A revised diet matrix to improve the parameterization of a West Florida Shelf Ecopath model for understanding harmful algal bloom impacts

Holly A. Perryman[a,b,*], Joseph H. Tarnecki[c], Arnaud Grüss[a,d], Elizabeth A. Babcock[a], Skyler R. Sagarese[e], Cameron H. Ainsworth[f], Alisha M. Gray DiLeone[g]

[a] Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
[b] Institute of Marine Research, Nordnesgaten 33, 5005 Bergen, Norway
[c] Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32608, USA
[d] School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98105-5020, USA
[e] Southeast Fisheries Science Center, Sustainable Fisheries Division, 75 Virginia Beach Drive, Miami, FL 33149-1099, USA
[f] College of Marine Science, University of South Florida, 140 7th Avenue South, St. Petersburg, FL 33701, USA
[g] NOAA/National Marine Fisheries Service, Southeast Regional Office, 263 13th Avenue South, St. Petersburg, FL 33701, USA

ARTICLE INFO

ABSTRACT

Harmful algal blooms (HABs) are a growing concern in the West Florida Shelf (WFS) region. An Ecopath with Ecosim (EwE) model of the WFS explicitly simulating HABs was previously developed to illuminate the potential impacts of blooms of the dinoflagellate *Karenia brevis* (colloquially referred to as "red tides") on the WFS ecosystem. However, the diet matrix of the Ecopath component of this EwE model (referred to as "WFS-HAB Ecopath") was based largely on sparse, cursory information and not on local survey data. Here, we revise the diet matrix of the WFS-HAB Ecopath model using predictions of a robust statistical model that incorporates local survey data and employs the Dirichlet distribution and maximum likelihood estimation. The relative impacts of both the revised diet matrix and red tide mortality scenarios on model structure are explored by comparing four alternative WFS-HAB Ecopath models: (i) the base model; (ii) a model employing the revised diet matrix; (iii) a model with elevated red tide mortality; and (iv) a model with both the revised diet matrix and elevated red tide mortality. Incorporating the revised diet matrix into the WFS-HAB Ecopath model had a relatively large impact on ecosystem structure (i.e., trophic organization, mortality rates, trophic interaction strengths, and omnivory). Elevated red tide mortality had virtually no impact on ecosystem structure aside from altering the contribution of fishing, natural, and red tide mortalities to the total mortality of functional groups; however, elevated red tide mortality might have meaningful implications in dynamic simulations, which should be explored in future studies. Collectively, results showed that incorporating the revised diet matrix into WFS-HAB Ecopath, which revealed a number of new predator-prey linkages, led to a more complex and interconnected food web. Specifically, prey items were generally consumed by a broader variety of predators, which contrasts with the base WFS-HAB Ecopath model where many prey, particularly juvenile fishes, were subjected to exceedingly high predation mortality rates from specific predators. The incorporation of the revised diet matrix into the WFS-HAB Ecopath model discussed herein is a fundamental step towards increasing the realism of trophic interactions in the model, which is particularly important as these trophic interactions define starting conditions for dynamic simulations.

1. Introduction

The ecosystem services provided by the Gulf of Mexico are invaluable for the U.S. economy, particularly those from the West Florida Shelf (WFS) (Fig. 1; Plantier-Santos et al., 2012; Chagaris, 2013; Karnauskas et al., 2013). However, the productivity of the WFS ecosystem may be greatly impacted by harmful algal blooms (HABs) (Walsh et al., 2011). The WFS regularly experiences blooms of the
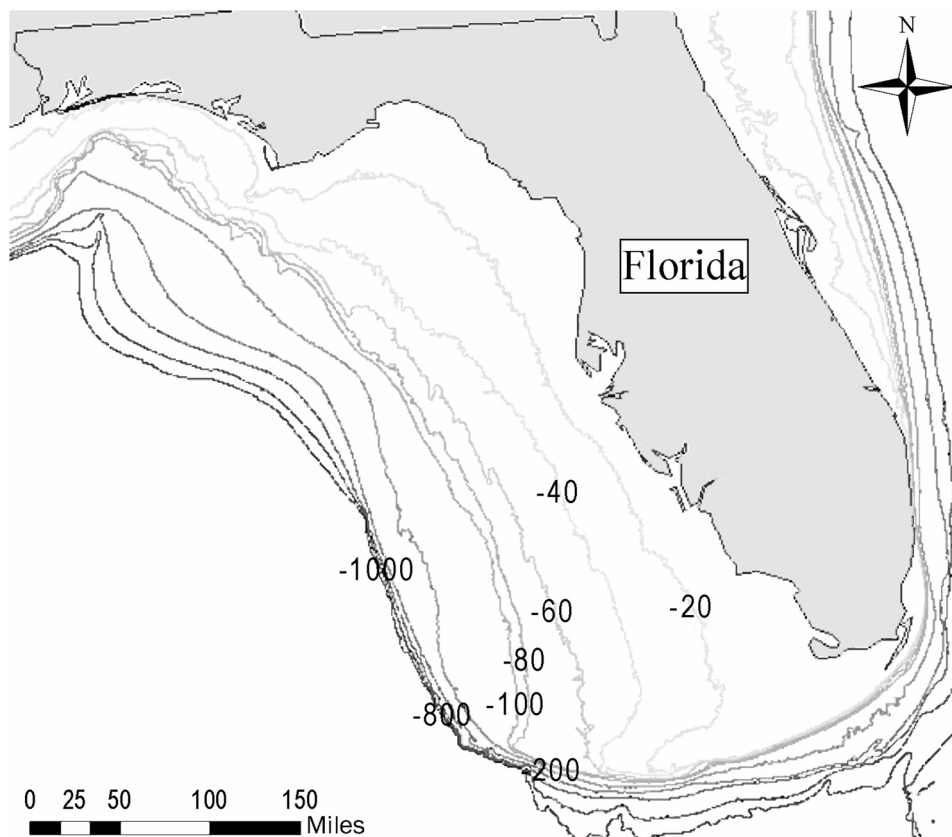
Fig. 1. Map of the West Florida Shelf (WFS) in the Gulf of Mexico. Depth contours are labeled in $20-$, $40-$, $60-$, $80-$, $100-$, $200-$, $800-$, and $1000-$ m contours. The area considered in the WFS-HAB Ecopath model spans approximately 170,000 km^2 between Florida's Gulf coast and the $200-$ m depth contour. This image was created with ArcGIS using political boundary data from French and Schenk (2005) and bathymetry data from Eakins et al. (2011).

dinoflagellate *Karenia brevis*, colloquially referred to as "red tides". When blooms of *K. brevis* become massive, the lysis of *K. brevis* cells results in the release of a neurotoxin called brevetoxin (Steidinger et al., 1998; Landsberg et al., 2009). Aerosolized brevetoxin can have strong negative impacts on local human communities via health issues (Kirkpatrick et al., 2004; Fleming et al., 2005). Moreover, direct exposure to brevetoxin can alter the sodium-potassium channels of aquatic vertebrates, eventually leading to death (Kirkpatrick et al., 2004). Blooms of *K. brevis* can also indirectly harm marine fauna by causing excessive hypoxia, turbidity, and shading (Okey et al., 2004; Landsberg et al., 2009; Klemas, 2012). Persistent blooms can result in widespread die-offs of fish and other aquatic animals, including protected species, ultimately impacting the structure of local marine communities through trophic cascades (Okey et al., 2004; Dupont and Coy, 2008; Landsberg et al., 2009; Flaherty and Landsberg, 2011) and reducing the catch rates of local fisheries (Landsberg et al., 2009; Driggers et al., 2016). Although HAB events have been documented on the WFS as early as 1844 (Ingersoll, 1881; Rounsefell and Nelson, 1966; Steidinger et al., 1998), their ecosystem effects are still relatively unclear and robust strategies for coping with their economic implications remain to be established. Understanding HABs is a top research priority in the Gulf of Mexico, partly because there are concerns that blooms of *K. brevis* are increasing in frequency and intensity over time (Brand and Compton, 2007; Grüss et al., 2017; Harford et al., 2018). Therefore, there is a need for tools designed specifically to evaluate the potential ecosystem impacts of HABs to assist management and mitigation efforts (Heil and Steidinger, 2009).

Sophisticated ecosystem simulation models such as applications of the trophodynamic Ecopath with Ecosim (EwE) with Ecospace (Walters et al., 1999, 2010) can explicitly consider a comprehensive suite of marine organisms, their trophic interactions and the effects of the abiotic environment on species dynamics. Such models have been identified as key tools for exploring the potential ecosystem impacts of HABs on the WFS (Grüss et al., 2017; O'Farrell et al., 2017). The

Ecopath component of EwE provides a static mass-balance representation of a food web, which serves as a starting point for dynamic modeling (Christensen and Pauly, 1992; Christensen and Walters, 2004). The Ecosim component of EwE allows one to simulate food web dynamics at monthly time steps by altering fishing mortality, fishing effort, and abiotic environmental forcing functions (Walters et al., 1997, 2000). Finally, the Ecospace component of EwE allows one to simulate food web and fishing fleet dynamics and changes in the abiotic environment over time and space (Walters et al., 2010; de Mutsert et al., 2016).

An EwE model explicitly simulating red tides was previously developed to evaluate the ecosystem impacts of HABs, referred to here as "WFS-HAB EwE" (Okey and Mahmoudi, 2002; Okey et al., 2004; Gray, 2014; Sagarese et al., 2015; Gray DiLeone and Ainsworth, 2019). However, the diet matrix of the basal component of WFS-HAB EwE – "WFS-HAB Ecopath" – was developed based on reports from the Florida Fish and Wildlife Research Institute (FWRI), information provided by FishBase (Froese and Pauly, 2018) and SeaLifeBase (Palomares and Pauly, 2018), and a variety of stomach content and feeding habit studies not necessarily specific to the WFS (see Okey and Mahmoudi (2002) for details). Because much of this information was qualitative and based on expert knowledge, there was a considerable amount of uncertainty regarding the diet matrix in the WFS-HAB Ecopath model. The diet matrix fed into sophisticated ecosystem models, such as EwE with Ecospace or the Atlantis modeling platform (Fulton et al., 2004, 2011), has a substantial impact on the predictions of these models. In particular, even small changes in the biomass of prey consumed in Ecosim, which is based on the diet matrix defined in Ecopath, can result in the severe depletion of some species, particularly juvenile fishes (Walters et al., 2008, 2010). Therefore, it is important to build a robust diet matrix for the Ecopath component of EwE with Ecospace models (Grüss et al., 2017; O'Farrell et al., 2017). Fortunately, detailed quantitative diet data on the WFS are now plentiful due to monitoring efforts (Grüss et al., 2018a). Moreover, robust statistical modeling approaches

using maximum likelihood are available to estimate diet proportions for informing ecosystem models (Ainsworth et al., 2010; Masi et al., 2014; Tarnecki et al., 2016; Sagarese et al., 2016, 2017).

The objectives of this study were to (i) develop a revised diet matrix for the WFS using predictions of a robust statistical model that incorporates local survey data and (ii) evaluate the changes in ecosystem structure for WFS-HAB Ecopath in response to modifications, including the revised diet matrix and elevated red tide mortality. Because the static ecosystem structure provided by Ecopath serves as a starting point for dynamic modeling with Ecosim and spatio-temporal modeling with Ecospace, the revised diet matrix would refine the representation of the spatio-temporal dynamics of red tides within the WFS and impacts on vulnerable species groups for future simulations (Grüss et al., 2018b). First, we reviewed the Ecopath modeling approach and the development of the base WFS-HAB Ecopath model considered in this study (i.e., Gray, 2014; Gray DiLeone and Ainsworth, 2019). Second, we developed a revised diet matrix for WFS-HAB Ecopath based on predictions from a statistical model using the Dirichlet distribution fitted to empirical diet data (Ainsworth et al., 2010; Masi et al., 2014; Tarnecki et al., 2016; Sagarese et al., 2016, 2017). We compared this revised diet matrix to the diet matrix described in the base WFS-HAB Ecopath model to evaluate changes in predator-prey linkages, prey preferences, and similarities. Third, we developed four alternative versions of the WFS-HAB Ecopath in a factorial design with the base and revised diet matrices, and low versus elevated red tide mortalities. Finally, we compared ecosystem structure across the four alternative versions of WFS-HAB Ecopath by exploring (i) PREBAL diagnostics (Link, 2010, 2016), (ii) basic estimates of Ecopath (e.g., trophic levels (TL), and mortality rates), and (iii) trophic metrics including mixed trophic impact indices (Ulanowicz and Puccia, 1990), trophic interaction strengths, and omnivory indices (Pauly et al., 1993).

2. Materials and methods

2.1. The Ecopath modeling approach and the WFS-HAB Ecopath model

2.1.1. The Ecopath modeling approach

Ecopath is a mass-balance approach for describing the trophic structure of an aquatic ecosystem (Christensen and Pauly, 1992; Pauly et al., 2000). In Ecopath, a comprehensive suite of functional groups (i.e., groups of species that have similar trophic, life history and niche characteristics) are explicitly considered, typically including detritus groups, primary producer groups, and invertebrate, fish, turtle, seabird and mammal groups (Pauly et al., 2000). These functional groups are represented either as single biomass pools or as multi-stanza functional groups that account for ontogenetic shifts in habitat and/or diet (Walters et al., 2008). Ecopath relies on two master equations that (i) limit loss terms to no more than that group's available production (Eq. (1)), and (ii) define the group's productivity with respect to its consumption and maintenance needs (Eq. (2)) (Christensen and Walters, 2004):

$$P_i = Y_i + B_i \bullet M2_i + E_i + BA_i + M0_i \tag{1}$$

$$P_i = Q_i - R_i - U_i \tag{2}$$

where P_i is the production of group i; Y_i is the fisheries yield for group i; B_i is the biomass of group i; $M2_i$ is the total predation mortality rate of group i; E_i is the net migration (emigration - immigration) rate of group i; BA_i is the biomass accumulation rate of group i; $M0_i$ is the "other mortality" rate of group i, which is equivalent to $P_i(1\text{-}EE_i)$, where EE_i is the ecotrophic efficiency of group i which represents the production of group i explicitly considered within the modeled system; Q_i is the consumption of group i; R_i is the respiration of group i; and U_i is the unassimilated food of group i.

These two equations can be re-expressed as:

$$B_i \bullet \left(\frac{P}{B}\right)_i = Y_i + \sum_j^n B_j \bullet \left(\frac{Q}{B}\right)_j \bullet DC_{ij} + E_i + BA_i + B_i \bullet \left(\frac{P}{B}\right)_i \bullet (1 - EE_i) \tag{3}$$

and

$$B_i \bullet \left(\frac{Q}{B}\right)i = B_i \bullet \left(\frac{P}{B}\right)_i + R_i + U_i \tag{4}$$

where $(P/B)_i$ is the production of group i per unit of biomass (i.e., the productivity of group i), which is equal to the total mortality rate of group i (Christensen and Walters, 2004); $(Q/B)_i$ is the consumption rate of group i per unit of biomass; DC_{ij} is the element of the diet matrix fed into Ecopath that describes the proportion of group i in the diet of group j; and n is the total number of groups represented in the Ecopath model. For each group i, an Ecopath model requires at least three of the following four data inputs: B_i; $(P/B)_i$; $(Q/B)_i$; and EE_i. If one of these four data inputs is not provided by the user, the missing data input is estimated during the mass-balance process. During the mass-balance process, Ecopath estimates several quantities that are useful to characterize the structure of the modeled system, such as the TL of functional groups.

2.1.2. The WFS-HAB Ecopath model

The conceptual model in Fig. 2 summarizes the evolution of the first WFS-HAB Ecopath model (Okey and Mahmoudi, 2002; Okey et al., 2004) to the WFS-HAB Ecopath model considered herein (Gray, 2014; Gray DiLeone and Ainsworth, 2019). First, the Ecopath model was updated to reflect the WFS ecosystem in 2014 by reparametrizing biomass, landings and productivity. Second, functional groups not present in the first WFS-HAB Ecopath model (Okey and Mahmoudi, 2002; Okey et al., 2004) but considered vulnerable to HABs were added based on literature (Steidinger et al., 1973) and the FWRI fish kill database (Florida Fish and Wildlife Research Institute, 2015). The FWRI fish kill database consists of publicly reported approximate numbers and species of dead fishes seen along the WFS coast during *K. brevis* blooms. In total, WFS-HAB Ecopath explicitly considers 81 functional groups, including two marine mammal groups (dolphins and manatees), one seabird group, one turtle group, 49 fish groups (of which 11 are multi-stanza groups representing adults and juveniles), 19 invertebrate groups (of which one is a multi-stanza group representing adults and juveniles, and four are zooplankton groups), one microbial heterotroph group, five autotroph groups, and three detritus groups (Appendix Table A.1). Third, catch-per-unit-effort (CPUE) time series of biomass and landings were used to reparametrize WFS-HAB Ecopath to 1980 values (i.e., the historical model, which serves as the starting point for future dynamic simulations). The historical model allowed for simulations to investigate the model's ability to recreate observed time series (Gray, 2014; Gray DiLeone and Ainsworth, 2019).

The fourth step for updating WFS-HAB Ecopath was the integration of HAB mortality (Fig. 2), which was accomplished using a pseudo-fishing fleet referred to as the "HAB fleet". This "fleet" comes in addition to the ten fishing fleets explicitly considered in WFS-HAB Ecopath (trawl, recreation, headboats, gill/trammel net, spear/gig, hook/line, purse seine, haul seine, long line, and traps). The HAB fleet is a discard-only fleet, so the biomass "caught" by the HAB fleet is immediately cycled into the detritus pools and, consequently, immediately available to detritivore functional groups (Gray, 2014; Gray DiLeone and Ainsworth, 2019). In essence, the HAB fleet acts as a mortality forcing function which differs from the forcing function routine within EwE (Christensen et al., 2008). The FWRI fish kill database (Florida Fish and Wildlife Research Institute, 2015) was used to determine the functional groups vulnerable to red tides, and to construct an index of vulnerability to red tides for each functional group based on their prevalence in the database (Gray, 2014; Gray DiLeone and Ainsworth, 2019). Gray DiLeone and Ainsworth (2019) described in detail how an index of vulnerability to red tides was developed such that the functional groups
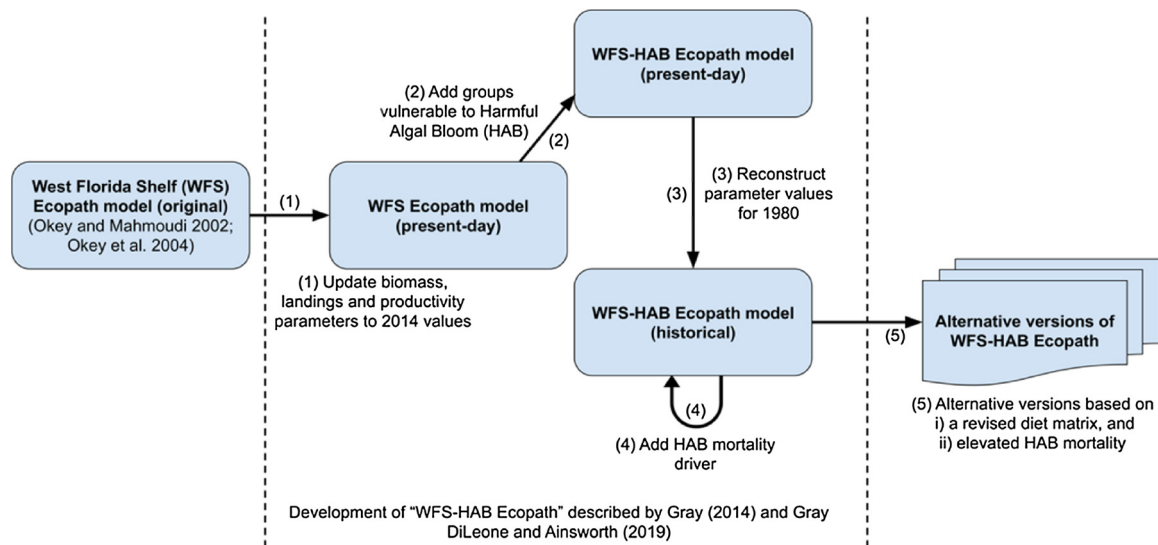
Fig. 2. Conceptual model showing the development of the West Florida Shelf (WFS) Ecopath model explicitly simulating Harmful Algal Bloom (HAB) mortality described by Gray (2014) and Gray DiLeone and Ainsworth (2019), referred to here as "WFS-HAB Ecopath" (1–4), which was used in this study to develop and evaluate four alternative Ecopath models (5).

that are more numerous in the fish kill database are more strongly affected by red tides in the WFS-HAB Ecopath model. Of the functional groups in WFS-HAB Ecopath, 38 correspond to species vulnerable to red tide (Appendix Table A.2; Gray, 2014; Gray DiLeone and Ainsworth, 2019). Applying the mortality effect to multiple functional groups allowed for the examination of interactions. Their method has been employed in other studies (e.g., Sagarese et al., 2017).

2.2. The development of alternative versions of WFS-HAB Ecopath

To evaluate the relative effects of improved diet information and elevated red tide mortality on the static snapshot in WFS-HAB Ecopath, we developed four alternative versions of WFS-HAB Ecopath: (i) the base WFS-HAB Ecopath model used in Gray (2014) and Gray DiLeone and Ainsworth (2019), which is fed with a highly uncertain diet matrix and represents WFS HABs of 1980, a year characterized by very weak red tide events; hereafter, we refer to this model as the "Base" model (Gray, 2014; Gray DiLeone and Ainsworth, 2019); (ii) a model with a revised diet matrix (referred to as the "Revised Diet" model): (iii) a model with elevated red tide mortality (referred to as the "Elevated HAB Mortality" model); and (iv) a model with both a revised diet matrix and elevated red tide mortality (referred to as the "Revised Diet and Elevated HAB Mortality" model). The rationale behind the consideration of these four alternative versions of WFS-HAB Ecopath was to evaluate the impacts of using a revised diet matrix on the trophic structure in WFS-HAB Ecopath, in the presence of very weak or severe red tide events.

2.2.1. Construction of a revised diet matrix for WFS-HAB Ecopath and attendant analyses

We constructed a revised diet matrix by employing a statistical model using the Dirichlet distribution and maximum likelihood estimation (Ainsworth et al., 2010; Masi et al., 2014; Tarnecki et al., 2016; Sagarese et al., 2016, 2017). This methodology allowed us to develop a diet matrix based on a large empirical diet dataset while (i) avoiding overestimation of the proportion of rarely consumed prey items in the diet of predators (Walters et al., 2006; Ainsworth et al., 2010); and (ii) allowing the estimation of error ranges of diet proportion estimates. Fish diet data for the statistical model were obtained from: (i) the Florida Fish and Wildlife Conservation Commission (FWC)'s Fisheries Independent Monitoring (FIM) database, and (ii) the Gulf of Mexico Species Interactions (GoMexSI) database (Simons et al., 2013; http://

gomexsi.tamucc.edu/). Samples in the FWC dataset consisted of individual stomach contents recorded in total volume of individual prey species, while samples in the GoMexSI dataset consisted of individual stomach contents recorded in volumetric proportions or weight (g) of individual prey species. Data for analyses were restricted to samples collected east of 88.0 °W to reflect the WFS ecosystem. A total of 14,989 samples across 43 predatory fish functional groups of the WFS-HAB Ecopath model were identified, with 14,643 samples obtained from FWC and 346 samples (from 18 predatory fish functional groups) obtained from the GoMexSI database, with no overlap between data sources. Prey diversity for each predatory fish group was measured using the Shannon-Wiener diversity index (Spellerberg and Fedor, 2003).

The diet matrix of WFS-HAB Ecopath was revised using the most recent and updated information from FWC and GoMexSI diet datasets. First, diet data was combined from FWC and GoMexSI datasets by normalizing all data to reflect percent prey proportions per individual fish. Individual fish species were then aggregated into the appropriate WFS-HAB functional group and fed into the statistical analysis described in Tarnecki et al. (2016). Briefly, we arranged the data into an 82×82 matrix (predator vs. prey) based on the WFS-HAB Ecopath functional groups. Given that it would be rare for each predatory fish group to feed on all WFS-HAB prey groupings, the most-frequently observed diet proportion throughout the matrix was zero. To correct for zero-inflation, pseudo-predator stomachs representing time-integrated diet compositions were created for each of the 43 predatory fish groups by randomly selecting 15 % of the observed stomachs and averaging the diet proportions together. Using bootstrapping with replacement 10,000 pseudo-predator stomachs were generated and the bootstrapped diet proportions were fitted to the Dirichlet density function using maximum likelihood method. The Dirichlet function is the multivariate generalization of the beta function – suitable for estimating diet proportions as it is defined on a [0, 1] interval and can take a variety of shapes (Ainsworth et al., 2010). The marginal beta distributions provided a mode corresponding to the diet proportion for a given predator-prey interaction that was most frequently observed, as well as confidence intervals around this mode (Tarnecki et al., 2016). We employed the "VGLM" function from the "VGAM" R package (Yee and Wild, 1996) for the maximum likelihood fitting procedure.

A food web diagram illustrating predator-prey connectivity on the WFS was created based on a hierarchical clustering analysis (Clarke et al., 2008; Masi et al., 2014). This analysis groups statistically similar

($α$ = 0.05) functional groups together based on similarity in the Bray-Curtis measures of distance (Bray and Curtis, 1957) between diets (Tarnecki et al., 2016). The Bray-Curtis dissimilarity measure was computed between each pair of samples as:

$$D_{jk} = \frac{\sum_{i=1}^{n} |y_{ij} - y_{ik}|}{\sum_{i=1}^{n} (y_{ij} + y_{ik})} \tag{5}$$

where y_{ij} is the count of the ith species in the jth sample; y_{ik} is the count of the ith species in the kth sample; and n is the number of species. A cluster analysis was performed on the dissimilarity measures by computing the cluster mode group averages, as well as a similarity profile analysis (Clarke et al., 2008) with 999 permutations to produce significant ($p < 0.05$) aggregations of predator groups as hierarchical clusters.

Comparisons of the revised diet matrix and the diet matrix used in the base WFS-HAB Ecopath model, referred to herein as the "base diet matrix", were made using analyses presented in Tarnecki et al. (2016). First, to determine differences in predator-prey connectivity between the base and revised diet matrices, we visually compared the presence/absence of prey groups amongst predator groups. Then, using similarity percentages (SIMPER; Clarke et al., 2008), we compared volume and prey composition between the base and revised diet matrices to measure resemblance; low percentages revealed high variability whereas high percentages revealed similar prey contributions and volumes between the base and revised diet matrices. The SIMPER analysis was streamlined by classifying predators into the following guilds: "elasmobranchs", "pelagic predatory fishes", "benthic/demersal fishes", "structure associated fishes", and "planktivorous fishes". Finally, we conducted a canonical analysis of principal coordinates (CAP; Anderson and Willis, 2003) using the Primer statistical package (v6; Clarke and Gorley, 2006) to reveal guild similarities and dissimilarities between food webs and potential refinements to guild correlation. The CAP was performed on the Bray-Curtis measures of distance (Bray and Curtis, 1957), resulting in CAP plots where groups clustered together have greater similarity in diet composition than groups far apart.

2.2.2. Representation of elevated HAB mortality

Both the Base model and the Revised Diet model used the baseline HAB mortality rates which represent WFS HABs in 1980, a year characterized by very weak red tide events (Gray, 2014; Gray DiLeone and Ainsworth, 2019). To represent elevated HAB mortality, both the Elevated HAB Mortality model and the Revised Diet and Elevated HAB Mortality model were developed to represent WFS HABs in 2005 – when the WFS experienced some of the most severe red tide events of the past 40 years (Sagarese et al., 2015). Gray (2014) estimated that the "effort" of the HAB fleet (i.e., the severity of the red tide events) in 2005 was around 256 % higher than the HAB fleet effort in 1980. Therefore, to capture elevated HAB mortality we multiplied the baseline HAB fleet mortality rates of the 38 functional groups vulnerable to HABs by 2.56. The HAB fleet mortality rates for all alternative versions of WFS-HAB Ecopath are provided in Appendix Table A.2.

2.3. Evaluation of the mass-balanced alternative versions of WFS-HAB Ecopath

Following recommended best practices in EwE models (Ainsworth and Walters, 2015; Heymans et al., 2016), we employed PREBAL diagnostics to evaluate each of the mass-balanced alternative versions of WFS-HAB Ecopath (Link, 2010, 2016). First, we examined trends in log-scaled biomass (B), production (P), consumption (C), respiration (R) and vital rates (i.e., P/B, C/B, and R/B) across functional groups and TLs, with the expectation of these metrics increasing with decreasing TL (Link, 2010). In addition, biomasses were expected to span five to seven orders of magnitude from the highest to lowest TL (Link, 2010). Next, we examined whether the biomasses relative to primary production

(PP), productions relative to PP, and P/B's relative to PP, as well as the predator-prey ratios of biomass and vital rates, were below 1 (Link, 2010, 2016). Lastly, additional metrics were calculated for each functional group, including: (i) P/C, which should range between 0.1 and 0.3; (ii) the consumption of the group relative to its production, which should remain below 1; (iii) the consumption by the group relative to its production, which should be greater than 1; and (iv) total human removals (i.e., fishing) relative to the consumption of the group, which should remain below 1 (Link, 2010).

2.4. Analysis of the trophic structure amongst the alternative versions of WFS-HAB Ecopath

To elucidate the impacts of the revised diet matrix and/or elevated red tide mortalities on the ecosystem structure of the WFS, we focused on three indices: (i) mixed trophic impact (MTI) indices, (ii) overall impact indices (ε), which measure trophic interaction strengths, and (iii) omnivory indices. The MTI analysis (Ulanowicz and Puccia, 1990) assesses direct and indirect interactions by quantifying the effect that group j has on group i, by taking the difference between a term expressing how much group i contributes to the diet of group j and a term giving the proportion of the predation on i that is due to j. Computed in Ecopath, MTI_{ji} indices for functional groups are based on predator-prey linkages whereas MTI_{ji} indices for fleets are based on fishing mortality rates. MTI_{ji} indices range from -1 to 1, where a positive MTI_{ji} index indicates that group j has a positive impact on group i, while a negative MTI_{ji} index indicates that group j has a negative impact on group i. The closer the MTI_{ji} index is to the bounds ($-1,1$) the stronger the impact, with -1 indicative of top-down control and 1 indicative of bottom-up control. We used the results from the MTI analysis to compute the overall impact index for each functional group. The overall impact from functional group j is the square root of the sum of squared MTI_{ji} indices, excluding MTI_{jj}. Lastly, the omnivory index was calculated for each functional group, which reflects the variance of prey trophic levels for a consumer (Pauly et al., 1993; Christensen et al., 2008). Lower omnivory indices indicate specialized consumers, feeding on few trophic levels, whereas larger indices indicate consumers that feed on a variety of trophic levels. Omnivory indices were provided by EwE Version 6.4.3, but all other indices were based on results from the "Network analysis" module in EwE Version 5 (Christensen and Walters, 2004) as initial attempts to use the Network analysis module in EwE Version 6.4.3 failed to converge due to the large number of trophic linkages in WFS-HAB Ecopath.

3. Results

3.1. Analyses of the revised food web

The diet compositions estimated in this study varied greatly from one predator to another (see Appendix Table A.3 for maximum likelihood diet estimates and 95 % confidence intervals). Piscivorous adult gag (*Mycteroperca microlepis*) preyed primarily (82 %) on fish functional groups including: structure associated coastal omnivores, structure associated coastal planktivores, juvenile pinfish (*Lagodon rhomboides*), structure associated coastal piscivores and the sardine-herring-scad complex. Coastal sharks had the most diverse diet overall (Appendix Table A.4), consuming crabs, fishes, shrimps and small infaunal invertebrates.

Hierarchical cluster analyses concentrated the 43 predatory fish groups into 21 clusters based on similarities in prey consumption (Appendix Table A.5). In addition, 9 non-fish boxes were created to complete the WFS food web diagram (Fig. 3). The cluster with the highest TL was that for large oceanic piscivores (e.g., swordfish, *Xiphias gladius*; Spanish mackerel, *Scomberomorus maculatus*; king mackerel, *S. cavalla*), while the groups dead carcasses and sediment detritus had the lowest trophic levels (Fig. 3). Sediment detritus was the sole food
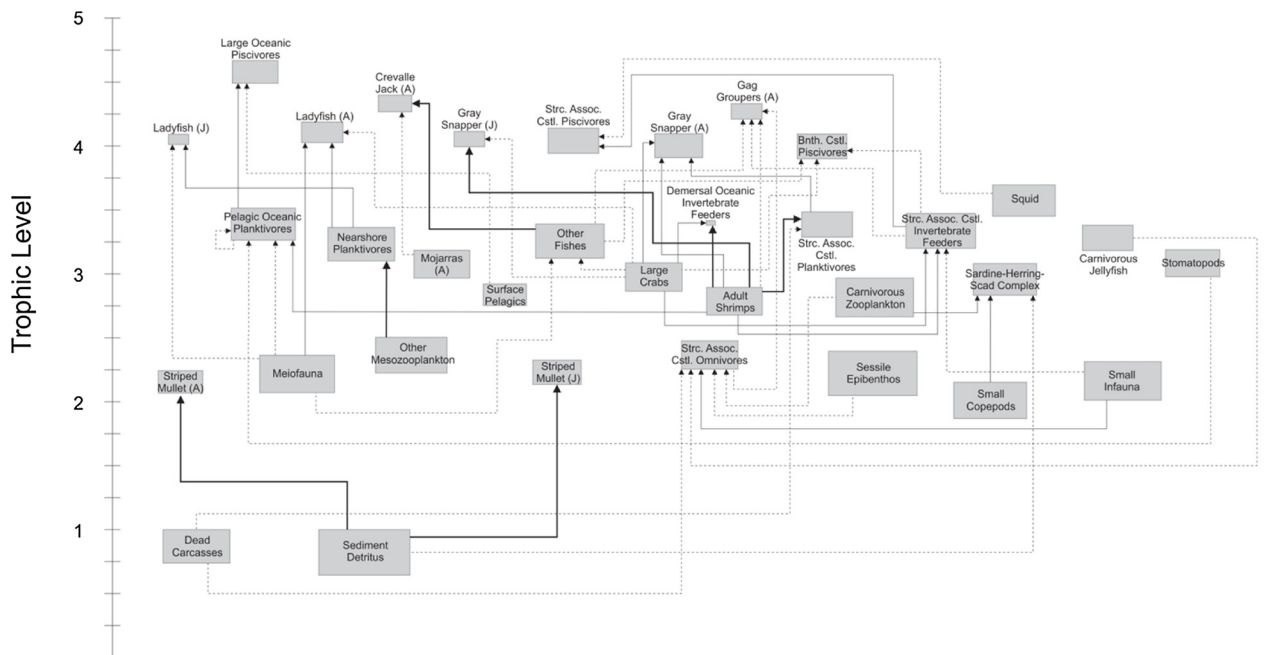
Fig. 3. Food web diagram illustrating predator-prey connectivity in the West Florida Shelf (WFS) region. Each box represents a cluster from the hierarchical cluster analysis and is named after the WFS-HAB Ecopath predator functional group containing the highest biomass estimates (Appendix Table A.5 details the WFS-HAB Ecopath functional groups composing the hierarchical clusters). Box areas are proportional to log biomass estimates and arrows indicate the flow of energy from prey to predators. Dotted lines indicate groups with ≥10 % − 20 % prey contributions, thin solid lines represent prey contributions ranging from > 20 % − 40 %, and thick solid lines indicate > 40 % prey contributions. Diets < 10 % were omitted from the food web diagram. The estimated trophic level of each grouping is indicated on the y-axis.

source for juvenile and adult striped mullet (*Mugil cephalus*), while the group "other mesozooplankton" was the sole food source for nearshore planktivores (Fig. 3). Adult shrimps were the main food source for demersal oceanic invertebrate feeders, juvenile gray snapper (*Lutjanus griseus*), and structure associated coastal planktivores (Fig. 3).

Comparing the base and revised food webs, we identified marked differences in predator-prey connections (Fig. 4). The revised food web incorporated 340 new prey linkages. Of the 43 predatory fish groups considered in the revised food web, 28 % had more than 10 prey groups added, 44 % had between 6 and 10 prey groups added, 23 % had between 1 and 5 prey groups added, and 5 % had no additional prey groups incorporated. Benthic coastal invertebrate feeders had the largest number of prey groups added (17). By contrast, juvenile ladyfish (*Elops saurus*) and nearshore planktivores showed no dissimilarity in prey groups between the base and revised food webs. Considering prey groups, 37 % experienced no change in the total number of predators with the revised food web, 27 % had between 1 and 5 new predators, 25 % had 6 to 10 new predators, 5 % had 11 to 15 new predators, and 6 % had 16 or more new predators. The largest increase in predator groups was for bivalves (20), followed by meiofauna (19).

The SIMPER analysis suggests that diet similarities between the base and revised food webs vary greatly among functional groups (Fig. 5). Planktivorous functional groups have the most similar diets between the base and revised food webs (median 78.25 %), whereas pelagic predatory fish functional groups have the most dissimilar diets (median 47.5 %). The diet of nearshore planktivores (e.g., anchovies) was the most similar (88.4 %) between food webs, largely because: (i) zooplankton, ichthyoplankton and copepods were the three main prey items of nearshore planktivores in the base food web; and (ii) with respect to nearshore planktivores, revising the WFS food web only resulted in an increase in the proportion of zooplankton, ichthyoplankton and copepods in the diet of this predator. By contrast, the diet of demersal oceanic invertebrate feeders (e.g., *Mullus auratus*) was the least similar (9.3 %) between food webs. While the base food web indicated that zooplankton, ichthyoplankton and copepods were the primary prey

items of demersal oceanic invertebrate feeders, the revised food web identified shrimps, crabs as the main prey items.

Regarding the CAP, similarity ranged between −0.2 and +0.4 along the x-axis (CAP1) and between −0.30 and +0.25 along the y-axis (CAP2) for the base food web (Fig. 6A). A distinct cluster formed for planktivorous fishes, while broader clusters formed for the remaining predator guilds, particularly benthic/demersal fishes and elasmobranchs. The distribution of predator functional groups differed in the revised food web (Fig. 6B). For the revised food web, similarity ranged between −0.4 and +0.2 along the x-axis and between −0.3 and +0.3 along the y-axis (Fig. 6B). A distinct cluster formed for pelagic predatory fishes, while tighter clusters formed for all other predator guilds. In addition, results from the revised food web generated less overlap amongst predator guilds than results from the base food web, especially for benthic/demersal fishes and elasmobranchs (Figs. 6B vs. A).

3.2. Balance of the alternative WFS-HAB Ecopath models and evaluation of the mass-balanced models

The alternative versions of the WFS-HAB Ecopath model developed for the present study did not immediately balance. For the Elevated HAB Mortality model, the ecotrophic efficiency (EE) of nearshore associated piscivores estimated by the Base model (0.9) was ultimately used as input because the initial estimated EE exceeded 1 (1.03). Both the Revised Diet model and the Revised Diet and Elevated HAB Mortality model did not immediately balance because: (i) the estimated biomass for large oceanic planktivores was 0 t km^{-2}; and (ii) the estimated EE for adult shrimps was over 1 (13.52). We employed the biomass of large oceanic planktivores (0.073 t km^{-2}) and the EE of adult shrimps (0.884) estimated by the Base model as inputs in both the Revised Diet model and the Revised Diet and Elevated HAB Mortality model. These decisions allowed all models to balance while keeping them directly comparable to the Base model.

A majority of the PREBAL diagnostics for the Base model were met,
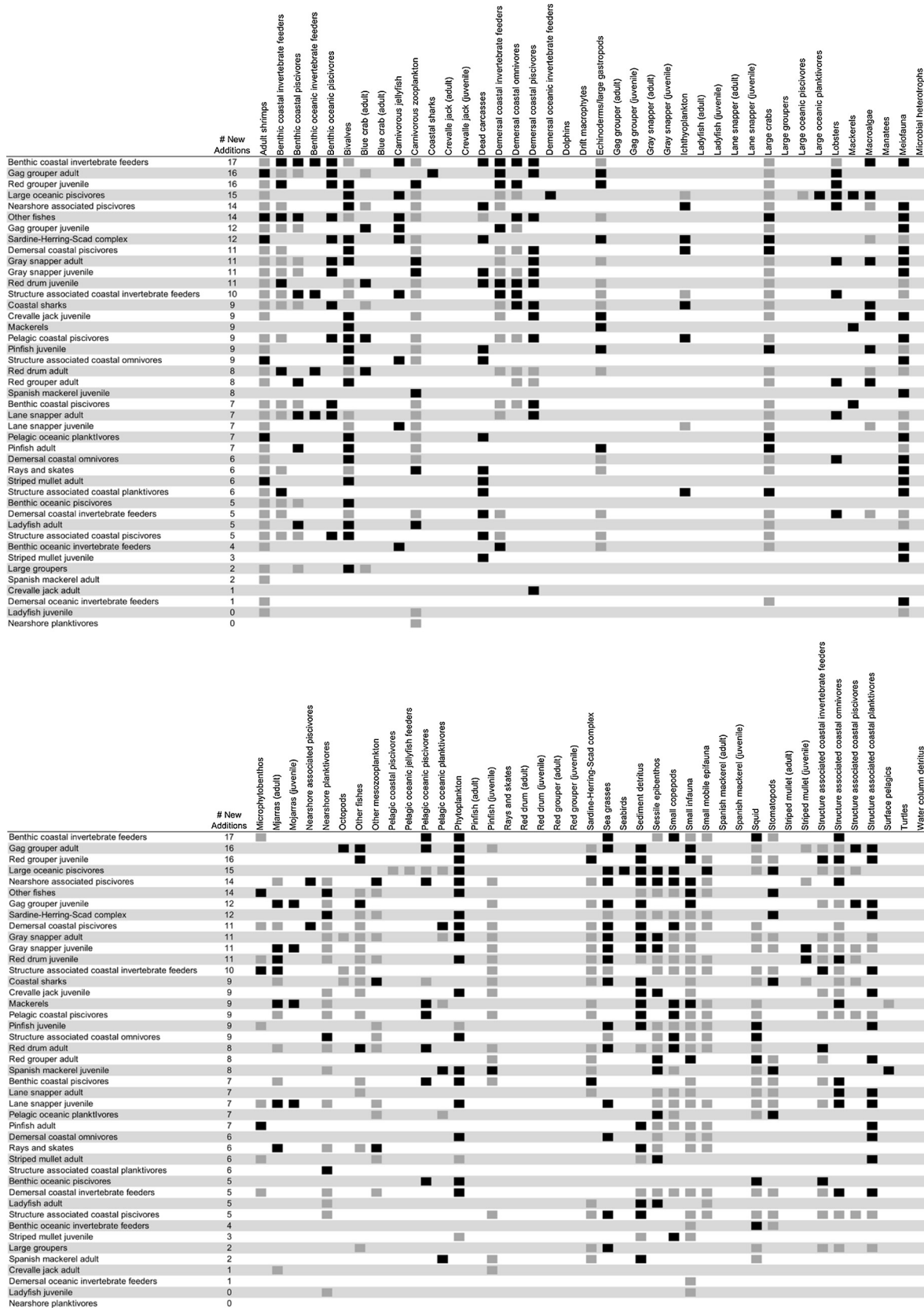
Fig. 4. Diet comparisons between the base and revised food webs for the WFS-HAB Ecopath model. Grey boxes indicate predator (rows) – prey (columns) linkages that are present in both food webs, while black boxes indicate predator – prey linkages that are present in the revised food web but not in the base food web. Predators are presented in order of number of new prey additions.
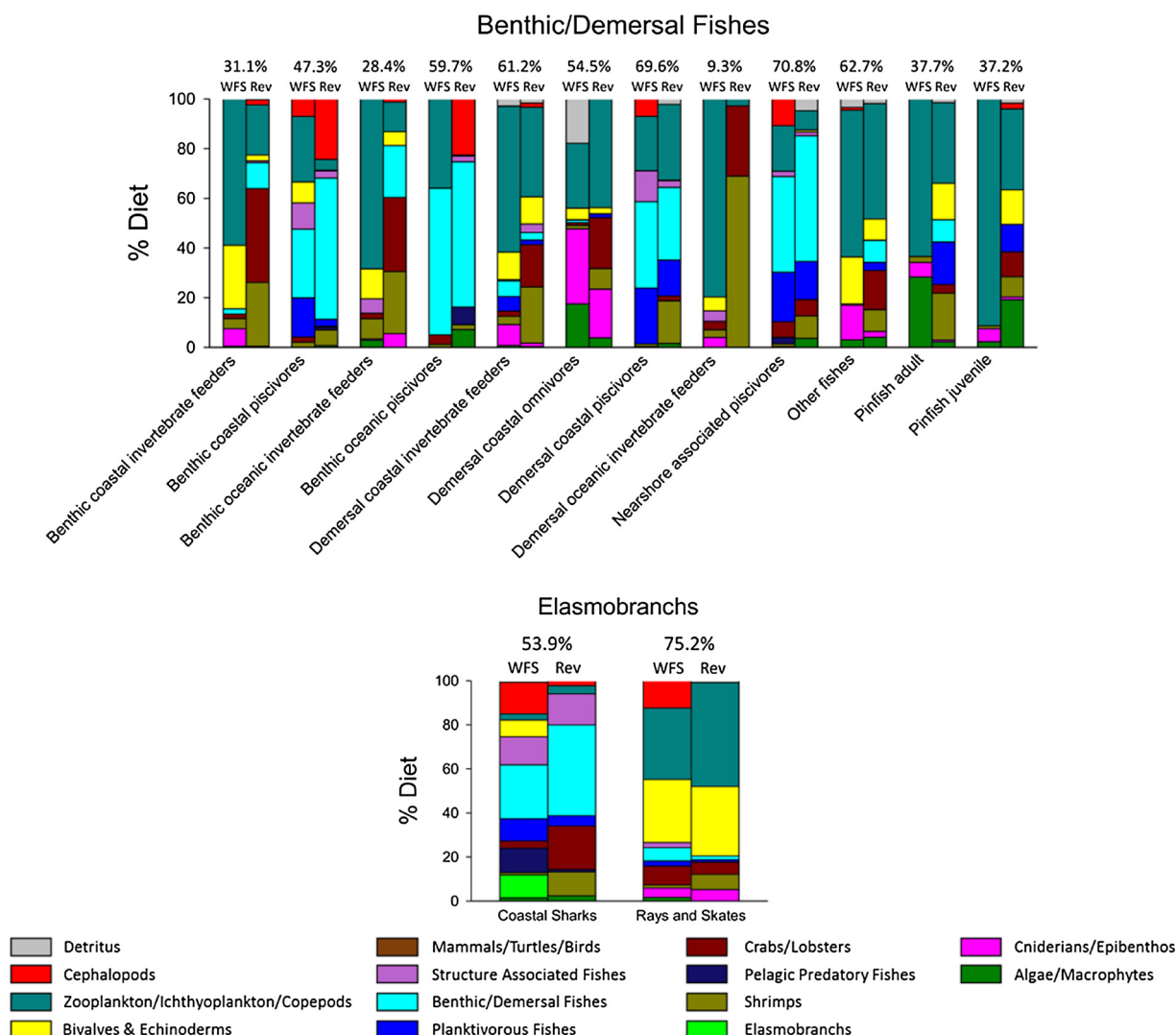
Fig. 5. Percent diet and similarity percentages (SIMPER, numbers above graph) of predator categories (x-axis) comparing the base and revised food webs for the WFS-HAB Ecopath model, referred to here as the "WFS" and "Rev" food webs, respectively. To facilitate comparisons, the graphs were constructed for predator groups using prey grouped into 14 guilds.

suggesting that the inputs and estimates of this model were biologically reasonable (Appendix Figs. B.1–B.4). Although some PREBAL diagnostics were not met, Link (2010) and Heymans et al. (2016) both emphasize this is acceptable as long as departures from the proposed guidelines can be explained (see Appendix B for details in our case). Using elevated red tide mortality rates in WFS-HAB Ecopath had no influence on PREBAL diagnostics. By contrast, incorporating the revised diet matrix into WFS-HAB Ecopath had a small impact on PREBAL diagnostics, largely due to the different TLs estimated in Ecopath (Appendix B).

3.3. Impacts of using the revised diet matrix or elevating red tide mortality on Ecopath estimates

Basic estimates from Ecopath consisted of the four data inputs required for initiating the mass-balance process (B, (P/B), (Q/B), and EE; see subsection 2.1.1), and quantities for characterizing the structure of the modeled ecosystem (e.g., the TL of functional groups). Overall, using elevated red tide mortality rates had a negligible impact on Ecopath basic estimates (results not shown), while employing the revised diet matrix in WFS-HAB Ecopath impacted only some of Ecopath basic estimates (Table 1).

Revising the Ecopath diet matrix had a large impact on the TLs of

functional groups (Table 1). TL estimates increased or decreased by more than 1 % for around 57 % of the functional groups represented in WFS-HAB Ecopath. Most of these functional groups (89 %) experienced an increase in TL, with the largest increase in TL observed for adult pinfish (34.3 %). A few functional groups experienced a (minor) decrease in TL. Adult and juvenile mullet experienced the largest reductions in TL (10 % and 7 %, respectively). Of the 22 % of functional groups that experienced no change in TL, most belonged to the base of the food web (e.g., detritus and plankton groups). The changes in TL estimates caused by using the revised food web resulted in a re-ordering and expansion of the system's trophic flow (Table 1). The Base model had TLs up to 4.58, with large oceanic piscivores occupying the top of the food web, followed by coastal sharks (TL = 4.41) and pelagic coastal piscivores (TL = 4.34). Employing the revised diet matrix resulted in a food web where adult Spanish mackerel had the largest TL (TL = 4.91), followed by large oceanic piscivores (TL = 4.85) and benthic oceanic piscivores (TL = 4.83).

Total mortality rates, equated to P/B's (Section 2.1.1), were similar across the alternative versions of WFS-HAB Ecopath, because they were defined before initiating the mass-balance process and, therefore, were unchanged during the mass-balance process. However, specifying elevated red tide mortality and/or employing the revised diet matrix often had an impact on the relative importance of the different sources of
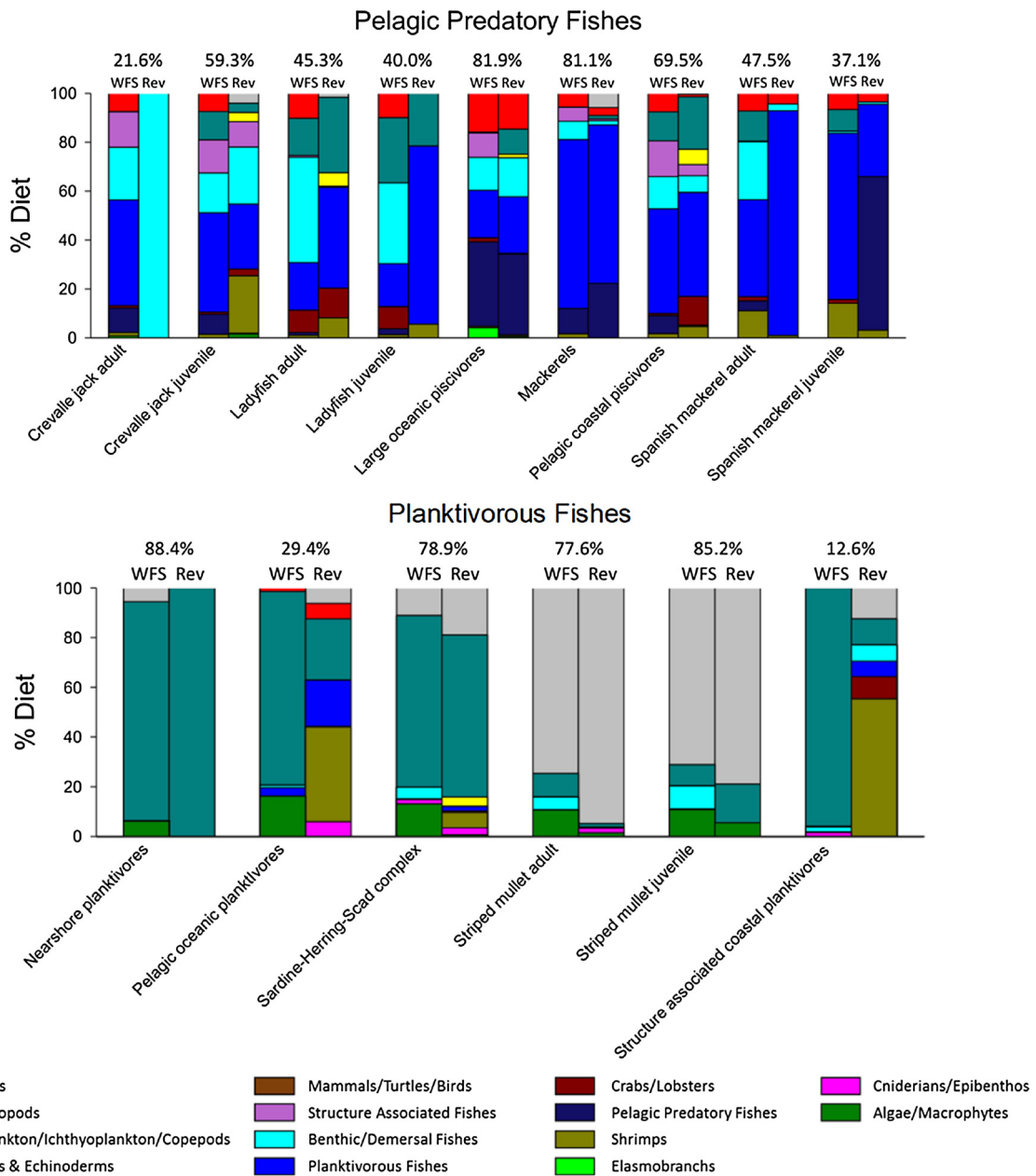
Fig. 5. (*continued*)

mortality of a functional group (Fig. 7 and Appendix Fig. A.1). As expected, specifying elevated red tide mortality increased the contribution of red tide mortality to the total mortality for all functional groups vulnerable to red tide. Because total mortality rate did not change for any functional group, Ecopath accommodated increased red tide mortality by reducing the contribution of natural mortality to the total natural mortality (Fig. 7); this was particularly the case for adult gag, demersal coastal invertebrate feeders and adult red grouper (*Epinephelus morio*). Specifying elevated red tide mortality slightly reduced the contribution of fishing mortality to the total mortality of nearshore planktivores and large groupers (Fig. 7). By contrast, using the revised diet matrix resulted in an increased contribution of fishing mortality to total mortality for some of the functional groups, which was accomplished by a reduction of the contribution of natural mortality to total mortality. The largest increases in fishing mortality occurred for large groupers and the "other fishes" group (Fig. 7). Moreover, employing the revised diet caused the contribution of red tide mortality to total mortality to increase for nearshore planktivores and large groupers

(Fig. 7). Results for the Elevated HAB Mortality and Revised Diet model suggest that changes in mortality patterns are not influenced by the interaction between elevated red tide mortality and the revised diet matrix (Fig. 7 and Appendix Fig. A.1).

3.4. Trophic structure amongst the alternative versions of WFS-HAB Ecopath

3.4.1. Mixed trophic impact (MTI) analysis

Elevated red tide mortality rates had minor impacts on the outcomes of the MTI analysis (Appendix Figs. C.1–C.4), whereas using the revised diet matrix in WFS-HAB Ecopath greatly altered the MTI outcomes (Appendix Fig. C.5). Changes in MTI indices were the most common amongst functional groups of macrofauna. First, using the revised diet matrix in WFS-HAB Ecopath reduced or reversed some of the negative impacts amongst some fish groups (Appendix Fig. C.5). For instance, in the Base model, large oceanic piscivores had some of the largest negative impacts on functional groups (i.e., large oceanic
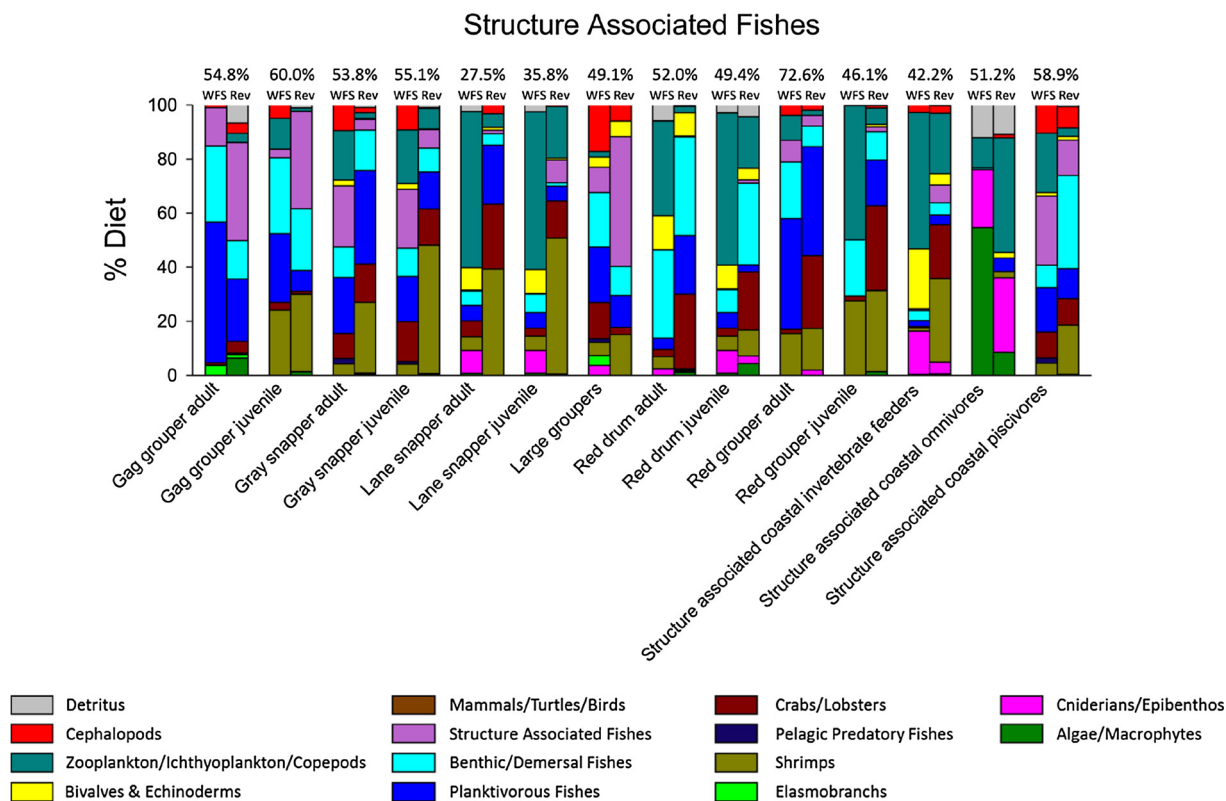
Fig. 5. (*continued*)

piscivores: −0.72; adult gray snapper: −0.44; mackerels: −0.33), whereas these impacts were reduced or reversed in the Revised Diet model (e.g., +0.01, -0.14, and +0.001, respectively). Second, using the revised diet matrix in WFS-HAB Ecopath resulted in the amplification or creation of positive impacts between fish groups (Appendix Fig. C.5). For instance, in the Base model, nearshore planktivores had minor positive impacts on juvenile ladyfish (+0.12) and adult ladyfish (+0.03), whereas these positive impacts were amplified in the Revised Diet model (+0.53 and +0.28, respectively). Third, benthic groups primarily benefited teleosts in both the Base and Revised Diet models, yet the positive impacts of benthic groups on teleosts were stronger in the Revised Diet model (Appendix Fig. C.5). This was particularly notable for adult shrimps, which generally had a very strong positive impact on teleosts when the revised diet matrix was employed in WFS-HAB Ecopath (e.g., juvenile gray snapper: +0.52; demersal oceanic invertebrate feeders: +0.50; juvenile lane snapper, *L. synagris*: +0.47; adult lane snapper: +0.45). Fourth, there were a few instances where substituting the base diet matrix with the revised diet matrix in WFS-HAB Ecopath led to an amplification of negative impacts from biota (Appendix Fig. C.5). This was particularly notable for squids, which had a very strong negative impact on many functional groups in the Revised Diet model (e.g., pelagic oceanic jelly feeders: −0.47; nearshore planktivores: −0.35; demersal coastal piscivores: −0.34).

The MTI analyses conducted for the Base and Revised Diet WFS-HAB Ecopath models indicated that biota positively influenced fishing fleets, while fishing fleets negatively influenced biota (Appendix Fig. C.5). However, employing the revised diet matrix in WFS-HAB Ecopath caused an intensification of some of the negative impacts that fishing fleets had on marine biota, while having no influence on the positive impacts that biota had on fishing fleets (Appendix Fig. C.5). The intensification of the negative impacts of fishing fleets on biota were particularly notable for the trawl and recreational fleets. In the Base model, the most deleterious impact from trawls was upon benthic oceanic piscivores (−0.30), whereas in the Revised Diet model, trawls had more prevalent intense, deleterious impacts on biota (e.g., benthic

oceanic piscivores: −0.71; demersal oceanic invertebrate feeders: −0.71; benthic oceanic invertebrate feeders: −0.5). In the Base model, the most deleterious impact from the recreational fleet was upon adult gag (−0.44), whereas, in the Revised Diet model, the recreational fleet had more intense and negative impacts on biota (e.g., adult grey snapper: −0.75; juvenile red grouper: −0.50; adult gag: −0.43). Moreover, employing the revised diet matrix in WFS-HAB Ecopath resulted in the longline fleet as the only fishing fleet with a notably positive impact on biota (juvenile gag: +0.87). This may be a result of the long line fleet reducing the seabird predation on juvenile gag given the strong negative impact the longline fleet has on seabirds (−0.88) and the strong negative impact seabirds have on juvenile gag (−0.97).

MTI indices from the red tide pseudo-fleet were predominantly negative across impacted groups for all WFS-HAB Ecopath models. However, red tide impacts were influenced by both specifying elevated red tide mortality and using the revised diet matrix (Fig. 8). Deleterious impacts from red tide were the least intense in the Base model because the structure of the WFS ecosystem in the Base model was characterized by a very weak red tide event (Gray, 2014). Employing the revised diet matrix in WFS-HAB Ecopath amplified the negative impacts of red tide on some functional groups and fishing fleets (Fig. 8), including skates and rays (−0.68), juvenile red drum (*Sciaenops ocellatus*) (−0.64), adult red grouper (−0.18), the red grouper fleet (−0.18), nearshore associated piscivores (−0.15), adult gag (−0.15) and sea turtles (−0.13). There were some instances where using the revised diet matrix in WFS-HAB Ecopath alleviated the negative MTI indices associated with the red tide pseudo-fleet (e.g., demersal coastal invertebrate feeders) or promoted positive MTIs from the red tide pseudo-fleet (e.g., structure associated invertebrate feeders and juvenile blue crab, *Callinectes sapidus*). As expected, specifying elevated red tide mortality in WFS-HAB Ecopath amplified the impacts from red tide (Appendix Figs. C.3 and C.4).

3.4.2. Overall impact (ε) indices

Substituting the base diet matrix with the revised diet matrix in
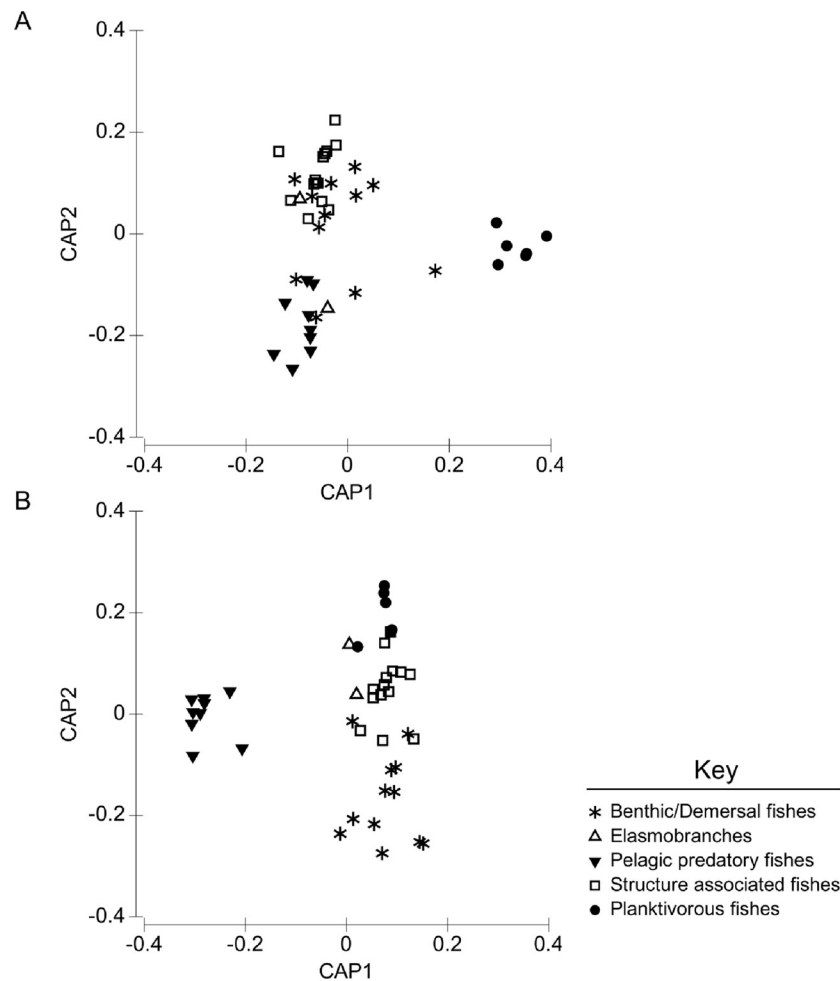
Fig. 6. Canonical analysis of principal coordinates (CAP) plots illustrating the distribution of predator fish functional groups in the base (A) and revised (B) food webs for the WFS-HAB Ecopath model with respect to diet. For both panels, each individual symbol represents a WFS-HAB Ecopath fish functional group, while symbol shapes indicate the predator guild to which the fish functional groups belong. Appendix Table A.5 details the WFS-HAB Ecopath functional groups composing the hierarchical clusters.

WFS-HAB Ecopath had an impact on ε indices (Fig. 9), whereas elevating red tide mortality had no impact on ε indices (Appendix Table C.1). Overall, the ε indices in the Revised Diet model differed from the Base model, with adult shrimps displaying the largest increase in the ε index with the revised diet matrix, followed by seabirds (Fig. 9). The increased overall impacts from seabirds, as well as dolphins, were particularly noteworthy as these groups are often underdeveloped in end-to-end models (Goedegebuure et al., 2017). Pelagic coastal piscivores had the second largest decrease in the ε index with the revised diet matrix, following juvenile striped mullet (Fig. 9). While the Base model suggested that pelagic coastal piscivores had the largest impact on ecosystem structure (ε = 1.52), the Revised Diet model suggested that adult shrimps filled that role (ε = 1.35). Pelagic coastal piscivores still had a relatively large impact in the Revised Diet model (ε = 0.92), but, by contrast, adult shrimps had no significant impact in the Base model (ε = 0.38). Third, dolphins (ε = 1.18), squid (ε = 1.17), structure associated invertebrate feeders (ε = 1.15) and sardine/herring (ε = 1.06) had relatively large impacts in the Revised Diet model, while small mobile epifauna (ε = 1.26) and sardines/herrings (ε = 1.21) had relatively large impacts in the Base model. Lastly, both the Base and Revised Diet models resulted in manatees having the weakest influence on the structure of the WFS ecosystem (ε = 0.001 for both models).

3.4.3. Omnivory indices (OI)

Substituting the base diet matrix with the revised diet matrix in

WFS-HAB Ecopath impacted omnivory indices (Fig. 10), while elevating red tide mortality had no impact on omnivory indices (Appendix Table C.2). The majority of functional groups (53 %) had higher omnivory indices in the Revised Diet model, indicating that groups had a tendency to be more omnivorous in this model. The omnivory index increased the most for juvenile pinfish (Base OI = 0.08; Revised Diet OI = 0.69), and surface pelagics displayed the highest omnivory index in both models (Base OI = 0.86; Revised Diet OI = 1.01). About 30 % of the functional groups became less omnivorous and more selective in the Revised Diet model. The omnivory index decreased the most for juvenile striped mullet between models (Base OI = 0.55; Revised Diet OI = 0.19). The system omnivory index (i.e., the average omnivory index of all consumers weighted by the logarithm of each consumers food intake; Christensen et al., 2008) from the Base model was 0.22, which is comparable to other models of the Gulf of Mexico (Okey et al., 2004; Sagarese et al., 2017). The Revised Diet model exhibited a slightly less omnivorous system (OI = 0.20) because groups with higher weighted food intakes had a tendency to have reduced omnivory indices in the Revised Diet model (Appendix Table C.2).

4. Discussion

In the present study, we estimated a revised diet matrix for an Ecopath model describing the structure of the WFS ecosystem from a large, empirical diet dataset. The revised diet matrix had around 340

Table 1

Basic estimates of the WFS-HAB Ecopath model. Values are presented for alternative versions of the WFS-HAB Ecopath model: the versions using the base diet matrix (Gray, 2014; the "Base" and "Elevated HAB Mortality" models); and the versions using the revised diet matrix (the "Revised Diet" and "Revised Diet and Elevated HAB Mortality" models). All alternative versions of the WFS-HAB Ecopath model exhibited the displayed values, but the alternative versions using the revised diet matrix had different values for some of the estimates which are displayed within square brackets. Values in bold were estimated by Ecopath. TL = trophic level; EE = ecotrophic efficiency; B = biomass; P = production; Q = consumption; R = respiration. The functional groups represented in WFS-HAB Ecopath were each assigned a short name and an ID, which are also given in this table.

Functional group (Abbreviation)	TL	EE	B (t. km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	R/B (yr^{-1})	P/Q
1 Dolphins (DOL)	**4.34 [4.60]**	0.01	0.04	0.16	40.44	**32.19**	**0.00**
2 Seabirds (SEA)	**4.21 [4.47]**	0.01	0.00	0.30	80.00	**63.70**	**0.00**
3 Turtles (TUR)	**3.32**	0.38	0.00	0.19	3.50	**2.61**	**0.05**
4 Manatees (MAN)	**2.00**	0.09	0.00	0.10	36.50	**21.80**	**0.00**
5 Large oceanic piscivores (LOP)	**4.58 [4.86]**	0.20	0.14	0.68	7.40	**5.24**	**0.09**
6 Large oceanic planktivores (LPL)	**3.73 [3.81]**	0.50	0.07[a]	0.11	1.80	**1.15**	**0.06**
7 Coastal sharks (SHK)	**4.41 [4.59]**	0.95	0.11	0.41	3.29	**2.22**	**0.12**
8 Rays and skates (RAY)	**3.63 [3.41]**	0.60	0.15	0.85	7.72	**5.33**	**0.11**
9 Pelagic oceanic piscivores (POP)	**4.34 [4.57]**	0.85	0.57	1.06	7.20	**4.70**	**0.15**
10 Pelagic coastal piscivores (PCP)	**4.25 [4.21]**	0.95	0.40	0.70	9.23	**6.68**	**0.08**
11 Mackerel (MAC)	**4.22 [4.42]**	0.95	0.08	0.80	8.00	**5.60**	**0.10**
12 Red grouper juvenile (RGR1)	**3.83 [4.15]**	0.80	0.02	0.50	14.60	**11.18**	**0.03**
13 Red grouper adult (RGR2)	**4.05 [4.42]**	0.78	0.17	0.31	6.25	**4.69**	**0.05**
14 Spanish mackerel juvenile (SMK1)	**4.08 [4.16]**	0.93	0.02	0.90	46.79	**36.53**	**0.02**
15 Spanish mackerel adult (SMK2)	**4.12 [4.91]**	0.95	0.08	0.55	21.78	**16.87**	**0.03**
16 Gag juvenile (GAG1)	**4.11 [4.22]**	0.95	0.00	2.00	18.90	**13.12**	**0.11**
17 Gag adult (GAG2)	**4.13 [4.41]**	0.40	0.03	0.44	4.97	**3.54**	**0.09**
18 Red drum juvenile (RDM1)	**3.53 [3.94]**	0.95	0.01	1.40	12.06	**8.25**	**0.12**
19 Red drum adult (RDM2)	**3.62 [4.26]**	0.95	0.01	0.95	5.75	**3.65**	**0.17**
20 Striped mullet juvenile (SMU1)	**2.32 [2.17]**	0.31	0.20	1.50	50.27	**38.72**	**0.03**
21 Striped mullet adult (SMU2)	**2.24 [2.03]**	0.95	0.13	1.00	29.7	**22.76**	**0.03**
22 Lane snapper juvenile (LSN1)	**3.53 [3.94]**	0.95	0.02	1.00	20.56	**15.45**	**0.05**
23 Lane snapper adult (LSN2)	**3.53 [4.20]**	0.95	0.19	0.6	8.02	**5.82**	**0.07**
24 Gray snapper juvenile (GSN1)	**4.05 [4.06]**	0.54	0.03	0.75	16.23	**12.24**	**0.05**
25 Gray snapper adult (GSN2)	**4.10 [4.34]**	1.00	0.19	0.75	7.29	**5.09**	**0.10**
26 Crevalle jack juvenile (CJK1)	**4.22 [4.29]**	0.74	0.02	2.00	14.48	**9.58**	**0.14**
27 Crevalle jack adult (CJK2)	**4.33 [4.47]**	1.00	0.04	0.80	5.06	**3.25**	**0.16**
28 Pinfish juvenile (PIN1)	**3.33 [3.44]**	0.95	1.14	2.00	26.34	**19.07**	**0.08**
29 Pinfish adult (PIN2)	**2.97 [3.99]**	0.95	1.49	0.91	11.34	**8.17**	**0.08**
30 Mojarras juvenile (MOJ1)	**3.23**	0.95	0.11	1.60	26.15	**19.32**	**0.06**
31 Mojarras adult (MOJ2)	**3.18**	0.95	0.54	0.80	10.96	**7.96**	**0.07**
32 Ladyfish juvenile (LDF1)	**4.05 [4.26]**	0.95	0.02	1.40	17.21	**12.36**	**0.08**
33 Ladyfish adult (LDF2)	**4.11 [3.97]**	0.95	0.09	0.58	6.84	**4.89**	**0.08**
34 Sardine-Herring-Scad complex (SAR)	**3.08 [3.20]**	0.98	1.70	2.30	12.11	**6.17**	**0.19**
35 Pelagic oceanic jelly eaters (PJL)	**4.17 [4.18]**	0.95	0.30	1.56	8.07	**4.90**	**0.19**
36 Pelagic oceanic planktivores (PPL)	**3.39 [4.03]**	0.95	1.94	0.87	11.71	**7.33**	**0.07**
37 Demersal oceanic invert. feeders (DOI)	**3.42 [3.93]**	0.95	0.01	1.20	15.76	**11.41**	**0.08**
38 Demersal coastal piscivores (DCP)	**4.13 [4.10]**	0.87	0.12	0.80	6.33	**4.27**	**0.13**
39 Demersal coastal invert. feeders (DCI)	**3.50 [3.68]**	0.98	0.34	0.85	7.92	**5.48**	**0.11**
40 Demersal coastal omnivores (DCO)	**2.93 [3.54]**	0.97	0.14	1.34	15.13	**10.76**	**0.09**
41 Benthic oceanic piscivores (BOP)	**4.10 [4.84]**	0.95	0.01	0.45	7.94	**5.90**	**0.06**
42 Benthic oceanic invert. feeders (BOI)	**3.50 [4.09]**	0.95	0.02	1.50	15.78	**11.12**	**0.10**
43 Benthic coastal piscivores (BCP)	**4.00 [4.71]**	0.91	0.24	0.55	8.39	**6.16**	**0.07**
44 Benthic coastal invert. feeders (BCI)	**3.43 [3.94]**	0.79	0.77	0.86	10.11	**7.23**	**0.09**
45 Surface pelagics (SPL)	**2.92 [2.97]**	0.95	**0.11 [0.24]**	2.60	11.70	**6.76**	**0.22**
46 Structure assoc. coastal piscivores (SAP)	**4.04 [4.64]**	0.95	0.26	0.63	5.40	**3.69**	**0.12**
47 Large groupers (LGP)	**4.17 [4.52]**	0.95	**0.03 [0.01]**	0.46	4.10	**2.82**	**0.11**
48 Structure assoc. coastal invert. feeders (SCI)	**3.47 [3.95]**	0.29	4.84	0.75	7.33	**5.12**	**0.10**
49 Structure assoc. coastal omnivores (SCO)	**2.48 [3.32]**	0.88	0.60	1.33	24.37	**18.17**	**0.05**
50 Structure assoc. coastal planktivores (SCP)	**3.48 [3.75]**	0.75	0.27	2.00	10.00	**5.00**	**0.20**
51 Nearshore assoc. piscivores (NRP)	**4.15 [4.52]**	**0.90 [0.38]** [b]	0.01	1.06	7.67	**5.08**	**0.14**
52 Nearshore planktivores (NPL)	**3.23 [3.49]**	0.99	**3.01 [2.57]**	2.00	15.92	**9.14**	**0.13**
53 Other fishes (OTH)	**3.39 [3.61]**	0.95	**4.05 [1.33]**	1.30	7.04	**4.33**	**0.18**
54 Squid (SQU)	**3.70 [3.72]**	0.99	1.50	3.00	35.00	**19.75**	**0.09**
55 Adult shrimps (SHP)	**2.89**	**0.88**[a]	0.52	5.38	19.20	**6.14**	**0.28**
56 Lobsters (LOB)	**2.92**	0.95	0.10	0.90	8.20	**4.43**	**0.11**
57 Large crabs (CRB)	**3.09**	0.95	0.61	2.30	8.50	**3.23**	**0.27**
58 Blue crab juvenile (BCB1)	**3.05**	0.95	0.01	2.00	18.02	**12.42**	**0.11**
59 Blue crab adult (BCB2)	**3.07**	**0.98 [0.36]**	0.10	1.10	9.94	**6.85**	**0.11**
60 Octopods (OCT)	**3.39 [3.43]**	0.95	**0.17 [0.0004]**	3.10	11.70	**7.08**	**0.26**
61 Stomatopods (STP)	**3.19 [3.20]**	0.92	0.43	1.34	**8.90**	**4.90**	0.15
62 Echinoderms and large gastropods (ECH)	**2.40**	0.45	19.25	1.20	3.70	**0.43**	**0.32**
63 Bivalves (BIV)	**2.15**	0.23	48.60	1.21	23.00	**10.29**	**0.05**
64 Sessile epibenthos (SEP)	**2.39**	0.28	219.00	0.80	9.00	**2.80**	**0.09**
65 Small infauna (SMI)	**2.31**	0.55	19.03	4.60	15.90	**3.35**	**0.29**
66 Small mobile epifauna (SME)	**2.35**	0.95	**14.12 [9.39]**	7.01	27.14	**7.92**	**0.26**
67 Meiofauna (MEI)	**2.36**	0.85	13.00	12.50	25.00	**1.25**	**0.50**
68 Small Copepods (COP)	**2.15**	0.95	8.60	17.30	60.00	**12.70**	**0.29**
69 Other mesozooplankton (OMS)	**2.50**	0.98	6.70	17.30	45.00	**5.20**	**0.38**

(*continued on next page*)

Table 1 (*continued*)

Functional group (Abbreviation)	TL	EE	B (t. km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	R/B (yr^{-1})	P/Q
70 Carnivorous zooplankton (CZO)	**2.97**	0.45	21.60	8.70	17.00	**1.50**	**0.51**
71 Ichthyoplankton (ICH)	**2.94**	0.86 [0.68]	0.05	50.45	132.13	**28.83**	**0.38**
72 Carnivorous jellyfish (CJL)	**3.38**	0.52	0.27	37.00	80.00	**35.00**	**0.46**
73 Microbial Heterotrophs (MHT)	**2.00**	0.88	40.00	40.00	80.00	**24.00**	**0.50**
74 Macroalgae (ALG)	**1**	0.46	36.05	4.00			
75 Microphytobenthos (MPB)	**1**	0.57	29.78	23.73			
76 Phytoplankton (PHY)	**1**	0.46	20.00	160.00			
77 Sea grasses (SGR)	**1**	0.02	175.62	9.01			
78 Dead carcasses (DCA)	**1**	**0.45 [0.46]**	3.00				
79 Sediment detritus (SED)	**1**	**0.51**	390.00				
80 Water column detritus (WDT)	**1**	**0.57**	125.00				
81 Drift macrophytes (DMA)	**1**	**0.12 [0.11]**	2.66				

^a The value estimated by the base WFS-HAB Ecopath model was employed as input in the alternative versions of WFS-HAB Ecopath using the revised diet matrix.

^b The value estimated by the base WFS-HAB Ecopath model was employed as input in the alternative version of WFS-HAB Ecopath with elevated harmful algal bloom mortality and using the base diet matrix.
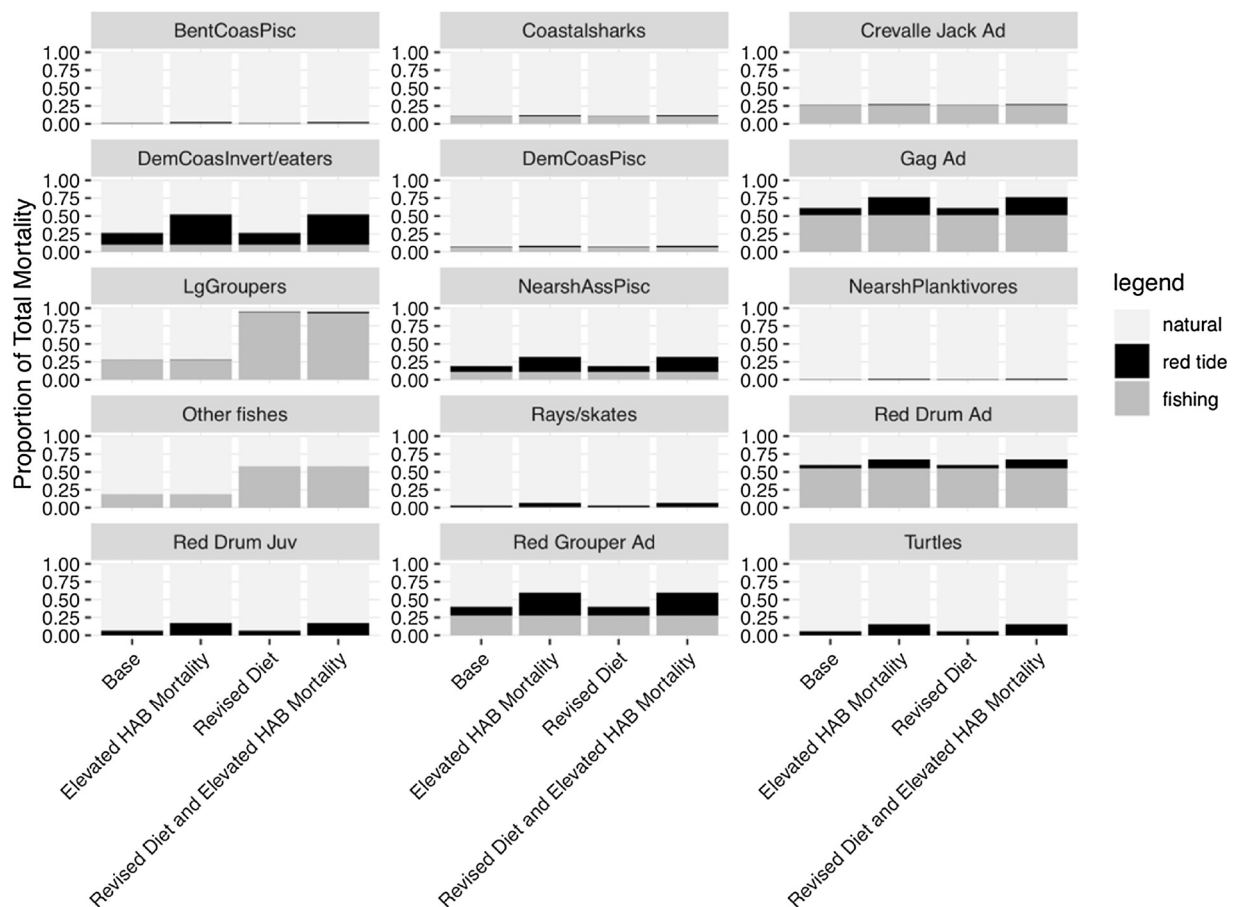

Fig. 7. Contribution of natural mortality, red tide mortality and fishing mortality to the total mortality of select functional groups represented in the WFS-HAB Ecopath model. Proportions of total mortality are provided here for each alternative version of the WFS-HAB Ecopath model: the base version ("Base"); the version with elevated red tide mortality ("Elevated HAB Mortality"); the version with the revised diet matrix ("Revised Diet"); and the version with both the revised diet matrix and elevated red tide mortality ("Revised Diet and Elevated HAB Mortality"). Here, we consider only the functional groups that experienced the largest changes in the contribution of natural mortality, red tide mortality and fishing mortality to the total mortality; results for all the other functional groups represented in WFS-HAB Ecopath are shown in Appendix Fig. A.1.

predator-prey linkages that were not present in the diet matrix used in the base WFS-HAB Ecopath model. Thus, the revised diet matrix represented a more complex food web. However, there were some predator-prey linkages in the base diet matrix that were not retained in the revised diet matrix because of the low frequency of those predator-prey interactions in the diet dataset employed in the present study. The more complex food web estimated for the WFS resulted in a reduction of the predation mortality rates of many of the prey groups represented in the

WFS-HAB Ecopath model, including many prey groups that are directly affected by red tides (e.g., adult gag, juvenile red grouper, adult red grouper). A large reduction in predation mortality rates may be reasonable for adult fish groups, but less so for juvenile fish groups, such as juvenile red grouper, as these juvenile fishes are generally reported to suffer high predation mortality rates in the wild (Sogard, 1997; Almany and Webster, 2006). To accurately estimate juvenile fish predation mortality rates, additional collection of predatory fish stomachs in the
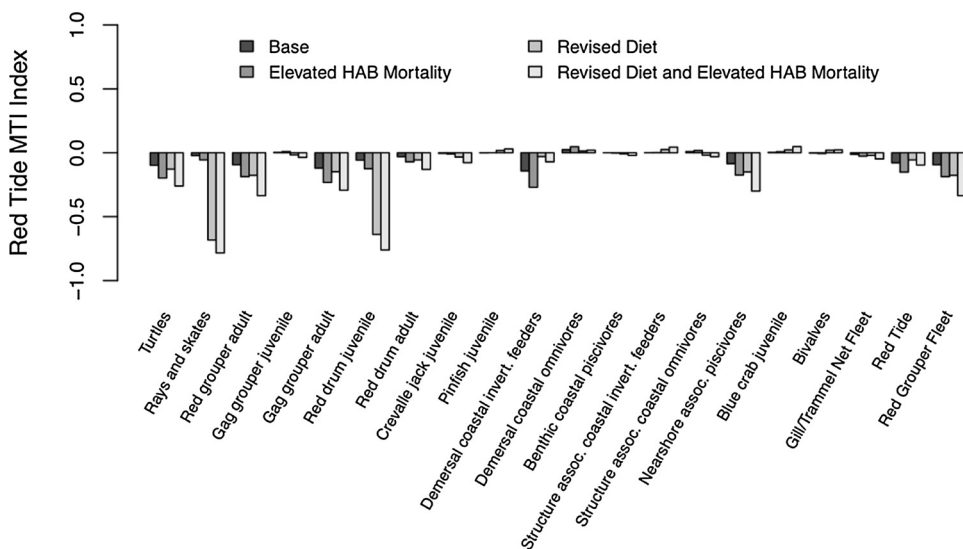
Fig. 8. Mixed Trophic Impact (MTI) indices for the red tide pseudo-fleet. MTI indices are provided here for all of the alternative versions of the WFS-HAB model: the base version ("Base"); the version with elevated red tide mortality ("Elevated HAB Mortality"); the version with the revised diet matrix ("Revised Diet"); and the version with both the revised diet matrix and elevated red tide mortality ("Revised Diet and Elevated HAB Mortality"). Here, we only show results for the functional groups for which the difference between the red tide MTI index from the Base model and alternative models was greater than 0.02. Results are shown in their entirety in Appendix Figs C.1-C.4.

WFS region will be needed, particularly in coastal (e.g., estuarine) habitats where the bulk of juvenile fishes occur. In addition, DNA-barcoding for prey identification (Sakaguchi et al., 2017) or a combination of DNA-barcoding and stable isotope analyses may further elucidate the energy flow of the WFS ecosystem (Carreon-Martinez and Heath, 2010; Tarnecki and Patterson, 2015; Nelson et al., 2017), as well as help us to properly distinguish between short-term and long-term diet trends in the WFS region (Kroetz et al., 2017; Nelson et al., 2017).

Substituting the base diet matrix with the revised diet matrix in the WFS-HAB Ecopath model had a large impact on trophic level estimates, but generally not on basic parameters estimated in balancing Ecopath. This was not surprising as many of the other basic parameters of Ecopath were specified, rather than estimated during the mass-balance process, and unchanged amongst the alternative models considered in this study. Adult pinfish had the largest increase in trophic level between the Base model and the Revised Diet model (2.97 and 3.98, respectively). Findings from previous studies suggest that the trophic level for this group within the WFS should be above 3. Hansen (1969) estimated that pinfish had a trophic level up to 3.4 in Florida estuaries, while Motta et al. (1995) found that pinfish had a trophic level of 3.2 in Apalachee Bay, Florida. Mullet groups (*Mugil* spp.) had the largest decrease in trophic levels between the Base model and the Revised Diet model (from 2.24 to 2.03 for adults and 2.32 to 2.17 for juveniles). This resulted from sediment detritus being the primary food source for mullet groups in the revised diet matrix, as indicated by the hierarchical cluster analyses. The trophic level of mugilids can vary greatly from one species to another and from one region to another (Whitfield, 2016), but reduced trophic levels obtained with the revised diet matrix are reasonable for the WFS. Collins (1981) found that mullets primarily fed on macrophytic detritus (40 %) and sand/shell particles (56 %) off Seahorse Key, Florida and on sediment particles (53 %) and algae (32 %) in Crystal River, Florida. A majority of functional groups had larger trophic level estimates in WFS-HAB Ecopath upon employing the revised diet matrix, which expanded the ecosystem structure modeled in WFS-HAB Ecopath. This is a significant implication of revising the diet matrix in WFS-HAB Ecopath as truncated marine food webs oversimplify the fish community, masking higher trophic levels and their associated interactions, which can bias ecosystem-based fisheries management advice derived from Ecopath outputs (Hussey et al., 2014).

Pelagic coastal piscivores was the most impactful group in WFS-HAB Ecopath when the base diet matrix was employed, due to their strong negative impacts on several teleost functional groups. Similar observations were made with other ecosystem models of the Gulf of
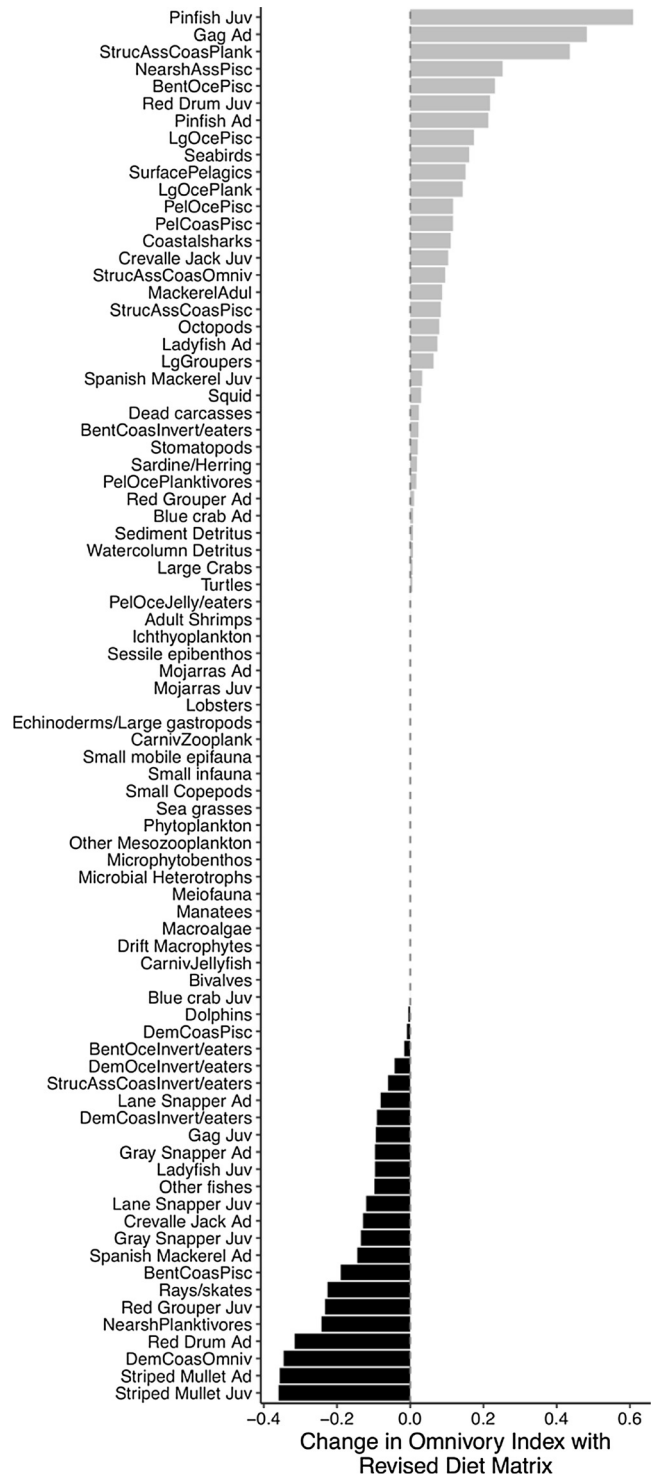
Mexico (e.g., Sagarese et al., 2017). However, many of the negative impacts of pelagic coastal piscivores were reduced when the revised diet matrix was employed in WFS-HAB Ecopath, subsequently reducing their trophic interaction strength. In fact, several top-predator groups had reduced trophic interaction strengths when the revised diet matrix was used in WFS-HAB Ecopath, including benthic oceanic piscivores, coastal sharks, and large oceanic piscivores. It is likely that the base diet matrix of WFS-HAB Ecopath was over-representing top-down pressures from some of the top-predatory groups as it was based on sparse, cursory information, and that the revised diet matrix improves the representation of these pressures as it is based on WFS survey data. It is worth noting that the revised diet matrix could be reflecting a reduction in top-down pressures as there is nearly a 20-year difference between the original development of the base diet matrix (Okey and Mahmoudi, 2002; Okey et al., 2004) and the development of the revised diet matrix (which was estimated from diet data collected mainly over the last ten years). Although highly debated in the literature, the reduction of top-down pressures due to changes in the populations of top-predators (e.g., loss of abundance, shifts in habitats) could have negative impacts on local ecosystems (Heithaus et al., 2008; Terborgh and Estes, 2010; Boaden and Kingsford, 2015), including leading to more pronounced HAB impacts (Walsh et al., 2011). This study does not provide evidence of reduced top-down pressures, especially considering that some top-predator groups had increased trophic interaction strengths when the revised diet matrix was employed in WFS-HAB Ecopath, including seabirds, dolphins, and benthic coastal piscivores. However, future studies involving the WFS-HAB Ecopath model, such as exploring dynamic simulations using the revised diet matrix, should bear in mind the ecosystem impacts from changing trophic pressures as they will likely have important implications for resource management efforts.

Squids and adult shrimp were the most impactful groups when the revised diet matrix was fed into the WFS-HAB Ecopath model. By contrast, squids and adult shrimp had no significant impact in WFS-HAB Ecopath when the base diet matrix was employed. When using the revised diet matrix, squids had a strong negative impact on a variety of groups in WFS-HAB Ecopath (e.g., jellyfish eaters, nearshore plankti-vores, demersal piscivores, pinfish and ladyfish). Squids have been identified as playing an essential role in the biological transfer of energy in a variety of marine ecosystems, including the South Brazil Bight (Gasalla et al., 2010), the eastern Pacific (Nigmatullin et al., 2001; Shchetinnikov, 1988), and the Antarctic Polar Frontal Zone (Rodhouse and White, 1995). Additionally, Coll et al. (2013) found that the ecological role of squid occupying the neritic zone may be important as, across a variety of Ecopath models, squid had strong top-down control
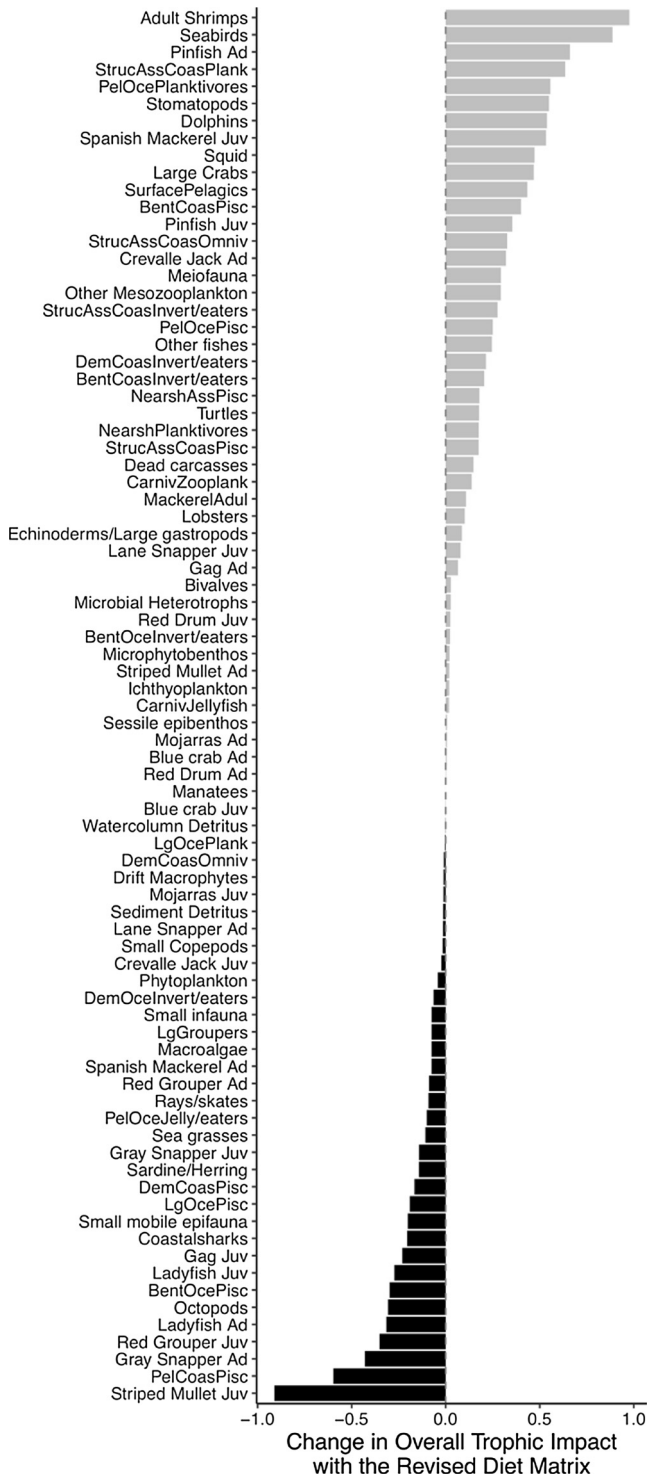
Fig. 9. Differences in overall impact indices between the WFS-HAB Ecopath model using the revised diet matrix and the base WFS-HAB Ecopath model. Grey bars highlight overall impact indices that increased upon substituting the revised diet matrix into WFS-HAB Ecopath, indicating groups with increased trophic interaction strength. Black bars highlight overall impact indices that decreased upon substituting the revised diet matrix into WFS-HAB Ecopath, indicating groups with reduced trophic interaction strength. Overall impact indices for all alternative versions of WFS-HAB Ecopath are detailed in Appendix Table C.1.

Fig. 10. Differences in omnivory indices between the WFS-HAB Ecopath model using the revised diet matrix and the base WFS-HAB Ecopath model. Grey bars highlight omnivory indices that increased upon substituting the revised diet matrix into WFS-HAB Ecopath, indicating groups becoming more omnivorous. Black bars highlight omnivory indices that decreased upon substituting the revised diet matrix into WFS-HAB Ecopath, indicating groups becoming less omnivorous. Omnivory indices for all alternative versions of WFS-HAB Ecopath are detailed in Appendix Table C.2.

on their prey and were important prey for top predators. Thus, it is plausible that squids play a critical role in the trophic structure of the WFS ecosystem, and that the revised diet matrix better reflected this

role in WFS-HAB Ecopath. When using the revised diet matrix in the WFS-HAB Ecopath model, adult shrimp had a strong positive impact on a variety of the modeled groups, including groups of snappers, groupers, and demersal coastal invertebrate feeders. Shrimps are

known for strongly influencing benthic communities (e.g., March et al., 2002) and to be essential for the recycling of nutrients (e.g., Welsh, 1975). Additionally, Fujiwara et al. (2016) found significant associations between shrimp abundance and the catch rates of fish in some regions of the Gulf of Mexico. Thus, it is plausible that the role adult shrimp have in the trophic structure of the WFS ecosystem was previously underrepresented, and that the revised diet matrix better reflects this role. Indeed, any scenario entailing large changes in squid and/or adult shrimp mortality rates tested with WFS-HAB EwE using the revised diet matrix will very likely result in major changes in the dynamics of the simulated WFS ecosystem (Sala and Sugihara, 2005).

Substituting the revised diet matrix into the WFS-HAB Ecopath model drove the minor differences in PREBAL diagnostics we observed (Appendix B). Although a majority of the PREBAL diagnostics for the alternative versions of WFS-HAB Ecopath were met, suggesting that model inputs and estimates were biologically reasonable, some were not met. This may be acceptable (Link, 2010; Heymans et al., 2016), yet we recommend future studies to complete an extended evaluation of the performance of WFS-HAB Ecopath to ensure the information extracted from this model that is used to assist resource management efforts is as robust as possible (Heymans et al., 2016).

Overall, this study found that compared to the base diet matrix of WFS-HAB Ecopath, the revised diet matrix estimated in this study had higher connectivity amongst functional groups, more generalist predators, and more omnivorous groups. These features are observed in a large number of marine food webs, particularly highly diverse ecosystems like the WFS (Link, 2002; Dunne et al., 2004; Shurin et al., 2006; Thompson et al., 2007). Diet matrices generally represent a mere portion of the complexity of real ecosystems. The increased connectivity and intricacy amongst functional groups provided by the revised diet matrix suggests an improved representation of an inherently complex and highly diverse marine ecosystem. Moreover, as indicated earlier, the WFS-HAB Ecopath model using the revised diet matrix is less likely to predict unreasonably high predation mortality rates due to specific predators, particularly for juvenile fishes, as prey items are generally consumed by a broader diversity of predators in the model (Sagarese et al., 2017). Therefore, we conclude that, as a starting point to evaluate the dynamic and spatio-temporal impacts of HABs and other ecosystem perturbations, using the revised diet matrix in the WFS-HAB Ecopath model is more reliable than using the diet matrix previously fed into WFS-HAB Ecopath. That being said, food web complexity and omnivory are often used to assess ecosystem stability, but no clear patterns between food web connectivity or omnivory and ecosystem stability have been established (Landi et al., 2018). We did not evaluate the impacts of the revised diet matrix on ecosystem stability, but future studies considering network approaches, energy flow analyses, and food web descriptors (e.g., weighted connectance; van Altena et al., 2016) could explore this issue (Landi et al., 2018).

Negative impacts of the fleets (i.e., red tides and fisheries) intensified in WFS-HAB Ecopath when the revised diet matrix was employed, confirming the concerns expressed in Gray DiLeone and Ainsworth (2019) about the limitations of WFS-HAB Ecopath due to the uncertainty of the base diet matrix. This suggests that part of the vulnerability to HABs is due to feeding dependencies (as opposed to direct toxicological effects). The negative impacts of the red tide pseudo-fleet intensified for most of the functional groups vulnerable to red tides, particularly for the skate/ray complex and juvenile red drum. The intensification of red tide impacts on juvenile red drum seems reasonable given that red drum recruitment declined markedly in 2005 and 2006, seemingly due to the severe HAB event that took place in 2005 (Flaherty and Landsberg, 2011). Moreover, Sagarese et al. (2017) found the skate/ray complex to be particularly vulnerable to red tides within the U.S. Gulf of Mexico. Using the revised diet matrix in WFS-HAB Ecopath also intensified the negative impacts of the red tide pseudo-fleet on gag and red grouper, as well as the negative impacts of the recreational fleet on these two species. Thus, the negative impacts of

recreational fishing and red tides on gag and red grouper may have been underestimated in the previous versions of WFS-HAB Ecopath that aimed to inform gag and red grouper assessments (Gray et al., 2013; Sagarese et al., 2015). This may explain why the red grouper mortality rates predicted by Sagarese et al. (2015) did not reflect the large mortality rates suggested by field observations.

This work represents an important advancement in the progression of ecosystem modeling tools for assisting resource management efforts for the WFS. The next step is to use the WFS-HAB Ecopath model with the revised diet matrix to conduct dynamic simulations with the Ecosim component of WFS-HAB EwE. We demonstrated the strong influence diet has on the trophic structure estimated by the WFS-HAB Ecopath model, and the more complex structure estimated by WFS-HAB Ecopath is likely to imply very different dynamics over time in Ecosim. Thus, the quantified uncertainty ranges in diet proportions we presented could be used to explore the impacts of diet uncertainty on advice for resource management based on dynamic simulations with Ecosim (Koehn et al., 2016; Morzaria-Luna et al., 2018; Bentley et al., 2019). Although we found that elevated red tide mortalities had virtually no impact on the trophic structure of WFS-HAB Ecopath, they did impact specific functional groups and could have stronger impacts in dynamic simulations with Ecosim. Future work should explore the impacts of uncertainty in the HAB mortality driver of WFS-HAB Ecopath, which is based on anecdotal observations reported to the FWRI fish kill database due to the lack of quantitative information on fish kills (Driggers et al., 2016; Sagarese et al., 2017). Finally, red tide blooms in the WFS can vary significantly in space and over time (Steidinger and Haddad, 1981; Steidinger and Vargo, 1988) and the catch-potential of targeted and bycatch species may increase during red tide blooms due to denser spatial patterns (Craig et al., 2005; Craig, 2012). Therefore, extending the WFS-HAB EwE model to an Ecospace model in order to simulate the spatio-temporal dynamics of red tides (O'Farrell et al., 2017) would allow for the estimation of red tide mortality rates based on the degree of spatial overlap between red tides and the functional groups that are vulnerable to them.

In conclusion, we found that using a large, empirical diet database to develop a more complex and more realistic diet matrix profoundly changed key ecological processes in WFS-HAB Ecopath pertinent for exploring HAB impacts and other important resource management questions. In particular, HAB mortality rates with the revised diet matrix were higher and more consistent with field observations for gag and red grouper, which are some of the species most effected by HABs. These findings show the importance of having accurate and up to date diet data when using ecosystem models to infer the impacts of ecosystem perturbations such as HABs throughout the food web.

Author contributions

Designed and analyzed the models: HAP, JHT, AG, EAB, SRS. Conceived the models: HAP, AG, SRS, CHA, AGdL. Wrote the paper: HAP, JHT, AG, EAB, SRS, CHA, AGdL. All authors have approved the final article.

Declaration of Competing Interest

None.

Acknowledgements

thank David Chagaris and Matthew Nuttall for the informative discussions and technical assistance regarding Ecopath. We are grateful to Amy Wallace for having produced the food web diagram presented in this study, and Trond Lindblom for having formatted the West Florida Shelf map presented in this study. We also thank the anonymous reviewers as their thoughtful comments and suggestions ultimately improved this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2019.108890.

References

Ainsworth, C.H., Kaplan, I.C., Levin, P.S., Mangel, M., 2010. A statistical approach for estimating fish diet compositions from multiple data sources: gulf of California case study. Ecol. Appl. 20, 2188–2202.

Ainsworth, C.H., Walters, C.J., 2015. Ten common mistakes made in Ecopath with Ecosim modelling. Ecol. Model. 308, 14–17.

Almany, G.R., Webster, M.S., 2006. The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25 (1), 19–22.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84 (2), 511–525.

Bentley, J.W., Hines, D., Borrett, S., Serpetti, N., Fox, C., Reid, D.G., Heymans, J.J., 2019. Diet uncertainty analysis strengthens model-derived indicators of food web structure and function. Ecol. Indic. 98, 239–250.

Boaden, A.E., Kingsford, M.J., 2015. Predators drive community structure in coral reef fish assemblages. Ecosphere 6 (4), 46. https://doi.org/10.1890/ES14-00292.1.

Brand, L.E., Compton, A., 2007. Long-term increase in *Karenia brevis* abundance along the southwest Florida coast. Harmful Algae 6 (2), 232–252.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Carreon-Martinez, L., Heath, D.D., 2010. Revolution in food web analysis and trophic ecology: diet analysis by DNA and stable isotope analysis. Mol. Ecol. 19 (1), 25–27.

Chagaris Jr., D.D., 2013. Ecosystem-Based Evaluation of Fishery Policies and Tradeoffs on the West Florida Shelf. PhD Dissertation. University of Florida.

Christensen, V., Pauly, D., 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61 (3–4), 169–185.

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Model. 172 (2), 109–139.

Christensen, V., Walters, C.J., Pauly, R., 2008. Ecopath with Ecosim Version 6 User Guide. Fisheries Centre, University of British Columbia, Vancouver, Canada.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J. Exp. Mar. Biol. Ecol. 366 (1), 56–69.

Coll, M., Navarro, J., Olson, R.J., Christensen, V., 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep-Sea Res. Part II 95, 21–36.

Collins, M.R., 1981. The feeding periodicity of striped mullet, *Mugil cephalus* L., in two Florida habitats. J. Fish Biol. 19 (3), 307–315.

Craig, J.K., Crowder, L.B., Henwood, T.A., 2005. Spatial distribution of brown shrimp (*Farfantepenaeus aztecus*) on the northwestern Gulf of Mexico shelf: effects of abundance and hypoxia. Can. J. Fish. Aquat. Sci. 62 (6), 1295–1308.

Craig, J.K., 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 445, 75–95.

de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan Jr., J.H., Christensen, V., 2016. Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. Ecol. Model. 331, 142–150.

Driggers III, W.B., Campbell, M.D., Debose, A.J., Hannan, K.M., Hendon, M.D., Martin, T.L., Nichols, C.C., 2016. Environmental conditions and catch rates of predatory fishes associated with a mass mortality on the West Florida shelf. Estuar. Coast Shelf Sci. 168, 40–49.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2004. Network structure and robustness of marine food webs. Mar. Ecol. Prog. Ser. 273, 291–302.

Dupont, J.M., Coy, C., 2008. Only the strong will survive: red tides as community structuring forces in the eastern Gulf of Mexico. In: Brueggeman, P., Pollock, N.W. (Eds.), Proceedings of the American Academy of Underwater Sciences 27th Scientific Symposium. American Academy of Underwater Sciences, Dauphin Island.

B. Eakins, J. Henderson, J. Varner. Bathymetry, Gulf of Mexico Data Atlas [Internet] Stennis Space Center (MS): National Centers for Environmental Information, [4 Screens] 2011; Available from: https://gulfatlas.noaa.gov/.

Flaherty, K.E., Landsberg, J.H., 2011. Effects of a persistent red tide (*Karenia brevis*) bloom on community structure and species-specific relative abundance of nekton in a Gulf of Mexico estuary. Estuar. Coast 34 (2), 417–439.

Fleming, L.E., Backer, L.C., Baden, D.G., 2005. Overview of aerosolized Florida red tide toxins: exposures and effects. Environ. Health Perspect. 113 (5), 618–620.

Fish and Wildlife Research Institute, 2015. Fish Kill Database Search. Accessed 1 June 2014. Available from:. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL. http://research.myfwc.com/fishkill/.

French, C.D., Schenk, C.J., 2005. Shaded relief image of the Gulf of Mexico (shade-drelief.jpg). Map Showing Geology, Oil and Gas Fields, and Geologic Provinces of the Gulf of Mexico Region Available at: https://pubs.usgs.gov/of/1997/ofr-97-470/OF97-470L/graphic/data.htm.

Froese, R., Pauly, D., 2018. FishBase. URL:. World Wide Web Electronic Publication. www.fishbase.org.

Fujiwara, M., Zhou, C., Acres, C., Martinez-Andrade, F., 2016. Interaction between *Penaeid* shrimp and fish populations in the Gulf of Mexico: importance of shrimp as forage species. PLoS One 11 (11), e0166479.

Fulton, E.A., Parslow, J.S., Smith, A.D., Johnson, C.R., 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. Ecol. Model. 173 (4), 371–406.

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D., Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish Fish. 12 (2), 171–188.

Gasalla, M.A., Rodrigues, A.R., Postuma, F.A., 2010. The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem. ICES J. Mar. Sci. 67 (7), 1413–1424.

Goedegebuure, M., Melbourne-Thomas, J., Corney, S.P., Hindell, M.A., Constable, A.J., 2017. Beyond big fish: the case for more detailed representations of top predators in marine ecosystem models. Ecol. Model. 359, 182–192.

Gray, A., Ainsworth, C., Chagaris, D., Mahmoudi, B., 2013. Red Tide Mortality on Gag Grouper 1980-2009. SEDAR33-AW21. SEDAR, North Charleston, SC, pp. 8.

Gray, A.M., 2014. Karenia Brevis Harmful Algal Blooms: Their Role in Structuring the Organismal Community on the West Florida shelf. Master Thesis. University of South Florida College of Marine Science.

Gray DiLeone, A.M., Ainsworth, C., 2019. Effects of *Karenia brevis* harmful algal blooms on fish community structure on the West Florida Shelf. Ecol. Model. 392, 250–267.

Grüss, A., Rose, K.A., Simons, J., Ainsworth, C.H., Babcock, E.A., Chagaris, D.D., de Mutsert, K., Froeschke, J., Himchak, P., Kaplan, I.C., O'Farrell, H., 2017. Recommendations on the use of ecosystem modeling for informing ecosystem-based fisheries management and restoration outcomes in the Gulf of Mexico. Mar. Coast. Fish. 9 (1), 281–295.

Grüss, A., Perryman, H.A., Babcock, E.A., Sagarese, S.R., Thorson, J.T., Ainsworth, C.H., Anderson, E.J., Brennan, K., Campbell, M.D., Christman, M.C., Cross, S., 2018a. Monitoring programs of the US Gulf of Mexico: inventory, development and use of a large monitoring database to map fish and invertebrate spatial distributions. Rev. Fish. Biol. Fish. 1–25.

Grüss, A., Chagaris, D.D., Babcock, E.A., Tarnecki, J.H., 2018b. Assisting ecosystem-based fisheries management efforts using a comprehensive survey database, a large environmental database, and generalized additive models. Mar. Coast. Fish. 10 (1), 40–70.

Hansen, D., 1969. Food, growth, migration, reproduction and abundance of pinfish, Lagodon rhomboids, and Atlantic croaker, Micropogon undulatus, near Pensacola, Florida. U.S. Fish. Comm. Bull. 68 (1), 135–146.

Harford, W.J., Grüss, A., Schirripa, M.J., Sagarese, S.R., Bryan, M., Karnauskas, M., 2018. Handle with care: establishing catch limits for fish stocks experiencing episodic natural mortality events. Fisheries 43 (10), 463–471. https://doi.org/10.1002/fsh.10131.

Heil, C.A., Steidinger, K.A., 2009. Monitoring, management, and mitigation of *Karenia* blooms in the eastern Gulf of Mexico. Harmful Algae 8 (4), 611–617.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23 (4), 202–210.

Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol. Model. 331, 173–184.

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G., Wintner, S.P., Fennessy, S.T., Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs. Ecol. Lett. 17 (2), 239–250.

Ingersoll, E., 1881. On the fish mortality in the Gulf of Mexico. Proc. U. S. Natl. Mus. 4 (195), 74–80. https://doi.org/10.5479/si.00963801.195.74.

Karnauskas, M., Schirripa, M.J., Kelble, C.R., Cook, G.S., Craig, J.K., 2013. Ecosystem Status Report for the Gulf of Mexico. NOAA Technical Memorandum NMFS-SEFSC, 653, pp. 52.

Kirkpatrick, B., Fleming, L.E., Squicciarini, D., Backer, L.C., Clark, R., Abraham, W., Benson, J., Cheng, Y.S., Johnson, D., Pierce, R., Zaias, J., Bossart, G.D., Baden, D.G., 2004. Literature review of Florida red tide: implications for human health effects. Harmful Algae 3, 99–115.

Klemas, V., 2012. Remote sensing of algal blooms: an overview with case studies. J. Coastal Res. 28 (1A), 34–43.

Koehn, L.E., Essington, T.E., Marshall, K.N., Kaplan, I.C., Sydeman, W.J., Szoboszlai, A.I., Thayer, J.A., 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California current ecosystem. Ecol. Model. 335, 87–100.

Kroetz, A.M., Drymon, J.M., Powers, S.P., 2017. Comparative dietary diversity and trophic ecology of two estuarine mesopredators. Estuar. Coast. 40 (4), 1171–1182.

Landi, P., Minoarivelo, H.O., Brännström, Å., Hui, C., Dieckmann, U., 2018. Complexity and stability of ecological networks: a review of the theory. Popul. Ecol. 60 (4), 319–345.

Landsberg, J.H., Flewelling, L.J., Naar, J., 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. Harmful

Algae 8 (4), 598–607.

Link, J., 2002. Does food web theory work for marine ecosystems? Mar. Ecol. Prog. Ser. 230, 1–9.

Link, J.S., 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecol. Model. 221 (12), 1580–1591.

Link, J.S., 2016. Corrigendum to "adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL" [Ecol. Model. 221 (2010) 1580–1591]. Ecol. Model. 337, 348–349.

March, J.G., Pringle, C.M., Townsend, M.J., Wilson, A.I., 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshw. Rev. 47 (3), 377–390.

Masi, M.D., Ainsworth, C.H., Chagaris, D., 2014. A probabilistic representation of fish diet compositions from multiple data sources: a Gulf of Mexico case study. Ecol. Model. 284, 60–74.

Morzaria-Luna, H., Ainsworth, C.H., Tarnecki, J., Grüss, A., 2018. Diet composition uncertainty determines impacts on fisheries following an oil spill. Ecosyst. Serv. 33, 187–198.

Motta, P.J., Clifton, K.B., Hernandez, P., Eggold, B.T., Giordano, S.D., Wilcox, R., 1995. Feeding relationships among nine species of seagrass fishes of Tampa Bay, Florida. Bull. Mar. Sci. 56 (1), 185–200.

Nelson, E.J., Holden, J., Eves, R., Tufts, B., 2017. Comparison of diets for Largemouth and Smallmouth Bass in Eastern Lake Ontario using DNA barcoding and stable isotope analysis. PLoS One 12 (8), e0181914.

Nigmatullin, C.M., Nesis, K.N., Arkhipkin, A.I., 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (*Cephalopoda: ommastrephidae*). Fish. Res. 54 (1), 9–19.

O'Farrell, H., Grüss, A., Sagarese, S.R., Babcock, E.A., Rose, K.A., 2017. Ecosystem modeling in the Gulf of Mexico: current status and future needs to address ecosystem-based fisheries management and restoration activities. Rev. Fish Biol. Fish. 27 (3), 587–614.

Okey, T.A., Mahmoudi, B. (Eds.), 2002. An Ecosystem Model of the West Florida Shelf for Use in Fisheries Management and Ecological Research: Vol. II. Model Construction. Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg.

Okey, T.A., Vargo, G.A., Mackinson, S., Vasconcellos, M., Mahmoudi, B., Meyer, C.A., 2004. Simulating community effects of sea floor shading by plankton blooms over the West Florida shelf. Ecol. Model. 172, 339–359.

Palomares, M.L.D., Pauly, D., 2018. SeaLifeBase. URL:. World Wide Web Electronic Publication. www.sealifebase.org.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57 (3), 697–706.

Pauly, D., Soriano-Bartz, M., Palomares, M.L., 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings No. 26, pp. 1–13.

Plantier-Santos, C., Carollo, C., Yoskowitz, D.W., 2012. Gulf of Mexico ecosystem Service Valuation Database (GecoServ): gathering ecosystem services valuation studies to promote their inclusion in the decision-making process. Mar. Policy 36 (1), 214–217.

Rodhouse, P.G., White, M.G., 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. Biol. Bull. 189 (2), 77–80.

Rounsefell, G.A., Nelson, W.R., 1966. Red Tide Research Summarized to 1964 Including an Annotated Bibliography. Spec. Sci. Rep. No. 535. US Fish and Wildlife Service, Washington, DC.

Sagarese, S.R., Gray, A.M., Ainsworth, C.H., Chagaris, D.D., Mahmoudi, B., 2015. Red Tide Mortality on Red Grouper (*Epinephelus Morio*) Between 1980 and 2009 on the West Florida shelf. SEDAR42-AW-01. SEDAR, North Charleston, SC, pp. 12p.

Sagarese, S.R., Nuttall, M.A., Geers, T.M., Lauretta, M.V., Walter III, J.F., Serafy, J.E., 2016. Quantifying the trophic importance of gulf menhaden within the northern Gulf of Mexico ecosystem. Mar. Coast. Fish. 8 (1), 23–45.

Sagarese, S.R., Lauretta, M.V., Walter, J.F., 2017. Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico. Ecol. Model. 345, 75–98.

Sakaguchi, S.O., Shimamura, S., Shimizu, Y., Ogawa, G., Yamada, Y., Shimizu, K., Kasai, H., Kitazato, H., Fujiwara, Y., Fujikura, K., Takishita, K., 2017. Comparison of morphological and DNA-based techniques for stomach content analyses in juvenile chum salmon *Oncorhynchus keta*: a case study on diet richness of juvenile fishes. Fish. Sci. 83 (1), 47–56.

Sala, E., Sugihara, G., 2005. Food web theory provides guidelines for marine conservation. In: Belgrano, A., Scharler, U.M., Dunne, J., Ulanowicz, R.E. (Eds.), Aquatic Food Webs: An Ecosystem Approach. Oxford University Press, Oxford, pp. 170–183.

Shchetinnikov, A.S., 1988. Feeding and Food Relations of Abundant Squids in Southeastern Part of the Pacific Ocean. Autoreferat Dissertatsii na Soiskanie Uchenoj Stepeni Kandidata Biologicheskikh, Nauka, Moscow, pp. 21 (in Russian).

Shurin, J.B., Gruner, D.S., Hillebrand, H., 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proc. R. Soc. B: Biol. Sci. 273 (1582), 1–9.

Simons, J.D., Yuan, M., Carollo, C., Vega-Cendejas, M., Shirley, T., Palomares, M.L.D., Roopnarine, P., Abarca Arenas, L.G., Ibañez, A., Holmes, J., Schoonard, C.M., Hertog, R., Reed, D., Poelen, J., 2013. Building a fisheries trophic interaction database for management and modeling research in the Gulf of Mexico large marine ecosystem. Bull. Mar. Sci. 89, 135–160.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60 (3), 1129–1157.

Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Glob. Ecol. Biogeogr. 12 (3), 177–179.

Steidinger, K.A., Burklew, M.A., Ingle, R.M., 1973. The effects of *Gymnodinium breve* toxin on estuarine animals. In: Martin, D.F., Padilla, G.M. (Eds.), Marine Pharmacognosy. Academic Press, New York and London, pp. 179–202.

Steidinger, K.A., Haddad, K., 1981. Biologic and hydrographic aspects of red tides. Bioscience 31 (11), 814–819.

Steidinger, K.A., Vargo, G.A., 1988. Marine dinoflagellate blooms: dynamics and impacts. In: Lembi, C.A., Waaland, J.R. (Eds.), Algae and Human Affair. Press Syndicate of the University of Cambridge, on behalf of the Phycological Society of America, Inc., New York.

Steidinger, K.A., Carlson, P., Baden, D.G., Rodriguez, C., Seagle, J., 1998. Neurotoxic shellfish poisoning due to toxin retention in the clam *Chione cancellata*. In: Reguera, B., Blanco, J., Fernandez, M.L., Wyatt, T. (Eds.), Harmful Algae. Xunta de Galicia/ Intergovernmental Oceanographic Commission of UNESCO, Vigo, pp. 457–458.

Tarnecki, J.H., Patterson III, W.F., 2015. Changes in Red Snapper diet and trophic ecology following the Deepwater Horizon Oil Spill. Mar. Coast. Fish. 7 (1), 135–147.

Tarnecki, J.H., Wallace, A.A., Simons, J.D., Ainsworth, C.H., 2016. Progression of a Gulf of Mexico food web supporting Atlantis ecosystem model development. Fish. Res. 179, 237–250.

Terborgh, J., Estes, J.A. (Eds.), 2010. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press.

Thompson, R.M., Hemberg, M., Starzomski, B.M., Shurin, J.B., 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88 (3), 612–617.

Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5 (1), 7–16.

van Altena, C., Hemerik, L., de Ruiter, P.C., 2016. Food web stability and weighted connectance: the complexity-stability debate revisited. Theor. Ecol. 9 (1), 49–58.

Walsh, J.J., Tomas, C.R., Steidinger, K.A., Lenes, J.M., Chen, F.R., Weisberg, R.H., Zheng, L., Landsberg, J.H., Vargo, G.A., Heil, C.A., 2011. Imprudent fishing harvests and consequent trophic cascades on the West Florida shelf over the last half century: a harbinger of increased human deaths from paralytic shellfish poisoning along the southeastern United States, in response to oligotrophication? Cont. Shelf Res. 31 (9), 891–911.

Walters, C., Pauly, D., Christensen, V., 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2 (6), 539–554.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7 (2), 139–172.

Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3 (1), 70–83.

Walters, C., Martell, S.J., Mahmoudi, B., 2006. An ecosim model for exploring ecosystem management options for the Gulf of Mexico: implications of including multistanza life history models for policy predictions. In: Presentation for Mote Symposium. 6 June. pp. 23.

Walters, C., Martell, S.J., Christensen, V., Mahmoudi, B., 2008. An Ecosim model for exploring Gulf of Mexico ecosystem management options: implications of including multistanza life-history models for policy predictions. Bull. Mar. Sci. 83 (1), 251–271.

Walters, C., Christensen, V., Walters, W., Rose, K., 2010. Representation of multistanza life histories in Ecospace models for spatial organization of ecosystem trophic interaction patterns. Bull. Mar. Sci. 86 (2), 439–459.

Welsh, B.L., 1975. The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. Ecology 56 (3), 513–530.

Whitfield, A.K., 2016. Ecological role of *Mugilidae* in the coastal zone. In: Crosetti, D., Blaber, S. (Eds.), Biology, Ecology and Culture of Grey Mullet (Mugilidae). CRC, Boca Raton, pp. 324–348.

Yee, T.W., Wild, C.J., 1996. Vector generalized additive models. J. Roy. Stat. Soc. B: Met. 58, 481–493.