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Pelagic Habitat Use By Benthic Fishes – Juvenile Scorpaenoids of the Oceanic Gulf of Mexico

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Thesis of Drew W. Mertzlufft

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Biology

Nova Southeastern University
Halmos College of Arts and Sciences

December 2021

Approved:
Thesis Committee

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

Pelagic Habitat Use by Benthic Fishes – Juvenile Scorpaenoids of the Oceanic
Gulf of Mexico

By
Drew W. Mertzlufft

Submitted to the Faculty of
Halmos College of Arts and Sciences
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The degree of Master of Science with a Specialty in:

Marine Biology

Nova Southeastern University
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ABSTRACT

The suborder Scorpaenoidei is among the most speciose fish taxa of the World Ocean, including the Gulf of Mexico (GoM). Most adult scorpionfishes are benthic and have a pelagic juvenile phase. Although the species descriptions and distributions of adult scorpionfishes within the GoM are well documented, their juvenile forms are largely undescribed. Due to the poorly resolved taxonomic status of juvenile scorpionfishes, their assemblage dynamics have not been accurately assessed. Specimens were collected from the GoM during seven research cruises (2010-2011), as part of the NOAA-supported Offshore Nekton Sampling and Analysis Program (ONSAP), and during six research cruises (2015-2018), as a part of the GOMRI-supported Deep Pelagic Nekton Dynamics of the Gulf of Mexico Consortium (DEEPEND). Members of the suborder Scorpaenoidei occurred within 47% of epipelagic trawls from the ONSAP and DEEPEND surveys. Juvenile scorpaenoids were as abundant within the upper 200 m of the GoM during the day from the DEEPEND survey as one of the most successful midwater fish groups, the Myctophidae. Nine unique morphotypes were defined, with putative identifications, based upon meristics, morphometrics, and internal and external features with an emphasis on head spines. *Pontinus rathbuni* accounted for the majority of specimens collected. Specimens of *P. rathbuni* that were of comparable size to juvenile myctophids (e.g., 15-19 mm standard-length) showed the same diet composition as myctophids but predated during the day as opposed to nocturnal feeding by the myctophids, suggesting a degree of niche partitioning between juvenile benthic and adult pelagic species in a low-latitude oceanic ecosystem.

Keywords: early life stages, oceanic Gulf of Mexico, scorpionfish ecology

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1. INTRODUCTION

1.1. Dominant Holopelagic Fishes and Meropelagic Scorpaenoids – Differing Body Plans Despite Habitat Co-occurrence

The fish families Gonostomatidae, Sternoptychidae, and Myctophidae are the numerically dominant constituents of the mesopelagic ichthyofaunal assemblage of the World Ocean, including the Gulf of Mexico (hereafter referred to as GoM), and thus exhibit a high frequency of occurrence in pelagic trawl catches (Hopkins & Baird 1981, 1985, Cook et al. 2013). These families define a “classic” deep-pelagic morphological ichthyotype, which includes bioluminescent photophores, a lack of spiny fin-rays, weak and low-density musculature, and the presence of countershading (Figure 1; Nafpaktitis 1975, Badcock & Merrett 1976, Kinzer & Schulz 1988, Sutton & Hopkins 1996). In contrast, pelagic-phase juveniles of the suborder Scorpaenoidei (scorpionfishes and allies) deviate from this “classic” form with the presence of heavy spination, relatively robust musculature, and a lack of both bioluminescence and countershading (Figure 2; Washington et al. 1984, Eschmeyer 1998, Nelson 2018). Despite this disparity in body form, pelagic-phase juvenile scorpaenoids have been collected in epipelagic (0-200 m depth) trawls of the GoM at a frequency of occurrence that is comparable to some of the numerically dominant deep-pelagic fishes in the GoM, such as the Myctophidae (anecdotal observation, T. Sutton and J.A. Moore).

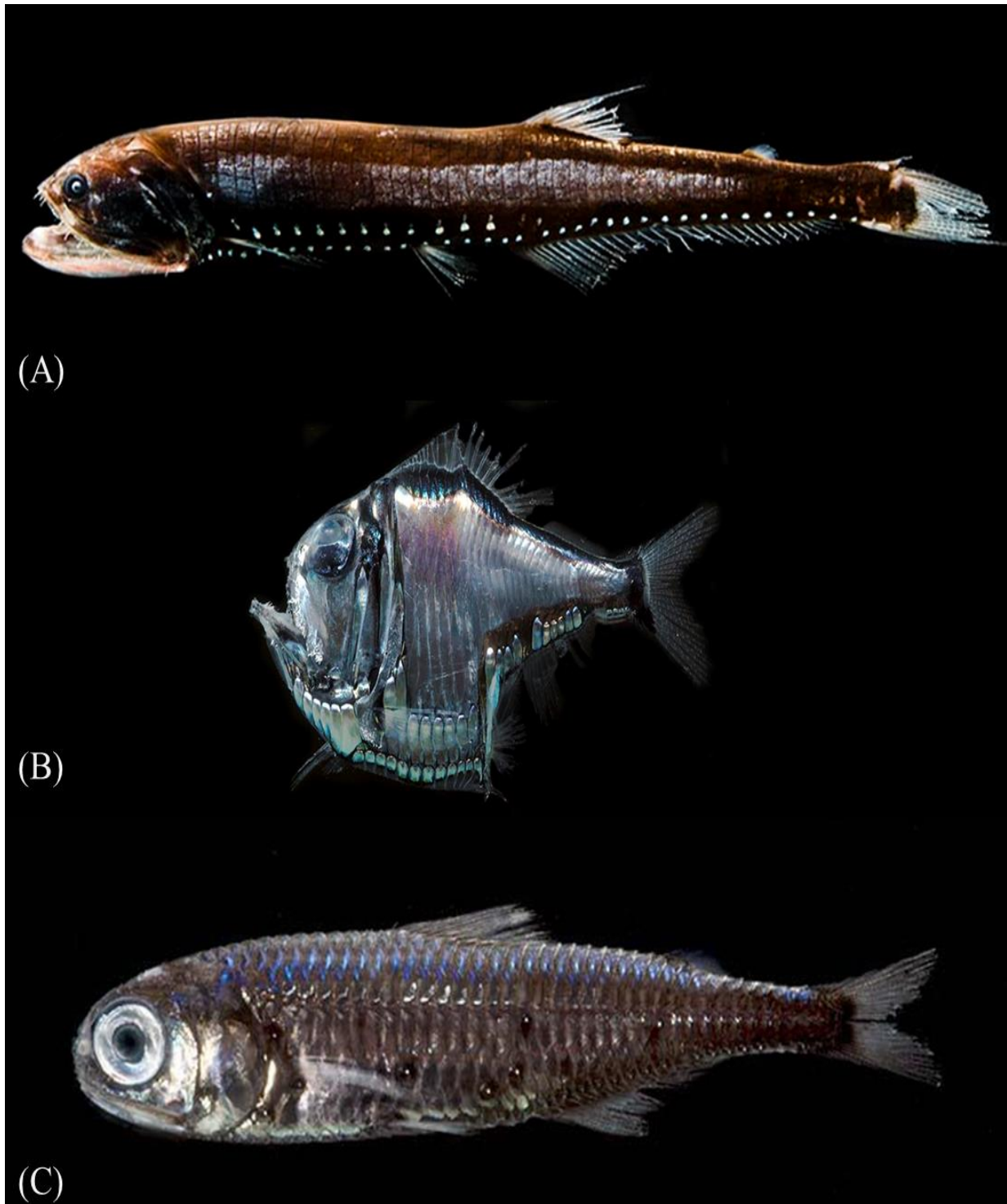


Figure 1. A) *Sigmops elongatus*, a member of Gonostomatidae. B) *Argyropelecus aculeatus*, a member of Sternoptychidae. C) *Myctophum asperum*, a member of Myctophidae. Image credit: DEEPEND/Danté Fenolio.

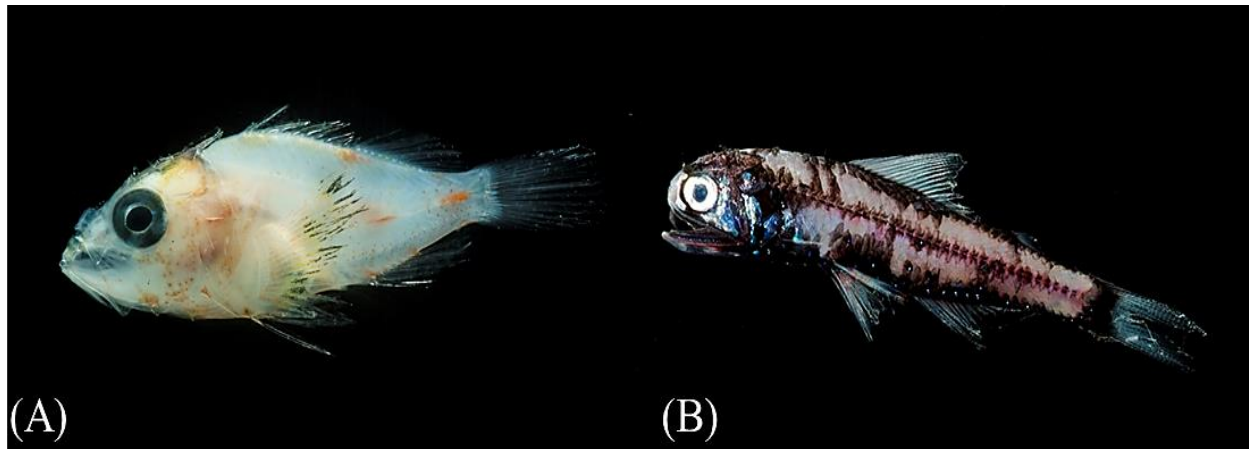


Figure 2. A) A pelagic-phase juvenile scorpaenoid. B) *Diaphus fragilis*, a myctophid exhibiting the classic deep-sea ichthyotype. Image credit: DEEPEND/Danté Fenolio.

1.2. Meropelagic Fish Body Forms, with Emphasis on Scorpaenoids

Meropelagic fishes, such as juvenile scorpaenoids, Anguilliformes (eel leptocephali), and Pleuronectiformes (Figure 3) rely primarily on transparency as juveniles to reduce visually oriented predation (Mukhacheva 1974, Smith 1979, Ahlstrom et al. 1984). Pelagic-phase scorpaenoids also have a diverse range of pigmentation (e.g., erythrin, melanin, and xanthin) in the pectoral fins and throughout the body. Additionally, the head is generally ornate with prominent spination (Figure 3). The head spines of scorpaenoids may aid with extended suspension in the water column by increasing surface area, which in turn increases drag, thus retarding sinking (Cowen & Guigand 2008, Nonaka et al. 2021). The form exhibited by juvenile scorpaenoids may have evolved to accommodate a protracted pelagic phase for greater species dispersal (Love et al. 1990, Rooker et al. 2013).

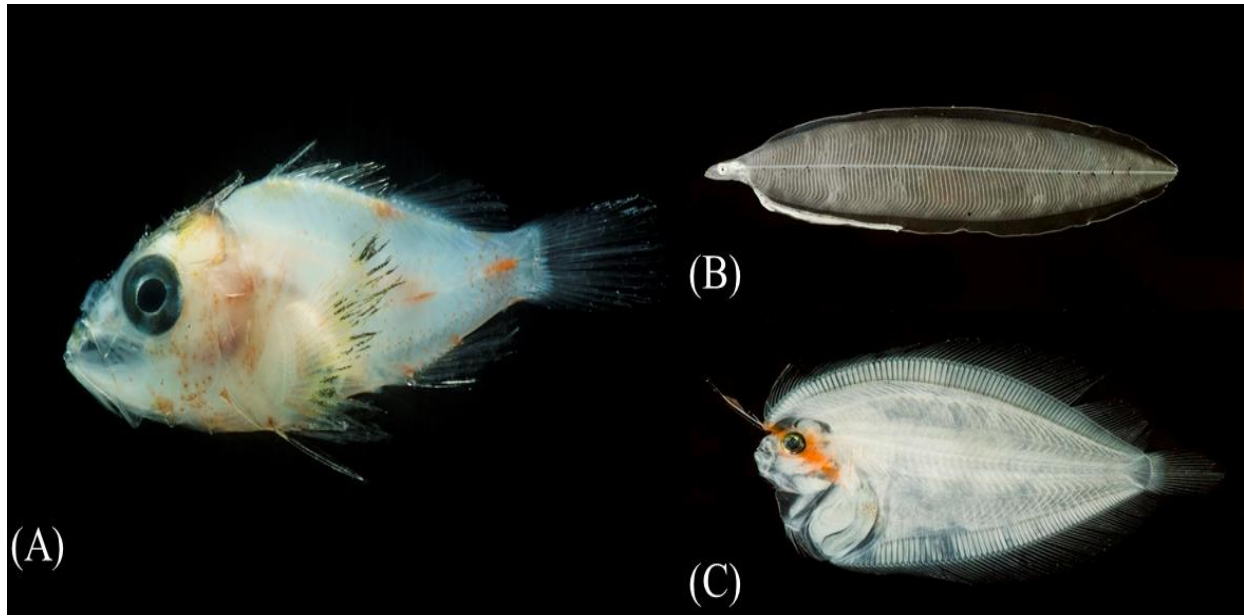


Figure 3. Body forms of: A) pelagic-phase juvenile scorpaenoid, B) eel leptcephalus and C) larval pleuronectiform. Image credit: DEEPEND/Danté Fenolio.

1.3. Scorpaenoid Life History Relative to Pelagic Existence

Scorpaenoids exhibit a wide array of reproductive modes, the most common of which is oviparity (Breder & Rosen 1966, Moyer & Zaiser 1981, Munehara et al. 1997, Sequeria et al. 2003). Members of Scorpaeninae, Pteroinae, Sebastidae, Setarchidae, and Sebastolobinae release a buoyant, gelatinous egg mass into the water column to be fertilized (Moser 1967, 1974, Washington et al. 1984). The gelatinous egg masses floats to the ocean surface and the juveniles develop within the epipelagic (0-200 m). The resulting progeny are carried by surface ocean currents and settle to the benthos after a maximum of one year in order to continue development into adulthood (Boehlert 1977, Moser & Boehlert 1991). Therefore, the pelagic early life history of scorpaenoids gives these fishes the ability to colonize a wide geographic range of benthic habitats.

1.4. Taxonomic Composition of Juvenile Scorpionfishes

The species composition of juvenile scorpaenoids worldwide is inadequately documented because of low taxonomic resolution. Specimens are routinely identified only to order

(Scorpaeniformes) or family (Scorpaenidae) due to knowledge gaps in scorpaenoid ontogeny and development, largely stemming from a lack of unique identifying external traits (Imamura 2004, Smith & Wheeler 2004, Nelson et al. 2018). Juvenile scorpaenoids have meristic overlaps across multiple genera in fin-spine, fin-ray, vertebral, and gill-raker counts (Eschmeyer 1965, 1969, Richards 2006). Therefore, little is known regarding the species-specific early life history of many juvenile scorpaenoids (Washington et al. 1984).

1.4.1. Systematic Background of Scorpionfishes

The order Scorpaeniformes is one of the most speciose orders of fishes, with 24-36 families, 250-280 genera, and over 1,400 species (Washington 1984, Washington et al. 1984, Eschmeyer 1998, Smith & Wheeler 2004), though the order is far from resolved systematically and phylogenetically (Washington et al. 1984, Johnson & Patterson 1993, Imamura & Yabe 2002, Imamura 2004). Some now place the Scorpaeniformes as a suborder within the Perciformes (Fricke et al. 2021), but the traditional classification is used herein pending consensus acceptance of this classification. In the Western Central Atlantic, the order Scorpaeniformes comprises three suborders: Scorpaenoidei (scorpionfishes/rockfishes), Platycephaloidei (gurnards/flatheads/sea robins), and Serranoidei (sea basses/groupers) (Imamura 1996, Poss 1999, Near et al. 2013, Hastings et al. 2015). The suborder Scorpaenoidei includes one family, 11 genera, 29 species, and one subspecies of scorpionfishes in the Western Central Atlantic, including the GoM, (Table 1; Richards 1990, 2006, Smith et al. 2018).

Table 1. Scorpaenoid species in the Western Central Atlantic (adapted from Richards 2006, Smith et al. 2018, Fricke et al. 2021).

Family	Genus and Species
Scorpaenidae	<i>Idiastion kyphos</i> Eschmeyer, 1965 <i>Neomerinthe beanorum</i> (Evermann & Marsh, 1900) <i>Neomerinthe hemingwayi</i> Fowler, 1935 <i>Phenacoscorpius nebris</i> Eschmeyer, 1965 <i>Pontinus castor</i> Poey, 1860 <i>Pontinus helena</i> Eschmeyer, 1965 <i>Pontinus longispinis</i> Goode & Bean, 1986 <i>Pontinus nematophthalmus</i> (Günther, 1860) <i>Pontinus rathbuni</i> Goode & Bean, 1896 <i>Pterois miles</i> (Bennett, 1828) <i>Pterois volitans</i> (Linnaeus, 1758) <i>Scorpaena agassizi</i> Goode & Bean, 1896 <i>Scorpaena albifimbria</i> Evermann & Marsh, 1900 <i>Scorpaena bergii</i> Evermann & Marsh, 1900 <i>Scorpaena brachyptera</i> Eschmeyer, 1965 <i>Scorpaena brasiliensis</i> Cuvier, 1829 <i>Scorpaena calcarata</i> Goode & Bean, 1882 <i>Scorpaena dispar</i> Longley & Hildebrand, 1940 <i>Scorpaena elachys</i> Eschmeyer, 1965 <i>Scorpaena grandicornis</i> Cuvier, 1829 <i>Scorpaena inermis</i> Cuvier, 1829 <i>Scorpaena isthmensis</i> Meek & Hildebrand, 1928 <i>Scorpaena plumieri</i> Bloch, 1789 <i>Scorpaenodes caribbaeus</i> Meek & Hildebrand, 1928 <i>Scorpaenodes tredecimspinosus</i> (Metzelaar, 1919) <i>Helicolenus dactylopterus</i> (Delaroche, 1809) <i>Trachyscorpia cristulata cristulata</i> (Goode & Bean, 1896) <i>Ectreposebastes imus</i> Garman, 1899 <i>Setarches guentheri</i> Johnson, 1862

1.4.2. Taxonomy of Pelagic-Phase Juvenile Scorpaenoids

Scorpaeniform fishes are distinguished from other fishes by the presence of a suborbital stay, a bony strut made of infraorbital bones that connect the lacrimal bone to the preopercle (Figure 4; Nelson 2018). While the suborbital stay is one of the only constant characters of the Scorpaeniformes, finer identification of scorpaeniform species, particularly within juvenile forms, is both complex and controversial (Eschmeyer 1969, Washington et al. 1984, Kendall 1991, Wiley & Johnson 2010). Therefore, the juvenile phases of many Western Central Atlantic scorpaenoids are poorly described (Eschmeyer 1969, Richards 1990, 2006).

The current morphological descriptions of juvenile scorpaenoids are limited to melanin pigmentation, fin-ray branching elements, and internal features within specific size classes (Kendall 1991, Richards 2006). The pigmentation of pectoral fins and their respective fin-ray counts (i.e. meristics) can be difficult to discern because fins and other soft external features are often damaged during collection (Wiebe et al. 1985, Judkins et al. 2017). Some diagnostic internal features are the pigmentation of the gut, the presence or absence of a swim bladder, and the presence or absence of a slit behind the fourth gill arch (McEachran & Fechhelm 2010). However, internal features are often difficult to discern and their use for field identification would require the dissection of individuals before preservation. Therefore, internal features are not helpful for identifications of scorpaenoids immediately following collection while hard external features are much easier to use for identification purposes. Although head spines are not only a salient and hard external feature (Figure 4), the characterization and use of head spination is missing from current taxonomic treatments (Moser et al. 1977, Richards 2006). All juvenile scorpaenoids exhibit spination of the head to varying degrees, and these spines can be useful distinguishing characters (Ginsburg, 1953).

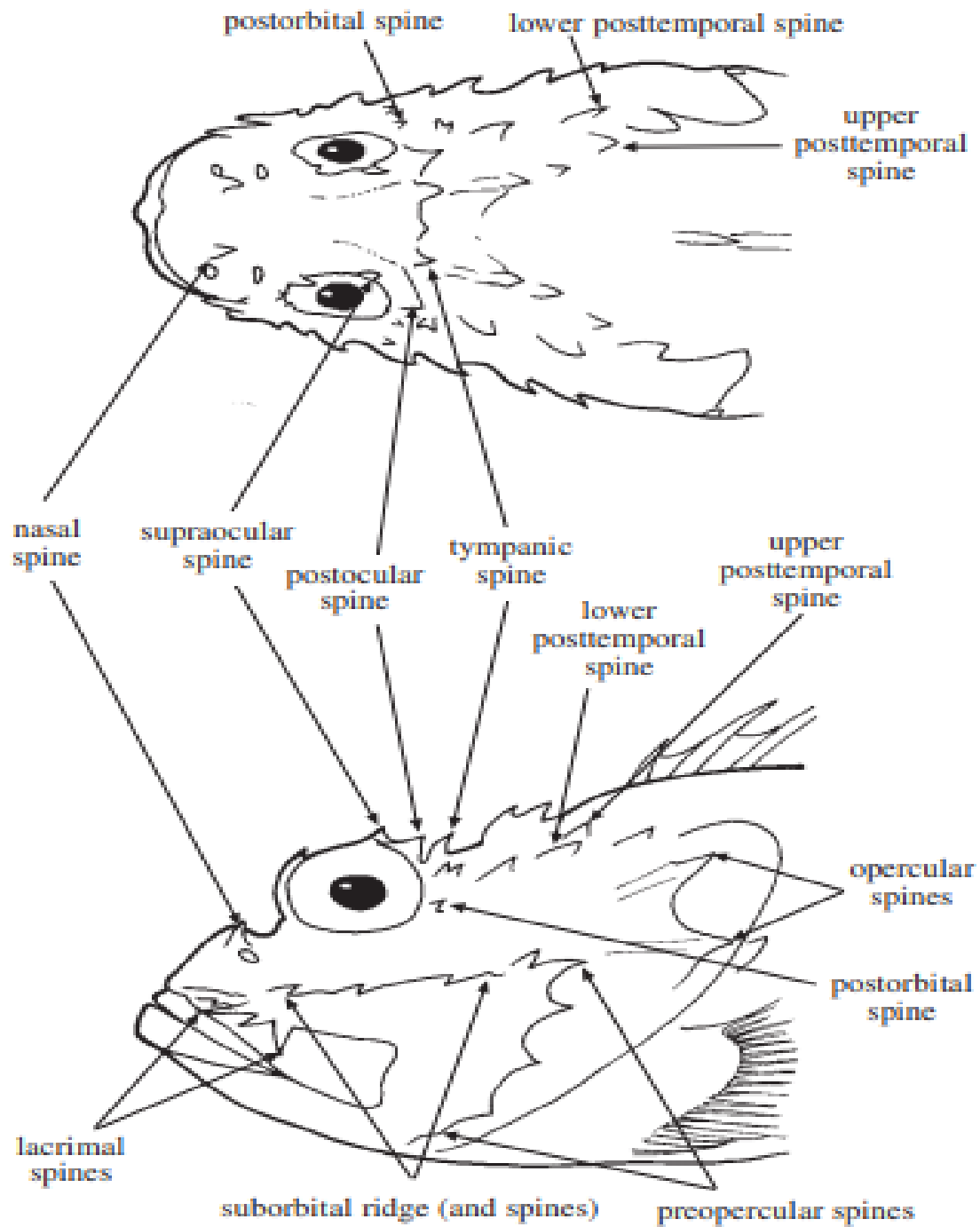


Figure 4. Head spination of a typical adult scorpaenoid (adapted from Eschmeyer 1969)

1.5. Trophic Ecology of Scorpaenoids and Other Pelagic Fishes

The trophic ecology of adult scorpaenoids is well-documented throughout the world, particularly in the Mediterranean and the Pacific (Russell 1983, Stergiou & Karpouzi 2002, Başçınar & Sağlam 2009). However, the diets of larval and juvenile scorpaenoids of the Western Central Atlantic are mostly unknown (Richards 2006). In comparison, the dominant prey of mesopelagic fishes, such as the Myctophidae and Sternoptychidae, is well known. The Myctophidae and some species of Sternoptychidae, like *Lampanyctus alatus* and *Valenciennellus tripunctulatus*, respectively, follow their prey during diel vertical migration and feed within the epipelagic at night (Hopkins & Baird 1985, Hopkins et al. 1996, Link & Almeida 2000). The diet of these species is known through extensive study to consist of copepods, euphausiids, and ostracods (Conley & Hopkins 2004, Stowasser et al. 2009, Drazen & Sutton, 2017). The categories of known prey items for dominant pelagic fishes and the presumed zooplanktivorous diets of juvenile scorpaenoids, as well as a shared use of the epipelagic as habitat, suggest the potential for niche overlap.

1.6. Objectives

The first aim of this thesis was to investigate and compare the frequency of occurrence (percent of trawls in which at least one scorpaenoid was collected) and standardized abundance (no. ind. 10^{-6} m^{-3}) of scorpaenoids within the epipelagic zone of the GoM with that of a well-documented pelagic fish taxon (e.g., Myctophidae). The influence of time of day (day/night) on the frequency of occurrence and standardized abundance of both scorpaenoids and myctophids was also examined. The spatial and temporal water column use of scorpaenoids within the epipelagic of the GoM in comparison to myctophids is described in support of this first aim.

The second aim of this thesis was to identify pelagic-phase juvenile scorpaenoids to genus or species level to provide a faunal inventory for the GoM. Morphotypes of scorpaenoid specimens were defined based on head spination in conjunction with meristics, morphometrics, and internal

features. Genus or species identifications were proposed for each morphotype using available literature. Diagnoses of scorpaenoids identified to species are presented.

The third aim of this thesis was to investigate the trophic ecology of the dominant pelagic-phase juvenile scorpaenoid species to better understand the resource utilization of this taxon within the epipelagic of the GoM. The number of prey types and the cumulative number of prey specimens per prey type were quantified. The diet of pelagic-phase juvenile scorpaenoids was compared with the reported diets of the dominant Myctophidae and Sternoptychidae species in the epipelagic GoM to investigate potential trophic niche partitioning.

2. METHODS

2.1. *Scorpaenoid Sample Collection*

Pelagic-phase juvenile scorpaenoids were collected in the GoM during the National Oceanic and Atmospheric Administration (NOAA)-supported Offshore Nekton Sampling and Analysis Program (ONSAP) from 2010-2011 (Figure 5, Figure 8) as well as during the Deep-Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) consortium research program from 2015-2018 (Figure 6). Seven ONSAP cruises were conducted aboard two vessels, the M/V *Meg Skansi* (MS6, MS7, and MS8) and the NOAA FRV *Pisces* (PC8, PC9, PC10, and PC12), to assess potential environmental damage imposed by the *Deepwater Horizon* oil spill (DWHOS) that started on April 20th, 2010 (Table 2; Cook et al. 2020). The DEEPEND consortium sampled the same stations occupied during the ONSAP from 2015-2018 aboard the R/V *Point Sur* (DP01-DP06) (Table 2). Sampling aboard both the M/V *Meg Skansi* and the R/V *Point Sur* utilized a 10-m² Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) with a mesh size of 3 mm (Wiebe et al. 1985). Sampling aboard the FRV *Pisces* utilized a commercial high-speed rope trawl (HSRT) with a 165-m² mouth area and 3.2-m to 19-mm mesh sizes.

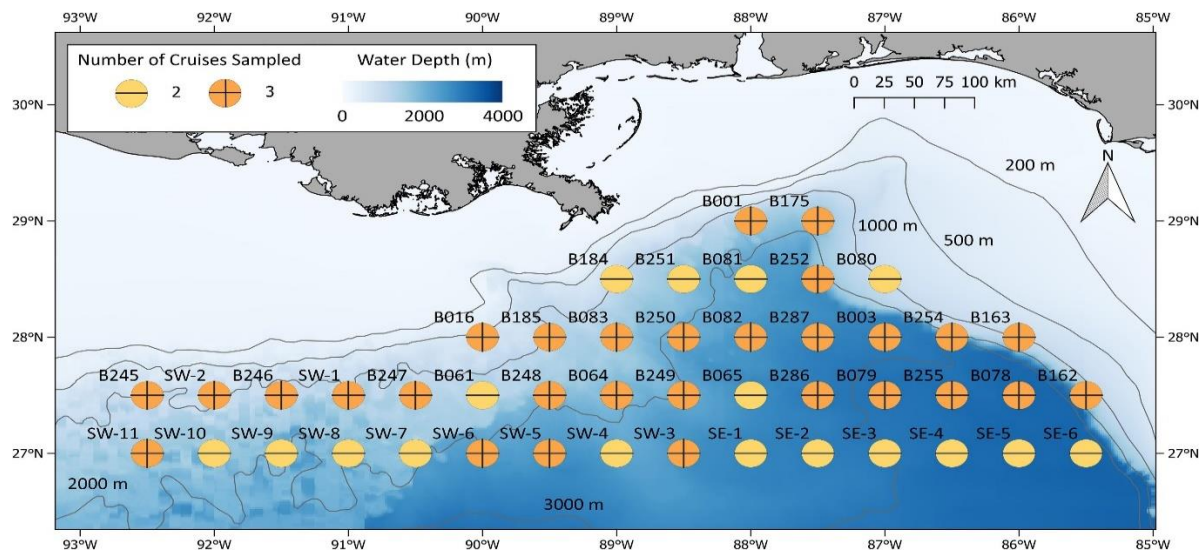


Figure 5. ONSAP MOCNESS sampling stations in the winter, spring, and summer 2011. Symbol colors represent the number of cruises that each station was sampled (adapted from Cook et al. 2020).

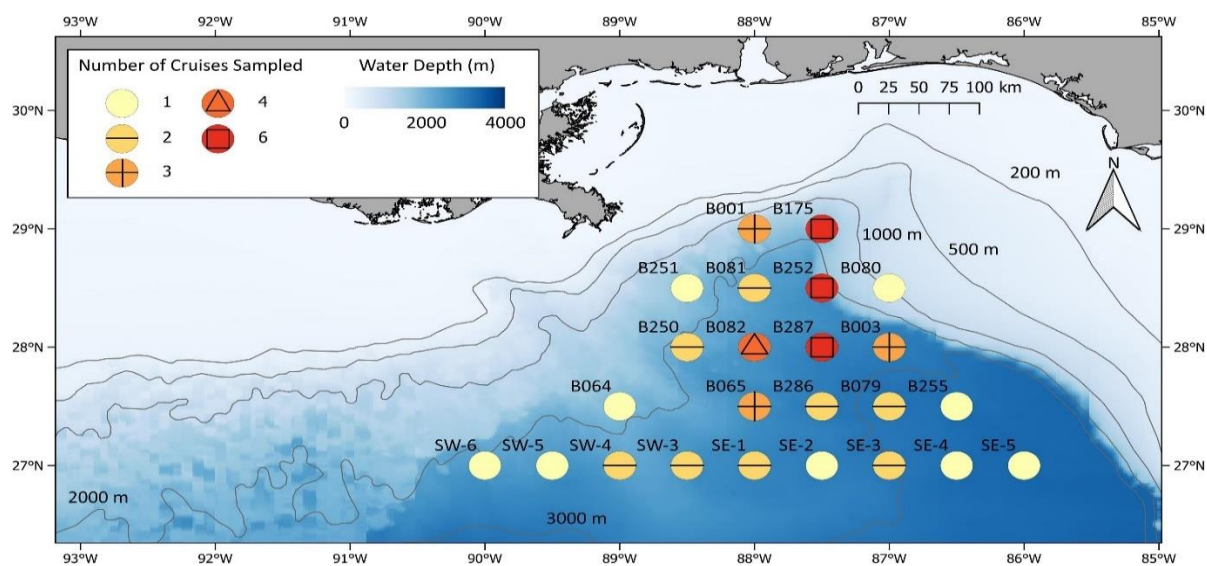


Figure 6. DEEPEND MOCNESS sampling stations between 2015-2018. Symbol colors represent the number of cruises that each location was sampled (adapted from Cook et al. 2020).

Table 2. Summary of the 13 research cruises conducted in the Gulf of Mexico. Three surveys were conducted during the ONSAP aboard the M/V *Meg Skansi*. Four surveys were conducted during the ONSAP aboard the FRV *Pisces*. Six surveys were conducted during the DEEPEND consortium aboard the R/V *Point Sur*. The column “No. of Samples” refers to the combined total number of quantitative tows per cruise. Combined volumes (m³) are reported as the total volume filtered across all samples during quantitative tows of each cruise.

Cruise	Sampling Dates	No. of Samples	Combined volumes (m ³)
MS6	January 28 th – March 30 th , 2011	207	7,960,547.20
MS7	April 14 th – June 30 th , 2011	285	9,625,358.60
MS8	July 18 th – September 30 th , 2011	356	10,740,501.45
DP01	May 1 st – May 8 th , 2015	34	1,179,842.00
DP02	August 8 th – August 21 st , 2015	95	2,880,308.00
DP03	April 30 th – May 14 th , 2016	75	2,230,905.80
DP04	August 5 th – August 19 th , 2016	112	2,674,249.30
DP05	May 1 st – May 11 th , 2017	80	3,455,683.10
DP06	July 19 th – August 1 st , 2018	57	1,568,427.20
PC8	December 2 nd – December 19 th , 2010	22	89,419,063.84
PC9	March 23 rd – April 6 th , 2011	3	11,714,434.26
PC10	June 23 rd – July 13 th , 2011	42	98,686,682.90
PC12	September 8 th – September 27 th , 2011	48	106,376,488.60

2.1.1. Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS)

Sampling.

The M/V *Meg Skansi* 6, 7, and 8 (MS6, MS7, and MS8, respectively) cruises utilized a MOCNESS with a 10-m² mouth diameter with a 3-mm mesh equipped with six nets to sample discrete depth ranges (*Meg Skansi* survey henceforth). The first net (net 0) sampled from the surface to 1500 m depth. The other five nets sampled the following depth ranges sequentially: 1500 – 1200 m (net 1), 1200 – 1000 m (net 2), 1000 – 600 m (net 3), 600 – 200 m (net 4), and 200 – 0 m (net 5) (Figure 7). Sampling efforts were conducted between 09:00-15:00 (Day) and 21:00-03:00 (Night). A magnetically sensing flowmeter (Tsurumi-Seiki-Kosakusho) determined the volume of water filtered by each net. The six DEEPEND research cruises aboard the R/V *Point Sur* used the same MOCNESS (10-m² mouth diameter with a 3-mm mesh), sampling scheme, and flowmeter used during the *Meg Skansi* survey.

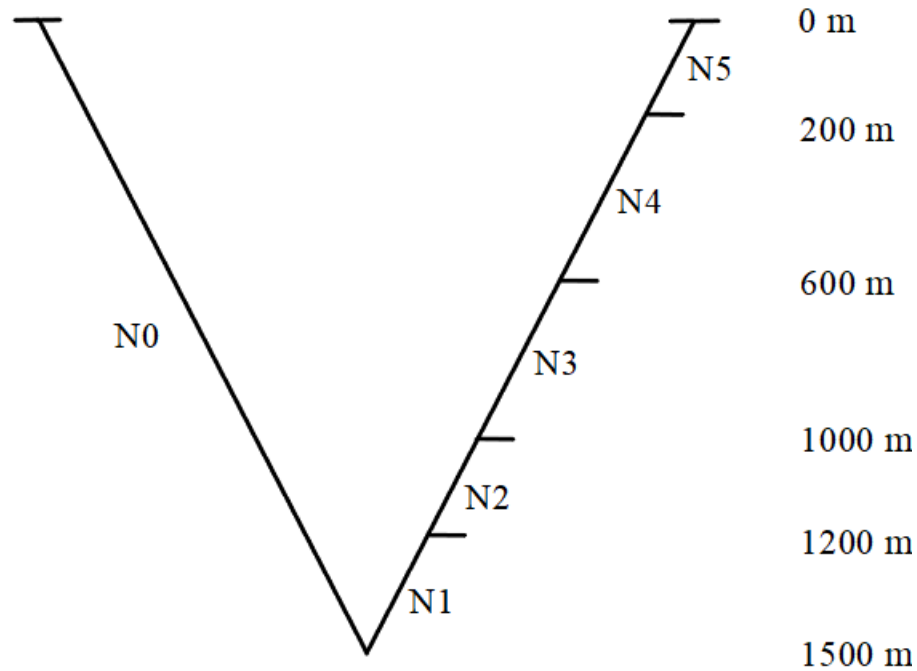


Figure 7. Depth strata sampled during the ONSAP and the DEEPEND MOCNESS surveys.

2.1.2. High-Speed Rope Trawl (HSRT) Sampling

All research cruises aboard the NOAA FRV *Pisces* used an oblique “V” pattern during sampling in which the HSRT was towed from the surface to depth and back to the surface without closing the mouth of the net. Two depth sampling patterns were used: “shallow” (0-700 m) and “deep” (0-1500 m). A subset of the stations sampled by the *Meg Skansi* survey was also sampled with the HSRT (Figure 8). This cruise series will be henceforth referred to as the *Pisces* survey.

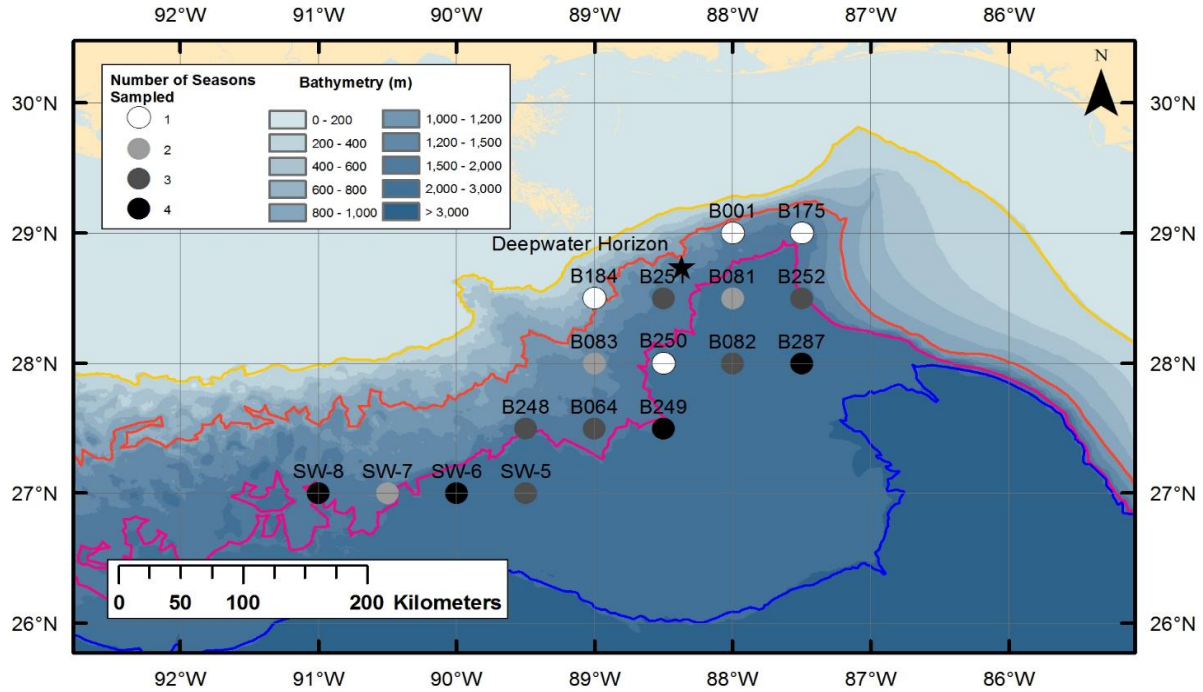


Figure 8. ONSAP HSRT sampling stations in winter 2010 and, spring, summer, and fall 2011. Symbol colors represent the number of seasons that each location was sampled. Contour lines, from north to south, correspond to 200 m, 1000 m, 2000 m, and 3000 m isobaths (adapted from Cook et al. 2020).

2.2. Spatiotemporal Distribution

The percent frequency of occurrence of both scorpaenoids and myctophids was calculated by dividing the sum of the quantitative samples in which at least one specimen from each taxon was caught per depth range (Figure 7) by the total number of quantitative samples that occurred in the respective depth range. The standardized abundance (no. ind. 10^{-6} m^{-3}) of both scorpaenoids and myctophids was calculated by dividing the sum of the raw count of scorpaenoids/myctophids collected by the sum of the volume of water filtered from each depth (Table 2). Due to differing gear types, abundance calculations did not include specimens obtained during the *Pisces* survey. Diel vertical distributions of scorpaenoids and myctophids were determined by plotting the standardized abundances by depth during day and night samples. Vertical distribution plots of standardized abundance were made using R Studio (version 4.1.0, R foundation for Statistical Computing). Additionally, both the number of individuals of the dominant scorpaenoid species and the length-frequency distributions were plotted against catch and depth data to examine spatiotemporal trends. Due to the non-normal distribution of data, a non-parametric Kruskal-

Wallis test was used to determine statistical significance between standard length and depth of occurrence of the dominant scorpaenoid species.

2.3. Scorpaenoid Specimen Processing

Specimens were preserved at sea in 10% buffered formalin:seawater solution and were later transferred into a 70% ethanol:water solution. Standard lengths (SL) were measured for specimens that were identified to species level prior to preservation. Most specimens were identified to family level (i.e. Scorpaenidae) during initial processing, and were therefore not measured prior to preservation. Specimens that were not initially identified to species level were measured during specimen processing for this study.

2.3.1. Specimen Morphology

Specimens were examined under a dissecting stereomicroscope (Carl Zeiss™ STEMI 2000-C). The left side of specimens was used for measurements and counts unless sufficient damage was observed. Seven morphometric traits were measured. Standard length (SL) was defined as the distance between the anterior-most point of the upper maxilla and the posterior end of the hypural plates. Pre-anal fin length (PAL) was defined as the length between the anterior-most point of the upper maxilla and the beginning of the anal vent. Snout length (SNL) was defined as the length between the anterior-most point of the upper maxilla and the beginning of the orbit. Head length (HL) was defined as the length between the anterior-most point of the upper maxilla and the posterior end of the operculum. Body depth (BD) was defined as the length between the origin of the pelvic fin to the highest point of the dorsal curvature. Pectoral depth (PD) was measured from the length between where the first pectoral ray connects to the body and where the last pectoral ray connects to the body. Orbit diameter (OD) was defined as the distance between the anterior edge of the orbit and the posterior edge of the orbit. The snout-orbit length (SNOL) was defined as the length between the anterior-most point of the upper maxilla and the posterior-most portion of the orbit (Figure 9).

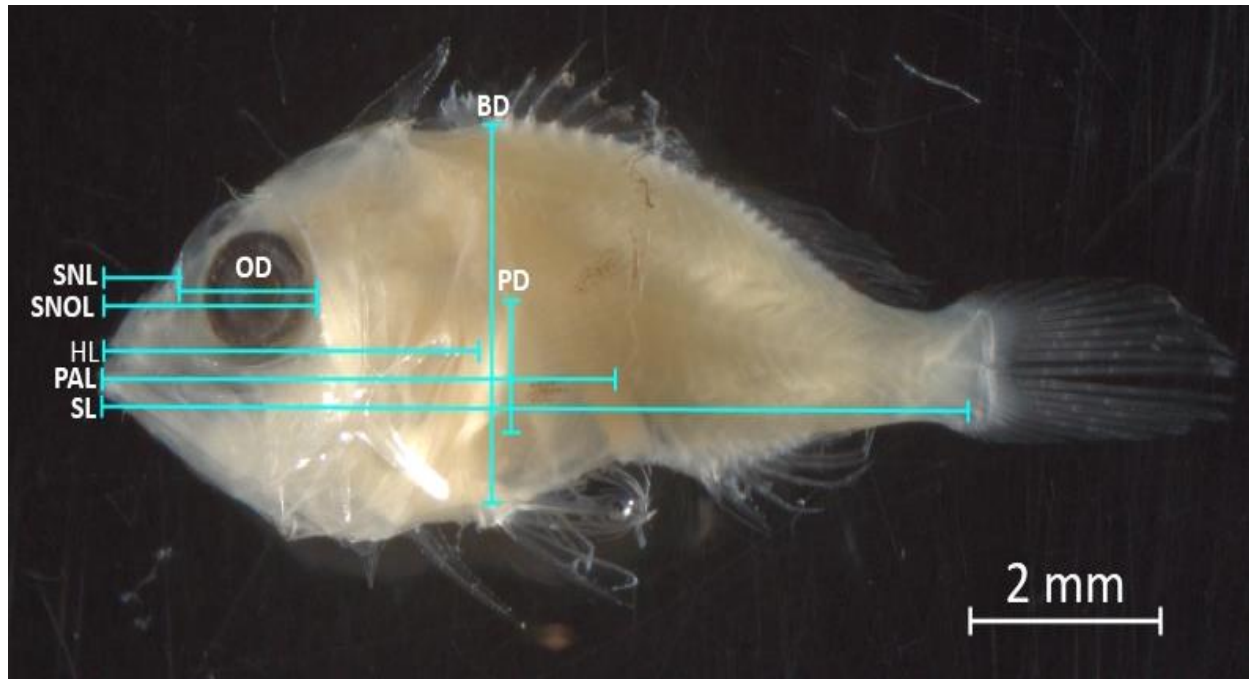


Figure 9. Morphometric analysis of juvenile scorpaenoid fishes from the Gulf of Mexico. SNL = snout length. OD = orbit diameter. SNOL = snout-orbit length. HL = head length. BD = body depth. PD = pectoral depth. PAL = pre-anal fin length. SL = standard length is represented by SL.

Digital images were taken with a camera attached to a stereomicroscope (ZEISS AxioCam ICc 3) and processed with the ZEN imaging software (version 2.6, blue edition). The SL and PAL of specimens that were too large to completely fit within the field of view of the stereomicroscope were measured using a ruler to the nearest mm. The SL and PAL of smaller specimens (<18 mm) were measured using imaging software to the nearest 0.01 mm. All remaining morphometrics were measured to the nearest 0.01 mm, regardless of specimen size, using the ZEN software. Ratios between morphometric measurements were calculated and reported as a percent with respect to SL.

In addition to lengths and meristic counts, external features were documented, including scale type, and the number, presence/absence, degree of curvature, and length of the preopercular, preorbital, supraorbital, parietal, and nuchal spines (Figure 10). Internal features documented include the presence/absence of a slit behind the fourth gill arch and the presence/absence of a swim bladder.



Figure 10. The head spines of a typical juvenile scorpaenoid: A. preorbital spines. B. supraorbital spine. C. parietal spine. D. nuchal spine. E. preopercular spines.

The spines of the first dorsal fin and the anal fin as well as the rays of the second dorsal fin, the pectoral fin, and the anal fin were counted with the stereomicroscope. The loss of body color during preservation in formalin made the identification and subsequent counting of some fin elements difficult. Select specimens were cleared and stained to facilitate counts of fin-spine/fin-ray elements and were processed in the Microbiology and Genetics Labs at the Nova Southeastern University Oceanographic Center. Alizarin red and Alcian blue 8GX were used with a 1% potassium hydroxide (KOH) solution following Dingerkus and Uhler (1977; Figure 11).



Figure 11. *Scorpaena plumieri* after being cleared and stained. Calcified elements appear pink (stained with Alizarin red) while cartilage appears blue (stained with Alcian blue) (Image created by Phillip-Eric Fortman).

2.4. Gut Content Analysis

Specimens between 15-19 mm standard-length (SL), the dominant size-class mode among available specimens, were dissected for gut content analysis. A longitudinal cut was made with a micro-knife in between the pelvic fins and proceeded posteriorly until the vent of the anus. A pair of blunt forceps peeled the trunk dorsally until the gastrointestinal tract was exposed. The esophagus was then severed by applying a small amount of manual force posteriorly. The gastrointestinal (GI) tract was excised by severing the anus from the trunk of the fish and subsequently placed into a small drop of water atop a glass microscope slide. Fuchsin acid was added to stain the GI tract contents. The stomachs were examined before being separated at the duodenum from the intestines via blunt forceps and all stomachs were given a value from five to zero based on stomach fullness, with a score of five representing an extremely full stomach and a score of zero representing an empty stomach (Table 3). Once all individual stomachs were assigned a fullness score, the stomach vacuity coefficient (Cv%) was calculated by dividing the number of empty stomachs by the total number of stomachs examined and the resultant was multiplied by

100 (Castriota et al. 2011). Both the stomach and the intestinal tract were opened, contents carefully transferred to a microscope slide, and examined separately. Prey items were then examined and identified to major taxon using a compound microscope (Carl Zeiss™ AXIO Scope A1).

Table 3. Indices of stomach fullness.

Categories of Stomach Fullness	
5	Stomach completely full with portions of stomach noticeably bulbous from prey.
4	Stomach largely full with only some prey items noticeable from outside.
3	Stomach moderately bulging with no prey items being noticeable from outside.
2	Stomach somewhat flat, not bulging, and no prey items noticeable from outside.
1	Stomach mostly flat with no prey items noticeable from outside.
0	Stomach nearly transparent, quite thin, and completely empty.

After prey items were identified, an index of state of digestion, from five to 0.5, was scored for all prey items that were extracted from stomachs (Figure 12, Table 4). A prey state of digestion score of five indicated a pristine specimen that exhibited no structural degradation, missing appendages, and/or a clear and defined body form. A prey state of digestion score of 0.5 would indicate mere remnants of prey such as bones, scales, shattered pieces of shell/carapace, and whole or fragmented appendages with no clear indication to the main body of the prey organism.

Table 4. Indices of prey state of digestion.

Categories of Prey State of Digestion	
5	Pristine specimen. The entire prey item is observed with no structural damage.
4	Prey item is observed with minor structural damage and full limb compliment.
3	Portions of the prey item body absent but the majority of limbs/appendages remain.
2	Main body of prey item recognizable with few limbs present, but no other body parts.
1	Main body of prey item recognizable with no other parts of the body present.
0.5	Reserved for the presence of bits of shell, scales, bones, and/or standalone limbs/appendages.

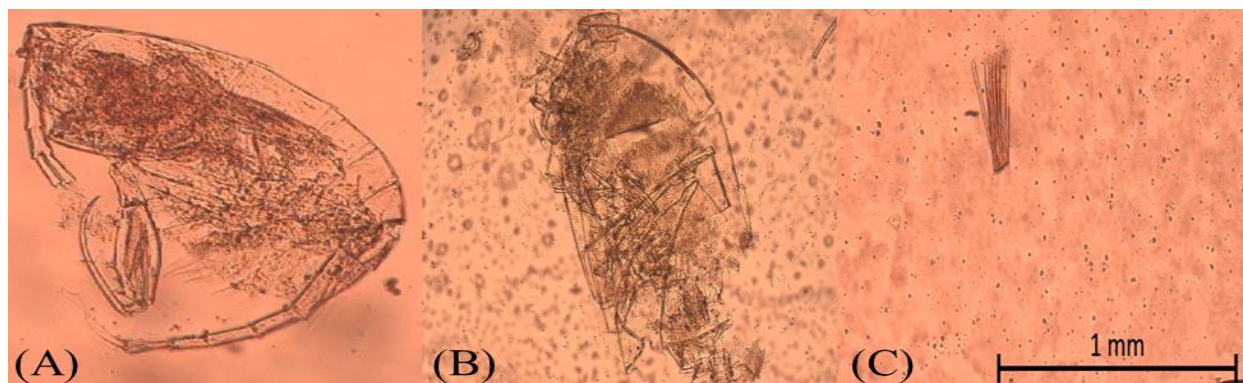


Figure 12. Varying states of digestion of prey items found within the stomachs of juvenile scorpaenoids. Left (A) and center (B) images are both copepods while the right image (C) is digested bone. From left to right the states of digestion are 5, 3, and 0.5.

A two-tailed two-sample nonparametric Mann-Whitney Wilcoxon t-test was applied to determine if varying degrees of stomach fullness and prey state of digestion were statistically related to time of day of capture ($p < 0.05$). All statistical analyses were conducted with R and R Studio (version 4.1.0, R foundation for Statistical Computing).

3. RESULTS

A total of 666 scorpaenoids were collected during the *Meg Skansi* (n=558), *Pisces* (n=37), and DEEPEND (n=71) surveys. Scorpaenoids collected during the *Pisces* survey were omitted from both frequency of occurrence and standardized abundance calculations due to incomparable sampling gear types (i.e. HSRT vs MOCNESS; widely disparate mesh sizes).

Of the 666 individuals collected, 347 were examined during this study. Nine unique morphotypes were discriminated based on fin-spine and fin-ray counts, head spine presence/absence, morphometric measurements, and the presence/absence of some internal features (Figure 9, Figure 10). Specimens were identified to the lowest taxonomic level possible.

Table 5. Morphotypes and species of pelagic-phase juvenile scorpaenoids collected in the Gulf of Mexico. The designation “N/A” means that neither a genus nor a species identification was possible.

Morphotype/Species	Individuals examined (no.)	Individuals examined (%)	Size Range (mm SL)	Putative ID
A	276	79.54	5-24	<i>Pontinus rathbuni</i>
B	1	0.29	8	N/A
C	17	4.90	6-10	<i>Scorpaena plumieri</i>
D	2	0.58	4-5	<i>Setarches guentheri</i>
E	1	0.29	12	<i>Pontinus longispinis</i>
F	3	0.87	4-9	<i>Scorpaena agassizi</i>
G	9	2.58	7-11	<i>Scorpaena</i> spp. A
H	2	0.58	8-9	<i>Scorpaena</i> spp. B
I	3	0.87	6-8	N/A
<i>Helicolenus dactylopterus</i>	4	1.15	7-11	<i>Helicolenus dactylopterus</i>
<i>Pterois</i> spp.	3	0.86	5-12	<i>Pterois</i> spp.
<i>Setarches guentheri</i>	17	4.90	6-48	<i>Setarches guentheri</i>
Damaged	9	2.59	6-11	N/A
Total	347	100	4-48	

3.1. Pelagic-Phase Juvenile Scorpaenoid Identification

A total of 347 pelagic-phase juvenile scorpaenoids were examined from the *Meg Skansi*, *Pisces*, and DEEPEND surveys. The scorpaenoid assemblage was dominated by morphotype A (~80%; Table 5). Morphotypes B–I made up approximately 10% of specimens. *Helicolenus dactylopterus*, *Pterois* spp., and *Setarches guentheri* composed approximately 7% of specimens. Several individuals (n=9) were damaged and could not be identified beyond the family level (~3%; Table 5). Morphotypes A–I were defined based on fin-spine and fin-ray counts, head spines, morphometric measurements, and some internal features (Appendix Tables 1 and 2, Appendix Figure 1).

3.1.1. Morphotype A

Morphotype A was the most numerous morphotype of the scorpaenoids collected from the *Meg Skansi*, *Pisces*, and DEEPEND cruise surveys. This morphotype was defined by the curvature and a comparatively large parietal spine, the presence of a supraorbital spine, and the longest preopercle spine being the second spine (Figure 13). Morphotype A was also characterized by having 11-12 dorsal fin-spines, 8-10 dorsal fin-rays, three anal fin-spines, five anal fin-rays, and

16-18 pectoral fin-rays. In addition, unbranched pectoral fin-rays, the presence of two preorbital spines, ctenoid scales (Figure 14), a small slit behind the fourth gill arch, and the presence of a swim bladder characterize morphotype A. The morphometric measurements and their respective ratios reported as a percent with respect to SL helped identify morphotype A. Morphometrics and ratios of morphotype A are presented in Table 6 and Table 7.



Figure 13. Image of morphotype A.



Figure 14. Ctenoid scales consistently observed in specimens larger than 15 mm SL from morphotype A.

Table 6. Average morphometrics (mm \pm SE) of 214 specimens of morphotype A.

Standard-Length (SL)	15.61 \pm 3.32
Snout Length (SNL)	1.53 \pm 0.47
Pre-anal Fin Length (PAL)	9.39 \pm 2.33
Head Length (HL)	6.82 \pm 1.36
Body Depth (BD)	5.46 \pm 1.06
Pectoral Depth (PD)	1.66 \pm 0.35
Orbit Diameter (OD)	2.48 \pm 0.49
Snout-Orbit Length (SNOL)	4.01 \pm 0.87

Table 7. Average morphometric ratios reported as percent (% \pm SE) of SL of 214 specimens of Morphotype A.

SNL:SL	9.82% \pm 1.89
PAL:SL	59.92% \pm 4.59
HL:SL	43.99% \pm 3.36
BD:SL	35.35% \pm 2.78
PD:SL	10.73% \pm 1.72
OD:SL	15.96% \pm 1.30
SNOL:SL	25.80% \pm 2.21

Putative identification was made based on the morphometric ratios and other traits reported above. The presence of unbranched pectoral fin-rays, two preorbital spines, ctenoid scales, a small slit behind the fourth gill arch, and a swim bladder indicate two possible genera: *Neomerinthe* or *Pontinus*. The genus *Neomerinthe* comprises two species in the Western Central Atlantic: *Neomerinthe beanorum* and *Neomerinthe hemingwayi* (Richards 2006, McEachran & Fechhelm, 2010). Morphotype A exhibits two preorbital spines over the maxilla, with the first curving ventro-posteriorly and the second curving posteriorly. This curvature is inconsistent with reports of preorbital spines for *N. beanorum* (McEachran & Fechhelm 2010). While the curvature of the preorbital spines is consistent with reports of *N. hemingwayi*, no specimen of morphotype A had the three dark spots of pigmentation on the posterior part of the lateral line, which is a key characteristic of *N. hemingwayi* (McEachran & Fechhelm 2010). Additionally, the morphometric ratios as a percent of SL in respect to SNL, OD, and BD for morphotype A were not within the ranges reported for either *N. beanorum* or *N. hemingwayi*.

The genus *Pontinus* comprises five species in the Western Central Atlantic: *Pontinus castor*, *Pontinus helena*, *Pontinus longispinis*, *Pontinus nematophthalmus*, and *Pontinus rathbuni* (Richards 2006). An identification of morphotype A as *P. helena* was ruled out, as it is documented to be endemic to the “Gulfo de Triste” in Venezuela (Richards 2006). Further separation of adult *P. castor*, *P. longispinis*, *P. nematophthalmus*, and *P. rathbuni* is possible via pectoral fin-ray counts; however, this has low taxonomic value for juvenile forms due to a high potential for changes ontogenetically (Washington et al. 1984). Despite the lack of more distinguishing characters of the remaining species, morphotype A appears most similar to the body form of *Pontinus rathbuni* illustrated in Sánchez & Acha (1988) (Figure 15). Additionally, larger specimens (~20 mm SL) exhibited four dusky saddles of pigmentation of the upper section of the body below the dorsal fin that is in accordance with pigmentation described for *P. rathbuni* in McEachran & Fechhelm (2010). Lastly, the morphometric ratios presented above are largely in accordance with those reported for *P. rathbuni*, with the exception of SNL (McEachran & Fechhelm 2010). Therefore, morphotype A is assigned *Pontinus rathbuni* herein.

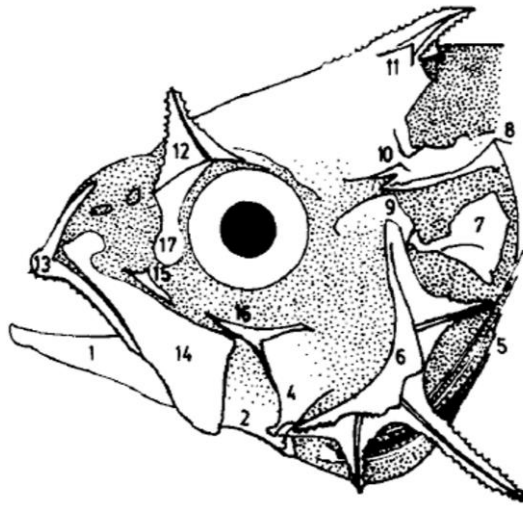


Figure 15. Head spination shown by pelagic-phase juvenile *Pontinus rathbuni* (adapted from Sanchez & Acha 1988).

3.1.2. Morphotype B

Morphotype B characterized and defined a single specimen. The key characteristics of this morphotype were the morphology of the supraocular and parietal spines (Figure 16). No other morphotype examined in this study possessed anteriorly oriented supraocular spines. The parietal spines extend far beyond both the pectoral- and dorsal-fin bases. The parietal spines also appeared much thicker than that of other morphotypes. The specimen designated as morphotype B had 12 dorsal fin-spines, 11 dorsal fin-rays, three anal fin-spines, six anal fin-rays, and 17 pectoral fin-rays. The presence of six anal fin-rays limited the identification of Morphotype B to a select few species within Scorpaenoidei: *Ectroposebastes imus*, *Pterois miles*, *Pterois volitans*, *Scorpaena plumieri*, and *Setarches guentheri*. Juvenile forms of both *S. plumieri* and *S. guentheri* are described below and both forms do not possess the head spine compliment shown by morphotype B. Morphotype B is also neither *P. miles* nor *P. volitans* because the parietal spines, anal fin-rays, pectoral fin-rays, and relative body length to head length do not match those described for either species (lionfishes: see account of *Pterois* spp. below). While the meristics of morphotype B are mostly consistent with *E. imus*, the head spine compliment of morphotype B does not match with published accounts and illustrations of juvenile *E. imus* (Richards 2006, McEachran & Fechhelm

2010). Therefore, it is possible that morphotype B is not a member of Scorpaenoidei, since morphotype B is also not a member of the families Triglidae or Peristediidae because the head shape is inconsistent with juvenile forms of Triglidae and/or Peristediidae and morphotype B does not display the elongated first through third pelvic fin-rays that are diagnostic features of either family (Richards 2006). Morphotype B might still belong to the order Perciformes. Due to the uncertainty surrounding finer identification of this morphotype, it will stay defined as morphotype B. Morphometrics and ratios of morphotype B are presented in Table 8 and Table 9.



Figure 16. Image of morphotype B.

Table 8. Morphometrics (mm) of one specimen of morphotype B.

Standard-Length (SL)	8.00
Snout Length (SNL)	0.91
Pre-anal Fin Length (PAL)	4.51
Head Length (HL)	3.31
Body Depth (BD)	2.99
Pectoral Depth (PD)	1.00
Orbit Diameter (OD)	1.20
Snout-Orbit Length (SNOL)	2.09

Table 9. Morphometric ratios reported as percent (%) of SL of one specimen of Morphotype B.

SNL:SL	11.39%
PAL:SL	56.39%
HL:SL	41.39%
BD:SL	37.36%
PD:SL	12.50%
OD:SL	15.00%
SNOL:SL	26.11%

3.1.3. Morphotype C

Morphotype C characterized 17 specimens. The key characteristics of morphotype C were branched pectoral rays, two preorbital spines, five or six preopercular spines with the first and third spines reaching close to the pectoral base, absence of a slit behind the fourth gill arch, heavy pigmentation of the pectoral fin, and some pigmentation of the gut (Figure 17). Morphotype C had 12 dorsal fin-spines, nine dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 18-20 pectoral fin-rays. The aforementioned features were sufficient to conclude morphotype C as *Scorpaena plumieri*. While the examples of *S. plumieri* were missing their distinctive coloration due to preservation in formalin, the body form and pectoral pigmentation matched that described for the early life history of *S. plumieri* (Richards 2006). Morphometrics and ratios of morphotype C are presented in Table 10 and Table 11.

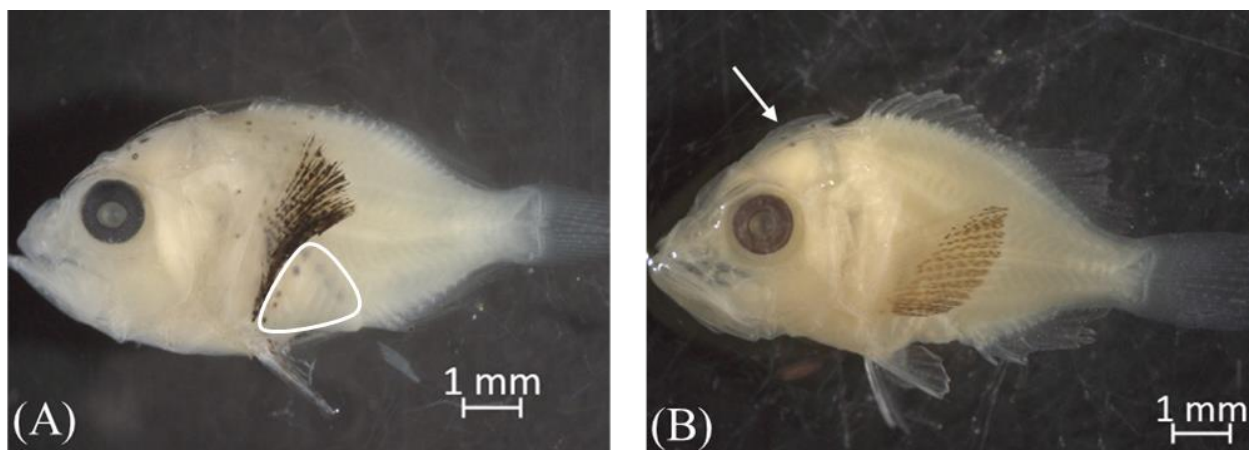


Figure 17. Images of morphotype C. A) pigmentation of the gut under the highly pigmented pectoral fin. B) head spines (arrow) and pectoral fin in a clearer view.

Table 10. Average morphometrics (mm \pm SE) of 17 specimens of morphotype C.

Standard-Length (SL)	7.88 \pm 0.97
Snout Length (SNL)	0.88 \pm 0.19
Pre-anal Fin Length (PAL)	4.95 \pm 0.57
Head Length (HL)	3.74 \pm 0.47
Body Depth (BD)	3.61 \pm 0.54
Pectoral Depth (PD)	1.14 \pm 0.22
Orbit Diameter (OD)	1.34 \pm 0.19
Snout-Orbit Length (SNOL)	2.23 \pm 0.27

Table 11. Average morphometric ratios reported as percent (% \pm SE) of SL of 17 specimens of Morphotype C.

SNL:SL	11.25% \pm 2.24
PAL:SL	63.08% \pm 5.01
HL:SL	47.69% \pm 4.31
BD:SL	45.98% \pm 4.97
PD:SL	14.72% \pm 3.50
OD:SL	17.19% \pm 2.54
SNOL:SL	28.42% \pm 3.25

3.1.4. Morphotype D

Morphotype D characterized two specimens. These individuals were also the smallest scorpaenoids examined (4-5 mm standard-length). This morphotype was defined by the presence of a largely transparent cranium, a weakly ossified skull, three preopercle spines, and some reddish-orange pigmentation on the pectoral fins (Figure 18). Specimens of morphotype D had 11 dorsal fin-spines, nine dorsal fin-rays, three anal fin-spines, five or six anal fin-rays, and 20 or 22 branched pectoral fin-rays. The combination of a maximum of six anal fin-rays and over 20 pectoral fin-rays limit identification to a single species: *Setarches guentheri*. Even though *S. guentheri* is documented to have four or five preopercle spines, the individuals examined are small enough to assume that they could still develop more preopercle spines at a larger size. Morphometrics and ratios of morphotype D are presented in Table 12 and Table 13.

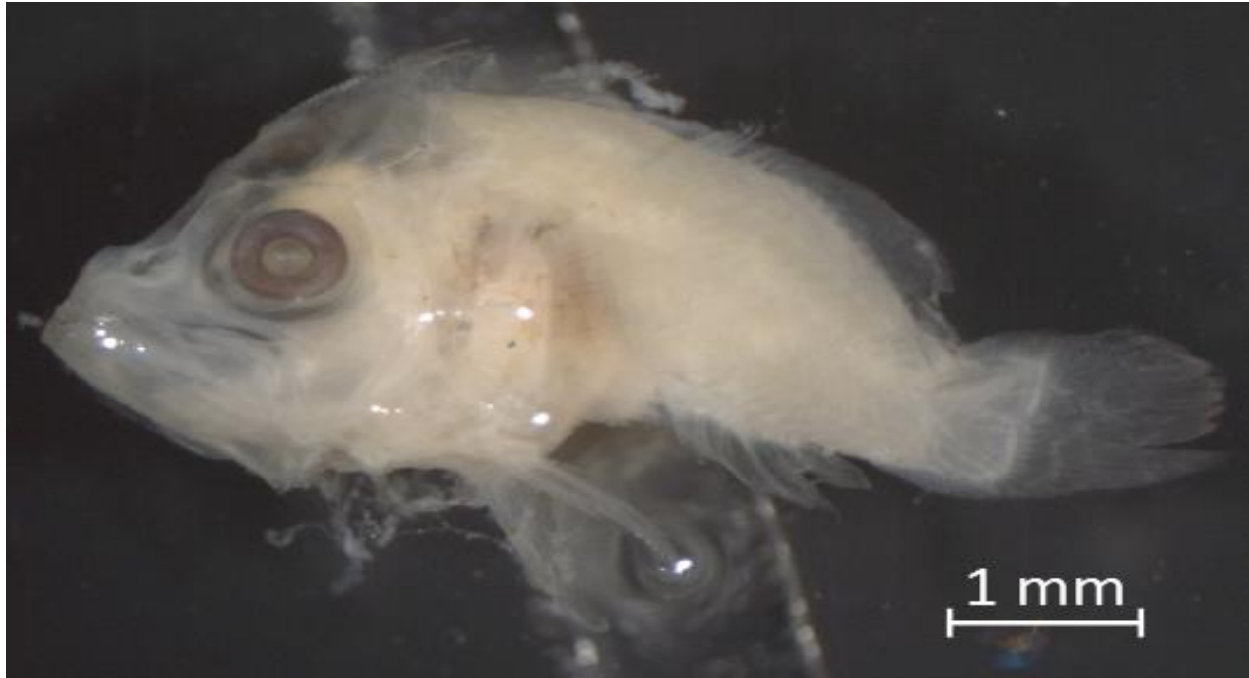


Figure 18. Image of morphotype D.

Table 12. Average morphometrics (mm \pm SE) of two specimens of morphotype D.

Standard-Length (SL)	4.55 \pm 0.78
Snout Length (SNL)	0.63 \pm 0.19
Pre-anal Fin Length (PAL)	2.73 \pm 0.32
Head Length (HL)	2.23 \pm 0.33
Body Depth (BD)	2.06 \pm 0.36
Pectoral Depth (PD)	0.81 \pm 0.30
Orbit Diameter (OD)	0.73 \pm 0.33
Snout-Orbit Length (SNOL)	1.47 \pm 0.38

Table 13. Average morphometric ratios reported as percent (% \pm SE) of SL of two specimens of Morphotype D.

SNL:SL	13.77% \pm 1.80
PAL:SL	60.23% \pm 3.21
HL:SL	49.19% \pm 1.15
BD:SL	45.16% \pm 0.22
PD:SL	17.52% \pm 3.56
OD:SL	15.73% \pm 4.57
SNOL:SL	32.10% \pm 2.97

3.1.5. Morphotype E

Morphotype E characterized one specimen and was defined by a relatively flat head and the absence of any frontal, parietal, or nuchal spines. The preopercle has three spines, with the second spine being the longest and extending beyond the pectoral fin base (Figure 19). Morphotype E also had a slit behind the fourth gill arch. The meristics of morphotype E were the same as those for *Pontinus rathbuni*: 12 dorsal fin-spines, nine dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 17 pectoral fin-rays. While meristics of morphotype E might match that of *P. rathbuni*, the body form clearly does not match. However, the body form did match that of *Pontinus longispinis*, a sister taxon to *P. rathbuni*, shown in Richards (2006). Morphometrics and ratios of morphotype E are presented in Table 14 and Table 15.



Figure 19. Image of morphotype E.

Table 14. Average morphometrics (mm) of one specimen of morphotype E.

Standard-Length (SL)	11.57
Snout Length (SNL)	1.28
Pre-anal Fin Length (PAL)	7.07
Head Length (HL)	5.11
Body Depth (BD)	3.96
Pectoral Depth (PD)	1.29
Orbit Diameter (OD)	1.87
Snout-Orbit Length (SNOL)	3.14

Table 15. Average morphometric ratios reported as percent (%) of SL of one specimen of Morphotype E.

SNL:SL	11.06%
PAL:SL	61.08%
HL:SL	44.17%
BD:SL	34.18%
PD:SL	11.12%
OD:SL	16.16%
SNOL:SL	27.12%

3.1.6. Morphotype F

Morphotype F characterized three specimens. This morphotype was defined by five preopercle spines (with the first and third being the longest), two preorbital spines over the maxilla, a very small supraorbital spine, branching pectoral fin-rays, absence of pigmentation on the dorsally distal portion of the pectoral fin, a distinct band of pigmentation at the pectoral base, pigmentation of the dorsal portion of the gut, and the absence of a slit behind the fourth gill arch (Figure 20). Morphotype F had 12 dorsal fin-spines, nine dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 19-20 pectoral fin-rays. The head spines, pigmentation, and meristics were enough to conclude morphotype F as *Scorpaena agassizi* based on the description of *S. agassizi* within Richards (2006). Morphometrics and ratios of morphotype F are presented in Table 16 and Table 17.

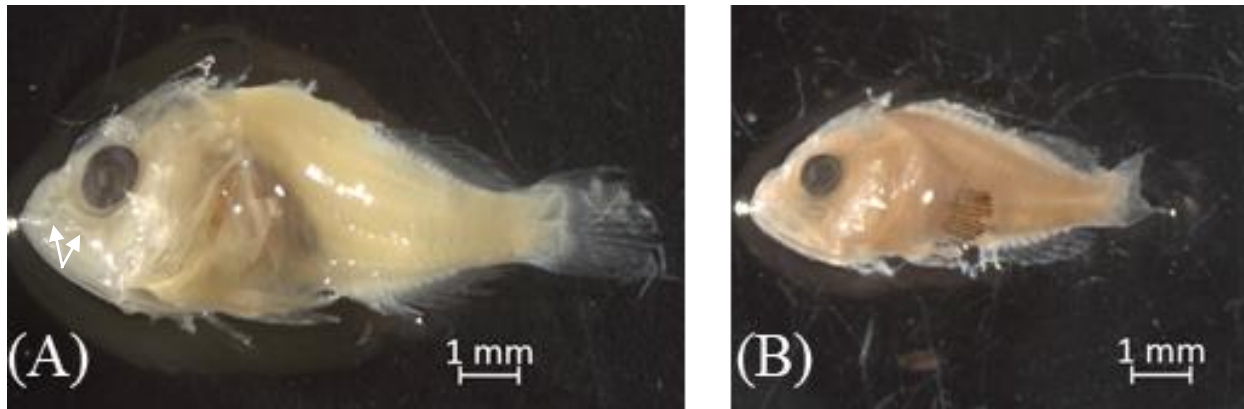


Figure 20. Morphotype F showing A) pigmentation of the gut and the presence of two preorbital spines (arrows), B) the pigmentation of the pectoral fin as well as the positioning and size of five preopercular spines.

Table 16. Average morphometrics (mm \pm SE) of three specimens of morphotype F.

Standard-Length (SL)	6.59 \pm 1.96
Snout Length (SNL)	0.71 \pm 0.18
Pre-anal Fin Length (PAL)	3.99 \pm 1.10
Head Length (HL)	2.73 \pm 0.58
Body Depth (BD)	2.29 \pm 0.96
Pectoral Depth (PD)	0.88 \pm 0.13
Orbit Diameter (OD)	1.12 \pm 0.21
Snout-Orbit Length (SNOL)	1.82 \pm 0.30

Table 17. Average morphometric ratios reported as percent (% \pm SE) of SL of three specimens of Morphotype F.

SNL:SL	10.94% \pm 2.09
PAL:SL	60.73% \pm 2.32
HL:SL	42.09% \pm 3.71
BD:SL	34.41% \pm 8.20
PD:SL	14.50% \pm 5.77
OD:SL	17.38% \pm 2.35
SNOL:SL	28.45% \pm 4.91

3.1.7. Morphotype G

Morphotype G characterized nine specimens. Two key characteristics were unique to this morphotype: the second portion of the dorsal fin began with a soft ray as opposed to a spine and the parietal spine appeared to be fused with the nuchal spine (however, osteological verification was not conducted). The parietal spine appeared shorter, positioned more anteriorly, and directed dorsally whereas the nuchal spine appeared slightly longer, positioned more posteriorly, and directed anteriorly (Figure 21). Morphotype G had 11-12 dorsal fin-spines, 9-10 dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 17 pectoral fin-rays. Meristics alone for morphotype G were not helpful in any further identification as the reported average fin-spines and fin-rays

overlapped with ranges reported for various genera and species of scorpaenoids (Richards 2006, McEachran & Fechhelm 2010). However, the absence of a slit behind the fourth gill arch did permit for a few potential identifications: *Trachyscorpia cristulata*, *Helicolenus dactylopterus*, or any species within the genus *Scorpaena*. Morphotype G cannot be *H. dactylopterus* due to missing pigmentation under the dorsal fin and the stomach. *Helicolenus dactylopterus* also does not exhibit the fused parietal spine shown in morphotype G. Therefore, morphotype G could be within the genus *Scorpaena* or *Trachyscorpia cristulata* but will remain defined as morphotype G since species identification cannot be confirmed. Morphometrics and ratios of morphotype G are presented in Table 18 and Table 19.

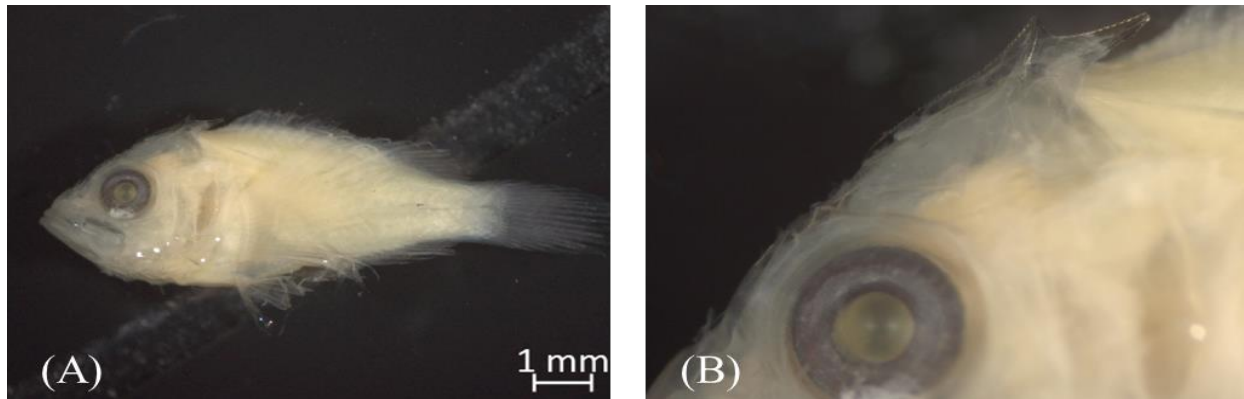


Figure 21. Images of morphotype G showing: A) the whole fish, B) a close-up of the parietal and nuchal spines.

Table 18. Average morphometrics (mm \pm SE) of nine specimens of morphotype G.

Standard-Length (SL)	8.57 \pm 1.19
Snout Length (SNL)	0.84 \pm 0.28
Pre-anal Fin Length (PAL)	4.84 \pm 0.89
Head Length (HL)	3.48 \pm 0.44
Body Depth (BD)	3.30 \pm 1.00
Pectoral Depth (PD)	1.54 \pm 0.63
Orbit Diameter (OD)	1.30 \pm 0.18
Snout-Orbit Length (SNOL)	2.14 \pm 0.37

Table 19. Average morphometric ratios reported as percent (% \pm SE) of SL of nine specimens of Morphotype G.

SNL:SL	9.66% \pm 2.79
PAL:SL	56.42% \pm 6.73
HL:SL	40.77% \pm 3.21
BD:SL	37.90% \pm 8.99
PD:SL	34.29% \pm 10.27
OD:SL	15.35% \pm 2.16
SNOL:SL	24.96% \pm 3.11

3.1.8. Morphotype H

Morphotype H characterized two specimens. A strong suborbital ridge, three preopercular spines of equal size, and parietal spines that pointed caudally (in-line with the dorsal ridge) defined this morphotype (Figure 22). The meristics of morphotype H were the same as morphotype G, with a dorsal fin-spine count of 12, a dorsal fin-ray count of nine, an anal fin-spine count of three, an anal fin-ray count of five, and a pectoral fin-ray count of 17. This morphotype also lacked a slit behind the fourth gill arch. Therefore, it can be concluded that morphotype H represents a species of the genus *Scorpaena* but will remain defined as morphotype H since species identification cannot be confirmed. Morphometrics and ratios of morphotype H are presented in Table 20 and Table 21.

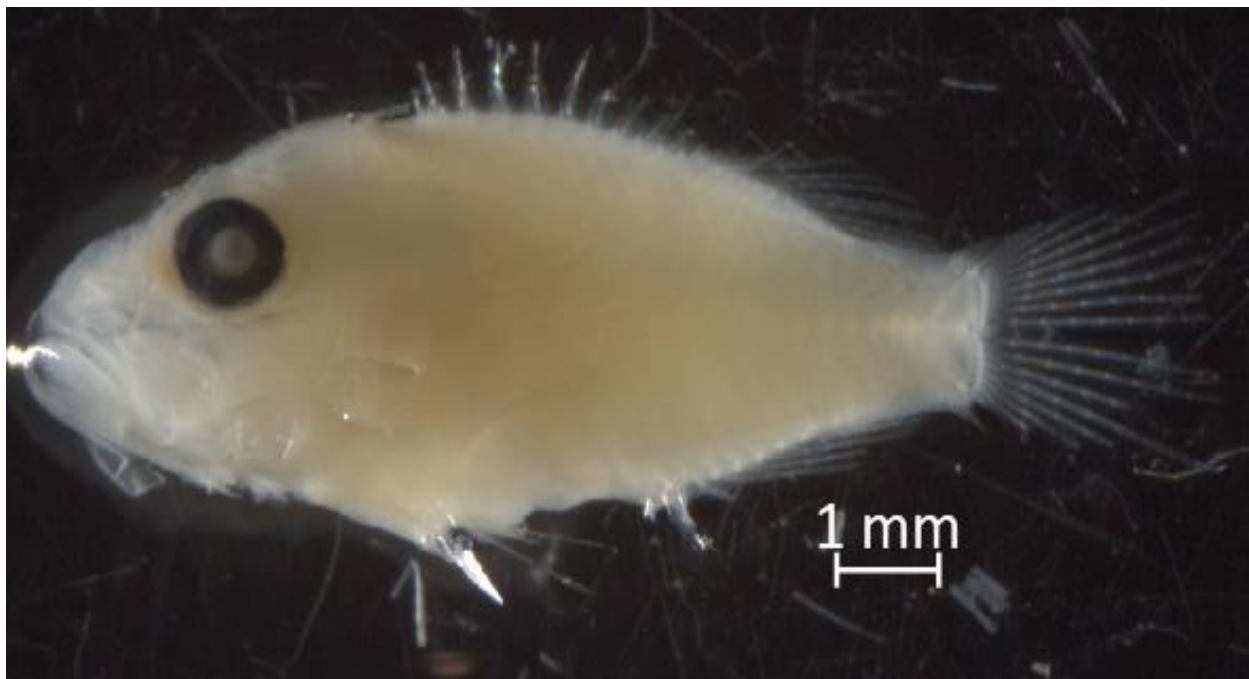


Figure 22. Image of morphotype H.

Table 20. Average morphometrics (mm \pm SE) of two specimens of morphotype H.

Standard-Length (SL)	8.50 \pm 0.71
Snout Length (SNL)	1.00 \pm 0.00
Pre-anal Fin Length (PAL)	5.50 \pm 0.71
Head Length (HL)	3.55 \pm 0.35
Body Depth (BD)	3.60 \pm 0.57
Pectoral Depth (PD)	1.65 \pm 0.21
Orbit Diameter (OD)	1.25 \pm 0.07
Snout-Orbit Length (SNOL)	2.25 \pm 0.07

Table 21. Average morphometric ratios reported as percent (% \pm SE) of SL of two specimens of Morphotype H.

SNL:SL	11.81% \pm 0.98
PAL:SL	64.58% \pm 2.95
HL:SL	41.74% \pm 0.69
BD:SL	42.22% \pm 3.14
PD:SL	19.58% \pm 4.12
OD:SL	14.72% \pm 0.39
SNOL:SL	26.53% \pm 1.37

3.1.9. Morphotype I

Morphotype I characterized three specimens. The most notable feature of this morphotype was the presence of parietal spines which displayed a dramatic curve caudally and protruded further from the body than was observed from any other morphotype (Figure 23). Morphotype I had 12 dorsal fin-spines, nine dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 18 pectoral fin-rays. This morphotype also possessed a slit behind the fourth gill arch, ruling out identifications like *H. dactylopterus*, *Scorpaena* spp., or *T. cristulata* and the presence of heavy head spines rule out the possibility of morphotype I as *Pterois* spp. (see account of *Pterois* spp. below). The combination of the meristics and the presence of a slit behind the fourth gill arch left the following species as potential identifications: *Ectreposebastes imus*, *Idiastion kyphos*, *Neomerinthe beanorum*, *Neomerinthe hemingwayi*, *Phenascorpius nebris*, *Pontinus castor*, *Pontinus helena*, *Pontinus nematophthalmus*, *Scorpaenodes caribbaeus*, *Scorpaenodes tredecimspinosus*, and *Setarches guentheri*. Morphotype I did not match published juvenile descriptions of *E. imus*, *S. caribbaeus*, *S. tredecimspinosus*, or *S. guentheri* (Richards 2006). Therefore, morphotype I could be any of the following: *I. kyphos*, *N. beanorum*, *N. hemingwayi*, *P. nebris*, *P. castor*, *P. helena*, or *P. nematophthalmus*. Due to the degree of uncertainty surrounding this morphotype, it will remain defined as morphotype I. Morphometrics and ratios of morphotype I are presented in Table 22 and Table 23.



Figure 23. Image of morphotype I.

Table 22. Average morphometrics (mm \pm SE) of three specimens of morphotype I.

Standard-Length (SL)	7.43 \pm 0.93
Snout Length (SNL)	0.77 \pm 0.25
Pre-anal Fin Length (PAL)	4.80 \pm 0.53
Head Length (HL)	3.47 \pm 0.47
Body Depth (BD)	2.93 \pm 0.40
Pectoral Depth (PD)	1.20 \pm 0.35
Orbit Diameter (OD)	1.13 \pm 0.31
Snout-Orbit Length (SNOL)	1.90 \pm 0.56

Table 23. Average morphometric ratios reported as percent (% \pm SE) of SL of three specimens of Morphotype I.

SNL:SL	10.18% \pm 2.46
PAL:SL	64.90% \pm 7.49
HL:SL	46.60% \pm 0.87
BD:SL	39.48% \pm 3.10
PD:SL	15.94% \pm 2.51
OD:SL	15.13% \pm 2.93
SNOL:SL	25.31% \pm 5.36

3.1.10. *Helicolenus dactylopterus*

Four individuals were identified as *Helicolenus dactylopterus* prior to the work of this thesis. This species can be easily identified by any combination of the following characteristics: a dorsal fin-ray count of 13 or 14, a pectoral fin-ray count of 19-20, and numerous pigmented

blotches of the gut (Figure 24). Specimens of *Helicolenus dactylopterus* examined during this study had 11 dorsal fin-spines, 13 dorsal fin-rays, three anal fin-spines, five anal fin-rays, and 20 pectoral fin-rays. *Helicolenus dactylopterus* is the only species of Scorpaenoidei that is documented to have 13 or 14 dorsal fin-rays. Therefore, the dorsal fin-ray count alone can serve as a sufficient diagnosis. Additionally, the parietal and nuchal spines were also helpful in identification. The parietal spine was larger than the nuchal spine in *H. dactylopterus*, whereas the parietal spine was smaller than the nuchal spine as shown in morphotype G (Figure 21). Also, both the parietal and nuchal spines point caudally. Gut pigmentation can also be used for identification in individuals up to 17 mm SL, as no other species of Scorpaenoidei are documented to have the numerous pigmented blotches of the gut. Morphometrics and ratios of *Helicolenus dactylopterus* are presented in Table 24 and Table 25.



Figure 24. Image of a pelagic-phase juvenile *Helicolenus dactylopterus*.

Table 24. Average morphometrics (mm \pm SE) of four specimens of *Helicolenus dactylopterus*.

Standard-Length (SL)	11.28 \pm 4.08
Snout Length (SNL)	1.24 \pm 0.28
Pre-anal Fin Length (PAL)	7.12 \pm 2.84
Head Length (HL)	4.74 \pm 1.03
Body Depth (BD)	4.22 \pm 1.78
Pectoral Depth (PD)	1.23 \pm 0.38
Orbit Diameter (OD)	1.70 \pm 0.25
Snout-Orbit Length (SNOL)	2.96 \pm 0.48

Table 25. Average morphometric ratios reported as percent (% \pm SE) of SL of four specimens of *Helicolenus dactylopterus*.

SNL:SL	11.31% \pm 1.33
PAL:SL	62.44% \pm 3.17
HL:SL	43.50% \pm 5.61
BD:SL	37.27% \pm 5.17
PD:SL	11.10% \pm 1.09
OD:SL	15.99% \pm 3.56
SNOL:SL	27.56% \pm 4.83

3.1.11. *Pterois* spp.

Three individuals were identified as juvenile *Pterois* spp. (lionfishes) prior to the work of this thesis. Juvenile *Pterois* spp. are easily distinguished from any other genera or species of Scorpaenoidei by their comparatively long and narrow body as opposed to the deep-bodied forms present in other juvenile scorpaenoids. Juvenile *Pterois* spp. also possess pectoral fins that extend far beyond the origin of the anal fin, a stout head comparative to body length, smaller head spines compared to other juvenile scorpaenoid species, and a maximum of seven or eight anal fin-rays (Figure 25). Additionally, finer identification between species of both adult and juvenile *Pterois* spp. is nearly impossible without genetic evidence. The meristics between *Pterois miles* and *Pterois volitans* are almost the same (Richards 2006). As a result, identification is left at the genus level for juvenile *Pterois* spp. Morphometrics and ratios of *Pterois* spp. are presented in Table 26 and Table 27.



Figure 25. Pelagic-phase juvenile lionfish (*Pterois* spp.)

Table 26. Average morphometrics (mm \pm SE) of three specimens of *Pterois* spp.

Standard-Length (SL)	9.49 \pm 2.91
Snout Length (SNL)	0.78 \pm 0.23
Pre-anal Fin Length (PAL)	4.83 \pm 1.70
Head Length (HL)	2.97 \pm 0.67
Body Depth (BD)	2.86 \pm 0.92
Pectoral Depth (PD)	1.17 \pm 0.79
Orbit Diameter (OD)	0.91 \pm 0.15
Snout-Orbit Length (SNOL)	1.70 \pm 0.37

Table 27. Average morphometric ratios reported as percent (% \pm SE) of SL of three specimens of *Pterois* spp.

SNL:SL	6.76% \pm 1.30
PAL:SL	40.91% \pm 5.12
HL:SL	26.03% \pm 6.57
BD:SL	24.36% \pm 2.99
PD:SL	9.00% \pm 4.67
OD:SL	8.15% \pm 2.86
SNOL:SL	14.91% \pm 4.07

3.1.12. *Setarches guentheri*

Seventeen individuals were identified as *Setarches guentheri* based on a pectoral fin-ray count of 21 to 25 prior to the work of this thesis (Figure 26). Three other scorpaenoid species are documented to have a pectoral fin-ray count of 20 or higher (e.g., *Trachyscorpia cristulata*,

Scorpaena agassizi, or *Scorpaena albifimbria*). However, *S. guentheri* differed from all other possible species in two distinct ways: the head of *S. guentheri* appeared cavernous and weakly ossified (opposed to heavy ossification in all other possibilities) and the presence of a slit behind the fourth gill arch that is not present in other possible species (Eschmeyer & Collette, 1966; McEachran & Fechhelm, 2010). Additionally, specimens of juvenile *S. guentheri* had five preopercle spines, all of which were nearly equal in size and distance from each other (Eschmeyer & Collette, 1966). Morphometrics and ratios of *Setarches guentheri* are presented in Table 28 and Table 29.



Figure 26. Image of a pelagic-phase juvenile *Setarches guentheri*.

Table 28. Average morphometrics (mm \pm SE) of 17 specimens of morphotype *Setarches guentheri*.

Standard-Length (SL)	12.45 \pm 9.14
Snout Length (SNL)	1.26 \pm 0.77
Pre-anal Fin Length (PAL)	8.23 \pm 6.83
Head Length (HL)	5.49 \pm 4.12
Body Depth (BD)	5.27 \pm 3.66
Pectoral Depth (PD)	2.40 \pm 1.37
Orbit Diameter (OD)	1.84 \pm 1.23
Snout-Orbit Length (SNOL)	3.17 \pm 2.25

Table 29. Average morphometric ratios reported as percent ($\% \pm \text{SE}$) of SL of 17 specimens of *Setarches guentheri*.

SNL:SL	11.49% \pm 2.87
PAL:SL	64.25% \pm 5.20
HL:SL	45.24% \pm 3.22
BD:SL	41.08% \pm 4.63
PD:SL	18.88% \pm 3.77
OD:SL	15.13% \pm 2.15
SNOL:SL	26.72% \pm 2.93

3.2. Frequency of Occurrence of Juvenile Scorpaenoids in the Pelagic GoM

The overall frequency of occurrence of scorpaenoids during the *Meg Skansi* and DEEPEND surveys was calculated to be a 47% within epipelagic depths (Table 30). Myctophids, by comparison, were collected in 62% of day trawls and 99% of night trawls in the upper 200 m.

Table 30. The percent frequency of occurrence of Scorpaenoidei and Myctophidae in the epipelagic zone of the Gulf of Mexico.

	Day	Solar Cycle	
		Night	Day & Night
Scorpaenoidei	48.6	44.1	46.6
Myctophidae	62.1	99.3	81.5

3.2.2. Abundance and Vertical Distribution

Scorpaenoids were primarily caught in the upper 200 m of the GoM during both daytime and nighttime (Table 31). There was a similar abundance ($\text{ind. } 10^{-6} \text{ m}^{-3}$) of pelagic-phase juvenile scorpaenoids during daytime and nighttime samples of the upper 200 m of the GoM from the *Meg Skansi* and DEEPEND surveys (Figure 27, Figure 28). Additionally, the abundance of pelagic-phase juvenile scorpaenoids for all other depths between day and night during the *Meg Skansi* survey was nearly zero and was zero for the DEEPEND survey (Table 31). In direct contrast, myctophids were primarily caught in the upper 200 m of the GoM at night and at deeper depths during the day (Table 32, Figure 27, Figure 28).

Table 31. Abundance of juvenile scorpaenoids from the open Gulf of Mexico as a function of depth. Values represent no. ind. 10^{-6} m^{-3} .

		Depth Ranges (m)				
		0-200	200-600	600-1000	1000-1200	1200-1500
<i>Meg Skansi</i>	Day	87.1	3.5	1.8	2.5	0.5
	Night	76.9	3.3	1.7	1.8	4.3
DEEPEND	Day	14.2	0	0	0	0
	Night	12.3	0	0	0	0

Table 32. Abundance of myctophids from the open Gulf of Mexico as a function of depth. Values represent no. ind. 10^{-6} m^{-3} .

		Depth Ranges (m)				
		0-200	200-600	600-1000	1000-1200	1200-1500
<i>Meg Skansi</i>	Day	179.3	1578.8	1410.7	477.7	222.0
	Night	3491.8	256.0	728.3	199.8	168.7
DEEPEND	Day	14.2	N/A	N/A	N/A	N/A
	Night	913.8	N/A	N/A	N/A	N/A

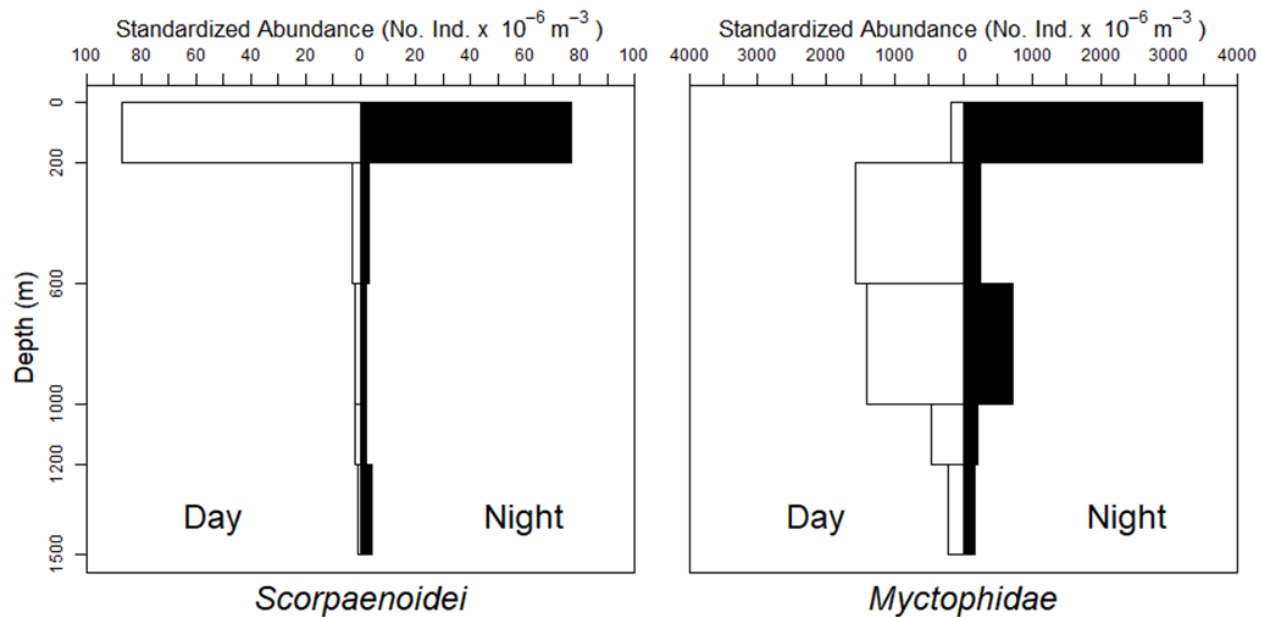


Figure 27. Vertical distribution of scorpaenoids and myctophids during the *Meg Skansi* survey.

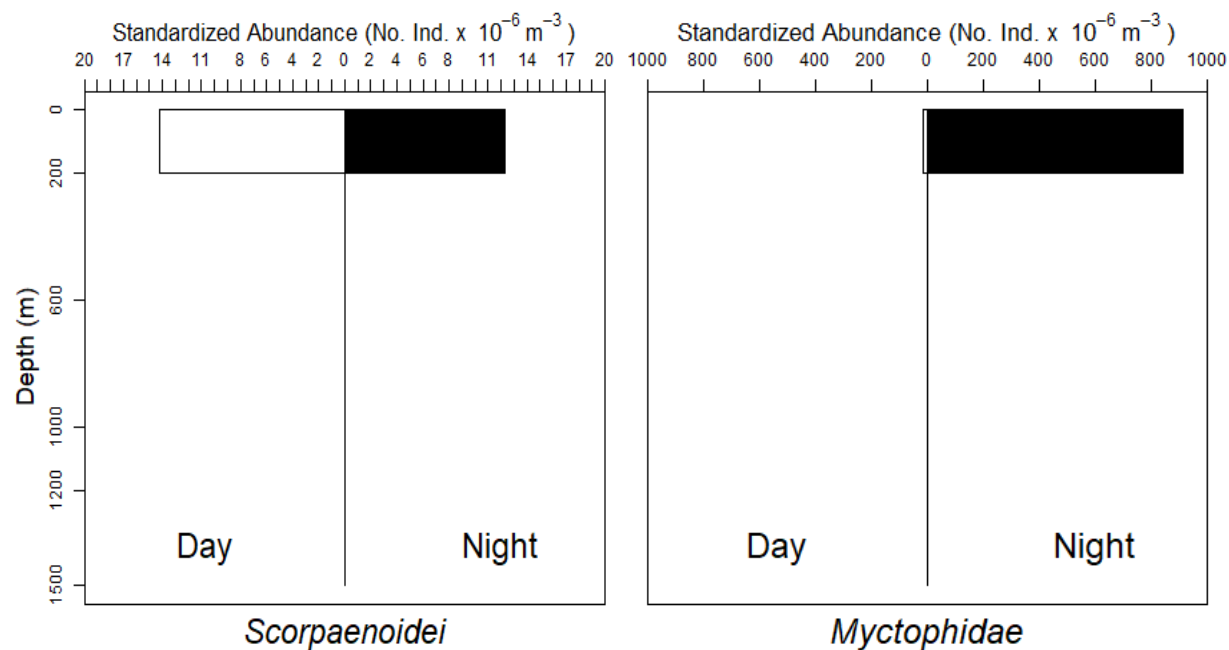


Figure 28. Vertical distribution of scorpaenoids and myctophids during the DEEPEND survey.

3.2.3. *Pontinus rathbuni* – Depth of Occurrence and Size at Depth

The majority (88%) of juvenile *Pontinus rathbuni* obtained from both the *Meg Skansi* and DEEPEND surveys were collected from the upper 200 m of the water column (n=177; Figure 29). No statistical difference was found between the SL of *P. rathbuni* at each depth range ($p>0.05$; Figure 30), though sample numbers below 600 m depth were too small for meaningful comparisons.

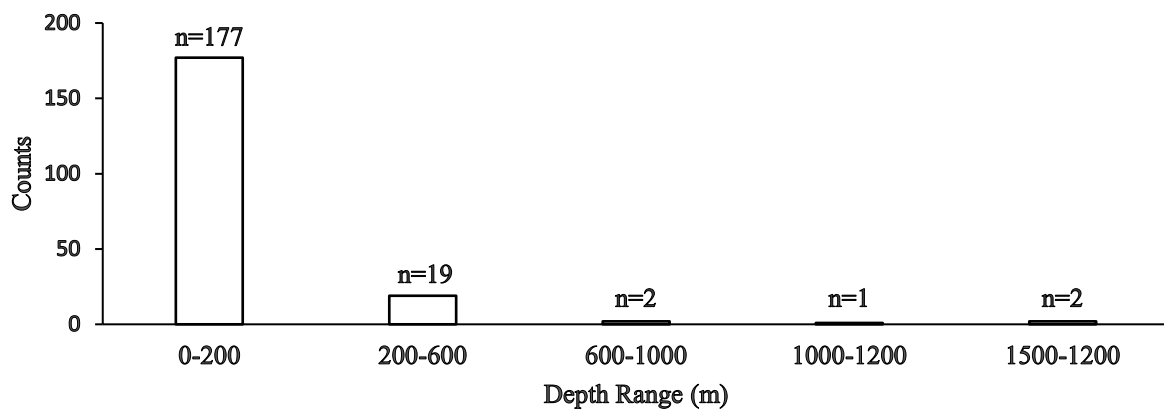


Figure 29. The number of pelagic-phase juvenile *Pontinus rathbuni* collected at varying depth ranges in the Gulf of Mexico during the *Meg Skansi* and DEEPEND surveys.

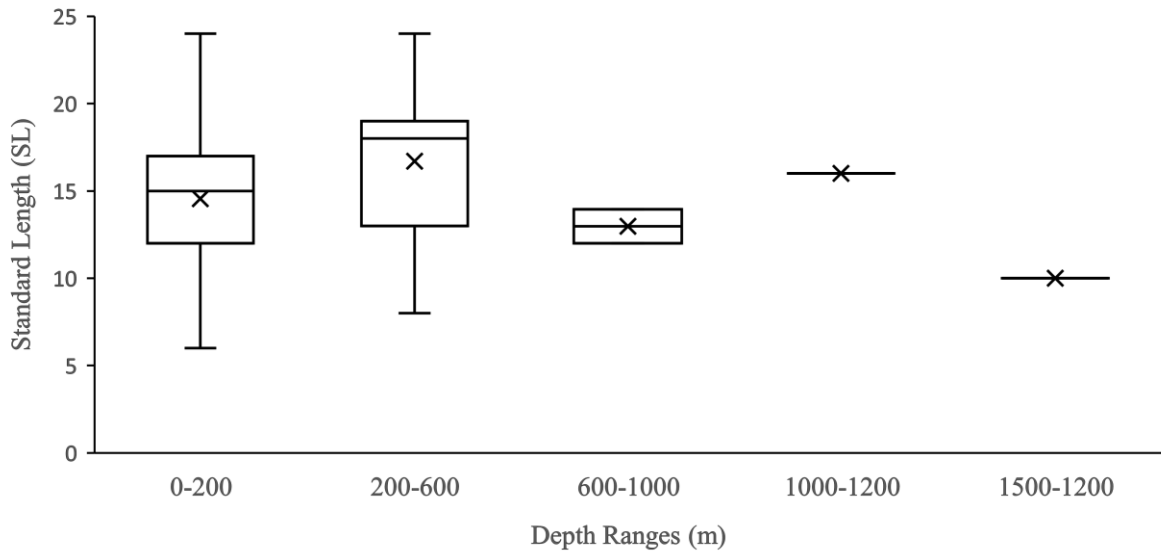


Figure 30. The standard lengths of pelagic-phase juvenile *Pontinus rathbuni* collected at varying depth ranges ($\bar{X} \pm$ mean). Error bars represent one standard deviation from the mean.

3.2.4. *Pontinus rathbuni* – Temporal Distribution

During the *Meg Skansi* survey, specimens were collected during a 9-month consecutive time span, allowing for a comparison of catches and sizes of individuals over time. The majority ($n=107$, ~60%) of juvenile *Pontinus rathbuni* were collected during February (Table 33; Figure 31). Additionally, the number of specimens caught between August 2016 ($n=4$) and July 2018 ($n=10$) were similar to the number of specimens caught during those same months in 2011 (e.g., $n=2$, $n=5$, respectively). While 60% of specimens were collected during February 2011, the average SL of specimens collected during March 2011 (~18.7 mm) was larger than February (~15.3 mm) (Figure 32). However, the average SL of specimens collected during July 2018 (e.g., ~12 mm) was approximately 4-mm larger than the average SL of specimens collected during July 2011 (e.g., ~9.6 mm) (Figure 32).

Table 33. Average standard lengths (mm \pm SE) of *Pontinus rathbuni* collected from the ONSAP and DEEPEND surveys.

Cruise Survey	Year	Month	Standard Length
<i>Meg Skansi</i>	2011	January	14.1 \pm 3.2
		February	15.3 \pm 2.9
		March	18.7 \pm 3.4
		May	7.2 \pm 2.1
		June	10.2 \pm 2.5
		July	9.6 \pm 2.3
		August	10.0 \pm 1.4
DEEPEND	2016	August	10.8 \pm 4.4
	2018	July	12.0 \pm 4.0

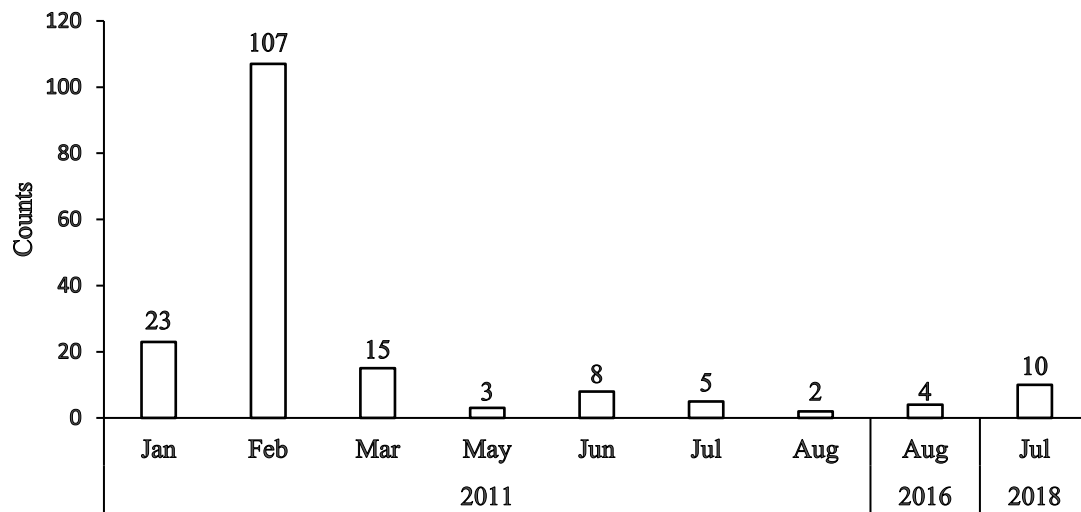


Figure 31. The number of juvenile *Pontinus rathbuni* collected in the upper 200 m from the Gulf of Mexico in 2011.

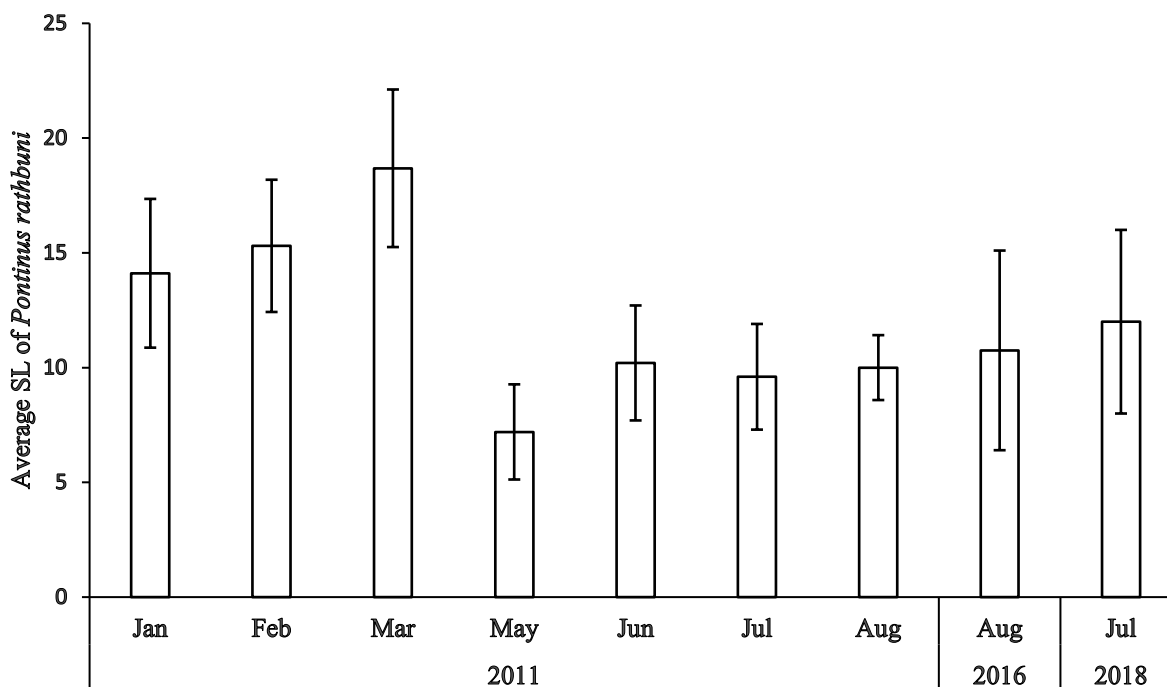


Figure 32. The average standard lengths of juvenile *Pontinus rathbuni* collected in the upper 200 m from the Gulf of Mexico in 2011. Error bars reflect calculated standard error of SL per month.

3.3 Trophic Ecology

A total of 113 specimens of the dominant scorpaenoid species, *Pontinus rathbuni*, were analyzed for gut contents. Analyses were performed only on specimens between 15-19 mm SL in order to compare stomach contents with those of juveniles of the Myctophidae and Sternoptychidae (Hopkins & Baird 1981, 1985).

3.3.1. Stomach Fullness and Vacuity

The overall average stomach fullness of juvenile *P. rathbuni* was 1.3. When delineated by time of day, the average stomach fullness became 3.0 for daytime, and 0.4 for nighttime. The overall average stomach fullness of prey-positive stomachs was 2.8. If delineated by time of day, the average stomach fullness for prey-positive stomachs was 3.1 during the day, and 1.3 at night (Table 34). The stomach fullness of *P. rathbuni* with respect to time of day was determined to be significantly different ($p=3.91 \times 10^{-16}$; non-parametric Mann-Whitney Wilcoxon; Figure 33).

Table 34. The average scores of stomach fullness for all stomachs and prey-positive stomachs (score \pm SE) of *Pontinus rathbuni*.

	Overall Average Stomach Fullness	Average Stomach Fullness of Prey-Positive Stomachs
Day	3.00 ± 1.45	3.10 ± 1.32
Night	0.40 ± 0.63	1.30 ± 0.48
Total	1.30 ± 1.60	2.50 ± 1.38

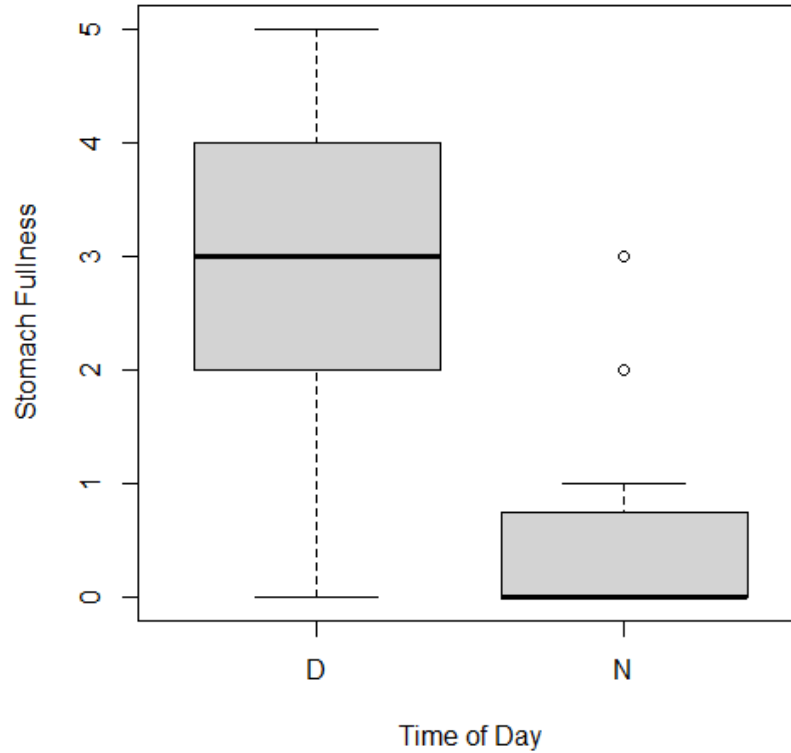


Figure 33. The stomach fullness of pelagic-phase juvenile *Pontinus rathbuni* collected during day and at night.

From the 113 dissected *P. rathbuni*, 42 were caught during the day and 71 were caught at night. Only two of the 42 stomachs of *P. rathbuni* caught during the day were empty, resulting in a 4.8% stomach vacuity index. The stomach vacuity index was calculated to be 73.2% for the *P. rathbuni* caught at night. Despite a larger number of specimens collected at night, the stomach vacuity index was lower and the average stomach fullness and the percent of prey-positive stomachs were higher for specimens collected during the day (Table 35).

Table 35. The total number of stomachs, the number and percentage of prey-positive stomachs, the number of empty stomachs, and the stomach vacuity of dissected pelagic-phase juvenile *Pontinus rathbuni*.

	No. of Stomachs	Prey Positive Stomachs (n)	Prey Positive Stomachs (%)	Empty Stomachs (n)	Stomach Vacuity (%)
Day	42	40	95.2%	2	4.8%
Night	71	19	26.8%	52	73.2%
Total	113	59	52.2%	54	47.8%

3.3.2. Prey Assemblage of *Pontinus rathbuni*

A total of 283 prey items were found within the 59 prey-positive stomachs of pelagic-phase juvenile *Pontinus rathbuni*. A variety of prey types were found including copepods, pteropods, ostracods, an amphipod, bits of carbonate shell, and/or appendages from unidentified zooplankton (UID invertebrate), as well as scales and fish bones (Figure 34). The majority of prey items were copepods (81.3%), which occurred in 73% of prey-positive stomachs. Pteropods composed 5.6% of prey items. However, the percentage of prey items with respect to pteropods is slightly misleading because 16 individual pteropods occurred within a single *P. rathbuni* stomach. While ostracods composed less of the prey assemblage than pteropods, ostracods occurred in 12% of prey positive stomachs as opposed to the single stomach filled with pteropods. Additionally, three stomachs were filled with the intermediate stage of an unknown digenean parasite (Figure 35).

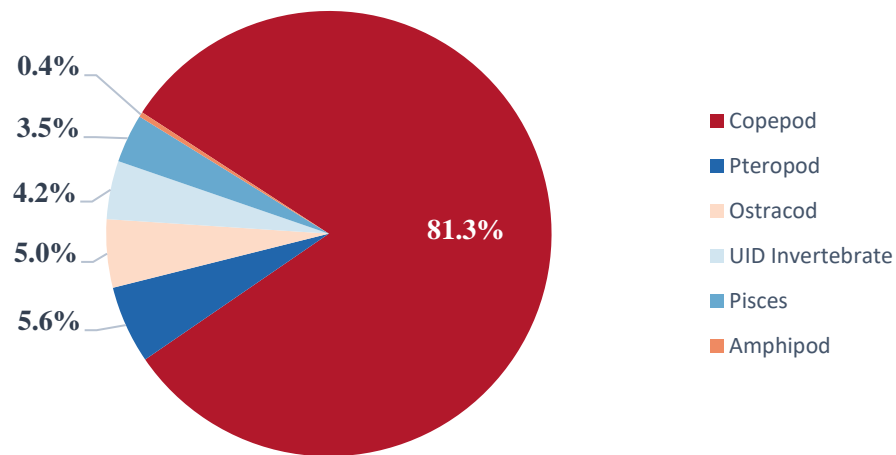


Figure 34. Prey assemblage found within the stomachs of pelagic-phase juvenile *Pontinus rathbuni*.

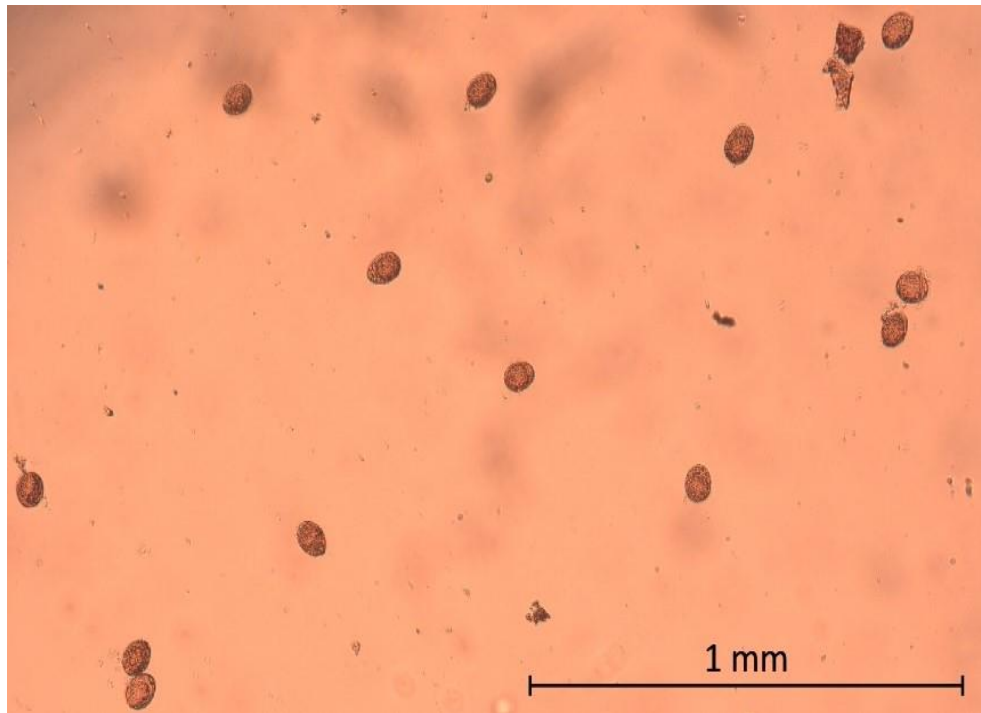


Figure 35. Intermediate stage of an unknown digenean parasite found in the stomachs of *Pontinus rathbuni*.

A total of 53 intestines contained prey items from the 113 juvenile *P. rathbuni* that were dissected. Within the 53 intestines, 115 individual prey items were identified. The same types of prey were found within the intestines as within the stomachs, with the exception of amphipods. The majority of prey were copepods (76.5%), which occurred in 75.5% of prey positive intestines. The remaining portion of the prey assemblage was represented by pteropods (6.1%), ostracods (6.1%), UID invertebrates (6.1%), and scales or bones from fish (5.2%; Table 36). Pteropods occurred in intestinal tracts of three specimens (5.7% of prey-positive intestines) while ostracods occurred in intestinal tracts of five specimens (9.4% of prey-positive intestines). Additionally, one fish had two copepods, two pteropods, and two ostracods within its intestinal tract. Lastly, three individuals had their intestines filled with an unknown digenean parasite. These individuals were also the same individuals that had their stomachs filled with the parasite. *Pontinus rathbuni* may be involved in the life cycle of some species of marine digenean parasite.

Table 36. Intestinal prey contents of *Pontinus rathbuni*.

	Copepod	Pteropod	Ostracod	UID Invertebrate	Pisces	Amphipod	Total
Number	88	7	7	7	6	0	115

3.3.3. Prey State of Digestion

There was a higher average state of digestion of prey from the stomachs of *P. rathbuni* that were collected during the day than at night (Table 37). The differences in state of digestion of prey items from the stomachs of *P. rathbuni* with respect to day and night were significantly different ($p=1.608 \times 10^{-5}$; non-parametric Mann-Whitney Wilcoxon t-test; Figure 36).

Table 37. The average scores of state of digestion (score \pm SE) of prey in pelagic-phase juvenile *Pontinus rathbuni*.

Average prey state of digestion	
Day	2.40 ± 1.20
Night	1.30 ± 1.10
Total	2.30 ± 1.30

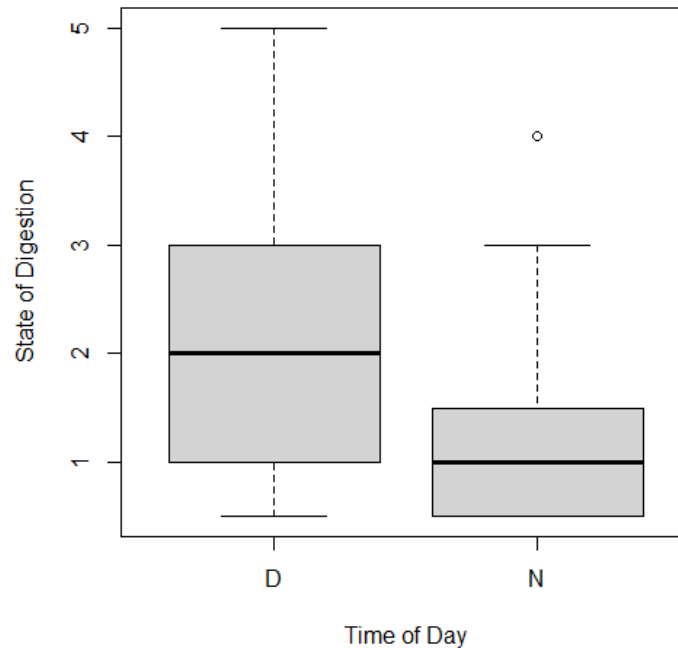


Figure 36. The state of digestion of prey items found within the stomachs of *Pontinus rathbuni* collected during day (D) and at night (N).

4. DISCUSSION

4.1. Spatiotemporal Distribution of Pelagic-Phase Scorpaenoids

Anecdotal observations suggested that pelagic-phase scorpaenoids were being predictably caught in a high frequency that is nearly par with other dominant midwater fishes in epipelagic samples of the GoM during the day (Sutton & Moore, personal communication). Therefore, this study sought to examine the frequency of occurrence and abundance of scorpaenoids to validate anecdotal observations.

Scorpaenoids are not historically considered as a prominent pelagic taxon. However, juvenile scorpaenoids were caught with an overall 47% frequency of occurrence within the epipelagic zone (0-200 m) during both the *Meg Skansi* and DEEPEND surveys. While the overall frequency of myctophids, the overall frequency of myctophids was nearly double that of juvenile scorpaenoids within the epipelagic GoM (Table 30), this was primarily due to nighttime occupation by the former. The disparity between the frequency of occurrence of juvenile scorpaenoids and myctophids was much less during the daytime (49% and 62%, respectively; Table 30). Thus, juvenile scorpaenoids appear to be successful enough in the pelagic realm to be caught nearly as often as the dominant myctophids during half of the diel cycle.

The standardized abundance of pelagic-phase juvenile scorpaenoids in the epipelagic of the GoM were lower from the DEEPEND survey than from the *Meg Skansi* survey both during the day and night (Table 31). This difference in abundance within the epipelagic of the GoM between cruise series could be attributed to the fact that the *Meg Skansi* survey sampled nearly double the volume of water and a larger geographical area than the DEEPEND survey (Table 2; Figure 5, Figure 6), or that pelagic-phase juvenile scorpaenoids were absent due to their spawning cycle. The species which composes most of the specimens collected, *Pontinus rathbuni*, may spawn during February, due to a huge spike of catches in 2011 (Figure 31). This hypothesis is based on the reproductive habits of other species, as the spawning season for *P. rathbuni* is not officially documented (Richards 2006). Future sampling efforts during the winter months (e.g., January, February, and March) of the year are needed to support this hypothesis.

The similarity in the abundance of juvenile scorpaenoids in the epipelagic zone of the GoM during daytime and nighttime suggests that this taxon do not vertically migrate on a diel cycle (Figure 27, Figure 28). In stark contrast, myctophids are strong diel vertical migrators and were found in higher abundances at depth during the daytime but are more abundant within the epipelagic at night (Figure 27, Figure 28). Thus, pelagic-phase juvenile scorpaenoids strongly co-occur with a dominant mesopelagic fish taxon half of the time (night) yet exhibit morphological and behavioral characteristics that deviate from the classic deep-pelagic ichthyotype defined by myctophids.

4.2. Scorpaenoid Faunal Assemblage Structure

Nine unique morphotypes and three scorpaenoid species that have been routinely identified to the genus or species level (e.g., *Helicolenus dactylopterus*, *Pterois* spp., and *Setarches guentheri*) comprised the faunal inventory of juvenile scorpaenoids in the pelagic GoM. Several anatomical and morphological aspects were used to define the nine morphotypes, but parietal spine(s) seemed to be the most diagnostic for differentiating morphotypes. Every juvenile scorpaenoid examined in this study, aside from *Pontinus longispinis*, had parietal spines. The presence/absence, shape, length, curvature, serration, angle, and position of the parietal spine(s) with respect to the nuchal spine(s) separated the scorpaenoids presented in this thesis. The fishes that were collected from the *Meg Skansi*, *Piscas*, and DEEPEND surveys comprised at least 11 species (Table 5). Morphotypes B and I are probably not scorpaenoids. Therefore, at least nine different species compose the pelagic-phase juvenile scorpaenoid assemblage of the GoM. One scorpaenoid species, *Pontinus rathbuni*, exhibited dominance, accounting for approximately 80% of scorpaenoids that were collected (Table 5). Future work may benefit from preserving one specimen for each morphotype described in this thesis for genetic analysis and validation of the putative identifications presented in this study.

4.3. Trophic Analysis of *Pontinus rathbuni*

4.3.1. *Pontinus rathbuni* Diet Composition and Comparison

The majority of the diet of pelagic-phase juvenile *Pontinus rathbuni* consisted of copepods, with occasional ostracods, pteropods, and amphipods. Comparatively, the diet of dominant pelagic vertically migrating taxa, like *Lampanyctus alatus* (family Myctophidae) and *Valenciennellus tripunctulatus* (family Sternoptychidae), also comprises of copepods, euphausiids (shrimps), and ostracods (Baird et al. 1975, Hopkins & Baird 1985, Link & Almeida 2000, Burdett et al. 2017). Even though the only dietary difference between *P. rathbuni* and *L. alatus/V. tripunctulatus* appeared to be that juvenile *P. rathbuni* feed upon pteropods and the dominant vertically migrating taxa prey upon euphausiids, these prey types are minor, approximately 10% or less of their respective diets. More importantly, the majority of the diet of both *P. rathbuni* and *L. alatus/V. tripunctulatus* comprised copepods. Therefore, both *P. rathbuni* and dominant vertically migrating taxa share copepods as their dominant source of prey and resource partitioning regarding prey type does not appear to occur between these common fish taxa (Horn & Ferry-Graham 2006, Burghart et al. 2010).

4.3.2. Stomach Fullness, Prey State of Digestion, and Stomach Vacuity

Gut content analysis of pelagic-phase juvenile *Pontinus rathbuni* suggests that *P. rathbuni* feed during the day and digest their prey at night. Due to the similarity in prey taxa, it can be reasonably concluded that *P. rathbuni* and adult, vertically migrating, mesopelagic fish taxa partition prey resources temporally.

5. CONCLUSION

This thesis focused on the epipelagic habitat use in the GoM by pelagic-phase juvenile scorpaenoids, morphotype characterization of juvenile scorpaenoids, and diet examination of juvenile *Pontinus rathbuni*. Juvenile scorpaenoids were collected in nearly half of all epipelagic samples in the GoM. While there was a large difference in abundance between juvenile scorpaenoids and adult myctophids in the epipelagic at night, abundances during the day were similar (approximately 14 ind. per 10^{-6} m^{-3}). There is no evidence to suggest that juvenile

scorpaenoids vertically migrate. Nine taxa of scorpaenoid were collected, with *Pontinus rathbuni* accounting for approximately 80% of the assemblage. The growth and development of *P. rathbuni* in the pelagic domain are made possible by a diet comprised mostly of energy-rich copepods, consumed primarily during the day, in contrast to the nocturnal feeding of most zooplanktivorous mesopelagic fishes. Understanding how a primarily benthic fish taxon utilizes the epipelagic for development, what juvenile stages eat, and how that predation and development interact with other fish taxa not only illuminates the complexity of the pelagic food web but also allows for insight into a historically overlooked group of fishes with respect to a low-latitude pelagic ecosystem.

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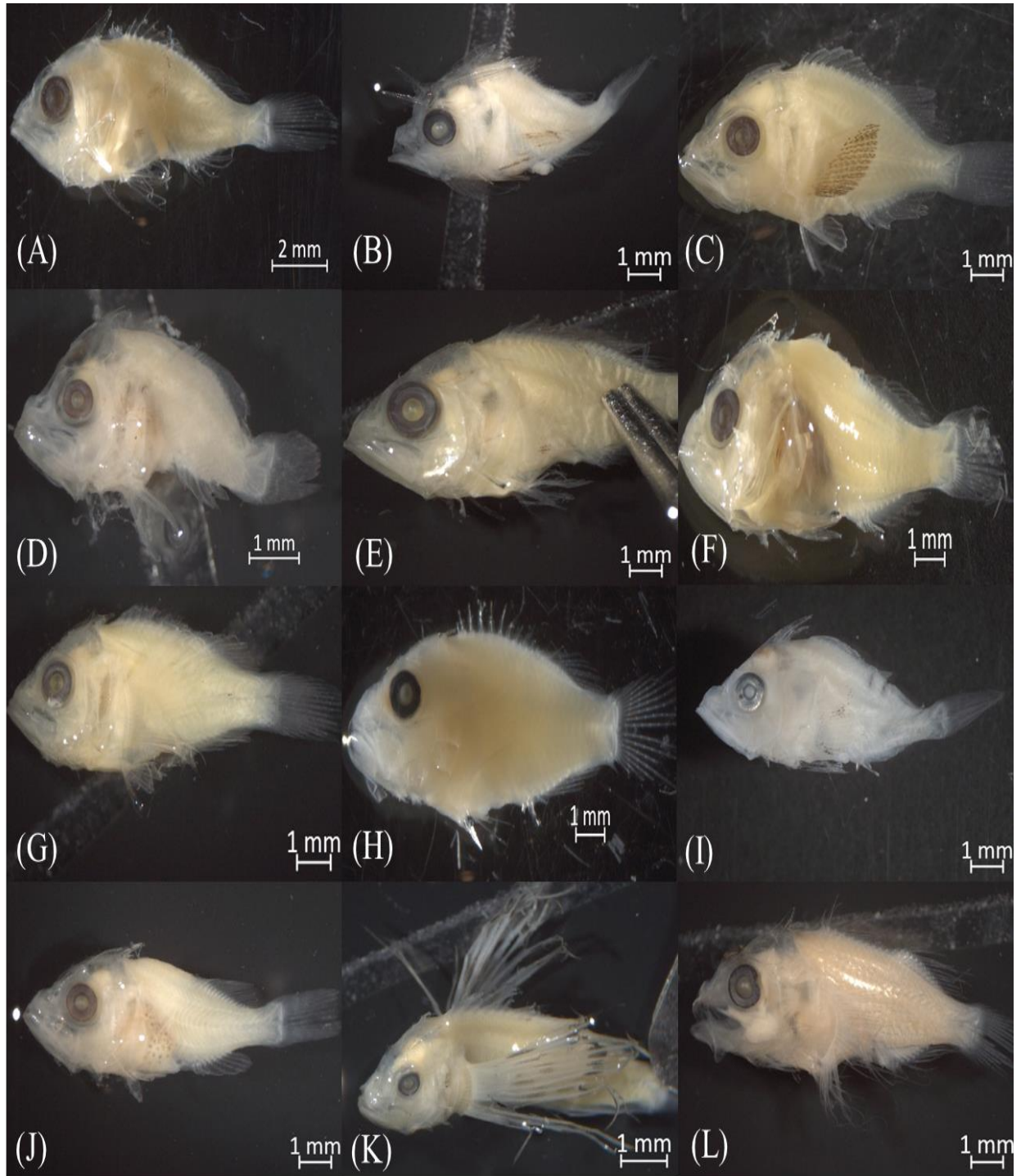
7. APPENDICES

Appendix Table 1. A combination of the morphometrics measured and their respective morphometric ratios reported as a percent of standard length for all morphotypes/species of pelagic-phase juvenile scorpaeonids examined.

	SL	SNL	PAL	HL	BD	PD	OD	SNOL	%SNL	%PAL	%HL	%BD	%PD	%OD	%SNOL
Morphotype A	15.61	1.53	9.39	6.82	5.46	1.66	2.48	4.01	9.82	59.92	43.99	35.35	10.73	15.96	25.80
Morphotype B	8.65	1.05	5.27	3.98	3.01	0.93	1.28	2.31	12.09	60.97	45.76	34.85	10.78	14.69	26.43
Morphotype C	8.00	0.91	4.51	3.31	2.99	1.00	1.20	2.09	11.39	56.39	41.39	37.36	12.50	15.00	26.11
Morphotype D	7.88	0.88	4.95	3.74	3.61	1.14	1.34	2.23	11.25	63.08	47.69	45.98	14.72	17.19	28.42
Morphotype E	4.55	0.63	2.73	2.23	2.06	0.81	0.73	1.47	13.77	60.23	49.19	45.16	17.52	15.73	32.10
Morphotype F	11.57	1.28	7.07	5.11	3.96	1.29	1.87	3.14	11.06	61.08	44.17	34.18	11.12	16.16	27.12
Morphotype G	6.59	0.71	3.99	2.73	2.29	0.88	1.12	1.82	10.94	60.73	42.09	34.41	14.50	17.38	28.45
Morphotype H	8.57	0.84	4.84	3.48	3.30	2.94	1.30	2.14	9.66	56.42	40.77	37.90	34.29	15.35	24.96
Morphotype I	8.50	1.00	5.50	3.55	3.60	1.65	1.25	2.25	11.81	64.58	41.74	42.22	19.58	14.72	26.53
Morphotype J	7.43	0.77	4.80	3.47	2.93	1.20	1.13	1.90	10.18	64.90	46.60	39.48	15.94	15.13	25.31
<i>Helicolenus dactylopterus</i>	11.28	1.24	7.12	4.74	4.22	1.23	1.70	2.96	11.31	62.44	43.50	37.27	11.10	15.99	27.56
<i>Pterois</i> spp.	9.49	0.78	4.83	2.97	2.86	1.17	0.91	1.70	6.76	40.91	26.03	24.36	9.00	8.15	14.91
<i>Setarches guentheri</i>	12.45	1.26	8.23	5.49	5.27	2.40	1.84	3.17	11.49	64.25	45.24	41.08	18.88	15.13	26.72

Appendix Table 2. Meristic ranges of all morphotypes and identified species of pelagic-phase juvenile scorpaenoids examined.

	Dorsal fin-spines	Dorsal fin-rays	Anal fin-spines	Anal fin-rays	Pectoral fin-rays	Branching pectoral fin-rays	Slit behind 4 th gill arch
Morphotype A (n=276)	XI-XII	9	III	5	16-18	N	Y
Morphotype B (n=1)	XII	11	III	6	17	N	N
Morphotype C (n=17)	XII	9	III	5	18-20	Y	N
Morphotype D (n=2)	XI	9	III	5-6	20-22	Y	Y
Morphotype E (n=1)	XII	9	III	5	17	N	Y
Morphotype F (n=3)	XII	9	III	5	19-20	Y	N
Morphotype G (n=9)	XI-XII	9-10	III	5	17	Y	N
Morphotype H (n=2)	XII	9	III	5	17	Y	N
Morphotype I (n=3)	XII	9	III	5	18	N	Y
<i>Helicolenus dactylopterus</i> (n=4)	XI-XII	12-13	III	5	19-20	Y	N
<i>Pterois</i> spp. (n=3)	XI	11	III	7	14	Y	N
<i>Setarches guentheri</i> (n=17)	XI-XII	9-10	III	5	22-24	Y	Y



Appendix Figure 1. Images representing the pelagic-phase juvenile scorpaenoid forms of morphotypes A-I (A-I) and three species identified before the work of this thesis: *Helicolenus dactylopterus* (J), *Pterois* spp. (K), and *Setarches guentheri* (L).