

4-22-2022

## Assemblage Composition and Vertical Distributions of Deep-Sea Anglerfishes (Suborder: Ceratioidei) of the Northern Gulf of Mexico

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# Thesis of Kimberly S. Schmutz

Submitted in Partial Fulfillment of the Requirements for the Degree of

## Master of Science Marine Science

Nova Southeastern University  
Halmos College of Arts and Sciences

April 2022

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HALMOS COLLEGE OF ARTS AND SCIENCES

Assemblage Composition and Vertical Distributions of Deep-Sea Anglerfishes (Suborder:  
Ceratioidei) of the Northern Gulf of Mexico

By Kimberly Schmutz

Thesis

Submitted to the Faculty of Halmos College of Arts and Sciences in Partial Fulfillment of the  
Requirements for the Degree of Master of Science with a Specialty in:

Marine Biology

Nova Southeastern University

Winter 2022

## **Acknowledgements**

I would like to first start off by thanking my major advisor, Dr. Tracey Sutton. I took his ichthyology class my second semester at NSU and became enamored with the ecology of fish, particularly those with unique adaptations. Thank you for accepting me into your lab, guiding me to become a better ecologist, as well as entrusting me with a project that I know was of extreme importance to you. I am forever grateful that you had the faith in me to see this project through.

To my friends and family, thank you for your endless support as I chased a dream of mine that I have had for as long as I can remember. Mom and Dad, thank you for giving me the opportunities that I know most people only dream of. I have been given the gift to see the world from a point of view that is as foreign as space to the rest of the world. Without your encouragement and support, I would not be the woman I am today. Kable, thank you for being there to remind me that even in the hardest times, it is important to find a reason to laugh, love, and adventure. I cannot imagine anyone else by my side through this journey we've taken.

Finally, to my NSU Academic Diving Program family, thank you for more than I can put into words. To my mentor, Bill Conrad, thank you for your guidance and always believing in me. In school, at work, and in life, you have made me realize all that I am capable of. To my fellow instructors, divemasters, and DMITS, thank you for creating the place I now consider home. I have an indescribable amount of love for all of you and the life you have helped me create.

## Abstract

The bathypelagic zone, despite being the largest cumulative ecosystem on the planet, represents the largest data gap in biological oceanography. In a deep environment with no solar light and pressures so high that survival is impossible for most marine organisms, some species have been able to adapt and overcome these challenges to radiate into diverse and successful taxa. Among the most notable of these successful taxa are the deep-sea anglerfishes (Lophiiformes: Ceratioidei). Ceratioid anglerfishes possess unique adaptations such as a symbiotic bioluminescent lure (females) and extreme dwarfism (males) that make them a particularly interesting group to study. Despite this research attractiveness, low sample sizes in ichthyological questions preclude detailed characterizations of fundamental assemblage properties, such as faunal composition, sex ratios, and vertical distributions in specific water bodies; i.e., most of what we know is compiled from sparse data across all oceans.

Ceratioids were collected in the Gulf of Mexico (GoM) as a part of an extensive pelagic survey following the *Deepwater Horizon* oil spill. Using high-speed rope trawls and a multiple opening and closing net system, ceratioids were collected day and night throughout the northern GoM. The faunal composition of females, males, and larvae were analyzed separately by life stage/sex and by family to gain insight into assemblage structure and vertical distribution.

A total of 1726 ceratioids were collected, representing all 11 families in the suborder. The assemblage was dominated numerically by females of the family Ceratiidae, in particular the species *Cryptopsaras couesii*. Males and larval numbers were dominated by the family Linophrynidae. The type of net used affected the size of specimens captured. Four patterns of vertical distributions were identified: 1) primarily epipelagic distribution with a rapid descent to great depth; 2) primarily mesopelagic residence; 3) a wide, “spanner” vertical distribution independent of solar cycle; and, 4) a primarily bathypelagic distribution. Larvae, particularly Linophrynidae larvae, best typified Pattern 1, the family Ceratiidae typified Pattern 2, the linophrynid species *Haplophryne mollis* typified Pattern 3, and males of many taxa typified Pattern 4. Vertical distribution patterns were not strictly related to taxon, sex, or life stage; for example, females within the same family (e.g., Linophrynidae) often displayed different patterns. This study demonstrates that ceratioid anglerfishes are not only among the most successful fish taxa of the bathypelagic zone, they also occupy one of the largest depth ranges among all taxa.

**Keywords:** Ceratioidei, anglerfishes, mesopelagic, bathypelagic, ecology, assemblage, Gulf of Mexico, vertical distribution, faunal composition.

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# 1. Introduction

## 1.1. The Bathypelagic Zone

The pelagic oceanic habitat is commonly separated into three depth zones: the epipelagic, mesopelagic, and bathypelagic (Figure 1). These zones are defined by the amount of solar light present during daytime (Herring, 2002; Priede, 2017). The epipelagic zone, in clearest ocean water, spans the surface to 200 m depth, with light levels allowing for photosynthesis (Randall and Farrell, 1997; Priede, 2017). The mesopelagic zone extends from 200 m to 1000 m, with primary production from solar illumination no longer possible, but still enough downwelling light for organisms to differentiate day and night (reviewed in Herring, 2002). The boundary between it and the bathypelagic zone below is generally considered the point at which solar illumination reaches 0% of surface levels during daytime (Priede, 2017).

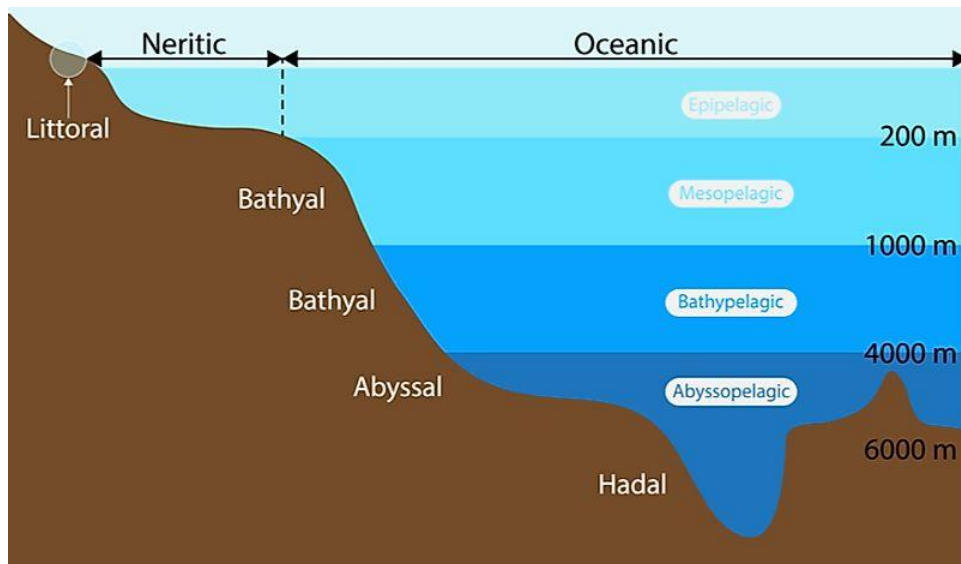


Figure 1. The depth zones of the pelagic ocean (www.worldatlas.com).

This deepest zone, the bathypelagic zone, is completely dark aside from the occasional flash of bioluminescence (Warrant, 2000; Pietsch, 2009; Priede, 2017). As is true for the mesopelagic zone, no photosynthesis can occur and chemosynthesis (which is another unique

mode of production) is a benthic phenomenon that does not contribute greatly to the bathypelagic zone (Herring, 2002; German et al., 2011). Without photosynthesis or chemosynthesis to form trophic guilds, food availability becomes a very large problem. Resource partitioning, either through vertical, diel, or ontogenic dimensions, has been the answer for some taxa to increase their encounters with potential prey items (Burghart et al., 2010; Besnard et al., 2021).

Accompanying the difficulty of attaining resources, the environment itself is constraining due to its cold temperatures, high pressures, and the general scarcity of individuals. With an average temperature of 4 °C and pressures as high as 100 times greater than that at sea level, highly specialized body systems and adaptations are required for organisms to live in this environment (Bertelsen and Nielsen, 1986; Herring, 2002). Likewise, the wide distribution of individuals makes mate location much more difficult.

The earliest hypotheses of deep-sea assemblages predicted that the deepest parts of the ocean were the least diverse and populated (Forbes, 1843; Wolff, 1977; Zezina, 1997) and thus less deserving of study. Technological developments, as well as increased research of the lower mesopelagic zones and bathypelagic zones over the last 60 years, have disproven these hypotheses - the deep-pelagic ocean holds ample life despite its extremely harsh conditions (Sutton, 2013; Danovaro et al., 2014). A lack of photosynthesizing organisms in the bathypelagic zone raises questions regarding energy acquisition to sustain the organisms within (Zezina, 1997; Herring, 2002). With such conditions affecting energy attenuation and food availability, the development of diversity in the bathypelagic zone is remarkable (Hessler and Sanders, 1967).

## **1.2. Fishes of the Bathypelagic Zone**

To survive in the inhospitable conditions of the bathypelagic realm, deep-sea fishes have developed unique adaptations. These adaptations can be a reduction or expansion of certain functions or behaviors (Priede, 2017). The lack of downwelling light results in adaptations at both ends of the spectrum: some teleosts have highly developed eyes while others have hardly any visual capacity at all. For those taxa that have evolved enhanced ocular specializations, the specializations include enlarged eyes with a large pupil area (Wagner et al., 1998) and densely packed rods to enhance light collection (Wagner et al. 1998, rev in Warrant, 2000). As a rule, bathypelagic fishes tend to have smaller eyes in relation to their body size than epi- and mesopelagic fishes (reviewed in Warrant and Locket, 2004).

The “visual-interaction” hypothesis presented by Childress et al. (1990) suggested that predator-prey interactions are decreased in the bathypelagic zone due to light limitation, and thus the selective pressure to maintain a high metabolism to support musculature required for evasion or predation is also decreased, a hypothesis supported by Drazen and Seibel (2007) and Priede (2017). The characteristic low metabolic rate of deep-sea teleosts is one of the most important evolutionary adaptations that has allowed them to succeed. Lowered metabolism reduces the resources required by organisms to sustain life, thereby minimizing the need for advanced locomotory functions to aid in the search for resources, and thus the need for metabolically demanding tissues such as muscles (Childress et al., 1990; Drazen and Seibel, 2007). Bathypelagic fishes tend to have a high water content, with soft, watery tissues rather than dense, hemoglobin-rich muscles (Graham et al., 1985; Randall and Farrell, 1997; Geringer, 2017; Priede, 2017). These gelatinous tissues can comprise nearly 33% of the mass of deep-sea species and in some species, it has been suggested that these tissues have the potential to serve as an energy reserve

(Eastman and DeVries, 1989; Priede, 2017). In deep-sea fishes lacking a swim bladder, this water content can be as high as 85-95% (Priede, 2017).

The most remarkable adaptation of deep-sea fishes is the ability to bioluminesce, though not all species living in the lower meso- and bathypelagic zones have that capability, and it manifests in many different forms (Suntsov et al., 2008; Waldenmaier et al., 2012; Priede, 2017). A striking example of bioluminescence in the deep sea exists in the lure of most adult female ceratioid anglerfishes (Pietsch, 2009; Freed et al., 2019). A specialized organ (the esca) at the end of a modified dorsal ray (illicium) is home to symbiotic bacteria that when present in a certain population size, emit a bioluminescent glow that is vital in prey attraction (Munk, 1999; Pietsch, 2009; Freed et al., 2019).

### **1.3. Order: Lophiiformes; Suborder: Ceratioidei**

The order Lophiiformes, suborder Ceratioidei, is believed to be the most species-rich taxon of fishes in the bathypelagic realm (Pietsch, 2009). Bertelsen (1951) provided an initial characterization of the seasonal, vertical, and geographical distributions of this suborder. Studies have shown that anglerfishes inhabit essentially all oceanic regions except for the Mediterranean Sea, whose bathypelagic fauna is severely restricted due to poor oxygenation (Bertelsen, 1951; Caruso, 1983; Barcala et al., 2019). Ceratioid systematics were summarized by Pietsch and Orr (2007) and recently updated in Eschemeyer's Catalog of Fishes from the California Academy of Sciences (Fricke et al., 2021). Of the 18 families in the order Lophiiformes, 11 are placed in the suborder Ceratioidei (Pietsch and Orr 2007). Within the 11 families comprising the Ceratioidei, there are 35 genera and 160 recognized species (Pietsch, 2009; Fricke et al., 2021). The Ceratioidei contains twice as many families and more than three times the number of species as

the next most species-rich fish taxon in the bathypelagic zone, the Stephanoberycoidei (whalefishes and allies) (Paxton, 1998; Herring, 2002).

The family Ceratiidae, the warty seadevils (Figure 2), are the largest known ceratioids, with females of one species, *Ceratias holboelli*, measuring up to 1.45 m in length (Pietsch, 2009; Coad, 2017). The defining feature of this family is the presence of two or three caruncles on the back near the origin of the soft-dorsal fin (Pietsch, 2009). The two genera containing four species are distinguished from one another by the shape of the luring apparatus, with either a long illicium (*Ceratias*) or one that is heavily reduced and nearly entirely contained within the esca tissue (*Cryptosaras*) (Pietsch, 2009; Rajeeshkumar et al., 2016; Fricke et al., 2021). The Ceratiidae is the best-known ceratioid family with over 1300 females documented (Pietsch, 2009).



Figure 2. Adult female (left) and larvae (right) of *Cryptosaras couesii*, of the family Ceratiidae. Photos not to scale.

The family Linophrynidae, the leftvent seadevils (Figure 3), are unique from all other ceratioid families in having three dorsal fin rays and three anal fin rays (Pietsch, 2009). Females have large mouths with prominent, dagger-like teeth as well as a sinistral anus (Pietsch, 2009). The family is also unique in that the genus *Linophyrne* possesses species-specific hyoid (chin)

barbels (Banon et al., 2006; Pietsch, 2009; Prokofiev, 2020). *Linophyrne* is the most speciose of the five genera in the family with 22 species, while five species are found in the other four genera (Pietsch, 2009; Fricke et al., 2021).



Figure 3. Varying sexes and life stages of the family Linophryinidae. Top left: adult female *Photocorynus spiniceps*; top right: adult male linophrynid; bottom center: larval linophrynid. Photos not to scale.

The family Melanocetidae, the black seadevils (Figure 4), visually represent their name well; females have black skin, globose bodies, and enormous mouths lined with sharp fangs (Bertelsen, 1951; Pietsch, 2009). Female melanocetids have a dorsal fin with more than three times the number of rays than that of the anal fin (Pietsch, 2009). The Melanocetidae is the second best-known ceratioid family with more than 1200 females documented (Pietsch, 2009). A single genus, *Melanocetus*, contains all six validated species within the family (Pietsch, 2009; Orlov et al., 2015).



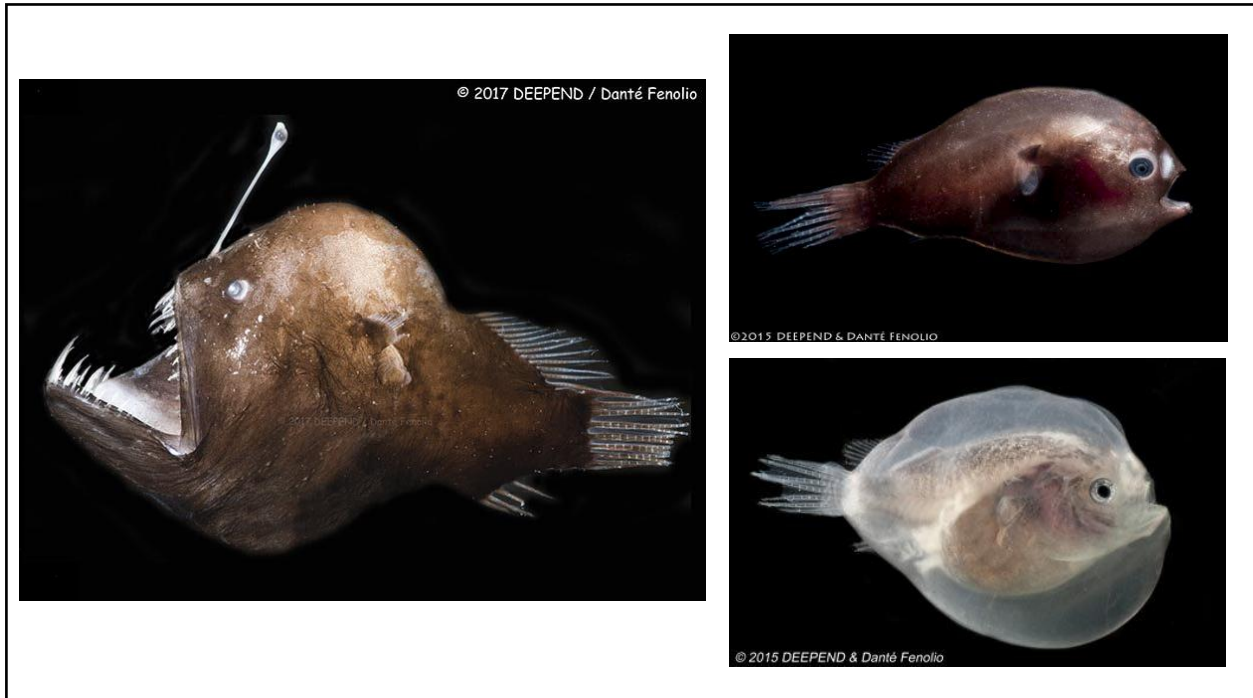


Figure 4. Varying sexes and life stages of the family Melanocetidae. Left: adult female *Melanocetus murrayi*; top right: male melanocetid; bottom right: larval melanocetid. Photos not to scale.

The Oneirodidae, or the dreamers (Figure 5), is the most diverse taxon of Ceratioidei (Pietsch, 2009; Coad, 2017), with 62 species across 16 genera. Adult body shapes are highly variable, from elongated and fusiform in *Leptacanthichthys* and *Dolopichthys* to globular in *Chaenophyrne* and *Oneirodes* (Pietsch, 2009; Fricke et al., 2021). Each oneirodid genus is morphologically unique; few share characteristics among them (Pietsch, 2009). The monophyly of this family is based on a rather obscure morphological character, a narrow, spatulate, anterodorsally directed process that overlaps the posterolateral surface of the respective sphenotic, though this is not readily apparent on gross inspection (Pietsch, 2009). It is difficult to identify an overarching feature or combination of features that describes the family as a whole due to the diversity present among the genera.



Figure 5. Representatives of the family Oneirodidae. Left: adult female *Oneirodes carlsbergi*; right: larva. Photos not to scale.

The Gigantactinidae, or whipnose seadevils (Figure 6), is one of most well-defined and specialized ceratioid families (Pietsch, 2009). Females are easily distinguished from other families by their long, streamlined, and laterally compressed shape with a small head and a long and slender illicium that emerges near the tip of the snout and can reach up to five times the standard length (Pietsch, 2009; Coad, 2017). These features suggest increased locomotory ability compared to more globose members of the suborder (Pietsch, 2009). The larvae have exceptionally large pectoral fins (which could also be an indicator of enhanced mobility) and males have highly reduced eyes accompanied by large nostrils (Pietsch, 2009; Coad, 2017).

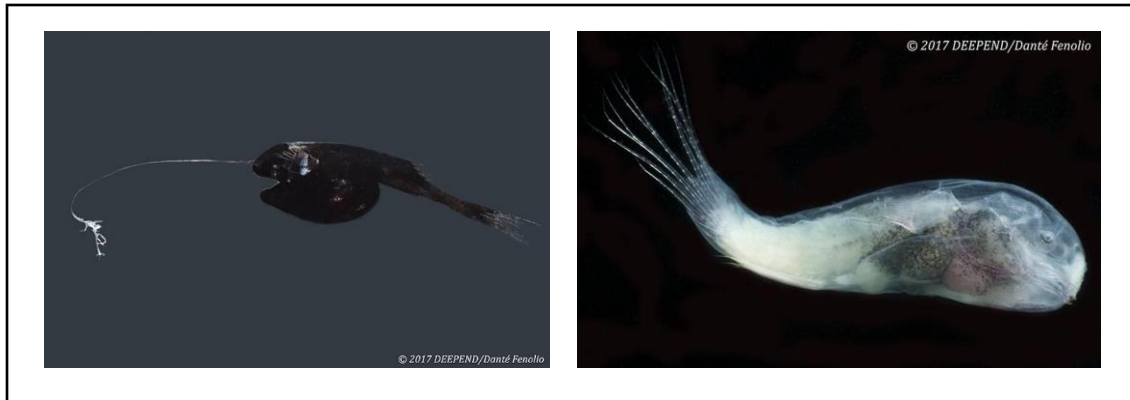


Figure 6. Representatives of the family Gigantactinidae. Left: adult female *Rhynchactis macrothrix*; right: male *Rhynchactis* sp. Photos not to scale.

The other six families within the Ceratioidei are Centrophrynidae (the prickly seadevils), Diceratiidae (the doublespine seadevils), Himatolophidae (the footballfishes), Thaumatchthyidae (the wolftrap seadevils), Caulophrynidae (the fanfin seadevils), and Neoceratiidae (the needlebeard or toothed seadevils) (Pietsch, 2009; Fricke et al., 2021). Combined, these seven families contain 11 genera and 66 species (Pietsch, 2009; Fricke et al., 2021). Centrophrynid females are laterally compressed with numerous teeth lining the gill arches and skin covered in dermal denticles (Pietsch, 2009). Diceratiid females bear a second dorsal fin spine with bioluminescent capabilities behind the base of the illicium (Rajeeshkumar et al., 2016). Himantolophid females are globular in shape with a blunt head, short snout, and skin with wart-like papillae (Pietsch, 2009; Coad, 2017; Prokofiev, 2020). Thaumatchthyid females have large, toothlike denticles associated with the esca; however, even more remarkable is the presence of an enormous upper jaw with long hooked teeth that forms a cage-like trap while feeding (Pietsch, 2009). Caulophrynid females have a long (*Robia*) or short illicia that may contain distal filaments (*Caulophryne*); however, the illicium lacks an esca organ (Pietsch, 2009). Neoceratiid females lack an illicium entirely and have many elongated yet mobile teeth (Pietsch, 2009; Prokofiev, 2020).

## Diagnosis of the Ceratioidei

The Ceratioidei have distinctive features that separate them from other closely related groups. From a morphological standpoint, repositioning of the pectoral fins, a loss of bony structures and therefore reduction in density, and the loss of palatine teeth support the monophyly of this group (Pietsch, 2009). That said, a single synapomorphic character distinguishes this suborder from its relatives: extreme sexual dimorphism and dwarfism of males (Pietsch, 2009). Bertelsen (1951) documented that in the most extreme cases of sexual dimorphism such as with *Ceratias holboelli*, the female may be 60 times the length of the male of the same species and weigh half a million times more. The lack of size in the males forces them to rely on other strategies for seeking out potential mates for reproduction. In an environment devoid of light other than bioluminescence and the inability to capitalize on symbiotic bioluminescence due to a lack of illicium, retinal acuity and sensitivity are imperative for success for male ceratioid anglerfishes (Collin and Partridge, 1996; Warrant, 2000). Their enhanced ocular specializations, such as densely packed rods and well-developed eyes, aids in their success in finding mates despite their size (Munk, 1966; Collin and Partridge, 1996; Warrant, 2000; Pietsch, 2005). Their ability to detect the pheromones of females that are species-specific is ostensibly facilitated by their large olfactory organs relative to their size (Bertelsen, 1951; Pietsch, 1976).

Bertelsen (1951) provided keys to distinguish males from females of most species, even in the larval stages, based on the illicial apparatus. This unique and complex structure is only present in females and is evolutionarily a modification of the first dorsal fin spine (Pietsch, 2009). These spines are supported by an elongated pterygiophore (Bertelsen, 1951). At the end of the illicium is a bulbous tissue structure called the esca or esca bulb (Bertelsen, 1951;

Shimazaki and Nakaya, 2004; Pietsch, 2009). This organ contains at least one small opening to the external environment and is filled with bioluminescent bacteria (Pietsch, 2009; Freed et al., 2019). The esca can also contain lenses, filters, and even multiple appendages in order to manipulate prey attraction or possibly mate attraction (Munk 1999; Freed et al., 2019). Pietsch (2009) claims that anglerfishes are even capable of altering the conditions within the esca in order to control the bacteria populations living within the bulb.

### Reproduction Strategies

Five of the 11 families of ceratioid anglerfishes are known to demonstrate a form of pair bonding that is unique among all vertebrates, sexual parasitism (Pietsch, 1975; Munk, 2000; Pietsch, 2005; Pietsch and Orr, 2007), but see below for discussion of this term. There are differences among taxa in the form of this phenomenon, including size differences between males and females and well as the duration of male attachment (Munk, 2000; Pietsch, 2005). Permanently attached males have been found in 23 species (Pietsch, 2005). It is proposed that in many species, sexual maturity is reached not at a certain size or age, but rather by the onset of the parasitic sexual association (Pietsch, 2005). In their free-living stage before parasitic attachment, the large eyes and nostrils of the dwarfed males are essential in conspecific mate selection. Once attachment is established, males begin to degenerate in order to allocate resources to reproduction (Bertelsen, 1951; Munk, 2000; Pietsch, 2009). Some females may be parasitized by multiple males, with as many as documented in the genus *Cryptopsaras* (Munk, 2000; Pietsch, 2005). For attachment, the male locks on to the female using either the lower jaw or both jaws and the location of this attachment is species-specific (Pietsch, 2009). After attachment, males fuse to the females, including the vascular system (Munk, 2000).

Regarding the classification of the phenomenon, it can be argued that this is not in fact parasitism, but rather genetic chimerism. Chimerism is the presence of two or more cell lines with different genetic origins within the same organism (Rejduch, 2001; Rejduch et al., 2016). Parasitism, *sensu stricto*, requires organisms to be from two different species (reviewed in Crofton, 1971) and thus, male ceratioids would not be considered parasites on members of their own species. The type of anatomical joining of ceratioids is unknown in any other organisms except for the unusual incidence of genetically identical conjoined twins (Nisbet, 1973; Swann et al., 2020). While the attachment of males to females can be vascular in nature, it does not illicit an immune response from the female (Swann et al., 2020), provides a benefit to the females by fertilizing the eggs, and therefore raises the question of the validity in calling this relationship parasitic.

Bertelsen (1951) detailed the reproductive life cycle of ceratioids in a schematic (Figure 7) that includes empirical data and conjecture (because the life cycle of many taxa is unknown). Ontogenic vertical migration plays a key role in the metamorphosis of ceratioids. It begins with fertilized eggs floating up to the surface after spawning and then hatching in the upper water column. Once the larvae get their start, at some point they migrate back down to depth to feed and reproduce.

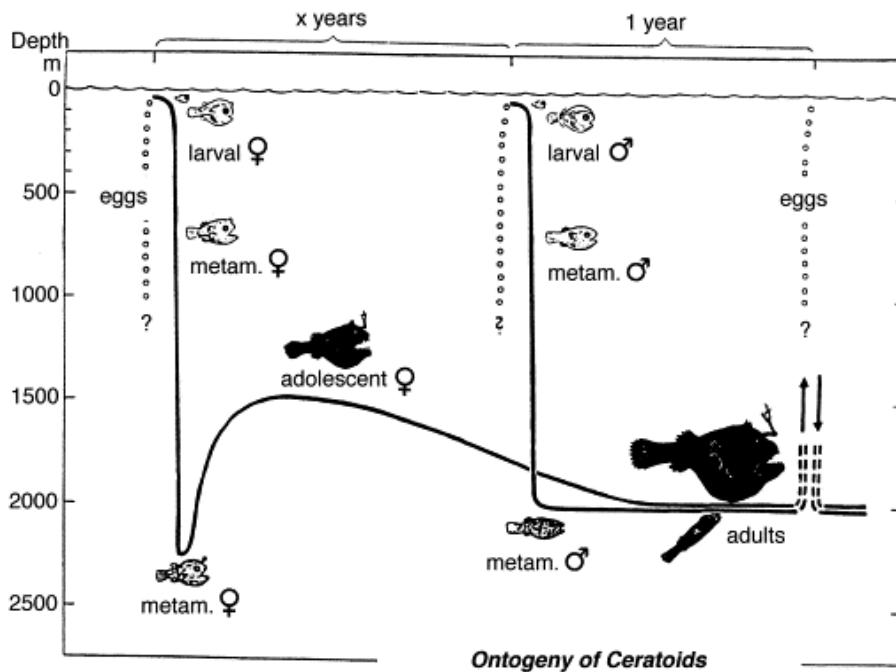


Figure 7. Diagrammatic representation of the ontogenic vertical migration of ceratioids (from Bertelsen, 1951).

### Feeding Strategies

The development of the illicial apparatus and its ability to house symbiotic bioluminescent bacteria has allowed females to attract and capture prey despite their decreased locomotory abilities (Pietsch, 2009). The light emitted from the esca bulb and the movement of the illicial structure lures prey to their oversized mouth. The suction created by the expansion of their jaws and the opening of their oral cavity devours their prey (Munk, 2000; Pietsch, 2009). Despite the ability of males to parasitize females and remain attached using denticular jaws, their alimentary canal is underdeveloped (Pietsch, 2009). The union of circulatory systems of males and females is such that males are nourished via female attachment. It is unknown how long free-living males can survive

#### **1.4. Significance of Work and Project Aims**

The ecology of the Ceratioidei, including age and growth, feeding, and how often they interact with others of their own species, is poorly known. McClain (2021) discussed how common it is for taxa to show extremely low abundances to exist in the deep sea. By understanding the ecology and habitat use of specific taxa, the factors leading to and maintaining rarity can be understood. Anglerfishes, particularly deep-sea ceratioids, are the “poster child” for rarity in the deep sea. Females may not interact with another female in their lifetime and potentially only a few males for reproductive purposes. Despite this, there is enough interaction between members of this taxon to allow for their success in an environment that has eliminated so many others.

The aims of this project are to: (1) document the faunal composition of the ceratioid anglerfish assemblage in the northern Gulf of Mexico; (2) characterize vertical distributions of assemblage members; and (3) examine these vertical distributions to identify major patterns and potential connectivity with the surface that supports this assemblage at its earliest life stage.

Through examination of the taxonomic composition, distribution, and life history characteristics of this key bathypelagic taxon in the Gulf of Mexico, we gain understanding of the ecological drivers of community structure in the largest ecosystem on Earth. Understanding the ecology of ceratioids in the ‘midnight zone’ illuminates pathways by which organisms can not only cope but also thrive in severe environments with limited resources.



## 2. Methods

### 2.1. Sample Collection

Following the 2010 *Deepwater Horizon* oil spill, two programs were created to assess the impacts of the spill. The first was a series of seven surveys that were conducted as part of the NOAA-supported Offshore Nekton Sampling and Analysis Program (ONSAP) between 2010 and 2011. The overall goal of ONSAP was to “survey and quantify the deep-pelagic life forms that could have been impacted by the oil spill” (Cook et al., 2020). This program included four surveys aboard the NOAA FSV *Pisces*: *Pisces 8* (PC8), *Pisces 9* (PC9), *Pisces 10* (PC10), and *Pisces 12* (PC12). Each sampling survey was three weeks long and occurred during all seasons from December 2010-September 2011. A total of 17 stations were sampled obliquely with shallow and deep deployments conducted both day and night (Figure 8). The trawls used during *Pisces* were commercial-sized, non-closing nets and therefore discrete-depth bins could not be sampled. High-speed rope trawls (HSRT) have been proven effective for sampling both young and adult pelagic fishes (Dotson and Griffith, 1996), however they limit the ability of quantifying taxa that vertically migrate due to the oblique nature of a net that cannot be opened and closed. Rather, the net sampled two large depth ranges, ‘shallow’ and ‘deep.’ The shallow-depth samples typically fished from the surface to 800 m. The deep samples typically fished from the surface to 1300-1500 m depth. In total, 84 shallow trawls and 87 deep trawls were conducted.

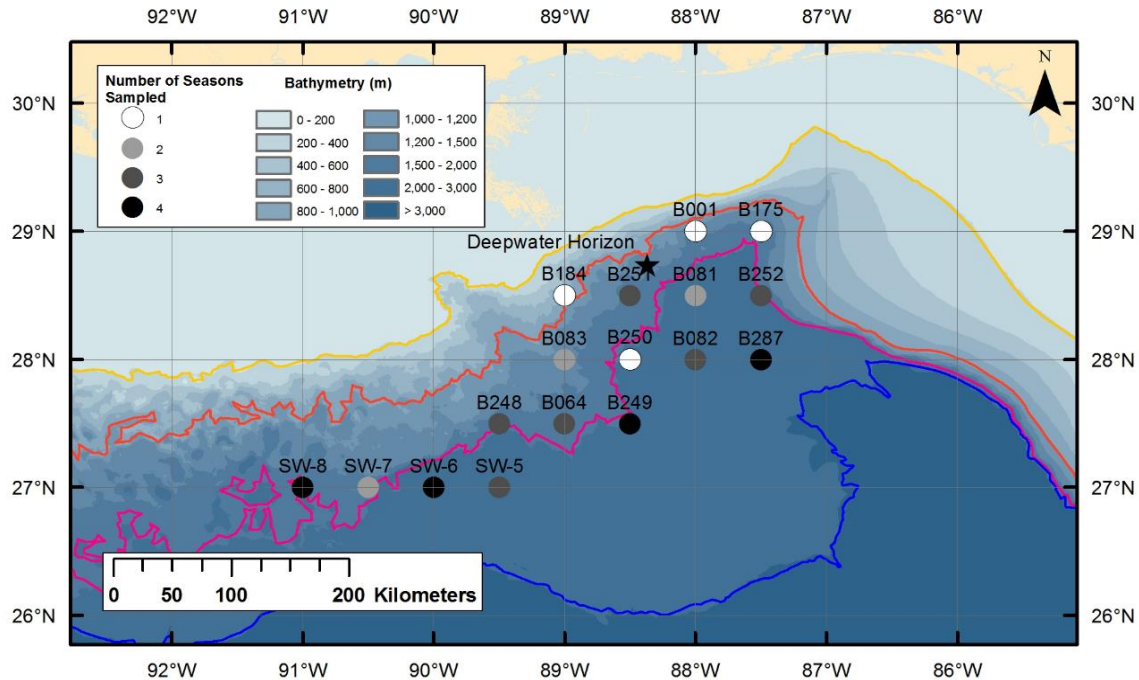


Figure 8. Station map of ONSAP cruises aboard the FSV *Pisces* from December 2010-September 2011.

A second research vessel, the M/V *Meg Skansi*, was used to conduct the other three ONSAP surveys: *Meg Skansi 6* (MS 6), *Meg Skansi 7* (MS 7), and *Meg Skansi 8* (MS8). Sampling was near continuous on this vessel from January to September 2011, with a total of 47 stations sampled day and night in triplicate (Figure 9). This vessel was equipped with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS). The MOCNESS had an opening dimension of 10 m<sup>2</sup> (from here on referred to as the MOC-10). The MOC-10 was equipped with six nets, and each of these nets had a 3-mm uniform mesh (Cook et al., 2020). The MOC-10, unlike those used on the *Pisces* deployments, was remotely opened and closed at different depths to sample discrete-depth bins. Five discrete-depth bins were sampled with the MOC-10 net: N1 = 1500 m-1200 m; N2 = 1200 m-1000 m; N3 = 1000 m-600 m; N4 = 600 m-200 m; and N5 = 200 m-surface. In total, 241 trawl deployments were conducted at 58 stations (936 quantitative discrete-depth samples).

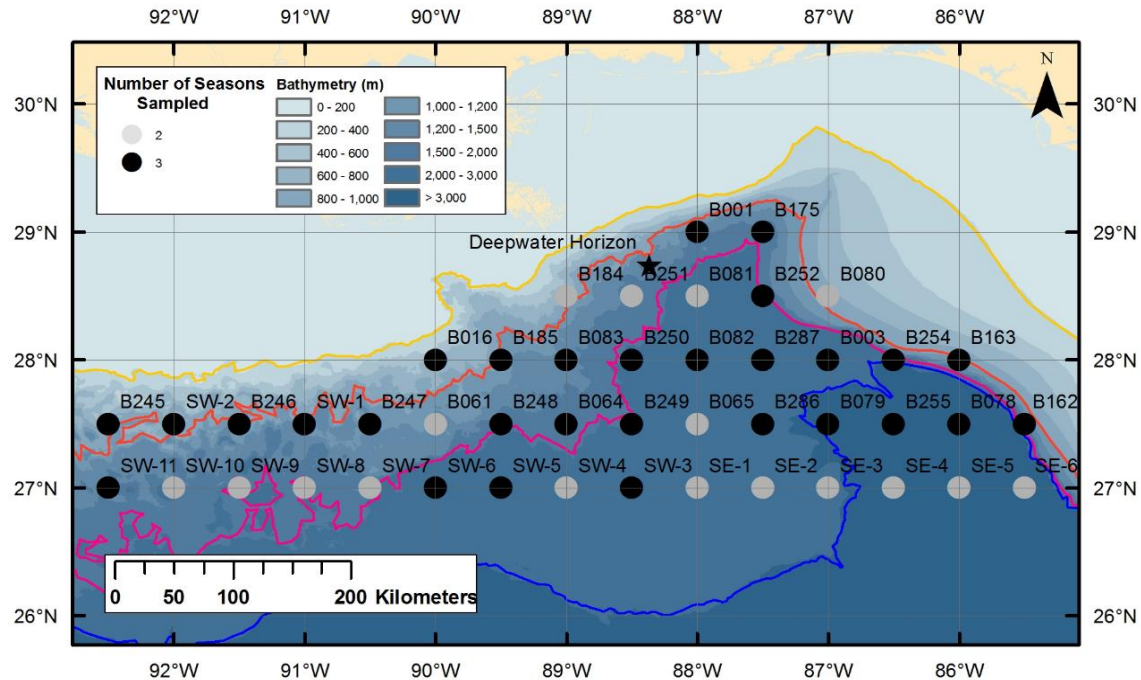


Figure 9. Station map of ONSAP cruises aboard the M/V *Meg Skansi* from January-September 2011.

After ONSAP, a second program was conceived and executed, the GoMRI-funded Deep Pelagic Nekton Dynamics (DEEPEND) Consortium. This project served as a continuation as well as an expansion of the ONSAP program by conducting additional types of sampling as well as addressing the drivers of variability in the GoM (Cook et al., 2020). Sampling was conducted aboard the R/V *Point Sur* over six cruises (DP01-DP06) in the northern Gulf of Mexico (Figure 10). Each color line in the figure represents a cruise track within the cruise series. Sampling was performed using the MOC-10 at the same discrete-depth intervals as in the *Meg Skansi* cruises. DP01 occurred in May 2015, DP02 occurred in August 2015, DP03 occurred in May 2016, DP04 occurred in August 2016, DP05 occurred in May 2017, and DP06 occurred in July/August 2017. In total, 122 trawl deployments were conducted at 24 stations (470 quantitative discrete-depth samples). Due to time constraints, the DEEPEND cruises were unable to sample the entire 46-

station grid created during the ONSAP cruises, resulting in the smaller sample size (Cook et al., 2020).

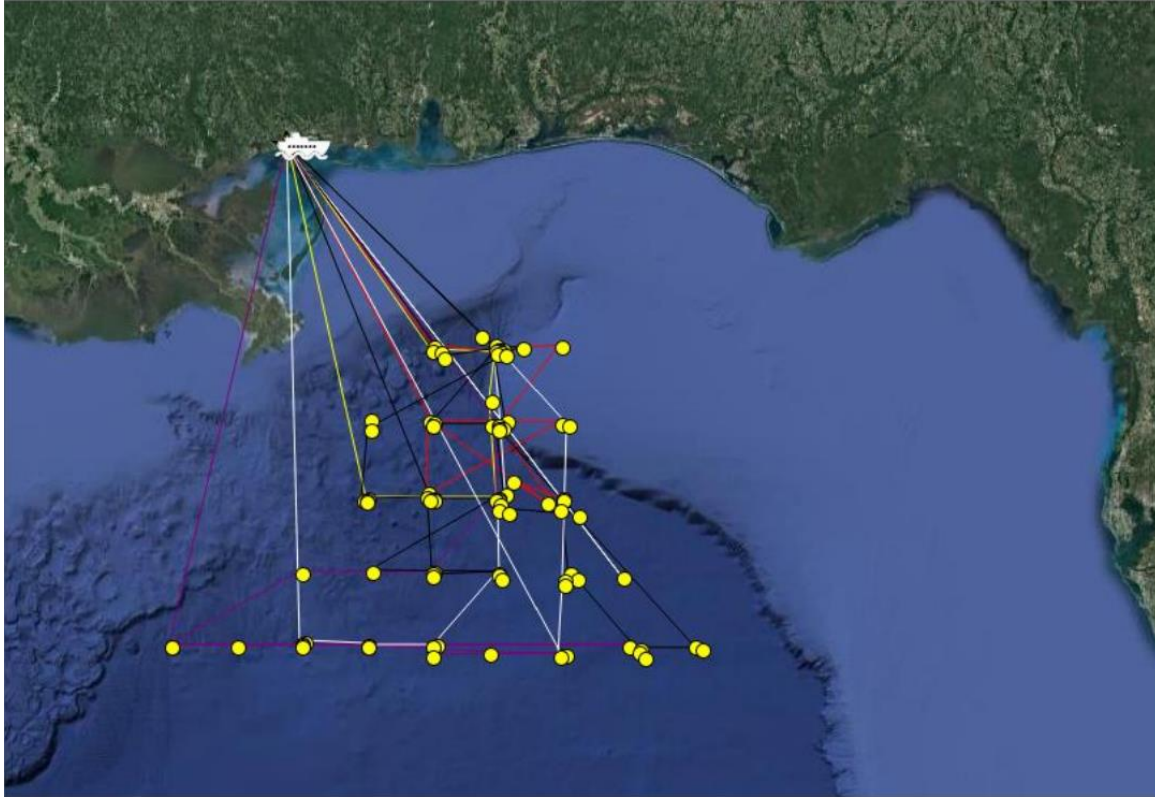


Figure 10. DEEPEND Cruise tracks aboard the R/V *Point Sur* (DP01, DP02, DP03, DP04, DP05, and DP06) from May 2015 to August 2017.

## 2.2. Sample Handling and Analysis

ONSAP samples were preserved in 10% buffered formalin:seawater at sea and transported to Nova Southeastern University (NSU). They were then sorted by major taxon by members of the Oceanic Ecology Laboratory, identified to the lowest taxonomic level possible, weighed (in batches by taxon), individually measured, and transferred to 70% ethanol:water solution. DEEPEND specimens were identified, weighed, and formalin-fixed at sea, and then transported to NSU for further evaluation.

Due to the extreme sexual dimorphism present in the Ceratioidei, the three main morphotypes (male, female, and larval) were considered separately in this thesis to account for differing expected ecologies and for the large difference in the resolution of taxonomic keys for each morphotype. Species-level keys are available for females only; most male and larval keys are resolved only to family. Issues still remain however with females in species validation and thus in some cases, family and or genus representing a group of females as the lowest taxonomic unit. Due to the rarity of this collection, specimens that lacked full taxonomic resolution due to damage sustained during sampling were still included. Ceratioidei are unique in the large size of their larvae, allowing capture of male, female, and larvae using the same nets and gear type. Specimens that were not characterized into one of these categories at sea previously or in the lab were reexamined and identified as either male, female, or larvae.

Male:female:larvae ratios were determined for each family. Deviations from a 1:1 male:female ratio were analyzed using a Chi Square Goodness of Fit test. For females, if the species could not be identified due to damage during collection, the notation DAM was assigned to the genus or family name. For any females that have yet to be identified to their lowest taxonomic unit but are not damaged, the notation TBD was assigned.

### **2.3. Abundance and Vertical Distribution**

Abundances of male, female, and larvae were standardized per unit effort for all quantitative MOC-10 samples. Aboard the vessel, volume of water filtered ( $m^3$ ) was calculated using the MOCNESS software for each trawl and depth bin. Abundances were then calculated by summing the counts of the lowest taxonomic unit (females) or family (males and larvae) and then divided by the sum of water filtered across that depth bin. Sampling selectivity of each net

type was assessed by analyzing standard length (SL) against type of net used for capture (MOC-10 versus HSRT) and time of day of capture (day versus night). Ceratioid vertical distributions were plotted in R Studio using a modified t-plot that compared day and night sampling efforts. Females were plotted by species while males and larvae were plotted by family.

### 3. Results

#### 3.1. Faunal Composition

In total, 1726 ceratioids were collected during the three cruise series and deposited at the NSU Oceanic Ecology Laboratory for further evaluation (Table 1). Five taxa comprised over 65% of the collection. The most collected taxon was Linophrynidae (primarily males) (25.7%), followed by *Cryptosaras couesii* (17.2%). During the *Pisces* cruises, 396 ceratioids were collected. Nearly 44% of the specimens collected belonged to four of the 51 taxa collected, with *Himantolophus* spp. being the most abundant, constituting 15.6% of the sample. During the *Meg Skansi* cruises conducted from in 2011, 936 ceratioids were collected. Of the specimens collected, 68% belonged to three of the 55 taxa collected, with Linophrynidae (primarily males) constituting 31.9% of the sample. During the DEEPEND Cruises, 394 ceratioids were collected. Of the specimens collected, 52% belonged to two of the 35 taxa collected, with Linophrynidae (primarily males) constituting 35.5% of the sample.

Table 1. Assemblage composition of ceratioid anglerfishes collected in the northern Gulf of Mexico (values equal number of specimens).

<b>Taxon</b>	<b>Totals</b>	<b><i>Pisces</i></b>	<b><i>Meg Skansi</i></b>	<b>DPND</b>
Linophrynidae	445	6	299	140
<i>Cryptosaras couesii</i>	297	26	205	66
<i>Linophryne</i> spp.	194	58	131	5
<i>Himantolophus</i> spp.	101	62	35	4
Oneirodidae	93	7	37	49
<i>Haplophryne mollis</i>	67	29	30	8
<i>Melanocetus johnsonii</i>	46	18	12	16
<i>Oneirodes</i> spp.	43	12	21	10
<i>Melanocetus murrayi</i>	40	24	10	6
<i>Ceratias</i> spp.	34	9	10	15
Gigantactinidae	27	1	11	15

<i>Melanocetus</i> spp.	26	6	11	9
<i>Gigantactis</i> spp.	23	8	13	2
<i>Chaenophryne draco</i>	18	2	12	4
<i>Dolopichthys pullatus</i>	15	7	7	1
<i>Spiniphryne gladisfenae</i>	15	1	8	6
<i>Dolopichthys</i> spp.	14	7	5	2
<i>Centrophryne spinulosa</i>	13	10	1	2
<i>Ceratias uranoscopus</i>	12	5	7	0
Ceratioidea	12	3	8	1
Himantolophidae	12	0	2	10
<i>Linophryne arborifera</i>	12	9	2	1
<i>Oneirodes carlsbergi</i>	11	3	3	5
<i>Photocorynus spiniceps</i>	10	4	5	1
<i>Gigantactis vanhoeffeni</i>	9	3	5	1
<i>Microlophichthys microlophus</i>	7	4	2	1
<i>Linophryne densiramus</i>	6	4	2	0
<i>Linophryne brevibarbata</i>	6	6	0	0
Ceratiidae	5	0	5	0
<i>Gigantactis microdontis</i>	5	3	0	2
<i>Himantolophus groenlandicus</i>	5	4	1	0
<i>Lasiognathus</i> spp.	5	3	2	0
<i>Lophodolos indicus</i>	5	3	1	1
<i>Thaumatichthys binghami</i>	5	5	0	0
<i>Caulophryne</i> spp.	4	0	4	0
<i>Danaphryne nigrifilis</i>	4	4	0	0
<i>Gigantactis gracilicauda</i>	4	3	0	1
<i>Chaenophryne longiceps</i>	3	2	1	0
<i>Chaenophryne</i> spp.	3	0	2	1
<i>Gigantactis longicauda</i>	3	3	0	0
<i>Lasiognathus dinema</i>	3	1	2	0
<i>Oneirodes macrosteus</i>	3	0	2	1
<i>Rhynchactis</i> spp.	3	0	0	3
<i>Bufoceratias wedli</i>	2	0	2	0
<i>Dolopichthys jubatus</i>	2	1	1	0
Diceratiidae	2	2	0	0
<i>Gigantactis longicirra</i>	2	0	2	0
<i>Gigantactis gargantua</i>	2	1	0	1
<i>Gigantactis herwigi</i>	2	2	0	0



<i>Gigantactis macronema</i>	2	2	0	0
<i>Lasiognathus beebei</i>	2	2	0	0
<i>Lasiognathus saccostoma</i>	2	0	2	0
<i>Oneirodes bradburyae</i>	2	1	1	0
<i>Oneirodes eschrichtii</i>	2	0	0	2
Thaumaticthyidae	2	1	1	0
<i>Chaenophryne melanorhabdus</i>	1	0	1	0
<i>Chaenophryne ramifera</i>	1	0	1	0
<i>Chirophryne xenolophus</i>	1	0	1	0
<i>Danaphryne</i> sp.	1	1	0	0
<i>Diceratias pileatus</i>	1	1	0	0
<i>Gigantactis watermani</i>	1	0	1	0
<i>Haplophryne</i> sp.	1	0	1	0
<i>Himantolophus albinares</i>	1	0	1	0
<i>Himantolophus paucifilosus</i>	1	1	0	0
<i>Linophryne algibarbata</i>	1	1	0	0
<i>Linophryne macrodon</i>	1	0	1	0
<i>Linophryne pennibarbata</i>	15	14	1	0
<i>Linophryne racemifera</i>	1	1	0	0
<i>Lophodolos acanthognathus</i>	1	0	1	0
Melanocetidae	1	0	1	0
<i>Neoceratias spinifer</i>	1	0	1	0
<i>Oneirodes theodorittissieri</i>	1	0	0	1
<i>Rhynchactis leptonema</i>	1	0	1	0
<i>Rhynchactis macrothrix</i>	1	0	0	1
<i>Spiniphryne</i> sp.	1	0	1	0
<b>Totals</b>	<b>1726</b>	<b>396</b>	<b>936</b>	<b>394</b>

### Sex Ratios

Of the ceratioids collected, 768 were female, 627 were male, and 291 were larvae/postlarvae. Any that did not receive a sex distinction were too damaged for evaluation. A Chi Square Goodness of Fit test indicated the female to male ratio was significantly different than 1:1 ( $p < 2.2 \times 10^{-16}$ ) with a higher abundance of females than males. Morphotype ratios among families differed, with Linophrynidae comprising 71% (N=216) of larvae and 62% (N=379) of

males in the assemblage, but only 19% (N=144) of females (Table 3, Figure 11). Females were distributed more widely among families, with Ceratiidae containing 35% (N=288), followed by Oneirodidae (22%, N=168), and then Linophrynidae (19%, N=144). The Ceratiidae were comprised of 10% (N=64) males and 3% larvae (N=10). Females were collected from all 11 ceratioid families in the northern GoM. No male specimens were caught from the families Centrophrynidae, Neoceratiidae, and Thaumatchthyidae. No larval specimens were caught from the families Centrophrynidae, Diceratiidae, or Neoceratiidae.

Table 2. Specimen counts by family for each morphotype.

<b>Family</b>	<b>Females</b>	<b>Males</b>	<b>Larvae</b>
Caulophrynidae	1	1	2
Centrophrynidae	13	0	0
Ceratiidae	268	64	10
Diceratiidae	3	2	0
Gigantactinidae	47	18	17
Himatolophidae	14	83	22
Linophrynidae	144	379	216
Melanocetidae	88	17	8
Neoceratiidae	1	0	0
Oneirodidae	168	49	27
Thaumatchthyidae	18	0	1

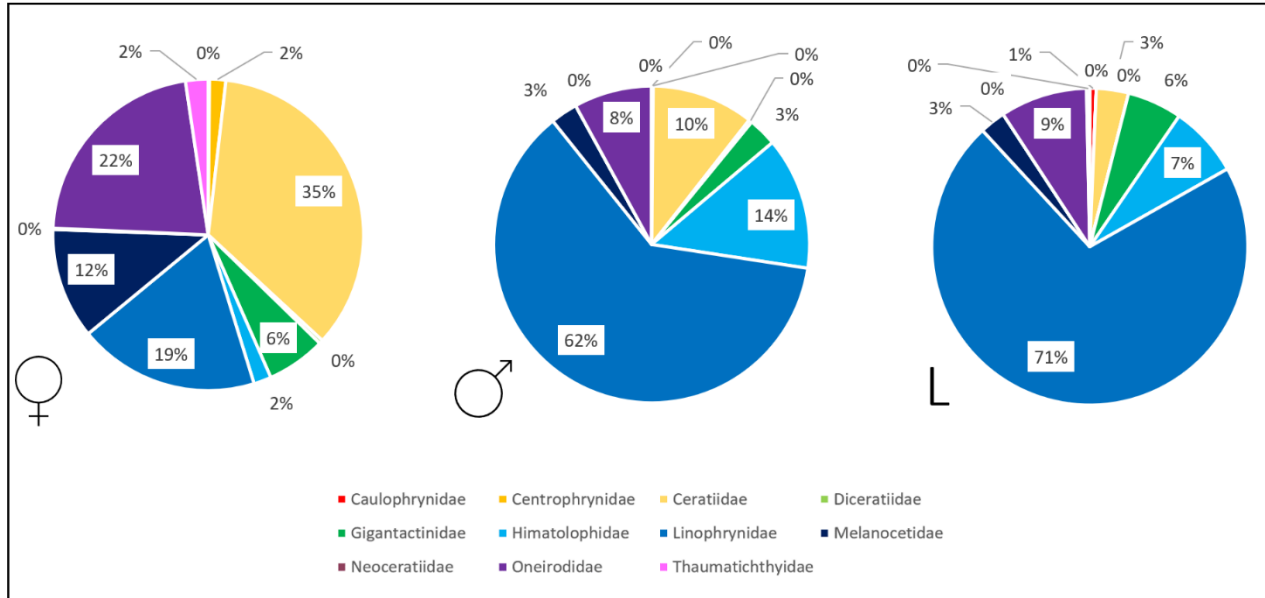


Figure 11. Family composition per morphotype in the order of females, males, and larvae, respectively.

#### Detailed Taxonomic Composition: Females

Females comprised 44.5% (N=768) of the collection. The four most abundant species belonged to three families: Ceratiidae, Oneirodidae, and Melanocetidae. The most abundant species, *Cryptopsaras couesii* (30%, N=228), belonging to the family Ceratiidae, was caught six times as much as the next closest species, *Haplophryne mollis* (5%, N=39) from Linophryniidae. *Melanocetus murrayi* (5%, N=39) and *Melanocetus johnsonii* (4.7%, N=36) from Melanocetidae were the next two most abundant species. These taxa were classified as “caught on most cruises” in abundance rank (Figure 12, Table 3).

The next three most abundant taxa were the family Linophryniidae (3.8%, N=29), the genus *Linophryne* (3.5%, N=27) and the genus *Oneirodes* (3.4%, N=26). Following these taxa were *Ceratias uranoscopus* (3%, N=23), Oneirodidae TBD (3%, N=23), and *Chaenophryne draco* (2.3%, N=18). These taxa were classified as “caught on some cruises” in abundance rank. The remaining taxa individually constituted no more than 2% of the whole assemblage, less than

37% of the female assemblage, and were only caught on few cruises. Taxa that were only caught once were listed separately (Table 4).

The most speciose family with respect to collected females was the Oneirodidae, with 17 species identified. The second-most speciose family was the Gigantactinidae, with 11 species identified. There were nine species identified from the Linophrynidae, four species from Thaumatchthyidae, three from Himantolophidae, and two each in Ceratiidae, Melanocetidae, and Diceratiidae. Neoceratiidae, Caulophrynidae, and Centrophrynidae each had one species identified.

Table 3. Specimens of female ceratioid anglerfishes, with relative abundance ranking across all cruise sampling.

<b>Taxon</b>	<b>Counts</b>	<b>Taxonomic Code</b>	<b>Relative Abundance</b>
<i>Cryptopsaras couesii</i>	228	C. cou	Most Cruises
<i>Haplophryne mollis</i>	39	H. mol	Some Cruises
<i>Melanocetus murrayi</i>	39	M. mur	Some Cruises
<i>Melanocetus johnsonii</i>	36	M. joh	Some Cruises
Linophrynidae TBD	29	Lino. TBD	Some Cruises
<i>Linophryne</i> spp. TBD	27	L. spp. TBD	Some Cruises
<i>Oneirodes</i> spp. TBD	26	O. spp. TBD	Some Cruises
<i>Ceratias uranoscopus</i>	23	C. ura	Some Cruises
Oneirodidae TBD	23	Oneiro. TBD	Some Cruises
<i>Chaenophryne draco</i>	18	C. dra	Some Cruises
<i>Ceratias</i> spp. DAM	16	Cer. spp. TBD	Some Cruises
<i>Spiniphryne gladisfenae</i>	16	S. gla	Few Cruises
<i>Dolopichthys pullatus</i>	15	D. pul	Few Cruises
<i>Gigantactis</i> spp. TBD	15	G. spp. TBD	Few Cruises
<i>Linophryne pennibarbata</i>	15	L. pen	Few Cruises
<i>Centrophryne spinulosa</i>	13	C. spi	Few Cruises
<i>Dolopichthys</i> spp. TBD	13	D. spp. TBD	Few Cruises
<i>Melanocetus</i> spp. DAM	13	M. spp. DAM	Few Cruises
<i>Linophryne arborifera</i>	12	L. arb	Few Cruises
<i>Oneirodes carlsbergi</i>	11	O. car	Few Cruises
<i>Gigantactis vanhoeffeni</i>	8	G. van	Few Cruises
<i>Himantolophus</i> spp. TBD	7	H. spp. TBD	Few Cruises
<i>Microlophichthys microlophus</i>	7	M. mic	Few Cruises
<i>Photocorynus spiniceps</i>	7	P. spi	Few Cruises
<i>Linophryne brevibarbata</i>	6	L. bre	Few Cruises
<i>Linophryne densiramus</i>	6	L. den	Few Cruises
<i>Oneirodes</i> spp. DAM	6	O. spp. DAM	Few Cruises
<i>Gigantactis microdontis</i>	5	G. mic	Few Cruises
<i>Himantolophus groenlandicus</i>	5	H. gro	Few Cruises
<i>Lasiognathus</i> spp. DAM	5	Las. spp. DAM	Few Cruises
<i>Lophodolos indicus</i>	5	L. ind	Few Cruises
<i>Oneirodes schmidti</i> group	5	O. SG	Few Cruises
<i>Thaumatichthys binghami</i>	5	T. bin	Few Cruises
<i>Danaphryne nigrifilis</i>	4	D. nig	Few Cruises
<i>Gigantactis gracilicauda</i>	4	G. gra	Few Cruises
Ceratiodea DAM	3	Cera. DAM	Few Cruises
<i>Chaenophryne longiceps</i>	3	C. lon	Few Cruises
<i>Gigantactis longicauda</i>	3	G. longicauda	Few Cruises
<i>Lasiognathus dinema</i>	3	L. dig	Few Cruises
<i>Oneirodes macrosteus</i>	3	O. mac	Few Cruises

<i>Bufoceratias wedli</i>	2	B. wed	Few Cruises
<i>Chaenophryne</i> spp. TBD	2	Cha. spp. TBD	Few Cruises
<i>Gigantactis gargantua</i>	2	G. gar	Few Cruises
<i>Gigantactis herwigi</i>	2	G. her	Few Cruises
<i>Gigantactis macronema</i>	2	G. mac	Few Cruises
<i>Lasiognathus beebei</i>	2	L. bee	Few Cruises
<i>Lasiognathus saccostoma</i>	2	L. sac	Few Cruises
<i>Oneirodes bradburyae</i>	2	O. bra	Few Cruises
<i>Oneirodes eschrichtii</i>	2	O. esc	Few Cruises
<i>Rhynchactis</i> spp. TBD	2	R. spp. TBD	Few Cruises

Table 4. Single-specimen collections of female ceratioid anglerfishes.

<b>Taxon</b>	<b>Counts</b>	<b>Taxonomic Code</b>
<i>Caulophryne</i> sp. TBD	1	Caul. sp. TBD
<i>Chaenophryne melanorhabdus</i>	1	C. mel
<i>Chaenophryne ramifera</i>	1	C. ram
<i>Chirophryne xenolophus</i>	1	C. xen
<i>Danaphryne</i> sp. DAM	1	Dan. sp. DAM
<i>Diceratias pileatus</i>	1	D. pil
<i>Dolopichthys jubatus</i>	1	D. jub
<i>Gigantactis longicirra</i>	1	G. longicirra
<i>Gigantactis watermani</i>	1	G. wat
<i>Himantolophus albinares</i>	1	H. alb
<i>Himantolophus paucifilosus</i>	1	H. pau
<i>Linophryne algibarbata</i>	1	L. alg
<i>Linophryne macrodon</i>	1	L. mac
<i>Linophryne racemifera</i>	1	L. rac
<i>Lophodolos acanthognathus</i>	1	L. aca
<i>Neoceratias spinifer</i>	1	N. spi
<i>Oneirodes theodorittissieri</i>	1	O. the
<i>Rhynchactis leptonema</i>	1	R. lep
<i>Rhynchactis macrothrix</i>	1	R. mac
Thaumatichthyidae TBD	1	Thaum. TBD

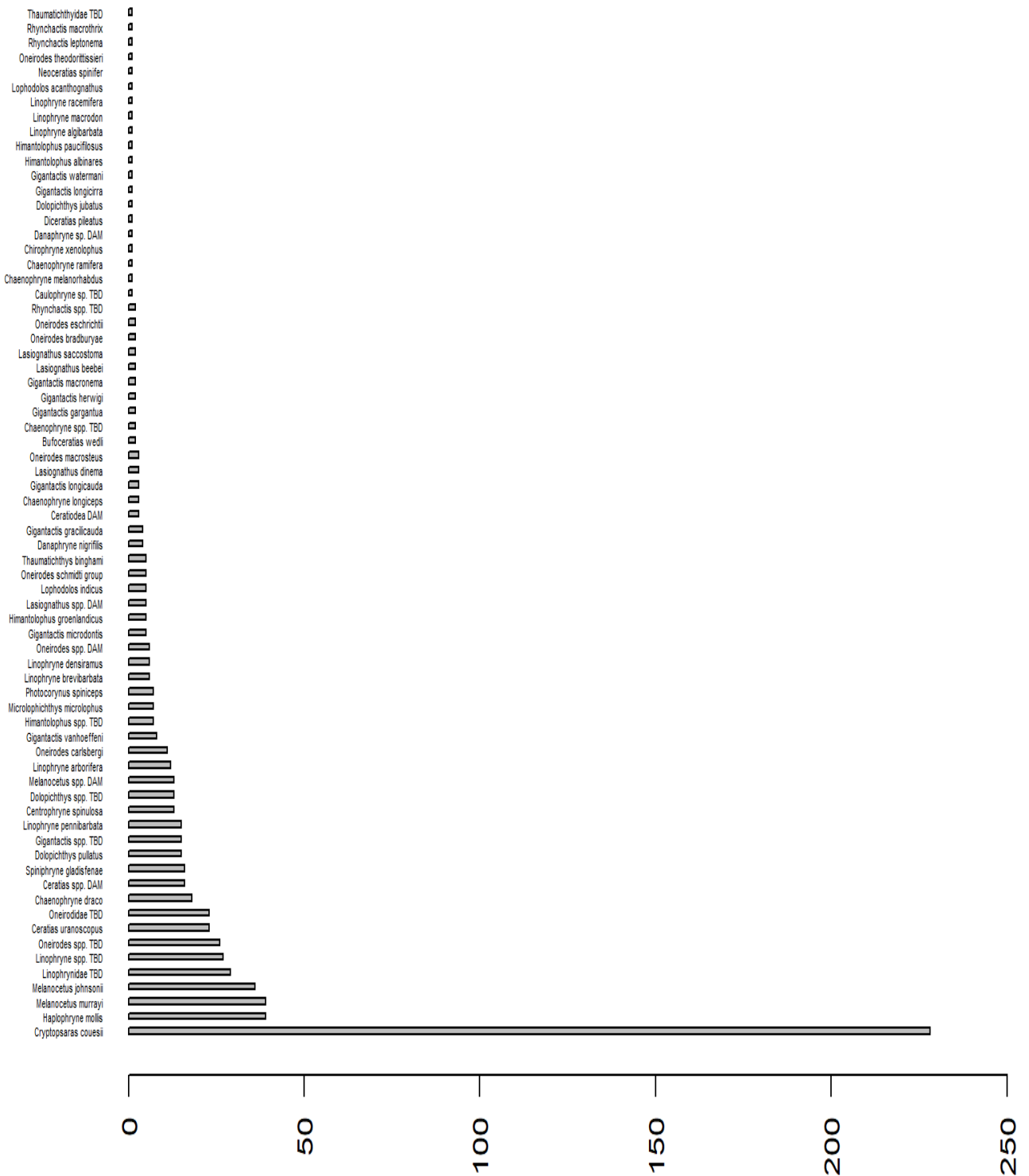


Figure 12. Sum of counts of each female taxa caught to the lowest taxonomic identification during all cruise series.

### Detailed Taxonomic Composition: Males

Males comprised 36.3% (N=627) of the collection (Table 2, Figure 11). There are very few species in which the males can be identified (ex. *Cryptopsaras couesii*). Linophryinidae was the most-abundant family (62% ,N=379). *Linophryne* was the most abundant genus identified and comprised 37.7% (N=143) of the male linophryinids caught. The second-most abundant family was Himantolophidae, comprising 14% (N=83) of the male assemblage. The third-most abundant family was Ceratiidae (10%, N=64).

The other families collectively represented 14% (N=87) of the male assemblage. Oneirodidae comprised 8% (N=49), and Gigantactinidae and Melanocetidae each comprised 3% (N=18 and N=17, respectively). Diceratiidae (N=2) and Caulophryinidae (N=1) comprised less than 1% of the assemblage combined. Of the 11 ceratioid families, males were caught in eight of them. Male members of the families Centrophryinidae, Neoceratiidae, and Thaumatchthyidae were not collected. .

### Detailed Taxonomic Composition: Larvae

Larvae comprised 19.2% (N=291) of the collection (Table 2, Figure 11). Linophryinidae was the most abundant family (71%, N=216). The second-most abundant family was Oneirodidae (9%, N=27), and third Himantolophidae (7%, N=22). The remaining eight families comprise 13% of the larval assemblage. Gigantactinidae (N=17) and Melanocetidae (N=8) each comprise 6% and 3%, respectively. Caulophryinidae (N=2) and Thaumatchthyidae (N=1) comprised less than 1% of the assemblage. Larval ceratioids were not caught from Centrophryinidae, Diceratiidae, or Neoceratiidae.



### 3.2. Size Frequency and Gear Type

A boxplot of the standard length (SL) of ceratioids grouped by net type demonstrates the disparity in specimen size distributions between the MOC-10 and the HSRT collections (Figure 13). The MOC-10 collected smaller specimens than the HSRT overall, while the HSRT collected a larger size range. Fifty percent of the specimens collected with the MOC-10 were between 13-21 mm, compared to 50% of HSRT specimens being between 24-48 mm. The largest specimens caught with the MOC-10 and HSRT were 191 mm (*Lasiognathus* sp.) and 290 mm (*Gigantactis gargantua*), respectively. The smallest specimens caught were 4 mm in the MOC-10, 12 mm in the HSRT, and both were *Cryptopsaras couesii*. The median specimen size was 17 mm for the MOC-10 and 34 mm for the HSRT.

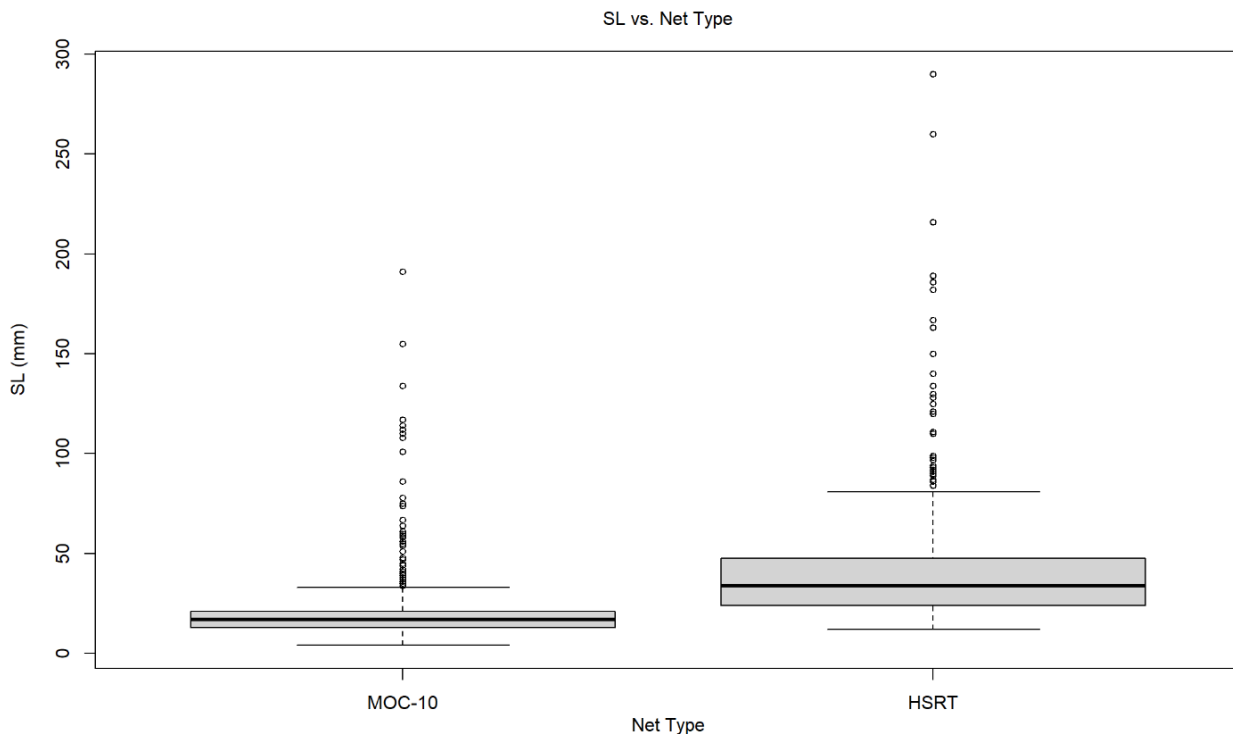


Figure 13. Ceratioid specimen size (SL [mm]) versus net type from GoM pelagic sampling.

### 3.3. Size Frequency and Solar Cycle

A boxplot of the standard length of ceratioids grouped by solar cycle using the MOC-10 (Figure 14) revealed that larger specimens were caught during the daytime trawls as well as a larger size range overall. Fifty percent of the samples collected during daytime trawls (N=437) and nighttime trawls (N=409) were between 13-21 mm. The largest specimen caught during the day was *Lasiognathus sp.* (191 mm SL), while at night was *Centrophryne spinulosa* (112 mm SL). The smallest specimen caught during daytime and nighttime trawls was the same: a 4 mm *Cryptopsaras couesii*. The median was 17 mm for daytime and nighttime trawls.

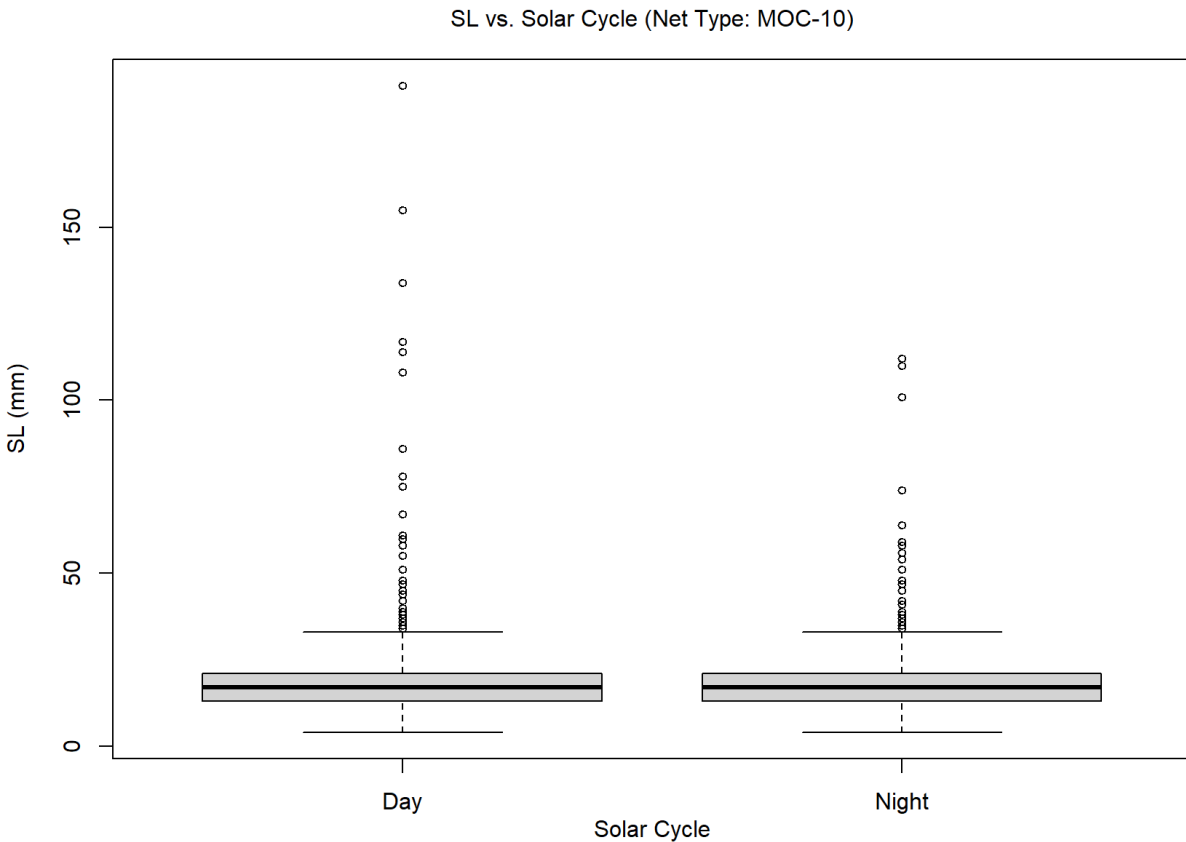


Figure 14. Ceratioid specimen size (SL [mm]) versus time of day trawled (solar cycle) of the MOC-10.

A boxplot of the standard length of ceratioids grouped by solar cycle using the HSRT (Figure 15) revealed that larger specimens were caught during the daytime trawls as well as a larger size range overall. Fifty percent of the samples collected during daytime trawls (N=193) were between 23-45 mm while 50% of the samples collected during nighttime trawls (N=154) were between 25-53 mm. The largest specimen caught during the day was *Gigantactis gargantua* (290 mm SL), while at night was *Gigantactis microdontis* (189 mm SL). The smallest specimen caught during daytime trawls was *Himantolophus sp.* (13 mm) while during nighttime trawls was *Cryptopsaras couesii* (12 mm). The median was 32 mm for daytime trawls and 34.5 mm for nighttime trawls.

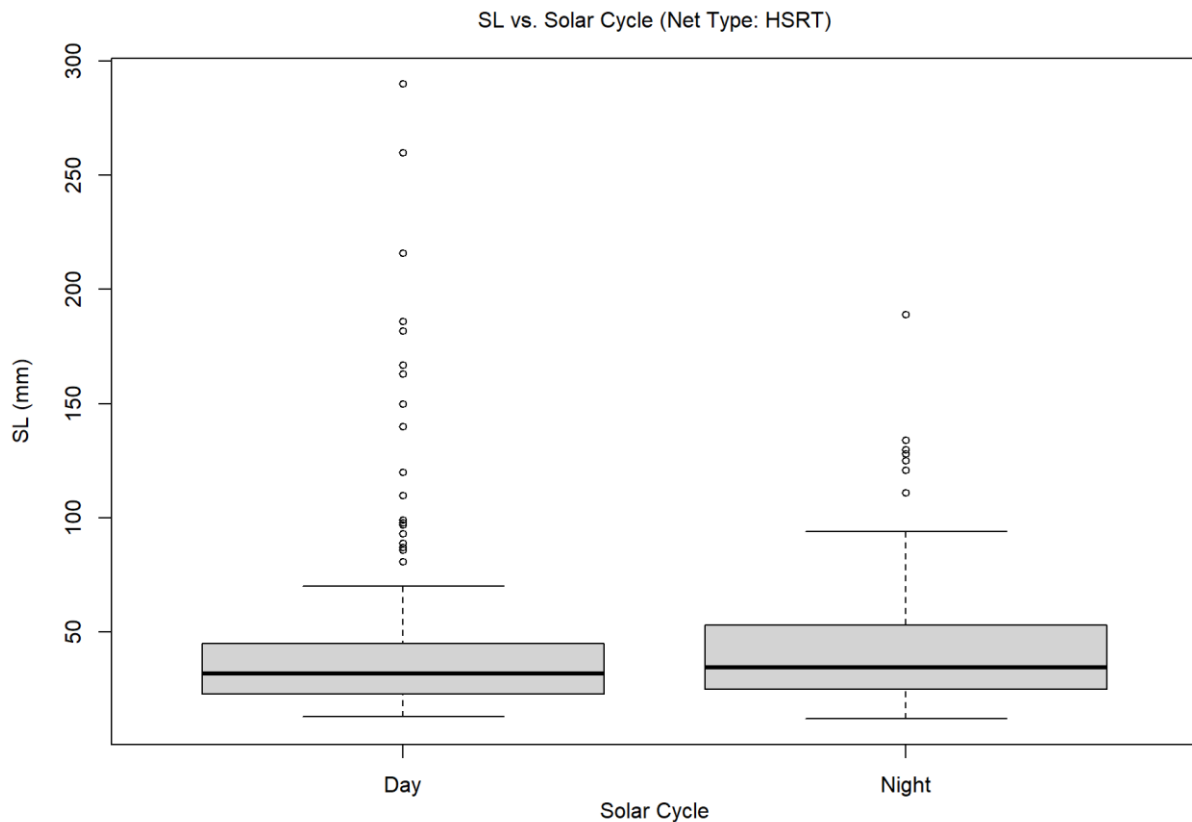


Figure 15. Ceratioid specimen size (SL [mm]) versus time of day trawled (solar cycle) of the HSRT.

### **3.4. Vertical Distributions**

Ceratioidei in the Gulf of Mexico were collected in every depth zone during both day and night. The fewest ceratioids were caught in the epipelagic zone and were primarily larvae. Four main patterns were identified for the vertical distribution of all quantitatively caught specimens. Below each pattern will be discussed in detail including the taxa showing that pattern.

#### 3.4.1. Pattern One – Epipelagic Residence with Ontogenic Descent

Pattern one (P1) comprised residents in the epipelagic zone with a rapid descent into mesopelagic or bathypelagic depths (Figure 16). During both day and night, abundance was highest in the epipelagic followed by a decrease in the upper mesopelagic (200-600 m), and finally an increase in abundance again to the maximum depth of the distribution in the lower mesopelagic/upper bathypelagic (600-1200 m) or to the maximum depth of the sampling, which includes part of the bathypelagic zone (1500 m). Of the taxa that showed this pattern, larvae are the predominate morphotype and thus the classification of this pattern as an ontogenic migration.

For Linophrynidae larvae, the majority (52.6%) were caught in the epipelagic (0-200 m). The mesopelagic (200-1000 m) showed the lowest abundance throughout the water column (13%). The two deepest strata (1000-1500 m) showed a higher abundance (34.4%) than the mesopelagic zone, however not as high as the epipelagic zone. Based on the 154 specimens caught, equal numbers were collected day and night in the two deepest strata thus suggesting limited or no vertical migration and constant occurrence during day and night.

For Himatolophidae, 50% were caught between 0-200 m. The lowest abundance was shown in the upper mesopelagic (200-600 m) at 8%. The lower mesopelagic/upper bathypelagic strata (600-1200 m) showed a higher abundance (42%) than the strata above it. Zero ceratioids

were collected in the deepest strata (1200-1500 m) suggesting the maximum depth of their occurrence is in the upper bathypelagic zone. Similar numbers were collected day and night suggesting constant occurrence and limited or no vertical migration.

Gigantactinidae larvae had a very low sample size (N=4). These low values still suggest an ontogenic migration due to the presence of larvae in the 0-200 m strata (epipelagic zone), followed by only one specimen caught between 200-1000 m, and then an increase in abundance caught (50%) in the upper bathypelagic (1000-1200 m). During daytime trawls, three specimens were collected compared to only one at night. However, this sample size is too small to assume that vertical migration is occurring.

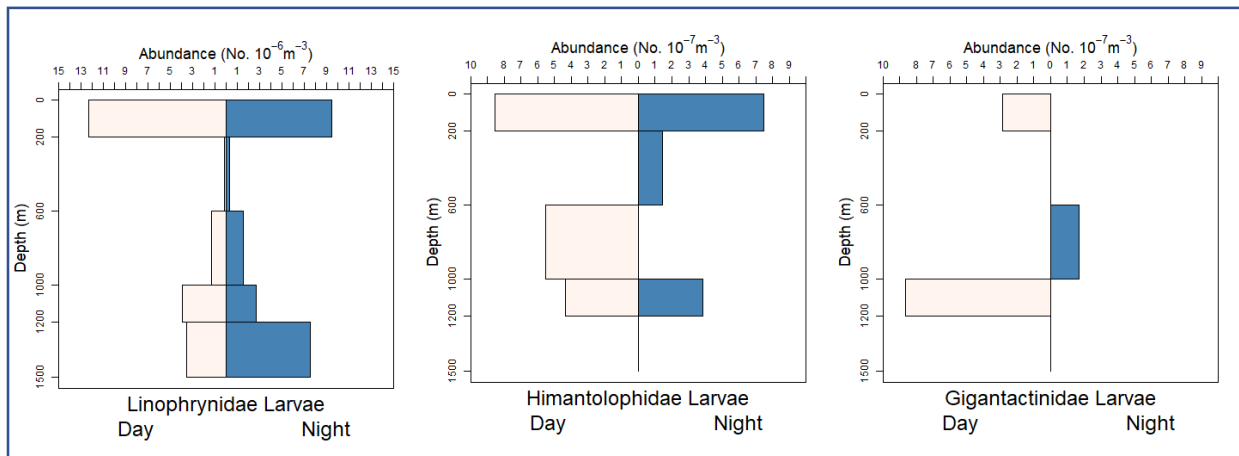


Figure 16. Pattern One (P1) vertical distributions. \*Note scale differences in abundance.

### 3.4.2. Pattern Two – Primarily Mesopelagic Occurrence

Pattern two (P2) comprised residents with a primarily mesopelagic residence. There was evidence of an upper bathypelagic presence in some taxa. Certain taxa also displayed a weak migration from upper bathypelagic depths (1500-1000 m) to lower mesopelagic depths (1000-

600 m) or from lower mesopelagic depths (1000-600 m) to upper mesopelagic depths (600-200 m). There is minimal, if any, epipelagic (0-200 m) presence in this pattern.

Ceratiidae are unique in that the females (two species), males, and larvae all displayed the same P2 vertical distribution pattern (Figure 17). *Cryptopsaras couesii* was the first of the two female species analyzed. The majority (86.8%) were collected in the mesopelagic zone (200-1000 m) with minimal presence from 0-200 m (4.2%) and 1000-1500 m (9%). Of the 143 *C. couesii* collected, similar numbers were collected day (N=64) and night (N=79) suggesting constant occurrence and a very weak or no vertical migration. The second female species analyzed was *Ceratiias uranoscopus* and this taxon had a small sample size (N=8). All of the *C. uranoscopus* caught were collected in the mesopelagic zone (200-1000 m). Similar numbers were collected across daytime (N=3) and nighttime trawls (N=5). A potential weak migration from lower mesopelagic depths to upper mesopelagic depths is possible; however, the sample size is too low to validate this. Ceratiid males were most abundant (78%) in the mesopelagic strata. There were no males caught in the epipelagic zone (0-200 m) and the remaining males (22%) were collected in the upper bathypelagic (1000-1200 m). Similar numbers were collected day (N=27) and night (N=32) suggesting constant abundance throughout the water column and a very weak or no vertical migration. The larvae did not show an ontogenic migration with zero collected in the epipelagic zone and the majority (67%) were collected in the mesopelagic zone (200-1000 m). There was also a presence (33%) of the Ceratiid larvae in the upper bathypelagic zone (1000-1200 m). More larvae were collected during daytime trawls (N=6) compared to nighttime trawls (N=3). However, low sample size prevents any assumptions regarding vertical migration for this taxon.

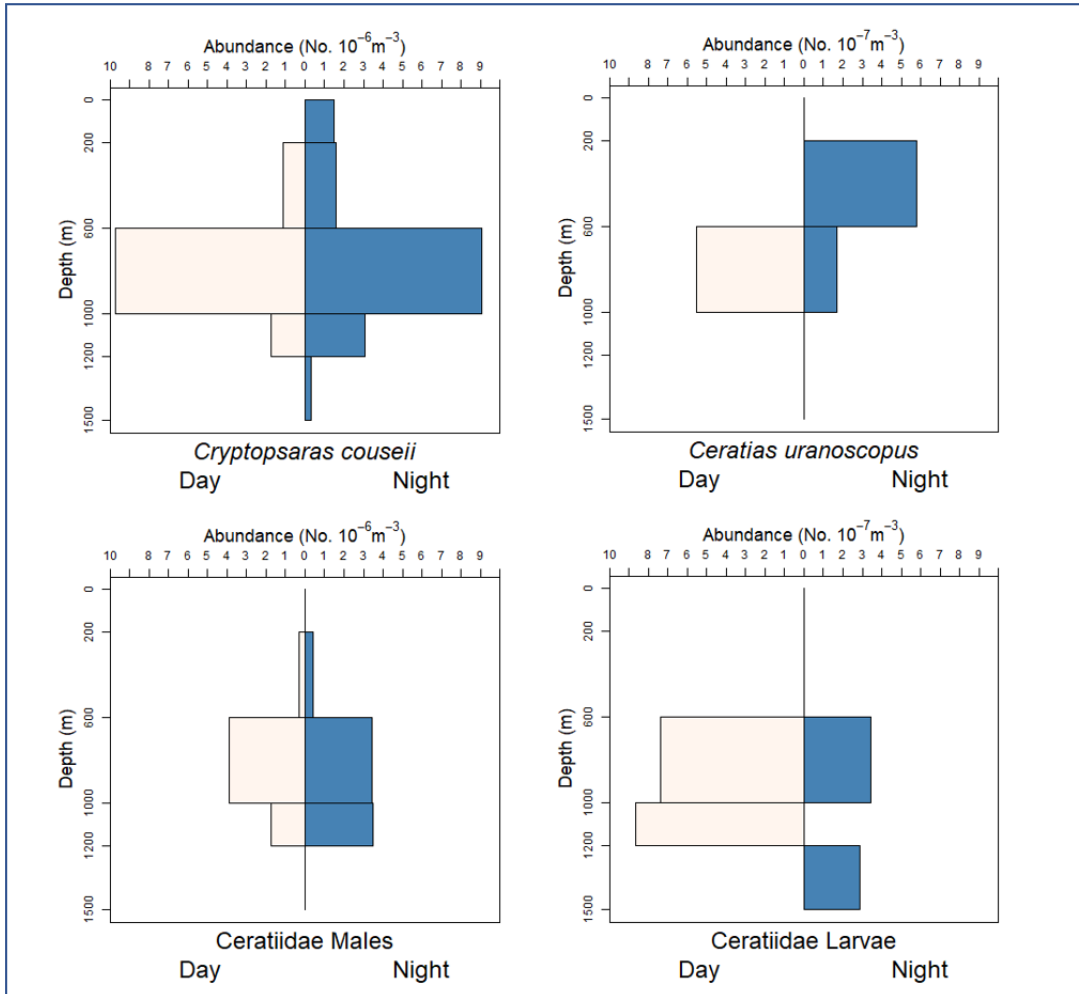


Figure 17. Pattern Two (P2) vertical distributions of the family Ceratiidae. \*Note scale differences in abundance.

Melanocetidae taxa analyzed all typified a P2 distribution except for the males (Figure 18). The first female species analyzed was *Melanocetus murrayi*. The majority of *M. murrayi* (82%) were caught in the lower mesopelagic zone (600-1000 m). Zero were collected in the epipelagic zone or upper mesopelagic (0-600 m) and the remaining 18% were collected in the upper bathypelagic zone (1000-1200 m). More *M. murrayi* were collected during daytime trawls (N=7) than nighttime trawls (N=4). This low sample size prevents any assumptions regarding

vertical migration for this taxon. The second female species analyzed was *Melanocetus johnsonii*. Similar to the other female species analyzed, the majority of *M. johnsonii* (86%) were collected in the lower mesopelagic zone (600-1000 m). Zero were collected in the epipelagic zone or upper mesopelagic (0-600 m) and the remaining 14% were collected in the bathypelagic zone to the maximum depth of sampling (1500 m). More *M. johnsonii* were collected during daytime trawls (N=9) compared to nighttime trawls (N=5). However, also similar to *M. murrayi*, low sample size prevents any assumptions regarding vertical migration. For melanocetid larvae, the majority (60%) were caught in the mesopelagic zone. Zero were collected in the epipelagic or upper mesopelagic zone (0-600 m) as seen with the female taxa analyzed. The remaining 40% were collected in the bathypelagic zone (1000-1200 m) and all were collected during daytime trawls. Similar numbers were collected during daytime (N=3) and nighttime (N=2) trawls suggesting constant abundance with limited or no vertical migration.

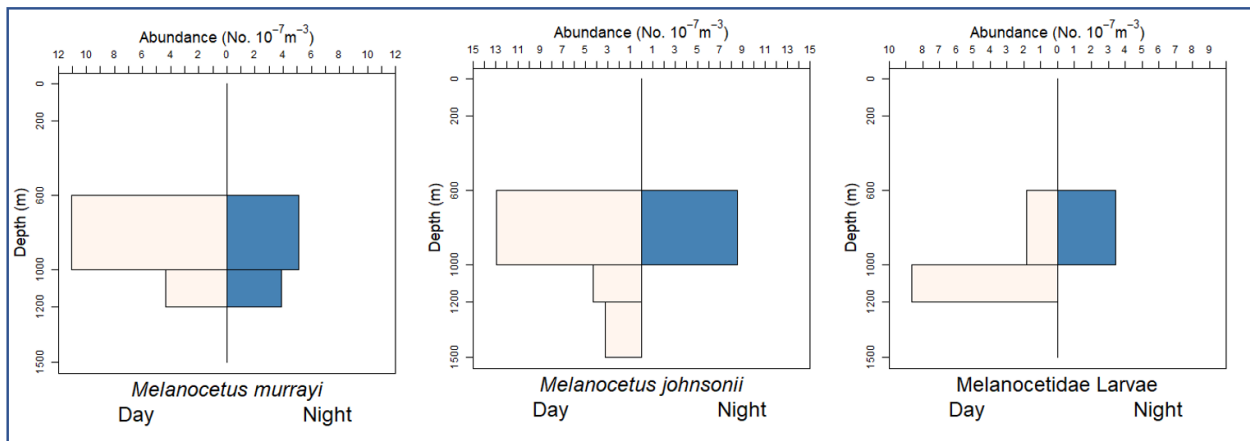


Figure 18. Pattern Two (P2) vertical distributions of the family Melanocetidae. \*Note scale differences in abundance.



Of the Oneirodidae taxa analyzed, the female groups all typified a P2 distribution (Figure 19). The first female taxa analyzed was *Chaenophyrne draco*. The majority of *C. draco* (69%) were collected in the mesopelagic zone (200-1000 m). Zero *C. draco* were collected in the epipelagic zone (0-200 m) with the remaining specimens (31%) collected in the upper bathypelagic zone (1000-1200 m). More *C. draco* were collected during nighttime trawls (N=9 versus N=4, respectively) suggesting the potential for a weak migration from upper bathypelagic/lower mesopelagic depths (600-1200 m) to lower mesopelagic/upper mesopelagic depths (1000-200 m). The second female taxa analyzed, *Oneirodes* spp. TBD, also had the majority of the taxon collected (74%) from the mesopelagic zone (200-1000 m). Zero were collected in the epipelagic zone (0-200 m) with the remaining 36% collected in the upper bathypelagic (1000-1200 m). Of the 19 ceratioids collected, nearly equal numbers of specimens were caught during daytime trawls (N=9) and nighttime trawls (N=10) suggesting constant occurrence and limited or no vertical migration. The third female taxa analyzed, Oneirodidae TBD, had the majority of the taxon (82%) collected in the lower mesopelagic zone (600-1000 m). Zero Oneirodidae TBD were collected in the epipelagic zone (0-200 m) and the remaining 18% were collected in the bathypelagic zone to the maximum depth of sampling (1500 m). Of the 11 specimens collected, nearly equal numbers were collected during daytime (N=6) and nighttime (N=5) trawls suggesting constant occurrence and limited or no vertical migration similar to *Oneirodes* spp. TBD. The final taxa that typified P2 in the Melanocetidae family were the larvae. The majority (58%) were collected in the mesopelagic zone (200-1000 m). Unlike other taxa typifying this pattern, 16% were collected in the epipelagic zone (0-200 m). It is important to note, however, that this was represented by only two specimens and the overall sample size was small. The remaining 26% were collected in the bathypelagic zone. More

Oneirodidae TBD were collected during nighttime trawls (N=8 versus N=5) suggesting the potential for a weak migration from upper bathypelagic/lower mesopelagic depths (600-1200 m) to lower mesopelagic/upper mesopelagic depths (1000-200 m).

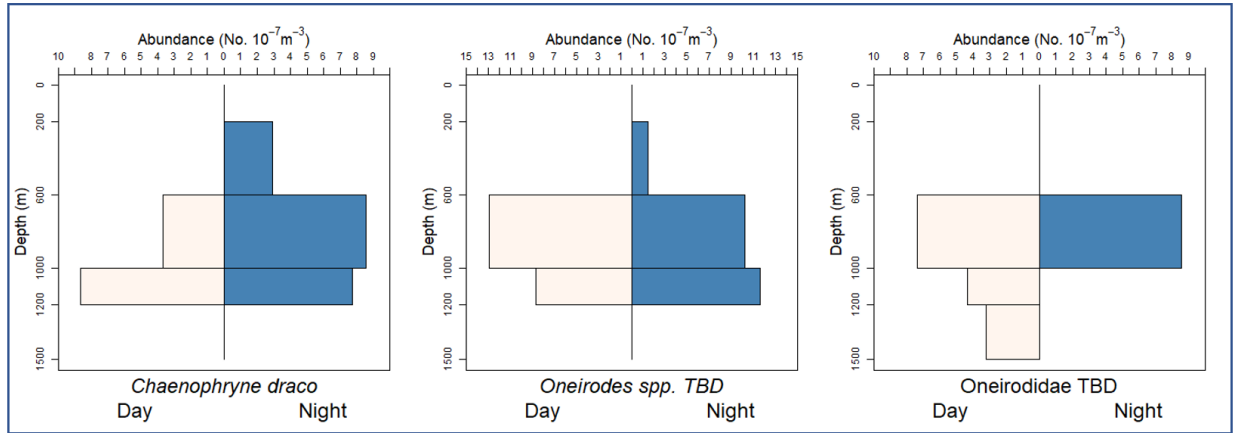


Figure 19. Pattern Two (P2) vertical distributions of the family Oneirodidae. \*Note scale differences in abundance.

### 3.4.3. Pattern Three – Wide Vertical Ranges

Pattern three (P3) comprised residents that move up and down the water column with no discernible pattern (Figure 20). These “spanner” groups occurred in all three depth zones, epipelagic, mesopelagic, and bathypelagic (0-1500 m) and during both day and night. This pattern was represented by the least number of taxa.

The first taxon that typified P3 was *Haplophryne mollis*. Similar percentages of abundance occurred throughout the three major depth strata: 33% in the epipelagic zone (0-200 m); 44% in the mesopelagic zone (200-1000 m); and the final 23% in the bathypelagic zone (1000-1500 m). *H. mollis* occurred in all depth zones both day and night. Of the nine *H. mollis* caught, nearly equal numbers were collected during daytime (N=4) and nighttime (N=5) trawls

suggesting constant occurrence in all depth strata as well as no vertical migration influencing that occurrence.

The second taxon that typified P3 was the Oneirodidae males. Similar percentages of abundance occurred throughout the lower mesopelagic (600-1000 m), upper bathypelagic (1000-1200 m) and lower bathypelagic to the maximum depth of sampling (1500 m). These percentages represented 27.3%, 33.3%, and 39.4% of the abundance respectively. While the males did not occur in the upper 600 m of the water column, the maximum abundance was at the maximum depth of sampling, suggesting sampling did not reach maximum depth of occurrence and thus an underrepresentation of the full distribution and potential spanner pattern.

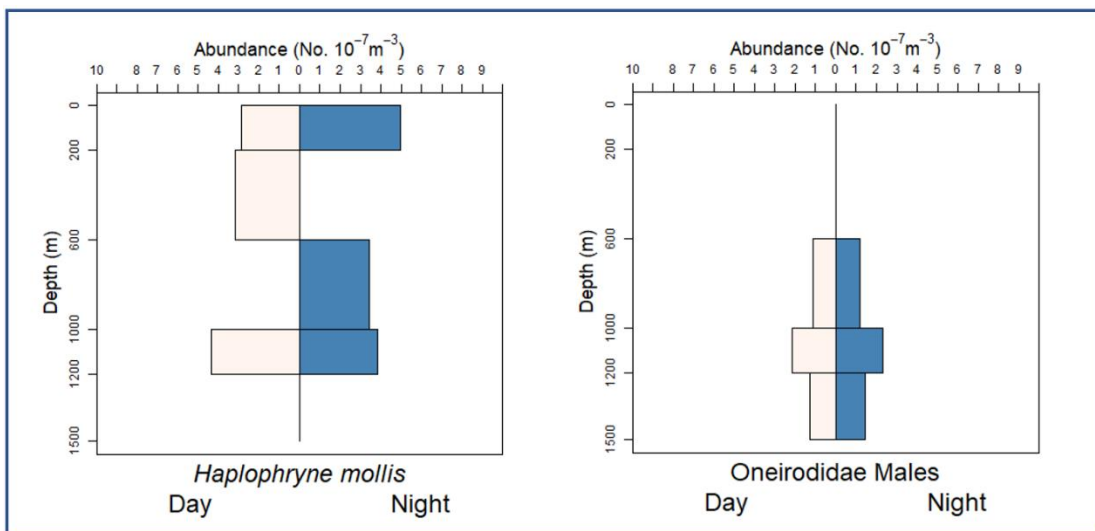


Figure 20. Pattern 3 (P3) vertical distributions. \*Note scale differences in abundance.

#### 3.4.4. Pattern Four – Primarily Bathypelagic Residence

Pattern four (P4) comprised fishes with a primarily bathypelagic residence (1000 m and below). There was evidence of a lower mesopelagic presence by some taxa (600-1000), and a

very limited presence of upper mesopelagic and epipelagic residents (600-0 m). Of the taxa that showed this pattern, males were the predominate morphotype. It is important to note that the bathypelagic zone reaches up to 4000 m while sampling only occurred to 1500 m and thus the potential for what is considered “bathypelagic” in this thesis may only be the top of a taxon’s full distribution.

Four male taxa typified this pattern (Figure 21). The first taxon that represented P4 was the Linophrynidae males. The majority of the males (88%) were collected in the bathypelagic zone (1000-1500 m). Few were collected in the mesopelagic (200-1000 m) and even less in the epipelagic (0-200 m). The shallower the depth strata, the lower the abundance of male linophrynids. Similar numbers of males were collected during daytime (N=107) and nighttime trawls (N=123) suggesting constant occurrence and limited or no vertical migration. For Melanocetidae males, 88% were also collected in the bathypelagic zone (1000-1500 m) with only one specimen being collected above 1000 m. Nearly equal amount of male melanocetids were collected during daytime and nighttime trawls (N=5 and N=4, respectively) also suggesting constant occurrence as seen with the male linophrynids. The Himantolophidae males were not as dominant in the bathypelagic zone as other P4 male taxa; however, the majority of their abundance (55%) still occurred between 1000-1500 m. The remaining abundances were divided out at 40% from the mesopelagic zone and 5% from the epipelagic. Similar numbers were collected during daytime (N=9) and nighttime trawls (N=11) suggesting a lack of vertical migration as seen with the other males displaying this pattern. The final male taxon that typified P4 was the Gigantactinidae males with the majority of their abundance (77%) in the bathypelagic zone (1000-1500 m). During the daytime, there were a small number of males collected in the epipelagic zone and mesopelagic zone. All specimens collected during nighttime trawls were

collected below 1000 m. Similar numbers in daytime and nighttime collections (N=13 and N=9, respectively) suggest the same pattern previously seen with males typifying P4: constant occurrence with limited or no vertical migration.

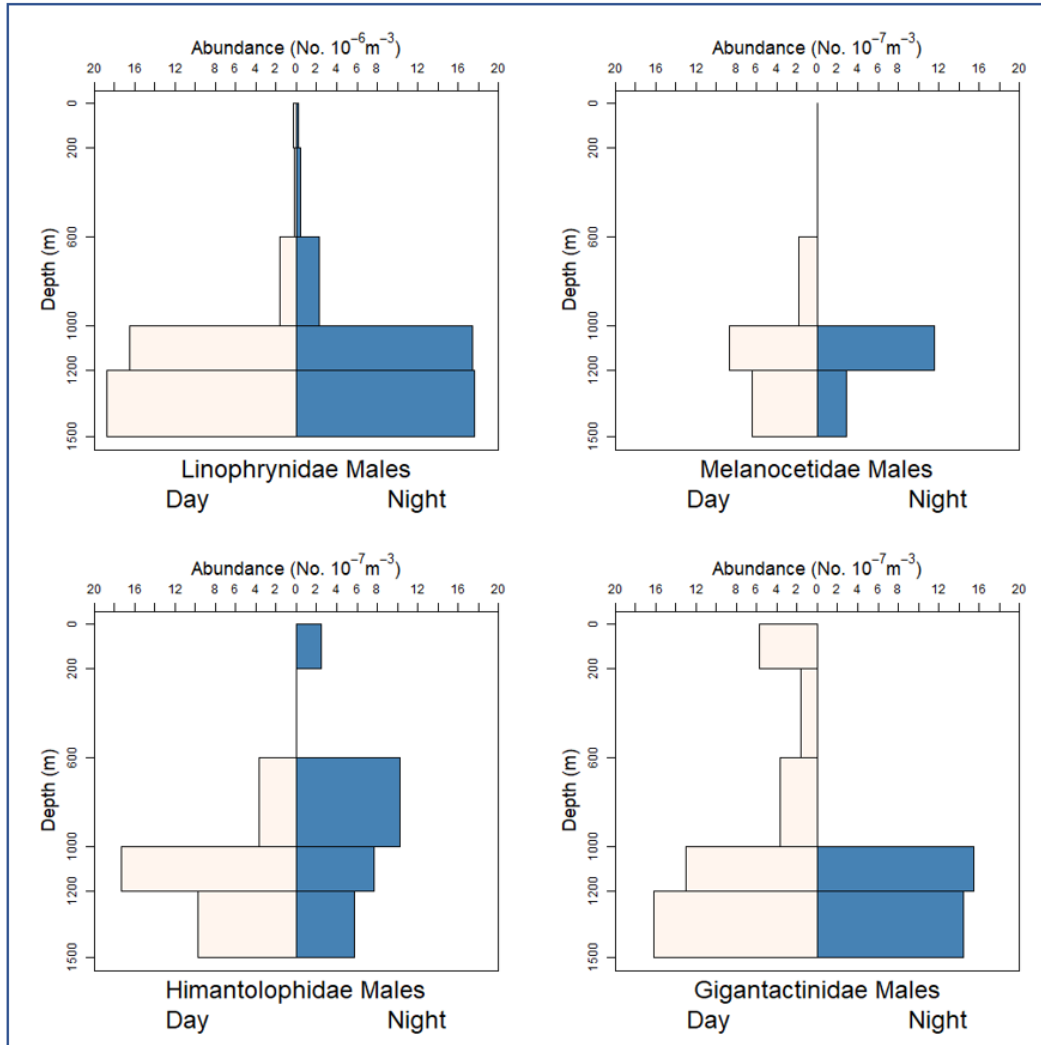


Figure 21. Pattern Four (P4) vertical distributions of male taxa. \*Note scale changes in abundance.

The final taxon that typified P4 was the Linophryniidae TBD (females) (Figure 22). This was the only female taxon to display a primarily bathypelagic distribution. While less than some of the other taxa that typified this pattern, the majority (52%) were collected in the bathypelagic

zone (1000-1500 m). There was a larger abundance in the epipelagic zone (36%) than other taxa displaying this pattern as well. However, the resolution for this family was particularly coarse due to further inquiries needed on certain specimens in this grouping. More Linophrynidae TBD were collected during daytime trawls than nighttime (N=13 and N=8, respectively) as well as deeper.

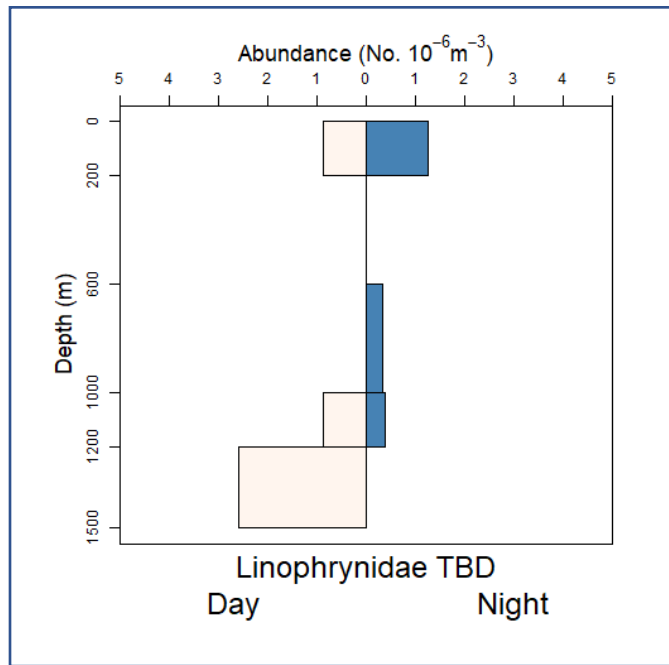


Figure 22. Pattern Four (P4) vertical distribution of Linophrynidae TBD.

### 3.4.5. – Limited Data

Not all taxa could be classified into a pattern due to sampling limitations and low relative abundance counts. Thaumatchthyidae larvae, *Linophryne* spp. TBD (females), Caulophrynidae males, and Caulophrynidae larvae were such taxa. Vertical distribution plots for these organisms are presented in Appendix A. Quantitative depth data were not collected for Neoceratiidae, Diceratiidae, and Centrophrynidae.

## **4. Discussion**

While previous studies have described new species (Pietsch and Sutton, 2015) and characterized microbial symbiosis (Freed, et al. 2019) of ceratioid anglerfishes in the Gulf of Mexico, this study represents the first examination the faunal composition and spatial dynamics of an entire ceratioid assemblage in the GoM. A summary of the biogeographic distribution of individual taxa is presented by Pietsch (2009), but this does not specifically describe the GoM assemblage. The last comprehensive analysis of Ceratiodei (Pietsch, 2009) examined 7095 specimens from 90 institutions around the world. NSU's collection from the GoM contained 1726. The analysis of gear type, sampling time, sampling effort, relative abundance, and vertical distribution of females, males, and larvae of all 11 families provides the most comprehensive summary of this suborder for any ecoregion of the World Ocean.

### **4.1. Faunal Composition**

From the three field programs, the *Meg Skansi* cruise series (comprised of 241 trawl deployments) collected the most ceratioids, followed by *Pisces* (171 trawl deployments), and then DEEPEND (122 trawl deployments). The most abundant taxon collected on the *Meg Skansi* and DEEPEND cruises was the family Linophrynidae (primarily males), whereas the most abundant taxon collected during *Pisces* cruises was *Himantolophus* spp.

The HSRT used on *Pisces* had a larger mouth opening (336.64 m<sup>2</sup> EMA for *Pisces* 8 and 9; 165.47 m<sup>2</sup> EMA for *Pisces* 10 and 12) than the MOC-10 (10 m<sup>2</sup>) (Cook, et al. 2020). The HSRT maximized the volume of water filtered, and therefore sampled more and larger specimens than the MOC-10. However, the HSRT lacked the vertical resolution of the MOC-10

sampling and was not flow-metered to allow for catch standardization. Despite size and faunal differences of the collections with the different gears, no significant difference was noted in size versus time of day of collection (day vs. night), suggesting that catchability does not vary on a diel basis.

### Sex Ratios

Females and males were not collected in a 1:1 ratio, but this was highly taxon-specific, as well as gear-specific. Of the two dominant taxa of anglerfishes collected, females dominated the catches of the ceratiid *Cryptopsara couesii*, while males dominated the catches of the family Linophrynidae. Both of these patterns were manifest in catches from the smaller trawl (MOC10), though it should be noted that large females (e.g., all taxa other than *Cryptopsaras*) were infrequently caught with the MOC10. Females dominated all large-trawl (HSRT) samples, ostensibly due to escape of the smaller males through the larger meshes. Given that trawl avoidance and/or escapement is a function of all midwater sampling and not unique to this study, this discussion will be focused on natural elements of variation. Males and females of teleost fish can be produced in equal proportions (Parker, 1992). However, the sexual dimorphism present in ceratioids is unlike any other documented taxon. Clarke (1983) reported uneven sex ratios (favoring females) in other deep-pelagic fish taxa, Myctophidae and Stomiidae. It is possible that the considerable difference in abundance between males and females is due to a reproductive strategy in which more energy is partitioned to the production of females rather than the males. Given that males are not known to feed, while females are considered voracious, opportunistic, ambush predators (Espinoza and Wehrmann, 2008; Haubrock et al., 2020), the main driver of assemblage success in the bathypelagic may be the severe partitioning of assemblage biomass in the egg-producing component. The extreme dwarfism and reduced abundance of males may



reduce male-male competition for mates, something postulated for other taxa with dwarfed males such as *Parexocoetus mento*, the African sailfin flying fish (Parker, 1992). Mortality rates of males may be higher due to their lack of feeding and weaker and/or smaller size.

## Females

The most abundant family with respect to females, the Ceratiidae, is circumglobal (Pietsch, 2009). The most abundant species caught, *Cryptopsaras couesii*, has the highest known number of metamorphosed females in collections (N=983 as of Pietsch, 2009). The ability of *C. couesii* females to accommodate more than one male at a time (potentially up to eight; Munk, 2000; Pietsch, 2005; Swann, et al., 2020) could be a factor in their success and ability to survive circumglobally and in the bathypelagic zone. The ability to amplify mate attachment increases the potential for higher reproductive success.

Oneirodidae is poorly represented in ichthyology thus lacks geographical and depth characterization (Pietsch, 2009). Due to it being so speciose, a broad overview of the family may not be particularly useful. In the GoM, it represented the second-most frequently caught family with respect to females. Many of the Oneirodidae specimens in this collection lack taxonomic resolution, and were classified simply to family or the genus *Oneirodes*. Species classification of Oneirodidae is difficult due to the minute differences between them, such as minimal differences between epibranchial tooth counts and escal bulb appendages (Key to Female Species of the Genus *Oneirodes*, retrieved from Pietsch, 2009). Very few characters are considered particularly robust (Sutton, pers. comm.). Clearly, more work is needed on this diverse taxon.

Caulophrynidae, Neoceratiidae, and Centrophrynidae contributed three species to the GoM female assemblage. The lack of motility in ceratioid anglerfishes suggests limited

avoidance capacity, further suggesting that these are indeed rare taxa in the GoM.

Caulophrynidae are well represented in all three oceans, typically between 65°N and 50°S and in the mesopelagic/upper bathypelagic zones (Pietsch, 2009). Their poor representation in the GoM may be a function of deeper residence in the bathypelagic zone than was sampled (1500 m).

Neoceratiidae has not been previously documented in the GoM. This deep-living bathypelagic family with a single species (Pietsch, 2009) may also reside below depths sampled here.

Centrophrynidae also contains one species, *Centrophryne spinulosa*, and contributed 13 specimens to the GoM assemblage. There has been previous documentation of *C. spinulosa* in the GoM (Pietsch, 2009). A mesopelagic and bathypelagic species, sampling efforts and a lack of quantitative samples limited the ability to create an accurate picture of their composition and distribution.

### Males

An important distinction when assessing male abundance by family is the presence of sexual parasitism and/or a free-living stage. The two most frequently caught families exhibit external sexual parasitism. The high catch rate of Linophrynidae and Oneirodidae males could be representative of a lower mortality rate in families with external attachment. Energy allocation could be dedicated to mate interaction and success prior to attachment and thus result in the higher abundance of males of certain species.

Due to the limited knowledge regarding environmental and temporal factors of reproduction in ceratioids, there may be seasons of high male abundances because they have yet to attach to a female to partake in sexual reproduction. Spawning seasonality could differ among families due to the differences in their ecologies. Spawning frequency dynamics are completely

unknown. There could be a large difference between spawning times of different families, and thus an increase in the abundance of one family while another is decreasing.

### Larvae

The relative abundances of larvae mirror that of the adults; the two most-collected families were the first- and second-ranking families of males and females collected, respectively. While typically considered “large” as far as larvae go, some families have small larvae such as in Ceratiidae. The high abundance of Ceratiidae females, but lower counts of larvae, could be a function of capture rates with certain gear types. The most frequently caught family, Linophrynidae, tends to have more elongated and highly inflated bodies than other ceratioid larvae (Pietsch, 2009). A larger mass and surface area would increase their probability of being caught compared to slender and compressed larval types that may easily be missed by the net.

## **4.2. Vertical Distributions**

Vertical migration is a common thread among mesopelagic fishes to allow for attenuation of resources, avoidance of predators, or multiple species to occupy the same niche in an assemblage but varying on a diel time scale (Easson et al., 2020; Ursella et al., 2021). Deep-pelagic predatory fishes of the GoM, such as stomiid dragonfishes, have been shown to undertake diel vertical migration (Sutton et al., 1996). Overall, ceratioids of the GoM demonstrated highly limited vertical migration patterns, representing an extreme dichotomy of ecologies with the other primary “lure-using” predatory fishes of the deep pelagial, the dragonfishes. Of the four distribution patterns identified, one displayed ontogenic vertical

migration and one displayed the potential for a weak migration in some taxa of the mesopelagic zone.

#### Pattern One Distribution - Epipelagic Residence with Ontogenic Descent

The pattern one distribution is most similar to that characterized by Bertelsen (1951) as ontogenic vertical migration (Figure 7). Lipid-filled eggs are released from females at depth and float to surface waters due to positive buoyancy. Once those eggs hatch, they feed in the plankton-rich epipelagic zone before beginning their descent to the adults' depths of occurrence. In this study, only larval specimens showed a large residence in the epipelagic zone with evidence of a descent into deeper waters and thus the classification as ontogenic. A total of 169 specimens from three families fit this pattern. Taxa that displayed this pattern were Linophrynidae larvae, Himantolophidae larvae, and Gigantactinidae larvae.

#### Pattern Two Distributions – Primarily Mesopelagic Occurrence

Pattern two is descriptive of a group of fishes who have established permanent residence in the mesopelagic zone such as myctophids (Sutton et al., 2017). This pattern was the most prevalent across all morphotypes, somewhat bucking the paradigm that ceratioid anglerfishes are primarily bathypelagic. Even though males, females, and larvae displayed this pattern, they were from different families indicating that phylogeny does not necessarily determine location in the pelagic water column. In some taxa, a weak vertical migration between the meso- and bathypelagic zones was apparent. While ceratioids have some of the most unique anatomical modifications witnessed in any taxon, the efficient swimming morphology is not one of them. The evidence of weak migration could be indicative of their limited mobility. A total of 305

specimens from three families fit this pattern. Taxa that displayed this pattern were Ceratiidae males, *Chaenophryne draco* (females), Oneirodidae larvae, Oneirodidae TBD (females), Ceratiidae larvae, *Oneirodes* spp. TBD (females), *Ceratias uranoscopus* (females), *Cryptopsaras couesii* (females), Himantolophidae males, *Melanocetus johnsonii* (females), *Melanocetus murrayi* (females), and Melanocetidae larvae.

#### Pattern Three Distributions – Wide Vertical Ranges

Pattern three taxa do not seem to exhibit any one pattern and was displayed by only one male taxon and one female taxon. The “spanner” grouping, as classified by Sutton et al. (2010), displayed a wide vertical distribution that occupies multiple depth zones and occurs throughout the pelagic water column without diel vertical migration. This pattern was the least represented in the assemblage. This group of non-migrators may have adapted to life in multiple depth zones. A total of 42 specimens from two families fit this pattern. Taxa that displayed this pattern were Oneirodidae males and *Haplophryne mollis* (females).

#### Pattern Four Distributions – Primarily Bathypelagic Residence

Sampling the bathypelagic zone during all three cruises reached a maximum depth of 1500 m. For some taxa, this may be only the top of their distribution and the majority of their population resides even deeper. A total of 302 specimens from four families fit this pattern. Taxa that displayed this pattern were Linophrynidae males, Linophrynidae TBD (females), Himantolophidae males, Melanocetidae males, and Gigantactinidae males.

### 4.3. Vertical Distributions by Family

#### Family Linophrynidae

With males and one taxon of females exhibiting a bathypelagic residence, the ontogenic migration pattern of the larvae from the surface to depth fits well with Bertelsen's (1951) reproductive cycle hypothesis. *Haplophryne mollis* however, appears to be an exception within this family. *Haplophryne mollis* is unique in its complete lack of color (Pietsch, 2009). Typically, ceratioids are black or darkly pigmented. No explanation currently exists for why out of all species of ceratioids, *Haplophryne mollis* is the only one with unpigmented skin throughout its life cycle. The stark color contrast between this species and all other ceratioids could explain their interesting vertical distribution. Their lack of pigmentation may have allowed them to take up residence in the epipelagic, mesopelagic, and bathypelagic realms. Their translucent skin may allow them to remain elusive in the epipelagic zone but may not affect them negatively in the unlit zones of the ocean, either.

#### Family Ceratiidae

The only family that displayed a mesopelagic pattern across all female taxa, males, and larvae, Ceratiidae may represent the evolutionary strategy of neoteny, or the retention of juvenile characteristics into adult life stages (Granden and Deesing, 2004). Larval females are hump-backed with a vertical mouth, as seen in the adult females (Pietsch, 2009). Sexual dimorphism is well developed even in small larvae, unlike other ceratioid families (Pietsch, 2009)

Larvae co-occupied the mesopelagic zone with males and females, without evidence of ontogenic descent. Due to the demonstration of neoteny in this family, the females may allocate resources differently during egg formation, decreasing the typical lipid amounts that cause

buoyancy, thus allowing hatching to occur within a similar depth zone to the adults. Eggs hatching at depth may decrease mortality due to predation. Males in this family are sexual parasites. By hatching at depth, they are already close to the females. The low abundance of larvae in the epipelagic zone could also be explained by sampling measures. Ceratiidae larvae can be very small despite already displaying adult characteristics. It is possible that the net was unable to retain young larvae due to their size.

#### Family Melanocetidae

The two female species analyzed in this study, *Melanocetus murrayi* and *Melanocetus johnsonii*, showed similar mesopelagic (P2) vertical distributions. Two congeneric species occupying the same depth zone of the ocean without causing competition for the same resources that could eliminate one another is an example of McClain's (2021) rarity in the deep-sea hypothesis in action. Despite occupying what would seem to be a similar ecological niche, it is likely that females of these species have no impact on their resources, obviating the need for specialization. Rarity works in their favor rather than hinders their success.

Males in this family are not parasitic and were found to have a deeper distribution than the females. If they do not eat and will eventually run out of energy, remaining deep may decrease their mortality rate by minimizing energy expenditure.

Low larval counts prevent a descriptive analysis of their distribution. While there was a higher presence of larvae in the upper mesopelagic at night, this cannot be validated as a meaningful portrayal of vertical migration because of the very low sample size and the difference between day and night collections varying by one specimen.

## Family Oneirodidae

The abundance of females in this family allowed for the analyses of three taxa. All three showed similar distributions and hence the same pattern. Due to the difficulty in species identification of Oneirodidae, it is possible that the females in the Oneirodidae TBD group are females from the other two analyzed (*Chaenophyrne draco* and *Oneirodes* spp. TBD) and thus the similarity in distribution. *Chaenophyrne draco* and *Oneirodes* spp. TBD had extremely similar distributions despite being in different genera. This could be another example of McClain's (2021) rarity in the deep-sea hypothesis, as seen with the melanocetids.

Males in this family had a deeper distribution that overlapped the females but was also deeper, also as seen in the melanocetids; however, unlike melanocetids, they are sexual parasites. The larvae were also found to be deeper than some of the females; however, they did display a residence in the epipelagic zone as well and evidence of an ontogenic descent. The highest mortality rate for fishes is in the beginning stages of their life, when the transition from endogenous to exogenous feeding occurs (Hjort, 1914; Sifa and Mathias, 1987). In the case of male ceratioids however, that "critical period" to their first meal does not exist if feeding does not occur. Their critical period would then instead change from finding a meal to finding a mate. Instead of using energy sources to locate a meal in depth zones of more nutrients, they are going right to the source, the females, which could explain their presence at depth. Once that descent begins after hatching in the epipelagic zone, they begin to metamorphose into males, and then they could be just descending until they find a mate.



### Family Himantolophidae

Another family that fit into Bertelsen's (1951) reproductive cycle, the Himantolophidae demonstrated higher larval abundance in the epipelagic followed by a descent to the mesopelagic zone. The males displayed a primarily bathypelagic presence as seen with other male taxa. Like the male melanocetids, they are also not parasitic. A lack of quantitative female data prevented an analysis of their vertical distribution as well as how the males compare vertically. If those data were available, it would be interesting to note if Himantolophidae follows a similar family distribution pattern to Linophrynidae: larvae hatch at the surface and then descend to the depth of the males and females. If mirroring the Linophrynidae distribution, there is also potential for female species to exhibit spanner distributions that overlap with the males, like *Haplophryne mollis*.

### Family Gigantactinidae

Males displayed residence in the full water column; however, the majority resided in the bathypelagic zone. Gigantactinids have increased mobility compared to other families in the suborder (Pietsch, 2009), which possibly explain their wide vertical distribution. The males in the epipelagic zone could have just metamorphosed from larvae and were nearing the descent to depth. The small sample of larvae demonstrated the potential for an ontogenic migration similar to Linophrynidae and Himantolophidae: presence in the epipelagic zone and then residence in the meso- and bathypelagic zones. Gigantactinidae larvae are unique from other ceratioids in their large pectoral fins (Pietsch, 2009). Increased locomotory abilities due to their fins may allow larvae to better evade capture.

The lack of female data can be explained by sampling measures not reaching the full extent of the bathypelagic zone. While the males may inhabit parts of the upper bathypelagic zone, as seen with other families, that does not necessitate that females are distributed in the same depth intervals. Females of this family are among the largest known ceratioids and are characterized by an extremely long illicium (Pietsch, 2009). That long illicium may allow mate and prey attraction from a farther distance and thus their ability to remain deeper and use rarity to their advantage.

## 5. Conclusions

The ceratioid anglerfishes of the Gulf of Mexico analyzed in this study represent the largest collection of known specimens in existence, as well as the largest study of a single ceratioid assemblage. The assemblage contained all 11 families of the suborder Ceratioidei, but differences in abundances and family composition existed across females, males, and larvae. For females, Ceratiidae comprised the largest abundance of a single family, with intensive contributions from *Cryptopsaras cosei*. Linophrynidae dominated the male and larval assemblages, with little contribution from other families. Across all morphotypes, the lower mesopelagic and upper bathypelagic zone (600-1200 m) contained the maximum species richness and abundance. Deeper sampling is needed to characterize faunal composition in the lower bathypelagic depths.

Diel vertical migration was not present in any ceratioid taxon analyzed; however, four main patterns of vertical distribution were identified: (P1) epipelagic residence followed by relatively rapid descent into deeper waters, most likely indicative of an ontogenic migration; (P2) primarily mesopelagic residence, with some taxa displaying weak vertical migration; (P3) a “spanner” distribution in which the taxa are found throughout the water column; and (P4) a primarily bathypelagic residence, likely deeper than was sampled here.

The survival and radiation of such a charismatic taxon seems to be explained by their ability to largely exist alone. Isolation has become their specialty in the deep Gulf of Mexico. Such a large part of the ocean that is low in food availability, completely lacks light, and lacks diversity in habitat is home to an extremely speciose taxon. Their rarity and isolation have promoted speciation instead of impeding it. Species-specific and sex-specific distributions have developed as an evolutionary response to environmental limiters. Understanding the ecology of

ceratioid anglerfish can aid in understanding other taxa in similar ecosystem structures. A more accurate representation of a highly successful taxa provides insight into evolutionary mechanisms and adaptations that have allowed explosive speciation to occur and thus survival in the most constraining environment on the planet.

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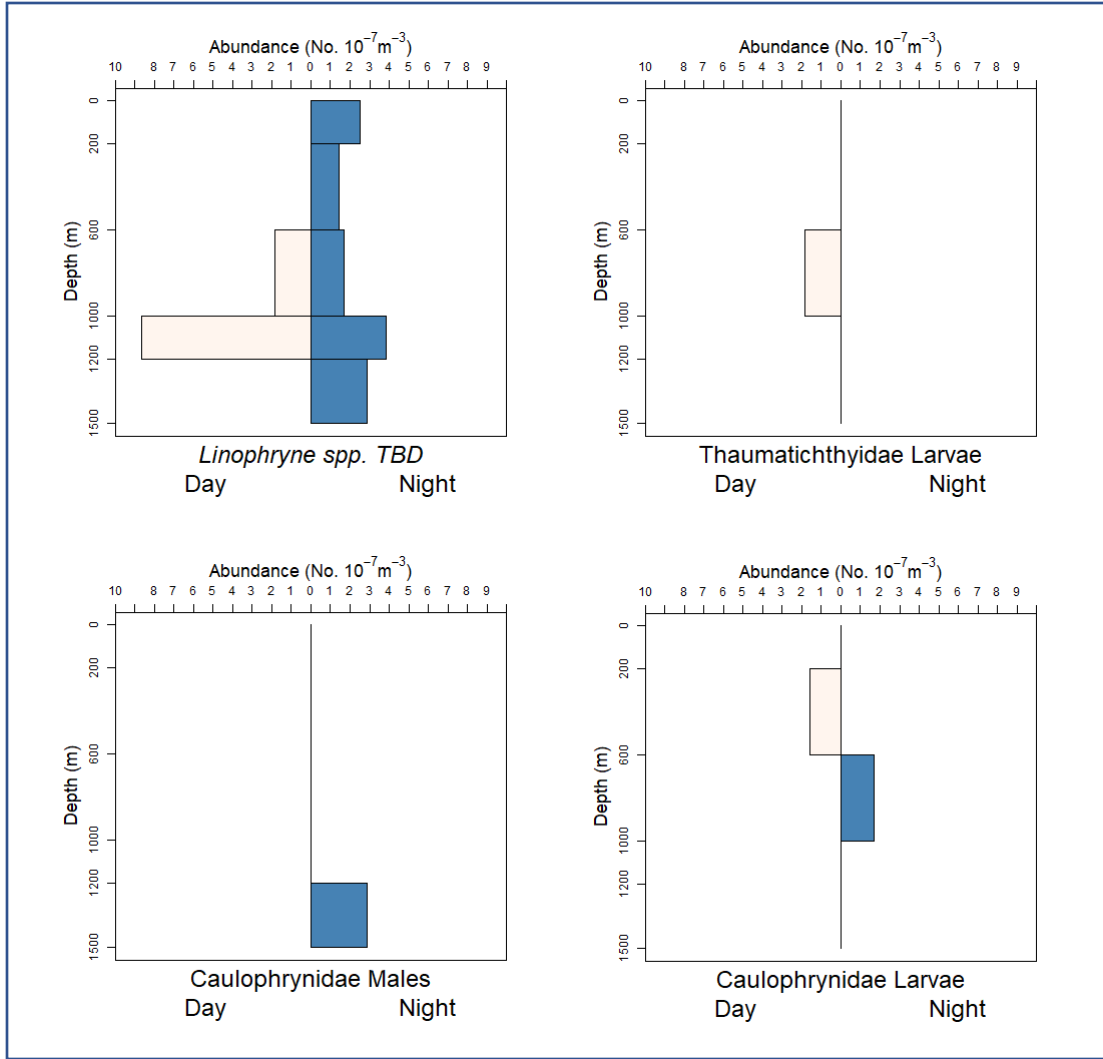
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## 7. Appendix A



Appendix Figure 1. Gallery of vertical distribution plots that lacked enough data to analyze or interpret a distribution pattern. \*Note scale differences in abundance.