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Construction and evaluation of a robust trophic network model for the northern Gulf of Mexico ecosystem

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ABSTRACT

A critical issue in understanding trophic connectivity in ecological systems is the lack in quality and quantity of information about feeding habits. In this work, we present a method for integrating a diversity of feeding habits data from published studies to evaluate the impact on indices that describe characteristics of individual taxa and their connectivity. We focus our study on feeding habits of the fishes of the northern Gulf of Mexico and seek to understand the importance of the forage fish Gulf Menhaden (*Brevoortia patronus*) in predator diets. We created a database of diet studies from the northern Gulf of Mexico that included six diet metrics: frequency of occurrence, wet weight, dry weight, number, volume, index of relative importance, and index of caloric importance. We then used this information to construct a set of traditional networks (all prey and predators were from a single taxonomic level and trophic connections were parameterized with a single diet metric). We also constructed a "robust" network where all taxa were identified to the lowest taxonomic level and trophic connections were parameterized using a resampling approach that included all available information. Linear regression and resampling methods were used to convert data reported in other diet metrics into the frequency of occurrence diet metric. For both traditional and robust networks, we used network indices to describe topological properties. With the robust network, we conducted removal simulations where the forage fish species Gulf Menhaden, and associated Clupeidae representatives, were removed from the network and the feeding effort of the predators was reallocated among their other prey items. We found that network and node-specific indices were sensitive to the choice of taxonomy and diet metric level. In the robust network, predator species with the greatest number of identified prey had the lowest precision in their connections and prey from the Arthropoda phyla had the lowest precision for connections. From the removal and reallocation simulations, we found that Actinopterygii and Arthropoda were the most impacted prey taxa with 1.2% to 4.3% increase in predation and approximately 23 taxa would receive 50% of the reallocated predation. Overall, the resampling methods we present provide a potential means for combining disparate diet data and enables a comprehensive understanding of trophic interactions within an ecosystem.

1. Introduction

An understanding of an ecosystem's trophic dynamics is becoming an increasingly critical aspect of population assessment and ecosystem management (Hughes et al., 2005). Of particular interest, is to understand the role of those taxa that belong to the multiphyletic group "forage fish" (Ruzicka et al., 2012). Forage fishes are comprised of bony fish (and invertebrate, e.g. krill) taxa that are small to intermediate sized, pelagic, and act as the primary food source for a variety of predators (Pikitch et al., 2014). Forage fish stocks are highly productive and support some of the world's largest fisheries (Essington et al., 2015). However, their role in the maintenance of predator populations remains an open question (Hilborn et al., 2017; Pikitch et al., 2018). They are thought to play a major role in transferring energy from primary production to higher trophic levels to species such as fishes, marine mammals, and seabirds (Cury et al., 2011). Pikitch et al. (2012) reported that 75% of $n = 72$ published ecosystem models predicted that at least one predator depended on forage fishes for at least 50% of their diet. They also reported that the diets of approximately 16% of all predators within an ecosystem was at least 50% forage fish (Pikitch et al. 2012). Because of the complexity and diversity of trophic interactions in an ecosystem, the variation in ecosystem conditions, and the necessity for precision in predictive and descriptive models for decision making, there is a critical need for efficient use of existing trophic

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information.

The trophic dynamics of ecosystems have been quantitively evaluated using a number of tools. Two methods have been widely used: mass balance and network models. The mass balance approach is most often employed using the Ecopath with Ecosim framework (termed EwE) (Pauly et al., 2000). EwE is an approach to understand energy flow among trophic groups and has been used to understand the ecosystem-level effects of harvest and environmental disturbance (Christensen and Walters, 2004; Fath et al., 2007). Recent applications using this approach have described the relative importance of Gulf Menhaden as a prey item in the northern Gulf of Mexico (Geers et al., 2014; Sagarese et al., 2016) as well as the role of competitors to Gulf Menhaden stock productivity in the region (Robinson et al., 2015). An alternative method for modeling trophic connectivity in ecosystems is network analysis. Network analysis is used to understand an ecosystem's trophic dynamics and the role of an individual taxonomic group in the trophic web but does not require information about trophic group production, is not dynamic, and is not a statistical approach. In the absence of this information, the inferences derived from the modeling framework are different and generally simpler because trophic group production and consumption components are not estimated from a dynamic model. Instead, network approaches provide a framework for summarizing, visualizing, and analyzing complex food webs. The application of network approaches includes the comparative studies of energy flow and connectivity of trophic groups in different ecosystems (Dunne et al., 2002), evaluation of compartmentation in trophic networks (Krause et al., 2003), and investigation of ecosystem resilience and fragility (Solé and Montoya, 2001). A variety of indices of networks have been developed and these are generally of two types, those that are node-specific and focused on the number and type of connections of a taxonomic node to its neighbors and those that summarize some aspect of connectivity and structure of the entire network. A critical issue in developing an EwE or a network model is to make decisions about the level of taxonomic or functional group aggregation that will be modeled and to quantify the magnitude of trophic interactions among groups.

Both the level of taxonomy and the measurement used to describe connectivity between predator and prey can have profound impacts on the understanding of trophic dynamics (Oshima and Leaf, 2018). In many cases it is not possible to describe the identity of prey to a low taxonomic level (e.g. the level of species) because biological material is degraded and becomes difficult to identify in stomachs (Hyslop, 1980). Variability of preservation among different prey items can lead to biases and material that is more easily digestible are difficult to identify (Michener and Schell 1994, Bowen and Iverson 2013). The limitations of taxonomic assignment serves to reduce the inferences that can be made about the relative importance of a given taxa in the diets of predators. Such limitations often require that the model under consideration be structured such that only taxa of a given taxonomic level are included. This requires either “lumping” taxa together at a higher taxonomic level (e.g. order, family, or genus) or removing from the network information from poorly characterized (taxonomically) prey items and only including information from groups defined at a low taxonomic level. Both approaches result in the loss of information and impact our understanding of an ecosystem. In the context of network models, Oshima and Leaf (2018) reported that a network composed with frequency of occurrence data and trophic groups aggregated at the genus level was the most resilient to directed perturbations, however, when nodes were aggregated at the order level, that network became the least resilient.

Another source of variation in using studies of stomach content analysis to parameterize predator-prey interactions are errors in measurement. In many studies a diversity of diet metrics are reported that provide redundant or complementary information (Cortés, 1997; Macdonald and Green, 1983). The choice of diet metric impacts predictions about the structure of the food web (Oshima and Leaf, 2018). Oshima and Leaf (2018) reported that the composition of a trophic network is sensitive to the diet metrics used in its formulation. For example, networks of Gulf of Mexico fishes composed with frequency of occurrence data had a maximum of 166 individual nodes compared to the networks composed with volumetric data, which had a maximum of 41 nodes and inferences about the connectivity of trophic groups was sensitive to the amount of information to support the network. Reporting differences (the choice of diet metric) may also lead to misidentification of key groups within a network. There are advantages and limitations of each metric and it might not be possible to report multiple metrics. Frequency of occurrence is a simple method for quantifying stomach contents, however weight, volumetric, and caloric methods require effort. However, a limitation of the frequency of occurrence metric occurs when the prey items is fragmented. Whereas, with metrics such as weight and volume, the total amount of a prey item is determined. In a review of elasmobranch diet metrics, Cortes (1997) proposed the standardized use of index of relative importance as the measure for diet analysis. Using multivariate statistical techniques, McDonald and Green (1983) found that the diet metrics; number of individuals, weight, and frequency of occurrence provided redundant, and not complementary, information. An additional complication in understanding magnitude of the predator-prey interaction is that most diet studies generally limit the reporting of the diet metric to point estimates (mean or median) and omit uncertainty (Tirasin and Jørgensen, 1999). It is likely that diet composition changes substantially among individuals, spatially, and temporally (Szoboszlai et al., 2015) and such variation is generally not accounted for in network models.

In this work we present an approach to integrate disparate diet information from studies of stomach content analysis that use different levels of taxonomic organization and that preserves the structure of the observation, measurement, and process error. We are particularly interested in understanding inferences about the “importance” of the forage fish Gulf Menhaden (*Brevoortia patronus*) to predators and evaluating the impacts of incorporating estimates from published diet studies, that use alternative metrics, to create a robust food web for fishes of the northern Gulf of Mexico in a network analysis framework. The robust network we present incorporates the maximum number of available taxa and all available diet information. We use this network and traditional formulations (uniform trophic level and a single diet metric) to evaluate a variety of descriptive network- and node-specific indices. Given the observed variation in trophic connections based on resampling, we describe the relative precision of trophic connections and we evaluate, using the robust network, how predation pressure is reallocated to other prey groups when fishes in the Order Clupeiformes, the Family Clupeidae, the Genus *Brevoortia*, and the Species *Brevoortia patronus* are removed from the network.

2. Materials and methods

We conducted a literature search of available (published peer reviewed and gray literature) diet studies in the northern Gulf of Mexico (nGoM) using the bibliography provided in the Gulf of Mexico Species Interactions (GoMexSI, www.gomexsi.tamucc.edu) online database and a search using Google Scholar (https://scholar.google.com). We compiled information from 69 published sources that described stomach contents of Gulf of Mexico fishes in the coastal zone. Studies describing diets of fish classes Actinopterygii (ray-finned fishes) and Elasmobranchii (cartilaginous fishes) were evaluated and we limited our analysis to those fish species reported to have a minimum depth range of no > 200 m and found in habitats “Coastal”, “Reef”, “Seagrasses”, “Beach”, “Estuary”, and “Soft Bottom” based on a query in the Fishbase online database (www.fishbase.org accessed using R package “rfishbase”, Boettiger et al. 2012). 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. In many of the studies, two or more metrics are included. We focused our analysis on those studies that included at least one of the following diet metrics: frequency of occurrence, dry weight, wet weight, number, volume, index of relative importance (IRI), and index of caloric importance (ICI). IRI is calculated for each prey item using three variables: the percent number (n), percent weight (w), and frequency of occurrence (f); IRI = f (n + w). The index of caloric importance, is calculated using C, the calories in dry weight (g^{-1}) of the diet item and percent number (n), ICI = f (n + C). For each predator evaluated, in each study, we scaled and centered the log-transformed values of each diet metric. Because we found that frequency of occurrence was the most widely reported diet metric, we used this as an independent variable in a series of linear regressions to understand its relationship to other reported diet metrics (dry weight, wet weight, number, volume, IRI, and ICI).

We categorized prey groups using seven taxonomic ranks: Kingdom, Phylum, Class, Order, Family, Genus, and Species. The taxonomic classification for each prey item were determined using the World Register of Marine Species (WoRMS) database (www.marinespecies.org). All ambiguous prey items were excluded if the taxonomy could not be resolved (anachronistic and colloquial names could not be found in the WoRMS database) or if the prey item was not organic. Similarly, all diet items that were of ambiguous organic origin (e.g. flesh, bone, spine) were omitted.

We constructed trophic networks of two types: the first we term a "robust" network that includes the lowest taxonomic categories of the prey items reported in the published literature and the predator fishes and the second we term "traditional" networks that are constructed using only those prey and predator taxa from a single taxonomic level (Order, Family, and Genus) and parameterized with connections from a single diet metric (frequency of occurrence, dry weight, wet weight, number, volume, and IRI). The incorporation of prey items into a single taxonomic level for the traditional networks required aggregating (summing) the value of the diet metric for those taxa that were identified to levels lower than that which the network specified. For example, if three crab taxa in in the family Portunidae were classified to the Genus or Species level, the associated diet metrics of each would be summed and added to the diet metric associated with Portunidae spp. (if present). Information about the diet metric for unidentified crabs identified to the Order or Class level would be omitted from the Family-level trophic network.

To construct the robust network, we parameterized the connections in the network, the edges, using a resampling approach: for each predator, we identified each unique prey taxa in our database, regardless of the study from which they were reported and regardless of taxonomic level. We determined the diet metric that was reported for each of the unique prey items. Each diet metric, for each prey item, was randomly sampled $n = 1000$ times. If the randomly sampled diet metric was frequency of occurrence, this value was used for the edge weight. However, if the randomly sampled diet metric was dry weight, wet weight, number, volume, IRI, or ICI, we used the 95% confidence interval of the mean predicted frequency of occurrence value from the linear regression associated with the value of the chosen diet metric to select the edge weight. A random sample was taken from a uniform distribution that was bounded by the 95% confidence interval of the mean prediction. The variation in the values represents the aggregated impacts of process, observation, and measurement errors associated with the predator and prey relationship. Traditional networks were also constructed using a resampling approach. We categorized all prey species to the Order, Family, and Genus from which they belonged even if they were identified to a lower taxonomic level. For each traditional network realization (combination of taxonomic level and diet metric), we identified each predator's unique prey taxa in our database, regardless of the study from which they were reported, and randomly sampled from the values reported of the given diet metric. Using this approach, we derived a distribution of $n = 1000$ values for each edge weight in each network.

Using the constructed networks, we performed three types of analysis. We evaluated the distribution of node- and network-specific indices for each network, described the precision of the edge weights, and simulated the allocation of predation pressure when Gulf Menhaden were removed from the network. We used a suite of node- and network-specific indices including weighted link density, weighted connectance, weighted average path length, and neighborhood size. Weighted link density is a network-specific metric that describes the edges-per-node and includes the edge weight, $LD_w = e^{0.5\Phi}$, where Φ is the network's degrees of freedom, or number of alternate paths in the network (Boit et al., 2014). Low LD_w values indicate that the majority of paths in the network are disconnected and that the paths are linear instead of circular. In ecosystems with many interspecies interactions, link density would be higher. Weighted connectance is a metric that indicates the number of alternate path lengths, $C_w = LD_w/N^2$ and incorporates the weight of the edge (Boit et al., 2014). Weighted connectance provides information on how complete and efficient the ecosystem is. Networks that have higher connectance have more alternate pathways, so that if a connection between a predator and prey is removed, the predator has alternative connections to prey. Networks with greater connectance can still function when disturbances (removal of nodes) occur but those with low connectance can be broken into isolated sub-networks. In this study, connectance values are an indication of the amount of data available in the network. Networks constructed with less information will generally exhibit lower connectance values. Weighted average path length is calculated by $\frac{1}{N(N-1)}\sum_{ij}^{N} d_{ij}$, where N is number of nodes and d_{ij} is the shortest distance between nodes i and j. The edge weights are incorporated in d_{ij} so that the shortest distance between each pair maximizes the sum of edge weights between the pair, meaning if there are multiple ways to connect two nodes, the "shortest" distance is the one that has the largest edge magnitude. This index provides information on the mean number of times energy is transferred within a trophic network. A neighborhood metric was calculated to determine the number of connections (edges) within two nodes of the specified target node of Gulf Menhaden. The neighborhood index indicates the magnitude of node connections and in the case of trophic networks, meaning they can act as a "hub", or core taxa, for trophic interactions. In the case of traditional networks that were described at the Order, Family, or Genus level, the neighborhood metric was calculated for target nodes Clupeiformes, Clupeidae, and *Brevoortia* spp. respectively.

To describe the precision of trophic interactions in the robust network, we described two aspects of uncertainty. The first is variation in frequency of occurrence of prey taxa. The second is variation in frequency of occurrence in predator diets. For both analyses, we calculated the coefficient of variation (CV) of the $n = 1000$ resampled values of the frequency of occurrence metric in the robust network. Each prey taxa have a CV value for each of the predators that it is connected to and each predator taxa have a CV value for each of the prey taxa it is associated with in the robust network. We evaluated uncertainty and variation in each prey taxa (across all predators) by ranking the calculated CV of frequency of occurrence values (from smallest to largest CV). We report the uncertainty and variation as the prey-specific sum of the rank of CV. Uncertainty and variation in predator diets is represented as the sum of the CV of all prey items in the diet.

Finally, we performed a set of simulations for the robust network to understand the role of the "forage fish" Gulf Menhaden (*Brevoortia patronus*) in the diets of predators. We were interested in understanding how predation effort would be reallocated when Gulf Menhaden were removed in the network. To estimate this reallocation, we calculated the sum of the edge weights for each identified predator of Gulf Menhaden and assumed that all individuals in the taxonomic groups (*Brevoortia patronus*, *Brevoortia* spp., and Clupeidae spp.) consisted entirely of Gulf Menhaden. We then calculated how the impact of reallocating feeding pressure changed the sum of edge weights for the remaining prey species for each of the 1000 network realizations of the

Table 1
Summary of the taxonomic composition of predator species evaluated in the published literature including the number of unique prey items from each of the studies and the diet metric reported for the prey items. Diet metric includes the number of individuals, frequency of occurrence, dry weight, wet weight, and volume.

Class	Order	Family	Genus	Species	Number of Unique Prey Items	Number of Studies	N	Freq. of Occurrence	Dry Weight	Wet Weight	Volume	IRI
Actinopterygii	Anguilliformes	Congridae	*Rhynchoconger*	*flavus*	2	1					X	
	Aulopiformes	Synodontidae	*Saurida*	*brasiliensis*	7	3	X				X	
			Synodus	*foetens*	5	4	X	X			X	
			Synodus	*poeyi*	3	2	X				X	
	Batrachoidiformes	Batrachoididae	*Porichthys*	*plectrodon*	10	3	X				X	
			Porichthys	*porosissimus*	10	1					X	
	Beryciformes	Holocentridae	*Holocentrus*	*adscensionis*	3	1	X					
			Sargocentron	*bullisi*	4	1	X					
	Clupeiformes	Engraulidae	*Anchoa*	*cubana*	5	2	X				X	
			Anchoa	*hepsetus*	16	5	X	X		X	X	X
			Anchoa	*lyolepis*	5	1					X	
			Anchoa	*mitchilli*	31	2	X					
	Elopiformes	Elopidae	*Elops*	*saurus*	23	1		X		X		
	Gadiformes	Macrouridae	*Bathygadus*	*macrops*	4	2	X				X	
			Coelorinchus	*caribbaeus*	6	2	X				X	
	Lepisosteiformes	Lepisosteidae	*Atractosteus*	*spatula*	9	1		X				
			Lepisosteus	*osseus*	13	1		X				
	Lophiiformes	Ogcocephalidae	*Halieutichthys*	*aculeatus*	15	5	X	X			X	
			Ogcocephalus	*declivirostris*	12	2	X	X				
			Ogcocephalus	*nasutus*	4	2	X				X	
			Ogcocephalus	*pantostictus*	13	2	X	X				
			Ogcocephalus	*parvus*	6	1					X	
	Ophidiiformes	Ophidiidae	*Lepophidium*	*brevibarbe*	7	3		X			X	
	Perciformes	Acropomatidae	*Synagrops*	*spinosus*	4	2	X				X	
		Apogonidae	*Apogon*	*pseudomaculatus*	3	1	X					
		Carangidae	*Caranx*	*hippos*	25	1		X			X	
			Chloroscombrus	*chrysurus*	5	3	X				X	
			Seriola	*dumerili*	32	1	X	X			X	
			Trachinotus	*carolinus*	16	3		X	X		X	
			Trachurus	*lathami*	3	1	X					
		Chaetodontidae	*Chaetodon*	*sedentarius*	5	1	X					
		Labridae	*Bodianus*	*pulchellus*	5	1	X					
			Decodon	*puellaris*	5	1	X					
			Halichoeres	*bathyphilus*	6	1	X					
Class	Order	Family	Genus	Species	Number of Unique Prey Items	Number of Studies	N	Freq. of Occurrence	Dry Weight	Wet Weight	Volume	
Actinopterygii	Perciformes	Lobotidae	*Lobotes*	*surinamensis*	36	3	X	X		X	X	X
		Lutjanidae	*Lutjanus*	*campechanus*	46	8	X	X	X	X		X
			Lutjanus	*synagris*	25	1	X	X		X		X
			Rhomboplites	*aurorubens*	9	2	X					

(*continued on next page*)

Table 1 (*continued*)

Class	Order	Family	Genus	Species	Number of Unique Prey Items	Number of Studies	N	Freq. of Occurrence	Dry Weight	Wet Weight	Volume	IRI
Actinopterygii	Perciformes	Malacanthidae	*Caulolatilus*	*chrysops*	4	1	X					
			Malacanthus	*plumieri*	5	1	X					
		Percophidae	*Bembrops*	*anatirostris*	7	1	X					
		Polynemidae	*Polydactylus*	*octonemus*	5	1	X					
		Pomatomidae	*Pomatomus*	*saltatrix*	17	1		X			X	
		Priacanthidae	*Priacanthus*	*arenatus*	4	1	X					
			Pristigenys	*alta*	4	1	X					
		Rachycentridae	*Rachycentron*	*canadum*	14	2	X	X				
		Sciaenidae	*Cynoscion*	*nebulosus*	38	7	X	X		X	X	X
			Cynoscion	*nothus*	17	5		X	X		X	
			Menticirrhus	*littoralis*	13	3	X	X			X	
			Menticirrhus	*saxatilis*	14	2	X	X			X	
			Pareques	*umbrosus*	4	1	X					
			Pogonias	*cromis*	35	3		X				
			Sciaenops	*ocellatus*	76	6	X	X		X	X	X
		Scombridae	*Acanthocybium*	*solandri*	35	2	X	X		X	X	X
			Euthynnus	*alletteratus*	14	1					X	
			Scomberomorus	*cavalla*	21	3	X	X			X	X
			Scomberomorus	*maculatus*	14	2	X	X			X	X
		Serranidae	*Epinephelus*	*adscensionis*	9	1				X		
			Paranthias	*furcifer*	12	2	X			X		
			Pronotogrammus	*martinicensis*	6	1	X					
			Serraniculus	*pumilio*	5	2	X				X	
			Serranus	*atrobranchus*	8	3	X				X	
			Serranus	*notospilus*	5	2	X				X	
			Serranus	*phoebe*	6	1	X					
		Sparidae	*Archosargus*	*probatocephalus*	25	2		X				
			Pagrus	*pagrus*	9	1	X					
			Stenotomus	*caprinus*	15	4	X		X		X	
		Stromateidae	*Peprilus*	*burti*	7	2	X				X	
		Trichiuridae	*Trichiurus*	*lepturus*	8	3			X			
	Pleuronectiformes	Bothidae	*Trichopsetta*	*ventralis*	6	2	X				X	
		Cynoglossidae	*Symphurus*	*plagiusa*	19	3	X	X			X	
		Paralichthyidae	*Citharichthys*	*spilopterus*	13	2	X	X			X	
Class	Order	Family	Genus	Species	Number of Unique Prey Items	Number of Studies	N	Freq. of Occurrence	Dry Weight	Wet Weight	Volume	
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Etropus*	*crossotus*	5	1					X	
			Etropus	*rimosus*	6	1	X					
			Paralichthys	*albigutta*	12	1		X				
			Syacium	*gunteri*	9	2	X				X	
			Syacium	*papillosum*	7	1	X					
	Scorpaeniformes	Scorpaenidae	*Pontinus*	*longispinis*	6	2	X				X	
			Pterois	*volitans*	59	1				X		
			Scorpaena	*calcarata*	5	2	X				X	
		Triglidae	*Bellator*	*militaris*	6	2	X				X	
			Prionotus	*alatus*	6	2	X				X	
			Prionotus	*roseus*	5	2	X				X	
			Prionotus	*scitulus*	5	2	X				X	
			Prionotus	*stearnsi*	7	3	X				X	
	Stomiiformes	Gonostomatidae	*Cyclothone*	*pallida*	4	1		X				
		Sternoptychidae	*Valenciennellus*	*tripunctulatus*	3	1	X		X			
		Stomiidae	*Stomias*	*affinis*	11	1		X		X		
	Syngnathiformes	Syngnathidae	*Syngnathus*	*scovelli*	7	2	X	X	X	X		X
	Tetraodontiformes	Balistidae	*Balistes*	*capriscus*	10	1				X		
		Tetraodontidae	*Canthigaster*	*rostrata*	4	1	X					
Elasmobranchii	Carcharhiniformes	Carcharhinidae	*Carcharhinus*	*limbatus*	13	1		X	X			
			Rhizoprionodon	*terraenovae*	23	1		X	X			
		Sphyrnidae	*Sphyrna*	*tiburo*	3	1						X

robust model. The reallocation of predation pressure to each prey group is proportional to that group's representation in the diet. From these we determined the expected percent increase in predation to other prey groups.

3. Results

The database compiled in this work described predator and prey interactions from 69 studies published between 1951 and 2014 of 95 predator species (Table 1). In aggregate, the studies documented 9564 trophic interactions of these predators on ten phyla, 32 classes, 69 orders, 150 families, and 162 genera. The taxonomic distribution of prey indicated that Actinopterygii was the dominant phyla in the diets of fish predators (n = 148 unique taxa), followed by representatives of the phyla Arthropoda (n = 121), and Mollusca (n = 29 unique taxa). Annelida, Bryzoa, Chaetognatha, Chelicerata, Cnideria, Echinodermata, and Urochordata each had four or fewer representatives in fish diets. A total of 133 unique prey taxa were identified to the species level. Frequency of occurrence was the most frequently reported diet metric reported (n = 2931) followed by percent volume (n = 2310), number of

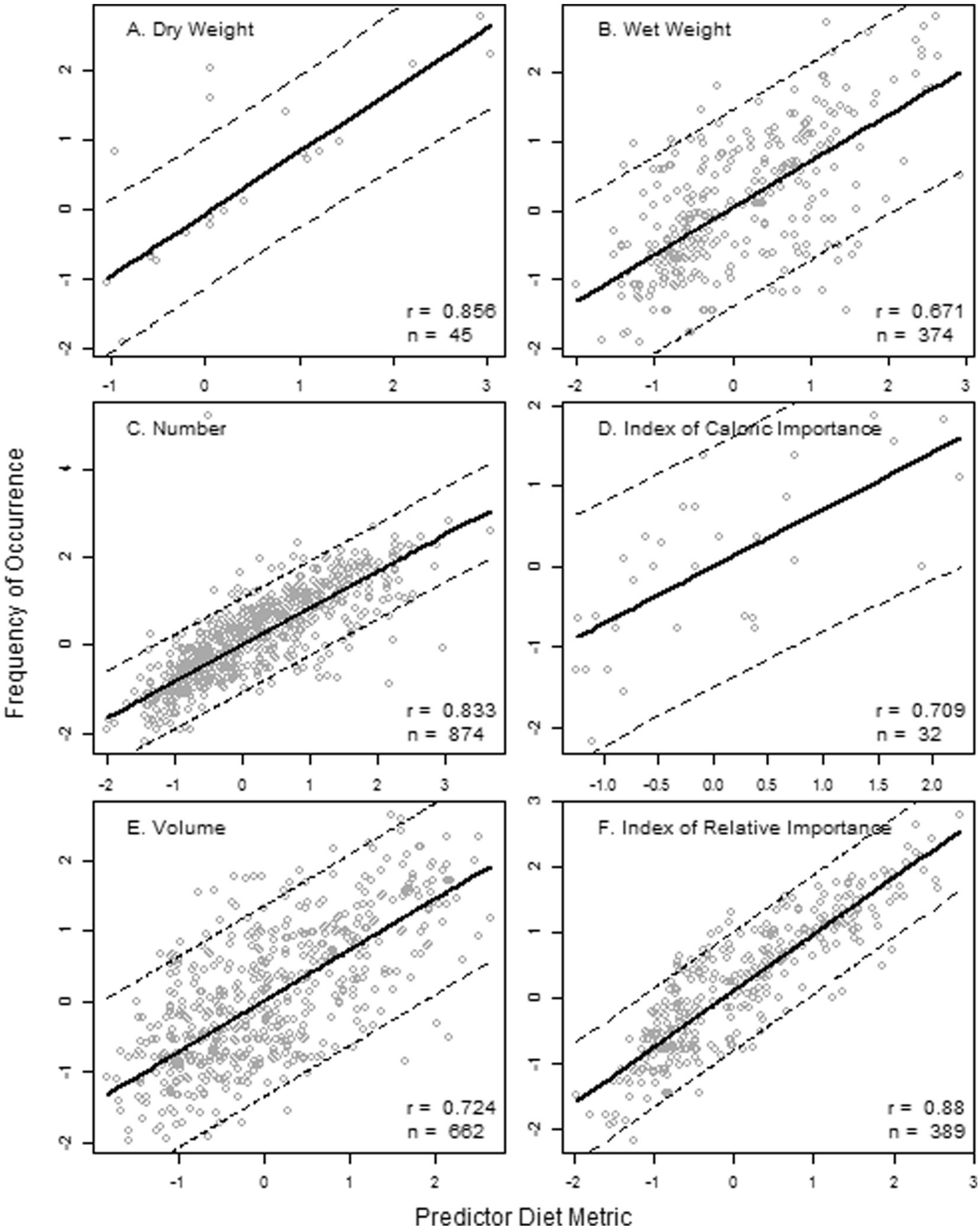

Fig. 1. Linear relationship of A. Dry weight, B. Wet Weight, C. Number, D. Index of Caloric Importance, E. Volume and F. Index of Relative Importance to Frequency of Occurrence. All values are derived from the literature and are log-transformed, centered, and scaled.

individuals (n = 2235), dry weight (n = 970), wet weight (n = 604), IRI (n = 418), and ICI (n = 96).

For those studies that reported multiple diet metrics, and included frequency of occurrence, we found a significant and positive relationship between the pooled, scaled, log-transformed diet metrics and the scaled, log-transformed frequency of occurrence (Fig. 1). Pearson product-moment correlation coefficient (r) values ranged from 0.671 to 0.880. The greatest correlation was found for the linear regressions of frequency of occurrence and IRI (r = 0.880), dry weight (r = 0.856), and number (r = 0.833). The diet metrics wet weight (r = 0.671), ICI (r = 0.709), and volume (r = 0.724) exhibited a lower correlation. Each of the slope values of the scaled and log-transformed diet metric to the scaled and log transformed frequency of occurrence were significantly different from zero ($p < 0.0001$).

The taxonomic level and the diet metric used in the construction of a diet network impacts the number of nodes and the associated pattern and weight of the connections among them (Fig. 2). We created a suite of traditional networks (n = 18) and a least-parsimonious robust network to represent the trophic web in the northern Gulf of Mexico (Table 2). Different numbers of nodes and orientation of connections serves to significantly change the indices used to describe the network characteristics. Each candidate network had a different topological structure and varied in the total number of nodes, ranging from 418 in the robust network model to 20 nodes in the network that was constructed using only the dry weight diet metric evaluated at the species level. The mean weighted link density decreases with the number of nodes and each value in the traditional network is significantly different ($\alpha > 0.05$) than the mean value reported for the robust network.

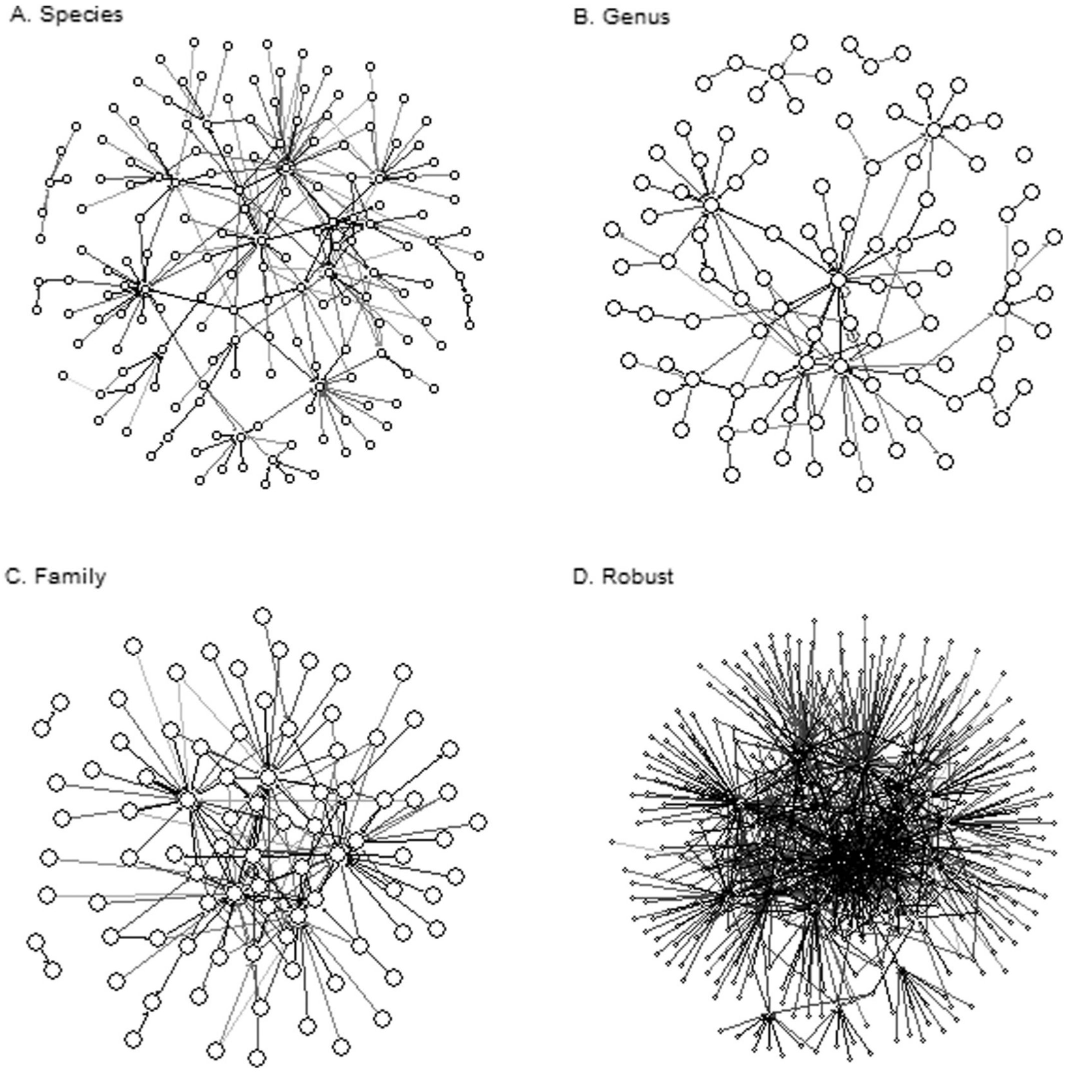

Fig. 2. Variation in the network topology using frequency of occurrence information for taxa at the A. Species, B. Genus, and C. Family level. Network representation that includes all taxa is presented in D.

Table 2
Node and network specific indices of the robust network and n = 18 traditional networks.

Diet Metric	Taxonomic Level	Number of Nodes	Weighted Link Density	Weighted Connectance	Weighted Average Path Length	Neighborhood
Robust	Lowest Identified	418	0.082 (0.080 to 0.084)	33.624 (34.117 to 35.235)	2.780 (2.840 to 3.017)	104
Frequency of Occurrence	Family	131	0.122 (0.118 to 0.125)	15.936 (15.499 to 16.363)	2.349 (2.259 to 2.442)	103
	Genus	153	0.076 (0.074 to 0.077)	11.606 (11.35 to 11.84)	3.226 (3.141 to 3.323)	80
	Species	132	0.07 (0.065 to 0.072)	9.235 (8.645 to 9.451)	3.577 (3.392 to 3.7)	78
Number	Family	101	0.115 (0.112 to 0.119)	11.661 (11.3 to 12.025)	2.524 (2.428 to 2.601)	60
	Genus	118	0.072 (0.07 to 0.074)	8.479 (8.217 to 8.755)	3.585 (3.419 to 3.749)	39
	Species	88	0.072 (0.069 to 0.075)	6.339 (6.047 to 6.615)	4.203 (3.949 to 4.404)	37
Volume	Family	62	0.191 (0.181 to 0.202)	11.858 (11.202 to 12.526)	1.915 (1.664 to 2.059)	61
	Genus	56	0.126 (0.122 to 0.129)	7.067 (6.829 to 7.203)	3.253 (3.194 to 3.409)	40
	Species	49	0.133 (0.132 to 0.135)	6.537 (6.465 to 6.603)	3.232 (3.2 to 3.349)	30
Wet Weight	Family	90	0.108 (0.104 to 0.111)	9.763 (9.375 to 10.018)	2.677 (2.578 to 2.74)	27
	Genus	102	0.074 (0.07 to 0.076)	7.582 (7.161 to 7.781)	2.878 (2.713 to 2.974)	32
	Species	88	0.063 (0.063 to 0.065)	5.586 (5.505 to 5.684)	3.815 (3.734 to 3.896)	30
Index of Relative Importance	Family	48	0.151 (0.138 to 0.16)	7.238 (6.647 to 7.659)	2.238 (1.942 to 2.524)	33
	Genus	54	0.123 (0.118 to 0.129)	6.666 (6.352 to 6.945)	3.388 (2.751 to 3.706)	21
	Species	41	0.128 (0.12 to 0.135)	5.235 (4.917 to 5.54)	2.977 (2.6 to 3.313)	22
Dry Weight	Family	26	0.242 (0.219 to 0.265)	6.305 (5.697 to 6.89)	1.929 (1.78 to 2.059)	20
	Genus	25	0.239 (0.21 to 0.265)	5.985 (5.239 to 6.622)	1.955 (1.787 to 2.07)	21
	Species	20	0.288 (0.288 to 0.288)	5.75 (5.75 to 5.75)	1.795 (1.795 to 1.795)	20

Table 3a

Table of the 25 prey taxa in the robust network with the lowest precision in their edge weights (connection to predator, presented as the sum of the ranks of the coefficient of variation,CV) ranked from largest to smallest. Frequency is the number of predator taxa that reported the prey item.

Phyla	Class	Order	Family	Genus	Species	Sum of Rank of CV	Frequency
Arthropoda	Malacostraca	Decapoda				641	68
Chordata	Actinopterygii					546	70
Arthropoda						436	56
Annelida						335	49
Arthropoda	Malacostraca	Amphipoda				311	45
Arthropoda	Malacostraca					205	35
Arthropoda	Malacostraca	Stomatopoda				185	31
Chordata	Actinopterygii	Clupeiformes	Engraulidae	*Anchoa*		178	9
Arthropoda	Malacostraca	Decapoda	Penaeidae			178	10
Arthropoda	Maxillopoda	Calanoida				165	19
Arthropoda	Malacostraca	Decapoda	Portunidae	*Callinectes*	*sapidus*	154	7
Mollusca	Bivalvia					147	23
Chordata	Actinopterygii	Perciformes	Serranidae			146	6
Chordata	Actinopterygii	Perciformes	Carangidae			138	8
Chordata	Actinopterygii	Scorpaeniformes	Triglidae			136	6
Mollusca	Cephalopoda					134	16
Arthropoda	Malacostraca	Decapoda	Portunidae			131	6
Mollusca	Gastropoda					119	16
Arthropoda	Malacostraca	Decapoda	Xanthidae			116	8
Arthropoda	Malacostraca	Decapoda	Squillidae	*Mantis*		110	4
Chordata	Actinopterygii	Clupeiformes	Clupeidae			108	8
Chordata	Actinopterygii	Clupeiformes	Clupeidae	*Brevoortia*	*patronus*	107	8
Arthropoda	Maxillopoda					101	7
Chordata	Actinopterygii	Perciformes	Blenniidae			93	3
Arthropoda	Maxillopoda	Harpacticoida	Harpacticidae			93	5

Conversely, weighted connectance increases with the number of nodes. The robust network had a significantly greater value of weighted connectance than any of the traditional networks. There was some overlap in weighted average path length index among the robust network and traditional network formulations. The neighborhood index for the robust network indicated that almost a quarter of the taxa are within two nodes of the nodes Clupeiformes, Clupeidae, and *Brevoortia* spp., and *Brevoortia patronus*.

The sum of the rank of the coefficient of variation values for the edges in the robust network indicated that a number of the prey taxa analyzed in the robust network are not well described in the diets of predators. Of the 418 unique prey items in the robust network model, taxa in the phyla Arthropoda, Chordata, Annelida, and Mollusca identified to the Class or Order level exhibited substantial variation and were also frequently occurring in the diets of predators (Table 3a). A diversity of Arthropod taxa represented 13 of the 25 of those taxa that exhibited greatest CV in their edge weight (the lowest precision). Only a single Arthropod, that was identified to the species level, was found to exhibit high variation in edge weight, the blue crab (*Callinectes sapidus*). The Arthropods identified to the Class, Order, and Family level that exhibit substantial variation in edge weight are a taxonomically and morphologically diverse group. Similarly, Phyla Annelida, and Gastropod, Cephalopod, and Bivalve Mollusca exhibit variations in edge weight. There is a general increase in the sum of the rank of CV and the frequency of occurrence, but this is not the case for Cephalopod and Gastropod mollusks which have moderate sum of ranked CV values and relatively large frequencies of occurrence. Most prey of the Phyla Chordata that are identified to the family level (Engraulidae, Serranidae, Carangidae, Triglidae, Clupeidae, and Blenniidae) exhibit relatively high variation in edge weight. We note the presence of Gulf Menhaden (*Brevoortia patronus*) as the only Chordate representative identified to the species level that was found to exhibit substantial variation in edge weight. A similar analysis of the variation in edge weights associated with the nodes of the unique predator fish species evaluated in the robust network ($n = 95$) indicated the variation in diet and the range of unique prey items reported in the literature. In general, those predator species with the fewest number of prey items identified (Table 3b) had the lowest precision in the estimates of prey. The most poorly estimated diets are allocated between those predator taxa with very few prey items (two to eight) and those with a larger number of prey items (12 to 36). The predator species represented include a taxonomically and ecologically diverse group.

The impacts of node removal in the robust model of *Brevoortia patronus*, *Brevoortia* spp., and Clupeidae spp. affected the 15 fish taxa that were predators on these taxa. The simulation of the allocation of predation to other prey taxa indicated that Actinopterygii and Arthropoda would be the most impacted, ranging from a 1.2 to 4.3% increase in predation. An estimated total of 23 prey taxa would receive approximately 50% of the predation impact given the extirpation of Gulf Menhaden and associated Clupeidae representatives (Table 4). We note that unidentified Actinopterygii (that may also include Clupeidae) exhibit the greatest increase in percent change of predation pressure.

4. Discussion

The success of quantitative models employed to describe the multispecies trophic dynamics of ecosystems are contingent on the quality and quantity of information used in their formulation. In the United States there have been systematic (temporal and spatial) studies of fish diets in some ecosystems including the north Pacific (http://www.afsc.noaa.gov), the Chesapeake Bay (http://www.vims.edu/research), California Current (Szoboszlai et al., 2015), and the northeast Atlantic (http://www.ngdc.noaa.gov). These descriptive efforts require substantial and consistent effort to characterize the variability in food habits. Such an effort has not been undertaken in the northern Gulf of Mexico. Given the gaps of information on food habits in the northern Gulf of Mexico and the critical need for this information to hasten ecosystem understanding, we focus our work on describing the information content available in the published literature from the region. In this work we find that although published studies differ in the reporting of diet metrics they may contain redundant information, that network analysis is a useful framework for understanding trophic connectivity but that the descriptive indices of networks are sensitive to the data used in their construction, and that the precision of estimates of predator diet and prey item frequency of occurrence can be low for some groups. Finally in our evaluation of the impacts of removal of Gulf

Table 3b

Table of the 25 predator taxa in the robust network with the lowest precision in their edge weights presented as the sum of the coefficient of variation (CV). The number of prey taxa is the total number of prey taxa reported (in all studies) for a given predator.

Order	Family	Genus	Species	Sum of CV	Number of prey taxa
Perciformes	Carangidae	*Chloroscombrus*	*chrysurus*	52793	5
		Trachinotus	*carolinus*	2667	16
Lophiiformes	Ogcocephalidae	*Halieutichthys*	*aculeatus*	2046	15
Perciformes	Acropomatidae	*Synagrops*	*spinosus*	1916	4
Pleuronectiformes	Paralichthyidae	*Citharichthys*	*spilopterus*	670	13
Anguilliformes	Congridae	*Rhynchoconger*	*flavus*	668	2
Lophiiformes	Ogcocephalidae	*Ogcocephalus*	*declivirostris*	631	12
Clupeiformes	Engraulidae	*Anchoa*	*mitchilli*	535	31
Pleuronectiformes	Paralichthyidae	*Syacium*	*papillosum*	508	7
Perciformes	Serranidae	*Serranus*	*atrobranchus*	504	8
Aulopiformes	Synodontidae	*Synodus*	*poeyi*	454	3
Pleuronectiformes	Paralichthyidae	*Etropus*	*rimosus*	412	6
Perciformes	Priacanthidae	*Priacanthus*	*arenatus*	380	4
Scorpaeniformes	Triglidae	*Bellator*	*militaris*	376	6
Ophidiiformes	Ophidiidae	*Lepophidium*	*brevibarbe*	349	7
Scorpaeniformes	Triglidae	*Prionotus*	*stearnsi*	349	7
Gadiformes	Macrouridae	*Bathygadus*	*macrops*	322	4
Perciformes	Serranidae	*Serranus*	*notospilus*	315	5
Scorpaeniformes	Triglidae	*Prionotus*	*roseus*	292	5
Perciformes	Serranidae	*Serraniculus*	*pumilio*	284	5
Clupeiformes	Engraulidae	*Anchoa*	*hepsetus*	280	15
Gadiformes	Macrouridae	*Coelorinchus*	*caribbaeus*	276	6
Perciformes	Serranidae	*Serranus*	*phoebe*	259	6
Lophiiformes	Ogcocephalidae	*Ogcocephalus*	*pantostictus*	258	13
Perciformes	Lobotidae	*Lobotes*	*surinamensis*	248	36

Menhaden (and members of family Clupeidae) from the robust network we show that the reallocation of feeding effort is spread among a variety of fish and invertebrate prey taxa.

In our survey of the published diet literature we found that there is a diversity of metrics used to describe stomach contents and that different workers represent and highlight different aspects of predator diet. Our approach to combine diet metrics allows a maximum number of interactions to be evaluated given the use of a common scale, frequency of occurrence. However, we note that in some cases the use of the predicted relationship may be problematic: The consumption of a single large prey item and the consumption of many small prey items of the same taxa would result in similar volume, dry weight, and wet weight measurements. Our use of the mean value of each diet metric in the regression is by necessity but may help to reduce potential individual-level biases. Diet metrics are generally reported as mean values and the associated variation (among individuals of the same taxa) is generally not reported.

A ubiquitous issue in diet studies is the challenge of assigning diet

Table 4

Table of the predicted mean and range of reallocation of predation pressure (percent increase in edge weight) to other prey items identified in predator diets. The simulation included the removal of all taxa of Order Clupeiformes, Family Clupeidae, and Genus *Brevoortia*.

						Percent Change in Edge Weight			
Phylum	Class	Order	Family	Genus	Species	Mean	Minimum	Maximum	Cumulative Sum of Mean
Chordata	Actinopterygii					0.043	0.039	0.046	0.043
		Perciformes	Sciaenidae			0.039	0.035	0.043	0.082
			Sciaenidae	*Micropogonias*	*undulatus*	0.029	0.025	0.035	0.111
Arthropoda	Malacostraca	Decapoda				0.028	0.025	0.032	0.139
	Malacostraca		Penaeidae			0.025	0.022	0.028	0.164
Chordata	Actinopterygii	Pleuronectiformes	Bothidae			0.025	0.021	0.028	0.189
		Clupeiformes	Engraulidae	*Anchoa*		0.023	0.02	0.026	0.212
		Perciformes	Sciaenidae	*Leiostomus*	*xanthurus*	0.023	0.02	0.028	0.235
			Carangidae			0.022	0.019	0.025	0.257
Arthropoda	Malacostraca					0.021	0.016	0.025	0.278
Chordata	Actinopterygii	Anguilliformes	Ophichthidae			0.021	0.018	0.024	0.299
		Perciformes	Trichiuridae			0.021	0.018	0.026	0.32
Mollusca	Cephalopoda					0.021	0.018	0.024	0.341
Arthropoda	Malacostraca	Isopoda				0.02	0.015	0.023	0.361
	Malacostraca	Stomatopoda				0.019	0.015	0.023	0.38
Chordata	Actinopterygii	Mugiliformes	Mugilidae	*Mugil*	*cephalus*	0.019	0.017	0.025	0.399
		Perciformes	Serranidae			0.017	0.015	0.02	0.416
		Aulopiformes	Synodontidae			0.016	0.013	0.02	0.432
		Perciformes	Labridae			0.016	0.013	0.02	0.448
		Clupeiformes	Engraulidae			0.015	0.012	0.019	0.463
		Perciformes	Sparidae	*Lagodon*	*rhomboides*	0.015	0.012	0.02	0.478
Arthropoda						0.014	0.012	0.016	0.492
Chordata	Actinopterygii	Pleuronectiformes	Cynoglossidae	*Symphurus*	*plagiusa*	0.014	0.011	0.019	0.506
		Siluriformes	Ariidae	*Ariopsis*	*felis*	0.013	0.01	0.017	0.519
		Perciformes	Sparidae			0.012	0.011	0.014	0.531

items unambiguously to the lowest taxonomic category possible. Taxonomic ambiguity in prey identification reduces the number of nodes available for analysis in traditional diet metrics but also may add some bias to the robust analysis presented in this work. The conversion of candidate diet metrics to the frequency of occurrence metric may be problematic for taxonomic prey groups that are poorly defined. These groups may contain a large variety of constituent taxa that exhibit heterogeneity in life-stage and sizes.

Alternative candidate diet metrics provided different ability to predict the frequency of occurrence metric. The diet metrics IRI, dry weight, and percent number explained a greater amount of variability of the frequency of occurrence metric than did the metrics ICI, wet weight and volume. In the case of IRI, this is expected – the frequency of occurrence metric is included in the IRI calculation and thus these metrics are not independent. The predictive capability of the dry weight metric was surprising, indicating that for the studies examined, the weights of each individual prey item of a taxa were consistent. The ICI and dry weight metrics have low relative sample sizes and were reported in few studies. Both of these metrics are more labor intensive to obtain than the other reported diet metrics (Li and Brocksen, 1977). In the case of ICI, low sample size likely contributes to the low precision of the relationship to frequency of occurrence. Additionally, the relationship of ICI and frequency of occurrence has been shown to exhibit marked seasonal relationships (Pope et al., 2001). The caloric value of prey items varies seasonally depending on the physiological and demographic characteristics of the prey, including reproductive status (Vollenweider et al., 2011) and age, size, and sex (Paul et al., 1998). These characteristics of the prey generally are not reported and may serve to contribute variation to the relationship. That ICI is highly influenced by temporal and demographic factors and has low sample size indicates that this diet metric may not provide the best predictive capability for frequency of occurrence. In our resampling approach we recognize the potential sources of variation in the relationship of one diet metric to another – they are fundamentally measuring different aspects of diet. Our synthesis approach (using regression and resampling) necessarily involves the explicit incorporation of the variation associated with the relationship of each diet metric to frequency of occurrence. Variation in some relationships are large and these need to be acknowledged and accounted for in the trophic modeling.

In understanding energy flow in an ecosystem, a challenge remains to understand how the diet metric frequency of occurrence relates to consumption rates and the metabolic demand of organisms. There are few studies that have described energy density of ecological systems in a systematic way (Golley, 1961). Although some studies have reported multi-taxa estimates of the caloric density of marine fishes (Perez, 1994), the caloric value of fishes varies with depth (Hunter et al., 1990) and in the case of Gulf Menhaden, oil content which can be considered a proxy for caloric value varies inter- (Leaf, 2017) and intra-annually (Leaf et al., 2018). Thus, each diet metric informs one aspect of diet and provides an indicator of the presence of given prey item, but much work still needs to be done to scale these values to an ecosystem level understanding of energy flow.

The contrasts in the node and network-specific indices highlight their sensitivity to taxonomic choice and diet metric value. The traditional networks allow a taxonomically unambiguous method to estimate trophic connectivity but the number of taxonomic groups that can be modeled is decreased and information about the relative contribution to diet of some prey items is necessarily omitted. Specificity is desirable when understanding the importance of a single prey species as a predator or prey. In many cases the evaluation of trophic dynamics of ecosystems are concerned with identifying the trophic role of specific functional groups, such as forage fishes (Chiaverano et al., 2018), or in the case of this analysis a specific taxonomic group, Gulf Menhaden. Taxonomic specificity is coincident with the traditional models used in fishery science that require information about single stock dynamics and, in the case of forage fishes, which are thought to play a critical role in the trophic dynamics of ecosystems, the determination of single species "ecosystem-based" target and limit reference points are desirable (Buchheister et al., 2017). The unique position of forage fishes as conduits of energy from lower to higher trophic levels is thought to make them a critical link in the trophic network for many larger predator species that provision commercial and recreational fisheries. The neighborhood analysis of the robust network indicated that Gulf Menhaden are connected, within two edges, to approximately 25% of other taxa, implying that any major changes to their populations would result in increased predation on small and unidentified Scianidae, other small fish species, and decapod and penaeid crustaceans. The observed low link densities indicate that the breadth of Gulf Menhaden predator's diets and that predators of Gulf Menhaden have a multi-taxa portfolio of low trophic level prey items that they exploit. The observed greater weighted connectance in the larger, robust network allows more connections to be realized and contrasts that of the traditional networks.

The coefficient of variation of the distribution of edge weights between predator and prey can be considered an indicator of information quality and quantity and a measure of the inherent variability of prey in predator diets. The coefficient of variation for prey edges was greatest for aggregated unidentified prey from four Phyla, the majority of the groups were identified to Order or Family level. These edges had low precision despite being common in diets. One reason for the low precision is the coarse taxonomic resolution of stomach contents. Species within the same Order or Family are very diverse in their morphology and ecology. In the case of bivalve, gastropod, and cephalopod molluscs, the hard parts are preserved such that even though they are of relatively high frequency they have moderate precision in their mean estimates, relative to other poorly categorized taxa. The error associated with this uncertainty is used in this work to highlight areas that need increased research efforts. Tools such as fatty acid characterization and DNA barcoding can serve to reduce taxonomic ambiguity (Dahl and Patterson, 2014; Sousa et al., 2016).

We found that a narrow feeding range was associated with low precision of edge weights. Predators with few prey taxa reported in the stomach had the lowest precision. It is likely that those studies of fish taxa that reported few prey items (≤ 10) also reported them at a high taxonomic level, compounding the imprecision of the estimate. These predator taxa are comprised of species that are generally not well studied because they are not the targets of recreational and commercial fisheries. However, because they can be numerically dominant and occupy a diverse range of habitats they are likely very important for energy flow in the northern Gulf of Mexico. Better quantification of their trophic niche is desirable because many feed at low trophic levels. The other group with low precision in the description of their diets have a large number of prey items. These taxa are characterized by having a diverse portfolio of identified prey items.

Our analysis of the removal of Clupeidae indicate that predators of this multi-species taxonomic group (that includes the forage fish Gulf Menhaden) have a range of potential prey items that they exploit. We found that 15 of the 95 predator fish species, for which diet information was available, have positive occurrence of Clupeidae and allied taxa in their diets. These fishes have positive records for 170 unique prey taxa reported. The diversity of prey items in a predator's diet portfolio likely allows them flexibility when prey abundances of one group is low and suggests they have a wide niche in terms of diet. Large prey niche is a common feature of fish predators and leads to ecosystem resilience. In a network context, as more pathways between predator and prey are included within a network, redundancy of the network increases. Ecosystems rely on redundant pathways in times of perturbations, such as heavy fishing pressure or other anthropogenic disturbances, to remain functional.

In this work, we present a method for integrating stomach content data from multiple sources and reported in different diet metrics to construct large inclusive trophic network. This method is advantageous because it is a flexible framework that can be used to evaluate trophic characteristics in a diversity of ecosystems. The utility of this approach is in the ability to describe overall structural properties of a trophic network, guide investigation by understanding where information gaps exist, identify key pathways and their impacts on neighboring taxa, and produce results that can be used to parameterize larger ecosystem models such as Atlantis or Ecopath with Ecosim.

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