



# An original model of the northern Gulf of Mexico using Ecopath with Ecosim and its implications for the effects of fishing on ecosystem structure and maturity



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## ABSTRACT

The Gulf of Mexico (GoM) is a valuable ecosystem both socially and economically, and fisheries contribute substantially to this value. Gulf menhaden, *Brevoortia patronus*, support the largest fishery in the Gulf (by weight) and provide forage for marine mammals, seabirds and commercially and recreationally important fish species. Understanding the complex interactions among multiple fisheries and myriad unfished species requires tools different from those used in traditional single-species management. One such tool, Ecopath with Ecosim (EwE) is increasingly being used to construct food web models of aquatic ecosystems and to evaluate fisheries management options within a broader, ecosystem context. Here, an EwE model was developed to examine the impact of Gulf fisheries on ecosystem structure and maturity. This model builds on previously published EwE models of the GoM, and is tailored to the range and habitat of Gulf menhaden. The model presented here consists of 47 functional groups, including 4 seabird groups, 1 marine mammal group, 3 elasmobranch groups, 26 bony fish groups, 9 invertebrate groups, 3 primary producer groups and 1 detritus group. A number of different management scenarios for Gulf fisheries were modeled and the results were evaluated in terms of impacts on ecosystem maturity and development. The results of the model simulations indicated that the northern Gulf of Mexico is in an immature state (*sensu* Odum, 1969). Management scenarios that increased fishing pressure over time consistently resulted in a decrease in the maturity indices. In particular, we found that Gulf menhaden, as a key forage fish in the ecosystem, plays a substantial role in the structure and functioning of the ecosystem.

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## 1. Introduction

Gulf menhaden, *Brevoortia patronus*, supports the second largest fishery, and largest forage fish fishery, in the United States (Vaughan et al., 2007); yet its ecosystem role and implications of its management on ecosystem structure and functioning are still not well understood. In the evolving field of ecosystem-based fisheries management (Hall and Mainprize, 2004; Pikitch et al., 2004; Marasco et al., 2007; Smith et al., 2007; Hilborn, 2011), the management of forage fish has emerged as an extremely relevant and essential topic due to its potentially far-reaching consequences on ecosystems. Empirical studies, modeling approaches and literature

reviews continue to demonstrate the critical role that forage fish play in marine ecosystems (e.g. Cury et al., 2011; Smith et al., 2011; Hall et al., 2012; Pikitch et al., 2012a, 2012b). Forage fish are often the main conduit of energy flow from lower to upper trophic levels in the ecosystems they inhabit (Pikitch et al., 2012a). As such, they can exact either top-down control on plankton or bottom-up control on predators (Cury et al., 2000) and are especially important to the structure and functioning of marine ecosystems.

Forage fish-dependent predators are common and can be quite sensitive to changes in prey abundance and distribution, which can be altered by fishing activities (Kaschner et al., 2006; Alder et al., 2008). Seabirds appear to be particularly affected by changes in forage populations (Jahncke et al., 2004; Piatt et al., 2007; Crawford et al., 2008; Pikitch et al., 2012a). In a study of Magellanic penguins (*Spheniscus magellanicus*), Boersma and Rebstock (2009) showed that increased foraging distance negatively impacted penguins' reproductive success. On a global scale, a meta-analysis of 14 seabird species in 7 ecosystems found that seabird breeding success was

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linked to a threshold abundance of forage fish prey (Cury et al., 2011). Predators dependent on forage fish are not limited to seabirds however, and include marine mammals, finfish and sharks. In the Chesapeake Bay, recreationally important fish species such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*) are heavily dependent on menhaden and other forage fish and may compete with the menhaden fishery for forage fish resources (Hartman, 2003; Uphoff, 2003). Insufficient menhaden abundance also appears to have contributed to a decline in the condition of striped bass in this region in the late 1990s (Uphoff, 2003). Nuttall et al. (2011) found that Atlantic menhaden had the greatest impact on other species in Great South Bay (Long Island, New York) in the 1880s, but as the population diminished due to overfishing, their role as a primary consumer was replaced by benthic fauna, which precipitated a decline in structural complexity of the Bay.

Given even these limited examples, it is clear that the ecosystem risks of overfishing forage fish are quite high. Even fishing for forage fish at traditional single-species target levels (e.g. maximum sustainable yield; MSY) can have substantial ecosystem consequences (Smith et al., 2011; Pikitch et al., 2012a). Through an analysis of 10 ecosystems around the world, Pikitch et al. (2012a) found that fishing for forage fish species at the traditional target level of MSY lead to a median decline in biomass of 27% for all forage fish predators and a median decline in biomass of 54% for all seabirds consuming forage fish. Forage fish fishing can also have indirect impacts on other fisheries. While the direct value of commercial forage fish fisheries is almost 6 billion USD, the value of commercial fisheries supported by forage fish as prey is nearly twice that (Pikitch et al., 2012b). However, the overall economic worth of forage fish is likely much greater due to their role in supporting recreational fishing and ecotourism opportunities such as whale watching. As such, forage fish may prove to be more valuable when left in the water than when fished directly (Pikitch et al., 2012b).

Within this context, it is clear that the role of Gulf menhaden in the northern Gulf of Mexico (GoM) needs to be better understood in order to characterize the ecosystem impacts of menhaden harvest. Gulf menhaden inhabit the northern GoM from Cape Sable, Florida north and west to Texas and south to Veracruz, Mexico (Ahrenholz, 1991; Lewis and Roithmayr, 1981; Vaughan et al., 2007). Menhaden are omnivorous filter-feeders consuming zooplankton, phytoplankton and detritus through a complex system of gill rakers (Ahrenholz, 1991). Menhaden provide important forage for fish, seabirds and marine mammals in the GoM (Ahrenholz, 1991; Vaughan et al., 2007). Many of the commercially and recreationally harvested fish species, including king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*Scomberomorus maculatus*), dorado (*Coryphaena hippurus*), crevalle jack (*Caranx hippos*), tarpon (*Megalops atlanticus*) and bonito (*Sarda sarda*), rely on the abundant schools of menhaden along the Gulf coast (Dailey et al., 2008; Franklin, 2007). Menhaden are also important in the diet of red drum (Boothby and Avault Jr., 1971). Red drum was historically a commercially important species in the Gulf, but due to past overfishing, current regulations prohibit commercial retention and possession of the species in federal waters (GMFMC (Gulf of Mexico Fishery Management Council), 2010). Recent research has found that blacktip (*Carcharhinus limbatus*), spinner (*C. brevipinna*), finetooth (*C. isodon*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks feed heavily on menhaden during all or part of their life cycles (e.g. Barry et al., 2008; Bethea et al., 2004, 2006; Hoffmayer and Parsons, 2003). Among marine birds, the brown pelican (*Pelecanus occidentalis*), Louisiana's state bird, is notable for having a diet of over 95% menhaden according to some studies (Hingtgen et al., 1985; Franklin, 2007).

The many varied interactions among fisheries, predators and prey pose a challenge for managers. Ecosystem models are

becoming an increasingly important tool for addressing these dynamics and have been used to answer a wide range of biological, physical and economic questions that were previously not feasible to address on such a large scale. Several types of modeling programs now exist, each with their pros and cons (for a review see Fulton, 2010). Ecopath with Ecosim (EwE) was chosen for this study, due to its widespread use (over 5600 users and 300 publications), user-friendly and freely distributed software, and its focus on fisheries management ([www.ecopath.org](http://www.ecopath.org)). Several EwE models have been developed for all, or parts, of the Gulf of Mexico and have evolved from small-scale Ecopath models to large-scale integrated Ecosim models (e.g. Vidal and Pauly, 2004; Walters et al., 2008). While some of these models have considered fisheries impacts in the GoM, none have focused on Gulf menhaden, an important prey item and major fishery in the region. In addition, many models are lacking top predators such as sharks, seabirds and marine mammals that are important consumers of menhaden and other forage fish.

The objective of this study was to develop a comprehensive ecosystem model for the northern Gulf of Mexico that fully addresses the ecosystem role of Gulf menhaden and evaluates management options for the species. Ecosim simulations were conducted to examine changes in ecosystem structure and maturity under different management scenarios. Such analyses contribute to a greater understanding of the role of Gulf menhaden in the GoM and therefore to the development of ecosystem-based management in the region.

## 2. Methods

### 2.1. Ecopath with Ecosim

Ecopath was originally developed to provide a simple method for generating information about the standing stock and energy flow within an ecosystem (Polovina, 1984). It has since been developed and updated (see e.g. Christensen and Pauly, 1992; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2008), but the basic principles have been maintained. There are two master equations in Ecopath, the first describes production (Eq. 1), and the second describes the energy balance of each group (Eq. 2). Ecopath model groups consist of the major biological components of the ecosystem of interest and can be a single species or a group of similar species (e.g. similar habitat, feeding habits, predators, etc.). Groups may also be broken down into two or more age classes to represent trophic differences between juveniles and adults. There are four Ecopath input parameters linked to each Ecopath group: biomass ( $B$ ), ratio of production to biomass ( $P/B$ ), ratio of consumption to biomass ( $Q/B$ ) and ecotrophic efficiency (EE), the proportion of production that is used within the system. In its original incarnation, Ecopath required the assumption of equilibrium or steady state (Polovina, 1984). Now, however, model parameterization is based on the assumption of mass balance over the time period modeled, usually a year (Christensen and Walters, 2004). Via this mass balance approach, modeled in the two master equations, the Ecopath software only requires the input of three of the four parameters for each group. In addition, diet information for each group must be input in terms of percent diet composition. The Ecopath master equation can be written as:

$$B_i(P/B)_i EE_i - \sum_{j=1}^n B_j(Q/B)_j DC_{ji} - Y_i - E_i - BA_i = 0 \quad (1)$$

where for a given group  $i$ ,  $B_i$  is the biomass,  $(P/B)_i$  is the production/biomass ratio,  $EE_i$  is the ecotrophic efficiency,  $B_j$  is the biomass of the predator group  $j$ ,  $(Q/B)_j$  is the consumption/biomass ratio,  $DC_{ji}$  is the fraction of prey ( $i$ ) in the average diet of predator ( $j$ ),  $Y_i$  is the total fishery catch rate,  $E_i$  is the net migration rate, and  $BA_i$  is the biomass

accumulation rate. The previous equation allows the model to estimate “missing parameters” (i.e. whichever is not entered of  $B$ ,  $P/B$ ,  $Q/B$  and  $EE$ ) so as to ensure mass balance between modeled groups, while the following equation ensures energy balance within a group:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

Walters et al. (1997) developed Ecosim, a time-dynamic simulation model coupled to Ecopath. Ecosim inherits its initial parameters from the balanced Ecopath model and produces dynamic estimates of biomass and catch rates over time. These biomass dynamics are expressed through a series of coupled differential equations of the form:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \quad (3)$$

where  $dB_i/dt$  is the growth rate in terms of biomass ( $B_i$ ) over time for group  $i$ ,  $g_i$  is the net growth efficiency (i.e. production/consumption ratio), and the two summations represent consumption rates.  $Q_{ji}$  is the total consumption by group  $i$ , while  $Q_{ij}$  is the predation by all predators on group  $i$ .  $I_i$  is the immigration rate,  $MO_i$  is the “other” natural mortality rate (unrelated to predation),  $F_i$  is the fishing mortality rate and  $e_i$  is the emigration rate (Christensen et al., 2008).

Predator–prey interactions are an important component of Ecosim dynamics. The availability of prey to predators and the ability of predator populations to grow in relation to their prey base greatly influence the biomass dynamics of the model. Consumption rate calculations are based on the foraging arena concept (Walters and Juanes, 1993), where the biomass of prey groups is divided into invulnerable and vulnerable components:

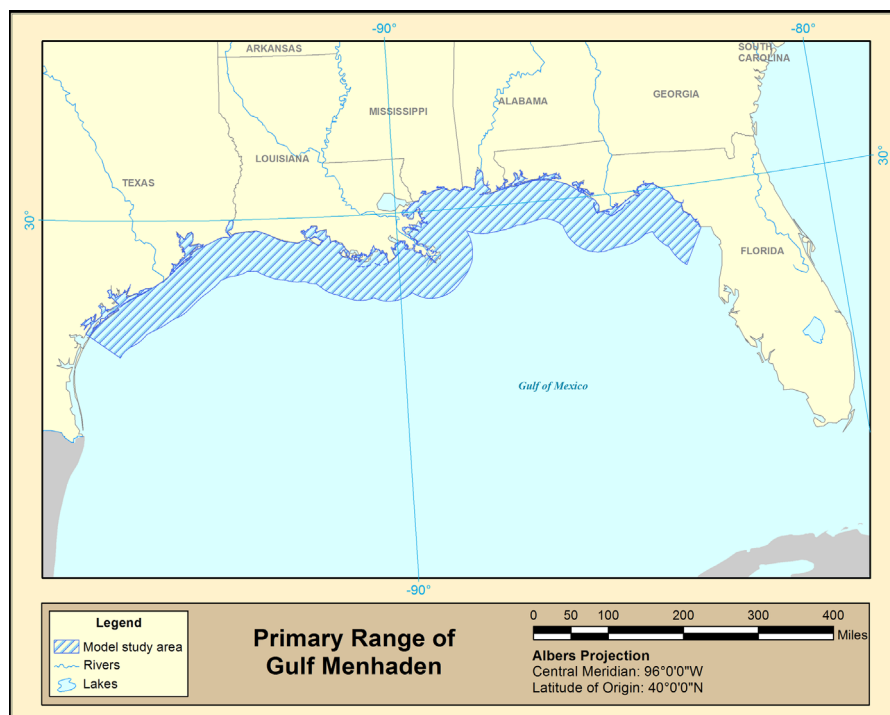
$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}B_iB_j}{(2v_{ij} + a_{ij}B_j)} \quad (4)$$

where  $Q_{ij}$  is the consumption of prey  $i$ , by predator  $j$ ,  $a_{ij}$  is the effective search rate for prey  $i$  by predator  $j$ ,  $v_{ij}$  is the vulnerability parameter, which expresses the rate that prey move between vulnerable and invulnerable states,  $B_i$  is the prey biomass, and  $B_j$  is the predator biomass (Christensen et al., 2008). The vulnerability

parameter is what determines top down (predator control) vs. bottom up (prey control) control. Low vulnerability values (close to 1) lead to bottom up control and an increase in predator biomass will not cause a substantial increase in predation mortality on its prey. Conversely, high vulnerabilities (approaching 100 or more) lead to top down control, where increases in predator biomass are directly proportional to increases in predation mortality (Christensen et al., 2008).

## 2.2. Model construction and data

The modeled area was approximately 145,000 km<sup>2</sup> and included the northern Gulf coast from Aransas Pass, Texas to Cedar Key, Florida from the coastline (i.e. littoral zone) to 80 km off shore (Fig. 1). This incorporated areas that are used during menhaden's seasonal migration offshore, as well as inshore nursery habitats. The model focused on the north-central region because Gulf menhaden are most abundant from the Florida panhandle to eastern Texas; although the species is found as far south as Veracruz, Mexico in the west and Cape Sable, Florida in the east (Vaughan et al., 2007). The ecological roles of the 1100–1300 fish species, numerous birds, marine mammals and reptiles, and countless invertebrates (Felder and Camp, 2009) in the region were represented through individual species or multi-species functional groups (Table S1). The focus on menhaden necessitated the explicit articulation of all its predators, competitors and prey. In addition, other major GoM fishery species were included in order to facilitate the examination of interactions among fisheries and the tradeoffs between fisheries and ecosystem health. Individual species were classified into groups representing similar size, dietary habits and habitat preferences. Three documents provided a jumping off point for creating and specifying the model groups, Gulf of Mexico models developed by Vidal and Pauly (2004) and Walters et al. (2008) and the Regional Management Plan for the Gulf Menhaden Fishery (VanderKoooy and Smith, 2002). Species that were important to fisheries and for which substantial data were available were left as individuals in order to accurately represent their roles in the Ecopath analysis. Additionally, certain species



**Fig. 1.** Map of the Gulf of Mexico depicting the region modeled (hatched area), which represents the primary habitat of Gulf menhaden. Area estimate and shapefile, courtesy of Andrew Hayslip, Florida Fish and Wildlife Research Institute.

groups (mackerels, red drum, spotted seatrout and menhaden) were divided into juvenile and adult categories to better represent trophic differences between life stages.

A full description of the estimation procedures and input parameters has been documented in Geers (2012) and is only briefly described below. For each functional group, biomass estimates were derived from the primary literature, survey data or stock assessments, or were estimated based on catch data and fishing mortality rates. Consumption and production estimates were calculated based on empirical relationships or were acquired from the primary literature or stock assessments. For these three parameters (biomass, consumption, production), maximum, minimum, and “best estimate” values were compiled and included estimates from previous models of the Gulf of Mexico. Parameterization was particularly influenced by other recent EwE models of the northern Gulf (e.g., Okey et al., 2004; Walters et al., 2008), though all available previously published EwE models of the Gulf were consulted (Abarca-Arenas and Valero-Pacheco, 1993; Arreguin-Sanchez et al., 1993a, 1993b, 2004; Browder, 1993; Chavez et al., 1993; De la Cruz-Aguero, 1993; Vega-Cendejas et al., 1993; Venier and Pauly, 1997; Arreguin-Sanchez and Manickchand-Heileman, 1998; Manickchand-Heileman et al., 1998a, 1998b; Rosado-

Solorzano and del Proo, 1998; Christian and Luczkovich, 1999; Vega-Cendejas and Arreguin-Sanchez, 2001; Althausen, 2003; Vidal and Pauly, 2004; Carlson, 2007; Cruz-Escalona et al., 2007; de Mutsert, 2010). An extensive literature review was conducted to estimate diet compositions for each species in the model (see Table S2 for the final diet composition matrix). For those groups exploited commercially and recreationally, catch data were acquired from the National Marine Fisheries Service Fisheries Statistics Division (NMFS-FSD) database (<http://www.st.nmfs.noaa.gov>). These data were also used to determine the fleets targeting different species; a total of 13 gear types were used (11 commercial, 2 recreational). Fleets and landings by model group can be found in Table S3. All parameter estimates were based on the most current data available. Once the initial input parameters were entered into Ecopath, it was necessary to “balance” the model, such that fluxes of energy into the model were equal to energy fluxes out of the model and each ecotrophic efficiency (EE) value was less than or equal to 1 (Christensen et al., 2008). A PREBAL analysis (Link, 2010) was conducted to determine which groups and input values should be prioritized during balancing. A list of the parameters of the balanced model can be found in Table 1.

**Table 1**  
Parameters of the balanced Ecopath model. Species comprising each model group are listed in Table S1. Values in bold were estimated by Ecopath.

	Group name	Trophic level	Biomass (t/km <sup>2</sup> )	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	EE
1	Birds of prey	4.0	5.150E-05	0.100	60.000	<b>0.000</b>
2	Loons	3.6	9.880E-05	0.100	28.634	<b>0.475</b>
3	Gulls and terns	3.9	1.473E-03	0.100	50.000	<b>0.087</b>
4	Pelicaniformes	3.7	7.468E-03	0.100	17.737	<b>0.006</b>
5	Coastal dolphins	4.0	3.064E-02	0.099	15.000	<b>0.106</b>
6	Large coastal sharks	4.0	8.443E-02	0.300	3.200	<b>0.033</b>
7	Small coastal sharks	4.0	7.576E-02	0.510	4.700	<b>0.315</b>
8	Skates and rays coastal pelagic	3.4	2.380E-01	0.380	4.000	<b>0.154</b>
9	Piscivores	3.8	1.000E-01	0.614	5.433	<b>0.934</b>
10	Tunas	4.1	2.444E-02	0.900	13.000	<b>0.587</b>
11	0–6 Mackerels	3.9	2.100E-04	4.000	32.683	<b>1.000</b>
12	6+ Mackerels	4.0	6.000E-02	0.700	5.400	<b>0.992</b>
13	0–8 Red drum	3.1	1.262E-03	3.447	24.965	<b>0.193</b>
14	8+ Red drum	3.5	1.800E-01	0.600	4.800	<b>0.677</b>
15	0–18 Spotted seatrout	3.5	3.694E-02	1.416	12.940	<b>0.086</b>
16	18+ Spotted seatrout	3.5	3.100E-01	0.700	5.100	<b>0.733</b>
17	Groupers	3.7	2.890E-01	0.469	2.800	<b>0.574</b>
18	Red snapper	3.7	4.000E-01	0.700	5.240	<b>0.130</b>
19	Ladyfish	3.5	9.880E-02	0.880	4.304	<b>0.668</b>
20	Spot	2.9	8.000E-01	1.100	6.900	<b>0.217</b>
21	Atlantic croaker	3.0	6.000E-01	1.500	10.000	<b>0.194</b>
22	Butterfish	3.1	<b>2.003E-01</b>	2.000	10.400	0.300
23	Black drum	3.1	5.000E-01	0.578	3.654	<b>0.319</b>
24	Flounders	3.5	4.140E-01	0.775	4.516	<b>0.328</b>
25	Gars	3.8	4.000E-02	0.562	3.471	<b>0.456</b>
26	Sea catfishes	3.3	5.000E-01	0.800	7.600	<b>0.225</b>
27	Mulletts	2.0	6.900E-01	0.978	10.021	<b>0.665</b>
28	Other demersals	3.2	2.200E+00	1.065	7.700	<b>0.986</b>
29	Nearshore omnivores	2.8	1.440E+00	0.996	8.600	<b>0.946</b>
30	Adult Menhaden	2.6	7.240E+00	1.900	8.100	<b>0.432</b>
31	Juvenile Menhaden	2.6	1.851E+00	2.300	19.617	<b>0.411</b>
32	Shads	3.0	1.793E+00	1.900	11.800	<b>0.425</b>
33	Other clupeids	3.0	5.448E+00	1.533	11.381	<b>0.429</b>
34	Anchovies etc.	2.8	3.032E+00	2.443	13.475	<b>0.880</b>
35	Squid	3.7	2.670E-01	4.000	<b>17.643</b>	0.990
36	Caridean shrimp	2.2	<b>3.243E+00</b>	2.400	18.000	0.800
37	Penaeid shrimp	2.5	<b>2.254E+00</b>	2.400	19.200	0.990
38	Stone crab	2.5	<b>1.029E+00</b>	2.000	7.000	0.950
39	Blue crab	2.6	<b>9.832E-01</b>	2.400	8.500	0.950
40	Benthic invertebrates	2.1	<b>2.499E+01</b>	4.500	22.000	0.800
41	Macrozooplankton	2.1	<b>6.434E+00</b>	22.000	67.000	0.500
42	Microzooplankton	2.0	<b>6.460E+00</b>	36.000	89.000	0.500
43	Infaua	2.0	2.000E+01	2.000	10.000	<b>0.229</b>
44	Algae	1.0	2.978E+01	25.000	0.000	<b>0.134</b>
45	Seagrass	1.0	1.756E+02	9.014	0.000	<b>0.001</b>
46	Phytoplankton	1.0	2.500E+01	182.130	0.000	<b>0.261</b>
47	Detritus	1.0	1.000E+02			<b>0.083</b>

Although Ecosim is capable of running simulations using only the initial Ecopath parameters, it is helpful to calibrate the model with time series of exploitation rates, abundance, catch, or total mortality rates (Christensen et al., 2008; Frisk et al., 2011). Originally all available time series were used, but some were removed during the fitting process due to concerns that they were not representative for particular species; time series spanned the period from 1950 through 2009, though not all series covered the entire range. Fitting the model to time series also required adjusting vulnerability parameters, which control top-down vs. bottom-up dynamics. Vulnerability values were manually adjusted for 15 groups during the fitting process to minimize the log sum of squares of the final model. Values for the remaining groups were assumed to be 2, the default value representing a mix of top-down and bottom-up control. For greater detail on the fitting procedure see Geers (2012).

### 2.3. Ecosim model runs

Once the fitting procedure was completed and a satisfactory fit to the time-series data was found, fishery management strategies and policy scenarios were tested (Table 2). Specifically, the impact of recreational fishing on the ecosystem was examined by halving and doubling recreational fishing mortality rates from their 2009 levels for all recreationally caught species (i.e. Half Rec and Double Rec). A scenario first developed by Walters et al. (2008) was used to look at the impact of fishing on potentially vulnerable fish groups (e.g. red drum, red snapper and groupers). In this scenario, fisheries were shut down entirely (i.e. Species Recovery), which allowed us to observe species recovery under continued fishing of their prey groups (e.g. menhaden and shrimp). Conversely, fisheries for menhaden and penaeid shrimp were shut down (i.e. No Menhaden  $F$  and No Shrimp Effort), also similar to Walters et al. (2008), to examine the impact of prey abundance on important predator groups. Scenarios were also developed that fished menhaden at the  $F_{target}$  ( $F=0.94$ ) and  $F_{limit}$  ( $F=1.46$ ) levels estimated in the 2007 stock assessment (Vaughan et al., 2007). Other forage fish groups in the model (e.g. shads, other clupeids and anchovies etc.) are currently fished at very low levels ( $F < 0.005$ ), but scenarios were developed to examine the impact of new forage fish fisheries on predators, should they arise in the future. The first, examined by Walters et al. (2008), involved fishing the three “new” forage fish (FF) groups at an  $F$  of 0.3, similar to the level of the 2009 menhaden fishery, while menhaden continued to be fished at 2009 levels (i.e. New FF fisheries). The second scenario fished all four forage fish groups (including menhaden) at their

single species  $F_{MSY}$  levels (i.e. FF at  $F_{MSY}$ ; Geers, 2012). The final set of scenarios involved increasing and decreasing fishing mortality rates for all fished groups (i.e. Increase All and Decrease All). Under these scenarios fishing rates were either increased or decreased by 5% per year for 25 years and then remained steady for the remainder of the simulation. A baseline scenario was also run, with which to compare the other scenarios; this “Standard Run” held fishing mortality rates at their 2009 levels for the duration of the simulation. All Ecosim simulations were run through 2109, 100 years after the end of current time series (Table 2).

### 2.4. Ecosystem metrics

Ecosystem metrics were estimated for comparison with other models and to evaluate Ecosim scenarios. The Ecopath modeling software contains a built-in routine for network analysis following the theory of Ulanowicz (1986). The indices estimated and used for analysis are described below. Primary production and respiration were estimated; net primary production represents the activity of lower trophic levels, while the activity of consumers is represented by the total respiration. The primary production to respiration ratio is expected to approach one as a system matures (*sensu* Odum, 1969). The diversity of upper trophic levels was measured by Kempton's  $Q$  index (Kempton and Taylor, 1976). Indices related to catch included the primary production required (PPR), the mean trophic level of the catch and the gross efficiency (ratio of total catches to net primary production). The trophic transfer efficiency, representing the average energy transferred between trophic levels, was also estimated.

Ecosystem development or succession, as described by Odum (1969), is the process by which an ecosystem progresses towards a mature state. This involves a directional, orderly and predictable process that results in a biomass maximum, optimization of energy, and overall homeostasis (Odum, 1969). Although anthropogenic and natural stressors can limit the maturity level an ecosystem can reach, comparisons of ecosystem maturity under different scenarios provide a metric to understand the relative state of system development.

Christensen (1995) developed a maturity index based on seven of Odum's (1969) attributes of ecosystem maturity. This maturity index was used to compare and contrast Ecosim scenarios. The primary production to biomass (excluding detritus) ratio is related to community energetics and is expected to decrease as a system matures due to the accumulation of biomass in mature systems (Christensen, 1995). Another measure of community energetics is the biomass supported per unit energy flow. This is represented by the ratio of biomass to total system throughput, where the total

**Table 2**  
Description of Ecosim scenarios developed for analysis.

Scenario Name	Description of Scenarios
Standard Run	Fishing mortality rates for all groups were maintained at their 2009 levels for the duration of the simulation
Half Rec	Recreational fishing mortality rates were halved from their 2009 levels
Double Rec	Recreational fishing mortality rates were doubled from their 2009 levels
Species Recovery	Fisheries for red drum, red snapper, and groupers were shut down (i.e., $F=0$ )
No Shrimp Effort	Fisheries for penaeid shrimp were shut down (i.e., effort set to 0)
No Menhaden $F$	Fisheries for Gulf menhaden were shut down (i.e., $F=0$ )
Menhaden at $F_{targ}$	Fishing mortality for Gulf menhaden was set to the target level of $F=0.94$
Menhaden at $F_{lim}$	Fishing mortality for Gulf menhaden was set to the limit level of $F=1.46$
New FF Fisheries	Fishing mortality for forage fish groups (shad, other clupeids, anchovies) was set to 0.3; Gulf menhaden $F$ was kept at 0.35
FF at $F_{MSY}$	Fishing mortality for forage fish groups was set to their single species $F_{MSY}$ levels
Increase All	Fishing mortality rates for all currently fished groups were increased by 5% per year for 25 years and then remained constant for the remainder of the simulation
Decrease All	Fishing mortality rates for all currently fished groups were decreased by 5% per year for 25 years and then remained constant for the remainder of the simulation

system throughput represents the size of the ecosystem in terms of the summation of flows from total consumption, respiration, export and flows to detritus. Food web connectivity is described by the proportion of flows in the system that originates from detritus (referred to as dominance of detritus) and represents a shift from herbivory to detritivory as a system matures (Odum, 1969; Christensen, 1995). Species diversity is also expected to increase as a system matures, but is difficult to measure when several species are grouped together to form the model groups. Christensen (1995) proposed flow diversity as a measure to use instead, which can be quantified by the statistical entropy ( $H$ ) for all groups in the system. Life history attributes can be quantified indirectly by the ratio of biomass to total system production, which is a proxy for organism size. Odum (1969) described nutrient recycling as one aspect of ecosystem maturity with mature systems displaying a higher degree of recycling than immature systems. Finn (1980) developed an index with which to measure energy cycling within an ecosystem. The Finn's cycling index (FCI) is the proportion of total throughput that is recycled (Christensen, 1995). Though Christensen (1995) did not include FCI in his maturity index, it has been included here. Path length, also developed by Finn (1980), is another descriptor of flows in the ecosystem and is expected to be highest for mature systems. It is calculated as the ratio of total system throughput to the sum of total export and total respiration. Species growth can also be described by the residence time of energy in the system, which is estimated as the ratio of total biomass to the sum of total respiration and total exports. Ascendency, which combines ecosystem growth (i.e., increase in size as measured by the total throughput) and organization (Ulanowicz, 1986; Christensen, 1995) was also estimated, though not as part of the maturity index.

### 3. Results

#### 3.1. Ecopath/ecosystem metrics

The model development and balancing process resulted in a balanced model with 47 functional groups (Table 1), including 4 seabird groups, 1 marine mammal group, 3 elasmobranch groups, 26 bony fish groups, 9 invertebrate groups, 3 primary producer groups and 1 detritus group. The trophic level of consumers varied from 2 (Infauna) to 4.1 (Tunas). Structural properties of the ecosystem, estimated by Ecopath, are listed in Table 3. Total system production was 7472 t/km<sup>2</sup>/yr. Primary production was 6881 t/km<sup>2</sup>/yr and respiration was 806 t/km<sup>2</sup>/yr, resulting in a primary production

**Table 3**  
Summary statistics of the northern Gulf of Mexico model.

Metric	
Sum of all consumption	2164.0 t/km <sup>2</sup> /yr
Sum of all exports	6074.7 t/km <sup>2</sup> /yr
Sum of all respiratory flows	806.1 t/km <sup>2</sup> /yr
Sum of all flows into detritus	6623.0 t/km <sup>2</sup> /yr
Total system throughput	15,667.7 t/km <sup>2</sup> /yr
Sum of all production	7472.0 t/km <sup>2</sup> /yr
Mean trophic level of the catch	2.6
Gross efficiency (catch/net p.p.)	0.000585
Total net primary production	6880.7 t/km <sup>2</sup> /yr
Total primary production/total respiration	8.5
Net system production	6074.6 t/km <sup>2</sup> /yr
Total primary production/total biomass	21.2
Total biomass/total throughput	0.02
Total biomass (excluding detritus)	324.7 t/km <sup>2</sup> /yr
Total catches	4.02 t/km <sup>2</sup> /yr
Connectance index	0.30
System omnivory index	0.19
Ecopath pedigree index	0.33

to respiration ratio (Pp:R) of 8.5. The primary production to biomass ratio was 21.2. The high value of these ratios indicates that the northern Gulf of Mexico ecosystem is in a developmental stage. The primary production required for catch was approximately 2% of the total primary production. The mean trophic level of the catch was 2.64. The average transfer efficiency of the energy between trophic levels is often assumed to be about 10% for marine systems (Lindeman, 1942; Christensen and Pauly, 1993). In this model, the mean trophic transfer efficiency was 11.4%, similar, but slightly more efficient than the assumed value. The Ecopath pedigree index was 0.33.

#### 3.2. Ecosim

The Ecosim model was fit to observed biomass data for large coastal sharks, small coastal sharks, adult mackerels, adult red snapper, squid, adult red drum, flounders, adult spotted seatrout, sea catfishes, butterfish, black drum, Atlantic croaker, spot, blue crab, adult menhaden, penaeid shrimp and mullets (Fig. 2). The model was also fit to catch time series for adult mackerels, coastal pelagics, red snapper, groupers, adult red drum, adult spotted seatrout, sea catfishes, other demersals, black drum, blue crab, adult menhaden, penaeid shrimp and benthic invertebrates (Fig. 3). The overall log sum of squares for these 30 fits to the base model was 151. The model was able to approximately recreate the observed values and trends in biomass for red snapper, adult red drum, blue crab, adult menhaden and penaeid shrimp (Fig. 2). To a lesser extent, the model captured the biomass trends of small coastal sharks, adult mackerels, squid, adult spotted seatrout, Atlantic croaker and spot (Fig. 2). The model did not capture the decline in flounder biomass, the high sea catfishes biomass in the 1980s, the decline in butterfish biomass in the 1980s, the increase in black drum biomass, or the decline in mullet biomass in the early 1990s (Fig. 2). The model also predicts an increase in large coastal shark biomass, whereas the observed data point to a leveling off of biomass at low levels (Fig. 2). The model reasonably reflected catch time series for adult mackerels, coastal pelagics, spotted seatrout, sea catfishes, other demersal fishes, black drum, blue crab, adult menhaden and penaeid shrimp; although it tended to overestimate catches of coastal pelagics and blue crab (Fig. 3). The model was unable to mimic the fluctuation in groupers or benthic invertebrate catches over time (Fig. 3). The model closely replicated the trend in red drum catches, though it overestimated the catch in the beginning and middle of the time series and underestimated the catch towards the end (Fig. 3). Red snapper catches were well modeled with the exception of the 1970s, during which the model showed an increasing trend while the observed data showed a decreasing trend (Fig. 3).

#### 3.3. Comparison of Ecosim scenarios

Several different fishery management scenarios were tested to determine the ecosystem impact of fishery policies exploiting recreational and commercial fisheries. Standard ecosystem metrics and indices of maturity were compared among the simulations (Fig. 4 and Table 4). Substantial increases in catches and corresponding decreases in overall system biomass occurred when menhaden were fished at higher than present levels (Menhaden at  $F_{targ}$  and Menhaden at  $F_{lim}$ ), when all fisheries were increased by 5% per year (Increase All) and when all forage fish groups (menhaden, anchovies etc., other clupeids, shads) were fished at  $F_{MSY}$  levels (FF at  $F_{MSY}$ ; Fig. 4). Slight increases in overall system biomass occurred under the No Menhaden  $F$  and the Decrease All scenarios (Fig. 4); these simulations also resulted in substantial decreases in overall catches (Fig. 4). The trophic level of the catch generally increased when low trophic level species were not fished (e.g. No Shrimp Effort, No Menhaden  $F$ ) and decreased when

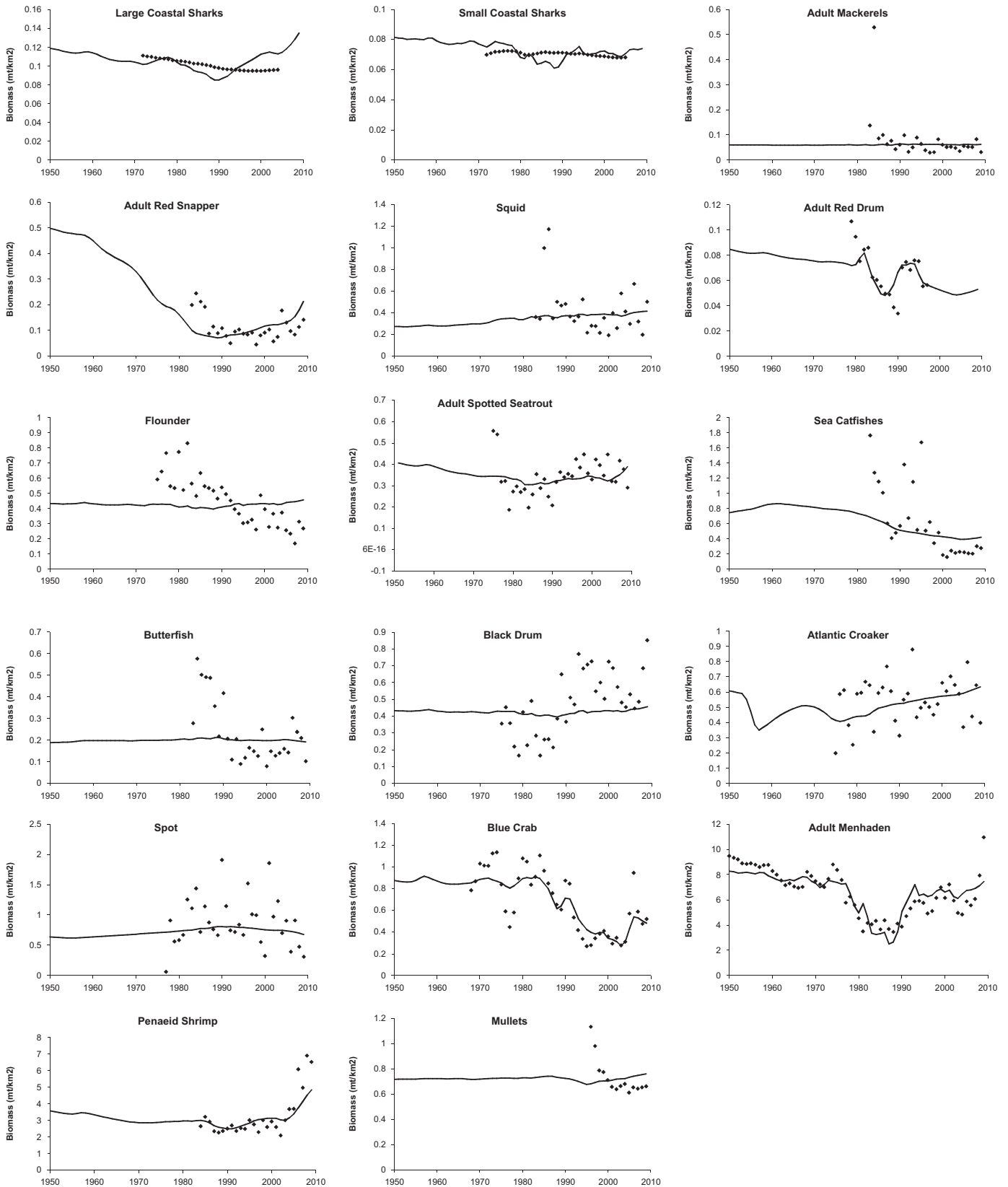


Fig. 2. Observed (dots) and predicted (solid lines) biomass for the northern Gulf of Mexico Ecosim model.

higher trophic level species were allowed to recover (e.g. Species Recovery, Half Rec; Fig. 4). The trophic level of the catch also increased under the New FF Fisheries scenario (Fig. 4). This may seem counterintuitive, but shad, other clupeids, and anchovies etc.

all have a higher trophic level than the other major fishery species (menhaden and shrimp). Therefore, increasing the catches of these three groups, despite their relatively low trophic level, actually increased the mean trophic level of the catch. Kempton's *Q* index

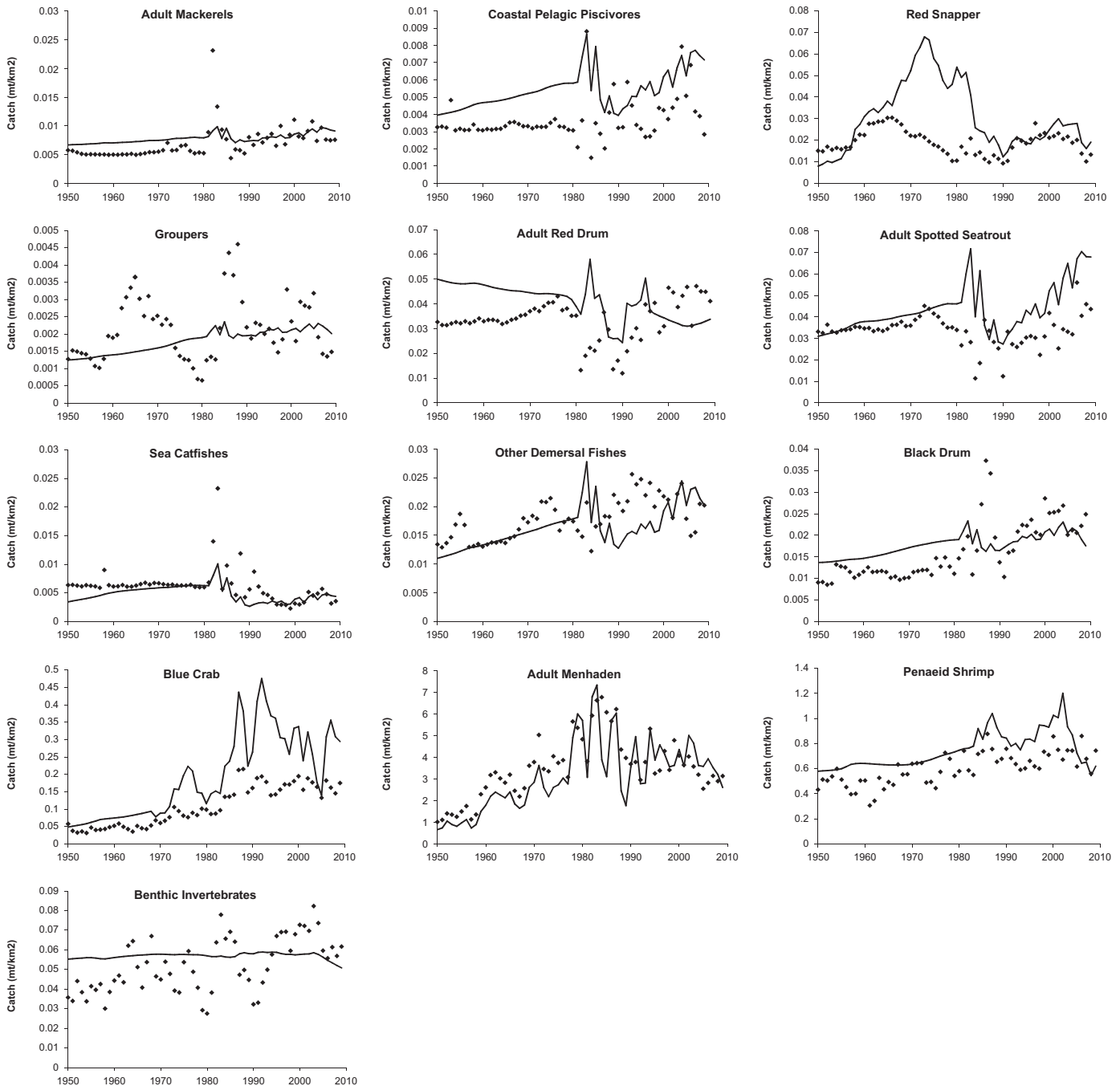


Fig. 3. Observed (dots) and predicted (solid lines) catches for the northern Gulf of Mexico Ecosim model.

represents the diversity of upper trophic level species. Upper trophic level diversity decreased under the Menhaden at  $F_{targ}$ , Menhaden at  $F_{lim}$ , Increase All, and Double Rec scenarios (Fig. 4).

The overall trends in maturity, relative to the standard run, for each of the Ecosim scenarios are presented in Table 4. Four runs resulted in an increase in ecosystem maturity based on these maturity indices: Species Recovery, No Menhaden  $F$ , Decrease All, and Half Rec. The remaining runs (No Shrimp Effort, New FF Fisheries, FF at  $F_{MSY}$ , Menhaden at  $F_{targ}$ , Menhaden at  $F_{lim}$ , Increase All, and Double Rec) all resulted in a decrease in system maturity. Not all indices used for the maturity index, in particular path length and dominance of detritus, fit with the overall trend (Table 4).

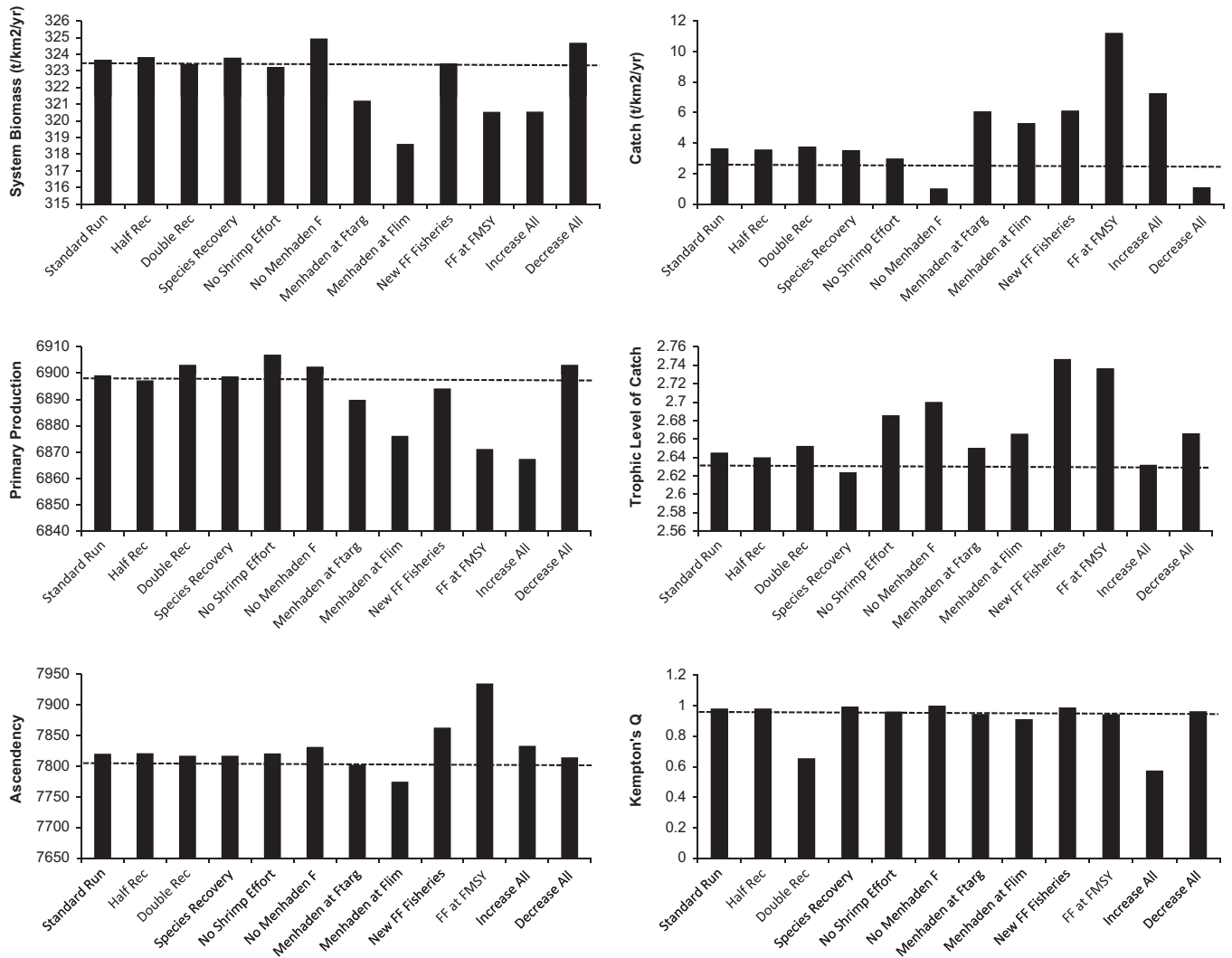
Six runs showed an increase in ascendency: No Shrimp Effort, No Menhaden  $F$ , New FF Fisheries, FF at  $F_{MSY}$ , Increase All, and Half Rec (Fig. 4). The other five runs showed a decrease in

ascendency: Species Recovery, Menhaden at  $F_{targ}$ , Menhaden at  $F_{lim}$ , Decrease All, and Double Rec.

#### 4. Discussion

The ecosystem role of Gulf menhaden and the species' importance as a prey resource for several top predators has been elucidated here through the development and analysis of an original and comprehensive model of the northern Gulf of Mexico ecosystem. The model was used to evaluate the impact of menhaden and other fisheries harvest on the Gulf ecosystem. We found that increased fishing for menhaden and other forage fish beyond 2009 levels lead to a decrease in system maturity, possibly resulting in a less stable system (i.e. less resistant to external perturbation). We also showed





**Fig. 4.** Comparison of select ecosystem metrics among different Ecosim runs. Metrics were calculated for 2109, the last year of the simulation. The horizontal dotted line is the reference level from the standard run; FF= forage fish. System biomass, primary productivity, ascendency and Kempton's Q index were used to compare maturity among Ecosim runs. Biomass is expected to increase with maturity, while primary production is expected to decrease, relative to respiration. Ascendency is generally thought to be positively correlated with maturity, though this may not always be the case (e.g. FF at  $F_{MSY}$ ). Kempton's Q index represents the diversity of upper trophic levels and is also positively correlated with maturity. Overall catch and trophic level of the catch were used to demonstrate the impact of the Ecosim scenarios on fisheries.

**Table 4**  
Trends in select maturity indices. Arrows represent an increase or decrease in maturity from the standard run.

Index	Trend with maturity	Half Rec	Double Rec	Species Recovery	No Shrimp effort	No Menhaden F	Menhaden at $F_{targ}$	Menhaden at $F_{tim}$	New FF Fisheries	FF at $F_{MSY}$	Increase All	Decrease All
Diversity (capacity/throughput)	+	↓	↓	↓	↓	↑	↓	↓	↑	↓	↓	↑
Biomass/throughput	+	↑	↓	↑	↓	↑	↓	↓	↓	↓	↓	↑
Finn's cycling index	+	↑	↓	↑	↓	↑	↓	↓	↓	↓	↑	↑
Mean path length	+	↓	↑	↑	↑	↓	↑	↑	↓	↓	↓	↑
Residence time	+	↓	↑	↑	↑	↑	↓	↓	↓	↓	↓	↑
Biomass/production	+	↑	↓	↑	↓	↑	↓	↓	↓	↓	↓	↑
Dominance of detritus	+	↑	↓	↓	↓	↑	↑	↑	↑	↑	↑	↓
Primary production/biomass	-	↑	↓	↑	↓	↑	↓	↓	↓	↓	↓	↑
Overall trend		↑	↓	↑	↓	↑	↓	↓	↓	↓	↓	↑

that increased fishing for menhaden resulted in a decrease in ascendency, which points to the species' role in maintaining a large and diverse flow structure in the ecosystem. These findings have important implications for managing the Gulf menhaden fishery

from an ecosystem perspective and highlight the potential value of setting ecosystem-based reference points for menhaden that ensure enough biomass is left in the system to meet the needs of predators and to maintain the integrity of the ecosystem. These findings are

also extremely relevant given that new catch limits recently set for Atlantic menhaden will reduce landings by 25% in 2013 (ASMFC, 2012), which may increase pressure on Gulf menhaden.

#### 4.1. Comparison of ecosystem structure with other Gulf of Mexico models

Network analysis and standard ecosystem metrics were used to characterize the northern Gulf of Mexico ecosystem, as well as to assess the impact of fishery management scenarios on ecosystem health and development. The results of the network analysis indicated that the northern Gulf of Mexico is in an immature state with high levels of primary productivity, comparatively few flow pathways and little build-up of age structure. Odum and Barrett (1971) suggested that in immature systems, primary production would greatly exceed respiration. The Pp:R ratio of this model is 8.5, which is high and outside of the commonly observed range (0.8–3.2) described by Christensen and Pauly (1993). However, it is similar to the value found by de Mutsert (2010) for Breton Sound, Louisiana and within the range estimated for other Gulf of Mexico models, 0.75 (Yucatan Shelf, Mexico, Arreguin-Sanchez et al., 1993) – 15.9 (Celestun Lagoon, Mexico, Vega-Cendejas and Arreguin-Sanchez, 2001). The P:B ratio is also fairly high, indicative of a developing system, but again falls within the range of other GoM models, 6.21 (Celestun Lagoon, Chavez et al., 1993) – 64 (Celestun Lagoon, Vega-Cendejas and Arreguin-Sanchez, 2001). The overall biomass of the system of 324 t/km<sup>2</sup>/yr is close to the estimate of 304 t/km<sup>2</sup>/yr found by Vidal Hernandez (2000) for the entire GoM. The model FCI value of 1.99% is relatively low compared to other ecosystems, although immature systems generally have lower FCI values. Christensen (1995) found that FCI was not always a good indicator of maturity, and did not use it in comparisons among ecosystems; however, path length (defined as the total throughput over the sum of total exports and total respiration) was found to be a good descriptor of flows and cycling (Finn, 1980; Christensen, 1995). Reefs, shelves and upwelling areas tend to have shorter path lengths, while estuaries tend to have longer path lengths (Christensen and Pauly, 1993). The path length of 2.28 determined by this model is towards the middle of the range of other ecosystems, which can be expected given its coastal nature. The trophic level of the catch in the GoM was relatively low compared to other heavily fished ecosystems (Pauly et al., 1998). The relatively high biomass of low trophic level groups in the catch is not, however, a result of “fishing down the food web”, as is the case in numerous other ecosystems (Pauly et al., 1998), but is rather due to menhaden and shrimp, the top two species targeted by fisheries in the region, having low trophic levels of 2.6 and 2.5, respectively. In fact, it has been noted that the trophic level of the catch in the Gulf of Mexico has actually risen slightly since the 1950s (de Mutsert et al., 2008), which appears to be due to an increase in catches of upper trophic level species, rather than to a decline in shrimp or menhaden.

#### 4.2. Comparison of maturity indices among Ecosim scenarios

While other modeling efforts have looked at similar harvest strategies to the ones examined here (e.g. Walters et al., 2008; Pikitch et al., 2012a), none have examined the impact of these policies on ecosystem development. Therefore, Odum's (1971) indices of ecosystem maturity were used to compare Ecosim scenarios within the present model. Overall trends in the indices for Species Recovery, No Menhaden F, Decrease All, and Half Rec indicated an increase in maturity, though certain indices did not follow the general pattern. The Species Recovery scenario resulted in a decrease in species diversity (i.e. flow diversity) and dominance of detritus, the opposite of what would be expected as

maturity increases. The large increases in red drum populations under the Species Recovery scenario could actually lead to a decrease in the diversity of flows if a greater proportion of flows were channeled through the red drum group. This could similarly lead to a reduction in the proportion of flows from detritus (i.e. dominance of detritus) if red drum were primarily consuming herbivores. The Decrease All scenario also led to a decrease in dominance of detritus, likely for similar reasons. That is, an increase in herbivorous species, as well as in the piscivores that eat them, resulted in a decrease in flows from detritus. The Half Rec scenario also led to a decrease in diversity of flows; similar to the Species Recovery scenario, halving recreational effort caused a large increase in red drum, which may have channeled flows through this model group. No Menhaden F resulted in a decrease in path length, or the average number of groups an inflow or outflow passes through. While path length is expected to increase with maturity, the decrease in path length observed here makes sense, as an increase in menhaden could potentially channel energy through this one species. This also points to the unique role of forage fish in structuring marine ecosystems. While high diversity, particularly in upper trophic levels, is often considered to be an indicator of a healthy ecosystem, ecosystems containing healthy forage fish populations are often dominated by just one or two of these planktivorous species (Cury et al., 2000).

The remaining runs (No Shrimp Effort, New FF Fisheries, FF at  $F_{MSY}$ , Menhaden at  $F_{target}$ , Menhaden at  $F_{lim}$ , Increase All, and Double Rec) all resulted in a decrease in system maturity. Notably all scenarios that increased fishing caused a decrease in maturity, a trend previously noticed in other studies (e.g. Christensen, 1995, Christensen and Pauly 1998, Christensen and Walters, 2004). Again, however, not all indices followed the general trend. In particular, all scenarios that increased forage fish fishing increased the dominance of detritus, contrary to what would be expected with a decrease in maturity. This is likely because these scenarios caused an increase in penaeid shrimp biomass. Half of the penaeid shrimp diet is composed of detritus compared to 5–20% for forage fish groups, resulting in greater flow from detritus when forage fish groups are reduced. As with a reduction in menhaden fishing, path length did not follow the general trend when menhaden fisheries were increased. Again, this is likely due to the critical positioning of menhaden at the middle of the food web. When menhaden biomass decreases, flows must pass through a greater number of groups to reach the same end. A similar increase in path length with the reduction of dominant forage fish species has been observed in the northern Benguela upwelling ecosystem (Heymans et al., 2004). In the 1970s, when anchovies and sardines dominated the lower trophic levels of the northern Benguela, path length was low (Heymans et al., 2004). However, path length increased in the 1980s as the biomass of sardines and anchovies declined, leading to a greater diversity of planktivorous fish species (Heymans et al., 2004). Interestingly, elimination of the penaeid shrimp fishery in the Gulf of Mexico resulted in a decrease in maturity. The trends in the maturity indices for this scenario are not intuitive and are likely a result of the many complex interactions affected by changes in lower trophic levels. The lack of a clear explanation for these trends may also highlight the lack of resolution in the invertebrate and other low trophic level groups in this model.

Changes in ascendancy (Ulanowicz, 1986) were also evaluated as an alternative index of ecosystem state. The relationship between ascendancy and Odum's indices of maturity is not straightforward. Typically, ascendancy and Odum's maturity indices are thought to be positively correlated (Christensen, 1995). However, in a review of ecosystem goal functions, Christensen (1995) found these two indices to be inversely related. Christensen hypothesized that maturity may be more closely correlated to ecosystem stability (resistance to external fluctuation), while ascendancy represents growth (as measured by total throughput) and organization. This explanation may

help to address the different trends in ascendancy and maturity for the various scenarios seen in this study. New FF Fisheries and FF at  $F_{MSY}$  resulted in a decrease in maturity, but an increase in ascendancy. Forage fish play a dominant role in the middle of the food web, transferring energy from primary producers to upper trophic levels. Scenarios that remove biomass of forage fish may actually cause an increase in the relative diversity of flows through the ecosystem, which could explain the increase in ascendancy. Furthermore, depleting several lower trophic level species is likely highly disruptive for the system, causing changes in the diet composition of predators and changing the ecosystem in potentially unpredictable ways. Several runs did result in a positive correlation between ascendancy and maturity, in particular those related to Gulf menhaden. No Menhaden F resulted in an increase in maturity and ascendancy, while increasing Menhaden at  $F_{lim}$  or  $F_{targ}$  resulted in a decrease in both maturity and ascendancy.

#### 4.3. Uncertainty in input parameters and model limitations

While substantial uncertainty exists about each individual input parameter in the model, the most up-to-date and accurate data available were used. Furthermore, boundaries were placed on the input parameters during the balancing process, based on a range of values obtained from the literature. Nevertheless, the uncertainty in input parameters highlights the need for further research. Estimates based on local, high-precision sampling were difficult to come by for the northern Gulf. Diet and catch data were fairly well quantified and for the most part came from quantitative regional studies and national statistics, respectively. However, there was a paucity of information on the diets of large shark species and coastal bird groups in the northern Gulf region. Consumption and production rates have not been studied for the majority of species; thus it was necessary to use empirical relationships. Uncertainty also arose when fitting the Ecosim model to observed time series. A balance was struck between adjusting parameters to provide a better fit and maintaining parameters within the bounds of reality. In general, the model generated biomass and catch trends that matched well with observed values for species that have important fisheries and/or play a key ecological role.

Following the Deepwater Horizon oil spill in 2010, a substantial amount of research was initiated, much of which is documented in this issue of Deep Sea Research II. Results to-date indicate that the short-term impacts of the spill on mobile fish and invertebrates and fisheries are minimal (Fodrie and Heck, 2011; Mendelsohn et al., 2012). If long-term changes occur, it seems likely that they will affect the composition and relative abundance of species, given species' varying response to oil exposure (Mendelsohn et al., 2012). Food web models may be best suited to address these questions and may further be able to tease apart impacts of the spill on growth and recruitment that were masked by other influences such as environmental variability and fishing. For example, the abundance of many species, in particular Gulf menhaden, appeared to increase following the spill due to release from fishing pressure. Future work with this model could test variable rates of larval mortality with lowered fishing pressure to ascertain the relative influence of these factors. It may also be useful to construct a post-spill model based on data collected following the spill that can be compared to the present model. The model presented here compiled data through 2009, making it ideal for comparison with a post-spill model. Another potential impact of the oil spill is on the quality of the prey available, either via reduced condition or through a reduced abundance of "high quality" prey. Although we did not examine prey quality in this model, there is the potential to use it for such.

#### 4.4. Conclusions

Here we have shown that the northern Gulf of Mexico is a relatively immature system with high levels of primary production, low levels of nutrient recycling, and moderate diversity. Increased disturbance due to higher fishing rates appears to further decrease system maturity, potentially changing ecosystem structure and decreasing biomass and diversity. Furthermore, while there were some differences in the trends seen in the maturity and ascendancy indexes, several runs did result in a positive correlation between ascendancy and maturity, in particular those related to Gulf menhaden. Eliminating menhaden fishing resulted in an increase in maturity and ascendancy, while increasing menhaden fishing to  $F_{lim}$  or  $F_{targ}$  levels resulted in a decrease in both maturity and ascendancy. These results point to menhaden's role in maintaining a healthy Gulf ecosystem; that is, one that is resistant to external perturbation and in which a large and diverse flow structure is maintained despite natural disturbance.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2014.01.009>.

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