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Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico

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ABSTRACT

Catastrophic disturbances to marine environments, such as the Deepwater Horizon oil spill in the northern Gulf of Mexico (GoM), emphasize the need to approach fisheries management and restoration from an ecosystem perspective. To evaluate the ecosystem dynamics within the GoM, we developed a mass-balanced Ecopath model ("nGoM Ecopath") which integrated ecosystem stressors, indirect effects of fishing (e.g. bycatch), and predator-prey dynamics. A meta-analysis of diet composition filled critical gaps in higher trophic level predator-prey linkages, such as predation on economically important groupers (Serranidae). Compared to previous Ecopath models of the GoM, nGoM Ecopath displayed higher ecosystem complexity including higher connectivity amongst trophic groups and increased omnivory. Mixed trophic impact analysis revealed species including snappers, groupers, pelagic coastal piscivores, oceanic piscivores, cephalopods, and dolphins as critical top-down predators. Bottom-up effects were identified for juvenile groupers and mackerels, which benefited from high production of invertebrates and small fishes. Network analysis revealed detrimental effects of red tides on sharks, skates and rays, and demersal coastal invertebrate feeders such as black drum, as well as adult red and gag grouper. Pelagic coastal piscivores (e.g. jacks (Carangidae)), snappers (Lutjanidae), and mobile epifauna (e.g. lobsters) imposed the largest influence on ecosystem structure as keystone predators. The nGoM Ecopath model using the dynamic module Ecosim can help guide restoration efforts through the evaluation of multispecies responses to management actions and identification of ecosystem trade-offs.

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1. Introduction

Events such as the Deepwater Horizon (DWH) oil spill have emphasized the need to approach fisheries management and restoration from an ecosystem perspective using the best available science. Ecosystem-based fisheries management requires explicit consideration of ecosystem processes such as multispecies interactions (e.g. predator-prey dynamics, competition), environmental effects (e.g. harmful algal blooms such as red tides), and fish-fisher interactions (e.g. bycatch) (Pikitch et al., 2004). Ecosystem restoration, defined as the process of assisting the recovery of damaged, degraded, or destroyed ecosystems (Abelson et al., 2016), can refer to rebuilding depleted coastal and marine resources and enhancing community resilience (e.g. Gulf of Mexico Regional Ecosystem Restoration Strategy, GCERTF 2011), for example through the reduction of bycatch of non-targeted species in large-scale fisheries.

Ecosystem models, such as Ecopath with Ecosim (EwE; Christensen and Pauly, 1992; Christensen and Walters, 2004), are a key tool for examining consequences of management actions on marine ecosystems (e.g. Chagaris et al., 2015) and can elucidate dominant inter-species interactions, energy transfer pathways, and community shifts (Pauly et al., 1998; Walters and Martell, 2004; Robinson et al., 2015). Mass-aggregate ecosystem models, such as EwE (Hollowed et al., 2000), require that critical predator-prey interactions are defined, as these relationships drive the flow of energy between trophic groups. When combined with other system inputs, including biomass, production, and consumption, biotic and abiotic factors are linked to species' population dynamics to provide a static "snapshot" of trophic structure (Hollowed et al., 2000; Pauly et al., 2000). Changes in the food web over time can be sim-

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ulated within Ecosim to explore past and future effects of fishing or other sources of mortality (e.g. harmful algal blooms such as red tides) on community dynamics (Walters et al., 1997; Walters et al., 2008; Christensen and Walters, 2004). As a result, Ecosim predictions of changes in food web structure are heavily dependent upon the parameterization of the species interactions and rates of consumption; this information is often lacking at the ecosystem scale (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015).

Applications of existing Gulf of Mexico (GoM) ecosystem models to elucidate ecosystem dynamics have highlighted substantial uncertainty of trophic interactions, due to (1) difficulty in obtaining quality stomach contents from reef species due to barotrauma (i.e. stomach eversion in deep-water species; Bradley and Bryan, 1975), (2) prevalence of baited gear which can attract "hungry" species with empty stomachs (Cortés, 1997; Joyce et al., 2002), (3) limited sampling intensity or spatial coverage (Chagaris et al., 2015), and (4) an inability to identify digested prey for reasons discussed in Baker et al. (2014). An EwE model designed around shrimp bycatch in Florida waters (Walters et al., 2008; hereafter referred to as "coastal GoM EwE") was previously employed to assess changes in ecosystem structure, but possessed a diet matrix largely derived from expert opinion rather than quantitative diet studies (Simons et al., 2013; Geers et al., 2014). Substantial efforts were expended by Geers et al. (2014) to alleviate this limitation, who adapted the coastal GoM EwE model to focus on Gulf menhaden (*Brevoortia patronus*) in the northern GOM (Geers et al., 2014; hereafter referred to as "GoM menhaden EwE"); however, this model was not designed to evaluate reef habitats, an essential fish habitat from both an ecological and economic standpoint (Geers, 2012). In addition, the GoM menhaden EwE model had a limited suite of predators on Gulf menhaden, subsequently documented in Sagarese et al. (2016), and did not include discard information from the menhaden reduction fishery and other large-scale commercial fisheries. The former represents a substantial amount of biomass removals of many economically important species such as Spanish mackerel (*Scomberomorus maculatus*) and sea trout (*Cynoscion* spp.) (Guillory and Hutton, 1982; de Silva et al., 2001). Robinson et al. (2015) developed a model designed to evaluate menhaden-jellyfish interactions in the Northern Gulf of Mexico with a focus on lower trophic level (TL) dynamics but did not have upper trophic groups identified to the level of detail necessary to compare with existing single-species assessment and management.

The limitations of previous ecosystem models (as discussed in Simons et al., 2013) have necessitated additional efforts, particularly in terms of capturing predator-prey interactions concerning higher TL organisms and economically important species, such as groupers (Serranidae). The socio-economic importance of groupers is well-recognized in the northern GoM where species such as red grouper (*Epinephelus morio*) are targeted by both commercial and recreational fisheries (Coleman et al., 1996; Agar and Carter, 2014; Sadovy de Mitcheson et al., 2013). However, despite their economic importance, there is a paucity of information regarding their role in the GoM food web, particularly as prey for large predators (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015). Parameterization of predator-prey interactions has rarely included groupers in past ecosystem models, with relatively few predators documented across studies (Table 1). Even within the West Florida Shelf reef fish EwE model (Chagaris, 2013; Chagaris et al., 2015; hereafter referred to as "WFS reef fish EwE"), which represents the most progressive and extensive EwE model in the region to date, predation on groupers is limited to pelagic coastal piscivores (e.g. mackerels (Scombridae)), cobia (*Rachycentron canadum*), and other groupers (Table 1). Further, in WFS reef fish EwE the sole predator of adult red grouper, gag grouper (*Mycteroperca microlepis*), black grouper (*M. bonaci*), and yellowedge grouper (*Hyporthodus flavolimbatus*) is the tuna/billfish functional group (Chagaris et al., 2015). A lack of trophic understanding, ranging from missing predation events on higher TLs to missing consumers of key forage fish such as menhaden, has complicated the estimation of predator-prey linkages required for ecosystem-based fisheries management (Pikitch et al., 2004). These have resulted in an incomplete picture of species interactions incorporated in previous models aimed at addressing ecosystem-based fisheries management (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015; Robinson et al., 2015) and/or restoration efforts (e.g. de Mutsert et al., 2012; Lewis et al., 2016).

Since publication of a suite of ecosystem models for the GoM, several key issues and limitations of previous models have emerged. Notably, the emergence of red tide as a key environmental stressor, has been explicitly considered in fisheries assessments and is critical to understanding ecosystem dynamics in the GoM. Secondly, given the high volume of discards and the fact that many fisheries are driven as much by their discards as by their target catch, it is critical to consider discards in ecosystem modeling. Third, the incomplete nature of the previous diet matrices left many functional groups either without predators or with incompletely represented diets. This paper addresses these three key processes and describes a mass-balanced northern GoM Ecopath model (hereafter referred to as "nGoM Ecopath") with explicit improvements compared to previous Ecopath models including: (1) the focus on socioeconomically important federally (e.g., red grouper) and internationally managed species (e.g., swordfish) on a gulf-wide scale matching the spatial extent of management; (2) statistically-derived, more comprehensive definitions of species interactions; (3) modeling of bycatch removals from the menhaden reduction fishery and other large-scale fisheries, and (4) inclusion of mortality effects from harmful algal blooms (i.e. red tides). A network analysis was employed to evaluate the direct and indirect species interactions within the GoM as well as to assess the impacts of fisheries and red tide events on species dynamics, with special emphasis placed on economically important groupers. Integration of these ecological processes with human dimensions is essential to enhance realism of ecosystem models, which will facilitate ecosystem-based fisheries management and restoration in the GoM (Mace et al., 2001; MSFCMA, 2007).

2. Materials and methods

2.1. Mass-balance modeling approach

Ecopath utilizes a mass-balanced framework composed of trophically-linked biomass pools representing major ecosystem functional groups (Polovina, 1984; Christensen and Pauly, 1992; Pauly et al., 2000). Ecosystem functional groups can reflect: (1) a group of species exhibiting similar life history, dietary or niche preferences (e.g. forage fish); (2) a single species of commercial or ecological importance (e.g. red snapper); or (3) a life-history stage ("stanza") ontogenetically distinct in diet and/or habitat (e.g. estuarine juveniles versus coastal adults) (Pauly et al., 2000; Walters et al., 2008). The production of stock *i* (P_i) is expressed as a function of all loss and gain processes to a functional group's biomass (B_i) and is estimated as:

$$P_i = Y_i + (B_i x M2_i) + E_i + BA_i + P_i(1 - EE_i) \quad (1)$$

where Y_i is the yield from the fishery, $M2_i$ is the total predation rate, E_i is the net migration rate (emigration − immigration), BA_i is the biomass accumulation rate, and EE_i is the ecotrophic efficiency, defined as a trophic group's production transferred within the system (e.g. by predation or fishery removals). The total consumption

Table 1
Comparison of predator-grouper linkages between the northern Gulf of Mexico (nGoM) Ecopath model and other regional studies. N refers to the total number of functional groups considered in each model (excluding imports). Predators include: marine mammals (MM), seabirds (SBD), sharks (SHK), tunas (TUN), billfishes (BIL), pelagic coastal piscivores (PCP; e.g. jacks), amberjacks (AMB), cobia (COB), mackerel (MAC), rays (RAY), groupers (GRP), snappers (SNP), and tilefishes (TLF).

Region/Area	N	References	MM	SBD	SHK	TUN	BIL	PCP	AMB	COB	MAC	RAY	GRP	SNP	TLF
Large Marine Ecosystem	40	Vidal and Pauly (2004)	X	–	X	–	–	–	–	–	–	–	–	–	–
Northern	63	Walters et al. (2008)	–	–	–	–	–	–	–	–	–	–	–	–	–
	75	Sagarese et al. (this study)	–	X	X	X	X	X	X	X	X	–	X	X	X
	47	Geers et al. (2014)	–	X	X	X	–	X	–	–	X	X	X	X	–
North-Central	54	Robinson et al. (2015)	X	–	–	–	–	–	–	–	–	–	–	–	–
West Florida Shelf	59	Okey et al. (2004)	–	–	X	X	X	X	–	–	–	–	X	–	–
	70	Chagaris et al. (2015)	–	–	–	X	X	X	X	X	X	–	X	–	–
Looe Key, FL (Atlantic)	20	Venier (1997)	–	–	X	–	–	–	–	–	–	X	–	–	–
Continental Shelf Yucatan	21	Arreguín-Sánchez and Valero (1996)	–	–	X	–	–	–	–	–	–	–	–	–	–
Western	21	Arreguín-Sánchez et al. (1993)	–	–	X	–	–	–	–	–	–	–	–	–	–
Southwest Continental Shelf	19	Manickchand-Heileman et al. (1998)	–	–	X	–	–	–	–	–	–	–	–	X	–

of predator *j* (Q_j), or removal of system production is modeled with the following equation:

$$B_i x M2_i = \sum_{j=1}^{n} \left(B_j x \frac{Q_j}{B_j} x DC_{ji} \right)_i \qquad (2)$$

where B_j is the biomass of predator *j*, Q_j/B_j is the ratio of the consumption to the biomass of predator *j*, and DC_{ji} is the proportion of predator *j*'s diet that consists of prey *i*. By assuming mass balance of these equations, Ecopath produces a 'snapshot' of ecosystem conditions which tracks trophic flows within the system for the time period investigated. Ecopath requires three of four data inputs for each trophic group, including relative biomass (B), the ratio of production to biomass (P/B), the ratio of consumption to biomass (Q/B) or EE. If one of the four data inputs required for a functional group is missing, it can be calculated through the mass-balance of the Ecopath model. Notably, the estimated diet composition (DC) of each trophic group is a required data input and, arguably, the most influential information for estimating time-dynamic changes in community structure, since the diet matrix is the sole determinant defining predator-prey interactions in the food web. Trophic interactions are the most critical feature of mass-aggregate ecosystem models such as Ecopath, and are also extremely critical in end-to-end modeling platforms such as Atlantis (Masi et al., 2014; Tarnecki et al., 2016). The refined definitions of predator-prey interactions in the nGoM Ecopath model were a primary focus of our effort, and represented an improvement in model structure.

2.2. Study area

The GoM is a semi-enclosed basin with a single connection to the Atlantic Ocean spanning the Straits of Florida and Yucatan Channel. The area modeled included approximately 310,000 km^2 within the northern GoM which covers 2,934 km of U.S. coastline from Brownsville, Texas to the Florida Keys and extended roughly to 400 m depth in the pelagic environment (Fig. 1) (Vidal and Pauly, 2004; Yáñez-Arancibia and Day, 2004). Over 100 species of fish, crustaceans, mollusks, and other invertebrates are commercially fished in the GoM, with total annual reported commercial landings from the GoM Large Marine Ecosystem (LME) averaging 850,000 t between 2000 and 2005 (McCrea-Strub et al., 2011). During this time period, it is important to note that approximately 60% and 13% of GoM LME landings were of menhaden (509,620 t ± 83,004 SD) and Penaeid shrimp (114,000 t ± 11,116 SD), respectively (SEDAR, 2013a; NMFS-FSD, 2014). The removals of these two important prey groups occurs from two fleets, the purse seine reduction fishery and shrimp trawl fishery, both of which have significant bycatch of finfish and other species.

2.3. ECOPATH model construction

2.3.1. Structure

A total of 75 functional groups were modeled, including one marine mammal group, one seabird group, one sea turtle group, eight shark groups, 53 fish groups, seven invertebrate groups, three primary producer (PP) groups, and one detritus group (see Table A.1 for specifics). Following Chagaris et al. (2015), functional groups were selected based on their socio-economic importance and management history (both federal and international). Economically-important grouper species including red grouper, gag grouper, black grouper, and yellowedge grouper were each separated into age-specific multi-stanza groups to capture ontogenetic foraging behavior and mortality: (1) age 0 s which remain inshore (Fitzhugh et al., 2005) and consume small invertebrates (Mullaney, 1994; Brulé et al., 2005; Stallings et al., 2010); (2) juveniles (ages 1–3) which move to nearshore reefs (Koenig and Coleman, 1998) where they consume invertebrates and small fishes (Brulé and Canché, 1993; Brulé et al., 2005, 2011; Stallings et al., 2010); and (3) adults (ages 3+) which inhabit deeper regions (Bullock and Smith, 1991) and prey upon invertebrates and large fishes (Randall, 1967; Bullock and Smith, 1991; Patterson et al., 2012; Tremain and Adams, 2012). A focus on groupers at the gulf-wide scale represented one of the major advancements of the nGoM Ecopath model.

2.3.2. Data inputs

Biomass estimates (B; t km^{-2}) were obtained from the primary literature, recent stock assessments, or survey data when feasible. For most functional groups, production per biomass (P/B; yr^{-1}) was approximated by assuming that P/B equaled the instantaneous rate of total mortality (*Z*), which itself is given as the summation of both natural mortality (M) and fishing mortality (F) (Allen, 1971). Consumption per biomass estimates (Q/B; yr^{-1}) were obtained using empirical equations of Pauly et al. (1990) and Palomares and Pauly (1989). Landings and discards (t km^{-2} yr^{-1}) were obtained from either stock assessment documents or from the National Marine Fisheries Service Fisheries Statistics Division (NMFS-FSD) database (http://www.st.nmfs.noaa.gov) (NMFS-FSD, 2014). Due to the unknown effects of the DWH oil spill on species abundance and catches, annual estimates of all data inputs (i.e., biomass, landings, and discards) were averaged between 2005 and 2009. Data from 2010 and subsequent years following the DWH oil spill (i.e., 2011-onwards) were excluded due to concerns over the impacts of the DWH Oil Spill on derived estimates of species abundance and community composition. Additional details on data inputs are provided in Appendix A.

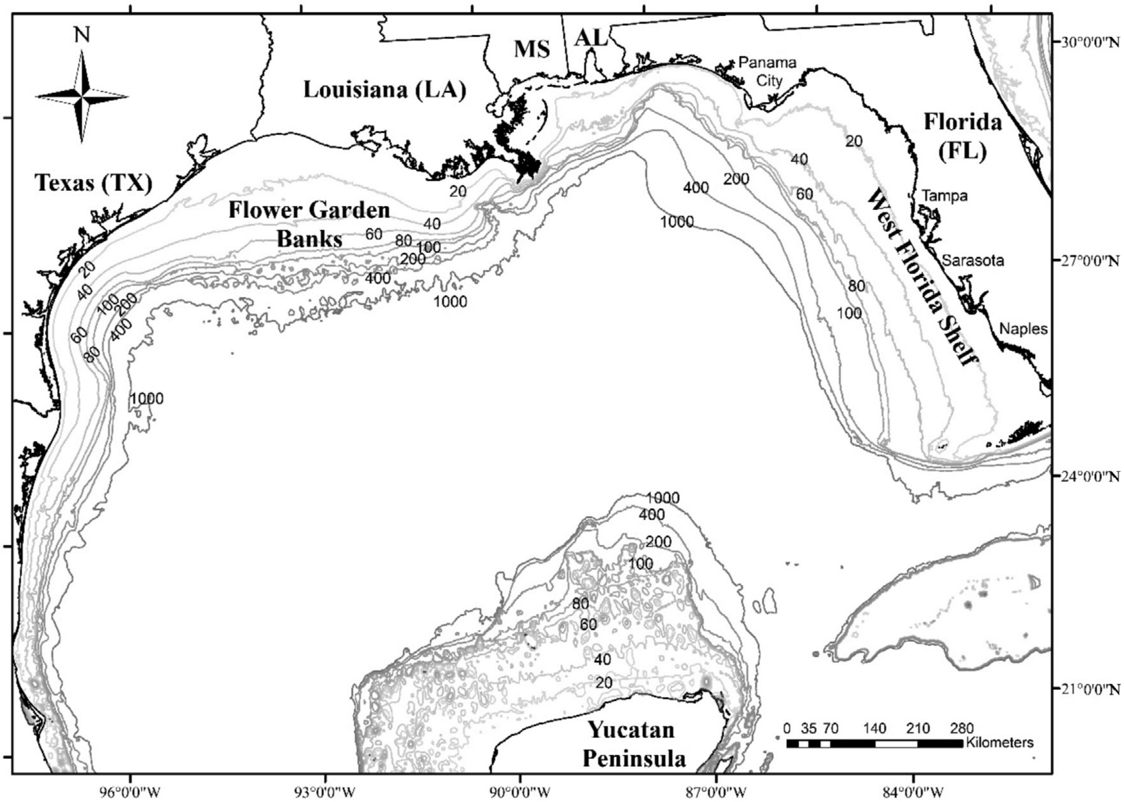

Fig. 1. Map of the northern Gulf of Mexico with depth contours (m) identifiable by solid lines. The modeled area spans approximately 310,000 km^2 in U.S. waters between the land mass and the 400-m dashed contour line. MS = Mississippi, AL = Alabama.

2.3.3. Diet

A probabilistic approach was employed to estimate diet composition of fishes based on a meta-analysis of trophic interactions (Sagarese et al., 2016). Briefly, the probabilistic method entailed: (1) drawing 10 random (with replacement) diet composition estimates for each predator from all available regions and/or studies; (2) estimating the weighted mean diet contribution of each prey item to each predator; (3) repeating steps (1) and (2) 10,000 times to generate probability distributions for these bootstrapped weighted, averaged diet observations; and (4) fitting a Dirichlet distribution to the bootstrapped diet composition data (for all prey items of each predator). The end-product is a marginal distribution of prey-specific predictions of the proportion of each prey item by weight or biomass from which maximum-likelihood estimates (MLE) of diet proportion and confidence intervals were obtained. These estimated distributions represented the likely contribution of prey groups to the predator's diet. If at least 10 random observations were not available, as was typically the case for juvenile life stages, five observations were used in the MLE approach.

Within the meta-analysis, the term comprehensive is used in the sense that all encountered diet studies for each predator (e.g. blacktip shark (*Carcharhinus limbatus*)) were consulted whether specific to the GoM or outside the GoM. Quantification of diets for some functional groups (e.g. butterfish (Stromateidae) among others) required diet composition from regions beyond the GoM. Inherent in this approach was the assumption of how to allocate unidentified prey. If a diet item was reported as a general class (e.g. unidentified [UNID] grouper), contribution was determined by weighting the diet metric by the relative biomass of each potential prey group. For example, if a diet study of a large coastal shark species (e.g. scalloped hammerhead (*Sphyrna lewini*)) identified UNID grouper as a diet item, this grouping was retained throughout the estimation process. After maximum likelihood estimation of the proportion of each prey item in the diet, the estimated proportion of UNID grouper was allocated based on relative biomass estimates from the mass-balanced nGoM Ecopath model to all potential grouper groups. This method assumed that all included species were potential prey items and were equally vulnerable to the predator (i.e. the catchability of different prey items was the same). These assumptions for allocating prey items played a key role in quantifying the consumption of species such as groupers which were rarely reported as specified prey items. Potential prey items were identified from either known trophic interactions (e.g. already identified as prey based on meta-analysis) or qualitative information (i.e. a prey item listed in a reference (e.g. Randall, 1967) with no corresponding metrics indicating proportion by weight, proportion by number, or frequency of occurrence).

2.3.4. Discards

The inclusion of fleet discard information, in particular the consideration of discards from the Gulf menhaden reduction fishery and from the red tide pseudo-fishing fleet, represented a major improvement to the ecosystem model for the nGoM. Discard estimates were obtained from stock assessment documents and from NOAA commercial and recreational statistics, when available. Although excluded from the coastal GoM EwE and GoM menhaden EwE models, bycatch estimates from the menhaden fishery were accounted for in the nGoM Ecopath to appropriately account for removals. The species composition and proportion of discards for the menhaden purse seine fishery reported in the early 1980s were used to infer bycatch (Guillory and Hutton, 1982). During 1980 and 1981, approximately 2.5% of menhaden landings in weight were deemed bycatch within the Louisiana menhaden fishery, although it is important to note that sampling occurred at the fish plants (i.e. large bycatch species were likely discarded at sea; Guillory and Hutton, 1982). Landings of bycatch species were allocated based on their percent by weight in the bycatch and an assumed average of 450,000 t for Gulf menhaden landings between 2005 and 2009 (Parker and Tyedmers, 2012; SEDAR, 2013a). Another bycatch study which sampled dead bycatch aboard commercial menhaden fishing vessels between 1994 and 1995 was used to infer bycatch landings for sharks (de Silva et al., 2001).

Following Gray (2014), a red tide fleet was included as a pseudo-fishing fleet to reflect removals due to mortality from harmful algal blooms (HAB). Functional groups susceptible to red tide events were identified from the Florida Fish and Wildlife Research Institute (FWRI) fish kill database (Fig. 2) (Gray, 2014; FWRI, 2015). The HAB fleet was parameterized as a discard-only fleet (Gray, 2014). The magnitude of removals was set using an 'anchor point' method based on gag grouper as discussed in Gray (2014). Within the nGoM Ecopath model, we employed the HAB discard estimates discussed in Gray (2014) with 100% discard mortality and adjusted the Gray (2014) estimates to reflect the larger area of the model coverage for the nGoM model. The reader is referred to Gray (2014) for additional details on their novel approach for estimating discards from red tide mortality.

2.4. Balancing the Ecopath model

To ensure Ecopath estimates were biologically realistic, the PREBAL procedure of Link (2010) was followed. Biomass, production, consumption, respiration (R), and vital rates (P/B, Q/B, and R/B) were examined across all taxa and TLs, with the expectation of an increasing trend when organized in decreasing order of TL (Link, 2010). Biomass estimates were expected to span between five and seven orders of magnitude from highest to lowest TL, while predator-prey ratios of biomass and vital rates were expected to remain below one (Link, 2010). Biomass relative to primary production (PP), production relative to PP, and P/B relative to PP were expected to remain below 1. Estimates of P/Q were calculated across taxa and expected to fall between 0.1 and 0.3 (Darwall et al., 2010; Link, 2010). For each functional group, the ratio of the consumption of that functional group to its production was expected to remain below one (i.e. P > consumption by predators) whereas the ratio of the consumption by that functional group to its production was expected to exceed one (i.e. P < consumption by functional group) (Link, 2010). Lastly, the ratio of total human removals (i.e. via fishing) to consumption was expected to remain below one (Link, 2010). In addition to the PREBAL diagnostics, the ecological and thermodynamic rules listed in Darwall et al. (2010) were examined.

During model balancing, only minor adjustments were made to the diet matrix where necessary since the diet matrix was statistically derived. Model inputs including biomass, P/B, and Q/B were re-evaluated and modified (while still maintaining the PREBAL limitations) to attain mass-balance, which was achieved when all EEs were below one (Darwall et al., 2010; Link, 2010).

2.5. Comparison of statistics to other regional Ecopath models

Summary statistics of the nGoM Ecopath model were compared to statistics from other available Ecopath models of the GoM including the coastal GoM EwE model (Walters et al., 2008), the GoM menhaden EwE model (Geers et al., 2014), and the West Florida Shelf reef fish EwE model (Chagaris et al., 2015). Summary statistics related to trophic ecology included: (1) an index of connectance, or the ratio of the number of actual links to the number of possible links (Heymans and Baird, 2000; Christensen and Walters, 2004); (2) system omnivory, or the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake which describes the distribution of feeding interactions between TLs (Heymans and Baird, 2000; Christensen and Walters, 2004); and (3) mean TL of the catch. Metrics are also presented concerning the proportion of functional groups impacted by discards as well as the proportion of realized predator-prey linkages to quantify improvements in modeled dynamics between the present Ecopath model and previous Ecopath models. For Ecopath models where TL estimates were reported, we assess the proportion of realized predator-prey linkages between TLs (i.e., <2 TL, 2.0–2.5 TLs, 2.5–3.0 TLs, etc.).

2.6. Trophic analysis

The mass-balance model accounted for trophic interactions as well as environmental drivers (e.g. mortality due to red tide) and removals due to the direct and indirect effects of fishing (e.g. bycatch). Direct and indirect trophic dynamics were quantified among biomass groups using a mixed trophic impact (MTI) analysis (Ulanowicz and Puccia, 1990) for each combination of impacting (e.g. predator or fishing fleet) and impacted (i.e. prey or resource) groups from the mass-balanced nGoM Ecopath model. For predator-prey combinations, MTI_{ij} values represent the net impact of prey *j* on predator *i* minus the negative impact of predator *i* on prey *j* (Ulanowicz and Puccia, 1990; Scharler and Fath, 2009). A large positive MTI_{ij} is indicative of a greater benefit of prey *j* on predator *i* (i.e. bottom-up control) whereas a large negative MTI_{ij} is evident of a detrimental impact of predator *i* on prey *j* (i.e. top-down control) (Ulanowicz and Puccia, 1990; Libralato et al., 2006; Hattab et al., 2013). For fishing fleet-biomass group combinations, MTI_{ij} values represent the net impact of resource *j* on fishing fleet *i* minus the negative impact of fishing fleet *i* on resource *j*, with large positive MTI values indicative of a greater benefit of resource *j* on fleet *i* and large negative MTI values indicative of a detrimental impact of fleet *i* on resource *j*. The net MTI was used to estimate the overall impact (ε) and the keystoneness index (KS) for each biomass group (Libralato et al., 2006). Keystone species are those which display a relatively low biomass but play an important role in the food web (Libralato et al., 2006). Network analysis was conducted with EwE version 5 after initial network analysis runs in EwE Version 6.4.3 failed to converge due to the vast amount of trophic linkages.

3. Results

3.1. Predation by higher trophic level organisms on economically important species such as groupers

Out of 568 references consulted in the meta-analysis both within and outside the GoM, 39 references identified grouper as potential prey for predatory species (Table 2; see Table A.4 for references). Of 59 observations of grouper as prey, approximately 73% solely reported family Serranidae as prey, which could represent hamlets, sea basses, or groupers. Ten observations of grouper as prey were specific to the GoM, although only three were reported to the genus level; both gag grouper and crevalle jack (*Caranx hippos*) preyed upon *Mycteroperca* sp. whereas scalloped hammerhead preyed upon *Epinephelus* sp. (Table 2). Outside the GoM, *Epinephelus* spp. were consumed by frigatebird (*Fregata minor*), blacktip shark, bull shark (*C. leucas*), sailfish (*Istiophorus* sp.), cobia, king mackerel (*Scomberomorus cavalla*), and mutton snapper (*L. analis*) (Table 2).

The meta-analysis of diet studies recognized a higher number of predators on groupers compared to previous studies, specifically amberjacks, cobia and tilefish (Malacanthidae) in the GoM menhaden EwE (Geers et al., 2014) and seabirds, sharks, snappers, and tilefish in the WFS reef fish EwE (Chagaris et al., 2015) (Table 1). Although both marine mammals (Robinson et al., 2015) and rays (Batoidea) (Geers et al., 2014) were considered predators of groupers in previous ecosystem studies, no empirical evidence was found during the meta-analysis.

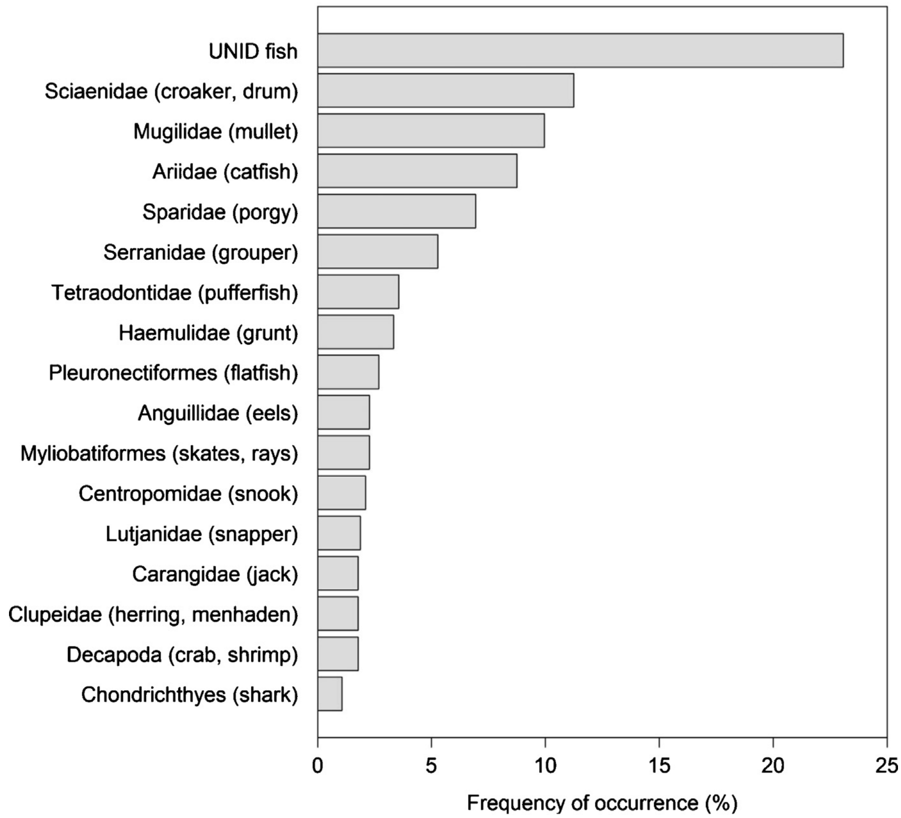

Fig. 2. Most frequently cited organisms in harmful algal bloom fish kills in the eastern Gulf of Mexico according to the Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute harmful algal bloom fish kill database. Note that only groups exhibiting a frequency of occurrence >1% in the database are shown for brevity. UNID = unidentified.

3.2. Balancing the Ecopath model

Input parameters including B (t km^{-2}), P/B (yr^{-1}), and Q/B (yr^{-1}) were incrementally modified to achieve a balanced nGoM Ecopath model (Table 3). In general, the most common error encountered during model balancing was predation mortality exceeding P/B estimates, which primarily stemmed from predation by a relatively abundant predator(s). Therefore, the most significant modification during model balancing was the reduction of these predation events from predators that included reef-associated invertebrate feeders (e.g. grunts (Haemulidae)), omnivores (e.g. filefish (Monacanthidae)), and forage fish (e.g. killifish (Fundulidae)), under the assumption that diet inputs were unrepresentative of average diets. For example, the meta-analysis predicted 6% of anchovy-silverside-killifish diet to be composed of menhaden prey, but this was based on a single observation of Gulf killifish (*Fundulus grandis*) diet. The amount of cannibalism by seabirds was reduced from 2.1% to 0.6% to achieve mass balance. Observed landings were assumed accurate such that in situations where fishing mortality exceeded P/B, either the functional group's biomass or P/B estimate was increased. This was necessary for many of the higher TL predators which exhibited low biomass but high landings (e.g. tunas), possibly a result of poor biomass estimates due to limited monitoring or violations of the assumptions required for estimating biomass from catch and F (see Appendix A).

Model balance diagnostics suggested that the model inputs and estimates were biologically realistic. On a log scale, biomass estimates spanned six orders of magnitude and declined with increasing TL at a rate of ~9%, showing an expected distribution of a trophic pyramid (Link, 2010). Production, consumption, respiration, and vital rates indicated a generally increasing linear trend with decreasing TL, with R^2 estimates ranging from 0.54 (R/B) to 0.73 (R) (Fig. 3). Estimates for multistanza groups often tended above or below the regression lines for most model inputs and estimates (Fig. 3). All predator prey ratios were below one with the exception of Q/B and R/B for marine mammals and birds to small pelagics (Table 4).

The majority of functional groups displayed P/Q ratios between 0.10 and 0.30 with the exception of dolphins, seabirds, and large oceanic planktivores (e.g. whale shark (*Rhincodon typus*)) (Fig. 4). These groups exhibited $P/Q < 0.05$ due to relatively low production and/or relatively high consumption estimates (Table 3). All EE estimates fell below one and were generally higher for groups that were both preyed upon and fished (e.g. sharks) (Table 3; Fig. 4). Multi-stanza groups tended to produce lower EE estimates, particularly age 0 groups for groupers, mackerel, and red snapper (Fig. 4). Other groups which exhibited relatively low EE estimates ($EE < 0.2$) included adult black and yellowedge groupers, tilefish, gray triggerfish (*Balistes capriscus*), butterfish, and primary producers (Fig. 4).

3.3. Comparison of statistics to other regional models

The nGoM Ecopath model displayed the highest indices of connectance and system omnivory among GoM models examined (Table 5). The connectance index nearly doubled that of the WFS reef fish EwE model and nearly tripled that of the coastal GoM EwE model (Table 5). Among broad-scale GoM Ecopath models available for network analysis (Walters et al., 2008; Geers et al., 2014), nGoM Ecopath produced higher estimates of respiration, exports, total system throughput, and production, but lower estimates of consumption and catch (Table 5). In contrast, estimates of consumption, respiration, total system throughput, and production were lower in nGoM Ecopath compared to WFS reef fish EwE (Table 5). Mean TL of the catch from the nGoM Ecopath model was

Table 2
Summary of predation events on groupers identified within a meta-analysis of trophic dynamics encompassing 568 references from within and outside the Gulf of Mexico (GoM). Note that the number of predation events does not always correspond to the number of references because multiple life history stages may have been examined. Additional details are provided in Sagarese et al. (2016). * indicates predators where interactions were identified outside the Gulf of Mexico. See Table A.4 for further details on regions.

Predator	*Epine-phelus*	*Myctero-perca*	*Acanth-istius*	*Cephalo-pholis*	Serra- nidae
Seabirds					
Frigatebird (*Fregata minor*)*	1				1
Sharks					
Blacktip shark (*Carcharhinus limbatus*)	1				2
Dusky shark (*Carcharhinus obscurus*)*			1		1
Bull shark (*Carcharhinus leucas*)*	2				1
Scalloped hammerhead (*Sphyrna lewini*)	1				4
Blacknose shark (*Carcharhinus acronotus*)*				1	
Tunas					
Bluefin tuna (*Thunnus thynnus*)*					1
Skipjack tuna (*Katsuwonus pelamis*)*					1
Yellowfin tuna (*Thunnus albacares*)*					3
Billfishes					
Sailfish (*Istiophorus platypterus*)*	1				2
Striped marlin (*Kajikia audax*)*					1
Piscivores					
Pelagic					
King mackerel (*Scomberomorus cavalla*)*	1				1
Almaco jack (*Seriola rivoliana*)*					1
Crevalle jack (*Caranx hippos*)		1			2
Greater amberjack (*Seriola dumerili*)*					1
Bluefish (*Pomatomus saltatrix*)					6
Cobia (*Rachycentron canadum*)	1				4
Dolphinfish (*Coryphaena hippurus*)*					1
Benthic					
Inshore lizardfish (*Synodus foetens*)					1
Groupers					
Gag grouper (*Mycteroperca microlepis*)		1			1
Red grouper (*Epinephelus morio*)					1
Scamp (*Mycteroperca phenax*)*					1
Yellowmouth grouper (*Mycteroperca interstitialis*)					1
Yellowfin grouper (*Mycteroperca venenosa*)*					1
Blueline tilefish (*Caulolatilus microps*)*					1
Snapper					
Red snapper (*Lutjanus campechanus*)					3
Mutton snapper (*Lutjanus analis*)*	1				
Dog snapper (*Lutjanus jocu*)*				1	1
Schoolmaster (*Lutjanus apodus*)*					1
Total	9	2	1	2	45

similar to other GoM models (range: 2.64–2.91), but lower than the WFS Ecopath model (3.54) (Table 5).

Improvements in both the proportion of functional groups with fishery discards and realized trophic linkages were evident in the present study compared to previous Ecopath models (Fig. 5). Consideration of discards was largest in the present study, likely due to the inclusion of discards by the harmful algal bloom "fleet" as well as bycatch of finfish and sharks in the Gulf menhaden reduction fishery (Fig. 5). Similarly, our meta-analysis of diet composition led to a greater proportion of realized predator-prey linkages in the present study for all TLs combined as well as for individual TL groups (Fig. 5). The literature review undertaken in the present study led to greater connectivity between higher TL predators (i.e., >3.5) and prey, with the proportion of realized linkages in the present study nearly doubling the proportions captured in previous studies. The proportions of realized lower TL linkages in the present study also remained higher than previous studies (Fig. 5).

3.4. Trophic analysis

Large oceanic sharks exhibited the highest estimated TL (4.25) followed by dusky shark (4.18) and blacktip shark (4.17). Estimated TLs for groupers ranged from 3.35 for adult black grouper to 3.92 for deep-water groupers, with relatively lower TLs estimated for age 0 s (range: 3.53 for black grouper to 3.76 for yellowedge grouper) compared to juveniles (3.62 for yellowedge grouper to 3.92 for black grouper) and adults (range: 3.35 for black grouper to 3.81 for gag grouper).

Predators of age 0 groupers included seabirds, blacktip shark, pelagic coastal piscivores, amberjacks, adult king mackerel, other groupers and snappers (Fig. 6). In addition to these predators, cobia, adult red snapper, mutton snapper and tilefish also consumed juvenile groupers (Fig. 6). Adult groupers were preyed upon by sharks, tunas, billfish, pelagic coastal piscivores, amberjacks, cobia, adult king mackerel, other adult groupers, and tilefish (Fig. 6). Total consumption of all groupers ranged from 0.00003 t km^{-2} yr^{-1} by bluefin tuna to 0.031 t $km^{-2} yr^{-1}$ by snappers excluding red, vermilion (*Rhomboplites aurorubens*), and mutton (hereafter referred to as "snappers"). Snappers fed upon juvenile gag, red, black, and yellowedge groupers, goliath grouper, deep-water groupers (e.g. speckled hind (*H. drummondhayi*)), and shallow-water groupers (e.g. yellowfin grouper (*M. venenosa*)) (Fig. 6).

Large negative mixed trophic impacts (MTIs) were indicative of a predator having a detrimental impact on prey. Detrimental impacts frequently outweighed the benefit of consumption for snapper and grouper functional groups, with MTIs ranging from −0.48 for age 0 yellowedge grouper to 0.00 for adult gag grouper (Fig. 7). Other instances of top-down predation (i.e. large negative MTIs) were identified for pelagic coastal piscivores preying upon oceanic species (−0.71 to 0.06), oceanic piscivores consuming tilefish (−0.59), cephalopods consuming reef omnivores (−0.52), Goliath grouper consuming sea turtles (−0.49), small coastal sharks

Table 3
Ecopath parameters from the balanced northern Gulf of Mexico (nGoM) Ecopath model. TL is the estimated trophic level, B is the relative biomass, P/B is the ratio of production to biomass, Q/B is the ratio of consumption to biomass, EE is the ecotrophic efficiency, P/Q is the ratio of production to consumption, and R/B is the ratio of respiration to biomass. Values in italics were estimated by the model. Additional details on model inputs are provided in Appendix A.

No	Group name	TL	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	R/B (yr^{-1})
1	Dolphins (DOL)	*3.97*	0.0156	0.16	40.00	*0.953*	*0.004*	*31.84*
2	Seabirds (SBD)	*3.73*	0.0119	0.25	33.00	*0.935*	*0.008*	*26.15*
3	Sea turtles (TUR)	*3.60*	0.0128	0.31	3.10	*0.649*	*0.100*	*2.17*
4	Blacktip shark (BKT)	*4.17*	0.0220	0.45	2.00	*0.962*	*0.225*	*1.15*
5	Dusky shark (DUS)	*4.18*	0.0110	0.39	2.00	*0.988*	*0.193*	*1.22*
6	Sandbar shark (SNB)	*3.94*	0.0138	0.28	2.60	*0.923*	*0.108*	*1.80*
7	Large coastal sharks (LCS)	*4.16*	0.0168	0.37	2.10	*0.990*	*0.176*	*1.31*
8	Large oceanic sharks (LOS)	*4.25*	0.0061	0.27	1.80	*0.997*	*0.150*	*1.17*
9	Atlantic sharpnose shark (ASN)	*3.83*	0.0382	0.65	5.30	*0.989*	*0.123*	*3.59*
10	Small coastal sharks (SCS)	*3.83*	0.0692	0.83	5.00	*0.989*	*0.166*	*3.17*
11	Yellowfin tuna (YFT)	*4.17*	0.0105	0.72	5.20	*0.996*	*0.138*	*3.45*
12	Bluefin tuna (BFT)	*3.97*	0.0098	0.94	3.40	*0.993*	*0.276*	*1.78*
13	Tropical tunas (TUN)	*4.12*	0.0148	0.93	5.00	*0.961*	*0.186*	*3.07*
14	Billfish (BIL)	*4.11*	0.0052	0.38	3.50	*0.993*	*0.109*	*2.42*
15	Swordfish (SWO)	*4.16*	0.0194	0.81	3.20	*0.991*	*0.253*	*1.75*
16	Pelagic coastal piscivores (PCP)	*3.84*	0.1120	1.80	6.00	*0.993*	*0.300*	*3.00*
17	Amberjacks (AMB)	*3.92*	0.0519	1.10	3.60	*1.000*	*0.306*	*1.78*
18	Cobia (COB)	*4.01*	0.0420	0.90	3.80	*0.931*	*0.237*	*2.14*
19	Juvenile king mackerel (KM0)	*3.87*	0.0011	1.40	12.12	*0.438*	*0.116*	*8.30*
20	Adult king mackerel (KM3)	*4.03*	0.0307	0.90	3.50	*0.992*	*0.257*	*1.90*
21	Juvenile Spanish mackerel (SM0)	*3.84*	0.0116	2.00	14.67	*0.779*	*0.136*	*9.74*
22	Adult Spanish mackerel (SM3)	*3.95*	0.0995	1.20	5.40	*0.979*	*0.222*	*3.12*
23	Skates and rays (RAY)	*3.43*	0.1365	1.10	7.80	*0.937*	*0.141*	*5.14*
24	Age 0 gag grouper (GGR0)	*3.66*	0.0032	1.90	19.41	*0.201*	*0.098*	*13.62*
25	Juvenile gag grouper (GGR1)	*3.88*	0.0334	1.00	6.94	*0.459*	*0.144*	*4.55*
26	Adult gag grouper (GGR3)	*3.81*	0.0697	0.61	3.20	*0.555*	*0.191*	*1.95*
27	Age 0 red grouper (RGR0)	*3.67*	0.0023	1.80	18.24	*0.194*	*0.099*	*12.79*
28	Juvenile red grouper (RGR1)	*3.69*	0.0310	0.80	6.55	*0.515*	*0.122*	*4.44*
29	Adult red grouper (RGR3)	*3.70*	0.1065	0.50	3.10	*0.529*	*0.161*	*1.98*
30	Age 0 black grouper (BGR0)	*3.53*	0.0023	2.00	17.03	*0.212*	*0.117*	*11.63*
31	Juvenile black grouper (BGR1)	*3.92*	0.0267	0.90	6.15	*0.494*	*0.146*	*4.02*
32	Adult black grouper (BGR3)	*3.35*	0.0867	0.50	2.90	*0.125*	*0.172*	*1.82*
33	Age 0 yellowedge grouper (YEG0)	*3.76*	0.0032	3.00	23.98	*0.254*	*0.125*	*16.18*
34	Juvenile yellowedge grouper (YEG1)	*3.62*	0.0230	1.20	7.97	*0.618*	*0.151*	*5.18*
35	Adult yellowedge grouper (YEG3)	*3.39*	0.0884	0.50	3.10	*0.111*	*0.161*	*1.98*
36	Goliath grouper (GOL)	*3.87*	0.0090	0.42	3.80	*0.665*	*0.110*	*2.62*
37	Other deep grouper (DWG)	*3.92*	0.0109	0.60	4.00	*0.404*	*0.150*	*2.60*
38	Other shallow grouper (SWG)	*3.75*	0.0180	0.80	6.20	*0.821*	*0.129*	*4.16*
39	Juvenile red snapper (RSN0)	*3.81*	0.0019	1.70	13.50	*0.514*	*0.126*	*9.10*
40	Adult red snapper (RSN6)	*3.65*	0.0745	0.70	3.48	*0.965*	*0.201*	*2.08*
41	Vermilion snapper (VSN)	*3.43*	0.0869	1.20	11.50	*0.696*	*0.104*	*8.00*
42	Mutton snapper (MSN)	*3.46*	0.0773	1.20	11.30	*0.206*	*0.106*	*7.84*
43	Other snapper (OSN)	*3.43*	0.1975	1.80	11.80	*0.383*	*0.153*	*7.64*
44	Coastal piscivores (CoP)	*3.59*	0.0754	1.65	9.50	*0.933*	*0.174*	*5.95*
45	Sea trout (ST)	*3.34*	0.2415	1.80	10.20	*0.656*	*0.176*	*6.36*
46	Oceanic piscivores (OcP)	*3.74*	0.1175	1.34	6.20	*0.993*	*0.216*	*3.62*
47	Benthic piscivores (BeP)	*3.70*	0.1350	1.54	6.20	*0.981*	*0.248*	*3.42*
48	Reef/rubble-associated piscivores (ReP)	*3.58*	0.1088	1.32	7.00	*0.636*	*0.189*	*4.28*
49	Reef-associated invertebrate feeders (RIF)	*3.07*	0.5650	2.80	12.50	*0.578*	*0.224*	*7.20*
50	Demersal coastal invertebrate feeders (DCIF)	*3.00*	1.0850	3.00	14.20	*0.547*	*0.211*	*8.36*
51	Red drum (RD)	*3.53*	0.1400	1.60	8.50	*0.267*	*0.188*	*5.20*
52	Benthic coastal invertebrate feeders (BCIF)	*3.04*	1.0255	3.10	15.60	*0.402*	*0.199*	*9.38*
53	Tilefish (TLF)	*3.47*	0.0859	1.80	10.00	*0.089*	*0.180*	*6.20*
54	Gray triggerfish (GTR)	*2.97*	0.0892	2.00	15.10	*0.110*	*0.132*	*10.08*
55	Coastal omnivores (CoOm)	*2.90*	0.3500	2.60	17.60	*0.923*	*0.148*	*11.48*
56	Reef omnivores (ReOm)	*2.80*	0.3200	2.70	22.20	*0.952*	*0.122*	*15.06*
57	Surface pelagics (SRF)	*3.12*	0.2290	2.70	11.70	*0.716*	*0.231*	*6.66*
58	Large oceanic planktivores (LOP)	*3.41*	0.1540	0.60	11.00	*0.221*	*0.055*	*8.20*
59	Oceanic planktivores (OPL)	*3.43*	0.3200	2.40	11.70	*0.817*	*0.205*	*6.96*
60	Sardine-herring-scad (SHS)	*3.02*	1.1000	2.65	12.10	*0.640*	*0.219*	*7.03*
61	Menhaden (MEN)	*2.53*	1.0700	2.70	13.90	*0.715*	*0.194*	*8.42*
62	Anchovy-silverside-killifish (ASK)	*2.93*	1.3980	3.50	15.90	*0.404*	*0.220*	*9.22*
63	Mullet (MUL)	*2.46*	0.5500	3.10	19.40	*0.265*	*0.160*	*12.42*
64	Butterfish (BUT)	*2.92*	0.4950	3.50	12.50	*0.090*	*0.280*	*6.50*
65	Cephalopod (CPH)	*3.30*	1.3800	3.50	13.70	*0.996*	*0.255*	*7.46*
66	Shrimp (SHR)	*2.77*	2.4000	3.80	19.20	*0.913*	*0.198*	*11.56*
67	Crabs (CRB)	*3.14*	2.2200	3.00	10.50	*0.995*	*0.286*	*5.40*
68	Sessile epifauna (SEP)	*2.01*	20.0000	5.00	17.00	*0.543*	*0.294*	*8.60*
69	Mobile epifauna (MEP)	*2.38*	15.0000	6.00	27.00	*0.989*	*0.222*	*15.60*
70	Zooplankton (ZOO)	*2.22*	13.0000	10.00	40.00	*0.999*	*0.250*	*22.00*
71	Infauna (INF)	*2.05*	18.5000	6.00	22.00	*0.975*	*0.273*	*11.60*
72	Algae (ALG)	*1.00*	29.8000	27.50		*0.083*		
73	Seagrass (SGR)	*1.00*	150.0000	25.00		*0.010*		
74	Phytoplankton (PHY)	*1.00*	25.0000	160.00		*0.208*		
75	Detritus (DET)	*1.00*	100.0000			*0.068*		

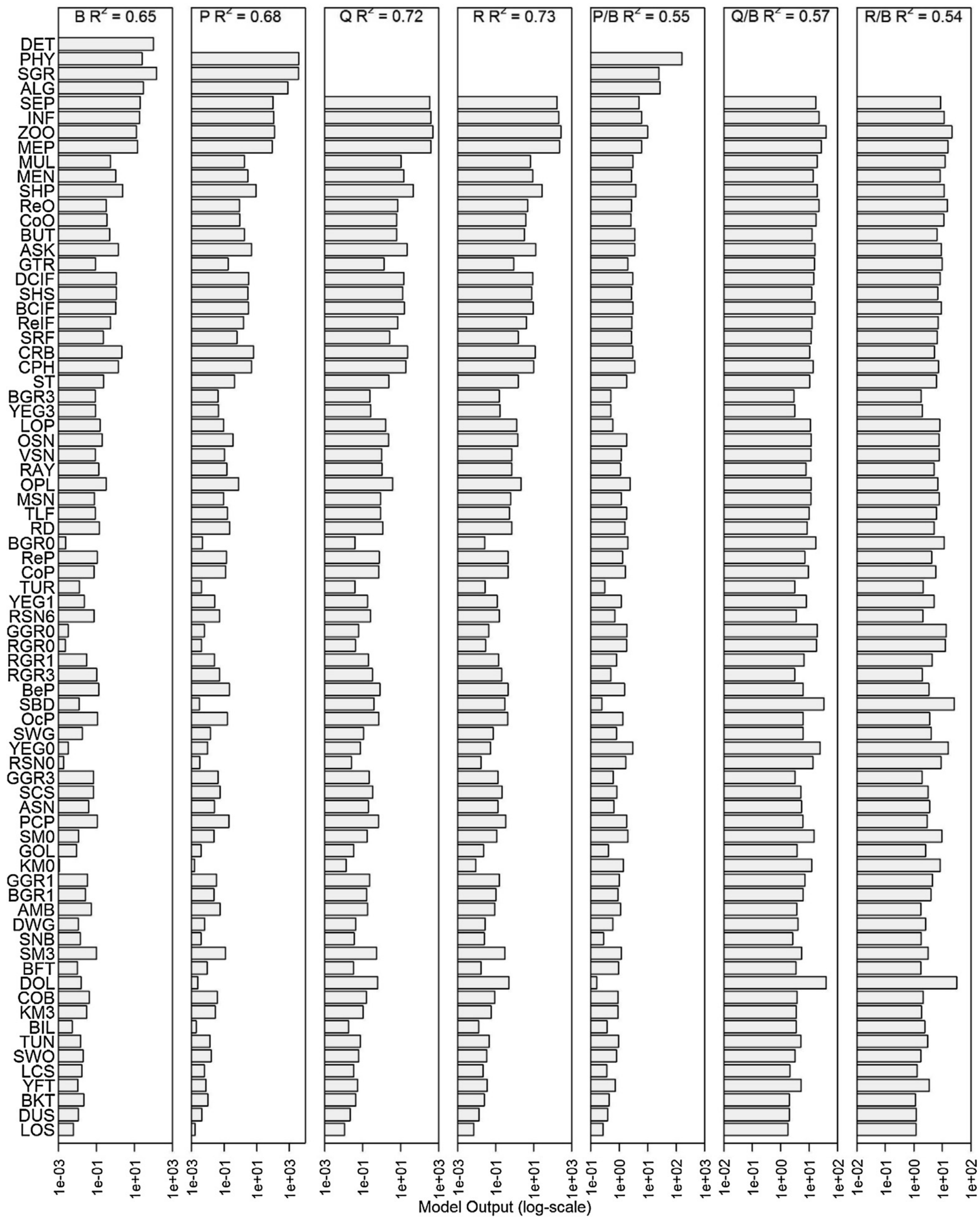

Fig. 3. Across trophic level trends in log-scaled biomass (B), production (P), consumption (Q), respiration (R), and vital rates (P/B, Q/B, R/B). Note that logarithms were used because biomass values span several orders of magnitude and groups are organized from increasing trophic level from top to bottom. Functional groups are as defined in Table 3. Note that homeothermic groups (dolphin, seabirds) are excluded from regression analyses for Q/B and P/B (Link, 2010).

Table 4
Predator prey ratios for biomass and vital rates for model diagnostics of the northern Gulf of Mexico (nGoM) Ecopath model. Parameters are as defined in Table 3.

Predator/prey ratio	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	R/B (yr^{-1})
Demersal/Benthic invertebrates	0.08	0.30	0.52	0.63
Demersal and medium pelagic piscivores/Small pelagics	0.17	0.46	0.52	0.54
Marine mammals and birds/Small Pelagics	0.00	0.07	2.58	3.52
Sharks/Small pelagics	0.02	0.18	0.22	0.23
Small pelagics/Zooplankton	0.48	0.31	0.35	0.38
Small pelagics/Phytoplankton	0.25	0.02	–	–
Planktivores/Zooplankton	0.04	0.15	0.28	0.35
Zooplankton/Phytoplankton	0.52	0.06	–	–

(e.g. bonnethead shark (*Sphyrna tiburo*)) preying upon shallow-water groupers (−0.41), dolphins feeding upon small coastal sharks (−0.37), and cannibalism by red snapper (−0.25) (Fig. 7).

Mixed trophic impacts indicative of a greater benefit of prey *j* to predator *i* were infrequently observed (Fig. 7). Age-1 yellowedge grouper benefited from mobile epifauna (+0.38), juvenile king and Spanish mackerels benefited from anchovies-silversides-killifish

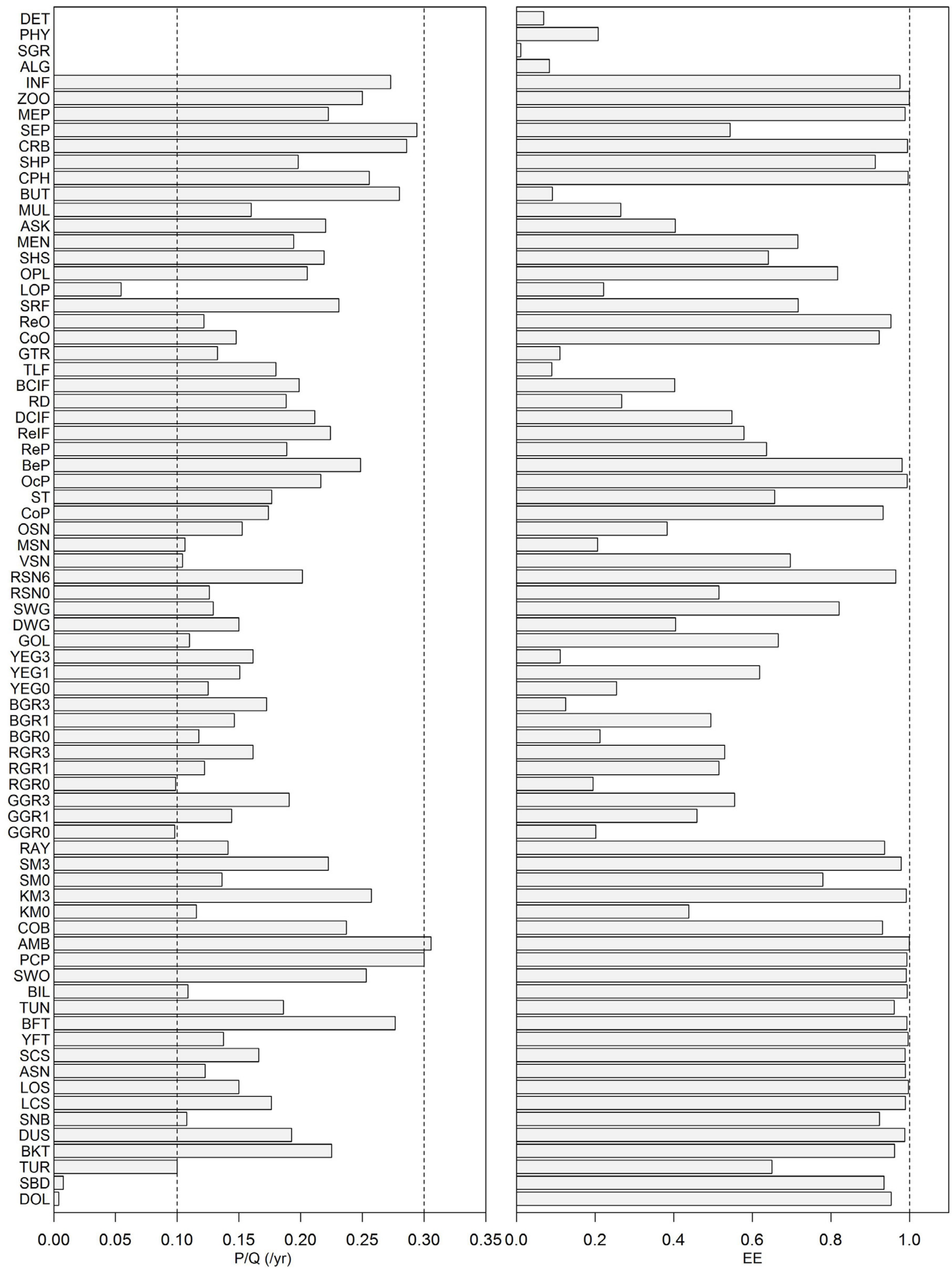

Fig. 4. Estimates of production/consumption (P/Q) and ecotrophic efficiency (EE) obtained from the balanced northern Gulf of Mexico (nGoM) Ecopath model. Dashed lines identify target values of 0.1 and 0.3 for P/Q and 1.0 for EE. Functional groups are as defined in Table 3.

(+0.29 to +0.33), and juvenile gag grouper benefited from benthic coastal invertebrate feeders (e.g. dusky flounder (*Syacium papillosum*)) (+0.27) (Fig. 7).

Harmful algal blooms had large detrimental impacts on skates and rays (−0.36), the Mexican shark fishery (-0.34), blacktip shark (−0.34), sandbar shark (−0.24), and demersal coastal invertebrate feeders (e.g. black drum (*Pogonias cromis*)) (−0.23). Species which benefited from red tide included cobia (+0.19) and dusky shark (+0.17), likely due to release of predation pressure (skates and rays upon cobia and blacktip shark upon dusky shark). Surprisingly, MTIs for most grouper functional groups remained near 0 (range: −0.06 to +0.01) with the exception of adult red (−0.11) and adult gag (−0.10) groupers. For juvenile groupers, HAB removals revealed a greater negative impact compared to fisheries but a

Table 5
Statistics, flows, and ecological indicators for the northern Gulf of Mexico (nGoM) Ecopath model in comparison to other regional models. (Walters et al., 2008) model available from http://www.ecopath.org/model/128, (Geers et al., 2014) model obtained from T. Geers, and (Chagaris et al., 2015) model obtained from Supplementary material therein.

Parameter	(Walters et al., 2008)	(Geers et al., 2014)	(Chagaris et al., 2015)	Sagarese et al., (this study)	Units
Statistics and flows					
Sum of all consumption	2707	2164	16613	1908	t km^{-2} yr^{-1}
Sum of all exports	5897	6075	1750	7530	t km^{-2} yr^{-1}
Sum of all respiratory flows	998	806	5229	1046	t km^{-2} yr^{-1}
Sum of all flows into detritus	6655	6623	18591	8078	t km^{-2} yr^{-1}
Total system throughput	16257	15668	42184	18563	t km^{-2} yr^{-1}
Sum of all production	7610	7472	13831	9050	t km^{-2} yr^{-1}
Total net primary production	6881	6881	6985	8570	t km^{-2} yr^{-1}
Total biomass (excluding detritus)	360	325	497	289	t km^{-2}
Community energetics					
Net system production	5883	6075	1755	7523	t km^{-2} yr^{-1}
Total primary production/total respiration	7	9	1	8	–
Total primary production/total biomass	19	21	14	30	–
Total biomass/total throughput	0.022	0.021	0.012	0.016	–
Exploitation indices					
Mean trophic level of the catch	2.91	2.64	3.54	2.84	–
Gross efficiency (catch/net primary production)	0.0032	0.0006	0.0001	0.0004	–
Total catch	21.86	4.02	0.41	3.18	t km^{-2} yr^{-1}
Connectance index	0.131	0.303	0.231	0.396	–
System omnivory index	0.119	0.190	0.199	0.410	–

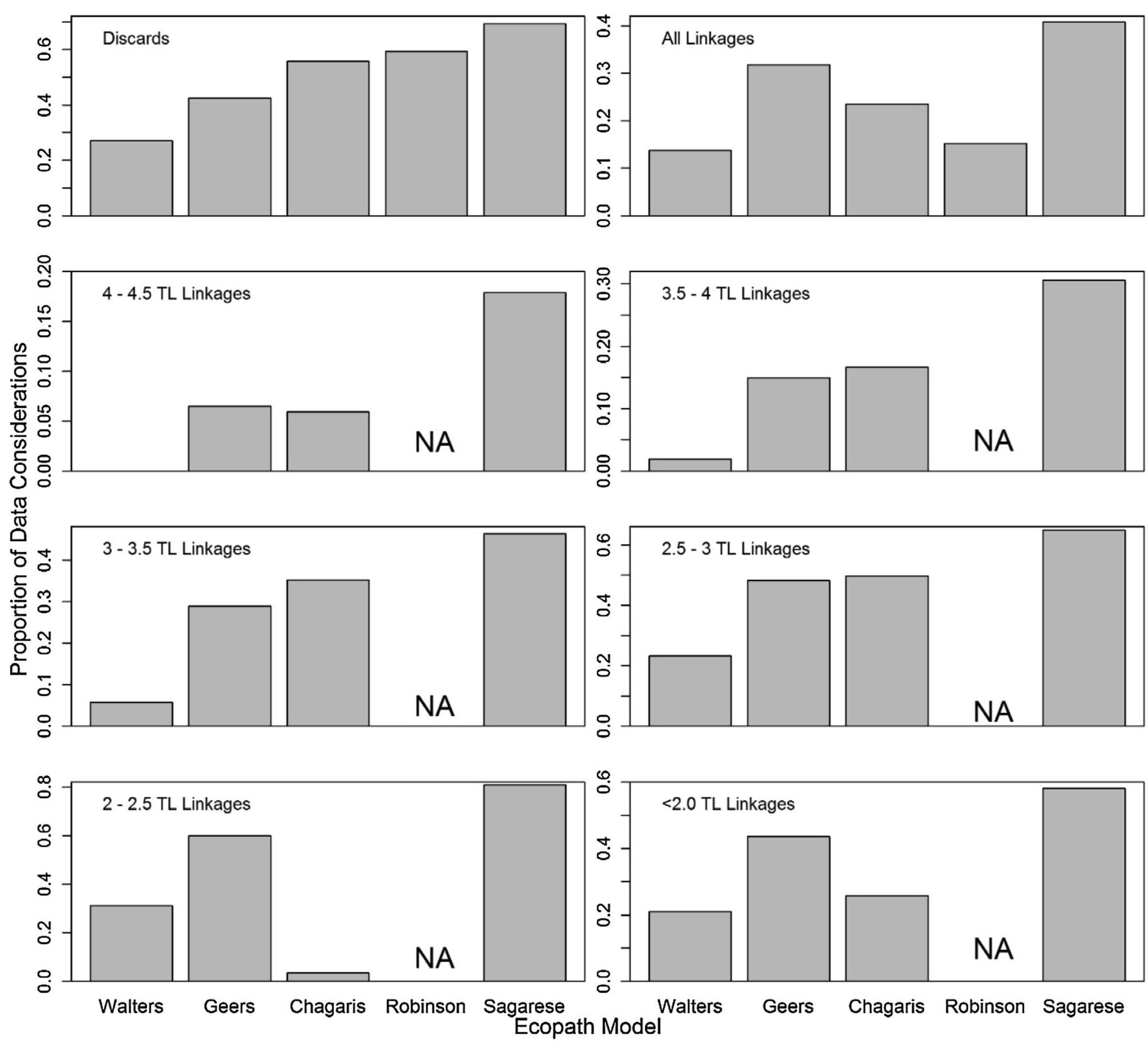

Fig. 5. Comparison of the proportion of species influenced by fishery discards and the proportion of realized predator-prey linkages for all functional groups combined and for subsets of trophic levels (i.e., 4.0–4.5, 3.5–4.0, etc.). Note that estimated trophic levels were not reported in (Robinson et al., 2015) or their Supplementary material.

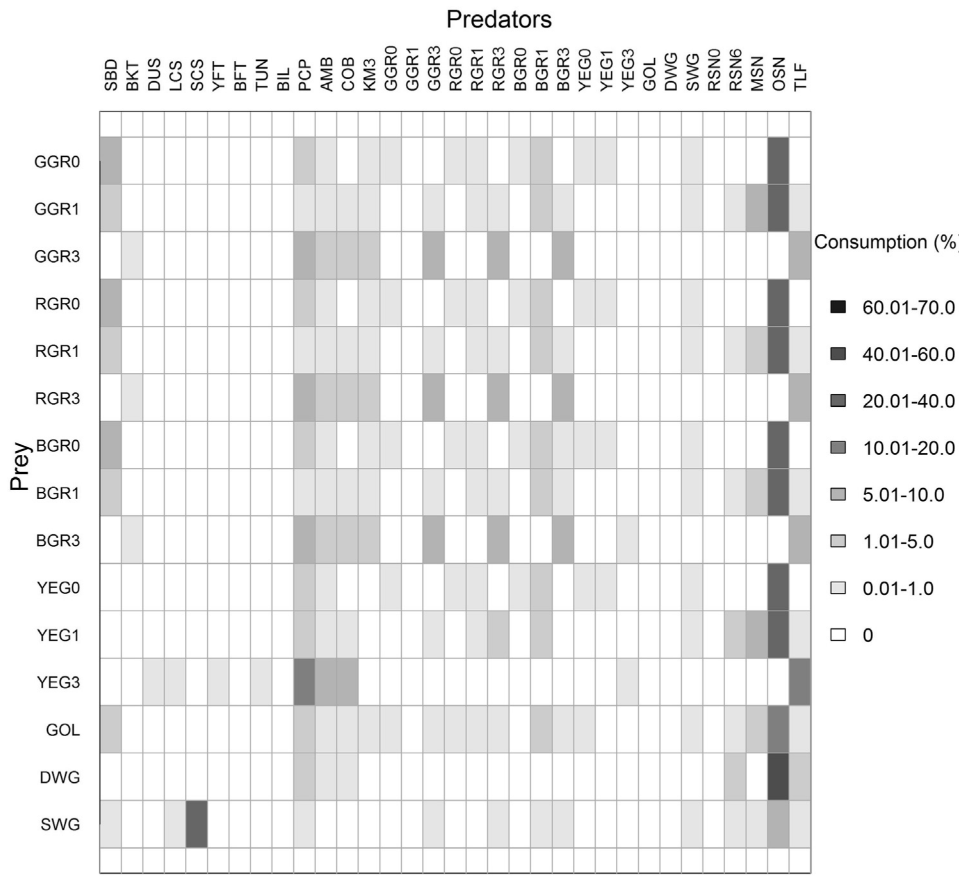

Fig. 6. Estimated consumption of groupers by predatory groups within the northern Gulf of Mexico (nGoM) Ecopath model. Both predator and prey functional groups are as defined in Table 3.

weaker influence compared to predators. For adult groupers, the most detrimental effects were exhibited by predatory species and commercial and recreational fisheries.

The largest positive MTIs were indicative of a greater benefit of resource *j* to fishing fleet *i*, such as the crab trap fishery benefiting from the increased production of crabs (+0.88), the fish trawl fishery benefiting from demersal coastal invertebrate feeder production (+0.84), the dredge fishery benefiting from sessile epifauna production (+0.83), the cast net fishery benefiting from mullet production (+0.83), the shrimp trawl fishery benefiting from shrimp production (+0.74), the seine fishery benefiting from mullet production (+0.71), the lobster trap fishery benefiting from mobile epifauna production (+0.60), the purse seine fishery benefiting from menhaden production (+0.59), and red grouper impacting the trap fishery (+0.52) (Fig. 7).

Groupers did not have a large influence on the ecosystem-wide scale according to keystoneness (−3.31 to −0.63) nor total impact rating (0.00–0.24). Pelagic coastal piscivores (e.g. carangids) and snappers had the largest influence on the ecosystem structure according to keystoneness and total impact (pelagic coastal piscivores: KS = 0.34, $\varepsilon = 2.16$; snappers: KS = 0.24, $\varepsilon = 1.72$), suggesting these two groups are the top trophic compartments in the northern Gulf of Mexico (Fig. 8) outside of fisheries. Relatively high keystone values were also exhibited by mobile epifauna (KS = −0.04) and oceanic piscivores (e.g. Atlantic cutlassfish (*Trichiurus lepturus*)) (KS = −0.19) whereas sharks, tunas and billfish were relatively low in keystoneness (KS range: −0.65 for small coastal sharks to −3.50 for bluefin tuna) (Fig. 8), despite their relative importance to fisheries.

4. Discussion

Here we present a detailed fisheries ecosystem model describing the upper TL dynamics in the GoM and employ this model to elucidate species interactions using the best empirical information on the system. Diet references from regions outside the GoM were critical in elucidating predator diets at higher TLs such as sharks, billfish, tunas, and seabirds, and helped capture predation pressure on species such as economically important groupers. Potential grouper predators, some of which have not been included in previous GoM models, included frigatebirds, various shark genera and species, tunas, billfish, coastal piscivores, snappers, groupers, tilefish, and benthic piscivores (e.g. inshore lizardfish (*Synodus foetens*)). The diet matrix enhanced biological realism by allowing for high connectance and a high level of omnivory in the system, likely a result of the high biodiversity within the northern Gulf of Mexico ecosystem (McEachran and Fechhelm, 1998, 2006; Fautin et al., 2010). The inclusion of additional energy pathways in the nGoM Ecopath model indicated the ecosystem may be more resistant to perturbations than previously thought, assuming a direct link between trophic complexity and ecosystem resilience (Vidal and Pauly, 2004; Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015).

Ecosystem studies are often specialized and designed to address specific questions (e.g. menhaden and jellyfish energy transfer, Robinson et al., 2015) and therefore may incompletely represent the effects of fisheries if modeled dynamics are missing critical trophic linkages or sources of mortality such as bycatch. Models designed to explore lower TL dynamics (e.g. WFS EwE model, Okey et al., 2004) may not adequately capture higher TL interactions

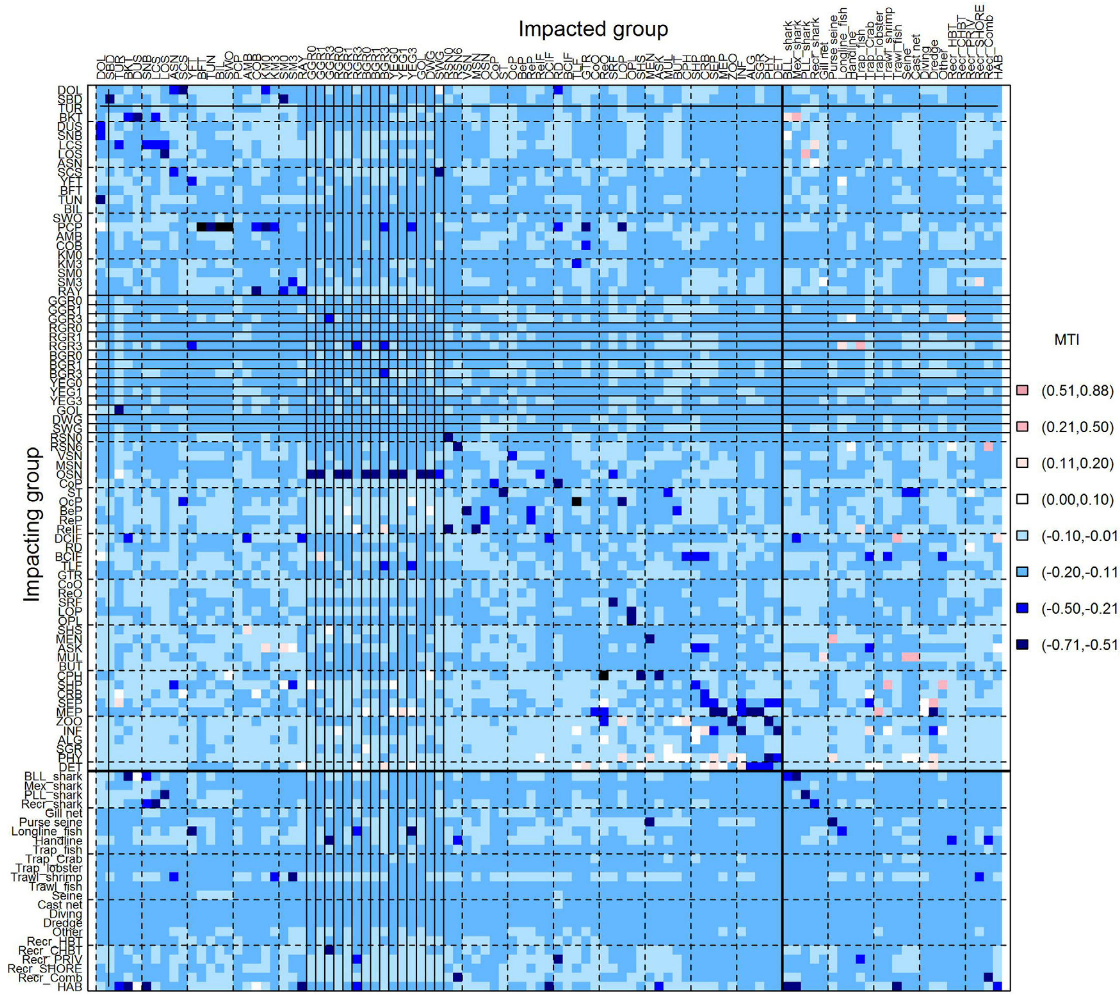

Fig. 7. Mixed trophic impacts analysis (MTI) from the northern Gulf of Mexico detailing the combined direct and indirect trophic impacts of impacting groups (i.e. predators or fishing fleets) on impacted groups (i.e. prey or resources). Thick solid lines separate species from fisheries. Horizontal and vertical solid lines identify grouper functional groups. Dashed lines are included at even intervals to enhance readability. Both impacting and impacted groups are as defined in Table 3.

(e.g. Apalachicola, FL EwE model, Carlson, 2007). The nGoM Ecopath model was developed with a focus on regional-scale GoM fisheries, as evident by the large number of higher TL functional groups (i.e. fishes) compared to lower TL groups (i.e. invertebrates). The advantage of focusing on fish predators in the nGoM, via a fish-centric model (Zeller and Reinert, 2004; Pinnegar et al., 2005; Chagaris et al., 2015), is that the model can provide advice on ecosystem-level perturbations due to changes in species abundance and fleet dynamics which can complement single-species fishery management. While it is possible that weak trophic links may exist between species, trophic linkages in the nGoM model were scrutinized and reduced if deemed unrealistic (e.g. 6% of anchovy-silverside-killifish diet was composed of menhaden due to one observation). However, we acknowledged that a rare prey group can be heavily affected by predation of an abundant predator (Walters et al., 2008; Ainsworth et al., 2010). All documented trophic linkages were included in the diet matrices, i.e., we did not exclude observed instances of consumption even if they were very rare as removal of weak links can lead to model instability (Pinnegar et al., 2005). However, we recognize the ongoing limitations of existing diet matrices particularly for lower TL invertebrates and for soft-bodied, digestion prone species that may be systematically underrepresented in diets.

The majority of federally managed species are assessed and managed on a single stock basis throughout the GoM, necessitating region-wide information such as biomass estimates and prey composition estimates to assess the system in a more holistic effort. In addition to substantially improving the parameterization of trophic interactions in the GoM, development of the nGoM Ecopath model included the explicit incorporation of bycatch from all fisheries operating in the region, including the large-scale purse seine and shrimp trawl fisheries which land a substantial amount of non-target, economically important species (Guillory and Hutton, 1982; de Silva et al., 2001). The incorporation of these two fundamental datasets in conjunction with the influence of red tides on species mortality represented a large advancement over previous models. Multiple diagnostics revealed that the mass-balance nGoM Ecopath model was biologically realistic and consistent with empirical information, such as decomposition of production with increasing TL (Link, 2010). Therefore, the nGoM Ecopath model is appropriate for the evaluation of ecosystem-based fisheries management because of its large-scale spatial domain, comprehensive trophic dynamics of ecologically and economically important species, and explicit integration of fisheries harvest, bycatch removals, and mortality due to red tides.

4.1. Trophic importance of groupers

Although ecosystem modeling has been undertaken in the northern GoM since the early 1990s (e.g. Browder, 1993), repre-

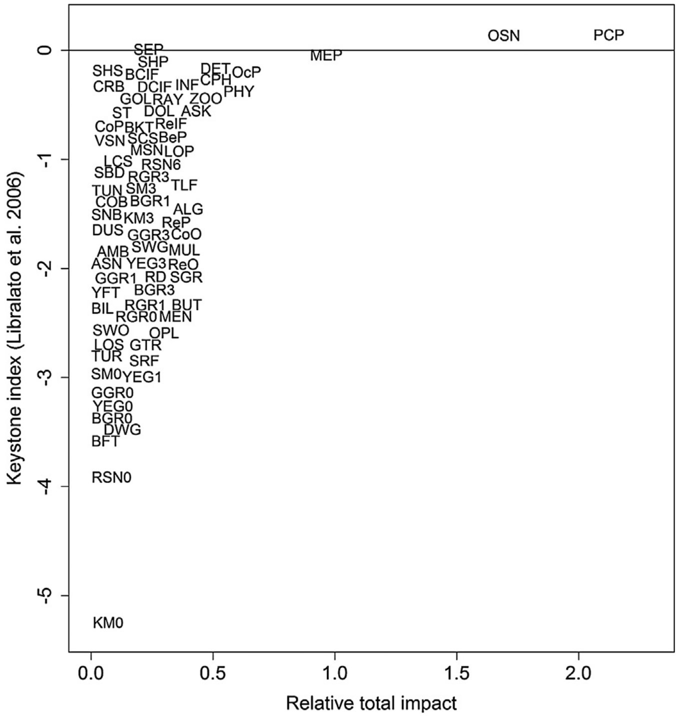

Fig. 8. Total ecosystem impact versus keystoneness for functional groups derived from the northern Gulf of Mexico (nGoM) Ecopath model. Groups with large values of relative total impact and keystone index represent groups that impose a large influence on the ecosystem. Functional groups are as defined in Table 3.

sentation of higher TL predator-prey linkages is often limited due to the lack of data specific to the GoM (Masi et al., 2014; Chagaris et al., 2015). Data limitations of top predator diets will likely persist until stomach contents can be routinely and comprehensively collected; however, our meta-analysis and evaluation of grouper as prey for top predators fills an important information gap necessary to understand the trade-off between grouper-targeted fisheries, management, and restoration of top predators in the GoM (e.g., can shark populations be restored if bycatch in the Gulf Menhaden purse seine reduction fishery is reduced).

A previous coastal GoM EwE model attempted to explore system responses to the effects of differing management options; however, its utility was questioned because of unexpected model results (Simons et al., 2013) such as the strong response of catfish abundance to reduced shrimp trawling and their uncertain trophic dominance (Walters et al., 2008). Further, simulations conducted with the coastal GoM EwE model did not consider the impact predators would have on grouper dynamics (Walters et al., 2008). In the GoM menhaden EwE model, simulated patterns in grouper abundance revealed puzzling trends, for example the lack of recovery of the species complex when fishing was removed, attributed partly to relatively large predation mortality rates by rebuilding of the red snapper population (Geers et al., 2014). It is anticipated that simulations with a tuned nGoM Ecopath model, due to its comprehensive and statistically-derived diet matrix, will provide a more representative picture of changes in ecosystem structure resulting from the impacts of fishing or ecological stressors (e.g. competition, predation).

Alternative means of identifying potential predators of groupers have been undertaken, specifically the estimation of trophic interactions within the WFS using the spatially-structured, individual-based multi-species model OSMOSE-WFS (Shin and Cury, 2004; Grüss et al., 2015, 2016). Within OSMOSE, predation is opportunistic and size-based, with predator-prey interactions determined by overlapping spatial distributions, predator/prey size ratios, and the accessibility of prey to predators which depends on their vertical distribution and morphology (Grüss et al., 2015, 2016). In contrast to Ecopath, which requires a diet matrix as model input, OSMOSE estimates a diet matrix based on species dynamics and behavior (Shin and Cury, 2004). Predators of gag and red groupers common to both OSMOSE-WFS and the nGoM Ecopath model included king mackerel, amberjacks, gag grouper, and red grouper (Grüss et al., 2015, 2016). In contrast to the nGoM Ecopath model, OSMOSE-WFS identified reef carnivores (e.g. grunts) as predators of age 0 gag (8%) and adult red snapper as a predator of age 0 red grouper (7%) (Grüss et al., 2016), likely due to the fact that OSMOSE-WFS can only accommodate a limited number of functional groups inhabiting the West Florida Shelf. Our meta-analysis did not identify reef carnivores including grunts, wrasses, and porgies as potential predators; however, additional sampling efforts in shallow waters using seines or spearfishing on reef habitats combined with the use of genetic DNA-barcoding tools (e.g. Hargrove et al., 2012) could greatly enhance our understanding of the predator assemblage for age 0 groupers and other juvenile fishes (Masi et al., 2014; Sagarese et al., 2016). Particularly within diet data derived from the GoM, there is a paucity of length measurements accompanying identified prey and therefore little understanding of which life-history stages are susceptible to predation for many ecologically important fish species.

For larger species which may be difficult to encounter and sample via traditional field surveys, an OSMOSE model focused on higher TL predators (e.g. seabirds, sharks, billfish, tunas) could further elucidate potential trophic interactions concerning groupers as prey, in the absence of diet observations. Unfortunately, this application would require substantial modifications to the current OSMOSE framework including: (1) the ability to include more higher TL groups, which is currently limited by computational power required for calibration; (2) accurate representation of seabird population dynamics; and (3) the representation of other marine organisms that have a life cycle very different from that of fish species (e.g. most marine mammals).

Within the dietary meta-analysis, the inclusion of studies that use a Serranidae prey group required some assumption of how best to allocate "unidentified Serranidae" diet amongst Serranid groups. We chose to allocate prey items based on relative biomass within the GoM ecosystem under the assumptions that the prey groups identified by the meta-analysis constitute potential prey items and that the proportional biomass contribution is homogeneous throughout the GoM. While an alternative approach involves allocating unidentified prey among identifiable prey groups, this was not an option because groupers were rarely identified as prey items due to the difficulty in obtaining stomach samples of higher TL piscivores (Geers et al., 2014; Masi et al., 2014; Chagaris et al., 2015). The benefit of the approach employed in the present study is that newly acquired data can easily be incorporated and used to update the diet matrix. As stomach-level information becomes available from the GoMexSI database (Simons et al., 2013), subsequent refinement of existing diet matrices (sensu Ainsworth et al., 2010; Masi et al., 2014) may be possible. In addition, GoMexSI may provide critical data regarding the diet composition of systematically underrepresented invertebrates.

4.2. Ecological implications

Although several Ecopath models exist for either the GoM as a whole or for its many subsystems including the continental shelf, estuaries, lagoons, and coral reefs (Vidal and Pauly, 2004; Geers 2012), only two Ecopath models have undergone a comprehensive network analysis (Libralato et al., 2006): WFS EwE (Okey et al., 2004) and a western Gulf of Mexico Ecopath model (Arreguín-Sánchez et al., 1993, 2004). The nGoM Ecopath model revealed possible trends in interspecies interactions, for example strong top-down control (e.g. pelagic coastal piscivore predation on some tunas and mackerels) and bottom-up control (e.g. epifauna production effects on juvenile grouper biomass).

Keystone species play a structuring role within ecosystems and food webs and frequently comprise higher TL predators such as seals, cetaceans, and sharks (Libralato et al., 2006; Valls et al., 2015). The removal of these species often triggers strong ecosystem responses (Sala and Sugihara, 2005). Generally, keystone species tend to exhibit relatively low biomass (Libralato et al., 2006) because keystoneness indices are penalized for high abundance (Nuttall et al., 2011). For the GoM, pelagic coastal piscivores and other snappers were identified as most influential on ecosystem dynamics according to keystoneness and total ecosystem impact, despite their relatively high biomass. These two functional groups displayed relatively high TLs (pelagic coastal piscivores: 3.84, snappers: 3.43) and the most frequent large negative MTIs. Snappers strongly affected groupers, reef-associated invertebrate feeders, and surface pelagics (e.g. flyingfish (Exocoetidae)) whereas pelagic coastal piscivores affected tunas, billfish, cobia, king mackerel, adult groupers, red drum, gray triggerfish, and large oceanic planktivores. A similar importance of pelagic coastal piscivores was identified by Libralato et al. (2006) for the WFS Ecopath model (Okey et al., 2004) and for jacks in the southwestern GoM Ecopath model (Arreguín-Sánchez et al., 1993, 2004). Species which exhibit bottom-up effects on the ecosystem can also be considered keystone species (Libralato et al., 2006), such as mobile epifauna (e.g. amphipods and ostracods among others) in the present study. That the current study identified two species groupings (other snapper and coastal piscivores) as keystone species indicates that there is substantial need to further refine these species groupings to understand the ecosystem dynamics of the GoM. The impact of the complex of species in these mixed groups is unlikely to be uniformly distributed.

Large-scale fisheries are capable of exhibiting high keystoneness within ecosystems (Kitchell et al., 2002). For example, the removal of top predators by fishing can initiate a trophic cascade, characterized by increased prey abundance of top predators and the simultaneous decrease of their prey abundance (Dulvy et al., 2004; Sala and Sugihara, 2005). Within the GoM, the influence of fisheries and other anthropogenic stressors (e.g. Campagna et al., 2011) have the potential to destabilize marine food webs by removing species at higher TLs (Sala and Sugihara, 2005). However, highly complex marine systems such as the GoM may be less likely to exhibit trophic cascades than other ecosystems because of high richness, connectance and degree of omnivory (Dulvy et al., 2004; Sala and Sugihara, 2005), as observed by Grüss et al. (2016).

4.3. Management implications

Within the GoM, red tides ("Florida red tides") caused by the dinoflagellate *Karenia brevis* frequently occur in the eastern GoM, can devastate populations of marine mammals and sea turtles (Landsberg et al., 2009), and can cause extensive fish kills (Flaherty and Landsberg, 2011). Blooms generally originate offshore (Steidinger and Vargo, 1988) and are transported inshore by winds and tidal currents (Steidinger and Haddad, 1981). Current understanding of how red tides impact marine resources is largely derived from accounts of dead fish washing inshore or opportune encounters with floating fish (e.g. Driggers et al., 2016). Herein, our network analysis revealed detrimental impacts of red tides on sharks, skates and rays, and demersal coastal invertebrate feeders such as black drum, as well as adult red and gag grouper. Significant impacts of red tide mortality have been suggested for groupers because much of their habitat coincides with areas susceptible to red tide blooms, with anecdotal evidence of mortality observed following the 2005 and 2014 red tide events (Walter et al., 2013; Driggers et al., 2016). Unfortunately, very little quantitative evidence exists due to the difficulty in recovering identifiable fish from areas impacted by red tide events. Although stock assessments for both gag and red groupers have incorporated red tide mortality into modeled dynamics, considerable uncertainty remains regarding which age classes are susceptible to red tides and the mechanisms behind red tide mortality.

The explicit incorporation of bycatch in the nGoM Ecopath model from all fisheries operating in the region, such as the large-scale purse seine fishery targeting Gulf menhaden (Guillory and Hutton, 1982; de Silva et al., 2001), represents a substantial improvement over past GoM models where the inclusion of fishery discards was relatively sparse. Discarded fish were mainly attributed to the shrimp trawl in Walters et al. (2008) and to recreational fisheries in Geers et al. (2014). The Gulf menhaden reduction fishery is the second largest U.S. commercial fishery by weight (Vaughan et al., 2007; NMFS, 2010; Geers et al., 2014), and represents a key source of bycatch for sharks (Guillory and Hutton, 1982; de Silva et al., 2001; SEDAR, 2006a), mackerels, pelagic coastal piscivores, coastal piscivores (e.g. seatrout), invertebrate feeders (e.g. Atlantic croaker *Micropogonias undulatus*), and other forage fish (e.g. threadfin shad *Dorosoma petenense*) (Guillory and Hutton, 1982; de Silva, 1998). This approach reflects the best available science and will enhance modeling of the dynamics between fishery removals and species biomass trends in the GoM. Research efforts should be expended to update the relative magnitude and species composition in the bycatch, particularly for the Gulf menhaden reduction fishery.

Additional research efforts are planned using the dynamic Ecosim module to tune the nGoM Ecopath model to long-term time series to calibrate the estimates of biomass and catches over time. Once calibrated, the model will be used by the Southeast Fisheries Science Center (SEFSC) to simulate potential restoration measures for the GoM, including changes in species biomass related to reduced fishing effort (e.g., reduction of fishing effort on forage fish), mortality, and bycatch. A better understanding of predator-prey interrelationships and the impact of massive prey removals may be gained by identifying key policies that target one component of the food web, evaluating the predicted responses of associated predators and prey using the ecosystem model, and monitoring the observed changes in populations. Upon completion, development of a nGoM EwE model is expected to advance ecosystem-based fisheries management efforts for the GoM by providing better informed predicted responses to restoration efforts such as bycatch reduction. Although the nGoM Ecopath model was developed to represent the ecosystem between 2005 and 2009, which can be considered pre-DWH, the results of our study create a baseline of ecosystem structure, prior to the large-scale disturbance, to compare with community structure post DWH (i.e. 2011–2015) to determine if changes in ecosystem structure are detectable.

Multiple diagnostics indicated that the modeled food web was biologically realistic, with intuitive and empirically supported estimates of species interactions identified through network analysis. However, there were some inconsistencies within diagnostics concerning trends in biomass, P/B, Q/B, and R/B. Many multi-stanza groups focused on age 0 s and juveniles exhibited lower than expected values of biomass (B), consumption (Q), and production (P) and ratios of production to biomass (P/B), consumption to biomass (Q/B), and respiration to biomass (R/B), likely due to limited data on abundance (e.g. juvenile groupers). When multi-stanza groups were excluded, diagnostics improved considerably (B: 0.65 to 0.82; P: 0.68 to 0.80; Q: 0.72 to 0.85; R: 0.73 to 0.86; P/B: 0.55 to 0.70; Q/B: 0.57 to 0.89; R/B: 0.54 to 0.86). The PREBAL analysis revealed ratios of human removals (i.e., fishing, bycatch) to consumptive removals of a taxa exceeding 1 for adult groupers, sharks, adult red snapper, menhaden, and scombrids, many of which represent key apex predators and may be exempt from the preferred ratio below 1 (Link, 2010). However, this result may suggest a continued incomplete understanding of trophic dynamics in the GoM, even following the comprehensive literature review and meta-analysis of predation events.

5. Conclusion

The present study represents a significant step towards enhancing our understanding of upper TL dynamics in the northern Gulf of Mexico ecosystem for ecosystem-based fisheries management and restoration. Further extensions of the modeling would benefit from a merger of the extensive lower TL complexity in Robinson et al. (2015) with the higher TL detail in our nGoM Ecopath model. Despite the well-recognized limitations in quantifying trophic interactions within the GoM, the methods used integrated the vast majority of available information on trophic dynamics within the ecosystem. By focusing on socioeconomically important trophic groups across coastal, reef, and pelagic communities, and on a region-wide scale, the nGoM Ecopath model advanced the knowledge of GoM food web structure and community dynamics. Ultimately, this model will facilitate exploration of species dynamics in response to both intentional (reducing bycatch, ecosystem restoration) and unintentional (oil spills, nutrient discharge) anthropogenic impacts and episodic events (e.g. harmful algal blooms).

Author contributions

Designed and analyzed the models: SS, ML. Conceived the models: SS, ML, JW. Wrote the paper: SS, ML, JW. All authors have approved the final article.

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Appendix A. Details on data inputs

Biomass: Biomass estimates ($t\,km^{-2}$) were obtained from the primary literature, recent stock assessments, or survey data when feasible. Estimates of absolute biomass were available for some federally assessed species from stock assessments (Table A.2). For higher TL functional groups lacking absolute biomass estimates, biomass was estimated as the mean annual removals (catch and dead discards where applicable during 2005–2009) divided by recent fishing mortality (F) estimates (2005–2009) obtained from stock assessments. However, it is important to note that this approach provides a good approximation of biomass but only over a limited range of low fishing mortality rates and assumes that catches are proportional to the biomass present in the area (Okey and Mahmoudi, 2002). For unfished species, parameter estimates were obtained from previous GoM and WFS Ecopath models and scaled to the area of our study region.

Production per biomass (P/B): For all fish functional groups where estimates were unavailable in the stock assessment literature, M was estimated using empirical equations (Pauly, 1980). If a proxy of F was unavailable, knowledge of stock status was used to estimate P/B with the following equations:

$$P/B = F + M, \tag{A.1}$$

where

$$F = (0.5 + P_{OF} + P_{OFO}) + M, \tag{A.2}$$

where both the probabilities of being overfished (P_{OF}) and of overfishing occurring (P_{OFO}) were based on stock status (yes, +0.25; unknown (UNK), +0.1; no, +0). As an example, an overfished stock not experiencing overfishing and with an M of one would have a P/B of 1.75 (P/B = (0.5 + 0.25 + 0.0) + 1). Additional details on P/B ranges for fish groups can be found in Table A.3.

Consumption per biomass (Q/B): Estimates of Q/B (yr^{-1}) were obtained using empirical equations of Pauly et al. (1990) and a temperature of 25 °C assumed representative of mean annual conditions within the GoM. The equation of Palomares and Pauly (1989) was also used to estimate Q/B if estimates of the aspect ratio ($(\text{tail height/area})^2$) were available. Additional details on Q/B ranges for fish groups can be found in Table A.3. For the marine mammal group (e.g. bottlenose dolphin *Tursiops truncatus*), Q/B was estimated using the equation modified from Innes et al. (1987) in Trites and Heise (1996). For the seabird group, Q/B was estimated using weight parameters presented in Okey and Mahmoudi (2002) and the equation given in Nilsson and Nilsson (1976).

Fleets, landings and discards: Seventeen commercial fishing fleets were considered including the bottom longline shark fishery, Mexican shark fishery, pelagic longline shark fishery, gill net, purse seine, pelagic longline (fish), handline, fish traps/pots, crab traps/pots, lobster traps/pots, shrimp trawl, fish trawl, haul seine, cast net, diving, dredge, and other. Six recreational fleets were considered including a shark fishery, headboat angling, charterboat angling, private sport angling, shore angling, and combined. Commercial and recreational fisheries for shark species were reported as separate fleets due to expected differences in fisher behavior (e.g. targeting) and gear (e.g. bottom versus pelagic longline). In addition, Mexican landings of blacktip shark and sandbar shark (*Carcharhinus plumbeus*) in U.S. waters were substantial and therefore reported as a Mexican fishery. Landings and discards of functional groups were obtained from stock assessment documents and from NOAA commercial and recreational statistics. Landings and discards ($t\,km^{-2}\,yr^{-1}$) were quantified by averaging values between 2005 and 2009 where possible (or as recent to that time period as available). For functional groups not federally or internationally assessed, including many of the invertebrate groups, landings were obtained from the National Marine Fisheries Service Fisheries Statistics Division (NMFS-FSD) database (http://www.st.nmfs.noaa.gov) (NMFS-FSD, 2014). When necessary, discard mortality rates were obtained from stock assessments. If no discard mortality information was available, an estimate of 100% was assumed.

Table A.1
Functional groups included in the northern Gulf of Mexico (nGoM) Ecopath model focused on important predators and managed species.

No	Functional group	Abbreviation	Included taxonomic groups
1	Dolphins	DOL	Delphinidae
2	Seabirds	SBD	Phalacrocoracidae, Pelecanidae, Laridae, Gaviidae, Sternidae, Hydrobatidae, Procellariidae, Pandionidae, Accipitridae
3	Sea turtles	TUR	Cheloniidae, Dermochelyidae
4	Blacktip shark	BKT	*Carcharhinus limbatus*
5	Dusky shark	DUS	*C. obscurus*
6	Sandbar shark	SNB	*C. plumbeus*
7	Large coastal sharks	LCS	Sphyrnidae, Odontaspididae, large Carcharhinidae
8	Large oceanic sharks	LOS	Lamnidae, Alopiidae, *Prionace glauca*
9	Atlantic sharpnose shark	ASN	*Rhizoprionodon terraenovae*
10	Small coastal sharks	SCS	Small Carcharhinidae, Triakidae, *Sphyrna tiburo*
11	Yellowfin tuna	YFT	*Thunnus albacares*
12	Bluefin tuna	BFT	*T. thynnus*
13	Tropical tunas	TUN	*Katsuwonus pelamis*, *T. obesus*, *T. atlanticus*
14	Billfish	BIL	Istiophoridae
15	Swordfish	SWO	*Xiphias gladius*
16	Pelagic coastal piscivores	PCP	Coryphaenidae, Pomatomidae, Carangidae, Echeneidae, Belonidae, Lobotidae, *Sarda* spp., *Euthynnus* spp., *Auxis* spp., *Acanthocybium solandri*
17	Amberjacks	AMB	*Seriola dumerili*, *S. fasciata*
18	Cobia	COB	*Rachycentron canadum*
19	Juvenile king mackerel	KM0	Ages 0 to 3 years *Scomberomorus cavalla*
20	Adult king mackerel	KM3	Ages 3 and older *S. cavalla*
21	Juvenile Spanish mackerel	SM0	Ages 0 to 3 years *S. maculatus*
22	Adult Spanish mackerel	SM3	Ages 3 and older *S. maculatus*
23	Skates/rays	RAY	Rajidae, Gymnuridae, Myliobatidae, Dasyatidae, Rhinobatidae, *Ginglymostoma cirratum*
24	Age 0 gag grouper	GGR0	Age 0 to 1 year *Mycteroperca microlepis*
25	Juvenile gag grouper	GGR1	Ages 1 to 3 years *M. microlepis*
26	Adult gag grouper	GGR3	Ages 3 and older *M. microlepis*
27	Age 0 red grouper	RGR0	Age 0 to 1 year *Epinephelus morio*
28	Juvenile red grouper	RGR1	Ages 1 to 3 years *E. morio*
29	Adult red grouper	RGR3	Ages 3 and older *E. morio*
30	Age 0 black grouper	BGR0	Age 0 to 1 year *M. bonaci*
31	Juvenile black grouper	BGR1	Ages 1 to 3 years *M. bonaci*
32	Adult black grouper	BGR3	Ages 3 and older *M. bonaci*
33	Age 0 yellowedge grouper	YEG0	Age 0 to 1 year *Hyporthodus flavolimbatus*
34	Juvenile yellowedge Grouper	YEG1	Ages 1 to 3 years *H. flavolimbatus*
35	Adult yellowedge grouper	YEG3	Ages 3 and older *H. flavolimbatus*
36	Goliath grouper	GOL	*E. itajara*
37	Other deep grouper	DWG	*H. niveatus*, *H. nigritus*, *E. drummondhayi*, *H. mystacinus*
38	Other shallow grouper	SWG	*E. striatus*, *M. venenosa*, *M. interstitialis*, *E. adscensionis*, *E. guttatus*, *M. phenax*
39	Juvenile red snapper	RSN0	Ages 0 to 6 years *Lutjanus campechanus*
40	Adult red snapper	RSN6	Ages 6 and older *L. campechanus*
41	Vermilion snapper	VSN	*Rhomboplites aurorubens*
42	Mutton snapper	MSN	*Lutjanus analis*
43	Other snapper	OSN	Lutjanidae
44	Coastal piscivores	CoP	Megalopidae, Elopidae, Centropomidae, Albulidae
45	Sea trout	ST	*Cynoscion* spp.
46	Oceanic piscivores	OcP	Trichiuridae, Gempylidae, Bramidae, *Merluccius albidus*
47	Benthic piscivores	BeP	Paralichthyidae, Uranoscopidae, Synodontidae, Ophichthidae, Squatinidae
48	Reef/rubble-associated piscivores	ReP	Holocentridae, Sphyraenidae, Muraenidae, Congridae, *Rypticus* spp.
49	Reef-associated invertebrate feeders	RIF	Serranidae, Labridae, Scorpaenidae, Chaetodontidae, Priacanthidae, Haemulidae, Sparidae, *Ocyurus chrysurus*
50	Demersal coastal invertebrate feeders	DCIF	Sciaenidae, Ariidae, Gerreidae, *Trachinotus* spp., *Chloroscombrus chrysurus*, *Oligoplites saurus*, *Pagrus pagrus*, *Haemulon aurolineatum*, *Orthopristis chrysoptera*
51	Red drum	RD	*Sciaenops ocellatus*
52	Benthic coastal invertebrate feeders	BCIF	Pleuronectiformes, Triglidae, Polynemidae, Gobiidae, Ophidiidae
53	Tilefishes	TLF	Malacanthidae
54	Gray triggerfish	GTR	*Balistes capriscus*
55	Coastal omnivores	CoO	Tetraodontiformes, Ephippidae, *Lagodon rhomboides*
56	Reef omnivores	ReO	Pomacanthidae, Acanthuridae, Pomacentridae, Scaridae
57	Surface pelagics	SRF	Exocoetidae, Hemiramphidae
58	Large oceanic planktivores	LOP	*Manta birostris*, *Cetorhinus maximus*, *Rhincodon typus*, *Mola mola*
59	Oceanic planktivores	OPL	Argentinidae, Nomeidae
60	Sardine-herring-scad	SHS	Clupeidae, *Decapterus* spp.
61	Menhaden	MEN	*Brevoortia* spp.
62	Anchovy-silverside-killifish	ASK	Engraulidae, Atherinidae, Fundulidae
63	Mullet	MUL	Mugilidae
64	Butterfish	BUT	Stromateidae
65	Cephalopod	CPH	Cephalopoda
66	Shrimp	SHR	Penaeidae, Caridea shrimp
67	Crabs	CRB	Portunidae
68	Sessile epifauna	SEP	Porifera, Anthozoa, Tunicata, Bryozoa, Hydrozoa, Crinoidea, Mytilidae
69	Mobile epifauna	MEP	Malacostraca, Ostracoda, Echinoderma, Gastropoda, Pectinidae
70	Zooplankton	ZOO	Copepoda, Euphausiacea, Scyphozoa, planktonic eggs/larvae

Table A.1 (*Continued*)

No	Functional group	Abbreviation	Included taxonomic groups
71	Infauna	INF	Annelida, Nematoda, Bivalvia, Thalassinidea, Hippidae
72	Algae	ALG	Rhodophyta, Chlorophyta, Phaeophyta, Cyanophyta, Xanthophyta, Cyanobacteria
73	Phytoplankton	PHY	Bacillariophyceae, Dinoflagellata, Protozoa
74	Seagrass	SGR	Marine angiosperms
75	Detritus	DET	Calcareous debris, mud, organic matter, fishery discards, detritus

Table A.2
Estimates of biomass (t km^{-2}) used as initial inputs for the northern Gulf of Mexico (nGoM) Ecopath model with methods or references consulted. *refers to estimates from other studies which may not necessarily reflect GoM trends and are therefore considered unreliable. Note that the mass-balance process focused on modifying biomass for groups in which biomass estimates were thought untrustworthy.

No	Group	Initial biomass (t km^{-2})	Biomass reference
1	DOL	0.0211*	Fulling et al. (2003); NMFS (2013)
2	SBD	0.0091*	GoM menhaden EwE (Geers et al., 2014)
3	TUR	0.0021*	WFS red tide EwE (Gray, 2014)
4	BKT	0.1275	SEDAR (2012); 1/3 of biomass assumed to occur in GoM
5	DUS	0.0009	B = C/F
6	SNB	0.0536	B = C/F
7	LCS	0.0011	SEDAR (2006a)
8	LOS	0.0015	B = C/F
9	ASN	0.1114	SEDAR (2013c)
10	SCS	0.0487	SEDAR (2007); SEDAR (2013d); SEDAR (2011a)
11	YFT	0.0032	B = C/F
12	BFT	0.0005	B = C/F
13	TUN	0.0073	B = C/F
14	BIL	0.0003	B = C/F
15	SWO	0.0056	B = C/F
16	PCP	0.1183	B = C/F
17	AMB	0.0028	SEDAR (2014)
18	COB	0.0092	SEDAR (2013b)
19	KM0	0.0008	Estimated using multistanza
20	KM3	0.0221	B = C/F
21	SM0	0.0084	Estimated using multistanza
22	SM3	0.0710	B = C/F
23	RAY	0.2380*	GoM menhaden EwE (Geers et al., 2014)
24	GGR0	0.0009	Estimated using multistanza
25	GGR1	0.0090	Estimated using multistanza
26	GGR3	0.0190	B = C/F
27	RGR0	0.0015	Estimated using multistanza
28	RGR1	0.0198	Estimated using multistanza
29	RGR3	0.0679	B = C/F
30	BGR0	0.0001	Estimated using multistanza
31	BGR1	0.0015	Estimated using multistanza
32	BGR3	0.0047	B = C/F
33	YEG0	0.0008	Estimated using multistanza
34	YEG1	0.0059	Estimated using multistanza
35	YEG3	0.0227	B = C/F
36	GOL	0.0030*	WFS reef fish EwE (Chagaris et al., 2015)
37	DWG	0.0108	B = C/F
38	SWG	0.0077	B = C/F
39	RSN0	0.0018	Estimated using multistanza
40	RSN6	0.0726	B = C/F
41	VSN	0.0070	SEDAR (2006b)
42	MSN	0.0253	SEDAR (2008)
43	OSN	0.5016	B = C/F
44	CoP	0.2365	B = C/F
45	ST	0.2460*	Coastal GoM EwE (Walters et al., 2008)
46	OcP	0.0102	B = C/F
47	BeP	0.0030	B = C/F
48	ReP	0.0030	B = C/F
49	RIF	1.6290*	WFS reef fish EwE (Chagaris et al., 2015)
50	DCIF	2.9000*	Coastal GoM EwE (Walters et al., 2008)
51	RD	2.1660*	Coastal GoM EwE (Walters et al., 2008)
52	BCIF	2.2000*	GoM menhaden EwE (Geers et al., 2014)
53	TLF	0.0043	SEDAR (2011b)
54	GTR	0.0056	B = C/F
55	CoO	1.7850*	WFS reef fish EwE (Chagaris et al., 2015)
56	ReO	0.5383*	WFS reef fish EwE (Chagaris et al., 2015)
57	SRF	0.5630*	WFS reef fish EwE (Chagaris et al., 2015)
58	LOP	1.9436*	WFS red tide EwE (Gray, 2014)
59	OPL	0.0750*	WFS red tide EwE (Gray, 2014)
60	SHS	1.7000*	WFS red tide EwE (Gray, 2014)

Table A.2 (*Continued*)

No	Group	Initial biomass (t km^{-2})	Biomass reference
61	MEN	1.4425	SEDAR (2013a)
62	ASK	3.2000*	Coastal GoM EwE (Walters et al., 2008)
63	MUL	3.3500*	Coastal GoM EwE (Walters et al., 2008)
64	BUT	0.2003*	GoM menhaden EwE (Geers et al., 2014)
65	CPH	0.2670*	GoM menhaden EwE (Geers et al., 2014)
66	SHR	4.8092	B = C/F
67	CRB	0.2000*	Coastal GoM EwE (Walters et al., 2008)
68	SEP	18.6988*	WFS reef fish EwE (Chagaris et al., 2015)
69	MEP	53.6534*	WFS reef fish EwE (Chagaris et al., 2015)
70	ZOO	12.8940*	GoM menhaden EwE (Geers et al., 2014)
71	INF	20.0000*	Coastal GoM EwE (Walters et al., 2008)
72	ALG	29.7780*	Coastal GoM EwE (Walters et al., 2008)
73	PHY	175.6170*	Coastal GoM EwE (Walters et al., 2008)
74	SGR	25.0000*	Coastal GoM EwE (Walters et al., 2008)
75	DET	100.0000*	Coastal GoM EwE (Walters et al., 2008)

Table A.3
Estimates of natural mortality (M, yr^{-1}), production per biomass (P/B, yr^{-1}), consumption per biomass (Q/B, yr^{-1}), and production per consumption (P/Q) for teleost functional groups. Overfished and overfishing status was used to estimate P/B by serving as a proxy for the fishing mortality (F) which was then added to natural mortality to obtain total mortality (Z) (i.e. M + F = Z). UNK = unknown status. Empirical formulae were used to calculate natural mortality (Pauly, 1980) and consumption per biomass (Palomares and Pauly, 1989, 1998; Pauly et al., 1990). Minimum (Min), average, and maximum (Max) values were obtained by summarizing empirical estimates and also parameters given on www.fishbase.org (Froese and Pauly, 2015). Average M and Q/B were input as initial values and modified as needed to achieve mass balance.

				M				Q/B			
Group	Overfished	Overfishing	mult	M_{MIN}	$M_{AVERAGE}$	M_{MAX}	P/B	Q/B_{MIN}	$Q/B_{AVERAGE}$	Q/B_{MAX}	P/Q
BKT	No	No	0.5	0.380	0.398	0.417	0.597	3.1	3.6	4.5	0.166
DUS	Yes	Yes	1	0.080	0.087	0.095	0.175	1.8	2.2	2.8	0.080
SNB	Yes	Yes	1	0.126	0.128	0.130	0.256	1.1	2.3	3.4	0.113
LCS	Yes	Yes	1	0.080	0.197	0.638	0.395	1.1	2.6	4.5	0.153
LOS	Yes	Yes	1	0.100	0.137	0.180	0.274	0.9	2.7	9.6	0.102
ASN	No	No	0.5	0.388	0.388	0.388	0.582	5.8	6.7	7.4	0.087
SCS	Yes	Yes	1	0.080	0.306	0.470	0.612	2.2	3.7	6.3	0.164
YFT	Yes	No	0.75	0.483	0.588	0.692	1.029	4.3	8.4	11.6	0.123
BFT	Yes	Yes	1	0.100	0.283	0.490	0.567	3.0	3.8	4.3	0.151
TUN	No	Yes	0.75	0.308	0.635	0.983	1.111	3.9	9.3	32.6	0.120
BIL	Yes	Yes	1	0.360	0.464	0.592	0.927	1.7	4.9	14.5	0.191
SWO	No	No	0.5	0.158	0.184	0.210	0.276	3.4	4.0	5.3	0.069
PCP	UNK	UNK	0.7	0.212	0.637	1.900	1.082	2.3	6.3	13.0	0.171
AMB	Yes	Yes	1	0.431	0.431	0.431	0.863	3.3	3.9	5.2	0.221
COB	No	No	0.5	0.457	0.548	0.640	0.822	3.4	4.1	4.8	0.203
KM0	–	–	0.5								
KM3	No	No	0.5	0.299	0.299	0.299	0.449	2.7	3.5	4.0	0.128
SM0	–	–	0.5								
SM3	No	No	0.5	0.531	0.531	0.531	0.797	6.0	7.0	8.3	0.115
RAY	UNK	UNK	0.7	0.169	0.388	0.760	0.660	1.0	7.6	64.6	0.087
GGR0	–	–	0.5								
GGR1	–	–	0.5								
GGR3	Yes	Yes	1	0.285	0.312	0.340	0.625	3.5	4.3	5.0	0.145
RGR0	–	–	0.5								
RGR1	–	–	0.5								
RGR3	No	No	0.5	0.270	0.325	0.380	0.487	4.8	5.5	6.3	0.088
BGR0	–	–	0.5								
BGR1	–	–	0.5								
BGR3	No	No	0.5	0.290	0.314	0.339	0.472	3.1	3.8	4.5	0.124
YEG0	–	–	0.5								
YEG1	–	–	0.5								
YEG3	No	No	0.5	0.200	0.222	0.245	0.333	3.2	3.9	4.6	0.086
GOL	UNK	UNK	0.7	0.230	0.246	0.262	0.418	2.7	3.3	4.0	0.126
DWG	UNK	UNK	0.7	0.131	0.210	0.297	0.357	1.4	3.7	7.8	0.095
SWG	UNK	UNK	0.7	0.170	0.329	0.592	0.560	2.8	5.7	8.7	0.098
RSN0	–	–	0.5								
RSN6	Yes	No	0.75	0.269	0.329	0.409	0.576	4.6	5.3	6.2	0.108
VSN	No	No	0.5	0.360	0.386	0.413	0.580	3.8	4.5	5.4	0.129
MSN	No	No	0.5	0.365	0.383	0.400	0.574	4.3	5.0	5.8	0.115
OSN	UNK	UNK	0.7	0.210	0.488	0.938	0.830	3.0	5.3	10.6	0.158
CoP	UNK	UNK	0.7	0.160	0.457	0.749	0.777	2.7	5.8	9.3	0.134
ST	UNK	UNK	0.7	0.290	0.485	0.749	0.825	3.2	6.2	9.1	0.134
OcP	UNK	UNK	0.7	0.130	0.664	1.110	1.129	1.2	6.6	24.2	0.172
BeP	UNK	UNK	0.7	0.220	0.498	0.770	0.846	2.3	6.8	11.0	0.125
ReP	UNK	UNK	0.7	0.160	0.794	2.310	1.350	1.8	6.3	15.2	0.215
RIF	UNK	UNK	0.7	0.280	1.007	2.280	1.712	2.5	11.5	64.6	0.149
DCIF	UNK	UNK	0.7	0.220	0.805	2.010	1.369	2.1	7.1	22.4	0.192
RD	UNK	UNK	0.7	0.660	0.717	0.775	1.220	4.0	5.0	6.2	0.245
BCIF	UNK	UNK	0.7	0.370	1.256	3.390	2.135	2.8	13.4	40.2	0.159

Table A.3 (*Continued*)

				M				Q/B			
Group	Overfished	Overfishing	mult	M_{MIN}	$M_{AVERAGE}$	M_{MAX}	P/B	Q/B_{MIN}	$Q/B_{AVERAGE}$	Q/B_{MAX}	P/Q
TLF	No	No	0.5	0.230	0.242	0.255	0.364	2.2	2.6	3.5	0.137
GTR	Yes	Yes	1	0.544	0.592	0.640	1.184	3.8	5.9	7.8	0.200
CoO	UNK	UNK	0.7	0.410	0.805	1.458	1.369	4.8	9.3	22.6	0.148
ReO	UNK	UNK	0.7	0.320	0.978	2.120	1.662	4.2	19.8	52.3	0.084
SRF	UNK	UNK	0.7	1.060	1.406	1.869	2.390	9.4	19.1	34.1	0.125
LOP	UNK	UNK	0.7	0.035	0.079	0.130	0.134	0.6	1.3	3.7	0.101
OPL	UNK	UNK	0.7	0.520	2.104	3.689	3.578	4.7	38.2	83.3	0.094
SHS	UNK	UNK	0.7	0.470	1.521	6.410	2.585	4.3	10.5	30.6	0.245
MEN	No	No	0.5	0.585	0.858	1.090	1.287	5.7	10.0	31.4	0.129
ASK	UNK	UNK	0.7	0.536	1.761	2.530	2.994	9.2	18.5	40.9	0.162
MUL	UNK	UNK	0.7	0.340	0.622	0.784	1.058	7.4	15.0	25.3	0.071
BUT	UNK	UNK	0.7	0.680	1.921	2.983	3.265	5.6	8.9	12.5	0.369

Table A.4
References documenting predation events on grouper or unidentified Serranids by predator groups (in bold) and by species. For all references outside the Gulf of Mexico, the general study region is given and includes the Pacific (Pac), Atlantic (Atl), Caribbean (Cari), Mediterranean (Med), and Indian (Ind). If no region is listed, the study was conducted in the Gulf of Mexico.

Predator	*Epinephelus* sp. references	*Mycteroperca* sp. references	*Acanthistius* sp. references	*Cephalopholis* sp. references	Serranidae references
Seabirds					
Great frigatebird (*Fregata minor*)	Schreiber and Hensley (1976) – Pac				Calixto-Albarrán and Osorno (2000) – Pac
Sharks					
Blacktip shark (*Carcharhinus limbatus*)	Dudley and Cliff (1993) –Ind				Dudley and Cliff (1993) – Ind; Heupel and Hueter (2002)
Dusky shark (*Carcharhinus obscurus*)			Smale (1991) – Atl		Simpfendorfer et al. (2001) – Ind
Bull shark (*Carcharhinus leucas*)	Cliff and Dudley (1991) – Ind				Cliff and Dudley (1991) – Ind
Scalloped hammerhead (*Sphyrna lewini*)	Avendaño-Alvarez et al. (2013)				Galván-Magaña et al. (2013) – Pac; Hussey et al. (2011) Atl/Ind
Blacknose shark (*Carcharhinus acronotus*)				Fischer et al. (2009) – Atl	
Tunas					
Yellowfin tuna (*Thunnus albacares*)					Dragovich and Potthoff (1972) – Atl; Lewis and Axelsen (1967) – Cari; Logan et al. (2013) – Atl
Bluefin tuna (*Thunnus thynnus*)					Karakulak et al. (2009) – Med
Other tunas					
Skipjack tuna (*Katsuwonus pelamis*)					Dragovich and Potthoff (1972) – Atl
Billfish					
Striped marlin (*Kajikia audax*)					Abitia-Cárdenas et al. (1997) – Pac
Sailfish (*Istiophorus platypterus*)	Rosas-Alayola et al. (2002) – Pac				Jolley (1977) – Atl; Rosas-Alayola et al. (2002) – Pac
Piscivores					
Pelagic					
King mackerel (*Scomberomorus cavalla*)	Saloman and Naughton (1983) – Atl				Menezes (1969) – Atl
Almaco jack (*Seriola rivoliana*)					Manooch and Haimovici (1983) – Atl
Crevalle jack (*Caranx hippos*)		Saloman and Naughton (1984)			Saloman and Naughton (1984)
Greater amberjack (*Seriola dumerili*)					Manooch and Haimovici (1983) – Atl
Bluefish (*Pomatomus saltatrix*)					Buckel et al. (1999) – Atl; Naughton and Saloman (1984)

Table A.4 (*Continued*)

Predator	*Epinephelus* sp. references	*Mycteroperca* sp. references	*Acanthistius* sp. references	*Cephalopholis* sp. references	Serranidae references
Cobia (*Rachycentron canadum*)	Rohit and Bhat (2012) – Ind				Franks et al. (1996); Gómez-Canchong et al. (2004) – Cari; Knapp (1951); Meyer and Franks (1996)
Dolphinfish (*Coryphaena hippurus*)					Lewis and Axelsen (1967) – Cari
Benthic					
Predator	*Epinephelus* sp. references	*Mycteroperca* sp. references	*Acanthistius* sp. references	*Cephalopholis* sp. references	Serranidae references
Inshore lizardfish (*Synodus foetens*)					Sheridan (2008)
Groupers					
Gag grouper (*Mycteroperca microlepis*)		Naughton and Saloman (1985)			Weaver (1996)
Red grouper (*Epinephelus morio*)					Weaver (1996)
Scamp (*Mycteroperca phenax*)					Matheson et al. (1986) – Atl; Nelson (1988)
Yellowmouth grouper (*Mycteroperca interstitialis*)					Nelson (1988)
Yellowfin grouper (*Mycteroperca venenosa*)					Randall (1967) – Cari
Blueline tilefish (*Caulolatilus microps*)					Ross (1982) – Atl
Snappers					
Red snapper (*Lutjanus campechanus*)					Schwartzkopf (2014); Szedlmayer and Lee (2004)
Mutton snapper (*Lutjanus analis*)	Freitas et al. (2011) – Atl				
Dog snapper (*Lutjanus jocu*)				Randall (1967) – Cari	Gómez-Canchong et al. (2004) – Cari
Schoolmaster (*Lutjanus apodus*)					Randall (1967) – Cari

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