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Journey into Midnight: Population Dynamics, Vertical Distribution, and Trophic Ecology of Whalefishes (Cetomimidae) in the Bathypelagic Gulf of Mexico

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Thesis of
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Submitted in Partial Fulfillment of the Requirements for the Degree of

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Marine Science

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Halmos College of Arts and Sciences

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HALMOS COLLEGE OF ARTS AND SCIENCES

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By

Rachel Marie Eckley

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Abstract

Despite comprising the largest biome on Earth, the bathypelagic zone inhabitants represent a “black hole” in the understanding of deep-oceanic functioning due to physical and monetary limitations. The characteristics of the global bathypelagic realm create a limiting environment only inhabitable by specially adapted fauna. These include whalefishes (Stephanoberycoidei: Cetomimidae), which are a taxonomically and systematically challenging group of primarily bathypelagic fishes.

Cetomimids were collected in the Gulf of Mexico using high-speed rope trawls and a multiple-opening-and-closing net system. Population dynamics were described using morphometric analysis. Vertical distributions, including diel variation, were described using a modified boxplot of abundance standardized by volume of filtered water. Finally, trophic ecology of male and larval *Cetomimus*/*Gyrinomimus* was described through gut-content analysis.

In total, 493 Cetomimidae were collected, including six new records for the region (*Cetomimus compunctus*, *C. picklei*, *Danacetichthys galathenus*, *Gyrinomimus bruuni*, *G. grahami*, and male *Cetomimus*/*Gyrinomimus* TBD) and one new record for the Atlantic Ocean (*C. compunctus*). The assemblage is dominated by *Cetostoma regani* and *Ditropichthys storeri* and is highly skewed to favor adult females. Cetomimids were collected most often in the upper bathypelagic zone, including the smaller males and larvae. Asynchronous diel vertical migration is likely in *C. regani* and *D. storeri* and possible in species of *Gyrinomimus*. Specimen SL and depth of capture were not correlated. Male *Cetomimus*/*Gyrinomimus* primarily consume copepods although opportunistic feeding of larger crustacea including euphausiids and/or mysids is likely. Larvae gorge on copepods (in quantities reaching 1709) and may display a selective feeding strategy targeting swarming copepods.

Keywords: Cetomimidae, deep-sea, faunal composition, species abundance, vertical range, diel variation, diet.

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1. Introduction

1.1. Bathypelagic zone

The deep sea (water depth > 200 m) is Earth's largest habitat covering roughly 65% of the planet's surface (Priede, 2017), with the bathypelagic zone leading by volume of the World Ocean. The bathypelagic zone begins at the base of the mesopelagic zone, roughly 1000 m water depth in most oceans, at which (measurable) solar light penetration effectively goes to zero. This zone reaches depths just above the abyssopelagic zone at roughly 4000 m (Figure 1). The environment of the bathypelagic zone is characterized by high hydrostatic pressure and average temperature of c. 4 ˚C and is referred to as the 'midnight zone' due to the complete lack of sunlight (Herring, 2002; Danovaro et al., 2014). One of the more inconspicuous qualities possessed by this zone is low food availability relative to overlying waters, and thus the attenuation of food energy with depth (Angel, 1997).

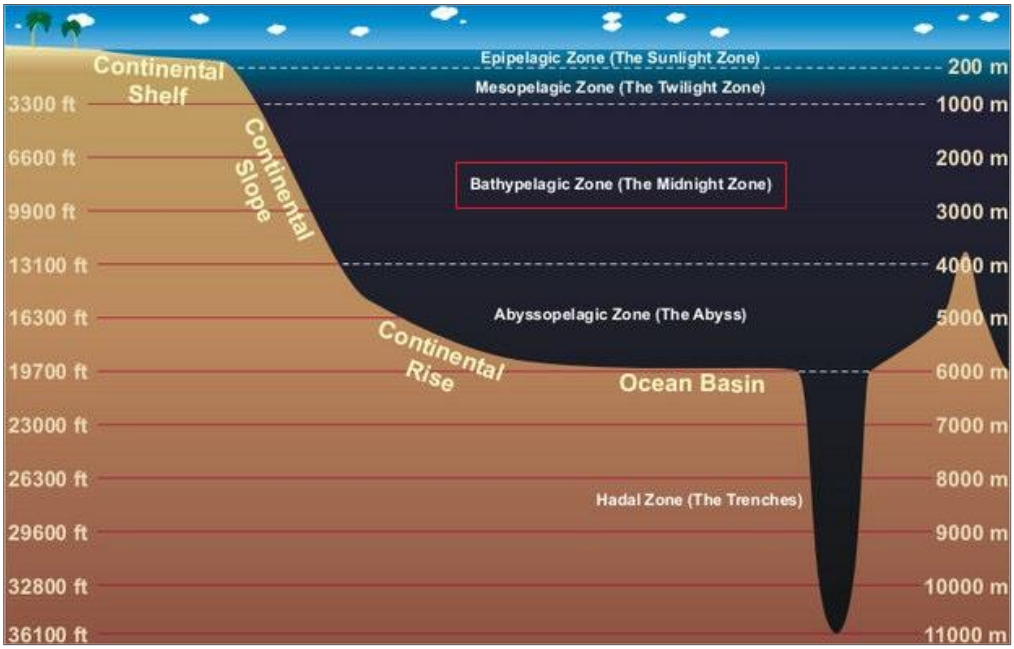


Figure 1. Diagram of the pelagial oceanic zones by depth with the bathypelagic zone indicated by the red box (www.eoearth.com).

Each oceanic biome possesses discrete habitat qualities that create unique domains and yield zone-specific biota. The bathypelagic and mesopelagic (c. 200 – 1000 m) zones in the Gulf of Mexico have been found to be distinctly separate, but highly connected, ecosystems containing

relatively discrete assemblages (Burghart et al., 2007). The prominent factor determining zone specificity of assemblages is depth, which is itself a multivariate ensemble that encompasses other environmental factors such as light, temperature, dissolved oxygen, and pressure (Burghart et al., 2007; Cruz-Acevedo et al., 2018; Powell & Haedrich, 2003).

Limiting environment

The conditions of high pressure, low food availability, low temperature, and an absence of solar light penetration create a limiting environment in the bathypelagic zone. Bathypelagic fishes maintain specializations and adaptations to live in this extreme environment (Bertelsen & Nielsen, 1986; Sutton et al., 2008). To obtain adequate food energy, many deep-sea fishes undergo diel vertical migrations in which predators inhabit deeper biomes during the day and rise to surface waters at night to feed (Hopkins et al., 1996; Merrett & Roe, 1974), including lanternfishes (Myctophidae) and dragonfishes (Stomiidae) migrating from the mesopelagic zone. The limiting characteristics of the bathypelagic zone create unique circumstances in which only few fishes can exist (Sutton et al., 2010). Morphological adaptations of deeper-dwelling pelagic fauna include a reduction in the ratio of eye size to head length and an enlarged mouth gape to utilize a generalist feeding strategy in an environment with low prey opportunities (Drazen & Sutton, 2017).

Knowledge gap

The most prevalent knowledge gap in marine diversity occurs in the bathypelagic zone (Wiebe et al., 2010). The known inhabitants of this region and below make up less than 15% of the limited pelagic biodiversity records (Webb et al., 2010). This deficiency in data could be attributed to the challenges in adequately sampling the deep ocean, coupled with elevated costs of equipment and ship time (Lord, 2016). Consequently, over a billion cubic kilometers of the deep ocean remain effectively unexplored (Kunzig, 2003).

Although the available knowledge of bathypelagic inhabitants is lagging, wide-ranging studies have proved that this biome hosts a variety of life and higher abundance than previously thought. Hanchet et al. (2013) discovered that indices of species richness, biodiversity, and evenness near the Ross Sea Region in the abyss (3000 – 3600 m), slope (600 – 2200 m), and seamounts (400 – 3000 m) were greater than those of the shelf (0 – 1200 m). Remotely operated vehicles exposed a diverse assemblage of tunicates, crustaceans, polychaetes, and fishes of the

Monterey Canyon in which abundance peaked in the upper bathypelagic region (Robison et al., 2010). During the Census of Marine Life Mid-Atlantic Ridge Ecosystem Project (MARECO; Vecchione et al., 2010), multiple-opening-and-closing nets revealed that the highest fish biomass occurred between 1500 and 2300 m (Sutton et al., 2008; Sutton, 2013). Finally, Cook et al. (2013) furthered these findings in determining that the waters of the deep-pelagic Mid-Atlantic Ridge contained the highest diversity index between 700 and 1900 m. Broad studies that utilize various sampling gears have demonstrated a diverse assemblage and increased abundance in deep-pelagic realms, although further investigation is required.

Gulf of Mexico

Knowledge of the inhabitants of the bathypelagic Gulf of Mexico has dramatically increased following the 2010 *Deepwater Horizon* oil spill (DWHOS) through various projects including the Gulf of Mexico Offshore Nekton Sampling and Analysis Program (ONSAP), funded by the National Oceanic and Atmospheric Administration, and the Deep Pelagic Nekton Dynamics (DEEPEND) Consortium, funded by the Gulf of Mexico Research Initiative. These projects aimed to understand the population and community dynamics of the Gulf of Mexico, as proper baseline data detailing the ecosystem before the spill occurred were lacking (Fisher et al., 2016). Current species counts, faunal composition of the assemblages, and ecological data of the bathypelagic Gulf of Mexico were recorded and estimated after the oil spill occurred, but without baseline data, the extent of the damage from the spill is not definitive.

The Gulf of Mexico is a semi-enclosed basin in which the deeper biomes are relatively stable environments. The Loop Current and associated eddies are the main oceanographic features responsible for circulation in the Gulf of Mexico, which produce observable effects as deep as 1000 m (Mooers, 1998). From roughly 700 to 900 m, Antarctic Intermediate Water (AAIW) is present. Water below 1000 m is primarily composed of North Atlantic Deep Water (NADW). Between these layers is a transitional water mass in which temperature begins to decrease to the characteristic 4 ˚C of the bathypelagic (Portela et al., 2018). The lack of physical features in the mesopelagic zone and above allows for an unchanging environment, excluding the effects of anthropogenic impacts. Biota may enter the Gulf of Mexico near the Yucatan Peninsula, utilizing the Loop Current, and exit at the Florida Straits, thus the Gulf of Mexico hosts a unique assortment of ichthyofauna at all depths. Through ONSAP and DEEPEND, scientists have found that the Gulf

of Mexico could contain one of the most diverse deep-pelagic biomes in the world (Sutton et al., 2017).

1.2. Cetomimidae

The suborder Stephanoberycoidei (*sensu* Fricke et al., 2021), comprises six families, of which three are termed "whalefishes:" Cetomimidae (whalefishes), Rondeletiidae (redmouth whalefishes), and Barbourisiidae (velvet whalefish). The three other families within the suborder Stephanoberycoidei are Stephanoberycidae (pricklefishes), Hispidoberycidae (hispidocerycids), and Gibberichthyidae (gibberfishes). While current literature classifies the three whalefish families as the superfamily Cetomimoidea (Nelson et al., 2016), the subclade is not yet accepted *sensu* Fricke et al. (2021). The family Cetomimidae, the topic of this thesis, comprises 11 genera and 21 valid species (Nelson et al., 2016).

Cetomimidae have been studied since the original description (Goode & Bean, 1895), but the group lacks the magnitude of research that coastal or shallow water fauna have received. Per the Ocean Biogeographic Information System (2020), the available data on cetomimid fishes are from only 764 known records. Despite the underrepresentation of Cetomimidae in scientific literature, the family is regarded as one of the most common and speciose groups of deep-sea fishes below 1800 m (Nelson et al., 2016; Paxton, 1989).

Systematics and taxonomy

Historically, Stephanoberycoidei have remained taxonomically and systematically challenging. Paxton (1989), Moore (1993), and Paxton et al. (2001) described changes to the classification of the deep-sea group as phylogenies between Stephanoberycoidei and other groups were investigated. Stephanoberycoidei were originally classified in a suborder of Beryciformes (Rosen & Patterson, 1969). This group was then considered to be the only fishes in the separate order Cetomimiformes (Ebeling & Weed, 1973). Other studies classified the group in the stephanoberycoid assemblage, in the basal clade Stephanoberyciformes, and in the clade Trachichthyiformes (Rosen, 1973; Johnson & Patterson, 1993; Moore, 1993, respectively). The present study follows the classification of Fricke et al. (2021) in that the whalefish families are placed within the suborder Stephanoberycoidei, which is within the order Beryciformes as described by Keene and Tighe (l984). Recent studies have further classified Beryciformes using

molecular evidence. Nelson et al. (2016) found that Cetomimidae, Rondeletiidae, and Barbourisiidae form a monophyletic subclade (Cetomimoidea) that separates the whalefishes from others within the Beryciformes. Dornburg et al. (2017) investigated conflicting molecular data and further reorganized the Beryciformes. The beryciform families Holocentridae, Berycidae, Melamphaeidae, Cetomimidae, Rondeletiidae, and Barbourisiidae constitute a sister group to the Percomorpha, while the remaining beryciform families constitute the clade Trachichthyiformes (Dornburg et al., 2017).

Cetomimids display extreme cases of sexual dimorphism and ontogenetic transformations, resulting in further taxonomic controversies. In unpublished data, Paxton described the *Gyrinomimus* species complex of *G. myersi*, *G. parri*, and *G. simplex*, in which previously described specimens of those species need reevaluation due to a lack of genus-to-species identification keys (Tolley et al., 1989). Larval cetomimids were initially described as being members of the order Beryciformes: suborder Stephanoberyciformes: family Mirapinnidae until mitochondrial DNA sequencing showed that mirapinnids and cetomimids were analogous (Miya et al., 2003). Johnson et al. (2009) examined this quandary further with mitogenomic sequencing and morphological examination of a transitional female specimen and revealed that three formerly described families of Beryciformes were in fact larvae (formerly Mirapinnidae; Bertelsen & Marshall, 1956), males (formerly Megalomycteridae; Myers & Freihofer, 1966), and females of the single family Cetomimidae. The male and larval cetomimid complexes of "*Ataxolepis"* and "*Eutaeniophorus"* are rooted within the genera *Cetomimus* and *Gyrinomimus* (Johnson et al., 2009). A shortage of genetic analyses, descriptions, and identification keys complicate the ability to identify larval or juvenile life stages; thus, many of these cetomimid forms have yet to be described. Few species descriptions are based on the complete ontogeny, and analyses estimate that as little as 10% of larval cetomimid species have been described (Leis, 2015). This lack of identified larval and juvenile forms of Cetomimidae further accentuates the knowledge gap of these deep-sea fishes and has inhibited studies regarding distribution and diet.

Global horizontal and vertical distribution

Despite the deficiency in widespread distribution analyses, studies suggest that Cetomimidae have a circumglobal distribution. The population throughout the World Ocean appears relatively less abundant than other bathypelagic fishes, although cetomimid abundance is

higher than previously thought (Paxton, 1989). Using historically whalefish-rich trawls from the South Atlantic, cetomimid abundance was estimated to be 2800 fish per km^3 of seawater between 1800 and 2300 m (Paxton, 1989). Knowledge gaps of Cetomimidae and the bathypelagic ecosystem are profound, as some species are known by only the holotype (e.g., *Gyrinomimus andriashevi*; Fedorov et al., 1987). This insufficiency of data limits the scientific understanding of Cetomimidae distributions and ranges.

The Cetomimidae is known to exist within the range of 52 °N to 72 °S and has been found in most major seas and ocean basins (Paxton, 1989). Cetomimids are considered to have a cosmopolitan distribution, as is typical of many bathypelagic species due to the weaker barriers between biomes and water masses at depth (Backus et al., 1977; Paxton, 1989). To date, seven taxa have been recorded from the Gulf of Mexico (Table 1).

Table 1. Known Cetomimidae occurring in the Gulf of Mexico prior to this study, including known depth range (summarized in McEachran, 2009). Note that *Gyrinomimus parri* was identified as *Gyrinomimus myersi.*

Taxa	Depth (m)	References
Cetomimus gillii	900 – 1300	McEachram & Fechhelm, 1998; Paxton, 1989; Paxton, 2002; Tolley et al., 1989
Cetomimus hempeli	1000 – 2000	McEachram & Fechhelm, 1998; Paxton, 2002; Stukus, 1963; Tolley et al., 1989
Cetomimus teevani	1000 – 4000	McEachram & Fechhelm, 1998; Paxton, 1989; Paxton, 2002
Cetostoma regani	600 – 1500	McEachram & Fechhelm, 1998; Paxton, 1989; Paxton, 2002; Tolley et al., 1989
Ditropichthys storeri	800 – 2150	McEachram & Fechhelm, 1998; Murdy et al., 1983; Paxton, 1989; Paxton, 2002
Gyrinomimus parri	1280	Bigelow, 1961; McEachram & Fechhelm, 1998; Paxton, 1989; Paxton, 2002
Eutaeniophorus festivus	0 – 2000	Bertelsen & Marshall, 1956; Bertelsen & Marshall, 1958; McEachram & Fechhelm, 1998; Paxton 2002

Larval and juvenile cetomimids have been collected shallower in the water column than the adults; however, the vertical ranges remain unknown as many species contain undescribed early life stages. One late flexion larval specimen believed to be either *Gyrinomimus* or *Cetomimus* was caught near Juan Fernandez Seamount between 0 and 450 m (Herrera et al., 2016), and three other larvae were collected near the North Pacific Gyre (Loeb, 1979). Another study described the collection of larval and post-larval *Parataeniophorus brevis*, *Eutaeniophorus festivus*, and

Cetostoma regani, and a juvenile *Gyrinomimus* specimen; however, all collections occurred in open nets and therefore the exact depth of capture is unknown (Johnson et al., 2009).

While larval and juvenile stage fishes of Cetomimidae are typically found shallower in the water column, adult cetomimids almost always appear within the bathypelagic zone below 1000 m (Paxton, 1989). There may be an exception in *Cetostoma regani* and *Ditropichthys storeri* in which smaller individuals display evidence of vertical migration (Paxton, 1989), although these results have not yet been confirmed. Owing to the fact that open-net trawling results in imprecise collection depths, the maximum depth of capture for Cetomimidae has been impossible to determine (Paxton, 1989). While the occurrence of cetomimids is estimated to be lower than other bathypelagic fishes in the World Ocean (e.g., bristlemouths of the genus *Cyclothone*), the lack of known distributions are likely due to inadequate sampling efforts rather than geographical limitations (Paxton, 1989). Additional analyses of historical captures and further studies utilizing discrete-depth trawls will bridge knowledge gaps of these bathypelagic fishes.

Trophic ecology

Dietary data of most bathypelagic fauna are severely lacking, especially for Cetomimidae. Although no comprehensive feeding estimates have been made, Drazen and Sutton (2017) postulate that bathypelagic fishes consume less than or between 0.5 – 5% of their body weight daily, as energy requirements and expenditures are less than those of mesopelagic ichthyofaunal counterparts. Few studies have analyzed the stomach contents of cetomimid specimens or made dietary assumptions based on form and function. Paxton (1989) analyzed 500 specimens of Cetomimidae and concluded that some bodily features, including a larger mouth, long abdominal section, and posterior dorsal and anal fins, are suggestive of consuming the largest possible prey item when available. Johnson et al. (2009) summarized the known dietary information for the larval and male life-history stages and reported that larvae and juveniles gorge on copepods and cease feeding after metamorphosing into the adult male form. At that time, the stomach shrinks and the nutrition and energy from the copepods are transferred to the liver, which enlarges and continues to sustain the individual. There is a deficit of dietary knowledge for the remaining species and life stages of Cetomimidae as well as predation on cetomimids. Without predator or prey documentation, the ecological importance of Cetomimidae remains largely unknown.

1.3. Statement of problem and significance of work

Cetomimidae remains one of the least-studied groups of deep-sea fishes. Few studies described form and function, while reproductive mechanisms and diet remain unexplored (Paxton, 1989). Aside from the original Cetomimidae population estimate by Paxton (1989), no further assessment has been made regarding abundance or faunal composition. The classification of these bathypelagic fishes has historically been questioned and will likely continue to be reassessed until further collections are made. Using previously analyzed specimens, studies have produced identification keys, including to genus (Paxton, 1989) and species of *Cetomimus* (Maul, 1969); however, these keys are potentially incomplete due to new species descriptions and reclassifications of the group. Understanding this basic information regarding life-history and diet of one of the most speciose deep-sea groups would considerably increase the scope of knowledge and understanding of the bathypelagic biome. Without this essential information, the ecology and population assemblage of the deep sea would remain an incomplete puzzle.

This study aimed to (1) analyze the population dynamics of the Gulf of Mexico Cetomimidae assemblage, (2) determine vertical distributions, including diel variation, of cetomimid species and life-history stages, and (3) analyze the diets of male and larval *Cetomimus*/*Gyrinomimus*. Through improved understanding of the bathypelagic zone ecology, a more thorough understanding of the deep-pelagic World Ocean can be attained. This study will substantially increase the available knowledge of the bathypelagic Gulf of Mexico, and thus better the understanding of global deep-pelagic environments.

2. Methods

2.1. Sampling and processing

Following the 2010 DWHOS, two projects were created to survey the deep-pelagic ecosystem of the Gulf of Mexico and assess the impacts of the spill. The NOAA-funded Offshore Nekton Sampling and Analysis Program (ONSAP) occurred from 2010 to 2015 as a component of NOAA's Natural Resource Damage Assessment and consisted of a 47-site survey grid aboard the M/V *Meg Skansi* and a four-cruise survey aboard the NOAA FRV *Pisces*. The GoMRI-funded Deep Pelagic Nekton Dynamics (DEEPEND) Consortium occurred from 2015 to 2020 and consisted of a six-cruise survey aboard the R/V *Point Sur*.

Multiple net types were utilized at varying solar cycles aboard the ONSAP and DEEPEND cruises, which allowed for the collection of a broad specimen size range. Larger specimens were collected using commercial-sized trawls during ONSAP, while smaller specimens were collected using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) during ONSAP and DEEPEND.

The ONSAP 47-site survey grid (Figure 2) was sampled over nine months and collected pelagic fauna in discrete depths using a 10-m^2 MOCNESS (MOC-10; Figure 3) with 3-mm mesh nets. Specimens were collected from surface to 1500 m (net 0; N0), 1500 to 1200 m (N1), 1200 to 1000 m (N2), 1000 to 600 m (N3), 600 to 200 m (N4), and 200 m to surface (N5). *Meg Skansi* 6 (MS6) occurred from 28 January – 30 March 2011, MS7 occurred from 14 April – 30 June 2011, and MS8 occurred from 18 July – 30 September 2011.

Figure 2. Locations and trawl trajectories of sampling sites during the ONSAP 47-site survey grid in the Gulf of Mexico aboard the M/V *Meg Skansi* (MS6, MS7, and MS8). Figure courtesy of DEEPEND.

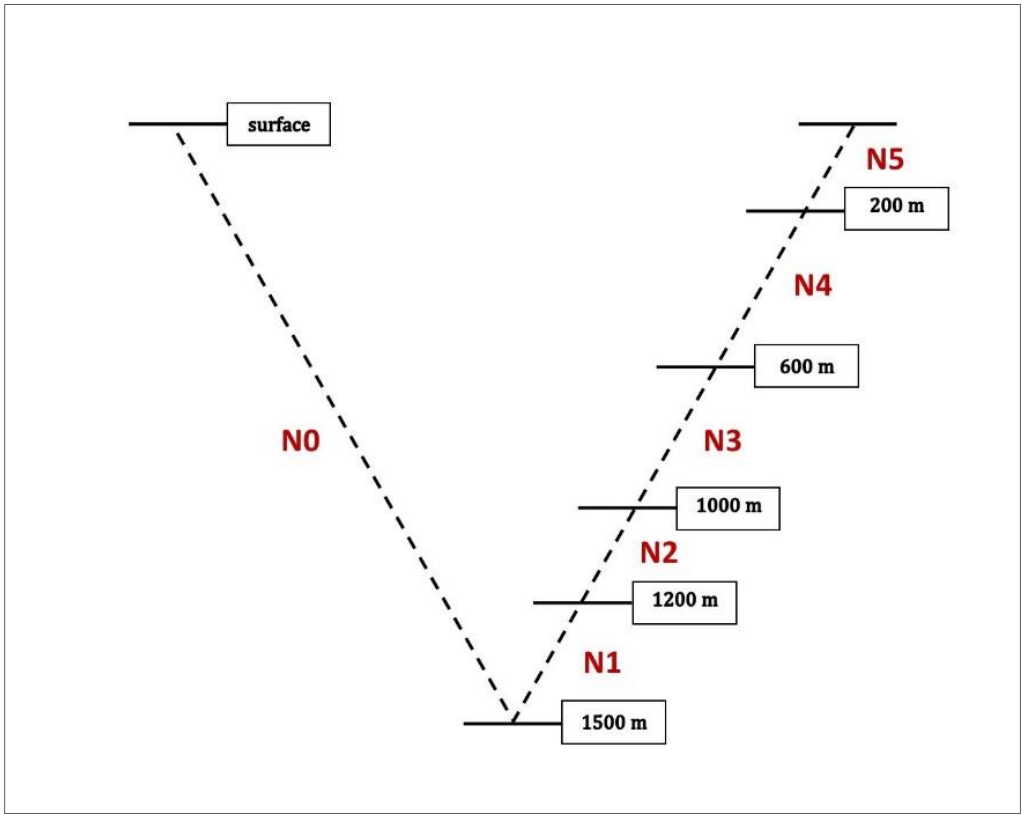


Figure 3. Depth sampling scheme utilized during the ONSAP and DEEPEND MOC-10 surveys in the Gulf of Mexico with the associated net names (e.g., N0, N1, etc.).

The ONSAP "*Pisces*" cruises (NOAA vessel *Pisces*) surveyed the pelagic fauna from surface to 1600 m in the Gulf of Mexico (Figure 4). These cruises utilized a series of large, commercial-sized, dual-warp trawls (high-speed rope trawl, Irish herring trawl, and International Young Gadoid Pelagic Trawl), fished obliquely, to emphasize sampling in the subsurface oil plume between 800 and 1400 m. *Pisces* 8 (PC8) occurred from 02 – 19 December 2010, PC9 occurred from 23 March – 06 April 2011, PC10 occurred from 23 June – 13 July 2011, and PC12 occurred from 08 – 27 September 2011. All ONSAP sampling occurred from 27 °N to 29 °N and 87 °W to 91 °W.

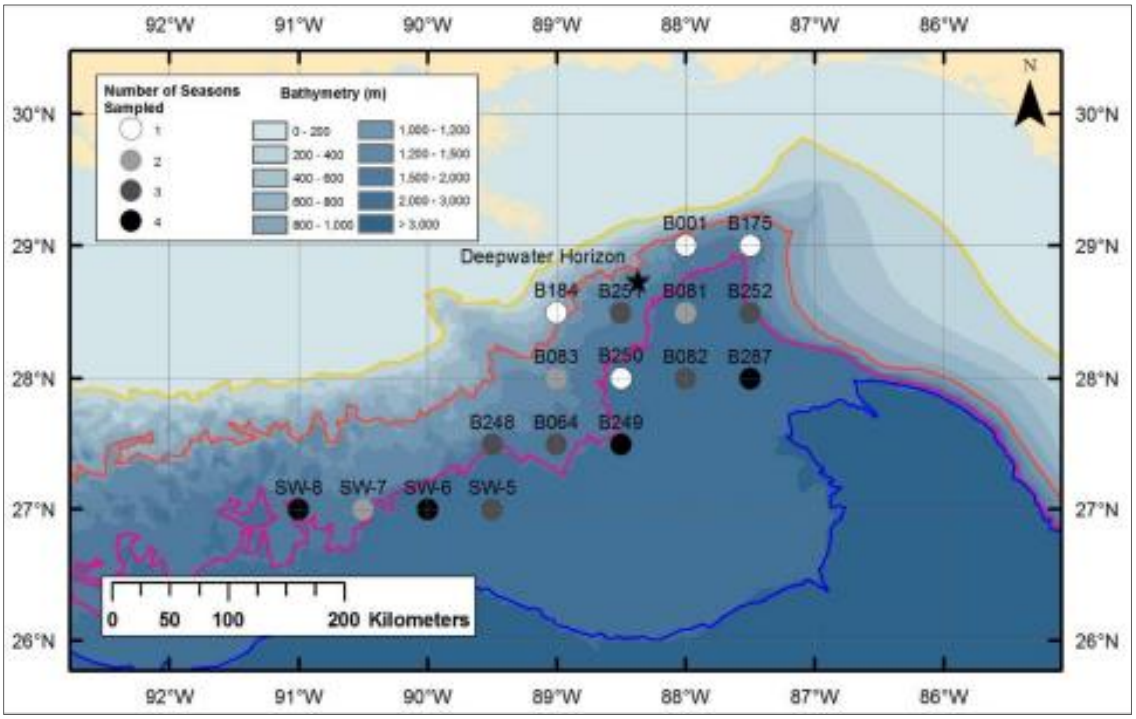


Figure 4. Locations sampled during all ONSAP cruises in the Gulf of Mexico aboard the NOAA FRV *Pisces* (PC8, PC9, PC10, and PC12). Figure courtesy of DEEPEND.

The DEEPEND cruises surveyed the deep-pelagic fauna at the same six depth intervals mentioned above, using the MOC-10 from surface to 1500 m in the Gulf of Mexico (Figure 5). The first DEEPEND cruise (DP01) occurred from 01 – 08 May 2015, DP02 occurred from 08 – 21 August 2015, DP03 occurred from 30 April – 14 May 2016, DP04 occurred from 05 – 19 August

2016, DP05 occurred from 01 – 11 May 2017, and DP06 occurred from 19 July – 02 August 2018. All DEEPEND sampling occurred from 26 °N to 29 °N and 86 °W to 90 °W.

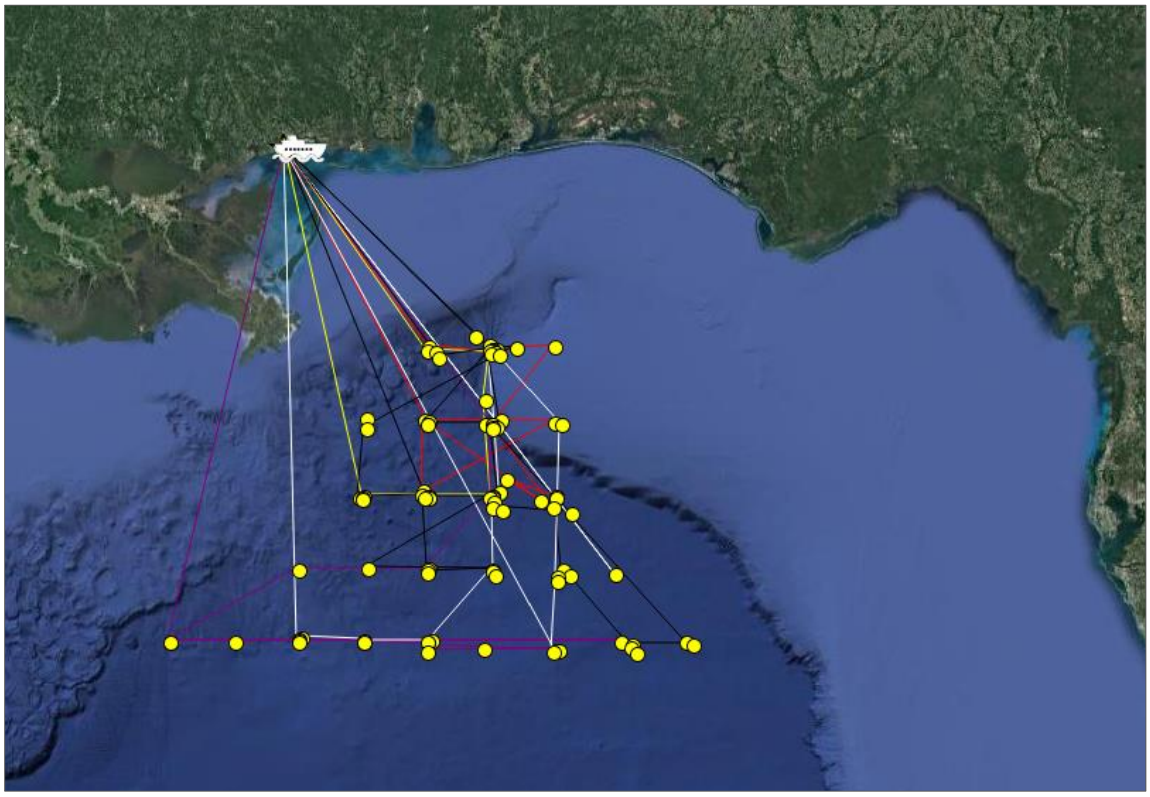


Figure 5. Cruise track of DEEPEND cruises in the Gulf of Mexico aboard the R/V *Point Sur* (DP01, DP02, DP03, DP04, DP05, DP06). Figure courtesy of DEEPEND.

Preliminary processing of all collected samples occurred onboard the research vessels for each cruise. Specimens were identified to the lowest possible taxonomic unit while at sea and preserved in 10% buffered formalin:seawater. Samples were later sorted and transferred to 70% ethanol:water by members of the Oceanic Ecology Laboratory at the Nova Southeastern University (NSU) Guy Harvey Oceanographic Center. All samples were deposited at the NSU Oceanic Ecology Laboratory collection.

2.2. Faunal composition and population dynamics

Morphometrics, meristic counts, and descriptive characteristics were recorded for each specimen to aid in identification efforts, faunal composition, vertical distribution, and dietary analyses. Initially, each of the analyzed specimens was blotted dry and weighed to the nearest 0.01

g. Standard length (SL), and all other measurements, were measured to the nearest 0.1 mm using dial calipers. Descriptive characteristics and meristic counts (e.g., dentition arrangement, lateral line pore count, etc.) were documented using abbreviations and methodology following Paxton (1989).

Each specimen was identified to the lowest possible taxonomic group (species as a default). The most updated available diagnostic keys were utilized during specimen identification (Maul, 1969; Paxton, 1989; Paxton, 2002). Unpublished, revised keys to the species of *Cetomimus* and *Gyrinomimus* provided by J.R. Paxton (personal communication, March 20, 2019) were also utilized during identification efforts.

The multiple net types utilized allowed for collection of larger adult females and smaller adult males, juveniles, and larvae. To describe the faunal composition, each specimen was assigned a life-history stage utilizing terminology described by Paxton (1989). Life-history stage was determined through morphometrics, meristic counts, and descriptive characteristics.

Morphometrics performed during faunal composition analysis are as follows: standard length (SL), head length (HL), eye diameter (ED), pre-orbital length, post-orbital length, snout length (SnL), upper jaw length, lower jaw length, dorsal base length (DB), anal base length (AB), pectoral fin length (PL), pectoral fin width (PW), pelvic fin length (PvL; pelvic fins present in larvae only), snout to dorsal origin (Sn-D), snout to anal origin (Sn-A), snout to pectoral base (Sn-P), snout to pelvic base (Sn-Pv; in larvae only), dorsal origin to anal origin (D-A), and anus to anal origin (An-AO; Figure 6). Meristic counts documented during faunal composition analysis are as follows: dorsal fin rays (D), anal fin rays (A), pectoral fin rays (P), principal caudal fin rays (C), lateral line pores on head canal, and lateral line pores on trunk canal. Descriptive characteristics documented during faunal composition analysis are as follows: existence and location of cavernous tissue and dentition arrangement.

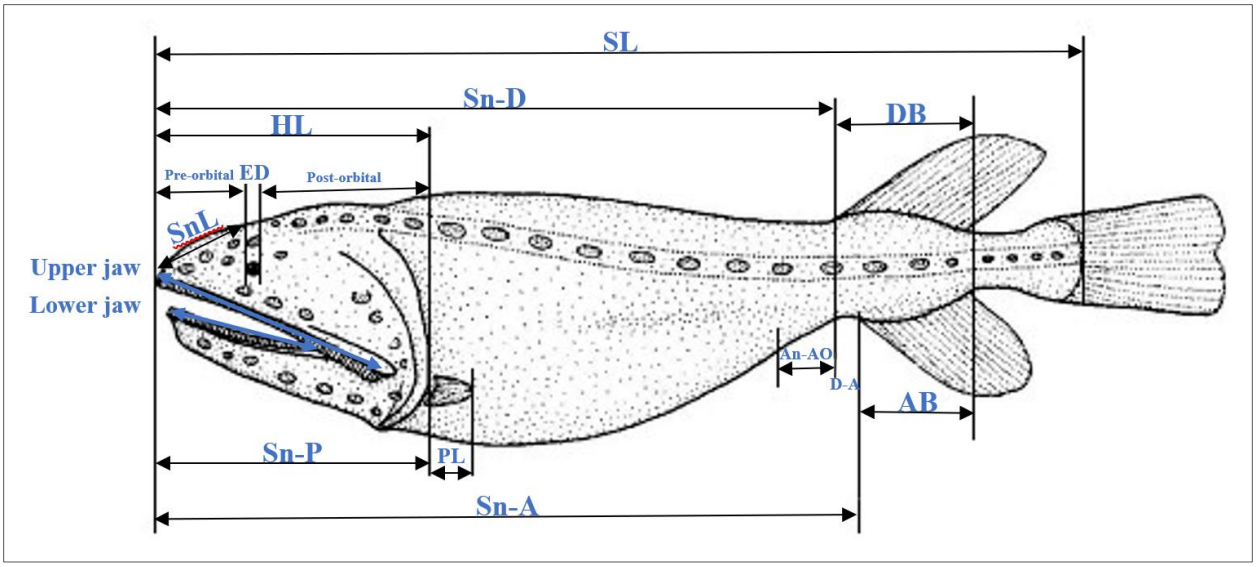


Figure 6. Diagram of morphometrics measured using dial calipers under a Stemi 2000-C stereomicroscope. Measurements not pictured: pelvic fin width and snout to pelvic fin. Image from Ayling & Cox 1982.

Paxton (1989) synthesized diagnostic characteristics for Cetomimidae species, including dentition, lateral line system, and cavernous tissue, while noting challenges in properly quantifying these characters. While tooth counts may be practical in diagnosing other deep-sea ichthyofauna (e.g., chiasmodontids; Prokofiev, 2014), this method is not feasible for some members of Cetomimidae. Teeth of *Gyrinomimus* continue to grow forming new rows throughout the lifetime as indicated by a longer inner row than outer row of jaw teeth (Paxton, 1989). Therefore, tooth counts are not viable in diagnosing species and thus only tooth arrangements were documented in the present study. Paxton (1989) described in detail the complex lateral line system observed in all cetomimid species, excluding that of the genera *Procetichthys* and *Rhamphocetichthys*. The system is composed of a canal with alternating perforated pores along the top and neuromast receptors along the bottom. The head canal is separated into various branches including the supraorbital, infraorbital, mandibular, and preopercular, while the trunk canal is the line of pores posterior of the operculum. The arrangement and counts of pores are determined externally while the connection of the branches is determined internally (Paxton, 1989). The complexity of this system is useful in distinguishing taxa, although challenging to determine depending on the condition of the skin after abrasion from the net; therefore, only the number of pores in each of the head and trunk canals were documented. The extent and location of cavernous tissue is also used to distinguish cetomimids. The tissue of unknown function is present near the anus, sometimes

extending ventrally and dorsally, in all cetomimids except *Rhamphocetichthys* and *Procetichthys* (Paxton, 1989). As cavernous tissue is located on the skin, a specimen in ideal condition is necessary to properly describe the tissue; therefore, only the existence and location of the tissue was noted in this study.

Cetostoma regani specimens were sexed (i.e. female/male) using available identification keys. Since all available identification keys for *Cetomimus* and *Gyrinomimus* describe females, all specimens were sexed as female. "*Ataxolepis*" specimens were sexed as male as this complex has been determined to represent male *Cetomimus* and *Gyrinomimus* species. The "*Eutaeniophorus*" complex represents larval *Cetomimus* and *Gyrinomimus* species and thus were not sexed. The adult male form of *Ditropichthys storeri* has not yet been described and thus all specimens not identified as larva or in transformation were identified as female. Sex ratios for Cetomimidae and *C. regani* were calculated and Chi Square Goodness of Fit Tests performed in R Studio to determine if the observed sex ratios significantly diverge from the expected ratio of 1:1 (female:male).

Cetostoma regani and *D. storeri* specimens were assigned a life-history stage using available identification keys. *Cetomimus* and *Gyrinomimus* specimens were all assumed to be adult as the larval stage is represented by "*Eutaeniophorus*." Male cetomimids were assigned as either the sub-adult or adult life-history stage during dietary analysis. During metamorphosis, male cetomimids transition to the adult stage that is heavily modified for reproduction (Johnson et al., 2009). The stomach reduces to nothing and the energy is transferred to the liver, which expands and sustains the individual. The gonads then enlarge to allow for a maximum chance of reproduction when in the presence of a female. Therefore, "*Ataxolepis*" specimens with enlarged gonads and lacking a stomach were identified as adult while specimens without enlarged gonads and still in possession of the stomach were identified as sub-adult (Figure 7). During morphometric analysis, the sub-adult stage was further divided into larval or sub-adult, as cetomimids lose the pelvic fins during metamorphosis. Specimens still in possession of the pelvic fins were identified as larva while specimens without such fins were identified as sub-adult.

Figure 7. Gastrointestinal tract of "*Ataxolepis*" in transformation (left) as indicated by the shrinking stomach (A) and a specimen in the adult phase (right) as indicated by the enlarged liver (B) and the enlarged gonads (C) surrounding the intestine (D).

To describe the species composition of cetomimids in the Gulf of Mexico, male and larval *Cetomimus*/*Gyrinomimus* specimens were clustered based on measurements as a function of SL using complete linkage hierarchical clustering in R Studio. Clustering analyses create discriminated groups based on similarity of multivariate data. Correlations were first performed for SL against all other measurements, eliminating specimens for which accurate measurements could not be made due to net abrasion. For significant correlations (i.e. with a p-value < 0.05) containing a high correlation coefficient (r-value), any missing measurements were interpolated. For the measurements in which a significant correlation was observed, the measurements were standardized as a function of SL (i.e. SL/measurement). Finally, the cluster analysis was performed. Those measurements for male cetomimids were snout to anal base (r-value 0.9229005) and snout to dorsal base (r-value 0.8892101), and those for larval cetomimids were head length (r-value 0.9143433) and pectoral fin base width (r-value 0.8835249).

To further assess the faunal composition of cetomimids in the Gulf of Mexico, species percent frequency and percent abundance were calculated. To assess the sampling selectivity of the different gear types, specimen SL was analyzed against gear type and collection time of day. Length-weight regressions performed in R Studio were also created to describe taxon-specific growth patterns. The appropriate growth model was selected by choosing the lowest Akaike Information Criterion (AIC value).

2.3 Abundance and vertical distribution

Abundance of Cetomimidae species and life history stages were standardized per unit effort for all quantitative MOC-10 samples. Volume of filtered water (m^3) was calculated for each trawl

and depth interval using the MOCNESS software. For the trawls in which an accurate volume was obtained, volumes were summed for each depth interval and solar cycle. Abundances were then calculated using quantitative trawls only by dividing the sum of counts for each species and/or life history stage by the sum of the depth interval volume. Cetomimid vertical distributions, including presence or absence of vertical migration, were described by plotting the standardized abundances of each taxon per depth interval per solar cycle using a modified boxplot in R Studio. These analyses were performed for each species, life-history stage, and sex to fully describe cetomimid vertical distribution in the Gulf of Mexico. Correlations were also examined between specimen size (mm SL) and depth of capture.

2.4. Dissection and trophic ecology

Dietary analyses were performed on male and larval *Cetomimus*/*Gyrinomimus* specimens. Using a Stemi 2000-C stereomicroscope, these specimens were transversely incised at the isthmus and anus, and ventrally incised to connect the original incisions. The entire gastrointestinal tract was removed and further separated into stomach and intestine via a small incision anterior to the stomach (Figure 8).

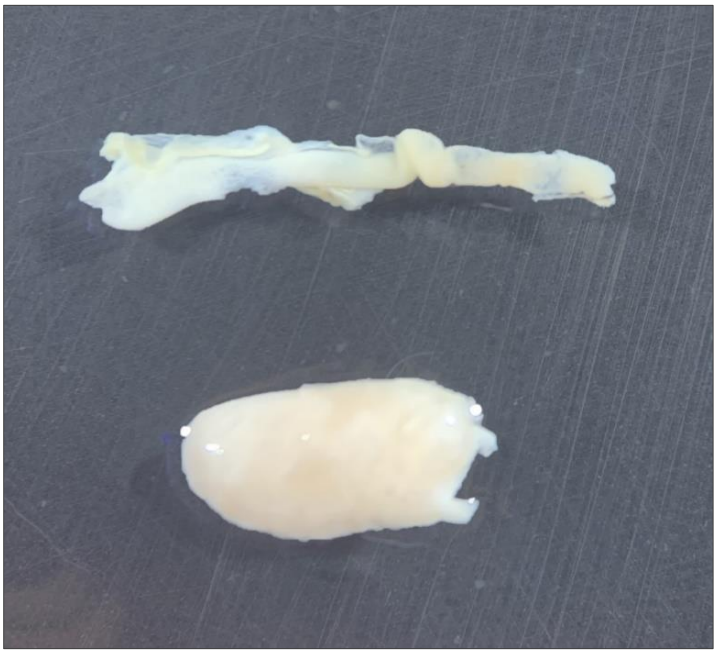


Figure 8. Larva intestine (top) and stomach (bottom) separated.

Stomach fullness was recorded on a scale of 0 – 5, with zero being empty and 5 being full (e.g., Figure 9). For each prey item from the stomach, the state of digestion was recorded on a scale of 0 – 5, with 0.5 being fresh and totally recognizable and 4.5 being nearly completely digested and unrecognizable (i.e. trace prey fragments). Prey items found in the stomach indicating no evidence of digestion (rating of 0) were likely due to net feeding and thus excluded from further dietary analyses, while fully digested prey items would not be found (rating of 5). Microscope slides were prepared for intestine and stomach contents of the males and intestine contents of the larvae. Prey items were deposited onto a slide with a 50/50 mixture of glycerin and water and stained with a few drops of Fuchsin Acid Powder for easy visibility. Slides were protected with a cover slip and sealed with clear nail polish. Prey items were described and photographed using a ZEISS Axio Scope A1 compound light microscope with camera and ZEN lite 2012 software.

Figure 9. Full, distended stomach of "*Eutaeniophorus*" containing 732 copepods. Image by Danté Fenolio, courtesy of DEEPEND.

The stomachs of cetomimid larvae were found to be engorged with copepods. Stomach contents were weighed by the batch and each copepod was counted with the help of a differential cell counting device. Eight initial copepods from each stomach were photographed and measured using a Stemi 2000-C stereomicroscope with camera and ZEN lite 2012 software and identified by analyzing pereiopods and metasome shape. The five (or four) pereiopods of each copepod were removed and deposited, in order, on a slide with a 50/50 mixture of glycerin and water and stained with Fuchsin Acid Powder for easy visibility. The pereiopods were viewed under a ZEISS Axio Scope A1 compound light microscope, enabling identification of copepods to the lowest possible taxonomic unit (species as a default), using the identification guide in Oyre and Foyo (1967). The number of taxa was plotted against number of copepods identified for each species. Additional copepods were identified, one by one, until a levelling off occurred indicating enough copepods were identified to accurately describe the diet (i.e. no new prey items were found).

The diet of cetomimid larvae was analyzed by calculating prey percent frequency of occurrence. Prey items for the males were highly digested and unable to be weighed or identified to species. Analysis for these items involved characterization and descriptions rather than quantitative methodology. Slides of prey items were analyzed and photographed using a ZEISS Axio Scope A1 compound light microscope with camera and ZEN lite 2012 software.

3. Results

3.1. Faunal composition and population dynamics

The NSU Oceanic Ecology Laboratory collection of Cetomimidae is the largest known, as the collection of specimens in discrete-depth intervals increases the known samples by 65% globally and by 948% in the Gulf of Mexico per the Ocean Biogeographic Information System (2021). Throughout the four *Pisces* cruises from 2010 – 2011, 274 cetomimids were collected (Table 2). Throughout the *Meg Skansi* cruises from 2010 – 2011, 143 cetomimids were collected (Table 3). Throughout the six DEEPEND cruises from 2015 – 2018, 76 cetomimids were collected (Table 4). In total throughout all surveys, 493 cetomimids were collected and deposited at the NSU Oceanic Ecology Laboratory collection (Table 5).

Table 2. Specimen counts by preliminary lowest taxonomic identification collected during *Pisces* cruises. Note: "*Ataxolepis*" and "*Eutaeniophorus*" are no longer valid names, but no replacement currently exists for male and larval *Cetomimus*/*Gyrinomimus*, respectively.

Lowest Taxonomic Identification	**N**
Cetostoma regani	97
Cetomimus spp.	72
Ditropichthys storeri	45
Gyrinomimus spp.	20
"*Ataxolepis*"	18
Cetomimidae	15
Gyrinomimus bruuni	4
"*Eutaeniophorus*"	2
Gyrinomimus parri	1
	274 Total

Table 3. Specimen counts by preliminary lowest taxonomic identification collected during *Meg Skansi* cruises. Note: "*Ataxolepis*" and "*Eutaeniophorus*" are no longer valid names, but no replacement currently exists for male and larval *Cetomimus*/*Gyrinomimus*, respectively.

Lowest Taxonomic Identification	**N**
Cetostoma regani	54
Ditropichthys storeri	28
Cetomimus spp.	19
"*Ataxolepis*"	14
Cetomimidae	10
"*Eutaeniophorus*"	9
Cetomimus gillii	4
Cetomimus hempeli	3
Cetomimus picklei	1
Gyrinomimus spp.	1
	143 Total

Table 4. Specimen counts by preliminary lowest taxonomic identification collected during DEEPEND cruises aboard the R/V *Point Sur*. Note: "*Ataxolepis*" and "*Eutaeniophorus*" are no longer valid names, but no replacement currently exists for male and larval *Cetomimus*/*Gyrinomimus*, respectively.

Lowest Taxonomic Identification	**N**
Cetostoma regani	29
Cetomimus spp.	17
Ditropichthys storeri	17
"*Eutaeniophorus*"	9
Cetomimidae	3
Gyrinomimus spp.	1
	76 Total

Table 5. Total specimen counts by preliminary lowest taxonomic identification of all ONSAP and DEEPEND cruises and site survey locations. Note: "*Ataxolepis*" and "*Eutaeniophorus*" are no longer valid names, but no replacement currently exists for male and larval *Cetomimus*/*Gyrinomimus*, respectively.

Lowest Taxonomic Identification	**N**
Cetostoma regani	180
Cetomimus spp.	108
Ditropichthys storeri	90
"*Ataxolepis*"	32
Cetomimidae	28
Gyrinomimus spp.	22
"*Eutaeniophorus*"	20
Cetomimus gillii	4
Gyrinomimus bruuni	4
Cetomimus hempeli	3
Cetomimus picklei	1
Gyrinomimus parri	1
	493 Total

Cetomimidae

In total, 493 Cetomimidae specimens were collected and deposited at the Nova Southeastern University Oceanic Ecology Laboratory collection. During this study, 275 specimens were analyzed to update identifications or obtain length and weight measurements to describe population dynamics and vertical distribution. Specimens in poor condition that obtained damages from the net were excluded from the analyses. Specimens in which length and weight measurements were already documented upon collection were not re-measured in this study. From the subsample, 184 individuals were identified as belonging to 10 valid species and five genera (Table 6). Due to damages that occurred during sampling, 37 specimens were identified only to genus and six were identified only to family. Using unpublished identification keys provided by J.R. Paxton (Personal communication, March 20, 2019), five additional specimens identified to genus could be further identified as potential new species of *Cetomimus* and *Gyrinomimus* (*Cetomimus* "*papilio*" sp. Nov. n=1, *Gyrinomimus* "*borealis*" sp. Nov. n=1, *Gyrinomimus* "*laciniosus*" sp. Nov. n=2, *Gyrinomimus* "*rosenblatti*" sp. Nov. n=1) while another was identified as the known species type of *Cetomimus* sp. K2. The remaining 42 specimens were identified as the "*Ataxolepis*" male complex (n=24, Figure 10) or the "*Eutaeniophorus*" larval complex (n=18, Figure 11). One species documented in this study represents a new record for the Atlantic Ocean and six taxa represent new records for the Gulf of Mexico.

Table 6. Cetomimidae collected in the Gulf of Mexico, with revised taxonomic identifications. Note: "*Ataxolepis*" and "*Eutaeniophorus*" are no longer valid names, but no replacement currently exists for male and larval *Cetomimus*/*Gyrinomimus*, respectively.

Lowest taxonomic identification	**N**
Cetostoma regani	87
Ditropichthys storeri	55
Cetomimus	35
"*Ataxolepis*"	24
"*Eutaeniophorus*"	18
Cetomimus teevani	15
Gyrinomimus	8
Cetomimidae	6
Gyrinomimus bruuni	6
Cetomimus compunctus	6
Cetomimus gillii	5
Cetomimus hempeli	5
Cetomimus picklei	2
Danacetichthys galathenus	2
Gyrinomimus grahami	1
	275 Total

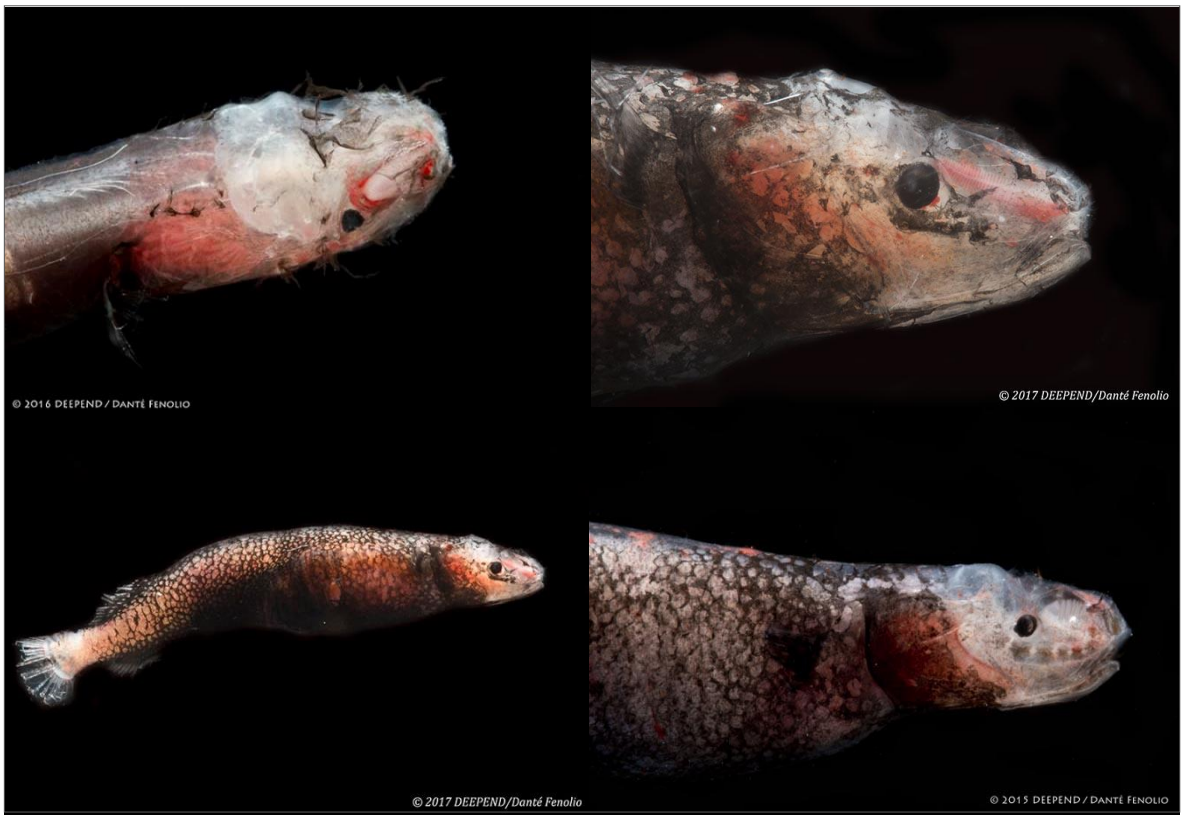


Figure 10. Male *Cetomimus*/*Gyrinomimus* specimens collected from the Gulf of Mexico. Images by Danté Fenolio, courtesy of DEEPEND.

Figure 11. Larval Cetomimidae specimen collected from the Gulf of Mexico. Image by Danté Fenolio, courtesy of DEEPEND.

The most collected cetomimid species in the Gulf of Mexico was *Cetostoma regani* and the least collected species were *Gyrinomimus grahami* and *Gyrinomimus parri* (Table 7; Figure 12). *Cetostoma regani* (35.4%), *Ditropichthys storeri* (19.2%, Figure 13), and *Cetomimus* spp. (17.8%, Figure 14) were the numerically dominant cetomimid taxa, while individual species of *Cetomimus* and *Gyrinomimus* (Figure 15) were the rarest (0.2% - 3.5%).

Table 7. Total specimen counts (N) and standardized abundance of cetomimids collected in the Gulf of Mexico.

Lowest taxonomic identification	N	Abundance (individual $10^{-8}m^{-3}$)
Cetostoma regani	184	59.1
Ditropichthys storeri	90	31.3
Cetomimus spp.	82	24.5
"*Ataxolepis*"	33	10.9
Cetomimus teevani	15	6.4
Cetomimidae	17	5.9
"*Eutaeniophorus*"	18	5.0
Gyrinomimus spp.	20	4.5
Cetomimus gillii	7	2.7
Cetomimus compunctus	6	2.3
Cetomimus hempeli	6	2.3
Gyrinomimus bruuni	8	2.3
Cetomimus picklei	3	1.4
Danacetichthys galathenus	2	0.9
Gyrinomimus grahami	1	0.5
Gyrinomimus parri	1	0.5
	493 Total	

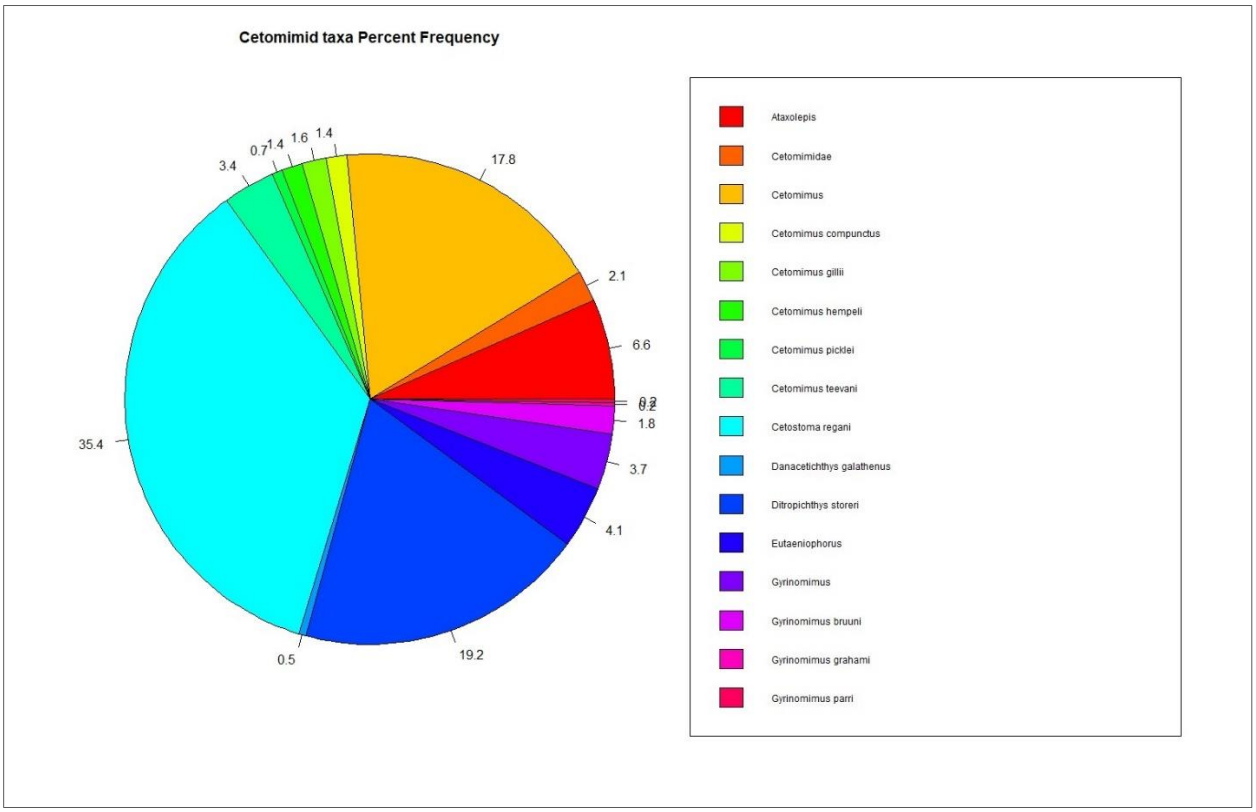


Figure 12. Cetomimid taxa percent frequency collected from the Gulf of Mexico.

Figure 13. *Ditropichthys storeri* specimens collected from the Gulf of Mexico. Images by Danté Fenolio, courtesy of DEEPEND.

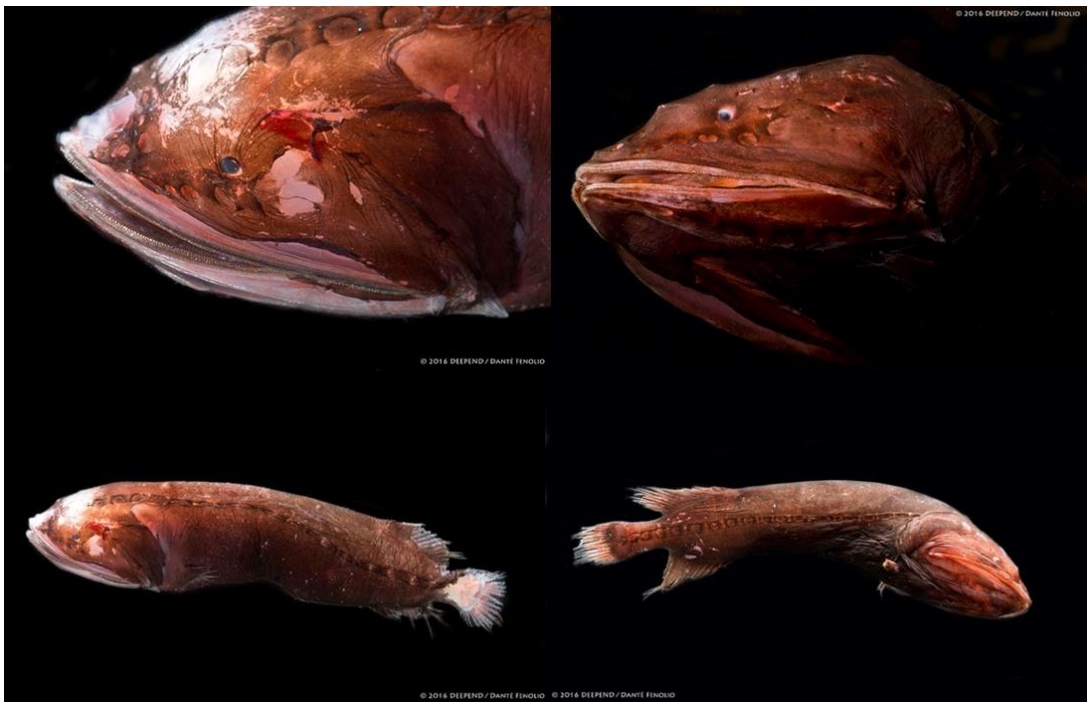


Figure 14. *Cetomimus* specimens collected from the Gulf of Mexico. Images by Danté Fenolio, courtesy of DEEPEND.

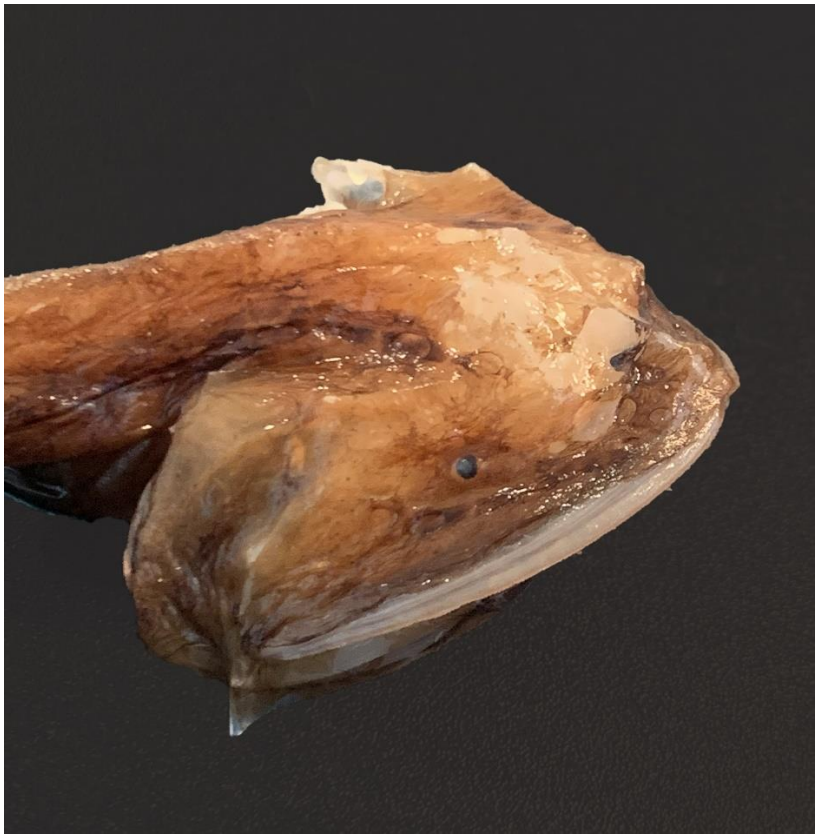


Figure 15. *Gyrinomimus* specimen collected from the Gulf of Mexico.

The fewest number of cetomimid species was collected in the epipelagic zone (n=3) while the largest number was collected in the mesopelagic zone (n=9). The entire depth range of the bathypelagic zone was not sampled, but eight species were collected in the depth strata that were sampled.

From the subsample of 275 cetomimid specimens, 174 were identified as being either female or male. Of these, 145 specimens were identified as female and 29 were identified as male, resulting in a female to male ratio of 5:1. A Chi Square Goodness of Fit test indicated that the observed female to male ratio of 5:1 significantly diverges from the expected ratio of 1:1 (p-value 2.2×10^{-16}).

From the subsample of 275 cetomimid specimens, 83 were assigned a life-history stage. Of these, 50 specimens were in the transformed adult stage, seven were in the sub-adult stage, 23 were in the larval stage, and three were in transformation from the sub-adult to the adult stage.

A boxplot of SL versus gear type revealed the relative size distribution of cetomimids between the two main gear types (Figure 16). Overall, the MOC-10 collected smaller cetomimids

while the commercial-sized dual-warp trawl gear collected larger specimens and a larger size range. The median specimen SL for both trawl gears was about 60 mm. Fifty percent of the samples collected from the MOC-10 were between about 50 and 75 mm SL, while 50% of the samples collected from the commercial-sized dual-warp trawl gear were between about 30 and 90 mm SL. The largest and smallest cetomimids collected from the MOC-10 were 150 mm SL (*Cetomimus teevani*) and 18.3 mm SL (*D. storeri*) respectively, while the largest and smallest collected from the commercial-sized dual-warp trawl gear were 404 mm SL (*Cetomimus*) and 19 mm SL (*C. regani*) respectively.

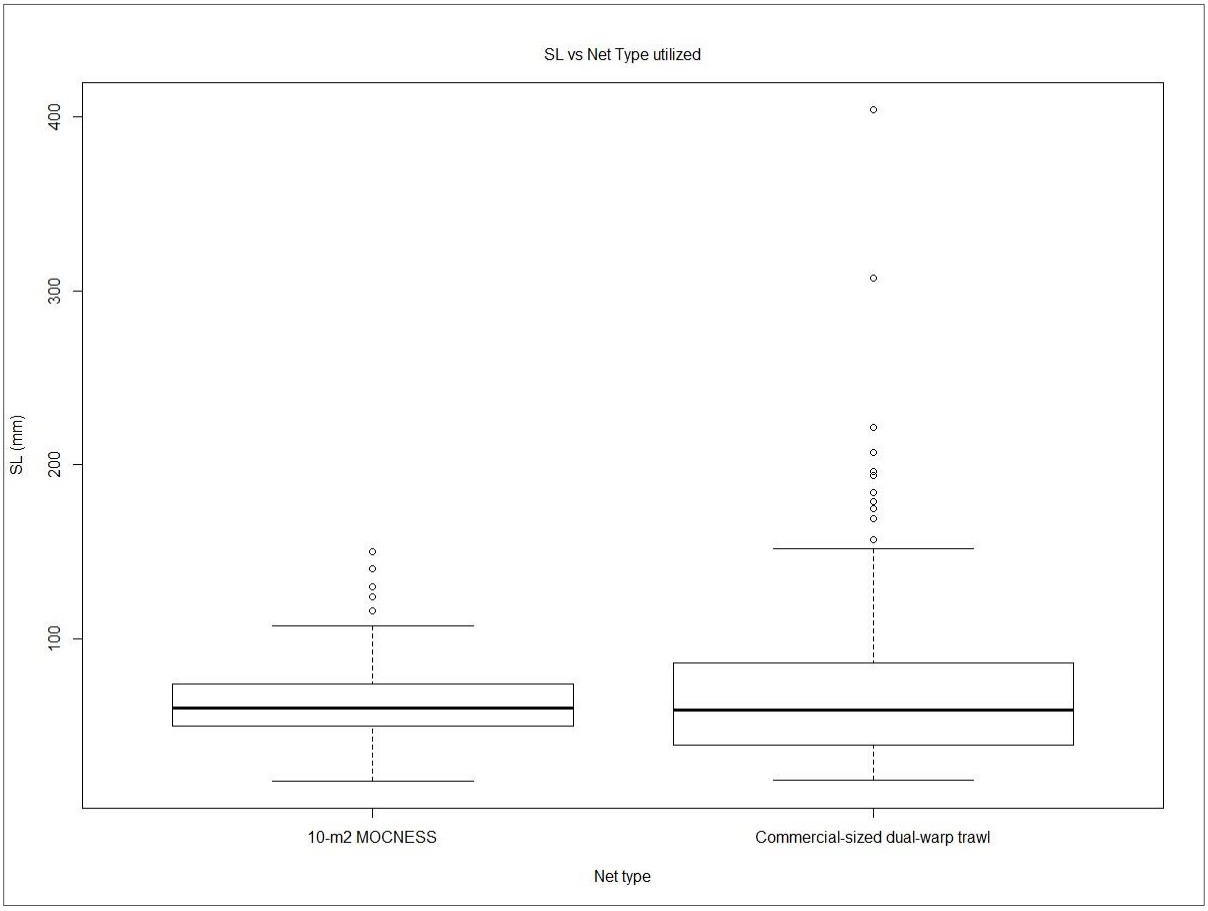


Figure 16. Specimen SL in mm versus net type utilized for Cetomimidae in the Gulf of Mexico (n=380).

The relative size distribution of cetomimids collected between day and night trawls is presented in Figure 17. Overall, larger cetomimids were collected during the day than night; however, the size difference was not significant (p-value 0.7664). Daytime trawls also accounted for a larger range of specimen SL. The median size collected during both the day and night was also about 60 mm SL. Fifty percent of the samples collected during the day were between about 50 and 90 mm SL, while 50% of the samples collected during the night were between about 50 and 80 mm SL. The largest and smallest cetomimids collected during the day were 130 mm SL (*C. regani*) and 18.3 mm SL (*D. storeri*), while the largest and smallest collected during the night were 404 mm SL (*Cetomimus*) and 19 mm SL (*C. regani*).

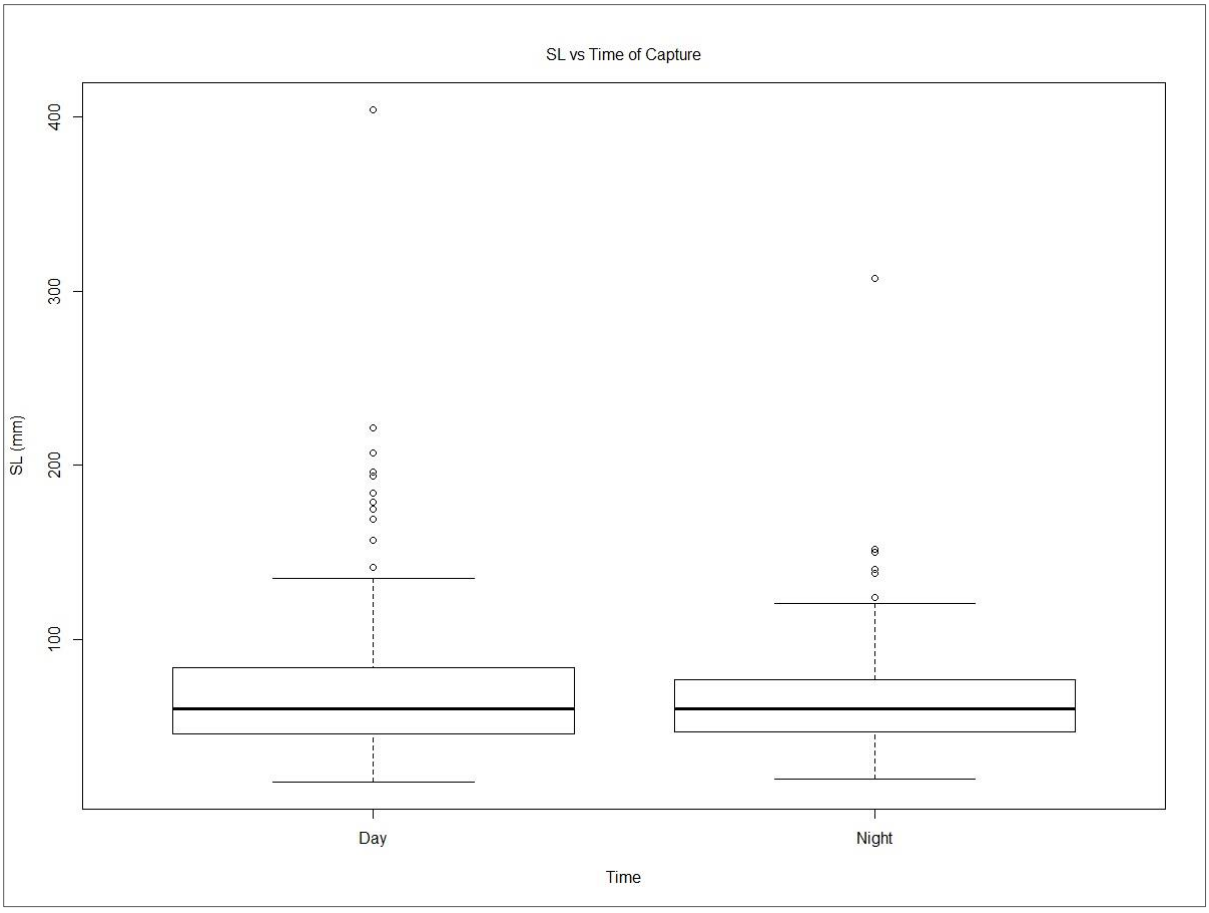


Figure 17. Specimen SL in mm versus collection time for Cetomimidae in the Gulf of Mexico (n=380).

Cetostoma regani

There were 155 specimens of *Cetostoma regani* collected throughout this study, of which 80 were identified to sex or assigned a life-history stage. Of these, 75 specimens were in the transformed adult life-history stage and five were in the larval stage (Figure 18). Of the 75 specimens in the transformed adult life history stage, 71 were identified as female (Figure 18) and four were identified as male (Figure 18), resulting in a female to male ratio of ~18:1 (17.75:1). A Chi Square Goodness of Fit test indicated that the observed female to male ratio of ~18:1 significantly diverged from the expected ratio of 1:1 (p-value 1.022×10^{-14}). A *C. regani* length-weight regression included 72 individuals. The curve was best fit by the Simple Logistic Non-Linear Regression model (Figure 19).

Figure 18. Larva (top left), male (top right), and adult female (bottom) *Cetostoma regani* collected from the Gulf of Mexico.

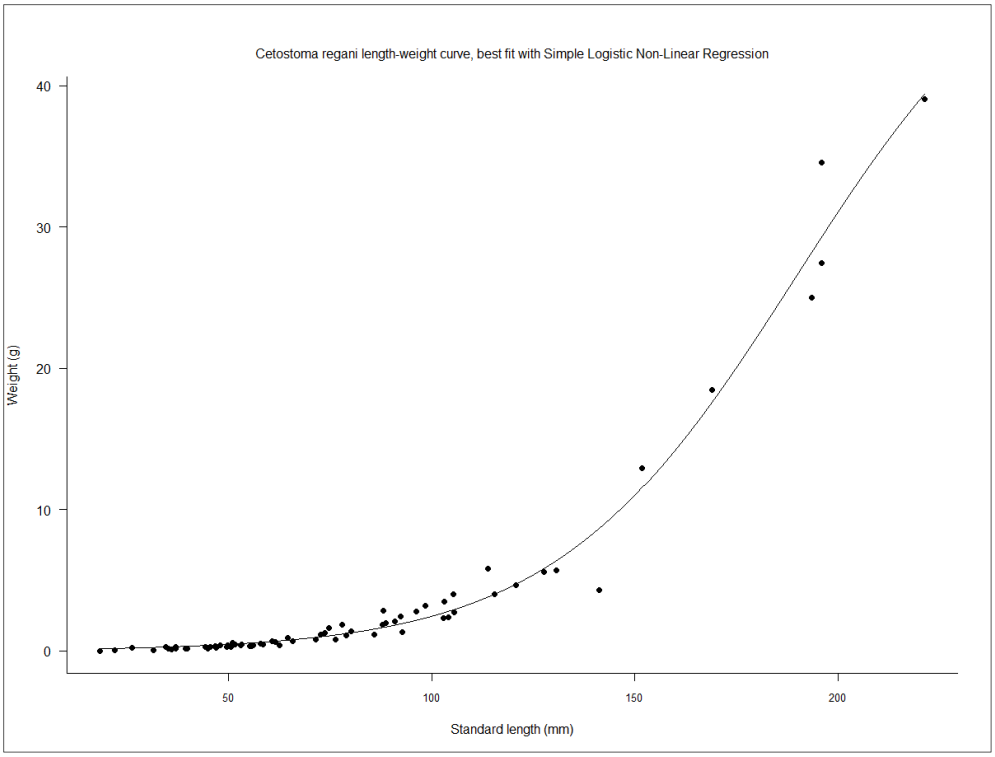


Figure 19. Length-weight curve of *Cetostoma regani* from the Gulf of Mexico (n=72).

Ditropichthys storeri

There were 84 specimens of *Ditropichthys storeri* collected throughout this study, of which 31 were identified to sex or assigned a life-history stage. Of these, 28 specimens were in the transformed female adult life-history stage, two were in transformation from the larval to the adult stage, and one was in the larval stage (Figure 20). A *D. storeri* length-weight regression included 33 individuals. The curve was best fit by the Gompertz Non-Linear Regression model (Figure 21).

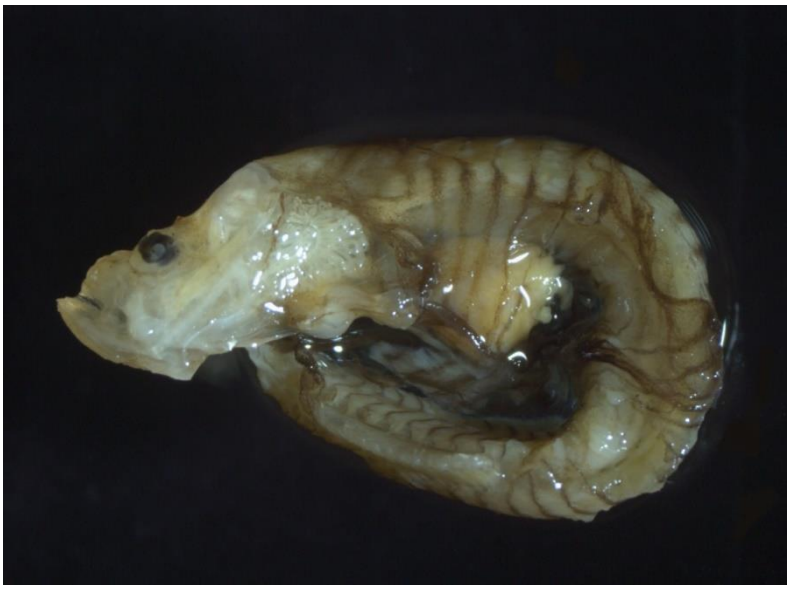


Figure 20. Larva *Ditropichthys storeri* collected from the Gulf of Mexico.

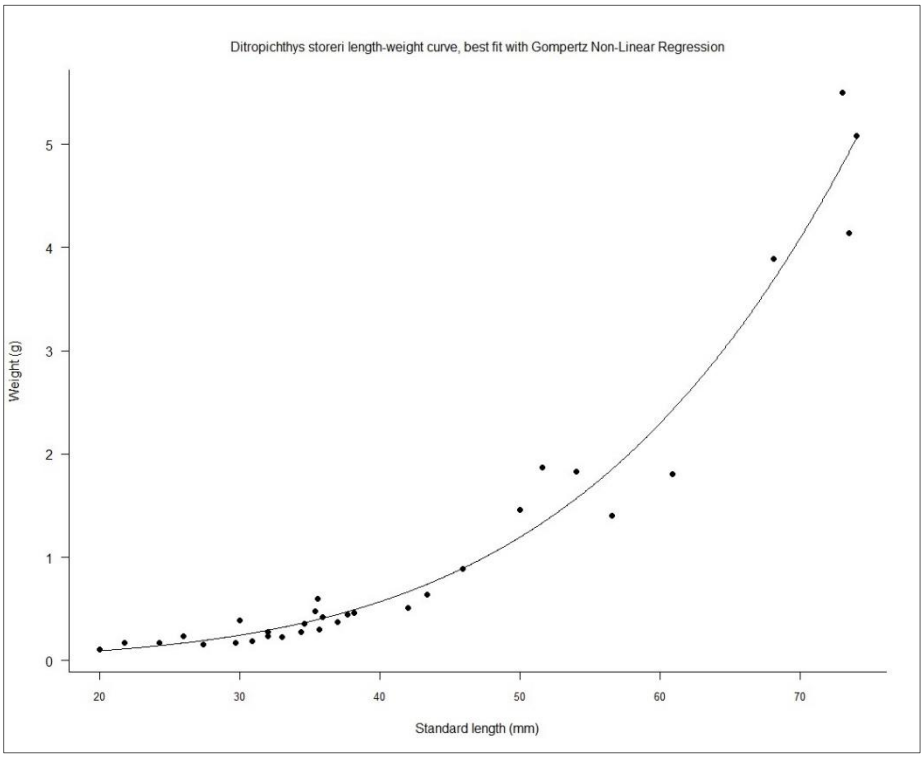


Figure 21. Length-weight curve of *Ditropichthys storeri* from the Gulf of Mexico (n=33).

Cetomimus

There were 115 specimens of *Cetomimus* collected throughout this study, of which 37 were identified to species and two were identified as potential new species of *Cetomimus* using an unpublished, revised key provided by J.R. Paxton (personal communication, March 20, 2019). All *Cetomimus* specimens were identified as transformed adult females, as the males are represented by "*Ataxolepis*" and the larvae are represented by "*Eutaeniophorus*." *Cetomimus teevani* was the only species of the genus with enough individuals to produce a length-weight regression (n=15). The curve was best fit by the Gompertz Non-Linear Regression model (Figure 22). The records of *Cetomimus compunctus* represent the first known occurrence in the Atlantic Ocean while the records of *Cetomimus picklei* and *C. compunctus* represent the first known occurrences in the Gulf of Mexico.

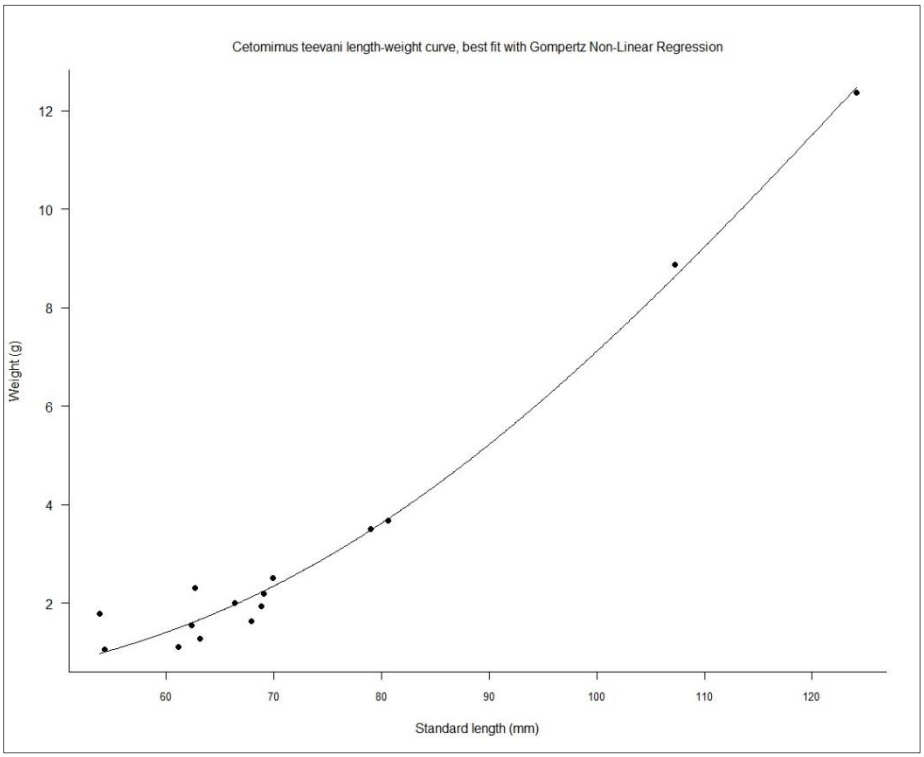


Figure 22. Length-weight curve of *Cetomimus teevani* from the Gulf of Mexico (n=15).

Gyrinomimus

There were 26 specimens of *Gyrinomimus* collected throughout this study, of which nine were identified to species and four were identified as potential new species of *Gyrinomimus* using an unpublished key provided by J.R. Paxton (personal communication, March 20, 2019). All *Gyrinomimus* specimens were identified as transformed adult females as the males are represented by "*Ataxolepis*" and the larvae are represented by "*Eutaeniophorus*." The records of *Gyrinomimus bruuni* and *Gyrinomimus grahami* represent the first known occurrences in the Gulf of Mexico. Too few individuals of any species in this genus were collected to produce meaningful growth curves.

Male *Cetomimus*/*Gyrinomimus* ("*Ataxolepis*")

There were 32 specimens collected throughout this study identified as male *Cetomimus/Gyrinomimus*, of which 22 were assigned a life-history stage. Ten specimens were in the transformed adult stage, eight were sub-adults with one in the last transition phase, and four were beginning transformation out of the larval stage. A male cetomimid length-weight regression included 22 individuals; one individual weight was an outlier and thus removed. The curve was best fit by the Exponential Non-Linear Regression model (Figure 23). These records represent the first published occurrence of male *Cetomimus* and/or *Gyrinomimus* in the Gulf of Mexico.

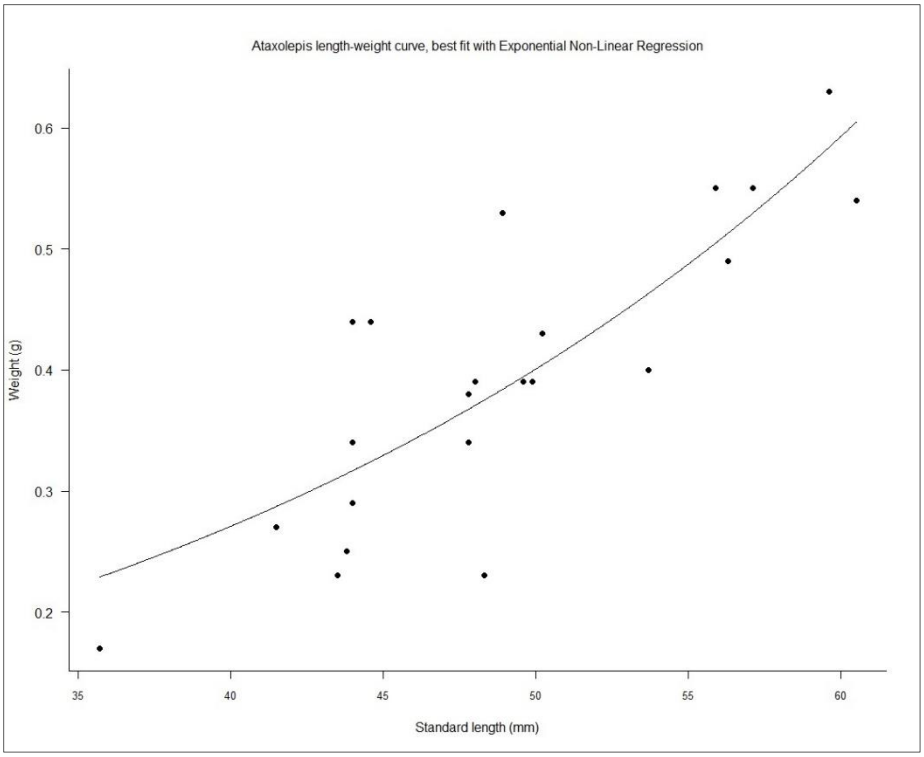


Figure 23. Length-weight curve of male *Cetomimus*/*Gyrinomimus* from the Gulf of Mexico (n=22).

Hierarchical cluster analyses of morphological measurement data discriminated at least three groups of males that are embedded within the *Cetomimus* and *Gyrinomimus* populations of the Gulf of Mexico (Figure 24). Clustering analysis is not a significance test; however, the groupings of specimens are distinguished based on multivariate structure and similarity to the next closest grouping. Fish ID 160 was considered an outlier and omitted during data interpretation.

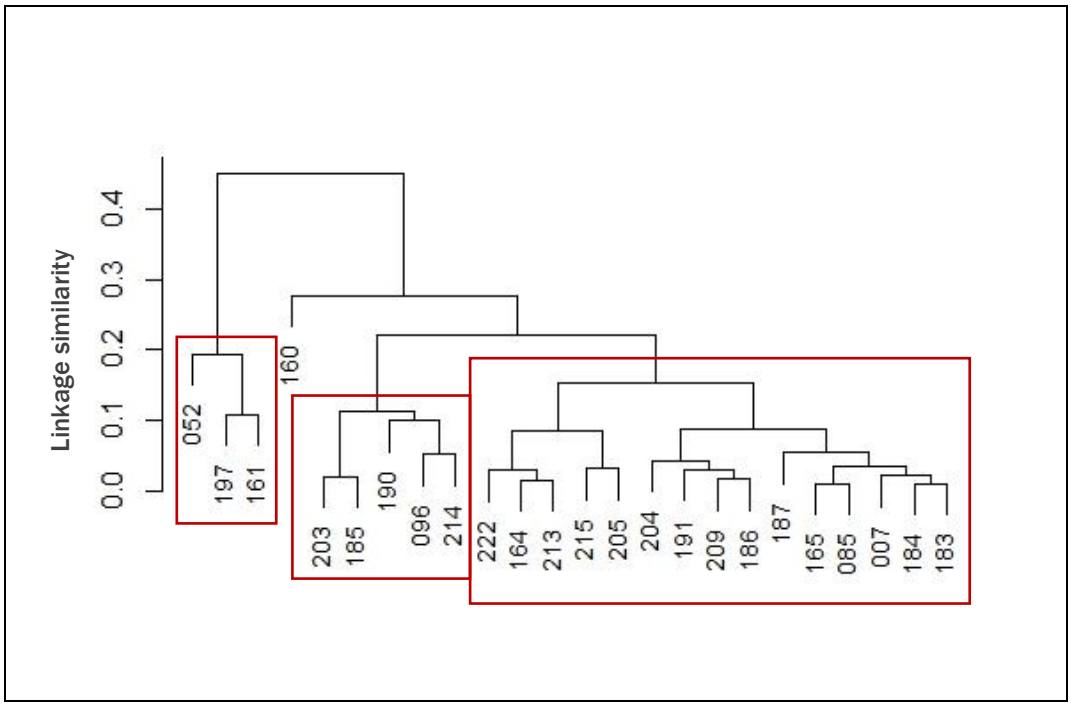


Figure 24. Dendrogram of complete linkage clusters based on similarity of measurements as a function of SL for male *Cetomimus*/*Gyrinomimus* from the Gulf of Mexico. Red boxes indicate discriminated clusters.

Larval *Cetomimus*/*Gyrinomimus* ("*Eutaeniophorus*")

Eighteen specimens collected in this study were identified as "*Eutaeniophorus*," an undefined designation carried over from the invalidated *Eutaeniophorus festivus* (Bertelsen and Marshall, 1956), now known to be the larva of an undetermined number of cetomimid species (Johnson et al., 2009). A larval cetomimid length-weight regression included ten individuals; two individual weights were outliers and thus removed. The curve was best fit by Gompertz Non-Linear Regression model (Figure 25).

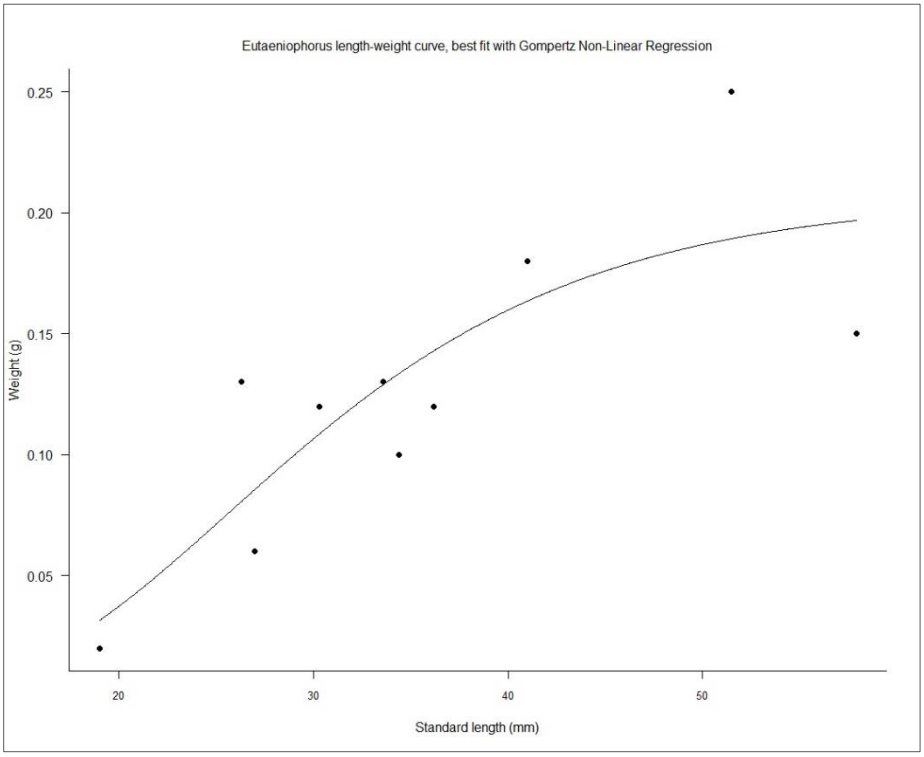


Figure 25. Length-weight curve of larval Cetomimidae ("*Eutaeniophorus*") from the Gulf of Mexico (n=10).

Hierarchical cluster analyses discriminated at least two groups of larvae that are embedded within the *Cetomimus* and *Gyrinomimus* populations of the Gulf of Mexico (Figure 26). Fish ID 221 was considered an outlier and omitted during data interpretation.

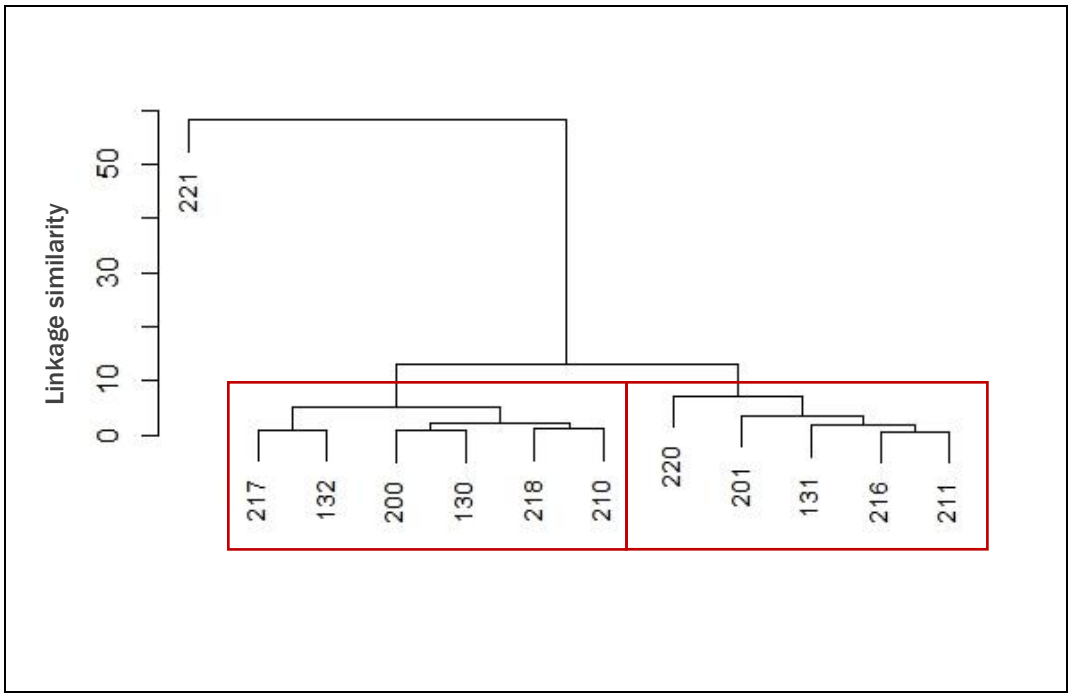


Figure 26. Dendrogram of complete linkage clusters based on similarity of measurements as a function of SL for larval Cetomimidae ("*Eutaeniophorus*") from the Gulf of Mexico. Red boxes indicate discriminated clusters.

Danacetichthys galathenus occurrence

There were two individual specimens collected during this study identified as *Danacetichthys galathenus* (58.3 and 44.6 mm SL). These records represent the first known occurrence of *D. galathenus* in the Gulf of Mexico. The specimens were not sexed or identified to life-history stage.

3.2. Abundance and vertical distribution

Cetomimidae

Cetomimidae in the Gulf of Mexico were collected most often between 1000 and 1200 m during both the day and night (Figure 27). Cetomimids were collected least often during the day between 200 and 600 m, and during the night between the surface and 200 m. A Kendall non-parametric correlation test (n=74) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.5697). Adult cetomimids were collected most often during the day and in the depth range of 1200 and 1500 m. During the night, adult cetomimids were collected most often between 1000 and 1200 m. No adult cetomimids were collected during the night in the uppermost depth range between the surface and 200 m. Female

cetomimids were collected most often during the day between 1200 and 1500 m; however, overall catch rates were highest between 1000 and 1200 m. Male cetomimids were primarily collected between 1000 and 1500 m with the highest catch rate occurring at night between 1000 and 1200 m. The only other depth range in which male cetomimids were collected was during the day between the surface and 200 m. Cetomimids in transformation (i.e. sub-adult or post-larva) were only collected in the lowermost depth ranges of 1000 to 1500 m with the highest catch rate occurring at night between 1000 and 1200 m. Larval cetomimids were collected most often during the night below 600 m with the highest catch rate occurring between 1000 and 1200 m.

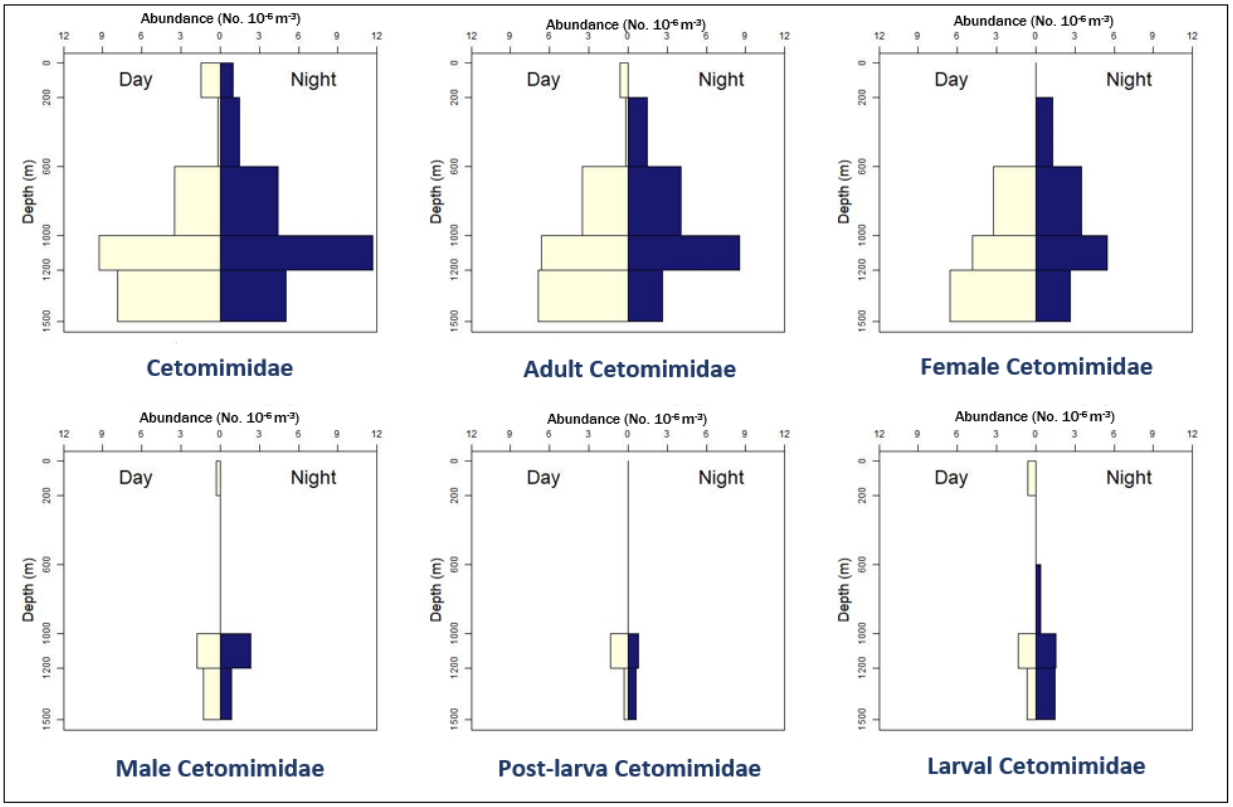


Figure 27. Abundance and diel vertical distribution of Cetomimidae in the Gulf of Mexico.

Cetostoma regani

Cetostoma regani was the most abundant species of Cetomimidae, with the highest catch rate occurring during the day between 1200 and 1500 m (Figure 28). During the night, *C. regani* was collected most often between 1000 and 1200 m. During the day, no *C. regani* specimens were collected shallower than 600 m and during the night no *C. regani* specimens were collected

shallower than 200 m. A Spearman non-parametric correlation test (n=24) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.08418). Adult *C. regani* were collected most often during the day and in the depth range of 1200 to 1500 m. During the night, adult specimens were collected most often between 1000 and 1200 m. The majority of adult *C. regani* specimens were identified as female and thus the vertical distribution closely resembles that of the adult assemblage. Male C. *regani* were only collected during the night and in deeper water with a slightly higher catch rate occurring between 1000 and 1200 m. Larval *C. regani* were collected most often during the night and between 1000 and 1200 m. within the sampled depth ranges. No larvae were collected from the surface to 600 m.

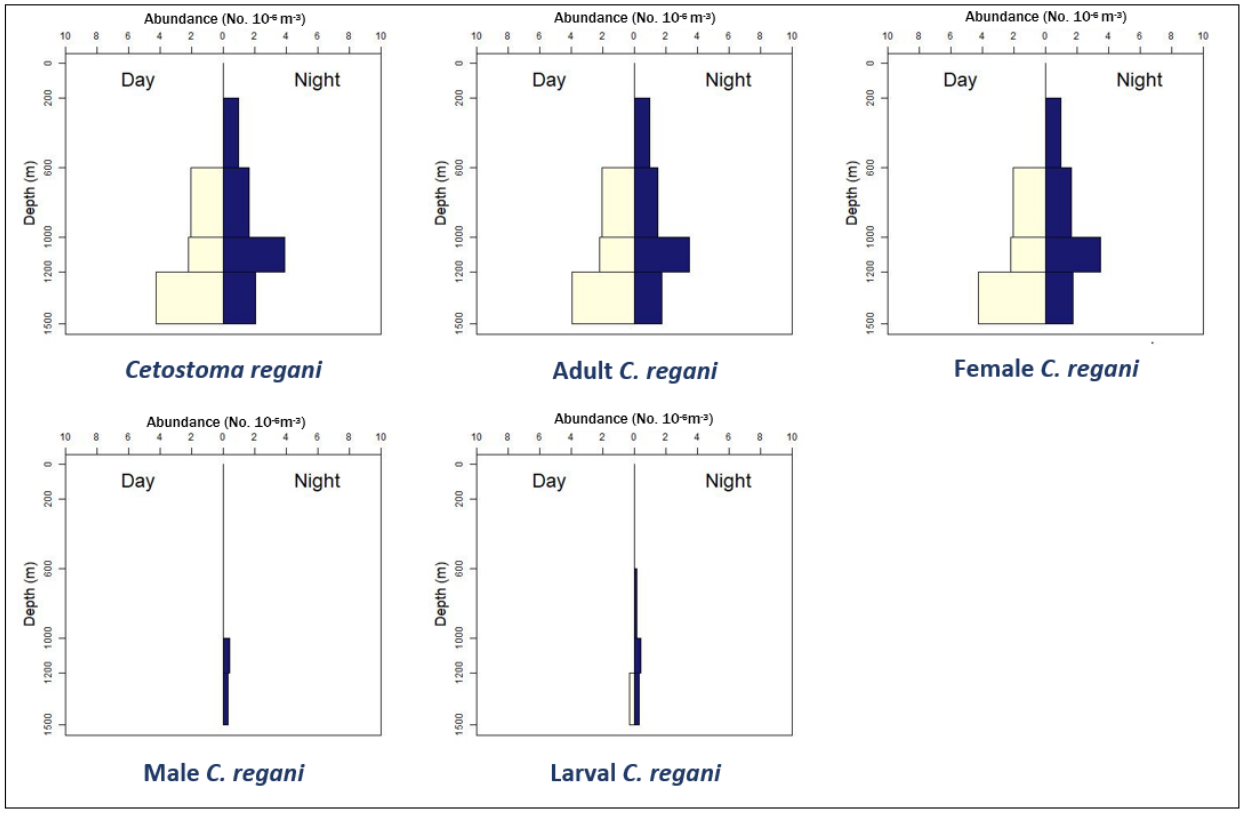


Figure 28. Abundance and diel vertical distribution of *Cetostoma regani* in the Gulf of Mexico.

Ditropichthys storeri

Ditropichthys storeri was the second-most abundant species of Cetomimidae, with the highest catch rate occurring during the day between 1000 and 1200 m (Figure 29). During the night, *D. storeri* was collected most often between 600 and 1000 m. No *D. storeri* specimens were

collected during the day or night in the uppermost depths from surface to 200 m. During the day, *D. storeri* was not collected shallower than 600 m. A Spearman non-parametric correlation test (n=15) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.8483). The majority of *D. storeri* specimens were identified as adult and thus the vertical distribution closely resembles that of the entire assemblage. Specimens in transformation (i.e. sub-adult or post-larva) were only collected during the day between 1000 and 1200 m.

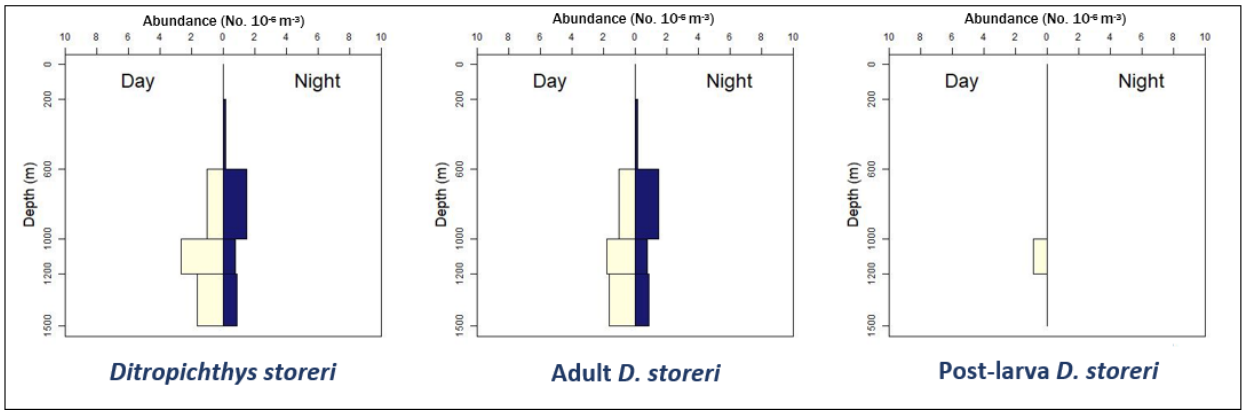


Figure 29. Abundance and diel vertical distribution of *Ditropichthys storeri* in the Gulf of Mexico.

Cetomimus

Cetomimus were collected most often during the night and in the depth range of 1000 to 1200 m (Figure 30). During the day, *Cetomimus* were collected in all depth ranges with the highest catch rate occurring between 1000 and 1200 m. During the night, no *Cetomimus* specimens were collected shallower than 200 m or deeper than 1200 m. All *Cetomimus* specimens were identified as adult females. A Spearman non-parametric correlation test (n=21) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.355). *Cetomimus compunctus* was only collected during the day and between 1000 and 1200 m. *Cetomimus gillii* was the most abundant species of *Cetomimus* identified from quantitative, discrete-depth samples, with the highest catch rate occurring during the night and in the depth range of 1000 to 1200 m. *Cetomimus hempeli* was only collected during the night with the highest catch rate occurring between 1000 and 1200 m. No *C. hempeli* were collected shallower than 600 m or deeper than 1200 m. *Cetomimus picklei* catch rates were equal between 1000 and 1200 m

during the day and night. The only other collection of *C. picklei* was during the day between the surface and 200 m. *Cetomimus teevani* catch rates were slightly higher during the day and in the depth range of 1000 to 1200 m. During the day, no *C. teevani* were collected between 600 and 1000 m. During the day and night, no *C. teevani* were collected shallower than 200 m or deeper than 1200 m.

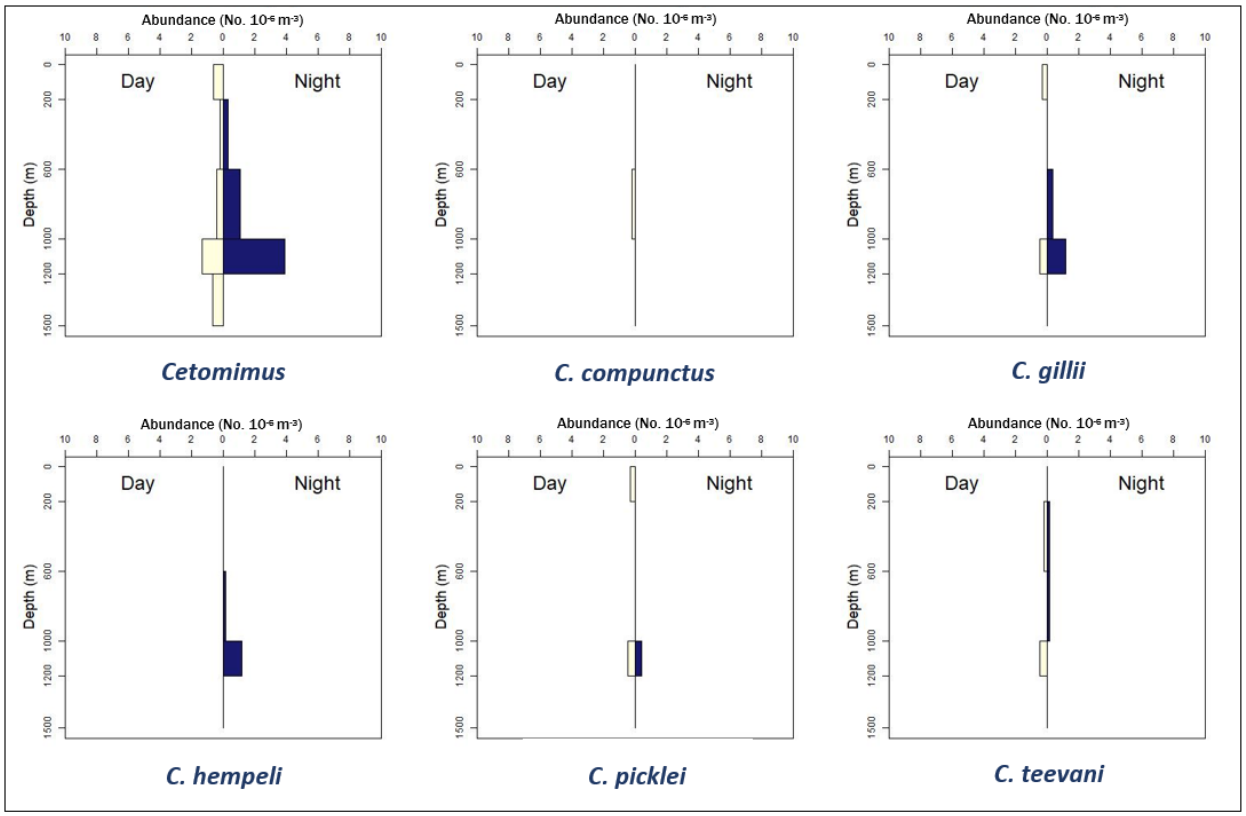


Figure 30. Abundance and diel vertical distribution of *Cetomimus* in the Gulf of Mexico. All individuals were identified as adult female.

Gyrinomimus

No *Gyrinomimus* specimens were collected in discrete-depth intervals using the 10-m^2 MOCNESS (MOC-10). Eight quantitative trawls using dual-warp commercial trawl gear collected nine specimens of *Gyrinomimus* (Table 8). These non-closing trawls were categorized into shallower (fishing depth 0 – 700 m) or deep water (rapid deployment to 700 m depth, sustained fishing between 700 – 1500 m depth, and rapid retrieval from 700 m to surface). That said, given the non-closing nature of the gear, the precise depth stratum of capture could not be determined. *Gyrinomimus* specimens were caught at approximately equal rates during the day (n=5) and night

(n=4), and in deep tows (n=5) and shallow water (n=4). Two *Gyrinomimus bruuni* specimens were collected during the day in deep tows while two were collected during the night in shallow tows. One *Gyrinomimus grahami* specimen was collected during the night in a deep tow. Two potentially undescribed species of *Gyrinomimus* were collected during the day, one in each a deep and shallow tow. One potentially undescribed species of *Gyrinomimus* was collected during the night in a shallow tow. One specimen collected during the day in a deep tow was too trawl-damaged to be identified to species level. All *Gyrinomimus* specimens were identified as adult females.

Table 8. Depth of capture of *Gyrinomimus* species in the Gulf of Mexico. D/N indicates solar cycle of capture.

Taxon	**SL (mm)**	**D/N**	**Depth fished (m)**
Gyrinomimus	67.7	Day	0 – 1401
Gyrinomimus "borealis" sp. Nov.	Damaged	Day	0 – 761
Gyrinomimus "laciniosus" sp. Nov.	131.7	Day	0 – 1419
Gyrinomimus "rosenblatti" sp. Nov.	74.0	Night	0 – 720
Gyrinomimus bruuni	48.9	Day	0 – 1419
Gyrinomimus bruuni	125.5	Day	0 – 1271
Gyrinomimus bruuni	81.9	Night	0 – 733
Gyrinomimus bruuni	88.9	Night	0 – 719
Gyrinomimus grahami	69.3	Night	0 – 1500

Male *Cetomimus*/*Gyrinomimus* ("*Ataxolepis*")

The center of distribution of male Cetomimidae occurred between 1000 and 1200 m (Figure 31). During the day, male cetomimids were collected from the surface to 200 m and below 1000 m. A Spearman non-parametric correlation test (n=9) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.6559). Adult male cetomimids were collected only in the deepest depth ranges with the highest catch rates occurring during the day and between 1000 and 1200 m. Male cetomimids in transformation (sub-adult or post-larva) were also only collected in the deepest depth ranges with the highest catch rate occurring between 1000 and 1200 m. Male cetomimids beginning transformation from the larval life-history stage were also only collected below 1000 m.

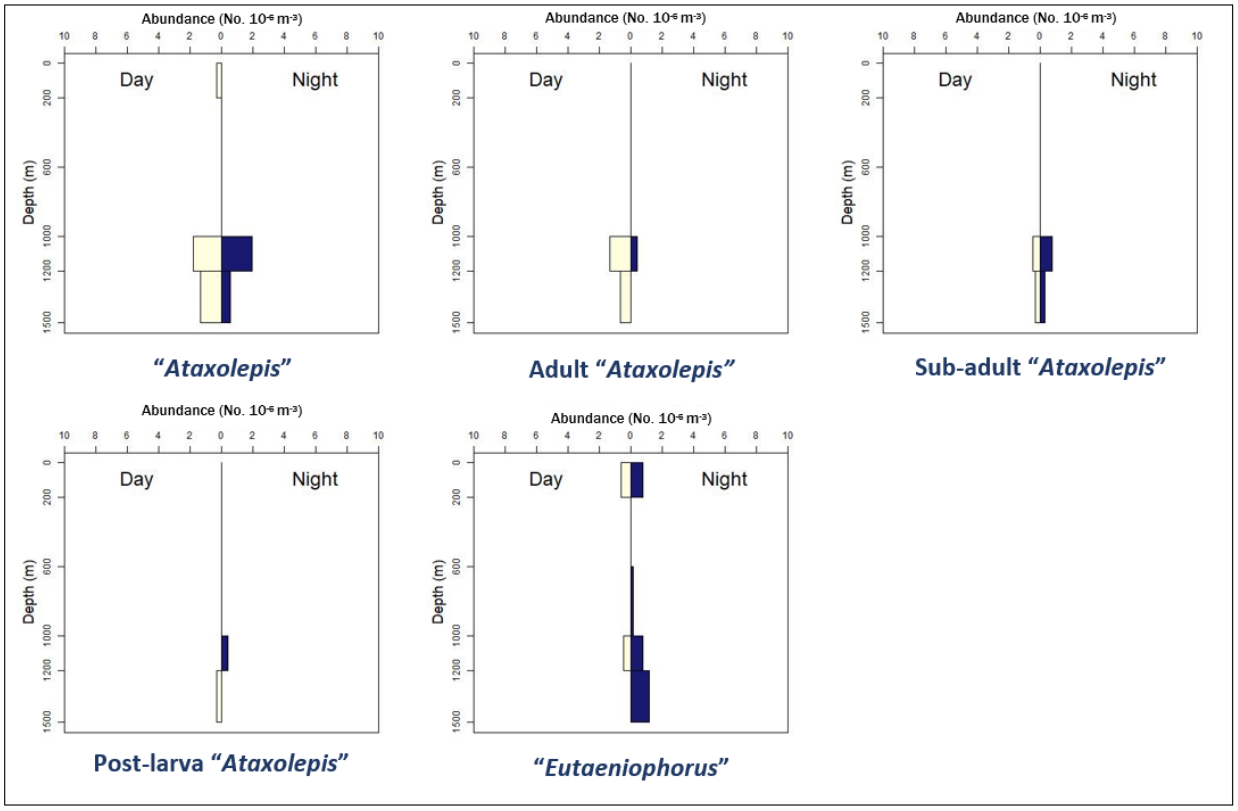


Figure 31. Abundance and diel vertical distribution of male *Cetomimus*/*Gyrinomimus* ("*Ataxolepis*") and larval Cetomimidae ("*Eutaeniophorus*") in the Gulf of Mexico.

Larval *Cetomimus*/*Gyrinomimus* ("*Eutaeniophorus*")

Larval Cetomimidae were collected most often during the night, with the highest catch rate occurring between 1200 and 1500 m (Figure 31). During the day, larval cetomimids were collected most often in the uppermost 200 m and the only other daytime collection was between 1000 and 1200 m. No larval cetomimids were collected between 200 m and 600 m. A Spearman non-parametric correlation test (n=5) suggested that there was no significant relationship between standard length and maximum depth of capture (p-value 0.2198).

Danacetichthys galathenus

The two identified specimens of *Danacetichthys galathenus* were taken only with dual-warp, commercial-sized trawl gear. Both specimens were collected during the night and in a deep tow with a potential maximum depth of 1313 m.

3.3. Trophic ecology

Male *Cetomimus*/*Gyrinomimus* ("*Ataxolepis*")

Of the available 22 male cetomimid specimens, 19 were in fair condition and dissected. Twelve individuals were not yet fully transformed into the adult stage and still had stomachs, four of which were positive (i.e. contained at least one prey item). The few specimens collected, and even lower incidence of positive stomachs (36%), prevented detailed analysis of feeding chronology. Positive stomachs consisted of highly digested crustacean fragments. These items were measured and photographed (Appendix Figures 1 and 2). Each stomach contained at least one highly digested exoskeleton and one contained a pereiopod exopodite. Another stomach contained two mandibles embedded in crustacean exoskeletons (Appendix Figure 3). The size of the exoskeleton fragments and size and shape of the mandibles suggest copepods as a likely prey taxon.

Positive intestines were observed in ten individuals, five of which were fully transformed adults and thus lacked a stomach. Each positive intestine contained highly digested crustacean fragments (Appendix Figures 4 – 7). All intestines contained exoskeletons, two of which contained appendages including exopodites and spines, one contained few mandibles, and two contained an individual ommatidium. The intestine containing the most items was from the smallest individuals (44.6 mm SL) and contained multiple exoskeletons, appendages, and 182 mandibles (Appendix Figures 8 – 10). The intestine containing the fewest items was from the largest individual (59.6 mm SL) and contained only exoskeleton. The size and nature of some prey fragments indicate that feeding on larger crustacea may occur.

Larval *Cetomimus*/*Gyrinomimus* ("*Eutaeniophorus*")

All available larvae were dissected, and prey items analyzed (n=13). Nine of the 13 stomachs were positive and contained prey items. Eight stomachs were engorged with copepods, with counts ranging from three to 1709 individual copepods (Table 9). Copepods were identified until a levelling off effect occurred and no new prey items were found. This effect was observed if after five copepods, no new species were identified (Figure 32). Stomachs that protruded from the body cavity were scored 5 for stomach fullness (n=4) while empty stomachs were scored 0 for stomach fullness (n=3). Although the greatest quantity of copepods was found in one of the largest individuals (38.9 mm SL), there was no overall trend identified in copepod quantity versus fish SL

(Table 10). Number of unique copepod taxa per stomach ranged from two to nine, with the largest number of taxa occurring in the smallest individual. Stomach weight was at least 80% of the body weight in four individuals.

Table 9. Stomach and intestine contents for each analyzed "*Eutaeniophorus*" specimen. Due to the size and condition of the specimen, sometimes the intestine was not found in the body cavity which are noted as did not find (DNF). Exoskeleton is noted as 'exo' and exopodite is noted as 'exp.'

SL (mm)	Stomach fullness	State of digestion	Stomach contents	Intestine contents
38.9	5	0.5	1709 copepods	Empty
57.9	5	0.5 - 2.5	1083 copepods	Empty
37.4	5	0.2 - 2	732 copepods	Empty
32.4	5	1.5 - 3	241 copepods	Exo
26.3	4	1.5 - 2	207 copepods	Exo, exp
36.1	3	2.5 - 3	61 copepods	Exo, exp
30.3	2	0.5 - 1.5	51 copepods	Empty
27.0	1	2	3 copepods	DNF
--	0.5	4	Exo	Empty
34.4	0	NA	Empty	Empty
33.6	0	NA	Empty	Exo
51.5	0	NA	Empty	DNF

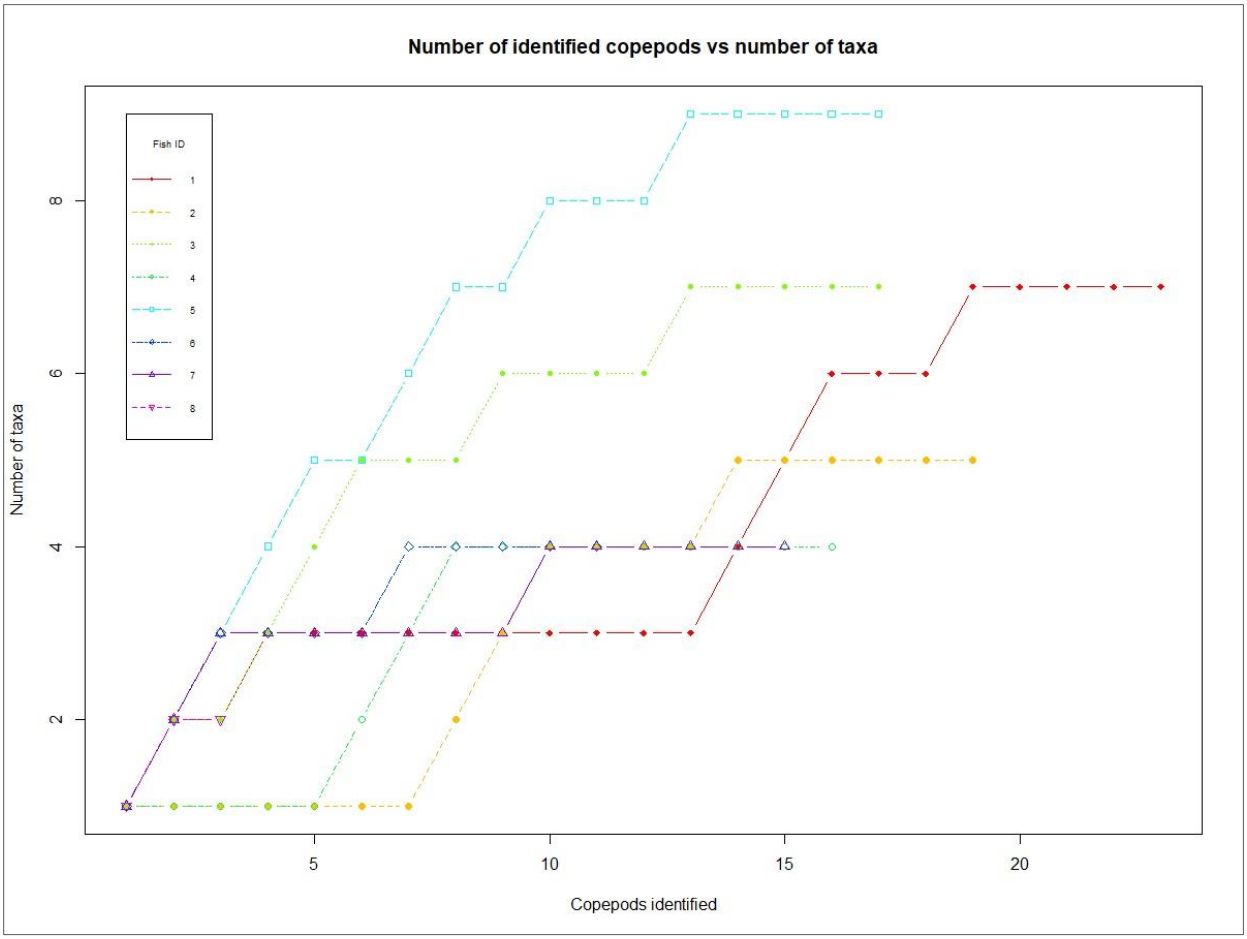


Figure 32. Number of copepod taxa versus number of identified copepods in the stomachs of eight "*Eutaeniophorus*" specimens from the Gulf of Mexico.

Table 10. Dietary information for eight "*Eutaeniophorus*" specimens engorged with copepods. *Weight values were calculated using a length-weight regression.

SL (mm)	Pre-dissection weight (g)	Stomach content weight (g)	Percent stomach weight in pre-dissection weight (g)	Copepod count	No. copepod taxa
38.9	1.95*	1.75	89.7	1709	7
57.9	1.75*	1.55	88.6	1083	5
37.4	0.89	0.74	84.3	732	7
32.4	0.60	0.48	80.0	241	4
26.3	0.13	0.06	46.2	207	9
36.1	0.27	0.03	25.0	61	4
30.3	0.12	0.05	41.7	51	4
27.0	0.06	0.01	16.7	3	2

The eight positive "*Eutaeniophorus*" stomachs engorged with copepods contained at least 14 calanoid copepod taxa (Table 11). *Undinula vulgaris* was the most frequently consumed copepod and accounted for 28.1% of the prey identified to species (Figure 33). *Pleuromamma gracilis* was the second-most frequently identified copepod and accounted for 27.3% of the diet. Copepods identified as Calanoid C were well-digested but different than all other calanoids and accounted for 9.1% of the diet. Copepods belonging to the genus *Pleuromamma* accounted for 8.3% of the diet. *Pleuromamma piseki* accounted for 4.1% of the diet. *Phaenna spinifera* accounted for 7.4% of the diet. Calanoid F accounted for 5% of the diet. Calanoid D accounted for 1.7% of the diet. Finally, Calanoid A, Calanoid B, Calanoid E, *Euchirella rostrata*, and *Pleuromamma abdominalis* each accounted for 0.8% of the diet. Unidentified Calanoid copepods accounted for 5% of the diet. An image gallery of the 12 identified copepod taxa, with ordered pereiopods, can be found in Appendix Figures 11 – 22.

Table 11. Copepod taxa identified in the diet of larval Cetomimidae ("*Eutaeniophorus*.")

Copepod species	**Prey percent frequency**		**Prey percent occurrence**	
	Count	**%**	**Count**	**%**
Undinula vulgaris	1148	28.1	6	75
Pleuromamma gracilis	1116	27.3	7	87.5
Calanoid C	372	9.1	4	20
Pleuromamma	339	8.3	5	62.5
Phaenna spinifera	302	7.4	4	50
Calanoid	204	5	3	37.5
Calanoid F	204	5	2	25
Pleuromamma piseki	168	4.1	2	25
Calanoid D	69	1.7	2	25
Calanoid A	33	0.8	1	12.5
Calanoid B	33	0.8	1	12.5
Calanoid E	33	0.8	1	12.5
Euchirella rostrata	33	0.8	1	12.5
Pleuromamma abdominalis	33	0.8	1	12.5
	4087 Total			

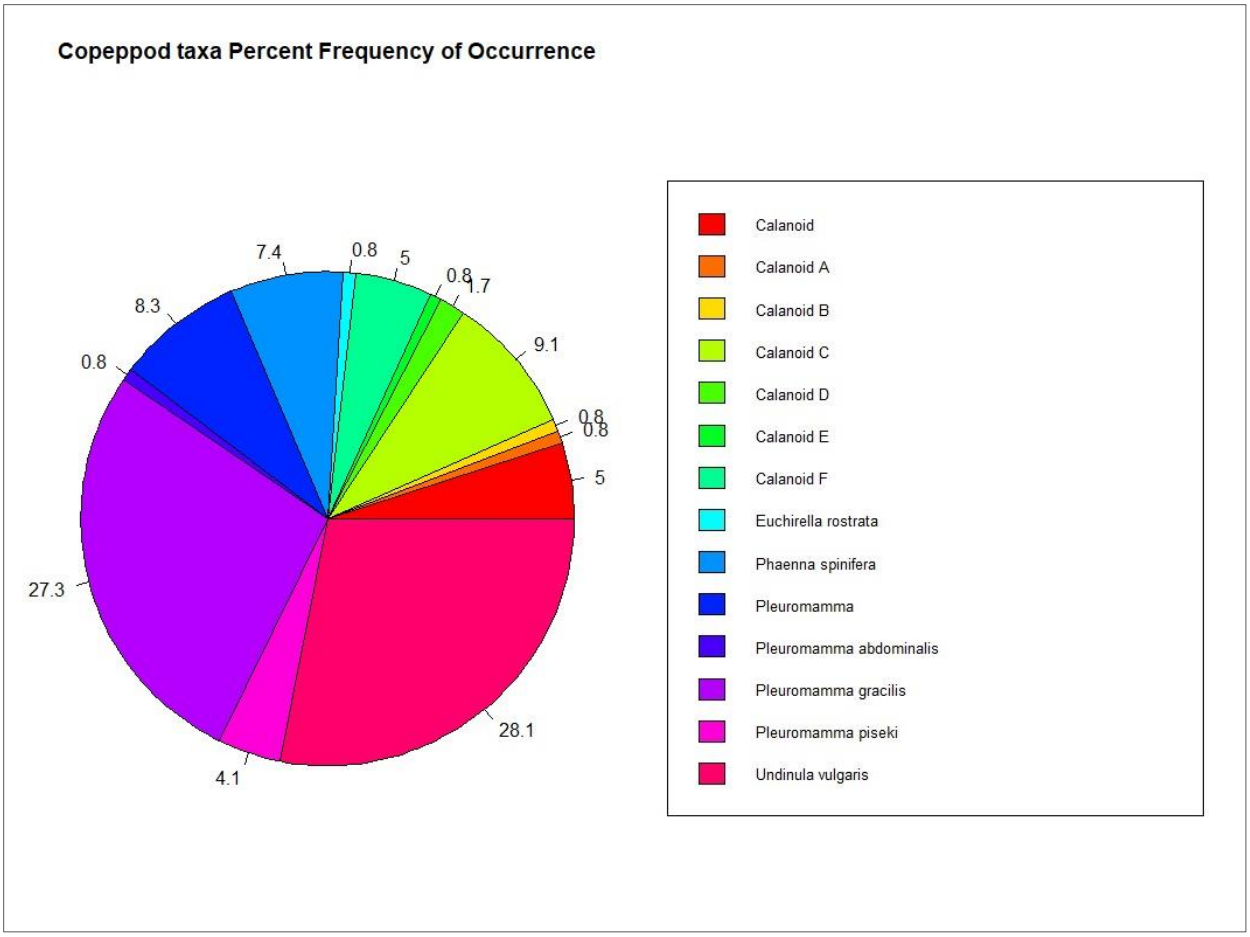


Figure 33. Copepod taxa percent frequency of larval Cetomimidae ("*Eutaeniophorus*") diet from the Gulf of Mexico.

Pleuromamma gracilis occurred most often and was consumed by 87.5% of the analyzed "*Eutaeniophora*" containing positive stomachs (Table 11). *Undinula vulgaris* occurred in 75% of the stomachs and *Pleuromamma* occurred in 62.5%. The next highest occurrence was *P. spinifera* in 50% of the stomachs. The remaining copepod taxa each occurred in less than 38% of larval stomachs, with the lowest occurrence of 12.5% belonging to Calanoid A, Calanoid B, Calanoid E, *E. rostrata*, and *P. abdominalis*.

The individual stomach that contained 1709 copepods also contained 20 unidentified fish scales (Appendix Figure 23). This stomach was so engorged that the contents spilled into the preservation jar. There was another highly damaged larval specimen preserved in the same jar, so the scales may not have been ingested.

The remaining positive larval stomach that was not engorged with copepods contained mostly digested crustacean exoskeletons (Appendix Figure 24). These items could not be identified due to the state of digestion and condition, but the size range suggested copepod fragments.

Positive intestines were observed in four individuals. Each of these intestines contained highly digested crustacean exoskeleton fragments while two contained pereiopod exopodites (Appendix Figures 25 and 26). The size and nature of these items also suggest a copepod diet.

4. Discussion

4.1 Faunal composition and population dynamics

Cetomimidae

Cetomimidae are known globally from 764 records per the Ocean Biogeographic Information System (2021). This study appreciably increases the known records by 493 individuals, one new record for the Atlantic, and six new records for the Gulf of Mexico. The new records are likely attributed to the sampling effort, which increased the probability of accurately describing the cetomimid assemblage, rather than new habitat usage by the Cetomimidae.

The most abundant cetomimid species, *Cetostoma regani* and *Ditropichthys storeri*, comprised over 54% of the assemblage, which further corroborates these as being the two most common cetomimids globally (Paxton, 1989). The genera *Cetomimus* and *Gyrinomimus* were less common, making up only 10.7% of the assemblage. Abrasion from the net and the need for further revision of the genera meant that many *Cetomimus* and *Gyrinomimus* specimens could not be identified to species.

Cetomimidae diversity was assessed by comparing the number of species collected in each of the major depth strata using the 10-m^2 MOCNESS (MOC-10). The lowest level of species richness occurred in the epipelagic zone, in which only three species were collected. The highest level of observed cetomimid species richness occurred in the lower mesopelagic zone (600 to 1000 m) where nine species were collected. Eight cetomimid species were collected in the bathypelagic zone. As only the upper limits of the bathypelagic zone were sample in this study and another 2500 m of under-sampled habitat exists, it could be surmised that species richness of the bathypelagic zone may surpass the mesopelagic.

Assuming that the gear types utilized in this study collect both males and females with the same efficiency, then females outnumber males in the sampled depth intervals as indicated by the significantly diverging sex ratio. It is possible that cetomimids display a large gap in the population sizes of females and males, partitioning more of the biomass into egg producers than the latter. Uneven sex ratios favoring larger females in low latitude ecosystems have been observed in other deep-sea fishes including some myctophids and stomiids of the central Pacific Ocean (Clarke, 1983) and perciforms of the upper-mesopelagic Arabian Sea (Khan, 1996). Morphology of the larger females suggests that they may be more equipped to evade capture in the nets, signifying even more that female cetomimids greatly outnumber males. Males also may primarily inhabit

deep bathypelagic water beyond the sampled depths of this study. Lastly, given that feeding in males is highly reduced or ceased altogether, it is possible that mortality is much higher for males than females, thus skewing *in situ* sex ratios.

Over half of the specimens collected during this study were captured using the commercial-sized, dual-warp trawl gear (274 individuals), in which over 297 million m^3 of seawater was filtered. While using the MOC-10, over 56 million m^3 of seawater was filtered and 219 cetomimids were collected (Cook et al., 2020). While the smallest and median specimen sizes collected were equivalent between the gear types, larger specimens and a larger size range were collected using the commercial-sized, dual-warp trawl gear. The various commercial-sized trawl gears, including a high-speed rope trawl and Irish herring trawl, had very large mouth openings to enhance sampling efficiency. Therefore, these trawls filtered a much larger volume of water than the MOC-10 and allowed for the opportunity to collect more and larger specimens. Cetomimidae have a remarkable lateral line system to detect movement in the surrounding water; however, no species are particularly muscled. The most substantial musculature observed occurs in *D. storeri* and was described as solid layers that increase with specimen size (Paxton, 1989). Therefore, the overall biology of Cetomimidae suggests a limited escape ability from the trawls and is especially true for smaller individuals.

Cetostoma regani

Paxton (1989) summarized the known biology of *Cetostoma regani* derived from 150+ records. This study increases the known records by 103% and 155 individuals. *Cetostoma regani* is the only cetomimid species in which the larval and male adult life-history stages have been successfully linked to the adult female form via genetic and morphological analyses (Johnson et al., 2009). As adults and larva were collected in this study, insight on the population dynamics of this monotypic genus is provided (though a putative second species is suggested based on genetic 'barcoding,' R. Eytan and M. Weber, personal communication). The significantly diverging sex ratio suggests that *C. regani* partition more of the species' biomass into females. As the males were only recently linked to the females in 2009, detailed analyses of their distribution are lacking. The possibility of males inhabiting deeper water could explain the observed unequal sex ratio. Another probable explanation is that the gear types utilized in this study selects for micronekton-sized cetomimids rather than for larvae and smaller males. All four larval *C. regani* were among

the smallest individuals collected during this study and the standard lengths fell within the 9th percentile of all measured specimens.

Ditropichthys storeri

Paxton (1989) summarized the known biology of *Ditropichthys storeri* derived from 80+ records. This study increases the known records by 105% and 84 individuals. Detailed life-history stages and associated descriptions for *D. storeri* are severely lacking. Johnson et al. (2009) demonstrated that a previously described species of *Parataeniophorus* is in fact the larvae of *D. storeri*, however the males have yet to be matched. Thus, all *D. storeri* specimens not identified as the easily differentiated larval stage or in transformation were assumed to be adult females.

Cetomimus

Paxton (1989) summarized the known biology of *Cetomimus* derived from 180+ records. This study increases the known records by 115 individuals. *Sensu* Fricke et al. (2021), seven valid species belong to the genus *Cetomimus*, and at least five were found in the Gulf of Mexico during the present study. The inclusion of the potential new species found in this study would increase these values to nine species globally and seven in the Gulf of Mexico. Continued revision of this genus coupled with genetics and matching of the adult males and larvae will lead to a more thorough understanding of *Cetomimus*.

Cetomimus picklei is believed to have been previously recorded in the Atlantic Ocean (Angulo, 2015), however the three individuals documented in the present study represent the first known occurrences in the Gulf of Mexico. *Cetomimus compunctus* has never been documented in the Gulf of Mexico or Atlantic Ocean, thus the six individuals recorded in this study represent new records for the region.

Gyrinomimus

Paxton (1989) summarized the known biology of *Gyrinomimus* derived from 125+ records. This study increases the known records by 26 individuals. *Sensu* Fricke et al. (2021), five valid species occur within the genus *Gyrinomimus*, and at least three were found in the Gulf of Mexico during this study. The inclusion of the potential new species found in this study would increase these values to eight species globally and six in the Gulf of Mexico. Ongoing revision of this genus

involving genetic matching of the adult males and larvae will lead to a more thorough understanding of *Gyrinomimus*. The eight records of *Gyrinomimus bruuni* and one record of *Gyrinomimus grahami* represent the first known occurrences of these species in the Gulf of Mexico.

Male and larval *Cetomimus*/*Gyrinomimus*

Until now, males belonging to *Cetomimus* and *Gyrinomimus* had not been documented as occurring in the Gulf of Mexico. The remarkable 32 individuals identified in this study represent the first known records for this region and drastically increase the understanding of the cetomimid assemblage.

Cluster analyses revealed that there may be at least three forms, which may or may not be separate species, within the "*Ataxolepis*" assemblage of the Gulf of Mexico. These analyses were based on correlations between snout to anal base and snout to dorsal base as a function of SL. It could be surmised that these distinct clusters may represent the various life-history stages of males; however, the clusters were not specific to adults or sub-adults. Adults were identified as having enlarged gonads and lacking a stomach while sub-adults were identified as still in possession of the stomach and lacking pelvic fins. Thus, it is possible that the discriminated clusters may represent separate species, indicating that at least three species of *Cetomimus* and/or *Gyrinomimus* males were collected during this study. Genetic matching is ongoing with the hope of linking the discriminated morphotypes with genotypes.

Cluster analyses determined that there may be at least two forms within "*Eutaeniophorus festivus"* in the Gulf of Mexico. These clusters were based on correlations between head length and pectoral fin base width as a function of SL. It could be theorized that these discriminated clusters may represent the various larval growth periods; however, the clusters were not specific to a SL range. The length-weight curve of "*Eutaeniophorus*" was best fit by the Gompertz Non-Linear Regression model, later discussed. It is also possible that the discriminated clusters may represent different species, indicating that at least two species of "*Eutaeniophorus*" were collected during this study.

Danacetichthys galathenus

The monotypic genus *Danacetichthys* (*D. galathenus* Paxton, 1989) was known globally by only six specimens (Paxton et al., 2016). The two specimens collected during the present study represent the first known records for the Gulf of Mexico. The specimens measured 44.6 mm and 58.3 mm SL, the latter represents the largest known individual globally as the prior record was 54 mm SL (Paxton et al., 2016).

Cetomimid growth models

The size distribution data for many Cetomimidae species were best described by the Gompertz model growth curve in which initial slow growth is observed, followed by exponential growth, and ending with another slow growth period. The rapid increase in *D. storeri* growth was observed when the fish reached 30 to 40 mm in SL. The only *D. storeri* in transformation included in the length-weight curve measured 35.9 mm. It is possible that the rapid increase in growth occurs during the transformation from larva to adult. Not enough large specimens were collected to observe the second period of slow growth; however this could likely be visible in specimens over 74 mm as that was the largest fish collected. The initial slow growth in *Cetomimus teevani*, the only species in the genus for which a length-weight curve could be produced, was not observed as only two specimens used to create this growth curve were less than 60 mm SL. The initial slow growth phase likely occurs before the fish reaches 60 mm SL and would be observed in a collection with more small individuals. The second period of slow growth appears to begin after the fish reaches 120 mm SL, as this is where the curve begins to plateau. The initial slow growth of "*Eutaeniophorus*" appears to end once the fish reaches 20 mm SL. The period of rapid growth is apparent between 25 to almost 40 mm SL. The final period of slow growth is visible as the fish nears 50 mm SL, likely indicating that the fish has begun transformation into the post-larval/sub-adult phase.

The size distribution of *C. regani* was best described by the Simple Logistic growth model. This model parallels the Gompertz model in which initial slow growth is observed, followed by a more rapid growth period, and ending with another slow growth period. Initial slow growth is observed until the fish reaches about 50 mm SL. The larvae ranged in size from 18 to 26 mm; however, no individuals were identified in the post-larval stage, likely indicating that 50 mm marks

the start of that ontogenetic transition. Growth then increases and appears to begin to plateau around 225 mm, indicating that this may be when the second period of slow growth begins.

The size distribution of "*Ataxolepis*" was best fit by the Exponential growth model in which length and weight increase proportionately over time. The high variance in growth from the model is likely caused by the multiple species represented by the male complex. Also, more individuals collected in which the SL was distributed more evenly on either side of the minimum and maximum measurements would likely improve the appearance of observable exponential growth in male *Cetomimus*/*Gyrinomimus*.

4.2. Abundance and vertical distribution

Paxton (1989) described what little is known regarding global vertical distribution patterns of Cetomimidae, noting that this apparent lack of information is likely due to non-closing net captures. As the present study utilized a multiple opening and closing net, vertical distributions were observed at both the family and species levels.

Cetomimidae were collected most often from the upper bathypelagic zone between 1000 and 1500 m, with the highest collection rates occurring from 1000 to 1200 m. Trawling of the bathypelagic zone using multiple-opening-and-closing nets suggests that adult ceratioid anglerfishes and chiasmodontids are among the few fishes considered uniquely bathypelagic (i.e. rarely collected shallower than 1000 m), while myctophids and stomiids are migrators and occasional residents of the bathypelagic (Sutton et al., 2010). As the majority of cetomimids are non-migrators (excluding *Cetostoma regani* and *Ditropichthys storeri* and possibly *Gyrinomimus,* later discussed), species of Cetomimidae appear to belong to the "spanner" and "holobathypelagic" categories as described by Sutton et al. (2010), in which some species exhibit a wide vertical distribution while others have specialized to a bathypelagic lifestyle, respectively. This variation may be explained by individual species habitat, life-history stage (adult, sub-adult, post-larva, larva) and reproductive biology. Cetomimids in metamorphic transition from the larval to the adult stage were only found in the bathypelagic zone, in contrast to reports that smaller individuals occur in surface waters (Herrera et al., 2016; Paxton, 1989). The wide-ranging vertical distribution observed in larval cetomimids suggests that ontogenetic descent may be rapid.

The Kendall non-parametric correlation test revealed that there was no significant correlation between specimen standard length (SL) and depth of capture. It was expected that

smaller individuals (males, young females, and larvae) inhabit shallower water while larger individuals (adult females) inhabit deeper water, as is commonly observed in deep-sea fishes. However, this lack of significant correlation indicates that SL, and thus sex and life-history stage, may not explain overall cetomimid vertical distribution patterns. An additional explanation for this pattern could be that certain cetomimid species inhabit epi- and mesopelagic waters while others inhabit meso- and bathypelagic waters.

Cetostoma regani and *D. storeri* occurred primarily in the bathypelagic zone. Nighttime collections in shallower water indicate that these species may perform asynchronous vertical migration. These results paralleled Paxton's (1989) results, which hypothesized that these species perform some form of vertical migration and that smaller individuals occur shallower in the water column. Given that these two species dominated the Gulf of Mexico cetomimid assemblage, this could explain shallower catches of adult Cetomimidae. Tolley et al. (1989) found a significant positive correlation between size of *C. regani* and maximum depth, demonstrating that larger individuals are found deeper in the water column. Results of the present study confirm that *C. regani* and *D. storeri* may perform limited vertical migration, though we did not find a significant relationship between specimen SL and depth of capture. Smaller individuals of both species were predominantly collected in deep water with male and larval *C. regani* occurring deeper than 600 m and *D. storeri* in a state of transition (post larva or sub-adult) occurring between 1000 and 1200 m. The 10-m^2 MOCNESS with 3-mm mesh sizing likely allowed for the collection of smaller individuals that previously evaded capture during larger-meshed open-net trawling.

Adult female *Cetomimus* were collected in all sampled depth intervals, with the highest collection rates occurring in water deeper than 200 m. Plotted abundances of *C. teevani*, the species with the highest collection rates, revealed a wide vertical distribution pattern, as approximately even abundances were observed throughout the water column in the middle three depth intervals (200 – 600, 600 – 1000, and 1000 – 1200 m depth). The few specimens collected of other species prevented detailed analyses of vertical distributions, although correlation between *Cetomimus* SL and collection depth was not observed. Open-net trawling and low collection rates of adult female *Gyrinomimus* also resulted in limited observable distribution patterns. As no *Gyrinomimus* specimens were caught in discrete-depth intervals using the MOC-10, exact depth of capture was unable to be determined. At night, several *Gyrinomimus* specimens were collected in shallow trawls (n=3), indicating some form of vertical migration may occur. Distribution of *G. bruuni*, the

species with the highest collection rate, also suggested vertical migration may occur, with equal individual counts (n=2) collected in deep trawls during the day (sustained fishing between 700 and 1500 m) and shallow trawls at night (surface to 700 m). Correlation analysis of *Gyrinomimus* SL and collection depth was not possible due to the open-net trawling; however, as small and large fish were collected in deep trawls, no trend was apparent.

Adult males embedded within the genera *Cetomimus* and *Gyrinomimus* were predominantly collected in the bathypelagic zone below 1000 m, while the larvae displayed a wider vertical distribution and were collected throughout the water column. Approximately equal abundances of larvae were seen for both day and night in shallow and deep water. A possible explanation for both deep and shallow occurrences is rapid ontogenetic descent. Little is known regarding cetomimid reproduction, but it has been shown in other bathypelagic taxa (e.g., ceratioid anglerfishes) that fertilized eggs rise to the surface and hatch where the larger food supply is able to sustain the individual (Pietsch, 2009).

These males and larvae are the smallest representatives of the Cetomimidae. The observed vertical ranges of these taxa generally inhabiting deeper water could be attributed to a few factors. First, the literature is based on numerically limited collections and may only partially describe the associated vertical ranges. The vertical distribution patterns presented here were derived from the largest known dataset and thus expand the known vertical habitat range for male and larval Cetomimidae. Second, the observed distributions could be explained by the use of both commercial-sized trawls and a MOC-10. The 3-mm mesh sizing of the MOC-10 allowed for the collection of smaller individuals that are likely sampled poorly in larger-meshed trawls. Likewise, the larger trawls process over an order of magnitude more water per deployment than a rectangular midwater trawl such as the MOC-10, an important consideration for fishes demonstrating a rare species strategy. The combined data show that cetomimids not only have a cosmopolitan horizontal distribution, but also a wider vertical range than previously known. Lastly, as these complexes likely represent multiple species of *Cetomimus* and *Gyrinomimus* (Johnson et al., 2009), it is possible that vertical distributions for these taxa are dependent on individual species habitats. Hierarchical cluster analyses indicated that there may be at least three and two discriminated groups of males and larvae, respectively, embedded within the Gulf of Mexico cetomimid population. As no *Gyrinomimus* specimens were caught using the MOC-10, this study is unable to investigate this hypothesis further.

Two specimens collected during this study were identified as *Danacetichthys galathenus* and both were taken in deeper trawls during the night. Historically, this species was thought to inhabit the Pacific, Indian, and Atlantic Oceans from 30° N to 20° S and has been taken in trawls from 1300 to 2000 m (Paxton et al., 2016). Until now, this species had not been found in the Gulf of Mexico, although this was not surprising given the known horizontal distribution. These collections further illustrate that current understandings of cetomimid distributions are minimal. During collection in the deep open-net trawls, the targeted maximum depth was 1500 m; however, the maximum depth occurred shallower in the locations in which the seafloor was near 1500 m. Although *D. galathenus* appears to inhabit deeper water in other ecosystems, the collections at 1300 m in the Gulf of Mexico may signify that this species inhabits water near the seafloor. Further investigation and bathypelagic trawling are necessary to be able to properly describe the distribution both globally and vertically.

4.3 Trophic ecology

Based on the observations of stomach and intestine contents, the diet of male cetomimids prior to transformation into the adult stage consists primarily, if not only, of Crustacea. The size and nature of many of the gut contents suggest that copepods are the primary diet component. The presence of ommatidia (photoreceptor cells in compound eyes) and larger crustacean fragments in multiple intestines indicate that euphausiids and/or mysids are also consumed, differing from the diet of larvae.

The two males containing ommatidia in the intestine measured 44.6 and 55.9 mm SL. Both specimens lacked a stomach and were identified as transformed adults. These individuals likely opportunistically fed on a larger meal before metamorphosis, ensuring a higher preservation of energy being transferred to the enlarging liver. These findings represent the first known record of male cetomimids feeding on larger crustacea other than copepods.

While "*Ataxolepis*" lose the stomach during metamorphosis, the size in which an individual begins this transformation is unknown (Johnson et al., 2009). The individual with the highest number of prey fragments in the intestine contained substantially more items than the other specimens combined and was among the smallest males of this study (44.6 mm SL). It is likely that the transition out of the sub-adult phase begins just before the fish reaches that size.

Most mandibles in the stomach and intestines of male cetomimids were of the same size and shape and likely belonged to omnivorous copepods based on appearance, as described by Geisecke and González (2004). The intestine contents of the individual mentioned above were the most varied compared to the other specimens and contained larger crustacean fragments (Appendix figure 9) and feeding appendages (Appendix Figure 10). The size and shape of these fragments align with large copepod species or larger Crustacea.

The only identifiable prey taxa of larval cetomimids ("*Eutaeniophorus*") were copepods of the order Calanoida. Most copepods were found intact and in near-perfect condition aside from indication of digestion. Cetomimid larvae have little to no dentition and it appears teeth grow as the fish matures. Of individuals having dentition, the teeth are tiny, jagged, and few in number. The lack of dentition coupled with the state of the prey indicate that the larvae consume copepods whole and in large numbers during individual feeding bouts (i.e. gorging).

Few studies have described the vertical distributions of calanoid species in the Gulf of Mexico through discrete-depth trawling. From stratified zooplankton trawls of the northern Pacific Ocean, *Pleuromamma* spp. have been collected as deep as 2500 m (Yamaguchi et al., 2015). *Phaenna spinifera* is also documented deeper, typically inhabiting meso- to bathypelagic water across the World Ocean (Bradford-Grieve et al., 1999; Dorgham et al., 2012). *Euchirella rostrata* is known to have a wide vertical range with the deepest known collection at 2000 m in the Gulf of Mexico (Markhaseva, 1996). However, *Undinula vulgaris*, the most commonly consumed copepod by larval cetomimids, is primarily an epipelagic species (Hopkins, 1982; Suárez-Morales et al., 2009). Although three of the engorged larvae were collected between 1000 and 1500 m, the vertical distribution of the prey indicates the feeding likely occurred in shallow water. After the fish has gorged on copepods and has begun ontogenetic transformations, it may rapidly descend to the bathypelagic zone, as indicated by the depth of collection. The other two engorged larvae were collected in open nets from the surface to 1500 m.

Considering the size range of the cetomimid specimens engorged with copepods (26.3 to 57.9 mm), the quantity of copepods in each stomach (510 on average) was quite remarkable. The eastern Gulf of Mexico has an average copepod biomass of ~1 gm^{-3} from surface to 1000 m (range: 0.7 to 5 gm^{-3}) for taxa similar to that observed as cetomimid prey (Hopkins, 1982). As the states of digestion of prey in each stomach did not drastically vary, fish of this size range should not have been able to process a large enough volume of water in such a short time to collect as many

copepods as they did if the prey were distributed evenly. There would appear to be four possibilities to explain massive copepod gorging in larval cetomimids: (1) the fish serendipitously encountered a large swarm of copepods or many smaller swarms, (2) the fish participated in 'net feeding,' where potential prey are concentrated in cod-ends along with the captured larval cetomimid, (3) the fish possess a means for locating a swarm of copepods (e.g., during mating or feeding), or (4) the fish possesses a means of attracting copepods to itself. For small fishes, viscous (frictional) forces dominate locomotion (i.e. low Reynold's number environment), causing the individual to use more energy for swimming than larger, more fusiform fishes. The possibility that cetomimid larvae can swim fast enough through the water to simultaneously consume large amounts of copepods also does not seem likely. The mesh of the 10-m^2 MOCNESS (3 mm) is much smaller than the mesh of the large dual-warp commercial trawl gear (> 1 m meter at mouth, grading to ~ 19 mm at cod-end). As the copepods ranged in standard length from 0.851 to 2.182 mm with a single outlier of 4.078 mm, they would not have been collected in high concentrations in the net, thus discounting the possibility of net feeding. Larval cetomimids would require excellent vision to locate and consume large swarms of copepods in an environment, and with no available downwelling light and extremely small eyes (Figure 34), the third possibility would be difficult although not impossible. The final idea that the copepods were attracted to the fish seems likely, although the mechanism for such means is unknown. It is also possible that only those individuals that locate copepod swarms survive (and are thus captured by us). Further research on the biology of larval cetomimids would be required to further develop these hypotheses. It is evident, however, that the larvae are highly specialized to survive in this limiting environment.

Figure 34. Cetomimidae larva ("*Eutaeniophorus*") collected from the Gulf of Mexico.

The 14 copepod taxa identified in the stomachs of larval cetomimids indicate that these fish participate in a highly selective feeding strategy rather than opportunistic feeding. The number of discrete copepod taxa in each stomach ranged from two to nine with an average of five. *Undinula vulgaris* was the most frequently consumed and was found in most positive stomachs (n=6). *Pleuromamma gracilis* was the second most frequently consumed and found in all but one positive stomach (n=7). *Phaenna spinifera* was consumed in low quantities but was found in half of the positive stomachs (n=4). These species are commonly collected in zooplankton tows of the pelagic Gulf of Mexico (Cummings, 1983; Hopkins, 1982; Suárez, 1992; Suárez-Morales et al., 2009). It is possible that large swarms of these species allow for the apparent larval cetomimid feeding selectivity and gorging.

Prior to this study, the largest quantity of copepods found in a single larval cetomimid stomach is ~600+ (J.R. Paxton. personal communication, September 5, 2020). This study collected three individuals in which the copepod record was drastically exceeded, including almost triple in one specimen containing 1709 copepods. Although these contents spilled out of the stomach and body cavity while in the preservation jar, it was confirmed that the fish was intact upon capture

and that the copepods belonged to the individual larva (T.T. Sutton, personal communication, January 4, 2021).

The 20 unidentified fish scales found in one larval stomach were likely reflexively gulped during the agonal phase as these fish are non-piscivorous (T.T. Sutton. personal communication, September 4, 2020). This does indicate, however, that larval cetomimids may survive for some time after capture in the net. The remaining positive stomach contents unable to be identified and intestine contents are likely appendages and exoskeleton from copepods. No mandibles were found but many pereiopod exopodites were observed. The size of these appendages agree that these items likely belonged to copepods.

5. Conclusion

The Cetomimidae assemblage of the Gulf of Mexico was analyzed from a collection of 493 individuals, which significantly increases the known records of this deep-sea fish family. The assemblage contained at least 16 species and five genera and was dominated by two species that are globally distributed, *Cetostoma regani* and *Ditropichthys storeri*. Six taxa identified from 53 individuals represent the first records in the Gulf of Mexico (*Cetomimus compunctus*, *Cetomimus picklei*, *Danacetichthys galathenus*, *Gyrinomimus bruuni*, *Gyrinomimus grahami*, and male *Cetomimus*/*Gyrinomimus*), while one species identified from six individuals represents the first record in the Atlantic Ocean (*C. compunctus*). The mesopelagic zone contained the highest observed cetomimid species richness in the Gulf of Mexico; however, further sampling of the lower bathypelagic region may indicate that species richness is highest below 1000 m. The life-history stage data suggest a highly skewed sex ratio favoring larger females in this low-latitude ecosystem.

Large size ranges for individual taxa were collected during this study, but deeper trawling is likely necessary to confirm maximum sizes. Growth models were analyzed for the more frequently caught taxa of Cetomimidae, representing the first known study to do so. Many cetomimids were best fit by the Gompertz growth model and experience an initial period of slow growth, followed by rapid growth until eventually slowing again. These periods of varying growth rates were observed in many species collected in the Gulf of Mexico and are believed to represent life-history stage transformations.

Morphometric analysis provided initial insight into the faunal makeup of the male and larval *Cetomimus*/*Gyrinomimus* assemblages. At least three morphologically discriminated groups of males and two discriminated groups of larvae were identified in this study. Genetic matching is in progress with the expectation that these undescribed morphotypes will be linked to the identified adult female forms.

Overall, cetomimids have a wide vertical range and can be found everywhere in the water column, but the adults are most common in the bathypelagic zone in which depth is greater than 1000 m. Some form of vertical migration likely occurs in the populations of *C. regani* and *D. storeri* and may occur in the adult female *Gyrinomimus* population. Prior to this study, smaller cetomimids were thought to inhabit shallow water while the larger adult females inhabit deeper water. The results of this study expand the known vertical ranges of cetomimid taxa, as males and

larvae of the genera *Cetomimus* and *Gyrinomimus* were observed to primarily inhabit the bathypelagic zone. In addition, we found no correlation between specimen standard length and depth of capture.

Male *Cetomimus*/*Gyrinomimus* may feed on crustaceans larger than copepods, including euphausiids and/or mysids. Prior to this study, males were thought to only gorge on copepods prior to metamorphosing and losing the stomach; however, the presence of ommatidia and larger crustacean fragments indicate that a diet of euphausiids and/or mysids is likely. Based on the quantity of prey items in the intestine, male cetomimids may begin transformation into the adult phase around 44 mm standard length.

The larvae ("*Eutaeniophorus*") gorge on massive amounts of copepods over a relatively short amount of time. Although the mechanism for encountering prey of this quantity remains unknown, we propose that either location of dense patches of copepods and/or attraction of copepods to the fish are the most likely explanations. The feeding strategy appears highly selective towards swarming copepod taxa including *Undinula vulgaris* and *Pleuromamma* spp. concentrated in the epipelagic zone. Trophic data and vertical distribution patterns indicate that ontogenetic descent is rapid.

6. References

Angel, M. V. (1997). What is the deep sea? In D. J. Randall & A. P. Farrell (Eds.), *Deep-Sea Fishes* (pp. 1–41). New York, NY: Academic Press.

Angulo, A. (2015). *Cetomimus gillii* Goode and Bean, 1895 (Cetomimiformes: Cetomimidae): range and extension and first records in the Tropical Eastern Pacific. *Marine Biodiversity Records, 8*(e22), 1-5. doi: 10.1017/S1755267215000019.

Backus, R. H., Craddock, J. E., Haedrich, R. L., & Robison, B. H. (1977). Atlantic mesopelagic zoogeography. In R. H. Gibbs, Jr. (Ed.), *Fishes of the western North Atlantic, part 7* (pp. 266-287). New Haven, CT: Sears Foundation for Marine Research.

Bertelsen, E., & Marshall, N. B. (1956). The Mirapinnatoidei: a new order of teleost fishes. *Dana Report 42*, 1-34.

Bertelsen, E., & Marshall, N. B. (1958). Notes on Mirapinnati (an addendum to Dana Report Number 42): A change of name and further records. *Dana Report 42*, 9-10.

Bertelsen, E. & Nielsen, J. G. (1986). Saccopharyngidae. In P. J. P. Whitehead (Ed.), *Fishes of the North-eastern Atlantic and the Mediterranean, volume 2* (pp. 530-533). Paris, France: Unesco.

Bigelow, H. B. (1961). A new species of the cetomimid genus *Gyrinomimus* from the Gulf of Mexico. *Breviora* 145: 1-2.

Bradford-Grieve, J. M., Boyd. P. W., Chang, F. H., Chiswell, S., Hadfield, M., Hall, J. A… Shushkina, E.A. (1999). Pelagic ecosystem structure and functioning in the Subtropical Front east of New Zealand in austral winter and spring. *Journal of Plankton Research 21*, 405–428.

Burghart, S. E., Hopkins, T. L., & Torres, J. J. (2007). The bathypelagic Decopoda, Lophogastrida, and Mysida of the eastern Gulf of Mexico. *Marine Biology, 152*, 315-327. doi: 10.1007/s00227-007-0691-3.

Clarke, T.A. (1983). Sex ratios and sexual differences in size among mesopelagic fishes from the central Pacific Ocean. *Marine biology, 73*. 203-209. doi: 10.1007/BF00406889.

Cook, A. B., Sutton, T. T., Galbraith, J. K., & Vecchione, M. (2013). Deep-pelagic (0–3000 m) fish assemblage structure over the Mid-Atlantic Ridge in the area of the Charlie-Gibbs Fracture Zone. *Deep-Sea Research II: Topical Studies in Oceanography, 98*(Part B), 279-291. doi: 1016/j.dsr2.2012.09.003.

Cook, A. B., Bernard, A. M., Boswell, K. M., Bracken-Grissom, H., D'Elia, M., deRada, S…. Sutton, T. T. (2020). A multidisciplinary approach to investigate deep-pelagic ecosystem dynamics in the Gulf of Mexico following *Deepwater Horizon*. *Frontiers in Marine Science, 7*:548880. doi: 10.3389/fmars.2020.548880.

Cruz-Acevedo, E., Tolimieri, N., & Aguirre-Villaseñor, H. (2018). Deep-sea fish assemblages (300−2100 m) in the eastern Pacific off northern Mexico. *Marine Ecology Progress Series, 592*, 225-242. doi: 10.3354/meps12502.

Cummings, J.A. (1983). Habitat dimensions of calanoid copepods in the western Gulf of Mexico. *Journal of Marine Research, 41*. 163-188.

Danovaro, R., Snelgrove, P. V. R., & Tyler, P. (2014). Challenging the paradigms of deep-sea ecology. *Trends in Ecology and Evolution, 29*(8), 465-475. doi: 10.1016/j.tree.2014.06.002.

Dorgham, M. M., Elsherbiny, M. M., & Hanafi, M. H. (2012). Vertical distribution of zooplankton in the epipelagic zone off Sharm El-Sheikh, Red Sea, Egypt. *Oceanologia 54*(3), 437-489. doi: 10.5697/oc.54-3.473.

Dornburg, A., Townsend, J. P., Brooks, W., Spriggs, E., Eytan, R. I., Moore, J. A…Near, T. J. (2017). New insights on the sister lineage of percomorph fishes with an anchored hybrid enrichment dataset. *Molecular Phylogenetics and Evolution, 110*, 27-38. doi: 10.1016/j.ympev.2017.02.017.

Drazen, J. C. & Sutton, T. T. (2017). Dining in the deep: the feeding ecology of deep-sea fishes. *Annual Review of Marine Science, 9*, 337-366. doi: 10.1146/annurev-marine-010816-060543.

Ebeling, A. W. & Weed, W. H. (1973). Order Xenoberyces (Stephanoberyciformes). In D. M. Cohen, A. W. Ebeling, T. Iwamoto, S. B. McDowell, N. B. Marshall, D. E. Rosen, P. Sonoda, W. H. Weed III, & L. P. Woods (Eds.), *Fishes of the western North Atlantic, part 6* (pp. 397-478). New Haven, CT: Sears Foundation for Marine Research.

Fedorov, V. V., Balushkin, A. V., & Trunov, I. A. (1987). A new whale-fish species, *Gyrinomimus andriashevi*, sp. nov. (Osteichthyes: Cetomimidae) from the Lazarev Sea (Antarctic). *Journal of Ichthyology, 27*(2), 47-54. Translated from *Voprosy Ikhtiologii, 1*, 12-18.

Fisher, C. R., Montagna, P. A., & Sutton, T. T. (2016). How did the Deepwater Horizon oil spill impact deep-sea ecosystems? *Oceanography, 29(3)*, 182–195. doi: 10.5670/oceanog.2016.82.

Fricke, R., Eschmeyer, W. N. & R. van der Laan, (Eds., 2021). Eschmeyer's Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Electronic version accessed 02 May 2021.

Goode, G. B. & Bean, T. H. (1895). On Cetomimidae and Rondeletiidae, two new families of bathybial fishes from the northwestern Atlantic. *Proceedings of the United States National Museum, 17*(1012), 451-454.

Geisecke, R. & González, H. E. (2004). Mandible characteristics and allometric relations in copepods: a reliable method to estimate prey size and composition from mandible occurrence in predator guts. *Revista Chilena de Historia Natural, 77*, 607-616.

Hanchet, S. M., Stewart, A. L., McMillan, P. J., Clark, M. R., O'Driscoll, R. L., & Stevenson, M. L. (2013). Diversity, relative abundance, new locality records, and updated fish fauna of the Ross Sea region. *Antarctic Science, 25*(5), 619-636. doi: 10.1017/S0954102012001265

Herrera, G. A., Landaeta, M. F., & Castro, L. R. (2016). Record of a larval whalefish (family Cetomimidae) from near the Juan Fernandez seamounts, southeastern Pacific Ocean. *Revista de Biología Marina y Oceanografía, 51*(1), 171-174. doi: 10.4067/50718-19572016000100016.

Herring, P. (2002). *Biology of Habits*. The Biology of the Deep Ocean. New York, NY: Oxford University Press.

Hopkins, T.L. (1982). The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep-Sea Research, 29*(9), 1069-1083.

Hopkins, T. L., Sutton, T. T., & Lancraft, T. M. (1996). The trophic structure and predation impact of a low latitude midwater fish assemblage. *Progress in Oceanography, 38*(3), 205-239. doi: 10.1016/S0079-6611(97)00003-7.

Johnson, G. D. & Patterson, C. (1993). Percomorph phylogeny – a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science, 52*(1), 554–626.

Johnson, G. D., Paxton, J. R., Sutton, T. T., Satoh, T. P., Sado, T., Nishida, M., & Miya, M. (2009). Deep-sea mystery solved: astonishing larval transformations and extreme sexual dimorphism unite three fish families. *Biology Letters, 5*, 235-239. doi: 10.1098/rsbl.2008.0722.

Keene, M. J. & Tighe, K. A. (1984). Beryciformes: development and relationships. In H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., & S. L. Richardson (Eds.), *Ontogeny and Systematics of Fishes* (pp. 383-392). American Society of Ichthyologists and Herpetologists.

Khan, M. F., Zacharia, P.U., Nandakumaran. K., Mohan, S., Arputharaj, M.R., Nagaraja, D., & Ramakrishnan, P. (1996). Catch, abundance and some aspects of biology of deep sea fish in the southeastern Arabian Sea. *Proceedings of the Second Workshop on Scientific Results of FORV Sugar Sampud*, 331-346.

Kunzig, R. (2003). Deep-sea biology: living with the endless frontier. *Science, 302*(5647), 991. doi: 10.1126/science.1090808.

Leis, J. M. (2015). Taxonomy and systematics of larval Indo-Pacific fishes: a review of progress since 1981. *Ichthyological Research, 62*(1), 9-28. doi: 10.1007/s10228-014-0426-7.

Loeb, V. J. (1979). Larval fishes in the zooplankton community of the North Pacific Central Gyre. *Marine Biology, 53*(2), 173-191.

Lord, H. K. (2016). *A history of research in the bathypelagic realm: Earth's largest habitat*. Capstone. Nova Southeastern University. Retrieved from NSUWorks, (321). https://nsuworks.nova.edu/cnso_stucap/321.

Markhaseva, E. L. (1996). Calanoid copepods of the family Aetideidae of the world ocean. *Zoological Institute, Russian Academy of Sciences, 268*: 1-331.

Maul, G. E. (1969). On the genus *Cetomimus* (Cetomimidae) with the description of a new species. *Bocagiana, 18*, 1-12.

McEachran, J. D. (2009). Fishes (Vertebrata: Pisces) of the Gulf of Mexico. In D. L. Felder & D. K. Camp (Eds.), *Gulf of Mexico Origin, Waters, and Biota, Volume 1: Biodiversity.* (pp. 1223-1316). College Station, Texas.

McEachran, J. D., & Fechhelm, J. D. (1998). Fishes of the Gulf of Mexico. Volume 1: Myxiniformes to Gasterosteiformes. University of Texas Press, Austin. pp. 1112.

Merrett, N. R. & Roe, H. S. J. (1974). Patterns and selectivity in the feeding of certain mesopelagic fishes. *Marine Biology, 28*(2), 115-126.

Miya M., Takeshima, H., Endo, H., Ishiguro, N. B., Inoue, J.G., Mukai, T…Nishida, M. (2003). Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution, 26,* 121-138. doi: 10.1016/S1055-7903(02)00332-9.

Mooers, C. N. K. (1998). Intra-Americas Sea Circulation. In K. H. Bring & A. R. Robinson (Eds.), The Global Coastal Ocean II: Regional Studies and Synthesis (pp. 186-208). New York, NY: John Wiley & Sons, Inc.

Moore, J. A. (1993). Phylogeny of the trachichthyiformes (Teleostei: Percomorpha). *Bulletin of Marine Science, 52*(1), 114-136.

Murdy, E. O., Matheson Jr., R. E., Fechhelm, J. D., & McCoid M. J. (1983). Midwater fishes of the Gulf of Mexico collected from the R/V *Alaminos*. *Texas Journal Science*, 35: 109–127.

Myers, G. S., & Freihofer, W. C. (1966). Megalomycteridae, a previously unrecognized family of deep-sea cetomimiform fishes based on two new genera from the North Atlantic. *Stanford Ichthyological Bulletin, 8*(3), 192-206.

Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the World* (5th ed.). Hoboken, NJ: John Wiley & Sons, Inc.

Ocean Biogeographic Information System. (2021). Family: Cetomimidae. Retrieved from OBIS 02 May 2021. https://obis.org/taxon/125460.

Owre, H. B. & Foyo, M. (1967). Copepods of the Florida Current: *Fauna Caribaea Number 1 Crustacea, Part 1: Copepoda*. Miami, Florida: Institute of Marine Science, University of Miami.

Paxton, J. R. (1989). Synopsis of the whalefishes (family Cetomimidae) with descriptions of four new genera. *Records of the Australian Museum, 41*(2), 135-206. doi: 10.3853/j.0067-1975.41.1989.141.

Paxton, J. R. (2002). Order Stephanoberyciformes. In K. E. Carpenter (Ed.), *The Living Marine Resources of the Western Central Atlantic, Volume 2: Bony Fishes part 1* (pp. 1171-1175). Rome, Italy: FAO.

Paxton, J. R., Johnson, G. D., & Trnski, T. (2001). Larvae and juveniles of the deepsea "whalefishes" *Barbourisia* and *Rondeletia* (Stephanoberyciformes: Barbourisiidae, Rondeletiidae), with comments on family relationships. *Records of the Australian Museum, 53*(3), 407-426. doi: 10.3853/j.0067-1975.53.2001.1352.

Paxton, J. R., Trnski, T., & Johnson, G. D. (2016). Order Stephanoberyciformes: Cetomimidae. In K. E. Carpenter (Ed.), *The Living Marine Resources of the Eastern Central Atlantic, Volume 3: Bony Fishes part 1* (pp. 2173-2181). Rome, Italy: FAO.

Pietsch, T. W. (2009). Reproduction and early life history. In *Oceanic Anglerfishes: Extraordinary Diversity in the Deep Sea* (pp. 277-308). University of California Press.

Portela, E., Tenreino, M., Pallàs-Sanz, E., Meunier, T., Ruiz-Angulo, A., Sosa-Gutiérrez, R., & Cusí, S. (2018). Hydrography of the central and western Gulf of Mexico. Journal of Geophysical Research: Oceans, 123, 5134-5149. doi: 10.1029/2018JC013813.

Powell, S. M. & Haedrich, R. L. (2003). The deep-sea demersal fish fauna of the northern Gulf of Mexico. *Journal of Northwest Atlantic Fishery Science, 31*, 19-33. doi: 10.2960/J.v31.a2.

Priede, I. G. (2017). Introduction. In *Deep-Sea Fishes: Biology, Diversity, Ecology and Fisheries* (pp. 1-67). Cambridge University Press. doi: 10.1017/9781316018330.002.

Prokofiev, A. M. (2014). Swallowerfishes (Chiasmodontidae) of the East Pacific. *Journal of Ichthyology, 54*(9), 631-641. Translated from *Voprosy Ikhtiologii, 54*(6), 643-653. doi: 10.1134/S0032945214060137

Robison, B. H., Sherlock, R. B., & Reisenbichler, K. R. (2010). The bathypelagic community of Monterey Canyon. *Deep-Sea Research Part II: Topical Studies in Oceanography, 57*(16), 1551-1556. doi: 10.1016/j.dsr2.2010.02.021.

Rosen, D. E., (l973). Interrelationships of higher euteleostean fishes. *Zoological Journal of the Linnean Society, 53,* Supplumental 1, 373-395.

Rosen, D. E. & Patterson, C. (l969). The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History, 141*(3), 357-474.

Stukus, R. D. (1963). Family Lepisosteidae. In H. B. Bigelow et al., (Eds.), *Fishes of the Western North Atlantic, Volume 3: Soft-rayed bony fishes* (pp. 68-88). Sears Foundation for Marine Research, Memoir 1, New Haven, Connecticut.

Suárez, E. M. (1992). Faunistic list of the calanoid copepods (Copepoda: Calanoida) of the Gulf of Mexico: zoogeographic considerations. *Marine Science 18*(2): 119-151. doi: 10.7773/cm.v18i2.889.

Suárez-Morales, E., Fleeger, J. W., Montagna, P. A. (2009). Free- Living Copepoda (Crustacea) of the Gulf of Mexico. In D. L. Felder & D. K. Camp (Eds.), *Gulf of Mexico Origin, Waters, and Biota, Volume 1: Biodiversity.* (pp. 841-869). College Station, Texas.

Sutton, T. T. (2013). Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of Fish Biology, 83*, 1508-1527. doi: 10.1111/jfb.12263.

Sutton, T. T., Porteiro, F. M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C. I. H.…Bergstad, O. A. (2008). Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep Sea Research Part lI: Topical Studies in Oceanography, 55*(1-2), 161-184. doi: 10.1016/j.dsr2.2007.09.013.

Sutton, T. T., Wiebe, P. H., Madin, L., & Bucklin, A. (2010). Diversity and community structure of pelagic fishes to 5000 m depth in the Sargasso Sea. *Deep Sea Research Part II: Topical Studies in Oceanography, 57*(24–26), 2220-2233. doi: 0.1016/j.dsr2.2010.09.024.

Sutton, T. T., Clark, M. R., Dunn, D. C., Halpinc, P. N., Rogers, A. D., Guinottee, J.… Heino, M. (2017). A global biogeographic classification of the mesopelagic zone. *Deep Sea Research Part I: Oceanographic Research Papers, 126,* (85-102). doi: 10.1016/j.dsr.2017.05.006.

Tolley, S. G., Gartner Jr., J. V., & Lancraft, T. M. (1989). Whalefishes (Beryciformes: Cetomimoidei) of the Gulf of Mexico. *Bulletin of Marine Science, 45*(3), 671-677.

Vecchione, M., Bergstad, O. A., Byrkjedal, I., Falkenhaug, T., Gebruk, A. V., Godø, O. R....Wenneck, T. (2010). Biodiversity patterns and processes on the Mid-Atlantic Ridge. In A. D. McIntyre (Ed.), *Life in the World's Oceans: Diversity, Distribution, and Abundance* (pp. 103–121). West Sussex, UK: Wiley-Blackwell. doi: 10.1002/9781444325508.

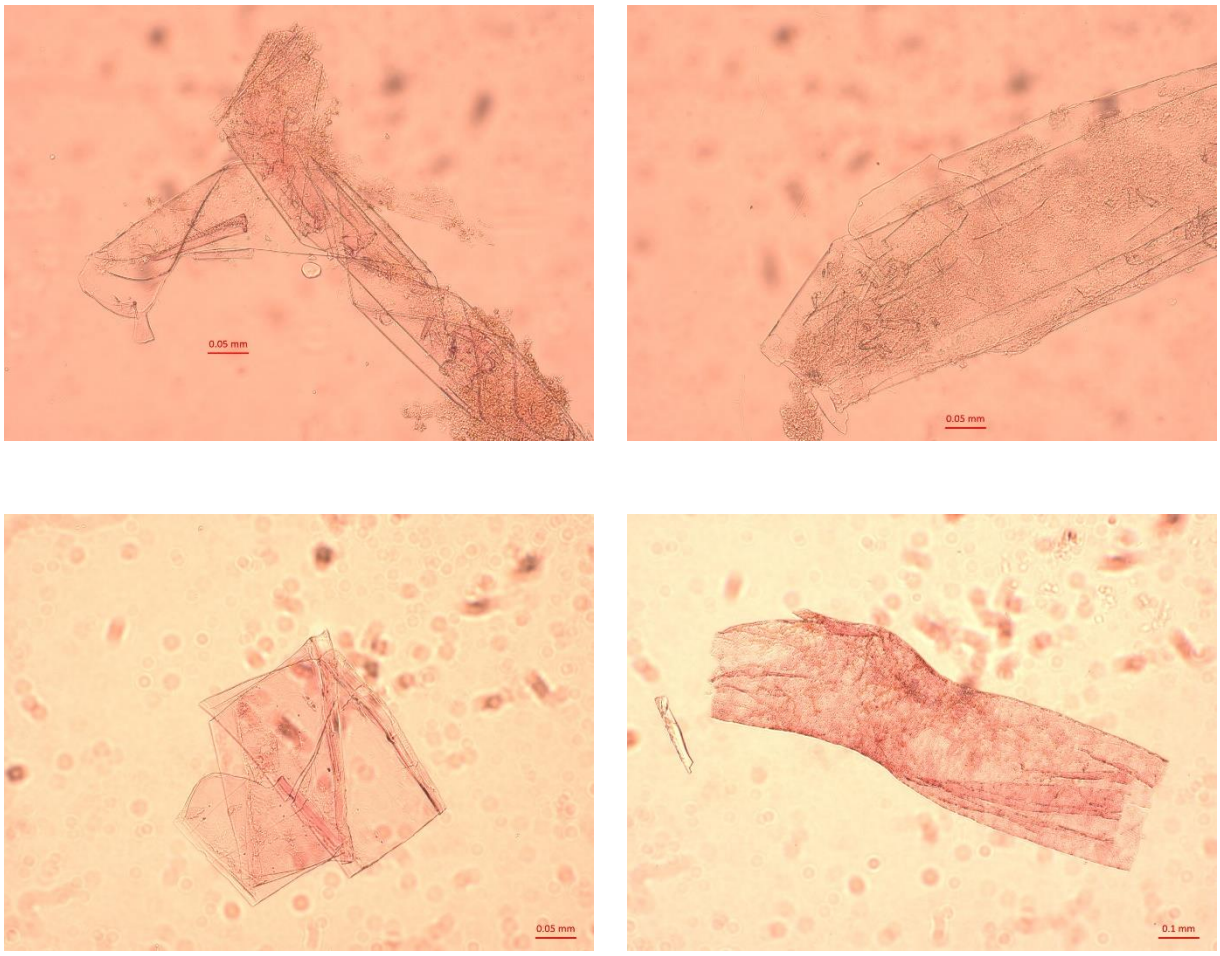
Webb, T. J., Berghe, E. V., & O'Dor, R. (2010). Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLoS ONE, 5*(8), e10223. doi: 10.1371/journal.pone.0010223.

Wiebe, P. H., Bucklin, A., Madin, L., Angel, M. V., Sutton, T., Pagés, F…Lindsay, D. (2010). Deep-sea sampling on CMarZ cruises in the Atlantic Ocean – an introduction. *Deep-Sea Research II: Topical Studies in Oceanography, 57*(24-26), 2157-2166. doi: 10.1016/j.dsr2.2010.09.018.

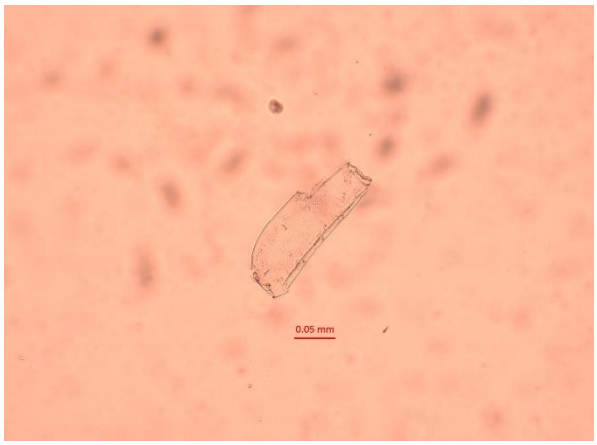
Wiebe, P. H., Morton, A. W., Bradley, A. M., Backus, R. H., Craddock, J. E., Barber, V...Flierl, G. R. (1985). New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Marine Biology, 87*(3), 313-323. doi: 10.1007/bf00397811.

Yamaguchi, A., Matsuno, K. & Homma, T. (2015). Spatial changes in the vertical distribution of calanoid copepods down to great depths in the North Pacific. *Zoological Studies, 54*(13), doi: 10.1186/s40555-014-0091-6.

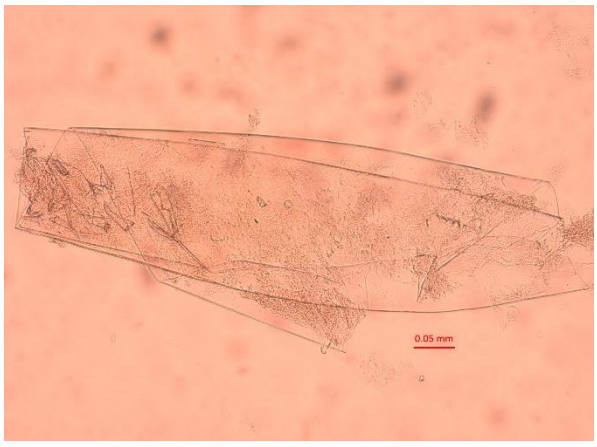
7. Appendices



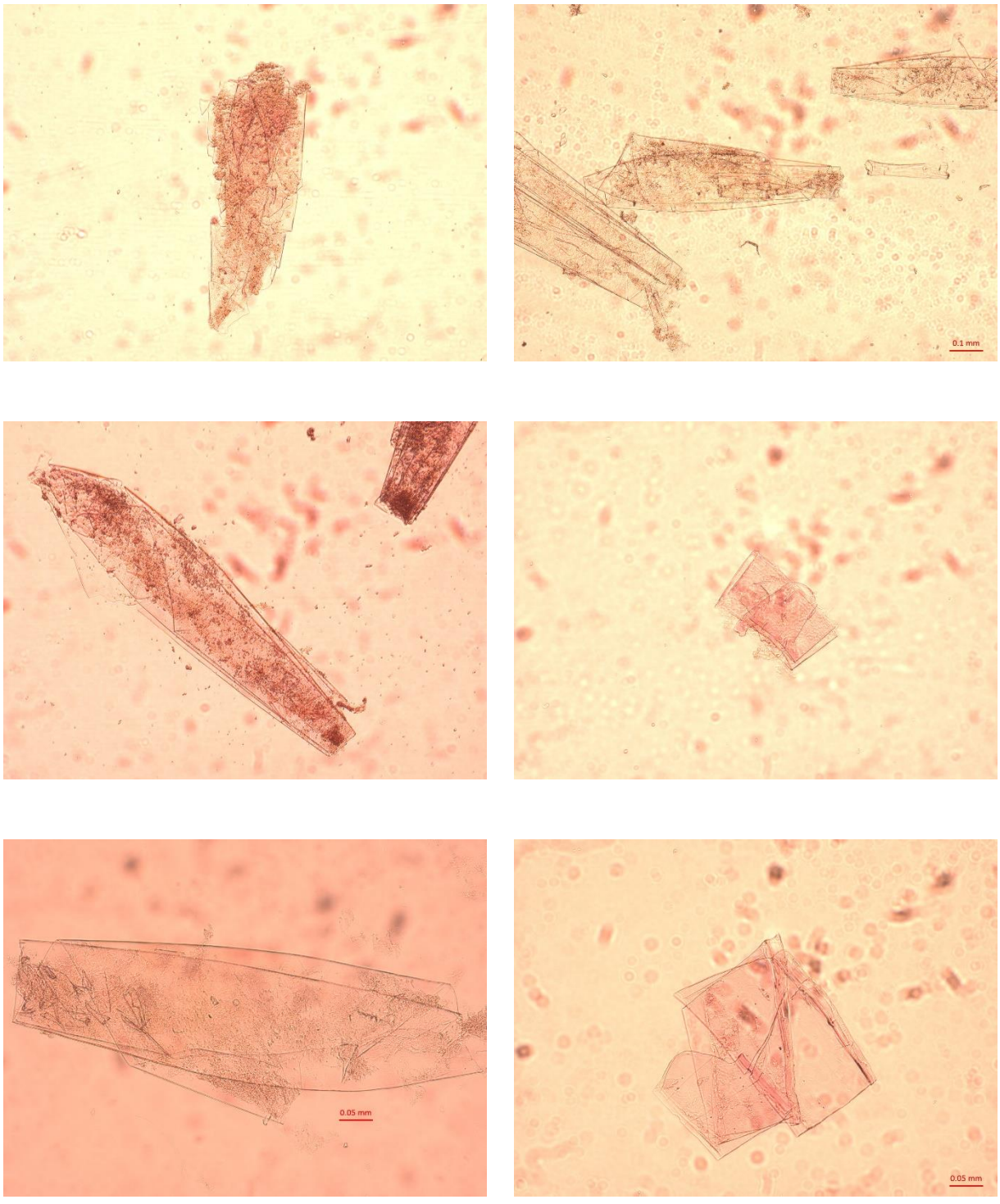
Appendix Figure 1. Image gallery of various crustacean exoskeletons found in the stomachs of four "*Ataxolepis*" specimens from the Gulf of Mexico.



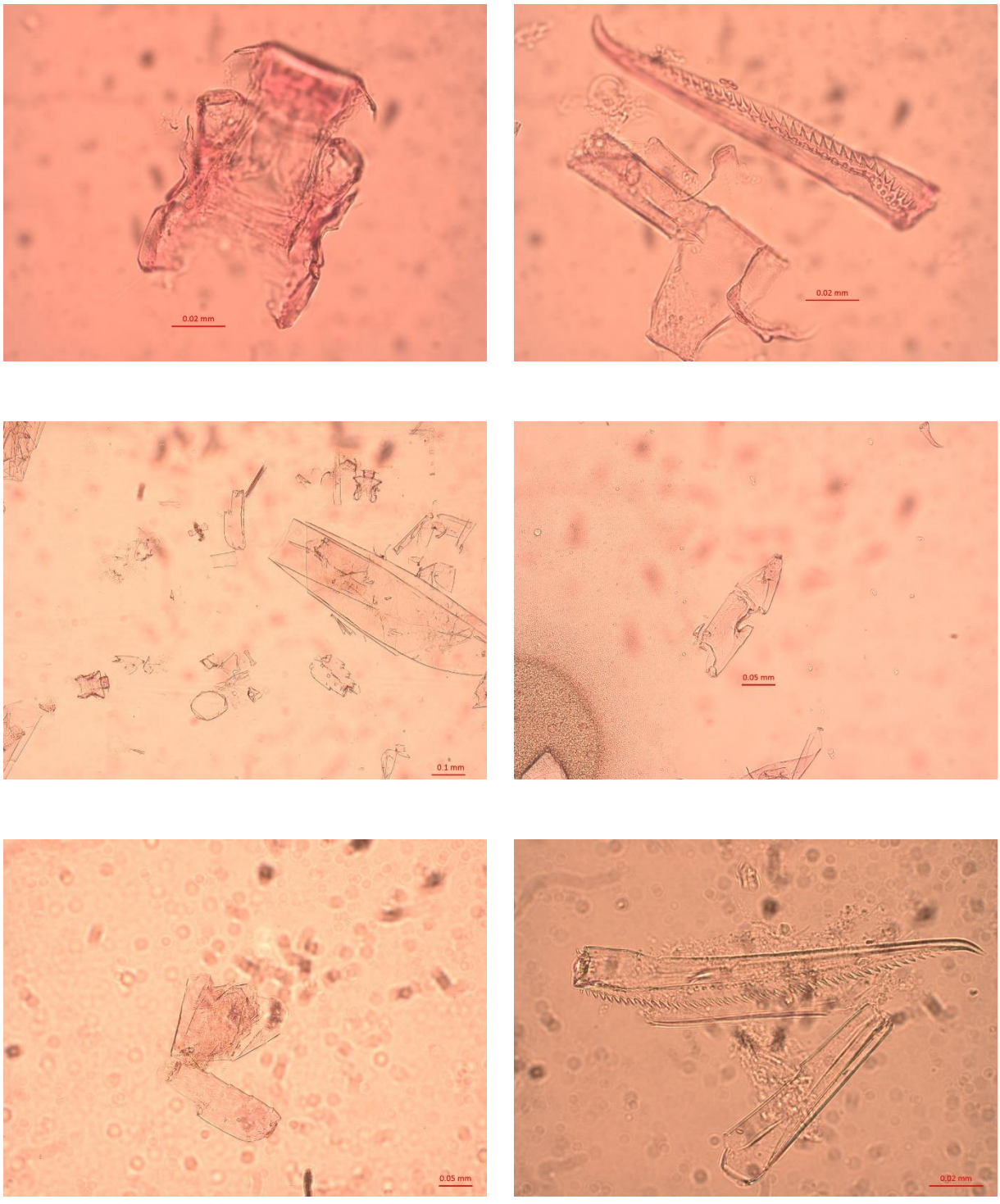
Appendix Figure2. Image of crustacean appendage found in the stomach of one "*Ataxolepis*" specimen from the Gulf of Mexico.



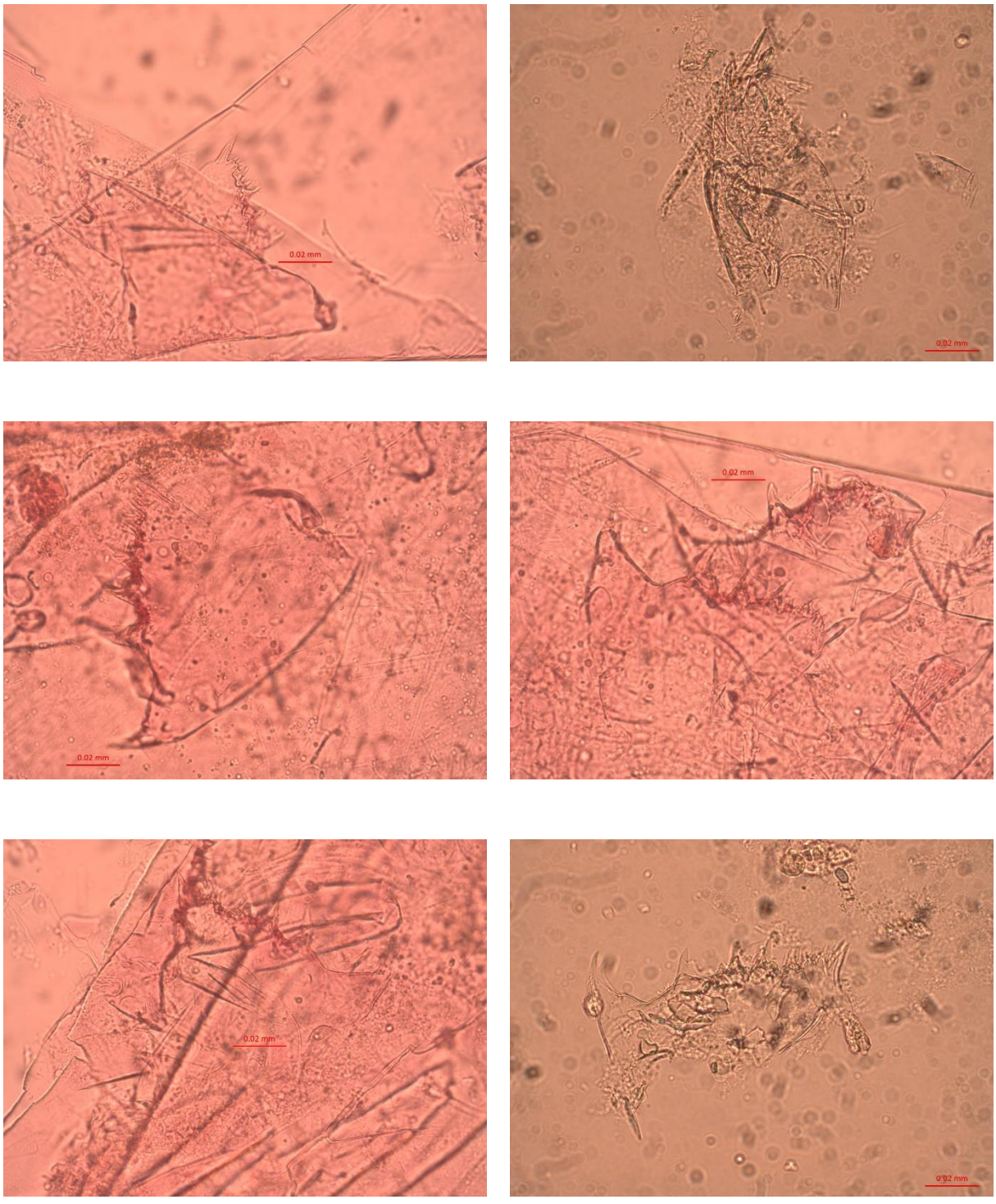
Appendix Figure 3. Image gallery of two crustacean mandibles found in the stomach of one "*Ataxolepis*" specimen from the Gulf of Mexico.



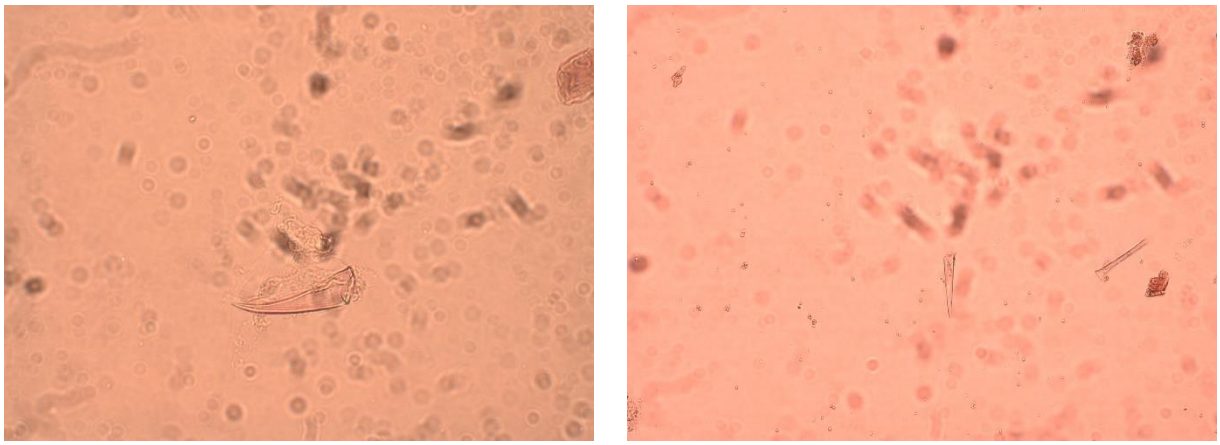
Appendix Figure 4. Image gallery of various crustacean exoskeletons found in the intestines of six "*Ataxolepis*" specimens from the Gulf of Mexico.



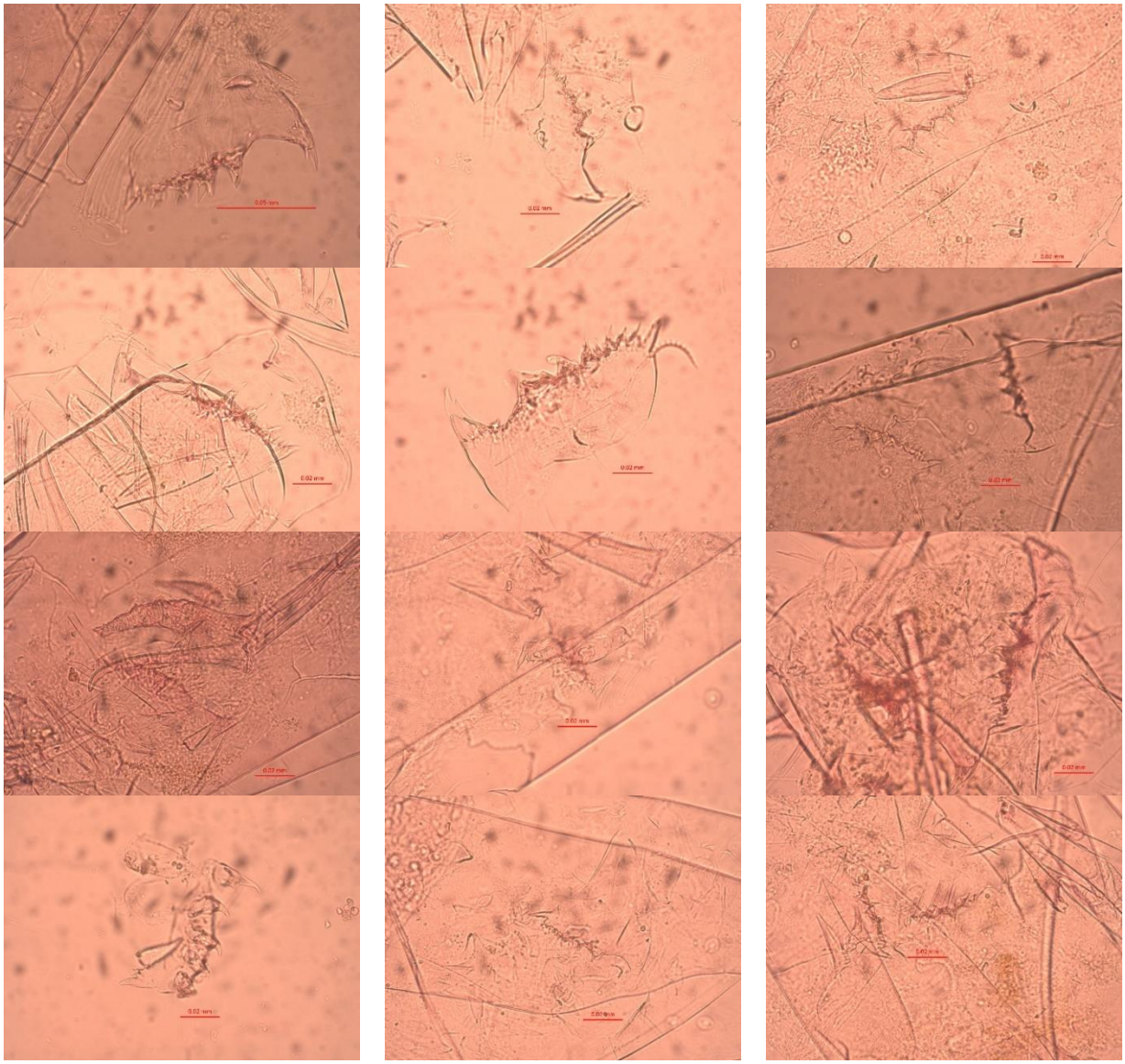
Appendix Figure 5. Image gallery of various crustacean appendages found in the intestines of four "*Ataxolepis*" specimens from the Gulf of Mexico.



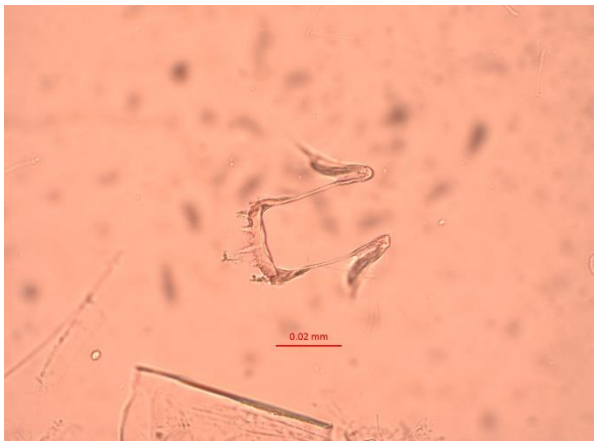
Appendix Figure 6. Image gallery of various crustacean mandibles found in the intestines of three "*Ataxolepis*" specimens from the Gulf of Mexico.

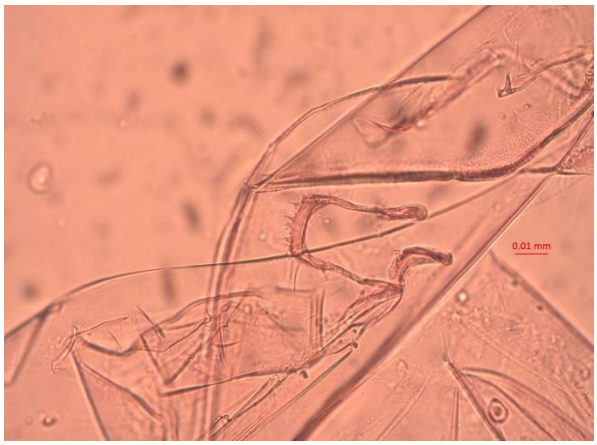


Appendix Figure 7. Image gallery of highly digested crustacean bits found in the intestines of two "*Ataxolepis*" specimens from the Gulf of Mexico. Left image shows a spine from a crustacean appendage. Right image shows a single ommatidia from a crustacean eye.

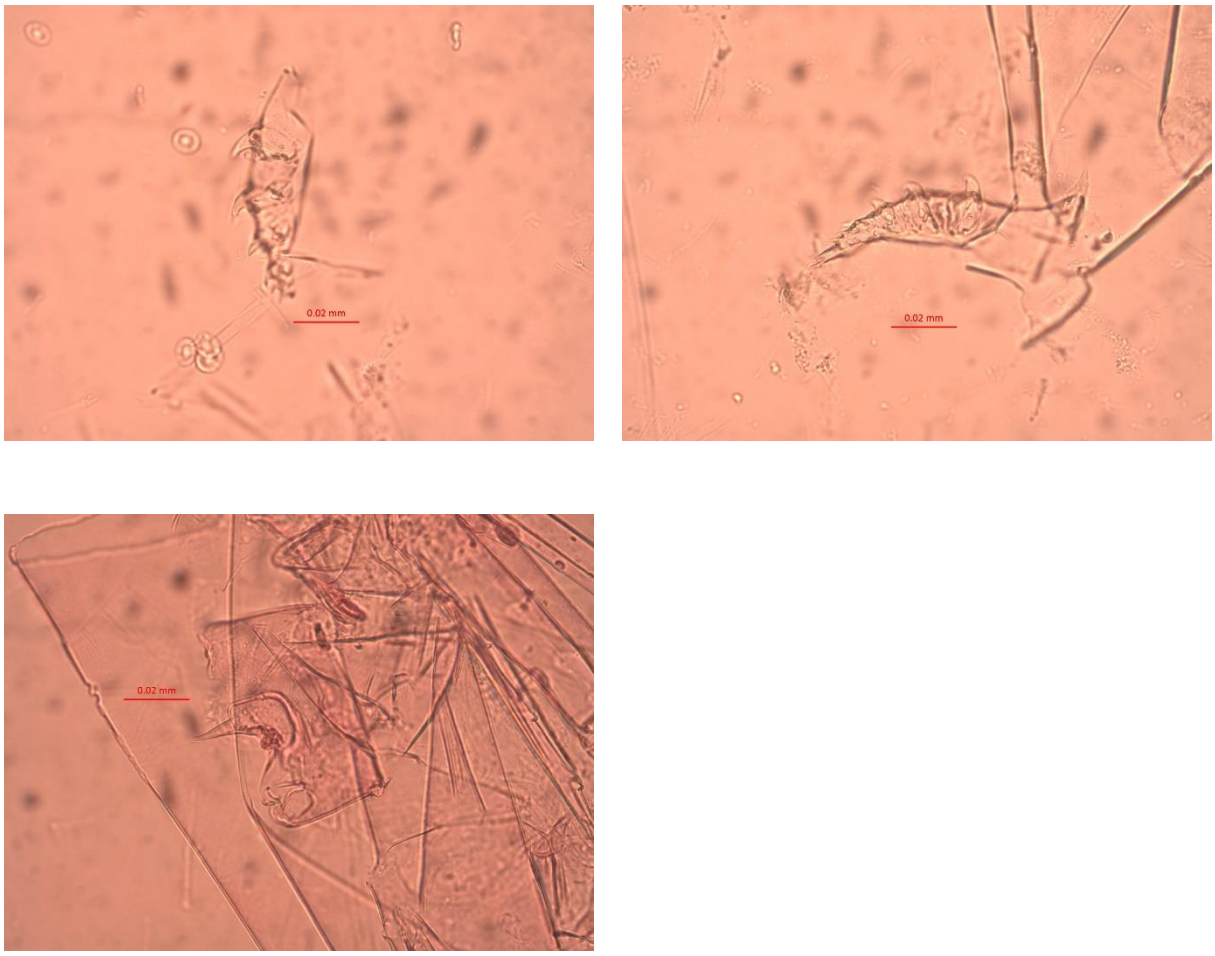


Appendix Figure 8. Image gallery of various crustacean mandibles (n=182) found in the intestine of one "*Ataxolepis*" specimen from the Gulf of Mexico.

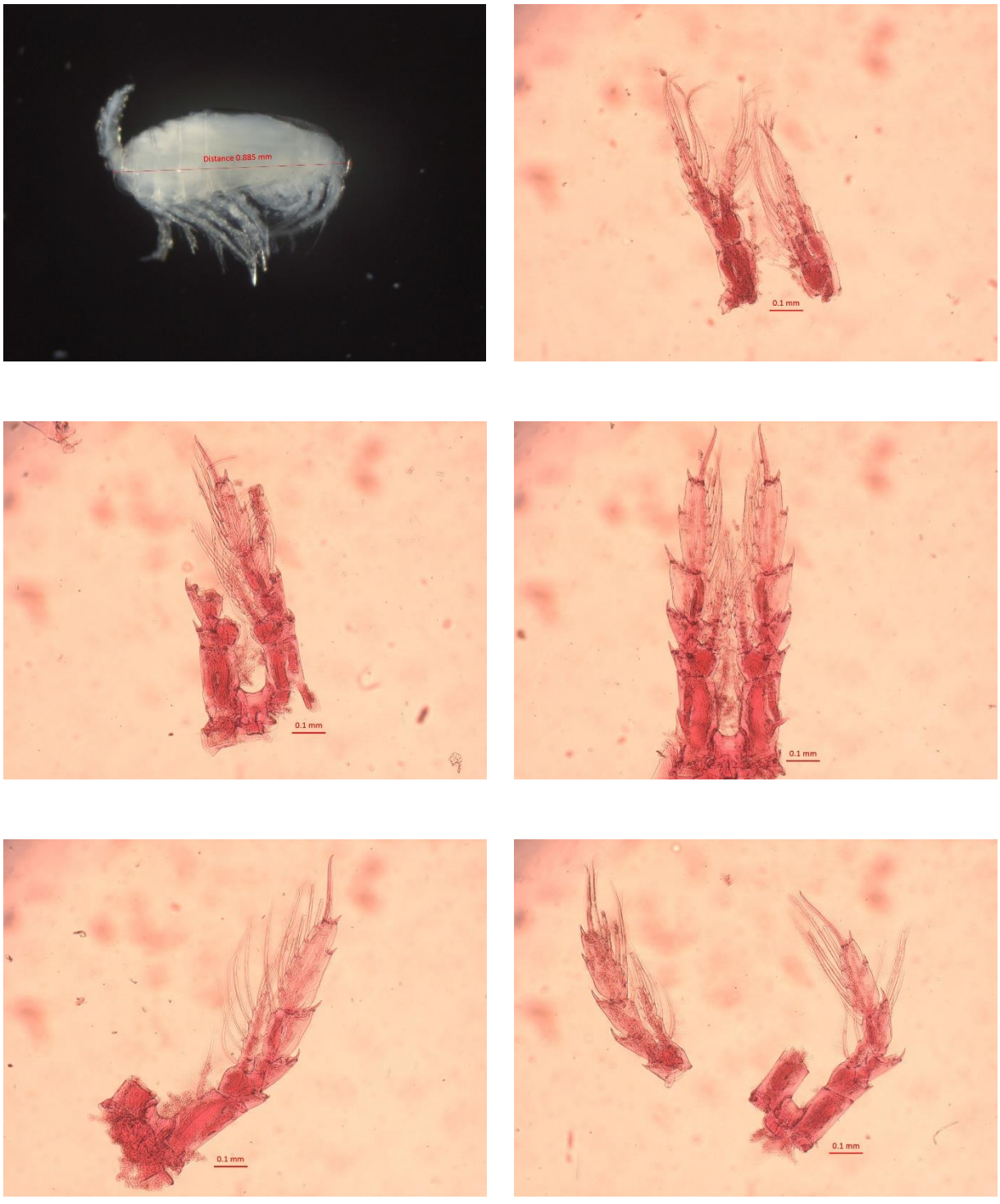




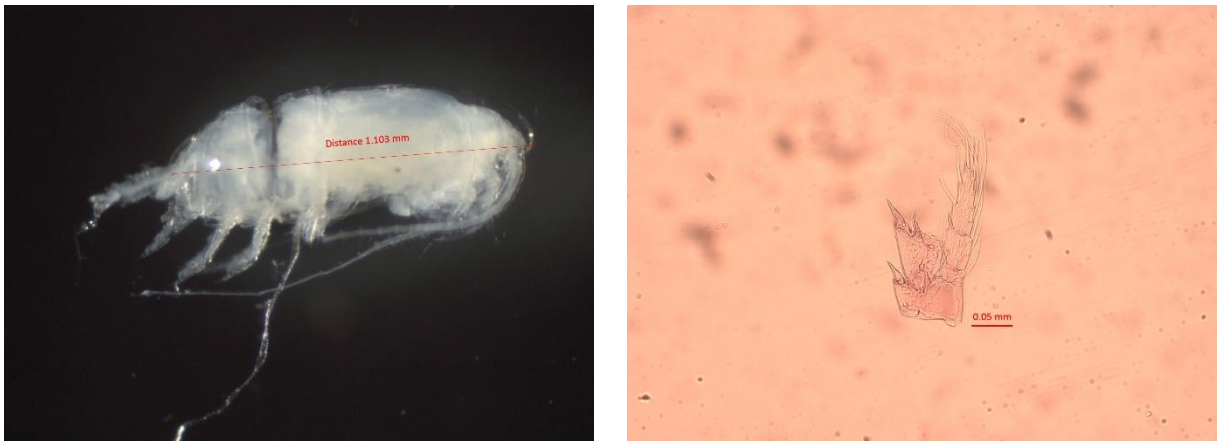
Appendix Figure 9. Image gallery of crustacean fragments found in the intestine of one "*Ataxolepis*" specimen from the Gulf of Mexico.



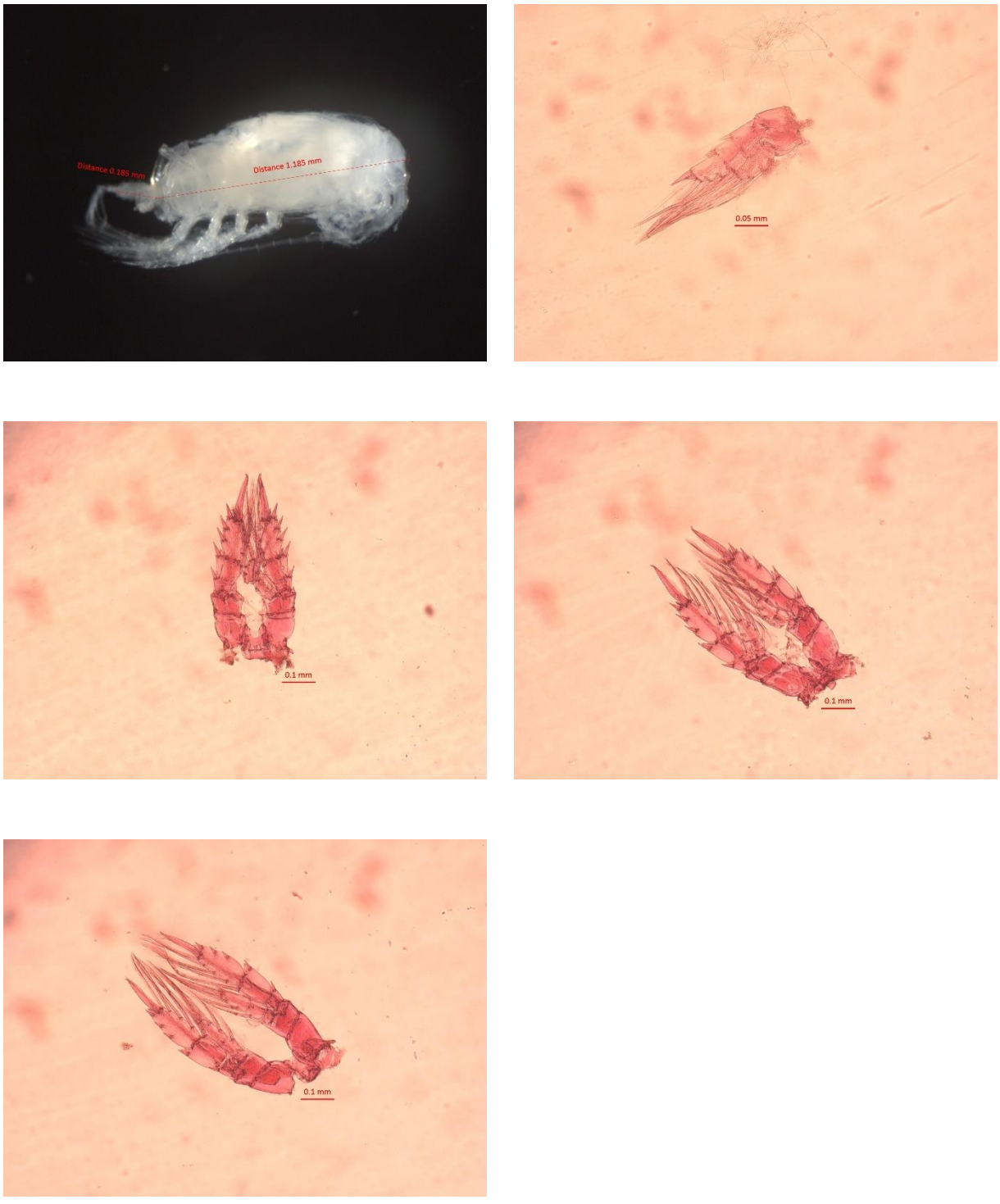
Appendix Figure 10. Image gallery of feeding appendages found in the intestine of one "*Ataxolepis*" specimen from the Gulf of Mexico.



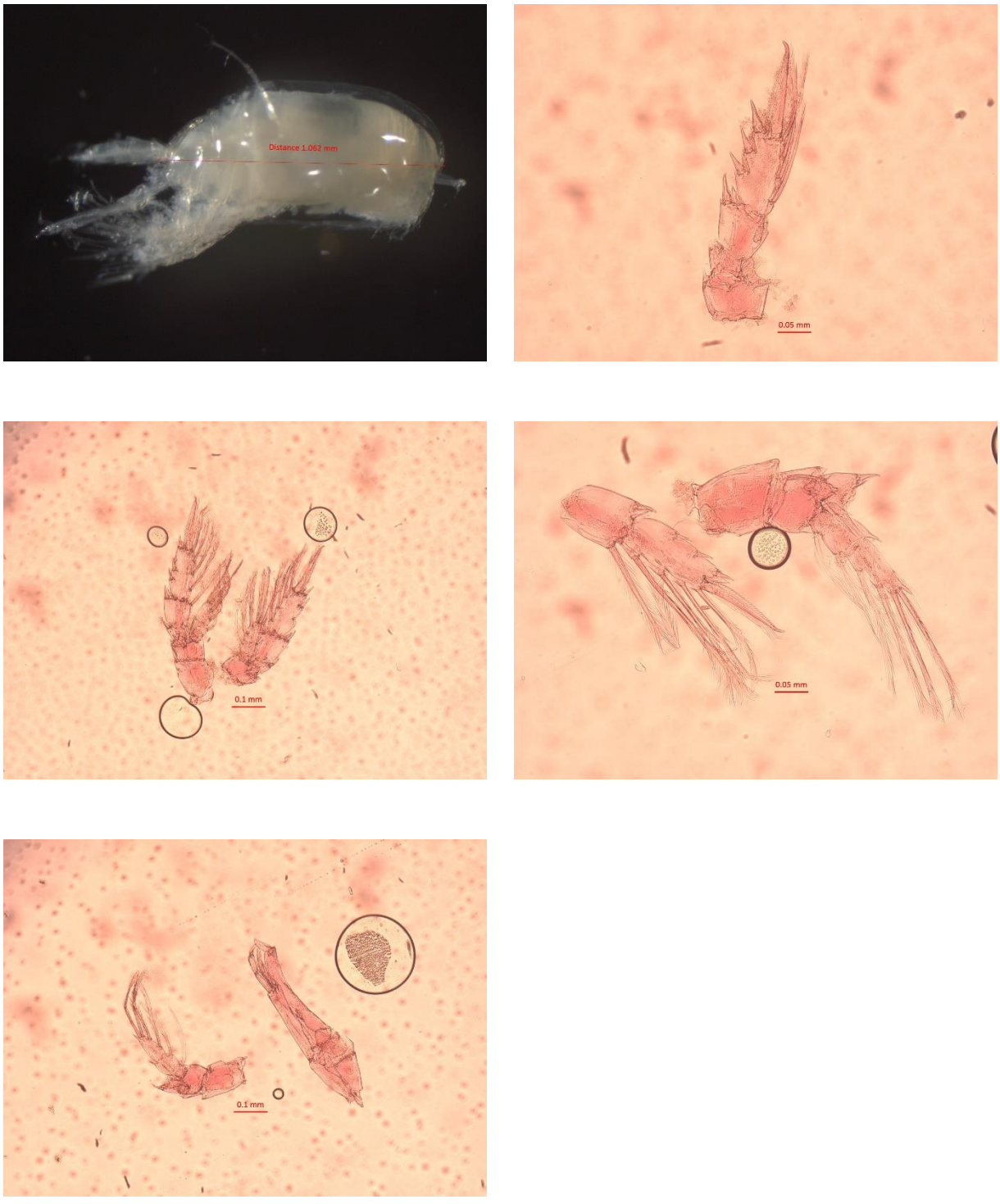
Appendix Figure 11. Image gallery of the copepod Calanoid A and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



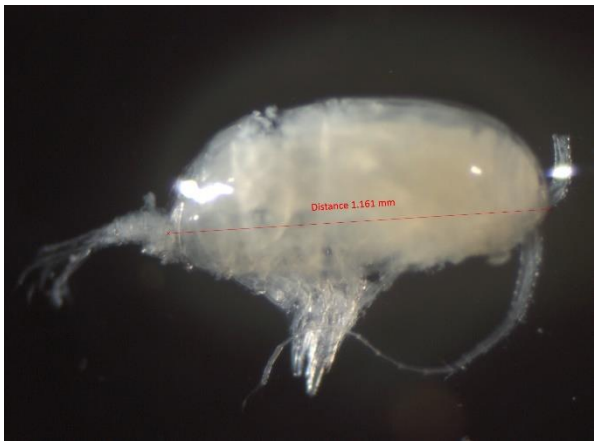
Appendix Figure 12. Image gallery of the copepod Calanoid B and pereiopod two (p5 absent) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.

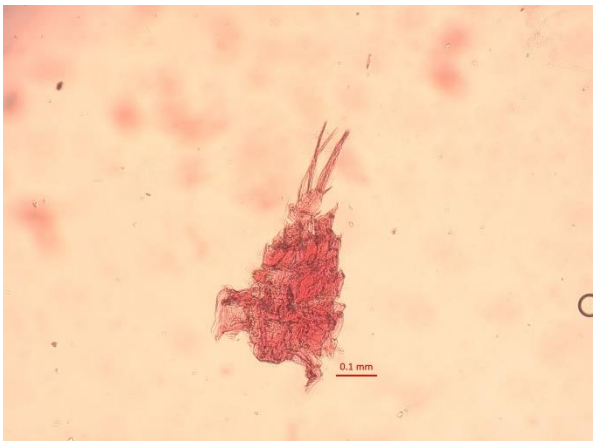


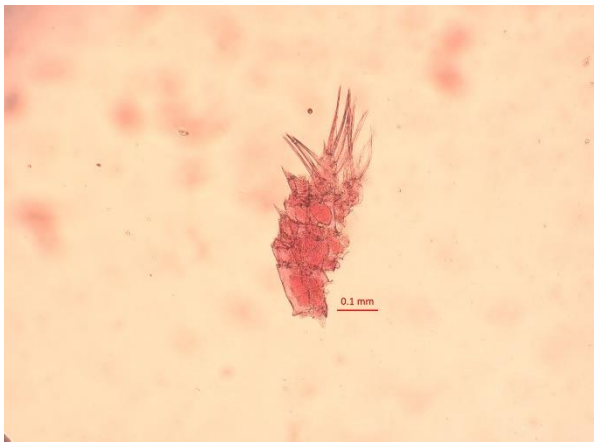
Appendix Figure 13. Image gallery of the copepod Calanoid C and the ordered pereiopods (p5 absent) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



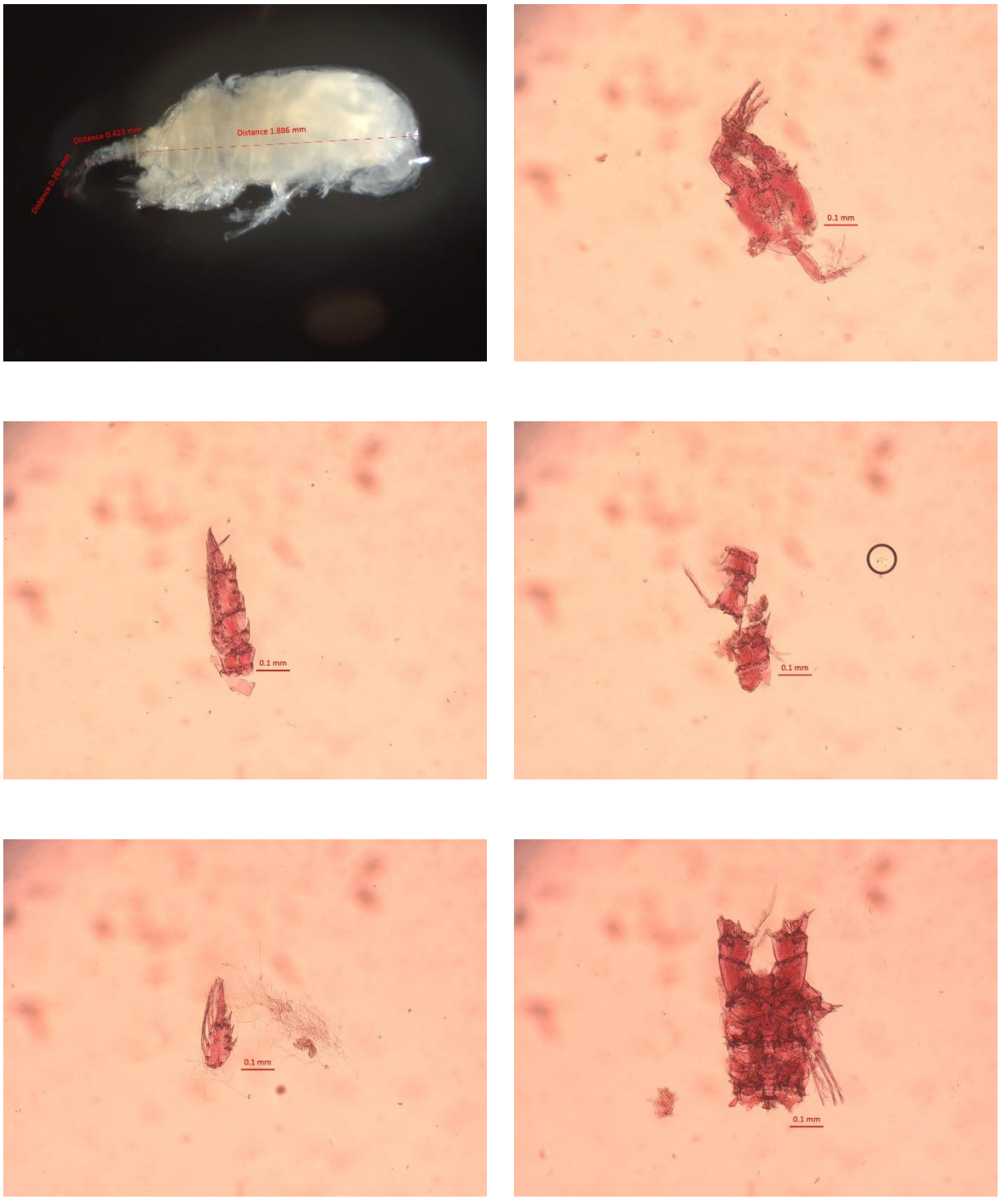
Appendix Figure 14. Image gallery of the copepod Calanoid D and the ordered pereiopods (excluding p2) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



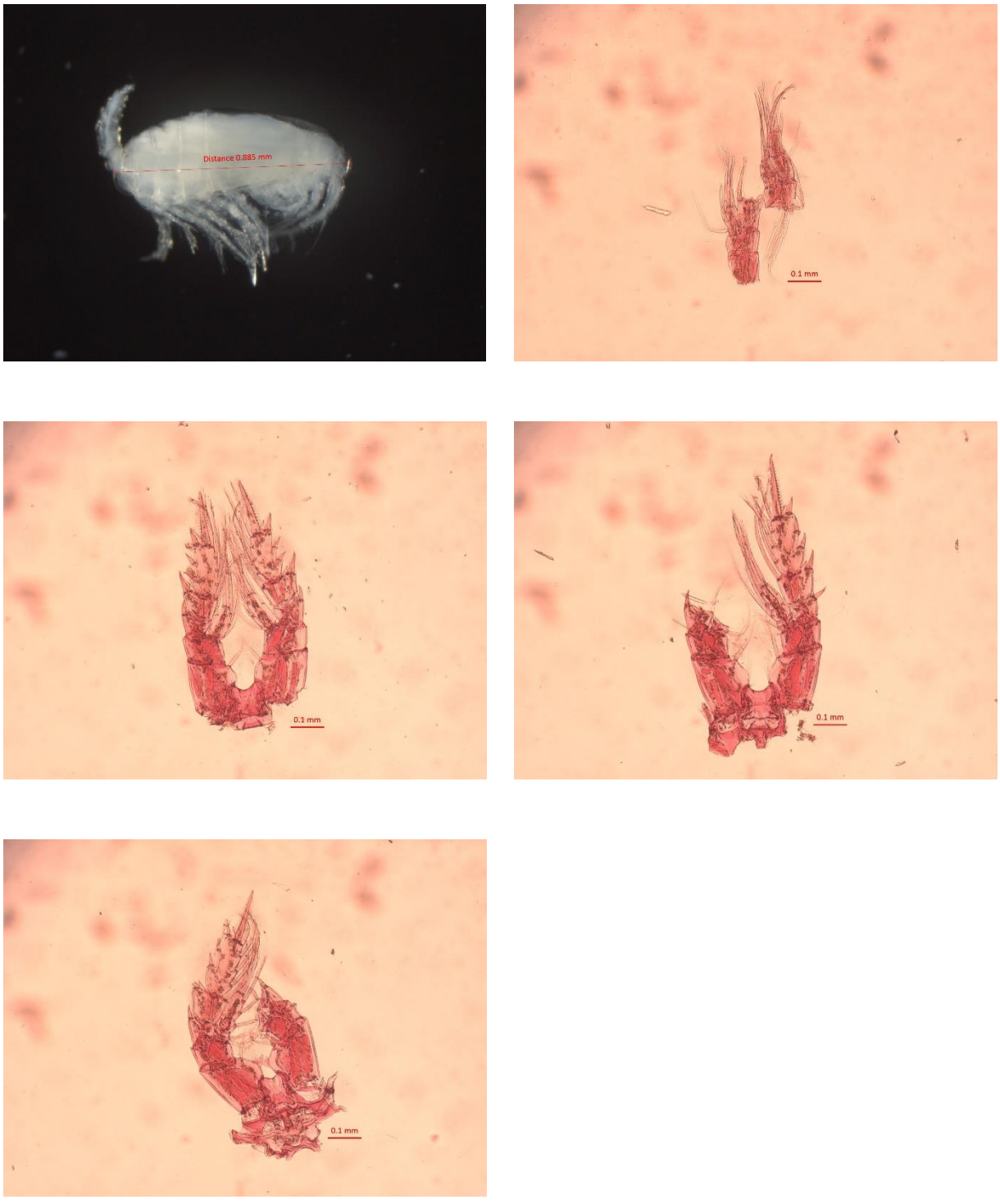




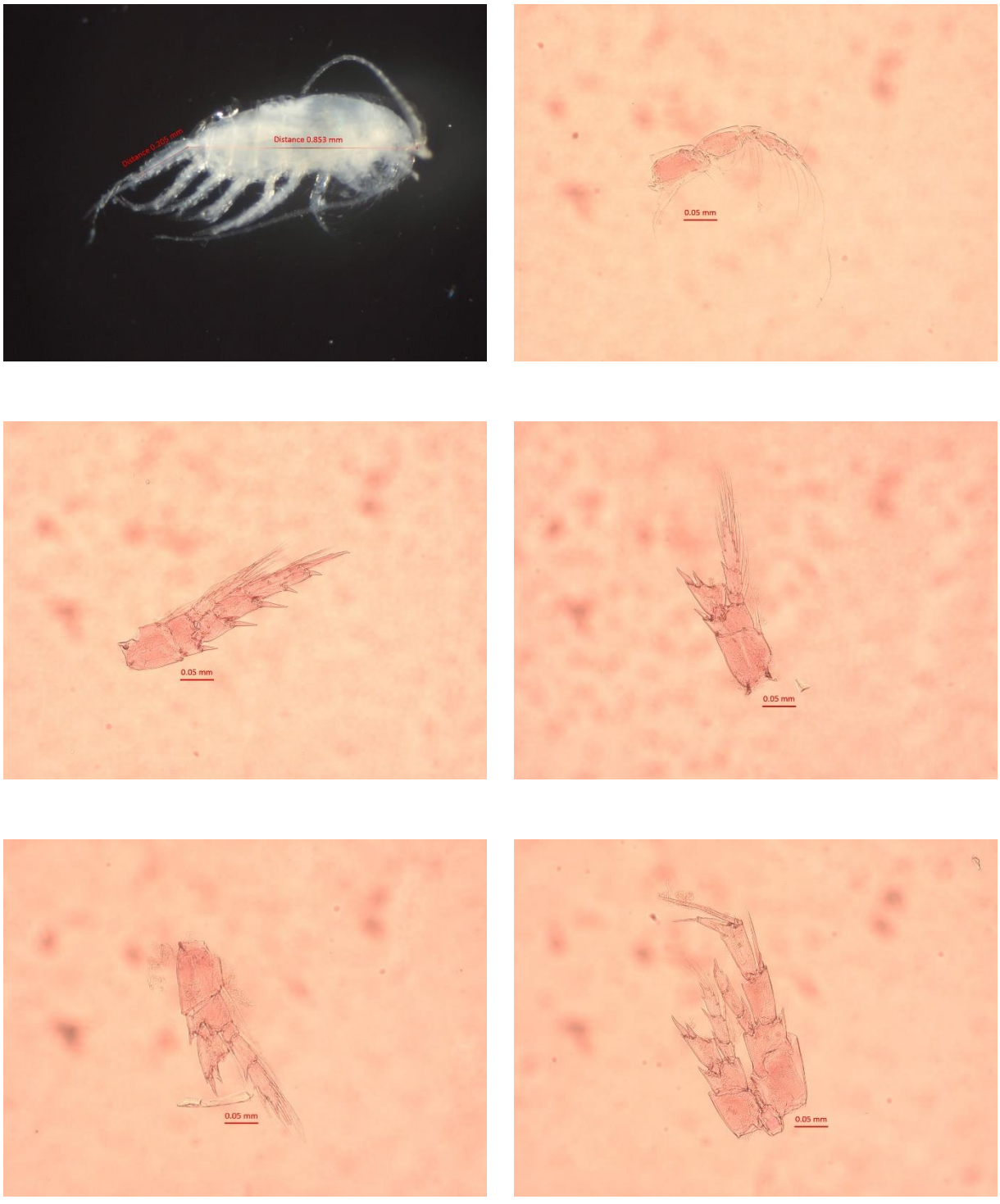
Appendix Figure 15. Image gallery of the copepod Calanoid E and the ordered pereiopods (p3 and p4 only) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



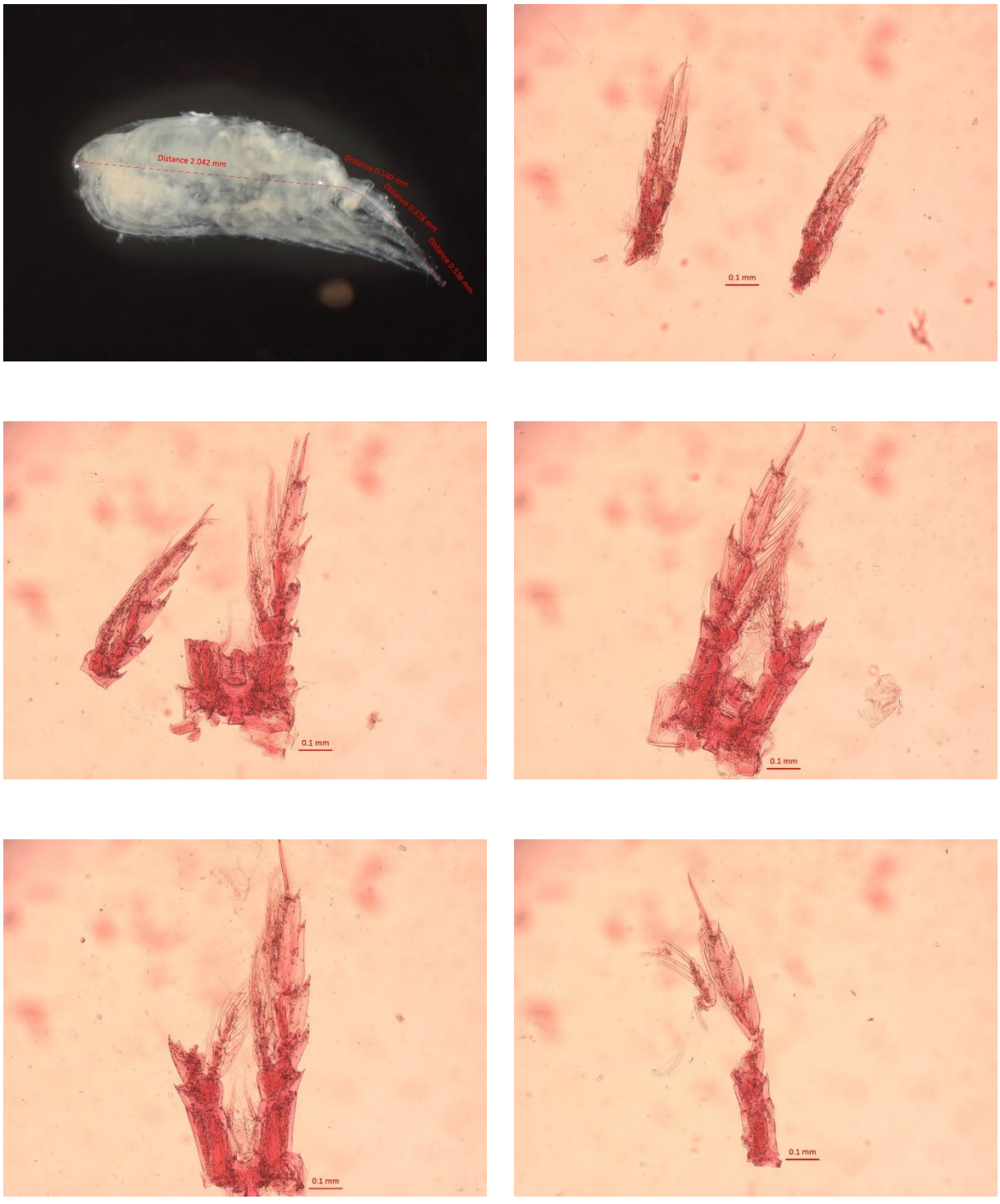
Appendix Figure 16. Image gallery of the copepod Calanoid F and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



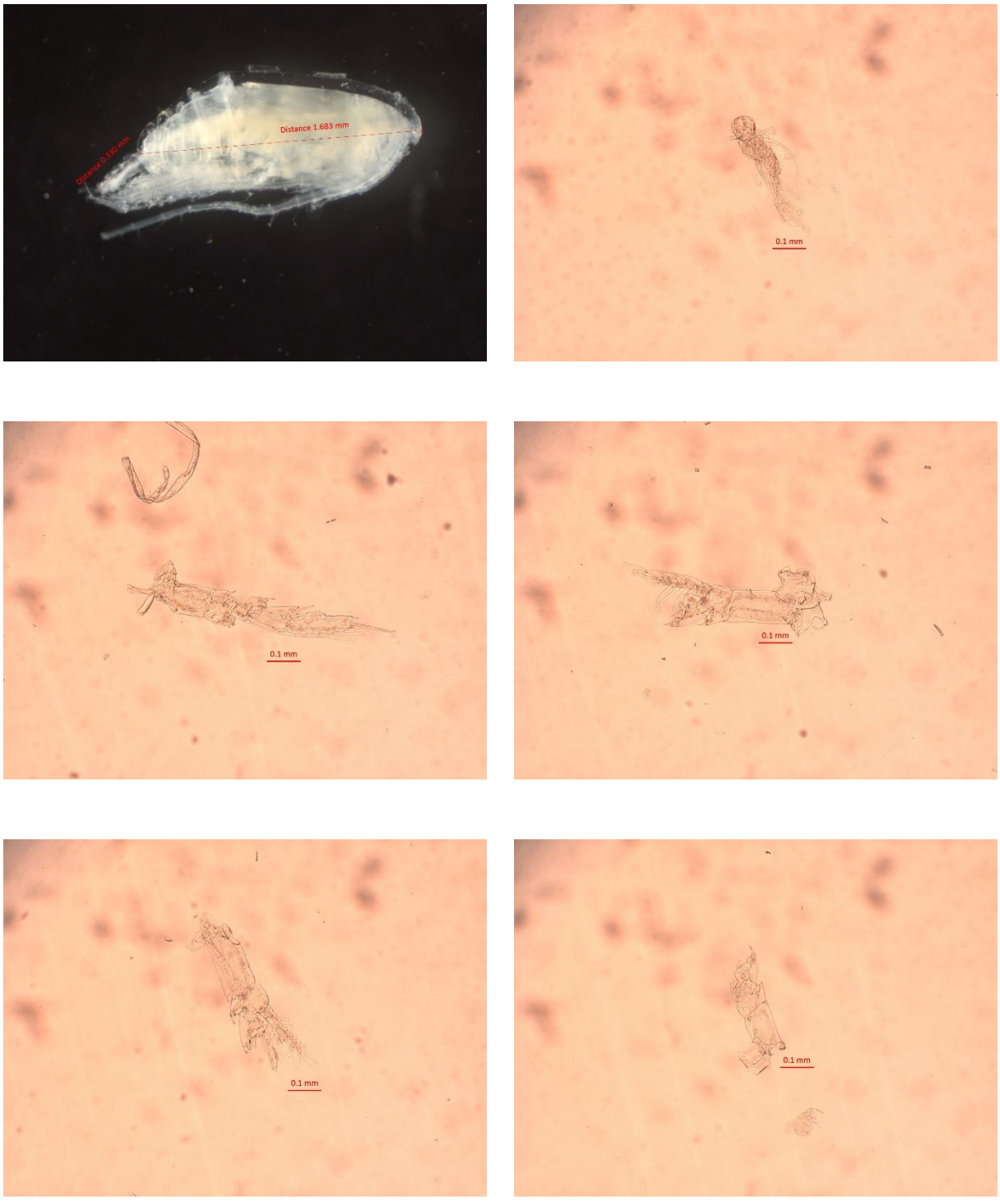
Appendix Figure 17. Image gallery of the copepod *Euchirella rostrata* and the ordered pereiopods (p5 absent) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



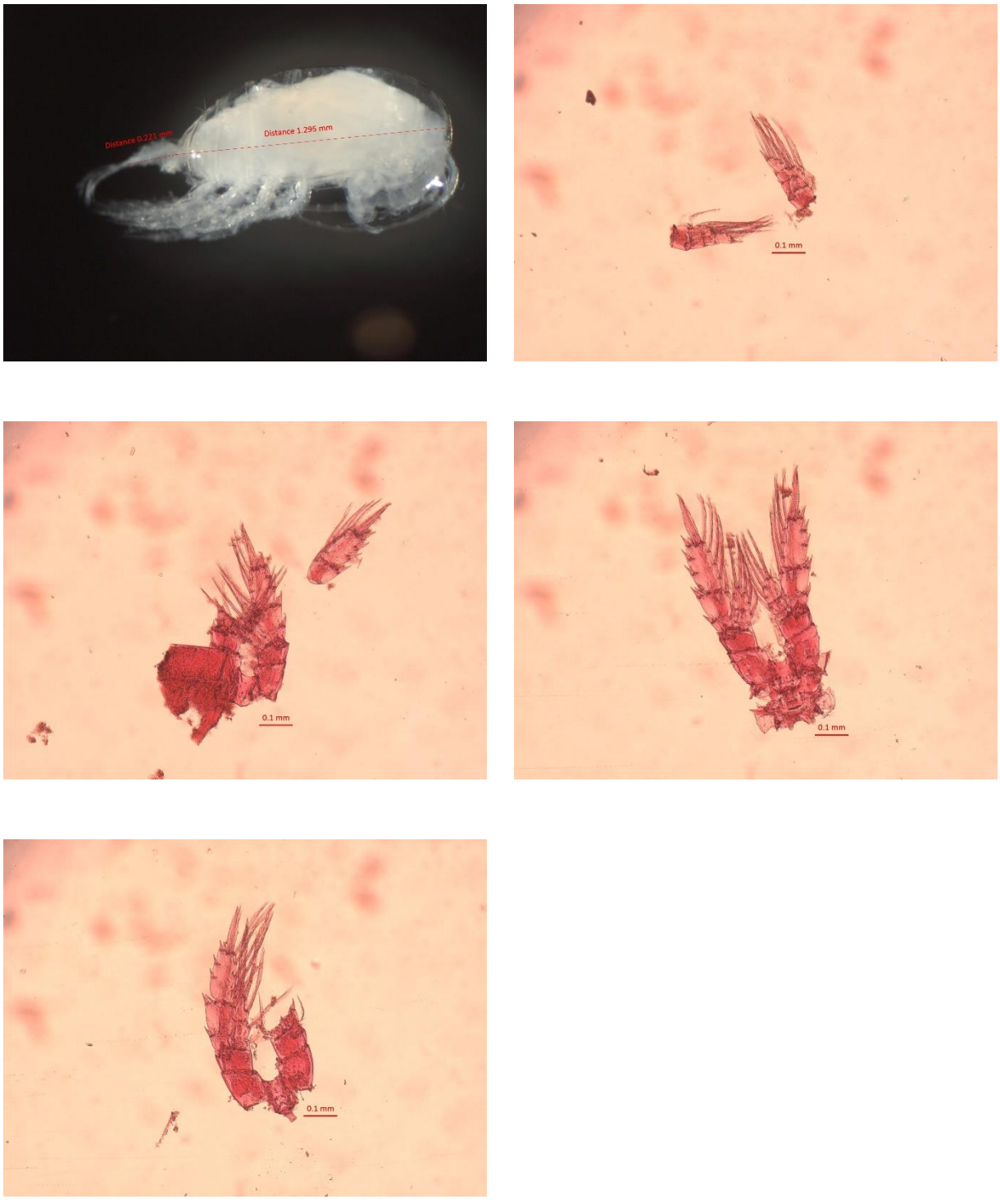
Appendix Figure 18. Image gallery of the copepod *Pleuromamma abdominalis* and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



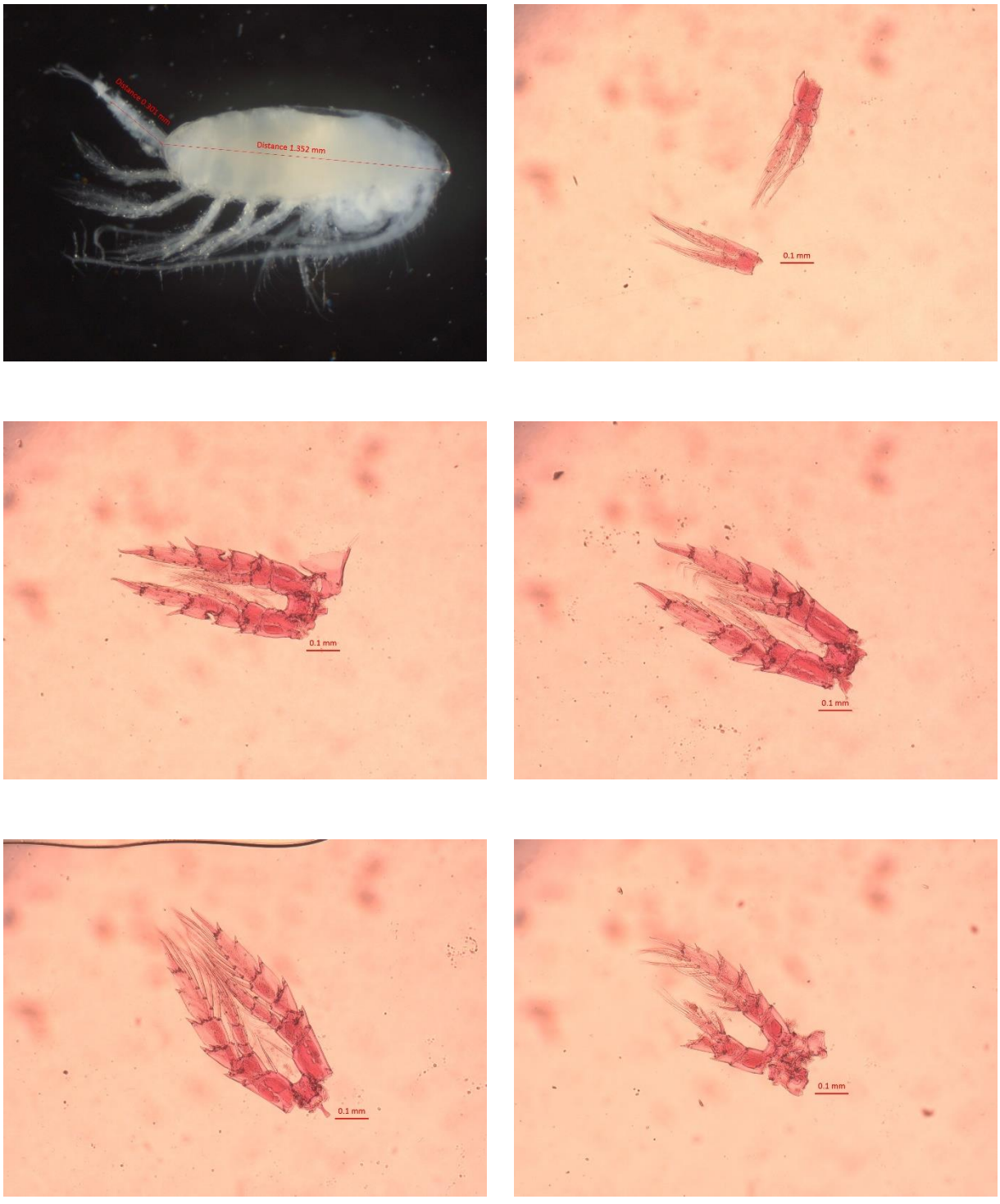
Appendix Figure 19. Image gallery of the copepod *Pleuromamma gracilis* and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



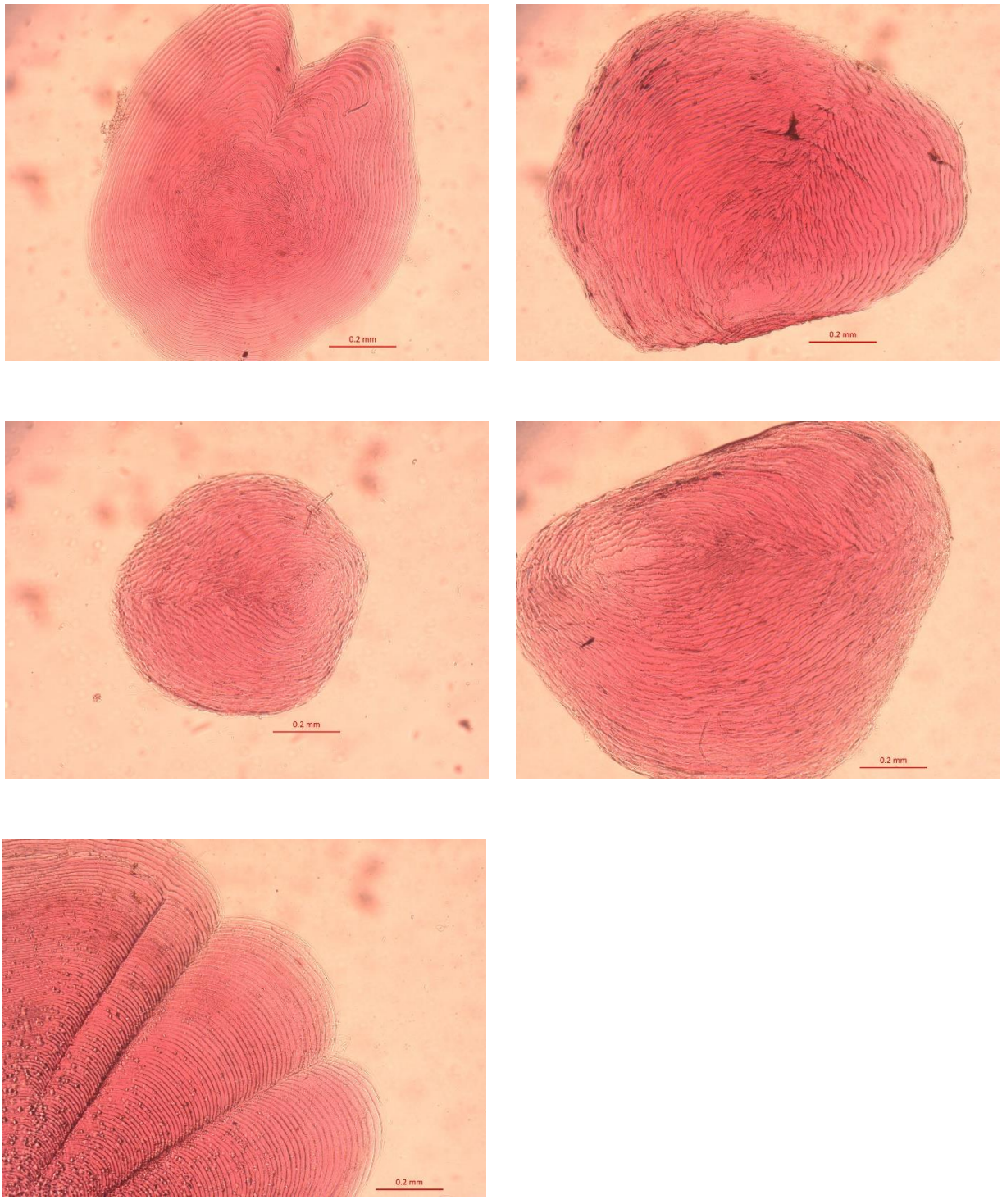
Appendix Figure 20. Image gallery of the copepod *Pleuromamma piseki* and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.



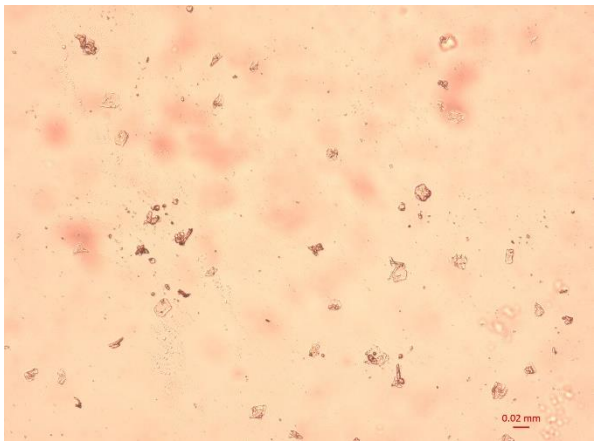
Appendix Figure 21. Image gallery of the copepod *Phaenna spinifera* and the ordered pereiopods (p5 absent) found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.

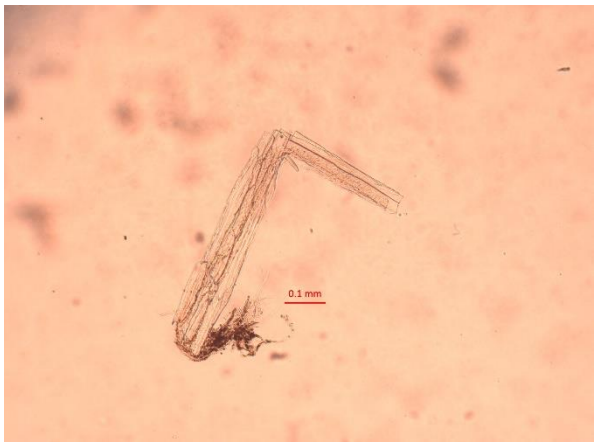


Appendix Figure 22. Image gallery of the copepod *Undinula vulgaris* and the ordered pereiopods found in the stomachs of "*Eutaeniophorus*" from the Gulf of Mexico.

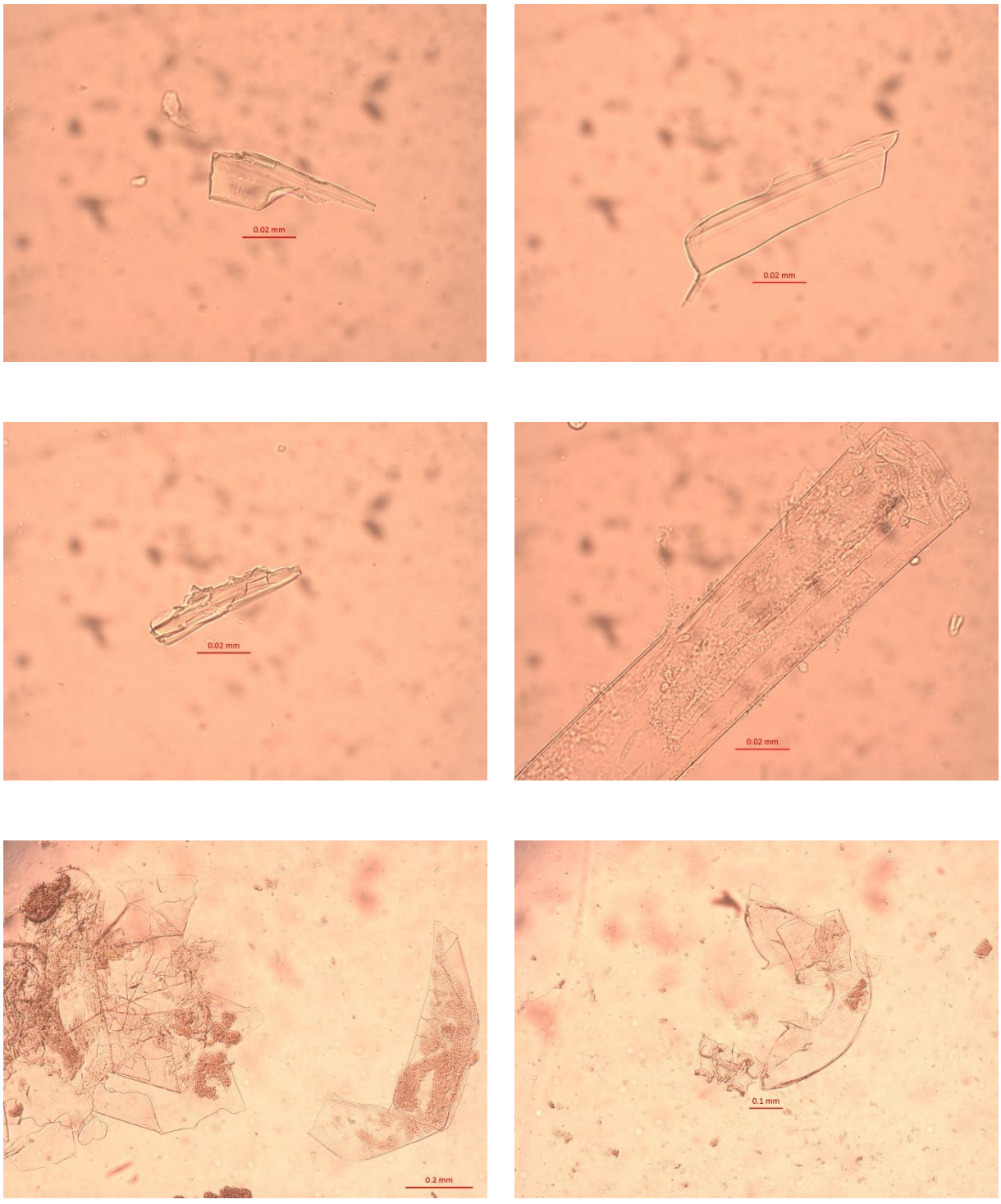


Appendix Figure 23. Image gallery of various fish scales (n=20) in the stomach of one "*Eutaeniophorus*" specimen from the Gulf of Mexico.

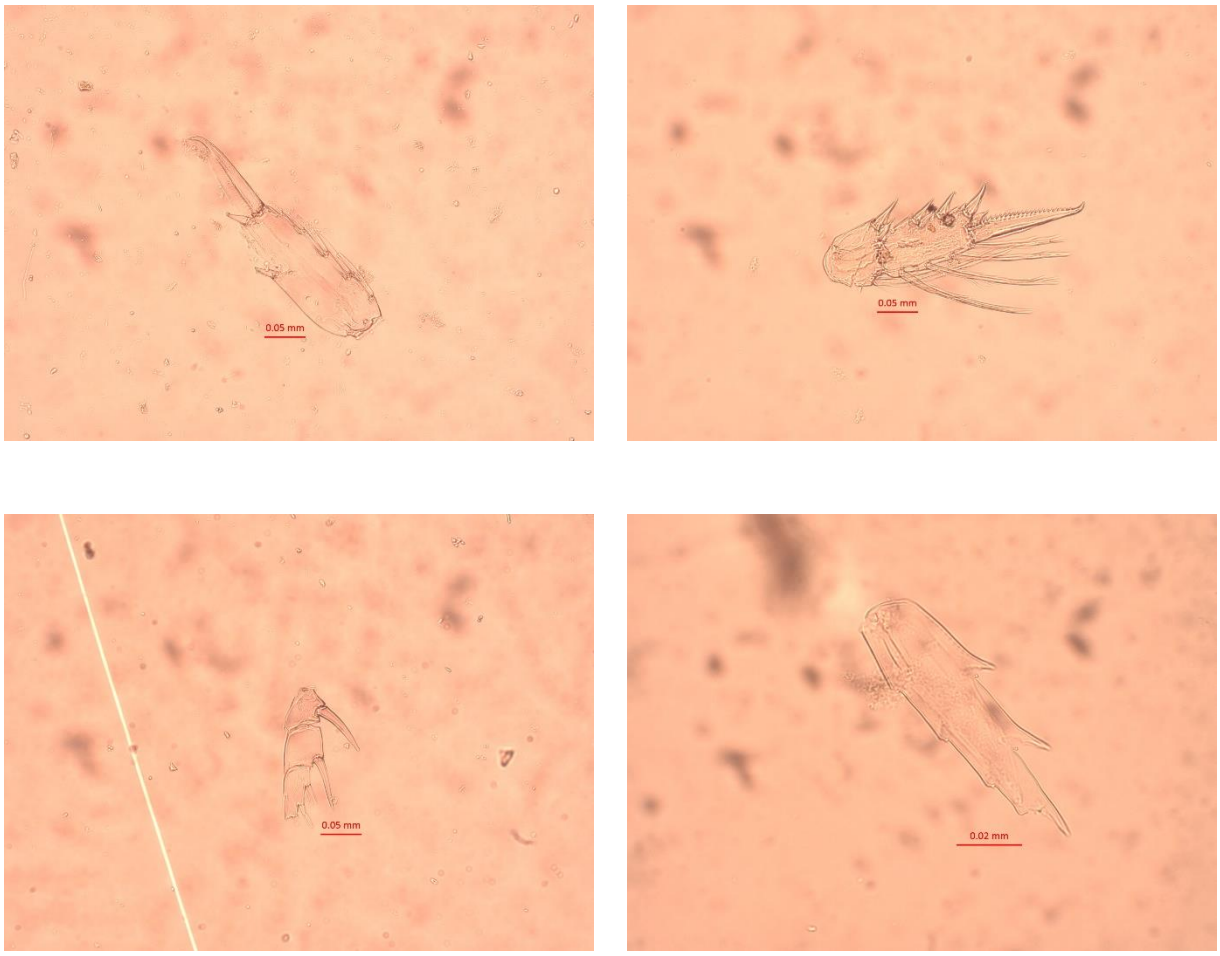




Appendix Figure 24. Image gallery of various crustacean exoskeletons found in the stomach of one "*Eutaeniophorus*" specimens from the Gulf of Mexico.



Appendix Figure 25. Image gallery of various crustacean appendages found in the intestines of four "*Eutaeniophorus*" specimens from the Gulf of Mexico.



Appendix Figure 26. Image gallery of various crustacean appendages found in the intestines of two "*Eutaeniophorus*" specimens from the Gulf of Mexico.