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Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico

Skyler R. Sagarese[a,*,1], Matthew V. Lauretta[b], John F. Walter III[b]

[a] Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

[b] Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, FL 33149, USA

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ABSTRACT

Catastrophic disturbances to marine environments, such as the Deepwater Horizon oil spill in the northern Gulf of Mexico (GoM), emphasize the need to approach fisheries management and restoration from an ecosystem perspective. To evaluate the ecosystem dynamics within the GoM, we developed a mass-balanced Ecopath model ("nGoM Ecopath") which integrated ecosystem stressors, indirect effects of fishing (e.g. bycatch), and predator-prey dynamics. A meta-analysis of diet composition filled critical gaps in higher trophic level predator-prey linkages, such as predation on economically important groupers (Serranidae). Compared to previous Ecopath models of the GoM, nGoM Ecopath displayed higher ecosystem complexity including higher connectivity amongst trophic groups and increased omnivory. Mixed trophic impact analysis revealed species including snappers, groupers, pelagic coastal piscivores, oceanic piscivores, cephalopods, and dolphins as critical top-down predators. Bottom-up effects were identified for juvenile groupers and mackerels, which benefited from high production of invertebrates and small fishes. Network analysis revealed detrimental effects of red tides on sharks, skates and rays, and demersal coastal invertebrate feeders such as black drum, as well as adult red and gag grouper. Pelagic coastal piscivores (e.g. jacks (Carangidae)), snappers (Lutjanidae), and mobile epifauna (e.g. lobsters) imposed the largest influence on ecosystem structure as keystone predators. The nGoM Ecopath model using the dynamic module Ecosim can help guide restoration efforts through the evaluation of multispecies responses to management actions and identification of ecosystem trade-offs.

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1. Introduction

Events such as the Deepwater Horizon (DWH) oil spill have emphasized the need to approach fisheries management and restoration from an ecosystem perspective using the best available science. Ecosystem-based fisheries management requires explicit consideration of ecosystem processes such as multispecies interactions (e.g. predator-prey dynamics, competition), environmental effects (e.g. harmful algal blooms such as red tides), and fish-fisher interactions (e.g. bycatch) (Pikitch et al., 2004). Ecosystem restoration, defined as the process of assisting the recovery of damaged, degraded, or destroyed ecosystems (Abelson et al., 2016), can refer to rebuilding depleted coastal and marine resources and enhancing community resilience (e.g. Gulf of Mexico Regional Ecosystem Restoration Strategy, GCERTF 2011), for example through the reduction of bycatch of non-targeted species in large-scale fisheries.

Ecosystem models, such as Ecopath with Ecosim (EwE; Christensen and Pauly, 1992; Christensen and Walters, 2004), are a key tool for examining consequences of management actions on marine ecosystems (e.g. Chagaris et al., 2015) and can elucidate dominant inter-species interactions, energy transfer pathways, and community shifts (Pauly et al., 1998; Walters and Martell, 2004; Robinson et al., 2015). Mass-aggregate ecosystem models, such as EwE (Hollowed et al., 2000), require that critical predator-prey interactions are defined, as these relationships drive the flow of energy between trophic groups. When combined with other system inputs, including biomass, production, and consumption, biotic and abiotic factors are linked to species' population dynamics to provide a static "snapshot" of trophic structure (Hollowed et al., 2000; Pauly et al., 2000). Changes in the food web over time can be sim-

* Corresponding author.
E-mail addresses: Skyler.sagarese@noaa.gov (S.R. Sagarese), matthew.lauretta@noaa.gov (M.V. Lauretta), john.f.walter@noaa.gov (J.F. Walter III).
[1] Present address: Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149, USA (305-361-4272).

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ulated within Ecosim to explore past and future effects of fishing or other sources of mortality (e.g. harmful algal blooms such as red tides) on community dynamics (Walters et al., 1997; Walters et al., 2008; Christensen and Walters, 2004). As a result, Ecosim predictions of changes in food web structure are heavily dependent upon the parameterization of the species interactions and rates of consumption; this information is often lacking at the ecosystem scale (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015).

Applications of existing Gulf of Mexico (GoM) ecosystem models to elucidate ecosystem dynamics have highlighted substantial uncertainty of trophic interactions, due to (1) difficulty in obtaining quality stomach contents from reef species due to barotrauma (i.e. stomach eversion in deep-water species; Bradley and Bryan, 1975), (2) prevalence of baited gear which can attract "hungry" species with empty stomachs (Cortés, 1997; Joyce et al., 2002), (3) limited sampling intensity or spatial coverage (Chagaris et al., 2015), and (4) an inability to identify digested prey for reasons discussed in Baker et al. (2014). An EwE model designed around shrimp bycatch in Florida waters (Walters et al., 2008; hereafter referred to as "coastal GoM EwE") was previously employed to assess changes in ecosystem structure, but possessed a diet matrix largely derived from expert opinion rather than quantitative diet studies (Simons et al., 2013; Geers et al., 2014). Substantial efforts were expended by Geers et al. (2014) to alleviate this limitation, who adapted the coastal GoM EwE model to focus on Gulf menhaden (*Brevoortia patronus*) in the northern GOM (Geers et al., 2014; hereafter referred to as "GoM menhaden EwE"); however, this model was not designed to evaluate reef habitats, an essential fish habitat from both an ecological and economic standpoint (Geers, 2012). In addition, the GoM menhaden EwE model had a limited suite of predators on Gulf menhaden, subsequently documented in Sagarese et al. (2016), and did not include discard information from the menhaden reduction fishery and other large-scale commercial fisheries. The former represents a substantial amount of biomass removals of many economically important species such as Spanish mackerel (*Scomberomorus maculatus*) and sea trout (*Cynoscion* spp.) (Guillory and Hutton, 1982; de Silva et al., 2001). Robinson et al. (2015) developed a model designed to evaluate menhaden-jellyfish interactions in the Northern Gulf of Mexico with a focus on lower trophic level (TL) dynamics but did not have upper trophic groups identified to the level of detail necessary to compare with existing single-species assessment and management.

The limitations of previous ecosystem models (as discussed in Simons et al., 2013) have necessitated additional efforts, particularly in terms of capturing predator-prey interactions concerning higher TL organisms and economically important species, such as groupers (Serranidae). The socio-economic importance of groupers is well-recognized in the northern GoM where species such as red grouper (*Epinephelus morio*) are targeted by both commercial and recreational fisheries (Coleman et al., 1996; Agar and Carter, 2014; Sadovy de Mitcheson et al., 2013). However, despite their economic importance, there is a paucity of information regarding their role in the GoM food web, particularly as prey for large predators (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015). Parameterization of predator-prey interactions has rarely included groupers in past ecosystem models, with relatively few predators documented across studies (Table 1). Even within the West Florida Shelf reef fish EwE model (Chagaris, 2013; Chagaris et al., 2015; hereafter referred to as "WFS reef fish EwE"), which represents the most progressive and extensive EwE model in the region to date, predation on groupers is limited to pelagic coastal piscivores (e.g. mackerels (Scombridae)), cobia (*Rachycentron canadum*), and other groupers (Table 1). Further, in WFS reef fish EwE the sole predator of adult red grouper, gag grouper (*Mycteroperca microlepis*), black grouper (*M. bonaci*), and yellowedge grouper (*Hyporthodus flavolimbatus*) is the tuna/billfish functional group (Chagaris et al., 2015). A lack of trophic understanding, ranging from missing predation events on higher TLs to missing consumers of key forage fish such as menhaden, has complicated the estimation of predator-prey linkages required for ecosystem-based fisheries management (Pikitch et al., 2004). These have resulted in an incomplete picture of species interactions incorporated in previous models aimed at addressing ecosystem-based fisheries management (Walters et al., 2008; Geers et al., 2014; Chagaris et al., 2015; Robinson et al., 2015) and/or restoration efforts (e.g. de Mutsert et al., 2012; Lewis et al., 2016).

Since publication of a suite of ecosystem models for the GoM, several key issues and limitations of previous models have emerged. Notably, the emergence of red tide as a key environmental stressor, has been explicitly considered in fisheries assessments and is critical to understanding ecosystem dynamics in the GoM. Secondly, given the high volume of discards and the fact that many fisheries are driven as much by their discards as by their target catch, it is critical to consider discards in ecosystem modeling. Third, the incomplete nature of the previous diet matrices left many functional groups either without predators or with incompletely represented diets. This paper addresses these three key processes and describes a mass-balanced northern GoM Ecopath model (hereafter referred to as "nGoM Ecopath") with explicit improvements compared to previous Ecopath models including: (1) the focus on socioeconomically important federally (e.g., red grouper) and internationally managed species (e.g., swordfish) on a gulf-wide scale matching the spatial extent of management; (2) statistically-derived, more comprehensive definitions of species interactions; (3) modeling of bycatch removals from the menhaden reduction fishery and other large-scale fisheries, and (4) inclusion of mortality effects from harmful algal blooms (i.e. red tides). A network analysis was employed to evaluate the direct and indirect species interactions within the GoM as well as to assess the impacts of fisheries and red tide events on species dynamics, with special emphasis placed on economically important groupers. Integration of these ecological processes with human dimensions is essential to enhance realism of ecosystem models, which will facilitate ecosystem-based fisheries management and restoration in the GoM (Mace et al., 2001; MSFCMA, 2007).

2. Materials and methods

2.1. Mass-balance modeling approach

Ecopath utilizes a mass-balanced framework composed of trophically-linked biomass pools representing major ecosystem functional groups (Polovina, 1984; Christensen and Pauly, 1992; Pauly et al., 2000). Ecosystem functional groups can reflect: (1) a group of species exhibiting similar life history, dietary or niche preferences (e.g. forage fish); (2) a single species of commercial or ecological importance (e.g. red snapper); or (3) a life-history stage ("stanza") ontogenetically distinct in diet and/or habitat (e.g. estuarine juveniles versus coastal adults) (Pauly et al., 2000; Walters et al., 2008). The production of stock i (P_i) is expressed as a function of all loss and gain processes to a functional group's biomass (B_i) and is estimated as:

$$P_i = Y_i + (B_i x M2_i) + E_i + BA_i + P_i(1 - EE_i) \quad (1)$$

where Y_i is the yield from the fishery, $M2_i$ is the total predation rate, E_i is the net migration rate (emigration − immigration), BA_i is the biomass accumulation rate, and EE_i is the ecotrophic efficiency, defined as a trophic group's production transferred within the system (e.g. by predation or fishery removals). The total consumption