *M. valdiviae* was excluded from prey fish family analysis.

3.1.8 Eustomias brevibarbatus

There were 12 prey items found in 17 dissected *Eustomias brevibarbatus* specimens collected from the GoM. Of those 12 prey items, six were only identified to Teleostei due to the digested condition of the prey. There were five additional fish prey items identified further to family Myctophidae (two of which were identified as *Lepidophanes guentheri*). One cephalopod was also found in the diet of *E. brevibarbatus* (Table 3).

Of the 17 specimens dissected, there were 10 prey-positive stomachs (58.8%) and two prey-positive intestines (11.8%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.81$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.59$; Table 6). The state of digestion values of 10 prey items were plotted on a 24-hour time scale and displayed no trend (Figure 8). Per feeding event, *E. brevibarbatus* ingested meals that were 27.2% of their body weight (Table 7) and 40.2% of their body size (Table 8).

The feeding selectivity analysis of *E. brevibarbatus* suggested slightly high selectivity for cephalopods and slightly negative selectivity for teleosts (Table 9). However, *E. brevibarbatus* was grouped within the primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. brevibarbatus* was highly selective for myctophids (Table 10) and thus was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.9 Leptostomias bermudensis

There were nine prey items found in 14 dissected *Leptostomias bermudensis* specimens collected from the GoM. Of those nine prey items, eight were only identified to Teleostei due to

the digested condition of the prey with one additional fish prey item identified further to family Myctophidae (Table 3).

Of the 14 specimens dissected, there were five prey-positive stomachs (35.7%) and four prey-positive intestines (28.6%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 1.00$; Table 5). State of digestion as a function of time of day was not significant ($p = 0.76$; Table 6). The state of digestion values of five prey items were plotted on a 24-hour time scale and showed no trend (Appendix Figure 1). Per feeding event, *L. bermudensis* ingested meals that were 0.9% of their body weight (Table 7). Percentage of body size consumed was unable to be calculated due to the digested condition of all prey found.

The feeding selectivity analysis of *L. bermudensis* suggested high selectivity for teleosts (Table 9). *Leptostomias bermudensis* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *L. bermudensis* was highly selective for myctophids (Table 10). *Leptostomias bermudensis* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.10 Bathophilus pawneei

Bathophilus pawneei was the most abundant *Bathophilus* species collected from the GoM, with four prey items found in 15 dissected specimens. Of these four prey items, three were only identified to Teleostei due to the digested condition of the prey with one additional fish prey item identified further to the family Stomiidae (Table 3).

Of the 15 specimens dissected, there were three prey-positive stomachs (20.0%) and one prey-positive intestine (6.7%; Table 4). The average stomach fullness was 0.6. Stomach fullness as a function of time of day was not significant ($p = 0.41$; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values for the three positive samples were plotted on a 24-hour time scale and showed no trend (Appendix Figure 1). Per feeding event, *B. pawneei* ingested meals that were 0.5% of their body weight (Table 7). Percentage of body size consumed was unable to be calculated due to the digested condition of all prey found.

The feeding selectivity analysis of *B. pawneei* suggested high selectivity for teleosts (Table 9). *Bathophilus pawneei* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") between UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *B. pawneei* was highly selective for stomiids (Table 10) with only one prey item included in the fish family selectivity analysis. *Bathophilus pawneei* was placed into their own feeding group (feeding group "b") between UPGMA clustering (Figure 11) and in multidimensional space (Figure 12).

3.1.11 Photonectes margarita

Photonectes margarita was the most abundant *Photonectes* species collected from the GoM, with a total of two prey items found in 15 dissected specimens. Of these two prey items, one was only identified to Teleostei due to the digested condition of the prey. There was one additional fish prey item identified further to the myctophid species, *Ceratoscopelus warmingii* (Table 3). Two prey items (both crustaceans – *Sergia regalis* of the family Sergestidae and *Bentheogennema* of the family Benthesicymidae) were determined to be net feeds and were, therefore, excluded from analyses.

Of the 15 specimens dissected, there were two prey-positive stomachs (14.3%) and zero prey-positive intestines (0.0%; Table 4). One stomach was excluded from analysis due to the presence of net feeds. The average stomach fullness was 1.0. Stomach fullness as a function of time of day was not significant ($p = 0.11$; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values of two prey items were plotted on a 24-hour time scale and exhibited no trend (Appendix Figure 2). Per feeding event, *P. margarita* ingested meals that were 0.2% of their body weight (Table 7) and 11.7% of their body size (Table 8).

The feeding selectivity analysis of *P. margarita* suggested high selectivity for teleosts (Table 9). *Photonectes margarita* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *P. margarita* was highly selective for myctophids (Table 10). *Photonectes margarita* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.12 Eustomias acinosus

There were nine prey items found in 13 dissected *Eustomias acinosus* specimens collected from the GoM. Of these nine prey items, six were only identified to Teleostei due to the digested condition of the prey. There were three additional fish prey items identified further to the howellid species, *Howella atlantica* (Table 3).

Of the 13 specimens dissected, there were seven prey-positive stomachs (53.8%) and two prey-positive intestines (15.4%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.76$; Table 5). However, state of digestion as a function of time of day was significant ($p = 0.05$; Table 6). The state of digestion values of seven prey items were plotted on a 24-hour time scale and demonstrated a trend with higher values at night and lower values during the day (Figures 8 and 13). Per feeding event, *E. acinosus* ingested meals that were 3.7% of their body weight (Table 7) and 15.3% of their body size (Table 8).

The feeding selectivity analysis of *E. acinosus* suggested high selectivity for teleosts (Table 9). *Eustomias acinosus* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. acinosus* was highly selective for howellids (Table 10). *Eustomias acinosus* was grouped into a separate feeding group (feeding group "a") from most of the species in this study in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) as *E. acinosus* primarily preyed upon howellids.

3.1.13 Eustomias filifer

There were four prey items found in 12 dissected *Eustomias filifer* specimens collected from the GoM. Of these four prey items, three were only identified to Teleostei due to the digested condition of the prey. There was one additional fish prey item identified further to the howellid species, *Howella atlantica* (Table 3).

Of the 12 specimens dissected, there were four prey-positive stomachs (33.3%) and zero prey-positive intestines (0.0%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.23$; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values of four prey items were plotted on a 24-hour time scale and demonstrated a trend where values increased during the night

and decreased during the day (Appendix Figure 2). Per feeding event, *E. filifer* ingested meals that were 11.3% of their body weight (Table 7) and 26.8% of their body size (Table 8).

The feeding selectivity analysis of *E. filifer* suggested high selectivity for teleosts (Table 9). *Eustomias filifer* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *E. filifer* was highly selective for howellids (Table 10). *Eustomias filifer* was grouped with *E. acinosus* (feeding group "a") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) as *E. filifer* also primarily preyed upon howellids.

3.1.14 Flagellostomias boureei

Flagellostomias is a monotypic genus with *Flagellostomias boureei* as the only known species. There were four prey items found in 10 dissected *F. boureei* specimens collected from the GoM. Of these four prey items, three were only identified to Teleostei due to the digested condition of the prey with one additional fish prey item identified further to family Myctophidae (Table 3).

Of the 10 specimens dissected, there were three prey-positive stomachs (30.0%) and one prey-positive intestine (10.0%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.26$; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values of three prey items were plotted on a 24-hour time scale and showed no trend (Appendix Figure 2). Per feeding event, *F. boureei* ingested meals that were 7.7% of their body weight (Table 7) and 16.9% of their body size (Table 8).

The feeding selectivity analysis of *F. boureei* suggested high selectivity for teleosts (Table 9). *Flagellostomias boureei* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *F. boureei* was highly selective for myctophids (Table 10). *Flagellostomias boureei* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.15 Melanostomias tentaculatus

There were four prey items found in 10 dissected *Melanostomias tentaculatus* specimens collected from the GoM. Of these four prey items, three were only identified to Teleostei due to the digested condition of the prey. There was one additional fish prey item identified further to family Myctophidae (Table 3).

Of the 10 specimens dissected, there were four prey-positive stomachs (40.0%) and zero prey-positive intestines (0.0%; Table 4). The average stomach fullness was 0.7. Stomach fullness as a function of time of day was not significant ($p = 0.34$; Table 5). State of digestion as a function of time of day was unable to be analyzed. The state of digestion values of three prey items were plotted on a 24-hour time scale and demonstrated no trend (Appendix Figure 2). All prey items for *M. tentaculatus* were well digested and therefore prey weight and lengths were unattainable to calculate instantaneous ration and percent of body size consumed.

The feeding selectivity analysis of *M. tentaculatus* suggested high selectivity for teleosts (Table 9). *Melanostomias tentaculatus* was grouped with most of the species in this study in a primarily piscivorous feeding guild (feeding guild "c") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). With respect to fishes consumed, *M. tentaculatus* was highly selective for myctophids (Table 10). *Melanostomias tentaculatus* was grouped with seven other dragonfishes (feeding group "c") in UPGMA clustering (Figure 11) and in multidimensional space (Figure 12) that also primarily preyed upon myctophids.

3.1.16 Bathophilus longipinnis

There were four prey items found in five dissected *Bathophilus longipinnis* specimens collected from the GoM. All four prey items were only identified to major prey taxon due to the digested condition of the prey with two teleosts and two cephalopods identified (Table 3).

Of the five specimens dissected, there were two prey-positive stomachs (40.0%) and two prey-positive intestines (40.0%; Table 4). The average stomach fullness was 0.7. Stomach fullness and state of digestion as functions of time of day were unable to be analyzed. The state of digestion values for the two positive samples were plotted on a 24-hour time scale with no trend (Appendix Figure 2). Per feeding event, *B. longipinnis* ingested meals that were 10.4% of their body weight

(Table 7). Percentage of body size consumed was unable to be calculated due to the digested condition of all prey found.

The feeding selectivity analysis of *B. longipinnis* suggested high selectivity for cephalopods and negative selectivity for teleosts (Table 9). *Bathophilus longipinnis* was grouped into their own feeding guild (feeding guild "a") in UPGMA clustering (Figure 9) and in multidimensional space (Figure 10). No prey items were identified to family level and thus *B. longipinnis* was excluded from prey fish family analysis.

Table 3. The sums of prey items per dragonfish species. Dragonfish species are abbreviated as followed: E. sch = *Eustomias schmidti*, E. bar = *Echiostoma barbatum*, E. hyp = *Eustomias hypopsilus*, M. mel = *Melanostomias melanops*, E. fis = *Eustomias fissibarbis*, L. gla = *Leptostomias gladiator*, M. val = *Melanostomias valdiviae*, E. bre = *Eustomias brevibarbatus*, L. ber = *Leptostomias bermudensis*, B. paw = *Bathophilus pawneei*, P. mar = *Photonectes margarita*, E. aci = *Eustomias acinosus*, E. fil = *Eustomias filifer*, F. bou = *Flagellostomias boureei*, M. ten = *Melanostomias tentaculatus*, and B. lon = *Bathophilus longipinnis*. A "-" represents that this prey item was not found in the diet

Prey Taxa	**E. sch**	**E. bar**	**E. hyp**	**M. mel**	**E. fis**	**L. gla**	**M. val**	**E. bre**	**L. ber**	**B. paw**	**P. mar**	**E. aci**	**E. fil**	**F. bou**	**M. ten**	**B. lon**
Teleostei	27	21	17	13	12	3	1	11	9	4	2	9	4	4	4	2
Gonostomatidae	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
C. acclinidens	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Howellidae	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-
H. atlantica	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-
Melamphaidae	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myctophidae	2	2	5	1	2	-	-	5	1	-	1	-	-	1	1	-
Bolinichthys	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
C. warmingii	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
D. rafinesquii	1		-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. guentheri	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-
N. resplendens	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Stomiidae	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Crustacea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopoda	-	5	-	-	-	-	-	1	-	-	-	-	-	-	-	2
Total	**27**	**26**	**17**	**13**	**12**	**3**	**1**	**12**	**9**	**4**	**2**	**9**	**4**	**4**	**4**	**4**

Table 4. Summary statistics of melanostomiine dragonfish feeding including percentage of prey-positive stomachs and intestines and average stomach fullness rating. A "*" represents that a net feed prey item was present and excluded from analysis.

Species	**Dragonfishes (n=)**	**Empty Stomachs (n=)**	**Percent Positive Stomachs**	**Avg. Stomach Fullness Index**	**Empty Intestines (n=)**	**Percent Positive Intestines**
Eustomias schmidti	88	71	19.3	0.6	79	10.2
*Echiostoma barbatum**	83	64	22.9	0.6	76	8.4
Eustomias hypopsilus	61	47	22.9	0.7	58	4.9
Melanostomias melanops	40	32	20.0	0.7	37	7.5
Eustomias fissibarbis	32	22	31.2	0.7	31	3.1
Leptostomias gladiator	17	14	17.6	0.5	17	0.0
Melanostomias valdiviae	19	19	0.0	0.0	18	5.3
Eustomias brevibarbatus	17	7	58.8	0.7	15	11.8
Leptostomias bermudensis	14	9	35.7	0.7	10	28.6
Bathophilus pawneei	15	12	20.0	0.6	14	6.7
*Photonectes margarita**	15	12	14.3	1.0	15	0.0
Eustomias acinosus	13	6	53.8	0.7	11	15.4
Eustomias filifer	12	8	33.3	0.7	12	0.0
Flagellostomias boureei	10	7	30.0	0.7	9	10.0
Melanostomias tentaculatus	10	6	40.0	0.7	10	0.0
Bathophilus longipinnis	5	3	40.0	0.7	3	40.0

Table 5. Results from a non-parametric Mann-Whitney Wilcoxon test analyzing stomach fullness as a function of time of day (i.e. day vs night). The t-test statistic is considered significant at $p < 0.05$ with a "*" representing statistical significance. No p-values were statistically significant in this analysis.

Stomiid Species	**n**	**W statistic**	**p-value**
Eustomias schmidti	88	978.5	0.90
Echiostoma barbatum	84	770.0	0.38
Eustomias hypopsilus	61	449.5	0.81
Melanostomias melanops	40	168.5	0.26
Eustomias fissibarbis	32	101.5	0.79
Leptostomias gladiator	17	29.5	1.00
Melanostomias valdiviae	19	45.0	NA
Eustomias brevibarbatus	17	28.5	0.81
Leptostomias bermudensis	14	23.0	1.00
Bathophilus pawneei	15	22.5	0.41
Photonectes margarita	14	16.0	0.11
Eustomias acinosus	13	18.5	0.76
Eustomias filifer	12	7.5	0.23
Flagellostomias boureei	10	15.0	0.26
Melanostomias tentaculatus	10	16.5	0.34

Table 6. Results from a non-parametric Mann-Whitney Wilcoxon test analyzing state of digestion of prey items as a function of time of day (i.e. day vs night). The t-test statistic is considered significant at $p < 0.05$ with a "*" representing statistical significance. Only one p-value was significant in this analysis. The analysis could not be conducted on eight species due to lack of data in either day or night level.

Stomiid Species	**n**	**W statistic**	**p-value**
Eustomias schmidti	17	47.5	0.28
Echiostoma barbatum	20	62.0	0.10
Eustomias hypopsilus	14	26.5	0.63
Melanostomias melanops	9	4.5	0.22
Eustomias fissibarbis	10	6.5	0.78
Eustomias brevibarbatus	10	5.5	0.59
Leptostomias bermudensis	5	2.0	0.76
Eustomias acinosus	7	0.0	0.05*

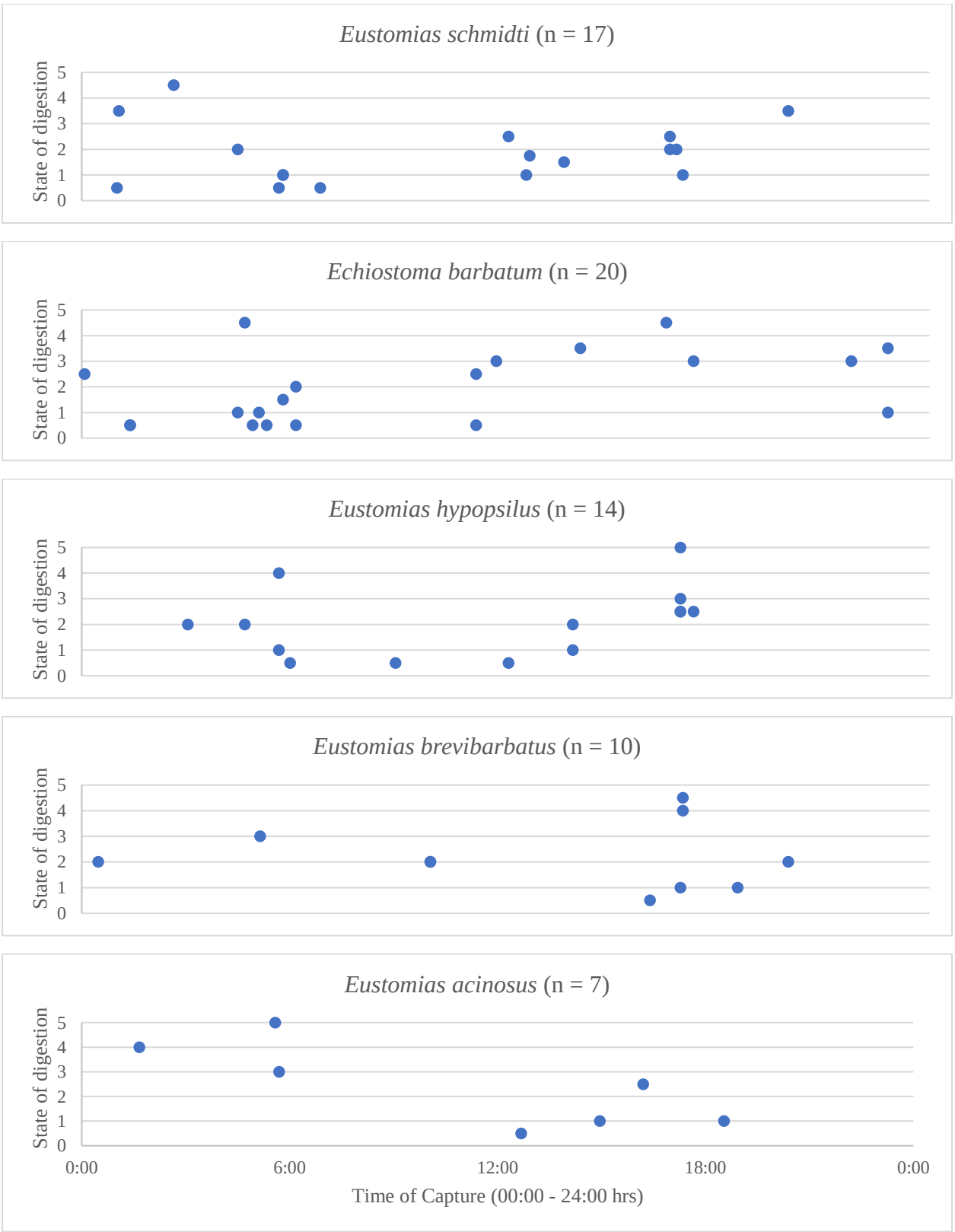

Figure 8. Feeding chronology of five melanostomiines within the Gulf of Mexico across 24-hours. State of digestion of prey items were graded from 0.5 (mostly digested) to 5.0 (fresh).

Table 7. Instantaneous ration estimates per melanostomiine species. Instantaneous ration is represented as a percentage of stomiid body weight. “E” represents a 70% ethanol weight was recorded and “F” represents a 10% buffered formalin weight was recorded. Predator weights of both ethanol and formalin were averaged together.

Species	**Avg. Predator Weight (E/F) (g)**	**Avg. Prey Weight (E)(g)**	**Instantaneous Ration**
Eustomias schmidti	36.89	2.60	7.0
Echiostoma barbatum	62.90	2.65	4.2
Eustomias hypopsilus	2.22	0.20	9.0
Melanostomias melanops	7.30	0.49	6.7
Eustomias fissibarbis	7.32	0.77	10.5
Leptostomias gladiator	11.99	0.16	1.3
Eustomias brevibarbatus	1.47	0.40	27.2
Leptostomias bermudensis	34.20	0.31	0.9
Bathophilus pawneei	9.61	0.05	0.5
Photonectes margarita	119.26	0.22	0.2
Eustomias acinosus	1.07	0.04	3.7
Eustomias filifer	2.47	0.28	11.3
Flagellostomias boureei	0.78	0.06	7.7
Bathophilus longipinnis	5.10	0.53	10.4

Table 8. Average percent of stomiid body size (standard length) consumed per feeding event.

Species	**Avg. Predator SL (mm)**	**Avg. Prey SL (mm)**	**Percent Stomiid Body Size Consumed**
Eustomias schmidti	156.00	43.60	27.9
Echiostoma barbatum	177.67	63.67	35.8
Eustomias hypopsilus	122.50	33.70	27.5
Melanostomias melanops	141.00	60.83	43.1
Eustomias fissibarbis	170.00	52.80	31.1
Eustomias brevibarbatus	94.50	38.00	40.2
Photonectes margarita	260.00	30.40	11.7
Eustomias acinosus	87.33	13.40	15.3
Eustomias filifer	108.00	28.90	26.8
Flagellostomias boureei	85.00	14.40	16.9

Table 9. Results of Chesson's selectivity index (1978) analyzing major prey taxon (Teleostei, Cephalopoda, and Crustacea) selectivity per dragonfish species. A "-" represents that this prey item was not found in the diet.

Stomiid Species	**n**	**Teleostei**	**Cephalopoda**	**Crustacea**
Eustomias schmidti	88	1	-	-
Echiostoma barbatum	83	0.17	0.83	-
Eustomias hypopsilus	61	1	-	-
Melanostomias melanops	40	1	-	-
Eustomias fissibarbis	32	1	-	-
Leptostomias gladiator	17	1	-	-
Melanostomias valdiviae	19	1	-	-
Eustomias brevibarbatus	17	0.35	0.65	-
Leptostomias bermudensis	14	1	-	-
Bathophilus pawneei	15	1	-	-
Photonectes margarita	15	1	-	-
Eustomias acinosus	13	1	-	-
Eustomias filifer	12	1	-	-
Flagellostomias boureei	10	1	-	-
Melanostomias tentaculatus	10	1	-	-
Bathophilus longipinnis	5	0.05	0.95	-

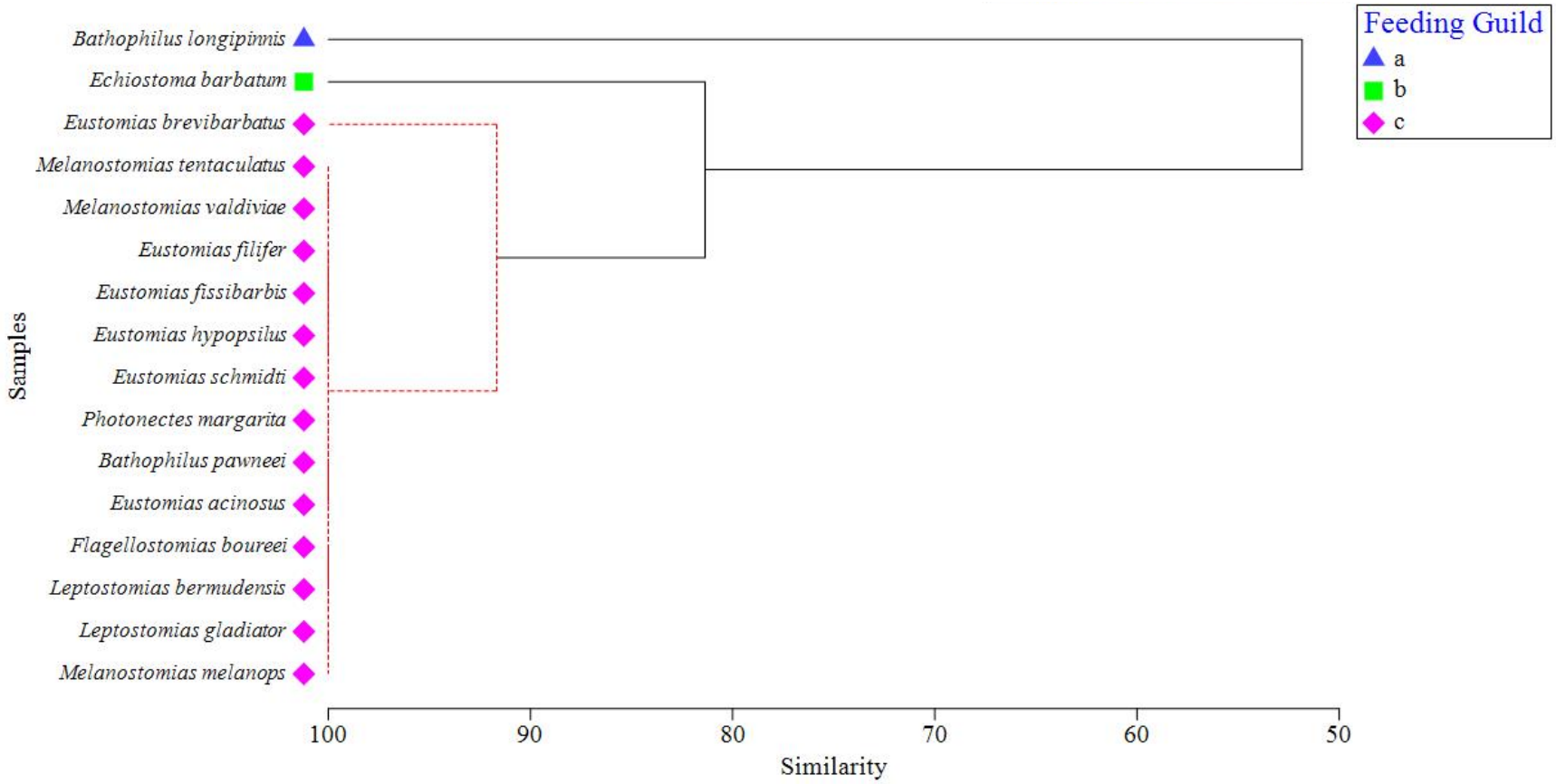

Figure 9. Hierarchical classification of feeding guilds by major prey taxon (Teleostei, Crustacea, and Cephalopoda) among dragonfishes in this study using Bray-Curtis similarity values. Feeding guilds are represented by symbols. Dashed red lines represent that these species could not be distinguished from one another by major prey taxon consumed and therefore are placed into a feeding guild together.

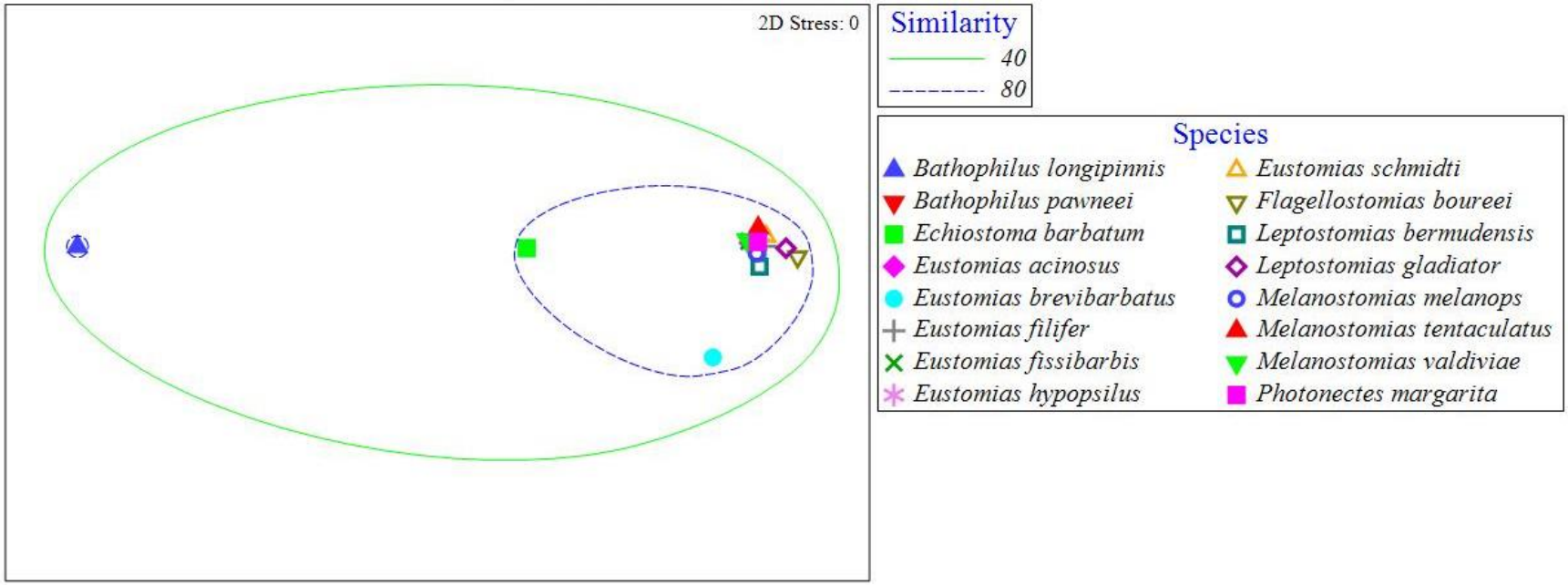

Figure 10. A non-metric multidimensional scaling plot depicting Bray-Curtis similarity values of melanostomiine diet by major prey taxon (Teleostei, Crustacea, and Cephalopoda). Ellipses are based on the clustering depicted in Figure 10. Dragonfish species are represented by symbols.

Table 10. Results of Chesson's selectivity index (1978) analyzing prey fish family selectivity per dragonfish species. Fish families are abbreviated as followed: Gono = Gonostomatidae, Howe = Howellidae, Mela = Melamphaidae, Myct = Myctophidae, and Stom = Stomiidae. A "-" represents that this prey item was not found in the diet.

Stomiid Species	**n**	**Gono**	**Howe**	**Mela**	**Myct**	**Stom**
Eustomias schmidti	88	-	-	-	1	-
Echiostoma barbatum	83	-	-	0.84	0.04	0.12
Eustomias hypopsilus	61	-	-	-	1	-
Melanostomias melanops	40	0.70	-	-	0.30	-
Eustomias fissibarbis	32	-	-	-	1	-
Eustomias brevibarbatus	17	-	-	-	1	-
Leptostomias bermudensis	14	-	-	-	1	-
Bathophilus pawneei	15	-	-	-	-	1
Photonectes margarita	15	-	-	-	1	-
Eustomias acinosus	13	-	1	-	-	-
Eustomias filifer	12	-	1	-	-	-
Flagellostomias boureei	10	-	-	-	1	-
Melanostomias tentaculatus	10	-	-	-	1	-

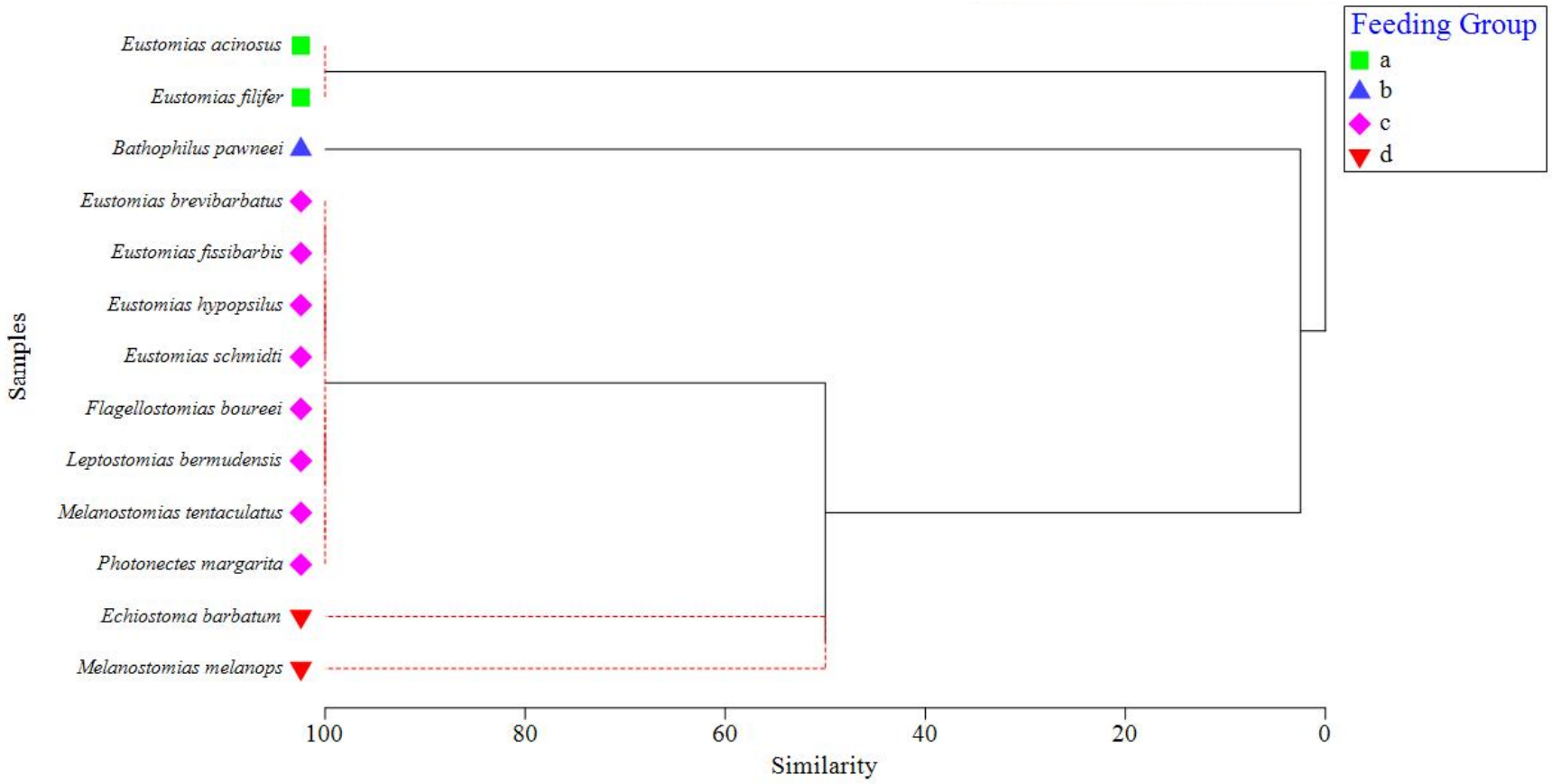

Figure 11. Hierarchical classification of feeding groups by prey fish family among dragonfishes in this study using Bray-Curtis similarity values. Feeding guilds are represented by symbols. Dashed red lines represent that these species could not be distinguished from one another by fish family consumed and therefore are placed into a feeding group together. Three dragonfish species were not included in this analysis due to all prey only identified to major prey taxon.

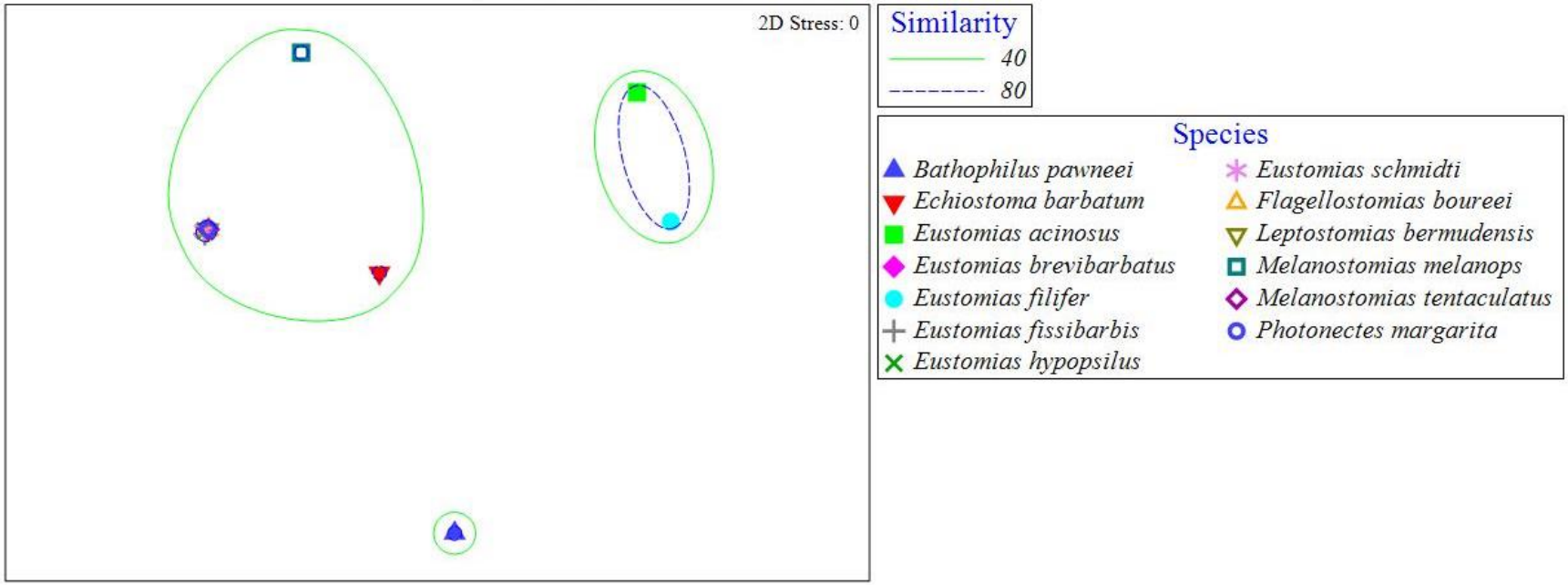

Figure 12. A non-metric multidimensional scaling plot depicting Bray-Curtis similarity values of melanostomiine diet by fish family. The ellipses are based on the clustering depicted in Figure 12. Dragonfish species are represented by symbols. Three dragonfish species were not included in this analysis due to all prey only identified to major prey taxon.

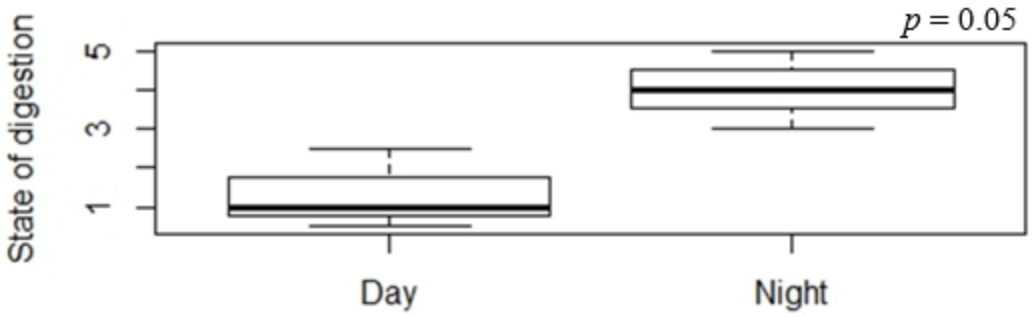

Figure 13. A boxplot representation of state of digestion (y-axis) as a function of time of day (x-axis; i.e. day vs. night) for *Eustomias acinosus*. This species was the only species that was significant in terms of state of digestion regarding day vs. night.

3.2 Functional Morphology

There were 471 fishes measured in this study, with 410 fishes included in morphological analysis. Specimens excluded from the analysis had one or more measurement landmarks that were damaged during collection methods. All quantitative morphometric measurements were transformed as a percentage of head length (Table 11). Regarding morphological analysis, there were five morphotypes identified via UPGMA clustering (Figure 14) with individuals in each morphotype shown (Figures 15, 16, 17, 18, and 19) and via MDS (Figure 20).

3.2.1 Eustomias schmidti

Individuals of the *Eustomias* genus had both upper and lower jaws that protruded. *Eustomias schmidti* had a vertical oral gape of 77.8%, horizontal maxillary oral gape of 44.4%, and a horizontal articular oral gape of 39.1% of their head length. Their longest premaxillary tooth and mandibular tooth were 10.5% and 8.9% of their head length, respectively. The eye size of *E. schmidti* was 21.4% of their head length. *Eustomias schmidti* had a barbel length that was 107.9% of their head length with three main branches on the barbel (Table 11).

Eustomias schmidti was grouped primarily into one morphotype (morphotype "c") in UPGMA clustering (Figures 14 and 17) and in multidimensional space (Figure 20) with a few individuals overlapped with morphotype "b" (Figure 16). *Eustomias schmidti* was grouped with *E. barbatum*, *P. margarita*, *E. fissibarbis*, and *M. valdiviae* with at least 80% morphological similarity. This group was defined by a short barbel, medium-sized vertical oral gape, and a medium-sized horizontal maxillary oral gape. There were some individuals within this morphotype from *E. brevibarbatus* and *B. longipinnis*.

3.2.2 Echiostoma barbatum

Echiostoma barbatum had a protrusible lower jaw with a vertical oral gape of 114.8%, horizontal maxillary oral gape of 64.5%, and a horizontal articular oral gape of 52.7% of their head length. Their longest premaxillary tooth and mandibular tooth were 14.5% and 18.4% of their head length, respectively. The eye size of *E. barbatum* was 18.9% of their head length. *Echiostoma barbatum* had a barbel length that was 71.4% of their head length with zero main branches on the barbel (Table 11).

Echiostoma barbatum was grouped into two morphotypes (morphotypes “b” and “c”) in UPGMA clustering (Figures 14, 16, and 17) and in multidimensional space (Figure 20) with some overlap between these groupings. *Echiostoma barbatum* was grouped with *M. valdiviae*, *P. margarita*, *E. schmidti*, and *E. fissibarbis* with at least 80% morphological similarity. These groups were defined by a short barbel, a large vertical oral gape, and a large horizontal maxillary oral gape. There was an overlap of *E. brevibarbatus* and *E. fissibarbis* with a third grouping and an outlying specimen of *B. longipinnis* and *E. acinosus* in morphotypes “b” and “c” as well.

3.2.3 Eustomias hypopsilus

Eustomias hypopsilus had a vertical oral gape of 76.4%, horizontal maxillary oral gape of 37.3%, and a horizontal articular oral gape of 30.7% of their head length. Their longest premaxillary tooth and mandibular tooth were 11.0% and 9.1% of their head length, respectively. The eye size of *E. hypopsilus* was 23.7% of their head length. *Eustomias hypopsilus* had a barbel length that was 369.5% of their head length with zero main branches on the barbel (Table 11).

Eustomias hypopsilus was grouped primarily into one morphotype (morphotype “e”) in UPGMA clustering (Figures 14 and 19) and in multidimensional space (Figure 20) with a few individuals overlapped with morphotype “d” (Figure 18). *Eustomias hypopsilus* was grouped with *E. acinosus*, *M. tentaculatus*, *B. pawneei*, *F. boureei*, and *L. gladiator* with at least 80% morphological similarity. This group was defined by a long barbel, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape. There was overlap with another group that included *E. filifer* (Figures 18 and 20). Also, there was a single *L. bermudensis* individual within this morphotype as well (Figures 19 and 20).

3.2.4 Melanostomias melanops

Melanostomias melanops had a protrusible lower jaw with a vertical oral gape of 125.3%, horizontal maxillary oral gape of 79.0%, and a horizontal articular oral gape of 67.1% of their head length. Their longest premaxillary tooth and mandibular tooth were 17.5% and 22.4% of their head length, respectively. The eye size of *M. melanops* was 18.7% of their head length. *Melanostomias melanops* had a barbel length that was 259.2% of their head length with zero main branches on the barbel (Table 11).

Melanostomias melanops was primarily grouped into one morphotype (morphotype "d") in UPGMA clustering (Figures 14 and 18) and in multidimensional space (Figure 20) with little overlap with other groups. *Melanostomias melanops* was grouped with *E. brevibarbatus*, *E. filifer*, *B. pawneei*, and *M. tentaculatus* with at least 80% morphological similarity. This group was defined by a long barbel, large vertical oral gape, and large horizontal maxillary oral gape. In this morphotype, there was an overlap of *E. filifer*, *E. fissibarbis*, and *M. valdiviae* with other groups (Figures 16 and 17).

3.2.5 Eustomias fissibarbis

Eustomias fissibarbis had a protrusible upper and lower jaw with a vertical oral gape of 66.3%, horizontal maxillary oral gape of 40.0%, and a horizontal articular oral gape of 31.9% of their head length. Their longest premaxillary tooth and mandibular tooth were 10.6% and 9.5% of their head length, respectively. The eye size of *E. fissibarbis* was 19.7% of their head length. *Eustomias fissibarbis* had a barbel length that was 136.3% of their head length with three main branches on the barbel (Table 11).

Eustomias fissibarbis was grouped into two morphotypes (morphotypes "c" and "d") in UPGMA clustering (Figures 14, 17, and 18) and in multidimensional space (Figure 20). *Eustomias fissibarbis* was grouped with *E. schmidti*, *E. brevibarbatus*, *E. acinosus*, *M. valdiviae*, and some individuals of *E. barbatum* and *P. margarita* with at least 80% morphological similarity. These groups were defined by a small to medium-sized barbel length, vertical oral gape, and horizontal maxillary oral gape.

3.2.6 Leptostomias gladiator

Leptostomias gladiator had a slightly protrusible lower jaw with a vertical oral gape of 68.9%, horizontal maxillary oral gape of 48.2%, and a horizontal articular oral gape of 42.3% of their head length. Their longest premaxillary tooth and mandibular tooth were 19.8% and 17.5% of their head length, respectively. The eye size of *L. gladiator* was 22.1% of their head length. *Leptostomias gladiator* had a barbel length that was 582.3% of their head length with zero main branches on the barbel (Table 11).

Leptostomias gladiator was grouped into two morphotypes (morphotypes "a" and "e") in UPGMA clustering (Figures 14, 15, and 19) and in multidimensional space (Figure 20).

Leptostomias gladiator was grouped with *L. bermudensis*, *B. pawneei*, *F. boureei*, *E. hypopsilus*, *E. acinosus*, and *E. filifer* with at least 80% morphological similarity. These groups were defined by a large barbel length, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.7 Melanostomias valdiviae

Melanostomias valdiviae had a protrusible lower jaw with a large vertical oral gape of 104.9%, horizontal maxillary oral gape of 57.7%, and a horizontal articular oral gape of 48.6% of their head length. Their longest premaxillary tooth and mandibular tooth were 18.9% and 18.6% of their head length, respectively. The eye size of *M. valdiviae* was 18.6% of their head length. *Melanostomias valdiviae* had a barbel length that was 111.6% of their head length with zero main branches on the barbel (Table 11).

Melanostomias valdiviae was grouped into two morphotypes (morphotypes "b" and "c") with two other individuals in a third morphotype (morphotype "d") in UPGMA clustering (Figures 14, 16, 17, and 18) and in multidimensional space (Figure 20). *Melanostomias valdiviae* was grouped with *E. schmidti*, *E. barbatum*, *P. margarita*, and *E. fissibarbis* with at least 80% morphological similarity. The two other individuals were grouped with the *M. melanops* cluster. These groups were defined by a short barbel, large vertical oral gape, and large horizontal maxillary oral gape.

3.2.8 Eustomias brevibarbatus

Eustomias brevibarbatus had a protrusible upper and lower jaw with a vertical oral gape of 80.1%, horizontal maxillary oral gape of 42.5%, and a horizontal articular oral gape of 38.1% of their head length. Their longest premaxillary tooth and mandibular tooth were 9.7% and 8.9% of their head length, respectively. The eye size of *E. brevibarbatus* was 21.7% of their head length. *Eustomias brevibarbatus* had a barbel length that was 211.1% of their head length with two main branches on the barbel (Table 11).

Eustomias brevibarbatus was grouped into two morphotypes (morphotypes "c" and "d") in UPGMA clustering (Figures 14, 17, and 18) and in multidimensional space (Figure 20). *Eustomias brevibarbatus* was primarily grouped with *M. melanops*, *M. tentaculatus*, and some individuals of *E. filifer* and *M. valdiviae* with at least 80% morphological similarity. There was

some overlap with another group where *E. brevibarbatus* overlapped with *E. fissibarbis* (Figure 20). These groups were defined by a long barbel, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.9 Leptostomias bermudensis

Leptostomias bermudensis had a slightly protrusible lower jaw with a vertical oral gape of 75.8%, horizontal maxillary oral gape of 46.6%, and a horizontal articular oral gape of 42.8% of their head length. Their longest premaxillary tooth and mandibular tooth were 14.6% and 15.3% of their head length, respectively. The eye size of *L. bermudensis* was 20.1% of their head length. *Leptostomias bermudensis* had a barbel length that was 997.1% of their head length with zero main branches on the barbel (Table 11).

Leptostomias bermudensis was primarily grouped into one morphotype (morphotype "a") in UPGMA clustering (Figures 14 and 15) and in multidimensional space (Figure 20). *Leptostomias bermudensis* was grouped with *L. gladiator* and an individual of *B. pawneei* with at least 80% morphological similarity. There was one other individual of *L. bermudensis* within the cluster including *F. boureei* and the other individuals of *L. gladiator* (Figure 19). This group was defined by an exceptionally long barbel, small vertical oral gape, and small horizontal maxillary oral gape.

3.2.10 Bathophilus pawneei

Bathophilus pawneei had both upper and lower jaws that could protrude with a vertical oral gape of 76.3%, horizontal maxillary oral gape of 43.9%, and a horizontal articular oral gape of 39.0% of their head length. Their longest premaxillary tooth and mandibular tooth were 12.6% and 10.1% of their head length, respectively. The eye size of *B. pawneei* was 18.5% of their head length. *Bathophilus pawneei* had a barbel length that was 359.1% of their head length with zero main branches on the barbel (Table 11).

Bathophilus pawneei was grouped into three morphotypes (morphotypes "a", "d", and "e") in UPGMA clustering (Figures 14, 15, 18, and 19) and in multidimensional space (Figure 20). *Bathophilus pawneei* was grouped with the *M. melanops* and *E. brevibarbatus* cluster and the *E. acinosus*, *E. hypopsilus*, *Leptostomias* species and *F. boureei* clusters with at least 80%

morphological similarity. These groups were defined by a long barbel length, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.11 Photonectes margarita

Photonectes margarita had a protrusible lower jaw with a vertical oral gape of 119.4%, horizontal maxillary oral gape of 63.0%, and a horizontal articular oral gape of 53.6% of their head length. *Photonectes margarita* was a larger species but possess small teeth with their longest premaxillary tooth and mandibular tooth measuring at 9.9% and 5.8% of their head length, respectively. The eye size of *P. margarita* was 22.5% of their head length. *Photonectes margarita* had a barbel length that was 61.0% of their head length with 6 – 8 main branches on the barbel (Table 11).

Photonectes margarita was grouped into two morphotypes (morphotypes "b" and "c") in UPGMA clustering (Figures 14, 16, and 17) and in multidimensional space (Figure 20). *Photonectes margarita* was grouped with *E. barbatum*, *M. valdiviae*, *E. schmidti*, and *E. fissibarbis* with at least 80% morphological similarity. These groups were defined by a short barbel, large vertical oral gape, and large horizontal maxillary oral gape.

3.2.12 Eustomias acinosus

Eustomias acinosus had a protrusible upper and lower jaw with a vertical oral gape of 70.4%, horizontal maxillary oral gape of 39.6%, and a horizontal articular oral gape of 33.4% of their head length. Their longest premaxillary tooth and mandibular tooth were 11.2% and 8.5% of their head length, respectively. The eye size of *E. acinosus* was 21.8% of their head length. *Eustomias acinosus* had a barbel length that was 276.6% of their head length with one main branch on the barbel (Table 11).

Eustomias acinosus was grouped into two morphotypes (morphotypes "d" and "e") in UPGMA clustering (Figures 14, 18, and 19) and in multidimensional space (Figure 20). *Eustomias acinosus* was grouped with *M. tentaculatus*, *E. filifer*, *E. hypopsilus*, *M. melanops*, and *B. pawneei* with at least 80% morphological similarity. There was one other individual of *E. acinosus* within the *E. schmidti* cluster. These groups were defined by a long barbel length, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.13 Eustomias filifer

Eustomias filifer had a protrusible upper and lower jaw with a vertical oral gape of 71.1%, horizontal maxillary oral gape of 40.5%, and a horizontal articular oral gape of 35.0% of their head length. Their longest premaxillary tooth and mandibular tooth were 11.6% and 12.5% of their head length, respectively. The eye size of *E. filifer* was 20.1% of their head length. *Eustomias filifer* had a barbel length that was 286.9% of their head length with three main branches on the barbel (Table 11).

Eustomias filifer was grouped into two morphotypes (morphotypes "d" and "e") in UPGMA clustering (Figures 14, 18, and 19) and in multidimensional space (Figure 20). *Eustomias filifer* was grouped with *M. melanops*, *E. acinosus*, *E. hypopsilus*, *M. tentaculatus*, *B. pawneei*, and some individuals of *M. valdiviae* and *E. fissibarbis* with at least 80% morphological similarity. These groups were defined by a long barbel length, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.14 Flagellostomias boureei

Only two specimens of *Flagellostomias boureei* were included in morphological analysis as the other specimens were omitted due to damaged morphological measurements. *Flagellostomias boureei* was the only species in this study with both jaws that did not protrude. *Flagellostomias boureei* had a vertical oral gape of 81.2%, horizontal maxillary oral gape of 46.7%, and a horizontal articular oral gape of 43.4% of their head length. This species had the largest premaxillary tooth and mandibular tooth percentages of 20.1% and 26.3% of their head length, respectively. The eye size of *F. boureei* was the largest percentage for eye size in this study at 26.2% of their head length. *Flagellostomias boureei* had a barbel length that was 450.9% of their head length with 4 – 5 main branches on the barbel (Table 11).

Flagellostomias boureei was grouped primarily into one morphotype (morphotype "e") in UPGMA clustering (Figures 14 and 19) and in multidimensional space (Figure 20). *Flagellostomias boureei* was grouped with *L. gladiator*, *E. hypopsilus*, *E. acinosus*, *E. filifer* and some overlap with the *M. melanops* cluster with at least 80% morphological similarity. This group was defined by a long barbel length, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape.

3.2.15 Melanostomias tentaculatus

Melanostomias tentaculatus had a protrusible lower jaw with a vertical oral gape of 91.4%, horizontal maxillary oral gape of 64.3%, and a horizontal articular oral gape of 54.3% of their head length. Their longest premaxillary tooth and mandibular tooth were 18.8% and 19.4% of their head length, respectively. The eye size of *M. tentaculatus* was 19.1% of their head length. *Melanostomias tentaculatus* had a barbel length that was 315.8% of their head length with zero main branches on the barbel (Table 11).

Melanostomias tentaculatus was grouped into two morphotypes (morphotypes "d" and "e") in UPGMA clustering (Figures 14, 18, and 19) and in multidimensional space (Figure 20). *Melanostomias tentaculatus* was grouped with *M. melanops*, *E. brevibarbatus*, *E. filifer*, *E. hypopsilus*, and *E. acinosus* with at least 80% morphological similarity. These groups were defined by a long barbel, large vertical oral gape, and large horizontal maxillary oral gape.

3.2.16 Bathophilus longipinnis

Bathophilus longipinnis had both upper and lower jaws that could protrude. *Bathophilus longipinnis* had a vertical oral gape of 76.4%, horizontal maxillary oral gape of 52.3%, and a horizontal articular oral gape of 43.3% of their head length. Their longest premaxillary tooth and mandibular tooth were 17.1% and 16.3% of their head length, respectively. The eye size of *B. longipinnis* was 20.4% of their head length. *Bathophilus longipinnis* had a barbel length that was 140.3% of their head length with zero main branches on the barbel (Table 11).

Only three specimens of *B. longipinnis* were used in morphological multivariate analysis due to one or more damaged measurements on the two remaining specimens. *Bathophilus longipinnis* was grouped into two morphotypes (morphotypes "c" and "d") in UPGMA clustering (Figures 14, 17, and 18) and in multidimensional space (Figure 20). *Bathophilus longipinnis* was grouped with *M. valdiviae* and *E. schmidti* with at least 80% morphological similarity. These groups were defined by a medium-sized barbel length, small vertical oral gape, and small horizontal maxillary oral gape.

Table 11. Average morphometric measurements of all 16 melanostomiine species. Quantitative measurements (i.e. barbel length, vertical oral (VO) gape, horizontal articular (HA) oral gape, horizonal maxillary (HM) oral gape, longest premaxillary (PM) tooth, longest mandibular (MDB), and eye size) were all transformed and shown as a percentage of head length. Qualitative measurements included number of main branches and jaw protrusion. Jaw protrusion was listed as Y = Yes, N = No, and S = Slight with "*" representing that both upper and lower jaws did protrude.

Species	**n**	**Barbel Length %**	**VO Gape %**	**HA Oral Gape %**	**HM Oral Gape %**	**Longest PM Tooth %**	**Longest MDB Tooth %**	**Eye Size %**	**Barbel Main Branches (n=)**	**Jaw Protrusion**
Eustomias schmidti	83	107.9	77.8	39.1	44.4	10.5	8.9	21.4	3	Y*
Echiostoma barbatum	87	71.4	114.8	52.7	64.5	14.5	18.4	18.9	0	Y
Eustomias hypopsilus	53	369.5	76.4	30.7	37.3	11.0	9.1	23.7	0	Y*
Melanostomias melanops	34	259.2	125.3	67.1	79.0	17.5	22.4	18.7	0	Y
Eustomias fissibarbis	30	136.3	66.3	31.9	40.0	10.6	9.5	19.7	3	Y*
Leptostomias gladiator	22	582.3	68.9	42.3	48.2	19.8	17.5	22.1	0	S
Melanostomias valdiviae	17	111.6	104.9	48.6	57.7	17.1	18.9	18.6	0	Y
Eustomias brevibarbatus	12	211.1	80.1	38.1	42.5	9.7	8.9	21.7	2	Y*
Leptostomias bermudensis	16	997.1	75.8	42.8	46.6	14.6	15.3	20.1	0	S
Bathophilus pawneei	8	359.1	76.3	39.0	43.9	12.6	10.1	18.5	0	Y*
Photonectes margarita	13	61.0	119.4	53.6	63.0	9.9	5.8	22.5	6-8	Y
Eustomias acinosus	14	276.6	70.4	33.4	39.6	11.2	8.5	21.8	1	Y*
Eustomias filifer	10	286.9	71.1	35.0	40.5	11.6	12.5	20.1	3	Y*
Flagellostomias boureei	2	450.9	81.2	43.4	46.7	20.1	26.3	26.2	4-5	N
Melanostomias tentaculatus	6	315.8	91.4	54.3	64.3	18.8	19.4	19.1	0	Y
Bathophilus longipinnis	3	140.3	76.4	43.3	52.3	17.1	16.3	20.4	0	Y*

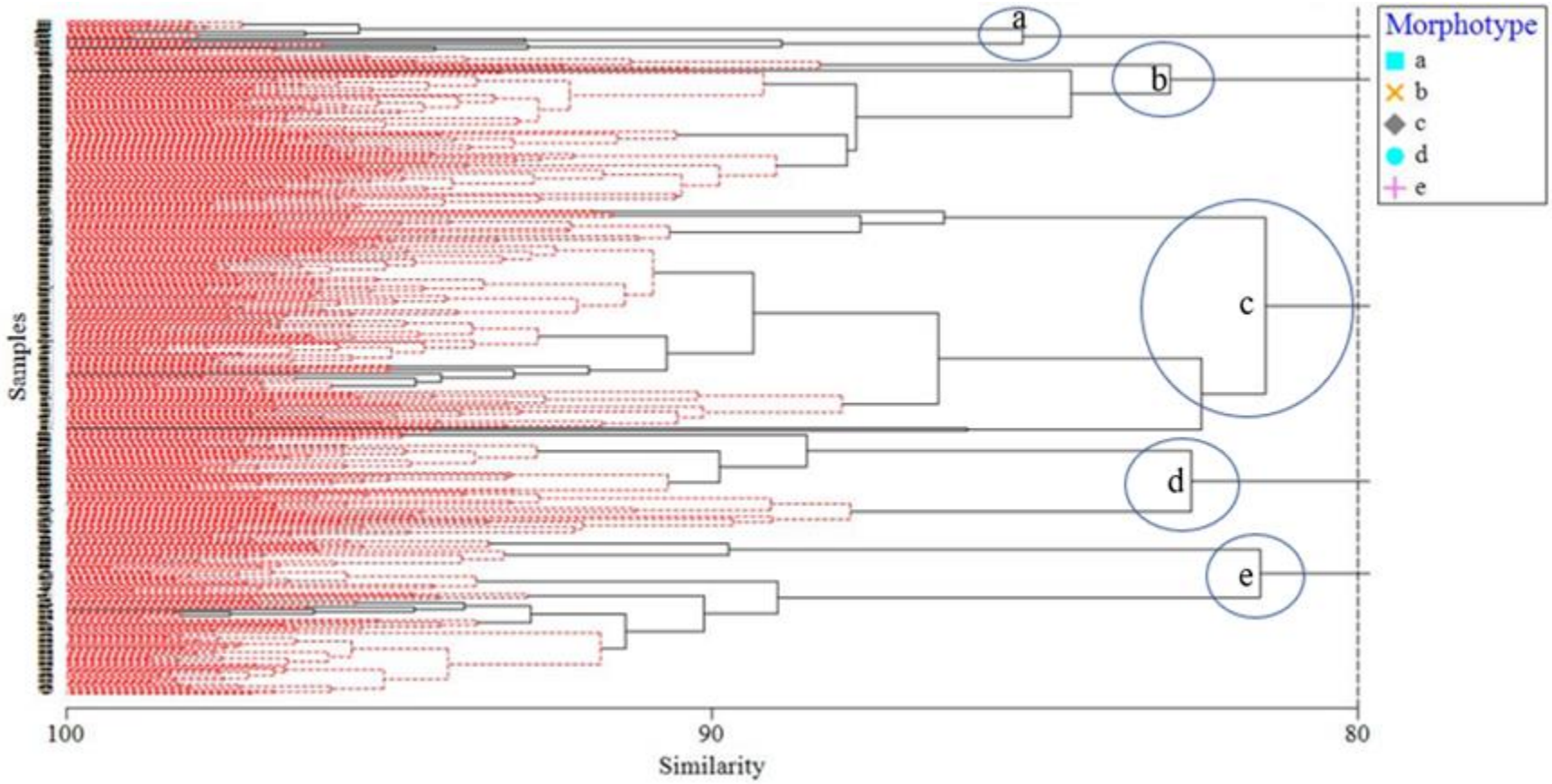

Figure 14. Hierarchical classification of morphotypes among dragonfishes in this study using Bray-Curtis similarity values. A slice was placed at 80% similarity to group these species into morphotypes. Morphotypes are represented by symbols and clusters are circled. Dashed red lines represent that these samples could not be distinguished from one another by morphology and therefore are placed into a morphotype together. See Figures 15 – 19 for individuals grouped into each morphotype

Figure 15. The stomiid individuals grouped into morphotype “a” from the hierarchical classification of morphotypes in Figure 14. These species cannot be distinguished from one another with 80% morphological similarity.

Figure 16. The stomiid individuals grouped into morphotype “b” from the hierarchical classification of morphotypes in Figure 14. These species cannot be distinguished from one another with 80% morphological similarity.

Figure 17. The stomiid individuals grouped into morphotype “c” from the hierarchical classification of morphotypes in Figure 14. These species cannot be distinguished from one another with 80% morphological similarity.

Figure 18. The stomiid individuals grouped into morphotype “d” from the hierarchical classification of morphotypes in Figure 14. These species cannot be distinguished from one another with 80% morphological similarity.

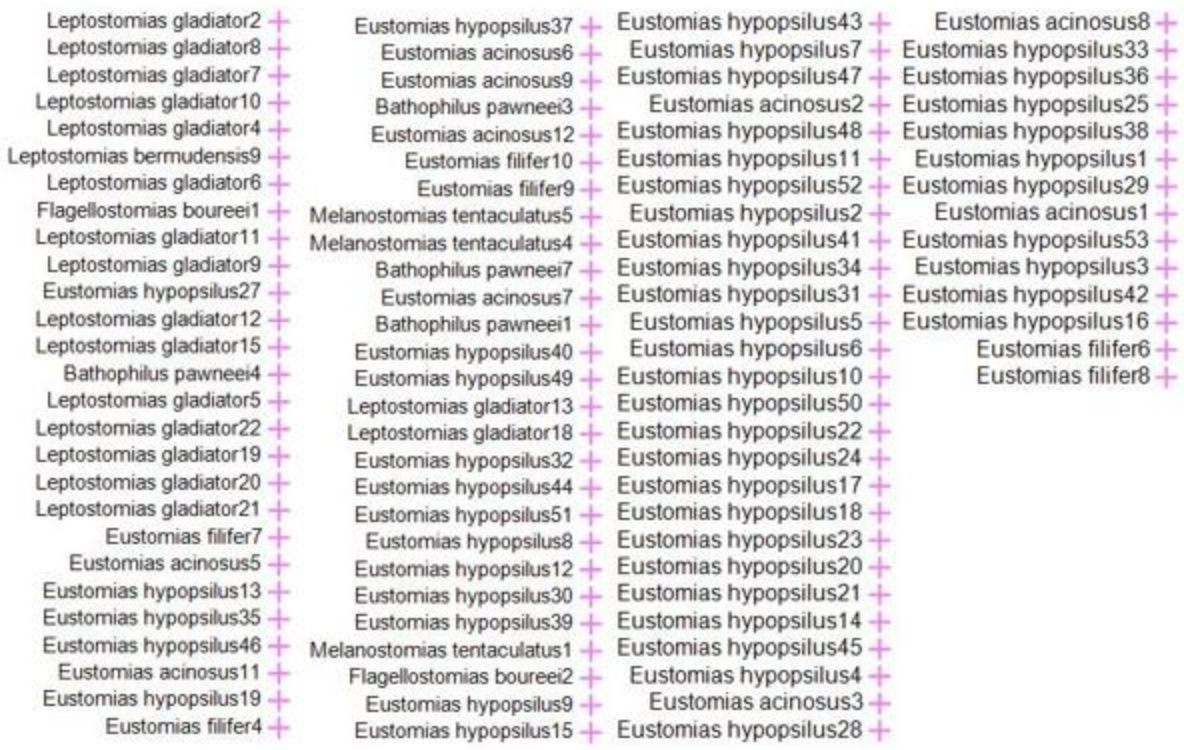

Figure 19. The stomiid individuals grouped into morphotype “e” from the hierarchical classification of morphotypes in Figure 14. These species cannot be distinguished from one another with 80% morphological similarity.

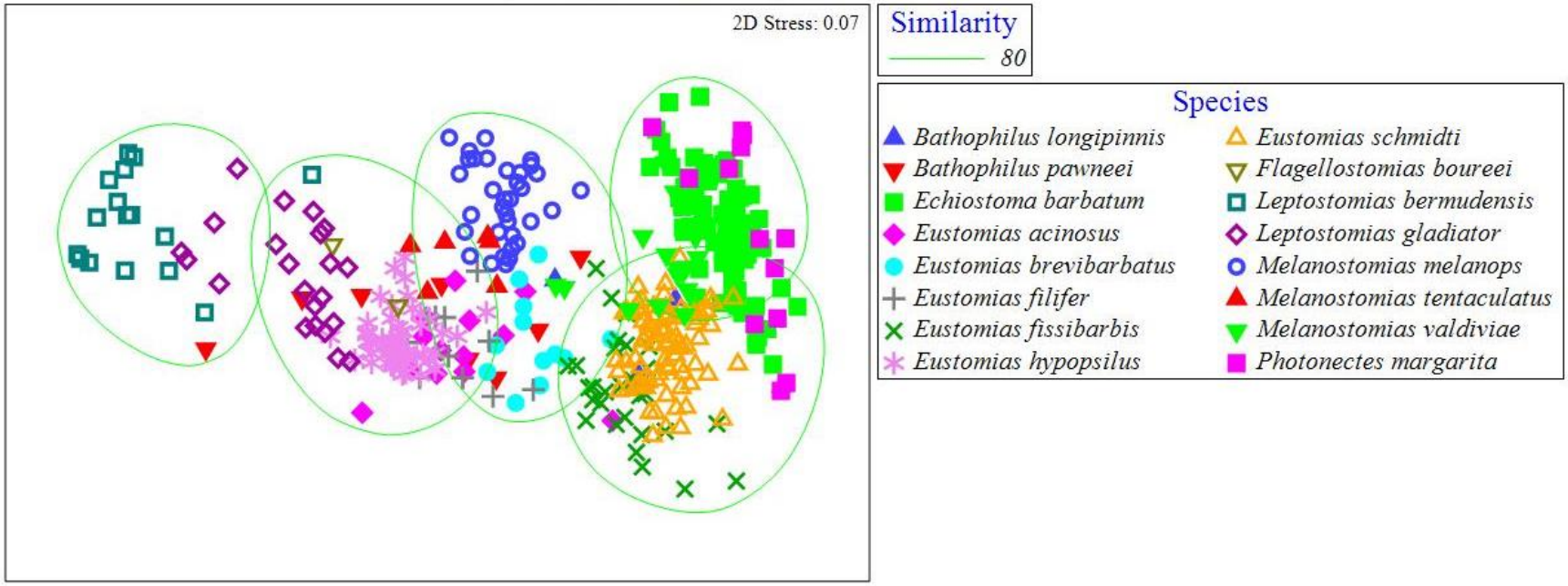

Figure 20. A non-metric multidimensional scaling plot depicting Bray-Curtis similarity values of melanostomiine morphotypes. The ellipsis is based on the clustering depicted in Figure 14. Dragonfish species are represented by symbols

3.3 Morphological-Dietary Relationships

The morphological-dietary relationships of melanostomiines were assessed by visually comparing the groups determined for both multivariate analyses (UPGMA clustering and non-parametric MDS) for both trophic ecology and functional morphology. From this assessment, there were no obvious morphological-dietary relationships in this study by major prey taxon or by prey fish family.

4. DISCUSSION

4.1 Trophic Ecology

4.1.1 Melanostomiine stomach vacuity

With feeding opportunities scarce in the deep sea, it is crucial to be a successful predator on any prey encounter. Out of 451 specimens in this study, approximately 29% of stomachs were prey-positive. The findings in this study aligned with other studies that also reported a high vacuity percentage among stomiids. For example, stomach vacuity of two non-melanostomiine genera, *Chauliodus* and *Stomias*, in the Arabian Sea ranged from 60% – 84% (*Chauliodus*) and 50% – 75% (*Stomias*) (Butler et al. 2001). A recent study by Woodstock et al. (2020) reported prey-positive stomachs for several fish families of the Gulf, with 28.6% of stomiid (non-melanostomiine) stomachs being prey-positive compared to 48.2% of gonostomatid stomachs and 88.7% of myctophid stomachs (both planktivorous fish families). The low percentage of prey-positive stomiid stomachs compared to zooplanktivores supported the notion that predators like stomiids do not have to vertically migrate to feed as often as zooplanktivores that consume smaller prey.

4.1.2 Feeding guilds

On a broader scale, dragonfishes are classified into either a pelagic micronektonivorous or pelagic generalist feeding guild (Gartner et al. 1997; Drazen & Sutton 2017). All 16 melanostomiine species in this study were grouped into feeding guilds by major prey taxon, with three guilds identified via UPGMA clustering and two guilds identified via MDS. All stomiids exhibited some form of piscivorous behavior, but there were some dragonfishes that also consumed cephalopods. The largest feeding guild, which included 14 species in UPGMA clustering (except *B. longipinnis* and *E. barbatum*) and 15 species in MDS (except only *B.*

longipinnis) fed primarily on teleosts, with some cephalopods in few of these melanostomiine diets. Cephalopods comprised 18.5% of the total diet of *E. barbatum* while comprising 50% of the diet in *B. longipinnis*. The feeding selectivity analysis for 13 of the 16 species suggested high selectivity for teleosts. Three species (*B. longipinnis*, *E. barbatum*, and *E. brevibarbatus*) were more selective for cephalopods than teleosts. There is one species of dragonfish that appears to specialize in cephalopod predation (*Heterophotus ophistoma*, subfamily Astronesthinae; Clarke 1982; Sutton & Hopkins 1996b), but overall this strategy is uncommon amongst melanostomiines.

Piscivorous dragonfishes were further grouped according to prey fish family. Previous data on stomiid diet suggested that dragonfishes preyed primarily on myctophids and only a small portion of the diets consisted of fishes from the families Gonostomatidae, Sternoptychidae, Bregmacerotidae, Argentinidae, and the order Beryciformes (Clarke 1982; Hopkins et al. 1996; Sutton & Hopkins 1996b). The analyses for prey fish family were conducted on dragonfish species with one or more fish prey items identified to family level. Many of the prey items in this study were well-digested and only identified to Teleostei. Among the 13 melanostomiines classified, four groups were discriminated via UPGMA clustering and three via MDS. The largest group, which contained eight species in UPGMA clustering and 10 species in MDS, preyed primarily upon myctophids. Both multivariate analyses placed *B. pawneei* in their own group and placed *E. acinosus* and *E. filifer* together in a group. *Bathophilus pawneei* was unique in having a stomiid as prey. Dragonfishes (e.g., *Chauliodus sloani*) have been documented with stomiids in their diet previously with some stomiids even exhibiting cannibalistic behavior (Battaglia et al. 2018; Eduardo et al. 2020). However, the feeding selectivity analysis of *B. pawneei* is likely an underestimate of their diet breadth, as the stomiid was the only prey item included in the analysis. *Eustomias acinosus* and *E. filifer* both fed primarily on howellids (pelagic basses). Howellids were previously found in the diet of *E. brevibarbatus* in an earlier study (Sutton & Hopkins 1996b). The only lack of concordance between the two multivariate analyses was with *E. barbatum* and *M. melanops*. Cluster analysis placed these two species into their group, separate from the primarily myctophid-eating group. However, *E. barbatum* and *M. melanops* were placed into the myctophid-eating group via MDS. *Echiostoma barbatum* seems to be opportunistic with their diet, which included several fish families (Melamphaidae, Myctophidae, and Stomiidae). This finding agrees with Sutton & Hopkins (1996b), who reported a mixed diet of fishes, decapods, and crustaceans. *Melanostomias melanops* preyed upon two fish families, Gonostomatidae and

Myctophidae. Therefore, it is suggested that *M. melanops* is also opportunistic with their diet as they preyed upon the two numerically dominant fish families in the Gulf.

Dragonfishes were originally thought to exhibit generalist feeding (Beebe & Crane 1939; Haffner 1952; Merrett & Roe 1974), however, the feeding data indicated that dragonfishes are highly selective in their diet. Apart from one gonostomatid prey item, 13 of the 16 species of melanostomiines fed upon myctophids. While myctophids are the second-ranking fish family in the mesopelagic zone, there was still a lack of representation of other dominant micronekton taxa (i.e. gonostomatids; Brodeur & Yamamura 2005; De Forest & Drazen 2009) in the diets of melanostomiine dragonfishes.

Feeding chronology

On a scale of 0 – 5 for stomach fullness (i.e. zero represents an empty stomach and five represents a completely full stomach), dragonfishes in this study had an average stomach fullness index of 0.6. This value is relatively low, which may emphasize the few feeding opportunities that occur for these predators. Since dragonfishes vertically migrate ostensibly to feed (Sutton & Hopkins 1996b; Hopkins & Sutton 1998), stomach fullness is hypothesized to be higher at night. In this study, stomach fullness did not vary significantly as a function of time of day (i.e. day vs. night) for any of the 16 melanostomiine species. This lack of diel feeding periodicity suggests that stomiids may feed at different times of day and/or may take several days to digest fish prey (Sutton & Hopkins 1996b). Larger prey items can take more than a day to digest and thus the pattern between feeding, space, and distribution can be difficult to determine.

Eight species of dragonfishes had samples sizes allowing assessment of feeding chronology via state of digestion as a function of time of day (the other eight species were data deficient for either day or night cycles). *Eustomias acinosus* had less digested prey at night, indicating that feeding occurs at night. There were no significant differences in state of digestion vs. time of day for the other seven melanostomiines assessed. These findings are similar to those reported for the three most abundant stomiid species (all non-melanostomiine) in the Gulf (*Chauliodus sloani*, *Photostomias guernei*, and *Stomias affinis*; Sutton & Hopkins 1996b).

4.1.3 Instantaneous Ration

Sutton & Hopkins (1996b) reported instantaneous ration estimates of Gulf stomiids ranging from 2.1% – 7.6%. In this study, instantaneous ration estimates ranged from 0.2% (*P. margarita*) to 27.2% (*E. brevibarbatus*), with an average of 7.2% of predator body weight consumed per feeding event. Concomitant with their high trophic position, individual prey of melanostomiine dragonfishes were large, ranging from 11.7% (*P. margarita*) to 43.1% (*M. melanops*), with an average of 27.6% of the predator length.

4.2 Functional Morphology

4.2.1 Adaptations for large prey

Feeding morphology of a species can be used to predict the relative prey size preference of a predator. The absolute mouth size and dentition of these predators dictate how large of a prey item can be ingested (Sutton 2005). In the species examined, vertical oral gape ranged from 66.3% (*E. fissibarbis*) to 125.3% (*M. melanops*), with an average 86.0% of the stomiid head length. *Melanostomias melanops* had the largest mouth gape which supported the hypothesis that they are opportunistic with their diet as a large mouth gape allows species to consume various sizes of prey available to them. With such a large mouth gape, these melanostomiines have increased their chance at success in prey capture for each of the limited opportunities available to feed. Also, with the ability to ingest large prey, melanostomiines do not have to expend energy in vertically migrating daily as larger prey items can sustain predators for longer than a day.

Dragonfishes possess fewer, longer jaw teeth than other midwater fishes. The fang-like teeth of stomiids are associated with ingestion of large prey. In this study, the longest premaxillary tooth ranged from 9.7% (*E. brevibarbatus*) to 20.1% (*F. boureei*), with an average 14.2% of the stomiid head length. The longest mandibular tooth ranged from 5.8% (*P. margarita*) to 26.3% (*F. boureei*), with an average 14.2% of the stomiid head length. With large fang-like teeth, these melanostomiines again have increased their chance at success in prey capture as larger teeth can not only aid in prey capture, but also reduce the chance of prey escape with the teeth acting as a cage inside the mouth. However, with fewer teeth, smaller prey have an increased chance of escape through the gaps between these fang-like teeth. The largest premaxillary and mandibular teeth of all melanostomiines in this study were both observed in *F. boureei* which was the only species that exhibited no jaw protrusion. Larger teeth may substitute the need for jaw protrusion by investing

more energy in teeth development unlike other melanostomiines. This may allow *F. boureei* to occupy a new niche to avoid competition with other stomiids. *Photonectes margarita* had the smallest mandibular teeth and second-smallest premaxillary teeth. Smaller teeth could confine smaller prey like crustaceans inside the mouth as there is less space between the teeth for the prey to escape. *Photonectes margarita* did ingest crustacean prey items, but they were deemed net feeds and thus excluded from analysis. Therefore, it is hypothesized that crustaceans and smaller prey are targeted by *P. margarita* which is supported by their low instantaneous ration (0.2) observed in this study.

4.2.2 Morphotypes

Three morphometric characters had the most influence in defining morphotypical groups. The most influential character was barbel length, followed by vertical oral gape, and then horizontal maxillary oral gape. Dragonfishes use their bioluminescent lure, when present, to aid in their predatory lifestyle (Partridge & Douglas 1995; Douglas et al. 1998). Barbel length was highly variable between species and ranged from 61.0% (*P. margarita*) to 997.1%, (*L. bermudensis*), with an average 296.1% of head length. With respect to barbel morphology, five morphotypes were distinguished: (1) long barbel, small vertical oral gape, and small horizontal maxillary oral gape (*L. bermudensis*, *L. gladiator*, and a *B. pawneei* individual), (2) long barbel, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape (*L. bermudensis*, *L. gladiator*, *F. boureei*, *E. filifer*, *E. acinosus*, *E. hypopsilus*, *M. tentaculatus*, and one *B. pawneei* individual), (3) long barbel, large vertical oral gape, and large horizontal maxillary oral gape (*M. melanops*, *E. filifer*, *M. tentaculatus*, *E. fissibarbis*, *E. brevibarbatus*, *B. pawneei*, *B. longipinnis*, and *M. valdiviae*), (4) short barbel, medium-sized vertical oral gape, and medium-sized horizontal maxillary oral gape (*E. schmidti*, *E. barbatum*, *P. margarita*, *M. valdiviae*, *E. fissibarbis*, *B. longipinnis*, *E. brevibarbatus*, and *E. acinosus*), and (5) short barbel, large vertical oral gape, and large horizontal maxillary oral gape (*E. barbatum*, *P. margarita*, *M. valdiviae*, and *E. schmidti*). These character combinations did not influence prey type, as all melanostomiines exhibited piscivorous behavior and therefore diet specialization was not the main factor that influenced melanostomiine hyperspeciation. However, these character combinations in these morphotypes supported a sit-and-wait predation strategy as large oral gapes increase prey capture per encounter which is vital in the deep sea.

In this study, diet specialization between melanostomiine genera was not apparent, suggesting that some other selective pressure may drive the intense speciation of melanostomiines. Dragonfishes were known to use their lure for predation (Partridge & Douglas 1995; Douglas et al. 1998), but studies have speculated that these lures could also be used for intraspecific communication. A study by Davis et al. (2014) demonstrated that myctophids and stomiids with species-specific bioluminescent structures have rapidly speciated more than other taxa that use bioluminescence for predation or camouflage. In this study, melanostomiine barbels varied regarding the number of main branches as several species (*E. barbatum*, *E. hypopsilus*, *M. melanops, L. gladiator*, *M. valdiviae, L. bermudensis*, *B. pawneei*, *M. tentaculatus*, and *B. longipinnis*) displayed a barbel with no branching and the largest amount of branching with 6 – 8 branches on the barbel displayed by *P. margarita*. The amount of branching may influence the number of bulbs and bulb structure on these barbels. The main selective pressure that drove the hyperspeciation observed may result from species recognition, intraspecific communication, and sexual selection. In an environment with few genetic isolating barriers, finding a mate could potentially be very difficult especially in low-light areas and therefore the ability to utilize bioluminescence to communicate intraspecifically could be useful. Barbel complexity could lead to sexual selection where individuals with barbels adorned with more bulbs and branches could be selected over other individuals which may explain the barbel variability observed between *Eustomias* species. The hyperspeciation observed from these melanostomiines may have in part been driven from other selective pressures like morphological changes, but it is inferred that species-specific bioluminescence is the main pressure that drove this intense speciation.

4.2.3 Vision

In this study, eye size was relatively consistent among melanostomiine species, ranging from 18.5% (*B. pawneei*) to 26.2% (*F. boureei*), with an average of 20.8% of the stomiid head length. A study conducted by De Busserolles et al. (2013) on eye size of myctophids determined that phylogenetic relationships were the sole factor to influence the eye size instead of ecological factors. The ecological factors analyzed (i.e. depth and bioluminescence) did not significantly affect eye size. However, some of the lanternfishes exhibited the trend where eyes are larger in shallow depths and smaller in deep depths. Similar to myctophids, stomiids possess an eye designed to detect both downwelling light and bioluminescence. Adaptations of the eye to detect

these sources of light is hypothesized to be influenced by the ecological task required (De Busserolles et al. 2013). Myctophid eyes are relatively larger that stomiid eyes regarding percentage of head length, which may emphasize a greater need for myctophids to see downwelling light for vertical migration and to search greater volumes of water to avoid predators. In contrast, a reduced eye size is less energetically costly but useful for seeing bioluminescence at a distance (Warrant et al. 2003). Melanostomiine eyes are hypothesized to be medium-sized as to partially accommodate both the need to see close for predation, but also the need to see farther to search for mates. Eye size was not related to barbel length, which suggested that bioluminescence was not driving the differences observed in eye size. Mode of feeding may have influenced eye size as dragonfishes are sit-and-wait predators and thus only need to see just a few meters around them for prey attracted by their lure. However, medium-sized eyes adapted to search for mates could also be useful to search large volumes of water for prey. Eye size may have several influences, but since eye size was relatively consistent among melanostomiines, it is hypothesized that all melanostomiines utilized their eyes for a similar task that is not derived from competitive pressure.

4.2.4 Jaw Protrusion

Jaw protrusion amongst melanostomiines was characterized as either protrusion, slight protrusion, or no protrusion. The only species that did not exhibit jaw protrusion was *F. boureei* which is in agreement with a recent taxonomic key (Sutton et al. 2020). Two species, *L. bermudensis* and *L. gladiator*, had slight protrusion in the lower jaw and no protrusion in the upper jaw. *Flagellostomias boureei*, *L. bermudensis*, and *L. gladiator* possessed the three largest barbel lengths and exhibit little to no jaw protrusion. With such a long barbel, these species should possess a protrusible jaw to capture the prey attracted to the lure that is not close to the mouth, however, this was not the case. The long barbel may be utilized to confuse predators to target the lure that is far away from the head of these stomiids. *Echiostoma barbatum*, *M. melanops*, *M. tentaculatus*, *M. valdiviae,* and *P. margarita* could protrude the lower jaw with the upper jaw not able to protrude. The ability to protrude the lower jaw increased the size that the mouth could extend which allowed these predators to consume larger prey. *Bathophilus* and *Eustomias* species exhibited both upper and lower jaw protrusion and were also observed to have a smaller mouth size compared to melanostomiines that exhibited only lower jaw protrusion. *Eustomias* had the

largest species count collected from the Gulf with 722 specimens and *Bathophilus* was the third-highest count with 161 specimens. It is hypothesized that *Bathophilus* and *Eustomias* aimed to occupy a new niche by possession of a more protrusible jaw to catch smaller prey instead of competing with larger melanostomiines that targeted larger prey. *Eustomias* and *Bathophilus* were amongst the highest species counts of melanostomiines collected from the Gulf, which suggested that the ability to protrude both jaws also influenced the hyperspeciation observed in these genera.

5. CONCLUSION

This thesis represents the most extensive study into the diet of the subfamily Melanostomiinae. There were three feeding guilds by major prey taxon, the largest of which was piscivory, which further divided into four feeding groups. All of the melanostomiine species preyed upon teleosts, but some also selected for cephalopods. With respect to fishes consumed, most melanostomiines were highly selective for myctophids, with some exceptions; a few also consumed Gonostomatidae, Howellidae, Melamphaidae, and Stomiidae. Melanostomiine dragonfishes take relatively large prey, averaging 7.2% of their own weight and 27.6% of their own length. Of the six morphological characteristics measured, the main characteristics that influenced dissimilarity amongst the morphotypes were barbel length, followed by vertical oral gape, and horizontal maxillary oral gape. Five morphotypes were identified from these three morphological characteristics. There were no obvious morphological-dietary relationships amongst these melanostomiines. Diet specialization may have influenced the hyperspeciation exhibited by the Melanostomiinae, but other factors such as intraspecific communication, interspecific competition, and predator avoidance, likely influenced this speciation as well. Lastly, barbel complexity was highly variable between genera, with the most variability observed within the genus *Eustomias*. Genera with more complex barbels were more speciose than genera with less complex barbels as barbel morphology dictated the number of species per genus, with *Eustomias* species accounting for half of the species within the family Stomiidae.

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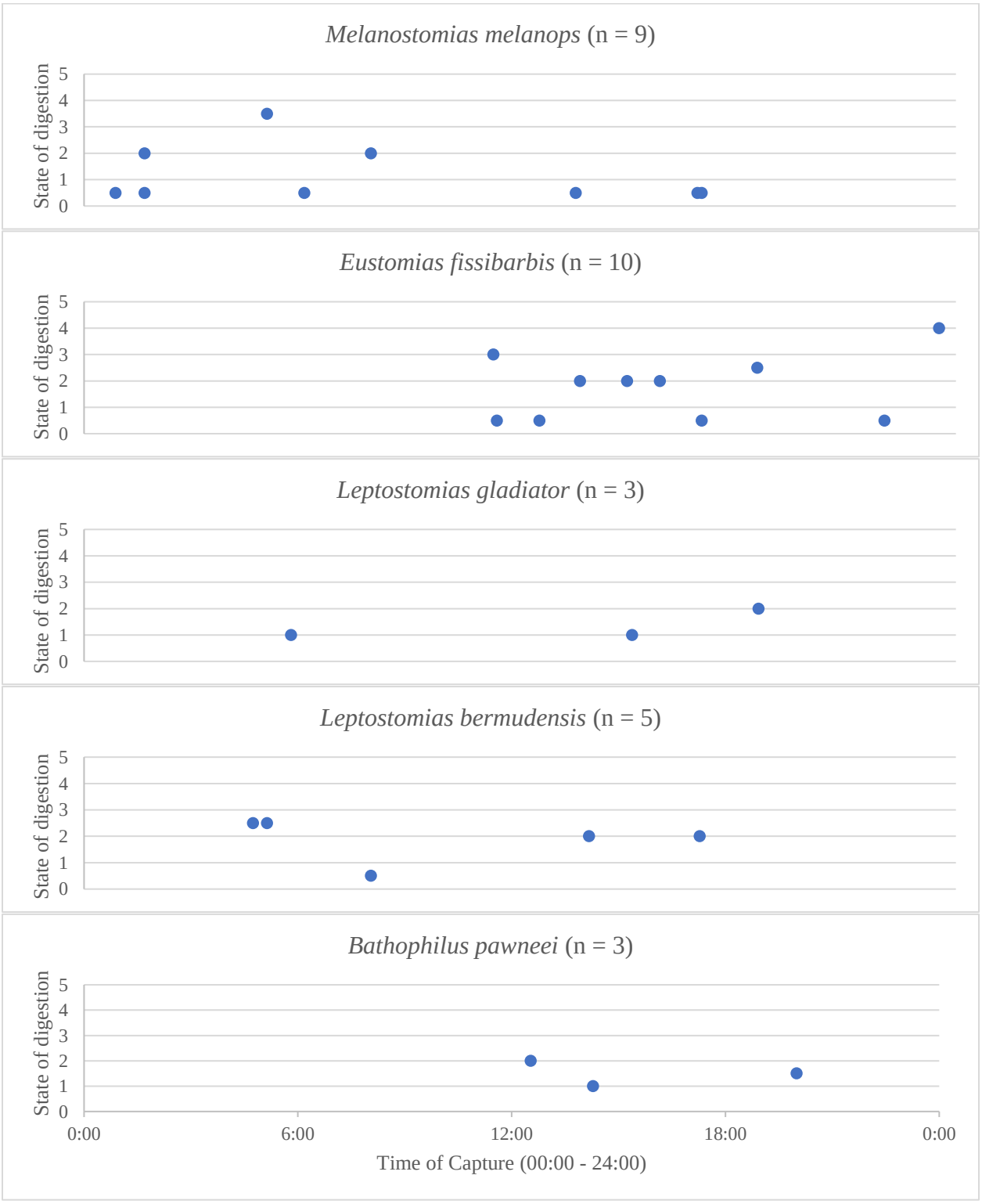
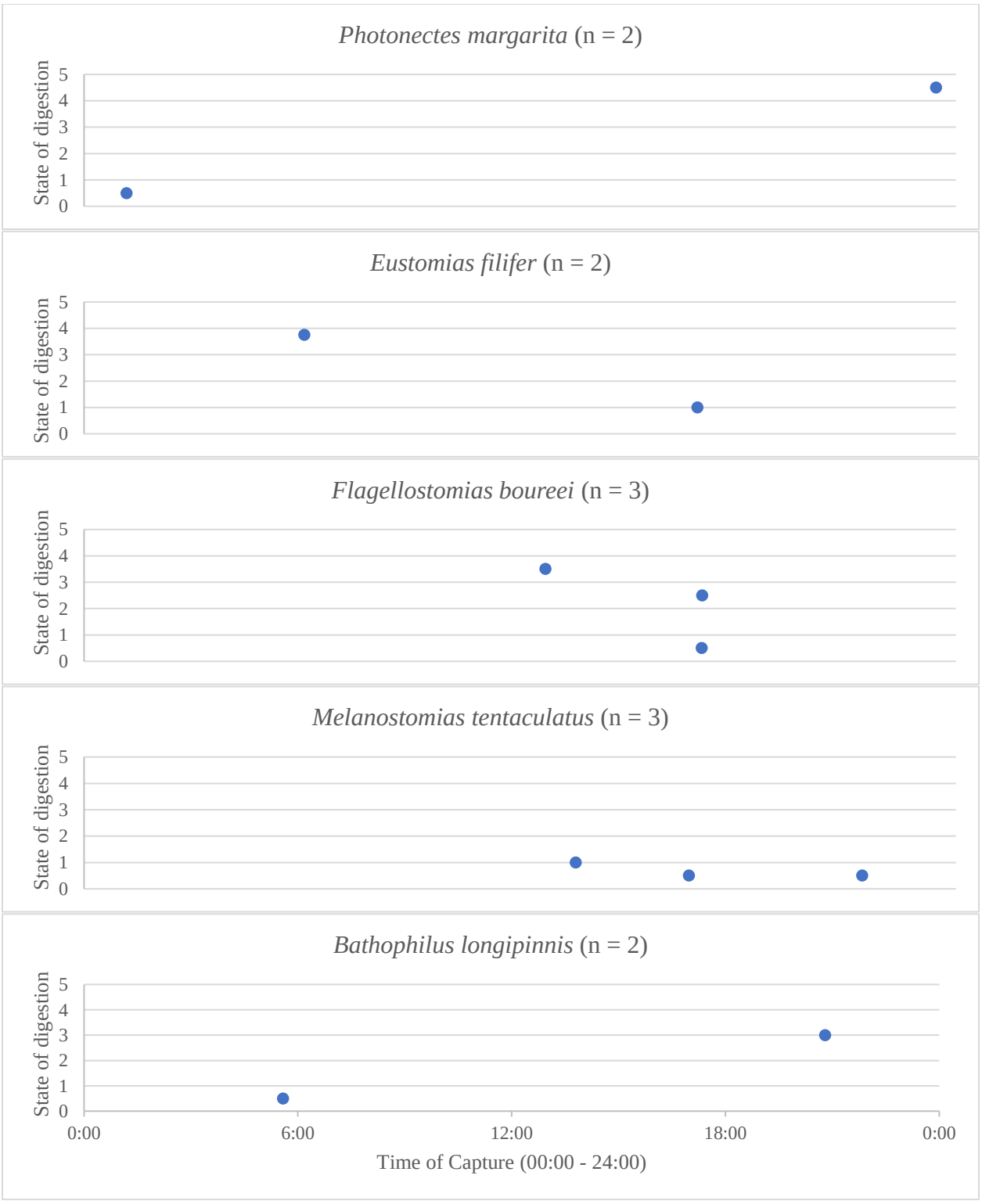
7. APPENDIX



Appendix Figure 1. Feeding chronology of five melanostomiines within the Gulf of Mexico. State of digestion of prey items graded from 0.5 (mostly digested) to 5.0 (fresh).



Appendix Figure 2. Feeding chronology of five melanostomiines within the Gulf of Mexico. State of digestion of prey items graded from 0.5 (mostly digested) to 5.0 (fresh).