Combining biotracer and stomach contents analysis to understand trophic dynamics in the northern Gulf of Mexico

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ABSTRACT

The northern Gulf of Mexico (nGOM) is a taxonomically rich ecosystem. Previous work based on a meta-analysis of stomach contents data has shown the trophic connectivity of predators and prey to be substantial. However, the trophic dynamics of many economically and ecologically important species are still not well understood. Sportfish, such as Spotted Seatrout (*Cynoscion nebulosus*), Red Drum (*Sciaenops ocellatus*), and Southern Flounder (*Paralichthys lethostigma*), support recreational fisheries throughout the region. Gulf Menhaden (*Brevoortia patronus*), a high biomass forage fish with the region's largest commercial fishery, is considered an important forage species. In this study, we use information from meta-analysis of stomach contents and stable isotope analysis to investigate the importance of prey taxa, including Gulf Menhaden, for nGOM nearshore predators. Stomach contents and stable isotope analyses are generally evaluated independently, with stomach contents used to directly identify trophic interactions, while stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide insight into a consumer's long-term feeding habits. We used a multispecies trophic model, EcoDiet, developed by Hernvann et al. (2022), that integrates information of both stomach contents and stable isotopes into a single framework to estimate trophic link probabilities and diet proportions. Data in the model include $n = 41$ predators, $n = 173$ prey, and $n = 497$ unique predator and prey interactions. The results indicate that nGOM nearshore predators are generalists using the diverse prey base, and in concordance with previous findings, there is no single Menhaden-dependent predator. Our findings better quantify the trophic interactions of the highly diverse nGOM region and have important implications regarding future ecosystem modeling and management considerations for the Gulf Menhaden stock.

1. Introduction

The Gulf of Mexico exhibits high ichthyofaunal diversity relative to the Pacific and Atlantic coasts of the United States, with more than 1443 finfish species, over 51 shark species, and at least 49 species of rays and skates (Chen, 2017) resulting in complex trophic dynamics (Oshima and Leaf, 2018). The fishes in the Gulf of Mexico range from low trophic level herbivorous groups (e.g. Mugilidae), families with members that feed on secondary production (e.g. Exocoetidae, Chaenopsidae, Epigonidae, Ogcocephalidae, and Ariommatidae), and high trophic level taxa (e.g. Sphyraenidae, Coryphaenidae, and Xiphiidae, Appendix A). The biogeographic setting, the diversity of habitats, and the nutrient-enriched river discharge in the nearshore coastal zone and continental shelf (Grimes, 2001) result in enhanced production and diversity of fish stocks.

One of the most productive fisheries in the northern Gulf of Mexico (nGOM) is the Gulf Menhaden (*Brevoortia patronus*) purse seine fishery. Gulf Menhaden is a low trophic-level forage fish, and like other forage fishes, their population dynamics and ecosystem services have received much attention (Geers et al., 2016; Lamb et al., 2020; Oshima and Leaf, 2018; Sagarese et al., 2016). Low trophic-level fishes are thought to provide a link between phytoplankton and zooplankton and higher trophic levels, such as fishes, birds, and mammals in some regions (Geers et al., 2016; Lamb et al., 2020; Sagarese et al., 2016). Gulf Menhaden is hypothesized to provide a critical provisioning role for higher trophic level taxa in the nGOM, although the importance of this provisioning and to what extent the harvest of Gulf Menhaden impairs other stocks is debated (Berenshtein et al., 2023; Hilborn et al., 2017; Pikitch et al., 2012, 2018).

Although much work has been done to understand the diets and trophic linkages of fishes in the nGOM, these are still not well understood for many predator species of management concern. This

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uncertainty presents challenges to natural resource managers who are confronted with conflicting demands to ensure the sustainability of the commercial Gulf Menhaden fishery while also ensuring that recreationally harvested stocks are not overfished (Berenshtein et al., 2023). Three species (Spotted Seatrout *Cynoscion nebulosus*, Red Drum *Sciaenops ocellatus*, and Southern Flounder *Paralichthys lethostigma*) have been and remain among the most iconic, highly targeted, and economically important finfish species in the nGOM (Holland et al., 1992; Keithly and Roberts, 2017; Midway et al., 2024; Vega et al., 2011). Likewise, these three species are managed or protected in all Gulf states' respective commercial sectors. These species have similar, yet distinct, habitat utilization patterns and niches (Moulton et al., 2017; Shaw et al., 2016) and are primarily targeted in the nearshore coastal zone.

Meta-analysis of stomach contents data has shown that there is a high degree of trophic connectivity among fishes in the region, with predators using a diversity of prey items (Leaf and Oshima, 2019; Oshima and Leaf, 2018). Trophic analysis models (such as network models and Ecopath with Ecosim) are often used in ecosystem assessment and have as their foundation a predator-prey matrix that describes the connectivity of predators and prey (Walters et al., 2008). Limitations in the availability of data (for some fish species), the precision of observation (identification of partially digested prey items), and biases in experimental design (imbalances of sampling in space and time) impact the accuracy and precision of estimates of prey presence and frequency. This will lead to biases in the predator-prey matrix, which is primarily built using data collected from stomach contents analysis (SCA, Walters et al., 2008; Sagarese et al., 2016).

Stomach contents and stable isotope analyses are often used independently to understand the trophic characteristics of predators. SCA is used to identify recently consumed prey and enables numerous diet metrics to be calculated, including the frequency of occurrence of a prey item in a collection of stomachs (Chipps and Garvey, 2007; Hyslop, 1980). SCA allows identification of the specific prey items that were consumed; however, each stomach provides only a snapshot of a consumer's diet that may not be indicative of long-term feeding habits. The speed of digestion limits the timescale and taxonomic resolution of information available from SCA (Buckland et al., 2017), and variable digestion rates can lead to biases in which more easily digestible materials are overlooked (Bowen and Iverson, 2013). Stable isotope analysis (SIA) is a complementary approach. Stable carbon isotope values (δ^{13}C) of an organism's tissues (generally muscle) reflect those of its dietary sources, while an organism's stable nitrogen isotope values (δ^{15}N) are enriched relative to its food sources and can be used to estimate an organism's trophic level in the food web (DeNiro and Epstein, 1978, 1981; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 1999). Thus, SIA allows for an understanding of trophic relationships among trophic levels of predators and prey but does not allow for an understanding of a predator's specific prey items. Unlike SCA, SIA results allow an understanding of diet integrated over some time frame which is dependent on the turnover rate of the tissue examined (Fry, 2008). The muscle turnover time for larger predatory fishes, such as Red Drum, in the nGOM is on the order of multiple months (Bennetts et al., 2023). Coupling SCA and SIA allows for a comprehensive view of consumer diets by maximizing the benefits of each method while minimizing their shortcomings (Layman et al., 2005; McClain-Counts et al., 2017; Sturbois et al., 2022).

To provide insight into the role of forage fishes, understand the trophic dynamics of fishes of management concern, and evaluate similarities in feeding habits among taxa, we employed a multispecies trophic model, EcoDiet, developed by Hernvann et al. (2022). EcoDiet is the first model to integrate SCA and SIA data in the same modeling framework (Hernvann et al., 2022). The EcoDiet model integrates three modules in a Bayesian framework: a joint prior distribution of the food-web topology and the proportions of prey in a predator's diet, the likelihood function which is used to integrate prey occurrences from stomach contents data, and the likelihood function used to assimilate stable isotope information to update the prior information on the diet proportions (Hernvann et al., 2022). By combining, in a quantitative framework, SCA and SIA using EcoDiet, we seek to provide a robust and integrated understanding of the trophic dynamics in the nGOM. In previous work, using network analysis, we found that the fishes and invertebrates of the nGOM have high connectivity (Leaf and Oshima, 2019; Oshima and Leaf, 2018). Our objective in this work is to use archived SIA and SCA data that has been collected to simultaneously estimate the food-web topology and diet matrix and assess the importance of prey taxa, including finfishes and invertebrates, for predators in the northern Gulf of Mexico.

2. Methods

To construct the EcoDiet model, we used three different sources of data: SCA data reported in the literature, δ^{13}C and δ^{15}N values for fishes and invertebrates collected and analyzed by the authors, and δ^{13}C and δ^{15}N values for fishes and invertebrates from the literature. Predators (fish species) and prey (fishes and invertebrate taxa) were included in the EcoDiet model only if there was information about their δ^{13}C and δ^{15}N values and they had positive frequency of occurrence values in the stomach contents data.

To develop the stomach contents data, we conducted a literature search of available diet studies from the nGOM (published and unpublished literature including academic theses and dissertations). Studies describing diets of fish in classes Actinopterygii (ray-finned fishes) and Elasmobranchii (cartilaginous fishes) were evaluated. For each source, we recorded the predator species, prey taxa, and the metric used to describe the magnitude of the prey encountered in the diet. The taxonomic classification (Kingdom, Phylum, Class, Order, Family, Genus, and Species) for each prey item was determined using the World Register of Marine Species (WoRMS) database (Costello et al., 2013). We note that Gulf Menhaden are classified as members of the family Alosidae (Wang et al., 2022); however, for the studies examined, Gulf Menhaden were classified as Clupeidae. All ambiguous prey items were excluded if the taxonomy could not be resolved (e.g., anachronistic or colloquial names that could not be assigned) or if the prey item was inanimate. Similarly, all diet items of biological origin that were ambiguous (e.g., flesh, bone, spine) were omitted. In many of the studies, multiple diet metrics are included; however, our analysis focused on those that included frequency of occurrence, as stomach contents data is entered into the EcoDiet model using this metric. Because the index of relative importance (IRI) has a strong correlation (Pearson's $\rho \geq 0.90$) to the frequency of occurrence (Leaf and Oshima, 2019) we used modeled FO using a linear relationship:

$$\widehat{FO} = 0.89 \times IRI + 8.01 \ (\text{R}^2 = 0.68)$$

If both frequency of occurrence and IRI values were provided for a predator-prey interaction within the same study, the frequency of occurrence value was used. If a predator-prey interaction was observed in multiple studies, a weighted mean estimate of the frequency of occurrence was calculated based on the number of predator stomachs evaluated.

We compiled a database of stable isotope values of carbon and nitrogen for fishes and invertebrates from data collected by the authors. We collected $n = 5094$ estimates of δ^{13}C and δ^{15}N from $n = 232$ fish and invertebrate taxa in various habitats and locations in the nGOM from 2010 to 2020. All organisms were identified to the lowest possible taxa. For all fishes, a small sample of dorsal muscle tissue of each individual was extracted. Individual invertebrates were processed whole. All tissues were stored frozen, freeze-dried, and pulverized into a fine homogenous powder using a mortar and pestle and stored in cone cap 20 ml scintillation vials kept in desiccant cabinets. Portions of samples were weighed with a Mettler Toledo XP26 microbalance, packed into tin capsules, and stored in 96-well plates in a desiccator until analysis could

be performed. Samples were analyzed at the University of Southern Mississippi's Gulf Coast Research Laboratory with a Thermo Delta V Advantage stable isotope ratio mass spectrometer coupled to a Costech model 4010 elemental analyzer via a Conflo IV interface. Results were expressed in the standard delta notation in per mil (‰) according to the equation:

$$\delta^{13}C \ or \ \delta^{15}N \ (‰) = \left[\left(R_{sample}/R_{standard} \right) - 1 \right] \times 1000,$$

where R is the ratio of heavy to light isotopes (^{13}C:^{12}C or ^{15}N:^{14}N). Values are relative to international standards of Pee Dee belemnite for carbon and atmospheric N$_2$ for nitrogen. All samples and secondary standards were referenced to certified standards (USGS-40 and USGS-41) from the National Institute of Standards and Technology (average difference between analyses of standards = 0.13 ‰ and 0.09 ‰ for δ^{13}C and δ^{15}N, respectively). Samples were not lipid extracted or mathematically lipid corrected. Of the 2625 fish samples analyzed, 92% had C:$N < 3.5$ and 95% had C:$N < 4$ indicating low lipid content (Logan et al., 2008). Like in previous work (Dillon et al., 2022), a crustacean-specific mathematical lipid correction (Bodin et al., 2007) was attempted for invertebrate prey items which resulted in irrelevant changes in δ^{13}C (mean δ^{13}C change = 0.26 ± 0.37 ‰, $n = 808$). Additionally, storage of carbon-rich compounds such as chitin and glycogen can also lead to elevated C:N for invertebrate tissue, and lipid extraction does not result in changes to C:N ratios or δ^{13}C values (Kiljunen et al., 2006; Logan et al., 2008).

For each taxon, we collected samples in different habitats and seasons of the year. This results in inflated variances of the mean δ^{13}C and δ^{15}N values. We processed the δ^{13}C and δ^{15}N data using the Stable Isotope Bayesian Ellipses in R (SIBER) package (version 3.5.1; Jackson et al., 2011). Isotopic values for each taxa were included in the analysis if the bivariate δ^{13}C and δ^{15}N values were contained in the taxa's core isotopic niche area. We delineated this area as an ellipse that contains approximately 40% of the data. The SIBER algorithm fits a standard ellipse area (SEA) and uses uninformative priors for the mean of the isotope values and an uninformative Inverse-Wishart prior for the covariance matrix. Only those taxa that had at least five samples of δ^{13}C and δ^{15}N were included in the analysis ($n = 84$ taxa). For those taxa that did not have at least five δ^{13}C and δ^{15}N samples ($n = 148$ taxa), we implemented a resampling technique using values from those organisms with a similar taxonomy. For example, if the lowest taxonomic level for the prey item was at the family level, we used δ^{13}C and δ^{15}N from all individuals from the preceding taxonomic level (in this case order). We then developed the SIBER ellipse for small sample sizes and randomly drew additional bivariate δ^{13}C and δ^{15}N samples, always including those bivariate δ^{13}C and δ^{15}N samples from the original data, such that five observations represented the taxa's $\delta13$C and $\delta15$N.

To augment the values of δ^{13}C and δ^{15}N that we collected, we conducted a literature search of available stable isotope studies. There were taxa recorded in the SCA literature that were not represented in our stable isotope data ($n = 494$ taxa). To supplement our data, we found estimates of the mean and variation (standard deviation and variance) of δ^{13}C and δ^{15}N of these fishes and invertebrates. To account for the correlation of measurements of δ^{13}C and δ^{15}N, we developed an estimate of the phyla-specific covariance matrix developed from the retained raw data filtered using SIBER as described above. The covariance matrix was weighted using the number of individual lowest identified taxa in each phylum. For each of the literature estimates, we took random samples from the bivariate normal distribution specified by the phyla-specific variance-covariance matrix and the mean estimate of δ^{13}C and δ^{15}N. Five samples were drawn for each of the taxa identified in the literature.

The collected and collated data was implemented into the statistical model, EcoDiet. EcoDiet provides Bayesian estimates of trophic link probability and diet proportions. EcoDiet is available as an R package (version 2.0.0; Hernvann et al., 2022; R Core Team, 2023). Our model used uniform priors to simultaneously estimate the food-web topology

and diet proportions by first using SCA data to update the prior information on food-web topology and then SIA data to update the prior information on diet proportions. EcoDiet writes and runs a JAGS model to approximate Bayesian posterior distributions via Monte Carlo Markov Chain methods (Hernvann et al., 2022). Three independent MCMC chains of 1,000,000 iterations were used. The first 500,000 iterations of each chain were discarded. After the burn-in period, a thinning rate of 500 was used to yield 3000 samples from the joint posterior. We performed an analysis to understand the effects of changing the trophic discrimination factors for δ^{13}C and δ^{15}N. The base model was constructed using trophic discrimination factors of 0.8‰ for δ^{13}C and 3.4‰ for δ^{15}N (DeNiro and Epstein, 1978; Hernvann et al., 2022; Vander Zanden and Rasmussen, 1999). The consumers evaluated in our work were relatively large fishes, for which stable isotope samples are largely taken as muscle tissue. The evaluation was performed with trophic discrimination factors of 1.3‰ for C and 2.9‰ for N between trophic levels following McCutchan Jr et al. (2003), who found such a shift when analyzing muscle tissue alone.

To understand the similarities in foraging habits among fishes, we used the Gauch (1982) percentage similarity index, hierarchical agglomerative cluster analysis, and principal components analysis (PCA). EcoDiet model output provides a credible interval for the trophic link probability and diet proportion for each predator/prey interaction. For pairwise comparisons of Spotted Seatrout, Southern Flounder, and Red Drum feeding habits, the Gauch (1982) percentage similarity index was calculated using the mean trophic link probability of all respective prey. To understand the diet similarities of predators in the model, we used hierarchical agglomerative cluster analysis and PCA using the mean value for diet proportion. To reduce dimensionality, we used a reduced set of predator species and prey taxa: predator species with fewer than three prey items were excluded (i.e. Bay Whiff *Citharichthys spilopterus*, Round Herring *Etrumeus teres*, Gulf Killifish *Fundulus grandis*, and American Stardrum *Stellifer lanceolatus*), and prey taxa included were the 25 most frequently observed (shown in Table 3), excluding the prey group Actinopterygii. The mean value for diet proportion was used to calculate a Bray-Curtis dissimilarity matrix using the vegan package in R (version 2.6–4, Oksanen et al., 2007). The cluster analysis was performed on this distance matrix using Ward Jr (1963) clustering criterion. The cluster analysis was evaluated using the cophenetic correlation and agglomerative nesting coefficients via the cluster package in R (version 2.1.6, Maechler et al., 2013). The cophenetic correlation coefficient is the correlation between the cophenetic distance and the original distance matrix and describes how well pairwise distances of unmodeled data points are preserved by the dendrogram (Saraçli et al., 2013). The agglomerative nesting coefficient ranges from 0 to 1 and describes the strength of the clustering structure (Kaufman and Rousseeuw, 2009). PCA was performed using mean diet proportions to determine which prey items influence clustering.

3. Results

Taxa were included in the model if there was available information on frequency of occurrence or IRI from the stomach contents data, as well as both δ^{13}C and δ^{15}N values for both the predator species and associated prey taxa. Data in the EcoDiet model included $n = 198$ unique taxa, consisting of $n = 41$ predator species and $n = 173$ prey taxa, resulting in $n = 497$ unique predator-prey interactions. The stomach contents information used in the model came from $n = 39$ studies (Table 1, citations in Appendix B1). The fish species used in the model were diverse in their feeding habits, trophic levels, and habitat occupancy (Appendix A). Drums (Family Sciaenidae) were the most represented family (Trophic Level 3.61, FishBase.org, Froese and Pauly, 2024). High trophic level taxa including Jacks (Carangidae), Flounders (Paralichthyidae), Mackerels (Scombridae), and Snappers (Lutjanidae) were well represented in the data (Trophic Level 3.57 to 4.23, FishBase. org, Froese and Pauly, 2024). Mid-trophic level fish including Porgies

Table 1
Summary of predator species stomach contents obtained from the literature and used in this study.

Family	Species	Studies	Fish Sampled	Prey Items	F	Sm	Sp	W	State	Duration of Sampling
Carcharhinidae	*Carcharhinus isodon*	1	20	28	x	x	x		MS	2001 to 2001
	C.limbatus	1	50	28	x	x	x		MS	2001to 2001
	Rhizoprionodon terraenovae	1	133	28	x	x	x		MS	1980 to 2001
Lepisosteidae	*Atractosteus spatula*	1	36	9	x				MS	1965 to 1965
	Lepisosteus oculatus	2	168	32	x	x			LA, MS	1965 to 1986
	L. osseus	1	168	13	x				MS	1965 to 1965
Lobotidae	*Lobotes surinamensis*	3	136	62	x	x	x		AL, MS	1995 to 2000
Synodontidae	*Synodus foetens*	4	24	14		x			AL, LA, MS, TX	1970 to 1991
Carangidae	*Caranx hippos*	1	72	44	x	x	x		LA, TX	1980 to 1981
	Seriola dumerili	2	6	34	x	x	x		AL, MS	1978 to 2000
	Trachinotus carolinus	3	92	21	x	x	x		LA, MS	1968 to 1976
Rachycentridae	*Rachycentron canadum*	2	11	14	x	x			MS, TX	1948 to 1972
Dorosomatidae	*Harengula jaguana*	2	45	12	x	x	x		FL, TX	1976 to 1990
Engraulidae	*Anchoa hepsetus*	5	23	27	x	x	x		AL, LA, MS, TX, FL	1970 to 1991
Cyprinodontidae	*Floridichthys carpio*	1		8	x	x			FL	1989 to 1990
Fundulidae	*Fundulus grandis*	1	75	3		x			TX	1981 to 1981
	F. similis	1		7	x	x			FL	1989 to 1990
Elopidae	*Elops saurus*	1	48	24		x	x		LA	1968 to 1969
Lutjanidae	*Lutjanus campechanus*	8		64	x	x	x	x	AL, MS, TX	1970 to 2010
	L.synagris	1	53	26	x		x	x	MS	1996 to 1997
Sciaenidae	*Bairdiella chrysoura*	1	15	14		x	x		MS	2002 to 2003
	Cynoscion arenarius	7	7	30		x			AL, LA, MS, TX	1970 to 1991
	C. nebulosus	7	86	53	x	x	x	x	LA, MS, TX	1960 to 2007
	C. nothus	5	31	30		x			MS, TX	1970 to 1982
	Micropogonias undulatus	11	53	102	x	x	x	x	AL, LA, MS, TX	1960 to 2007
	Pogonias cromis	3	84	57					LA, MS	1960 to 1982
	S. ocellatus	6	54	84	x	x	x	x	LA, TX, MS	1960 to 1998
	Stellifer lanceolatus	1	20	2		x			TX	1981 to 1981
Sparidae	*Archosargus probatocephalus*	2	43	31					LA, MS	1960 to 1982
	Lagodon rhomboides	3	102	20	x	x	x	x	TX, FL	1981 to 1990
Paralichthyidae	*Citharichthys spilopterus*	2	27	13	x	x	x	x	MS, LA	1970 to 1992
	Paralichthys albigutta	1	90	13	x	x	x	x	TX	1974 to 1975
	P. lethostigma	3	305	55	x	x	x	x	LA, MS, TX	1963 to 1982
Pomatomidae	*Pomatomus saltatrix*	1	111	62					LA	1977 to 1981
Scombridae	*Acanthocybium solandri*	1	321	26					LA	1997 to 2007
	Scomberomorus cavalla	3	126	58	x	x	x	x	FL, LA,TX	1977 to 1987
	S. maculatus	1	508	6					FL	1985 to 1987
Ariidae	*Ariopsis felis*	1	16	5		x			TX	1981 to 1981
Diodontidae	*Chilomycterus schoepfi*	1		6	x	x			FL	1989 to 1990
Dussumieriidae	*Etrumeus teres*	1	26	5				x	LA	1982 to 1982
Ogcocephalidae	*Halieutichthys aculeatus*	5	20	20	x	x			AL, LA, MS, TX	1970 to 2003

Citations in Appendix B1. F = Fall, Sm = Summer, Sp = Spring, W = Winter. FL = Florida, AL = Alabama, MS = Mississippi. LA = Louisiana, TX = Texas.

(Sparidae), Herrings (Clupeidae), Anchovies (Engraulidae), and Triggerfishes (Balistidae) were present in the stomach contents analysis data (Trophic Level 3.29 to 3.38, FishBase.org, Froese and Pauly, 2024), as were higher trophic level predators Mackerels (Scombridae) and Cobia (Rachycentridae, Trophic Level 4.23 to 4.26, FishBase.org, Froese and Pauly, 2024). The taxa included in the model were found in a variety of habitats, including estuaries, mangroves, neritic, oceanic, and intertidal areas.

Stable isotope values ($n = 3983$) from $n = 103$ taxa collected by the authors were used in the model (Table 2a). Arthropoda and Chordata had the greatest species richness and the largest number of individuals (99.3% of total number of individuals). After SIBER evaluation, δ^{13}C and δ^{15}N values collected by the authors show high overlap at the phylum level (Fig. 1). The phylum Mollusca has a small sample size (n = 3), with a complete overlap of Arthropoda and Chordata. Arthropoda ($n = 1116$) shows high overlap with Chordata ($n = 2840$), although Chordata are enriched in δ^{15}N relative to Arthropoda. After SIBER evaluation, SI values collected by the authors of fish families are generally well-grouped, with more variation in δ^{13}C than δ^{15}N within families (Fig. 1B). Sample sizes vary among families, with some families well represented and others not. The families Ariidae, Sciaenidae, Lutjanidae, Pomatomidae, and Carcharhinidae show highly enriched δ^{15}N values, while the families Balistidae, Carangidae, and Lobotidae show depleted δ^{15}N values.

Stable isotope values from the literature search used in the model describe $n = 136$ different taxa (Table 2b). Stable isotope data from the 6 phyla were developed from $n = 67$ studies (citations in Appendix B2). Similar to values collected by the authors, literature stable isotope information was largest for Arthropoda and Chordata (95.1% of total number of individuals). After evaluating the observed data with the SIBER algorithm, stable isotope values from the literature show a wider range than those collected by the authors (Fig. 1C). Literature stable isotope values have a high overlap among Arthropoda, Mollusca, and Chordata, with the largest isotopic niche space belonging to the phylum Chordata.

Modeled predator species exhibit diverse diets, utilizing both low-trophic level fishes and invertebrates. The predators with the most diverse diets (i.e. observed trophic linkages from SCA) were Red Drum
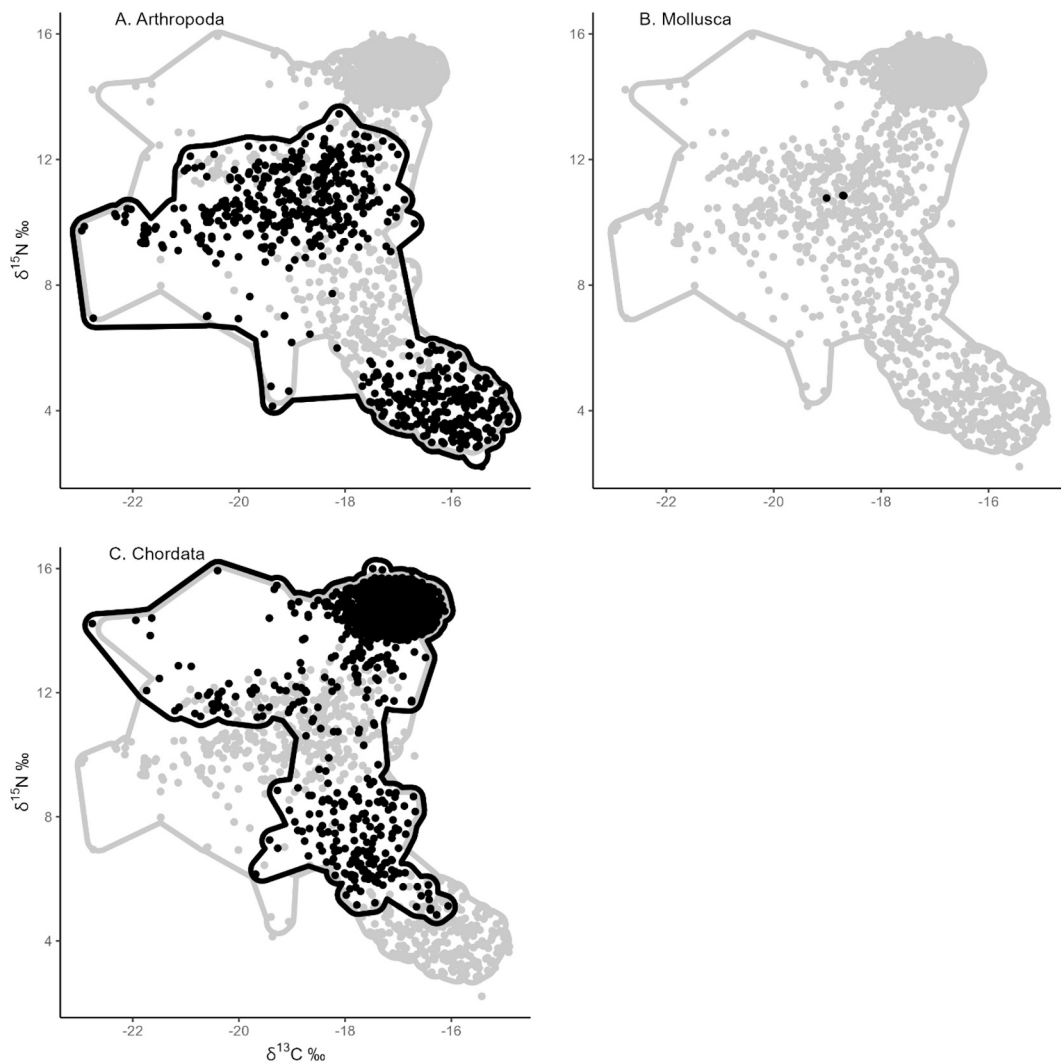
Table 2a
Summary of phylum-specific frequency of stable isotope δ^{13}C and δ^{15}N collected by the authors and used in this study. The columns Class, Order, Family, Genera, and Species are the frequency of this taxonomic level within each phylum and n is the number of samples.

Phylum	Classes	Orders	Family	Genera	Species	n
Annelida	1	1	1	1	1	9
Arthropoda	4	5	12	9	30	1116
Chordata	6	17	32	37	65	2840
Cnidaria	1	1	1	1	1	4
Mollusca	4	3	3	1	6	14

Fig. 1. A. Bivariate distribution of phylum-specific (black points) δ¹³C and δ¹⁵N values with all (gray points) stable isotope values collected by the authors. Polygons are minimum convex polygons.

B. Bivariate distribution of family-specific (black points) δ¹³C and δ¹⁵N values of fishes with all (gray points) stable isotope values collected by the authors. Polygons are minimum convex polygons.

C. Bivariate distribution of phylum-specific (black points) δ¹³C and δ¹⁵N values with all (gray points) stable isotope values obtained from the literature. Polygons are minimum convex polygons.

($n = 46$ prey), Atlantic Croaker (*Micropogonias undulatus*, $n = 40$ prey), Tripletail (*Lobotes surinamensis*, n = 28 prey), Greater Amberjack (*Seriola dumerili*, n = 28 prey), and Southern Flounder ($n = 25$ prey). The prey groups observed in the greatest number of predator species' diets were Actinopterygii ($n = 29$ predators), Decapoda ($n = 26$ predators), Amphipoda ($n = 16$ predators), Bivalvia ($n = 15$ predators), and *Anchoa* spp. ($n = 14$ predators) (Table 3 A). Prey taxa identified to lower taxonomic levels appear in a wide range of predator diets. The most frequently observed prey items identified to the family or genus levels were *Anchoa* spp. (n = 14 predators), Penaeidae (n = 13 predators), Clupeidae ($n = 7$ predators), Sciaenidae ($n = 7$ predators), and Gobiidae (n = 6 predators). The most frequently observed prey species were Gulf Menhaden ($n = 11$ predators), Atlantic Croaker ($n = 11$ predators), Blue Crab (*Callinectes sapidus*, $n = 10$ predators), Striped Mullet (*Mugil cephalus*, n = 7 predators), and Hardhead Catfish (*Ariopsis felis*, n = 6 predators). Across their respective predators, the mean trophic link probabilities for the ten most widely consumed prey taxa identified to at least the family level are: Penaeidae (0.19), Gulf Menhaden (0.19), *Anchoa* spp. (0.18), Clupeidae (0.15), Blue Crab (0.10), Sciaenidae

(0.07), Striped Mullet (0.06), Hardhead Catfish (0.05), Gobiidae (0.04), Atlantic Croaker (0.04) (Fig. 2).

Spotted Seatrout, Southern Flounder, and Red Drum display generalist diets, with 21, 25, and 46 different prey items observed from SCA, respectively (Fig. 3). The Spotted Seatrout's three highest mean trophic link probabilities are with Actinopterygii (0.40), Decapoda (0.18), and Penaeidae (0.16). Southern Flounder's highest mean trophic link probabilities are with Penaeidae (0.32), Striped Mullet (0.24), and Sciaenidae (0.23). Red Drum's highest mean trophic link probabilities are with Actinopterygii (0.34), Penaeidae (0.32), and Decapoda (0.31). The Gauch percentage similarity (Gauch, 1982) was used to investigate the similarity between these predator's mean trophic link probabilities. The percent similarity between Southern Flounder and Red Drum is 28.9%. The percentage similarity between Southern Flounder and Spotted Seatrout is 33.4%. The percentage similarity between Spotted Seatrout and Red Drum is 43.8%.

In our evaluation of Gulf Menhaden, we found that 17 of the 41 modeled predator species were observed to contain either Gulf Menhaden, *Brevoortia* spp., or Clupeidae in their diets (Fig. 4). We found that
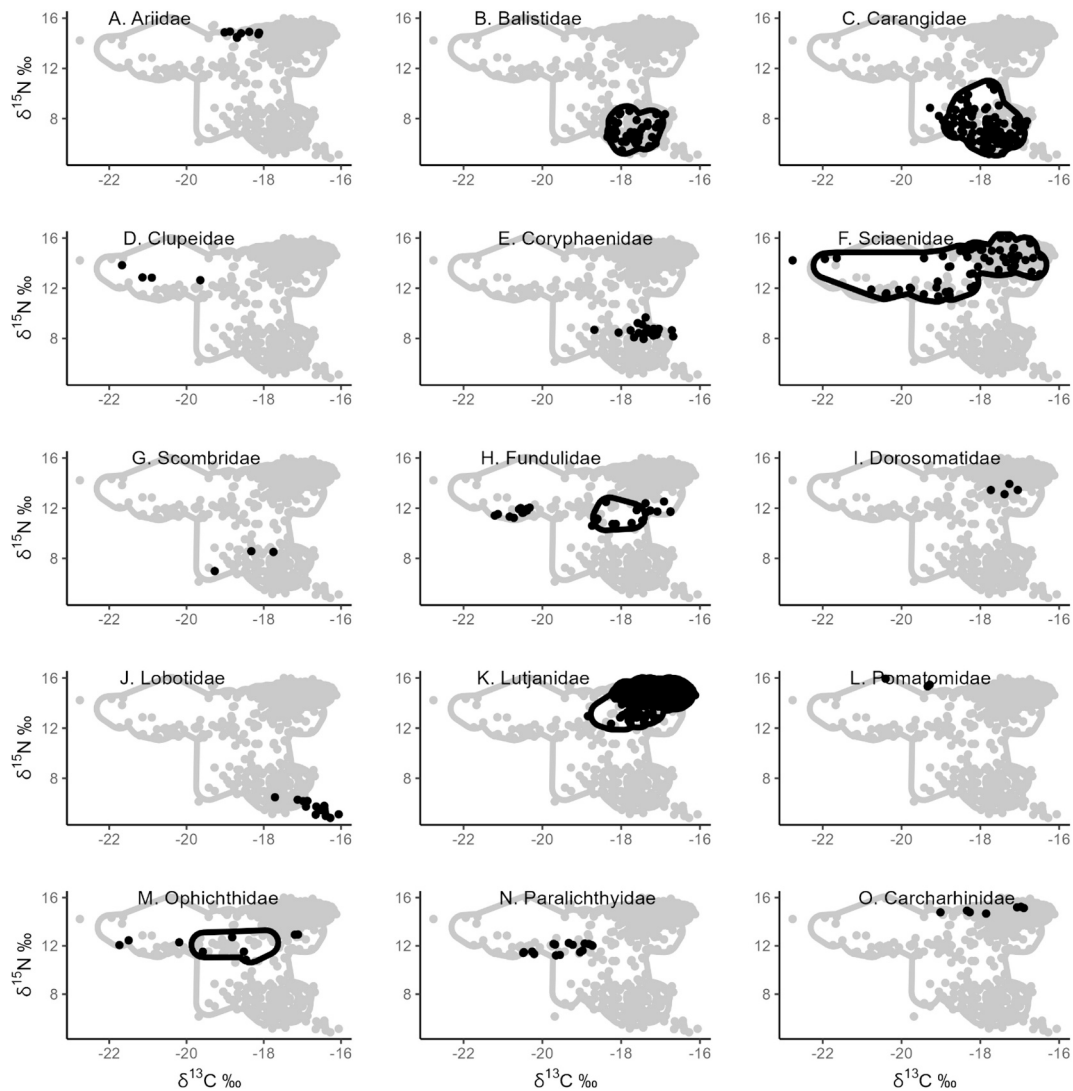
Fig. 1. (*continued*).

three predator species contained two of the three Gulf Menhaden groups within their diets: Red Drum (Gulf Menhaden and *Brevoortia* spp.), Crevalle Jack (*Caranx hippos*; Gulf Menhaden and Clupeidae), and Tripletail (Gulf Menhaden and Clupeidae). A total of 11 predator species were found to prey on Gulf Menhaden with mean diet proportions ranging from 2.2 to 43% (Red Drum and Longnose Gar L. *osseus*, respectively*)*; however, the second largest diet proportion was 15.4% (Ladyfish *Elops saurus*). Spotted Seatrout and Red Drum were found to prey on *Brevoortia* spp. with mean diet proportions of 4.6 and 2.1%, respectively. Of the seven predator species observed to feed on Clupeidae, mean diet proportions ranged from 3.2 to 20% (Tripletail and Spanish Mackerel *Scomberomorus maculatus*, respectively).

Our analysis of altering the trophic discrimination factor indicated that the EcoDiet model is robust to changes in the values of this parameter. The observed difference between mean estimated trophic link probabilities for respective predator and prey interactions ranged from −0.006 to 0.006. The range of the difference between mean diet proportions from the base and evaluation of the alternative trophic discrimination factor is −0.11 to 0.16; however, the first and third quartiles of differences are −0.002 and 0.003, respectively.

Hierarchical agglomerative cluster analysis resulted in an agglomerative nesting coefficient of 0.69, indicating strength within clustering structures, and a cophenetic correlation coefficient of 0.70, indicating that the original structure of the data is preserved after clustering. Five

predator groups were delineated from the dendrogram (Fig. 5). The partitioning of these groups was analyzed qualitatively within the PCA plot (Fig. 6). Group 1 is comprised largely of low trophic level consumers; the group is influenced by highly aggregated invertebrate prey taxa such as Amphipoda, Ostracoda, Gastropoda, and Bivalvia. Group 2 contains relatively large-bodied generalists, and their location indicates Clupeidae, Carangidae, Cephalopoda, and *Anchoa* spp. influence the group. Group 3 contains relatively smaller nearshore predators including Hardhead Catfish, Sand and Silver Seatrout (*C. arenarius, C. nothus*), Spanish Mackerel, and the Inshore Lizardfish (*Synodus foetens*); *Anchoa* spp., Gobiidae, and Decapoda influence this group. Group 4 contains predators with diverse diets that are generally intermediately sized between Groups 1 and 5 and Groups 2 and 3. Within Group 4, two branches group together in ordination space. Sheepshead (*Archosargus probatocephalus*), Lane Snapper (*Lutjanus synagris*), and Black Drum (*Pogonias cromis*) are influenced by the loadings Penaeidae, *Callinectes* spp., and other invertebrates. Spotted Gar (*L. oculatus*), Tripletail, Atlantic Croaker, Red Drum, Spotted Seatrout, and Southern Flounder are influenced by Penaeidae, Blue Crab, and the lower trophic level fish species Atlantic Croaker, Striped Mullet, Spot, Hardhead Catfish, and Gulf Menhaden. Group 5 contains Cobia (*Rachycentron canadum*), three nearshore shark species, Ladyfish, two gar species, and Bluefish (*Pomatomus saltatrix*); this group is influenced by low trophic level species such as Atlantic Croaker, Striped Mullet, Spot (*Leiostomus*

Fig. 1. (*continued*).

Table 2b

Summary of phylum-specific frequency of studies of stable isotope $\delta^{13}C$ and $\delta^{15}N$ obtained from the literature and used in this study. The columns Class, Order, Family, Genera, and Species are the frequency of this taxonomic level within each phylum and n is the number of samples. Sources is the number of studies used to obtain estimates for each phylum. Citations in Appendix B2.

Phylum	Classes	Orders	Family	Genera	Species	n	Sources
Annelida	1	2	3	3	3	14	5
Arthropoda	4	9	19	20	26	1981	25
Chordata	4	17	29	45	54	1648	40
Echinodermata	1	1	1	1	1	3	1
Mollusca	4	8	8	10	10	150	11
Porifera	1	1	1	1	1	21	1

xanthurus), Hardhead Catfish, and Gulf Menhaden.

4. Discussion

As researchers and managers focus their efforts on multi-taxa ecosystem assessment, the ability to leverage information from diverse data sources is critical. Incomplete diet data is often a limiting factor in exploring a region's trophic dynamics, impacting the ability to employ ecosystem-based assessment approaches and management (Sagarese et al., 2016; Walters et al., 2008). In this work, we found that the information for stomach contents and stable isotopes in the nGOM was extensive. When these data were integrated into the EcoDiet model, we

found that fish predators exhibit diversity in their diets, including the fishery-targeted species Spotted Seatrout, Southern Flounder, and Red Drum. We identified five predator guilds based on prey consumption patterns using multivariate analysis. Our work leverages information from SIA and SCA with the intention of maximizing the information in both data sources to develop a comprehensive understanding of trophic connectivity in the nGOM. Our findings have implications for the management of low trophic-level fishes in an ecosystem context. Consistent with previous findings, our results indicate that the trophic linkages of fishes and their prey in the northern Gulf of Mexico are generally weak.

In general, most of the fishes that we examined are generalists with

Table 3

Mean estimated value of (A) trophic link probability and (B) diet proportion between all predators and the 25 most widely consumed prey items.

Family	Species	Amphipoda	Gammaridae	Decapoda	Penaeidae	Callinectes	Callinectes sapidus	Xanthidae	Maxillopoda	Ostracoda	Bivalvia	Cephalopoda	Gastropoda	Actinopterygii	Ophichthidae	Carangidae	Clupeidae	Brevoortia patronus	Anchoa	Gobiidae	Mugil cephalus	Bothidae	Ariopsis felis	Sciaenidae	Leiostomus xanthurus	Micropogonias undulatus
								Arthopoda				Mollusca								Chordata						
Carcharhinidae	*Carcharhinus isodon*						0.02							0.11				0.05							0.03	0.02
	Carcharhinus limbatus				0.07									0.33	0.02			0.04			0.02				0.03	0.02
	Rhizoprionodon terraenovae				0.24		0.05							0.45	0.05			0.12			0.04		0.05	0.02	0.05	0.02
Lepisosteidae	*Atractosteus spatula*																	0.03			0.04		0.13		0.06	0.06
	Lepisosteus oculatus			0.09			0.06							0.31				0.09	0.02		0.02		0.02			0.02
	Lepisosteus osseus			0.03										0.22				0.88	0.13		0.05				0.06	0.06
Lobotidae	*Lobotes surinamensis*			0.08	0.4	0.12	0.08							0.23		0.02	0.02	0.1				0.02				
Synodontidae	*Synodus foetens*				0.27						0.03			0.56					0.48							
Carangidae	*Caranx hippos*				0.41						0.03	0.13	0.02	0.25	0.03	0.09	0.1	0.04				0.03		0.05		
	Seriola dumerili				0.05							0.22		0.39		0.02	0.22					0.09		0.02	0.02	
	Trachinotus carolinus	0.55	0.38	0.16	0.16						0.46		0.29	0.11												
Rachycentridae	*Rachycentron canadum*				0.46									0.05										0.05		0.05
Dorosomatidae	*Harengula jaguana*	0.67		0.36						0.3	0.76		0.2													
Engraulidae	*Anchoa hepsetus*	0.33		0.36						0.43			0.5													
Cyprinodontidae	*Floridichthys carpio*	0.6		0.2						0.6	0.21		0.4													
Fundulidae	*Fundulus grandis*													0.02												
	Fundulus similis	0.3		0.16						0.17	0.83		0.3													
Elopidae	*Elops saurus*			0.05										0.17				0.45	0.07		0.02					
Lutjanidae	*Lutjanus campechanus*			0.07								0.17		0.37	0.06											
	Lutjanus synagris	0.2		0.2	0.09	0.09		0.25	0.07		0.09			0.21					0.49							
Sciaenidae	*Bairdiella chrysoura*	0.08	0.08	0.11							0.08															
	Cynoscion arenarius			0.46										0.19						0.02						
	Cynoscion nebulosus	0.03	0.02	0.18	0.16		0.06		0.14	0.04	0.03			0.4					0.11		0.02			0.02		0.04
	Cynoscion nothus			0.21								0.02		0.18					0.2	0.09						
	Micropogonias undulatus	0.11		0.09	0.11	0.1	0.08	0.06	0.09	0.21	0.28	0.03	0.07	0.09					0.04	0.02						
	Pogonias cromis	0.11		0.17	0.03		0.16	0.2	0.05		0.33			0.12	0.02							0.08				
	Sciaenops ocellatus	0.09	0.07	0.31	0.32	0.03	0.29	0.04	0.11	0.06	0.21		0.12	0.34	0.04			0.21	0.05		0.06	0.02		0.02		0.07
	Stellifer lanceolatus			0.35															0.26							
Sparidae	*Archosargus probatocephalus*		0.1	0.08	0.08		0.08	0.04			0.09			0.11												
	Lagodon rhomboides	0.6		0.23						0.23	0.3		0.41													
Paralichthydae	*Citharichthys spilopterus*																									
	Paralichthys albigutta	0.04												0.08		0.04									0.11	
	Paralichthys lethostigma	0.11		0.03	0.32	0.07				0.07				0.17			0.13				0.08	0.02	0.24	0.02	0.23	0.03
Pomatomidae	*Pomatomus saltatrix*										0.06			0.29						0.07						0.04
Scombridae	*Acanthocybium solandri*										0.14			0.59		0.17										
	Scomberomorus cavalla			0.09							0.19			0.76			0.12	0.19	0.11					0.03		
	Scomberomorus maculatus													0.3				0.36	0.39							
Ariidae	*Ariopsis felis*			0.26							0.04			0.1												
Diodontidae	*Chilomycterus schoepfi*	0.08		0.04							0.6		0.72													
Dussumieriidae	*Etrumeus teres*									0.16																
Ogcocephalidae	*Halieutichthys aculeatus*	0.22							0.1																	

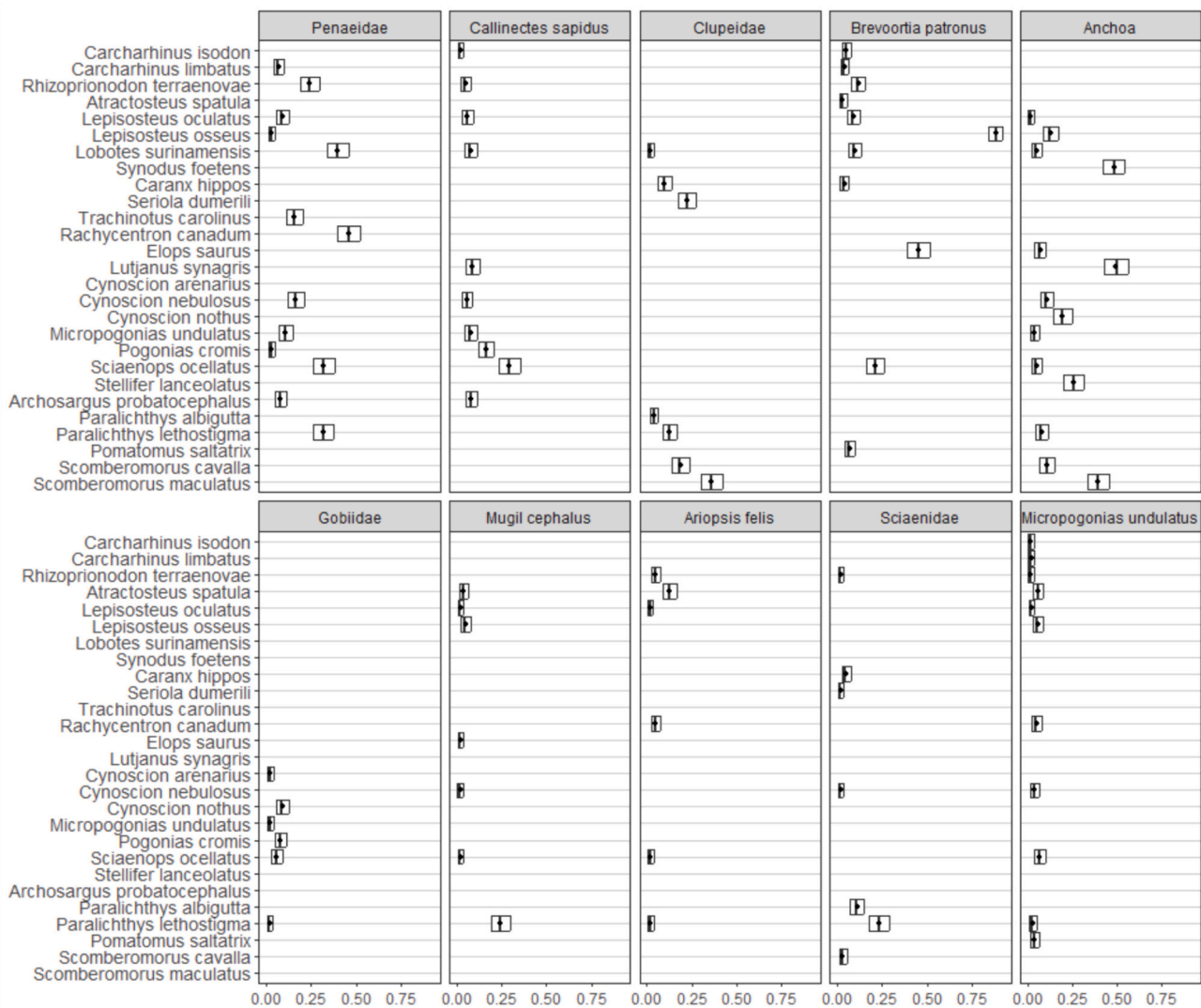| Family | Species | Arthopoda | | | | | | | | | Mollusca | | | Chordata | | | | | | | | | | | | |
		Amphipoda	Gammaridae	Decapoda	Penaeidae	Callinectes	Callinectes sapidus	Xanthidae	Maxillopoda	Ostracoda	Bivalvia	Cephalopoda	Gastropoda	Actinopterygii	Ophichthidae	Carangidae	Clupeidae	Brevoortia patronus	Anchoa	Gobiidae	Mugil cephalus	Bothidae	Ariopsis felis	Sciaenidae	Leiostomus xanthurus	Micropogonias undulatus
Carcharhinidae	*Carcharhinus isodon*						0.1							0.13				0.11								0.09
	Carcharhinus limbatus			0.09										0.22	0.07			0.07					0.07		0.07	0.07
	Rhizoprionodon terraenovae			0.05			0.05							0.04	0.04			0.04				0.05	0.04	0.05	0.04	0.04
Lepisosteidae	*Atractosteus spatula*																	0.11			0.14		0.16		0.14	0.12
	Lepisosteus oculatus			0.05			0.03							0.09					0.05	0.03	0.06		0.02			0.02
	Lepisosteus osseus			0.06										0.08					0.43	0.11	0.12				0.06	0.03
Lobotidae	*Lobotes surinamensis*			0.04	0.04	0.04	0.04							0.04		0.04	0.03	0.03	0.04					0.03		
Synodontidae	*Synodus foetens*			0.27								0.1		0.3				0.33								
Carangidae	*Caranx hippos*			0.04							0.04	0.05	0.05	0.03	0.05	0.05	0.05	0.05				0.05			0.04	
	Seriola dumerili			0.04								0.04		0.03		0.04	0.04					0.04		0.03	0.04	
	Trachinotus carolinus	0.34	0.03	0.1	0.07						0.23		0.18	0.05												
Rachycentridae	*Rachycentron canadum*			0.21										0.06									0.07			0.06
Dorosomatidae	*Harengula jaguana*	0.26		0.22						0.18	0.19		0.14													
Engraulidae	*Anchoa hepsetus*	0.21		0.25						0.22			0.32													
Cyprinodontidae	*Floridichthys carpio*	0.38		0.03						0.32	0.06		0.2													
Fundulidae	*Fundulus grandis*													1												
	Fundulus similis	0.1		0.07						0.06	0.7		0.08													
Elopidae	*Elops saurus*			0.11										0.1				0.15	0.07		0.04					
Lutjanidae	*Lutjanus campechanus*			0.09								0.1		0.21	0.09											
	Lutjanus synagris	0.06		0.06		0.06	0.06	0.07	0.05		0.07			0.06					0.06							
Sciaenidae	*Bairdiella chrysoura*	0.2	0.06	0.28							0.2															
	Cynoscion arenarius			0.41										0.4						0.19						
	Cynoscion nebulosus	0.05	0.05	0.05	0.05		0.05		0.05	0.05	0.05			0.05					0.05		0.05			0.04		0.04
	Cynoscion nothus			0.19								0.15		0.23					0.27	0.16						
	Micropogonias undulatus	0.02		0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.03	0.03	0.02	0.03					0.03	0.02						
	Pogonias cromis	0.05		0.05	0.05		0.05	0.05	0.06		0.05			0.05	0.05				0.05							
	Sciaenops ocellatus	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02		0.02	0.02	0.02			0.02	0.02	0.02	0.02		0.02			0.02
	Stellifer lanceolatus			0.37															0.63							
Sparidae	*Archosargus probatocephalus*		0.05	0.11	0.1		0.12	0.09			0.09			0.11												
	Lagodon rhomboides	0.2		0.14						0.12	0.09		0.21													
Paralichthyidae	*Citharichthys spilopterus*																									
	Paralichthys albigutta	0.2												0.11		0.08									0.12	
	Paralichthys lethostigma	0.04		0.04	0.04	0.04			0.04					0.04		0.04					0.04	0.04	0.04		0.04	0.04
Pomatomidae	*Pomatomus saltatrix*										0.09			0.22							0.12					0.07
Scombridae	*Acanthocybium solandri*										0.05			0.14		0.07										
	Scomberomorus cavalla			0.09							0.11			0.34			0.1	0.06		0.08					0.06	
	Scomberomorus maculatus													0.19			0.2		0.29							
Ariidae	*Ariopsis felis*			0.27							0.06			0.23												
Diodontidae	*Chilomycterus schoepfi*	0.12		0.09							0.36		0.43													
Dussumieriidae	*Etrumeus teres*								1																	
Ogcocephalidae	*Halieutichthys aculeatus*	0.29							0.27																	

Fig. 2. Box plots represent the median and 80% credible interval of trophic link probability between the 10 most widely consumed prey items (identified to at least family level, represented in individual panels) and their respective consumers (y-axis). Points represent the mean trophic link probability value.

diets comprised of a wide range of prey taxa including both invertebrates and low trophic-level fishes. Although there are several low trophic-level taxa present in high biomass and abundance in the nGOM (e.g. Gulf Menhaden and Atlantic Croaker), our results do not indicate that there is a high dependence on a single prey taxon. Predators may be highly dependent on a small suite of prey sources seasonally or during certain life stages, but we were unable to identify a single overwhelmingly dominant prey taxa in the region. Penaeid shrimps are found in high biomass and account for the most valuable fishery in the Gulf of Mexico (Fujiwara et al., 2016; Keithly and Roberts, 2017). The migratory nature of the Penaeid shrimps limits their temporal availability as forage for nearshore species (Overstreet and Heard, 1982), and we hypothesize that their importance as a prey item is determined by their availability relative to other potential forage (Fujiwara et al., 2016). *Anchoa* spp. are found in extremely high abundance and biomass and seasonally play a key role in the region's trophic dynamics as a direct link between zooplankton and higher trophic level predators (Griffith and Bechler, 1995; Johnson et al., 1990; Overstreet and Heard, 1982). Other highly abundant low trophic-level fishes include Striped Mullet, Atlantic Croaker, and Hardhead Catfish (Gunter, 1941); however, gape and body size may limit the community of predators that can utilize these species as prey (Bethea et al., 2004; Modde and Ross, 1983; Scharf et al., 2000). The taxonomic richness in the nGOM may confer

resilience and stability to buffer response rates to changing conditions and species loss through functional redundancy, food web flexibility, and utilization of distinct energy channels (Hooper et al., 2005; Rooney et al., 2006).

Gulf Menhaden's biomass in the nGOM has led to its provisioning of one of the largest fisheries in the United States with recent harvests of 400,000 to 600,000 mt y^{-1} (GSMFC (Gulf States Marine Fisheries Commission), 2021). The Gulf Menhaden stock is not overfished or undergoing overfishing and continues to account for a significant portion of the nGOM's commercial fishery production (GSMFC (Gulf States Marine Fisheries Commission), 2021). The Gulf Menhaden fishery largely operates in the coastal zone in Mississippi and Louisiana and overlaps with some of the nGOM's most productive recreational fisheries (O'Connell et al., 2005; GSMFC (Gulf States Marine Fisheries Commission), 2015; Keithly and Roberts, 2017). Despite its biomass and widespread spatial overlap with many predators, we did not find that Gulf Menhaden constituted large proportions of many predators' diets. Our modeling approach does not allow us to understand the taxonomic composition of unidentified material. It is possible that *B. patronus, Brevoortia* spp., and members of the family Clupeidae are more readily digestible and thus have either a greater likelihood of being assigned to a higher trophic level or being removed from analysis because of being characterized as unidentifiable. We found that predators utilized the
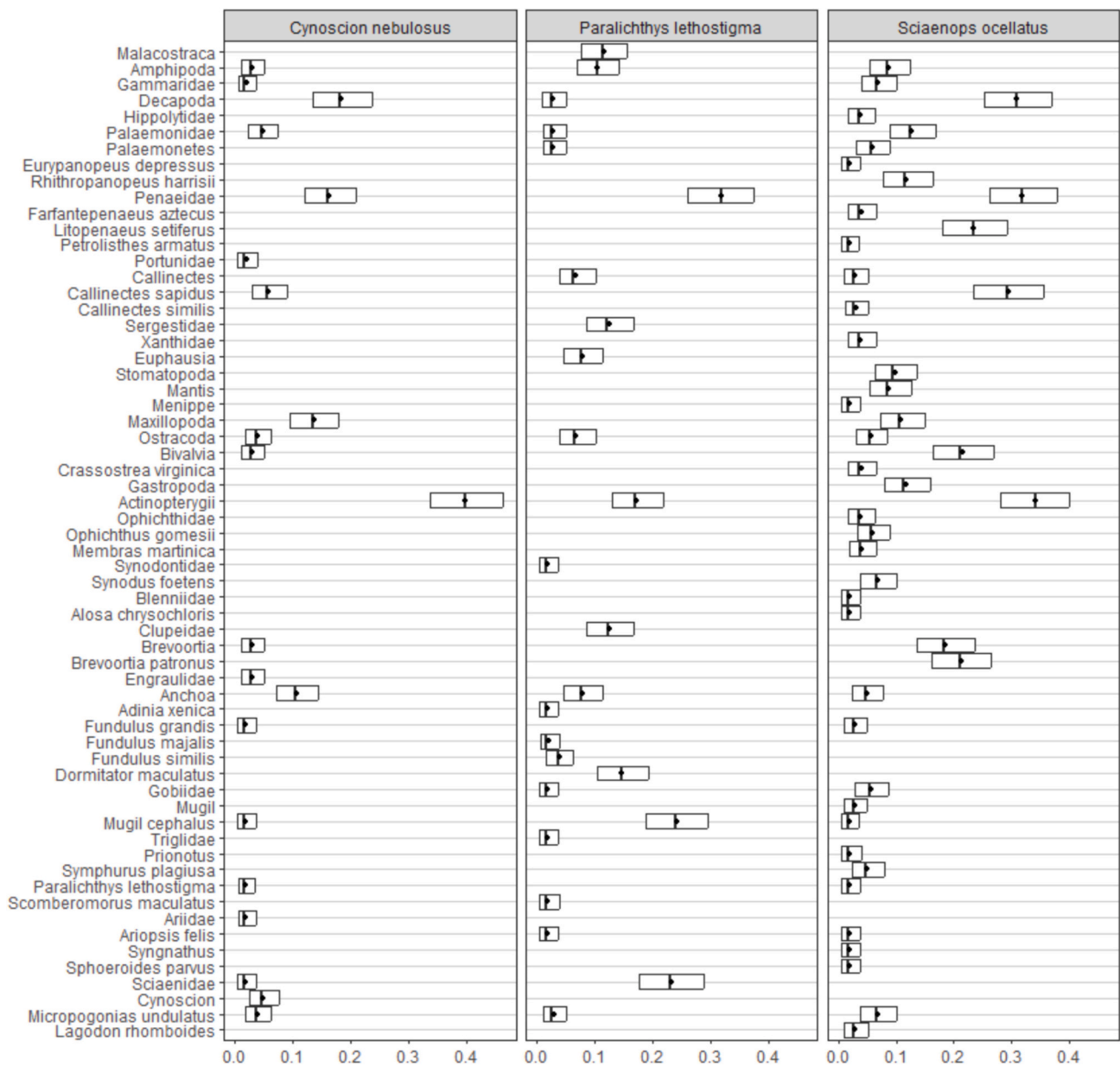
Fig. 3. Box plots represent the median and 80% credible interval of trophic link probability between Spotted Seatrout, Southern Flounder, and Red Drum (represented in individual panels, respectively) and their observed prey items (y-axis). Points represent the mean trophic link probability value.

nGOM's wide prey base, and this is especially true for predator species of management interest, such as Spotted Seatrout, Southern Flounder, and Red Drum. The notable exception is Longnose Gar; the estimated proportion of Gulf Menhaden in its diet is high. The large, estimated contribution of Gulf Menhaden in Longnose Gar's diet may be attributed to limitations in both stomach contents and stable isotope data. Estimates of $\delta^{13}C$ and $\delta^{15}N$ were obtained from $n = 4$ Longnose Gar along the Florida Big Bend (Peterson, 2014). Stomach contents data describing Longnose Gar diet was limited to collections from June, July, and August along the Mississippi coast, showing a high prevalence for Gulf Menhaden (Goodyear, 1967). A 5-year diet study conducted along the US Atlantic coast described Longnose Gar as a generalist predator with seasonal reliance on prey, such as White Perch (*Morone americana*), Atlantic Menhaden (*B. tyrannus*), killifishes (*Fundulus* spp.), Atlantic Croaker, and Spot (McGrath et al., 2013). The finding that high trophic level nGOM fishes have a diverse diet aligns with those of Leaf and Oshima (2019) and Berenshtein et al. (2023) who did not identify any predators that they considered to be highly dependent on Gulf

Menhaden. Similarly, Sagarese et al. (2016) showed that Gulf Menhaden contributes to only 2 to 3% of the diets of most predators.

Both sources of data were collected over multiple seasons and years, over a large geographic range, and for a range of life stages. The combination of data likely results in inflated variation of the mean carbon and nitrogen stable isotope estimates (Bennetts et al., 2023; Dillon et al., 2015; Wells et al., 2017) and the frequency of occurrence estimates of stomach contents. We reduced the observed variability in the stable carbon and stable nitrogen isotope values by processing these data using SIBER, resulting in a constrained estimate (40% of the data). This was a deliberate choice that likely resulted in constrained estimates of prey item's proportion in a predator's diet. Predators in the nGOM have been documented to undergo changes in diet over ontogeny (Bethea et al., 2004; Livernois et al., 2024; Wells et al., 2008). Predator diets may also vary spatially (Bethea et al., 2006; Livernois et al., 2024), and many of the predator species evaluated in our model exhibit seasonal movement (e.g. Cobia, Red Drum, Spotted Seatrout, Southern Flounder) (Dippold et al., 2017; Moulton et al., 2017; Steffen et al., 2023). Digestive
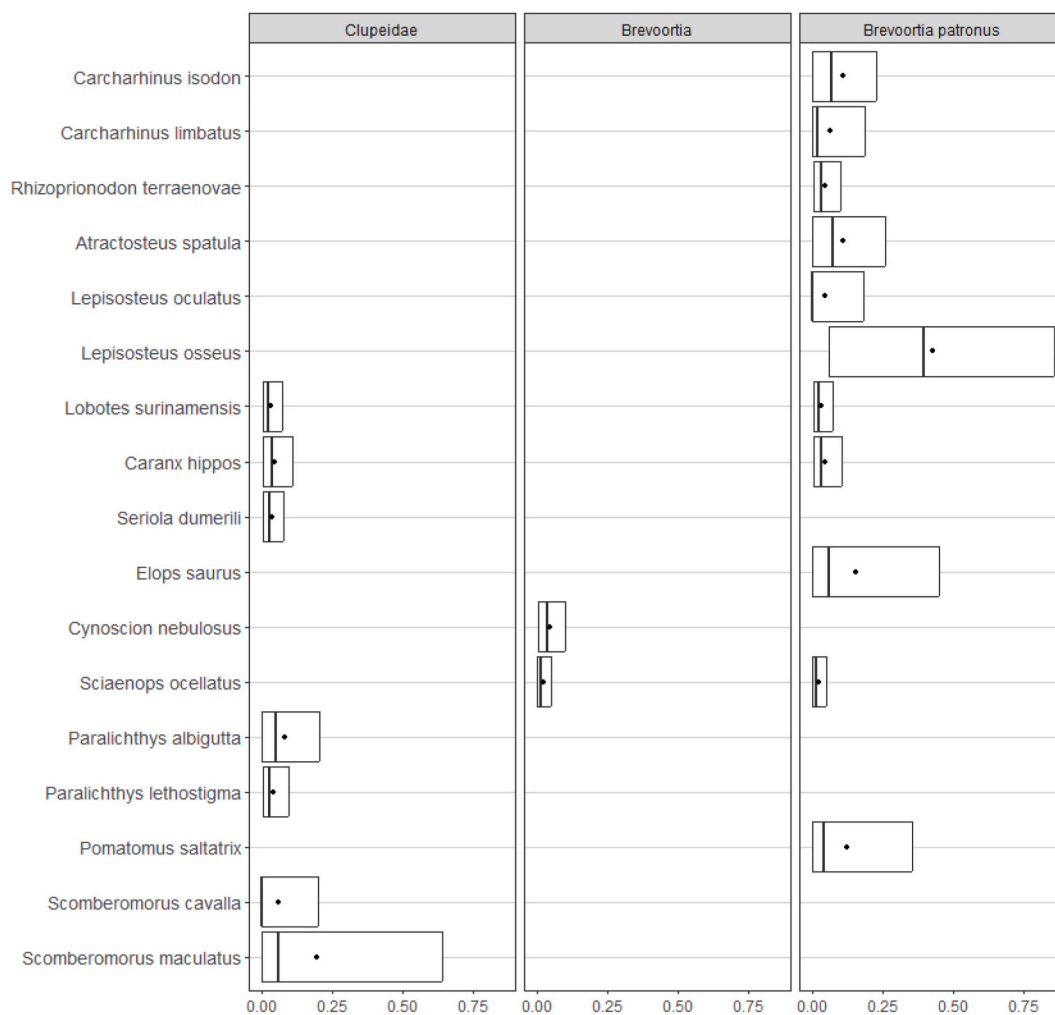
Fig. 4. Box plots represent the median and 80% credible interval of diet proportion constituted by Clupeidae, *Brevoortia* spp., or *Brevoortia patronus* (represented in individual panels) for their observed consumers (y-axis). Points represent the mean diet proportion value.

processes of predators necessitate that some prey in stomach contents data is assigned to taxonomic levels higher than species, reducing the ability to identify species-specific trophic relationships and the taxonomic resolution of frequency of occurrence estimates (Buckland et al., 2017). The precision of the EcoDiet predictions is constrained when the input data have inflated variance. Additionally, the model may have difficulty in discerning diet proportions when a predator's prey groups are isotopically similar (Phillips et al., 2014). Trophic enrichment factors vary spatiotemporally, by methodology, and between species (McCutchan Jr et al., 2003); however, changing trophic enrichment factors did not result in considerable differences.

The EcoDiet model does not provide predictions of the biomass of predators, but it can inform models that have that capacity. Changes in abundance and diversity at one trophic level can affect diversity and abundance at other trophic levels (Hooper et al., 2005). Of interest in the region is to understand the impacts a decline in Gulf Menhaden abundance would have on other groups. Given the diversity of low trophic-level species in the nGOM, responses to a decrease in Gulf Menhaden abundance would likely include prey-switching by predators and increases in biomass of other forage through competitive release (Hilborn et al., 2017; Jutila and Grace, 2002). Other forage species that traditionally do not constitute as large of a portion of predator's diets would see an increase in predation pressure; however, they would also see a decrease in competition (e.g. on spatial overlap or foraging opportunities) for themselves. Ecosystem-based models (such as Ecopath with Ecosim) can project community responses to proposed shifts (e.g.,

harvest levels or oceanographic changes). However, these models require numerous inputs and assumptions to which the models can be extremely sensitive (Walters et al., 2008). Using this modeling framework, Robinson et al. (2015) suggested that, through competitive release, an increase in Gulf Menhaden harvest would lead to increases in other forage fish abundances and jellyfish biomass. They found that Gulf Menhaden transfer considerably more energy and more efficiently to higher trophic levels than jellyfish, which are historically characterized as a "trophic dead end". Geers et al. (2016) reported an increase in penaeid shrimp biomass in response to increased forage fish harvest. Berenshtein et al. (2023) reported that increased Menhaden harvest would lead to an increase in the biomass of other low trophic-level fishes. The expected response of higher trophic level species to changes in Gulf Menhaden abundance is mixed. Robinson et al. (2015) did not observe a large decline in consumers' populations in response to a simulated 50% increase in removals by the Menhaden fishery. Walters et al. (2008) found that an increase in Menhaden abundance had relatively little impact on the abundance of its consumers. When analyzing individual forage fish populations from observed indices of relative abundance, Hilborn et al. (2017) found little evidence that forage fish abundance is positively related to predator population growth; however, others using ecosystem-based modeling approaches have shown that the harvest of forage fishes has direct and indirect impacts on predator biomass (Berenshtein et al., 2023; Pikitch et al., 2012). Our modeling work cannot provide information about the population dynamics of trophically-linked taxa to simulated changes in prey abundance but does
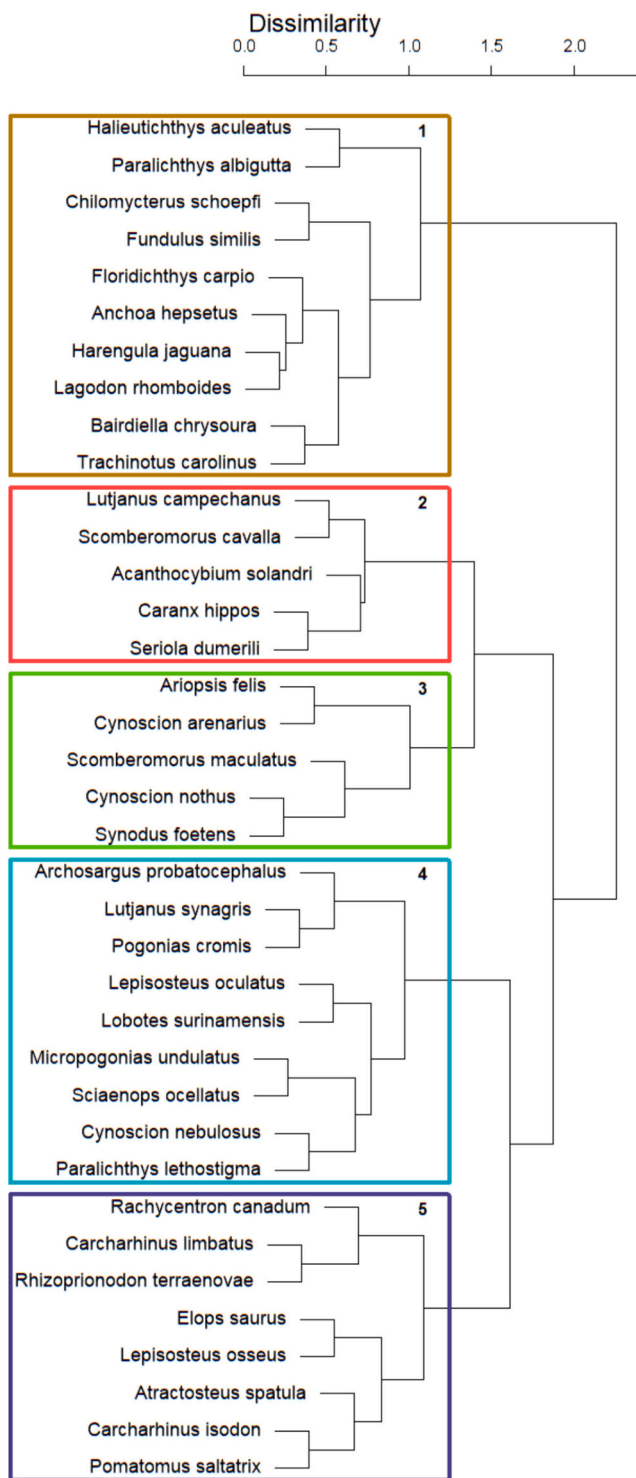
Fig. 5. Dendrogram from hierarchical cluster analysis based on mean diet proportions. 5 groups were delineated from the dendrogram: Group 1 = gold, Group 2 = red, Group 3 = green, Group 4 = blue, Group 5 = purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

quantify trophic dynamics of the nGOM region. Diet matrices that describe the extent of trophic interactions of taxa are at the foundation of ecosystem models. Results from EcoDiet can be used to inform larger, more complex ecosystem-based models by estimating a key input: the diet matrix (Hernvann et al., 2022).

In this work, there was stomach contents data that was not entered into the EcoDiet model due to results being reported in a different metric. The importance of the diet matrix as an input in ecosystem-level models necessitates a standardized method for stomach contents analysis that is not yet agreed upon (Amundsen and Sánchez-Hernández, 2019; Buckland et al., 2017; Chipps and Garvey, 2007). The ability to utilize information from different sources will aid in the utility of multispecies models and ecosystem-based management approaches. This is particularly apparent for ecosystem assessments of forage fishes (e.g. Gulf Menhaden), where there are efforts to establish ecological reference points based on understanding bottom-up control of forage species on high trophic level predators. Ecosystem-level models rely on time series of abundance data to verify model fit. Ecosystem models are often condensed to include only taxa of utmost management and ecological importance (Chagaris et al., 2020). In the nGOM, many taxa could be considered important, yet some of these taxa lack the time series of abundance data necessary to inform ecosystem models. The utility of ecological reference points as a viable management strategy in the nGOM is constrained by a paucity of data and uncertainty in model inputs. Our identification of feeding guilds may be useful for ecosystem assessment in this context. It is likely that the relative abundances of multispecies groups or "stock complexes" may be more tractable in an ecosystem context, than single species.

Our findings from a combination of 39 stomach contents studies, 67 stable isotope studies, and a decade of stable isotope values collected by the authors support the assertion that high trophic level predators in the nGOM target a wide prey base and no single predator exhibits strong dependence on Gulf Menhaden to provision its diet. A meta-analysis of 72 ecosystem trophic models using Ecopath by Pikitch et al. (2012) reported that 54 of the Ecopath models examined had at least one model group that was highly ($\geq$50% to <75%) or extremely dependent ($\geq$75% of diet) on forage fishes. The extent of the dependence of predator production on forage fishes was variable, in part depending on the location and type of ecosystem: Pikitch et al. (2012) reported that high latitude and upwelling systems had the greatest ecosystem support service contribution from forage fishes. The support service contribution to predator production was minimal in subtropical and tropical systems, including the Gulf of Mexico. Understanding the role of forage fishes to provision predators continues to be both necessary (for ecosystem-based management) and contentious (Hilborn et al., 2017; Pikitch et al., 2018). Although our work indicates that there is a diverse prey field that fish predators in the Gulf of Mexico are utilizing, we recognize that much work must be done to understand trophic linkages to promote assessment and management in the economically important fisheries in the region. We propose that future work to advance knowledge of trophic dynamics in the nGOM should be focused on understanding temporal, spatial, and life-history-dependent variation in diets of recreationally and commercially important predators in the region. Additionally, the resolution of unidentified prey through DNA barcoding approaches is promising. Ultimately, this work serves to highlight the limitations of our current methods of diet description and despite these limitations, provides a more complete understanding of the trophic dynamics of nearshore fishes in the northern Gulf of Mexico.

CRediT authorship contribution statement

Calvin Chee: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation. **Robert T. Leaf:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Kevin S. Dillon:** Validation, Methodology, Investigation, Data curation.

Data availability

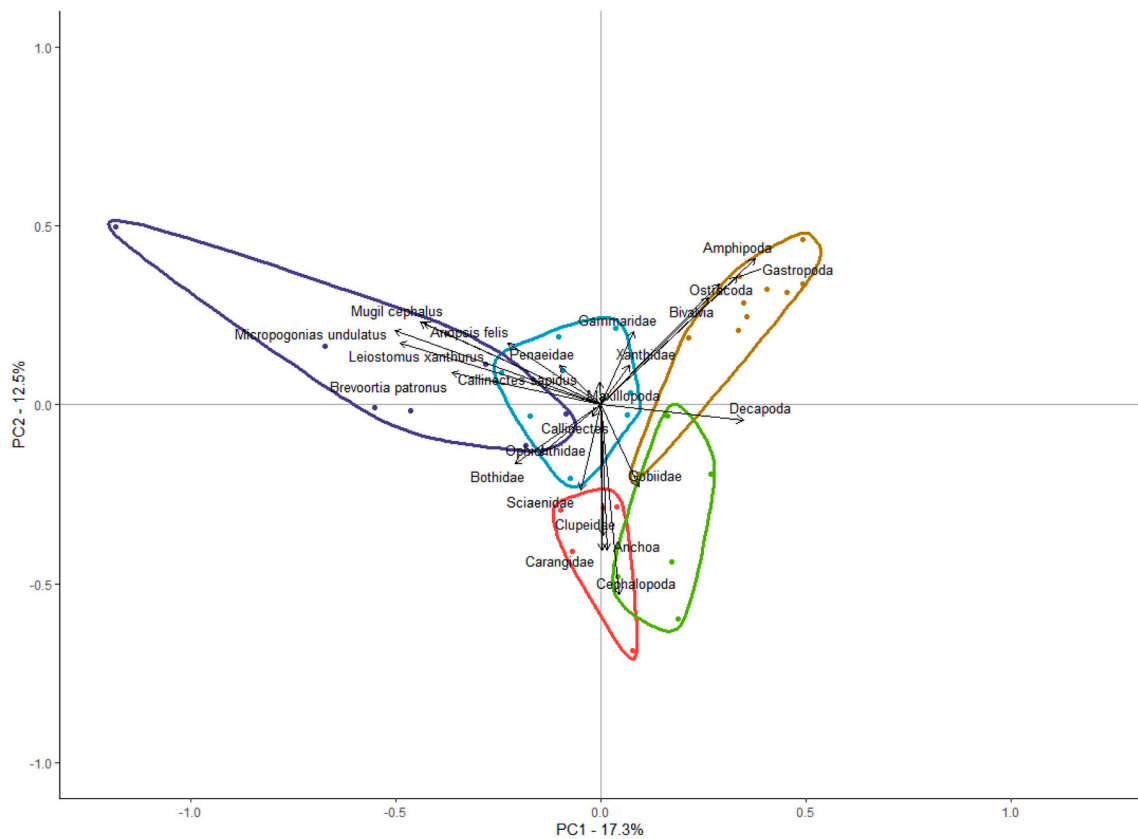Data will be made available on request.

Fig. 6. PCA biplot based on mean diet proportions. Arrows and labels represent PCA loadings: the prey taxa influencing position in ordination space. Points are predator species (unlabeled). Encircled groups are those delineated from cluster analysis. Colors correlate to Fig. 5: Group 1 = gold, Group 2 = red, Group 3 = green, Group 4 = blue, Group 5 = purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102746.

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