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Thesis of
Travis J. Kirk

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 2024

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NOVA SOUTHEATERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

Trophic Ecology of Black Swallowers (Scombriformes: Chiasmodontidae: *Chiasmodon*) In the Deep-Pelagic Gulf of Mexico

By

Travis J. Kirk

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 Science

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Abstract

The ecology of deep-pelagic predatory fishes remains poorly understood despite their importance as ecosystem regulators and energy transfer vectors. This study investigated the trophic ecology of three species of the predatory fish genus *Chiasmodon* ("black swallowers") in the Gulf of Mexico, a region that serves as an analog for the global low-latitude deep pelagial, the world's largest cumulative ecosystem. Foraging habits (e.g., selectivity, chronology, daily ration) of an "advanced" evolutionary fish in a system that is otherwise dominated by basal fish taxa, were quantitatively estimated via high-resolution stomach content analysis. A quantitative dataset of both predator and prey abundance, the largest and most complete of its kind in existence, was utilized. A total of 337 *Chiasmodon* individuals were dissected, of which 138 had prey-positive stomachs (41%). Stomach content analysis revealed a strong selectivity for cephalopods as prey, while teleost fishes were consumed in proportions as predicted to those in the environment. Crustaceans, though highly abundant as potential prey, appeared to be actively avoided. Identifiable teleost prey taxa included Stomiidae (dragonfishes), Sternoptychidae (hatchetfishes), *Dolicholagus* (deep-sea smelts), *Cyclothone* (bristlemouths), and *Bregmaceros* (antenna codlets). These results differ substantially from the Stomiidae, another top mesopelagic predator in the Gulf of Mexico that have been shown to feed almost exclusively on Myctophidae, teleosts, and certain crustaceans. The preponderance of cephalopod predation within the same system for *Chiasmodon* is notable due to its rarity, and promotes future research opportunities comparing predation impact between these top predators. Daily ration was calculated as 3.64%, suggesting that *Chiasmodon* feeds more often than dominant "lie-in-wait" predators such as dragonfishes, and therefore likely exerts more top-down control per fish than more basal fishes.

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1. **Introduction**

1.1 *Chiasmodon* History

  Chiasmodon (family Chiasmodontidae) is a genus of deep-sea fishes found circumglobally in the mesopelagic and bathypelagic depths of the ocean. These fishes are commonly known as the black swallowers (Prokofiev & Kukuev, 2009) due to their ability to swallow prey larger than their own body size (Wiecaszek et al., 2011). Very little is known about the genus *Chiasmodon*, as a significant amount of the existing literature has been published by only two scientists, whom both focused on taxonomy. These researchers are Marcelo Roberto Souto de Melo of the University of São Paulo and Artem Mikhailovich Prokofiev of the Russia Academy of Sciences. While found circumglobally, the dynamics, systematics, and behaviors of *Chiasmodon* in different regions have not been well studied. Systematically, there has been recent revision of the classification of the family Chiasmodontidae, as they are now classified in the order Scombriformes (Fricke et al., 2022), having been historically classified in the order Perciformes (Johnson, 1969).

  Regarding their taxonomy, there are conflicting assertions between the two scientists regarding the number of species within the genus *Chiasmodon*. Prokofiev claims there to be only two species of *Chiasmodon*, listed as *Chiasmodon niger* and *C. lavenbergi*, with any fish located outside of the western Pacific considered as *C. niger* (Prokofiev, 2011, Prokofiev 2010). In contrast, Melo suggests there are seven species of *Chiasmodon*, and has developed an identification key that lists the appropriate characters to identify each species (Melo, 2009a). Genetic barcoding studies have shown Melo's conclusions to be more accurate, especially in his distinctions of species in the Pacific Ocean. These conclusions are not definitive, as the multiple Atlantic-based species that Melo has classified are found to be within the same genetic clade (Kenchington et al., 2017). With very little research done elsewhere on *Chiasmodon*, there is not enough direct evidence to confirm either claim. The uncertainty and debate regarding these fishes displays how much more research is needed to gain a better understanding of them and their ecology.

1.2 Trophic Ecology of the Deep Sea

Trophic ecology involves investigation of feeding relationships among organisms (Garvey & Whiles, 2016) and is often used to trace energy flow (i.e., food web dynamics) through ecosystems (Finlay et al., 2010). Such studies investigate what a consumer eats, ideally in a quantitative fashion (da Silveira et al., 2020). Trophic ecology results highlight many aspects of ecosystem structure, such as predator-prey interactions, regulation of prey abundance by predators, and cycling of organic material in ecosystems (Ahlbeck et al., 2012).

Trophic ecology of the bathypelagic biome remains poorly known due to the lack of quantitative assessments of its inhabitants and the limited understanding of their roles in food webs (Golikov et al., 2019, Powell et al., 2003, Sutton et al., 2010). Some deep-sea fishes are known to utilize specific trophic niches (Gill et al., 2013), with some feeding more opportunistically as generalists (Gartner & Musick, 1989), while other fishes are highly selective feeders (Sutton & Hopkins, 1996). Generalist feeding strategies appear to be rare in the deep sea, contradicting initial expectations that most predators forage on a wide number of taxa (Gartner et al., 1997). *Chiasmodon*'s morphology makes them an ideal predator, as their sizeable mouth allows them to swallow a considerably larger maximum prey size (Sutton, 2005). Moreover, their larger teeth and more advanced jaw structures are believed to allow for more efficient prey capture in environments limited by food availability, such as the deep sea (Kenaley, 2012).

Trophic ecology studies of deep-pelagic fishes have mainly focused on zooplanktivorous families (e.g., Myctophidae, Sternoptychidae, and Gonostomatidae), while research has focused less on micronektivores (Richards et al., 2019). Previous studies have merged data on several chiasmodontid genera (i.e., *Pseudoscopelus, Kali,* and *Dysalotus*) to integrate data across the family Chiasmodontidae (Prokofiev, 2014). Consequently, there is a lack of information regarding the trophic ecology of the dominant genus *Chiasmodon* specifically. This study aims to provide a detailed trophic study of *Chiasmodon* in the "upper mile" (0-1500 m depth) of the Gulf of Mexico, a hyper-diverse pelagic ecosystem that has been intensively sampled (Sutton et al., 2020). This study entails a detailed, quantitative trophic study of *Chiasmodon*, and the results can be used as a baseline for future trophic studies covering this genus and the rest of Chiasmodontidae. This study

provides a fundamental counterpoint to what is currently know about top predators of the mesopelagic zone, a system numerically dominated by basal fish taxa (e.g., Stomiiformes and Myctophiformes). The trophic ecology and predation impact of an "advanced" (i.e., spiny-rayed) fish taxon will be investigated, with additional comparisons of the foraging strategies of the basal and advanced predatory fish lineages.

1.3 Ecological Role

Deep-pelagic fishes are key elements of oceanic food webs, with many fishes migrating daily from deeper depths during the day to shallower depths at night in search of greater feeding opportunities (Afonso et al., 2014). During vertical migrations, these fishes become prey for larger pelagic predators (Hopkins & Gartner, 1992). Mesopelagic fishes are a primary food source for epipelagic predators and contribute to the transfer of energy between depths (Young et al., 2015). Previous studies have shown the presence of species in the family Chiasmodontidae are present in the diet of epipelagic predators. For example, Moteki et al. (2001) found swallowers in the stomach contents of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Small proportions of Chiasmodontidae have also been found in the stomachs of common dolphins (*Delphinus delphis*) in the Bay of Biscay, Atlantic Ocean (Spitz et al., 2010). Moreover, Lin et al. (2020) found chiasmodontids present in the stomachs of 16 individual bigeye tuna (*Thunnus obesus*) in the Indian Ocean. Collectively, these studies show that *Chiasmodon* is both a prey and a predator, suggesting an important linkage between higher trophic levels.

Studying pelagic food webs is important for open-ocean management. As epipelagic fisheries resources have been overexploited, fishing has progressed deeper, putting mesopelagic fish populations at risk for overfishing (Norse et al., 2012). Given that mesopelagic fishes act as a prey source for the top epipelagic predators, this can further impact the population sizes of commercially valuable apex predator species. Connectivity of mid-trophic mesopelagic species with apex predators has become of significant interest in recent years (Choy et al., 2016).

1.4 Stomach Content Analysis

Stomach content analysis remains the most quantitative approach for trophic ecology studies, as it provides direct evidence of what fishes have eaten, how much was eaten (i.e., biomass converted to carbon for ecosystem modeling), and how often a fish eats (Parzanini et al., 2017). When quantitative data are available regarding prey abundance and productivity, the predation impact of a predator can be estimated. Fishes are ideal subjects for stomach content analysis because prey are often consumed whole rather than highly masticated (as with Crustacea and Mollusca). Given the near impossibility of directly observing deep-pelagic fish foraging behavior, stomach content analysis is the most effective method when quantitative, species-specific prey data are desired (Amundsen & Sánchez-Hernández, 2019).

Stomach content analysis provides the foundation for more complex questions to be answered using various statistical indices (Manko, 2016, Chipps & Garvey, 2007). For this study, the first question to be answered is "What prey taxa do *Chiasmodon* feed upon?" and whether they are selective feeders. Selectivity is estimated via a computed electivity index, which reflects the proportion of specific prey types in diets relative to their abundance in the environment (Lechowicz, 1982). These indices indicate whether a predator is selecting for or against specific prey in their environment (Tilghman et al., 2001).

The second question this project aims to answer is when, where, and at what depths *Chiasmodon* feed, and whether they feed throughout the 24-hour period or only at certain times of day (Darnell & Meierotto, 1962). Stomach fullness, prey degree of digestion, and time of capture are important factors for determining feeding chronology. Fuller stomachs or prey items with lower states of digestion in fishes collected during late hours may indicate nighttime foraging, or vice versa (Hopkins & Baird, 1981, Ozawa et al., 1977). Knowing when a fish eats can then be compared to its depths of collection (i.e., vertical distribution) and the known vertical distribution of prey, thus allowing insight into foraging strategies.

The third question of this study is to determine how much and/or how often *Chiasmodon* feed. This is the key parameter for estimating daily ration, or how much of their body weight

Chiasmodon are consuming per day. This parameter is critical for ecosystem modeling (e.g., mass-balance models, such as ECOPATH) and in the calculation of predation impact of a predator on its prey. Like most aspects of deep-sea trophic ecology, daily ration has rarely been quantified, despite its ecological importance (Madurell & Cartes, 2005).

The final goal of this study is to compare the feeding strategies of widely evolutionary disparate deep-pelagic predators. Most deep-sea fishes are considered relatively basal and less evolved compared to "higher" spiny-rayed fishes that make up most of the fish fauna in coastal marine ecosystems (Haedrich, 1996). What makes *Chiasmodon* and other swallowers unique is that they are considered "advanced," or more evolved, fishes due to the presence of true spines on their fins (Melo, 2009b). The results of this study can be used to compare *Chiasmodon* as a top predator in the deep-pelagic Gulf of Mexico with the other described top-predator fishes, namely the Stomiidae (e.g. dragonfishes), with respect to foraging mode (e.g., hunt and seek vs. lie-in-wait), prey composition, and feeding rate.

1.5 Significance of Work

Predators play important roles in marine ecosystems, influencing species interactions and flow of energy and nutrients through food webs, and hence ecosystem structure and function. In top-down systems, the removal of certain predators can cause dramatic increases in lower-trophic fish and zooplankton assemblages (Spiers et al., 2016). Fishes are important predators of lower-trophic organisms (e.g., krill and other planktivores; Kock et al., 2012), likely playing a key role in stabilizing species composition in open-ocean ecosystems. This study determines the impact of *Chiasmodon* predation in a low-latitude oceanic ecosystem. In an environment dominated by basal fish taxa, this study further aims to determine the foraging habits and predatory impact that an "advanced" fish has in these environments, which is a currently unknown assessment. Through stomach content analysis and the calculation of various statistical indices, this study increases the understanding of the role that a top predator like *Chiasmodon* plays in deep-pelagic environments and provides a useful foundation which can be utilized towards future trophic studies of other deep-pelagic predators.

2. Methods

2.1 Sample Collection

Following the *Deepwater Horizon* oil spill in April 2010, there was a need to assess the impact the spill had on deep-sea fish populations. As a result, the Offshore Nekton Sampling and Analysis Program (ONSAP) was created to collect and provide scientific evidence for NOAA's National Resource Damage Assessment (NRDA) (Sutton et al., 2020). Field sampling took place on research cruises from 2010 through 2011 aboard NOAA's FRV *Pisces* and the M/V *Meg Skansi* (Figure 1, Table 1). Each research cruise used their own unique sampling techniques depending on the target species and depth ranges. On the FRV *Pisces*, a high-speed midwater rope trawl (HSRT) was used to conduct "shallow-water" (surface - 700 m) and "deep-water" (surface - 1500 m) trawls (Figure 2). The *Meg Skansi* utilized a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS), which had a 10-m^2 mouth area and a 3-mm mesh size (Judkins et al., 2017). This apparatus allowed for sampling at various depths sequentially (Wiebe et al., 1985) (Figure 2, Table 2).

Following collection at sea, all samples were transported and stored at the Oceanic Ecology Laboratory located at Nova Southeastern University's Guy Harvey Oceanographic Center. The specimens were initially fixed at sea in a 10% formalin:seawater mixture, then transferred to 70% ethanol:water for longer preservation. A total of 764 total Chiasmodontidae specimens were collected across the seven cruises, with 535 of them identified to the genus *Chiasmodon*. Of those specimens, 456 were captured with the HSRT on the *Pisces* cruises, while 79 were captured using the MOCNESS on the *Meg Skansi* cruises.
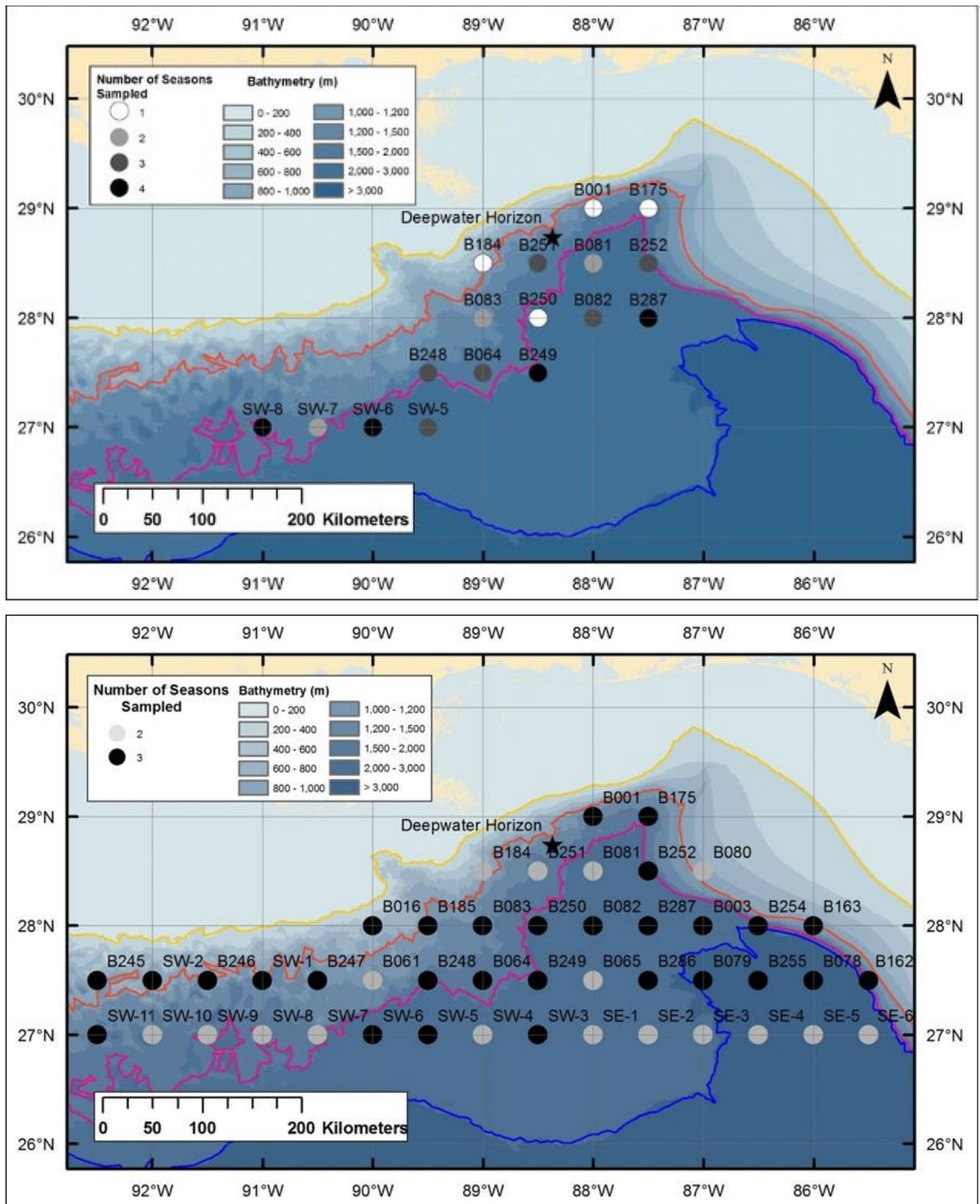
Figure 1. Locations of sites sampled by FRV *Pisces* (top) and M/V *Meg Skansi* (bottom) during the Offshore Nekton Sampling and Analysis Program. (Image from Marks, 2016).
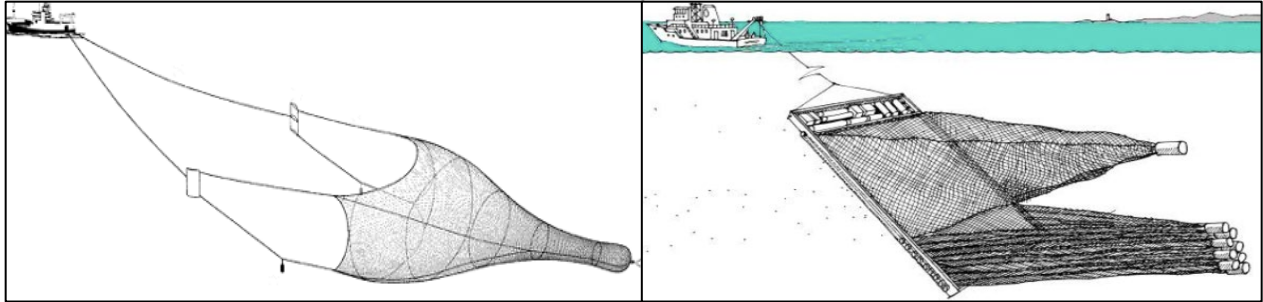
Figure 2. Sampling techniques utilized during the FRV *Pisces* cruises using the High-Speed Rope Trawl (left) (image from Tomljenović & Rusak, 2014) and the M/V *Meg Skansi* cruises using the Multiple Opening/Closing Net and Environmental Sensing System (right) (image courtesy of U.S. GLOBEC, 2002).

Table 1. Dates of research cruises during the NOAA-sponsored Offshore Nekton Sampling and Analysis Program.

Cruise	Research Vessel	Dates
PC8	FRV *Pisces*	2 Dec. 2010 – 19 Dec. 2010
PC9	FRV *Pisces*	23 Mar. 2011 – 6 Apr. 2011
PC10	FRV *Pisces*	23 Jun. 2011 – 13 Jul. 2011
PC12	FRV *Pisces*	8 Sep. 2011 – 27 Sep. 2011
MS6	M/V *Meg Skansi*	28 Jan. 2011 – 30 Mar. 2011
MS7	M/V *Meg Skansi*	14 Apr. 2011 – 30 Jun. 2011
MS8	M/V *Meg Skansi*	18 Jul. 2011 – 30 Sep. 2011

Table 2. The depths sampled of the Multiple Opening and Closing Net and Environmental Sensing System during the M/V *Meg Skansi* cruises.

Net	Depths Sampled
N_0	Surface – 1500 m
N_1	1500 m – 1200 m
N_2	1200 m – 1000 m
N_3	1000 m – 600 m
N_4	600 m – 200 m
N_5	200 m – Surface

2.2 Identification

All *Chiasmodon* specimens were identified to species level using a taxonomic key developed by Melo (2009a). In the key, seven species have been described worldwide: *Chiasmodon asper*, *C. braueri*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. pluriradiatus*, and *C. subniger* (Figure 3). Any specimen that was unable to be identified to species, due to either extensive physical damage or a lack of diagnostic morphometric features, was labeled "*C. niger* complex." Diagnostic features included the number of pectoral fin rays, the number of head pores, and the presence/absence of basibranchial and hypobranchial teeth (Table 3). Standard length (SL) was measured to the nearest 0.01 mm, starting at the anterior end of the head, and continuing until the end of the hypural plate. Each individual fish was given a unique identification code to be used in further analysis.
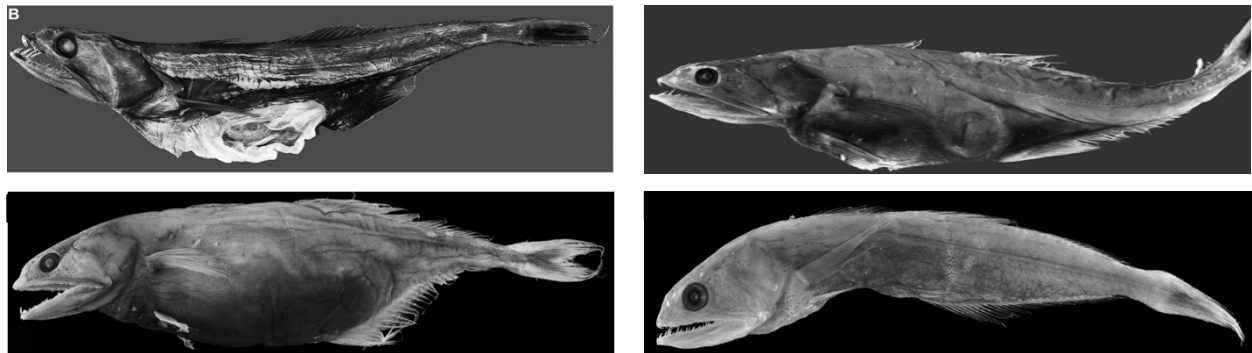
Figure 3. *Chiasmodon niger* (top left), *C. braueri* (top right), *C. microcephalus* (bottom left), and *C. pluriradiatus* (bottom right). Images from Melo (2009a).

Table 3. Distinguishing physical features among seven species of *Chiasmodon* following Melo (2009a) identification key.

Species	Pectoral Fin Ray Count	Fangs	Head Pores	Basibranchial/ Hypobranchial Teeth Present?
C. asper	15-16	2	9	No
C. braueri	12-14	1	8	Yes
C. harteli	12-14	1	6	Yes
C. microcephalus	12-14	1	7	No
C. niger	12-14	1	7	Yes
C. pluriradiatus	15-16	2	8	No
C. subniger	12-14	1	7	No

2.3 Dissection

Following identification, all specimens were dissected to remove their stomachs and intestines. Dissection began with a transverse incision located at the isthmus, followed by a vertical cut down the ventral body margin to the anus. The body cavity was then folded open, and the stomach and intestines were removed using forceps. The liver and pyloric caeca were separated from the stomach and properly disposed of. Gut fullness was measured visually on a scale from 0 to 5, with 0 representing an empty stomach and 5 representing a completely full and distended stomach (Figure 4). A drop of water was applied to the stomach prior to opening. The stomach was then "unzipped" along one side using fine forceps. All prey items were removed, recorded, and identified to the lowest taxonomic level based upon the condition of their morphological characteristics (Buckland et al., 2017) (Figure 6). The state of digestion of each prey item was also recorded using a visual numbering scale of 1-6, represented by: $1 =$ empty stomach, $2 = < 25\%$ intact items, $3 = 25 - 50\%$ intact, $4 = 50 - 75\%$ intact, $5 = > 75\%$ intact, $6 =$ no digestion (Riaz et al., 2020). All prey items were blotted dry and weighed to the nearest 0.01 g. The smaller and thinner prey items were mounted on microscope slides with glycerin, while larger prey items were stored in vials labeled with their corresponding identification code. All prey items and their diagnostic features were photographed using the Carl Zeiss Labscope imaging software. Intestinal contents were assessed qualitatively (presence/absence) by major prey taxa. In cases where

intestinal contents were from the same taxa as stomach contents, it was assumed they were derived from the same prey. Specimens that were extensively damaged during collection were not dissected. Additionally, specimens that served as vouchers for genetic barcoding studies were not dissected.

Figure 4. *Chiasmodon* specimens analyzed for stomach fullness values: 1 (top left), 2 (top right), 4 (bottom left), and 5 (bottom right).

2.4 Feeding Selectivity

All prey items were identified, and numbers of each prey taxon were used to quantify feeding selectivity, expressed using Ivlev's electivity index (Ivlev, 1961),

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i equals prey percentage in the diet of prey type i and p_i equals percentage of that prey type in the environment (Ivlev, 1961). Prey relative abundance in the environment was calculated using sample collection data from the Oceanic Ecology Lab. Selectivity was calculated for three major prey taxa: Teleostei, Cephalopoda, and Crustacea. The values for E_i range between -1 and 1, with -1 indicating complete negative selection for a given prey taxa (i.e., no consumption), 0 indicating consumption similar to the prey's relative abundance in nature, and 1 indicating complete positive prey selection. Feeding selectivity of major prey taxa was compared with frequency of occurrence of the same taxa to elucidate *Chiasmodon*'s predatory behavior. High frequency of occurrence and high selectivity for a prey type would signify *Chiasmodon* actively targeting that particular prey taxon. Low frequency of occurrence and high feeding selectivity would indicate that *Chiasmodon* strongly preferred that specific prey type when it was encountered. And a high frequency of occurrence and low selectivity value would indicate a more opportunistic feeding strategy without a preference for that certain prey type.

2.5 Feeding Chronology

Feeding chronology was determined by comparing stomach fullness and state of digestion data to the time of capture of the predator specimen (Sutton and Hopkins, 1996). Each graph was visually scrutinized to determine whether predation occurs preferentially at specific times of day. For example, higher stomach fullness and lower prey digestion at night would indicate primarily nocturnal feeding. A two-sample t-test was utilized to assess the effect of time of capture (day vs. night) on both state of digestion and gut fullness to determine if they were a function of time of day. The results of the t-test were considered significant with a p-value < 0.05. Five t-tests were run for each continuous variable, with a test for each of the four classified species and the fifth test being representative of the entire collection. The null hypothesis of each test was that the respective variable (stomach fullness and state of digestion) during the day was greater than or equal to the same variable during the night. Time as capture was categorized as during the day when the time was between 0600 and 1800. For night, the time slots were listed as between 1800 and 0600. All statistical analysis for feeding chronology was conducted in the programming software R Studio.

2.6 Daily Ration

Daily ration, representing how much *Chiasmodon* feed in a 24-h cycle relative to their own weight, is generally difficult to estimate in deep-sea fishes due to the lack of feeding interval information (Macpherson, 1985). Estimating daily ration requires a multi-step approach, starting with calculating the instantaneous ration, defined as the weight of each meal as a percentage of the predator's weight (Sutton & Hopkins, 1996). This was calculated as the sum weight of all prey items divided by the sum wet weight of all prey-positive predators. Prey item weights were calculated as the weight of the prey item at the time of consumption (i.e., fresh weight, not digested weight). For highly digested prey items where major prey taxon could be determined, the smallest identifiable individual of that prey taxon was substituted (a conservative proxy). Prey that weighed more than that lowest value was retained in its original weight.

The next step required knowledge of the digestion time of the prey items. However, this information must be obtained indirectly in deep-sea fishes due to the inability to acquire it in a laboratory setting (Tseitlin, 1980). Digestion estimates of prey were obtained via literature review and through other quantitative approaches done throughout this study. If feeding chronology results suggested a diel feeding pattern, indicating daily feedings, a digestion time of one day was assumed. In contrast, if chronology results did not display a diel feeding pattern, it was assumed that it took more than one day for the prey to be digested. This digestion time range was then compared to the frequency of empty stomachs to estimate the time *Chiasmodon* spends with an empty stomach before their next feeding event. Once the digestion time and the time spent with an empty stomach were confirmed, they were summed together to acquire the number of days *Chiasmodon* went between meals. Instantaneous ration was then divided by the number of days between meals, resulting in a daily ration estimation.

3. Results

3.1 Chiasmodon species in the Gulf of Mexico.

Of the 535 *Chiasmodon* specimens collected, 337 were utilized for stomach content analysis. Of the seven known species of *Chiasmodon*, three were identified from the Gulf of

Mexico sample set: *Chiasmodon braueri*, *C. niger*, and *C. pluriradiatus*. Of the 337 analyzed specimens, 66 were *C. braueri*, 62 were *C. niger*, 178 were *C. pluriradiatus*, and 31 identified as "*C. niger* complex" (Table 4). Individuals identified as "*C. niger* complex" were excluded from separate selectivity and chronology analysis and were instead considered with the pooled collection of *Chiasmodon*. Length-weight regressions of all species were produced (Figures 5-8).

Table 4. Quantitative stomach content results of *Chiasmodon* (n = 337).

	Chiasmodon	*C. pluriradiatus*	*C. niger*	*C. braueri*	*C. niger complex*
Dissected Specimens	337	178	62	66	31
Prey-Positive Stomachs	138	79	20	28	11
Proportion of Prey Positive Stomachs	0.41	0.44	0.32	0.42	0.35
Average Stomach Fullness	0.86	0.97	0.55	0.85	0.87
Average State of Digestion	2.27	2.45	1.79	2.19	2.18
Average Stomach Fullness W/ Prey	2.1	2.19	1.7	2	2.25
Average State of Digestion W/ Prey	3.41	3.51	3.12	3.26	3.35
Average Standard Length (mm)	74.9	76.4	75	76.7	62.6
Average Wet Weight (g)	4.75	4.67	5.52	5.29	2.39
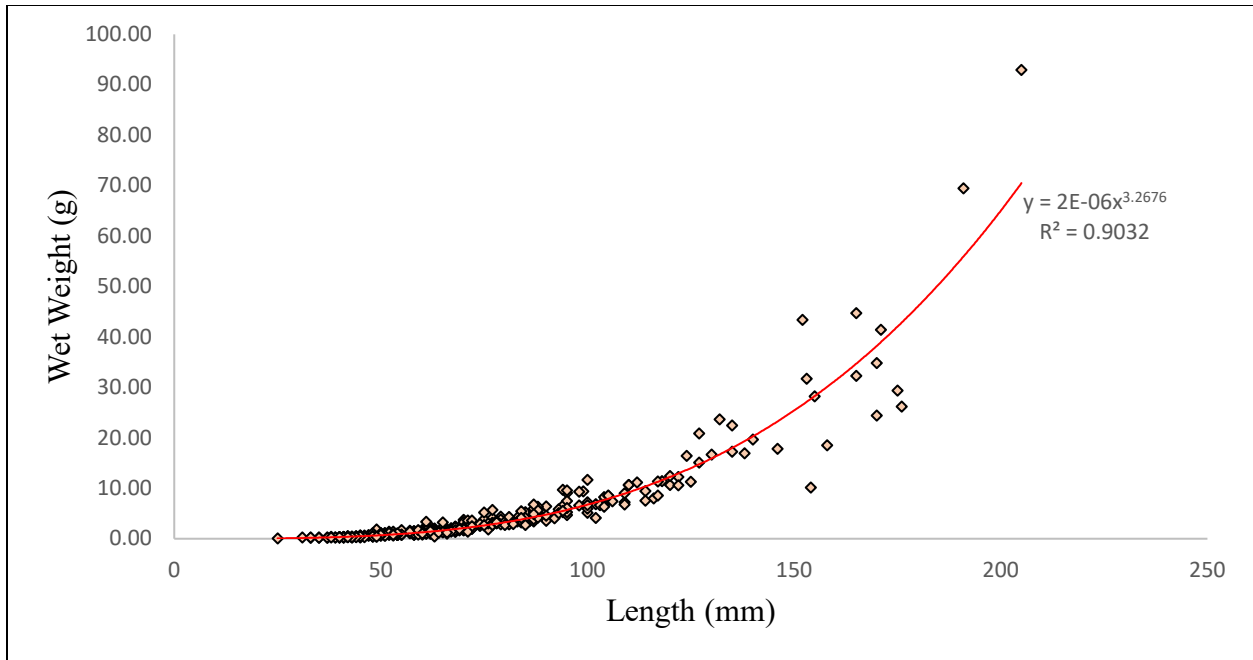
Figure 5. Length-weight regression of all dissected *Chiasmodon* specimens.
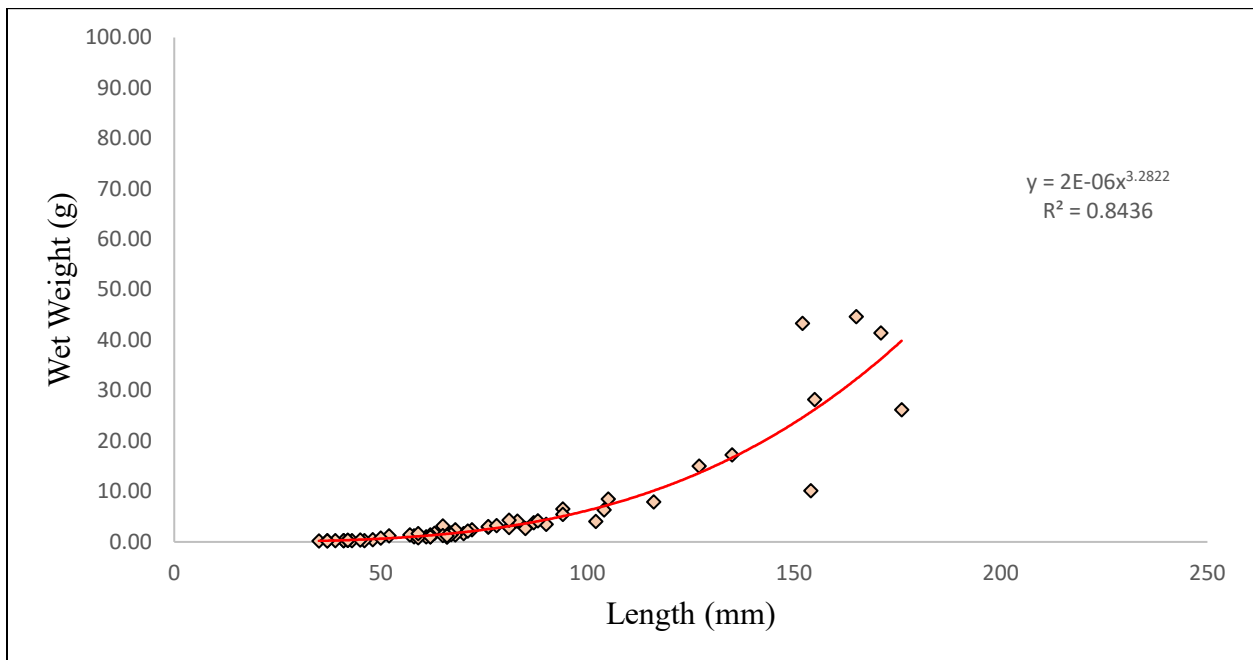
Figure 6. Length-weight regression of all dissected *Chiasmodon braueri* specimens.
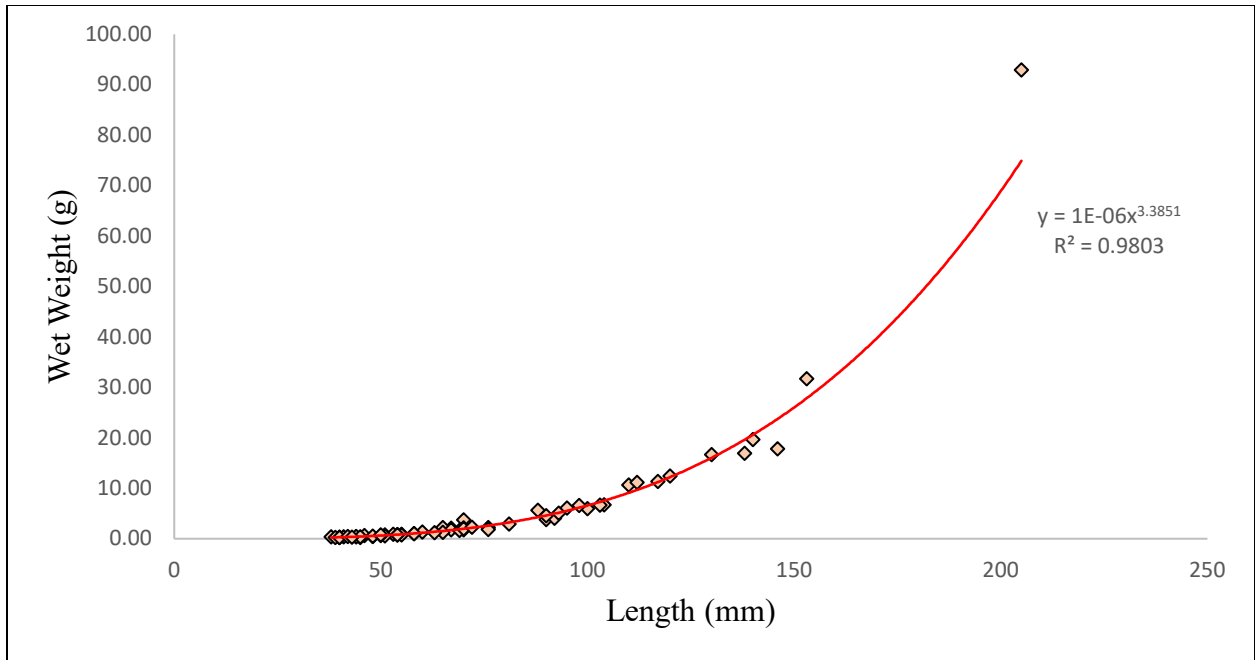
Figure 7. Length-weight regression of all dissected *Chiasmodon niger* specimens.
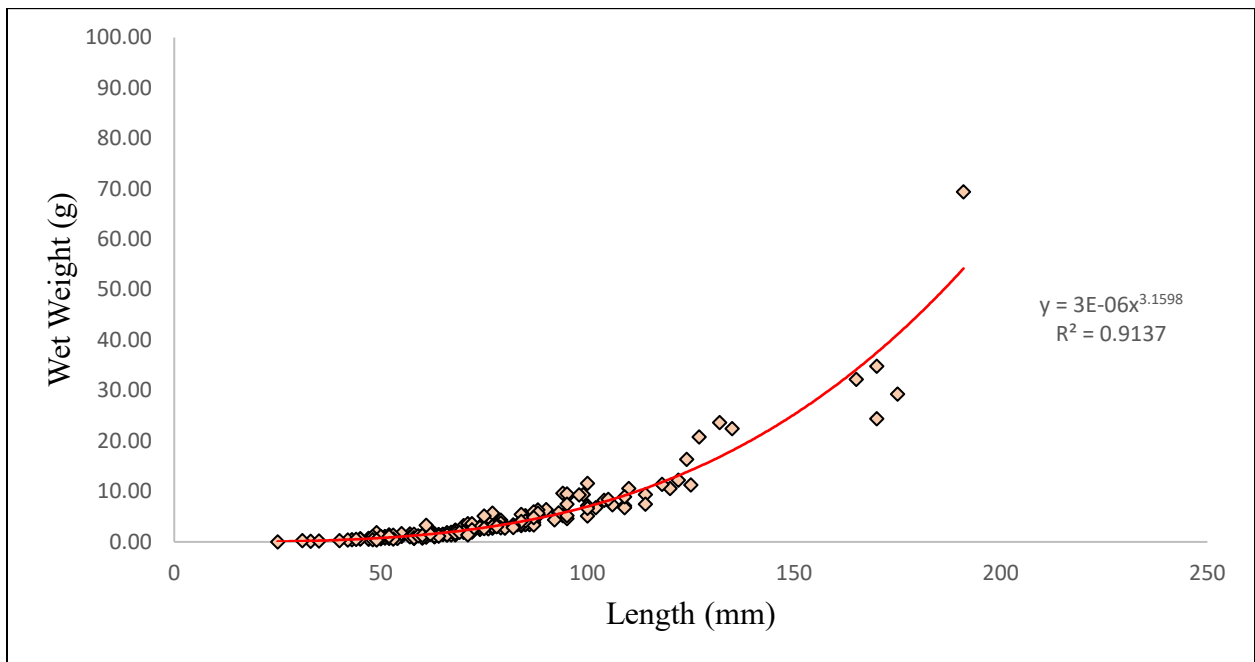
Figure 8. Length-weight regression of all dissected *Chiasmodon pluriradiatus* specimens.

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3.1.1 Chiasmodon - all species.

Of the 337 specimens of *Chiasmodon* that were dissected, 138 (41%) contained prey items in their stomachs. Average stomach fullness of all specimens was 0.86, and the average state of digestion of all prey items was 2.27. When only including specimens with prey-positive stomachs, the average stomach fullness was 2.10 and the average state of digestion of prey items was 2.10 (Table 4). In total, 54 cephalopods (%F = 39%), 49 teleosts (%F = 35%), and three crustaceans (%F = 2%) were identified as prey (Table 5). The remaining 33 prey items (%F = 24%) were unidentifiable to major prey taxon.

3.1.2 Chiasmodon pluriradiatus

Of the 178 specimens of *C. pluriradiatus* that were dissected, 79 (44%) contained prey items in their stomachs. The average standard length of *C. pluriradiatus* examined was 76.4 mm, with an average wet weight of 4.67 g. Average stomach fullness was 0.97, and the average state of digestion of all prey items was 2.45. When only including specimens with prey-positive stomachs, the average stomach fullness was 2.19 and the average state of digestion of prey items was 3.51 (Table 4). A total of 25 prey items were identified as Teleostei (%F = 32%). Of those 25, there was one instance of *Bregmaceros*, *Dolicholagus*, and Monacanthidae, and two instances of *Cyclothone* and Stomiidae. The remaining 18 teleosts could not be identified further. However, the Monacanthidae was believed to be a net feed, as it showed no sign of digestion or a slime coating, and thus was excluded from further analysis. There were 43 prey items were identified as cephalopods (%F = 54%). No crustaceans were found within this species. The remaining 11 prey items were unable to be identified and were classified as unknown (%F = 14%) (Table 5).

3.1.2 Chiasmodon braueri

Of the 68 specimens of *C. braueri* that were dissected, 28 (42%) contained prey items in their stomachs (Table 5). The average standard length of *C. braueri* was 76.7 with an average wet weight of 5.29. Average stomach fullness of all dissected individuals was 0.85, and average state of digestion of all prey items was 2.19. For the specimens that contained prey items, average stomach fullness was 2.00 with an average state of digestion of prey items of 3.26 (Table 4). A total of 12 prey items were identified to Teleostei (F = 43%). Of those 12, there were two instances

of Stomiidae, and the remaining 10 could not be identified further. Five prey items were identified as cephalopods (%F = 18%), and two were identified as crustaceans (%F = 7%). The remaining nine prey items were unable to be identified and were classified as unknown (%F = 32%) (Table 5).

3.1.3 Chiasmodon niger

Of the 62 specimens of *C. niger* that were dissected, 20 (32%) contained prey items in their stomachs (Table 4). Average standard length of *C. niger* was 75.0 mm, with an average wet weight of 5.52. Average stomach fullness of all dissected individuals was 0.55, and average state of digestion of all prey items was 1.79. For the specimens that contained prey items, average stomach fullness was 1.70 with an average state of digestion of prey items of 3.12 (Table 4). A total of four prey items were identified to Teleostei (%F = 20%). There was one instance of *Cyclothone* and one instance of Sternoptychidae. The remaining two teleosts could not be identified further. Three prey items were identified as cephalopods (%F = 15%). One item was identified as a crustacean (%F = 5%). Most of the prey items of *C. niger* were unable to be identified, with 12 being classified as unknown (%F = 60%) (Table 5).

3.1.4 Chiasmodon niger complex

Of the 31 specimens of *C. niger* complex that were dissected, 11 (35%) contained prey items in their stomachs (Table 4). Average standard length of *C. niger* complex was 62.6, with an average wet weight of 2.39. Average stomach fullness of all dissected individuals was 0.87, and average state of digestion of all prey items was 2.18. For the specimens that contained prey items, average stomach fullness was 2.25 with an average state of digestion of prey items of 3.35 (Table 4). A total of eight prey items were identified to Teleostei (%F = 73%). Of those eight, there was one instance of *Cyclothone*. The remaining seven teleosts were unable to be identified further. Three prey items were identified as cephalopods (%F = 27%). No crustaceans were found within this species. There was only one prey item that was unable to be identified and classified as unknown (%F = 9%) (Table 5).

Table 5. Stomach content analysis results of *Chiasmodon* species in the Gulf of Mexico (n = 337)

Prey Taxa	C. pluriradiatus	C. niger	C. braueri	C. niger complex
Teleostei	25	4	12	8
Bregmaceros sp.	1	-	-	-
Cyclothone sp.	2	1	-	1
Dolicholagus longirostris	1	-	-	-
Argyropelecus sp.	-	1	-	-
Stomiidae	2	-	2	-
Cephalopoda	43	3	5	3
Crustacea	-	1	2	-
Unknown	11	12	9	1
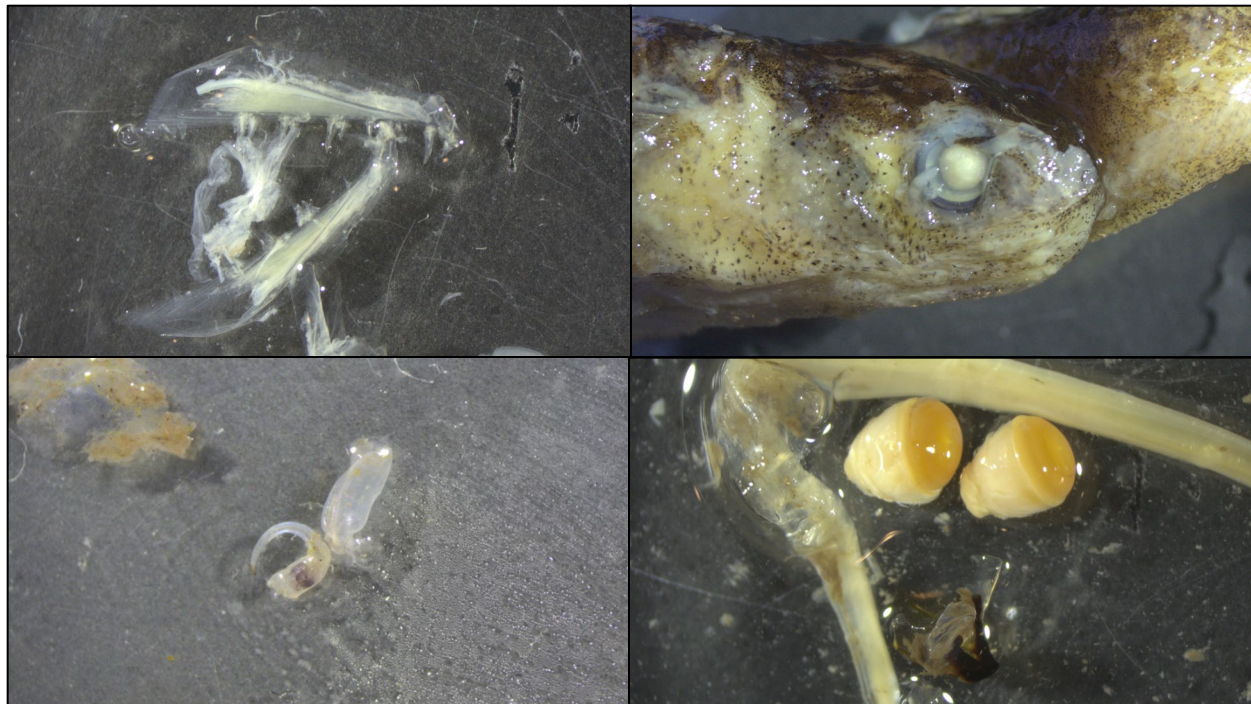
Figure 9. Prey items of *Chiasmodon* identified as: Teleostei/Stomiidae (top left), Teleostei/*Bregmaceros* (top right), Amphipod crustacean (bottom left), Cephalopod eyes (bottom right).

3.2 Feeding Selectivity

Prey abundance raw counts (individuals) in the environment derived from quantitative net sampling were 129,440 teleost fishes, 1,284 cephalopods, and 122,439 crustaceans. As a result, the P_i values for the Ivlev equations were 0.5113, 0.0051, and 0.4836, respectively (Table 6).

3.2.1 Chiasmodon spp.

The Ivlev index suggested consumption of Teleostei (-0.0513) at rates relative to their abundance in the environment, but a strong preference for Cephalopoda (0.9803), and a strong avoidance of Crustacea (-0.9493) (Table 6).

3.2.2 Chiasmodon pluriradiatus

The Ivlev index suggested consumption of Teleostei (-0.1634) at rates relative to their abundance in the environment, but a strong preference for Cephalopoda (0.9841), and a strong avoidance of Crustacea (-1.000) (Table 6).

3.2.3 Chiasmodon braueri

The Ivlev index suggested consumption of Teleostei (0.1052) at rates relative to their abundance in the environment, but a strong preference for Cephalopoda (0.9620), and a strong avoidance for Crustacea (-0.6425) (Table 6).

3.2.4 Chiasmodon niger

The Ivlev index suggested consumption of Teleostei (-0.0112) at rates relative to their abundance in the environment, but a strong preference for Cephalopoda (0.9732), and a strong avoidance for Crustacea (-0.5892) (Table 6).

Table 6. Feeding selectivity of *Chiasmodon* species in the Gulf of Mexico. Values denote Ivlev electivity indices. The variable r signifies prey occurrence in the diet and p signifies prey relative abundance in the environment.

Species	r_i	p_i	E_i	Conclusion
Chiasmodon – all species				
Cephalopoda	0.5094	0.0051	0.9803	Strong preference
Teleostei	0.4623	0.5113	-0.0504	Predicted consumption
Crustacea	0.0283	0.4836	-0.8894	Strong avoidance
C. pluriradiatus				
Cephalopoda	0.6324	0.0051	0.9841	Strong preference
Teleostei	0.3676	0.5113	-0.1634	Predicted consumption
Crustacea	0.0000	0.4836	-1.0000	Strong avoidance
C. braueri				
Cephalopoda	0.2632	0.0051	0.9620	Strong preference
Teleostei	0.6316	0.5113	0.1052	Predicted consumption
Crustacea	0.1053	0.4836	-0.6425	Strong avoidance
C. niger				
Cephalopoda	0.3750	0.0051	0.9732	Strong preference
Teleostei	0.5000	0.5113	-0.0112	Predicted consumption
Crustacea	0.1250	0.4836	-0.5892	Strong avoidance

3.3 Feeding Chronology

3.3.1 Chiasmodon spp.

Stomach fullness did not differ between daytime and nighttime (p = 0.7934). Similarly, a t-test comparing prey state of digestion with time of day indicated state of digestion values during the daytime were not significantly less than or equal to state of digestion values during the nighttime (p = 0.2259). Therefore, neither variable was determined to be a function of time of day. Of the 53 individuals captured in the shallow trawls, 43 were captured during the night solar cycle,

with the remaining 10 captured during the day. The remaining 284 (84%) fishes were captured in the deep trawls. Of those 284 individuals, 127 were captured during the night solar cycle, with the remaining 157 captured during the day (Figure 10).

3.3.2 Chiasmodon pluriradiatus

A total of 32 (18%) specimens were caught in the shallow trawls, with the remaining 146 (82%) caught in the deep trawls. In the shallow trawls, five specimens were caught during the day and the remaining 26 were caught at night. In the deep trawl, 87 specimens were caught during the day and 59 were caught at night (Figure 10). The two-sample t-test comparing stomach fullness with time of day concluded that *C. pluriadiatus* stomach fullness values during the daytime were not significantly less than or equal to stomach fullness values during the nighttime ($p = 0.2219$). Similarly, the t-test comparing state of digestion with time of day concluded state of digestion values during the daytime were not significantly less than or equal to state of digestion values during the nighttime ($p = 0.8168$). Therefore, neither variable was determined to be a function of time of day (Figures 11, 12).

3.3.3 Chiasmodon braueri

A total of five (7%) specimens were caught in the shallow trawls, with the remaining 61 (93%) caught in the deep trawls. In the shallow trawls, two specimens were caught during the day and the remaining three were caught at night. In the deep trawl, 28 specimens were caught during the day and 33 were caught at night (Figure 10). The two-sample t-test comparing stomach fullness with time of day concluded that *C. braueri* stomach fullness values during the daytime were not significantly less than or equal to stomach fullness values during the nighttime ($p = 0.7129$). Similarly, the t-test comparing state of digestion with time of day concluded state of digestion values during the daytime were not significantly less than or equal to state of digestion values during the nighttime ($p = 0.3652$). Therefore, neither variable was determined to be a function of time of day (Figures 11, 12).

3.3.4 Chiasmodon niger

A total of 10 (16%) specimens were caught in the shallow trawls, with the remaining 52 (84%) caught in the deep trawls. In the shallow trawls, two specimens were caught during the day and the remaining eight were caught at night. In the deep trawl, 25 specimens were caught during the day and 27 were caught at night (Figure 10). The two- comparing stomach fullness with time of day concluded that *C. niger* stomach fullness values during the daytime were not significantly less than or equal to stomach fullness values during the nighttime (p = 0.2506). Similarly, the t-test comparing state of digestion with time of day concluded state of digestion values during the daytime were not significantly less than or equal to state of digestion values during the nighttime (p = 0.6662). Therefore, neither variable was determined to be a function of time of day (Figures 11, 12).
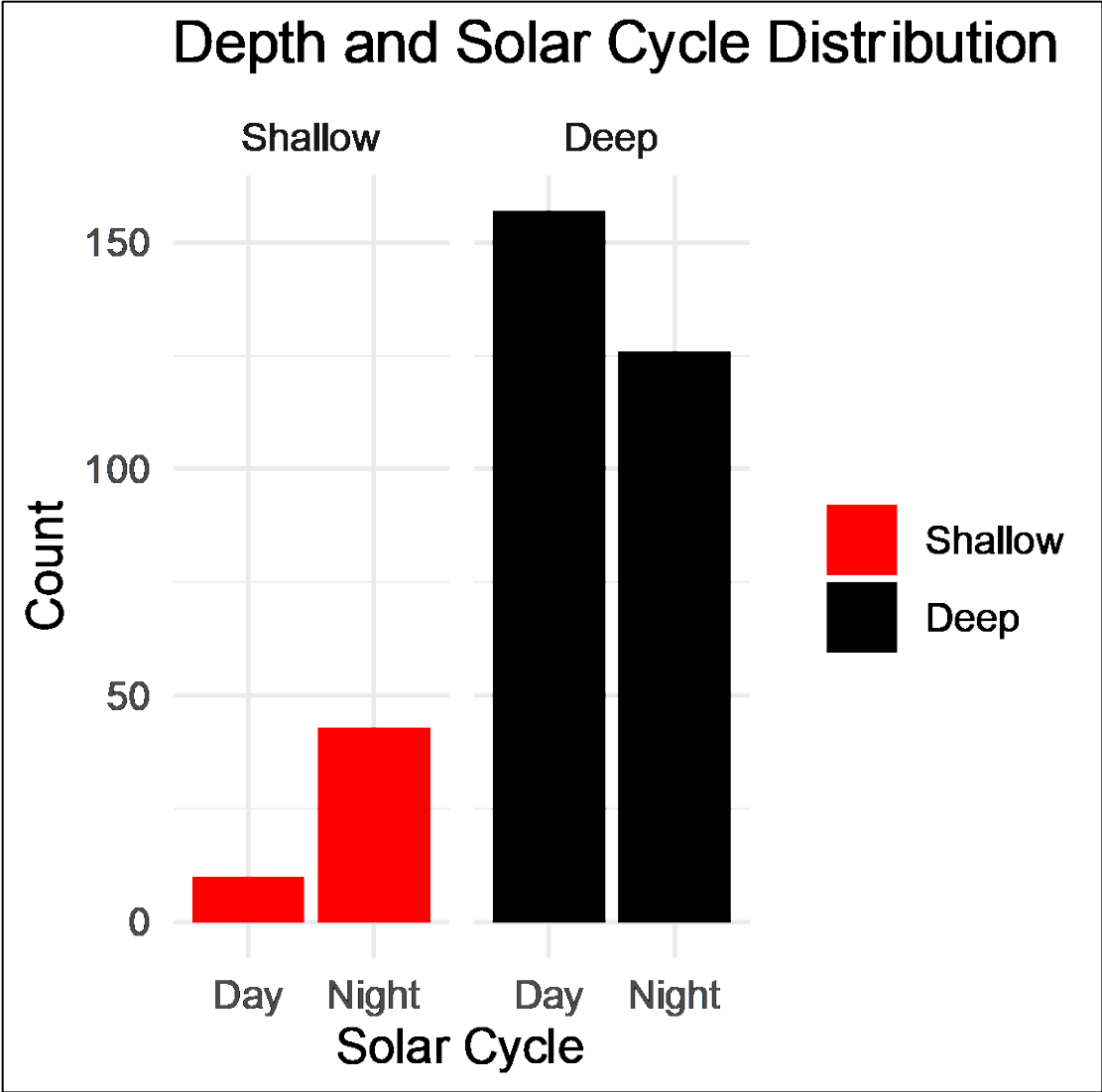
Figure 10. Depth and time of capture data of *Chiasmodon*. Collection time-sampling depth pairs were: Shallow-Day, Shallow-Night, Deep-Day, and Deep-Night.
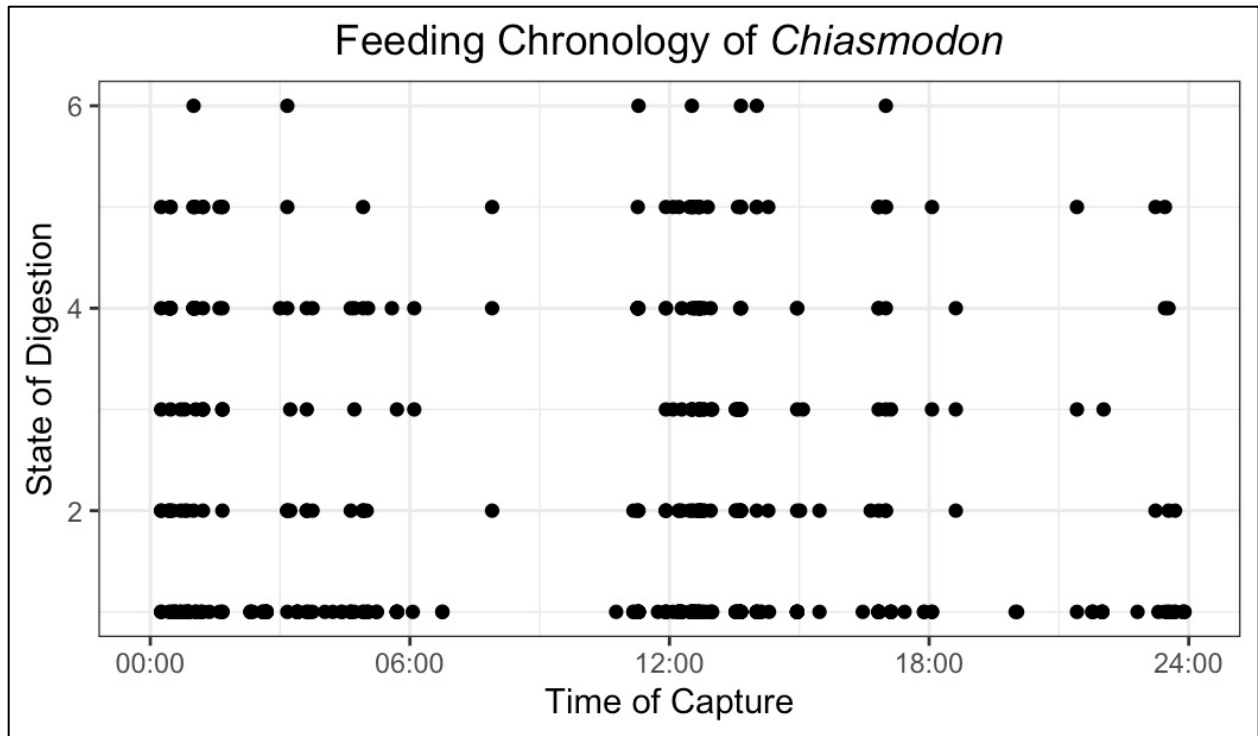
Figure 11. Feeding chronology of *Chiasmodon* species in the Gulf of Mexico, represented by prey state of digestion vs time of capture across a 24-hour cycle.
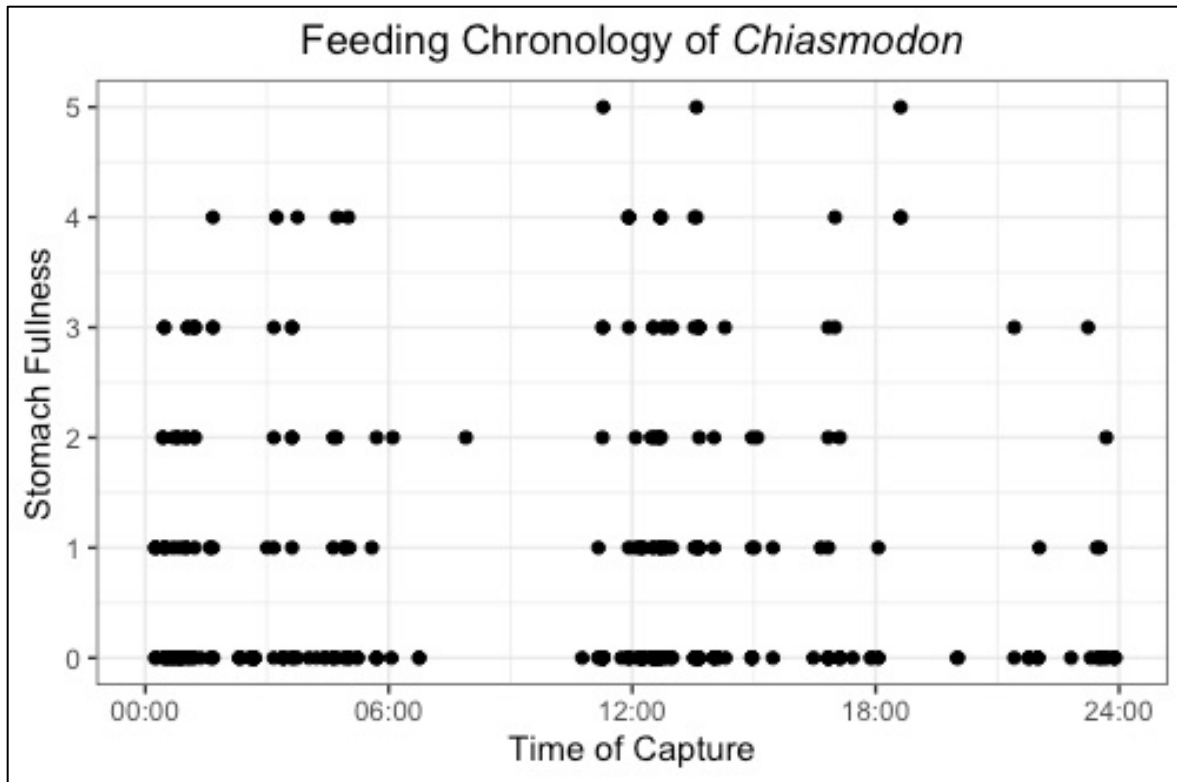
Figure 12. Feeding chronology of *Chiasmodon* species in the Gulf of Mexico, represented by prey stomach fullness vs time of capture across a 24-hour cycle.

3.4. Feeding Intervals and Daily Ration

Since feeding chronology results did not suggest a recurrent diel feeding cycle, it was inferred that *Chiasmodon* either took longer than one day to digest most prey or fed on an irregular schedule within the diel cycle. When compared with literature estimating the digestion times of a fish in similar cold-water temperatures of 4-8°C, it was estimated that *Chiasmodon*'s digestion time was two days for an average prey item (He & Wurtsbaugh, 1993; Drazen & Seibel, 2007). Time with an empty stomach was derived from the proportion of prey-positive stomachs, which was 41%. This suggests that on average *Chiasmodon* goes ~1.4× the time it takes to digest the prey (0.59/0.41) with an empty stomach before its next feeding event. Multiplying the two days of digestion time by this factor yields 2.8 days spent with an empty stomach. This value was added to the digestion time, resulting in a total time spent in between meals calculated as 4.8 days.

3.4.1 Instantaneous Ration

The lowest taxon-specific prey weights were 1.38 g for Teleostei, 0.29 g for Cephalopoda, and 0.28 g for Crustacea. Instantaneous ration (average meal size) of all *Chiasmodon* specimens containing prey was calculated as 13.35% the predator's own weight. The sum of all prey items was 86.27 g, and the sum of all predators was 493.85 g. Daily ration was calculated to be 3.64% (Table 7). The instantaneous ration of *C. pluriradiatus* specimens was calculated as 14.27% of the predator's weight. The sum of all prey items was 49.32 g, and the sum of all predators was 345.71 g. Daily ration was calculated to be 2.97% (Table 7). Instantaneous ration of *C. braueri* was calculated as 24.53%. The sum of all prey items was 20.41 g, and the sum of all predators was 83.21 g. Daily ration was calculated to be 5.11% (Table 7). Instantaneous ration of *C. niger* was calculated as 23.07%. The sum of all prey items was 7.29 g, and the sum of all predators was 31.60 g. Daily ration was calculated to be 4.81% (Table 7).

Table 7. Instantaneous and daily ration estimates of *Chiasmodon* species in the Gulf of Mexico.

Species	Sum of Prey (g)	Sum of Predators (g)	$R_{Instantaneous}$	$\dfrac{R_{Instantaneous}}{4.8\ days}$	Daily Ration Percent (%)
All	86.27	493.85	17.47%	0.0364	3.64
C. pluriradiatus	49.32	345.71	14.27%	0.0297	2.97
C. niger	7.29	31.60	23.07%	0.0481	4.81
C. braueri	20.41	83.21	24.53%	0.0511	5.11

4. Discussion

4.1 Trophic Ecology

A total of 41% (n = 138) of stomachs examined in this study were found to be prey-positive, which is a significantly larger proportion compared to other Gulf of Mexico deep-pelagic fishes. McGonagle (2021) reported 29% of prey-positive stomachs in 451 analyzed Stomiidae (dragonfishes) (McGonagle, 2021). Woodstock et al. (2020) performed stomach content analysis on a wide array of mesopelagic fish taxa, with stomiids containing 28.6% prey-positive stomachs (Woodstock et al., 2020). The higher percentage of prey-positive stomachs found in this study suggests that *Chiasmodon* may exert higher predation impact per fish than stomiids.

Stomach content analyses are time-intensive, and identification of soft, highly digested, and crushed prey can be quite difficult for all but the most skilled taxonomists (Fanelli & Cartes, 2008). This was exemplified in this study by the 66 prey items classified as unidentified, and further illustrated by the limited number of fish prey identifiable beyond the level Teleostei (n = 12) (Table 5). Diagnostic features that identified prey as Teleostei included the presence of jaws, otoliths, scales, and a distinct spherical eye shape. In parallel with previous stomach content analysis studies, cephalopod flesh was found to digest very quickly, but features such as the beaks,

gladii, and eyes remained intact and relatively undigested (Santos et al., 2001). There was also a hard rock-like structure with a brown and green coloration which was found consistently amongst the cephalopod prey, although its anatomical function remained unknown. Prey was identified to the class level with very high confidence because of these features. Crustacean prey was identified from setae and segmented appendages, which were not present in teleosts and cephalopods. In the end, quantitative stomach content analyses require large sample sizes, which tends to return more instances of identifiable prey. This requirement provides the impetus for continued sampling of the deep pelagial, and perhaps most importantly, more training of new generations of deep-pelagic taxonomists.

4.2 Feeding Selectivity

Due to the extremely large volume of the deep-pelagic biome (Webb et al., 2010), prey population density tends to be low in most ecosystems, making it crucial for predators to maximize potential feeding opportunities. This particularly applies to *Chiasmodon*, as the bathypelagic depths they inhabit are even less populated with prey than the overlying mesopelagic and epipelagic zones (Angel & Baker, 1982). Results of selectivity analyses will be discussed below by major prey taxon.

4.2.1 Cephalopoda

Feeding data revealed a strong preference towards cephalopod predation for *Chiasmodon*. Notably, cephalopod predation is not commonly reported for deep-pelagic fishes, being carried out only by a limited number of known fish taxa (Drazen and Sutton, 2017). Since prey selectivity is a function of prey catchability in midwater trawls, and cephalopods were much rarer than fishes or shrimps in Gulf collections, some elements of potential bias will be discussed. Most importantly, deep-sea cephalopods may be more abundant in the environment than the trawl data suggest. Cephalopods are highly mobile and visually advanced organisms, giving them an advantage in evading incoming trawl nets (Hoving et al., 2014). Although most cephalopod species tend to reside in epipelagic and mesopelagic depths, some species of deep-sea cephalopods have been found to migrate to deep bathypelagic depths (Stewart et al., 2013, Collins et al., 2001). Like other deep-sea fauna, cephalopods in deeper depths have reduced need for locomotory function (Rosa

et al., 2008). This may make them an easier prey item for *Chiasmodon* to capture rather than other potential prey taxa in their depth range. Judkins and Vecchione (2020) found that 95% of oceanic cephalopod species of the northern Gulf of Mexico spend time in the upper bathypelagic zone (1000 – 1500 m), whether that be permanently living or temporarily migrating through that specific area (Judkins & Vecchione, 2020). This depth range aligns with *Chiasmodon*'s depth range (Figure 7), suggesting a possible greater abundance of cephalopods in *Chiasmodon*'s preferred depth distribution.

4.2.2 Teleostei

Teleost predation appeared to reflect the taxon's ambient relative abundance among potential prey. While this study focused on the major taxon Teleostei for statistical analysis, individuals that were identified further warrant discussion. Of the fishes that were identified lower, there was a wide range of taxonomic representation, with five families (Bathylagidae, Gonostomatide, Bregmacerotidae, Sternoptychidae, and Stomiidae). This differs markedly from the feeding of the numerically dominant predatory fishes of the deep-pelagic Gulf, the Stomiidae, who feed primarily on one fish family (Myctophidae; Sutton and Hopkins, 1996). This wide diet breadth within the Teleostei likely results from an active swimming mode of predation in *Chiasmodon* versus a vertically migrating, sit-and-wait luring strategy of stomiids. One individual fish was identified as a juvenile monacanthid (filefish). This was an outlier, as juveniles of this fish family are strictly epipelagic (Sutton et al., unpubl.). The most logistical explanation for this occurrence is net feeding after capture.

4.2.3 Crustacea

Chiasmodon exhibited a strong avoidance of crustacean predation. With only three prey-positive stomachs containing crustacean prey, it was apparent that this is not the prey taxon of choice for *Chiasmodon*. Gulf of Mexico mesopelagic fishes have been found to consume copepods and other larger crustaceans, with some fishes having crustaceans as their main prey source (McClain-Counts et al., 2017). As a result, *Chiasmodon*'s exclusion of crustaceans from their diet is surprising. It is possible *Chiasmodon* may not encounter crustaceans as often in the deeper

depths than they would in the epipelagic and mesopelagic zone, but it is also possible, even probable, that crustaceans do not elicit an attack response when detected.

4.2.4 Selectivity Conclusions

Although they live in an environment where cephalopods appear to be relatively rare, *Chiasmodon* appear to have a distinct preference for this taxon as prey. When compared to the feeding selectivity of numerically dominant deep-pelagic predatory fishes, *Chiasmodon* species prey selection appears to differ. Most members of the family Stomiidae feed exclusively on myctophids, while never eating the numerically dominant fish genus *Cyclothone*, suggesting a high degree of selectivity (Sutton & Hopkins, 1996). Ceratioid anglerfishes, the most speciose clade of fishes in the bathypelagic zone, feed mainly on teleosts, with a small proportion of cephalopods and crustaceans making up the rest of the diet (López et al., 2016). *Chiasmodon* appears to have a unique diet relative to the other dominant fish predators, namely a mixed consortium of cephalopods and teleosts and an avoidance of crustaceans.

4.3 Feeding Chronology

The results of this study did not provide any conclusive evidence that *Chiasmodon* feed at a certain time of the day. Trawl capture data confirmed the notion that *Chiasmodon* is found in both the mesopelagic and bathypelagic depths, but also confirmed that their abundance is much greater deeper than 700 m (Figure 7). The specimens captured during the shallow (surface – 700 m) trawls are of interest, as there was a greater number of *Chiasmodon* individuals caught during the night cycle (n = 53) compared to the day (n = 10). The smaller number of specimens captured deep (700 m – 1500 m) at night may indicate some level of diel vertical migration to shallower depths at night. However, this cannot be confirmed, as the wide vertical sampling range of large midwater trawls does not discriminate the exact depth at which specimens were captured. Specimens caught in the epipelagic depths at nighttime could indicate allow levels of diel vertical migration, though most of the fishes were caught below 700 m (Figure 7). It is likely that the specimens caught in the shallow trawls were caught at depths closer to 700 m than the surface. This idea arose from the 53 individuals found in the shallow trawls. Of those 53 fishes, 16 contained prey-positive stomachs. Out of those 16 individuals, eight contained teleost prey, seven

contained cephalopod prey, one prey item was unknown, and none contained crustaceans. If *Chiasmodon* moves up the water column at night for feeding opportunities, it is not likely in search of a specific prey type. The results of this study indicate that it is unlikely *Chiasmodon* undergoes a diel vertical migration for feeding.

4.4 Daily Ration

The results of the daily ration estimates for *Chiasmodon* fall within previously estimated ranges for deep-sea fishes. It has been estimated that most mesopelagic fishes have relatively low daily ration rates, consuming anywhere between 0.5 – 5% of their own body weight day^{-1} (Drazen & Sutton, 2017). These lower values are due to the declining metabolic function coinciding with colder water temperatures (Drazen & Seibel, 2007). Vertically migrating species tend to be on the higher end of this range, as Myctophids have been found to have a daily ration between 2.4% – 5.6% (Hopkins and Baird, 1985, Sassa et al., 2023, Saunders et al., 2019). Other fishes remain on the lower end of this range, as Macpherson (1985) studied the daily rations of three deep-sea fishes (*Lophius upsicephalus*, *Coelorhynchus fasciatus*, *Helicolenus dactylopterus dactylopterus*) to be 0.55 - 1.3% (Macpherson, 1985).

A noteworthy development throughout this project was the high number of low stomach fullness values. Only three specimens had a stomach fullness value of 5, and only 14 had a value of 4. Every other specimen had a value of 3 or lower. This pattern differs markedly from that of the Stomiidae, who have larger average lengths (Marks, 2016) and daily ration ranges of 1.5% – 2.7% (Sutton & Hopkins, 1996). This is smaller than the 3.64% daily ration estimation of *Chiasmodon* from this study, inferring that *Chiasmodon* feed more often than their predatory counterparts.

4.5 Ecological Niche

Unlike the other customary deep-sea predators – dragonfishes (Stomiidae) and anglerfishes (Lophiidae), *Chiasmodon* do not have any luring appendages that can be used in a "lie-in-wait" feeding style. This feeding strategy is designed to attract potential prey items to the predator, an effort to limit swimming and energy usage. Once the prey is within lunging range, the predator

strikes in a sudden burst movement (Nilsson et al., 2010). Since they lack this apparatus, *Chiasmodon* must actively swim to catch its prey. This is a less common trait for a deep-sea predatory fish, as the food-limiting environment usually results in more passive predation tactics (Drazen et al., 2007). However, *Chiasmodon*'s morphology promotes an active predation style (Melo, 2009a). This style, combined with their higher daily ration value of 3.64%, may indicate that *Chiasmodon* feed more often than dragonfishes, thus displaying a greater predation impact "per fish" in the deep-pelagic realm.

Conclusions

This study contains the most comprehensive trophic analysis of the deep-pelagic predatory fish genus *Chiasmodon*, to date. These "black swallowers" are commonly depicted with enormously distended stomachs. Results of this study reveal novel information about this iconic deep-sea predator. *Chiasmodon*'s high degree of preference for cephalopods contrasts with the notion that this type of predation is rare among deep-pelagic fishes. Furthermore, the consumption of dragonfishes indicates that *Chiasmodon* displays characteristics of a super-predator among deep-pelagic fishes. It is also likely that *Chiasmodon* species exercise a top-predator role in the deep-pelagic ocean. More information is needed to gain a full understanding of bathypelagic ecology, but this study provides valuable insight into the roles of advanced fishes in the ultra-deep pelagic ocean.

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