Modeling the dynamics of ecosystem for the American lobster in the Gulf of Maine

Yuying Zhang · Yunkai Li · Yong Chen

Abstract The objective of this study is to evaluate impacts of different management scenarios for American lobster (*Homarus americanus*) and Atlantic cod (*Gadus morhua*) fisheries on the dynamics of ecosystem for the lobster in the Gulf of Maine (GOM). The GOM lobster supports one of the most economically valuable commercial fisheries in the northeastern United States. The GOM ecosystem has experienced a great change over the last two decades, switching from a groundfish-dominated ecosystem to a lobster-dominated ecosystem. An evaluation of the GOM ecosystem dynamics can help identify possible causes of such a change and improve our understanding of interactions between lobster and other species in the same ecosystem. In this study, we developed a 24-group Ecosim model to quantify the ecosystem dynamics in the GOM from 1985 to 2007. We developed a Monte Carlo simulation approach to incorporate uncertainties for 15 most sensitive vulnerabilities. We found that the GOM ecosystem dynamics could be generally well simulated using the Ecosim model compiled in this study. A high fishing mortality in cod could result in high lobster stock biomass, suggesting that higher fishing pressure on cod in the 1980s might contribute to the high lobster biomass in recent years. A higher fishing mortality for lobster would have led to a lower lobster biomass. The change in the fishing mortality of cod and lobster would also affect the biomass dynamics of other functional groups, indicating that the Atlantic cod and American lobster fisheries played an important role in the change of the GOM ecosystem in the last two decades.

Keywords American lobster · Atlantic cod · Ecosim · Fishing impact · Gulf of Maine · Vulnerability

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Introduction

The Gulf of Maine (GOM) is well known for its high productivity (Ji et al. 2007). Its unique geographic characteristics and well-mixed and nutrient-rich ecosystem support some important commercial shellfish and finfish fisheries. Of all the fisheries, the American

lobster (*Homarus americanus*) fishery is one of the largest and most valuable single-species fisheries in the northeastern United States and Atlantic Canada. This decapod crustacean, distributed from the north-west Atlantic from the Newfoundland to North Carolina (Cooper and Uzmann 1980), has the highest population size in the GOM (Palma et al. 1999). The average annual landing from 2005 to 2007 for the American lobster was over 35,000 metric tons (ASM-FC 2009), with more than 75 % landings occurred in the coastal waters of Maine.

The American lobster plays an important role in the Gulf of Maine ecosystem (Zhang and Chen 2007). Contrasting to the decrease in groundfish populations (NEFSC 2000, 2001, 2002) in the region, the GOM lobster population increased even with dramatic increases in landing and fishing effort over the last two decades (Chen et al. 2005; Cook 2005). It seemed that the GOM ecosystem switched from a groundfish-dominated ecosystem to an ecosystem dominated by American lobster. Many hypotheses were developed to explain such a shift including warming ocean temperatures (Spees et al. 2002), increased herring bait discards in the lobster fishery (Grabowski et al. 2010), and fluctuations in lobster larval supply in the GOM (Steneck and Wilson 2001). The mesopredator release hypothesis was also one of the hypotheses explaining the substantial decline in biomass of the predators, such as Atlantic cod (*Gadus morhua*), which might be responsible for the increase in American lobster (Crooks and Soulé 1999; Hanson and Lanteigne 2000). One of the objectives of this study is to evaluate potential interactions of the dynamics of American lobster, Atlantic cod, and other ecological groups in the GOM.

Trophic cascade indicates an indirect effect that a predator might have on the abundance/biomass of the lower trophic levels of its preys, and this effect tends to be stronger in an aquatic ecosystem than in a terrestrial system (Schmitz et al. 2000; Berger et al. 2008; Lroux and Loreau 2008). Changing the harvest strategies of Atlantic cod or American lobster would not only affect their own biomass dynamics, but also influence the dynamic of some other species that have trophic interactions with these two species. We conducted a quantitative analysis to assess how lobster stock dynamics might interact with population dynamics of cod and other ecological groups. Such a study can improve our understanding of possible trophic interactions among the groups in the ecosystem, leading to improved understanding of the GOM ecosystem dynamics.

Zooplankton is a main food source for lobster larvae and postlarvae during their first year (Lavalli 1988). In larval stomach analyses performed by Juinio and Cobb (1992), nine taxonomic prey groups were found. Copepods and decapod larvae were common preys, but cladocerans, fish eggs, nematodes, and diatoms were also found. Juvenile lobster was also reported as easy preys to many groundfish such as Atlantic cod, cunner (*Tautogolabtus adspersus*), sculpin, bass, and tautog (*Tautoga onitis*) (Herrick 1911; Carter and Steele 1982b; Bowman et al. 2000; Okey 2001). However, little information is available with respect to the percentage of the juvenile lobster in the diet composition of its predators.

The adult lobster is the largest mobile benthic invertebrate in the North Atlantic. Their size and large claws make them an important predator (Elner and Campbell 1981; Moody and Steneck 1993). Adult lobster is omnivorous, feeding largely on crabs, mollusks, polychaetes, sea urchin, and sea stars (Ennis 1973; Carter and Steele 1982a, b). Live fish and macroalgae are also part of their diets. The lobster is an opportunistic feeder, and their diets vary spatially depending upon the local prey species composition and abundance. On their main fishing grounds, baits (mostly Atlantic herring, *Clupea harengus*) discarded in the lobster fishery is also an important component of their diets.

This study is an extension of the ecosystem models developed by Zhang and Chen (2007), in which two mass-balance ecosystem models (Ecopath) were developed for the GOM ecosystem for the 1980s and 1990s, respectively. These two models, considered as two "snapshots" in the evolution of the GOM ecosystem, describe the structure of the ecosystem in the defined time (i.e., 1980s and 1990s). However, they are unable to describe the dynamic nature of the ecosystem and are not suitable for testing the trophic interactions between lobster and their preys and predators. In this study, we build a temporally dynamic model (Ecosim) to explore the contribution of different groups in driving the dynamics of lobster-dominated ecosystem. Ecopath with Ecosim (EwE) has been widely used worldwide in analyzing ecosystem structure and dynamics and evaluating impacts of fisheries on ecosystems (Mackinson et al. 2003;

Tsehaye and Nagelkerke 2008; Araújo and Bundy 2011). However, of all the applications of the EwE, only a small percentage looked at the vulnerability coefficients in Ecosim, and even fewer studies focused on uncertainty of the ecosystem dynamics resulting from the uncertainty associated with vulnerability coefficients, which indicate the likelihood that the functional groups in an ecosystem being affected by the top-down or bottom-up control.

Understanding of the dynamics of ecosystem is important in developing ecosystem-based fisheries management. In this study, we used the Ecosim model and applied various fishing mortality (F)-based harvest strategies in the American lobster fishery and the Atlantic cod fishery to explore possible interactions among the lobsters, cod, and other related functional groups in the GOM ecosystem. The model can also be used to forecast possible responses of lobster population to possible recovery of groundfish populations in the GOM (NEFSC 2011, 2012). The uncertainty of the flow control mechanism (i.e., vulnerability) was fully and explicitly considered in this study. The results of this study could provide us with critical information about the dynamics of lobster-dominated ecosystem in the GOM.

Methods and materials

General process and harvest strategy scenarios

The Ecosim model simulates the dynamics of ecosystem based on the following equation:

$$\mathrm{d}B_i/\mathrm{d}t = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M_i + F_i + e_i)B_i,$$

$$(1)$$

where $\mathrm{d}B_i/\mathrm{d}t$ is the growth rate of stock biomass B_i for group i; g_i is the net growth efficiency of group i; Q_{ji} is the consumption rate of predator group j on the prey group i; M_i is the non-predation natural mortality rate; F_i is the fishing mortality rate; and I_i and e_i are the emigration and immigration rates, respectively (Walters et al. 1997; Christensen et al. 2004). This equation describes how the biomass of each organism group in the ecosystem changes with time, which provides the information on the dynamics of ecosystem.

We developed an Ecosim model which uses the output of the 24-group mass-balanced Ecopath model

in the mid-1980s (Zhang and Chen 2007) as the initial status of the Ecosim model. The names of functional groups, as well as trophic levels, biomass, production/biomass ratios, consumption/biomass ratios, and eco-trophic efficiency are listed in Table 1. The parameters used to define the ecosystem in 1985 were same as those defined for the mid-1980s in the previous study (Zhang and Chen 2007). We then identified time series data from 1985 to 2007 for functional groups (Table 2), loaded the data as input of the simulation, and let Ecosim to fit the time series data by varying the vulnerability coefficients among groups (Christensen et al. 2004; Shannon et al. 2009). These groups were selected because of their importance to the lobster population dynamics and local ecosystem (Zhang and Chen 2007). To be compatible with the previous Ecopath model, the Ecosim model considers American lobster as a stanza/split group that is split into adult and juvenile subgroups (Christensen et al. 2004; Zhang and Chen 2007).

The lobster-dominated ecosystem dynamics were also evaluated under different levels of fishing mortalities for the American lobster and Atlantic cod, which described how changes of fishing intensity in the GOM lobster and cod fisheries might influence, directly or indirectly, their own biomass as well as biomasses of other species in the ecosystem. To evaluate impacts of alternative harvest strategies on the lobster and Atlantic cod population dynamics, 12 hypothetical fishing mortality levels were assumed for the American lobster and Atlantic cod, 6 for each of the species from 0 year^{-1} to 1 year^{-1} with an interval of 0.2 year^{-1}. Consistent with the EwE, fishing mortality is defined as the ratio between catch and biomass (Christensen et al. 2004). Each of the fishing mortality rates was applied to manage the fisheries throughout the management time period. For example, when we applied fishing mortality of 0.2 year^{-1} to manage the American lobster fishery, this fishing mortality would be set constantly every year from 1985 to 2007, while for the other group, that is, Atlantic cod, we would use the observed historical fishing mortality rates.

We also used percentage change of relative biomass (p_k) to quantify the effect of different fishing mortality levels of Atlantic cod and American lobster to the key group, i, in the GOM in year k:

$$p_k = (B_{f,k} - B_{f=0,k})/B_{f=0,k},$$

$$(2)$$

Table 1 Input data for the Gulf of Maine lobster Ecosim model

Group	Effective trophic level	B in habitat area (t/km^2)	P/B (/year)	Q/B (/year)	EE
Phytoplankton	1	97.8	88	–	0.483
Macroalgae	1	54	4	–	0.407
Microzooplankton	2	25	40	125	0.402
Macrozooplankton	2.28	61	7	21.87	0.041
Microbenthods	2.11	25.38	1.8	3	0.359
Shelled mollusk	2.01	9.8	1.22	23	0.989
Crab	3.22	2.74	1.38	8	0.99
American lobster (juvenile)	3.15	0.222	2.4	12.3	0.99
American lobster	2.72	0.285	1.2	8.2	0.462
Echinoderms	2.29	12.096	1.2	3.7	0.557
Squid	3.22	1.938	1.5	7	0.988
Shrimp	2.43	1.628	4	15	0.357
Atlantic herring	3.09	1.809	0.7	10.1	0.99
Silver hake	3.89	0.777	0.735	4.26	0.99
Skate	3.96	0.39	0.296	1.4	0.988
Cunner	3.63	0.0624	0.4	4.1	0.99
Cusk	3.55	0.391	0.341	2.2	0.99
Atlantic cod	4.22	0.752	1.05	2.58	0.99
Red hake	3.54	0.0468	0.323	2.6	0.807
Tautog	2.98	0.352	0.752	2	0.98
Atlantic wolfish	3.28	0.0297	0.418	1.8	0.982
Other fishes	3.71	1.945	2.6	3.6	0.99
Bait (herring)	1	1.86	1	–	0.99
Detritus	1	155.7	–	–	0.04

where $B_{f,k}$ is the relative biomass in year k under the fishing mortality of f.

Fisheries-dependent and independent data

The time series of data used in the Ecosim model included fishing mortality for the American lobster and the Atlantic cod, which acted as forcing drivers, as well as the relative biomass of American lobster, Atlantic cod, Atlantic herring, Atlantic wolfish (*Anarhichas lupus*), squid, silver hake (*Merluccius bilinearis*), skate, and shrimp, which acted as reference data for evaluating the accuracy of results. Relative biomass data for all species, except for American lobster and Atlantic herring, were from the Northeast Fisheries Science Center (NEFSC) fishery-independent survey programs, and annual fishing mortality data were from the NEFSC Stock Assessment Workshop (SAW) reports and other NEFSC reference documents (Hendrickson 2006; NEFSC 2006, 2007a,

b, 2009). The biomass data for American lobster were derived from a recent stock assessment using the University of Maine American lobster stock assessment model (Chen et al. 2005; Kanaiwa et al. 2008; ASMFC 2009). The relative biomass was calculated from the estimated lobster biomass in the GOM, and the fishing mortality was estimated for fully recruited lobster. For the Atlantic herring, the relative biomass is the stock biomass estimated for herring older than age 2 (Shepherd et al. 2009).

For other functional groups, different approaches were used for estimating their stock biomass or index (Zhang and Chen 2007). For example, the relative biomass of Atlantic cod from 1985 to 2007 was calculated from the standardized stratified mean catch per tow in weight (kg) in the NEFSC fall bottom trawl surveys, while the annual fishing mortality from 1982 to 2007 was estimated from virtual population analysis for cod ages 5–7 (Mayo et al. 2009). For the skate, the relative biomass is the mean catch weight per tow from

Table 2 The csv file of input data for the Gulf of Maine lobster Ecosim

	Lobster F	Cod F	Lobster Rel. Bio	Cod Rel. Bio	Herring Rel. Bio	Wolfish Rel. Bio	Skate Rel. Bio	Shrimp Rel. Bio	Squid Rel. Bio	Silver hake Rel. Bio
Pool code	9	18	9	18	13	21	15	12	11	14
Type	4	4	0	0	0	0	0	0	0	0
1985	0.24	0.87	1	1	1	1	1	1	1	1
1986	0.25	0.86	0.95	0.57	1.27	0.53	1.3	1.31	0.72	1.72
1987	0.25	0.97	1.07	0.41	1.46	0.21	0.98	1.36	4.3	1.28
1988	0.26	0.88	1.19	0.8	1.48	0.58	0.72	1.18	8.44	0.86
1989	0.30	0.87	1.29	0.55	1.82	0.74	0.64	1.03	9.32	1.58
1990	0.31	0.98	1.33	0.59	2.54	0.58	0.7	1.26	6.76	1.85
1991	0.32	1.22	1.37	0.34	3.25	0.68	0.69	1.33	1.95	1.5
1992	0.30	1.37	1.44	0.3	3.87	0.68	0.42	1.17	2.26	1.69
1993	0.28	1.24	1.49	0.12	4.4	1	0.35	0.96	4.49	0.95
1994	0.30	1.6	1.56	0.33	4.45	0.58	0.39	0.78	2.42	0.86
1995	0.31	1.42	1.6	0.44	4.53	0.79	0.39	1.03	1.97	1.6
1996	0.29	1.23	1.69	0.28	5.7	0.05	0.38	1.18	2.61	0.86
2007	0.31	1.04	1.89	0.23	5.93	0.37	0.39	0.85	1.47	0.74
1998	0.29	0.69	2.01	0.18	5.78	0.05	0.49	0.48	3.94	2.62
1999	0.27	0.55	2.05	0.42	5.26	0.26	0.62	0.4	0.54	1.38
2000	0.29	0.36	2.06	0.56	6.12	0.05	0.56	0.4	1.99	1.6
2001	0.26	0.46	2.04	0.89	5.66	0.21	0.54	0.37	0.91	1.08
2002	0.28	0.52	2.24	2.98	4.8	0.16	0.7	0.4	1.25	0.92
2003	0.22	0.68	2.34	0.73	4.83	0.42	0.86	0.49	5.48	1.05
2004	0.24	0.53	2.45	0.59	5.09	0.05	0.58	0.67	1.16	0.37
2005	0.22	0.66	2.38	0.35	4.9	0.26	0.53	1.05	2.52	0.25
2006	0.25	0.55	2.24	0.51	4.94	0.21	0.55	1.87		
2007	0.21	0.57	2.23	0.33	4.99	0	0.47	2.95		

The unit for the fishing mortality is year^{-1}. *F* fishing mortality, *Rel. Bio* biomass relative to that in the year of 1985, *pool code* the group ID in the Ecosim model, *type*: *data type*: 0 = relative biomass. 4 = fishing mortality

the GOM to mid-Atlantic region (offshore) fall survey for all the skates including winter skate (*Leucoraja ocellata*), little skate (*Leucoraja erinacea*), thorny skate (*Amblyraja radiata*), barndoor skate (*Dipturus laevis*), and smooth skate (*Malacoraja senta*) (NEFSC 2007a). The relative biomass for shrimp was estimated from the Collie–Sissenwine analysis (NEFSC 2007b). For other groups, such as silver hake, squid, and the Atlantic wolfish, their relative biomasses were all derived from the NEFSC fall research vessel surveys (Hendrickson 2006; NEFSC 2006, 2009). The details of input data are summarized in Table 2.

Flow control mechanism: vulnerability

The Ecosim model uses foraging arena theory to define the probability of an organism that is exposed to

predation risk (Walters and Martell 2004; Ahrens et al. 2011) and quantifies the risk by a vulnerability coefficient (Christensen et al. 2004). According to Walters and Martell (2004), prey group *i* can be partitioned into available biomass (V_i) and unavailable biomass (B_i–V_i) because of the behavior of prey group *i* and one of its predator groups, *j*. The vulnerability coefficient, v_{ij}, represents the exchange rate between the available and unavailable biomass. It is related to the biomass of prey group *i*, B_i, the abundance of predator group *j*, P_j, and the consumption rate of predator group *j* on the prey group *i*, Q_{ji} (see Eq. 1):

$$Q_{ji} = a_{ij}v_{ij}B_iP_j / \left(v_{ij} + v'_{ij} + a_{ij}P_j\right), \quad (3)$$

where a_{ij} is the effective search rate for predator *i* feeding on a prey *j*. In this way, the predator–prey

interactions affect the energy flows within the ecosystem (Walters and Juanes 1993; Walters and Korman 1999; Walters and Martell 2004).

In the Ecosim model version 5 (Christensen et al. 2004), parameters "vulnerabilities" were defined in three categories: A low vulnerability (= 1) indicates that the prey is well protected and seldom exposed to its predators. In this case, predator–prey interaction is controlled only by the prey density (bottom-up control). A high vulnerability approaching to the infinity ($\gg$1) implies a predator-driven interaction (top-down control), in which the natural mortality of the prey is also a function of the predator abundance (i.e., Lotka–Volterra model). The theory behind this definition links vulnerability coefficient with the biomass of predator relative to the carrying capacity with regard to a prey: That is, when predator biomass approaches the carrying capacity, the vulnerability will be close to 1; when biomass of predator is close to 0, the vulnerability is $\gg$1 (Christensen et al. 2004). Ecosim uses 2 as the default value of the vulnerability, which implies that the predator biomass is a certain proportion of the carrying capacity, and meanwhile, the mid-trophic level groups exert both top-down control on its preys and bottom-up control on its predators (mixed trophic control). Because the estimated ecosystem dynamics tend to be sensitive to vulnerability coefficients and the vulnerability is sensitive to Ecosim model input values and assumptions (Ahrens et al. 2011), it is important to evaluate impacts of uncertainty in vulnerability coefficients for the key functional groups in estimating the ecosystem dynamics.

A set of improved vulnerability coefficient estimates can often be achieved by "fitting" the Ecosim model to a time series of data. The goodness of fit can be measured by a weighted sum of squared deviation of log observed biomass from log predicted biomass (Christensen et al. 2004), and the most sensitive SS between predators and preys could be identified. However, the probability density function of vulnerability coefficient is unknown, and there is no built-in function in Ecosim to evaluate uncertainty of the vulnerability coefficients. In this study, we identified 15 most sensitive vulnerability coefficients from the fitted Ecosim model and then evaluated the impact of uncertainty of these vulnerability coefficients. The vulnerability coefficients were assumed to follow a piecewise uniformly distributed probability density

function described below based on their definition in Christensen et al. (2004):

$$
vij = \begin{cases} 1 & \gamma \in [0, 0.3) \\ 10\delta + 1 & \gamma \in [0.3, 0.6), \\ 10^{10}\delta + 10 & \gamma \in [0.6, 1] \end{cases} \tag{4}
$$

where γ indicates the piece that v_{ij} belongs to and δ is used to define the value of v_{ij} in each piece. They are independent numbers that were randomly and independently generated from 0 to 1. Essentially, this assumes that the vulnerability coefficients have 30 % probability to have a value of 1; 30 % probability to have a value from 1 to 11; and the remaining 40 % probability of having values from 10 to infinite. This effectively assumes the similar probability among the three types of vulnerability representing mainly bottom-up, mixed trophic control, and mainly top-down controlled systems, respectively. This was somewhat arbitrary because we did not have strong evidence to support any of these three controlled systems for the GOM lobster. It should be noted that we applied this approach to evaluate impacts of possible uncertainty associated with vulnerability on the ecosystem dynamic modeling, which is commonly not considered in the previous studies. One thousand of Monte Carlo simulation runs were conducted for the base case as well as each of the 12 alternative harvest strategy scenarios. For each run, the Ecosim model yielded a time series of biomass for the 24 groups included in the ecosystem model from 1985 to 2007.

Results

We identified 15 most sensitive vulnerability coefficients and examined their predators and preys. Among these vulnerability coefficients, 47 % of the predators were attributed to Atlantic cod, and 27 % of the predators to silver hake. This result suggests that the biomass of above two species would highly affect the dynamics of GOM lobster-dominated ecosystem.

The predicted temporal change of relative biomass from 1985 to 2007, its uncertainty derived from the 1000 Monte Carlo simulation runs, and observed survey data (relative survey indices) were plotted for American lobster and Atlantic cod, as well as the other six commercial fish groups in Fig. 1 and e1 (please see electronic appendix). For most of these groups, the temporal trends of the median predicted relative

Fig. 1 Relative biomass fitting for eight commercial fish groups from 1985 to 2007: predicted (*line*) versus observed (*circles*). The *gray shades* represent the uncertainty associated with the predicted relative biomass resulting from uncertainty associated with vulnerability coefficients
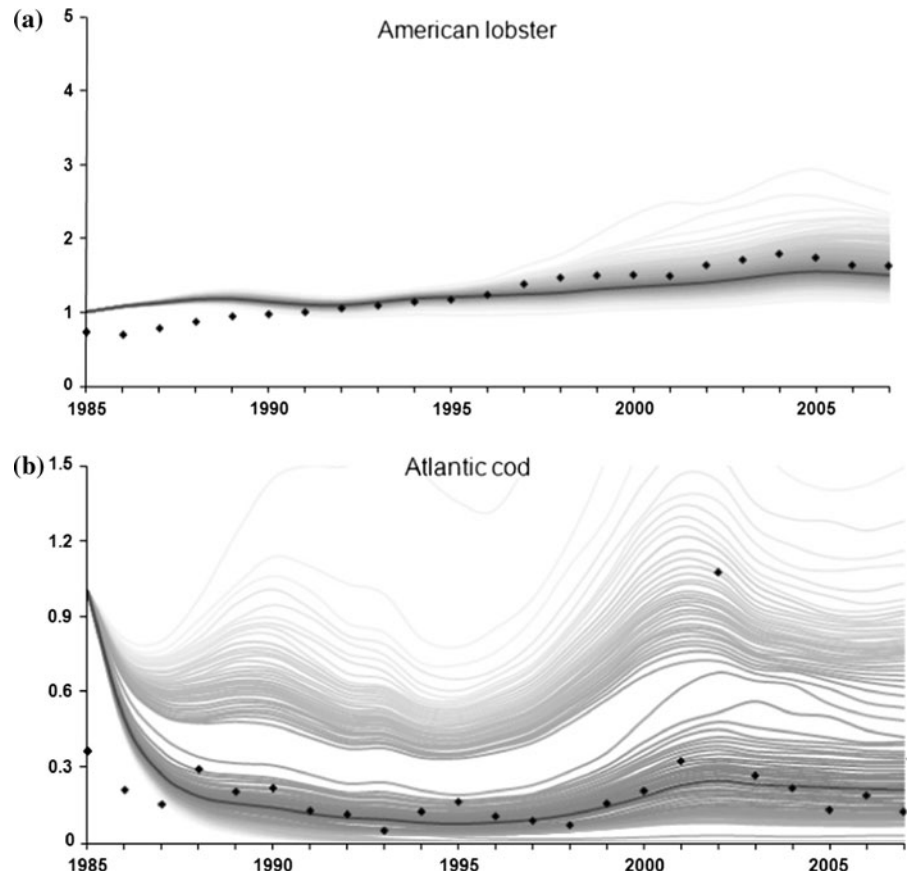
biomass were similar to those for the observed data, with the positive correlation coefficients (*R*s) (Table 3). However, for some groups, such as skate, shrimp and silver hake, the temporal trends of their predicted data are not consistent with those of the observed data. Moreover, there were discrepancies between the observed and predicted relative biomasses for some species in some years (e.g., biomass of Atlantic cod in 2002). For some species such as American lobster, the population biomass predicted by the Ecosim model was similar to the "observed" biomass estimated from the single-species stock assessment model. This may suggest the adequacy of the developed ecosystem model in describing the dynamics of most fish populations.

Fish populations such as American lobster, Atlantic herring, skate, shrimp, and sliver hake experienced increases from 1985 to 2007 (Fig. 1 and e1). Some organisms (e.g., squid) did not show large changes from 1985 to 2007. Atlantic cod and Atlantic wolfish experienced substantial decreases from 1985 to 2007.

Their biomasses at the end of 2007 were only around 20 % of what they were at the beginning of 1985.

By running the Ecosim model for 1,000 Monte Carlo simulation runs, the uncertainty associated with the predicted biomass could be estimated (Fig. 1 and e1). Most of the relative biomasses that were portrayed by the 1,000 simulation runs were consistent with the "observed" relative biomass.

The biomass dynamics of fish groups from 1985 to 2007 were estimated under alternative levels of fishing mortality rates for Atlantic cod using the Ecosim model. Six hypothetical fishing mortality levels were assumed for the Atlantic cod (Fig. 2 and e2). When the fishing mortality for Atlantic cod was assumed to be low over the 23-year time period (e.g., $F = 0.2$ year^{-1}), cod stock biomass in year 2007 would have been kept in the similar biomass levels as mid-1980s. If the cod fishing mortality rates were set high (e.g., $F = 0.8$ year^{-1}), the cod stock biomass would have decreased substantially from 1985 to 2007. The adult American lobster stock biomass would increase

Table 3 Correlation coefficients (R) between observed and predicted relative biomass for key species in the Gulf of Maine lobster-dominated ecosystem

| Group	R
American lobster	0.93
Atlantic cod	0.29
Atlantic herring	0.92
Atlantic wolfish	0.57
Skate	−0.5
Shrimp	−0.32
Squid	0.54
Silver hake	−0.14

continuously regardless of fishing mortality rates for the cod. The differences among the different cod fishing mortality scenarios were that the biomass of adult lobster would increase slightly under the scenarios of low cod F, but dramatically under higher cod fishing mortality scenarios.

This analysis also showed how the median stock biomasses might have changed compared with what they would be when no cod were caught during the same time period (Fig. 3 and e3). The general trend that adult lobster biomass responded to an increased

cod fishing mortality was opposite to the trend of the cod biomass. This suggests that a large reduction in the cod stock biomass might contribute to the increase in the lobster stock biomass. However, the effect of changing harvest level of Atlantic cod on adult lobster could only be seen after 10 years of applying the fishing mortality, while for the juvenile lobster, the effect could be seen immediately but started to decrease after 7 years. On the other hand, the decrease in juvenile lobster biomass with an increasing cod fishing mortality was associated with an increase in Atlantic herring and shrimp.

Increasing the fishing mortality of cod would not only affect the biomass of American lobster, but also reduce the biomass of cusk, wolfish, and echinoderms group. However, increasing trends could be found in the biomass of silver hake, skate, and tautog. The biomass of cunner, red hake and other fish would fluctuate with less than 5 % change over the time. The biomass dynamics of squid and crab were complicated and difficult to interpret (Fig. 3 and e3).

Six different hypothetical levels of fishing mortality were applied to the adult lobster for the period of 1985–2007, which would lead to large changes in both adult lobster biomass and juvenile lobster biomass
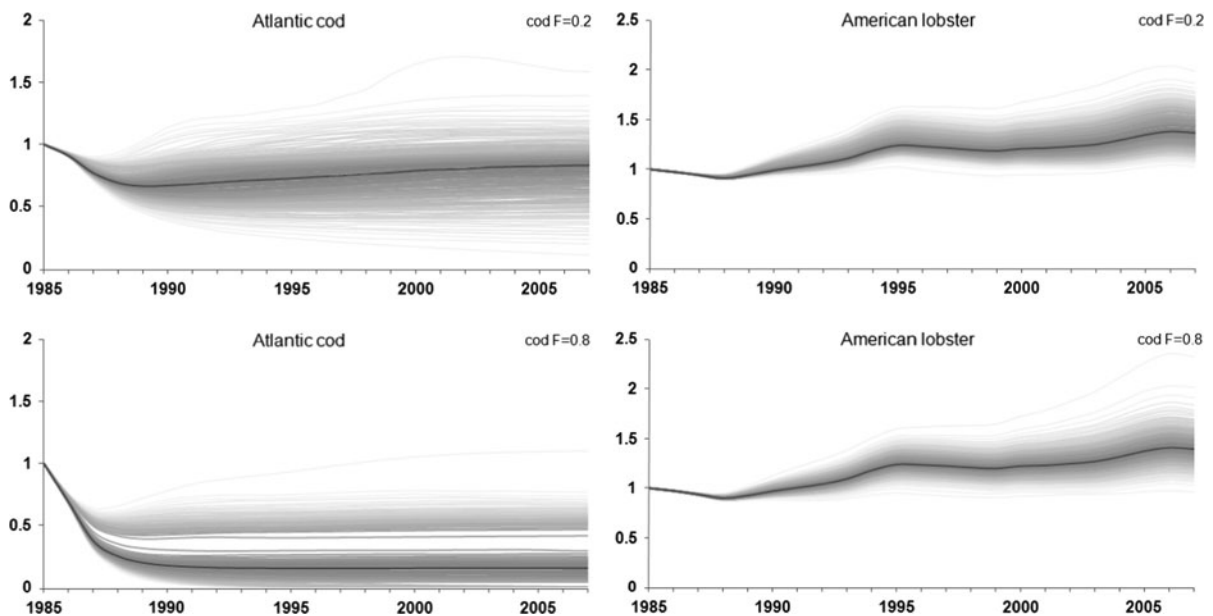
Fig. 2 Time series of relative biomasses for American lobster and Atlantic cod estimated from the Ecosim model from 1985 to 2007 under different scenarios of fishing mortality for the management of Atlantic cod. The *gray shades* represent the

uncertainty associated with the predicted relative biomass resulting from uncertainty associated with vulnerability coefficients
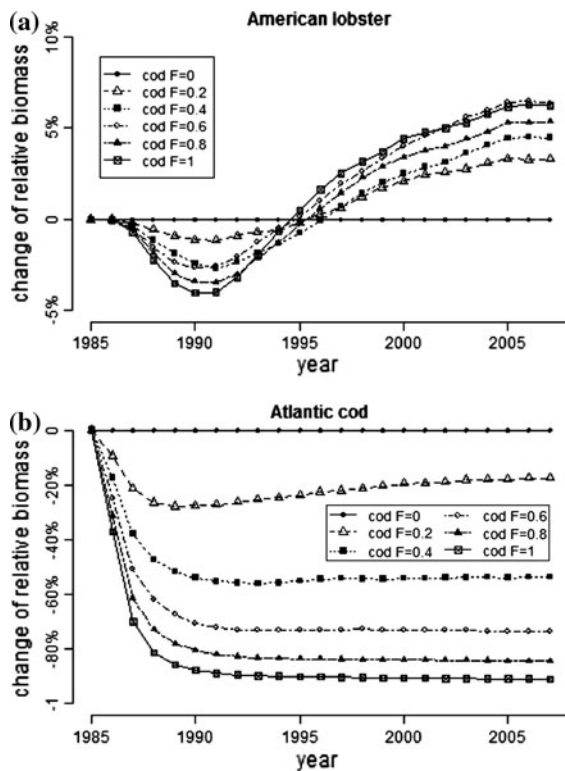
Fig. 3 Percentage change of relative biomasses for **a** American lobster and **b** Atlantic cod from 1985 to 2007 under different scenarios of fishing mortality for the management of Atlantic cod

(Fig. 4 and Fig. e4 and e5). When the fishing mortality for lobster was less than 0.6 year^{-1}, the adult lobster stock biomass at the end of 2007 would have been higher than that at the end of 1985. When the F was higher than 0.8 year^{-1}, the lobster stock biomass would have decreased dramatically. Increasing the fishing mortality for lobster would have led to a great decrease in lobster biomass after 1990 (Fig. 4 and e4).

The Atlantic cod would continue decreasing even the level of fishing mortality for American lobster was reduced to 0 year^{-1}, but interaction did exist between these two species. Increasing the adult lobster F would result in the biomass of cod stock increasing 20–40 % in the late 1990s. However, this built-up biomass would have disappeared in the mid-2000s.

When the F for adult lobster increased, the stock biomass for juvenile lobster, crab, cusk, and other fish group would increase greatly, but the Atlantic herring, tautog, echinoderms, and shrimp would decrease. The impact of increased adult lobster F on the biomass dynamics of Atlantic wolfish was complicated:

The biomass of wolfish would decrease with an increased F for the adult lobster after the 1990s, but then rebound later. For the other groups such as skate, squid, silver hake, red hake, and cunner, changes in their biomass dynamics were small (Fig. 5 and e5).

Discussion

Using the Ecosim model and parameters estimated in the Ecopath model established for the GOM ecosystem (Zhang and Chen 2007), we simulated the dynamics of the lobster-dominated ecosystem in the GOM from 1985 to 2007 and evaluated the long-term impact on the ecosystem under different harvest strategy scenarios for the Atlantic cod and adult American lobster. Such a study can help us understand the responses of the GOM ecosystems to the exploitations of lobsters and its predators. In addition, it can also be used to evaluate the performance of alternative harvest strategies for some other key species and how they may affect the dynamics of ecosystem. Similar work was conducted in assessing and managing fisheries and their related ecosystems (Arreguín-Sánchez 2000; Coll et al. 2008; Ortiz 2008; Overholts and Link 2009). It has been agreed that inappropriate harvest strategies with high ecological risk identified in such an exercise should be avoided in fisheries management before it causes unintentional irreversible damage to the ecosystem (Cochrane 2002).

Increasing F for Atlantic cod would have opposite effects on juvenile and adult lobster groups. The positive effect on juvenile lobster in the initial years, as a result of an increased fishing mortality for cod, may contribute to the positive effects on the adult lobster biomass several years later. This difference between juvenile and adult lobster in time lags in response to cod fishing mortality changes reflected the time duration lobster needs on average to grow from juveniles to legal-sized adults (ASMFC 2000). Complicated trophic interactions among different species in the ecosystem can make the interpretation of some results difficult. The impact of cod on the lobster was likely to result from direct predation as well as indirect interactions such as via changes in the biomass of lobster competitors (for foods) and preys, for example, the crab group. Both crab and lobster could be found in each other's stomach content (Carter and Steele 1982b; Ojeda and Dearborn 1991; Grabowski et al.
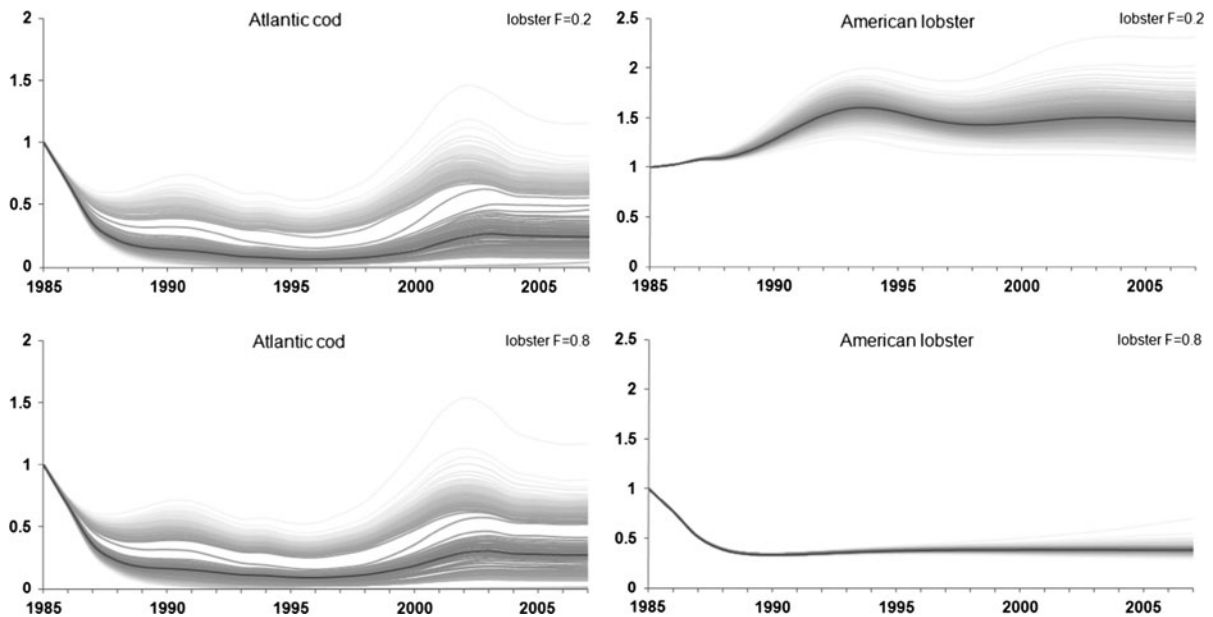
Fig. 4 Time series of relative biomasses for American lobster and Atlantic cod estimated from the Ecosim model from 1985 to 2007 under different scenarios of fishing mortality for the management of adult American lobster. The *gray shades* represent the uncertainty associated with the predicted relative biomass resulting from uncertainty associated with vulnerability coefficients

2010). Meanwhile, they also shared and competed for the same preys such as shelled mollusk and microbenthods. Decreasing the fishing mortality of cod would cause an immediate increase in crab in the first few years (Fig. e3), which might cause the decrease in adult lobster during the same time.

The result of reducing F of cod suggests a general negative relationship between the dynamics of Atlantic cod and American lobster (Figs. 2 and 3, Fig. e2 and 3a). Thus, we could not reject the mesopredator release hypothesis. The increase in lobster stock biomass since the 1990s may relate to reduced cod stock biomass (Wahle and Steneck 1991; Steneck and Wilson 1998). This also implies that a full recovery of the cod over the spatial range of the American lobster in the GOM may lead to a decrease in the American lobster stock, although the magnitude of such an impact depends on the recovered cod biomass and their spatial overlaps with the lobster in the GOM.

Increasing the fishing mortality for adult lobster would have resulted in a higher relative biomass of cod for the first 10 years, but the built-up biomass would disappear after 20 years (Fig. 5b). In this case, an increase in the cod biomass might result from the biomass increase in the other fish group, juvenile

lobster, and silver hake, while a decrease later might result from the decrease in Atlantic herring. The Ecosim model developed for the GOM ecosystem performed well in describing the population dynamics of lobster and some other key commercial fish species groups, such as Atlantic herring and Atlantic cod. The currently used single-species stock assessment model for American lobster could not incorporate interactions between the lobster and other fish species. The Ecosim model developed in this study could be used for exploring potential impacts of changes in managing of one fishery (i.e., changes in fishing mortality) on the dynamics of other species in the ecosystem. For example, we can use the Ecosim model to evaluate impacts of managing the lobster fishery on the cod stock and vice versa.

The interactions of Atlantic cod and American lobster with other species should also be explored (Fig. e3 and e5). For example, in addition to juvenile lobster, both Atlantic herring and silver hake were important food resources of cod. A small proportion (~2 %) of the cod diets was juvenile lobster, while 14.7 % was Atlantic herring and 12.2 % was silver hake (Bowman et al. 2000; Okey 2001; Zhang 2005). A reduction in cod biomass might increase the survival
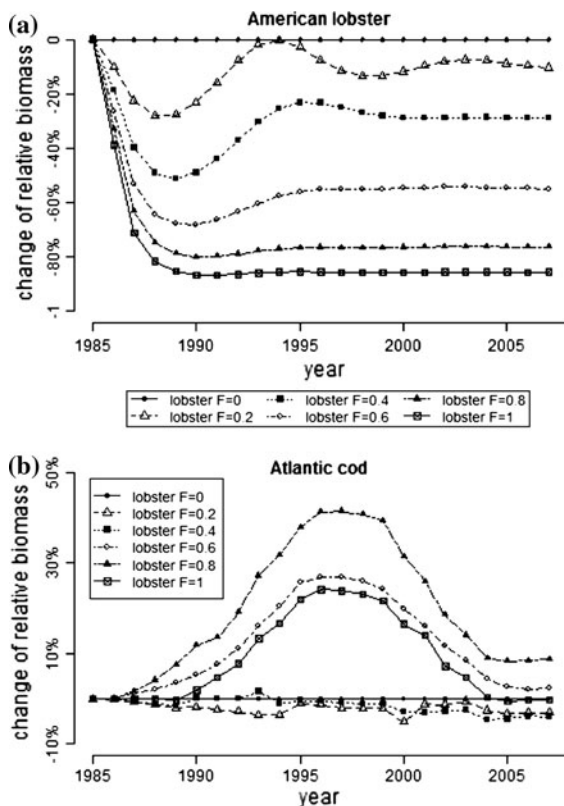
Fig. 5 Percentage change of relative biomasses for **a** American lobster and **b** Atlantic cod from 1985 to 2007 under different scenarios of fishing mortality for the management of adult American lobster

rate of herring. However, Atlantic herring was also the third most important food of silver hake (herring consisted of 16.8 % in the stomach content of silver hake). Therefore, according to trophic cascade hypothesis, a reduction in cod biomass could increase in the biomass of silver hake and then indirectly reduce the biomass of Atlantic herring. In addition, both Atlantic herring and silver hake were predators of macrozooplankton (Bowman et al. 2000; Okey 2001; Zhang 2005), which would make the dynamics of Atlantic herring more complicate. From our modeling results, we can conclude that increasing fishing mortality of cod would result in a 60 % increase in herring biomass at the end of 2007 (Fig. e3). Such an analysis can not only improve our understanding of possible interactions among different species in the ecosystem, but also identify the key species in an ecosystem that might dominate the dynamics of the ecosystem. It can provide information essential for

developing ecosystem-based fisheries management (Link 2010; Hilborn 2011).

The vulnerability coefficient is used to indicate whether a predator–prey interaction is predator- or prey-controlled. It is one of the most important parameters in the Ecosim to determine the dynamics of ecosystem (Christensen et al. 2004). However, our understanding of this parameter is limited for most ecosystems. It is important to incorporate uncertainty resulting from such a lack of knowledge in modeling an ecosystem. Ecosim only provides one set of output results based on the "best" set of estimates of vulnerabilities between preys and their predators (Christensen et al. 2004; Shannon et al. 2004). Some studies used default or fitted values for vulnerability suggested in the Ecosim (Taylor et al. 2008). In other studies, vulnerability of each group was adjusted according to the corresponding trophic level of the group (Buchary et al. 2003; Chen et al. 2008) with the assumption that the groups in the top and bottom trophic levels would be subject to either the "top-down" control or the "bottom-up" control, while the mid-trophic-level groups would be impacted by the mixed trophic control. This definition is not consistent with the definitions of vulnerability as the vulnerability value should be decided by both prey and predator groups (Christensen et al. 2004; Walters and Martell 2004). The assumption is not consistent with the flow control mechanisms, either. The top- and bottom-trophic-level groups in one ecosystem can have more than one control mechanisms based on different environmental conditions (Griffiths et al. 2010; Pereira et al. 2010). These inconsistencies call for the incorporation of uncertainty associated with vulnerability.

In this study, we used a piecewise uniformly distributed probability density function to quantify the uncertainty associated with the vulnerability (i.e., Eq. 3). This distribution function has similar probability for the three discrete intervals, implying that each predator–prey relation in the ecosystem has similar probabilities of being bottom-up controlled, top-down controlled, or mixed trophic controlled. This piecewise function incorporates uncertainty resulting from our lack of understanding of the ecosystem dynamics and can also be used to describe vulnerability when the availability of prey to its predators varies dramatically. Although this is rather arbitrary, this function represents our best understanding of the

vulnerability. As we stated in the method section, this is intended to evaluate potential impacts of uncertainty in vulnerability on modeling ecosystem dynamics. We used this approach to highlight the importance of identifying well-defined vulnerability coefficients. Any interpretation of ecological meanings of the uncertainty associated with vulnerability coefficients derived in this study should be cautious. The probability distribution should be better defined for vulnerability in the future.

Previous studies also indicated that the results from an Ecosim model tended to be sensitive to the choice of vulnerability (Arreguín-Sánchez 2000; Mackinson et al. 2003; Cheung and Sumaila 2008). However, limited studies had considered uncertainty for such critical but sensitive parameters. In our study, the uncertainty of vulnerability was fully considered with an incorporation of 1,000 sets of vulnerability matrix generated randomly and independently according to the distributional function defined in Monte Carlo simulations. The uncertainty analysis in the Ecosim model revealed the potential dynamics of the biomass. For most of the "observed" relative biomass data, the general trends were well represented by the median predicted relative biomass, and most of the "observed" data fell into the shade areas that represented 1,000 sets of biomass projections with the uncertainty of vulnerability. However, if some inappropriate vulnerability coefficients were defined, there might be some extreme predictions in the biomass dynamics.

For some species, such as skate and silver hake, the predicted and observed relative biomasses differed, which might result from inaccurate estimates of stock biomass for these species. The observed data were from the NEFSC fall surveys, and data collected in different seasons could yield different biomass estimates. Using survey abundance index data instead of estimated biomass might also cause discrepancies. Thus, a continuing effort to update the model with more accurately estimated stock biomass is necessary for the future evaluation of the GOM ecosystem.

Another reason for the inconsistent trend or the discrepancy between the observed and predicted stock biomass for some species is that in our Ecosim model we did not incorporate temporal variations in physical environments, such as water temperature and salinity. The impacts of these external variables that might determine the physical habitats of the ecosystem were

assumed to be incorporated into modeling via a single parameter called "other natural mortality" (death due to reasons other than predations). This parameter was assumed to be constant over the modeling time period. Thus, the physical environment of the ecosystem implicitly was assumed to be time invariant. However, this assumption is unlikely to be realistic, which might result in large uncertainties in modeling. In the future, more effort will be made to explore the relationship between the other mortality of key groups and the environmental variables. Also, input data used in this study were derived from different sources and varied greatly in their quality (Zhang and Chen 2007). Large errors associated with these data might also contribute to the errors in modeling. Therefore, the uncertainty of input data should also be evaluated in the future. Current approach, although is not perfect, provides us with an analytical tool to explore the interactions between different species in the ecosystem, which cannot be accomplished with a single species-based population model that is currently used in the GOM.

The Ecosim model developed in this study, although preliminary in nature and data input, provides a framework to evaluate trophic interactions between lobsters and other organisms in the GOM, improves understanding of the GOM ecosystem dynamics, and yields the information critical to the development of an ecosystem-based management for the lobster fishery in the GOM. More studies are needed, however, to reduce the uncertainty in input data, to explore the function of vulnerability coefficient, and to evaluate the performance of the model.

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