Ecosystem modeling in the Gulf of Mexico: current status and future needs to address ecosystem-based fisheries management and restoration activities

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Abstract

Many ecosystem-based fisheries management (EBFM) measures and restoration projects have been implemented to address the stressors that have negatively affected the United States (U.S.) Gulf of Mexico (GOM). Ecosystem simulation models are useful tools for tackling EBFM and restoration questions. Here, we review the current status of ecosystem modeling efforts for the U.S. GOM and whole GOM large marine ecosystem and identify future needs to address EBFM and restoration in these regions. Existing ecosystem models of the GOM are diverse, ranging from simple conceptual and qualitative models to biogeochemical-based end-to-end models and coupled and hybrid model platforms. Many models have focused on understanding the structure and functioning of GOM ecosystems and the impacts of EBFM measures such as bycatch reduction strategies and marine protected areas. By contrast, a small number of ecosystem models have been used specifically to address the other EBFM issues of the GOM and to assess restoration efforts (e.g., marsh restoration). The demands for EBFM and state and gulf-wide restoration activities will both be increasing in the GOM. Therefore, there is a critical need to better employ and enhance existing ecosystem models of the GOM, and to develop new ecosystem models, to more comprehensively address the different EBFM and restoration needs in the region. We provide suggestions to facilitate this endeavor. The development of consistent libraries of ecosystem models and gap analyses such as ours will help fisheries scientists to effectively tackle specific resource management questions in the different marine regions of the world.

Keywords: ecosystem modeling, ecosystem-based fisheries management, restoration, gap analysis, Gulf of Mexico

Introduction

The Gulf of Mexico (GOM) large marine ecosystem (LME) is home to a diversity of natural habitats, including wetlands, marshes, coral and oyster reef habitats, and artificial habitats, such as oil platforms and artificial reefs (Fig. 1). The GOM provides many ecosystem services, including seafood, oil and gas, recreational opportunities, and infrastructure protection (Gulf Coast Ecosystem Restoration Task Force 2011; Karnauskas et al. 2013; National Research Council 2014). Many of these services are inter-connected with the habitats and associated biota. Annual fisheries landings in the U.S. GOM amount to 589,700 metric tons (Karnauskas et al. 2013) and represent about one-third of the total U.S. seafood harvest (Gulf Coast Ecosystem Restoration Task Force 2011). Primary fisheries in the U.S. GOM include shrimp, oyster (*Crassostrea virginica*), blue crab (*Callinectes sapidus*), menhaden (*Brevoortia* spp.), red snapper (*Lutjanus campechanus*), gag grouper (*Mycteroperca microlepis)*, red grouper (*Epinephelus morio*) and mackerel (*Scomberomorus* spp.) fisheries (Karnauskas et al. 2013). The shrimp trawl and menhaden purse seine fisheries generate, respectively, the highest revenues and highest landings (by weight) in the U.S. GOM (Vaughan et al. 2007; Karp et al. 2011). Fisheries in the U.S. GOM Exclusive Economic Zone (EEZ) are managed under the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) that aims to prevent overfishing (see Glossary), rebuild overfished stocks, maximize long-term fisheries benefits, and ensure safety and sustainability in seafood (MSFCMA 2007). The GOM is also home to over 90% of the U.S. offshore oil and gas production and 23% of U.S. crude oil production (Gulf Coast Ecosystem Restoration Task Force 2011; Karnauskas et al. 2013). Finally, tourism in the U.S. GOM supports over 800,000 jobs (Gulf Coast Ecosystem Restoration Task Force 2011) and brings $20 billion to the U.S. economy per year (Karnauskas et al. 2013).

Traditionally, fisheries management has been conducted on a single-species basis in the GOM and throughout the world (Christensen and Walters 2011; Fogarty 2014; Hyder et al. 2015). However, the strong interconnectedness of resources, processes and stressors in the GOM calls for the added consideration of broader fisheries impacts on ecosystem components, motivating an ecosystem approach to fisheries management (EAFM) and a move toward ecosystem-based fisheries management (EBFM) (FAO 2008). Patrick and Link (2015) define EAFM as the "inclusion of ecosystem factors into a (typically single species) stock focus to enhance our understanding of fishery dynamics and to better guide stock-focused management decisions" and EBFM as "recognizing the combined physical, biological, economic, and social tradeoffs for managing the fisheries sector as an integrated system, specifically addressing competing objectives and cumulative impacts to optimize the yields of all fisheries in an ecosystem." EAFM provides additional tools for fisheries managers to assess and manage marine populations that are strongly influenced by species interactions and abiotic environmental factors, while EBFM is necessary to manage the collateral impacts of fishing, evaluate interactions between fisheries, and ensure the sustainability of the marine ecosystem as a whole. EAFM and the broader EBFM efforts in the U.S. GOM include the implementation of marine protected areas (MPAs), measures to reduce bycatch, culling programs, and the integration of ecosystem considerations into single-species stock assessments (Online Resource 1).

Due to the substantial dependence of humans on the resources of the GOM, and the continuing population growth and coastal development, the GOM is also under strong and increasing anthropogenic pressures other than fishing (Karnauskas et al. 2013). In 2010, the *Deepwater Horizon* (DWH) blowout in the GOM resulted in the largest oil spill in U.S. history (Bjorndal et al. 2011; Roberts 2012). Negative impacts on the environment and GOM coastal communities included an economic blow to the fishing industry due to fishery closures and consumer concern about seafood safety following the oil spill (Upton 2011). The detrimental impacts of the DWH oil spill have required the U.S. Government to call for long-term plans to mitigate the effects of anthropogenic pressures and other stressors that have negatively affected the GOM (Online Resource 2), and to bring the region back to healthy environmental and economic conditions (Gulf Coast Ecosystem Restoration Task Force 2011; Upton 2011; National Research Council 2014). Thus, over the recent years, a diversity of large research programs has been implemented in the GOM, including the Environmental Protection Agency (EPA)'s Gulf Coast Ecosystem Restoration Task Force (Gulf Coast Ecosystem Restoration Task Force 2011), the Gulf of Mexico Research Initiative (GoMRI) (Anonymous 2015), and the NOAA's RESTORE Act (Resources and Ecosystems Sustainability, Tourist Opportunities, and Revived Economies of the Gulf Coast States Act) Science Program (NOAA 2015). All these research programs complement large restoration activities that are in progress as a result of the DWH oil spill, as well as ongoing major efforts initiated prior to DWH, such as the plan put forth by the state of Louisiana for addressing land loss (Coastal Protection and Restoration Authority of Louisiana 2012). There are also action plans established by the Hypoxia Task Force to address the nutrient loading issue in the northwestern GOM (Hypoxia Task Force 2015) (Online Resource 1). The scope and level of activity related to restoration includes a wide range of actions that affect many different aspects of the GOM ecosystems and habitats and will increase dramatically over the next decades (National Academies of Sciences and Medicine 2016).

Ecosystem simulation models can be a useful tool for achieving EBFM and for aiding in the design and evaluation of restoration activities. Ecosystem models provide an understanding of the relationships between different types of drivers and pressures and resulting states in an ecosystem, as well as the implications and trade-offs of fisheries management and restoration efforts at multiple spatial and temporal scales (Plagányi 2007; Christensen and Walters 2011; Collie et al. 2016). A number of ecosystem models, such as Ecopath with Ecosim (EwE) (Walters et al. 1997; Pauly et al. 2000; Christensen and Walters 2004), OSMOSE (Shin and Cury 2001, 2004; Grüss et al. 2016c) and Atlantis (Fulton et al. 2004; Fulton et al. 2007; Fulton et al. 2011a) applications (Online Resource 3), have been developed for the GOM for either the whole LME or for its many subsystems including the continental shelf, estuaries, bays and coral reefs (see Geers (2012) for a partial review of EwE models). These models have been designed to address certain research questions and are not necessarily applicable to other questions related to EBFM and restoration in the GOM (Online Resource 1). For instance, ecosystem models designed to explore the dynamics of lower trophic level functional groups (i.e., groups of species that share similar life-history traits and ecological niches) may not appropriate for investigating the impacts of EBFM measures on higher trophic level functional groups. Therefore, there is a need to make a detailed inventory of ecosystem models of the GOM, so as to be able to better use or modify existing models or to develop new models to address specific EBFM and restoration objectives (Pikitch et al. 2004; Plagányi 2007; FAO 2008; NOAA 2015; Collie et al. 2016).

In the present paper, we review the current status of ecosystem modeling efforts in the GOM and identify future needs to address EBFM and restoration activities related to EBFM in the region. We first propose updated terminologies of ecosystem models and review the purposes, capabilities, use, and main findings of ecosystem models in the GOM. Subsequently, we discuss how existing ecosystem models of the GOM could be better employed and, eventually, enhanced to more comprehensively address EBFM and restoration needs in the region. We also discuss how ecosystem-modeling approaches not currently implemented in the GOM may provide useful insights to EBFM and restoration programs and projects. For practical reasons, the present paper focuses on the U.S. GOM, including the GOM side of the Florida Keys, and on the GOM LME as a whole.

Ecosystem modeling efforts in the Gulf of Mexico: current status

Ecosystem models are capable of delivering insights into the potential effects of fishing and other stressors and into the effects of management measures under an ecosystem perspective (Plagányi et al. 2007; Fulton 2010). Ecosystem models complement single-species modeling approaches by taking into consideration the impacts that trophic interactions and abiotic environmental influences on species dynamics may have on the effects of stressors and management measures (Hollowed et al. 2000a; Latour et al. 2003). Ecosystem models vary in terms of structure, assumptions and complexity and are used to address a variety of ecological situations and ecosystem management objectives (Plagányi et al. 2007; Fulton 2010; Shin et al. 2010; Espinoza-Tenorio et al. 2012).

Terminologies for classifying ecosystem models

Terminology based on model structure

An extensive terminology of ecosystem models based on their structure was provided by Plagányi (2007). We propose an updated version of this terminology (Table 1) based on Plagányi (2007), Fulton (2010) and Espinoza-Tenorio et al. (2012):

(1) Conceptual and qualitative models, which represent the ecosystem of interest qualitatively using simple depictions that show the ecosystem's components or connections; such

models are often the first step towards the development of quantitative ecosystem models (Dambacher et al. 2003; Marzloff et al. 2011; Kelble et al. 2013).

(2) Extensions of single-species models, which simply add a few additional features such as the influence of the abiotic environment to existing models. These extensions often remain single-species analyses with the effect of the environment or other factors incorporated as an effect on the vital rates of the focal species (Hollowed et al. 2000b; Clark et al. 2001).

(3) Dynamic multispecies models, which represent a limited number of species or functional groups that are most likely to exhibit large interactions with the species of focal interest (Livingston and Jurado-Molina 2000; Kinzey and Punt 2009; Begley 2012; Plaganyi et al. 2014).

(4) Aggregated (or whole ecosystem) models, which attempt to consider all trophic levels to explore energy flows among ecosystem components; these models typically represent a large number of species or functional groups (Odum 1983; Pauly et al. 2000; Bartell 2003; Christensen and Walters 2004; Fulford et al. 2010; Steenbeek et al. 2016).

(5) Biogeochemical-based end-to-end models, which consider both bottom-up and top-down interactions via the representation of a very large number of nutrient components, planktonic organisms, fish, and other top predators (Fulton et al. 2004; Fulton et al. 2007; Fulton et al. 2011a; Kishi et al. 2011; Rose et al. 2015).

(6) Coupled and hybrid model platforms, which also consider both bottom-up and top-down interactions through the coupling or combination of different types of model platforms (Gray et al. 2006; Houle et al. 2012; Travers-Trolet et al. 2014; Grüss et al. 2016c).

Terminology based on the model major purpose

Ecosystem models can also be categorized as: (1) conceptual models whose goal is to develop an understanding of processes in the study ecosystem; (2) strategic models, or models that deliver strategic advice to resource management, i.e., advice that relates to broad management issues such as ecosystem services and biodiversity objectives; or (3) tactical models, or models that provide short-term advice that directly leads to management actions such as setting an annual quota (FAO 2008; Plaganyi et al. 2014; Collie et al. 2016).

Overview of the current status of ecosystem modeling in the Gulf of Mexico

We conducted a search on the *ISI Web of Science*^{TM} and *Google* to identify the ecosystem models of the GOM. We supplemented this search through email exchanges with ecosystem modelers of the GOM. A total of 45 ecosystem models, which differ in their purposes, study area, structure, assumptions and components, were identified (Table 2 and Online Resource 4).

Strategic ecosystem models, which address broad management issues (e.g., the ecosystem impacts of rebuilding policies), were the most common type in the GOM (82%). Only 16% of the ecosystem models of the GOM provided tactical advice for short-term management objectives, and these were extensions of single-species assessment models (ESAMs). Only one conceptual model for the GOM has been published, which was the ecosystem-based management (EBM)-DPSER model designed by Kelble et al. (2013). The integration of ecosystem considerations into stock assessments for EBFM was the issue most addressed by ecosystem models of the GOM (16%), followed by fishing pressures suited for a sustainable marine ecosystem (11%), reduction of bycatch (11%), MPAs (9%), and changes to water flow (9%). Single examples of models addressed EBFM/restoration issues including mitigation of the impacts of invasive species, management strategy evaluation (MSE) integrating ecosystem considerations, and management of nutrient loads.

Ecosystem models were generally developed for ecological regions within a specific U.S. state, with only 9% covering the entire GOM LME (Fig. 2a). Florida ecosystems have received the most attention (38%), followed by Louisiana (12%), Texas (2%), Alabama (2%), and Mississippi (0%).

The majority of ecosystem models of the GOM have, at least in part, included a trophodynamic structure (61%; Fig. 2b). A single ecosystem model ("Atlantis-GOM"; Ainsworth et al., 2015) used a trophodynamic approach to simulate the dynamics of invertebrate functional groups and an age-structured approach for the vertebrate functional groups.

Aggregated (whole ecosystem) models, such as EwE applications, dominated the ecosystem models of the GOM (58%), followed by extensions of single-species models (22%), dynamic multispecies models (7%), coupled and hybrid model platforms (7%), and conceptual and qualitative models (4%) (Fig. 2c). A single biogeochemical-based end-to-end model (Atlantis-GOM) was identified.

Nearly all of the ecosystem models represented pelagic-demersal (91%) and benthic (82%) functional groups, and included fish functional groups (91%). More than 50% of ecosystem models explicitly considered invertebrates, phytoplankton groups, marine plants and detritus, whereas marine mammals, sea turtles and seabirds were included in less than 50% of the models (Fig. 2d). Among the key species or species groups represented, shrimps were explicitly considered (i.e., as an individual functional group) in the majority of the models (73%), while other key species such as mackerels, blue crab, red snapper, menhaden, gag grouper, red grouper and jellyfish were explicitly considered in more than 20% of the models. Oysters were explicitly considered in three models, while lionfish (*Pterois* spp.) was explicitly considered only in the

EwE model of Chagaris et al. (2015a). The influence of the abiotic environment on marine organisms was frequently represented, to various degrees, in the models of the GOM (71%), whereas fishing fleet dynamics (fishers' movement) were only simulated in 24% of the models.

Conceptual and qualitative models

Two ecosystem models of the GOM belonged to the category of conceptual and qualitative models: (1) the EBM-DPSER model, a conceptual DPSIR (driver-pressure-state-impact-response) model of the Florida Keys and Dry Tortugas ecosystem that integrated ecosystem services instead of impacts (Kelble et al. 2013); and (2) a loop analysis, which used a qualitative representation of the Galveston Bay (Texas) food web to evaluate the ecosystem's response to sustainable fishing of blue crab and the management of nutrient loads (Carey et al. 2014) (Table 2 and Online Resource 4). In actuality, a number of other conceptual and qualitative models have been developed in the GOM, but they were either part of the quantitative modeling process or reported in the gray literature (Swannack et al. 2012; Rose and Sable 2013).

Conceptual and qualitative models are useful operational tools for guiding any EBFM effort or restoration activity in that they integrate knowledge of ecosystem components while focusing management attention upon the most important aspects of the ecosystem under consideration. Conceptual and qualitative models are also easily communicated and their presentation is familiar to many model users, resource managers, and other stakeholders. However, their potential is limited to providing qualitative or semi-quantitative insights, which are not always sufficient, into the potential impacts of management measures.

Extensions of single-species models

Among the ten extensions of single-species models identified that aim to incorporate ecosystem considerations, such as natural mortality due to red tides, seven were extensions of single species assessment models or ESAMs (Hart 2012; GDAR 2013; ICCAT 2013; Muller and Taylor 2013; SEDAR 2013, 2014, 2015), and three were extensions of single-species individual-based models or ESIBMs (Butler IV 2003; Roth et al. 2008; Creekmore 2011) (Table 2 and Online Resource 4).

The purpose of ESAMs is to improve the accuracy of stock assessment models to better guide single-species fisheries management. By integrating ecosystem considerations, ESAMs can improve the fits of stock assessment models to time series data, provide more accurate estimates of stock status relative to reference points, and provide more realistic projections of stock dynamics under proposed management tactics (SEDAR 2013, 2014, 2015). However, there remains little formal consideration of when and how environmental factors should be considered. The incorporation of ecosystem processes in stock assessments is generally viewed with caution throughout the U.S. (Patrick and Link 2015), largely due to concerns about data limitations (Christensen and Walters 2011; Patrick and Link 2015). Also, observed correlations between environmental indices and processes (e.g., recruitment) may be due to chance (see, e.g., Myers (1998); Hare et al. (2015)), and the use of model outputs as inputs for subsequent models may introduce unknown biases (Brooks and Deroba 2015).

ESIBMs have the ability to integrate data across hierarchical scales of organization and can yield ecological insights useful to single-species stock assessments. ESIBMs also have the potential to yield insights useful to EBFM and restoration activities, yet none of the ESIBMs of the GOM (Butler IV 2003; Roth et al. 2008; Creekmore 2011) were developed to specifically address EBFM or restoration questions.

Dynamic multispecies models

The only dynamic multispecies models in the GOM were: (1) a spatially explicit, dynamic, multispecies model, which was developed to investigate the effects of no-take MPAs in the Florida Keys (Ault et al. 2005); and (2) the MICEs (Models of Intermediate Complexity for Ecosystem assessment) developed by Gaff et al. (2000) and Sable et al. (unpublished data) (Table 2 and Online Resource 4). The MICE of Gaff et al. (2000), which is called ALFISH, is a spatially-explicit model aiming to evaluate the impacts of alternative water regulation scenarios in the Florida Everglades under the Central and South Florida Comprehensive Project Review Study. The MICE of Sable et al. (unpublished data) is a spatially-explicit model of a tidal marsh community, which was designed to investigate how enhanced marsh degradation imposed on individuals can be scaled to population and community responses, but which has not been employed to assess the impacts of EBFM or proposed restoration measures.

MICEs focus on a few species or functional groups that are most likely to have significant interactions with the species of focal interest (Plaganyi et al. 2014) (Online Resource 3). MICEs integrate the best characteristics of single-species models of relative simplicity and the ability to use standard statistical methods for estimating model parameters, but also consider broader ecosystem considerations that depend on the management objectives being addressed. Their complexity is intermediate between that of single-species models and that of end-to-end models in terms of the number of components and processes explicitly considered (Plaganyi et al. 2014). The main advantages of existing MICEs within the GOM is that they offer a sophisticated representation of abiotic environmental influences on marine organisms, which allows a realistic simulation of water levels and water regulation in the case of Gaff et al. (2000) and marsh degradation in the case of Sable et al. (unpublished data).

Aggregated (whole ecosystem) models

Of the 26 aggregated (whole ecosystem) models identified for the GOM, three were energy flow models, 22 used the EwE modeling platform (four of them were Ecopath models, 11 were EwE models, and seven were Ecospace models), and one used the CASM (Comprehensive Aquatic System Model) approach (Table 2 and Online Resources 3 and 4).

Energy flow models were the first ecosystem models developed for the GOM and were used to address the issue of bycatch in shrimp fisheries (Browder 1982; Sheridan et al. 1984; Martinez et al. 1996). These models initiated energy flow modeling in the GOM. However, they were based on limited empirical data (i.e., biomasses and diets) and are thus difficult to validate.

The four Ecopath models of the GOM (Browder 1993; Christian and Luczkovich 1999; Robinson et al. 2015; Sagarese et al. 2017) focused on evaluating the structure of ecosystems of the region and were not used to explore the impacts of EBFM or restoration measures (Table 2 and Online Resource 4).

EwE models of the GOM include ecosystem models for the West Florida Shelf (WFS) developed by Chagaris and Mahmoudi (2013), Chagaris et al. (2015a, 2015b), Gray (2014) and Sagarese et al. (2015). Chagaris and Mahmoudi (2013)'s EwE model focused on managed reef fish. The purpose of this model was to estimate the natural mortality rate of young-of-the-year, juveniles and adults of gag grouper from 1950 to 2009, so as to support gag grouper stock assessment. Chagaris et al. (2015b) updated the model of Chagaris and Mahmoudi (2013) to simulate, among other things, the ecosystem impacts of rebuilding gag grouper or reducing longline fishing effort, so as to support EBFM on the WFS. Chagaris et al. (2015a)'s EwE model buillt upon the model of Chagaris et al. (2015b) and was created to explore the impacts of measures to mitigate lionfish invasion in the WFS ecosystem over a 30 year-period. Finally, the purpose of the EwE models of Gray (2014) and Sagarese et al. (2015) was to provide an index of natural mortality due to red tides for inclusion in the stock assessment for gag grouper and red grouper, respectively.

Other EwE models of the GOM include the models of Carlson (2007), Walters et al. (2008) and de Mutsert et al. (2012). The EwE model of Carlson (2007) focused on the Apalachicola Bay, Florida and was designed to evaluate fishing and MPA scenarios. Walters et al. (2008) developed an EwE model for the whole U.S. GOM and, among other things, explored the consequences of a reduction of bycatch mortalities by the shrimp fishery and evaluated the implications of changes in the fishing mortality rate of long-lived fish species, forage fish species or menhaden. Finally, by contrast with the other EwE models of the GOM, the model of de Mutsert et al. (2012) focused on a restoration issue; this model was designed to evaluate changes in the fish and shellfish community caused by changes in salinity due to freshwater diversion (to restore marsh) in the Breton Sound estuary, Louisiana.

Among the seven Ecospace models in the GOM, three were employed to address EBFM or restoration issues: (1) the model of Walters et al. (2010) for the U.S. GOM; (2) the model of Chagaris (2013) for the WFS; and (3) the model of de Mutsert et al. (2015) for the Louisiana coastal zone. Walters et al. (2010)'s Ecospace model was constructed from Walters et al. (2008)'s EwE model, and was used to explore the effects of a reduction of bycatch mortalities by the shrimp fishery and of the implementation of MPAs forbidding shrimp trawling. The Ecospace model of Chagaris (2013) was constructed from the model of Chagaris et al. (2015b) and was used to examine different MPA scenarios. Finally, the Ecospace model of de Mutsert et al. (2015) was developed to inform the Louisiana Coastal Protection and Restoration Authority about the consequences of changes to water flow in the Louisiana coastal zone. An important feature of de Mutsert et al. (2015)'s model is that it utilized Ecospace's habitat capacity model to simulate local changes in percent wetland, and its effect on biota, over time.

The EwE modeling approach benefits from a graphical user interface and from a dynamic user community (Coll et al. 2015; Colleter et al. 2015). Ecopath, EwE and Ecospace models have been developed for the GOM ecosystems addressing a range of stressors, natural processes and management objectives (Table 2). However, these models also have their limitations. These models are strongly driven by the inputted diet matrices, which have, in general, been developed using limited diet data with sparse spatial and temporal coverage. Sagarese et al. (2017) constructed a diet matrix for their Ecopath model based on a recently developed probabilistic approach using maximum likelihood estimation to quantify trophic interactions within the GOM (Sagarese et al. 2016a; Tarnecki et al. 2016). Specification of the diet matrix remains one of the major uncertainties in configuring an EwE model. The issue of the Ecopath diet matrix is exemplified by the outcomes of the bycatch reduction scenarios simulated with the EwE model of Walters et al. (2008) and the Ecospace model of Walters et al. (2010) (Table 2). Even relatively small changes in diet fractions in these model led to the depletion of major prey groups such as juvenile fishes; this is concerning because the diet patterns assumed in Ecopath often rely on data inadequate for estimation (Walters et al. 2010). EwE models should be evaluated by means of appropriate diagnostics. For example, the Ecopath model of Sagarese et al. (2017) was evaluated using the PREBAL diagnostics of (Link 2010) as well as diagnostics from Darwall et al. (2010). Another criticism of the EwE models of the GOM is that the calibration to multiple time series data has been too limited (Althauser 2003; Okey et al. 2004; Vidal and Pauly 2004; Carlson 2007; de Mutsert et al. 2012).

CASM is a trophodynamic modeling approach similar to Ecospace (Bartell 2003; Fulford et al. 2010). Some of the major differences between CASM and Ecospace are that the temporal dynamics of the populations represented in CASM are simulated using a bioenergetics-based process-oriented approach, and that fish movement patterns are not represented in CASM. Because it does not represent fish movement patterns, CASM is a "pseudo spatial" modeling platform and, therefore, the dynamics of its individual spatial units are analyzed in isolation as separate small point locations spread out within the model domain. CASM applications can be forced by fields of abiotic environmental parameters (e.g., surface light intensity, water temperature) and can be coupled to a landscape model, e.g., for evaluating the impacts of nutrient loading and toxic trace elements.

Currently, only one operational version of CASM is available in the GOM (Dynamic Solutions 2016). This implementation of CASM for the Mississippi River Delta was constructed for assessing the impacts of freshwater and sediment diversion on economically and ecologically important fish and invertebrate species to inform the Louisiana Coastal Protection and Restoration Authority.

CASM is a relatively sophisticated modeling approach that is suited to the evaluation of the effects of freshwater and sediment diversion projects in the GOM and similar restoration issues. The main limitation of this modeling approach is that it does not consider fishing and, therefore, cannot contribute to fisheries management in the face of significant changes in salinity due to diversion projects. Moreover, CASM does not simulate animal movement because only a 0-dimensional (point) version is presently available for the GOM and so it is limited to questions that can be feasibly addressed with a well-mixed assumption about the organisms.

Biogeochemical-based end-to-end models

The Atlantis-GOM model (Ainsworth et al. 2015) was the only biogeochemical-based end-to-end model in the GOM (Table 2 and Online Resources 3 and 4). Atlantis-GOM was primarily designed to investigate the consequences of the DWH oil spill and to provide insights into the potential impacts of EBFM and restoration actions as part of NOAA's GOM Integrated Ecosystem Assessment (IEA) program (Ainsworth et al. 2015). While the model has the potential to tackle many EBFM and restoration issues, none of these applications is yet published. Also, additional work remains on Atlantis-GOM, namely increased data collection (e.g., biomass estimates, spatial distributions, diet composition) and better calibration. During the calibration process of Atlantis-GOM to date, some functional groups experienced large decreases under a "no fishing" scenario, suggesting a problem caused by over-predation, reduced productivity, or both, whereas some functional groups collapsed in the presence of fishing (Ainsworth et al. 2015).

Coupled and hybrid model platforms

Coupled and hybrid model platforms identified for the GOM are all variants of an OSMOSE model of the WFS called "OSMOSE-WFS", which has been developed within NOAA's GOM IEA program (Table 2 and Online Resources 3 and 4) (Grüss et al. 2015; Grüss et al. 2016b; Grüss et al. 2016c). The two first versions of OSMOSE-WFS were designed to estimate size- and age-specific natural mortality rates for gag and red grouper, for use in single-species stock assessments, and to evaluate the ecosystem impacts of fishing scenarios for red grouper to provide information to the GOM Fishery Management Council (Grüss et al. 2015; Grüss et al. 2016c). The third and last version of OSMOSE-WFS was two-way coupled to a management procedure within an MSE framework. Analyses were then performed to evaluate harvest quota strategies for red grouper in the face of episodic events of natural mortality (due to, e.g., red tides or oil spill) (Grüss et al. 2016b). All versions of the OSMOSE-WFS model were validated using the pattern-oriented modeling approach of Grimm et al. (2005) and employed a specific algorithm ensuring that the fishing mortality rates provided in the model output were identical to fishing mortality rates provided to the model.

Future needs to address ecosystem-based fisheries management and restoration activities

A diversity of ecosystem models has been developed for the U.S. GOM and GOM LME between 1983 and the present, and these models have been used to tackle a number of EBFM and ecosystem restoration issues. Based on our review, we can identify several improvements that would further the EBFM and restoration questions that can be addressed by these models. More ecosystem models have been designed for Florida than for other regions of the GOM, yet regions like the northwestern GOM are facing critical EBFM and restoration issues (e.g., marsh restoration and freshwater diversion). Also, ecosystem models of the GOM have paid less attention to restoration issues than to EBFM issues. In this section, we discuss how existing ecosystem models of the GOM could be better employed and, eventually, enhanced to more comprehensively address EBFM and restoration needs in the region. In addition, we identify additional ecosystem models recommended for development.

Conceptual and qualitative models

Conceptual and qualitative models such as those of Kelble et al. (2013) and Carey et al. (2014) are useful in illustrating and developing an understanding of the components and connections of the ecosystem of interest. Such models should ideally be used for any EBFM or restoration project of the GOM, in particular as a first step towards the development of more complex, quantitative ecosystem models (FAO 2008; Swannack et al. 2012; Hyder et al. 2015; Rose et al. 2015). For example, to address the specific questions of habitat and water quality restoration and marine mammal recovery that are central in the state of Alabama (Online Resource 1), an EBM-DPSER model or a loop analysis with the following components could be employed: "Oil activities", "Invasive species", “Fishing”, "Marsh", "Barrier island", "Oyster reef", “Seagrass”, "Marine mammal", “Fish”, "Water quality", "Storm protection", "Marsh restoration", "Barrier island restoration", "Oyster reef restoration", “Seagrass restoration”, "Marine mammal recovery program", "Water quality restoration", and “Fisheries management”. Conceptual models have been used with other major ecosystem restoration efforts (e.g., DiGennaro et al., 2012).

Quantitative ecosystem models

To best use and enhance quantitative ecosystem models in the GOM, it is recommended that the following approach be used for each unique topic and set of goals: (1) identify the critical questions and/or management goals that need to be answered and addressed; (2) determine the required features that the ecosystem model should have to approach these questions/goals; (3) determine the existing ecosystem models that could be used and identify how these existing models should be enhanced; and (4) determine possible new ecosystem models to tackle the questions and goals. For a more detailed description of best practices in ecosystem modeling, the reader is referred to Rose et al. (2015). Characteristics of ecosystem models that must be considered for any particular EBFM or restoration issue include: (1) the appropriate spatial domain and spatial resolution; (2) the appropriate temporal extent and time step; (3) which ecosystem components must be included such as environmental processes, fleet dynamics, and species or life-stages of species that must be modeled as separate model components; (4) whether data are available to parameterize modeled processes accurately; and (4) how the model can be validated and tested. In many cases, important EBFM and restoration questions could be addressed using existing models, or using existing models with a finer spatial or temporal scale, better data inputs, including additional functional groups, life stages, or processes.

Integration of ecosystem considerations into stock assessments

ESAMs have the potential to improve the accuracy of stock assessment outcomes for many species of the U.S. GOM and should, therefore, see more widespread use in the GOM in the future. However, ESAMs require careful consideration as to whether the added complexity from environmental linkages is justified. In general, including an environmental driver because of a hypothesized mechanism for the impact is preferable to testing many variables looking for correlations (Punt et al. 2014). Further, it is necessary to also conduct simulation analyses to determine: (1) for which species of the U.S. GOM ecosystem considerations are necessary (i.e., how are ecosystem factors already captured in modeled processes?); (2) how best to parameterize ecosystem considerations; and (3) the cost of a false positive relationship and including an ecosystem covariate in an assessment model when no such relationship exist in reality (e.g., Hare et al. 2015). Ecosystem models more complex than ESAMs have the potential to provide ecosystem parameters to ESAMs if they represent species and processes that can yield outputs constituting relevant inputs to ESAMs.

Management strategy evaluation integrating ecosystem considerations

NOAA Fisheries recently laid out a Gulf of Mexico Regional Action Plan (GMRAP) in accordance with NOAA Fisheries Climate Science Strategy (Link et al. 2015), which calls, among other things, for MSE studies evaluating the impacts of harvest control rules implemented for individual species under climate change scenarios. The ecosystem models used for conducting these kinds of MSE studies should simulate the population dynamics of the species of interest over multiple years, and represent (either explicitly or implicitly) the influence of climatic changes on the vital rates of the species of interest. If an MSE is needed to evaluate the impacts of harvest control rules for a specific species under the assumption that climatic changes affect the survival of that species, then it would be relevant to employ an ESAM representing the effects of climatic changes on natural mortality to conduct that MSE. If it is assumed that climate change affects vital rates other than survival rates (i.e., growth, reproduction or movement rates), then it will be appropriate to use an ecosystem model other than an ESAM (e.g., an ESIBM, a MICE or a more complex ecosystem model, depending on the requirements of the MSE study). For example, to investigate the performance of harvest control rules implemented for red grouper or gag grouper in the face of climate change, the MSE framework developed for OSMOSE-WFS and reported in Grüss et al. (2016b) could be employed, provided that new capacities are introduced into the OSMOSE modeling platform to allow abiotic environmental parameters to affect relevant vital grouper rates. The Atlantis-GOM model integrates MSE capabilities and could be enhanced to more accurately simulate climate change scenarios either using adjusted oceanographic data or output from climate models with sufficient variation to capture inter-annual variation (Ainsworth et al. 2015).

Fisheries management in a context of red tides

In addition to using ecosystem models to evaluate how red tides would affect the inputs (e.g., natural mortality rates) of single-species models, ecosystem models can also be used to examine how red tides would affect community and food web responses. The EwE model developed by Gray (2014), and later modified to include red grouper by Sagarese et al. (2015), delivered estimates of natural mortality rates due to red tide to the stock assessments of red and gag groupers. Such a model could also be used to examine food web and fisheries responses to red tide, and could be expanded into an Ecospace model to incorporate the spatio-temporal patterns of red tides.

Bycatch reduction

The ecosystem model developed by Walters et al. (2008, 2010) is appropriate for reexamining the issue of reducing bycatch in the GOM shrimp fisheries in that it models all the necessary system components including detritus from shrimp trawl bycatch. However, the diet matrix of Walters et al. (2008)'s EwE model should be improved, with additional diet data stemming from genetics and dietary studies and using probabilistic approaches such as those employed by Sagarese et al. (2016a) and Tarnecki et al. (2016) to represent more accurate trophic interactions. Size spectrum models are another potential means to reexamine the consequences of measures aiming to reduce bycatch in U.S. GOM shrimp fisheries (Houle et al. 2012). The issue of bycatch in the menhaden purse seine fishery also deserves some attention in future ecosystem modeling efforts in the GOM (Rester and Condrey 1999; Vaughan et al. 2007; Karp et al. 2011; Sagarese et al. 2016b).

Marine protected areas

The GOM Fishery Management Council frequently requests investigations of the potential impacts of MPAs, particularly of whether MPAs can rebuild stocks without reducing fisheries yields and whether they can have some indirect negative effects on fish and fisheries. An ecosystem model suited for addressing these issues should: (1) consider spatial heterogeneity in habitat quality; (2) have the potential to simulate the movements of marine organisms (to represent "spillover" from MPAs) and spatial age structure; and (3) represent fishing fleet dynamics to be able to simulate reasonable spatial patterns of fishing effort following the implementation of MPAs. Ecospace has the potential to represent spatial age structure for multi-stanza populations using an individual-based modeling approach, and fishing fleet dynamics using a simple "gravity model" (Christensen et al. 2008; Walters et al. 2010). Suprenand et al. (2015) added an Ecospace component to the Walters et al. (2010) model, which has a higher spatial resolution and better characterizes the habitats of the U.S GOM (Table 2). The spatio-temporal data framework and the habitat capacity model could be introduced in Suprenand et al. (2015)'s Ecospace model, so as to improve the representation of spatio-temporal changes in habitat attributes in the model. Then, the enhanced Suprenand et al. (2015)'s Ecospace model could be employed to explore the direct and indirect impacts of existing and new MPAs for fish stocks and fisheries yields in the U.S. GOM.

Mitigation of the impacts of invasive species

Only one ecosystem model, Chagaris et al. (2015a)'s EwE model for the WFS, evaluated the potential impacts of actions to mitigate lionfish invasion in the GOM. An Ecospace model exploring the effects of measures for mitigating lionfish invasion is under development for the north-central GOM (David Chagaris, University of Florida, personal communication). However additional ecosystem models that simulate spatial overlap between predators and prey, and can represent the pressure exerted on the lionfish populations by the sponsored derbies and culling programs are needed in many other regions of the GOM impacted by the invasion (e.g., the western GOM, the Florida Keys). The invasion of Australian spotted jellyfish (*Phylloriza punctate*) is another important issue in the north-central GOM (Online Resource 2; Sheehy and Vik, 2010; Robinson et al. 2015).

Mitigation of oil spill effects

The DWH oil spill has been shown to have affected the vital rates of the different life stages of marine organisms of the GOM, including the survival of fish larvae (Goodbody-Gringley et al. 2013). Therefore, ecosystem models addressing the issue of the mitigation of oil spill effects should ideally simulate the full life cycle of marine organisms. The Atlantis-GOM model was primarily developed to assess the consequences of the DWH oil spill (Ainsworth et al. 2015). Recent studies establishing relationships between exposure to oil and larval recruitment, natural mortality and growth were conducted specifically to enhance the Atlantis-GOM model (Dornberger et al. 2016). After these relationships and an improved diet matrix (Tarnecki et al. 2016) have been fed into Atlantis-GOM and the model has been recalibrated, it will be possible to use Atlantis-GOM to analyze the impacts of efforts to mitigate oil spill effects in the GOM LME.

Habitat restoration

Ecosystem models guiding habitat restoration efforts necessarily need to be dynamic and spatial and must have the capacity to simulate changes in the structure and surface area of the physical habitat through time. The currency of these models (e.g., age or size-structured for some species) is dependent upon the life stages using the habitat of interest. For instance, marsh habitats serve as nursery for many fish and shellfish species, such as blue crab and brown shrimp (*Farfantepenaeus duorarum*) (Minello et al. 2012); thus, ecosystem models aiming to explore the impacts of marsh restoration and representing, say, blue crab, should distinguish between the juvenile and adult stages of the species. The processes represented (i.e., survival, growth, reproduction, and movement) depend on how changes in the physical habitat are assumed to influence the ecology of the species or functional groups represented in the ecosystem model.

Many existing ecosystem models have the capacity to evaluate the consequences of habitat restoration efforts in different GOM ecosystems or will have this capacity once enhanced (Althauser 2003; Vidal and Pauly 2004; Roth et al. 2008; de Mutsert et al. 2015; Lewis et al. 2016). For instance, the spatially-explicit MICE of Sable et al. (unpublished data) for the northern GOM represents habitat (channel, creek, marsh edge, marsh interior or pond) and simulates hourly variations in water depth in each habitat cell based on the elevation of the habitat cells which is related to the distance from marsh edge. In this model, the mortality for juveniles and adults of grass shrimp (*Palaemonetes pugio*) and blue crab is multiplied by habitat-specific multipliers to reflect added predation refuge in the vegetated habitats. Thus, the MICE of Sable et al. (unpublished data) is available for assessing the effects of the restoration of marshes on grass shrimp and blue crab production in the northern GOM.

The Ecospace model for Barataria Bay, Louisiana by Lewis et al. (2016) employs the methodology presented in de Mutsert et al. (2015), which uses Ecospace's habitat capacity model to simulate changes in the physical habitat through time. Lewis et al. (2016)'s model was designed to ascertain whether a given relationship between marsh edge and effective search rate could precisely hindcast the historical biomasses of functional groups of Barataria Bay (Table 2). This model could be utilized to guide marsh restoration activities in Barataria Bay. Althauser (2003)'s EwE model, which was developed to evaluate how the Weeks Bay (Alabama) food web may respond to different river flow scenarios, could be turned into an Ecospace model and applied to other relatively small estuaries to simulate the consequences of seagrass, oyster reef and marsh habitats through time, so as to support habitat restoration activities in Alabama (Online Resource 1). Another relevant new model for guiding habitat restoration in GOM ecosystems would be an Ecospace model for the Texas coastal zone, which would use the methodology reported in de Mutsert et al. (2015) to provide insights into the potential consequences of marsh and oyster reef restoration in Texas (Online Resource 1).

Assessing the effects of habitat restoration activities at the scale of the entire northern GOM could start with the InVitro modeling approach (Gray et al. 2006). InVitro is a highly sophisticated three-dimensional, dynamic, individual-based modeling approach, whose components are all 'agents"; these agents are numerous and include, among others, fish and crustaceans, sea turtles, benthic communities, seagrass meadows, mangroves, fisheries, and "catastrophic agents" (such as storms/cyclones) (Gray et al. 2006) (Online Resource 3). InVitro considers flora (e.g., mangrove forests, seagrass meadows) in the form of "polyorganism agents", which are two- or three-dimensional patches represented via polygons. Therefore, an InVitro model the northern GOM could simulate the impacts of habitat restoration in the region by altering the attribute values of existing polygons of polyorganism agents and by adding new polygons to polyorganism agents.

Artificial reefs

The GOM Fishery Management Council also requested studies assessing the effects of artificial reefs, especially their potential to improve fisheries yields without substantially decreasing the biomasses of some marine species. Ideally, an ecosystem model addressing these issues should represent fishing fleet dynamics to be able to simulate how fishers reallocate their fishing effort as new artificial reefs are created and fish re-distribute themselves. The beginnings of such a model is provided by Campbell et al. (2011) who simulated individuals of five fish species as they moved among a two-dimensional spatial grid of different arrangements of open and reef cells; feeding opportunities and predator protection were enhanced when individuals were in reef-designated cells.

Nutrient loading/hypoxia mitigation

During summer, the nutrients brought to the GOM by the Mississippi and Atchafalaya Rivers results in severe hypoxic conditions in Louisiana and Texas, which can have impacts on fish and shellfish (Rabalais et al. 2002; Hypoxia Task Force 2015). To guide efforts to mitigate nutrient loading/hypoxia in the northwestern GOM, spatially-explicit ecosystem models with a fine temporal resolution (i.e., with a monthly or smaller time step) should be employed, with the ability to simulate the impacts of varying dissolved oxygen levels on the vital rates of juveniles and adults of species or functional groups. The Ecospace model of de Mutsert et al. (2016) for the Louisiana coastal zone can separate the negative impact of nutrient loading on dissolved oxygen concentrations and their positive impact of primary production, to ultimately assess the net effects of hypoxia on the biomass and catches of functional groups in the Louisiana coastal zone and shelf (Table 2). It would be interesting to compare the results of de Mutsert et al. (2016) with the individual-based model of Atlantic croaker (*Micropogonias undulatus*) population dynamics in response to hypoxia by Creekmore (2011) to determine how food web interactions (Ecospace versus population model) affect the croaker population response to reduced nutrient loadings and improved hypoxia.

Freshwater diversion

Ecosystem model simulations are needed to evaluate the impacts of freshwater diversion for restoring natural hydrologic flows in Louisiana (Coastal Protection and Restoration Authority of Louisiana 2012). Dynamic spatial ecosystem models with a fine temporal resolution (e.g., with a daily or monthly time step) are preferred to be able to analyze the effects of freshwater diversion under different gradients of salinity just after, during, and post releases. These models should be age-, size- or stage-structured to capture the differing effects of changes in salinity on the vital rates of juveniles of some fish and shellfish species that inhabit estuarine systems and their adults that occur in marine habitats. A version of CASM developed by Dynamic Solutions (2016) for the Mississippi River Delta region is available but it is presently a series of separate point models spread out within the estuary, which limits how movement affects the responses. The EwE model of de Mutsert et al. (2012) has been applied to assessing diversion effects at a monthly time; this model could be expanded into an Ecospace model. Some combination of this Ecospace model and the CASM developed by Dynamic Solutions (2016) seems appropriate to allow for the explicit treatment of spatial variation and movement at fine enough spatial scales and temporal resolution.

Discussion

Some EBFM-related measures and multiple restoration projects have already been implemented in the U.S. GOM. Bycatch reduction strategies and MPAs have been employed and therefore many of the existing ecosystem models of the GOM have been developed to address issues relating to the structure and functioning of ecosystems and the impacts of bycatch reduction strategies and MPAs (Table 2). The GOM is a highly diverse ecosystem that is strongly influenced by environmental and anthropogenic factors (Fautin et al. 2010; National Ocean Service 2011), suggesting that ecosystem modeling that can account for bottom-up and top-down effects should play a large role. Our review identified a surprisingly small number of examples of ecosystem models being used specifically to address many of the EBFM issues of the GOM and to assess restoration efforts. EBFM endeavors such as ESAMs (seven ecosystem models), MSEs integrating ecosystem considerations (one ecosystem model) and simulations to evaluate the impacts of efforts to mitigate invasive species such as lionfish (one ecosystem model) have been initiated only recently. Many of the restoration projects in the GOM are also recent, particularly the large diversion and habitat restoration projects in Louisiana, which explains why a limited number of ecosystem models have been designed to specifically tackle GOM restoration issues. The demands for EBFM and state and gulf-wide restoration activities will both be increasing in the GOM (National Academies of Sciences and Medicine 2016). Therefore, there is a critical need to better employ and enhance existing ecosystem models of the GOM, and to develop new ecosystem models, to more comprehensively address the different

EBFM and restoration needs in the region.

Our review of existing ecosystem models of the GOM revealed that these models are diverse, ranging from simple conceptual and qualitative models to biogeochemical-based end-to-end models (Fig. 2). As is the case elsewhere in the world (Fulton 2010; Christensen and Walters 2011), most ecosystem models of the GOM have been used for strategic analyses, such as providing information and long-term assessments of alternative management actions. While most existing ecosystem models of the GOM account for abiotic environmental influences on functional groups, very few represent fishing fleet dynamics (i.e., fishers' movement). There has also been a focus of the ecosystem modeling for ecological regions near the eastern GOM (Florida). This is partly a result of funding opportunities and the availability of the well-studied WFS. Many of the models included representations of both pelagic-demersal and benthic species or functional groups, which reflects that GOM ecosystems are strongly influenced by the benthic component (Fautin et al. 2010). However, marine mammals, sea turtles and seabirds were often not explicitly considered in existing models.

We see an opportunity for a surge in ecosystem modeling to address the demands of EBFM in the GOM and to assist in the design and performance evaluation of the many restoration projects being implemented and planned in the region. Conceptual models and loop analysis could be employed in support of many of the EBFM and restoration issues, primarily for communication and as early step in the development of quantitative ecosystem models (FAO 2008; Swannack et al. 2012; Hyder et al. 2015; Rose et al. 2015). These conceptual models should be prepared within a common format (e.g., DiGennaro et al., 2012) to ensure effective use across modelers, resource managers, other stakeholders, ecosystems and models.

Ecosystem modeling, like all ecological modeling, must be question driven. The tendency or appearance that certain models are being used because they are available or known by the modelers must be avoided. However, the existing models provide an excellent database as a foundation for developing models into the future. Many of the questions to be addressed about EBFM and restoration overlap with the questions addressed by the earlier existing models. Our review provides a modeling inventory as ecosystem modeling for the GOM goes forward; such inventories are an important step in adapting and modifying existing models and developing new models to address the new resource management questions (Rose et al. 2015). Given the ongoing restoration efforts, and the influx of new funds for restoration from the DWH oil spill, ecosystem modeling should be used to help scale-up the ecological responses across multiple restoration projects to get to regional-level benefits (National Academies of Sciences and Medicine 2016).

When abiotic environmental factors or trophic interactions are shown to be important, ESAMs can be used within the stock assessment process, essentially to meet the recommendations of the revised MSFCMA (MSFCMA 2007) and the Marine Fisheries Stock Assessment Improvement Plan (Mace et al. 2001). More complex ecosystem models should be better employed, improved or designed in the future to address specific EBFM and restoration questions. Candidate issues include the potential impacts of marsh and oyster reef restoration, effects of artificial reefs, the control of invasive species such as the lionfish, and the assessment and scaling-up of restoration actions within and across regions (Online Resource 1).

There are several issues related to ecosystem modeling that span all modeling efforts whose careful attention would benefit the use of ecosystem modeling as it goes forward in the GOM. These issues are: (1) enhancing the calibration and validation processes of ecosystem models of the GOM and examining the behavior of these models in more detail; (2) allowing empiricists, resource managers and other stakeholders to properly understand and review the strengths and limitations of ecosystem models and to contribute to these models, which requires detailed descriptions of model assumptions; and (3) fostering capacity building and the maintenance of ecosystem models.

Firstly, the calibration of ecosystem models using empirical data needs to be improved in both quality (e.g., measurements of multiple biota) and quantity (e.g., longer time series) (FAO 2008; Steele et al. 2013; Rose et al. 2015). Also, ecosystem models that aim to support fisheries management should be calibrated to historical time series and demonstrate that they can adequately replicate historical trends, so as to lend confidence to the predictions derived from these models (Christensen and Walters 2011). Validation is another important step to complete before ecosystem models are used to answer certain questions (Steele et al. 2013; Rose et al. 2015). Diagnostics such as the PREBAL diagnostics of Link (2010) should become standard procedures for ecosystem models such as EwE, CASM and Atlantis models, while individual-based models such as OSMOSE and InVitro applications should be assessed using the pattern-oriented modeling approach of Grimm et al. (2005). Finally, the behavior of ecosystem models must be scrutinized and well understood before these models are used to explore scenarios. Sensitivity and uncertainty analyses, and the examination of alternative process formulations, are useful tools to evaluate the validity and robustness of the outcomes from ecosystem models (Lehuta et al. 2010; 2013; Collie et al. 2016; Peck et al. 2016). Model behavior should also be studied under “extreme” scenarios, such as high fishing and extreme abiotic environmental pressures. Determining that an ecosystem model can be used to examine scenarios that involve previously unobserved conditions is critical as ecosystem models receive more consideration by resource managers (Rose 2012).

Secondly, stronger interactions among ecosystem modelers, empiricists, resource managers and other stakeholders will be necessary in the GOM in the future (Espinoza-Tenorio et al. 2012; Hyder et al. 2015; Rose et al. 2015). The constitution of multidisciplinary teams involving ecosystem modelers, data collectors and statisticians in continued communication will ensure that the inputs provided to ecosystem models rely on the best available information (Rose 2012; Hyder et al. 2015). Moreover, long-term exchanges between ecosystem modelers and managers and other stakeholders are necessary for ecosystem modeling predictions to be properly considered and interpreted by managers. These exchanges have to start at the time where conceptual and qualitative models are designed and continue throughout the project, so as to make sure that the ecosystem models under development capture all the important resources, processes and stressors of the ecosystem of interest (Espinoza-Tenorio et al. 2012; Swannack et al. 2012; Rose et al. 2015). Such interactions and communication requires an investment of time but they will ensure the transparency of ecosystem modeling efforts in the GOM, caution when ecosystem models are gradually constructed, and trust between scientists and managers and other stakeholders (Rose 2012; Swannack et al. 2012). The extensive review and quality control of the Atlantis model of the U.S. West coast for use of its outputs in resource management is an example to follow in the GOM (Kaplan and Marshall 2016).

Lastly, there is a critical need for capacity building in the GOM and for viewing ecosystem modeling as an iterative and adaptive process. Conceptual models, loop analysis and ESAMs are tools that are easy to communicate and can be fairly easily used by a large number of users (especially conceptual models and loop analysis). In contrast, aggregated (whole ecosystem) models, biogeochemical-based end-to-end models and coupled and hybrid model platforms are highly complex, involve many assumptions, concepts and large computational costs, and require years of experience to be fully understood and their limitations appreciated

(Espinoza-Tenorio et al. 2012; Rose and Sable 2013; Hyder et al. 2015). In the future, more scientists of the GOM should be trained in the use of sophisticated modeling platforms such as EwE, Atlantis, InVitro and OSMOSE to foster the effective development and utilization of applications of these platforms for addressing EBFM and restoration needs as data collection improves. Such efforts would be greatly facilitated by the creation of a graphical user interface, a user guide and a web interface to query parameters for Atlantis, InVitro and OSMOSE. Beyond capacity building, maintenance of ecosystem models is also important. Our review provides a small step towards the development of an ecosystem modeling database. Similar to circulation models used in physical oceanography, ecosystem models should be viewed as iterative and adaptive tools, which need to be updated as new information and data become available (Christensen and Walters 2011; Espinoza-Tenorio et al. 2012; Swannack et al. 2012; Rose et al. 2015; Peck et al. 2016).

Several ecosystem components were underrepresented in the current ecosystem models of the GOM and should be given more consideration in future ecosystem modeling efforts. These ecosystem components include marine mammals, sea turtles and seabirds (i.e., very-high-trophic-level organisms), which can all have a very large impact on food web dynamics in the GOM (Rose et al. 2010). In addition, only a few existing ecosystem models of the GOM consider fishing fleet dynamics, while one ecosystem model represents interactions between resources and managers through the use of a MSE framework (the OSMOSE-WFS model presented in Grüss et al. (2016b)). Humans are other “very-high-trophic-level organisms” that can have a very large impact on food webs and should be given more consideration in ecosystem models of the GOM in the future (Fulton 2010; Rose et al. 2010; Fulton et al. 2011b). Existing models of fisher decision-making could be linked to ecosystem models (e.g. Saul and Die, 2016).

The improvement of the MSE framework designed for OSMOSE-WFS and the development of MSE frameworks for Ecospace and Atlantis models will allow a better integration of the human dimension via explicit representation of the fishers' dynamics and situation-specific incorporation of the stock assessment process and management decisions.

It is important to emphasize that a major pressing need to improve ecosystem modeling capabilities in the GOM is the collection of data for model development (e.g., parameterizing trophic interactions from diet studies), calibration (e.g., fitting model predictions of biomass to observed biomass trends), and validation (e.g., comparing model predictions of biomass with observed trends). Whether ecosystem models are conceptual or of higher complexity, each modeling framework integrates various sources of data and, as a result, model outputs are only as reliable and as realistic as the process formulations, input data, and spatial and temporal assumptions. Key data limitations within the GOM include estimates of absolute or relative abundance, spatial distributions, environmental and habitat associations and diet compositions. For example, results from EwE, CASM and Atlantis models are reliant upon the input diet matrix, as this information is the primary driver of ecosystem dynamics and can result in conclusions likely to be heavily challenged. We recommend that the diet matrix of the different EwE, CASM and Atlantis models of the GOM should be constructed or reconstructed with the best possible diet data stemming from genetics and/or dietary studies and using probabilistic approaches such as those employed by Sagarese et al. (2016a). The diet information contrains the degree of predation interactions and connectance within the food web that determines higher-order propreties such as system resilience (Masi et al. 2014; Sagarese et al. 2017). There are several ongoing projects in the GOM to compile existing data on diets, spatial distributions of functional groups and other key inputs to ecosystem models, and new data collections are also needed to address key uncertainties in the models (Grüss et al. 2016a; Tarnecki et al. 2016).

One important direction for future ecosystem modeling efforts in the GOM is the multi-model approach, which consists of using several ecosystem models that differ greatly in their structure and assumptions to tackle the same research questions (FAO 2008; Fulton 2010; Espinoza-Tenorio et al. 2012; Steele et al. 2013; Hyder et al. 2015). All ecosystem models have their qualities and flaws and, as a result, there is no "best" ecosystem model, even to address a particular research issue (Fulton 2010; Espinoza-Tenorio et al. 2012). Using a multi-model approach therefore deals with the issue of the conceptual, structural and predictive uncertainties of ecosystem models (Fulton 2010; Peck et al. 2016). In particular, if several ecosystem models, despite their different structure and assumptions, provide consistent and converging results, then one can have more confidence in their predictions and in supporting specific management measures (FAO 2008; Espinoza-Tenorio et al. 2012).

In the present paper, we focused on the U.S. GOM and GOM LME. The GOM is one of the largest LMEs of the world (National Ocean Service 2011), and is expecting to see increasing use of EFBM and large-scale restoration efforts. The situation is ripe for the use of ecosystem modeling. However, ecosystem modeling efforts in the Mexican and Cuban GOM were not considered in this review, for two main reasons. Firstly, we wanted to conduct a comprehensive review of ecosystem modeling efforts in the U.S. GOM and GOM LME as a whole, and use the review to outline some pressing questions that would benefit from more modeling and highlight some issues that will facilitate the use of the models in the U.S. GOM and GOM LME. Such a large endeavor deserved its own paper. Secondly, locating the published literature to identify ecosystem models of the Cuban GOM and, to a lesser extent, ecosystem models of the Mexico GOM, proved challenging. With Cuba, the political climate has long inhibited trans-boundary collaboration. Especially because the U.S. embargo with Cuba has been recently relaxed, it would be advantageous to expand the work conducted here to the Mexican and Cuban GOM. While our focus in the present paper was on the GOM, many of the models, questions, and issues apply to other systems. We hope that consistent libraries of ecosystem models will be developed through collaborative efforts between ecosystem modelers, empiricists, resource managers and other stakeholders for effectively tackling specific resource management questions in the different marine regions of the world (FAO 2008; Hyder et al. 2015).

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Glossary

Overfishing: situation where a fish population is subjected to a fishing mortality rate higher than that resulting in maximum sustainable yield (Blackhart et al. 2006)

Overfished status: situation where the spawning stock biomass of a fish population is below its spawning stock biomass at maximum sustainable yield (Blackhart et al. 2006)

Ecosystem approach to fisheries management (EAFM): EAFM provides additional tools for fisheries managers to assess and manage marine populations that are strongly influenced by species interactions and/or abiotic environmental factors. Patrick and Link (2015) define EAFM as the "inclusion of ecosystem factors into a (typically single species) stock focus to enhance our understanding of fishery dynamics and to better guide stock-focused management decisions".

Ecosystem-based fisheries management (EBFM): EBFM focuses on fisheries. Patrick and Link (2015) define EBFM as "recognizing the combined physical, biological, economic, and social tradeoffs for managing the fisheries sector as an integrated system, specifically addressing competing objectives and cumulative impacts to optimize the yields of all fisheries in an ecosystem."

Ecosystem-based management (EBM): EBM is interested in all sectors of activities, including fisheries. EBM considers the biological, physical and socio-economic complexities of managing marine ecosystems to find the management actions most appropriate to optimize ecosystem structure and functioning while maintaining the delivery of ecosystem services to humans (Patrick and Link 2015).

Integrated ecosystem assessment (IEA): IEA is an incremental approach and "formal synthesis and quantitative analysis" of the relevant natural and socioeconomic factors as they relate to management objectives. Scientific understanding aids management choices and is guided by changing ecosystem objectives (Levin et al. 2009).

Functional groups: groups of species that share similar life-history traits and ecological niches. Functional groups also usually share similar body size ranges and exploitation patterns.

Drivers: overarching stressors that cause ecosystem change and lead to a cascade of other stressors.

Pressures: stressors caused or intensified by drivers that afflict the ecosystem and change its state.

States: stressors that describe the status of the ecosystem and/or communities resulting from pressures created or intensified by drivers.

Marine protected areas (MPAs): marine zones where fishing activities and other human extractive activities are partially ("partial-take MPAs") or totally prohibited ("no-take MPAs" or "marine reserves"), year-round or seasonally, except when these activities are performed for scientific purposes.

Restoration: process of assisting the recovery of damaged, degraded, or destroyed ecosystems (Abelson et al. 2016).

Driver-Pressure-State-Impact-Response (DPSIR) model: conceptual modeling framework that depicts how human society affects a marine ecosystem through the use of cause and effect relationships among driver, pressure, state, impact and response indicators (Kelble et al. 2013)

Trophodynamic models: models that represent food webs and energy budgets, and no or very few non-trophic processes (Anonymous 2008).

Individual-based models: simulation models that describe individual agents, which represent individual organisms or groups of organisms ("super-individuals") that function as individuals as the lowest level of the modeled system (Grimm et al. 2006)

Mediation (in Ecopath with Ecosim): an interaction in which a third party organism prevents or assists a predator-prey interaction (Chagaris 2013).

Management strategy evaluation (MSE): process simulating alternative management strategies to identify those strategies that are robust to natural variation and uncertainties and that can balance conservation and exploitation objectives. MSE essentially relies on the two-way coupling of an operating model mimicking the real world with a management procedure deciding of management actions such as harvest quotas.

Calibration: the fitting of trends predicted by the model to observed trends in time series (e.g., relative or absolute biomass, fishing effort, fishing mortality, fisheries catch) to increase confidence in model results (Latour et al. 2003).

Validation: comparison of trends predicted by the model to an independent time series (e.g., relative or absolute biomass, fishing effort, fishing mortality, fisheries catch) not utilized in model calibration (Latour et al. 2003).

Tables

Table 1. Terminology of ecosystem models based on their structure. The different ecosystem modeling approaches mentioned in this table are extensively described in Online Resource 3

Category of ecosystem model	Ecosystem modeling approaches	Reference publications
(1) Conceptual and qualitative models	● Conceptual model	● Kelble et al. (2013)
	● Loop analysis	● Dambacher et al. (2003); Marzloff et al. (2011)
(2) Extensions of single-species models	● Extensions of single-species assessment models (ESAMs)	● Hollowed et al. (2000b)
	● Extensions of single-species individual-based models (ESIBMs)	● Clark et al. (2001)
(3) Dynamic multispecies models	● MSVPA (multispecies virtual population analysis) and MSFOR (multispecies forward simulation)	● Livingston and Jurado-Molina (2000); Kinzey and Punt (2009)
	● Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox)	● Begley (2012)
	● MICE (Model of Intermediate Complexity for Ecosystem assessment)	● Plaganyi et al. (2014)
(4) Aggregated (or whole ecosystem) models	● Energy flow model	● Odum (1983)
	● Ecopath with Ecosim (EwE)	● Pauly et al. (2000); Christensen and Walters (2004); Steenbeek et al. (2016)
	● CASM (Comprehensive Aquatic System Model)	● Bartell (2003); Fulford et al. (2010)
(5) Biogeochemical-based end-to-end models	● Atlantis	● Fulton et al. (2004); Fulton et al. (2007); Fulton et al. (2011a)
	● NEMURO models (NEMURO.FISH and NEMUROMS.FISH)	● Kishi et al. (2011); Rose et al. (2015)
(6) Coupled and hybrid model platforms	● OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation)	● Shin and Cury (2001, 2004); Travers-Trolet et al. (2014); Grüss et al. (2016c)
	● InVitro	● Gray et al. (2006)
	● Size spectrum model	● Houle et al. (2012)

Table 2. Main purpose of some of the ecosystem models of the United States (U.S.) Gulf of Mexico (GOM) and GOM large marine ecosystem (LME). The ecosystem models that addressed ecosystem-based fisheries management and/or restoration questions are highlighted in grey. An extensive description of each ecosystem model of the GOM and its major results is provided in Online Resource 4.

Ecosystem model	Modeling approach	Main purpose
Kelble et al. (2013)	Conceptual model	● Evaluating the response of pressures and/or states and/or ecosystem services to management scenarios in the Florida Keys and Dry Tortugas
Carey et al. (2014)	Loop analysis (qualitative model)	● Evaluating the response of the Galveston Bay (Texas) ecosystem to sustainable fishing of blue crab (*Callinectes sapidus*) and the management of nutrient loads
Butler IV (2003)	Extension of single-species individual-based model (ESIBM)	● Investigating the impacts of environmental events on spiny lobster (*Panulirus argus*) recruitment in the Florida Keys
Roth et al. (2008)	ESIBM	● Evaluating brown shrimp (*Farfantepenaeus aztecus*) production in the northwestern GOM, under different marsh fragmentation and inundation scenarios
Creekmore (2011)	ESIBM	● Assessing the effects of hypoxia on Atlantic croaker (*Micropogonias undulates*) dynamics in the northwestern GOM
Ault et al. (2005)	Dynamic multispecies model	● Exploring the impacts of no-take marine protected areas (MPAs) for species such as red snapper (*Lutjanus campechanus*), gag grouper (*Mycteroperca microlepis*) and red grouper (*Epinephelus morio*) in the Florida Keys
Gaff et al. (2000) (ALFISH)	Model of Intermediate Complexity for Ecosystem assessments (MICE)	● Evaluating the impacts of alternative water regulation scenarios in the Florida Everglades under the Central and South Florida Comprehensive Project Review Study
Sable et al. (unpublished data)	MICE	● Investigating how enhanced marsh degradation imposed on individuals can be scaled to population and community responses in the northern GOM
Browder (1982)	Energy flow model	● Evaluating the effects of reducing the discarded bycatch of the shrimp fishery of the north-central GOM, with a focus on reducing the quantity of the bycatch and catching a smaller quantity of fish
Sheridan et al. (1984)	Energy flow model	● Exploring the effects of reducing the discarded bycatch of the shrimp fishery in the northern GOM
Martinez et al. (1996)	Energy flow model	● Assessing the effects of reducing the discarded bycatch of the shrimp fishery of the northern GOM, looking at finfish release and size effects
Robinson et al. (2015)	Ecopath	● Assessing changes in the productivity of the north-central GOM ecosystem in response to changes in the consumption rates of Gulf menhaden (*Brevoortia patronus*) and jellyfish and to changes in the catch rates of forage fish
Sagarese et al. (2017)	Ecopath	● Developing a next-generation fisheries ecosystem model to address issues such as bycatch in key fisheries
Althauser (2003)	Ecopath with Ecosim (EwE)	● Investigating the structure of the Weeks Bay (Alabama) food web, and the responses of the food web to bottom-up perturbations
Okey et al. (2004)	EwE	● Evaluating the potential effects of shading by phytoplankton blooms on community organization on the West Florida Shelf (WFS)
Gray (2014)	EwE	● Assessing the response of the WFS ecosystem to red tide (*Karenia brevis*) blooms, with a focus on gag grouper
Sagarese et al. (2015)	EwE	● Assessing the response of the WFS ecosystem to red tide blooms, with a focus on red grouper
Chagaris and Mahmoudi (2013)	EwE	● Estimating natural mortality rates for young-of-the-year, juveniles and adults of gag grouper on the WFS from 1950 to 2009

Chagaris et al. (2015b)	EwE	● Simulating the impacts of fishing and environmental scenarios, including Reef Fish Fishery Management Plan Amendment 30B (which aims to rebuild gag grouper) and Amendment 31 (which reduces effort in the longline fishery), in the WFS ecosystem
Chagaris et al. (2015a)	EwE	● Assessing changes in the biomasses of reef fish functional groups of the WFS ecosystem in response to (1) changes in lionfish catch rates and (2) changes in the fishing mortality exerted on reef fish functional groups
Carlson (2007)	EwE	● Investigating how relative changes in fishing mortality on sharks and MPAs affect the structure and function of the Apalachicola Bay (Florida) ecosystem
Walters et al. (2008)	EwE	● Assessing the responses of the northern GOM ecosystem to changes in fisheries and primary productivity
de Mutsert et al. (2012)	EwE	● Simulating the effects of salinity changes caused by freshwater diversion on species biomass distributions of estuarine nekton in the Breton Sound (Louisiana) estuary
Geers et al. (2014)	EwE	● Examining the impact of fisheries, particularly the Gulf menhaden fishery, on the structure and maturity of the north-central GOM ecosystem
Vidal and Pauly (2004)	Ecospace	● Synthesizing Ecopath models into a single integrated, spatially explicit model for the entire GOM large marine ecosystem (LME), from which various inferences on the ecological functioning of, and fisheries impacts on the LME can be drawn
Walters et al. (2010)	Ecospace	● Developing an Ecospace model for the northern GOM for evaluating policies such as MPAs
Suprenand et al. (2015)	Ecospace	● Evaluating the information produced from 14 fisheries independent monitoring programs in the northern GOM
Chagaris (2013)	Ecospace	● Identifying ecological tradeoffs that arise through predator-prey interactions, tradeoffs between conflicting management objectives, and tradeoffs associated with MPAs in the WFS ecosystem
de Mutsert et al. (2015)	Ecospace	● Developing an Ecospace model for the Louisiana coastal zone that has the potential to evaluate the impacts of scenarios of changes to water flow and wetland restoration scenarios
de Mutsert et al. (2016)	Ecospace	● Developing an ecosystem model for the Louisiana coastal zone that is able to separate the effects of nutrient loading on secondary production from those of hypoxia and to evaluate net effects of hypoxia on fish biomasses and fisheries landings
Lewis et al. (2016)	Ecospace	● Determining if a suitable response mechanism between the organisms inhabiting the Barataria Bay (Louisiana) estuary and marsh edge distance could be developed
Dynamic Solutions (2016)	Comprehensive Aquatic System Model (CASM)	● Assessing the consequences of freshwater and sediment diversion for economically and ecologically important fish and invertebrate species of the Mississippi River Delta
Ainsworth et al. (2015) (Atlantis-GOM)	Atlantis	● Developing an Atlantis model for the whole GOM LME that has the potential to be employed to examine the consequences of resource management scenarios and the impacts of many different abiotic environmental events (e.g., climate change and harmful algal blooms)
Grüss et al. (2015) (OSMOSE-WFS)	OSMOSE	● Exploring the trophic structure of the WFS in the 2000s and estimating size-specific natural mortality rates for gag grouper
Grüss et al. (2016c) (update of OSMOSE-WFS)	OSMOSE	● Evaluating natural mortality rates and fishing scenarios for the red grouper population of the WFS

Grüss et al. (2016b) (update of OSMOSE-WFS)	OSMOSE	● Applying the management strategy evaluation (MSE) framework to the OSMOSE-WFS model to conduct an evaluation of harvest quota strategies for red grouper in a context of episodic events of natural mortality

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Figure captions

Fig. 1 Map of the Gulf of Mexico (GOM). Important features are labeled. LA = Louisiana - MS = Mississippi - AL = Alabama. The black dashed-dotted line delineates the United States exclusive economic zone

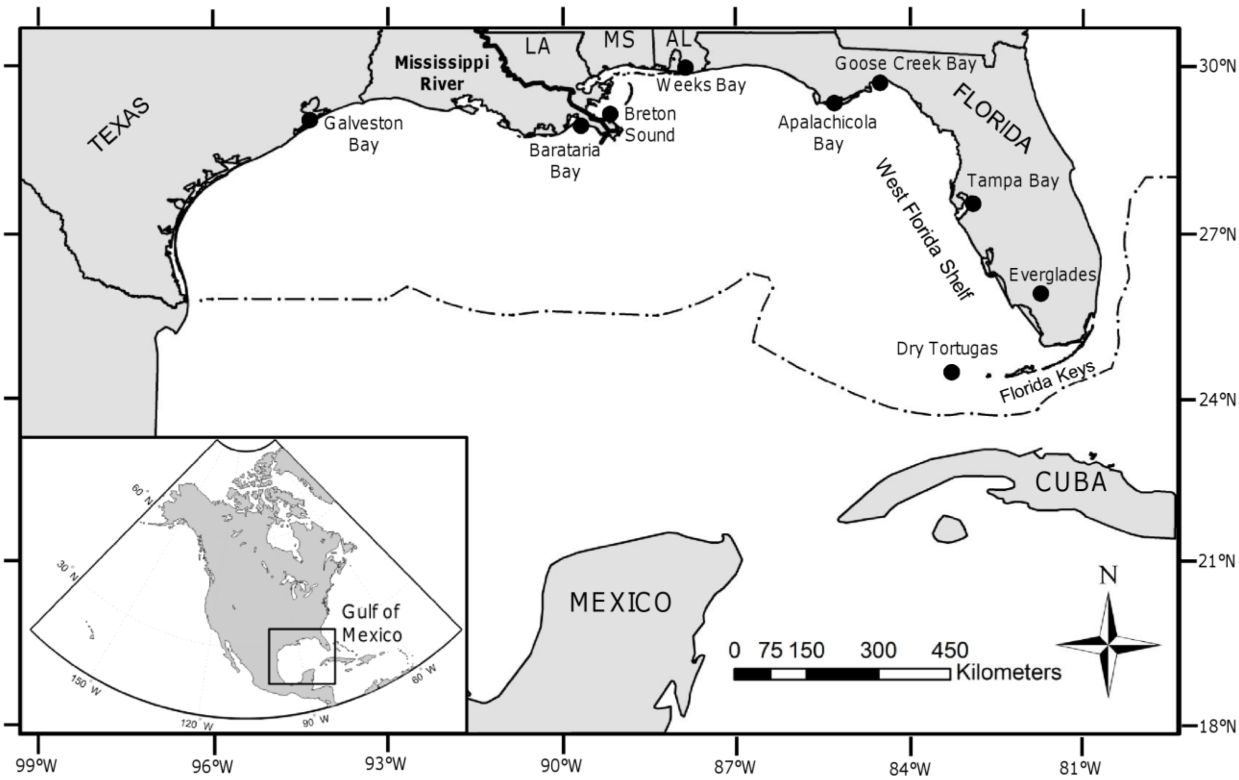
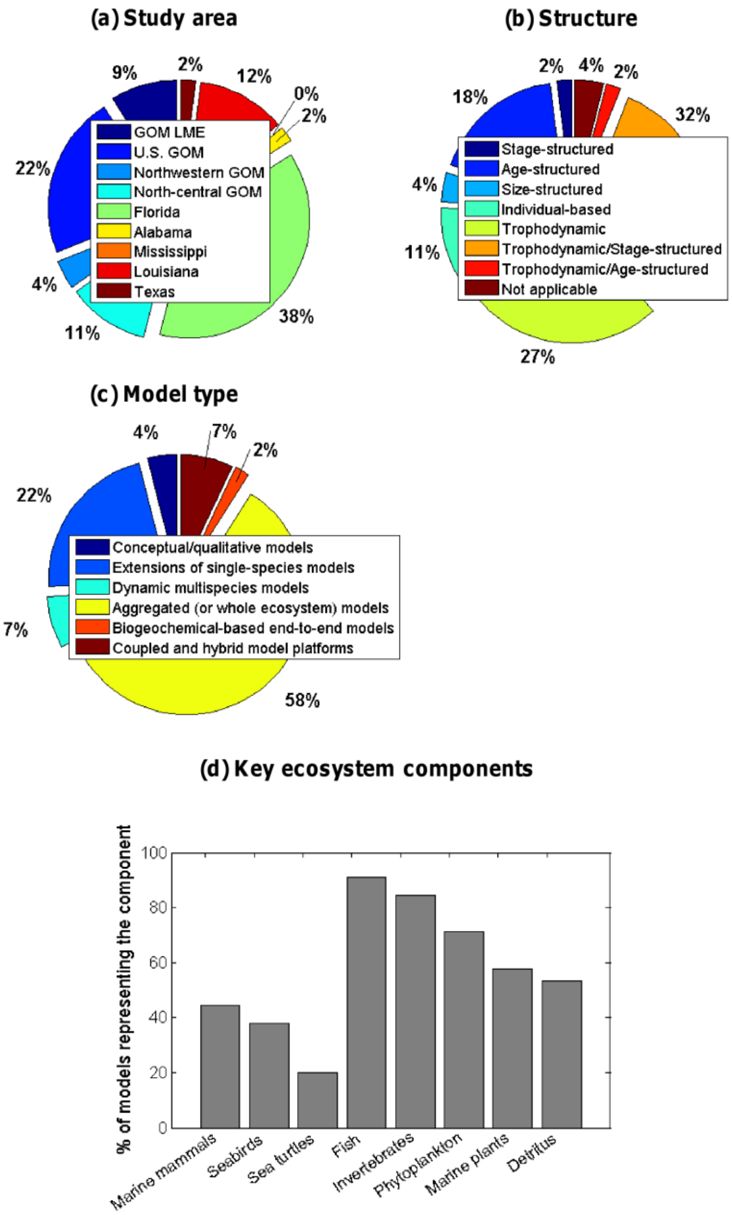


Fig. 2 Forty-five ecosystem models were identified for the U.S. Gulf of Mexico (GOM) and GOM Large Marine Ecosystem (LME). These ecosystem models differ greatly in (a) their study area, (b) their structure, (c) the model type to which they belong based on the first terminology of ecosystem models that we established in the present study, and (d) the key ecosystem components they represent.



Electronic supplementary material

Online Resource 1. Overview of ecosystem-based fisheries management (EBFM) efforts and restoration programs and projects related to EBFM in the United States (U.S.) Gulf of Mexico (GOM)

Online Resource 2. Overview of stressors in the Gulf of Mexico (GOM)

Online Resource 3. Main features of existing ecosystem modeling approaches

Online Resource 4. Features and main results of the existing ecosystem models of the United States (U.S.) Gulf of Mexico (GOM) and GOM large marine ecosystem (LME)