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ARTICLE

Quantifying the Trophic Importance of Gulf Menhaden within the Northern Gulf of Mexico Ecosystem

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Abstract

The Gulf Menhaden *Brevoortia patronus* is frequently cited as playing a predominant role in the trophic structure and function of the northern Gulf of Mexico (GOM) marine ecosystem, yet much work remains in quantifying its ecological importance. We performed a meta-analysis of diet studies to quantify the trophic role of Gulf Menhaden within this ecosystem. Of the 568 references consulted, 136 identified predator–prey interactions involving Gulf Menhaden, menhaden *Brevoortia* spp., or unidentified clupeid prey items. Overall, 79 species were reported to consume menhaden, and no significant difference was detected between the Atlantic Ocean and the GOM in the mean occurrence of *Brevoortia* spp. in predator stomachs. We employed a probabilistic approach using maximum likelihood estimation to quantify trophic interactions within the northern GOM, with a focus on the trophic role of Gulf Menhaden. The estimated contribution of identifiable menhaden to the diets of all predators generally ranged between 2% and 3%; the largest dietary contribution was identified for Blacktip Sharks *Carcharhinus limbatus* (8%), and lower estimates (<2%) were obtained for oceanic species, including sharks, billfishes, and tunas. When diet compositions were adjusted for unidentified prey by using the proportion of fish species biomass in the ecosystem, five predator groups showed a relatively large dependence on menhaden prey: juvenile King Mackerel *Scomberomorus cavalla*, juvenile Spanish Mackerel *Scomberomorus maculatus*, adult Spanish Mackerel, Red Drum *Sciaenops ocellatus*, and Blacktip Sharks. The quantification of trophic linkages and key predators identified herein will be fundamental to future modeling efforts focused on the northern GOM ecosystem.

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Events such as the Deepwater Horizon oil spill highlight the need for ecosystem-based fisheries management (EBFM) in the northern Gulf of Mexico (GOM), as the oil spill presented a significant threat to multiple organisms, habitats, and ecosystems and required an assessment of its ecosystemwide impacts (NRDA 2012). Furthermore, the federal Magnuson–Stevens Fishery Conservation and Management Reauthorization Act (Magnuson–Stevens Fishery Conservation and Management Act 2007) emphasizes the integration of ecosystem considerations into fisheries management, thus motivating EBFM (Pikitch et al. 2004). Ecosystem models, which are used to aid EBFM, require a comprehensive understanding of trophic interactions for all modeled species and/or functional groups (Walters et al. 1997; Ainsworth et al. 2010). Unfortunately, most GOM ecosystem models suffer from a lack of diet data for certain taxa (Simons et al. 2013), which hinders a full exploration of trophic dynamics within the modeled region. Indeed, the enormous biodiversity of GOM fauna and flora (e.g., Felder and Camp 2009); the lack of long-term monitoring in this region; and the difficulties associated with collecting dietary information from complex habitat types (e.g., mangroves, seagrasses, coral reefs, and artificial reefs), deep depths (some fish species tend to evert their stomachs when brought from depth; e.g., Bradley and Bryan 1975), and protected species (many birds and marine mammals) impede the ability to obtain adequate diet data for all components of the northern GOM ecosystem.

Menhaden *Brevoortia* spp. have been described as "the most important fish in the sea" because of their economic and ecological value in the USA (Franklin 2007). As forage fish, menhaden support fisheries both directly via a targeted reduction fishery and indirectly by providing sustenance for higher-trophic-level predators (e.g., Striped Bass *Morone saxatilis* in Chesapeake Bay; Pikitch et al. 2014). The reduction fishery for Gulf Menhaden *Brevoortia patronus* is the second-largest commercial fishery (by weight) in the USA (Vaughan et al. 2007; NMFS 2010; Geers et al., in press). Between 2000 and 2011, an average of 490,000 metric tons of Gulf Menhaden were removed by the reduction fishery each year, with removals ranging from 380,000 metric tons (in 2010) to 613,000 metric tons (in 2011; Parker and Tyedmers 2012; SEDAR 2013).

As the target of massive industrial landings and as a potentially critical forage species in the GOM ecosystem, the Gulf Menhaden has received particular attention as a subject for EBFM consideration (Pikitch et al. 2014). Several studies have referenced the fundamental role played by Gulf Menhaden—and to a lesser extent, its congeners (Finescale Menhaden *Brevoortia gunteri* and Yellowfin Menhaden *Brevoortia smithi*)—in the ecological structure of the northern GOM (Vaughan et al. 2007; Olsen et al. 2014; Geers et al., in press). An Ecopath with Ecosim (EwE; Pauly et al. 2000) model that was developed with Gulf Menhaden as the focal species highlighted this forage fish's role in structuring the ecosystem but recognized the lack of available diet information, particularly for higher-trophic-level organisms (Geers et al., in press). The Gulf Menhaden is a key forage species for commercially important fishes (e.g., Red Drum *Sciaenops ocellatus*; Scharf and Schlicht 2000), recreationally important fishes (e.g., King Mackerel *Scomberomorus cavalla*; Godcharles and Murphy 1986), seabirds (Fogarty et al. 1981; Withers and Brooks 2004), and marine mammals (Pauly et al. 1998). Menhaden have been identified as a more efficient energy transfer pathway to higher trophic levels than jellyfish, and increased forage fish harvest has led to reduced production of pelagic piscivorous fishes, seabirds, and apex predatory fishes (i.e., sharks; Robinson et al. 2015).

Despite its potential importance in the GOM system, the trophic role of the Gulf Menhaden as both prey and consumer remains unresolved (SEDAR 2013), thereby limiting the ecosystem modeling efforts that are necessary to support EBFM. Recreational anglers, industry, marine resource agencies, and environmental foundations hold a wide diversity of opinions about the trophic connections and importance of Gulf Menhaden in the GOM system and the bycatch impacts of the Gulf Menhaden reduction fishery. An early model of the GOM ecosystem parameterized the diet largely based on expert opinion and focused on evaluating the dynamics of shrimp trawling (Walters et al. 2008). In that model, reductions in shrimp trawling had a counterintuitive result: rather than increasing the populations of all fishes that were taken as bycatch in the shrimp fishery, the decreases in shrimp trawling were predicted to generate increases in saltwater catfish populations, which in turn limited population growth for many of the more desirable species (Walters et al. 2008). These surprising results highlighted the need to better characterize (1) the diets throughout the system and (2) the sensitivity of results to the diet assumptions. More recent ecosystem models continue to have a high level of uncertainty in diet compositions, particularly for higher-trophic-level groups (Chagaris et al. 2015; Geers et al., in press) and juvenile fishes (Masi et al. 2014). In ecosystem modeling for the West Florida Shelf, Chagaris et al. (2015) noted the uncertain diets of offshore predators; the reduced quality of diet information for deepwater reef species due to stomach eversion; the reliance of diet studies on baited gear, which can bias the results of stomach content analysis; and the low sample sizes for diets over the entire region. Other efforts to evaluate menhaden ecosystem dynamics within the GOM have similarly been limited by the lack of data, as only a few potential fish predator groups (namely coastal sharks, offshore sharks, and pelagic piscivores) were explicitly modeled (Robinson et al. 2015). Although current surveys have begun to collect more comprehensive diet data, the historical absence of systematic diet sample collection continues to limit the development of a diet matrix for the Gulf Menhaden and its predators.

Contrary to the potential importance of Gulf Menhaden as forage or in supporting a fishery, many of the GOM

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TABLE 1. Incorporation of menhaden into ecosystem models for the northern Gulf of Mexico (GOM) region by using Ecopath with Ecosim (N_{FG} = total number of functional groups considered; EE = ecotrophic efficiency, or the proportion of menhaden biomass that is used by the ecosystem; dash [−] = no consideration of menhaden; UNR = unreported).

GOM region	N_{FG}	Model objective	References	Menhaden group	EE
Large Marine Ecosystem	40	Synthesis of existing models	Vidal 2000; Vidal and Pauly 2004	Clupeidae	0.73
Continental shelf	15	Pilot model	Browder 1993	−	−
Coastal	63	Shrimp fishery bycatch	Walters et al. 2008	Juvenile (0–12 months)	0.58
				Adult (12 months and older)	0.70
Northern	47	Menhaden fishery impacts on ecosystem	Geers 2012; Geers et al., in press	Juvenile (0–12 months)	0.41
				Adult (12 months and older)	0.43
	54	Energy transfer pathways	Robinson et al. (2015)	Gulf Menhaden	0.89
Breton Sound, Louisiana	39	Salinity on nekton	de Mutsert 2010; de Mutsert et al. 2012	Gulf Menhaden	UNR
Weeks Bay, Alabama	17	Response to bottom-up perturbations	Althauser 2003	Gulf Menhaden	UNR
West Florida Shelf, Florida	59	Seafloor shading	Okey and Mahmoudi 2002; Okey et al. 2004	Sardines, herrings, and scads	1.00
	70	Reef fish complex	Chagaris et al. 2015	Sardines, herrings, and scads	0.50
	81	Red tide impacts	Gray 2014	Sardines, herrings, and scads	0.98
Apalachicola, Florida	21	Fishing on sharks	Carlson 2007	Pelagic forage fishes (including *Brevoortia* spp.)	0.90
Saint Marks, Florida	48	Winter seagrass food web	Christian and Luczkovich 1999; Luczkovich et al. 2002	−	−

Ecopath models that have explicitly included Gulf Menhaden have estimated a relatively low ecotrophic efficiency (EE), which measures the percentage of production that is accounted for in the model (Hollowed et al. 2000; Pauly et al. 2000; Table 1). The EE for the GOM EwE model that was specifically tailored to address Gulf Menhaden (Geers et al., in press) was only 43%, indicating that most of the production was unaccounted for (i.e., nothing was documented to be able to consume 57% of the overall production). This is in direct contrast to adult Atlantic Menhaden *Brevoortia tyrannus* in Chesapeake Bay, which have no lack of identified predators and have an EE of 0.94 (Christensen et al. 2009). It is possible that the low EE could result from a large Gulf Menhaden biomass and relatively depleted predators, but given the Gulf Menhaden's ecological importance it seems improbable that the majority of this species' biomass is being recycled into the detrital pool rather than consumed by predators. Ecotrophic efficiencies in other GOM models have also been relatively low (0.58 for juveniles; Walters et al. 2008) or unreported (Althauser 2003; de Mutsert et al. 2012), thus making it difficult to evaluate the role of menhaden in each model.

Numerous GOM feeding ecology studies have identified and quantified predator–prey interactions involving Gulf Menhaden. However, the majority of those studies were limited in scope temporally (e.g., seasonal), spatially (e.g., local bay), or both. Therefore, it is uncertain whether the findings from those studies are applicable at larger ecosystem scales. The objectives of the present study were to (1) review species-specific predators of Gulf Menhaden as obtained from an extensive literature search for studies conducted in the GOM and surrounding regions (i.e., meta-analysis); (2) estimate and compare the proportional contribution of Gulf Menhaden to each predator's diet based on data from this meta-analysis and by using simple arithmetic means, weighted means, and a probabilistic averaging approach (Ainsworth et al. 2010; Masi et al. 2014); and (3) produce a realistic representation of the Gulf Menhaden's trophic interactions in the GOM. Ideally, this study will be used in future ecosystem modeling efforts, with the goal of alleviating concerns stemming from uncertain and/or implausible trophic dynamics in previous GOM ecosystem models.

METHODS

Data Sources

A comprehensive literature search was undertaken to locate as many quantitative diet studies for GOM predatory species as possible. Here, the term "comprehensive" is used in the sense that all diet studies found for a GOM predator (e.g., Blacktip Shark *Carcharhinus limbatus*) were consulted

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whether they were specific to the GOM or conducted outside of the GOM. Diet studies were obtained through Google Scholar internet searches for individual species, the Gulf of Mexico Species Interactions Database (GoMexSI; Simons et al. 2013), FishBase (www.fishbase.org; Froese and Pauly 2015), an annotated bibliography of fish diet studies conducted in the southeastern USA and Gray's Reef National Marine Sanctuary (Marancik and Hare 2005), and diet studies used to support other ecosystem models (e.g., Geers et al., in press). A study was excluded if it was not easily locatable by using university and government subscriptions to online journals, library visits, and outside library requests. We incorporated a wide variety of references, including biological field reports (e.g., fishes of Cedar Key; Reid 1954), specialized studies (e.g., Gulf Menhaden predation by bycatch species; Knapp 1950), academic theses (e.g., food habits in Lavaca Bay, Texas; Wrast 2008), and peer-reviewed studies (e.g., Bethea et al. 2004). Both GoMexSI and FishBase were used to locate diet studies; primary data sources were used whenever feasible.

Our meta-analysis approach considering diet studies both inside and outside of the GOM maximized the potential trophic linkages between species to ensure that sample sizes were large enough for statistical analyses (see Supplementary Tables S.1 and S.2 available online for a complete list of references that were consulted during meta-analysis). There were no existing diet studies for large oceanic sharks, Bluefin Tuna *Thunnus thynnus*, Swordfish *Xiphias gladius*, tilefishes, or oceanic planktivores within the GOM (see Table 2 for functional group composition). In these instances, diets were obtained solely from outside sources, including the Atlantic, Pacific, and Indian oceans and Mediterranean Sea.

Data

For this work, we defined a diet observation as the combined composition of all prey items found within the stomachs of individuals representing a particular predator species and as reported by a single study for a particular region and/or a particular length-class. For example, seven site-specific diet observations for Bonnetheads within the eastern GOM were obtained from Bethea et al. (2007), who reported diets for neonates (at one location), juveniles (at three locations), and adults (at three locations). Special attention was paid to study location, time period, the life history stage examined, and sample size to ensure that particular samples were not duplicated in our data set (e.g., Saloman and Naughton 1983 and Browder et al. 1990 summarized diet data from the same King Mackerel samples).

Ecosystem models such as EwE (Pauly et al. 2000) require diet composition in terms of biomass (Christensen et al. 2008). Therefore, preference was given to data reported in either percent weight (%W), percent biomass (%B), percent volume (%V), or percent mass (%M) under the assumption that these metrics were equivalent (Ainsworth et al. 2010). Although percent frequency of occurrence (%FO) can be considered the most representative metric of diet composition (Baker et al. 2014), this metric is not directly applicable to mass-balance models that define trophic interactions in units of biomass (e.g., Ecopath; Christensen et al. 2008). For situations in which diet composition was not reported by weight, %FO was converted into relative weight composition via the empirical relationships reported by Stobberup et al. (2009) for fish, benthic invertebrates, crustaceans, echinoderms, mollusks, phytoplankton, plankton, plants, and worms; these relationships were based on 62,102 stomach samples collected throughout the northwest Atlantic, South Africa, Senegal, and the Azores (Stobberup et al. 2009). If only qualitative data were provided, this information was considered when allocating unidentified (UNID) prey to functional groups but was not incorporated into quantitative analyses.

Diet Estimation

Simple arithmetic mean.—The first method used to summarize data across all diet observations was a simple, unweighted arithmetic mean (SM_i) for prey type i,

$$\mathrm{SM}_i = \frac{\sum_{j=1}^{J} \mathrm{DC}_{ij}}{\sum_{j=1}^{J} \sum_{i=1}^{I} \mathrm{DC}_{ij}}, \tag{1}$$

where J is the number of diet observations for a given predator; and DC_{ij} is the diet contribution of prey type i averaged across all stomachs of predator species j (Ainsworth et al. 2010; Masi et al. 2014). This procedure has frequently been used when multiple observations of diet composition are available (Okey and Mahmoudi 2002; Cruz-Escalona et al. 2007; Walters et al. 2008). However, the SM method can produce biased predictions of %W if rare predation events are not taken into account—for example, when a predator consumes an abnormal prey item in a single event, but that prey is large relative to all other prey groups consumed by the predator (Masi et al. 2014). Other sources of uncertainty include the lack of information on the variance and the interdependence of prey types found within the stomach contents (Masi et al. 2014).

Weighted arithmetic mean.—The second method of summarizing the data accounted for differences in the study region (Reg), method reported (Md), and sample size (N) by applying weights to individual observations based on these factors. An arithmetic weighted mean (WM_i) was then calculated by using a weighting factor (w) for each predator j (Chagaris et al. 2015; Geers et al., in press),

$$w_j = \frac{\mathrm{Reg}}{\mathrm{Reg}_{TOTAL}} + \frac{\mathrm{Md}}{\mathrm{Md}_{TOTAL}} + \frac{N}{N_{TOTAL}}. \tag{2}$$

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TABLE 2. Predator functional groups that were investigated during a meta-analysis to quantify Gulf Menhaden trophic interactions within the Gulf of Mexico for use in developing an Ecopath with Ecosim model. Lower-trophic-level functional groups that were considered during the meta-analysis are also described. Number (*N*) refers to the number of diet observations obtained and used in analyses; note that the probabilistic approach to diet estimation was focused on fishes and was only conducted on groups with at least five diet observations.

Functional group	*N*	Included families, genus, or species
		Predator groups
Dolphins	27	Delphinidae
Seabirds	58	Phalacrocoracidae, Pelecanidae, Laridae, Gaviidae, Sternidae, Hydrobatidae, Procellariidae, Pandionidae, and Accipitridae
Sea turtles	13	Cheloniidae and Dermochelyidae
Blacktip Shark	15	Blacktip Shark *Carcharhinus limbatus*
Dusky Shark	15	Dusky Shark *Carcharhinus obscurus*
Sandbar Shark	14	Sandbar Shark *Carcharhinus plumbeus*
Large coastal sharks	50	Sphyrnidae, Odontaspididae, and Carcharhinidae
Large oceanic sharks	32	Lamnidae, Alopiidae, and Blue Shark *Prionace glauca*
Atlantic Sharpnose Shark	19	Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*
Small coastal sharks	33	Carcharhinidae, Triakidae, and Bonnethead *Sphyrna tiburo*
Yellowfin Tuna	22	Yellowfin Tuna *Thunnus albacares*
Bluefin Tuna	18	Bluefin Tuna *Thunnus thynnus*
Tropical tunas	16	Skipjack Tuna *Katsuwonus pelamis*, Bigeye Tuna *Thunnus obesus*, and Blackfin Tuna *Thunnus atlanticus*
Billfishes	38	Istiophoridae
Swordfish	17	Swordfish *Xiphias gladius*
Pelagic coastal piscivores	111	Pomatomidae (Bluefish *Pomatomus saltatrix*), Carangidae, Echeneidae, Belonidae, Lobotidae, bonitos *Sarda* spp., tunnies *Euthynnus* spp., mackerels *Auxis* spp., and Wahoo *Acanthocybium solandri*
Amberjacks	12	Greater Amberjack *Seriola dumerili* and Lesser Amberjack *Seriola fasciata*
Cobia	11	Cobia *Rachycentron canadum*
Juvenile King Mackerel	3	Age-0–3 King Mackerel
Adult King Mackerel	18	Age-3 and older (age-3+) King Mackerel
Juvenile Spanish Mackerel	3	Age-0–3 Spanish Mackerel *Scomberomorus maculatus*
Adult Spanish Mackerel	10	Age-3+ Spanish Mackerel
Skates and rays	42	Rajidae, Gymnuridae, Myliobatidae, Dasyatidae, Rhinobatidae, and Nurse Shark *Ginglymostoma cirratum*
Age-0 Gag	7	Age-0–1 Gags *Mycteroperca microlepis*
Juvenile Gag	10	Age-1–3 Gags
Adult Gag	9	Age-3+ Gags
Age-0 Red Grouper	5	Age-0–1 Red Grouper *Epinephelus morio*
Juvenile Red Grouper	7	Age-1–3 Red Grouper
Adult Red Grouper	5	Age-3+ Red Grouper
Age-0 Black Grouper	5	Age-0–1 Black Grouper *Mycteroperca bonaci*
Juvenile Black Grouper	3	Age-1–3 Black Grouper
Adult Black Grouper	2	Age-3+ Black Grouper
Age-0 Yellowedge Grouper	0	Age-0–1 Yellowedge Grouper *Hyporthodus flavolimbatus*
Juvenile Yellowedge Grouper	0	Age-1–3 Yellowedge Grouper
Adult Yellowedge Grouper	1	Age-3+ Yellowedge Grouper
Atlantic Goliath Grouper	8	Atlantic Goliath Grouper *Epinephelus itajara*
Other deepwater groupers	7	Snowy Grouper *Hyporthodus niveatus*, Warsaw Grouper *Hyporthodus nigritus*, Speckled Hind *Epinephelus drummondhayi*, and Misty Grouper *Hyporthodus mystacinus*

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TABLE 2. Continued.

Functional group	*N*	Included families, genus, or species
Other shallow-water groupers	23	Nassau Grouper *Epinephelus striatus*, Yellowfin Grouper *Mycteroperca venenosa*, Yellowmouth Grouper *Mycteroperca interstitialis*, Rock Hind *Epinephelus adscensionis*, Red Hind *Epinephelus guttatus*, and Scamp *Mycteroperca phenax*
Juvenile Red Snapper	38	Age-0–6 Red Snapper *Lutjanus campechanus*
Adult Red Snapper	20	Age-6+ Red Snapper
Vermilion Snapper	13	Vermilion Snapper *Rhomboplites aurorubens*
Mutton Snapper	6	Mutton Snapper *Lutjanus analis*
Other snappers	41	Lutjanidae
Coastal piscivores	40	Megalopidae, Elopidae, Centropomidae, and Albulidae
Seatrout	59	Seatrout *Cynoscion* spp.
Oceanic piscivores	41	Trichiuridae, Gempylidae, Bramidae, and Offshore Hake *Merluccius albidus*
Benthic piscivores	77	Paralichthyidae, Uranoscopidae, Synodontidae, Ophichthidae, and Squatinidae
Reef- or rubble-associated piscivores	37	Holocentridae, Sphyraenidae, Muraenidae, Congridae, and soapfishes *Rypticus* spp.
Reef-associated invertebrate feeders	148	Serranidae, Labridae, Scorpaenidae, Chaetodontidae, Priacanthidae, Haemulidae, Sparidae, and Yellowtail Snapper *Ocyurus chrysurus*
Demersal coastal invertebrate feeders	239	Sciaenidae, Ariidae, Gerreidae, pompanos *Trachinotus* spp., Atlantic Bumper *Chloroscombrus chrysurus*, Leatherjack *Oligoplites saurus*, Red Porgy *Pagrus pagrus*, Tomtate *Haemulon aurolineatum*, and Pigfish *Orthopristis chrysoptera*
Red Drum	23	Red Drum *Sciaenops ocellatus*
Benthic coastal invertebrate feeders	82	Pleuronectiformes, Triglidae, Polynemidae, Gobiidae, and Ophidiidae
Tilefishes	8	Malacanthidae
Gray Triggerfish	14	Gray Triggerfish *Balistes capriscus*
Coastal omnivores	90	Tetraodontiformes, Ephippidae, and Pinfish *Lagodon rhomboides*
Reef omnivores	57	Pomacanthidae, Acanthuridae, Pomacentridae, and Scaridae
Surface pelagics	20	Exocoetidae and Hemiramphidae
Large oceanic planktivores	6	Manta rays *Manta* spp., Basking Shark *Cetorhinus maximus*, Whale Shark *Rhincodon typus*, and Ocean Sunfish *Mola mola*
Oceanic planktivores	0	Argentinidae and Nomeidae
Sardine–herring–scad complex	49	Clupeidae and scads *Decapterus* spp.
Menhaden	8	Menhaden *Brevoortia* spp.
Anchovies–silversides–killifishes	62	Engraulidae, Atherinidae, and Fundulidae
Mullets	29	Mugilidae
Butterfishes	10	Stromateidae
		Lower-trophic-level groups
Cephalopods		Cephalopoda
Shrimp		Penaeidae and Caridea
Crabs		Portunidae
Sessile epifauna		Porifera, Anthozoa, Tunicata, Bryozoa, Hydrozoa, Crinoidea, and Mytilidae
Mobile epifauna		Malacostraca, Ostracoda, Echinoderma, Gastropoda, and Pectinidae
Zooplankton		Copepoda, Euphausiacea, Scyphozoa, and planktonic eggs or larvae
Infauna		Annelida, Nematoda, Bivalvia, Thalassinidea, and Hippidae
Algae		Rhodophyta, Chlorophyta, Phaeophyta, Cyanophyta, Xanthophyta, and Cyanobacteria
Phytoplankton		Bacillariophyceae, Dinoflagellata, and Protozoa
Seagrass		Marine angiosperms
Detritus		Calcareous debris, mud, organic matter, fishery discards, and detritus

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For region, all studies conducted within the GOM were given the highest priority (weight = 4), and weights for other regions were based on their proximity to the GOM and similarity in habitat and diversity (Caribbean Sea: weight = 3; Atlantic Ocean: weight = 2; all other regions: weight = 1). For method, the highest weight was given to weight-based metrics (weight = 3), whereas all other metrics were downweighted (unreported: weight = 2, under the assumption that this was weight; %*W* converted from %FO: weight = 1; %*W* converted from percent number [%*N*]: weight = 0.5; %*W* converted from percent index of relative importance [%IRI]: weight = 0.5). Lastly, individual observations were weighted by sample size (i.e., the total number of stomachs with food contents) to minimize bias resulting from differences in sampling intensity and, as a result, downweighting observations that may have been unduly affected by a single, rare predation event. When sample size was not reported, a sample size of 1 was used.

*Statistical combination.—*A bootstrap approach was used to combine observations in a manner that would reduce bias associated with any study-specific sampling effects (Ainsworth et al. 2010; Figure 1). Briefly, this probabilistic method entailed (1) drawing 10 random diet observations with replacement for each predator from all possible regions and/or studies; (2) estimating the weighted mean contribution of each prey type to each predator's diet (equation 2); (3) performing 10,000 repetitions of steps 1 and 2 to generate probability distributions for the weighted, averaged diet observations; and (4) fitting a Dirichlet distribution to the bootstrapped diet composition data (for all prey types consumed by each predator). The end product was a marginal distribution of prey-specific %*W* predictions from which maximum likelihood estimates (MLEs) and confidence intervals were

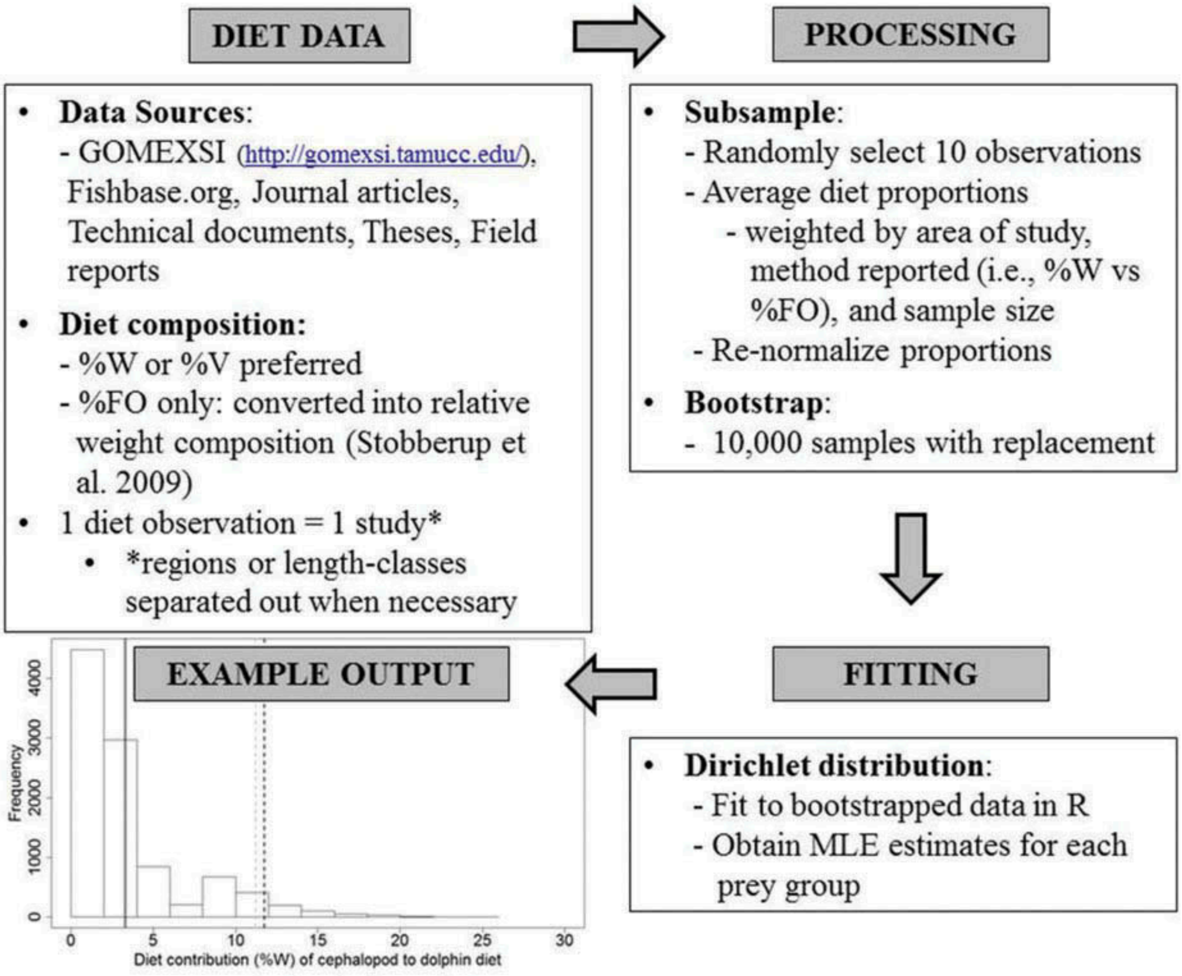

FIGURE 1. Bootstrap procedure followed for meta-analysis to quantify trophic interactions within the northern Gulf of Mexico and to identify the importance of Gulf Menhaden in predator diets (%*W* = percent weight; %*V* = percent volume; %FO = percent frequency of occurrence). Results from the maximum likelihood estimate (MLE) based on a probabilistic bootstrap approach (solid black line) are compared to the simple mean (dashed black line) and weighted mean (dashed gray line). The probabilistic approach was adapted from Ainsworth et al. (2010) and Masi et al. (2014).

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obtained, representing the likely contribution of particular prey groups to the predator's diet. If at least 10 random observations were not available, as was typically the case for juvenile stages, five observations were used in the maximum likelihood estimation approach. Although this sample size is smaller than those previously used in MLEs (Ainsworth et al. 2010; Masi et al. 2014), it was only pursued when necessary (see Table 2) and was calculated simultaneously with the SM and WM methods, thus representing the best available data in the absence of sufficient diet observations.

Comparison of Methods

The diet proportions estimated with the SM and WM methods were compared to the MLEs by using Student's paired *t*-test under the null hypothesis that the two samples originated from the same population (Ainsworth et al. 2010; Masi et al. 2014). The relative absolute error (RAE) was calculated for each predator–prey combination and each method (WM, SM, and MLE) to quantitatively compare the proportion of prey type *i* in the diet of predator *j* from each method ($\mathrm{DC}_{ij,Method}$) against the corresponding bootstrapped diet proportion ($\mathrm{DC}_{ij,Bootstrap}$),

$$\mathrm{RAE}_{ij,Method} = \frac{\left|\mathrm{mean}\left(\mathrm{DC}_{ij,Method}\right) - \mathrm{mean}\left(\mathrm{DC}_{ij,Bootstrap}\right)\right|}{\mathrm{mean}\left(\mathrm{DC}_{ij,Bootstrap}\right)}. \tag{3}$$

Larger RAE values indicate greater divergence in diet proportions between the method mean and the bootstrapped mean, whereas smaller RAE values suggest that diet proportions are similar between the method and bootstrapped data. Inherently, we assumed that the bootstrapped diet data reflected the "known truth"—but only for the purposes of comparing diet proportions between methods.

Assumptions

No difference in consumption between the Atlantic Ocean and the GOM.—Quantification of diets for some migratory functional groups (e.g., billfishes and tunas, among others) required the inclusion of diet studies from regions beyond the GOM due to the lack of GOM-specific diet information based on our comprehensive literature search. Although these studies sampled the diets of predators outside of the GOM, these highly migratory predators also exist within the GOM and potentially overlap with Gulf Menhaden. As a result, our meta-analysis was conducted with the assumption that diet observations from other ecosystems were representative of predator behavior within the GOM. For example, if a predator consumed a menhaden in the Atlantic, this was considered analogous to the consumption of a menhaden in the GOM. We recognize that consumption of a menhaden in one ecosystem may not translate directly into consumption of a menhaden in a system with a different dominant forage species. However, the assumption of diet similarity among regions was necessary and proved important, as many records of menhaden consumption in the literature involved Atlantic Menhaden rather than Gulf Menhaden. Given differences in biotic diversity (number of species) between the Atlantic ecosystem and the GOM ecosystem (Fautin et al. 2010) and potential differences in the trophic role of Atlantic Menhaden and Gulf Menhaden, we used a nonparametric Mann–Whitney *U*-test to assess the validity of our assumption that diets were similar between regions. Specifically, tested were differences in the relative contribution of *Brevoortia* spp. to the diets of predators from two broad regions (the Atlantic and the GOM) under the null hypothesis that the two samples of observations originated from an identical distribution (Quinn and Keough 2002). Differences in *Brevoortia* spp. consumption between the Atlantic and the GOM were also explored within functional groups when sample sizes allowed ($N \geq 5$ for each region).

To test whether diet metrics for *Brevoortia* spp. differed among multiple subregions within the GOM (e.g., Louisiana, Texas, and Florida) and among multiple general predator groups (e.g., sharks, dolphins, and tunas), a nonparametric Kruskal–Wallis one-way ANOVA was employed under the null hypothesis that two or more samples originated from the same distribution (Sokal and Rohlf 1995). Nonparametric tests were performed due to the prevalence of nonnormal data (i.e., Dirichlet proportions) and unsuccessful attempts to transform those data to meet normality assumptions. All analyses were conducted in R software (R Development Core Team 2013), with α set at 0.05.

Allocation of unidentified prey items.—The prevalence of UNID prey groups (e.g., UNID fish, crustaceans, animal remains, etc.) found throughout this meta-analysis required an assumption that the relative biomass of all prey groups corresponding to UNID classifications could be used to allocate UNID prey items to identified groups. Relative biomass estimates were obtained from a balanced Ecopath model for the northern GOM that is currently under development at the National Marine Fisheries Service's Southeast Fisheries Science Center, with initial biomass estimates derived from GOM stock assessment reports or fishery-independent surveys (where available) or from other Ecopath studies focused on the GOM (Walters et al. 2008; Geers et al., in press) or the West Florida Shelf (Okey and Mahmoudi 2002; Gray 2014; Chagaris et al. 2015). In Table S.3, relative biomass estimates from our balanced Ecopath model are presented along with other estimates from published ecosystem modeling studies throughout the GOM region. As an example of this procedure, consider the inclusion of a single diet study that has an UNID clupeid prey item. "Clupeidae" can refer to herrings, shads, Alewives *Alosa pseudoharengus*, sprats *Sprattus* spp., sardines, pilchards, or menhaden (Helfman et al. 2009). This

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UNID grouping is retained throughout the estimation process such that an MLE of %*W* for UNID Clupeidae is provided; the %*W* prediction is then partitioned between the two clupeid prey groups used in the analysis (sardines–herrings–scads and menhaden) based on their relative biomasses within the GOM (Table S.3). Inherent in this approach were the assumptions that (1) the prey groups identified by the meta-analysis constituted potential prey items and (2) the proportional biomass contribution was homogeneous throughout the GOM. Potential prey items were identified from known trophic interactions (e.g., already identified as prey based on the meta-analysis) and qualitative information.

RESULTS

Data Sources

In total, 568 references were used to quantify trophic interactions in the GOM. The references provided 1,906 diet observations for various life history stages and various regions (both within and outside of the GOM). As might be expected, the greatest number of diet observations was found for broad functional groups (e.g., 239 observations for demersal coastal invertebrate feeders, which include sea catfishes [Ariidae], drums and croakers [Sciaenidae], and mojarras [Gerreidae]), whereas the lowest number of diet observations was available for grouper species (e.g., zero observations for both age-0 and juvenile Yellowedge Grouper; Table 2).

Data

Observations of menhaden predation.—Of the 568 references examined, 136 referenced some form of predation on menhaden (i.e., consumption of Gulf Menhaden, *Brevoortia* spp., or UNID clupeids); the number of such studies from the GOM (73 studies) and the number from the Atlantic (69 studies) were relatively equal (Table 3). This set of references and the studies therein provided a total of 296 diet observations involving predation on menhaden, with roughly half occurring in the GOM (Table 3). Within the GOM, the majority of menhaden predation events occurred in Florida (61 events) and Texas (41 events), from which similar numbers of studies were examined (Texas: 19 studies; Florida: 22 studies; Table 3). Within the Atlantic, the majority of predation events occurred in the southeastern U.S. region (35 events) and the Mid-Atlantic region (29 events), for which the numbers of studies examined were also similar (southeastern USA: 22 studies; Mid-Atlantic: 17 studies; Table 3).

The majority of studies that identified menhaden as potential prey reported only one diet metric (38%); 35% of studies reported three metrics (%FO, %*W*, and %*N*), 25% reported two metrics, and 3% reported no metric (i.e., qualitative diet data). For these studies that identified menhaden, %FO was the most commonly reported metric (77% of the studies), followed by %*W* (56%) and %*N* (49%). The most frequently reported prey types in these studies were UNID clupeids (37.8% of the studies) followed by *Brevoortia* spp. (29.1%), which included UNID menhaden and less common species, such as the Finescale Menhaden. Nearly 20% of menhaden prey items were specifically reported as Gulf Menhaden, whereas Atlantic Menhaden constituted the least reported menhaden prey item (13.2%).

Potential predators of menhaden (i.e., based upon proximity and overlap in the GOM) clearly consumed clupeid prey (in most cases recorded as UNID clupeids) in other regions that were not inhabited by menhaden, including the Pacific Ocean (7 predator species; billfishes, seabirds, Yellowfin Tuna, skates and rays, and large coastal sharks), the Indian Ocean (4 predator species; seabirds and oceanic piscivores), and the Great Lakes (1 predator species; a seabird). We assumed that these observations reflected the possibility of a menhaden predation event by that predator in the GOM ecosystem; therefore, the observations contributed to our predictions of Gulf Menhaden consumption.

Menhaden predators.—In total, 79 species were reported to consume menhaden (either *Brevoortia* spp. or UNID clupeids; Table 4; see Table S.4 for references). Among those predator species, predation events specifically involving Gulf Menhaden were documented for common bottlenose dolphins, double-crested cormorants, neotropic cormorants, multiple shark genera and species, pelagic piscivores (including the Little Tunny, King Mackerel, Spanish Mackerel, Crevalle Jack, Bluefish, and Cobia), and coastal piscivores (including the Sand Seatrout, Spotted Seatrout, and Ladyfish; Table 4).

Four grouper species, two tilefish species, and three snapper species were also identified as potential predators of menhaden. Although Gulf Menhaden were identified in the diets of 20–30-cm Gags, most of those predation events consisted of UNID clupeids (Table 4) or qualitative reports of clupeid and/or menhaden predation. Invertebrate feeders, including two sea catfish species (Gafftopsail Catfish and Hardhead Catfish), Red Drum, and Silver Perch, also consumed Gulf Menhaden (Table 4). One instance of Gulf Menhaden predation by a Gulf Killifish in a brackish Mississippi marsh was reported, although no details were provided (e.g., prey length or stage; Rozas and LaSalle 1990).

Differences in the mean contribution of Gulf Menhaden to the diets of different predator species were detected for %*W* (χ^2 = 13.80, df = 6, *P* = 0.031) but not for %FO (χ^2 = 13.25, df = 7, *P* = 0.066) or %*N* (χ^2 = 7.24, df = 5, *P* = 0.203). The dietary contribution of Gulf Menhaden was relatively high for coastal sharks and coastal piscivores (Figure 2). Low sample sizes for many broad predator groups likely increased the probability of type II errors in this analysis.

Assumptions

Regional differences in diet contribution.—Using diet metrics reported by each study and based on %FO, we found

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TABLE 3. Summary of diet observations (by region) that documented predation on Gulf Menhaden, menhaden *Brevoortia* spp., or unidentified Clupeidae and that were used in the meta-analysis. Note that diet observations can reflect different life history stages, different regions, or both. The total number of references that cited potential menhaden prey was 136 of 568 references. "Studies" refers to the number of studies per region (because some studies covered multiple regions, there are more studies [n = 156] than references [n = 136]). References for areas outside of the Gulf of Mexico (GOM) were necessary for many predator groups, including sharks, billfishes, tunas, and seabirds.

Region	Number of studies	Number of diet observations	Range of years
GOM			
Southeastern USA and GOM	7	10	1983–1990
GOM (unspecified)	5	14	1977–2008
Texas	19	41	1945–2008
Louisiana	14	24	1958–2013
Mississippi	4	7	1975–2003
Northwestern Florida	7	32	1985–2011
Western Florida	15	29	1965–2009
Yucatan	2	2	2009–2013
GOM subtotal	73	159	
Caribbean Sea			
West Indies	1	2	1958–1961
East Caribbean (Barbados)	1	1	1981–1982
Caribbean subtotal	2	3	
Atlantic Ocean			
Atlantic (unspecified)	3	9	1990–1993
Northeastern USA	10	16	1978–2010
Mid-Atlantic USA	17	29	1975–2009
Southeastern USA	22	35	1959–2012
Northeast Atlantic	4	5	1971–1972, 1990–2005
Southeast Atlantic	2	7	1978–2006
Eastern tropical Atlantic	2	2	1965–1968
Mediterranean Sea	7	12	1989–1994, 1998–2000, 2003–2006
Southwest Atlantic (Brazil and Argentina)	2	2	2004–2007
Atlantic subtotal	69	117	
Pacific Ocean			
Eastern tropical Pacific	4	5	1987–1989, 1991
Northwest Pacific	2	3	1999–2001
Hawaii	1	1	1980–1986
Pacific subtotal	7	9	
Indian Ocean			
Northern Australia	1	1	1980–1987
Southwestern Australia	1	1	2002–2006
Western Indian Ocean	1	2	2005–2007
Northern Indian Ocean	1	3	1976
Indian Ocean subtotal	4	7	
Great Lakes			
Great Lakes	1	1	1994
Great Lakes subtotal	1	1	
Grand total	156	296	

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TABLE 4. Summary of menhaden predation by each predator group and species, as reported in the diet literature. Prey types include Atlantic Menhaden, Gulf Menhaden, menhaden *Brevoortia* spp. (Finescale Menhaden, Yellowfin Menhaden, Brazilian Menhaden *Brevoortia aurea*, and Argentine Menhaden *Brevoortia pectinata*), and clupeids (unidentified fish belonging to Clupeidae, Clupeiformes, or Clupeoidea). Asterisks indicate predators for which Gulf of Mexico diet data were lacking, and therefore diet data were derived from other regions (regions are described in Table S.4).

	Reported prey type			
Predator group or species	Atlantic Menhaden	Gulf Menhaden	*Brevoortia* spp.	Clupeids
Dolphins				
Common bottlenose dolphin *Tursiops truncatus*	X	X	X	X
Seabirds				
Osprey *Pandion haliaetus**	X		X	X
Bald eagle *Haliaeetus leucocephalus**				X
Black skimmer *Rynchops niger**			X	
Brown pelican *Pelecanus occidentalis*			X	
Magnificent frigatebird *Fregata magnificens**				X
Double-crested cormorant *Phalacrocorax auritus*		X		X
Neotropic cormorant *Phalacrocorax olivaceous*		X		
Common tern *Sterna hirundo**			X	
Royal tern *Sterna maxima**				X
Caspian tern *Hydroprogne caspia**				X
Audouin’s gull *Larus audouinii**				X
European herring gull *Larus argentatus**				X
Lesser black-backed gull *Larus fuscus**				X
Audubon’s shearwater *Puffinus lherminieri**				X
Wedge-tailed shearwater *Puffinus pacificus**				X
Sea turtles				
Loggerhead sea turtle *Caretta caretta**	X			
Sharks				
Blacktip Shark	X	X	X	X
Sandbar Shark	X		X	X
Dusky Shark			X	X
Bull Shark *Carcharhinus leucas*		X	X	
Spinner Shark *Carcharhinus brevipinna*		X	X	X
Silky Shark *Carcharhinus falciformis*	X		X	
Requiem shark *Carcharhinus* sp.			X	
Sand Tiger *Carcharias taurus*	X		X	
Scalloped Hammerhead *Sphyrna lewini*		X	X	X
Great Hammerhead *Sphyrna mokarran*			X	
Shortfin Mako *Isurus oxyrinchus**	X			X
Blue Shark*				X
Atlantic Sharpnose Shark		X	X	X
Blacknose Shark *Carcharhinus acronotus**			X	
Finetooth Shark *Carcharhinus isodon*	X	X	X	
Smooth Dogfish *Mustelus canis**	X			X
Dogfishes (Squalidae)			X	
Australian Angel Shark *Squatina australis**				X
Tunas				
Yellowfin Tuna	X			X
Bluefin Tuna*	X			X
Blackfin Tuna				X
Skipjack Tuna*				X

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TABLE 4. Continued.

Predator group or species	Reported prey type			
	Atlantic Menhaden	Gulf Menhaden	*Brevoortia* spp.	Clupeids
Little Tunny *Euthynnus alletteratus*		X	X	X
Billfishes				
Sailfish *Istiophorus platypterus*			X	X
Blue Marlin *Makaira nigricans**				X
Striped Marlin *Kajikia audax**				X
White Marlin *Kajikia albida**				X
Swordfish*	X			
Pelagic piscivores				
King Mackerel	X	X	X	X
Spanish Mackerel	X	X	X	X
Crevalle Jack *Caranx hippos*	X	X	X	X
Greater Amberjack*				X
Almaco Jack *Seriola rivoliana**				X
Bluefish	X	X	X	X
Cobia	X	X	X	X
Dolphinfish *Coryphaena hippurus*				X
Pompano Dolphinfish *Coryphaena equiselis**				X
Coastal piscivores				
Sand Seatrout *Cynoscion arenarius*		X		X
Spotted Seatrout *Cynoscion nebulosus*		X	X	
Ladyfish *Elops saurus*		X		
Common Snook *Centropomus undecimalis*			X	X
Tarpon *Megalops atlanticus*			X	
Oceanic piscivores				
Atlantic Cutlassfish *Trichiurus lepturus**				X
Offshore Hake				X
Benthic piscivores				
Southern Flounder *Paralichthys lethostigma*			X	
Inshore Lizardfish *Synodus foetens*				X
Reef piscivores				
Great Barracuda *Sphyraena barracuda**				X
Groupers				
Gag		X		X
Atlantic Goliath Grouper				X
Red Grouper				X
Snowy Grouper*				X
Tilefishes				
Tilefish *Lopholatilus chamaeleonticeps**	X			
Blueline Tilefish *Caulolatilus microps**				X
Snappers				
Cubera Snapper *Lutjanus cyanopterus**				X
Yellowtail Snapper				X
Red Snapper				X
Invertebrate feeders				

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TABLE 4. Continued.

Predator group or species	Reported prey type: Atlantic Menhaden	Gulf Menhaden	*Brevoortia* spp.	Clupeids
Gafftopsail Catfish *Bagre marinus*		X	X	X
Hardhead Catfish *Ariopsis felis*		X	X	
Kingfish *Menticirrhus* spp.			X	
Red Drum		X	X	
Silver Perch *Bairdiella chrysoura*		X		
Forage fish				
Gulf Killifish *Fundulus grandis*		X		

that the contribution of *Brevoortia* spp. to predator diets (all predators combined) did not significantly differ between the GOM and the Atlantic (Mann–Whitney U-test: U = 2,260.5, P = 0.269), suggesting that menhaden occurrence in predator stomachs did not differ regionally. Menhaden %FO averaged 11 ± 19% (mean ± SE) in the Atlantic and 17 ± 25% in the GOM. However, the mean %W of *Brevoortia* spp. in the combined predator diets was significantly different between the two regions (U = 1,175.5, P = 0.010) and was nearly two times greater in the GOM (mean ± SE = 22 ± 28%) than in the Atlantic (14 ± 25%; Figure 3). The largest significant difference between regions was observed for mean %N (U = 386.5, P = 0.006), which was approximately four times greater in the GOM (mean ± SE = 24 ± 30%) than in the Atlantic (6 ± 12%; Figure 3). For individual functional groups with sufficient sample sizes ($N \geq 5$) for each region (i.e., coastal sharks, dolphins, mackerels, and pelagic fishes), no significant regional trends in %FO, %W, or %N were identified (Figure 3).

Within the GOM, among-state differences in the mean contribution of Gulf Menhaden to predator diets were not detected for any diet metric examined (%FO: χ^2 = 4.91, df = 4, P = 0.296; %W: χ^2 = 4.58, df = 3, P = 0.206; %N: χ^2 = 5.64, df = 3, P = 0.130; Supplementary Figure S.1).

Diet Estimation

Application to adult Red Snapper.—Diet composition estimates based on the SM, WM, and MLE frequently led to different results. Figure 4 illustrates this with the example of adult Red Snapper, for which the SM and WM methods both tended to generate lower diet proportions and higher RAE estimates than the MLE values and bootstrapped data (Figure 4). Exceptions were noted for groups such as crabs, UNID fish, mobile epifauna, shrimp, and zooplankton (Figure 4), with the SM and WM techniques estimating higher values of prey importance.

For adult Red Snapper, the top-five prey items based on the SM and WM methods were as follows: UNID fish (SM = 39.7%; WM = 39.1%); crabs (SM = 11.2%; WM = 10.9%); sessile epifauna (SM = 6.4%; WM = 6.1%); mobile epifauna (SM = 5.2%; WM = 5.1%); and zooplankton (SM = 4.8%; WM = 4.7%) or detritus (SM = 4.5%; WM = 4.9%) depending upon the method. Based on the probabilistic approach, the top-five prey groups identified for adult Red Snapper were UNID prey items (9.3%), UNID fishes (8.5%), sessile epifauna (4.7%), detritus (4.2%), and cephalopods (3.9%). Note that the groups constituting the top five differed among the three methods. Crabs were not included in the top five for the probabilistic approach because the percentages estimated by the SM and WM methods were higher than that from the bootstrapped data (Figure 4).

Final estimates of diet composition for adult Red Snapper were obtained by partitioning UNID prey items into clupeids, fishes, flatfishes, groupers, invertebrates, crustaceans, and Reptantia (i.e., walking crustaceans). After UNID prey items were allocated to potential prey groups by weighting on the basis of their relative biomasses (Table S.3), the top-five prey groups predicted by the probabilistic approach were mobile epifauna (7.9%), benthic coastal invertebrate feeders (7.5%), reef-associated invertebrate feeders (6.3%), sardines–herrings–scads (6.2%; *does not* include menhaden), and sessile epifauna (6.0%).

General trends.—The means from all three approaches tended to be quite similar when we considered all predator–prey interactions across all predator species included in the meta-analysis (paired t-test with MLE values, SM: P = 0.992; WM: P = 0.989). The variance, however, was significantly greater for the probabilistic approach (F-test, SM and WM: P < 0.001).

Contribution of menhaden.—The majority of predators displayed MLE values that differed from SM and WM values, and RAE estimates were generally lower for the maximum likelihood estimation method than for the SM and WM methods (Figure 5). Instances of poor MLE fits for menhaden data were noted for groups such as Yellowfin Tuna, billfishes, and Red Drum; however, MLE fits for other prey groups to the bootstrapped data were adequate. Estimated contributions of menhaden to the diets of seabirds, coastal

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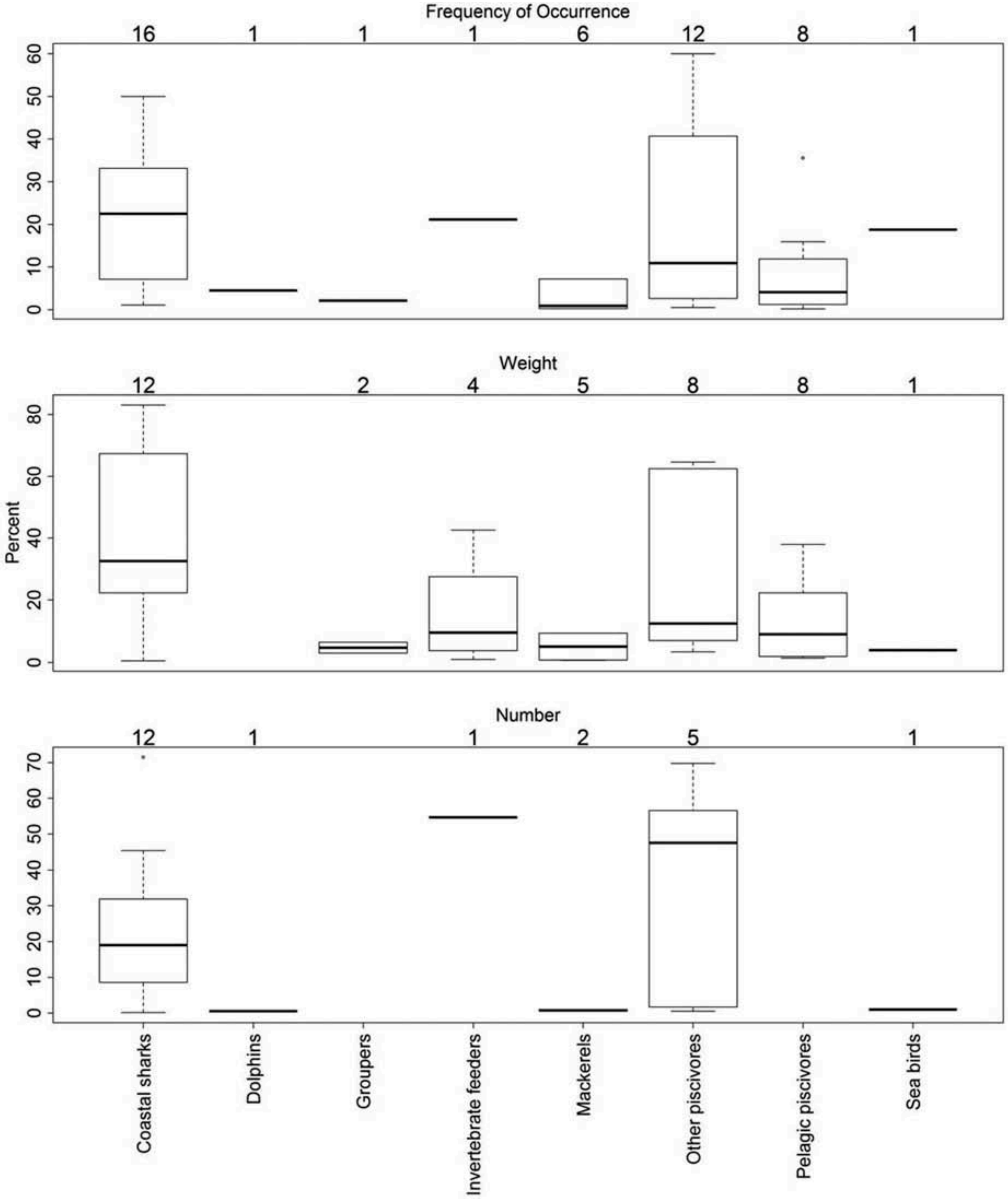

FIGURE 2. Percent contribution (percent frequency of occurrence, percent weight, or percent number) of Gulf Menhaden to predator diets. The numbers above each panel reflect the number of diet observations (i.e., a predation event by a given life history stage or species in a given region). The thick horizontal line within each box represents the median, the ends of the box represent the interquartile range (25th and 75th percentiles), and the ends of the whiskers represent either the maximum value or 1.5 times the interquartile range.

sharks, and coastal piscivores were higher from the SM and WM methods than from the maximum likelihood estimation approach. In contrast, for oceanic sharks, Yellowfin Tuna, Gags, benthic piscivores, Cobias, demersal coastal invertebrate feeders, and anchovies–silversides–killifishes, the menhaden contributions based on the SM and WM methods were lower than the MLEs. According to MLE values and before allocation of UNID prey to functional groups, the contribution of menhaden to the diet generally ranged between 2% and 3% for most predators (Figure 5).

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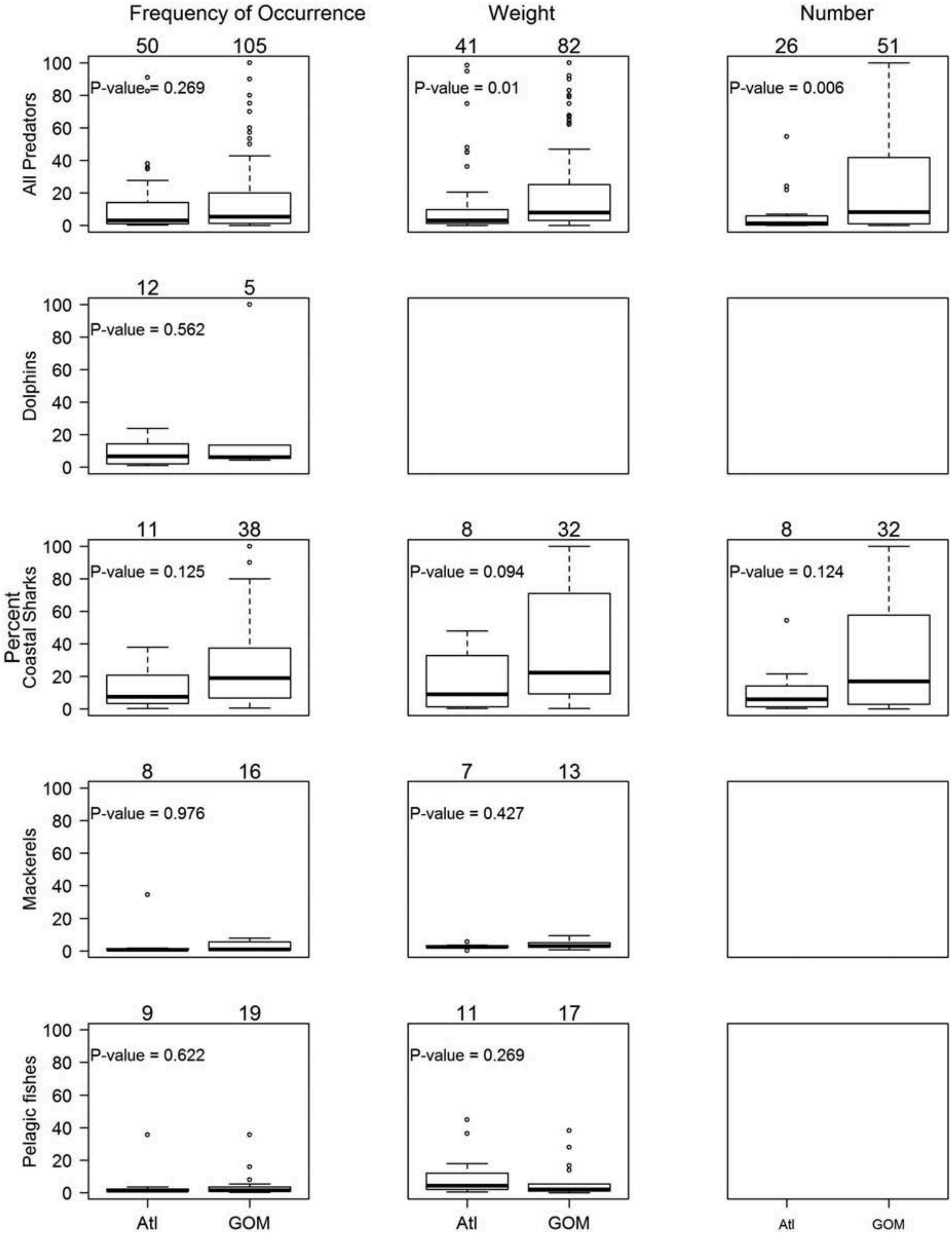

FIGURE 3. Percent contribution (percent frequency of occurrence, percent weight, or percent number) of menhaden *Brevoortia* spp. to predator diets in the Atlantic (Atl) and Gulf of Mexico (GOM) regions. Predator groups include all predators combined, dolphins, coastal sharks, mackerels, and pelagic fishes (includes the Almaco Jack, Bluefish, Cobia, Crevalle Jack, Dolphinfish, Greater Amberjack, Little Tunny, and Pompano Dolphinfish). Analyses were restricted to predator groups with at least five diet observations per region. Empty boxes denote a lack of data (i.e., < 5 diet observations for either region). See Figure 2 for definition of box plot elements.

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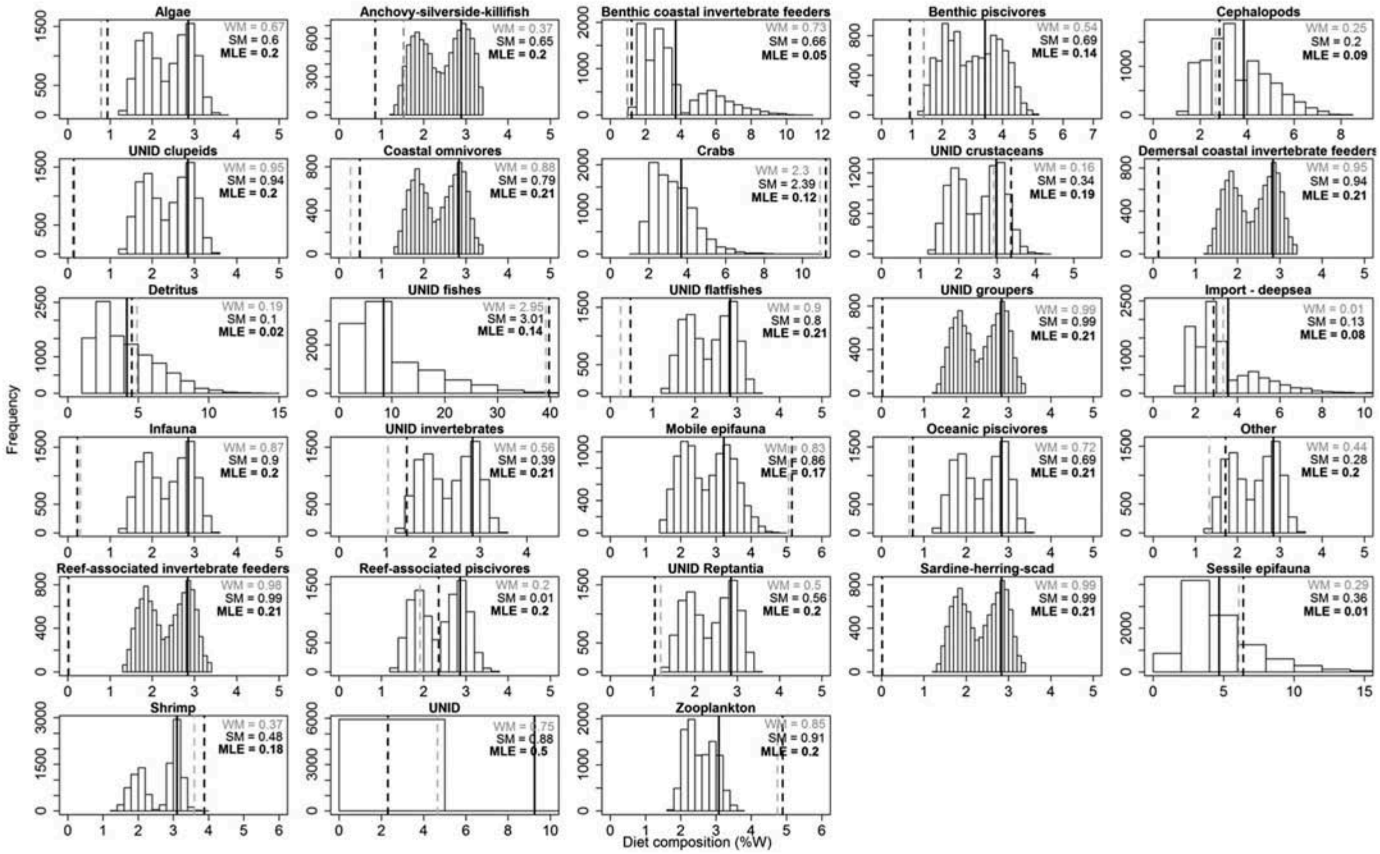

FIGURE 4. Example output of diet composition (percent weight [%*W*]) for adult Red Snapper, as derived from a meta-analysis assessing trophic interactions within the northern Gulf of Mexico. Histograms reflect bootstrapped samples obtained from randomly selecting 10 diet observations. Methods of estimation include the simple mean (SM; dashed black line), weighted mean (WM; dashed gray line), and maximum likelihood estimate (MLE; solid black line). Relative absolute errors are calculated for each method from the bootstrapped diet data. Descriptions of the prey groupings are provided in Table 2 (UNID = unidentified prey).

Lower estimates were obtained for oceanic species, including sharks (1.1%), tunas (1.0–1.8%), and billfishes (1.7%), whereas the highest dietary contribution of menhaden was predicted for Blacktip Sharks (8%).

After UNID clupeid prey were allocated to each predator's diet based on relative biomass (Table S.3), the contribution of menhaden to the total diet ranged from 0.3% for skates and rays to 11.8% for juvenile King Mackerel (Figure 6). Menhaden contributions to the diet were relatively large for juvenile King Mackerel (11.8%), juvenile and adult Spanish Mackerel (11.0% and 9.8%, respectively), Red Drum (9.1%), and Blacktip Sharks (7.2%). However, it is important to note that due to low sample sizes ($N < 5$), estimates for the juvenile mackerel groups were based on the WM method rather than the probabilistic approach.

DISCUSSION

A key challenge for EBFM is the quantification of trophic linkages. For the GOM in particular, there have been systematic difficulties in accounting for predation upon the economically and ecologically important Gulf Menhaden. Ecosystem models developed for the GOM have received criticism for diet composition matrices that appeared to be implausible (e.g., high mortality of Gulf Menhaden due to predation by killifishes; Geers et al., in press) or incomplete (e.g., lacking higher-trophic-level predator–prey linkages; Walters et al. 2008; Chagaris et al. 2015; Geers et al., in press). In the present study, a comprehensive literature review coupled with statistical methodology enabled the most complete quantification to date of the Gulf Menhaden's trophic role in the GOM food web. Among the 568 references consulted, 136 references reported menhaden prey items, including Gulf Menhaden, *Brevoortia* spp., or UNID clupeids. Overall, 79 species were documented as predators of menhaden. Gulf Menhaden were consumed by a range of predators, including dolphins, seabirds, sharks, tunas, pelagic piscivores (e.g., mackerels), coastal piscivores (e.g., seatrout), invertebrate feeders, and forage fishes; the estimated diet contribution of menhaden was generally between 2% and 3% for the

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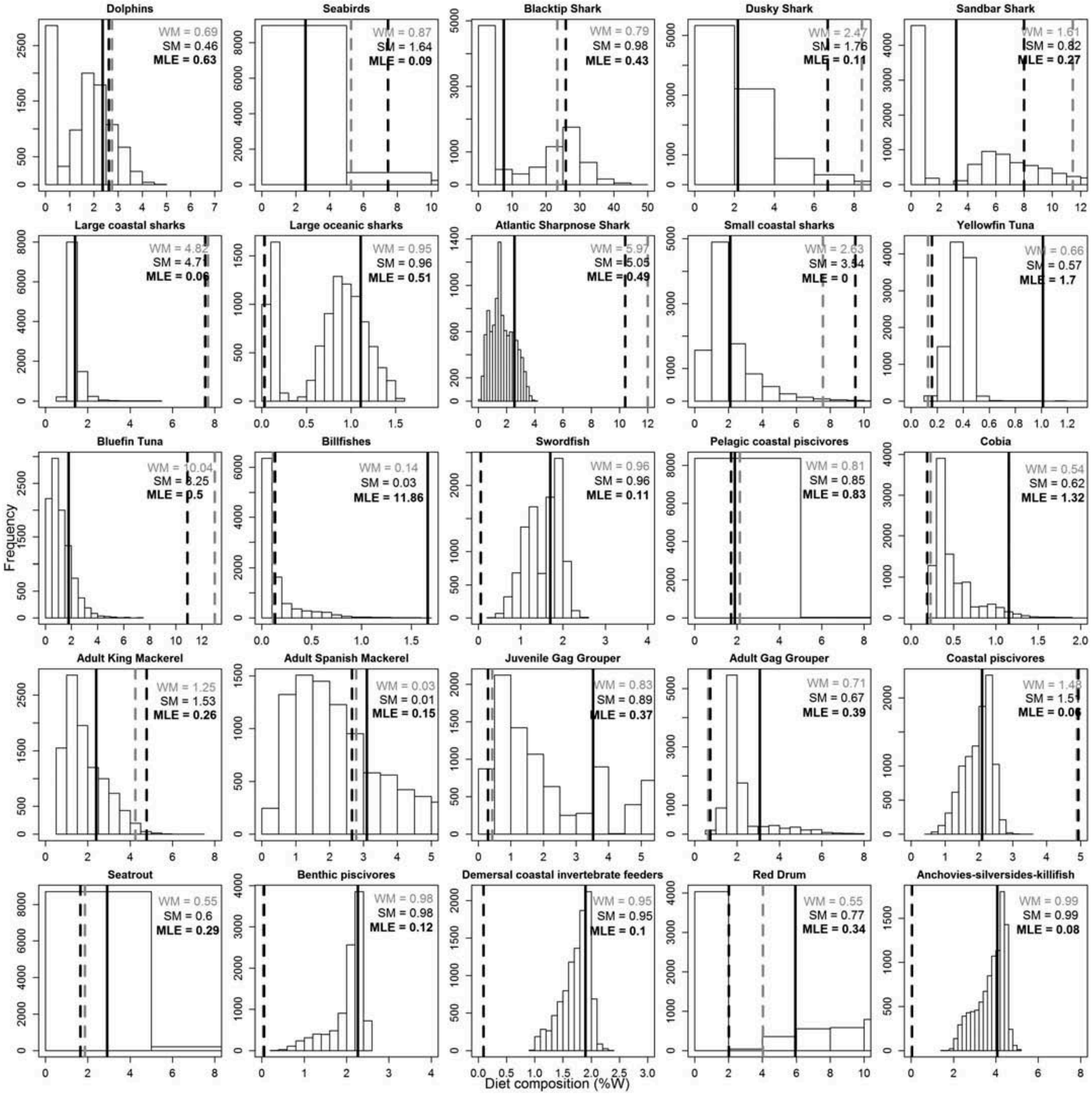

FIGURE 5. Maximum likelihood estimates (MLEs) of Gulf Menhaden contributions (percent weight [%*W*]) to predator diets based on a meta-analysis assessing trophic interactions within the northern Gulf of Mexico. Descriptions of the predator groups are provided in Table 2; additional definitions are provided in Figure 4.

majority of functional groups. When we accounted for UNID prey, the overall contribution of Gulf Menhaden to predator diets ranged from 0.3% for skates and rays to 11.8% for juvenile King Mackerel; the key predators included juvenile King Mackerel, juvenile Spanish Mackerel, adult Spanish Mackerel, Red Drum, and Blacktip Sharks.

Within other ecosystems, forage fish consumption is reportedly as high as 10% of predator dietary requirements (Pikitch et al. 2014); in contrast, Gulf Menhaden appear to have a smaller role than other forage fish in maintaining predator dynamics within the GOM. Overall, based on menhaden prey types (and prior to the allocation of UNID prey items),

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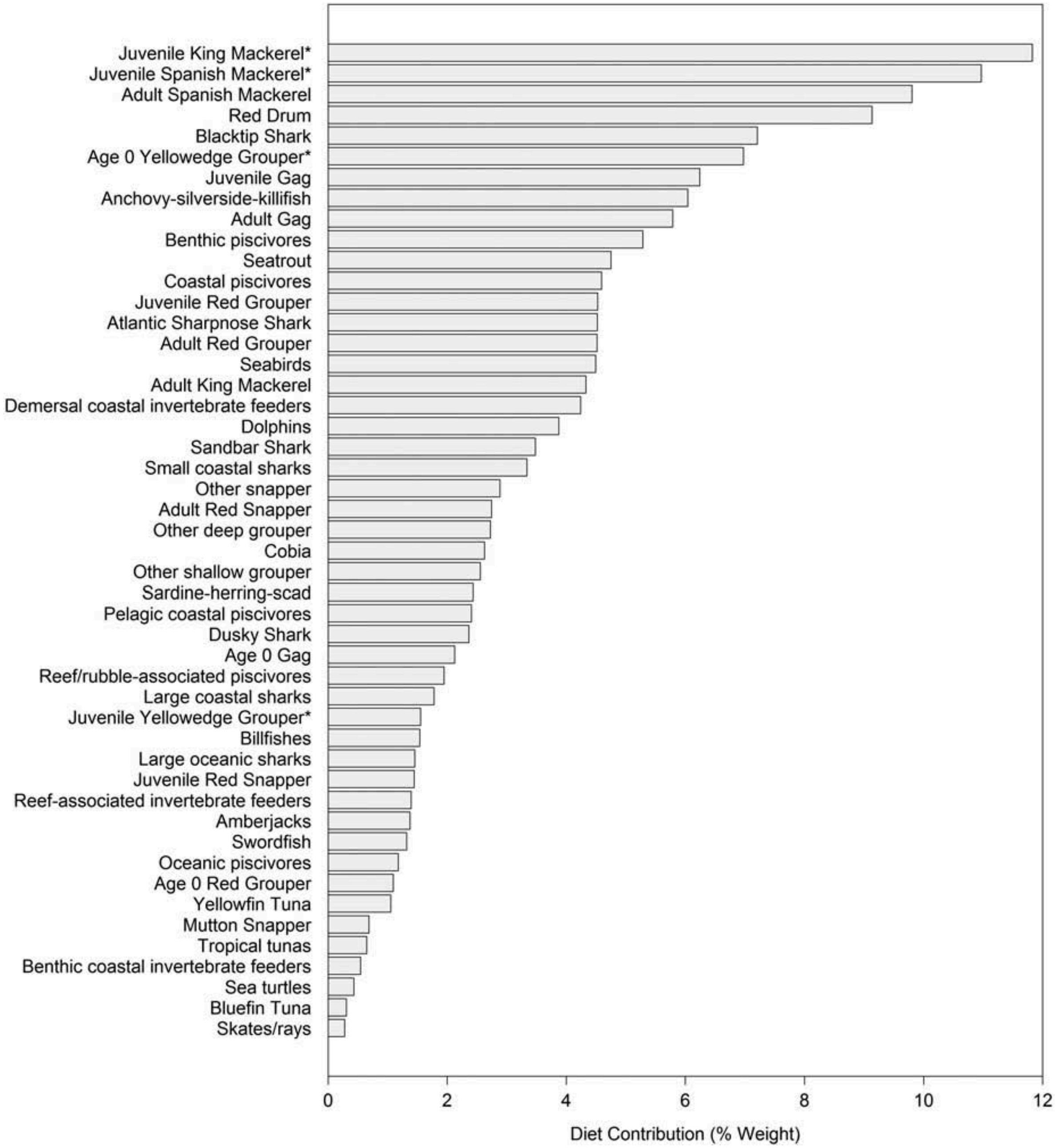

FIGURE 6. Contribution (percent weight) of menhaden *Brevoortia* spp. to predator diets, as determined by meta-analysis and after allocation of unidentified prey items. Asterisks identify predator groups for which estimates were based on weighted means because low sample sizes ($N < 5$) prevented estimation by probabilistic analysis. Descriptions of the predator groups are provided in Table 2.

we found that Gulf Menhaden contributed between 2% and 3% to the diet for the majority of predator species examined. Given the greater diversity of predator species and forage fishes at lower latitudes relative to higher latitudes (Christensen and Pauly 1993), predators likely have a wider prey spectrum and do not limit their prey consumption to a single forage fish species. Considering all forage fishes in the GOM, including 16 clupeid species and 10 engraulid species (i.e., anchovies; McEachran and Fechhelm 1998), we found that clupeids other than menhaden (i.e., herrings and sardines) contributed 4.3 ± 0.6% (mean ± SE) to predator diets, whereas engraulids contributed 4.5 ± 0.8%. Collectively, the percentage of forage fish (menhaden, clupeids, and engraulids) in predator diets was approximately 11 ± 1.7%, with the largest dietary contributions occurring for juvenile King Mackerel and juvenile Spanish Mackerel (~56%).

The reduced role of Gulf Menhaden in predators' diets within the GOM, as indicated by their relatively low diet contribution (~2

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–3%), challenges the perceived ecological importance of this species (e.g., Franklin 2007). While we found similarly, and slightly lower percentages, of menhaden in the diets of all the predators combined for the Atlantic, when we compared species groups, the differences were nonsignificant. The reason for the low percentages of menhaden in Atlantic diets was that the suite of predators was chosen from only species that largely co-occurred with the GOM; thereby excluding some key Atlantic predators of menhaden such as Striped Bass (Hartman and Brandt 1995; Walter et al 2003; Garrison et al. 2010), Silver Hake *Merluccius bilinearis* (Bowman et al. 2000) and Weakfish *Cynoscion regalis* (Hartman and Brandt 1995; Bowman et al. 2000). Including these species in the Atlantic diets would have increased the dietary percentage of menhaden well above that of the GOM. Furthermore, ecosystem models for the Atlantic region also generally have high ecotrophic efficiencies (>90%) for menhaden (Christensen et al. 2009; Nuttall et al. 2011), indicative of more complete accounting for consumption of menhaden. The question remains that if there is substantial menhaden consumption in the GOM, the key players remain elusive; though the predators in the Atlantic might provide some clues. Striped Bass and Weakfish are largely coastal and estuarine predators, particularly as juveniles. Substantial predation occurs in estuaries and shallow coastal regions which appear undersampled in the GOM, particularly in the Louisiana delta and adjacent coastal waters. Perhaps these areas, and the predator guilds found there, may hold the key to who and what many be consuming menhaden.

The relative contribution of Gulf Menhaden to predator diets suggests that the trophic role of Gulf Menhaden on an individual species level or a functional group level is relatively low. However, Gulf Menhaden may still be important at the ecosystem level due to (1) the number of different species that consume Gulf Menhaden and (2) the large total biomass of all species that consume Gulf Menhaden. We expected that menhaden would have a greater contribution to predator diets given their well-recognized ecological importance (Franklin 2007). Interestingly, our findings of low relative contributions by Gulf Menhaden to predator diets may in fact represent the reduced trophic role of menhaden in the GOM, as suggested by the relatively low EEs estimated by past ecosystem models. However, additional investigation of predator–prey dynamics that specifically separates menhaden from other clupeids is encouraged to test the plausibility of our findings. Gut content studies may have underestimated or even missed predation events entirely, resulting in our estimated Gulf Menhaden contribution of 2–3% to the diets of most functional groups. In addition, the majority of diet studies (78%) occurred after 1980 and during the period of large-scale fishery removals of Gulf Menhaden (>500,000 metric tons) from the GOM (Figure 7). During that period, the species' trophic role in the food web could have been greatly reduced.

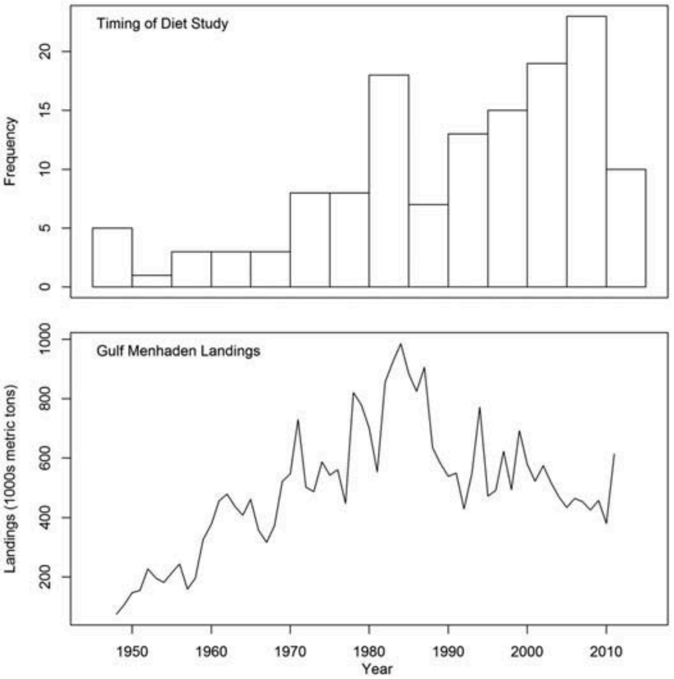

FIGURE 7. Comparison between the timing (year of publication) of diet studies used in the present study and the total landings of Gulf Menhaden (thousands of metric tons; combined commercial and recreational landings, SEDAR 2013).

Estimates of predation on menhaden may have been systematically reduced in diet studies from the GOM due to (1) more rapid digestion in the GOM than in other areas and (2) more common aggregation to higher taxonomic levels. The Gulf Menhaden and its congeners reach smaller maximum sizes than Atlantic Menhaden; the smaller menhaden sizes and warmer average water temperatures in the GOM could lead to greater digestion rates of these fish and a reduced ability to determine the prey species. In Atlantic studies, it was possible to identify Atlantic Menhaden by the digestion-resistant gizzard and from the presence of the parasitic isopod *Olencira praegustator* (Gannon and Waples 2004), which only infects menhaden in certain locations (e.g., North Carolina and Chesapeake Bay). For many of the predator species we examined (sharks, tunas, billfishes, and Red Snapper), the dietary percentage of menhaden was often low, likely due to reduced spatial overlap with coastal menhaden. The generalization of prey items as "UNID clupeids" may have blurred ecological interactions, since taxonomic families may contain any number of prey groups. The inclusion of studies that used a clupeid prey group required assumptions about how best to allocate the UNID clupeid portion of the diet among the clupeid groups. Another option is to allocate UNID clupeids to identified prey groups based on the observed proportions within the diet. However, such an approach can be biased by differential digestive rates (Baker et al. 2014), influenced by the experience level of technicians (e.g., their ability to identify prey items based on hard parts, etc.), or dependent upon the assumption that the relative proportions of prey groups identified in stomach contents are representative of the predator's actual diet. Particularly, the presence of the Gulf Menhaden's

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congeners (Finescale Menhaden and Yellowfin Menhaden) may have led researchers to err on the side of aggregation and simply report UNID clupeids, whereas the single menhaden species in the Atlantic made it more likely to be reported as Atlantic Menhaden.

Genetic analysis of stomach contents may help to resolve the issue of species identification by removing the reliance on morphological characteristics (Hargrove et al. 2012). Such DNA-based approaches have been implemented for individual species, including the French Grunt *Haemulon flavolineatum* in the U.S. Virgin Islands (Hargrove et al. 2012) and the Steller sea lion *Eumetopias jubatus* in the northeast Pacific (Tollit et al. 2009). However, such an analysis would entail a comprehensive field study to collect invertebrates and fishes for use in generating a reference data set of DNA sequences for potential prey items (Hargrove et al. 2012).

The limited appearance of Gulf Menhaden in diets from the northern GOM is further surprising given the species' considerable biomass. The 2013 stock assessment model for Gulf Menhaden estimated 107.67×10^9 age-0 fish and 58.1×10^9 age-1 and older fish in 2011 (SEDAR 2013). Within the assessment model (SEDAR 2013), higher natural mortality is implemented for younger individuals due to the assumption that they are subject to higher levels of predation. Unfortunately, the lack of size-based trends in diet prevented any examination of predation on juvenile menhaden, which is suggested to be a key component of natural mortality (SEDAR 2013). The perceived importance of predation on juvenile menhaden suggests that the prevalence of age 1 and older fish in gut contents may underestimate predation on Gulf Menhaden by missing instances of predation on superabundant juveniles. Furthermore, despite the fact that Louisiana waters are the center of the Gulf Menhaden fishery and constitute an area of high estuarine productivity for menhaden, there is a paucity of diet studies from Louisiana, where presumably a high amount of predation occurs. Future trophic research should focus on sampling Louisiana waters of the GOM to more completely evaluate the trophic role of Gulf Menhaden.

The diet composition estimated in this study is the most complete representation compiled to date, but there remain some limitations, which can be classified as errors of commission and errors of omission. As an example of the first situation, the presence of a single instance of menhaden predation by Gulf Killifish (Rozas and LaSalle 1990) has a very pronounced and likely unrealistic impact on ecosystem models. Several EwE models for the GOM have combined anchovies, silversides, and killifishes, which together represent a very large biomass pool. The single predation event by Gulf Killifish resulted in a 6% contribution of menhaden to the diet for the anchovy–silverside–killifish group; due to their extremely high biomass, these species are substantial predators upon menhaden in past GOM EwE models (Geers et al., in press). It remains doubtful that this single observation stems from active predation—if for no other reason than gape limitation in Gulf Killifish; instead, the event likely represents the scavenging of bait or the consumption of detritus.

Errors of omission would most certainly have been severe in our diet estimates had we not *imported* information from predators (birds, oceanic fishes, etc.) that most likely feed on Gulf Menhaden but had not been reported to do so in the GOM. This borrowing of information is absolutely critical to parameterization of diet matrices in situations where the available published studies do not permit full elucidation of the diets. Furthermore, small sample sizes ($N < 5$) for juvenile groupers and mackerels often prevented application of the probabilistic estimation approach; as a result, our estimates of dietary habits for juvenile predators were based on the WM method, potentially resulting in a biased diet composition. Even though mean contribution was weighted by sample size, the WM method relied heavily on the assumption that sample size is large enough to offset a rare predation event, which may not be the case when sample sizes are low (Table 2). Thus, additional data on juvenile predators are needed to enable a more statistically rigorous estimation of dietary habits. Indeed, collection of individual stomachs from the field could easily be incorporated into the present analysis as individual diet observations (sensu Ainsworth et al. 2010; Masi et al. 2014). Field studies that address juvenile diets in coastal waters, where many commercially important species (e.g., groupers and snappers) remain during their early life stages, are particularly needed.

Small-scale diet studies are often difficult to publish in peer-reviewed journals due to criticisms that such studies are too localized or limited in scale and sample size when compared with modeling and testing of hypotheses about broad concepts (Braga et al. 2012). Such notions are inherently inhibitive to EBFM efforts, as standardized diet composition data (Cortés 1999) are needed in most ecosystem-based models. The literature contains many papers that debate the best methods for describing trophic interactions (e.g., IRI [Cortés 1997] versus %FO [Baker et al. 2014]). For ecosystem modeling, reporting diet composition in terms of $\%W$ is critical since many ecosystem models are based on mass-balance approaches (e.g., Ecopath; Christensen et al. 2008). However, this method does have its challenges because the physical separation of different prey types is often difficult due to differential digestion rates (Baker et al. 2014), the order of prey ingestion, prey handling, and evacuation rates (Rindorf and Lewy 2004; Baker et al. 2014). Empirical relationships have been developed to convert %FO to relative weight composition based on samples obtained outside of the GOM (Stobberup et al. 2009), but this is an approximation and should only be used in the absence of more direct measurements. A similar analysis conducted using data collected within the GOM could help to refine these generalized

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relationships for the GOM region. The impending completion of GoMexSI may also provide a wealth of information to aid with such analyses.

An alternative approach to addressing predation on Gulf Menhaden could be to employ size-based ecosystem models (e.g., OSMOSE; Shin and Cury 2004) that do not prespecify the diet matrix but rather estimate it based on gape size and spatial overlap (e.g., Grüss et al. 2015). Although OSMOSE does not require diet composition directly, it does require a priori information about which predators to consider within model construction, and such information is elucidated within the present study. The use of size-based models to evaluate menhaden predation may provide critical insight into the trophic role of juvenile menhaden—insight that is not currently available from the published literature. Very few studies have distinguished between predation on Gulf Menhaden and predation on other clupeids, and even fewer studies have commented on the size-classes of consumed menhaden, thus leaving a gap in our understanding of trophic relationships.

We have provided a statistically derived diet matrix based on an intensive literature search for quantitative diet data, with the goal of alleviating major criticisms of past GOM ecosystem models that were based largely on expert opinion (Walters et al. 2008) and/or WM methods (Chagaris et al. 2015; Geers et al., in press). This statistically derived diet matrix will be used to parameterize an updated EwE model of the northern GOM, allowing the simulation of changes in ecosystem structure in response to changing fishing pressures. This work highlights the need for future research in trophic ecology to facilitate EBFM in the GOM.

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