

An early warning sign: trophic structure changes in the oceanic Gulf of Mexico from 2011—2018



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ABSTRACT

Ecosystem-based modeling is rapidly becoming an established technique to investigate the health and stability of ecosystems. In the Gulf of Mexico, ecosystem models are applied to neritic systems, but less focus has been placed on the oceanic domain. Since 2011, severe declines have been observed in many micronekton groups that occupy the mesopelagic zone (200–1000 m depth). Here we present an ecosystem model for the oceanic northern Gulf of Mexico for the year 2011, simulate that model according to micronekton trends through 2018, and quantify the top-down and bottom-up impacts that each functional group has on one another. These trends were examined to determine whether interactions between the two groups have changed directionally over time. In 2011, zooplankton (trophic level = 2) occupied greater than one-third of the total metazoan biomass, and also 40% of the total energy throughput ascended to higher trophic levels in the system. Of the 1849 possible functional group interactions (most of which are indirect), approximately 27% showed significant changes between 2011 and 2018, which were related to shifts in biomass and diet throughout the simulation. Direct top-down interactions changed more frequently than other types of trophic relationships. The frequency of direct changes that occurred in the simulation was not observed evenly among all functional groups, as opposed to indirect interactions. These changes between functional group interactions can be used to further examine potential shifts in the trophic structure of marine ecosystems under various forcing scenarios.

1. Introduction

The open ocean is Earth's largest biome. This complex and dynamic consortium of ecosystems is subject to continual anthropogenic inputs and disturbances. Globally, anthropogenic stressors have influenced commercial fisheries stocks (Hilborn, 2011), non-commercial species' populations (Guinotte and Fabry, 2008), and abiotic drivers (Hoegh-Goldberg and Bruno, 2010) in marine systems. Increased stress exerted on an ecosystem reduces the system's stability and resiliency towards future disturbances (Costanza and Magaeu, 1999). In order to examine the health and stability of an ecosystem, a multi-species modeling approach is useful to track the interactions of many species within the same model. Ecosystem modeling is a tool that combines information regarding all known biotic and abiotic components of an ecosystem with the goal of quantifying ecosystem services and food-web topology (Levin et al., 2008). In ecosystem models, both direct (trophic connection exists) and indirect interactions (no trophic interaction between species) can be investigated (Monaco and Ulanowicz, 1997). However,

ecosystem models require many input values, and simulations involve the changing of many parameters. This increases the uncertainty of an ecosystem model when compared to a single-species model. Due to a lack of sufficient data, there are few ecosystem models for the oceanic realm (seaward of the 200-m isobath) when compared to neritic zones (Webb et al., 2010). A lack of ecosystem models hinders our ability to predict shifts in the trophic structure of oceanic ecosystems over time.

The trophic structure of an ecosystem is often classified as a series of "top-down" and "bottom-up" interactions among species and is associated with predator and prey abundances within the system (Verity and Smetacek, 2002). Fluctuations in the population size of a predator species may have an impact on the population size of a prey species, but this effect is not equal across all prey of a single predator species (Worm and Myers, 2003). Ulanowicz and Puccia (1990) developed the mixed trophic impact measurement (MTI): a metric to determine the effect an infinitesimal increase in the population size of one functional group would have on each other functional group within an ecosystem. This index ranges from -1 to 1, where large negative values indicate

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top-down feedback and large positive values indicate bottom-up feedback. MTI has been used extensively in ecosystem models to recognize keystone species (Libralato et al., 2006), important trophic connections (Sagarese et al., 2017), and the importance of fishing pressure towards the future status of a fishery (Walters et al., 1997). Given that the MTI is a measure of the relative effect of one functional group on another within the ecosystem, changes in MTIs among multiple pairs of functional groups over time indicate changes to the system's trophic structure. When simulating an ecosystem across time, it may be valuable to model a series of individual time steps as static ecosystems and analyze this positioning as a time series. This method is usually developed for ecosystem-level indicators, such as biomass (Coll and Steenbeek, 2017), yield (Coll et al., 2008), and trophic level (Shannon et al., 2014). Calculating MTI at each time step in the simulation may reveal potential trends in the top-down/bottom-up impacts one species exerts on another (relative to other species within the model).

Akin to other low-latitude systems, large finfishes (e.g., tunas, billfishes, and sharks) are the predominant apex predators in the epipelagic (0 – 200 m depth) Gulf of Mexico (GoM, hereafter), while marine mammals exist in lower abundances. Many of these upper trophic level predators make routine dives into mesopelagic depths to prey upon micronekton assemblages (Watwood et al., 2006; Wilson and Block, 2009). Many mesopelagic organisms (particularly those in the deep-scattering layer) ascend into the epipelagic zone during nighttime to prey upon zooplankton or other mesopelagic migrants and descend back into mesopelagic depths during the daytime to avoid predators (Frost and McCrone, 1978). Deeper-dwelling pelagic predators (e.g., swordfishes) make a diel vertical migration into the epipelagic zone during the night as well, presumably following micronekton prey (Lerner et al., 2013). However, the micronekton assemblage is diverse, and predators are likely not confined to a single prey source. Instead, upper trophic level predators in the upper ocean are likely opportunistically feeding on the entire assemblage, suggesting the ecosystem may be resilient to severe declines in a singular functional group (Ménard et al., 2006). Micronekton feed on diverse zooplankton and micronekton assemblages in a manner that may be taxon- or size-class-specific to partition resources among species (Hopkins and Sutton, 1998). Overall, the food web of the oceanic GoM is complex, with depth layers connected by vertical migrations. Changes in the population size of functional groups within the ecosystem may alter the trophic structure of the system.

Recently, a large emphasis has been placed on ecosystem-based management in the northern GoM (Grüss et al., 2016). This emphasis can be attributed to the large amounts of data collected since the 2010 *Deepwater Horizon* oil spill and an increase in data sharing capabilities through online data repositories, such as GRIIDC (www.data.gulfresearchinitiative.org). These models have focal points that address ecosystem restoration (de Mutsert et al., 2012), harmful algal blooms (Perryman et al., 2020), hypoxia (de Mutsert et al., 2016), fishery policy decisions (Chagaris et al., 2015), and trophic interactions (Geers et al., 2016). Ecosystem models constructed in the GoM have primarily focused on the coastal realm, with just a few exceptions expanding into the open ocean (Vidal and Pauly, 2004; Ainsworth et al., 2015). Rigorous data collection of non-commercial species in the open ocean since 2011 has filled data gaps, providing data necessary to develop an ecosystem model for this domain (Sutton et al., 2020). A model devoted to the offshore GoM would highlight the importance of micronekton as prey resources and predators of other organisms in the ecosystem, as is apparent in other oceanic systems (Griffiths et al., 2013; Choy et al., 2016).

In this study, we present the first ecosystem model in the northern GoM devoted to the offshore waters seaward of the 1000-m isobath. The model is simulated from 2011 to 2018, using observed trends in mesopelagic micronekton as the driver of the simulation. We explore the uncertainty in input parameters and use this potential error to provide confidence intervals towards model output results. The trophic structure

of the ecosystem is characterized in the context of relative top-down and bottom-up relationships among species. We estimate how these trophic interactions have changed from 2011 to 2018. Finally, we discuss these changes in the context of ecosystem health and stability.

2. Methods

2.1. Model structure

The modeled area encompasses the GoM portion of the U.S. Exclusive Economic Zone, seaward of the 1000-m isobath, approximately 350,000 km² (Zeller and Pauly, 2015; Fig. 1). The vertical domain of the model region is from the surface to 1000-m depth. The functional groups in the ecosystem model included all species that occupy the ecosystem at any time throughout the year. Nine species: yellowfin tuna (*Thunnus albacares*), blue marlin (*Makaira nigricans*), bigeye tuna (*Thunnus obesus*), white marlin (*Kajikia albida*), swordfish (*Xiphias gladius*), sailfish (*Istiophorus albicans*), bluefin tuna (*Thunnus thynnus*), albacore tuna (*Thunnus alalunga*), and skipjack tuna (*Katsuwonus pelamis*) were each divided into two-stage multi-stanza groups (juvenile and adult) to account for ontogenetic changes in diet and fishing selectivity. Larval conspecifics were included in the juvenile life stage, as tuna and billfish larval stages are much shorter than one year and growth rates are rapid (Fromentin and Powers, 2005; Sponaugle et al., 2010). The age of each multi-stanza division was determined by the age at maturity referenced in stock assessments. Roundscale spearfish (*Tetrapurus georgii*) is included with white marlin because of difficulties in distinguishing between the two species by fishers (Shivji et al., 2006). Mesopelagic fishes included the four biomass-dominant fish families in the GoM (Myctophidae, Sternopychidae, Gonostomatidae, and Stomiidae). Mesopelagic fishes from other families were aggregated based on the known (Hopkins et al., 1996) or assumed trophic positions. Juvenile neritic fishes that either migrate or are advected offshore by currents were included in the epipelagic forage feeder group, as this would be their ecological role. Aggregate groups of invertebrates and primary producers were necessary to complete the food web. The resulting model consists of 42 functional groups, including three marine mammal groups, sea turtles, seabirds, 29 fish groups (10 of which are larval or juvenile), six invertebrate groups, one primary producer, and one detritus group. Additionally, one fishery is included in the model.

2.2. Ecopath with ecosim

Ecopath with Ecosim (EwE) is a mass-balanced ecosystem software that assumes the ecosystem is in equilibrium. EwE was initially developed as a method to provide information about the standing stock of functional groups and the flow of energy throughout an ecosystem (Polovina, 1984). Since its initial release, EwE has undergone extensive development with the inclusion of additional plug-in procedures (Steenbeek et al., 2016), but the original framework still exists in the current software. Two master equations control the mass-balance assumption within Ecopath: One describes production, and the second describes energy balance (*sensu* Christensen et al., 2008). Four Ecopath parameters are necessary for each group: Biomass (B), Production/Biomass (P/B), Consumption/Biomass (Q/B), and Ecotrophic Efficiency (EE; Table 1). Ecotrophic efficiency is defined as the proportion of production that is used within the system and is best calculated as an estimated parameter when all other information is known. A Biomass Accumulation (BA) parameter can be included to reflect population trends leading into the initial model year and can increase the reliability of model results in data-limited ecosystems (Natugonza et al., 2020). Ecopath once required the assumption of a steady state (Polovina, 1984), but advancements have reduced this assumption so that each functional group must achieve mass balance throughout each time step in the model and can otherwise be dynamic. An additional input parameter is the diet composition (i.e., the proportion of annual diet by

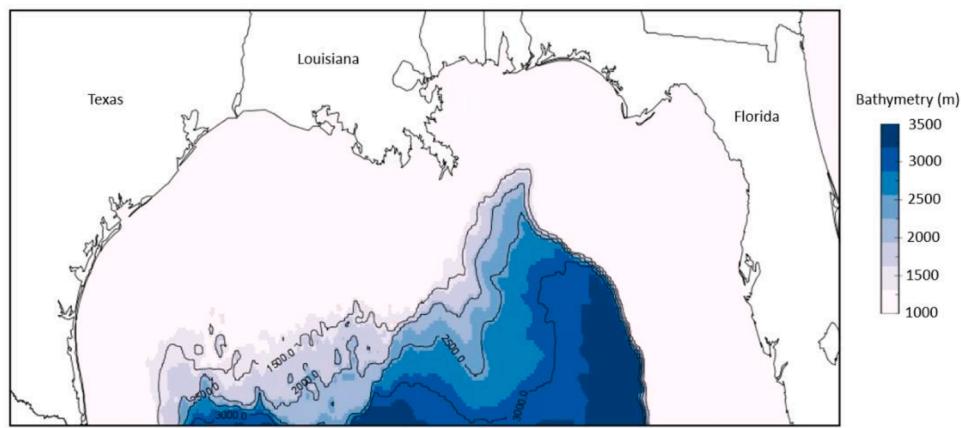


Fig. 1. Map of the model domain. This model includes the area of the U.S. Exclusive Economic Zone of the northern Gulf of Mexico, seaward of the 1000-m isobath. Color shading is included to show bathymetry. The average depth of the model domain is 2297 m.

Table 1

Input values of the original Ecopath model. Values estimated by the software are in bold. Trophic level is derived as a fractionated value from the diet matrix.

Group No.	Group name	Trophic level	Biomass (t/km ²)	P/B (/year)	Q/B (/year)	EE	P/Q (/year)	BA rate (/year)
1	Toothed Whales	4.50	1.10E-03	0.020	4.113	0.021	0.005	–
2	Baleen Whales	4.15	2.21E-04	0.020	4.684	0.000	0.004	–
3	Dolphins	4.22	1.39E-02	0.020	14.119	0.357	0.001	–
4	Seabirds	3.76	1.66E-03	0.300	1.000	0.100	0.300	–
5	Sea Turtles	3.43	1.21E-02	0.190	0.950	0.100	0.200	–
6	Oceanic Sharks	4.63	3.11E-03	0.454	3.165	0.100	0.144	–
7	Adult Albacore	4.46	4.87E-04	0.550	11.024	0.345	0.050	2.30E-06
8	Juvenile Albacore	4.03	9.23E-04	0.750	20.819	0.361	0.036	2.30E-06
9	Adult Bigeye	4.25	2.81E-05	0.700	6.915	0.259	0.101	-9.00E-07
10	Juvenile Bigeye	3.80	1.85E-05	0.800	12.889	0.051	0.062	-9.00E-07
11	Adult Bluefin	4.07	7.07E-04	0.500	4.815	0.168	0.104	4.10E-06
12	Juvenile Bluefin	3.62	3.04E-02	0.700	9.243	0.038	0.076	4.10E-06
13	Adult Sailfish	4.05	2.99E-03	0.407	7.216	0.245	0.056	3.50E-04
14	Juvenile Sailfish	3.73	7.92E-04	0.356	12.350	0.317	0.029	3.50E-04
15	Adult Yellowfin	3.93	1.09E-01	0.477	10.820	0.058	0.044	-5.50E-03
16	Juvenile Yellowfin	3.82	1.02E-01	1.179	20.106	0.125	0.059	-5.50E-03
17	Adult Swordfish	4.15	2.46E-02	0.679	8.339	0.106	0.081	-2.40E-03
18	Juvenile Swordfish	3.56	2.50E-02	0.448	15.087	0.054	0.030	-2.40E-03
19	Adult White Marlin	4.24	5.71E-03	0.350	8.132	0.256	0.043	4.50E-05
20	Juvenile White Marlin	3.81	1.99E-04	0.550	18.358	0.093	0.030	4.50E-05
21	Adult Skipjack	3.75	3.69E-05	1.441	14.564	0.039	0.099	-8.10E-06
22	Juvenile Skipjack	3.49	5.37E-06	0.864	30.778	0.010	0.028	-8.10E-06
23	Adult Blue Marlin	4.19	1.26E-03	0.500	5.580	0.349	0.090	3.90E-05
24	Juvenile Blue Marlin	3.81	4.92E-04	0.600	10.066	0.123	0.060	3.90E-05
25	Small Tunas and Other Large Predators	4.05	6.36E-03	1.069	8.342	0.400	0.128	–
26	Dragonfishes	3.95	2.70E-03	1.119	5.595	0.800	0.200	–
27	Other Mesopelagic Zooplanktivores	3.30	2.43E-02	1.138	3.498	0.950	0.325	–
28	Epipelagic Forage Feeders	3.15	3.30E+00	1.017	22.122	0.600	0.046	–
29	Other Mesopelagic Micronektonivores	3.91	5.13E-02	0.875	2.915	0.950	0.300	–
30	Hatchetfishes	3.33	1.10E-02	4.588	15.293	0.403	0.300	–
31	Bristlemouths	3.27	7.92E-02	3.386	11.288	0.247	0.300	–
32	Lanternfishes	3.31	2.22E-02	3.600	12.000	0.718	0.300	–
33	Leptocephali	2.07	4.00E-02	0.381	1.270	0.200	0.300	–
34	Cephalopods	3.30	1.66E+00	4.000	20.000	0.700	0.200	–
35	Decapods	2.65	1.16E-02	6.000	20.000	0.916	0.300	–
36	Euphausiids	2.42	6.79E-02	22.500	75.000	0.950	0.300	–
37	Mesozooplankton	2.11	2.50E+00	22.000	67.000	0.950	0.328	–
38	Ichthyoplankton	2.50	2.32E+00	15.000	45.000	0.990	0.333	–
39	Gelatinous zooplankton	2.47	8.02E-01	37.000	80.000	0.990	0.463	–
40	Microzooplankton	2.00	1.96E+00	36.000	89.000	0.990	0.404	–
41	Phytoplankton	1.00	2.55E+00	160.000	–	0.650	–	–
42	Detritus	1.00	5.00E+00	–	–	0.993	–	–

"P/B" = Production/Biomass, "Q/B" = Consumption/Biomass, "EE" = Ecotrophic Efficiency, "P/Q" = Production/Consumption, "BA" = Biomass Accumulation.

biomass) of each predator group on each prey group in the model. The diet of each functional group must be entered and cannot be estimated (including cohorts of multi-stanza groups). In this model, diet information is provided from bibliographic sources (Supplementary Material A).

Walters et al. (1997) developed Ecosim, a temporal-dynamic model that uses input parameters from a balanced Ecopath model and estimates changes in an ecosystem over time. The dynamics of an Ecosim model are expressed through two differential equations, one that estimates changes in biomass over time, and another that estimates changes

in consumption rates at each time step (*sensu* Christensen et al., 2008). During an Ecosim simulation, additional parameters monitor the change in a predator's ability to find and consume prey. The changes in consumption rates are derived from the foraging arena concept (Walters and Juanes, 1993), where prey groups can shift between vulnerable (available to the predator) and invulnerable (unavailable to the predator) states. A high vulnerability parameter signifies top-down control, while a low vulnerability parameter is indicative of bottom-up forcing. Vulnerability parameters were estimated for each functional group using an iterative fitting procedure (Christensen et al., 2008). This procedure tests different vulnerability values for each species and searches for the values that provide the best statistical fit towards a reference time series (Heymans et al., 2016). The vulnerability of larval and juvenile fishes was set at 1 (bottom-up forcing), which significantly improved model performance towards expected adult tuna and billfish trends.

2.3. Parameterization

Information regarding specific sources used to parameterize the model are in Supplementary Material B. Biomass (B ; metric tons km^{-2}) values derive from single-species stock assessments or from fisheries-independent survey data. The finfish stock assessment species that occupy the oceanic GoM have a wider distribution than the model domain. The adult biomass for each multi-stanza group was determined as the quotient of nominal catch in the GoM and fishing mortality that occurs in the model domain ($B = C/F$). Fishing mortality in the model domain was calculated as the product of the proportion of catches in the GoM relative to the entire stock and the fishing mortality of the entire stock. The data originate from the International Commission for the Conservation of Atlantic Tunas (ICCAT; www.iccat.int/en/). This calculation forces the assumption that standardized catches throughout a stock are a suitable proxy for the distribution of the stock and was chosen in favor of assuming the stock is distributed uniformly across the stock area. Marine mammal and micronekton functional group biomasses were calculated as the product of the standardized abundance (N individuals km^{-2}) and mean weight of an organism from either literature values (Trites and Pauly, 1998; NMFS 2019) or survey data. The production/biomass ratio (P/B ; year^{-1}) or total mortality (Z ; year^{-1}) is calculated as the sum of natural mortality and fishing mortality from stock assessments or through empirical relationships (Pauly, 1980; Eq. (1)):

$$M = K^{0.65} * L_{\infty}^{-0.279} * T_C^{0.463} \quad (1)$$

where M is natural mortality (year^{-1}), K is the curvature parameter from the von Bertalanffy growth equation, L_{∞} is the asymptotic length, and T_C is the mean water temperature in Celsius. Consumption values (Q/B) were estimated based on empirical relationships concerning diet, morphometrics, and water temperature at mean depth (Palomeres and Pauly, 1989; Eq. (2)):

$$\log\left(\frac{Q}{B}\right) = 5.847 + 0.280\log Z - 0.152\log W_{\infty} - 1.360T' + 0.062A + 0.510h + 0.390d \quad (2)$$

where W_{∞} is the asymptotic weight (g), T' is the mean water temperature expressed as 1000/temperature in Kelvins, A is the aspect ratio, and h and d are factors correcting for herbivores and detritivores. The values input into Equation 6 are derived from FishBase (Froese and Pauly, 2019).

The diet compositions of all functional groups were estimated from literature values and adjusted to match the requirements of input into an Ecopath model (% weight in diet). To account for uncertainty among input values, each parameter was assigned a rank in EwE's pedigree

table, which places a confidence interval around the input value to be used along with resampling techniques. Trophic levels are calculated as fractional values (Odum and Heald, 1975) for use in simulation-based analyses. For energy flow related results (i.e., non-Ecosim), a trophic aggregation technique (Ulanowicz, 1995) reorganized functional groups into integer-based trophic levels, as first described in Lindeman (1942).

One commercial fishing fleet was incorporated: U.S. Pelagic Longline. Landings and fishing effort (No. of hooks) from the longline fleet was obtained from ICCAT databases for the years 2011–2018. Bycatch values for the U.S. Pelagic Longline fleet and bycatch mortality rates were gathered from literature sources (Pacheco et al., 2011; Kerstetter and Graves, 2008; Garrison and Stokes, 2014). If bycatch data were not available for a functional group, all catches were assumed to be landed. The resulting model requires model balancing, a systematic process in which the parameters that were believed to have the greatest uncertainty were adjusted first.

2.4. Time series

The EwE model was developed with the reference year of 2011 and simulated through 2018. The Ecosim model was calibrated to 25 time series of relative changes in catch and biomass values over the eight-year period. Declines in the biomass of five micronekton groups (lanternfishes, bristlemouths, hatchetfishes, decapods, and euphausiids) were forced during simulations (i.e., the user controls the value at each time step; Christensen et al., 2008) according to survey information in 2011 and 2015–2018 (Cook and Sutton, 2017a, 2017b; Sutton et al., 2017; Cook and Sutton, 2018, 2020). Time-series biomass values for micronekton groups were calculated as the product of the median standardized abundance and the average weight of an individual of that functional group per sampled year. Only "Gulf Common Water" sampling stations (*sensu* Johnston et al., 2019) were included in micronekton biomass calculations to reduce sample bias caused by the Loop Current. Euphausiid biomass values were estimated at the start of the simulation, so the forced change over time is relative to the initial start value. Dragonfish (Stomiidae) biomass values were not forced during simulations because a significant portion of the population is believed to avoid capture by 10-m² MOCNESS deployments (the standard gear used to catch micronekton in the modelled region; Marks et al., 2020). Due to an absence of reference data, changes in biomass for micronekton functional groups from 2012–2014 are assumed to be a linear function between 2011 and 2015. Interannual changes in the fishing effort for the longline fleet were also forced.

2.5. Shifts in trophic structure

Using the aforementioned pedigree as a guide for confidence intervals and the original input parameter as a prior value, Monte Carlo simulations (1000 iterations) were run to explore the variation in final output based on original uncertainty (Heymans et al., 2016). Variance among input parameters from the Monte Carlo iterations is displayed in Supplementary Material C. Similar to Choy et al. (2016), feeding guilds were established for all functional groups with a trophic level greater than 3.5 to differentiate among feeding of top predators. A trophic level of 3.5 was chosen as a cut-off because this group contains adult cohorts of tunas and billfishes, micronektivorous fishes, and marine mammals. We employed this method for both 2011 (start of simulation) and 2018 (end of simulation) to identify trophic shifts among top predators in the ecosystem. The average diet matrix (mean of 1000 iterations) for each year was calculated. A hierarchical clustering method performed on a Bray-Curtis similarity matrix determined the feeding guilds in each year using 60% similarity as a cut-off (Clarke and Gorley, 2006). These guilds were overlaid with fitted eigen vectors on an MDS plot to aid in the interpretation of clustering results. All multivariate analyses were conducted using the R vegan package (Oksanen et al., 2019).

The mixed trophic impact (MTI) was calculated (Ulanowicz and

Puccia, 1990) individually for each iteration, for each functional group pair in the model ($N = 1849$), and for each year ($n = 8$). Averages and standard deviations were calculated for every functional group pair every year, treating the iterations as replicates. For each pair, a linear model was developed to examine whether the trend in MTI was a significant change or not. A p-value of less than 0.05 was considered statistically significant. The code used to calculate the MTI from the Monte Carlo model output is available as an R Markdown document on GitHub (www.github.com/mwood078-oGom-EwE).

3. Results

3.1. Ecopath results

The model comprises approximately five trophic levels, with sharks, marine mammals, and adult tunas and billfishes occupying the top of the food web. The micronekton groups that were forced in this simulation occupied trophic levels ranging from 2.42 to 3.33. A decomposition of the origin of flows by integer-based trophic level for each functional

group revealed that for all mesopelagic zooplanktivorous fish functional groups, greater than 75% of the energy they receive placed them in the third trophic level (Fig. 2). The two primary producer groups (including detritus) accounted for 29.1% of the total standing stock biomass in the system, while upper trophic level organisms ($TL > 4$) amounted to just 10.1% of the total biomass. The largest proportion of biomass was zooplankton ($TL = 2$), which accounted for 35.9% of the total biomass in the system. Zooplankton was responsible for 38.4% of the total system throughput (sum of consumption by predators, export, flow to detritus, and respiration), while upper trophic level organisms were only responsible for 3.7% of the total throughput. Detritus was the origin of a significant proportion of the total flow through the system (36%), which can be a sign of a mature ecosystem (Odum and Heald, 1975) and highlights the importance of detritus in the oceanic GoM.

3.2. Simulated processes

Throughout the eight-year simulation, all functional groups experienced some change in their biomass and trophic level, but many changes

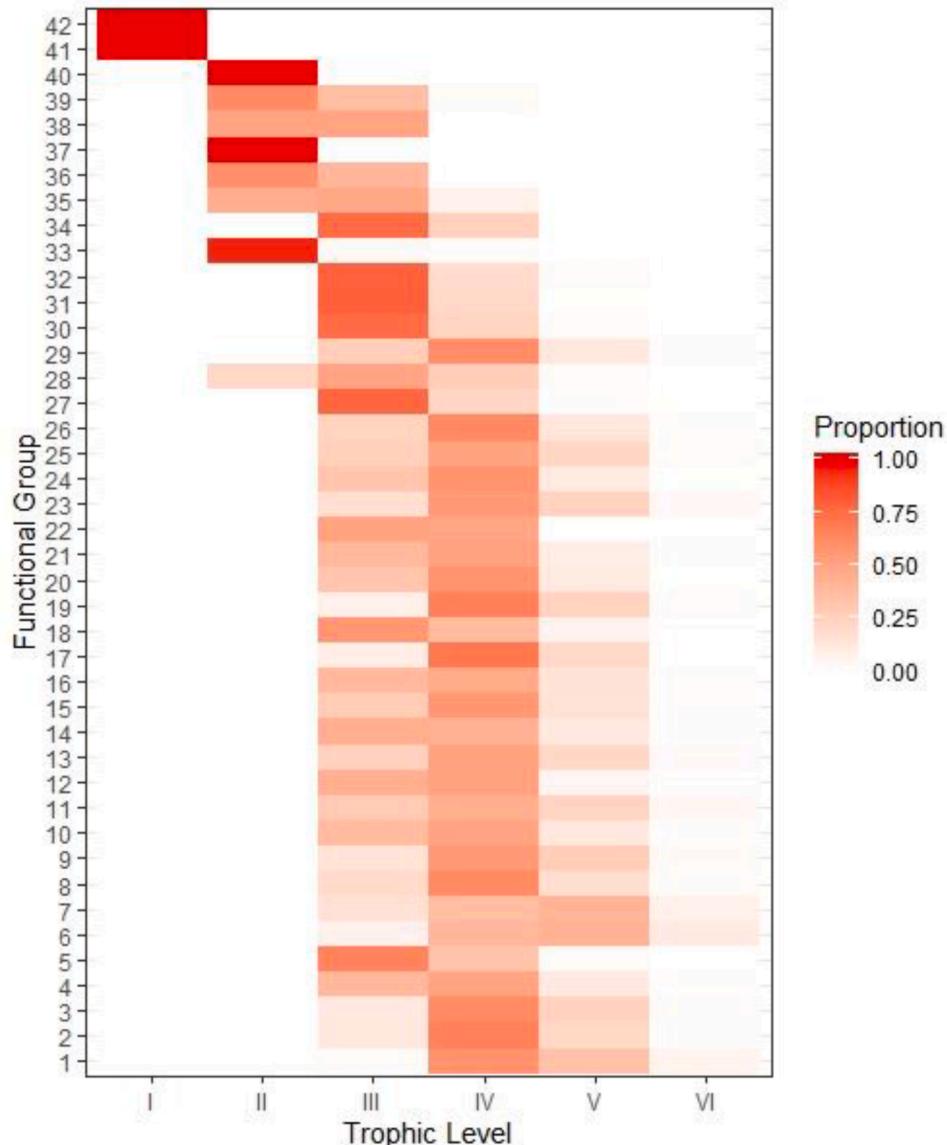


Fig. 2. Shade plot of the trophic level decomposition for each functional group based on diet composition. Red values are positive, shaded to proportion. Functional groups with positive values in multiple trophic levels indicate feeding on a variety of trophic levels (i.e., omnivory). Weighted averages equate to the mean trophic level of the functional group in Table 1.

were discrete (Fig. 3). Thirty-one of the 42 functional groups within the model showed a decrease in biomass throughout the simulation. The three functional groups that benefited the most throughout the simulation were juvenile skipjack (13.18% increase), oceanic sharks (7.79% increase), and mesozooplankton (3.01% increase). The most negatively affected functional groups in terms of percentage change were decapod crustaceans (81.10% decrease), bristlemouths (65.2% decrease), and dragonfishes (61.5% decrease). Twenty-five functional groups experienced a decrease in trophic level throughout the simulation. The largest overall changes in trophic level (TL) occurred in fishes that rely heavily on mesopelagic micronekton as a prey source: adult albacore tuna (0.08 TL decrease), juvenile albacore tuna (0.08 TL decrease), and dragonfishes (0.04 TL increase). In general, 19 functional groups decreased in both trophic level and biomass, while just eight increased in both (Fig. 3).

3.3. Shifts in diet

The underlying mechanics behind an Ecopath with Ecosim model rely on the predator-prey relationships driven by the diet matrix. Any change in the trophic structure that is not captured by changes in the trophic level of a functional group should be reflected in the diet matrix as a significant shift in prey taxa consumed (% biomass) relative to other predators at a similar trophic level. To target the effect of declines in micronekton biomass, two sets of feeding guilds were established for functional groups with a trophic level greater than 3.5. In 2011, 12 feeding guilds were established based on the similarity of diets (Fig. 4a). Predation on bristlemouths, decapod crustaceans, epipelagic forage feeders, cephalopods, ichthyoplankton, and dragonfishes best explained the food web structure. Lanternfishes are notably absent from this list because they are eaten by nearly all upper trophic level organisms, and do not contribute to diverging diets. Although marine mammals consume mesopelagic prey, their diets were separated from many tuna and billfish species because of an affinity for cephalopods and larval fishes (Fig. 4a). Seven single-group feeding guilds were present: oceanic sharks, adult albacore tuna, adult bigeye tuna, adult bluefin tuna, adult white marlin, small tunas and other large predators, and dragonfishes. An epipelagic-fish feeding guild was composed of seabirds, juvenile bluefin tuna, and juvenile yellowfin tuna. Dragonfishes were a bit of an outlier among the other functional groups, as their diet composition is primarily mesopelagic zooplanktivores. Other diets are more diverse than dragonfishes, including cephalopods and micronektonivores, so the dragonfish placement in this plot was more indicative of a vastly

different diet compared to other top predators in the ecosystem.

In 2018, eleven feeding guilds were recognized, and some functional groups have transitioned to have similar diets to other functional groups (i.e., changed feeding guild; Fig. 4b). Decapod crustaceans, bristlemouths, and dragonfishes no longer explained the majority of the food web structure, and instead were replaced by adult albacore tuna, juvenile yellowfin tuna, and other mesopelagic fishes. Compared to 2011, other upper trophic level organisms explained more of the food web structure than mesopelagics, which can be interpreted as a reduction in the mesopelagic biomass constricting the diversity of prey available to top predators.

3.4. Mixed trophic impact analysis

Individual linear models ($n = 1849$) indicated that there was a change in 27.3% of the functional group interactions during this simulation (Fig. 5). Although each functional group acted as both the impacting and impacted group towards each other functional group in the model, a change in one end of the interaction was reciprocated with a change in the other side of the relationship 47 times, which is likely an indication ecosystem complexity. Of the interactions where there was a direct trophic relationship (i.e., predator-prey interaction; $n = 505$), 32.3% of the interactions showed a change from 2011–2018 (Table 2). An uneven number of direct top-down and bottom-up interactions was the result of cyclical relationships (e.g., “cannibalism”). During the simulation, direct relationships strengthened more frequently than they weakened for both top-down and bottom-up interactions (Table 2). Contrary to direct interactions, indirect interactions weakened more frequently than strengthened (Table 2). Indirect interactions were the most common type of relationship ($n = 1344$) and changed less frequently than direct interactions (24.7% frequency). Direct top-down interactions changed more than the other three types of interactions, suggesting these types of relationships are more labile in the oceanic GoM.

When organizing groups by trophic level, there was no apparent trend in the proportion of changed interactions related to a functional group role in the ecosystem (Fig. 6). The changes seen in direct interactions were focused on certain functional groups, as opposed to being shared across all groups in the system (i.e., some functional groups had zero interactions change, while others had many). Changes among direct top-down interactions were more frequent than among direct bottom-up interactions (Fig. 6). Both types of indirect interactions (top-down and bottom-up) changed in small proportions for all functional

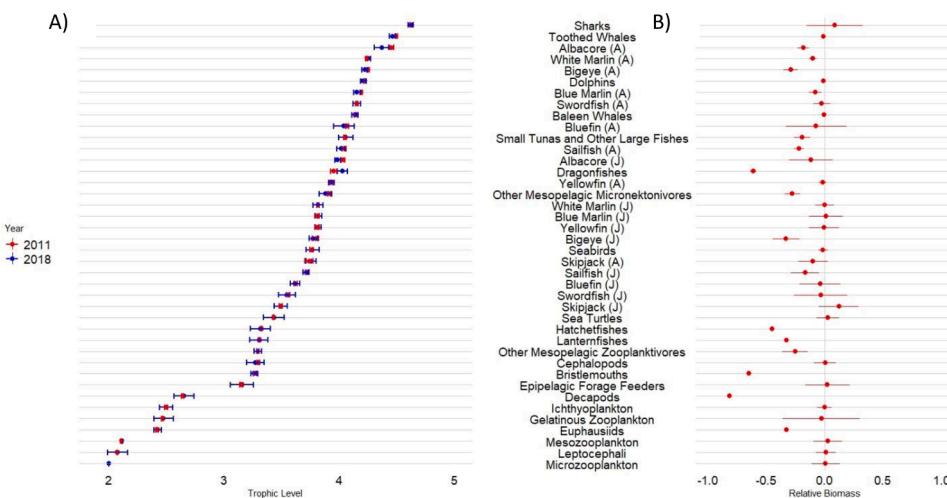


Fig. 3. Trophic level and biomass changes between 2011 and 2018. Functional groups are ordered by trophic level. “A” and “J” correspond to “adult” and “juvenile” as determined by the age of maturity. Error bars are 95% confidence intervals originating from 1000 model iterations. A) Mean trophic level by functional group for 2011 (red) and 2018 (blue). B) Relative biomass calculated as: (final – initial) / initial.

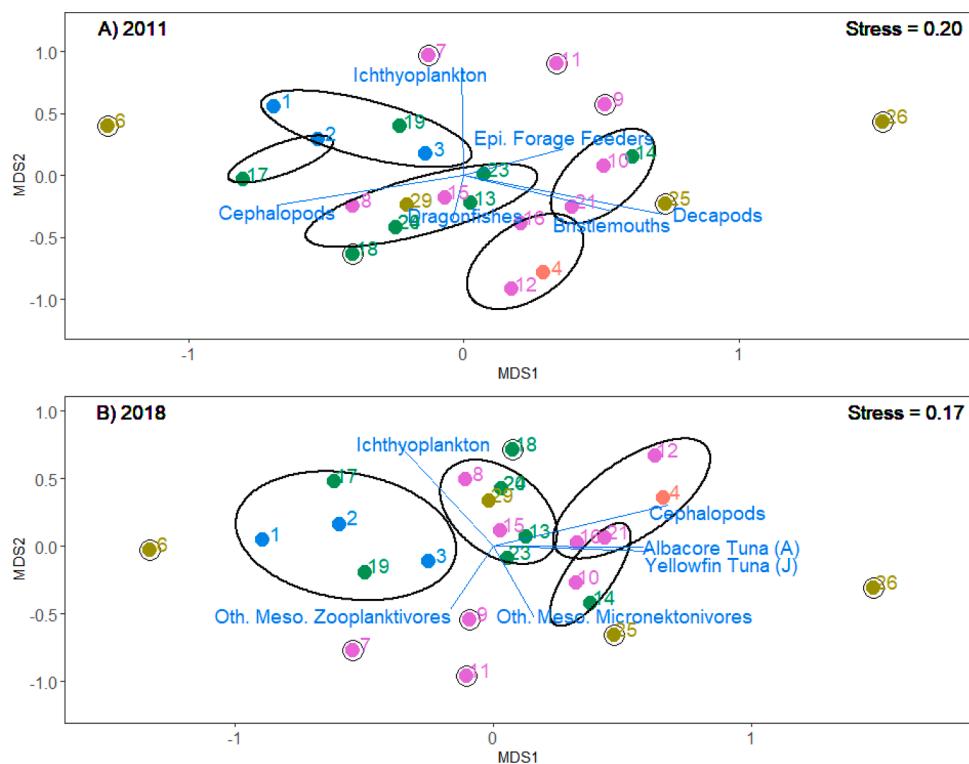


Fig. 4. Ordination plots of the upper trophic level organisms ($TL > 3.5$) according to Bray-Curtis similarity matrices. Guilds are displayed by ellipses. The prey groups that explained the majority of the matrix structure are shown as blue vectors and labeling. Predator groups are distinguished by taxon: blue = marine mammals, red = seabirds, purple = tunas; green = billfishes; yellow = other fishes.

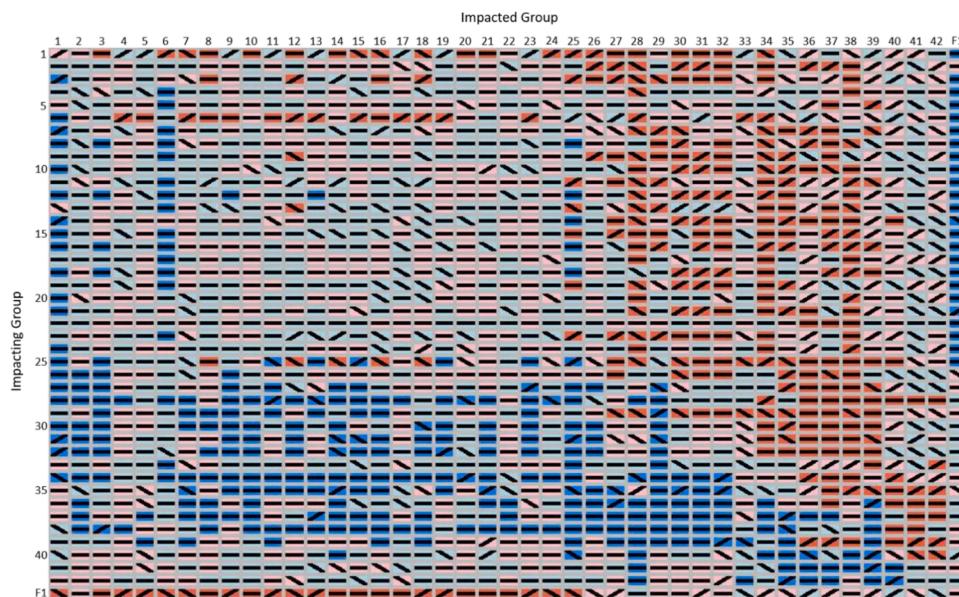


Fig. 5. Matrix of the trend observed in all functional group pairs over time. The background colors represent the initial role that functional group serves in the interaction: dark blue = prey (bottom-up), dark red = predator (top-down), light blue = indirect bottom-up, light red = indirect top-down. Lines represent the trend in the interaction over time: flat = no change, increasing = strengthened, decreasing = weakened. Numbers correspond to functional groups in Table 1. F1 corresponds to the U.S. Pelagic Longline fishing fleet.

Table 2

Contingency table of the number of functional group interactions that showed a change throughout the time series. The total number of interactions is in parentheses.

Interaction	Strengthened	Weakened	Unchanged
Direct Top-Down (318)	30.82%	18.87%	50.31%
Direct Bottom-Up (323)	8.98%	6.19%	84.83%
Indirect Top-Down (618)	9.71%	12.62%	77.67%
Indirect Bottom-Up (590)	5.42%	21.69%	72.88%

groups in the model, suggesting that the entire ecosystem experienced some change between 2011 and 2018. The preponderance of weakening indirect interactions (and scarcity of strengthening) suggests ecosystem resiliency has decreased (Bertness et al., 2015), as future ecosystem processes will now be more driven by direct interactions.

4. Discussion

The role of mesopelagic micronekton as ‘wasp-waist’ controllers in pelagic ecosystems is well documented (Griffiths et al., 2013; Choy et al.,

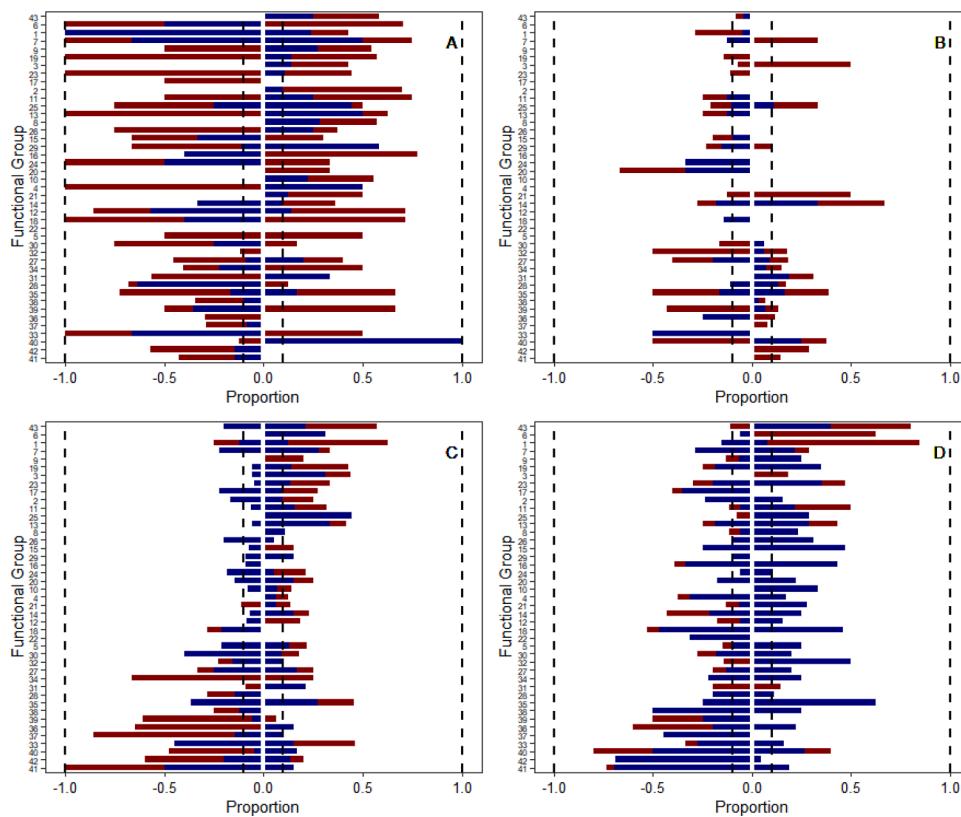


Fig. 6. Stacked barplots showing the proportion of interactions that changed for each functional group between 2011 and 2018. Values to the right of 0 represent the functional group acting as the impacting group, and values to the left of 0 are when the group is the impacted group. Total bar height is the overall proportion of changed interactions (0–1). Colors represent the directionality of change, where red indicates interactions that strengthened and blue indicates interactions that weakened. Vertical black lines mark 10 and 100% of interactions for readability. Functional groups are organized in descending order by trophic level, beginning with the fishery (Functional group 43). A) Direct top-down interactions, B) direct bottom-up interactions, C) indirect top-down interactions, and D) indirect bottom-up interactions.

2016). Compared to neritic habitats, pelagic organisms have less specific diets, but preferential preys exist (Drazen and Sutton, 2017). The feeding guilds that mesopelagic fishes can occupy are limited because the concentration of particulates in the water column is too low for filter feeding at mesopelagic depths (Herring, 2002), and herbivory is rare (Robison, 1984). Thus, carnivory dominates the feeding mode of mesopelagic fishes. Just three of the direct top-down interactions that involve myctophids, sternopychids, gonostomatids, and other mesopelagic zooplanktivores as predators strengthened throughout the simulation, while seven weakened (all from the aggregate group). A dearth of change among these functional groups, which had significant declines in biomass, is evidence of a poor ability to switch prey among a diminished prey field. These restricted diet options, combined with declines in macrozooplankton populations, will likely inhibit the recovery of micronekton fish populations as food is less prevalent. Furthermore, the direct top-down interactions exerted on the mesopelagic zooplanktivorous fish groups strengthened in 23 of 60 possible interactions and weakened in only five. Decreased mesopelagic zooplanktivorous fish populations in the oceanic GoM should hypothetically be relieved of predation pressure (regardless of where the population was pre-2011), but in many instances, the role they provide as prey has become more intense. Similar to the euphausiid-capelin (*Mallotus villosus*) trophic relationship in Newfoundland waters (Obrovich et al., 2014), a persistent decline in micronekton populations may have inauspicious effects on predator population growth.

Zooplankton populations are pivotal to the stability of oceanic ecosystems, as they are the food-web link between autotrophic organisms and secondary consumers. Filter-feeding zooplankton package pico- (10^{-12} m) and nano-size particles (10^{-9} m) into a consumable material for other consumers. Others, such as decapod crustaceans and some euphausiids, consume microzooplankton and mesozooplankton, occasionally competing with small fishes (Heffernan and Hopkins, 1981; Kinsey and Hopkins, 1994; Hopkins and Sutton, 1998). This wide niche breadth throughout the trophic level is why approximately two-fifths of

the total system throughput occurs at the zooplankton trophic level. Similar to fishes, the direct interactions involving zooplankton were labile. Therefore, pelagic zooplankton was predicted to experience greater predation pressure in 2018 despite their population decline. However, an underrepresented portion of many food-web models is the role of gelatinous zooplankton in the transfer of energy through the ecosystem. Although this model incorporates occurrences of gelatinous feeding by upper trophic level organisms (Cardona et al., 2012), these values are believed to be heavily underreported in the literature (Drazen and Sutton, 2017). The stability of the oceanic GoM ecosystem is dependent on the stability of the zooplankton trophic level, so it is imperative to understand the interactions that control their population dynamics.

Approximately one-quarter of all possible trophic interactions in the oceanic GoM changed between 2011 and 2018. For each functional group pair, i and j , there are two types of interactions. One interaction is where group i is the group exerting impact on group j , and another is where group i is receiving the impact from group j . In an ecosystem with high modularity (i.e., several guilds of organisms only interact with each other), a change in the top-down impact of one group to another should result in a change of the bottom-up impact in the reciprocating interaction, as a result of ecosystem simplicity. However, in this exercise, a change in the interaction between two groups did not often result in a change in the opposite direction. For example, the direct top-down pressure that dragonfishes exert on hatchetfishes weakened, but the direct bottom-up support hatchetfishes provide to dragonfishes did not change from 2011–2018. This phenomenon is likely attributable to the complexity of the oceanic GoM micronekton assemblage (Hopkins and Lancraft 1984) that allows upper trophic level predators to shift their diet to new preys rather than starve. The importance of mesopelagic micronekton in the diet of apex predators in the oceanic zone suggests that changes in population sizes within the micronekton community could have a direct impact on the predatory success of these apex predators (Duffy et al., 2017), as this exercise shows. Declined predator

success will result in declined biomass, but GoM-specific abundance indices suggest that yellowfin and bluefin tuna populations may be relatively stable or increasing (Anon, 2017, 2019). The potential underestimates in apex predator biomass is likely a product of an inability to model an “open-system” where organisms could leave but suggests that the results related to the top-down pressure on micronekton may be conservative. In reality, opportunistic predation and long-distance migrations by apex predators likely provide a buffer towards the stability of these predator populations (Ménard et al., 2006), despite declines in major prey resources in the GoM. These diet shifts were reflected in the calculation of the MTI as the declined prey group was predicted to experience less predation pressure from the predator, and the predator now benefits less from the existence of the former prey group (lower diet contribution). In stable ecosystems, individual populations can fluctuate because species that occupy a similar niche can replace declining populations (Holling, 1973). In the context of this exercise, changes among top-down and bottom-up effects may not reflect permanent changes to the trophic structure of the ecosystem, but instead, a temporary change based on fluctuations in prey abundances. However, simulated biomass declines in other micronekton groups (e.g., dragonfishes, cephalopods, and other mesopelagic micronektivorous fishes) indicates the northern GoM may no longer be a plentiful foraging ground for upper trophic level organisms compared to 2011.

Changes in the MTI of one functional group on another will mostly be influenced by changes in diet and biomass. Significant changes in diet (relative to the rest of the ecosystem) should adjust the trophic level of a functional group throughout a simulation, and diet is influenced by shifts in the biomass of prey groups over time (Shannon et al., 2014). Declines in several micronekton groups in this model led to a slight increase in the biomass of groups of a similar niche that were not forced (e.g., mesozooplankton), but to a decline in those dependent on mesopelagic micronekton as a prey resource (e.g., dragonfishes). An investigation of the MTI over time provides a more refined view into potential shifts in the role of each organism relative to others within the system and could be used to assess other oceanic ecosystems.

The total effort of fishers on an annual basis is a dynamic process influenced by the availability of target fishes, length of the fishing season, and unexpected shutdowns (Monroy et al., 2010). In an ecosystem model, the role of each fishing fleet is to remove biomass (similar to an apex predator). Fluctuations in the effort of a fishing fleet influence the amount of fishing pressure exerted on each commercial species. Since 2011, the fishing effort by the U.S. Pelagic Longline Fleet in the GoM has declined as a response to fishing regulations implemented in the region to reduce bluefin tuna bycatch (NMFS, 2020). This decline in the fishing effort has lessened the fishing mortality exerted on commercial groups, having a negative indirect effect on many intermediate trophic level groups. Micronekton interact on a much smaller spatial scale than large pelagic fishes but exist in large numbers as a well-dispersed assemblage (Milligan and Sutton, 2020). Still, the commercial impact of declines in mesopelagic micronekton in the GoM is untested. Future addenda to management and conservation policies in the oceanic GoM should be cognizant of declined prey abundances that could influence the direct trophic relationships with species of economic concern and energy flows throughout the ecosystem.

The 2010 *Deepwater Horizon* oil spill likely had an immediate negative impact on oceanic biota (Abbriano et al., 2011), but intense data collection regimes began after the disturbance (Sutton et al., 2020). Without a pre-disturbance reference point, it is difficult to discern between natural changes and human-influenced changes. Therefore, this exercise does not imply that anthropogenic impacts are responsible for changes within the ecosystem. Instead, these results may provide an example of the dynamic nature of complex ecosystems with opportunistic apex predators and diverse intermediate trophic level communities.

Author contribution

MW, TS, and YZ conceived the project, MW and YZ developed the methodology, TS, TF, and MW collected micronekton data for parameterization, MW analyzed the data, MW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109509.

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