



Original Article

Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico ecosystem

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Fishery management production models tend to stress only the elements directly linked to fish (i.e. fish, fish food, and fish predators). Large coastal jellyfish are major consumers of plankton in heavily fished ecosystems; yet, they are frequently not included as model components. We explore the relationship between gulf menhaden (*Brevoortia patronus*) and the large scyphozoan jellyfish (*Aurelia* spp. and *Chrysaora* sp.), and provide an examination of trophic energy transfer pathways to higher trophic levels in the northern Gulf of Mexico. A trophic network model developed within the ECOPATH framework was transformed to an end-to-end model to map foodweb energy flows. Relative changes in functional group productivity to varying gulf menhaden consumption rates, jellyfish consumption rates, and forage fish (i.e. gulf menhaden, anchovies, and herrings) harvest rates were evaluated within a suite of static, alternative energy-demand scenarios using ECOTRAN techniques. Scenario analyses revealed forage fish harvest enhanced jellyfish productivity, which, in turn, depressed menhaden productivity. Modelled increases in forage fish harvest caused pronounced changes in ecosystem structure, affecting jellyfish, marine birds, piscivorous fish, and apex predators. Menhaden were found to be a more efficient and important energy transfer pathway to higher trophic levels compared with jellyfish. A simulated increase in jellyfish abundance caused the relative production of all model groups to decline. These outcomes suggest that jellyfish blooms and forage fish harvest have demonstrable effects on the structure of the northern Gulf of Mexico ecosystem.

Keywords: ECOPATH, ecosystem-based fishery management, ecosystem model, ECOTRAN, forage fish, foodweb, Gulf menhaden, Gulf of Mexico, jellyfish.

Introduction

Forage fish are relatively small, planktivorous fish that form large, dense schools in productive coastal marine ecosystems. They are a

major prey source for piscivorous fish, seabirds, and marine mammals, and support large commercial fisheries (Pikitch *et al.*, 2014). Direct harvest for industrial reduction and human

consumption comprises 27% of global marine catch by tonnage in 2011, making forage fish fisheries among the biggest in the world (FAO, 2014). Because forage fish serve as a key conduit for energy transfer between lower and higher trophic levels, variability in their production can significantly affect ecosystem structure and function (Cury et al., 2000; Smith et al., 2011). Forage fish production is highly sensitive to oceanographic variability and intense fishery harvest (Bakun and Broad, 2003; Chavez et al., 2003), with effects of production changes cascading upwards and downwards through the foodweb (Cury et al., 2000; Daskalov et al., 2007; Utne-Palm et al., 2010). These sensitivities have made the conservation of healthy forage fish populations a management priority, prompting calls for policy-makers and managers to implement ecosystem-based fishery management (Fluharty and Cyr, 2001; Alder et al., 2008; Pikitch et al., 2012).

Ecosystem production models generally tend to focus on only the elements with direct linkages to fish (i.e. fish, fish food, and fish predators; Walters et al., 1997, 2008; Pauly et al., 2009). This tendency is problematic because ecologically important components like large jellyfish, which are undeniably major consumers of plankton production, including the early life stages of fish (Purcell and Arai, 2001; Purcell and Sturdevant, 2001; Hansson et al., 2005), may exert strong pressures upon those linkages. Large jellyfish in particular are perhaps ignored because survey data are lacking (Condon et al., 2012) or because of the perception that they represent an ecologically unimportant “trophic dead end”. The latter arising because, except for a few species such as leatherback sea turtles (*Dermochelys coriacea*) and the ocean sunfish (*Mola mola*), jellyfish are widely thought not to comprise a large fraction of the diets of many high-level consumers. However, this perception is changing, with data indicating jellyfish are often eaten by fish in appreciable amounts (Mianzan et al., 1996; Cardona et al., 2012).

The absence of jellyfish in production models used for application to heavily fished ecosystems may be short-sighted. Their ecological impacts are not well known. In only a few regions such as the Northern California Current (Ruzicka et al. 2012), Gulf of Alaska (Ruzicka et al. 2013), and the Black Sea [see Kideys et al. (2005) for review] have the ecosystem-wide effects of their blooms been investigated. Evidence suggests that jellyfish blooms can become larger or more frequent as a consequence of anthropogenic pressures, including climate change (Purcell, 2005; Lynam et al., 2011; Robinson and Graham, 2014), habitat modification (Lo et al., 2008; Duarte et al., 2012), cultural eutrophication (Oguz, 2005), the expansion of hypoxic waters (Purcell et al., 2001; Graham, 2001; Riisgård et al., 2012), and overfishing (Roux et al. 2013). Importantly, the role of forage fish harvest in enhancing jellyfish production, ostensibly though the release from competition for shared prey, is not well understood. Forage fish and jellyfish can overlap in diet (Brodeur et al., 2008; D’Ambra 2012) and in space in ecosystems where forage fish are intensively harvested (Brodeur et al., 2014; Robinson et al., 2014). Thus, harvest of forage fish may indirectly enhance jellyfish production by increasing prey availability.

Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico (GoMex) supports the largest forage fish fishery in the United States and the second largest commercial fishery (by weight) in the United States at 590 909 tonnes, valued at \$87.4 million USD ca. 2012 (Van Voorhees, 2012). Gulf menhaden (referred to hereafter as “menhaden”) are distributed throughout GoMex continental shelf waters, wintering on the inner and mid shelf at water depths of 20–88 m and migrating shoreward to

depths of ≤ 20 m in spring (Roithmayr and Waller, 1963; Smith, 2001). Menhaden are an important food source for large predatory fish such as mackerels and jacks, which themselves support valuable recreational fisheries (Van Voorhees, 2012), and they are an important food source for marine birds and marine mammals (Fogarty et al., 1981; Pauly et al., 1998; McGinnis and Emslie, 2001).

Menhaden share nearshore waters in the northern GoMex each summer and fall with blooms of large, planktivorous Scyphomedusae *Aurelia* sp. and *Chrysaora* sp. (Graham, 2001; Robinson and Graham, 2013). During periods of high abundance, these jellyfish can dominate the pelagic biomass with populations consisting of billions of individuals (Robinson and Graham, 2013). The spatio-temporal overlap between jellyfish and menhaden likely leads to predatory and competitive interactions as evidence suggests that they consume the same zooplankton prey (D’Ambra, 2012; Olsen et al., 2014). This interaction is expected to intensify with the harvest of menhaden by the commercial fishery and it may explain apparent jellyfish–menhaden replacement cycles observed in recent decades (Robinson et al. 2014).

Several ecosystem models previously developed for the northern GoMex have included or even focused specifically on menhaden (Walters et al., 2008; Mutsert et al., 2012; Geers et al., 2014). We are aware of only one GoMex model inclusive of jellyfish (Okey and Mahmoudi, 2002); however, its domain on the West Florida Shelf is outside menhaden’s centre of distribution along the Louisiana to Alabama coasts. Thus, we developed a holistic ecosystem “foodweb” model inclusive of jellyfish to elucidate the roles of menhaden and jellyfish as trophic energy transfer pathways in the northern GoMex ecosystem and the effects of fishery harvest on jellyfish and overall ecosystem structure.

Methods

Northern Gulf of Mexico foodweb

A foodweb model for the northern Gulf of Mexico was developed to represent the spatio-temporal extent of the menhaden reduction fishery during April to November (Ahrenholz, 1991; VanderKooy and Smith, 2002) and seasonal peaks in abundances of scyphozoan jellyfish, *Aurelia* spp. (August–November), and *Chrysaora* sp. (May–July; Graham, 2001; Robinson and Graham, 2013) for the years 1985–2009. This static model is representative of the area (42 310 km²) from east of Mobile Bay, Alabama (88°W) to west of the Louisiana-Texas border (94°W), and cross-shelf from the coastline to the 20-m isobath (Figure 1). Over 90–92% of all menhaden are harvested within 16 km of the coastline (Ahrenholz, 1991; Smith, 2001; VanderKooy and Smith, 2002).

The foodweb model for the northern Gulf of Mexico was constructed using the ECOPATH foodweb modelling platform (Polovina, 1984; Christensen and Pauly, 1992; www.ecopath.org). ECOPATH models use a mass-balance approach to estimate energy flows between defined functional groups. ECOPATH models are constructed by parameterizing Equation (1) such that a group’s net production (terms on the left) balances energy losses (terms on the right) via predation, fishery catch rates, senescence, and net migration.

$$b_p \times \left(\frac{P}{b}\right)_p \times ee_p = y_p + \sum b_c \times \left(\frac{q}{b}\right)_p \times D_{pc} + ba_p + nm_p. \quad (1)$$

Specifically, b_p is the biomass of a producer or prey group (p), b_c is the biomass of a consumer group (c), $(P/b)_p$ is the production rate per unit of biomass, ee_p is the ecotrophic efficiency (the fraction of total group production utilized within the ecosystem), y_p is the

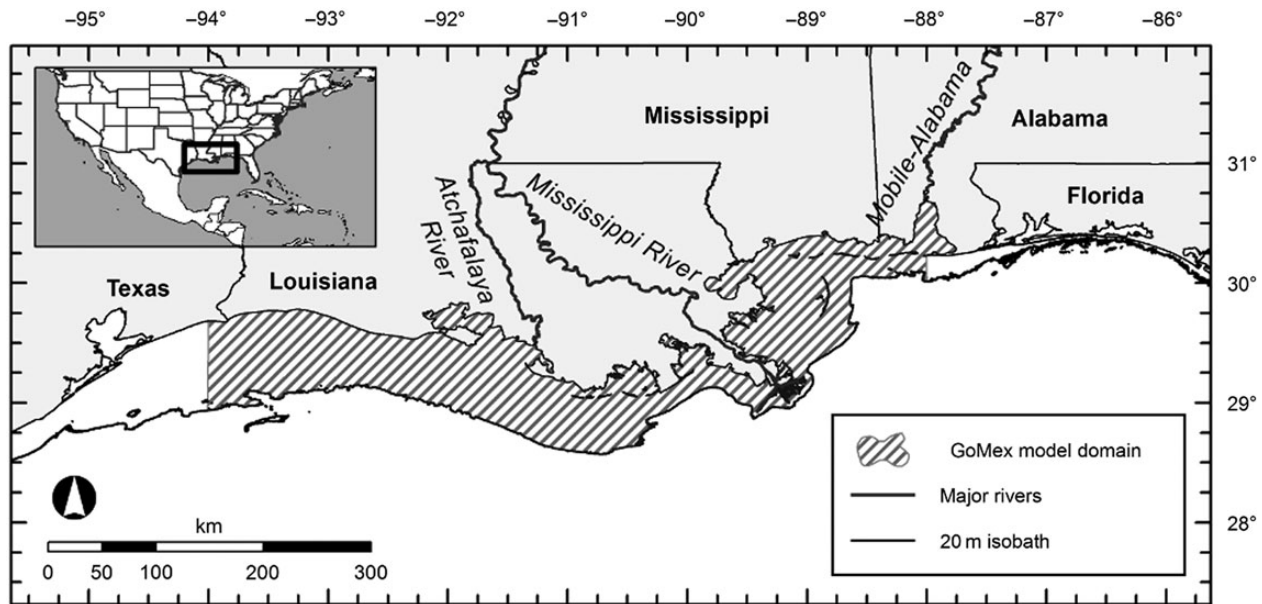


Figure 1. Spatial domain (hashed area) of the Northern Gulf of Mexico foodweb model over the continental shelf from the 0- to 20-m isobath of Louisiana, Mississippi, and Alabama, USA.

fisheries catch rate per unit area and time, $(q/b)_c$ is the food consumption rate per unit of biomass of consumer (c), D_{pc} is the contribution of producer (p) to the diet of consumer (c), ba_p is the biomass accumulation rate, and nm_p is the net migration rate of the producer. Using a system of linked linear equations [Equation (1)] representing each functional group and wet weight biomass as its currency, ECOPATH solves for Q_{pc} a matrix describing the consumer energy demand along each trophic linkage of the foodweb.

Model parameterization and community composition

The full, trophically resolved northern Gulf of Mexico (GoMex) model defines 50 living groups (2 primary producers, 6 non-gelatinous zooplankton, 3 gelatinous zooplankton, 3 macro-invertebrates, 18 fish, 4 elasmobranch, 4 benthic invertebrates, 3 marine birds, 4 marine turtles, and 3 marine mammals), 2 fisheries, fish eggs, and 3 detritus pools (Supplementary Table S2). Taxa were assigned to functional groups using four main criteria: (i) trophic classification (e.g. planktivore, piscivore, and detritivore), (ii) broad taxonomic classification (e.g. zooplankton, bony fish, and elasmobranch), (iii) primary habitat (e.g. pelagic, demersal, or reef-associated), and (iv) size (small or large; Supplementary Table S2). Functional group resolution was greatest among the pelagic groups given our focus on trophic energy transfer pathways involving and affecting gulf menhaden and jellyfish. Some fish were singled out as for snappers and groupers, red drum, and penaeid shrimp because they support highly valued fisheries. In other instances, we wished the flexibility to explore in the future energy transfer between groups like sea turtles, butterflyfish, and Atlantic bumper that feed on large jellyfish during their life histories. Detritus groups included pelagic detritus, benthic detritus, fishery offal. Two fishing fleets were used: commercial and recreational. Finally, because the GoMex model was developed to serve a template model for ecosystems where blooms of large jellyfish and forage fish overlap, we included groups like euphausiids to facilitate across-ecosystem comparisons. Euphausiids are not a major contributor to the pelagic biomass in the northern Gulf of Mexico; however, they are a major mid-trophic group in other coastal ecosystem such

the Northern California Current (Ruzicka *et al.*, 2012) and the Eastern Bering Sea (Aydin and Mueter, 2007). We summarize below the data sources and data processing used to construct the model. Additional details are provided in Supplementary Appendices.

Biomasses for five groups (eels, mesopelagic fish, large flatfish, suspension-feeders, and benthic infauna) were estimated by the model based on the demands of the consumer groups they support. Biomass densities of “small copepods” and of “seagrass and other macroalgae” were borrowed from the west Florida shelf model of Okey and Mahmoudi (2002) and the northern Gulf of Mexico model of Geers *et al.* (2014), respectively. All other functional group biomass estimates, including those for menhaden and large jellyfish, were derived from observational studies conducted in or immediately next to the model domain (Figure 1 and Supplementary Table S1).

Physiological rate parameters were taken from the literature or borrowed from other trophic models (Supplementary Table S3). Diet compositions (Supplementary Table S4) were obtained from the literature, www.fishbase.org, or were based on the authors’ expertise (Supplementary Table S5). Commercial and recreational fisheries landings data were extracted from the US National Marine Fisheries Service (NMFS) Fishery Statistics Division, the NMFS Marine Recreational Fisheries Statistics (MRFSS), and NMFS Marine Recreational Information Program (MRIP) online databases (Supplementary Tables S1, S20, and S22).

Donor-driven expression of the foodweb

The mass-balanced, steady-state ECOPATH solution for the foodweb as a “top-down” map of consumer demands upon prey groups (Q_{pc}) was re-expressed as a “bottom-up” map of production fate (A_{cp}) following the ECOTRAN technique of Steele and Ruzicka (2011):

$$A_{cp} = \frac{D_{pc}q_c}{\sum_c D_{pc}q_c}, \quad (2)$$

where A_{cp} is the production matrix, the fraction of the total

production of each producer p consumed by each consumer c , and q_c is the total consumption rate of consumer c . Expressed in this donor-driven format, the model can readily be used in simulation analyses to estimate the consequences of changes in forage fish and jellyfish abundances or in fishery harvest rates upon the rest of the ecosystem (Ballerini *et al.*, 2014; Robinson *et al.*, 2014; Treasure *et al.*, 2015).

Production matrix A_{cp} (Supplementary Table S12) was expanded to include (i) senescence and egestion flows to detritus pools and (ii) nutrient pools as explicitly defined functional groups supporting phytoplankton production and being supported by microbial metabolism of detritus and the metabolic excretion of consumer groups. The model is then an end-to-end model in the strict sense of the term: tracking production flow upwards through the foodweb from the input of nutrients, to the production of top trophic level consumers and fisheries, and back to base of the foodweb via the recycling of detritus and nutrients. Egestion production and metabolic excretion (ammonium) terms were obtained directly from defined ECOPATH physiological rate parameters (Table 1; Ruzicka *et al.*, 2012). Detritus and ammonium production were distributed between pelagic and benthic pools based on the general life histories and behaviours of each model group (Supplementary Table S6).

Analyses and metrics

The importance of each functional group as a producer and as a consumer can be characterized by two non-dimensional metrics: “reach” and “footprint” (Ruzicka *et al.*, 2012). “Reach” is the fractional contribution of the group of interest to total consumer production in the ecosystem via all direct and indirect pathways. “Footprint” is the fraction of total producer production in the ecosystem supporting the group of interest via all direct and indirect trophic pathways (Ruzicka *et al.* 2012). We also calculated the footprint and reach metrics of menhaden and jellyfish upon individual producer and consumer groups.

Structural scenarios were performed to evaluate the ecosystem-wide effects of changes in the biomass and consumption demands of large jellyfish and menhaden and the consequences of changes in fishery catch rates. Structural scenarios models estimate the immediate consequences of changes in energy flow pathways (Steele, 2009; Steele and Ruzicka, 2011). Four scenarios were run: (1) large jellyfish consumption increased by 50%, (2) menhaden removal via forage fish harvest increased by 50% and menhaden standing stock decreased by 59%, (3) forage fish harvest reduced by 50% and menhaden standing stock increased by 41%, and (4) the closing of all fisheries with a proportional increase in the standing stock biomass for each fished group. The altered energy demand of the manipulated group(s) was offset proportionally among all other consumers of a shared prey type, so that total predation pressure on each prey type remained unchanged (i.e. transfer efficiencies and unconsumed production flow to detritus were unchanged). For these simulation analyses, the 50 living functional groups of the fully resolved model were aggregated into 32 groups (Table 2) using production-weighted mean physiological rates (Supplementary Table S9) and diets (Supplementary Table S10).

Indices of confidence about all model-derived metrics and scenario analyses were estimated following the Monte Carlo techniques described in Ruzicka *et al.* (2013) and adapted from the principles of “ECOSENSE” routines developed by Aydin *et al.* (2007). Randomly generated models were produced by re-sampling each model parameter from a normal distribution defined by its quality (Supplementary Tables S7 and S8). Uncertainty and variability

about each biomass and diet parameter were estimated using coefficients of variation derived from field study data (Supplementary Tables S7 and S8). Uncertainties about physiological rate parameters were defined using the data quality “pedigree” recommendations of Christensen and Walters (2004). Each randomly generated model was evaluated for mass-balance such that predation demands did not exceed the production rate of any functional group. Analyses were simultaneously performed across 1000 “valid” mass-balanced models, and the distribution of results provides an index of confidence about all reported model responses.

Results

Foodwebs

Comparative foodweb diagrams highlighting energy flow patterns to (footprint) and from (reach) menhaden and jellyfish in the northern Gulf of Mexico show how menhaden serve as a more direct pathway for energy flowing from primary producers to upper-level consumers relative to large jellyfish (Figure 2). This relative greater energy transfer efficiency is illustrated by the large fraction of energy flowing from phytoplankton and zooplankton groups to menhaden (dark and wide green lines showing “footprint”), then again from menhaden to upper trophic level consumers like “apex predatory fish”, “piscivorous fish”, “seabirds”, and “fisheries” (dark and wide red lines showing “reach”; Figure 2a). In contrast, jellyfish can act as an energy loss pathway for these same consumers, diverting lower trophic production away from top trophic levels, indicated by the smaller fractions of energy being transferred upwards (lightly coloured and thin red lines, Figure 2b). Jellyfish, however, are not a “trophic dead-end”. Energy flow from them is diffusive, with small fractions of energy supporting a few, direct predators such as turtles, and additional consumers across multiple trophic steps via indirect pathways (Figure 2b). Nonetheless, relative to the total energy flow in the ecosystem, menhaden have a 10-fold higher reach to footprint ratio than the large jellyfish (Figures 3 and 4), signifying that menhaden are much more important in transferring energy upwards in the northern Gulf of Mexico foodweb.

Scenarios

When we attempted to increase jellyfish consumption by 50% (Scenario 1), the modelled northern Gulf of Mexico ecosystem could only support a 45% increase (Figure 4 and Table 3). The response of all groups to the simulated 45% increase in jellyfish was a decline in productivity. Baleen whales exhibited the largest decrease (−8.7%), followed by cephalopods (−7.6%), forage fish (−4.6%), and odontocetes (−4.6%). The production of menhaden (−1.9%) and pelagic planktivorous fish (−3.0%) also decreased (Table 3).

The impacts of reducing menhaden and other forage fish on the ecosystem were explored using Scenario 2, which increased fishery removal of menhaden and other forage fish by 50%. Total fisheries productivity declined by 10.5% as did the production of pelagic piscivorous fish, seabirds, and apex predatory fish (Figure 5 and Table 3). However, the response of most consumer groups (including jellyfish) was an increase in relative productivity (Figure 5 and Table 3).

Reduction of fishery catch rates by 50% (Scenario 3) resulted in an increase in the productivity of several functional groups (Figure 6). Overall fishery productivity declined by 28%. Production rates of marine birds (6.7%), pelagic piscivorous fish (6.7%), and apex predatory fish (3.1%) also increased. Changes in the net productivity of all other functional groups were minimal (Table 3 and Figure 6).

Table 1. Fully resolved ECOPATH model parameterization.

Code	Functional group	Biomass (t km ⁻² year ⁻¹)	p/b (year ⁻¹)	q/b	p/q	ae	ee	Landings (t km ⁻² year ⁻¹)		Discards (t km ⁻² year ⁻¹)	
								Rec	Comm	Rec	Comm
1	Phytoplankton	24.19	254.06	–	–	1.00	0.99	0	0	0	0
2	Seagrass and macroalgae	205.38	17.01	–	–	1.00	0.22	0	0	0	0
3	Microzoo	13.84	200.00	215.00	–	0.90	0.99	0	0	0	0
4	Large copepods	4.39	27.00	67.50	0.40	0.90	0.91	0	0	0	0
5	Small copepods	8.30	45.00	112.50	0.40	0.90	0.32	0	0	0	0
6	Euphausiids	1.25	20.70	51.75	0.40	0.90	0.62	0	0	0	0
7	Other mesozooplankton	195.95	19.00	47.50	0.40	0.90	0.90	0	0	0	0
8	Fish larvae	0.21	90.45	110.00	–	0.55	0.85	0	0	0	0
9	Penaeid shrimp	1.52	14.68	58.72	0.25	0.85	0.97	0	5.15E–02	0	1.74E–04
10	Large jellyfish	4.80	18.25	60.00	–	0.90	0.42	0	0	0	3.34E–07
11	Gelatinous filter-feeders	1.42	90.10	225.25	0.40	0.90	0.23	0	0	0	0
12	Small gelatinous carnivores	4.17	19.83	49.57	0.40	0.90	0.94	0	0	0	0
13	Anchovies	9.18	2.44	12.11	–	0.80	0.75	0	0	0	1.09E–06
14	Atlantic bumper	7.18	0.60	11.00	–	0.80	0.01	2.53E–06	0	2.73E–06	1.65E–06
15	Butterfish	17.27	0.80	1.85	–	0.80	0.00	1.25E–06	8.01E–06	2.31E–07	1.46E–06
16	Eels	3.04	0.86	12.92	–	0.80	0.80	6.35E–08	0	8.14E–08	7.57E–06
17	Herrings	10.84	1.60	13.26	–	0.80	0.53	8.82E–06	7.17E–04	2.19E–05	4.55E–07
18	Gulf menhaden	8.72	2.10	13.64	–	0.80	0.89	4.30E–05	5.54	3.58E–05	1.59
19	Mullet	0.32	1.80	18.23	–	0.80	0.93	1.18E–04	1.74E–03	1.11E–05	0
20	Red drum	0.24	0.35	3.67	–	0.80	0.64	4.49E–02	4.27E–05	6.81E–03	1.60E–03
21	Snapper–grouper	0.05	0.57	4.95	–	0.80	0.37	1.14E–05	9.62E–05	2.65E–06	2.86E–04
22	Skates and rays	0.36	0.38	7.84	–	0.80	0.70	8.36E–06	1.50E–06	3.24E–05	2.36E–06
23	Mesopelagic	0.37	0.87	11.71	–	0.80	0.80	0	0	0	0
24	Small flatfish	0.32	2.45	4.52	–	0.80	0.95	1.83E–05	0	6.17E–07	3.81E–07
25	Large flatfish	1.37	0.77	9.46	–	0.80	0.99	5.74E–04	5.41E–05	3.09E–05	1.35E–06
26	Large coastal sharks	0.15	0.43	2.48	–	0.80	0.01	8.10E–05	3.54E–04	2.91E–05	2.68E–04
27	Small coastal sharks	1.35	1.04	4.70	–	0.80	0.00	7.74E–05	1.39E–03	6.32E–06	6.32E–06
28	Offshore sharks	0.00	0.43	2.48	–	0.80	0.00	5.22E–08	1.92E–07	1.54E–08	1.54E–08
29	Reef invert feeder	0.92	2.45	9.67	–	0.80	0.98	2.32E–04	1.57E–04	3.01E–05	3.01E–05
30	Reef piscivore	0.55	0.40	10.21	–	0.80	0.06	4.07E–06	4.81E–05	2.88E–06	2.88E–06
31	Small pelagics	17.78	2.60	25.54	–	0.80	0.79	4.16E–06	4.65E–05	1.29E–05	1.29E–05
32	Large pelagics	10.37	0.70	5.40	–	0.80	0.37	1.60E–03	3.15E–03	2.97E–04	2.97E–04
33	Small demersal	83.09	1.58	5.41	–	0.80	0.93	1.35E–02	4.74E–03	2.12E–03	2.12E–03
34	Large demersal	0.55	1.58	3.67	–	0.80	0.97	1.10E–03	1.22E–03	1.14E–04	1.14E–04
35	Small squids	4.10	4.30	10.00	–	0.80	0.75	0	2.24E–06	0	0
36	Blue crab	1.93	2.40	8.50	–	0.80	0.92	2.07E–02	7.81E–02	4.14E–03	4.14E–03
37	Suspension-feeders	16.91	0.80	9.00	–	0.40	0.80	0	0	0	0
38	Benthic infauna	14.69	12.50	25.00	0.50	0.50	0.80	0	0	0	0
39	Bivalves	36.49	2.30	23.00	–	0.50	0.52	4.47E–03	9.48E–02	8.94E–04	8.94E–04
40	Benthic epifauna	38.47	6.40	7.43	–	0.87	1.00	0	0	0	0
41	Brown pelican	0.00	5.40	80.00	–	0.80	0.00	0	0	0	0
42	Terns	0.00	5.40	80.00	–	0.80	0.00	0	0	0	0
43	Black skimmer	0.00	5.40	80.00	–	0.80	0.00	0	0	0	0
44	Green sea turtle	0.00	0.19	3.50	–	0.80	0.01	0	0	0	0
45	Loggerhead sea turtle	0.00	0.19	3.50	–	0.80	0.04	0	0	0	0
46	Kemp Ridley's sea turtle	0.00	0.19	3.50	–	0.80	0.90	0	0	0	0
47	Leatherback sea turtle	0.00	0.19	3.50	–	0.80	0.04	0	0	0	0
48	Dolphins	0.04	0.10	24.98	–	0.80	0.15	0	0	0	0
49	Odontocetes	0.00	0.05	6.61	–	0.80	0.06	0	0	0	0
50	Baleen whales	0.00	0.04	7.57	–	0.80	0.00	0	0	0	0
51	Pelagic detritus	5.00	–	–	–	1.00	0.90	0	0	0	0
52	Fish eggs	0.02	–	–	–	1.00	0.89	0	0	0	0
53	Fishery offal	0.05	–	–	–	1.00	0.00	0	0	0	0
54	Benthic detritus	15.00	–	–	–	1.00	0.31	0	0	0	0

Bolded text indicates values estimated by Ecopath.

p/b, weight-specific production rate; q/b, weight-specific consumption rate; p/q, production efficiency; ae, assimilation efficiency; ee, ecotrophic efficiency; Rec, recreational fishery; Comm, commercial fishery.

Similar directional changes in productivity for functional groups occurred when all fisheries were closed (Scenario 4; Figure 7). Menhaden production increased by 80.7% relative to the baseline

model. Production of pelagic, piscivorous fish, and marine birds rose by 15 and 16%. Other groups that benefited from the fishery closure included baleen whales and apex predatory fish (Figure 7).

Table 2. Aggregated model functional group definitions. See Supplementary Appendices for fully resolved model functional group definitions.

Code	Group	Full resolved model functional groups
4	Phytoplankton	Phytoplankton
5	Macroalgae and other seagrass	Seagrass and macroalgae
6	Microzooplankton	Microzooplankton
7	Mesozooplankton	Large copepods, small copepods
8	Macrozooplankton	Fish larvae, penaeid shrimp
9	Euphausiids	Euphausiids
10	Gelatinous zooplankton	Gelatinous filter-feeders, small gelatinous carnivores
11	Large jellyfish	Large jellyfish
12	Gulf menhaden	Gulf menhaden
13	Forage fish	Anchovies, herrings, mullet
14	Pelagic fish—planktivore	Atlantic bumper, butterfish, small pelagics
15	Demersal fish—piscivore	Eels, red drum, snapper/grouper, reef piscivore, large demersal
16	Demersal fish—benthivore	Skates and rays, reef invert feeder, small demersal
17	Pelagic fish—apex predator	Small coastal sharks, large coastal sharks, offshore sharks
18	Pelagic fish—piscivore	Large pelagics
19	Cephalopods	Small squids
20	Benthos—epifauna	Blue crab, benthic epifauna
21	Benthos—filter-feeders	Suspension-feeders, bivalves
22	Benthos—infauna	Benthic infauna
23	Seabirds	Brown pelican, terns, black skimmer
24	Turtle	Green sea turtle, loggerhead sea turtle, Kemp Ridley's sea turtle, leatherback sea turtle
25	Odontocetes	Dolphins, odontocetes
26	Baleen whales	Baleen whales
27	Detritus—pelagic	Pelagic detritus, fish eggs
28	Detritus—offal	Fishery offal
29	Detritus—benthic	Benthic detritus
30	Fisheries	Recreational fisheries, commercial fisheries
31	Biomass accumulation	Biomass accumulation
32	Emigration	Emigration

Reduced productivity was observed for non-menhaden forage fish (−3.8%) and large jellyfish (−3.5%; Table 3).

Discussion

Our analyses represent the first attempt to examine the foodweb effects of increasing jellyfish biomass in the Northern Gulf of Mexico, particularly on the production of menhaden, an ecologically and commercially important fish species. Despite our assumptions of steady-state (no net change in production) and closed ecosystem (no net immigration or emigration), we feel that our model captures the main biomass pools and energy flows in this region and has allowed us to conduct structural scenarios to look at potential perturbations of key ecosystem components and examine their effects on multiple trophic levels.

The decline in the productivity of nearly all other northern Gulf of Mexico functional groups in response to a 50% increase in jellyfish consumption (Scenario 1) is similar to the ecosystem-wide responses observed in the Northern California Current (Ruzicka *et al.*, 2012). Because scenario analyses account for trophic energy flows to functional groups via all direct and indirect pathways, declines in the productivity of mammals were likely due to the declines in the production of their zooplankton prey (baleen whales, specifically) and forage fish (−4.6%) and pelagic planktivorous fish (−3.0%) prey (baleen whales and odontocetes). Increased jellyfish consumption would reduce the availability of large copepods upon which baleen whales directly feed on as well the production of other two prey groups, euphausiids and small pelagic fish, which compete directly with jellyfish for zooplankton prey. It is for this latter reason that the productivity of forage fish, menhaden, and pelagic planktivorous fish productivity also

declined in response to a simulated increase in jellyfish since all four groups are primarily zooplanktivorous.

Increasing fishery removals of menhaden and other forage fish by 50% (Scenario 2) resulted in declines in the productivity of a few upper-level consumers as well as an increase in the production rate of jellyfish (Figure 5). The absence of large changes in the relative productivity of most consumer groups was somewhat unexpected given their presumed role as key forage fish species in the northern Gulf of Mexico. An explanation for this outcome may be that menhaden predators compensated for reduced availability of menhaden by consuming more of the other pelagic planktivorous fish (e.g. mullet, anchovies, and non-menhaden herrings) that also contributed to their diets. The production of these fish was enhanced, presumably due to reduced competition with menhaden for planktonic prey. Nonetheless, the modelled decrease in high-level consumer productivity and the increase in the production rate of large jellyfish support findings from other heavily fished ecosystems, indicating intensifying the harvest of forage fish can lead to structural changes in marine ecosystems (Cury *et al.*, 2000; Pikitch *et al.*, 2012), including more jellyfish (Daskalov *et al.*, 2007; Lynam *et al.*, 2011; Roux *et al.*, 2013). The positive response of other mid-trophic level groups also supports the result that menhaden regulate large fraction of the ecosystem's total primary and secondary production (Figure 3). An interesting outcome of these analyses was that fisheries productivity declined by over 10% overall (despite the simulated increase of forage fish harvest by 50%), suggesting menhaden may be more valuable if left in the ecosystem as doing so may enhance the productivity of non-forage fish fisheries (Pikitch *et al.*, 2012; Essington and Munch, 2014).

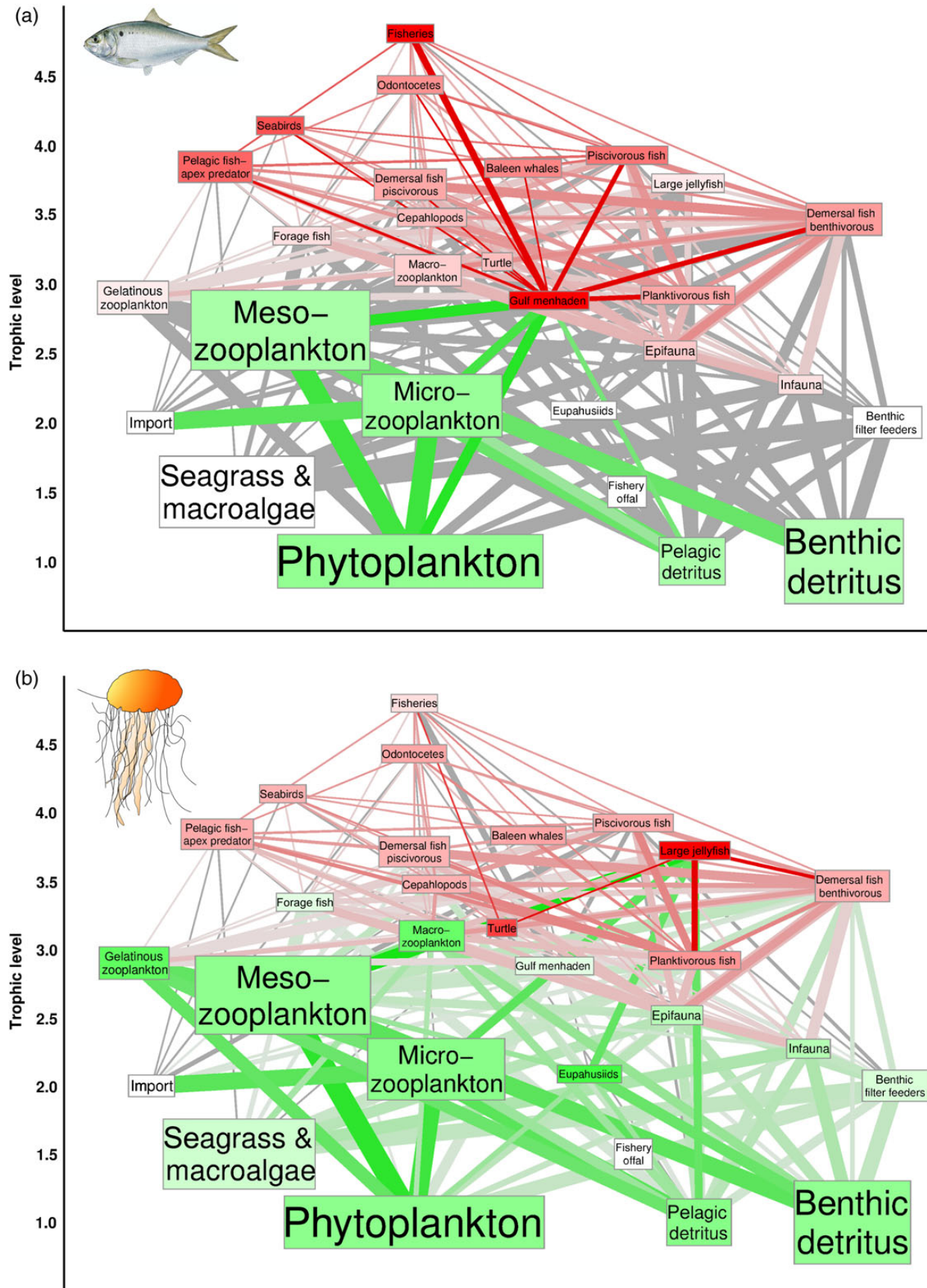


Figure 2. Reach (red) and footprint (green) of (a) menhaden and (b) large jellyfish to all functional groups in the northern Gulf of Mexico foodweb. Box size scales with functional group biomass. Colour intensity and line width indicate the relative size of energy flows and the footprint and reach relationships between Gulf menhaden and large jellyfish and all other functional groups.

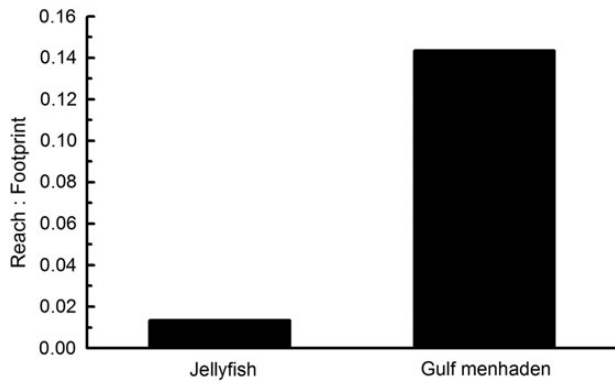


Figure 3. The ratio of the two metrics indicating the relative importance of each group in transferring energy upwards in the foodweb.

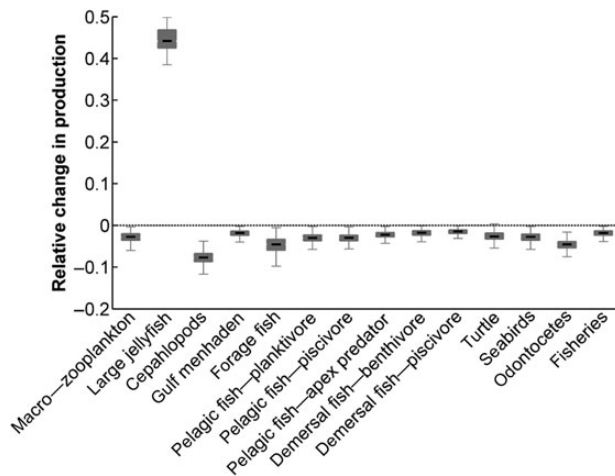


Figure 4. Ecosystem response to a 50% increase in consumption by jellyfish (Scenario 1). Interquartile range box plots represent the distribution of 1000 randomly drawn models where each term of the bottom-up production index was allowed to vary within $\pm 50\%$ of the base model (box = first–third quartile, waist (thick black bar) = median, whiskers cover 1.5 above and below interquartile range). Relative change in the productivity = (productivity in scenario model – productivity in base model)/productivity in base model. Unit of productivity is tonnes WWT $\text{km}^{-2} \text{year}^{-1}$.

Outcomes from the structural scenarios suggest that there is a dynamic interplay between menhaden, jellyfish, and forage fish fisheries in the northern Gulf of Mexico. Increases in jellyfish consumption ultimately resulted in lower menhaden productivity while the removal of menhaden and other forage fish through fisheries harvest enhanced jellyfish productivity, ostensibly through the release competition for shared prey resources. Thus, there appears a potential negative feedback loop for menhaden involving fishery harvest and jellyfish. This response matches the outcomes of simulations run for several other ecosystems (Mackinson *et al.*, 1997), where forage fish competitors increased with fishery removal. These responses would also explain the apparent replacement cycles between menhaden and jellyfish that occur in the northern Gulf of Mexico during periods of high jellyfish abundance.

Total menhaden and forage fish production declined by 6.5% in our jellyfish bloom scenario (Scenario 1), which was equivalent to

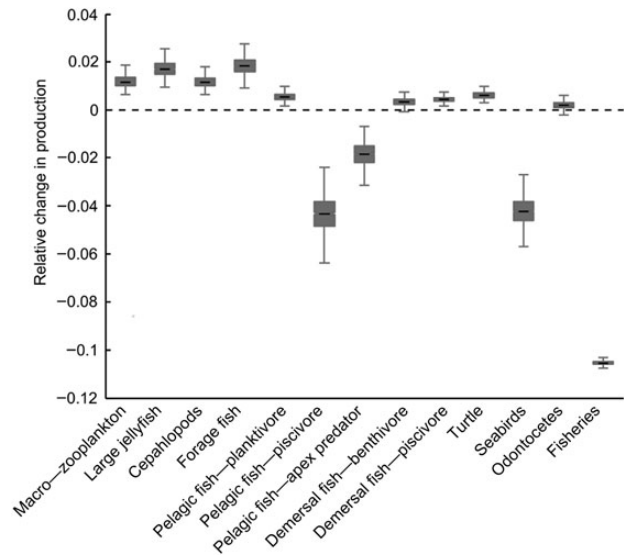


Figure 5. Ecosystem response to increasing forage fish (menhaden and forage fish) harvest by 50% (Scenario 2). Menhaden (not shown) productivity declined by 40.7%.

the ecosystem supporting 10.9 tonnes wet weight (WWT) km^{-2} of jellyfish biomass. It is not unrealistic to expect consideration of the jellyfish effect would be particularly necessary during years with exceptionally large blooms, such as 1992 and 1994 when biomass levels within the 20-m isobath reached an estimated 14.1 and 40.0 t WWT km^{-2} , respectively. Harvest rates of menhaden may need to be adjusted downwards during “high jellyfish” phases that occur in the northern Gulf of Mexico (Robinson and Graham, 2013) to leave enough production of menhaden to support higher trophic-level groups like seabirds and piscivorous fish (Pikitch *et al.*, 2012).

The simulated closure of all fishing (Scenario 4) provided some insights to how the northern Gulf of Mexico ecosystem would potentially respond to a total fishery moratorium. The modelled increase in the relative productivity of apex predatory fish and large piscivorous fish was likely due to the increased availability of menhaden as prey. Comparison of the these scenario results to those simulated for the Northern California Current and the Bering Sea ecosystems indicate that the simulation predicted the same trends (or lack thereof) in the response of some functional groups, but that jellyfish and menhaden biomass were much more responsive to a complete fishery closures (Robinson *et al.*, 2014).

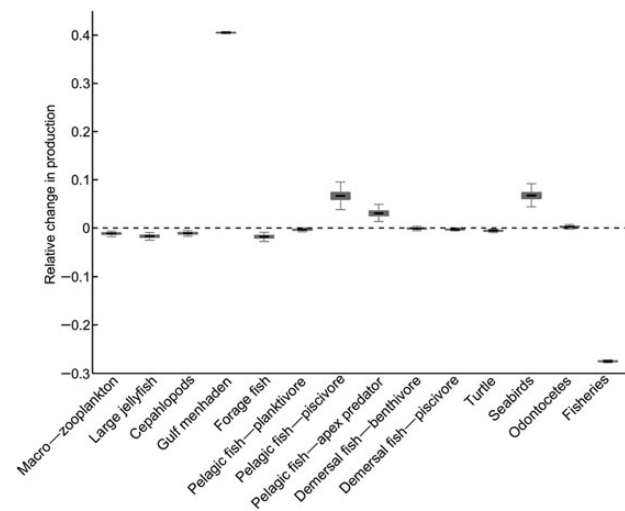
Foodwebs

The footprint and reach metrics derived from this inferred foodweb indicated that when jellyfish become more dominant in the pelagic community, the fraction of total ecosystem production and the efficiency at which it is transferred upwards in the foodweb is reduced compared with times when menhaden are dominant. Although jellyfish have historically been characterized as a “trophic dead-end”, our analyses of energy flows via all direct and indirect pathways in the northern Gulf of Mexico indicate that large jellyfish support a multitude of lower-, mid-, and higher-order consumers in the region (Figure 2b). This finding is consistent with earlier works, demonstrating jellyfish can directly support the production of a number of taxa, including bacteria, parasitic amphipods, juvenile fish, sunfish, seas turtles, and large predatory fish (Purcell and Arai, 2001; Masuda, 2009; Condon *et al.*, 2011; Cardona *et al.*, 2012; D’Ambra, 2012).

Table 3. Mean (± 1 standard deviation) fractional changes in the production of aggregated functional groups in response to the five structural scenarios.

Aggregated group code	Aggregated functional group	Scenario			
		1	2	3	4
1	NO ₃ ⁻	–	–	–	–
2	Pelagic NH ₄ ⁺	–0.30 \pm 0.13	–0.66 \pm 0.12	0.72 \pm 0.12	1.45 \pm 0.25
3	Benthic NH ₄ ⁺	0.46 \pm 0.17	0.57 \pm 0.15	–0.56 \pm 0.14	–1.06 \pm 0.28
4	Phytoplankton	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
5	Macroalgae and other seagrass	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
6	Micro-zooplankton	–0.01 \pm 0.00	0.43 \pm 0.11	–0.43 \pm 0.11	–0.88 \pm 0.23
7	Meso-zooplankton	–0.52 \pm 0.34	0.64 \pm 0.21	–0.64 \pm 0.21	–1.30 \pm 0.42
8	Macro-zooplankton	–2.85 \pm 1.17	1.19 \pm 0.25	–1.16 \pm 0.25	0.47 \pm 0.50
9	Euphausiids	–0.99 \pm 0.41	0.59 \pm 0.11	–0.59 \pm 0.11	–1.27 \pm 0.21
10	Gelatinous zoopl	–1.91 \pm 0.76	1.08 \pm 0.19	–1.08 \pm 0.19	–2.20 \pm 0.37
11	Large jellyfish	44.77 \pm 2.87	1.72 \pm 0.30	–1.70 \pm 0.30	–3.48 \pm 0.59
12	Gulf menhaden	–1.89 \pm 0.76	–40.71 \pm 0.04	40.51 \pm 0.10	80.72 \pm 0.25
13	Forage fish	–4.64 \pm 1.83	1.86 \pm 0.36	–1.84 \pm 0.35	–3.80 \pm 0.69
14	Pelagic fish—planktivore	–3.02 \pm 1.05	0.54 \pm 0.17	–0.37 \pm 0.18	–0.68 \pm 0.38
15	Demersal fish—piscivore	–1.52 \pm 0.61	0.44 \pm 0.12	–0.29 \pm 0.13	0.60 \pm 0.29
16	Demersal fish—benthivore	–1.83 \pm 0.78	0.35 \pm 0.16	–0.11 \pm 0.19	0.04 \pm 0.43
17	Pelagic fish—apex predator	–2.26 \pm 0.77	–1.88 \pm 0.49	3.08 \pm 0.72	7.37 \pm 1.74
18	Pelagic fish—piscivore	–2.97 \pm 1.00	–4.37 \pm 0.79	6.71 \pm 1.10	16.06 \pm 2.62
19	Cephalopods	–7.59 \pm 1.69	1.19 \pm 0.23	–1.11 \pm 0.23	–2.36 \pm 0.46
20	Benthos—epifauna	–0.54 \pm 0.23	0.35 \pm 0.09	–0.33 \pm 0.09	–0.61 \pm 0.18
21	Benthos—filter-feeders	0.01 \pm 0.01	0.15 \pm 0.05	–0.15 \pm 0.05	–0.15 \pm 0.10
22	Benthos—infauna	–0.12 \pm 0.06	0.15 \pm 0.06	–0.14 \pm 0.06	–0.47 \pm 0.11
23	Seabirds	–2.81 \pm 1.09	–4.25 \pm 0.60	6.74 \pm 0.92	15.43 \pm 2.26
24	Turtle	–2.32 \pm 1.66	0.61 \pm 0.15	–0.57 \pm 0.15	0.63 \pm 0.30
25	Odontocetes	–4.56 \pm 1.21	0.20 \pm 0.16	0.25 \pm 0.20	0.26 \pm 0.46
26	Baleen whales	–8.69 \pm 1.61	–0.50 \pm 0.19	1.38 \pm 0.28	3.29 \pm 0.68
27	Pelagic detritus	–0.07 \pm 0.03	0.43 \pm 0.11	–0.43 \pm 0.11	–0.87 \pm 0.22
28	Detritus—offal	–2.70 \pm 0.97	–1.63 \pm 0.44	1.89 \pm 0.45	3.99 \pm 0.93
29	Benthic detritus	0.46 \pm 0.25	–0.10 \pm 0.07	0.11 \pm 0.07	0.22 \pm 0.14
30	Fisheries	–1.86 \pm 0.75	–10.53 \pm 0.09	–27.53 \pm 0.12	–100.00 \pm 0.00

Fractional change = ((scenario model – base model)/base model) \times 100. Scenarios: (1) jellyfish biomass increased by 50%, (2) menhaden removal by forage fishing increased by 50%, (3) forage fishing reduced by 50%, and (4) total fishery closure. Aggregated group codes are from Supplementary Table S9.

**Figure 6.** Ecosystem response to a 50% reduction in consumption by forage fish removal by fisheries (including both landings and discards; Scenario 3).

These trophic relationships suggest instead that northern Gulf of Mexico jellyfish are energy diffusers, routing plankton production to functional groups at several different trophic levels. In contrast,

menhaden act as a direct energy conduit through which a large percentage of ecosystem production moves from producers to top-level consumers as discussed in [Robinson et al. \(2014\)](#). Despite the relative unimportance of jellyfish compared with menhaden in the northern Gulf of Mexico, the reach of jellyfish in this system is great than in more boreal ecosystems such as the Northern California Current and Bering Sea ([Robinson et al., 2014](#)).

Conclusion

We present here a comprehensive ecosystem model for the northern Gulf of Mexico inclusive of menhaden and jellyfish. As with all models, there are some aspects that could be improved. Chief among them is additional, quantitative estimates of the proportion gelatinous plankton contribute to the diets of other coastal consumers. Future research should aim to resolve whether gelatinous plankton are an important food source (or not) for juvenile or adult fish as suggested by a few, relatively isolated, studies (e.g. [Mianzan et al., 1996](#); [Cardona et al., 2012](#); [Brodeur et al., 2014](#)). Other improvements to the model include refining biomass estimates of coastal sharks and pelagic fish with values generated from surveys using gears specifically targeting those taxonomic groups as well as using observed biomasses for benthic infauna and eels. Despite these limitations, we demonstrate using best available data that menhaden are an important and efficient energy transfer pathway between producers and top-level consumers. Energy

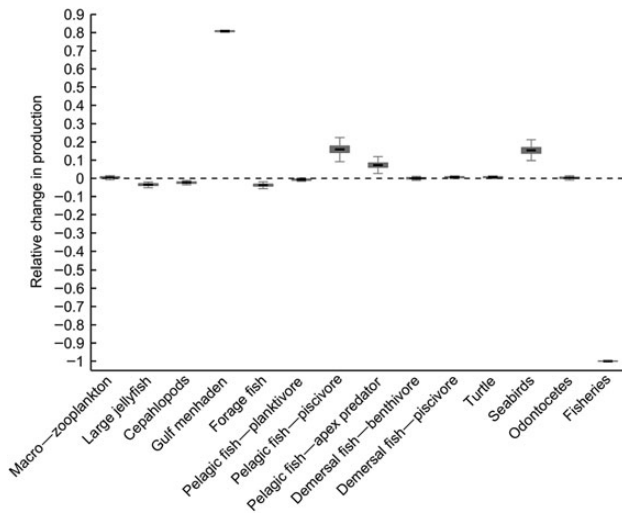


Figure 7. Ecosystem-wide response to a total fishery closure in the northern Gulf of Mexico (Scenario 4).

flow through jellyfish is characterized as diffusive, with energy from plankton producers flowing to a multitude of consumers at lower, mid-, and upper trophic levels after being consumed by jellyfish. Structural scenario analyses of the ecosystem responses to changes in jellyfish, menhaden, and forage fish harvest revealed a potential negative feedback loop for menhaden where forage fish harvest enhanced the production of jellyfish, which, in turn, depressed the productivity of menhaden. This series of interactions has implications for the broader ecosystem as lower menhaden production results in reduced productivity of seabirds and economically important pelagic fish. These findings suggest that the effects of jellyfish blooms on ecosystem productivity and the role of forage fish harvest plays in promoting them should be considered when implementing ecosystem-based approaches to fishery management in the northern Gulf of Mexico.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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